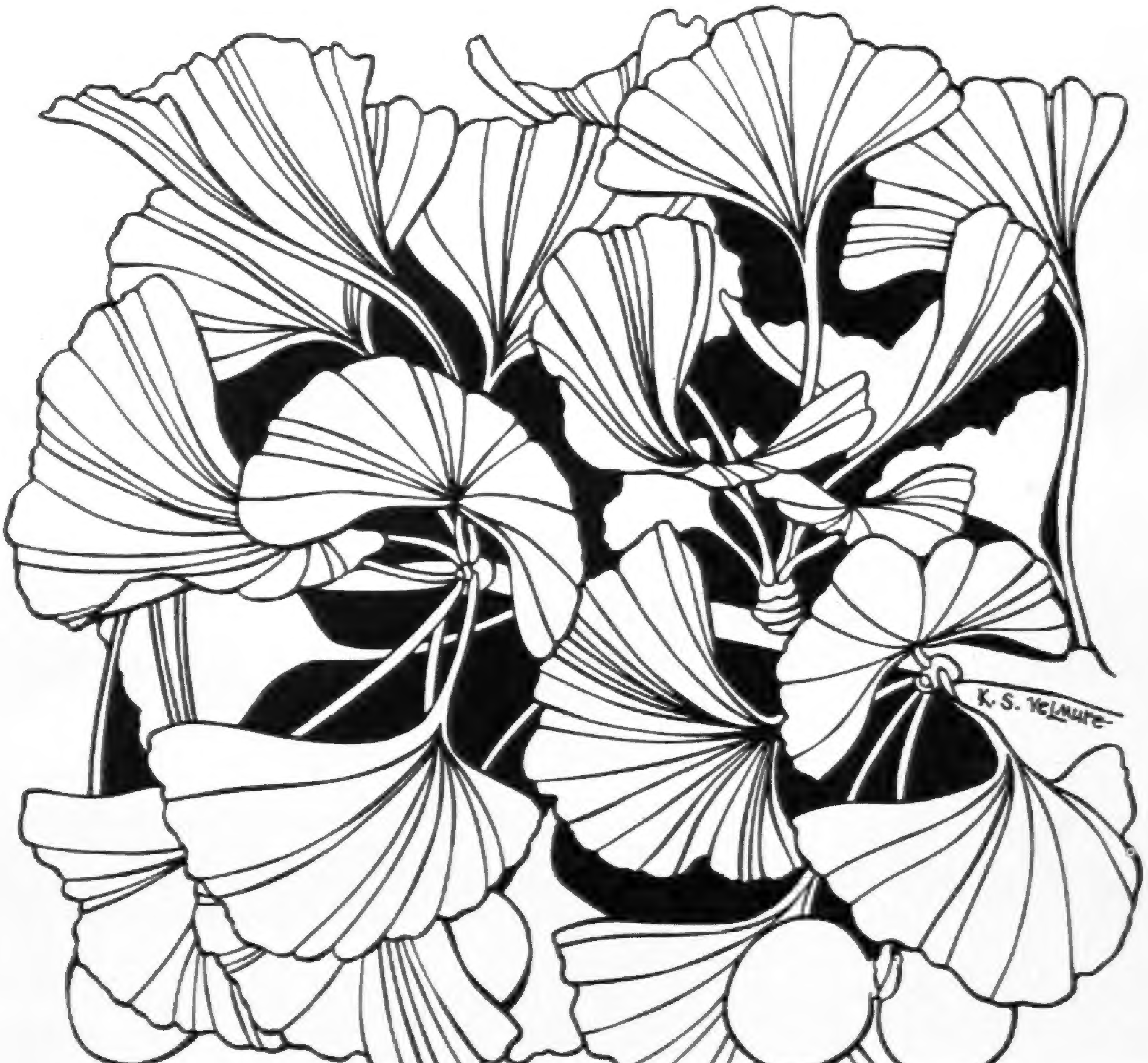
QK1
.J7655

JOURNAL OF THE
ARNOLD ARBORETUM



Volume 55 HARVARD UNIVERSITY 1974

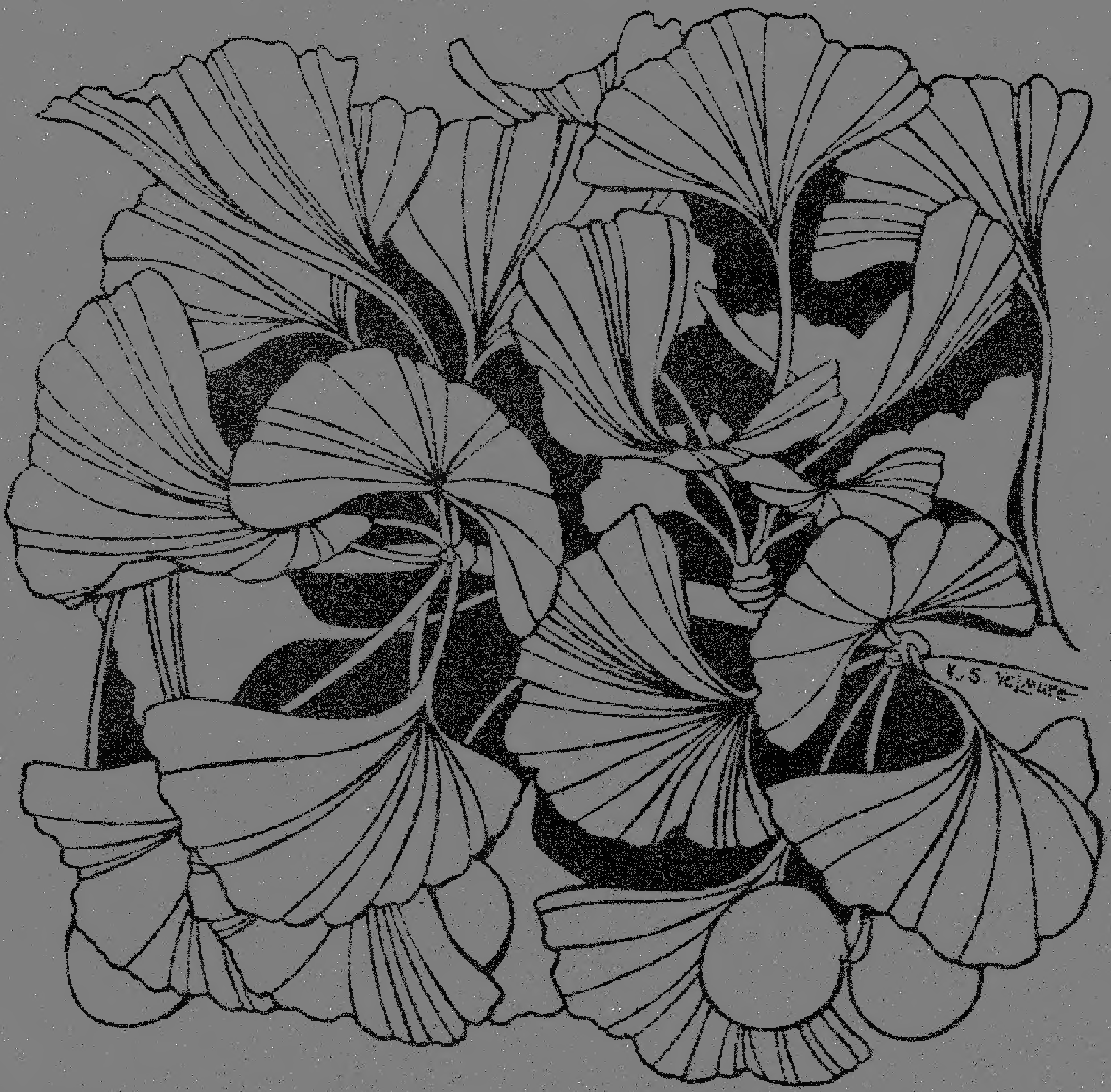
MISSOURI BOTANICAL
GARDEN LIBRARY

Dates of Issue

No. 1 (pp. 1–124) issued 30 January, 1974
No. 2 (pp. 125–332) issued 30 May, 1974
No. 3 (pp. 333–524) issued 24 September, 1974
No. 4 (pp. 525–695) issued 30 November, 1974

Contents of Volume 55 *1974*

JOURNAL OF THE ARNOLD ARBORETUM



Volume 55 HARVARD UNIVERSITY Number 1

US ISSN 0004-2625

Journal of the Arnold Arboretum

Published quarterly in January, April, July, and October by the Arnold Arboretum, Harvard University.

Subscription price $16.00 per year.

Subscriptions and remittances should be sent to Ms. Kathleen Clagett, Arnold Arboretum, 22 Divinity Avenue, Cambridge, Massachusetts 02138, U.S.A. Claims will not be accepted after six months from the date of issue.

Volumes I–XLV, reprinted, and some back numbers of volumes 46–50 are available from the Kraus Reprint Corporation, Route 100, Millwood, New York 10546, U.S.A.

EDITORIAL STAFF

B. G. Schubert, Editor

C. E. Wood, Jr.

S. A. Spongberg

CIRCULATION

K. Clagett

Printed at the Harvard University Printing Office, Boston, Massachusetts

COVER: *Ginkgo biloba* L., the maidenhair tree, so-called from the fancied resemblance of its leaves to those of the maidenhair fern. In China it has also been called the silver apricot, from the hard inner seed coat which is silvery when cleaned and vaguely resembles an apricot pit, and the duck-foot tree, from the resemblance of the leaves to the webbed feet of ducks.

The drawing for the cover and the devices for the back cover and reprints were planned and drawn by Karen Stoutsenberger Velmure from specimens taken from a tree cultivated in the Arnold Arboretum of Harvard University.

We want to assure the purists among our readers that our *Ginkgo* does not have leaves with open parallel venation. We think, however, that an exact reproduction of the dense dichotomous veins would have produced a much less dramatic design.

Second-class postage paid at Boston, Massachusetts

JOURNAL
OF THE
ARNOLD ARBORETUM

VOL. 55 JANUARY 1974 NUMBER 1

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

A. LINN BOGLE

NYCTAGINACEAE A. L. de Jussieu, Gen. Pl. 90, 1789, "Nyctagines," nom. cons.

(FOUR-O'CLOCK FAMILY)

Annual or perennial herbs, sometimes scandent shrubs, or trees; stems procumbent to erect, sometimes climbing by means of stout recurved thorns; roots fibrous or fleshy to tuberous; leaves mostly opposite, exstipulate, simple, entire, equal or unequal, sessile or petiolate, membranaceous or fleshy, glabrous or pubescent; inflorescence terminal or lateral, cymose [or racemose], diffuse or congested, bracteate, the bracts sometimes large and bright colored, either free or united in an involucre around one or more flowers and sometimes simulating a calyx [or flowers axillary and solitary]; flowers incomplete, perfect or imperfect (the plants monoecious or dioecious), showy or inconspicuous; perianth uniseriate, usually pen-

---

[1] Prepared for a Generic Flora of the Southeastern United States, a 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 of 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 in this area, with additional information from extra-regional taxa in brackets. References followed by an asterisk are those that I have been unable to check.

Most of this manuscript was completed while the author was directly associated with the Generic Flora as an Assistant Curator of the Arnold Arboretum; it was updated and concluded during the summer of 1973 in Cambridge and at the University of New Hampshire. I am grateful to Dr. Wood for his encouragement and help at various stages and for his careful editing of the manuscript, as well as for various additions and changes he has made. The illustrations were prepared in Cambridge, Massachusetts, by Virginia Savage from my dissections, which came, in part, from materials collected in Florida by Drs. R. A. Howard (*Okenia*), C. E. Wood, Jr., and A. Strahler. I should also like to thank Dr. A. R. Hodgdon, Dr. Y. T. Kiang, and Dr. A. C. Mathieson for reading the manuscript and making many helpful suggestions.

This paper is published with the approval of the Director of the University of New Hampshire Agriculture Experiment Station as Scientific Contribution Number 703.

tamerous, of five fused sepals, the calyx small, fleshy and inconspicuous to large, membranaceous, petaloid and colorful, simulating a corolla; aestivation induplicate-valvate (plicate or contorted); corolla none; stamens one to many, hypogynous, filaments filiform, unequal, free or united basally in a shallow collar, the anthers small, tetrasporangiate, 2-loculate at maturity, dehiscing by longitudinal slits; carpel one, ovary superior, unilocular, ovule solitary, basal, hemianatropous to anacampylotropous, integuments 1 or 2; style long filiform; stigma capitate to penicillate. Fruit an achene or utricle inclosed within the persistent fleshy (berry-like) to hard and leathery glabrous or pubescent, often 5(–10) ribbed base of the perianth tube, the ribs often viscid glandular or bearing stalked capitate glands; seed solitary, the seed coat membranaceous; embryo straight or curved, cotyledons foliaceous, endosperm sparse, perisperm abundant. TYPE GENUS: *Nyctago* A. L. de Jussieu, nom. illegit. = *Mirabilis* L.

A family of about 26 (to 30) genera, containing about 300 species distributed primarily in the tropical and subtropical regions of the New World, and represented in our area by about 14 species of four indigenous genera (*Boerhavia* L., *Mirabilis* L., *Okenia* Schlechtend. & Cham., *Pisonia* L.). In contrast, about 19 species of four genera (*Boerhavia*, *Bougainvillea* Commerson, *Mirabilis*, *Pisonia*) occur in Malaysia, but only *Pisonia* among these is unquestionably native to southeastern Asia (Stemmerik). *Boerhavia* is a pantropical weed. Several species of *Bougainvillea* are widely cultivated as ornamentals in the tropics, and *Mirabilis Jalapa* L. has escaped from cultivation in many tropical areas.

The systematics of the family are problematical, there being no consensus as to either the number of tribes represented or the number or circumscription of some of the larger and more important genera (e.g., *Mirabilis* sensu lato, *Pisonia* sensu lato). The genera have been disposed in four subfamilies (Fiedler) or tribes (Heimerl, 1889) or, more recently, in five tribes (Heimerl, 1934; Eckardt), or eight tribes (Hutchinson). Standley (1918), considering only the genera of North America, recognized six tribes. Depending upon the system consulted, two (Heimerl) or three (Hutchinson) tribes are represented by the four genera indigenous to our area.

The tribe Nyctagineae (Mirabileae Meissner),[2] taken in the broad

---

[2] A nomenclatural problem concerning the correct name of the tribe and subtribe containing the type genus of this family occurs because of a conflict in the wording of Article 19 of the International Code of Botanical Nomenclature in both the 1966 and 1972 editions, neither of which makes clear whether these names should be Nyctagineae and Nyctagininae or Mirabileae and Mirabilinae. In the 1966 edition, two criteria are given for the names of taxa below the level of family and above that of genus: 1) such names are formed by adding the appropriate suffix to the stem of a *legitimate name* of an included genus, and 2) "the name of any taxon of a rank below family and above genus which includes the type of the next higher taxon must be based on the *same stem as the name of the next higher taxon* . . ." (italics mine). In the 1972 version, the first criterion is retained, and the second is modified so that "the name of any taxon of a rank below family and above genus which *includes the*

sense of Heimerl (1934) and of Eckardt, is characterized by generally herbaceous to shrubby habit, mostly perfect flowers, the fruit inclosed in the persistent base of the calyx tube, and more or less folded or hooked embryos. Four subtribes are recognized in the Nyctagineae, of which subtribe Nyctagininae (Boerhaviinae) [2] is the largest (13 genera) and the only subtribe represented in our area by indigenous genera (*Boerhavia*, *Mirabilis*, *Okenia*). The other three subtribes are all monogeneric (Abroniinae, *Abronia*; Bougainvilleinae, *Bougainvillea*; Phaeoptilinae, *Phaeoptilum*). The genera *Abronia* and *Bougainvillea* are cultivated as ornamental plants in our area, but have apparently not become naturalized. *Phaeoptilum* Radlk. is an endemic of Angola and Southwest Africa.

The tribe Pisonieae Meissner, containing six genera but consisting principally of *Pisonia* L. and *Neea* Ruiz & Pavón, is characterized by trees or woody shrubs with mostly imperfect flowers; accessory fruits, the accrescent calyx base inclosing the utricle or achene; and straight embryos. Only *Pisonia* is found in our area. *Neea* occurs in South and Central America, approaching our area in the islands of the Caribbean.

The three remaining tribes of the family are small. Tribe Colignonieae Standley contains only the genus *Colignonia* Endl., with about eleven species in the South American Andes. Tribe Boldoeae Heimerl contains only the monotypic genus *Boldoa* Cav. of Mexico and Central America, while tribe Leucastereae Bentham & Hooker consists of four monotypic South American genera (*Andradea* Allemão, *Leucaster* Choisy, *Ramisia* Baillon, *Reichenbachia* Sprengel).

The relationships of the Nyctaginaceae are recognized by most authors

---

type genus of the correct name of the family to which it is assigned is to be based on the *name of that genus* . . ." (italics again mine). Under either version of the Code these two criteria come into conflict in the case of any of the dozen conserved family names that are based on an illegitimate generic name (e.g., Caryophyllaceae, Nyctaginaceae, Sapotaceae). Under Article 18, Note 1, these conserved family names are both valid and legitimate, but Article 19 does not deal with the conflict noted above.

Nowicke (1970) was aware of this problem and, following the 1966 edition of the code then applicable, emphasized the second criterion, the name of the next higher taxon, concluding that "the tribe Mirabileae, subtribe Boerhaaviinae, which contains this genus *Mirabilis*, must become the tribe Nyctagineae, subtribe Nyctagininae." If the second criterion is to be used, Nowicke's names would also stand under the changed wording of the 1972 Code, in which "the same stem as the name of the next higher taxon" is replaced by the stem of the name of the type genus (*Nyctago*). But the first criterion of both versions of the Article, requiring the stem of a legitimate name of an included genus, is not met, since conservation of the family name Nyctaginaceae with *Nyctago* as the type genus does not validate the illegitimate name *Nyctago* Juss. It can, therefore, be argued that *Mirabilis* L. remains the legitimate name and stem for the designation of higher taxa, which then become tribe Mirabileae and subtribe Mirabilinae.

Since it is clear that the intent of the Code is to indicate the subfamily, tribe, and subtribe that include the type genus of the family name, Nowicke's decision to follow the second interpretation is adopted here, even though Nyctagineae and Nyctagininae are based upon an illegitimate generic name. It is desirable, however, that Article 19 be studied and amended to account for this problem in the Nyctaginaceae and other families, the names of which are conserved but are based on illegitimate generic names.

to lie among the families of the order Centrospermae (Bentham & Hooker, 1880; Heimerl, 1889, 1934; Standley, 1909, 1918; Eckardt, 1964), or more recently the Caryophyllales (Buxbaum, 1961; Cronquist, 1968; Takhtajan, 1969), where they are considered either to be derived directly from the primitive phytolaccaceous stock or to be in an unclear position (Buxbaum). With this group of families the Nyctaginaceae share several distinctive characteristics, including the presence of betalains rather than anthocyanins (Hegnauer, 1969), the frequent occurrence of anomalous secondary growth, the basal placentation of the ovule, and a constellation of embryological characteristics unique to the order (Cronquist, 1968). Hutchinson (1920, 1967) placed the family in his order Thymelaeales after the Thymelaeaceae ("for want of a better position") on the basis of the apetalous flowers and increasingly woody habit among the genera of Nyctaginaceae. This position was supported by Venkateswarlu (1948) on the basis of embryological evidence from *Pisonia aculeata*, but the bulk of morphological and anatomical evidence favors affinity with the Caryophyllales. Physiological evidence also supports this affinity, since Kendrick & Hillman have demonstrated in *Mirabilis Jalapa* L. and other species of Centrospermae the absence of a dark reaction which converts the far-red absorbing form of phytochrome to the red absorbing form. The presence of such a reaction is typical of other dicotyledons, but is lacking in monocotyledons, and its absence in these species is seen as a further suggestion of common physiology and ancestry between the Centrospermae and monocotyledons.

The Nyctaginaceae are distinguished from the closely related Phytolaccaceae by their usually opposite leaves, mostly cymose inflorescences, synsepalous and often corolla-like calyces that are plicate or contorted in the bud, solitary uniovulate carpel, and fruit an achene inclosed in the accrescent calyx base.

Gametic and somatic chromosome counts reported in the literature indicate diploid numbers of $2n = 92$, ca. 92, ca. 88–92 in *Abronia*; $2n =$ ca. 58 in *Allionia*; $2n = 26$, 42, and 116 in *Boerhavia*; $2n = 20$, 34, 51 in *Bougainvillea*; $2n =$ ca. 40 in *Commicarpus* Standley; and $2n = 52$, 58, ca. 58 in *Mirabilis* (incl. *Oxybaphus*). Counts are apparently lacking for *Okenia*, *Pisonia*, and other North American genera.

Several unusual floral modifications occur in the family. The flowers are apetalous and the calyx is inconspicuous in many genera, but in *Mirabilis Jalapa* and *Okenia* the calyx tube is large and colorful, simulating a corolla, while several involucral bracts form an apparent calyx. In *Bougainvillea* three large, brightly colored petaloid involucral bracts surround a cluster of flowers with relatively small and inconspicuous calyx tubes. The extremely sticky fruits of some *Pisonia* species are disseminated by adherence to the feathers of birds, while the fruits of *Okenia* are geocarpic, being pushed underground by their elongating pedicels.

Joshi & Rao found basic similarities in the floral plan and vasculature of *Boerhavia diffusa*, *B. repanda*, *Bougainvillea spectabilis*, and *Mirabilis Jalapa*. In *Bougainvillea* the perianth receives many traces from both the inner and outer rings of primary bundles in the pedicel; but in *Boerhavia* and *Mirabilis* only the inner ring of pedicellar bundles contributes to the perianth, providing ten traces in two cycles of five each in *B. repanda* and *M. Jalapa*, but only a single cycle of five traces in *B. diffusa*. Reduction in the number of stamens is accompanied by reduction in the number of traces to the androecium, from seven or eight in two cycles (*Bougainvillea*) to five or fewer traces in one cycle (*Boerhavia, Mirabilis*). Gynoecial structure is stated to be similar to that of *Rivina* L., of the Phytolaccaceae, and unlike that of the Thymelaeaceae, as exemplified by *Stellera* L. Joshi & Rao conclude that the ancestral nyctaginaceous flower had a perianth supplied by 10 traces in two cycles, two whorls of stamens, and a single carpel. They propose relationships to the Phytolaccaceae, as opposed to the Thymelaeaceae, despite resemblances in perianth form to the latter.

The term "anthocarp" has been used traditionally in connection with the Nyctaginaceae to designate the combination of the fruit (an achene or utricle) and the persistent, accrescent, hard, leathery, or fleshy base of the calyx tube that incloses it. There is, however, considerable confusion in the use of the term. Some authors say that there is a union between the perianth base or receptacle and the fruit, although, as will be seen in FIGURES 1–5, this is not the case in Nyctaginaceae. Jackson (Glossary Bot. Terms, ed. 4. 1928) defined an anthocarp as "a fruit formed by the union of the floral organs or part of them, with the fruit itself, as in the Nyctaginaceae." Similarly Munz & Keck (Calif. Fl. 1577. 1959) and Correll & Johnston (Man. Vasc. Pl. Texas 1746. 1970) say that an anthocarp is "a structure in which the fruit proper is united with the perianth or receptacle." Henderson & Henderson (Dict. Biol. Terms, ed. 8. 1963) define anthocarp as "a collective or aggregated fruit formed from an entire inflorescence, . . ." and both Jackson and Featherly (Taxonomic Terminol. Higher Pls. 1954) write that anthocarpous is said of "fruits with accessories, sometimes termed pseudocarps, as the strawberry and pineapple."

Asa Gray took perhaps the most general view of the anthocarpous fruit (Structural Botany, 300, 301. 1879). He wrote, "Accessory or Anthocarpous Fruits are those of which some conspicuous portion of the fructification neither belongs to the pistil nor is organically united with it, except by a common insertion. The part thus imitating a fruit, while it is really no part of the pericarp, is sometimes called a Pseudocarp. This condition may occur in either simple, in aggregate, or in multiple fruits." After giving the fruits of *Gaultheria procumbens* and *Shepherdia* [*canadensis*] as examples of simple anthocarpous fruits he added, "So, also, the apparent achenium or nut of Mirabilis, or Four-o'clock, and of its allies, is the thickened and indurated base of the tube of a free calyx, which contracts at the apex and encloses the true pericarp (a utricle or thin akene), but does not cohere with it."

In view of the multiple ways in which the term is used, the use of "anthocarp" in the Nyctaginaceae hardly seems worth continuing, particularly since some of the definitions incorrectly include union of the accrescent calyx base and the fruit. It seems better, although more wordy, to refer to the components of the accessory fruit of members of this family as the accrescent calyx base that incloses the fruit, which is itself an achene or utricle. (In this connection it should be added that Buxbaum interprets the structure in *Mirabilis Jalapa* that most workers have called the perianth or calyx base as being axial in nature, forming a hypanthium around the ovary and fruit, and bearing the corolla-like calyx at its summit.)

Embryological studies by numerous workers on several of the common genera and species indicate 4-sporangiate anthers and pollen grains that usually are 3-celled (rarely 2-celled) at anthesis. Ovules are crassinucellar and unitegmic (*Abronia*, *Boerhavia*, *Mirabilis*) or bitegmic (*Bougainvillea*, *Oxybaphus*, *Pisonia*), with the inner integument forming the micropyle. Endosperm formation is nuclear, becoming mostly cellular except at the chalazal end of the curved embryo sac. Development of the embryo is of the Asterad type (Davis, Schnarf).

The form and development of the fruits, seeds, embryos, and seedlings of 14 species of six genera have been described in detail in the extensive comparative surveys of Lubbock and Martin. In *Abronia* one cotyledon is abortive, resulting in a "monocotyledonous" embryo.

Recent comprehensive light microscope and scanning electron microscope studies of nyctaginaceous pollen morphology (Nowicke; Nowicke & Luikart) reveal a broad range of variation in such characteristics as pollen size (22–210 micra in diameter), shape (commonly spheroidal but with some prolate and oblate types, aperture form (variously 3–18-colpate or 12 or more pantoporate, the pores frequently operculate), and exine sculpturing (either spinulose and tubuliferous, the spinules varying in size and distribution, or coarsely reticulate with modification in the ornamentation of the muri and lumina). Sexine pattern is seen as a more significant characteristic than aperture pattern in establishing systematic relationships, and a correlation between pollen morphology and various selective pressures (xeric conditions, pollination vectors, stigma types) is suggested. Nowicke (1971) suggests that this correlation of form with ecological conditions may possibly be demonstrated in the subtribe Nyctagininae, which contains thirteen genera (sensu stricto) of plants of warm, dry habitats, the pollen grains of which are characterized by thickened walls and small, frequently sunken, operculate pores. Nowicke's evidence supports the integrity of the tribal and subtribal delimitations of Heimerl (1934), but pollen morphology within the large subtribe Nyctagininae (Boerhaviinae) is relatively uniform and of very limited value at the generic level.

Stem and root anatomy in the few genera of Nyctaginaceae that have been studied (*Boerhavia*, *Bougainvillea*, *Heimerliodendron*, *Mirabilis*) is anomalous in that: 1) the primary vascular bundles are scattered in the ground tissue, rather than being arranged in a cylinder, and show very limited secondary growth; and 2), secondary thickening is due to a single, permanently acting, extra-fascicular meristematic zone of cortical origin, termed the primary thickening meristem. The latter produces anomalous secondary tissue consisting of alternating bands of lignified fibers and vessels, and nonlignified parenchyma and phloem (Maheshwari; Balfour; Studholme & Philipson). Most studies of anomalous secondary growth in the family have dealt mainly with the initiation of the primary thickening meristem and its derivatives in mature stems, but recent interest has turned to its initiation in the major organs of the seedlings. Mikesell & Popham found that in seedlings of *Mirabilis Jalapa* the primary thickening meristem first appears in the base of the stem. Subsequent development is acropetal in the stem and basipetal into the hypocotyl and root, where further differentiation is also acropetal. This sequence differs slightly in seedlings of *Bougainvillea spectabilis*, where the primary thickening meristem first appears at the base of the primary root and later at the base of the hypocotyl. Secondary vascular bundles (desmogen strands) arising from meristematic activity in stems of *B. spectabilis* exhibit limited cambial activity, producing tertiary xylem and phloem cells (Stevenson & Popham). Length of photoperiod has been shown to affect cell size and time of lignification in conjunctive tissue of hypocotyls and root bases of *Mirabilis Jalapa* seedlings (Mikesell & Popham).

Stomatal structure and ontogeny vary among the genera, with both anomocytic (ranunculaceous) and paracytic (rubiaceous) types recorded (Metcalf & Chalk). Inamdar reports a perigenous ontogenetic pattern for both types in three genera of the family.

In the fledgling field of ultrastructural systematics Behnke (1969, 1972) has described "P-type" plastids, i.e., leucoplasts that elaborate primarily proteinaceous inclusions, rather than starch granules as in "S-type" plastids, in the sieve tubes of *Mirabilis longiflora* L., and *Pisonia Brunoniana* Endl. Calcium oxalate raphide crystals are particularly abundant throughout plants of *Boerhavia*, and are also abundant in *Bougainvillea, Mirabilis, Okenia*, and *Pisonia* (Heimerl, 1890).

The family is of no economic significance apart from a few widely cultivated ornamental species of *Abronia* (Sand Verbena), *Mirabilis* (Four-o'clock), both annuals, and *Bougainvillea*, a woody vine. Less often plants of the herbaceous *Boerhavia* or woody *Pisonia* may be found in cultivation.

REFERENCES:

BAILLON, H. Nyctaginacées. Hist. Pl. **4**: 1–22. 1873.

BALFOUR, E. Anomalous secondary thickening in Chenopodiaceae, Nyctaginaceae, and Amaranthaceae. Phytomorphology **15**: 111–122. 1965.

BEHNKE, H. D. Über Siebröhren-Plastiden und Plastidenfilamente der Caryophyllales. Untersuchungen zum Feinbau und zur Verbreitung eines Weiteren spezifischen Plastidentyps. Planta **89**: 275–283. 1969. [*Mirabilis longiflora, Pisonia Brunoniana.*]

———. Sieve-tube plastids in relation to Angiosperm systematics — an attempt towards a classification by ultrastructural analysis. Bot. Rev. **38:** 155–197. 1972.

BENTHAM, G., & J. D. HOOKER. Nyctaginaceae. Gen. Pl. **3:** 1–11. 1880.

BOLKHOVSKIKH, A., V. GRIF, T. MATVEJEVA, O. ZAKHARYEVA. Chromosome numbers of flowering plants. A. FEDOROV, Ed. (Russian and English prefaces.) 926 pp. Leningrad. 1969. [Nyctaginaceae, 442.]

BUXBAUM, F. Vorlaüfige Untersuchungen über Umfang, systematische Stellung und Gliederung der Caryophyllales (Centrospermae). Beitr. Biol. Pflanzen **36:** 1–56. 1961. [*Mirabilis Jalapa*, 28.]

CHITTENDEN, F. J. The Royal Horticultural Society dictionary of gardening. Ed. 2. by P. M. SYNGE. 4 vols. Oxford. 1965. [Nyctaginaceae, **3:** 1386; *Mirabilis*, **3:** 1307, 1308.]

CHOISY, J. D. Nyctaginaceae. DC. Prodr. **13**(2): 425–458. 1849.

CRONQUIST, A. The evolution and classification of flowering plants. x + 396 pp. Boston. 1968. [Nyctaginaceae, 181. Detailed discussion of phylogenetic relationships among families of subclass Caryophyllidae.]

DAVIS, G. L. Systematic embryology of the angiosperms. ix + 528 pp. New York. 1966. [Nyctaginaceae, 187, 188.]

DIERS, L. Der Anteil an Polyploiden in den Vegetationsgürteln der West Kordillere Perus. Zeitschr. Bot. **49:** 437–488. 1961. [*Commicarpus*, *Mirabilis*, 449; *Allionia*, 455.]

ECKARDT, T. Centrospermae. *In*: H. MELCHIOR, A. Engler's Syllabus der Pflanzenfamilien. ed. 12. vol. 2. 1964. [Nyctaginaceae, 84–86.]

FIEDLER, H. Beiträge zur Kenntnis der Nyctaginaceen. Bot. Jahrb. **44:** 572–605. 1910.

GIDON, F. Sur l'interprétation anatomique de l'anomalie des tiges chez les dicotylédones cyclospermées et sur le plan structural de leurs pétioles. Actes Congrès Int. Bot. Paris. 204–207. 1900.

GRAY, A. Brief character of some new genera and species of Nyctaginaceae. Am. Jour. Sci. II. **14:** 259–268. 1853.

HEGNAUER, R. Chemotaxonomie der Pflanzen. Band 5. Dicotyledoneae: Magnoliaceae-Quiinaceae. 506 pp. Basel & Stuttgart. 1969. [Nyctaginaceae, 199–206.]

HEIMERL, A. Einlagerung von Calciumoxalat in die Zellwand der Nyctagineen. Bot. Jahrb. **8**(Lit.): 62. 1887.

———. Nyctaginaceae. Nat. Pflanzenfam. III. **1b:** 14–32. 1889.

———. Nyctaginaceae. Nat. Pflanzenfam. ed. 2. **16c:** 86–134. 1934.

HJELMQVIST, H., & F. GRAZI. Studies on variation in embryo sac development. 2. Bot. Not. **118:** 329–360. 1965. [*Oxybaphus nyctagineus*, 329–335; *Mirabilis Jalapa*, 335–344.]

HUTCHINSON, J. The families of flowering plants. Vol. I. Dicotyledons. London. 1926. [Nyctaginaceae, 152, 153.] *Ibid.* ed. 2. Oxford. 1959. [Nyctaginaceae, 216, 217.]

———. The Genera of Flowering Plants (Angiospermae). Dicotyledones. Vol. II. xi + 659 pp. Oxford. 1967. [Nyctaginaceae, 260–271.]

INAMDAR, J. A. Epidermal structure and ontogeny of stomata in some Nyctaginaceae. Flora **158:** 159–166. 1968. (*Boerhavia diffusa*, *B. repanda*; *Bougainvillea spectabilis*; *Mirabilis Jalapa*.)

JOSHI, A. C., & V. S. R. RAO. Vascular anatomy of the flowers of four Nyctaginaceae. Jour. Indian Bot. Soc. **13:** 169–186. 1934.

KENDRICK, R. E., & W. S. HILLMAN. Absence of phytochrome dark reversion in seedlings of the Centrospermae. Am. Jour. Bot. **58:** 424–428. 1971. [*Mirabilis Jalapa.*]

KERNER VON MARILAUN, A. The natural history of plants: their forms, growth, reproduction, and distribution. Translated by F. W. OLIVER. 2 vols. in 4. New York. 1895.

LUBBOCK, J. A contribution to our knowledge of seedlings. Vol. 2. 646 pp. London. 1892. [Nyctagineae, 400–409; *Abronia, Mirabilis, Oxybaphus.*]

MAHESHWARI, P. An introduction to the embryology of Angiosperms. x + 453 pp. New York. 1950. [*Abronia,* 429; *Boerhavia,* 29, 186, 203; *Bougainvillea,* 32; *Mirabilis,* 394; *Oxybaphus,* 191, 200, 210, 269.]

MARTIN, A. C. The comparative internal morphology of seeds. Am. Midl. Nat. **36:** 513–660. 1946. [Nyctaginaceae, 566–567.]

MEISSNER, C. F. Plantarum vascularum genera. 2 vols. Leipzig. 1841. [Tribes Mirabileae, Pisonieae, vol. 1, 229, 230; vol. 2, 318.]

METCALFE, C. R., & L. CHALK. Anatomy of the Dicotyledons. Vol. 2. Oxford. 1950. [Nyctaginaceae, 1059–1067.]

MIKESELL, J. E., & R. A. POPHAM. Effects of different photoperiods upon development of the primary thickening meristem of *Mirabilis Jalapa* L. (Abstr.). Am. Jour. Bot. **59:** 654. 1972.

NOWICKE, J. W. Pollen morphology in the Nyctaginaceae. I. Nyctagineae (Mirabileae). Grana **10:** 79–88. 1970.

——— & T. J. LUIKART. Pollen morphology of the Nyctaginaceae. II. Colignonieae, Boldoeae, & Leucastereae. Grana **11:** 145–150. 1971.

PANT, D. D., & B. MEHRA. Stem anatomy of some Nyctaginaceae. Curr. Sci. Bangalore **31**(5): 199–201. 1962.

RICKETT, H. W. Wildflowers of the United States. Vol. 2. The Southeastern States. Part 1. New York. 1966. [*Mirabilis, Okenia,* 147, *pl. 51.*]

ROCÉN, T. Zur Embryologie der Centrospermen. Inaug. Diss., Uppsala, 1927. [Includes *Mirabilis Jalapa, M. multiflora, M. longiflora; Oxybaphus nyctagineus, O. micranthus, O. viscosus; Abronia umbellata; Bougainvillea glabra.*]

SCHERMERHORN, J. W., & M. W. QUIMBY, Editors. Lynn Index. A Bibliography of Phytochemistry. Monograph I. Order Centrospermae. 1957. [Nyctaginaceae, 40, 41.]

SCHNARF, K. Vergleichende Embryologie der Angiospermen. vii + 354 pp. Berlin. 1931. [Nyctaginaceae, 52–54.]

STANDLEY, P. C. The Allioniaceae of the United States with notes on Mexican species. Contr. U. S. Natl. Herb. **12:** 303–389. *pls. 28–43.* 1909.

———. Allioniaceae. N. Am. Fl. **21:** 171–254. 1918.

———. Studies of American Plants — V. Publ. Field Mus. Bot. **8**(5): 293–398. 1931a. [Nyctaginaceae, 304–310; *Mirabilis, Torrubia, Bougainvillea, Neea, Allionia. Allioniella, Hesperonia, Oxybaphus, Quamoclidion* here united with *Mirabilis.*]

———. The Nyctaginaceae and Chenopodiaceae of northwestern South America. *Ibid.* **11**(3): 71–126. 1931b.

STEMMERIK, J. F. Nyctaginaceae. *In*: C. G. G. J. VAN STEENIS, Flora Malesiana I. **6:** 450–468. 1964. [*Mirabilis, Boerhavia, Bougainvillea, Pisonia.*]

STEVENSON, D. W., & R. A. POPHAM. Ontogeny of the primary thickening meristem in seedlings of *Bougainvillea spectabilis.* Am. Jour. Bot. **60:** 1–9. 1973.

STUDHOLME, W. P., & W. R. PHILIPSON. A comparison of the cambium in two woods with included phloem: *Heimerliodendron Brunonianum* and *Avicen-*

nia resinifera. New Zealand Jour. Bot. **4**: 355–365. 1966. [*H. Brunonianum* (Endl.) Skottsb. = *Pisonia Bruroniana* Endl.]

TAKHTAJAN, A. Flowering Plants. Origin and dispersal. x + 310 pp. Washington, D.C. 1969. [Nyctaginaceae, 214, 250.]

UPHOF, J. C. T. Dictionary of economic plants. ed. 2. 591 pp. Lehre. 1968.

VENKATESWARLU, J. A contribution to the morphology of *Pisonia aculeata* Linn. (Abstr.) Proc. 34th Indian Sci. Congr. **1947**(3): 156. 1948.

WOHLPART, A., & T. J. MABRY. The distribution and phylogenetic significance of the betalains with respect to the Centrospermae. Taxon **17**: 148–152. 1968. [Betacyanins identified in 21 species of 10 genera of Nyctaginaceae, incl. *Boerhavia, Mirabilis, Oxybaphus.*]

KEY TO THE GENERA OF NYCTAGINACEAE IN THE SOUTHEASTERN UNITED STATES

General characters: *Annual or perennial herbs or shrubs, trees, or woody vines with mostly opposite (to alternate) simple, entire to sinuate, exstipulate leaves; inflorescences terminal or lateral, basically cymose, bracteate to involucrate, the involucres containing 1 to several flowers; flowers perfect or imperfect, small and inconspicuous to large and showy, regular, hypogynous; sepals 5, united, fleshy and inconspicuous to membranaceous and corolla-like, constricted above the ovary, the limb ephemeral; corolla lacking; stamens 1 to many, or few, reduced, and sterile, unequal, free or basally united, the anthers didymous; carpel solitary, the ovary unilocular; ovule 1, basal. Fruit accessory, the accrescent calyx base berry-like to hard and leathery, inclosing the fruit (an achene or utricle).*

A. Plants herbaceous, or woody only at the base; flowers perfect; stigma capitate; embryo curved.
  B. Flowers involucrate, involucres solitary in leaf axils or in terminal or lateral loose to congested cymes; involucres 1 to several flowered.
    C. Involucral bracts 5, united, calyx-like, campanulate to rotate and veiny in fruit; flowers 1 or 2–6 per involucre; stamens 3–5. .... 1. *Mirabilis.*
    C. Involucral bracts 3 or 4, small, free; flowers solitary, axillary; perianth densely pubescent without; stamens 9–18; pedicels elongating after flowering, the fruit hypogeous. .... 2. *Okenia.*
  B. Flowers exinvolucrate, numerous, small (less than 1 cm.); inflorescence a diffuse lateral or terminal cyme, the ultimate flower clusters usually subumbellate; stamens 1–3(–5). .... 3. *Boerhavia.*
A. Plants woody, sometimes armed; flowers usually imperfect; stigma penicillate; embryo straight. .... 4. *Pisonia.*

Tribe NYCTAGINEAE [Mirabileae Meissner]

Subtribe **Nyctagininae** [Boerhaviinae Bentham & Hooker]

1. **Mirabilis** Linnaeus, Sp. Pl. 1: 177. 1753; Gen. Pl. ed. 5. 82. 1754.

Annual or perennial herbs with one to numerous stems from a tuberous root or woody rootstock; the stems stout or slender, slightly 4-angled, simple or dichotomously branched, erect or decumbent, as much as 1–2 m. high, densely pubescent, pubescent in lines, or glabrous, sometimes viscid

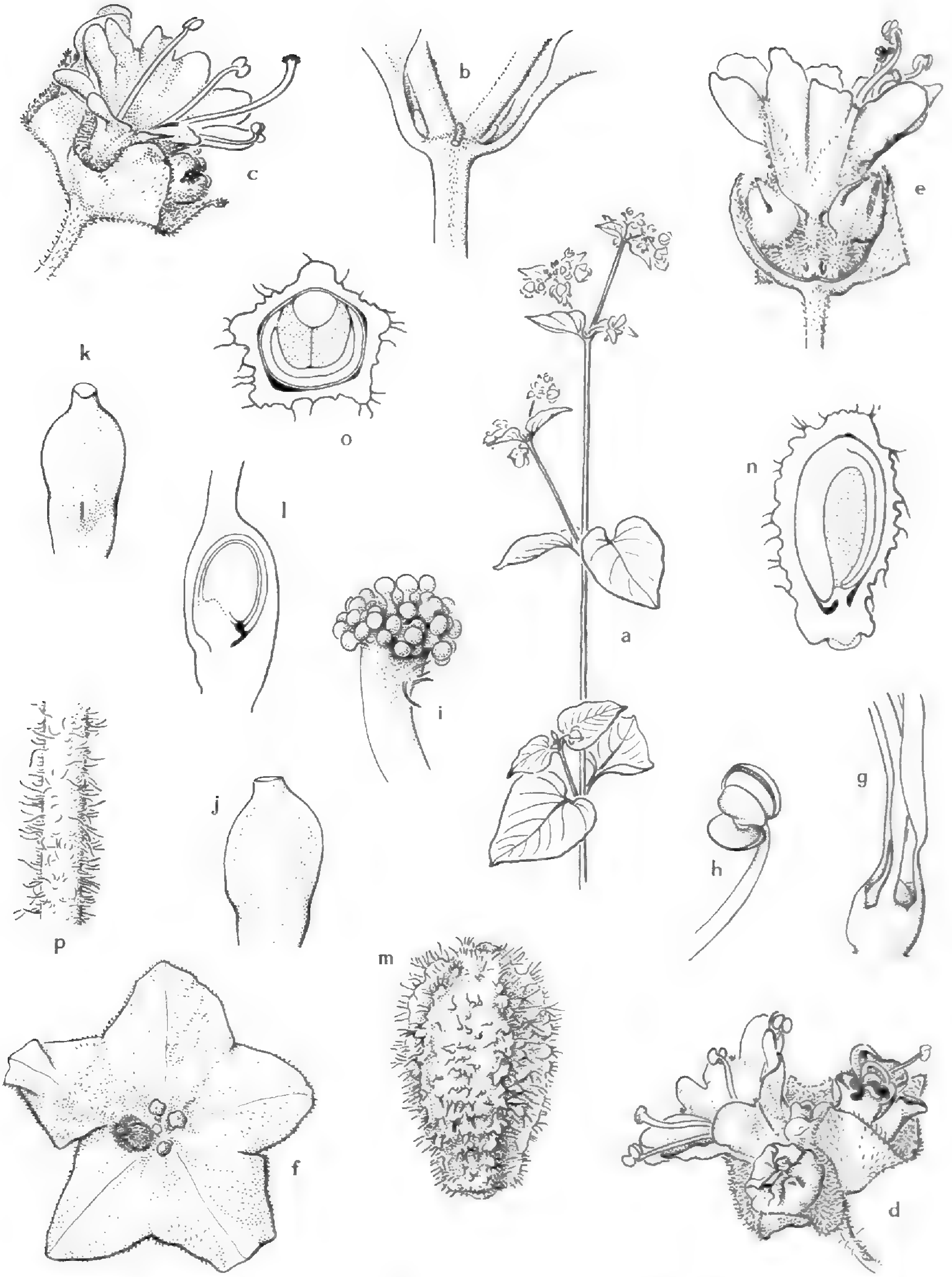


FIGURE 1. **Mirabilis.** a–o, *M. nyctaginea*: a, flowering branch, × 1/4; b, leaves at base of inflorescence with aborted terminal flower, × 2; c, d, two views of cymule of flowers with involucre, × 3; e, same, lateral view, portion of involucre removed to show flower and two buds, × 3; f, involucre from above, showing developing fruit and pedicels of three unpollinated flowers, × 2; g, base of androecium showing connation of staminal filaments around ovary, × 12; h, anther after dehiscence, × 12; i, stigma, × 25; j, k, two views of ovary, × 25; l, ovary in diagrammatic vertical section, showing basal ovule, × 25; m, mature accrescent calyx base inclosing fruit, × 10; n, same in vertical section showing fruit with embryo surrounding perisperm (stippled), ovary wall and seed coat too thin to be shown except at base, × 10; o, same in cross section, the embryo cut through cotyledons and hypocotyl, perisperm stippled, × 10. p, *M. hirsuta*: portion of stem, hairy, in contrast with stem of *M. nyctaginea*, × 2.

or glaucous, nodes slightly swollen; leaves opposite, exstipulate, petioled or sessile, entire; inflorescence an axillary or terminal, loose or congested thyrsiform or paniculate cyme of involucrate flowers, or involucres solitary in the axils; involucres one to few flowered, calyx-like, 5-lobed, the lobes equal or unequal, erect, imbricate in bud, green (the margins sometimes tinged purple) glabrous or pubescent, ± campanulate, often accrescent, becoming rotate and conspicuously veiny in fruit; flowers perfect, calyx tubular, corolla-like, the tube mostly very short, in a few species long to very long (3–17 cm.), constricted above the ovary, the limb campanulate to funnel-form or rotate (or not conspicuously expanded), 5-lobed, the lobes retuse or emarginate, induplicate-valvate or -plicate, the perianth ephemeral, falling after anthesis but the base persistent about the ovary and thickening in fruit; stamens 3–5, hypogynous, free or basally connate, filaments capillary, unequal, anthers didymous, exserted, dehiscing by slits; pollen polyporate; ovary superior, sessile, of one carpel; style filiform, longer or shorter than the stamens, stigma capitate, papillose; ovule solitary, anacampylotropous, integuments two; fruit accessory, the persistent calyx tube thickened, hard or leathery, 5-angled or -ribbed, the angles and surfaces smooth, rugose, or verrucose, pubescent or glabrous, the ovary wall membranaceous; embryo ± folded, cotyledons foliaceous, unequal (the inner smaller), curved around an abundant perisperm, radicle about as long as the cotyledons. (Including *Allionia* Loefl. [not *Allionia* L., nom. cons.]), *Oxybaphus* L'Hér., *Calymenia* Pers., *Jalapa* Miller, *Nyctago* Juss., *Trimista* Raf., *Admirabilis* Nieuwl.) TYPE SPECIES: *M. Jalapa* L. (From Latin, wonderful, presumably in reference to the large colorful flowers of *M. Jalapa.*) — Four-o'clock, marvel of Peru, umbrella-wort.

A New World genus of perhaps 45(–60) species, disposed most recently in six sections (Heimerl, 1934). The genus is best developed in southwestern North America but ranges from southern Canada and New England south to southern South America, with one species in Asia. As many as thirty-two species (under several generic synonyms) have been reported from the southwestern United States (Standley, 1918), but only five occur in our area.

Section MIRABILIS (sect. *Eumirabilis* Hook. f. in Heimerl, 1934) is characterized by one-flowered, more or less campanulate involucres that change little in fruit. Each flower has a conspicuous corolla-like, salverform, or funnel-shaped (to almost cylindric) calyx, five stamens, and a nonmucilaginous, glabrous or hairy, angled or ribbed, smooth or warty accessory fruit. The section is represented in our area only by *Mirabilis Jalapa*, four-o'clock or marvel of Peru, $2n = 54, 58$, a popular garden annual (or perennial in warmer regions). The erect, much-branched, tuberous-rooted plants of this species reach a meter in height, bear mostly ovate-deltoid to broadly ovate, glabrous, petiolate leaves with subcordate to rounded bases, and flowers with a showy salverform calyx tube 3–6 cm. long, which varies in color from purplish to red, yellow, white, or variegated. The species escapes from cultivation and is naturalized in waste places in some areas of the Southeast.

The four remaining species of our area were assigned by Heimerl (1934) to sect. EUOXYBAPHUS Heimerl, which contrasts with section MIRABILIS in having 2–6-flowered, campanulate involucres that become enlarged, veiny, and more or less rotate at maturity; a shorter campanulate to funnelform (or rotate) calyx limb that lacks a long tube and is deeply constricted above the ovary; 3–5 stamens; and fruit with a strongly 5-ribbed, usually hairy calyx base that becomes gelatinous when wet. *Mirabilis nyctaginea* (Michx.) MacM. (*Allionia nyctaginea* Michx., *Oxybaphus nyctagineus* (Michx.) Sweet), wild four-o'clock or heart-leaved umbrellawort, $2n = 58$, forms stout, erect, much-branched glabrous (or pubescent in lines above) plants bearing definitely petioled, usually deltoid-ovate leaf blades with rounded to cordate bases, pedunculate, congested-cymose inflorescences, basally short-pilose or puberulent involucres, magenta to pale-pink (or white) calyx tubes about 10 mm. long, and a fruit with a densely short-pilose obovoid calyx base with more or less rugose angles. It prefers rich soil in dry open ground in prairies and waste places, ranging in our area from Alabama to Louisiana and Arkansas, westward to Texas and Mexico, northward east of the Rocky Mountains to Tennessee, Wisconsin, Manitoba, and Montana. To the east and west it is reported as a rare adventive weed of waste places, especially along railroad beds and roadsides. *Mirabilis albida* (Walter) Heimerl (*Allionia albida* Walter, *Oxybaphus albidus* (Walter) Sweet) is a variable species having more or less glabrous stems bearing inconspicuous hairs in two lines along the internodes; sessile or nearly sessile leaves with usually lanceolate blades about 4–12 times longer than broad that vary in shape from linear-lanceolate to narrowly elliptic or oblong; a white or pale-pink perianth about 8–10 mm. long; and fruiting calyx bases with tuberculate angles. The species ranges from Georgia to Texas, northward to South Carolina, Tennessee, Iowa, and Kansas. It is usually found in open ground in prairies and meadows, the edges of bluffs, and limestone glades, as well as in waste places.

The stems of *Mirabilis hirsuta* (Pursh) MacM. (*Allionia hirsuta* Pursh, *Oxybaphus hirsutus* (Pursh) Sweet) are conspicuously and often densely pubescent or viscid pubescent. The pubescent leaves are sessile or borne on short, stout petioles, with broadly to narrowly ovate, cuneate, or linear-lanceolate blades, truncate to rounded or attenuate bases, and gradually narrowed, obtuse apices. The mostly three-flowered, viscid-pilose involucres may be solitary and axillary on younger plants, or grouped in diffuse, long-pedunculate thyrsiform or paniculate cymes on mature plants. The white to pink calyx tubes are 8–10 mm. long, and have 3–5 exserted stamens. In fruit, the accrescent calyx bases have more or less smooth angles and warty surfaces. A species of the Great Plains, *M. hirsuta* occurs in dry, open soil of prairies, sandhills, and gravelly areas and is probably adventive in our area from its native range, which extends from Texas, Oklahoma, and western Missouri, northward to Wisconsin and

Saskatchewan, and westward to the Rockies. *Mirabilis linearis* (Pursh) Heimerl (*Allionia linearis* Pursh, *Oxybaphus linearis* (Pursh) Robinson), $2n = 52$, is distinguished by its thick, linear leaves 5–15 cm. long and usually less than 5 mm. broad. The stems are usually glabrous (sometimes puberulent in lines) and often slightly woody below, developing from a woody rootstock. The pale-pink to purplish-red perianth is about 10 mm. long, and the perianth base in fruit is smooth angled. This species is apparently a rare adventive in our area from its range in western Missouri, Oklahoma, Arizona, and Mexico, northward to Minnesota and Montana (Steyermark, 1963).

Taxonomic opinion has varied as to the number of genera represented in the *Mirabilis* group. Gray (1859) separated *Mirabilis* (incl. *Quamoclidion* Choisy) and *Oxybaphus* (including the four indigenous species of our area) on characters of the involucre, stamen number, and fruit, while Heimerl (1889) recognized only *Mirabilis* (incl. *Oxybaphus*, *Quamoclidion*). Many species now included in *Mirabilis* have synonyms in *Allionia* Loefl., *Allioniella* Rydb., *Hesperonia* Standley, *Oxybaphus* L'Hér., and *Quamoclidion* Choisy. All of these genera were recognized by Rydberg (1902) and by Standley (1909, 1911, 1918) in his earlier papers. However, Standley (1931), the principal American student of the family, finally concluded that "If only the species of North America are considered, such genera as *Oxybaphus*, *Quamoclidion*, and *Hesperonia* seem to be differentiated by good and constant characters; but as so often happens, when extra limital species are taken into account, the characters supposed to separate the groups break down. It seems necessary, therefore, to follow Heimerl in considering all the plants of the group as repsenting a single genus." In his last revision of the genus Heimerl (1934), the leading European student of the family, recognized about 60 species arranged in six sections. Subgenera were recognized in *Mirabilis* (excl. *Oxybaphus*) by Gray (1859), Jepson (1909), and Macbride (1917, 1918). Shinners (1951) considered the species of *Oxybaphus* to be quite distinct, but satisfactory as a subgenus of *Mirabilis*. Most authors now recognize only *Mirabilis* (e.g., Reed, 1969), but *Oxybaphus* has been maintained as distinct from *Mirabilis* on a traditional basis in some recent floristic works, with the acknowledgment that the two might better be united (Gleason, 1952; Gleason & Cronquist, 1963).

Shinners noted that extreme seasonal, genetic, and environmental polymorphism exists in most of the species. He suspected hybridization in the genus, particularly in *Mirabilis albida*, which shows variation suggesting the influence of *M. linearis* and *M. gigantea* (Standley) Shinners, and possibly other species. A modern systematic study and revision of the genus is needed.

Chromosome counts recorded for six species of the genus show $2n = 52$, 54, or 58 (Bolkhovskikh, Bowden, Löve & Löve).

Related genera include *Allionia* L. (nom. cons., *A. incarnata*, $2n =$ ca. 58; incl. *Wedelia* Loefl., and *Wedeliella* Cockerell), which can be distinguished by its usually three-flowered, three-parted involucres of fused bracts, and compressed fruits bearing two rows of stipitate glands on the dorsal surface of the calyx base, and the monotypic *Hermidium* S. Watson (*H. alipes* S. Watson), in which the flowers are aggregated in headlike clusters and the pedicel of each flower is adnate to the midrib of a subtending foliaceous bract. Barneby (1942) suggested that *Hermidium alipes* is morphologically little more than a primitive relative of "subgenus Quamoclidion" and should be united with *Mirabilis*.

The best known species is *Mirabilis Jalapa* ($2n = 58$). Because of its easy cultivation it has been the subject of numerous investigations in many fields. It figured significantly in early genetic investigations on the inheritance of flower color (see Heimerl, 1934, p. 109, for citations of early literature; Kiernan & White, 1926; Showalter, 1934b). Although largely attributable to Mendelian inheritance patterns, non-Mendelian variation in flower color and plant habit due to somatic or gametic mutation has also been reported (Showalter, 1934a, b; Nakajima, Melcher). Clute reported a case of amphichromy, with both red and white flowers on the same plant, and even in the same cluster.

Hybrids between cultivated plants of *Mirabilis Jalapa* and *M. longiflora*, $2n = 54, 58$, have been known since the mid-eighteenth century, and have also been synthesized and studied extensively with regard to the cytological aspects of hybrid sterility (Tischler, Prakken), and to hybrid variation and the inheritance of parental characteristics (Prakken, Bazavluk, Kruszewska). Jost found that the cross *M. Jalapa* × *M. longiflora* works, but that the reciprocal cross never succeeds because the pollen tube of the relatively short-styled *M. Jalapa* stops growing before it has traversed the length of the much longer style of *M. longiflora*, thus preventing fertilization.

In the developing seedling of *Mirabilis Jalapa* a transition from monopodial to falsely dichotomous sympodial branching occurs between the level of the cotyledons and the fifth node. This change is brought about by the inhibition of the terminal apex and the accelerated development of the two lateral axillary buds at each node. It is accompanied by a change in the organization of the apical meristem that persists until the appearance of the first (terminal) flower (Champagnat & Laurent). Other morphological and anatomical studies dealing with *M. Jalapa* include those of Beal & Whiting; Champagnat, Champagnat, & Laurent; Lloyd; Mirskaja; Morot; Regnault; Vardar; and Wibaut.

Clements described in detail the histogenesis of the root-stem transition zone, lateral roots, and vegetative apex in *Mirabilis hirsuta* and *M. nyctaginea*. The ontogeny and course of the complex primary vascular system of the internodes, nodes, petioles and lateral branches of *M. Jalapa* is described by Inouye. Secondary tissues are derived from a primary thickening meristem that in *M. Jalapa* is extrafascicular in origin, developing acropetally in the stem and downward through the hypocotyl into the root, where further growth is also acropetal (Maheshwari; Mikesell & Popham).

Floral ontogeny is acropetal in sequence, the carpel arises on one side of and gradually incloses an apparently terminal nucellus. The carpel margins are fused in *Mirabilis Jalapa*, but are free for a short distance in *M. nyctaginea* (as *Oxybaphus Cervantesii*), forming a small pore (Payer). Heimerl (1887) described and illustrated in detail the anatomy and development of the flowers and fruits of *M. Jalapa*, *M. longiflora*, and *M. nyctaginea*. According to Joshi & Rao, the perianth of *Mirabilis Jalapa* is supplied by ten traces arising as two pentamerous cycles from the pedicellar stele, while a series of five stamen-traces originates above and opposite the upper set of perianth traces. A single (dorsal) bundle supplies the carpel, providing one trace to the basal ovule. Both the accrescent calyx base and the basal "coalesced" portion of the androecium which bears nectariferous tissue on its inner surface are interpreted by Buxbaum as being outgrowths of the floral axis rather than modifications of the perianth and androecium. The anatomy of the style and stigma of *M. Jalapa* are described by Guéguen.

The earlier embryological literature on the genus was reviewed by Rocén, who described the details of development and structure of the stamens, carpels, ovules before and after fertilization, and that of the endosperm for eight species of *Mirabilis* and *Oxybaphus* (including *M. Jalapa* and *M. nyctaginea*). Development of the female gametophyte is of the Polygonum type, and two gametophytes are sometimes formed. Each locule of the tetrasporangiate anther of *M. nyctaginea* contains 8–24 large pollen grains that are 3-celled when shed (Cooper). During embryo development (Asterad type) almost all the free-nuclear endosperm is absorbed by the embryo. Only a small portion of the endosperm becomes cellular; this persists as a cap over the tip of the radicle. The pollen tube is stated to persist throughout seed development, functioning as a haustorium in the transfer of nutrient materials from secretory cells of the funiculus to the developing embryo (Cooper; Hedeman; Schnarf; Woodcock). The stalk of the mature ovule is densely packed with white raphide crystals (Pobeguin, Cooper).

One of the most interesting morphological features of the genus is the progressive reduction in the number of flowers (as many as 12) included within the involucre, culminating in the one-flowered inflorescences evident in sect. MIRABILIS, in which the involucre imitates a calyx and the calyx a brightly colored corolla. The flowers of *Mirabilis* are ephemeral, opening in the late afternoon or evening and closing by early to mid-morning. The time of anthesis varies among the species (Kerner, Cruden), and poor weather conditions may delay opening and closing of flowers. The time of anthesis may also be genetically controlled, with continuous variation demonstrated among F_1 hybrid progeny resulting from crosses between *M. Jalapa* and *M. longiflora* (Kruszewska). The mechanism controlling anthesis is not known, but Meeuse concludes that the daily flowering time of *M. Jalapa* may be determined by the time of sunset on the preceding day.

Both self-compatible (*M. Jalapa, M. longiflora, M. nyctaginea, M. violacea*) and self-incompatible (*M. Froebelii, M. Greenei, M. multiflora*) breeding systems are reported in the genus (Kerner; Baker, 1961, 1964; Cruden, 1973). In *M. nyctaginea* pollination is by bees in both afternoon and morning and by small noctuid moths at night. Chasmogamous flowers are produced in early summer, cleistogamous ones in later summer. Chasmogamous flowers can be self pollinated as the flower closes, the coiling of the style and then the stamens bringing the stigma in contact with the pollen. (Cruden, 1973). Both insect pollination and self pollination are recorded for *M. Jalapa.* As the flower closes the coiling of the style carries the stigma through the stamens at least once, sometimes twice (Cruden, 1973; Heimerl, 1888).

Hawkmoths pollinate the white, night-blooming flowers of *M. longiflora* and *M. multiflora,* while hawkmoths and hummingbirds are the principal pollinators for *M. Froebelii,* along with bees and butterflies (Kerner; Baker, 1961; Cruden, 1970). The "apparent" tristyly observed in *M. Froebelii* by Baker (1964) is suggested by Bateman to be an early stage in speciation by divergent adaptation to different pollinators. Cruden (1970) suggests that selection for a single class of pollinators (hawkmoths) has occurred in *M. multiflora.*

Species of *Mirabilis* have long been cultivated as garden annuals or for use in folk medicine. *Mirabilis Jalapa* was introduced into European horticulture, supposedly from Peru, in 1596 (Curtis, 1797; Showalter. 1934b). However, a plant reputed to be *M. Jalapa* is illustrated in the Badianus Manuscript (ca. 1552; cf. Emmart), and Standley (1931) suggested that the species may have originated in Mexico, since its nearest relatives are indigenous there, while none occur in Peru. The specific epithet derives from the very early but erroneous belief that this species was the source of the medicinal resin "Jalap," the actual source of which is *Exogonium Purga* (Hayne) Lindley, of the Convolvulaceae (Hill, 1952). *Mirabilis nyctaginea* was also early cultivated in European botanical gardens, and some species, e.g., *Oxybaphus floribundus* Choisy, were described from such plants (Shinners). About ten species or hybrids of the genus are now cultivated as ornamentals (Bailey & Bailey; Chittenden). In areas where the plants are not hardy the fleshy roots can be lifted in the fall and stored over the winter like *Dahlia* roots.

Apart from its horticultural value the genus is of no economic importance. The roots of *Mirabilis Jalapa* are mildly purgative and are also used in folk medicine for dropsy. The leaves are bruised or ground for use in poultices for boils, abscesses, and scabies. When steeped in water the flowers provide a crimson dye used in China for tinting cakes and also jellies prepared from seaweed. A cosmetic powder is made in Japan from the powdered seeds (Stemmerik, Uphof).

REFERENCES:

Under family references see BAILLON; BENTHAM & HOOKER; BOLKHOVSKIKH *et al.*; BUXBAUM; CHITTENDEN; FIEDLER; HEGNAUER; INAMDAR; JOSHI &

Rao; Kerner; Maheshwari; Mikesell & Popham; Rocén; Schermerhorn & Quimby; Schnarf; Standley, 1909, 1931a; Stemmerik; Uphof.

Ahles, H. E., & A. E. Radford. Species new to the flora of North Carolina. Jour. Elisha Mitchell Sci. Soc. **75:** 140–147. 1959. [*M. nyctaginea.*]

———, C. R. Bell, & A. E. Radford. Species new to the flora of North or South Carolina. Rhodora **60:** 10–32. 1958. [*M. Jalapa,* 14.]

Bailey, L. H., & E. Z. Bailey. Hortus Second. 778 pp. New York. 1941.

Baker, H. G. The adaptation of flowering plants to nocturnal and crepuscular pollinators. Quart. Rev. Biol. **36:** 64–73. 1961.

———. Variation in style length in relation to outbreeding in *Mirabilis* (Nyctaginaceae). Evolution **18:** 507–509. 1964.

Barneby, R. C. A new species of *Mirabilis,* with remarks on *Hermidium* and related genera. Leafl. West. Bot. **3:** 175–179. 1942.

Bateman, A. J. The role of heterostyly in *Narcissus* and *Mirabilis.* Evolution **22:** 645–646. 1968.

Bazavluk, V. IU. The emergence of characteristics of two paternal forms which took part in the pollination of *Mirabilis Jalapa.* Trudy Inst. Genet. Akad. Nauk SSSR. **23:** 65–78. 1956.*

Beal, J. M., & A. G. Whiting. Effect of indoleacetic acid in inhibiting stem abscission in *Mirabilis Jalapa.* Bot. Gaz. **106:** 420–431. 1945.

Champagnat, M., & E. Laurent. Recherches morphologiques sur la ramification de *Mirabilis Jalapa* L. Rev. Gén. Bot. **63:** 181–192. 1956.

———, P. Champagnat, & M. Laurent. Evolution morphologique du point végétatif de *Mirabilis Jalapa* L. VIII^{e} Cong. Int. Bot. Paris 1954. Rap. Comm. Sect. 7/8: 202, 203. 1957.

Clements, F. E. Contributions to the histogenesis of the Caryophyllales. I. Trans. Am. Microscop. Soc. **20:** 97–160. *pls. 8–25.* 1899. [*M. hirsuta, M. nyctaginea,* as species of *Allionia.*]

Clute, W. N. Perennial four o'clocks. Am. Bot. **30:** 139–140. 1924.

Cooper, D. C. Flower and seed development in *Oxybaphus nyctagineus.* Am. Jour. Bot. **36:** 348–355. 1949.

Cruden, R. W. Hawkmoth pollination of *Mirabilis* (Nyctaginaceae). Bull. Torrey Bot. Club **97:** 89–91. 1970.

———. Reproductive biology of weedy and cultivated *Mirabilis* (Nyctaginaceae). Am. Jour. Bot. **60:** 802–809. 1973. [*M. nyctaginea, M. Jalapa, M. multiflora,* and *M. Froebelii.*]

Curtis, W. *Mirabilis Jalapa,* Common Marvel of Peru. Bot. Mag. **11:** *pl. 371.* 1797.

Emmart, E. W. The Badianus Manuscript (Codex Barberini, Latin 241). An Aztec Herbal of 1552. xxiv + 341 pp. Johns Hopkins Press, Baltimore. 1940.

Gray, A. Brief characters of some new genera and species of Nyctaginaceae, principally collected in Texas and New Mexico. Am. Jour. Sci. II. **15:** 319–324. 1853.

———. Nyctaginaceae. Pp. 168–175 *in* J. Torrey, Bot. Mex. Bound. Surv. 1859. [*Mirabilis, Oxybaphus, Allionia.*]

Guéguen, M. F. Anatomie comparée du tissu conducteur du style et du stigmate des Phanérogames (I. Monocotylédones, apétales et gamopétales). Jour. Bot. Morot **16:** 15–30. 1902. [Nyctaginées, *25, 26, pls. 11, 12; M. Jalapa.*]

HARLAND, S. C., & J. C. HAIGH. Counted grain pollinations in *Mirabilis Jalapa* L. Am. Nat. **61**: 95–96. 1927.

HEDEMANN, E. Über experimentelle Erzeugung von Adventivembryonen bei *Mirabilis uniflora* und *Mirabilis Froebelii.* Biol. Zentralbl. **51**: 647–652. 1931.

HEIMERL, H. Beiträge zur Anatomie der Nyctagineen. I. Denkschr. Akad. Wiss. Wien Math-Naturw. 53. 1887. [*M. Jalapa, M. longiflora, O. nyctagineus.*]

———. Die Bestaübungseinrichtungen einiger Nyctaginaceen. Verh. Zool.-Bot. Ges. Wien **38**(Abhandl.): 769–774. *figs. 1–3.* 1888.

———. Studien über einige Nyctaginaceen des Herbarium Delessert. Ann. Conserv. Jard. Bot. Genève **5**: 12–197. 1901. [New species or combinations in *Mirabilis*, incl. *M. Jalapa, M. nyctaginea, M. albida, M. linearis.*]

———. Beiträge zur Kenntnis amerikanischer Nyctaginaceen. Österr. Bot. Zeitschr. **56**: 249–255, 406–414, 424–429. 1906.

HILL, A. F. Economic Botany. Ed. 2. ix + 560 pp. New York. 1952.

HJELMQVIST, H., & F. GRAZI. Studies on variation in embryo sac development. 2. Bot. Not. **118**: 329–360. 1965. [*M. Jalapa,* 335–344; *Oxybaphus nyctagineus,* 329–335.]

INOUYE, R. Anatomical studies on the vascular system of *Mirabilis Jalapa* L. Bot. Mag. **69**: 554–559. 1956.

JEPSON, W. L. A flora of California. 2 vols. University of California, Berkeley. 1909. [Nyctaginaceae, Vol. 1, pt. 2, pp. 451–459.]

JOST, L. Über die Selbsterilität einiger Blüten. Bot. Zeit. **65**: 77–117. 1907. [*Mirabilis,* 109, 110.]

KIERNAN, F. P., & O. E. WHITE. Inheritance in four o'clocks. Jour. Hered. **17**: 383–386. 1926.

KRUSZEWSKA, A. The heredity of specific traits in the hybrid *Mirabilis Jalapa* × *Mirabilis longiflora.* Acta Polsk. Towarz. Bot. **30**: 611–648. 1961.*

LECOQ, H. Recherches sur les variétés et les hybrides des *Mirabilis Jalapa* et *longiflora.* Clermont. 1852.*

LLOYD, F. E. Abscission in *Mirabilis Jalapa.* Bot. Gaz. **61**: 213–230. *pl. 13, figs. 1, 2.* 1916.

LÖVE, A., & D. LÖVE. Chromosome numbers of central and northwest European plant species. Op. Bot. **5**: 1–581. 1961. [Nyctaginaceae, 132.]

MACBRIDE, J. F. Notes on the Hydrophyllaceae and a few other North American spermatophytes. Contr. Gray Herb. **49**: 23–59. 1917. [*Mirabilis,* 49.]

———. A revision of *Mirabilis*, subgenus *Hesperonia. Ibid.* **56**: 20–24. 1918.

MEEHAN, T. *Oxybaphus hirsutus.* Meehan's Monthly **9**: 177, 178. *pl. 12.* 1899. [Color plate; notes on floral biology, nomenclature, distribution; discussion of history, morphology, and relationships among *Mirabilis, Allionia, Oxybaphus.*]

MEEUSE, B. J. D. The story of pollination. x + 243 pp. Ronald Press, New York. 1961. [*Mirabilis Jalapa,* p. 63.]

MELCHER, R. Some observations and experiment on *Mirabilis Jalapa* L. chimeras. Zeitschr. Pflanzenzucht. **46**: 301–306. 1961.*

MIRSKAJA, L. Ergänzungsvorgänge an längsgespaltenen Stämmen von *Mirabilis Jalapa.* Flora **124**: 315–332. 1930. [Regeneration studies on surgically wounded stems.]

MOROT, L. Recherches sur le péricycle ou couche périphérique du cylindre central chez les Phanérogames. Ann. Sci. Nat. Bot. VI. **30**: 217–309. *pls. 9–14.* 1885. [*Mirabilis, pls. 7, 14, fig. 44.*]

NAKAJIMA, G. The tetraploid plants of *Mirabilis Jalapa* raised by the colchicine method. Kromosoma **34–36**: 1207–1210. 1958.*

PAYER, J. B. Traité d'organogénie comparée de la fleur. vii + 748 pp., *145 pls.* Paris. 1857. [Nyctaginées, 297–300.]

POBEDIMOVA, E. Concerning the biology of blossoming of *Allionia nyctaginea* Michx. (In Russian.) Soviet. Bot. **14**: 177–182. 1946.*

POBEGUIN, T. L'oxalate de calcium chez les *Mirabilis*: disposition particulière des raphides dans la fleur et le fruit. Ann. Sci. Nat. Bot. XI. **11**: 1–19. 1950.

PRAKKEN, R. Contributions to the genetics and cytology of *Mirabilis.* Hereditas **30**: 201–212. 1944. [Experimental hybridizations, *M. Jalapa* × *M. longiflora.*]

REED, C. F. Nyctaginaceae. *In*: C. L. LUNDELL, *et al.* Flora of Texas. **2**: 151–220. 1969.

REGNAULT, M. Recherches sur les affinités de structure des tiges des plantes du groupe des Cyclospermées. Ann. Sci. Nat. Bot. IV. **14**: 73–166. *pls. 4–9.* 1860. [Nyctaginées, 144–149, *pl. 9.*]

ROGERS, K. E., & F. D. BOWERS. Notes on Tennessee plants. Castanea **34**: 394–397. 1969. [*Oxybaphus nyctagineus.*]

SHINNERS, L. H. The North Texas species of *Mirabilis* (Nyctaginaceae). Field & Lab. **19**: 173–182. 1951.

SHOWALTER, H. M. The box type four-o'clock. A mutation of stalk character in *Mirabilis Jalapa.* Jour. Hered. **25**: 323–325. 1934a.

———. Self flower-color inheritance and mutation in *Mirabilis Jalapa* L. Genetics **19**: 568–580. 1934b.

———. A study of the chromosomes and degenerating microspore tissue in *Mirabilis.* Am. Jour. Bot. **22**: 594–608. *pls. 1–3.* 1935.

TAYLOR, R. L., & R. P. BROCKMAN. Chromosome numbers of some Western Canadian plants. Canad. Jour. Bot. **44**: 1093–1103. 1966. [*M. linearis,* $2n = 52$.]

TISCHLER, G. Zellstudien an sterilen Bastardpflanzen. Archiv. Zellforschung **1**: 33–151. 1908.

USTINOVA, E. I., M. I. D'YAKOVA, & R. N. SHCHEDRINA. Development of the embryo and the endosperm in *Mirabilis Jalapa* L. after limited pollination. Nauchn. Dokl. Vyssh. Shkoly Biol. Nauki **3**: 173–179. 1961.*

WIBAUT, C. Ontogenesis of the vegetative and reproductive organs of *Mirabilis Jalapa* L. (Nyctaginaceae). Rev. Cytol. Biol. Veg. **28**: 43–132. 1965.*

WOODCOCK, E. F. Seed studies in Nyctaginaceae. Pap. Michigan Acad. Sci. **9**: 495–502. *pls. 90, 91.* 1929.

2. **Okenia** Schlechtendal & Chamisso, Linnaea **5**: 92, 93. 1830.

Densely and finely glandular-pubescent annual herbs, with diffuse prostrate branches 2–7 feet long radiating from a short ligneous caudex on a long narrow taproot, forming mats. Leaves opposite, markedly unequal, the large and small alternating in position on the stem, the smaller often not as long as the petiole of the larger; petioles long, stout, exstipulate; blades ovate-deltoid, ovate or elliptic-ovate, the base rounded, truncate, or subcordate, sometimes inequilateral, the apex acute to rounded, the

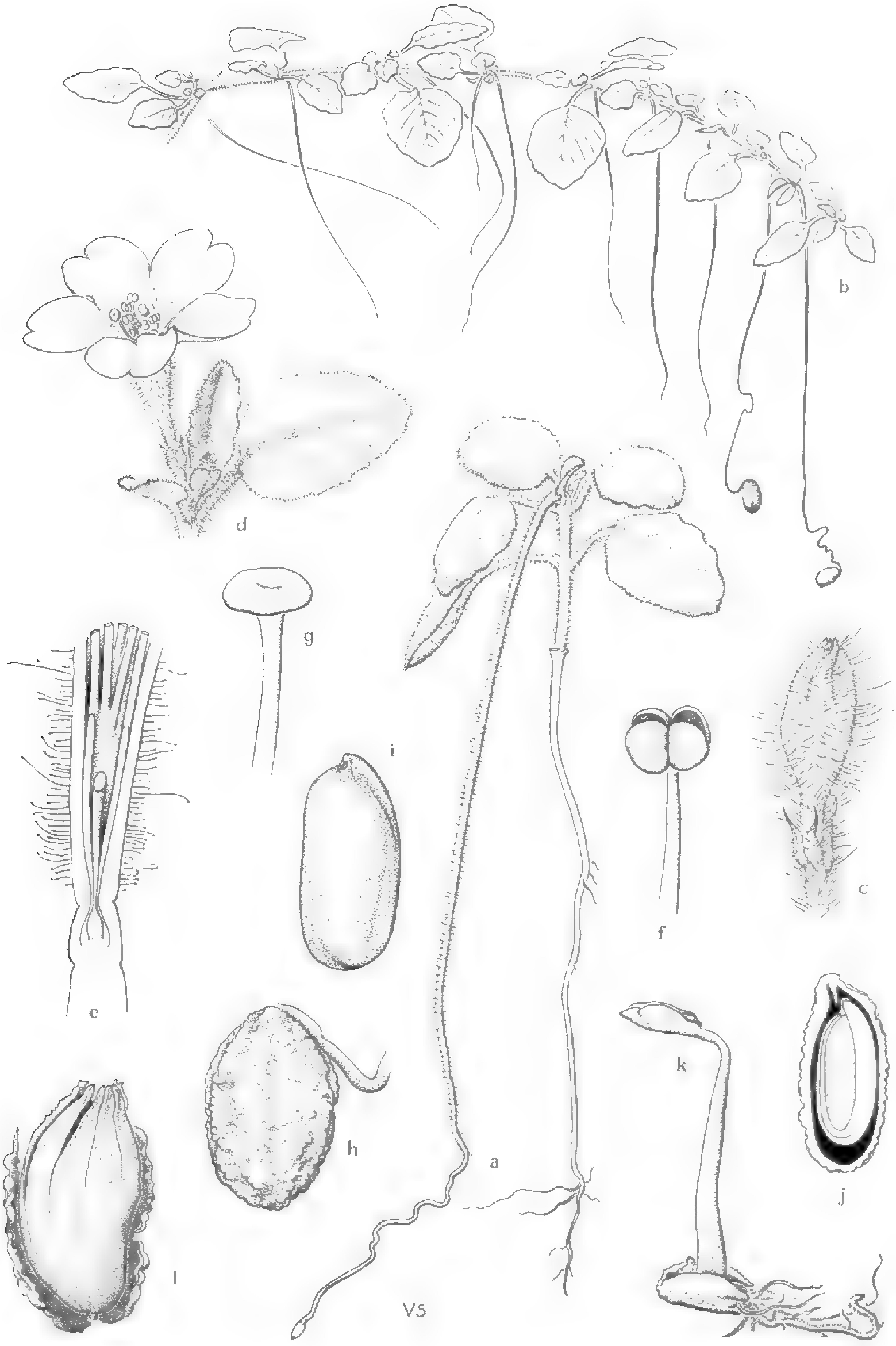


FIGURE 2. **Okenia.** a–l, *O. hypogaea*: a, seedling (in July) bearing developing fruit from first flower, the peduncle greatly elongated, × 3/4; b, branch from prostrate fruiting plant (in October) with two mature fruits and withered peduncles of earlier fruits, × 1/3; c, bud with bractlets, × 3; d, open flower, × 1 1/2; e, lower part of flower in partial section to show connation of staminal filaments — note ovary free from stamens and calyx base, × 12; f, anther, × 12; g, stigma, × 12; h, nearly mature accessory fruit, × 2; i, mature fruit removed from accrescent calyx base, × 3; j, mature accessory fruit in vertical section to show embryo surrounding perisperm (stippled), × 2; k, seedling with remains of calyx base, × 1; l, remains of calyx base after germination of seed, × 3.

margin entire to shallowly sinuate; both surfaces densely viscid-villous, the epidermis marked by the small brown dots of the trichome bases. Flowering stems axillary, ascending at anthesis, later deflected, pushing underground. Flowers incomplete, perfect, cleistogamous (?); terminal, solitary at each node, on long, often naked peduncles axillary to the small leaf of each pair, subtended by an involucre of 3–4 small, narrow, subulate bracts and a short pedicel. Sepals 5, united in a short, slender, funnelform tube, densely pubescent without, constricted above the ovary, 5-lobed, the lobes notched, brilliant magenta [dark blue to violet or white]; earlier flowers 25–30 mm. in diameter, later flowers much smaller; aestivation induplicate-plicate. Stamens 9–18; filaments filiform, unequal, united below into a short tube, magenta above to white below; anthers didymous, the lobes subglobose, attached to each other and the filament at the middle, dehiscing laterally by simple longitudinal slits. Style filiform, long; stigma large, capitate-peltate. Ovary small; ovule campylotropous (?). Fruit hypogeous, the thin-walled pericarp enclosed in the ± oblong thickened corky base of the calyx tube that is longitudinally ribbed, transversely plicate between the ribs, dark brown to whitish. Embryo peripheral, conduplicate; cotyledons large, obovate, unequal, enclosing the starchy perisperm; radicle about as long as the cotyledons, ascending. TYPE SPECIES: *O. hypogaea* Schlechtendal & Cham. (Named after the German naturalist Lorenz Oken, 1779–1851). — Dune-groundnut.

A very small and little-known genus, probably of two species, best known in our area as a maritime dune-plant on the Keys of southeastern Florida, where it is represented by the type species. The genus is also distributed in Mexico on both the eastern and western coasts and in the interior.

Standley (1911) described two new species (*O. grandiflora* and *O. rosei*) from specimens collected in Jalisco, Mexico, but later (1918) reduced them to synonymy under *O. hypogaea*. More recently, Wilson (1958) described *O. parviflora* P. G. Wilson from inland Mexico (Michoacán, Guerrero), a plant that is said to differ from *O. hypogaea* in its much smaller flowers and fewer (ca. 5) stamens.

The genus is notable for its subterranean fruits, which mature at depths of 10–30 cm. below the surface and germinate in place to give rise to new plants. After the ephemeral corolline calyx tube has fallen the peduncle becomes deflected and, through rapid elongation, pushes the developing fruit inclosed in the calyx base beneath the surface of the sand. A conical cap of cells, much like a thick root-cap, develops over the tip of the calyx base, protecting the ovary from abrasion as it is pushed beneath the sand (Karsten). Heimerl (1911) published brief observations on the morphology and anatomy of the fruit, seed, embryo, and seedling, but the vegetative anatomy, embryology, and chromosome number of the genus are apparently unknown. This interesting genus requires further study, particularly with regard to its floral biology and its taxonomy in Mexico.

REFERENCES:

Under family references see BAILLON; BENTHAM & HOOKER; CHOISY; HEIMERL; NOWICKE, 1970; RICKETT; STANDLEY, 1911, 1918.

HEIMERL, A. Zur Kenntnis der Gattung *Okenia.* Verh. Zool. Bot. Ges. Wien **61:** 461–467. 1911 (1912). [Morphology and anatomy of the accrescent calyx base, fruit, seed, embryo, seedling.]

KARSTEN, G. Notizen über einige mexikanische Pflanzen. Ber. Deutsch. Bot. Ges. **15:** 10–16. *pl. 2, fig. 2.* 1897. [*O. hypogaea,* 13–16, *pl. 2, fig. 2;* morphology and development of the fruit.]

SMALL, J. K. *Okenia hypogaea* Schlechtend. & Cham. Addisonia **4:** 11, 12. *pl. 126.* 1909. [Color plate with description and discussion of the species in Florida.]

———. Flora of the Florida Keys. xii + 162 pp. New York. 1913. [*Okenia,* 48. Distribution in the upper keys paralleling the mainland.]

WILSON, P. G. Contributions to the flora of tropical America: LXIII. Plantae Hintonianae: XII. Kew Bull. **13:** 155–170. 1958. [*O. parviflora,* 169, 170.]

3. **Boerhavia** Linnaeus, Sp. Pl. **1:** 3. 1753; Gen. Pl. ed. 5. 4. 1754.

Annual or perennial, glabrous, pubescent, or glandular herbs, often much branched from a narrow taproot or thickened woody rootstock; stems slender, diffuse, erect, ascending or decumbent, becoming ± woody below with age, the nodes swollen. Leaves simple, opposite, exstipulate, petiolate, those of a pair unequal, the large leaves alternating on the stem; blades gradually reduced upwards on the stem, slightly thickened, sometimes inequilateral, pinnipalmately veined, sometimes minutely dark dotted below, often tinged purplish, in outline broadly to narrowly deltoid, ovate-deltoid, or ovate to elliptic-oblong or linear-lanceolate above; margins entire; apex rounded or obtuse to acute, often mucronate; base subcordate or truncate to rounded or in the upper leaves acutely tapering. Lateral branches alternating on the stem, developing from the axil of the smaller leaf, accompanied by a short, deciduous, extra-axillary branch. Inflorescence lateral or terminal, cymose, paniculiform or thyrsiform, bracteate or bracteolate, ± diffuse, the ultimate flower clusters often subumbellate. Flowers small, perfect, sessile or on short- to long-jointed, accrescent pedicels, subtended by 1–3 small bracteoles; perianth tubular below, ± thick, 4–5[–10]-ribbed, glabrous or glandular-pubescent along the ribs, constricted near the middle around the top of the gynoecium, the limb campanulate, corolla-like, ± 5-lobed, aestivation plicate, white or pink to lavender or purple, limb deciduous. Stamens 1–3[–5], hypogynous, filaments slender, free or united basally in a shallow tube around the gynophore, anthers exserted, 4-sporangiate, 2-loculate at anthesis, didymous, dehiscing by simple slits; pollen forate, binucleate (sometimes trinucleate) when shed. Ovary shortly stipitate; style filiform; stigma capitate-peltate, slightly exserted; ovule anacampylotropous, with a single integument. Accrescent calyx base fleshy, clavate or obovate to narrowly obpyramidal, closed at the apex, 4 or 5[–10] ribbed, glabrous or sparsely

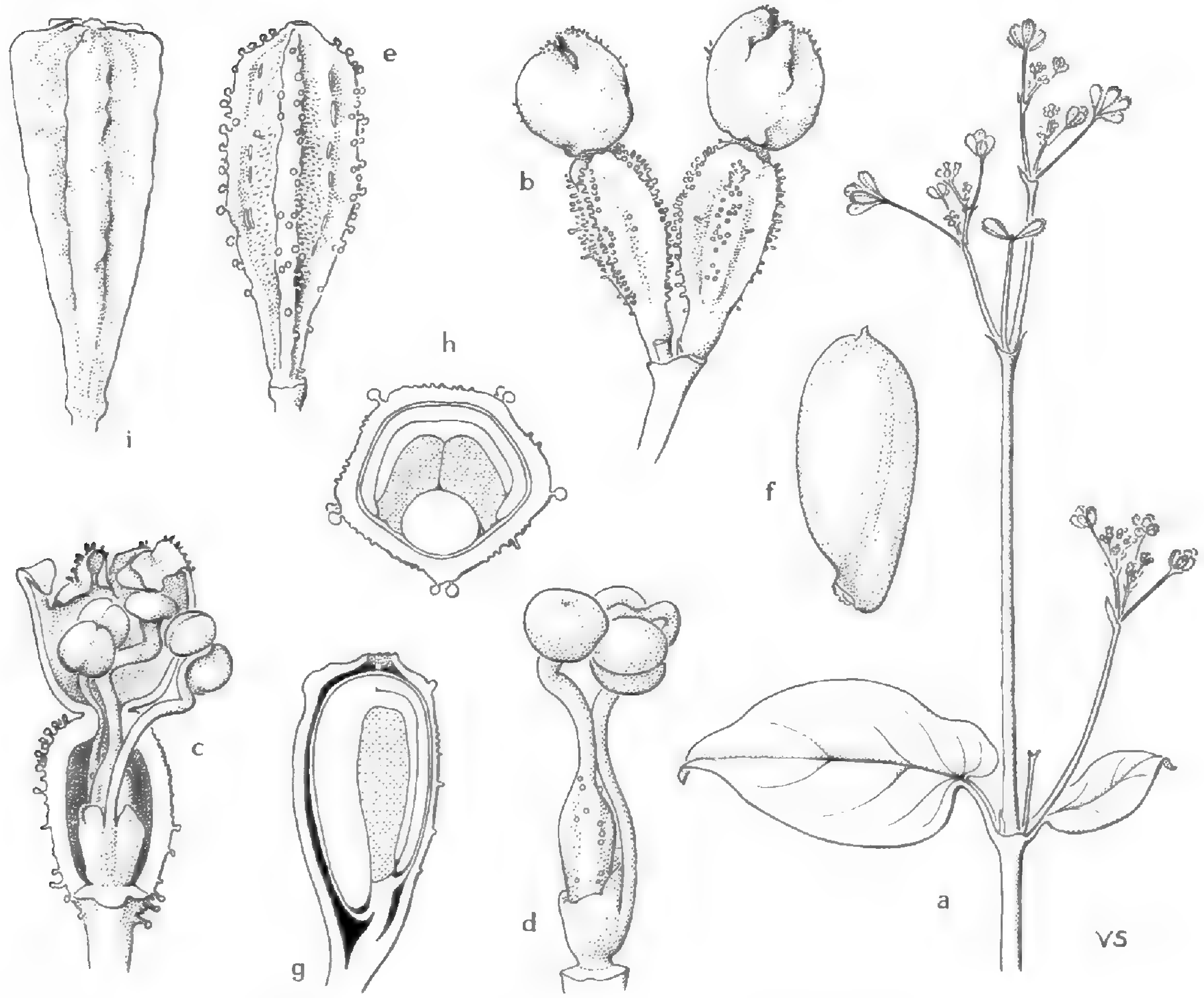


FIGURE 3. **Boerhavia.** a–h, *B. diffusa*: a, tip of flowering stem, × 3/4; b, two flowers, × 12; c, flower in vertical section to show perianth tube surrounding androecium and gynoecium, × 15; d, gynoecium and one of four stamens, three removed, × 25; e, accrescent calyx base inclosing fruit, × 12; f, fruit, × 12; g, calyx base and fruit in vertical section, the embryo white, the perisperm stippled — note that calyx is not adnate to fruit, × 12; h, same, in cross section, cotyledons of embryo above, hypocotyl below, × 15. i, *B. erecta*: mature accrescent calyx base inclosing fruit, × 12.

glandular pubescent, the grooves sometimes transversely wrinkled or longitudinally streaked with white raphides, falling with the inclosed fruit at maturity. Fruit a utricle, carpel wall membranaceous; embryo longitudinally folded at the hypocotyl, radicle straight, cotyledons unequal, curved inward around a columnar, mealy perisperm. LECTOTYPE SPECIES: *B. erecta* L.; see Standley, Contrib. U. S. Natl. Herb. 12: 375. 1909. (Named in honor of Herman Boerhaave, 1668–1738, Dutch naturalist and Professor in Leiden.) — Spiderlings, Wine-flower.

A weedy genus of perhaps 3–30 species distributed in the tropical and subtropical regions of the world, but best developed in southwestern North America. Up to fifteen species have been recognized in the southwestern United States (Tidestrom & Kittell, 1941). Two species occur as weeds of waste places in our area.

The morphologically variable pantropic weed *Boerhavia diffusa* L. (incl.

B. caribaea Jacq., *B. coccinea* Miller, *B. decumbens* Vahl, *B. hirsuta* Willd., *B. paniculata* Rich., *B. viscosa* Lag. & Rodr.), wine-flower, of sect. CLAVATAE of Heimerl (1934), is a prostrate to ascending, often viscid-pubescent weed of cultivated ground, pinelands, and waste places, with reddish-green to red or purplish [rarely white] flowers. Its narrowly obovoid 4- or 5-ribbed calyx bases have more or less rounded apices and bear short-stalked capitate glandular hairs along the ribs. It is widely distributed in Florida, but apparently infrequent in the Gulf States, and ranges westward to Texas and southern California, and southward to the West Indies, Mexico, Central America, and South America. *Boerhavia erecta* L., spiderling, of sect. PYRAMIDATA of Heimerl (1934), is an erect or ascending, essentially glabrous annual up to 1 m. tall, with leaves characteristically minutely and darkly spotted below, white or cream to pink or pale lavendar flowers, and narrowly obpyramidal, truncate, and glabrous accrescent calyx bases. It is also a pantropical weed, distributed in the southern United States from Florida to Texas and Arizona, northward along the Coastal Plain to North Carolina, in the Piedmont to South Carolina, and in the Mississippi embayment to Missouri, Arkansas, and Oklahoma. It extends southward in the Antilles, Mexico, and Central America to the tropics of South America.

The systematics of the genus is chaotic and badly in need of critical study. Heimerl (1889) divided twenty species of *Boerhavia* among five sections, but later (1897) reduced the sections to four. Three of these were subsequently segregated by Standley (1909, 1911), as genera of questionable validity. *Anulocaulis* Standley (1909) (sect. *Solenanthe* Heimerl, 1889) was considered distinct from *Boerhavia* in its large, thick leaves, distinctly tubular perianth, 10-ribbed turbinate or biturbinate fruits, and sticky-banded internodes. The plants appear to be obligate gypsophiles (Waterfall, 1945). About five species have been described (Waterfall, 1945; Johnston, 1944). *Commicarpus* Standley (sect. *Adenophorae* Heimerl) was set apart on the basis of a climbing or reclining habit, short funnelform perianth, and weakly 10-ribbed clavate fruits bearing numerous large mucilaginous glands. About sixteen species have been recognized, ranging from the southwestern United States, the Antilles, and Mexico, southward to northern South America, as well as in Africa, the Middle East, and Asia (Heimerl, 1934; Balle, 1951). *Cyphomeris* Standley (1911) (sect. *Senckenbergia* of Heimerl; incl. *Lindenia* Mart. & Gal., *Tinantia* Mart. & Gal., *Senkenbergia* Schauer), has been distinguished by its asymmetrical, clavate eglandular calyx bases and racemose inflorescences. Two species are known from Texas, New Mexico, and Mexico.

Heimerl (1934) accepted these segregates and revised the remaining species (sects. PTEROCARPON and MICRANTHAE, 1889), establishing four sections, but various authors of regional floras have rejected the segregates in whole (Tidestrom & Kittell, 1941) or in part, and the number of species recognized in *Boerhavia* varies accordingly. Standley later (1931) reduced *Commicarpus* to synonymy under *Boerhavia*, a course also followed by Stemmerik (1964 a,b), but some other workers maintain the genus. Several recent authors (Balle, 1951; Stemmerik, 1964; Woodson, 1961) have concluded that only two (or three if *Commicarpus* is included) variable, pantropic species constitute the genus *Boerhavia* proper. Woodson found "no tangible differences between *B. caribaea* and *B. coccinea* of the New World and *B. diffusa* of the Old World," and recognized only *B. diffusa* and *B. erecta*. This view is adopted here.

The generic name frequently appears in the literature with the spelling *Boerhaavia*, but Linnaeus latinized Boerhaave's name to "Boerhavius," and deliberately adopted the spelling *Boerhavia*, which should be used (Sprague, 1928). Although *B. erecta* L. is the accepted lectotype (Standley 1909), *B. repens* L. (Standley, 1918; Abrams, 1944), and *B. diffusa* L. (Hitchcock, 1930) have also been cited as "types."

Widely differing chromosome numbers are reported for the genus, including $2n = 26$ and 116 for *Boerhavia diffusa* L., $2n = 42$ for *B. repanda* Willd. (*B. chinensis* of Stemmerik, 1964), and $2n = 40$ for *Commicarpus tuberosus* (Lam.) Standley (*B. tuberosus* Lam.). I know of no counts from species of the southern United States.

Woodson (1961) suggests that hybridization probably occurs between *B. diffusa* and *B. erecta* in areas where they grow together, but that it is not sufficient to blur the species lines.

A diffuse vascular system and anomalous secondary growth characterize the stems of *Boerhavia diffusa* and *B. repanda* (Maheshwari, 1929, 1930; Bhargava, 1932) and give rise to a complex nodal anatomy, with 1–3 (*B. diffusa*) or 5 (*B. repanda*) leaf traces supplying the petiole. The leaf traces are derived from the middle ring of three concentric cycles of bundles in the young stem, while traces from the innermost "medullary bundles" supply the axillary branches (Pant & Mehra, 1961). The bundles of the outer ring become connected by an interfascicular cambium that initiates the development of up to 5 or more successive rings of anomalous secondary growth containing distinct collateral bundles embedded in a conjunctive tissue of elongated living cells that become lignified. Successive supernumerary cambia arise in the outer parenchyma cells of the phloem produced outwardly by the previous cambium (Maheshwari, 1930; Esau, 1965).

Floral ontogeny is acropetal in sequence, with no evidence of a second perianth whorl in either *B. diffusa* or *B. repanda* (Joshi & Rao, 1934). A single carpel arises from one side of the base of a terminal nucellus and gradually incloses it. Development of the male and female gametophytes is normal, and embryo development is of the Capsella type (Bhargava, 1932; Maheshwari, 1929). The scanty endosperm, which is initially nuclear in its development, is used up in the development of the embryo, leaving a substantial central column of whitish mealy perisperm (nucellar tissue) as a reserve food for the embryo (Bhargava, 1932; Maheshwari, 1929). The five-ribbed perianth of *B. diffusa* is supplied by one cycle of five traces, while the ten-ribbed perianth of *B. repanda* receives ten traces derived as two pentamerous cycles from the pedicellar stele (Joshi & Rao, 1934).

Betacyanin pigments have been demonstrated in five species of *Boerhavia* (*B. coccinea*, *B. erecta*, *B. intermedia*, *B. scandens*, *B. spicata*), as well as in *Anulocaulis gypsogenus* and *Cyphomeris gypsophiloides* (Wohlpart & Mabry, 1968). The reported presence of the alkaloid punarnavine in *B. diffusa* L. has been proven incorrect (Sircar, 1944). Raphides of calcium oxalate are extremely abundant in leaves, floral parts, and fruits of *Boerhavia*. When immersed in water the accrescent perianth base of *B. erecta* develops along the ribs extensive swellings of whitish slime, the significance of which is not known (Heimerl, 1889).

Boerhavia is of no economic significance, but various species are used locally in folk-medicine, as food, or as fodder. Roots of *B. diffusa* (syn. *B. repens*) are eaten by natives in Australia and used as a purgative, anthelmintic, or febrifuge in Malaysia. Leaves of *B. diffusa* are used as a pot-herb or in soups, or a liquid extract of them may be used for asthma and jaundice, or as a diuretic, emetic, or expectorant. Roots of *B. tuberosa* Lam. are eaten by natives in Peru, and plants of *B. pentandra* are grazed by livestock in South Africa (Cooke, 1910; Stemmerik, 1964; Uphof, 1968).

REFERENCES:

Under family references see BOLKHOVSKIKH; HEGNAUER; HEIMERL, 1889, 1934; INAMDAR; JOSHI & RAO; NOWICKE, 1970; PANT & MEHRA; STANDLEY, 1909, 1918; STEMMERIK; WOHLPART & MABRY.

ABRAMS, L. Illustrated flora of the Pacific States. vol. 2. viii + 635 pp. Stanford Univ. Press. 1944. [*Boerhavia*, incl. *Anulocaulis*, 102–104.]

BALLE, S. Nyctaginaceae. Fl. Congo Belg. Ruanda-Urundi **2:** 82–91. 1951. [*Boerhavia*, 83–85; *Commicarpus*, 86–90, *pl. 7*.]

BHARGAVA, H. R. Contribution to the morphology of *Boerhaavia repanda*. Jour. Indian Bot. Soc. **11:** 303–326. *pls. 1–4*. 1932.

———. The anatomy of the flower of *Boerhaavia repanda* Willd. Am. Midl. Nat. **47:** 508–512. 1952.

BUCHHOLZ, J. T., & E. J. PALMER. Supplement to the catalogue of Arkansas plants. Trans. Acad. Sci. St. Louis **25:** 91–155. *pls. 6–13*. 1926. [*B. erecita* (sic!), 112.]

COOKE, T. Nyctaginaceae. *In*: W. T. THISELTON-DYER. Fl. Capensis **5**(1): 392–398. 1912. [*Boerhavia*, 393–396.]

ESAU, K. Plant Anatomy. ed. 2. xx + 767 pp. New York. 1965. [*B. diffusa*, stem structure illustrated, *fig. 15, 19B*.]

GOODMAN, G. J., & U. T. WATERFALL. Notes on Oklahoma plants. Proc. Okla. Acad. Sci. **29:** 20, 21. 1949. [*B. erecta*, 20.]

HEIMERL, A. Beiträge zur Anatomie der Nyctaginaceen-Früchte. Sitz-ber. Math.-Naturw. Akad. Wiss. Wien **97**(Abt. 1): 692–703. *pl. 1*. 1888 (1889).

———. Beiträge zur Systematik der Nyctaginaceen. Jahresber. Staatsober-Realschule Wien 23. 40 pp. 1897. [*Boerhavia*, 4 sections, 24 species, 24–29.]

HITCHCOCK, A. S. Int. Bot. Congr. Cambridge Nomencl. Prop. Brit. Bot. (p. 115). 1929.

IRWIN, H. S. Roadside flowers of Texas. xvi + 295 pp. Austin. 1961. [*B. coccinea*, *B. erecta*, 105, 106, *pl. 7* (color).]

JOHNSTON, I. M. Plants of Coahuila, eastern Chihuahua, and adjoining Zacatecas and Durango. V. Jour. Arnold Arb. **25**: 133–182. 1944. [Incl. spp. of *Boerhavia* (9), *Cyphomeris* (3), *Commicarpus* (1), and *Anulocaulis* (4).]

KAJALE, L. B. Embryo and seed development in the Nyctaginaceae. I. Studies in the genus *Boerhaavia*. Jour. Indian Bot. Soc. **17**: 243–254. 1938.

KENNEDY, P. B. Getting acquainted with *Anulocaulis leiosolenus*. Muhlenbergia **6**: 75, 76. 1910. [= *B. leioselina* Torrey; cover picture of plant in natural habitat.]

MAHESHWARI, P. Contributions to the morphology of *Boerhaavia diffusa*. I. Jour. Indian Bot. Soc. **8**: 219–234. 1929. [Floral morphology, ontogeny, embryology.]

———. Contribution to the morphology of *Boerhaavia diffusa*. II. *Ibid*. **9**: 42–61. 1930. [Stem structure and development.]

——— & B. M. JOHRI. The occurrence of persistent pollen tubes in *Hydrilla*, *Ottelia*, and *Boerhaavia*, together with a discussion of the possible significance of this phenomenon in the life-history of angiosperms. *Ibid*. **29**: 47–51. 1950.

RADFORD, A. E., H. E. AHLES, & C. R. BELL. Manual of the vascular flora of the Carolinas. lxi + 1183 pp. Chapel Hill. 1968. [*B. coccinea*, *B. erecta*, 429, map.]

SAMANTARAI, B., & H. PATTNAIK. Response of *Boerhaavia diffusa* L. twigs to synthetic hormones. (Abstr.) Indian Sci. Cong. Proc. **40**: 113–114. 1953 (1954).

SIRCAR, N. N. Identification of indigenous drugs: *Boerhaavia diffusa* Linn. vs. 'Punarnava.' Indian Jour. Pharm. **6**: 9–12. 1944. [Source of drug "Punarnava" of Ayurvedic medicine identified as *Trianthema monogyna* (Aizoaceae).]

SPRAGUE, T. A. The correct spelling of certain generic names. III. Bull. Misc. Inf. Bot. Gard. Kew **1928**: 337–365. 1928. [*Boerhavia*, 348.]

STANDLEY, P. C. The Allioniaceae of Mexico and Central America. Contr. U. S. Natl. Herb. **13**: 377–430. 1911. [*Boerhavia*, 418–427; *Cyphomeris*, 428; *Commicarpus*, 428, 429; *Anulocaulis*, 430.]

STEYERMARK, J. A. Flora of Missouri. lxxxiii + 1725 pp. Ames. 1963. [*B. erecta*, 630; map no. 895; *pl. 152*, *fig. 4*.]

TIDESTROM, I., & T. KITTELL. A flora of Arizona and New Mexico. xxvi + 897 pp. Washington, D.C. 1941. [*Boerhavia*, 652–655.]

WOODSON, R. E., JR. Nyctaginaceae. *In*: R. E. WOODSON, R. W. SCHERY, *et al*., Flora of Panama. Ann. Missouri Bot. Gard. **48**: 51–65. 1961. [*Boerhavia*, 52–55, *fig. 172*.]

Tribe PISONIEAE Meissner

4. **Pisonia** Linnaeus, Sp. Pl. **2**: 1026, 1027. 1753; Gen. Pl. ed. 5. 451. 1754.

Dioecious [or monoecious] trees, erect to lax or scandent shrubs, or scrambling woody vines; stems armed or unarmed; lateral branches some-

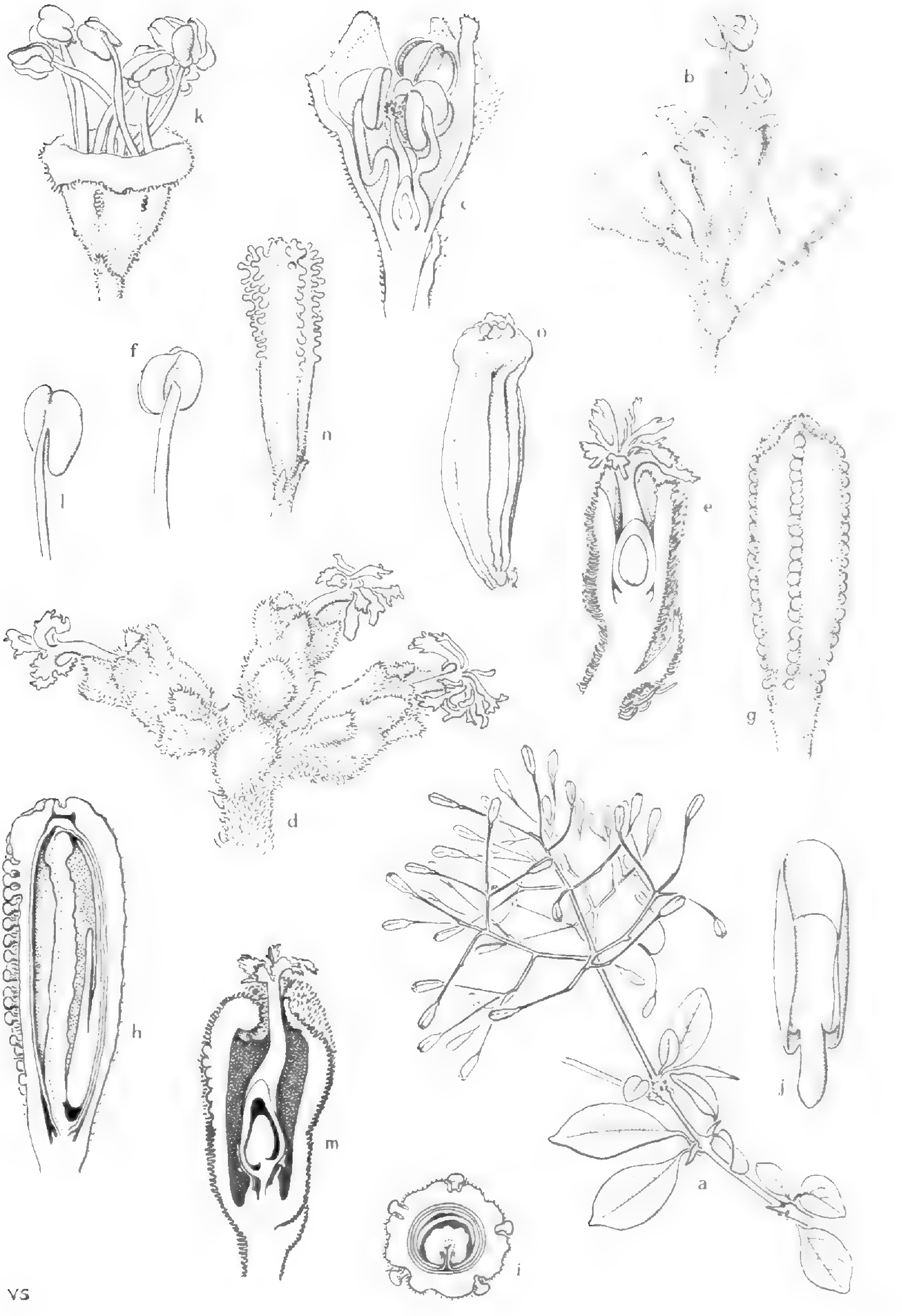


FIGURE 4. **Pisonia.** a–j, *P. aculeata*: a, branch with young fruit, one inflorescence removed, × 1/2; b, cluster of staminate flowers, × 6; c, staminate flower in vertical section, × 12; d, cluster of carpellate flowers, × 12; e, carpellate flower in partial section, the funiculus not visible behind ovule, × 15; f, stamen, × 12; g, mature accessory fruit (accrescent calyx base inclosing fruit), × 5; h, same, in section to show fruit with single seed, embryo with endosperm (flat stipple), × 6; i, same in cross section, the embryo cut through cotyledons, endosperm white stipple on black, × 6; j, embryo — note unequal cotyledons, × 6. k–n, *P. rotundata*: k, staminate flower, × 8; l, stamen, × 12; m, carpellate flower in partial section — note staminodia, × 15; n, mature accessory fruit, × 5. o, *P. floridana*: mature accessory fruit, × 5.

times short, stout, rigid and spine-like, terminating in a short, curved spine; axillary buds sometimes modified as a short recurved thorn, with accessory buds producing lateral growth from the axil. Leaves opposite to subopposite [or alternate], simple, entire, exstipulate, petiolate, glabrous or pubescent, more or less coriaceous. Inflorescence terminal or lateral, diffuse to congested, umbelliform to corymbosely thyrsiform pedunculate cymes. Flowers small, imperfect [or perfect], subtended by 1–3 small, subverticillate to verticillate bracteoles, sessile or pedicellate; perianth more or less fleshy, purple or reddish to yellowish green or greenish white. Staminate perianth ± obconic-campanulate, the limb 5-dentate, with short teeth, aestivation induplicate-valvate; stamens 6–10 [or up to 40], exserted [or included], filaments filiform, unequal, basally connate [or free]; anthers oblong or didymous, basifixed or dorsifixed; pollen tricolpate [6- or 12-rugate]; reduced sterile ovary present. Carpellate perianth tubular, narrowly campanulate to urceolate, the limb short, erect or spreading, 5 (–10)-toothed, persistent; staminodes about as long as the ovary, with rudimentary anthers, or reduced in varying degree to a low, occasionally glandular-dentate disc adnate to the stipe of the carpel; gynoecium a solitary carpel; ovary superior, sessile or stipitate; style terete, elongate, slightly exceeding the perianth; stigma penicillate [to capitate], persistent; ovule solitary, basal, anacampylotropous; integuments two, the outer forming the micropyle. Accrescent calyx glabrous or pubescent, fleshy to coriaceous, terete or angular, eglandular or glandular, the viscid capitate glands subsessile to shortly stipitate, uniseriate to biseriate on (or in costae along) the angles, the stalk of glands whitish to blackish, the head usually blackish. Fruit an elongate, membranaceous or coriaceous utricle enclosed within the persistent calyx. Seed with a deep longitudinal furrow; seed coat translucent, adhering to the pericarp. Embryo straight, the short radicle inferior; cotyledons broad, involute, surrounding the scanty, gelatinous endosperm and abundant mealy perisperm. (*Guapira* Aublet, *Pallavia* Vell., *Torrubia* Vell.) TYPE SPECIES: *P. aculeata* L. (Named in commemoration of William Piso, 1611–1678, a Dutch physician and naturalist who travelled in Brazil.) — Pisonia, blolly.

A large and variable genus of perhaps 35–75 species distributed in the tropics and subtropics of the World. The genus has its primary center of development and distribution in the West Indies, Central America, and South America, and a secondary center in the southwest Pacific, with about eight species occurring in Malaysia (two of these extending to Australia and New Zealand) and about five species endemic to Melanesia and Polynesia. Three of the Malaysian species also reach Madagascar and Africa (Stemmerik, 1964a). About six species of the genus have been recognized in our area in coastal southeastern Florida and the Florida Keys, and one of these (*P. aculeata*) also occurs in Texas.

Two of our species belong to section PISONIA (sect. *Glanduliferae* of Heimerl 1889, 1934), which is characterized by Stemmerik (1964b) as having "prickles [stipitate glands] on the anthocarp, no rostrum [elongate sterile apex of the accrescent calyx]. Stamens 6–10." The pantropical *Pisonia aculeata*, cock-spur, devil's-claws, pull-and-hold-back, old-hook, occurs on sea beaches, and in hammocks of southern peninsular Florida and the Keys as a thorny, densely branched scrambling vine with greenish-yellow or purple (?) calyx, and small, slender longitudinally 5-angled clavate fruits bearing a single row of low, blackish (in herbarium specimens) stipitate glands along the length of each angle, and 6–8 stamens in the staminate flowers. The species ranges from southern Texas, Florida, and the West Indies southward to tropical South America in the New World.

A single collection of a plant possibly referable to *Pisonia aculeata* var. *macranthocarpa* Donn. Sm. (*Pisonia macranthocarpa* Donn. Sm.) collected in 1881 by A. H. Curtis, is in the Arnold Arboretum herbarium. In a field note attached to the sheet Curtis states "A *Pisonia* found in hammock W. of Bay Biscayne. Except for the fr. I would have called it *P. aculeata* — tall-climbing like the latter & just as prickly." The mature dried fruits are 16–17 mm. long and 4–5 mm. wide and are more or less elliptic-oblong, bearing along the length of the angles of the calyx base five rows of stout uniseriate to biseriate whitish stipitate glands up to 1 mm. long, with small blackish heads. *Pisonia aculeata* var. *macranthocarpa* is otherwise known from Cuba and Central America to Venezuela.

Pisonia rotundata Griseb. (*P. subcordata* var. *rotundata* of Heimerl, *Torrubia rotundata* (Griseb.) Sudw.) is a low spreading shrub or small tree with broadly elliptic or ovate to obovate, pubescent, leathery leaves, with the veins strongly raised on the lower surface, dense cymes of greenish to whitish flowers, and small broadly to narrowly obovoid fruits about 5–7 mm. long bearing 5 rows of uniseriate stipitate glands along the angles of the distal third (or half) of the accessory fruit. The species is known from the Florida Keys, the Bahamas, Puerto Rico, Cuba, and the Isle of Pines.

The remaining species of our area differ from those of sect. PISONIA in having eglandular, fleshy, reddish [to black], drupe-like calyx bases. These were placed by Heimerl (1889, 1934) in his sect. EUPISONIA, but were transferred to *Torrubia* Vell. by Britton (1904), and later to *Guapira* Aublet (Little 1968; Lundell, 1968). Stemmerik (1964b) did not consider this group of species, and a formal category (section) apparently does not now exist for them within the genus *Pisonia*. Two taxa from our area, originally described as species of *Torrubia* (*T. Bracei* Britton, *T. globosa* Small), and recently transferred to *Guapira*, have never appeared under the name *Pisonia*. They are poorly represented in our collections, and their systematic position remains problematical. They are cited here as species of *Guapira*.

The well known *Pisonia discolor* Sprengel var. *longifolia* Heimerl (*P. longifolia* (Heimerl) Sargent, *Torrubia longifolia* (Heimerl) Britton, *Guapira longifolia* (Heimerl) Little), commonly called the beef-tree, beef-wood, pork-wood, pigeon-wood, or long-leaf blolly, is a tree 5–15 m. in height, with obovate-oblong leaves broadest above the middle, greenish-yellow imperfect (or perfect?) flowers that appear in autumn, and pink to red or magenta obovoid fruits that are rounded to slightly depressed at the apex, and become obviously ribbed on drying. The variety is found in Florida in dune-scrub, along the shores of salt-water lagoons, and in pinelands and woods from Cape Canaveral to the southern Keys, where

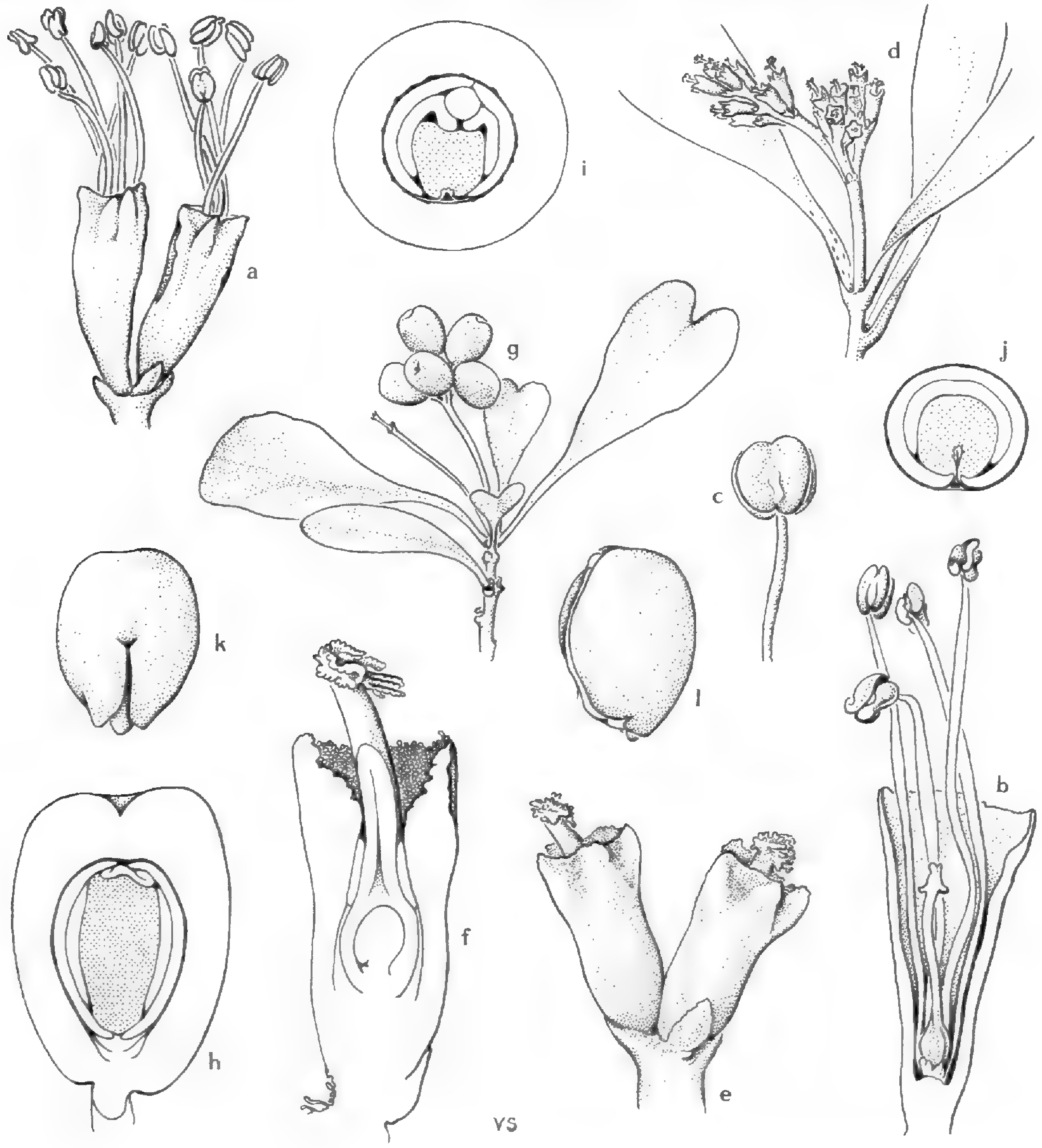


FIGURE 5. **Pisonia.** a–l, *P. discolor* var. *longifolia* (*Guapira longifolia*): a, staminate flowers, × 8; b, staminate flower in vertical section, × 12; c, stamen, × 15; d, carpellate inflorescence, × 2; e, carpellate flowers, × 12; f, carpellate flower in vertical section — note staminodia and penicillate stigma, × 20; g, infructescence, accrescent calyx bases berry-like and glabrous, × 1; h, mature accessory fruit in vertical section to show single seed — note parts of two unequal cotyledons on each side, surrounding perisperm (stippled), × 6; i, same, in cross section, embryo cut through cotyledons and hypocotyl, perisperm stippled — note longitudinal groove formed by intrusion of seed coat, × 6; j, fruit in cross section above epicotyl to show unequal cotyledons surrounding perisperm, seed coat intruding into perisperm, × 6; k, embryo, dorsal view, to show basal lobes of outer, larger cotyledon covering hypocotyl, × 6; l, same, side view, × 6.

the largest specimens were reported (Sargent, 1905) to occur on Elliot's Key and Old Rhodes Key. It is also common in the West Indies and ranges southward to Brazil. The typical *P. discolor* var. *discolor*, with leaves ovate to lance-ovate, broadest at or below the middle, is less well represented in our area, occuring in hammocks and thickets principally along the east coast of southern Florida. *Guapira globosa* (Small) Little (*Torrubia globosa* Small), the roundleaf blolly, is a small tree with small orbicular-cuneate to suborbicular leaves 1–2 cm. long, greenish-purple flowers, and subglobose juicy dark-red fruits. It is reported in hammocks of southeastern coastal Florida and the Keys. *Guapira Bracei* (Britton) Little (*Torrubia Bracei* Britton) is a gray-barked shrub or small tree with obovate leaves that are broadest above the middle and cuneately narrowed at the base, purplish flowers, and red, oblong-obovoid, apically truncate fruits about twice as long (7–8 mm.) as broad. The species was described from the Bahamas and is reported to occur in hammocks and adjacent pinelands on the lower eastern coast of peninsular Florida and in the Keys. *Pisonia floridana* Britton in Small (*Torrubia floridana* (Britton) Britton, *Guapira floridana* (Britton) Lundell) was described from incomplete material collected only once over a century ago on Rock Key near Key West. Its spatulate to obovate leaves are 2–3.5 cm. long and are supposedly distinctive in their dense puberulence.

In the late nineteenth century many specimens of this group of species from our area were incorrectly referred to *Pisonia obtusata* Swartz (Chapman, 1860, 1897; Heimerl, 1896; Sargent, 1894, Small, 1903). Britton (1904), however, established *P. obtusata* Sw. as a synonym of the West Indian and South American *P. inermis* Jacq. (*Torrubia inermis* (Jacq.) Britton) and assigned the Floridian specimens to his *Torrubia longifolia* (Heimerl) Britton. Heimerl (1896) recognized some specimens of our area only as varieties of West Indian species (*P. discolor* Sprengel var. *longifolia* Heimerl, *P. subcordata* Sw. var. *rotundata* (Griseb.) Heimerl).

More recently the material of *Pisonia* from our area has been studied by R. W. Long (Long & Lakela, 1971), who considers the various and intergrading eglandular forms in Florida to represent only phases of the West Indian *P. discolor* Sprengel. He recognizes two varieties in our area: var. *discolor*, with ovate, oval or lance-ovate leaf blades broadest at or about the middle, and *P. discolor* var. *longifolia* Heimerl (incl. *T. Bracei* Britton, *G. Bracei* (Britton) Little, *T. globosa* Small, *G. globosa* (Small) Little, *T. longifolia* (Heimerl) Britton) with leaf blades obovate or oblanceolate to narrowly spatulate, broadest above the middle.

Very few herbarium specimens bear field notes of any kind regarding plant size, habit, bark or wood form and color, flower color or odor, pollinators, fruit dispersal, etc. There are apparently no chromosome counts for the species of our area and possibly none for the genus. A modern monographic study of this genus, defining generic as well as specific boundaries, is badly needed.

The floral ontogeny and embryology of *Pisonia aculeata* have been briefly described by Venkateswarlu. He found floral organogeny to be acropetal in sequence. Embryological details include the presence of a secretory tapetum in the anthers; tricolpate pollen grains that are trinucleate when shed; the formation of an obturator-like structure in the ovary; formation of a nucellar cap; Polygonum-type embryo-sac development; nuclear endosperm; and an Asterad type of embryogeny. The woods of the genus are notable chiefly for their anomalous secondary growth in the form of successive rings of vascular bundles (Metcalfe & Chalk).

In the Pacific region the sticky-viscid fruits of *Pisonia grandis* R. Br. and *P. umbellifera* (Forster) Seem. are noted for catching insects, small lizards, and birds. Fruits or inflorescences of these species are hung as fly-catchers. Birds disseminate the sticky fruits, but excessive accumulation of fruits on the bodies of small birds may render them incapable of flight and cause their eventual death (St. John, Stemmerik, White, Govett, Kirk). Airy Shaw speculates that the unusual distribution of *P. grandis*, which is largely confined to small, often uninhabited "bird islands," may be partly linked to a need for a supply of bird-guano in association with a coral or limestone substrate for its germination and early development.

The generic limits of *Pisonia* are not clear. The genus has been considered on a world-wide basis only by Heimerl. His concept of the over-all limits of the genus changed over the years, as evidenced by his later recognition or acceptance of segregate genera, but he consistently maintained a broader view of *Pisonia* proper than most regional workers by retaining both glandular- and eglandular-fruited species within the genus. In his earlier papers (1889, 1897) he reduced several genera of previous authors either to sectional rank or to synonymy and recognized six sections in the genus. He revised the species of the two sections occuring in our area in 1896. Britton (1904) disagreed with Heimerl's concept of the genus, and segregated as the genus *Torrubia* the Floridian and West Indian species with unarmed stems and eglandular, red drupelike calyx bases while maintaining in *Pisonia* the armed, glanduliferous, and coriaceous-fruited species typified by *P. aculeata*. The segregation of *Torrubia* was accepted by Standley (1911), and later by Small (1933), who had earlier (1903) recognized only *Pisonia* in the southeastern United States. Standley (1911) also elevated Heimerl's sect. PISONIELLA to generic rank, and later (1918) re-established sect. CEPHALOTOMANDRA at the generic level. In 1934, Heimerl recognized only two sections in *Pisonia* (GLANDULIFERAE and EUPISONIEAE), which he considered to differ only in the presence or absence of glands on the calyx tube. The other four sections of his earlier treatments were established as segregate genera, including *Pisoniella* (Heimerl) Standl., *Calpidia* du Petit Thouars (*Pisonia* sects. *Timeroya* and *Prismatocarpae* of Heimerl, 1889), *Rockia* Heimerl (*Pisonia sandwicensis* Hillebr.), and *Cephalotomandra* Karsten & Triana (*Pisonia* sect. *Cephalotomandra* of Heimerl, 1889).

Woodson & Schery (1961) revived the earlier name *Guapira*, which had been established as a synonym of *Pisonia* by Hallier (1918), to replace *Torrubia* as the generic name for the fleshy-fruited eglandular species.

The name *Torrubia* was then proposed for conservation over *Guapira* (Little, 1964) but was rejected (McVaugh, 1968). Consequently a large number of new combinations have been made in *Guapira* (Lundell, 1968; Little, 1968).

Stemmerik (1964a, b) revised the Old World species of *Pisonia*, but did not consider the New World species. He again reduced the segregate genera *Calpidia*, *Heimerliodendron* Skottsb. (*Heimerlia* Skottsb.), and *Rockia* to synonymy under *Pisonia*, and tentatively proposed for the Pacific species four sections based on the presence or absence of stipitate glands and of a rostrum on the calyx tube, and on the number of stamens in the flowers, but stated that, except for historical precedent, he probably would not have proposed such subdivisions.

Meissner (1841) established a tribe Pisonieae, including the genera *Neea* Ruiz & Pavón, *Pisonia*, *Reichenbachia* Sprengel, and *Salpianthus* Humb. & Bonpl. Choisy, in DeCandolle's *Prodromus*, placed *Pisonia* in his suborder (subfamily) Boerhavieae, and separated the known species into two groups, those with stems armed (incl. *P. aculeata* L.) and those with stems unarmed. The species of the latter group were then divided on a geographical basis. Bentham & Hooker (1883) recognized a tribe Pisonieae in which they included *Pisonia*, *Timeroya* Montrousier and *Cephalotomandra* Karsten & Triana (both subsequently reduced by Heimerl to sections under *Pisonia*), and the closely related *Neea* Ruiz & Pavón (which had been included in *Pisonia* by Baillon, 1872). The tribe has been maintained in subsequent major treatments of the family (Heimerl, 1889, 1896, 1897, 1934; Eckardt, 1964).

Berry described fossil material of *Pisonia* (*P. apalachicolensis* Berry), probably dating from the end of the Oligocene, from the Alum Bluff Formation in Liberty County, Florida, stating that about fifteen fossil species of the genus have been described, the earliest being from the Upper Cretaceous of both America and Europe.

The genus is of little economic significance. Branches of *P. aculeata* are reported to be used as barrel hoops in Jamaica, and a decoction of its leaves is used against rheumatic and venereal disease in Jamaica and Yucatán. A decoction of the fruits of *P. capitata* (S. Watson) Standley is used against fevers by certain Indians in Mexico. The wood of *Pisonia Zapallo* Griseb., of Argentina, is strong enough to be used in box-making and for general building construction. The light-yellowish, chlorotic leaves of a cultivated race of *P. grandis* are boiled and eaten as a pot-herb in Malaysia, where the trees are known as "Mollucan cabbage," "cabbage-tree," or "lettuce-tree" (Airy Shaw, Stemmerik, Uphof). The leaves of *P. umbellifera* (*P. Brunoniana*) Endl. are used as a diuretic and the roots as a purgative in the Pacific Islands (Uphof).

REFERENCES:

Under family references see BAILLON; BENTHAM & HOOKER; CHOISY; ECKARDT; HEGNAUER; HEIMERL 1889, 1897, 1934; HUTCHINSON, 1967; MEISSNER;

SMALL, 1903, 1933; STEMMERIK; STUDHOLME & PHILIPSON; UPHOF; VENKATESWARLU.

AIRY SHAW, H. K. On the distribution of *Pisonia grandis* R. Br. (Nyctaginaceae), with special reference to Malaysia. Kew Bull. **1**: 87–97. 1952.

AUBLET, M. F. Histoire des plantes de la Guiane Françoise. **1**: 308–310; **3**: *pl. 119*. 1775. [Original publication of *Guapira*.]

BERRY, E. W. The physical conditions and age indicated by the flora of the Alum Bluff formation. U. S. Dep. Int. Geol. Surv. Prof. Paper **98–E**: 41–59. *pls. 7–10*. 1916. [*P. apalachicolensis* Berry.]

BRITTON, N. L. On *Pisonia obtusata* and its allies. Bull. Torrey Bot. Club **31**: 611–615. 1904. [With key to species of *Torrubia* in Florida and the West Indies.]

CHAPMAN, A. W. Flora of the southern United States. xxxviii + 621 pp. New York. 1860; ed. 3. xxxix + 655 pp. Cambridge. 1897.

GOVETT, R. H. A bird-killing tree. Trans. & Proc. New Zealand Inst. **16**: 364–366. 1884. [*P. Brunoniana* Endl., *P. Sinclairii* Hook. f. Both = *P. umbellifera* (Forster) Seem., according to Kirk.]

HALLIER, H. Über *Juliania*, eine Terebinthaceen-Gattung mit Cupula, und die wahren Stammeltern der Kätzchenblütler. 210 pp. Dresden. 1908. [Citation of *Guapira* Aublet as a synonym of *Pisoria*, 110, in footnote.]

———. Ueber Aublet's Gattungen unsicherer oder unbekannter Stellung und ueber pflanzengeschichtliche Beziehungen zwischen Amerika und Afrika. Leyden Rijksherb. Meded. **35**: 3–33. 1918. [Discussion of *Guapira* as a synonym of *Pisonia*, 18–20.]

HEIMERL, A. Nyctaginaceae. *In*: I. URBAN. Additamenta ad cognitionem florae Indiae occidentalis. III. Engler's Bot. Jahrb. **21**: 514–638. 1896. [*Pisonia*, 623–633.]

HESS, R. W. Zapallo caspi. Trop. Woods **87**: 35. 1946. [Brief description of wood characteristics and uses of *P. Zappallo*.]

KIRK, T. Botanical notes. Trans. Proc. New Zealand Inst. **16**: 367–368. 1884. [*P. umbellifera*, distribution and locations in New Zealand.]

LITTLE, E. L., JR. Proposal to conserve the generic name (2354) *Torrubia* Vell. (1825) against *Guapira* Aubl. (1775), *Gynastrum* Neck. (1790), *Bessera* Vell. (1825), and *Columella* Vell. (1825) (all of Nyctaginaceae). Regnum Veg. **34**: 58, 59. 1964.

———. Transfers to *Guapira* from *Torrubia* (Nyctaginaceae). Phytologia **17**: 367, 368. 1968. [*G. Bracei*, *G. globosa*, *G. longifolia*.]

LONG, R. W., & O. LAKELA. A Flora of Tropical Florida. A Manual of the Seed Plants and Ferns of Southern Peninsular Florida. xvii + 962 pp. Univ. of Miami Press, Coral Gables. 1971.

LUNDELL, C. L. Studies of Tropical American Plants — V. Wrightia **4**: 79–96. 1968. [Two new species and 61 new combinations in *Guapira*. *G. floridana*, 80. See also Wrightia **3**: 21–35. 1962.]

MCVAUGH, R. Conservation of generic names, X. Taxon **17**: 462–466. 1968. [*Torrubia* Vell. rejected for conservation over *Guapira* Aublet 62, 463.]

METCALFE, C. R., & L. CHALK. Anatomy of the Dicotyledons. vol. 2. Oxford. 1960. [Including *Calpidia*, *Pisonia*, *Rockia*, *Torrubia*.]

SARGENT, C. S. *Pisonia*. Silva N. Am. **6**: 109–112. *pl. 297*. [*P. obtusata*, 109–112, *pl. 297*.]

———. Manual of the trees of North America. xxiii + 826 pp. Boston. 1905. [*P. longifolia* Sarg. nom. nov., 313–315.]

SKOTTSBERG, C. The arboreus Nyctaginaceae of Hawaii. Sv. Bot. Tidskr. **30:** 722–743. 1936. [Description and transfer of species from segregate genus *Calpidia* to *Ceodes*; segregation of monotypic genus *Heimerlia.*]

ST. JOHN, H. The distribution of *Pisonia grandis* (Nyctaginaceae). (Pacific Plant Studies no. 10.) Webbia **8:** 225–228. 1951. [Map.]

STANDLEY, P. C. The Allioniaceae of Mexico and Central America. Contr. U. S. Natl. Herb. **13:** 377–430. 1911. [*Pisonia*, 386–391; *Pisoniella*, 385, 386; *Torrubia*, 385.]

———. Allioniaceae. N. Am. Fl. **21**(3): 171–254. 1918. [*Cephalotomandra*, *Pisonia*, *Pisoniella.*]

STEMMERIK, J. F. Florae Malesianae Precursores XXXVIII. Notes on *Pisonia* L. in the Old World (Nyctaginaceae). Blumea **12:** 275–284. 1964b. [Includes both glandular and eglandular species of the Pacific in *Pisonia.* Segregate genera in synonymy include *Calpidia*, *Ceodes*, *Heimerlia*, *Heimerliodendron*, *Rockia*, *Timeroyea*, *Vieillardia.*]

WHITE, C. T. An insect-catching tree. Austral. For. Jour. **7:** 36. 1924. [*P. Brunoniana.*]

WOODSON, R. E. Nyctaginaceae. *In*: WOODSON, R. E., & R. W. SCHERY. Fl. Panama 4 (4). Ann. Missouri Bot. Gard. **48:** 61–64. 1961. [*Guapira*, 61–4, *fig. 125*; *Pisonia*, 64, 65, *fig. 126.*]

DEPARTMENT OF BOTANY
UNIVERSITY OF NEW HAMPSHIRE
DURHAM, NEW HAMPSHIRE 03824

MARTICORENIA: A NEW GENUS OF MUTISIEAE (COMPOSITAE)

JORGE VICTOR CRISCI

IN THE COURSE OF A revisionary study of the genus *Leuceria* Lagasca (Compositae, tribe Mutisieae, subtribe Nassauviinae), *Leuceria foliosa*, a species described by the Chilean botanist R. Philippi in 1856, seemed to be out of place. The species grows in the Andean region of central Chile. A careful study of this species and of all the genera of this subtribe convinces me that *Leuceria foliosa* should be recognized as a new genus.

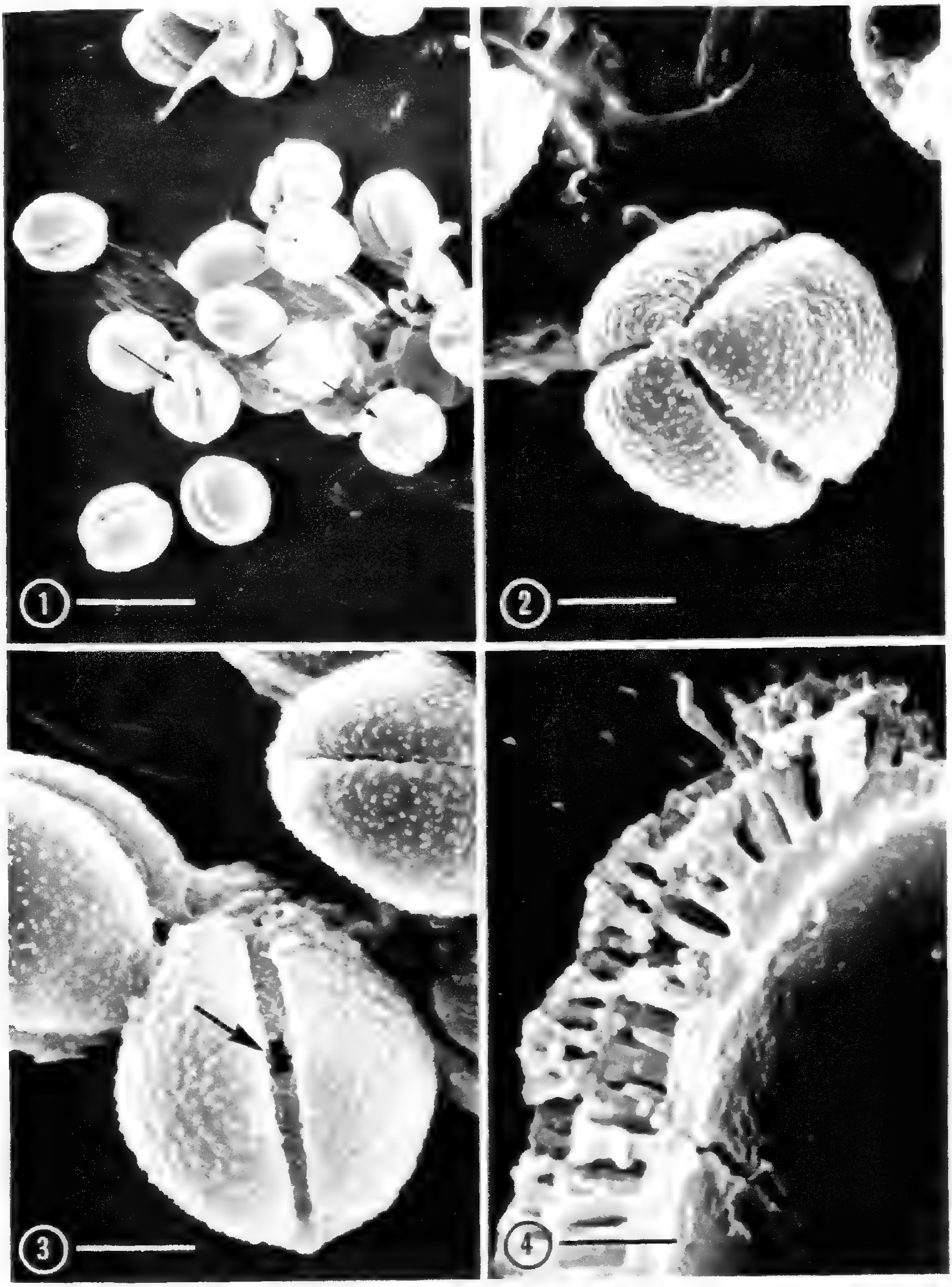
A description of the new genus and its one species, with illustrations, pollen analysis, chromosome number, and discussion of the generic relationships of the new taxon is presented in this paper. The abbreviations for herbaria listed in the citations of specimens are taken from the fifth edition of the *Index Herbariorum* (Lanjouw & Stafleu, 1964).

MATERIAL AND METHODS

Some pollen grains were acetolysed according to the method outlined by Erdtman (1960); other pollen grains were placed in 95 per cent ethanol stained with basic fuchsin and mounted in glycerine jelly. For Scanning Electron Microscopy (SEM) the acetolysed pollen grains were used. After acetolysis the pollen samples were washed several times in glass-distilled water to remove traces of acids. Each sample was dispersed in a drop of distilled water and placed on a specimen holder. The samples were then air dried, coated with 50 Å to 100 Å carbon and about 200 Å to 300 Å gold-palladium alloy for conductivity. Finally the specimens were photographed using a high resolution SEM, AMR model 900. FIGURES 1–4.

To obtain the chromosome number, flower buds were collected from plants growing in their native habitat. Buds were killed and fixed in ethanol and glacial acetic acid (3:1), transferred to 70 per cent ethanol after 24 hours, and refrigerated. Anthers were squashed in aceto-carmine.

Marticorenia Crisci, gen. nov. Capitulum multiflorum, homogamum; flores hermaphroditi. Involucrum hemisphaericum; bracteae lineari-lanceolatae, biseriatae. Receptaculum vix concavum, paleaceum; paleae rigentes vix amplexiflorae. Flores albo-violacei, bilabiati, labio interiore bipartito lobis revolutis, labio exteriore latiore ligulato tridentato. Antherae glabrae, basi longe sagittatae. Stylus bifidus; rami semiteretes, apice truncati penicillatisque, divergentes non revoluti. Achaenia cylindrata, papilloso-puberula. Pappus uniseriatus, pilis plumosis albis. Frutex dense pilosus; foliis alternis, sessilibus, ovatis lobatisque, basi cordatis et semiamplexicaulibus. Capitula pedunculata laxe cymosa. Pedicellus unibracteatus. SPECIES TYPICA: *Marticorenia foliosa* (Philippi) Crisci.



FIGURES 1–4, scanning electron micrographs (SEMG) of **Marticorenia foliosa** (from *West 5250*). 1, several acetolysed pollen grains, arrows indicate the pollen grains shown in FIGURES 2 and 3, the bar at the lower left hand corner represents ca. 40 µm; 2, a pollen grain in polar view, note the furrow showing zonocolporate condition, the bar represents ca. 10µm; 3, a pollen grain in equatorial view with arrow pointing toward the germ pore, the bar represents ca. 10 µm; 4, portion of pollen grain mechanically broken to show different wall components, the bar represents ca. 2 µm.

Shrubs more or less flabelliform in aspect, with short caudex woody at the base. Roots stout, woody with dissected vascular bundles. Stems branched from the base. Leaves alternate, sessile, decurrent, ovate-elliptic, lobulate, becoming linear-lanceolate above. Inflorescence a much branched terminal cyme. Pedicels each with a linear-lanceolate accessory bract, acute at apex. Heads numerous, terminal. Head with several flowers; flowers all equal, hermaphroditic, fertile. Involucre hemispherical, composed of bracts in two series, linear-lanceolate, acute at the apex, pubescent on the abaxial surface. Receptacle slightly concave, paleaceous; paleae scarious, conduplicate around the flowers, lanceolate, the abaxial surface densely pubescent, the apex incised. Corolla white-violaceous, bilabiate, tube broader toward the apex; outer lip lanceolate, liguliform with four veins, the apex three-toothed; inner lip bifid, each lobe revolute, acute at apex. Stamens five, the filaments inserted at a point halfway from the base of the tube; anthers connate with oblong apical appendage tailed at base, partially exserted in the mature flowers. Style bifid, its branches flattened, truncate with a crown of elongate collecting hairs at the apex and papillose with shorter ones on the adaxial surface, glabrous on the abaxial surface. Achenes more or less cylindric with long double trichomes. Pappus of numerous white plumose hairs in one series.

Pubescence of three kinds of trichomes, e.g., (1) *glandular uniseriate* (60–150μm), four—nine-celled (borne on leaves, stem, paleae, receptacle, involucre, corolla, and sparsely on the achenes); (2) *non-glandular uniseriate,* few-celled (on the corolla); (3) *double hairs* or "Zwillingshaare" (Hess, 1938) (200–250μm) of two cells joined along their inner wall but not quite meeting at the apex (on the achenes). One species.

It is a pleasure to name this new genus *Marticorenia* for Professor Clodomiro Marticorena of the Instituto Central de Biología, Universidad de Concepción, Concepción, Chile, who has made important contributions to our knowledge of the Chilean flora and to the study of palynology in Chile.

Marticorenia foliosa (Philippi) Crisci, comb. nov. FIGURE 5a–g.

Leuceria foliosa Philippi, Linnaea **28:** 720. 1856.
Lasiorrhiza foliosa (Philippi) Kuntze, Rev. Gen. Pl. **1:** 350. 1891.

Shrubs 40–50 cm. tall. Stems erect, much branched from the base, hirsute. Leaves sessile, ovate-elliptic, lobulate, sparsely pubescent beneath and densely so above, semiamplexicaul, the lower 5–10 cm. long, 3–5 cm. wide; lobules 1 cm. long, 1 cm. wide at the base; upper leaves linear-lanceolate 2 cm. long, 0.7 cm. wide. Inflorescence a dichotomous cyme; heads numerous (2–23); pedicels with a linear-lanceolate accessory bract acute at apex, abaxial surface pubescent, adaxial surface glabrate, 11–12 mm. long, 2 mm. wide; involucre hemispherical, 1.5–2 cm. in diameter, formed by 2 rows of bracts 2 cm. high; involucral bracts linear-lanceolate, acute at apex, abaxial surface pubescent, the adaxial glabrous,

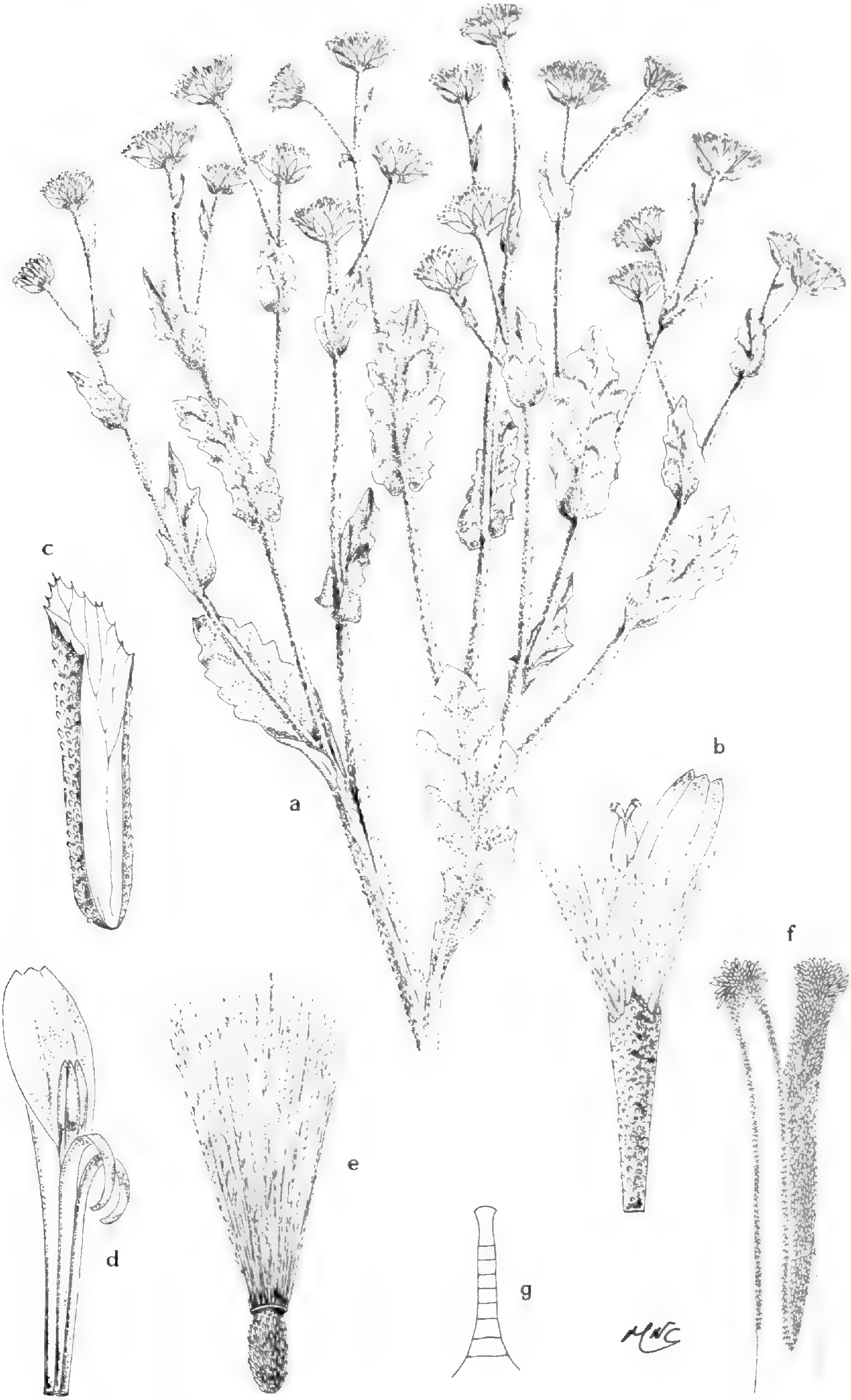


FIGURE 5. **Marticorenia.** a–g, *M. foliosa* (from *Zöllner 2994*): a, habit of the plant, × 1/4; b, flower with paleae, × 4; c, paleae, × 6 1/4; d, corolla, × 4; e, achene and pappus, × 4; f, style, × 13; g, trichome from stem, × 150.

8–15 mm. long, 1.5–2 mm. wide; receptacle slightly concave, paleaceous, slightly pubescent; paleae broadly obovate incised at apex, scarious, slightly conduplicate around flowers (amplexiflorous), adaxial surface glabrous, abaxial surface densely pubescent, 7 mm. long, 2 mm. wide. Flowers about 33; corolla white-violaceous 13–15 mm. long; tube 5–8 mm. long, 1 mm. in diameter at the base and 1.5 mm. at apex; outer lip with 4 veins, three-toothed at apex, abaxial surface and margins sparsely pubescent, 8–9 mm. long, 2.5 mm. wide; inner lip bifid, abaxial surface sparsely pubescent, 5–6 mm. long, each lobe 0.5 mm. wide; anthers tailed, glabrous, 6–8 mm. long; style bifid with branches 2 mm. long. Achenes 2–4 mm. long, 0.5–1 mm. wide, cylindric, with long hairs; pappus of 18–20 white plumose hairs, 10 mm. long, in one series.

POLLEN. Grains zonocolporate (3), subprolate to prolate-spheroidal, 34–45μm. Colpi 20–41 × 2–3.5μm, extremes rounded; apocolpium 2–3.5μm in diameter, mesocolpium 15–17μm; membrane of the colpi rather smooth as seen with optical light microscope. Exine 4–5μm thick at the pole, 5–6μm at the equator. Infratectum 1–1.5μm thick at the pole and 2–2.5μm at the equator. Nexine 1–1.5μm thick at the pole and 1.5–2μm at the equator. Tectum and infratectum separated from each other by a thick layer parallel to the nexine.

CHROMOSOME NUMBER: $n = 22$ (Chile, Provincia de Aconcagua, Maintencillo sobre Río Blanco, 2750 m., 6 May 1973, *O. Zöllner 6460*, GH).

NEOTYPE: Chile, Provincia de Santiago, Las Arañas (Cajón del Mapocho), Jan. 1862, ***Philippi 1132*** **(LP).**

DISTRIBUTION: Andean region of central Chile above timberline between 32°S and 35°S and 70°W and 71°W, from 2700 to 3300 meters altitude. Flowering from January to May.

SPECIMENS EXAMINED. **Chile.** Provincia Aconcagua, Valle de Aliste al Norte de Río Blanco, 2800 m., 3 Mar. 1970, *O. Zöllner 3899* (LP); Valle Castro cerca de Río Blanco, 3000 m., 21 Feb. 1968, *O. Zöllner 2994* (LP); Tres Lagunas, 2800 m., 10 Apr. 1971, *O. Zöllner 4963* (LP); Río Blanco, 2750 m., 2 Apr. 1971, *O. Zöllner 4756* (LP); Maintecillo sobre Río Blanco, 2750 m., 6 May 1973, *O. Zöllner 6460* (GH); between Laguna del Inca and transandine railroad tracks, 2840 m., 5 Feb. 1936, *James West 5250* (GH); Provincia Santiago, Cordillera Las Arañas, Jan. 1861, Landbeck *s.n.* (SGO); Cordillera de Santiago, Feb. 1857, *s. coll.* and *s.n.* (SGO); Tal los Castaños (Olivares-Colorado-Maipo-Tal) Cordillera de Santiago, 3300 m., 3 Feb. 1939, *C. Grandjot 3803* (GH, SI); near Laguna Negra, 10,000 feet, 6 Feb. 1902, *G. T. Hastings 615* (US).

Professor Carlos Muñoz Pizarro (1960), who published a book about Philippi's type specimens, was unable to find the type of *Leuceria foliosa*. My own search, which included the herbarium of the Museo de Historia Natural de Santiago, Chile, in which are housed the main collections of Philippi, was also negative. The material cited originally and its duplicate are believed to be lost or destroyed. It was, therefore, necessary to choose a neotype; the specimen chosen was collected and identified by Philippi and comes from the area of the type locality.

The combination *Lasiorrhiza foliosa* was made by Kuntze because he considered *Lasiorrhiza* the appropriate generic name to adopt for *Leuceria*. However, the two genera, published at the same time by the same author had been combined previously by Bentham and Hooker where *Leuceria* was adopted with *Lasiorrhiza* in its synonymy.

RELATIONSHIPS OF THE NEW GENUS

Marticorenia is a member of the tribe Mutisieae, subtribe Nassauviinae, which has characteristic bilabiate corollas with the outer lip three-toothed and the inner lip bifid; anthers long tailed at the base; and style bifid with branches truncate at the apex.

Philippi described *Marticorenia foliosa* as a species of *Leuceria*. However, *Marticorenia* is very different from the other species of *Leuceria* as is shown in TABLE 1.

TABLE 1

Leuceria	Marticorenia
Herbs, perennial or annual.	Shrubs.
Leaves variable in shape but never ovate-lobulate, basal leaves always petiolate.	Leaves all ovate-lobulate, sessile.
Receptacle glabrous, without paleae or with only a few paleae in the flowers of the margin.	Receptacle pubescent, with paleae in all flowers.
Corolla glabrous.	Corolla pubescent.
Pollen: exine with tectum and infratectum of the same thickness and separated from each other by a thin layer not parallel to the nexine (zigzag).	Pollen: exine with tectum and infratectum of different thicknesses and separated from each other by a thick layer parallel to the nexine.
Chromosome number: $n = 20$ (7 species counted).	Chromosome number: $n = 22$ (1 species).

Marticorenia can be easily distinguished from most of the other genera of the subtribe Nassauviinae by the presence of paleae in all of the flowers of the head. This character is shared with *Jungia* Linnaeus f. and *Pleocarphus* D. Don, genera that also have other characters in common with *Marticorenia*.

With *Pleocarphus, Marticorenia* shares the following characters: shrubby perennial habit; entire leaves; cymose inflorescence; pedicellate heads; hemispherical involucres with 2 rows of bracts; pubescent receptacle; pubescent flowers; glabrous anthers; pollen: exine stratification and grain without polar elevations; and style truncate at apex. The distribution of both genera is in the Andean region of central Chile.

With *Jungia*, *Marticorenia* shares these characters: entire leaves; cymose inflorescence; pedicellate heads; pubescent receptacle; uniseriate pappus; involucre with 2 rows of bracts; pubescent flowers; glabrous anthers; pollen: exine stratification, grain subprolate to prolate spheroidal without polar elevations; style truncate at apex.

However, *Marticorenia* is easily distinguished from both *Pleocarphus* and *Jungia* by the following characters:

Pleocarphus has tomentose pubescence; linear, petiolate, stipulate leaves with revolute margins; yellow flowers; linear (five times longer than wide), beaked, and sparsely pubescent achenes; hispidulous pappus in more than one series; prolate to subprolate pollen grains, membrane of the colpi with sexine process.

Jungia, a genus composed of shrubs or vines (rarely herbs), has tomentose pubescence; leaves cordate at base, petiolate and stipulate; campanulate, cylindric or turbinate involucre; beaked linear achene (five times longer than wide), glabrous or sparsely pubescent; pollen grain with membrane of the colpi with sexine process. The distribution of *Jungia* is in Central America (only one species) and the subtropical areas of South America.

Summarizing, we can establish that *Marticorenia* is easily distinguished from most of the genera of the subtribe Nassauviinae by the presence of paleae in all of the flowers of the head but it shares that character with *Jungia* and *Pleocarphus* from which it may be distinguished by the characters noted in the following key:

A. Lower leaves with sparsely tomentose pubescence, petiolate, stipulate.
  B. Flowers yellow, pappus in more than one series; leaves linear, margin entire, revolute. .... *Pleocarphus.*
  BB. Flowers white, pink-violet (rarely yellow), pappus in one series; leaves orbicular, cordate or widely lanceolate, margin lobulate. .... *Jungia.*
AA. Lower leaves lacking tomentose pubescence, sessile, exstipulate. .... *Marticorenia.*

ACKNOWLEDGMENTS

The present study was completed at the Gray Herbarium of Harvard University during my tenure as a Fellow of the John Simon Guggenheim Memorial Foundation. I am grateful to the officers of both organizations for their support of my work. I appreciate especially the privilege of consulting the rich collections and library of the Gray Herbarium and the Arnold Arboretum.

I also appreciate the help and advice of U. Banerjee, K. Bawa, A. L. Cabrera, C. Marticorena, B. G. Schubert, E. A. Shaw, O. T. Solbrig, C. E. Wood, O. Zöllner, and especially the assistance of my wife Marta who prepared the illustrations. The scanning electron microscope work was possible through the generosity of Professor Reed C. Rollins who made funds available for the purpose.

BIBLIOGRAPHY

Crisci, J. V. 1971a. Sobre una especie de *Jungia* (Compositae) del Perú. Bol. Soc. Arg. Bot. **13**(4): 341–346.

———. 1971b. Sobre una especie de *Leuceria* (Compositae) de Chile. Darwiniana **16**(3–4): 627–633.

Erdtman, G. 1960. The acetolysis method. A revised description. Sv. Bot. Tidskr. **54**: 561–564.

Hess, R. 1938. Vergleichende Untersuchungen über die Zwillingshaare der Compositen. Bot. Jahrb. **68**: 435–496.

Lanjouw, J., & F. A. Stafleu. 1964. Index Herbariorum I. ed. 5. Regnum Veg. **31**: 1–251.

Marticorena, C., & J. Crisci 1972. Sobre *Haplopappus scrobiculatus* (Compositae) de Chile y Argentina y su sinonimia. Darwiniana **17**: 467–472.

Muñoz Pizarro, C. 1960. Las especies de plantas descriptas por R. A. Philippi en el siglo XIX. Edic. Universidad de Chile, Santiago.

Parra, O., & C. Marticorena. 1972. Granos de polen de Plantas Chilenas II. Compositae-Mutisieae. Gayana **21**: 1–107.

Gray Herbarium
Harvard University
Cambridge, Massachusetts 02138

Permanent address:
División Plantas Vasculares
Museo de La Plata
La Plata, Argentina

BIGELOW'S "AMERICAN MEDICAL BOTANY"

GÜNTHER BUCHHEIM

AMERICAN MEDICAL BOTANY by Jacob Bigelow (1787–1879) is a three-volume work in which 60 species of American medicinal plants are described and illustrated. Its publication dates are usually given as "1817–1820." These are the inclusive title-page dates of the volumes: vol. 1 is dated 1817, vol. 2: 1818, vol. 3: 1820. However, this work was originally published in six parts, and not in volumes: two parts forming each volume. With the exception of volume 1 part 1, the other five parts are provided with part titles, each being an integral part of the first gathering of each part. These part titles are in the form of a half title and are undated, thus they are of no value in elucidating the dates of publication. The copy of this work in the Duke University, Medical Center Library, Trent Collection, at Durham, North Carolina (NcD–MC) was loaned to the Hunt Botanical Library for this study through the kindness of Dr. G. S. T. Cavanagh, librarian. This copy is distinctive in that the six parts are preserved in their original green boards, and with the paper untrimmed; features that proved to be of high bibliographical importance, especially for determination of dates, collation, and paper size.

The outside front covers give the title as

AMERICAN | MEDICAL BOTANY | WITH | COLOURED ENGRAVINGS. | BY JACOB BIGELOW, M.D. | Member of the American Academy of Arts and Sciences; of the American Philosophical | Society, &c. Rumford Professor and Lecturer on Materia Medica and | Botany in Harvard University.

After the volume and part number, there follows enumeration of the plants described in each part (10 species), together with the plate numbers. The place of publication, and name of publisher and printer, is the same as on the title-pages. Significantly, the dates imprinted on each cover differ from those on the title-pages. Although Graesse, *Trésor de livres rares et précieux* 1: 424. 1950 [reprint], Jackson, *Guide to the literature of botany* p. 360. 1881, and Savage (Comp.), *Catalogue of the printed books and pamphlets in the library of the Linnean Society of London* ed. 2, p. 67. 1925, list the correct inclusive dates (1817–1821), no reference is known which gives the correct publication dates of all the parts.

The dates recorded on the front boards are: Vol. I. Part I: 1817; Vol. I. Part II: 1818; Vol. II. Part I: 1819; Vol. II. Part II: 1819; Vol. III. Part I: 1820; Vol. III. Part II: 1821. In conclusion, volume 1 was published in 1817–1818 (title-page dated 1817), volume 2 in 1819 (title-page dated 1818), and volume 3 in 1820–21 (title-page dated 1820).

Additionally, a printed text is on the outside back covers of the parts belonging to volumes 1 and 2. That on volume 1, part 1 is an announcement by the publisher that part 2 of the same volume will shortly be published, followed by an advertisement of books, none of them botanical. Volume 1, part 2 represents a prospectus of the present work. It is dated May 1818 and states that "Two half volumes are already published." Volume 2, part 1 bears advertisements of books either published by Cummings and Hilliard, or which are in the press. The first item mentioned is AMERICAN MEDICAL BOTANY, Nos. 1, 2, & 3. That for Volume 2, part 2, reports an error on the front cover of Volume 2, part 1, where the plate numbers are reported as "I, II" etc. instead of "XXI, XXII" etc. It reports further that a work titled *Outlines of Botany* . . . by John Locke is in press [this work was published in 1819] and lists additional nonbotanical titles.

Using these data, and considering the contents and bibliographical characteristics of both the NcD–MC and HBL copies, the following formal treatment has been prepared:

American medical botany. 3 vols. Boston, 1817–1820 [1817–1821].

AMERICAN | MEDICAL BOTANY, | BEING A COLLECTION | OF THE | NATIVE MEDICINAL PLANTS | OF THE | UNITED STATES, | CONTAINING THEIR | BOTANICAL HISTORY AND CHEMICAL ANALYSIS, | AND PROPERTIES AND USES | IN | MEDICINE, DIET AND THE ARTS, | WITH | COLOURED ENGRAVINGS. | [very short thick-thin double rule] | BY JACOB BIGELOW, M.D. | RUMFORD PROFESSOR AND LECTURER ON MATERIA MEDICA AND BOTANY | IN HARVARD UNIVERSITY. | [very short thin-thick double rule] | VOL. I. | [5 dots in line] | BOSTON: | PUBLISHED BY CUMMINGS AND HILLIARD, AT THE | BOSTON BOOKSTORE, NO. 1, CORNHILL. | * * * * | UNIVERSITY PRESS . . . . HILLIARD AND METCALF. | 1817.

[Vol. II]: . . . | VOL. II. | . . . | BOSTON BOOKSTORE, NO. 1 CORNHILL | . . . | 1818.

[Vol. III]: . . . | MEDICINE, DIET, AND THE ARTS, | WITH | COLOURED ENGRAVINGS, | [short double rule] | BY JACOB BIGELOW, M.D. | RUMFORD PROFESSOR, AND PROFESSOR OF MATERIA MEDICA IN HARVARD UNIVERSITY. | [short double rule] | VOL. III. | [short thick-thin double rule] | BOSTON: | PUBLISHED BY CUMMINGS AND HILLIARD, AT THE BOSTON | BOOKSTORE, NO. 1 CORNHILL. | [very short double rule] | UNIV. PRESS . . . . HILLIARD AND METCALF. | 1820.

COLLATION: 8° in 4's: Vol. 1: *1*^{4} 2^{2} 3–14^{4} (—14$_{4}$) *15*^{4} 16–25^{4}; *i–v* vi–xi *xii* *17* 18–32 *33* 34–38 *39* 40–51 *52* 53–59 *60* 61–65 *66* 67–74 *75* 76–83 *84* 85–89 *90* 91–95 *96* 97–110 *111–113* 114–124 *125* 126–132 *133* 134–141 *142* 143–148 *149* 150–154 *155* 156–160 *161* 162–168 *169* 170–176 *177* 178–186 *187* 188–191 *192* 193–197 *198.*

Vol. 2: *1*^{4} 2–13^{4} *14*^{4} 15–25^{4}; *i–v* vi–vii *viii–ix* x–xiii xiv (in NcD–MC copy as "xvi") *15* 16–26 *27* 28–33 *34* 35–40 *41* 42–50 *51* 52–58 *59* 60–66 *67* 68–72 *73* 74–81 *82* 83–96 *97* 98–104 *105–107* 108–114 *115* 116–120 *121* 122–136 *137* 138–141 *142* 143–147 *148* 149–153 *154* 155–159 *160* 161–165 *166* 167–170 *171* 172–187 *188* 189–199 *200.*

Vol. 3: *1*^{4} 2–12^{4} 13^{2} (—13$_{2}$) *14*^{4} 15–25^{4} 26^{2}; *i–v* vi–x *11* 12–18 *19* 20–31 *32* 33–42 *43*

44–48 *49* 50–54 *55* 56–60 *61* 62–75 *76* 77–81 *82* 83–91 *92* 93–98 *99–101* 102–106 *107* 108–118 *119* 120–128 *129* 130–133 *134* 135–140 *141* 142–146 *147* 148–150 *151* 152–155 *156* 157–162 *163* 164–173 *174–175* 176–177 *178–179* 180–187 *188–189* 190 *191* 192–193 *194–195* 196–197 *198*.

Contents: Vol. 1: $\mathit{1}_1$r title, $\mathit{1}_1$v registration certification for vol. 1, dated 18 October 1817. $\mathit{1}_2$r dedication to Reverend John Thornton Kirkland (1770–1840), president of Harvard University, Cambridge, Mass., dated "*Boston, October*, 1817," $\mathit{1}_2$v ☐. $\mathit{1}_3$–2_2r preface. 2_2v ☐. 3_1–14_3 text: description of species and their medical uses, including botanical and medical references and explanation of the figures depicted on each plate. $\mathit{15}_1$r part title for vol. 1 part 2, $\mathit{15}_1$v ☐. $\mathit{15}_2$–25_1r continuation of the text. 25_1v–25_4r notes. 25_4v contents of vol. 1.

Vol. 2: $\mathit{1}_1$r part title for vol. 2 part 1. $\mathit{1}_1$v ☐. $\mathit{1}_2$r title, $\mathit{1}_2$v registration certification for vol. 2, dated 28 October 1818. $\mathit{1}_3$–$\mathit{1}_4$r advertisement by the author. $\mathit{1}_4$v ☐. 2_1–2_3 preface. 2_4–13_4 text. $\mathit{14}_1$r part title for vol. 2 part 2, $\mathit{14}_1$v ☐. $\mathit{14}_2$–24_2r continuation of the text. 24_2v–25_4r notes. 25_4v contents of vol. 2.

Vol. 3: $\mathit{1}_1$r part title for vol. 3 part 1, $\mathit{1}_1$v ☐. $\mathit{1}_2$r title, $\mathit{1}_2$v ☐. $\mathit{1}_3$–2_1 preface. 2_2–13_1 text. $\mathit{14}_1$r part title for vol. 3 part 2. $\mathit{14}_1$v ☐. $\mathit{14}_2$–23_2r continuation of the text. 23_2v ☐. 23_3–23_4r notes. 23_4v ☐. 24_1–25_1r appendix. 25_1v ☐. 25_2rv systematic index. 25_3–25_4r index of Latin names. 25_4v ☐. 26_1–26_2r index of English names. 26_2v contents of vol. 3.

Running titles vary with the plants described, the Latin binomial being used on the versos, the English name on the rectos. Language used: English.

Plates: 60 colored (colorprinted and handcolored) or partly colored, mixed intaglio plates (engraving, aquatint, stipple engraving) of medicinal plants, numbered I–LX (XIX as "XI"), titled binomially at foot; 207 × 136 mm. (pl. 2); plates facing descriptions; indexed by Stapf, *Index londinensis* (pl. 14, *Spigelia marilandica*, erroneously stated to be in black and white).

Illustrators:

Artist: the author, Jacob Bigelow. All plates unsigned. However, in the work itself (Vol. 1, p. xi; Vol. 2, p. vi) it is clearly stated that the figures have been prepared from original drawings made by the author himself, "with the exception of two or three presented by his friends" (Vol. 2: p. vi).

Engravers: Annin, W. B. (dates unknown): 2 plates, and additionally 23 (or 21) plates in collaboration with Smith; Smith, ——— (dates unknown): 23 (or 21) plates, all in collaboration with W. B. Annin. 35 (or 37) plates without indication of engraver (pls. 2–6, 8–28, 30, 41, 43–49; also pls. 31 and 58 in NcD–MC copy).

Paper: Halfsheets; size of halfsheet 358 × 530 mm. [NcD–MC, untrimmed]; white, wove. Plates: white, wove.

Printer: The firm of Hilliard and Metcalf, owner of University Press, Cambridge, Mass.

Publisher: Cummings and Hilliard, Boston booksellers.

Dates of Publication: The work was published in 6 parts. Vol. 1, part 1, pp.

i–xii, 17–110, pls. I–X: 1817 (November or late in October). Vol. 1, part 2, pp. 111–198, pls. XI–XX: 1818 (May). Vol. 2, part 1, pp. i–xiv, 15–104, pls. XXI–XXX: 1819 (early in the year, no later than March). Vol. 2, part 2, pp. 105–200, pls. XXXI–XL. 1819 (before December). Vol. 3, part 1, pp. i–x, 11–98 pls. XLI–L: 1820. Vol. 3, part 2, pp. 99–198, pls. LI–LX. 1821 (January).

Supporting evidence: A) Prepublication announcements in *Portico (Baltimore)* **4**(1/2): 131. 1817 [July/Aug.] ("in press") and in *N. Amer. Rev. Misc. J.* **5**(15): 434. 1817 [Sept.] ("about to be published"). B) Registration certification on the verso of the title-pages of vols. 1 and 2 (18 Oct. 1817; 28 Oct. 1818). C) Prospectus dated May 1818 on outside back cover of vol. 1, part 2; year date 1819 on front cover of vol. 2, part 1 (NcD–MC copy). D) Publication announcements in *N. Amer. Rev. Misc. J.* **6**(16): 145–146. 1818 [Nov. 1817] (Vol. 1, part 1 "just issued"); *Amer. Monthly Mag. Crit. Rev.* **4**(50): 388. 1818 [Mar. 1819] (Vol. 2, part 1); *Med. Chir. Zeitung* **1819.** IV(97): 293–295. 1819 [6 Dec.] (Vol. 2, part 2); *N. Amer. Rev. Misc. J.* **12**(30): 230–231. 1821 [Jan.] (Vol. 3, part 2). No announcement for vol. 3, part 1 and published in 1820 has been yet found by the present author; the earliest seen for this part is in *N. Amer. Rev. Misc. J.* **12**(30): 230–231. 1821 [Jan.].

Reviews: *Analectic Mag.* **11**(1): 1–9. 1818 [Jan.]. — *New England J. Med. Surg.* **7**(1): 61–70. 1818 [Jan.]; **10**(2): 157–166. 1821 [Apr.]. — *N. Amer. Rev. Misc. J.* **6**(18): 344–368. 1818 [Mar.]; **9**(24): 23–26. 1819 [June]. — *Ecl. Repert.* **8**(4): 487–497. 1818 [Oct.]. — *Med.-Chir. Zeitung* **1818.**IV(89): 161–163. 1818 [5 Nov.]; **1819.**III(60): 140–143. 1819 [29 July]; **1819.**IV(97): 293–295. 1819 [6 Dec.]. — *Gött. Gel. Anz.* **1819.**III(144/145): 1433–1444. 1819 [9 Sept.]; **1820.**II(111): 1111–1112. 1820 [10 July]; **1823.**II(113): 1121–1126. 1823 [17 July]. — *Neue Entdeck. Pflanzenk.* **1**: 386–393. 1820. — *N. Amer. Rev.* **13**(32): 100–134. 1821 [July]. — *London Med. Phys. J.* **47**(277): 242–244. 1822 [Mar.] — *Allg. Lit.-Zeitung (Halle & Leipzig)* **1822.**IV(36): 281–284. 1822 [Mar.]. — *Bull. Sci. Nat. Géol.* **3**([9]): 59. 1824 [Sept.]. — *Bull. Sci. Méd. (Paris)* **3**([9]): 69–75. 1824 [Sept.]. — *Boston Med. Surg. J.* **20**(26): 412. 1839 [7 Aug.].

Variants: Two states of leaf 2_3 of volume 2 are known, differing only in the pagination of the verso: xvi [misprint for xiv] and xiv [correct pagination]. The original incorrect pagination occurs in the NcD–MC copy, the corrected version e.g. in the HBL copy.

Copies Studied: HBL, NcD–MC; other copies known: AzU, BM, BMNH, CaBVaU, CSfA, CSmH, CSt, CtHT, DLC, DLNM, E–UL, FU, G, GOET-UB, GRO–UB, IaAS, IaDaM, ICF, ICJ, IEN–M, In, InNd, K, KyLxT, KyU, LE (vol. 2, part 1 only), Linn., LNT–M, MB, MBAt, MBC, MBHo, MBM, MdBM, MdBP, MeBat, MH–A (Harv. Herb. Libr.), MH–M, MiEM, MiU, MnS, MSaP, MWA, MWCH, MWiW, NB, NBLiHi, NBMS, NcAS, NcD, NcU, Nh, NhM, NjP, NN, NNA, NNNAM, NNS, NRU, NYBG, OC, OClGC, OKU, OO, OrU, PPA, PPAP, PPC, PPF, PPH, PPHor, PPL–R, PU, RPB, RPM, ScCMu, ScU, TNV, ViRMC, ViU, ViW, VtU, W (vol. 1 only), WIS–R. — US library holdings according to NUC (The National Union Catalog. Pre-1956 imprints) **57**: 283. 1969, and Shaw and Shoemaker (American Bibliography) **1817**: 44. 1963.

NOTES: The continuous sequence of roman and arabic page numbers is worth being mentioned. The gap in pagination in volume 1 (pp. xiii–xvi are lacking) proves that the preliminaries were printed later than the text proper and that the original estimate of 16 preliminary pages was not realistic.

Leaves 14_4 of vol. 1 and 13_2 of volume 3, both blank, are present in the NcD–MC copy. The pagination, however, indicates that these blank leaves were intended to be cut out, as was done in the HBL copy.

The wrong folding of gathering *1* of volume 2 in the NcD–MC copy results in the following irregular arrangement: 1_2 1_1 1_4 1_3; *iii–iv* *i–ii* vii *viii* *v* vi.

In volumes 2 and 3 of the HBL copy the part titles for part 1 are inserted at the wrong places:

Vol. 2: 1_2–1_4 2_1–2_3 1_1 2_4; *iii–v* vi–vii *viii–ix* x–xiv *i–ii* *15* 16.
Vol. 3: 1_2–1_4 2_1 1_1 2_2–2_4; *iii–v* vi–x *i–ii* *11* 12–16.

This work is considered Bigelow's most important contribution to medical botany. It is outstanding for the mixed intaglio processes used for the preparation of the copper plates, being a combination of engraving and aquatint and sometimes stipple engraving. Of the 60 species figured, four are illustrated here for the first time (*Gentiana catesbaei* Walt., *Solidago odora* Ait., *Statice caroliniana* Walt. [= *Limonium carolinianum* (Walt.) Britton] and *Polygala rubella* Willd. [= *P. polygama* Walt.]).

HUNT INSTITUTE FOR BOTANICAL DOCUMENTATION
CARNEGIE-MELLON UNIVERSITY
PITTSBURGH, PENNSYLVANIA 15213

THE GROWTH OF DRACAENA DRACO — DRAGON'S BLOOD TREE

D. E. SYMON

THE DRAGON'S BLOOD TREE is a striking member of the Liliaceae (or Agavaceae). The species is native to the Cape Verde and Canary Islands and an account of it in its natural habitat is given by Bystrom (1960). Considerable age has been attributed to several venerable specimens in the Canary Islands. The monstrous tree at Orotava, Teneriffe Island, was described by Humboldt (1850). When he examined the tree in 1799 the circumference close to the ground was 24 m. (78 ft.); several feet above ground it was 15 m. (48 ft.); and at 3 m. (10 ft.) above ground it was 3.6 m. (12 ft.); the tree was 21 m. (69 ft.) high.

The earliest record of this tree appears to have been made in 1402 when it was already very large and hollow. Bystrom, *l.c.* p. 181, suggests that it could be 600 to 700 years old. It was severely damaged by storm in 1819 and finally destroyed in 1868. Another massive specimen survives at Icod also on Teneriffe, but I do not have any actual measurements. Calculations of its size from a photograph suggest that it is about 10 m. (33 ft.) high, has a spread of 12 m. (36 ft.), branching starts quite low down. Bystrom suggests an age of 200 years, but this is probably an underestimate when compared with the 100 year old tree recorded below. The figures cited highlight the massive tapered bases common to some allied members of the arborescent monocotyledons, e.g. *Beaucarnea*, some *Aloe*, and to a lesser extent *Cordyline*, which no doubt contribute to the attribution of great age to them but particularly to *Dracaena draco*. Wright (1901) at Peradeniya, Ceylon, records the size of a specimen of *D. reflexa* Lam. which at 54 years old was 10 m. high, 9 m. wide, and whose trunk, which branched low down, was irregular in shape but nearly 1 m. in diameter. This species is bushier and much more finely branched than the massive *Dracaena draco*, but it obviously reached considerable size quite quickly.

Bystrom (*l.c.* p. 202), records details of a few plants of *D. draco* of known age on Brava Island, Cape Verde Islands. One planted in 1880 was 11 m. high in 1959 and had a trunk 1 m. in diameter; four others planted about 1902 were 7 m. high and had trunks 60 cm. in diameter. He also suggests that branching occurs after 10 to 25 years.

Possibly two forms of the species can be identified in Australia. The first has a more erect branching habit with relatively massive trunks and longer leaves. This may have originated from the Canary Islands, as it agrees fairly well with Bystrom's account and a plant grown from seed collected from a cultivated plant at Las Palmas is of this form. The second has a more spreading canopy, very umbrella-like, lower and more slender branches and shorter leaves, and corresponds best with the plants described in the Cape Verde Islands. In Adelaide, South Australia, it is the more common form in cultivation.

The species grows well in the warmer temperate areas of the world and has been planted in many gardens in Adelaide. The climate is of the Atlantic Mediterranean type with a cool wet winter and a drier, warm to hot summer. In this locality frosts are rare, but light frosts of short duration can occur.

Two specimens of *Dracaena draco* were planted in the Waite Arboretum in 1929. The plants came from Bowels Nursery, and there is no record of their origin or whether they were seedlings or cuttings. However, it was the practice to establish the trees in 9 liter tins for a year or so before planting, and one can safely assume that the plants were several years old and possibly up to 1 m. high when planted. They are of the stout-limbed Canary Island form. After planting, the trees were watered in the summer until well established but later were dependent on natural rainfall.

For the two older trees in the Waite Arboretum no records of the first flowering or first branching are available, but both trees flower in summer in December and January and ripen fruit in spring over a long period from August to October. Rarely would more than half a dozen branches flower in one season, and as Bystrom indicates, there may be flowers and both green and ripe fruits on the tree at the same time.

The branching of *Dracaena* is sympodial (see Tomlinson & Zimmermann (1969) for an account of this and for a summary of earlier literature). The inflorescence is terminal and after it has matured it is pushed aside as one or more axillary buds develop in the axils of the leaves immediately below the inflorescence. This new shoot replaces the parental axis. Occasionally two buds develop to produce a pseudo-dichotomous division. "Each axis is, therefore, a sympodium consisting of many successive growth units. The sympodium appears articulate both from the scars of the dried inflorescence stalks and from a swelling which marks each joint" (Zimmermann & Tomlinson, 1969). These slightly swollen units marked by constrictions are the "generations of branches" referred to by Bystrom and are better described as "orders of branching." In the young plants referred to in TABLE B, no branching occurred until after the first flowering when six and three buds, respectively, developed below the inflorescence. No detailed records are available for the older plants, but it is thought that each of the sympodial units was probably initiated after an inflorescence had matured.

FIGURE 1 shows tree No. *467* in 1944, 15 years after planting; FIGURE 2 shows the same tree in 1968, 39 years after planting, and FIGURE 3, taken in 1968, shows the nature of the stems and branching. The dimensions of these two trees are given in TABLE A (refer to page 53).

The trees each have 4 orders of branches, but division of the axis does not always occur after each constriction in the stem. Nor do they reflect synchronous flowering; in fact only a small number of the leaf tufts produce an inflorescence in any one year. However, the trees are

Figure 1. *Dracaena draco*, No. *467*, planted in 1929 and photographed in 1944.

Table A. Growth of two specimens of Dracaena draco planted in 1929.

	1934	1958	1968	1973
No. *363*, height in m.,	—	4.5	5.0	5.5
diam. in cm.	—	43	52	51
No. *467*, height in m.,	2.6	5.4	6.0	6.0
diam. in cm.	—	53	68	70

now 45 years old and this gives an order of branching about every 10 to 11 years on each axis which agrees reasonably with Bystrom's (*l.c.*, p. 205) calculation of 10 to 14 years. The trunks of these two trees are still relatively cylindrical between root level and initial branching at about

FIGURE 2. *Dracaena draco*, No. *467*, planted in 1929 and photographed in 1968.

2.25 m., the trunk diameter differing by only 5 to 6 cm. between these points. The massive tapering bases reported for old trees has shown little sign of development in the first 45 years. Neither of the trees has produced the adventitious roots described and illustrated by Bystrom. This may be due to the particular genotype being grown or to the much drier atmosphere in Adelaide compared with the peaks in the Cape Verde Islands which are frequently shrouded in clouds.

TABLE B. **Growth and flowering of three young specimens of Dracaena draco.**

	1957	1960	1964	1966	1967	1968	1969	1973
No. *1714*	seed	planted out	—	1st flowering	—	six branches	—	—
Height in m.					1.5	1.5	2	2
Diam. in cm.					16	20	18	22
No. *1715*	seed	planted out	—	—	—	1st flowering	three branches	—
Height in m.						2.6	3	3.5
Diam. in cm.						30	30	32
No. *1711*			seed	—	planted out	—	—	—
Height in m.						0.3		1
Diam. in cm.						—		25

FIGURE 3. *Dracaena draco*, No. *467*, showing the relatively massive branches.

In recent years three more plants have been established from seed: one (No. *1714*) from a plant in the Sydney Botanical Gardens of the Cape Verde form, the second (No. *1715*) from a plant in a garden at Las Palmas, and the third (No. *1711*) from seed collected from the large old tree at Icod, Teneriffe. Their performance to date is given in TABLE B (refer to page 54).

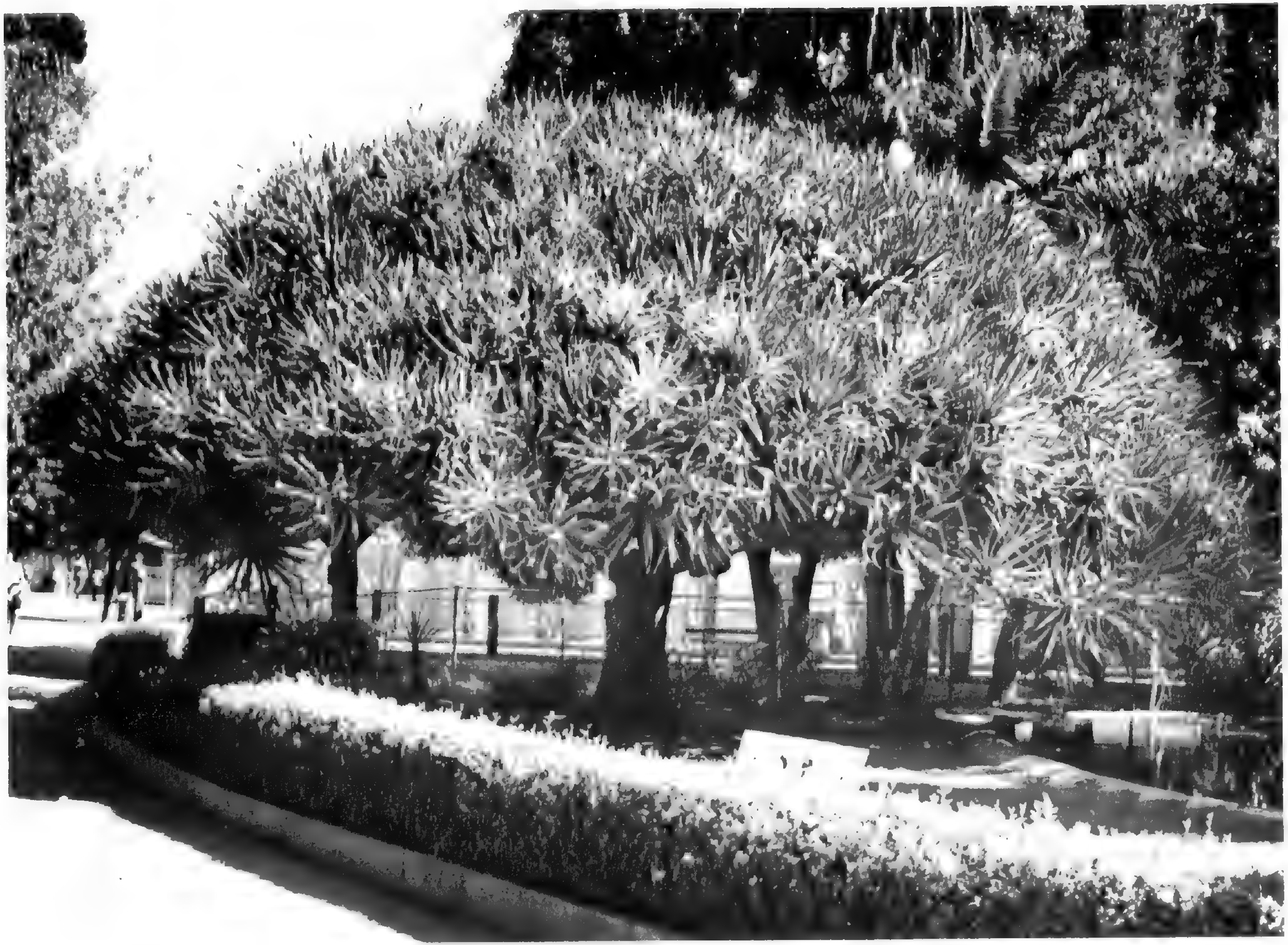


FIGURE 4. *Dracaena draco* in the Adelaide Zoological Gardens, 100 years old, photographed in 1973.

FIGURE 5. *Dracaena draco*, showing the more slender branches of the tree in FIGURE 4.

It will be seen that the first flowering occurred 9 to 11 years from seed and in both cases this was immediately followed by branching.

Two other trees of known age but of unknown origin have been examined. The first is in the Adelaide Zoological Gardens. It is of the Cape Verde form. The records are not precise, but this was probably sown before 1871 and planted out before 1875 and is not earlier than 1865. The specimen is then almost exactly 100 years old (see FIGURE 4). This striking spreading tree has a trunk diameter of 70 cm. at ground level and 60 cm. below the branch at 2 m. Its height is 6 m. and it has a spread of 7.5 m. About 11 orders of branches (or constrictions) can be counted, giving a sympodial unit every 9 to 10 years which agrees well with the trees grown in the Waite Arboretum (see FIGURE 5).

The second is in the Victoria Park Gardens and was planted about 70 years ago. This tree has thicker branches than the one above, the leaves have a distinct twist to them, and some thick adventitious roots 15–20 cm. long hang from some branches. The trunk is 64 cm. in diameter and branches at 1.2 m.; the tree is 5.5 m. high with a spread of 7.6 m. About 5 to 6 orders of branching can be counted, but the sympodial units are relatively long and in this case flowering is indicated every 11 to 14 years.

SUMMARY

These records show that flowering and branching of *Dracaena draco* may occur quite early but that the massive tapered trunks are not evident in the first 100 years.

Trunk diameter in young trees (50–100 years) increases at the rate of about 1 cm. per year in both the Cape Verde Islands and at Adelaide, and in both sites sympodial units, indicated by branch constrictions and probably the result of flowering, occur about every 10 years.

BIBLIOGRAPHY

BYSTROM, K. 1960. *Dracaena draco* L. in the Cape Verde Islands. Acta Horti-Gotoburgensis **23:** 179–214.

HUMBOLDT, F. H. A. VON. 1850. Views of nature, or contemplation on the sublime phenomenon of creation. English ed. xiv + 452 pp. Henry G. Bohn, London.

TOMLINSON, P. B., & M. H. ZIMMERMANN. 1969. Vascular anatomy of the monocotyledons with secondary growth — an introduction. Jour. Arnold Arb. **50:** 159–179.

WRIGHT, H. 1901. Observations on *Dracaena reflexa* Lam. Ann. Roy. Bot. Gdns. Peradeniya **1:** 165–172.

ZIMMERMANN, M. H., & P. B. TOMLINSON. 1969. The vascular system in the axis of *Dracaena fragrans* (Agavaceae). 1. Distribution and development of primary strands. Jour. Arnold Arb. **50:** 370–383.

WAITE AGRICULTURAL RESEARCH INSTITUTE
GLEN OSMOND
SOUTH AUSTRALIA, 5064

A NEW SPECIES OF RUPPIA IN HIGH SALINITY IN WESTERN AUSTRALIA

J. S. Davis [1] and P. B. Tomlinson [2]

The systematic position of *Ruppia*, whether isolated from or closely associated with the larger genus *Potamogeton*, has occasioned some disagreement in the taxonomic literature. Hutchinson (1934, 1959) represents a minority view by including *Ruppia* in a family (Ruppiaceae) separate from *Potamogeton*, whereas other authors include the two genera in the same family. Although there are obvious differences between *Potamogeton* and *Ruppia*, Hutchinson's view stresses them at the expense of their considerable similarities. However, this attitude, in turn, should be viewed against the modern tendency to dismember the originally large assemblage of the Potamogetonaceae (*sensu lato*) and erect smaller families like Cymodoceaceae, Posidoniaceae, Zannichelliaceae, Zosteraceae. This approach is reflected in the system of Takhtajan (1966) as well as that of Hutchinson. The question might therefore be asked about *Ruppia* — does it show the same degree of difference from *Potamogeton* as do these families from each other, sufficient to warrant its segregation in the Hutchinsonian manner? In views of the many evident similarities between *Potamogeton* and *Ruppia*, in terms of vegetative morphology and anatomy, but particularly of floral morphology (Uhl, 1947), the question would seem still to be an open one. The discovery of a new species of *Ruppia* (described here) with certain hitherto unrecorded morphological peculiarities which recall *Potamogeton* is of interest. The distinctive diagnostic features may be related, in part, to the unusual environment in which the plants were growing; so the habitat, which has been studied by the senior author, also deserves description.

The number of taxa within *Ruppia* remains uncertain chiefly because the plant is polymorphic and species are distinguished by relatively slight morphological differences of the reproductive parts, but especially of the fruits (e.g. Mason, 1967). Setchell (1924, 1946) laid emphasis on the ecotypic variation within *Ruppia*, and he considered that most diagnostic criteria which had been used to separate taxa were subject to this variation. The only careful cytotaxonomic survey has been carried out by Reese (1962) on the European forms, and his approach is very illuminating.

---

[1] J.S.D. The opportunity to study the flora and fauna of the solar salt system of J. O. Clough and Son Pty. Ltd. of Perth, Western Australia, is gratefully acknowledged.

[2] P.B.T. Work on the anatomy and morphology of monocotyledons was supported by National Science Foundation grants GB–5762x and GB–31844–x. A general account of the morphology and anatomy of *Ruppia* which will be published in a forthcoming volume (vol. VII, the Aquatic Monocotyledons. Alismatales-Najadales of "Anatomy of the Monocotyledons," ed. C. R. Metcalfe) is subsequently referred to as "Tomlinson, unpublished."

MATERIAL

Specimens were collected by one of us (J.S.D.) during the last week of August and the first weeks of September, 1970, in two ponds and several ditches on the property of Shark Bay Gypsum Company of Western Australia. The locality is at Useless Inlet on the Heirisson Prong of the Carrang Peninsula in the southern part of Shark Bay. The ponds (which are identified by letters) and the ditches are the intermediate part of the solar salt system in which sea water is evaporated to produce sodium chloride. In addition to herbarium specimens (deposited in the Herbarium of the University of Florida, FLAS), material was fixed in 70% alcohol. This provided opportunity for morphological study (by P.B.T.). Habit drawings and detailed illustrations were also prepared from this pickled material.

OBSERVATIONS

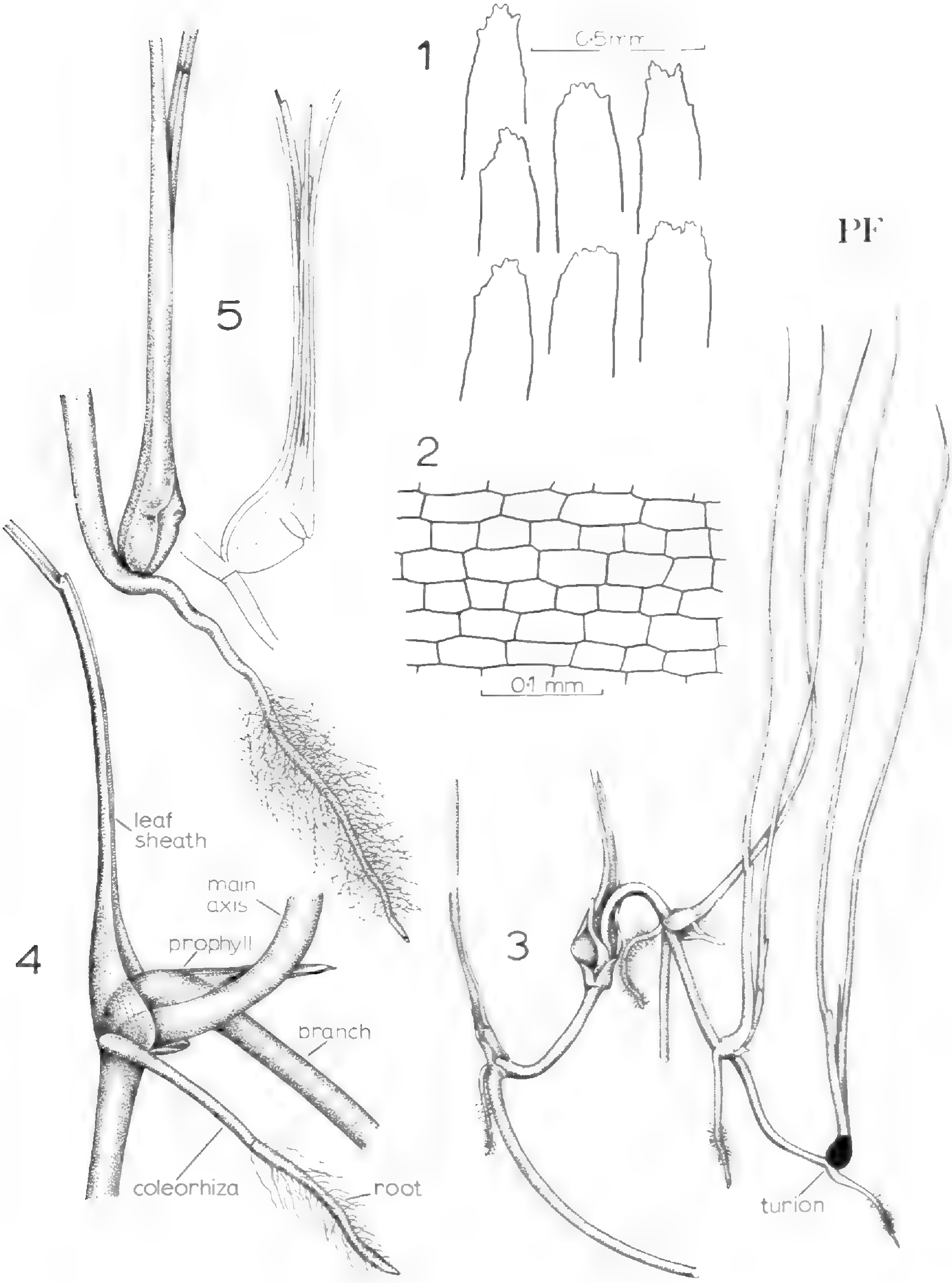
Ecology. The time of collection was the early spring of this part of Australia. At this time the plants were flowering and shedding their anthers, these often becoming concentrated by the wind into yellow films up to several square feet in area in certain parts of the pond. Many plants, however, were producing fruits. Plants were abundant in Pond V and Pond W of the solar system and in the ditches parallel to these two ponds. The plants grew in dense tufts covering up to several square feet of the bottom. Plants in various stages of maturity and varying in size were evident everywhere, from seedlings (FIGURES 1–7) to flowering specimens (FIGURES 8–10).

All the mature plants were dark green, firmly rooted, and with their rhizomes completely buried; they looked healthy and appeared to be growing vigorously.

The water in which the plants grew was clear, with depths varying from about three inches to two feet; the temperature range was 68–70° F. Of chief interest was the salinity of the water at the *Ruppia* locations, which ranged from 92 to 132 parts per thousand of dissolved salts, as determined with a corrected Bäume hydrometer. This represents a range of salinity from 2.6 to nearly 4 times that of ocean sea-water.

Ruppia was absent from the large pond which is used to supply water to Pond V (of about 1,000 acres), even though the salinity in both these bodies of water was the same. During windy days, however, wave action on the larger pond was noticeably severe. The ponds receiving the water of Pond W contained no *Ruppia*. These ponds are small and shallow but salinities were over 200 parts per thousand.

Ruppia tuberosa Davis & Tomlinson, sp. nov. Foliis brevibus (usque ad 8 cm. longibus), angustis (usque ad 0.3 mm. latis); apice folii rotundato irregulariter. Carpella plurima (usque ad 12); fructi sessili (deficientes podogynam), crista prominenti laterali dentato, non rostrata.



FIGURES 1–5. **Ruppia tuberosa:** 1, outline of leaf apex, × 45; 2, epidermal cells of leaf, × 150; 3, monopodial branching system of proximal parts, × 2; 4, detail of node on proximal parts, × 6; 5, detail of turion, × 6, in diagrammatic longitudinal section to right.

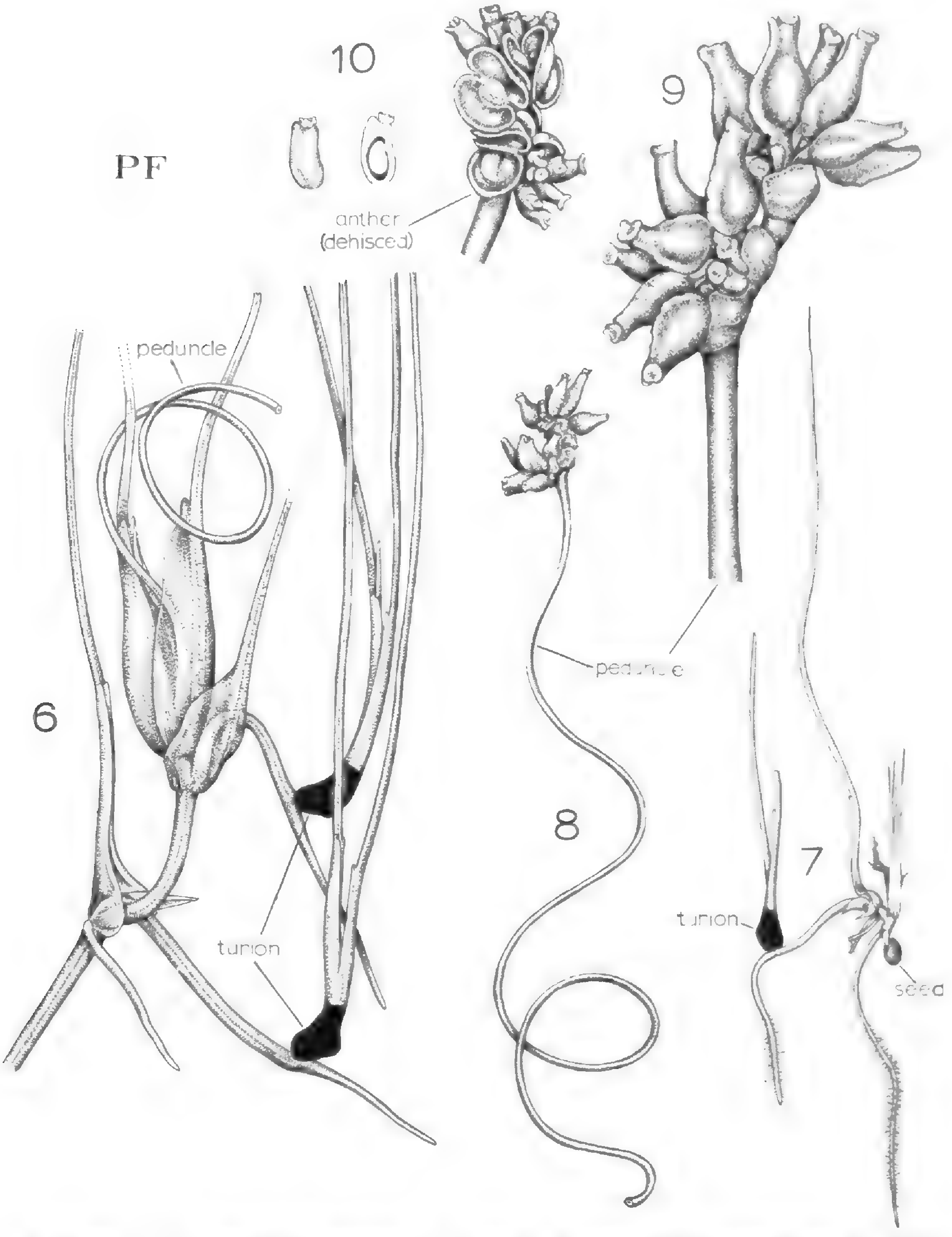
Surculi evolventes tubera tumida aut turiones conspicuos (usque ad 1.5 mm. diametro). TYPE: In hypersaline water (up to about 4 times the salinity of sea-water) in salt ponds, Useless Inlet, Shark Bay, Western Australia. *J. S. Davis s.n.* 4 Sept. 1970 (FLAS).

Leaves to 8 cm. long, narrow; blade scarcely 0.3 mm. wide at a level halfway between its base and apex; apex (FIGURE 1) irregularly rounded with 1- to few-celled apical teeth, rarely bidentate; epidermal cells of the order of 60 μm long, 30 μm wide (FIGURE 2). Shoots ending in conspicuous starch-filled swollen tubers (turions) up to 1.5 mm. wide. Peduncle long, exceeding the leaves, sometimes helically coiled; carpels (female flowers) numerous, always more than 4 (up to 12), with a prominent lateral crest. Fruits sessile (lacking a podogyne), more or less regularly flask-shaped and without a pronounced apical beak, but with a prominent transversely ridged lateral crest when young.

This species differs from all previously described forms of *Ruppia* in its sessile fruits and turions. The leaves are exceptionally narrow and short for the genus. It resembles *R. polycarpa* Mason in its numerous carpels, narrow leaves, and blunt leaf apex, but the shape of the fruit seems to be very different. We have no chromosome counts, which in view of the work of Reese (1962) and Mason (1967) would be very desirable.

Morphological details. In its general morphology the Australian *Ruppia* resembles other *Ruppia* species in so far as they have been described (e.g. Gamerro, 1968; Graves, 1908; Irmisch, 1858; Tomlinson, unpublished). For our present purposes, comparative material has been provided by a population of *Ruppia* (tentatively identified as *R. maritima*) in the brackish-water lakes towards the seaward side of Fairchild Tropical Garden and by a population in high salinities in the Bahamas. The transition from monopodial growth in the proximal vegetative parts (FIGURES 3, 4) to sympodial growth in the distal reproductive parts (FIGURE 6), which is characteristic of *Ruppia*, is clearly shown. In the former phase each foliage leaf subtends an axillary bud and each node has one adventitious root (sometimes more). In other *Ruppia* species roots are infrequent or lacking distally, but in *R. tuberosa* they seem present at all nodes, even distal ones (FIGURE 6). Modified leaves with inflated sheaths are associated with each terminal inflorescence (FIGURE 6). Renewal shoots (one or more) arise singly either in the axils of these modified distal leaves, or in those of the lower ones.

In the Australian *Ruppia* the extremity of each shoot tends to be abruptly recurved (FIGURES 3, 6, and 7). The terminal bud itself is then usually represented by a swollen structure which is conspicuously white or yellowish. These tuberous organs, which we may refer to as "turions" are displaced into a pseudolateral position so that the adventitious root appears to be a direct continuation of the main axis (FIGURE 5). Dissection and free-hand sectioning show that the turion consists largely of a single short internode in which the cortical parenchyma is distended and filled with starch. There is a single unextended root primordium at the upper node, visible externally, and in section obviously continuous with the stele (FIGURE 5). The turion is enveloped by the leaf inserted at its proximal end; the insertion of the leaf at its distal end is obscure,



FIGURES 6–10. **Ruppia tuberosa:** 6, detail of sympodial branching of distal parts in association with terminal peduncle, × 3; 7, seedling, × 2, with initiation of turion in post-seedling phase; 8, peduncle with young fruits, × 4; 9, detail of fruiting head, × 6; 10, old inflorescence with dehisced anthers and female flowers, × 6, inset to the left, detail of female flower in side view and longitudinal section.

largely because the ground tissue at the base of this leaf is also somewhat enlarged and starch-filled. A number of unexpanded leaf primordia are present in the turion. Turions occur throughout the plant and have been seen on seedlings which had produced very few leaves (FIGURE 7). They also had developed on renewal branches from nodes at or close to terminal inflorescences (FIGURE 6). Turions themselves remain unbranched, although there is a bud in the axil of their lowest leaf. Turions may be contrasted with normal shoots in which developing internodes are not swollen and the youngest extended root is obviously lateral (FIGURE 4).

In the material available the reproductive parts all represent relatively late flowering stages. Peduncles are long and often spirally twisted (FIGURE 8). The youngest stages were flowers which still retained dehisced thecae together with mature carpels (FIGURE 10) or fruits (FIGURE 9). These fruits were in groups of up to 12. Large numbers of ripe fruits were developed on some inflorescences. Individual fruits lack the podogyne which is otherwise normal in *Ruppia*. They are sessile and each has a pronounced dorsal and transversely ridged crest (FIGURE 9).

DISCUSSION

This species is unusual in several respects. Most obvious are the turions, which are modified shoots which serve for storage and possibly propagation, although we had no means of verifying this. Such organs seem never to have been described for *Ruppia*, and several authors (e.g. Graves, 1908; Kirchner et al., 1908) specifically mention the absence from *Ruppia* of any winter bud or other organ comparable to the structures commonly developed in several species of *Potamogeton* (e.g. Irmisch, 1858; Hagström, 1911). Setchell (1946) mentions the lack of storage starch in *Ruppia*. The similarity between the types of "resting" structure in *Ruppia* and *Potamogeton* is not close, however, since those of *Ruppia* include only one internode, whereas those of *Potamogeton* usually include several internodes. Winter buds or turions otherwise appear not to develop in those families of aquatic monocotyledons closely allied to the Potamogetonaceae (sensu stricto). The only possible confusion could be with the "tubercles" developed in *Ruppia* (and other genera), which are known to be a pathological response (e.g. Hisinger, 1887). There is no evidence that the modified shoots developed by the Australian *Ruppia* are pathological. It seems unlikely that these organs have been induced by the high salinity of their environment, since *Ruppia* is known to endure a wide range of salinities (Setchell, 1924). For example, our collection of *Ruppia* from Long Island, Bahamas, came from salt ponds with a salinity approximately twice that of sea-water. The only recorded morphological effect of salinity is on fruit size (Mayer, 1971). Tolerance of *Ruppia* to high salt concentration may be subject to genetic variation. Graves (1908) showed that leaf and root cells of *Ruppia maritima* were plasmolyzed at salt concentrations little higher than that of sea-water, suggesting to him that *Ruppia* might not endure high salt concentrations; on the other hand, *Ruppia* evidently exists in high salinities.

The presence of turion-like organs and sessile fruits in this species, both features of the genus *Potamogeton*, can be cited as evidence for a relationship between *Potamogeton* and *Ruppia* which is best expressed by including them in the same family.

SUMMARY

A new species, *Ruppia tuberosa*, is described from Western Australia occupying hypersaline habitats (with up to 4 times the salt concentration of sea-water). A morphological peculiarity is the development of swollen shoots, rich in starch, at the end of almost all axes. These recall the turions or winter-buds of *Potamogeton*. Organs of this kind have not been recorded for *Ruppia* before and are used as evidence to demonstrate the close relationship between these two genera. Additional peculiarities include the individually sessile fruits, each of which has a prominent dorsal ridge.

ACKNOWLEDGMENTS

We are indebted to Priscilla Fawcett, Botanical Illustrator at Fairchild Tropical Garden, for the habit drawings. The opinion of Dr. C. den Hartog, Rijksherbarium, Leiden, and Mr. J. E. Dandy, British Museum (Natural History), on the identity of the new *Ruppia* is also appreciated. Dr. Wm. T. Gillis provided the Latin diagnosis.

LITERATURE CITED

Ascherson, P., & P. Graebner. 1907. Potamogetonaceae. *In*: Engler, Das Pflanzenreich IV. **11**(Heft 31): 1–184.

Gamerro, J. C. 1968. Observaciones sobre la biología floral y morfología de la Potamogetonácea *Ruppia cirrhosa* (Petag.) Grande (= *R. spiralis* L. ex Dum.). Darwiniana **14**: 575–608.

Graves, A. H. 1908. The morphology of *Ruppia maritima*. Trans. Connecticut Acad. Arts Sci. **14**: 59–170.

Hagström, J. O. 1916. Critical researches on the Potamogetons. Sv. Vet. Akad. Handl. **55**(5): 1–281.

Hisinger, E. 1887. Recherches sur les tubercules du *Ruppia rostellata* et du *Zanichellia polycarpa* provoqués par le *Tetramyxa parasitica*. Med. Soc. Fauna Fl. Fenn. **14**: 53–62.

Hutchinson, J. 1934 & 1959. The Families of Flowering Plants. II. Monocotyledons. Eds. 1 & 2. Macmillan, London & Clarendon Press, Oxford.

Irmisch, T. 1858. Ueber einige Arten aus der natürlichen Pflanzenfamilie der Potameen. Abh. naturwiss. Ver. Sachsen Thüringen **2**: 1–56.

Kirchner, O. von., E. Loew, & C. Schröter. 1906. Lebensgeschichte der Blütenpflanzen Mitteleuropas. 1 Abt. 1. Stuttgart.

Mason, R. 1967. The species of *Ruppia* in New Zealand. New Zealand Jour. Bot. **5**: 519–531.

MAYER, F. L. S., JR. 1971. Influence of salinity on fruit size in *Ruppia maritima* L. Proc. Utah Acad. Sci. Arts & Letters **46**(2): 140–143.

REESE, G. 1962. Zur intragenerischen Taxonomie der Gattung *Ruppia* L. Zeitschr. Botanik. **50**(Heft 3): 237–264.

SETCHELL, W. A. 1924. *Ruppia* and its environmental factors. Proc. Nat. Acad. Sci. **10**(6): 286–288.

———. 1946. The genus *Ruppia* L. Proc. Calif. Acad. Sci. IV. **25**(18): 469–478. *Pls. 47, 48.*

TAKHTAJAN, A. 1967. Systema et Phylogenia Magnoliophytorum. Moscow-Leningrad.

UHL, N. W. 1947. Studies in the floral morphology and anatomy of certain members of the Helobiae. [Ph.D. Thesis, Cornell University.]

J. S. D.
DEPARTMENT OF BOTANY
UNIVERSITY OF FLORIDA
GAINESVILLE, FLORIDA 32601

P. B. T.
HARVARD FOREST
PETERSHAM, MASS. 01366

THE GENERA OF MIMOSOIDEAE (LEGUMINOSAE) IN THE SOUTHEASTERN UNITED STATES[1]

THOMAS S. ELIAS

Subfamily MIMOSOIDEAE A. P. de Candolle, Prodromus 2: *tab.* inter 94 & 95. 424. 1825, "Mimoseae"

(MIMOSA SUBFAMILY)

Trees, shrubs, vines, or herbs, often armed with prickles or stipular spines. Leaves alternate, evenly twice pinnate [or rarely once pinnate or modified as phyllodia or scales, or absent], persistent to deciduous, petiolate, the petiole with a conspicuous pulvinus, nectaries present in most genera on petiole and/or rachis, the pinnae usually opposite; leaflets large and few or, more frequently, small and numerous. Inflorescences subterminal, axillary, ramiflorous, or cauliflorous pedunculate spikes, racemes, or heads, the peduncles often fascicled. Flowers mostly small, regular, (3–)5(–7)-merous, perfect, staminate, or sterile (neutral, and then becoming showy in some genera), usually densely clustered, sessile to long-pedicellate, bracteate. Sepals valvate or rarely imbricate in bud, rarely free, usually connate, the lobes usually short. Corolla usually longer than calyx, the petals valvate in bud, free or more usually connate, the lobes long to short, usually exceeding the calyx. Stamens 4–10 (usually as many as or twice as many as corolla lobes) or numerous, free or the filaments connate to form a staminal tube or adnate to corolla, usually exserted; filaments usually white, yellow, pink, or red and often the con-

---

[1] Prepared for a Generic Flora of the Southeastern United States, a 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, the seventy-first to be published, follows the format established in the first paper of 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 information in brackets [ ]. References that I have not seen are marked by an asterisk.

I am most grateful to Dr. Wood for his numerous suggestions in the course of this study, his review of the manuscript, and the many corrections, changes, and additions he has made to it. I am further indebted to my botanical colleagues who have given freely of their time, knowledge, and materials in the course of this study. Among these are George Avery, W. T. Gillis, R. A. Howard, L. I. Nevling, K. R. Robertson, Bernice G. Schubert, and D. R. Windler. Drs. Schubert and Gillis have kindly read the entire manuscript, and Dr. Windler has reviewed the treatment of *Neptunia*. Their thoughtful comments are much appreciated. Mrs. Nancy Dunkly checked much of the bibliography and typed the original manuscript. The illustrations of ***Acacia, Albizia, Neptunia,*** and ***Schrankia*** were drawn by Virginia Savage; that of ***Leucaena*** is by Arnold D. Clapman.

spicuous part of the flower; anthers small, basifixed to dorsifixed, often versatile, sometimes with an apical gland; pollen grains shed singly (as monads) or more frequently as compound grains (polyads or pollinia) of 4–64 grains. Gynoecium 1-carpellate [or apocarpous with up to 15 carpels per flower], mostly bilaterally symmetrical, sessile to stipitate, glabrous to pubescent; style usually filiform and slightly exceeding the stamens; stigma terminal, generally minute and concave, or less often dome-shaped; ovary superior, ovules [1 to] many, in two alternating rows along the adaxial suture, hemianatropous to anatropous, obliquely ascending or pendulous, two integumented, crassinucellate. Fruit various, generally a dry to fleshy legume dehiscing along both adaxial and abaxial sutures [rarely explosively] or the adaxial suture dehiscing before the abaxial one, or tardily dehiscent or indehiscent, straight, twisted or variously contorted, continuous within or variously interrupted, or fruit a dry loment. Seeds various, generally plano-compressed, oriented transversely, obliquely, or longitudinally in the fruit, mainly with a leathery to very hard seed coat [or seed coat rarely lacking, the seeds then embedded in a fleshy pulp], often arillate (the aril often fleshy), almost always with a distinct U-shaped line (pleurogram) on each side; endosperm often absent or scarcely developed; embryo minute to large, straight, often with large, flat cotyledons, the radicle generally superior. Embryo-sac development of the Polygonum type; embryogeny of the Onagrad type. Base chromosome numbers 13, 14. (Mimosaceae R. Br. in Flinders, Voy. Terra Austr. 2: 551. 1814, "Mimoseae," nom. cons.; tribe Mimoseae Bronn, De Formis Pl. Leguminosarum 127, 130. 1822.) TYPE GENUS: *Mimosa* L.

The Mimosoideae is one of three widely recognized subfamilies of the large and important family Leguminosae (Fabaceae). Although some contemporary botanists (e.g., Cronquist, Hutchinson, Takhtajan) treat them as separate families of a single order, the distinguishing characters between the three taxa break down to such a degree that it seems far better to keep them at the rank of subfamily. The Mimosoideae are characterized by actinomorphic (regular) perianth and androecium, by both corolla and calyx valvate in bud (except the calyx imbricate in *Parkia*, *Pentaclethra*, and *Mimozyganthus*), and by seeds usually marked by pleurograms. By contrast, in the Caesalpinioideae the flowers are actinomorphic to zygomorphic, the corolla is imbricate in bud, the calyx usually is imbricate (rarely valvate), and the seeds generally lack pleurograms. The two subfamilies appear to be connected through the caesalpiniaceous genera *Burkea* and *Dimorphandra* and the mimosaceous *Pentaclethra*. The more specialized subfamily Mimosoideae appears to have arisen from the Caesalpinioideae. The relationship between the Mimosoideae and the Faboideae is not so close, the papilionaceous legumes tending, instead, to approach some of the zygomorphic-flowered caesalpiniaceous genera.

A number of artificial assemblages have been established in the Mimosoideae, and it is evident that many of the criteria used to delimit genera are unsatisfactory. Linnaeus placed all the mimosoid legumes known to him (with the exception of *Adenanthera pavonina*) in a single genus, *Mimosa*. In 1805, Willdenow divided *Mimosa* into five genera, and, by 1875, Bentham, in his now classic revision of the subfamily, enumerated six tribes containing 29 genera. Since 1875 generic delimitation has proceeded either toward a reduction in the number of genera (e.g., Kuntze, 1891) or toward the recognition of numerous segregate genera (e.g., Britton & Rose, 1928).

The subfamily Mimosoideae contains approximately 55 to 60 genera distributed throughout tropical, subtropical, and warm-temperate regions of the world. The distribution of species among the 56 genera recognized by Hutchinson (1964) is very uneven. Almost two-thirds of the known species fall into three genera: *Acacia*, with 700–800 species; *Mimosa*, with 400–450 species; and *Inga*, with 350–400 species. Many of the genera are small, and nearly one-half of those recognized by Hutchinson are monotypic. Most of the monotypic ones are African. Obviously, generic lines in this subfamily are in need of a complete re-examination.

Bentham's six tribes (Parkieae, Piptadenieae, Adenanthereae, Eumimoseae [= Mimoseae], Acacieae, and Ingeae) were based mainly on floral and seed characters. Taubert (1894) used the same characteristics in the second major account of the mimosoid legumes. Most authors have maintained these tribes until recently (1964), when both Hutchinson and Schulze-Menz combined the Piptadenieae (endosperm present) with the Adenanthereae (endosperm absent). Both authors also considered the monotypic *Mimozyganthus* Burkart to represent a distinct tribe, Mimozygantheae. Although the tribes recognized by Hutchinson and by Schulze-Menz may have some degree of integrity, they still appear to be largely artificial. For example, the separation of the Mimoseae from the Adenanthereae on the basis of the presence or absence of a gland at the tip of the anther is at best a tenuous distinction (see *Schrankia* and *Desmanthus*). However, considerably more data are needed, especially about the poorly known genera of tropical areas, before more natural infrageneric groupings can be made. Consequently, the genera treated here are assigned to the tribes of Hutchinson and of Schulze-Menz in a very tentative way.

The great variability in the pollen of the Mimosoideae is shown by the occurrence of single grains and several types of compound grains, various aperture systems, and variation in stratification and relief of the pollen exine. The pollen of many genera is shed as single grains (monads), usually tricolporate. Pollen in tetrads is found in *Schrankia* and some species of *Mimosa*, while eight-grained polyads, although infrequent, occur in some species of both *Mimosa* and *Calliandra*. Flattened, disc-shaped, 16-grained polyads are the most frequently encountered of the polyad types (cf. *Acacia*, *Albizia*, *Lysiloma*, and *Pithecellobium* and many species of *Calliandra* and *Inga*). Large 32-grained polyads are found in *Affonsea*, *Samanea*, *Enterolobium*, and some species of *Pithecellobium* and *Inga.* The individual grains of a polyad are often asymmetrical, heteropolar, and 4- to 8-porate.

Sorsa (1969) and Guinet (1969) independently obtained similar data from palynological surveys of the subfamily, but each regarded a different type of pollen as primitive. Guinet considered the tricolporate pollen types to be more complex than the porate ones, while Sorsa contended that the development of the various aperture systems proceeded from colpate and colporate toward the more advanced porate condition. Pollen grains shed individually are isopolar, while those shed as polyads are almost always heteropolar. Guinet linked heteropolarity with the simplest pollen features and isopolarity with the more complex, but Sorsa took the opposite view. Although these differences are unresolved, the many features of the pollen of the Mimosoideae, when correlated with other characteristics, undoubtedly will prove to be very helpful in understanding the complex relationships within this group.

The Mimosoideae are poorly known cytologically, perhaps because of difficulties in obtaining buds at the proper stage of development and because the number of pollen mother cells in an anther is reduced in many genera. The chromosomes are small and have not been studied morphologically. The genera in our range appear to have a base number of 13, except for *Desmanthus* and *Neptunia,* both of which have 14. Polyploids are few but occur in at least *Acacia* and *Mimosa.*

Although variable in size, the seed of members of the Leguminosae generally is compressed, has a large embryo, and a hard but smooth seed coat. Seeds without endosperm occur in all three subfamilies, except in tribes Adenanthereae and Mimoseae of the Mimosoideae. The most distinctive feature of almost all seeeds of the Mimosoideae is the pleurogram (or areole, ligne de suture, lineafisural; see Brenan, Corner) a fine U-shaped groove in the seed coat on each side of the seed. Except for the pleurogram, the significance of which appears to be unknown, the seeds of the Mimosoideae and those of the Caesalpinioideae are very similar.

Leguminous seeds, in general, are long lived, and those of a number of mimosoids have been shown to be remarkable in this respect. Seeds of *Mimosa pudica* have germinated 44 years after collection, *Acacia* after more than 50 years, *Mimosa glomerata* after 81, *Leucaena leucocephala* after 99, and *Albizia Julibrissin* after 50, 70, and 147 years (cf. *Albizia*; under subfamily references see Crocker).

The secondary xylem is either ring porous or diffuse porous, and the mostly solitary vessels are composed of elements with simple perforation plates. Senn (1943) concluded on the basis of the length and configuration of the vessel elements that the Leguminosae are highly specialized. Paratracheal parenchyma is usually abundant in the secondary xylem, except in a few species that have apotracheal parenchyma. The paratracheal parenchyma varies from the simple vasicentric type to confluent or even broadly banded types. Parenchyma patterns of the Mimosoideae are quite similar to those found in the Caesalpinioideae, but patterns in the

Faboideae show considerably more variation than in the other subfamilies.

Septate fibers occur in all three subfamilies, but are most frequent in the Mimosoideae and are very rare in the Faboideae. The occurrence of relatively specialized rays in the secondary wood indicates the advanced nature of the family. Storied rays are absent in the Mimosoideae, infrequent in the Caesalpinioideae, and most frequent in the Faboideae.

The nodal anatomy of the Mimosoideae is of the trilacunar type, with three traces and three gaps. Each of the two lateral traces gives rise to an accessory bundle that supplies one of the stipules. The main vascular supply of the petiole consists of a ring of vascular bundles with accessory bundles found in the adaxial position.

Most mimosoid legumes have extrafloral nectaries on the petiole and/or the rachis of the leaves. These nectaries are generally small, usually cup- or trough-shaped, and secrete a sugar-rich nectar. Some physiologists consider them to be organs for the elimination of waste products or an over-abundance of carbohydrates, but other investigators, mostly naturalists and ecologists, hold that the foliar nectaries entice ants, which, in turn, protect the plant from herbivores. Although the nectaries do indeed attract ants which provide some degree of protection, especially in some tropical species, and there are some remarkable examples of mutualism (see *Acacia*), the available data are inconclusive as to the primary function of these organs. Whatever their function, the many types of foliar nectaries can be useful taxonomically because each type is relatively invariable within a species.

Records of Mimosoideae as fossils, especially those from the southeastern United States, are based almost entirely upon fragments of leaflets. Species of the tropical genera *Inga* and *Pithecellobium* have been reported from deposits of the lower Eocene (Wilcox group) and the middle Eocene (Claiborne group) of the Mississippi Embayment region (Berry, 1916, 1924). The northernmost reported occurrence is *Inga wickliffensis* Berry from Ballard County, Kentucky. The identifications of angiosperms remains from the Mississippi Embayment are being reviewed, and detailed studies of the fragments are beginning to yield more accurate identifications. The presence of *Inga* and *Pithecellobium* in the deposits of the area needs verification.

Species of the Mimosoideae are of less economic importance than those of the Faboideae, but many members of the subfamily are useful. Gum arabic is obtained from *Acacia Senegal* Willd., while tannins are derived from the bark of other acacias, especially from certain species of Australia, South Africa, India, and some regions of the New World. The hard wood of many mimosoid trees is very attractive and takes an excellent polish. Lumber is obtained from species of *Acacia*, *Albizia*, *Xylia*, *Enterolobium*, *Lysiloma*, and many other genera of lesser importance.

The leaves of most mimosoid legumes found in the United States (except those with well-developed spines) are of value as forage for cattle, horses, and some of the larger native mammals. The seeds of all species of our range are eaten by various wildlife, especially birds and rodents. Flowers of some species of *Acacia* and *Leucaena* are prodigious nectar producers and are often important sources of honey. Some of the thicker, fleshier pods (as in species of *Inga*) are used to feed livestock or as an occasional food supplement by the Indians of the lowlands of Central and South America. Many of the small to medium-sized trees with spreading crowns are used as shade trees in coffee- (and to a lesser extent in cacao-) plantations.

Nearly all of the mimosoid legumes grown for their ornamental value are unable to tolerate freezing temperatures and, consequently, can be grown out-of-doors only in southern Florida and southern California. Several species of *Calliandra* are in cultivation, especially the well-known and widely cultivated *C. haematocephala* Hassk., powderpuff tree, and to a lesser extent *C. surinamensis* Bentham. Many species of *Acacia*, especially Australian ones, are cultivated in southern Florida and California for their fragrant and attractive flowers. Occasionally species of *Inga* and *Pithecellobium* are found in cultivation, and the rain tree, *Samanea Saman* (Jacq.) Merr. is grown in southern Florida. Specimens of *Anadenanthera colubrina* (Vell.) Brenan and *Enterolobium cyclocarpum* (Jacq.) Griseb. are in cultivation but are not widely grown.

Representatives of two genera introduced as ornamentals, *Dichrostachys* (DC.) Wight & Arn. and *Adenanthera* L., show signs of becoming naturalized in southern Florida and are, consequently, included in the key that follows. *Dichrostachys cinerea* (L.) Wight & Arn., apparently indigenous to India and Africa, has been introduced into southern Florida from Cuba. Despite the very attractive pink-and-yellow inflorescences, the thorny branches and rampant growth of this shrub or small tree have made it a serious pest in Cuba. Its possible spread in southern Florida should be watched carefully.

The Old World *Adenanthera pavonina* L., red sandalwood, also introduced into the West Indies and Central America, is cultivated as an ornamental tree. The twice-pinnately compound leaves are large with relatively large leaflets, and the valves of the fruits coil and twist upon dehiscence, much like those of *Pithecellobium*, exposing the bright red lens-shaped seeds, which remain attached to the valves. Birds probably serve as effective dispersal agents.

REFERENCES:

ATCHISON, E. Studies in the Leguminosae. IV. Chromosome numbers and geographical relationships of miscellaneous Leguminosae. Jour. Elisha Mitchell Sci. Soc. **65:** 118–122. 1949.

———. Studies in the Leguminosae. VI. Chromosome numbers among tropical woody species. Am. Jour. Bot. **38:** 538–546. 1951.

BAILLON, H. Légumineuses. Sous-famille des Mimosées. Hist. Pl. **2:** 21–68. 1870. (English ed. **2:** 20–68. 1872).

BELL, E. A. Canavanine in the Leguminosae. Biochem. Jour. **75**: 618–620. 1960.

BENTHAM, G. Notes on Mimoseae, with a short synopsis of species. Jour. Bot. Hooker **4**: 323–418. 1841–42; London Jour. Bot. **1**: 318–392, 494–528. 1842; **3**: 82–112, 195–226. 1844; **4**: 577–622. 1845; **5**: 75–108. *pl. 1.* 1846.

———. Revision of the suborder Mimoseae. Trans. Linn. Soc. London **30**: 335–664. *pls. 66–70.* 1875.

——— & J. D. HOOKER. Mimoseae. Gen. Pl. **1**: 588–600. 1865.

BERGER, C. A., E. R. WITKUS, & R. M. MCMAHON. Cytotaxonomic studies in the Leguminosae. Bull. Torrey Bot. Club **85**: 405–415. 1958.

BERRY, E. W. The Lower Eocene floras of southeastern North America. U.S. Geol. Surv. Prof. Pap. **91.** 481 pp. 1916. [Mimosaceae, 222–228.]

———. Upper Cretaceous floras of the eastern Gulf region in Tennessee, Mississippi, Alabama, and Georgia. *Ibid.* 112. 177 pp. 1919. [Mimosaceae, 96, 97.]

———. The Middle and upper Eocene floras of southeastern North America. *Ibid.* 92. v + 206 pp. 1924. [Mimosaceae, 62, 63.]

BIRDSONG, B. A., R. ALSTON, & B. L. TURNER. Distribution of canavanine in the family Leguminosae as related to phyletic groupings. Canad. Jour. Bot. **38**: 499–505. 1960.

BOELCKE, O. Estudio morfológico de las semillas de Leguminosas mimosoideas y caesalpinoideas de interés agronómico en la Argentina. Darwiniana **7**: 240–321. 1946.

BOLKHOVSKIKH, Z., V. GRIF, T. MATVEJEVA, & O. ZAKHARYEVA. Chromosome numbers of flowering plants. (Russian and English prefaces.) 926 pp. Leningrad. 1969. [Fabaceae, incl. Mimosoideae, 279–326.]

BRENAN, J. P. M. Leguminosae subfamily Mimosoideae. 173 pp. London. 1959. *In*: C. E. Hubbard & E. Milne-Redhead, eds., Flora of Tropical East Africa. [Includes 19 genera, excellent illustrations; includes *Adenanthera, Dichrostachys, Mimosa, Neptunia, Leucaena, Acacia, Albizia, Pithecellobium.*]

BRITTON, N. L., & J. N. ROSE. Mimosaceae. N. Am. Fl. **23**: 1–194. 1928.

——— & E. P. KILLIP. Mimosaceae and Caesalpiniaceae of Colombia. Ann. N.Y. Acad. Sci. **35**: 101–208. 1936.

BURKART, A. Las Leguminosas argentinas silvestres y cultivadas. ed. 2. xv + 569 pp. Buenos Aires. 1952.

CACCAVARI DE FILICE, M. A. Granos de polen de Leguminosas de la Argentina. I. Subfam. Mimosoideae; Tribu Acacieae. Darwiniana **16**: 144–174. 1970. II. Subfam. Mimosoideae; Tribu Adenanthereae. (In press). III. Subfam. Mimosoideae; Tribus Piptadenieae y Mimozygantheae. *Ibid.* **17**: 326–340. 1972.

CAMPO, M. VAN, & P. GUINET. Les pollens composés. L'exemple des Mimosacées. Pollen Spores **3**: 201–218. 1961.

COMPTON, R. H. An investigation of the seedling structure in the Leguminosae. Jour. Linn. Soc. Bot. **41**: 1–122. *9 pls.* 1912. [Mimosoideae, 5–10.]

CORNER, E. J. H. The leguminous seed. Phytomorphology **1**: 117–150. 1951.

CROCKER, W. Life-span of seeds. Bot. Rev. **4**: 235–274. 1938.

CRONQUIST, A. The evolution and classification of flowering plants. xii + 396 pp. Boston. 1968. [See p. 369.]

CANDOLLE, A. P. DE. Mémoires sur la famille des Légumineuses. 515 pp. + *71 pls. + 2 tableaux.* Paris. 1825–1827. [Mimosées, 415–451.]

———. Leguminosae. Prodr. **2**: 93–524. 1825. [Mimoseae, 424–473.]

DAVIS, G. L. Systematic embryology of the angiosperms. x + 528 pp. New York. 1966. [Mimosaceae, 176, 177.]

DORMER, K. J. An investigation of the taxonomic value of shoot structure in angiosperms with special reference to Leguminosae. Ann. Bot. II. **9**: 141–153. 1945.

DUKE, J. A. On tropical tree seedlings. I. Seeds, seedlings, systems, and systematics. Ann. Missouri Bot. Gard. **56**: 125–161. 1969. [Mimosaceae, 148.]

DNYANSAGAR, V. R. Embryological studies in the Leguminosae. XI. Embryological features and formula and taxonomy of the Mimosaceae. Jour. Indian Bot. Soc. **34**: 362–374. 1955.

ERDTMAN, G. Pollen morphology and plant taxonomy. V. On the occurrence of tetrads and dyads. Sv. Bot. Tidskr. **39**: 286–297. 1945. [Mimosoid legumes, 291.]

FAHN, A., & M. ZOHARY. On the pericarpial structure of the legumen, its evolution and relation to dehiscence. Phytomorphology **5**: 99–111. 1955.

GATES, F. C. Influence of moonlight on movements of leguminous leaflets. Ecology **4**: 37–39. 1923.

GATES, R. R. Epigeal germination in the Leguminosae. Bot. Gaz. **113**: 151–157. 1951.

GRAHAM, E. H. Legumes for erosion control and wildlife. U.S. Dep. Agr. Misc. Publ. **412.** ii + 153 pp. Washington, D.C. 1941.

GUIGNARD, M. E. Recherches d'embryogénie végétale comparée. I. Légumineuses. Ann. Sci. Nat. Bot. VI. **12**: 5–166. 1881.

GUINET, P. Les Mimosacées, étude de palynologie fundamentale, corrélations, évolution. Inst. Franç. Pondichéry Trav. Sci. Tech. **9**: 1–293. *pls. 1–20.* 1969.

HARBORNE, J. B., D. BOULTER, & B. L. TURNER, eds. Chemotaxonomy of the Leguminosae. xv + 612 pp. Academic Press, London & New York. 1971.

HENBEST, O. J. A preliminary report on the legumes of the Arkansas uplands. Proc. Arkansas Acad. Sci. **1**: 21–23. 1941.

HUTCHINSON, J. The genera of flowering plants. vol. 1. xi + 516 pp. Clarendon Press, Oxford. 1964. [Mimosaceae, 277–297.]

ISELY, D. Observations on seeds of the Leguminosae: Mimosoideae and Caesalpinioideae. Proc. Iowa Acad. Sci. **62**: 142–145. 1955.

———. Key to seeds to Caesalpinioideae and Mimosoideae of North Central States. *Ibid.* 146–149. 1955.

———. Leguminosae: nomenclatural notes. Rhodora **59**: 116–119. 1957. [*Schrankia* & *Acacia.*]

———. Leguminosae of the north-central United States. III. Mimosoideae and Caesalpinioideae. Iowa State College Jour. Sci. **32**: 355–393. 1958.

———. Legumes of the United States V. *Albizia, Lysiloma, Leucaena, Adenanthera*; rejected genera of Mimosoideae. Castanea **35**: 244–259. 1970.

———. Leguminosae of the United States: I. Subfamily Mimosoideae. Mem. N.Y. Bot. Gard. **25** (1). 1973.

JONES, G. N. Leguminales: A new ordinal name. Taxon **4**: 188, 189. 1955.

KRAUSS, G. J., & H. REINBOTHE. Die freien Aminosaüren in Samen von Mimosaceae. Phytochemistry **12**: 125–142. 1973.

KURZ, H., & R. K. GODFREY. Trees of northern Florida. xxxiv + 311 pp. Gainesville, Florida. 1962. [Leguminosae, 174–181.]

LITTLE, E. L., JR. Check list of native and naturalized trees of the United

States (including Alaska). U. S. Dep. Agr. Forest Serv. Agr. Handb. **41.** 472 pp. 1953.

——— & F. H. WADSWORTH. Common trees of Puerto Rico and the Virgin Islands. U. S. Dep. Agr. Forest Serv. Agr. Handb. **249.** x + 548 pp. 1964. [Mimosoideae, 142–168; illustrated; includes *Acacia farnesiana, Adenanthera pavonina, Albizia Lebbeck, Leucaena leucocephala, Pithecellobium dulce.*]

LONG, R. W., & O. LAKELA. A flora of tropical Florida. xvii + 962 pp. Coral Gables, Florida. 1971. [Mimosoideae, 447–455; includes all our genera.]

LUBBOCK, J. A contribution to our knowledge of seedlings. Vol. 1. 608 pp. New York. 1892. [Leguminosae, 382–476.]

MAHLER, W. F. Manual of the legumes of Tennessee. Jour. Tenn. Acad. Sci. **45:** 65–96. 1970.

MOHLENBROCK, R. H. Reorganization of genera within tribe Ingeae of the mimosoid Leguminosae. Reinwardtia **6:** 429–442. 1963.

PAMMEL, L. H. Anatomical characters of the seeds of Leguminosae, chiefly genera of Gray's Manual. Trans. Acad. Sci. St. Louis **9:** 91–273. *pls. 7–35.* 1899.

PELLEGRINI, O. Systematic affinity between Pruneae and Leguminosae demonstrated by the homologous pericarp tissue. (In Italian; English summary.) Delpinoa **5:** 7–48. 1952.

PIJL, L. VAN DER. Classification of the leguminous fruits according to their ecological and morphological properties. Nederland. Akad. Wetensch. Proc. C. Biol. Med. Sci. **59:** 301–313. 1956.

RECORD, S. J., & R. W. HESS. Timbers of the New World. xv + 640 pp. *pls. 1–58.* Yale Univ. Press, New Haven. 1943. [Leguminosae, pp. 227–336.]

RICKETT, H. W. Wild flowers of the United States. Vol. 2, pt. 1. x + 322 pp. New York. 1967. [Mimosaceae, 317–320 [incl. *pls. 115, 116*]; *Desmanthus illinoensis, Mimosa strigillosa, Neptunia pubescens, Schrankia microphylla, S. Nuttallii* illustrated.]

RIDLEY, H. N. The dispersal of plants throughout the world. xx + 744 pp. *22 pls.* Ashford, England. 1930. [Notes on dispersal of *Acacia farnesiana, Leucaena leucocephala, Mimosa pudica,* & *Pithecellobium dulce.*]

SARGENT, C. S. Leguminosae. Silva N. Am. **3:** 33–138. 1892. [Mimosoid legumes, 99–138, *pls. 136–147.*]

———. Manual of the trees of North America (exclusive of Mexico). ed. 2. xxvi + 910 pp. Boston & New York. 1922. [Mimosoideae, 585–603.]

SCHERY, R. W. Leguminosae subfamily Mimosoideae. *In:* R. E. WOODSON, R. W. SCHERY, *et al.*, Flora of Panama. Ann. Missouri Bot. Gard. **37:** 184–314. 1950. [16 genera treated.]

SCHULZE-MENZ, G. K. Rosales. *In:* H. MELCHIOR, A. Engler's Syllabus der Pflanzenfamilien. ed. 12. **2:** 193–242. 1964. [Mimosoideae, 223–226.]

SENN, H. A. Chromosome number relationships in the Leguminosae. Bibliogr. Genet. **12:** 175–336. 1938.

———. The relation of anatomy and cytology to the classification of the Leguminosae. Chron. Bot. **7:** 306–308. 1943.

SHAH, G. L., M. H. PARABIA, & M. J. KOTHARI. Epidermal structures and stomatal ontogeny in some Mimosaceae. Ann. Bot. II. **36:** 823–835. 1972.

SORSA, P. Pollen morphological studies on the Mimosaceae. Ann. Bot. Fenn. **6:** 1–34. 1969.

STAFLEU, F. A., & W. T. STEARN. De Candolle's Legumineuses. Taxon **9:** 169–171. 1960.

TAKHTAJAN, A. Flowering plants, origin and dispersal. (Transl. C. JEFFREY.) x + 310 pp. Edinburgh. 1969. [Mimosaceae, 223.]

TAUBERT, P. Leguminosae. Nat. Pflanzenfam. III. **3:** 70–384. 1891–1894. [General account, including Mimosoideae, 70–99; Mimosoideae, 99–112, 1891; 113–125, 1892.]

TURNER, B. L. The legumes of Texas. xii + 284 pp. Univ. of Texas, Austin. 1959. [Mimosoideae, 27–65; includes *Pithecellobium*, *Albizia*, *Calliandra*, *Acacia*, *Leucaena*, *Schrankia*, *Mimosa*, *Desmanthus*, *Neptunia*, *Prosopis*.]

——— & O. S. FEARING. Chromosome numbers in the Leguminosae. III. Species of the southwestern United States and Mexico. Am. Jour. Bot. **47:** 603–608. 1960.

U. S. DEP. AGR. FOREST SERV. Woody-plant seed manual. U. S. Dep. Agr. Forest Serv. Misc. Publ. **654.** 1948. [Includes *Acacia*, *Albizia*.]

VINES, R. A. Trees, shrubs and woody vines of the Southwest. xii + 1104 pp. Austin, Texas. 1960. [Mimosoid legumes, 491–518.]

WARD, D. B. Checklist of the legumes of Florida. 21 pp. Offset. Agr. Exp. Sta., Univ. Florida, Gainesville, Florida. 1972.

WATARI, S. Anatomical studies on some leguminous leaves with special reference to the vascular system in petioles and rachises. Jour. Fac. Sci. Tokyo Univ. Bot. **4:** 225–365. *pls. 5–8.* 1934.

WEST, E., & L. ARNOLD. The native trees of Florida. xx + 212 pp. Gainesville, Florida. 1946. [Mimosoid legumes, 86–89.]

WILBUR, R. L. The leguminous plants of North Carolina. N. Carolina Exp. Sta. Tech. Bull. **151.** 294 pp. 1963. [Mimosoideae, 14–18.]

WILLDENOW, K. Linn. Sp. Pl. ed. 4. vol. 4. 1157 pp. Berlin. 1805. [*Inga*, 1004–1027; *Mimosa* 1028–1041; *Schrankia* 1041–1045; *Desmanthus* 1045–1049; *Acacia* 1049–1093.]

WILSON, P. W. Symbiotic nitrogen-fixation by the Leguminosae. Bot. Rev. **3:** 365–399. 1937.

KEY TO THE GENERA OF MIMOSOIDEAE IN THE SOUTHEASTERN UNITED STATES

General characters: *Woody or herbaceous plants with alternate, bipinnately compound leaves usually with one or more nectaries present on the petiole and/or rachis; inflorescences of spikes, heads, or racemes; flowers small, regular, usually 5-merous and perfect or some staminate or infrequently neutral; calyx and corolla small, valvate in aestivation; staminal filaments conspicuous and often showy, 5, 10, or numerous, free or connate; anthers minute; fruit usually a legume or loment, sometimes indehiscent; seeds usually small, with a hard coat and a U-shaped line (pleurogram) on each face.*

A. Stamens 5 or 10.
  B. Plant an unarmed tree; stamens 10.
    C. Inflorescences capitate, axillary; petals free; anthers without an apical gland; pollen shed as single grains; fruit flat, not coiling; seeds compressed, brown. .... 1. *Leucaena.*
    C. Inflorescences racemose, terminal; petals nearly free, united at base; anthers with a deciduous gland at apex; pollen shed in flattened 16-grained polyads; valves of fruit coiling upon dehiscence, persistent,

bearing the brilliant red lens-shaped seeds along the margin. . . . . [*Adenanthera*.]

B. Plant an armed or unarmed shrub, subshrub, or herb; corolla sympetalous (petals distinct or only basally connate in *Desmanthus*); pollen shed as single grains or in tetrads.

D. Flowers pink to white, never yellow; anthers with an apical gland (or this rarely lacking); fruit without a conspicuous stipe.

E. Legume prickly or spinescent; staminal filaments bright pink; pollen in tetrads.

F. Fruit flattened, oblong, the valves separating from the persistent margins and dividing into 1-seeded segments; seeds plano-compressed, ovoid, ovate to orbicular; stems and leaves variously prickly, peduncle of inflorescences unarmed. . . . . 2. *Mimosa*.

F. Fruit tetragonal, splitting into 4 segments; seeds tetragonal to rhomboid; stems, leaves, and peduncles armed with numerous recurved prickles. . . . . 3. *Schrankia*.

E. Legume unarmed, bivalved and splitting along the margin into two segments; staminal filaments light green to white; pollen grains single; plant unarmed. . . . . 4. *Desmanthus*.

D. Flowers, at least the perfect ones, bright yellow, neutral flowers when present with conspicuous yellow, pink, or purplish staminodia; anthers without an apical gland; fruit with or without a conspicuous stipe.

G. Plants perennial, herbaceous, generally prostrate, branchlets unarmed; inflorescences congested spikes; flowers yellow; fruit compressed, not twisting, distinctly stipitate, marginally dehiscent by two valves. . . . . 5. *Neptunia*.

G. Plant woody; branchlets armed; inflorescences elongated spikes; flowers usually yellow and pink; fruit compressed, twisting, lacking a conspicuous stipe, usually indehiscent. . . . [*Dichrostachys*.]

A. Stamens numerous (more than 10); pollen shed in 16-grained, flattened polyads.

H. Stamens usually 50 or more, free. . . . . 6. *Acacia*.

H. Stamens usually 12–50, united at the base or into a distinct tube that generally equals the corolla tube.

I. Fruit dehiscent, the valves separating from the persistent margin; stamens united only at the base; stipules large, becoming foliaceous, deciduous to subpersistent. . . . . 7. *Lysiloma*.

I. Fruit indehiscent or dehiscing along one or both margins, the margin never persistent and separating from the valves; stamens united into a distinct tube; stipules setaceous and caducous or spinescent and persistent.

J. Flowers of an inflorescence dimorphic, the central one or two flowers having an elongated tubular corolla and a long-exserted staminal tube; fruit thin, flattened, membranaceous to chartaceous; seeds without an aril; leaves with many leaflets; branches unarmed. . . . . 8. *Albizia*.

J. Flowers of an inflorescence all alike; fruit usually thick, leathery, coiling; seed arillate; leaves with few leaflets; branches armed or unarmed. . . . . 9. *Pithecellobium*.

Tribe MIMOSEAE Bronn

1. **Leucaena** Bentham, Jour. Bot. Hooker 4: 416. 1842.

Trees or shrubs of tropical to subtropical habitats; sapwood yellowish, heartwood reddish brown; wood strong, durable, straight-grained; branches unarmed, slender to stout. Leaves persistent, with numerous pairs of pinnae and small leaflets [or with few pinnae and larger leaflets borne in pairs], petiolate, a petiolar nectary often present below the lowest pair of pinnae; stipules minute and caducous or becoming spinescent and persistent. Inflorescences of many-flowered, globose heads, the peduncles axillary, often fascicled or in terminal racemes. Flowers usually perfect, 5-merous, sessile or short-pedicellate, white; subtending bracts small, peltate, usually villous at the apex. Calyx campanulate to tubular, with 5 small lobes. Petals 5, free, narrowly obovate, acute to rounded at apex, narrowing at base, pubescent to glabrous. Stamens 10, free, attached at base of ovary, exserted; filaments filiform; anthers introrse, oblong, pilose [to glabrous], eglandular [rarely glandular], versatile; pollen generally shed as 3-colporate grains [or rarely in 16–28-grained polyads]. Stigma terminal, minute, invaginated and concave; style filiform; ovary stipitate, ovules numerous, anatropous. Legume many-seeded, stipitate, broadly to narrowly plano-compressed, linear-oblong to oblong, dehiscent, the valves thickened on the margins, continuous within, often pubescent when young, glabrous at maturity, the outer pericarp thin and papery, dark-colored, the inner thicker, woody, pale brown. Seeds ovate to obovoid, compressed, transversely oriented, suspended on a long slender funiculus; seed coat thin, crustaceous, brown and lustrous, with a distinct pleurogram; embryo inclosed by a thin horny endosperm; radicle slightly exserted. Base chromosome number 13. (*Ryncholeucaena* Britton & Rose; *Caudoleucaena* Britton & Rose). LECTOTYPE SPECIES: *L. glauca* sensu Bentham[2] (*Mimosa glauca* sensu L., 1763, non 1753) = *L. leucocephala* (Lam.) De Wit; see Britton, N. Am. Trees 526. 1908; Wilbur, Taxon 14: 246. 1965. (Name from Greek *leukos*, white, in reference to the color of the flowers.) — LEADTREE.

A genus of approximately 40 species distributed mainly in Central America, northern South America, and the West Indies. The Polynesian *Leucaena Forsteri* Bentham is better placed in the genus *Schleinitzia*. Three species occur in the United States: two are restricted to Texas, and the third occurs in California, Texas, and, in our range in southern Florida.

A small spreading tree, *Leucaena leucocephala* (Lam.) De Wit[3] (*L.*

---

[2] Isely (1970) has revived Williams's argument (1964) for selecting *L. diversifolia* as the lectotype species and for rejecting *L. glauca*. Williams holds that "If *Leucaena* is typified by *Mimosa glauca* L. then it will become a generic synonym of *Mimosa*." This argument is untenable as is clearly stated by Art. 10, ICBN, 1972. It is the species that Bentham had (not the name of that species) that is the type of the name *Leucaena*. There is no question about the identity of the species; he merely had the wrong name for it.

[3] Drs. William T. Gillis and William T. Stearn have reached still another conclusion

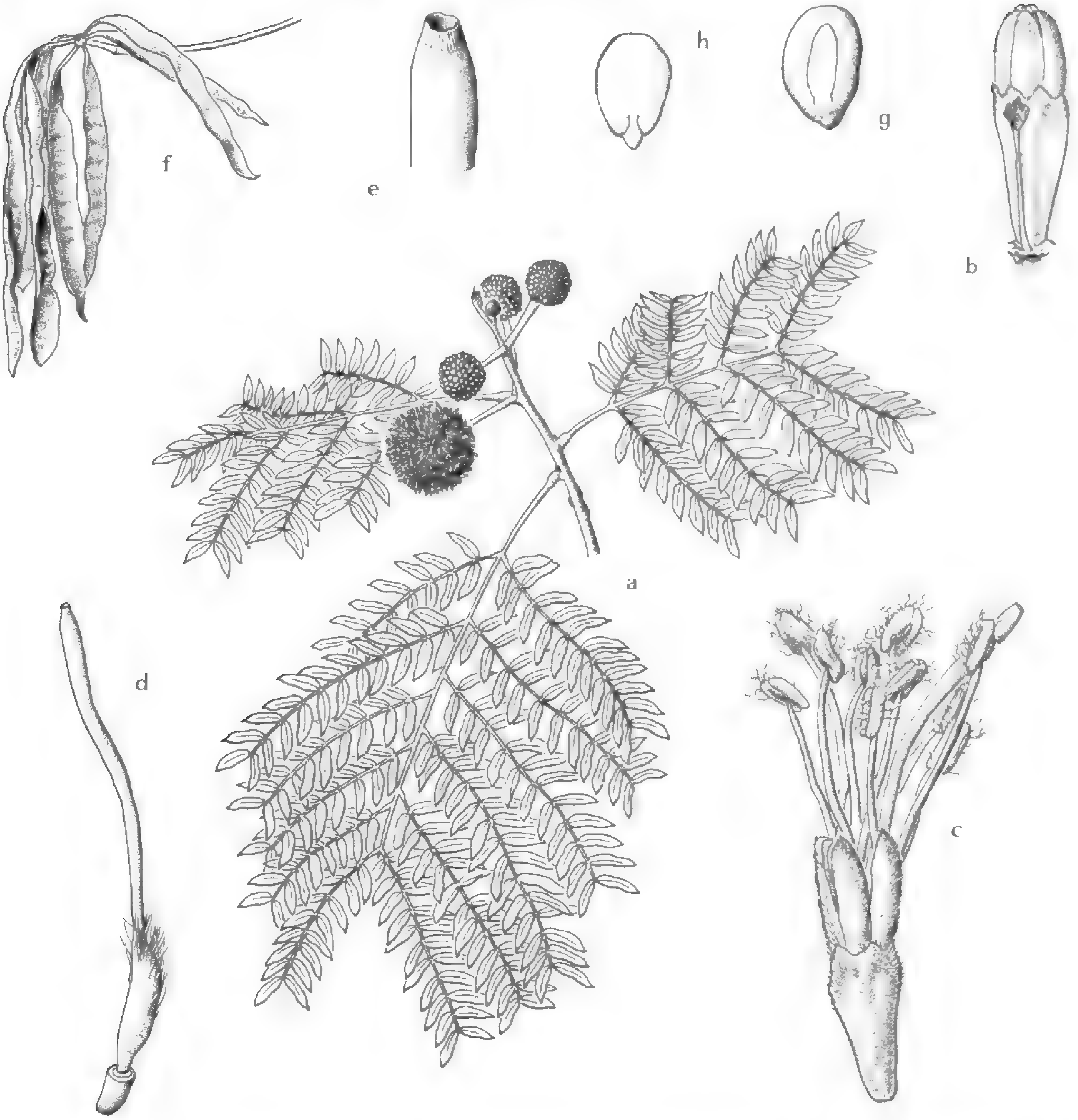


FIGURE 1. **Leucaena.** a–h, *L. leucocephala*: a, branchlet with inflorescences in bud and at anthesis, × 1/2; b, bud and subtending bract, × 6; c, perfect flower, showing pilose anthers, × 6; d, gynoecium, showing substipitate ovary, style, and minute stigma, × 6; e, stigma, showing concave, pore-like construction, × 24; f, infructescence, × 1/4; g, seed, showing pleurogram, × 2; h, embryo, showing slightly exserted radicle, × 2.

glauca (L.) Bentham sensu many authors), leadtree, $2n = 26, 104$, is indigenous from northern South America to southern Mexico, the West Indies (including the Bahamas), and possibly southern Florida. It has been introduced into southern Texas, California, Bermuda, and southward to Argentina and Chile. Widespread introduction and subsequent naturalization of *L. leucocephala* in the Old World tropics has also occurred. The unarmed plants of this species (trees or shrubs) are distinguishable from other mimosoid legumes of the southeastern United States by the leaves

---

about the correct name for this species and are basing a new combination on *Mimosa latisiliqua* L. Their arguments are presented in "Typification of the names of the species of *Leucaena* and *Lysiloma* in the Bahamas" (Taxon, in press).

with several pinna-pairs bearing numerous small leaflets; by the capitate inflorescences borne in a terminal raceme, the free petals, the 10 free stamens, and the eglandular pilose anthers; and by the legume with valves that separate along both margins but do not recurve.

The individual inflorescences comprising the flowering raceme develop acropetally. The flowers of a single inflorescence are largely synchronous in anthesis and are short lived, generally opening in the morning and remaining open until the following day when they show signs of wilting. The next higher inflorescence usually comes into flower as its predecessor fades. Since a raceme may bear 20–30 inflorescences, the time of flowering can be spread over two or three weeks. The ability of this species to invade cleared areas quickly and successfully is indicative of both its reproductive success and its competitiveness. In Puerto Rico flowering and fruiting have been reported throughout the year, with individual trees of *L. leucocephala* producing large numbers of fruit and viable seeds. In Central America mature plants of *L. leucocephala* are scattered, with relatively few seedlings, and they do not occur in dense stands (Janzen, 1970). Janzen reports that upwards of 90 per cent of the seed crop produced in Central America is lost to bruchid beetle predation. In Puerto Rico, however, bruchid attacks are less frequent, and most of the large number of seeds produced each year are viable, thus accounting for the dense stands. It is theorized that plant species invading islands may leave their predators and parasites behind. If this is so, *L. leucocephala* is a Central American species that has successfully invaded first the West Indies, and then Florida.

Two distinct types of pollen occur in *Leucaena* (Sorsa). In most species the grains are 3-colporate, subspheroidal, medium sized, with an exine 2–4 μm. thick, and are shed as single grains (monads). In a few species the pollen is in 16- to 28-grained polyads with the individual grains having 6–8 paraiso- or hetero-polar pores and being rounded pyramidal with a pointed proximal face and with the exine about 1.5–2 μm. thick. Guinet recognized a third type, which he considered to be intermediate, that is, being shed singly but having the characters of a grain found in a polyad. It seems likely that this type resulted from the acetolysis treatment, which separated the polyads into individual grains thus leading to misinterpretation.

The very high chromosome number $2n = 104$ that has been reported several times may be due to somatic polyploidy, a phenomenon known in several genera of this subfamily. The polyploidy is often present in young primary roots but disappears as the roots age.

Leucaena leucocephala is used as shade for coffee and cacao, and it is also used frequently as either a hedge or a living fence. The leaves are used as green fertilizer (Work) or, when dried, as forage for livestock in place of alfalfa. Gnatt concluded that *L. leucocephala* is superior to common grades of alfalfa meal, and the leaves were shown by Henke to be high in protein content. It has, however, been known for a long time that when moderate to large quantities of the leaves and legumes are eaten by horses, donkeys, mules, and hogs, the animals seem to be in generally poor condition and lose their hair. From a comparison of the symptoms Arnold attributed this effect to selenium accumulated by the plant from the soil and concentrated in the young leaves and seeds, but the poisonous principle has proved to be mimosine, an alpha-amino acid. Conflicting results with feeding experiments in various tropical areas suggest that there may be geographical genetic variation in the amount of mimosine produced by the plant. A recent account of *L. leucocephala* in cultivation is given by Oakes.

REFERENCES:

Under subfamily references see BERGER, WITKUS & MCMAHON; BOLKHOVSKIKH *et al.*, p. 304; BRENAN; COMPTON; F. C. GATES; GRAHAM; HUTCHINSON; ISELY, 1970; LITTLE, p. 224; LITTLE & WADSWORTH; RECORD & HESS, 1960; SARGENT, p. 109; TAUBERT; WEST & ARNOLD, p. 87; VINES, pp. 503–507.

ARNOLD, H. L. Poisonous plants of Hawaii. 71 pp. Tokyo. 1968. [*L. glauca*, 45, *pl. 17*.]

CARANGAL, A. R., & A. D. CATINDIG. The mimosine content of locally grown ipil-ipil (*Leucaena glauca*). Philip. Agr. **39**: 249–254. 1955.*

DNYANSAGAR, V. R. Degenerations in *Leucaena glauca* Benth. Curr. Sci. Bangalore **16**: 290. 1947.*

———. Embryological studies in the Leguminosae. I. A contribution to the embryology of *Leucaena glauca* Benth. Jour. Indian Bot. Sci. **28**: 95–107. 1949.

———. Embryological studies in the Leguminosae. X. Supplementary observation on the development of the endosperm and embryo in *Leucaena glauca* Benth. and *Mimosa hamata* Willd. *Ibid.* **33**: 433–442. 1954.

GATES, F. C. The daily movements of leguminous leaflets. Pl. World **19**: 42–45. 1916. [Includes *L. glauca*.]

GNATT, P. A. Utilization of *Leucaena glauca* as a feed in the Philippines. Proc. 8th Pacific Sci. Congr. 1953. **4B**: 601–603. 1958.* (See also Proc. 8th Pacific Sci. Congr. Abstr. Pap. 297, 298. 1953.)

GRAY, S. G. Hot water seed treatment for *Leucaena glauca* (L.) Benth. Austral. Jour. Exper. Agr. Anim. Husb. **2**: 178–180. 1962.*

GUINET, P. Les caractères du pollen dans le genre *Leucaena* (Mimosaceae). Pollen Spores **8**: 37–48. 1966.

HEGARTY, M. P. The isolation and identification of 5-hydroxypiperidine-2-carnoxylic acid in *Leucaena glauca* Benth. Austral. Jour. Chem. **10**: 484–488. 1957.*

HENKE, L. A. Value of *Leucaena glauca* as a feed for cattle. Proc. 8th Pacific Sci. Congr. 1953. **4B**: 591–600. 1958.* (See also Proc. 8th Pacific Sci. Congr. Abstr. Pap. 298, 299. 1953.)

JANZEN, D. Herbivores and the number of tree species in tropical forests. Amer. Nat. **104**: 501–528. 1970. [*L. glauca*, 522.]

KINGSBURY, J. M. Poisonous plants of the United States and Canada. xiii + 626 pp. Englewood Cliffs, New Jersey. 1964. [*L. leucocephala*, as *L. glauca*, 332, 333.]

MATSUMOTO, H., E. G. SMITH, & G. D. SHERMAN. The effect of elevated temperatures on the mimosine content and toxicity of koa haole (*Leucaena glauca*). Arch. Biochem. Biophys. **33**: 201. 1951.*

OAKES, A. J. *Leucaena leucocephala*, description — culture — utilization. Advanc. Front. Pl. Sci. **20:** 1–114. 1968. [Includes extensive bibliography.]

PELLEGRINI, O. Osservazioni sull'endosperma du *Leucaena glauca* Benth. (Mimosaceae). (In Italian.) Delpinoa II. **9:** 183–188. 1956.

SAMPATH, S., & K. RAMANATHAN. Chromosome numbers in Indian economic plants — III. Curr. Sci. Bangalore **18:** 408, 409. 1949. [Includes *L. glauca.*]

SAN BUENA VENTURA, P., & F. ASIDDAO. Preliminary tests on aerial seeding of ipil-ipil (*Leucaena glauca* (L.) Benth.) Philip. Jour. Forestry **13:** 119–133. 1959.*

TJIO, J. H. The somatic chromosomes of some tropical plants. Hereditas **34:** 135–146. 1948. [*L. glauca*, $2n = 104$.]

WILBUR, R. L. The lectotype of the mimosaceous genus *Leucaena* Benth. Taxon **14:** 246, 247. 1965. [*L. glauca* sensu Benth. = *L. leucocephala* (Lam.) De Wit.]

WILLIAMS, L. O. A lectotype for the genus *Leucaena* Benth. Taxon **13:** 300. 1964. [Chooses *L. diversifolia* (Schlecht.) Bentham.]

WIT, H. C. D. DE. Typification and correct names of *Acacia villosa* Willd. and *Leucaena glauca* (L.) Benth. Taxon **10:** 50–54. 1961.

WORK, S. H. *Leucaena glauca* in the Americas. Proc. 8th Pacific Sci. Congr. 1953. **4B:** 587–590. 1958.* (See also Proc. 8th Pacific Sci. Congr. Abstr. Pap. **289.** 1953.)

YLAGAN, M. M., & S. S. SANCHEZ. Carotene and nitrogen content of ipil-ipil (*Leucaena glauca*) leaves. Philip. Agr. **41:** 238, 239. 1957.

2. **Mimosa** L. Sp. Pl. 1: 516. 1753; Gen. Pl. ed. 5. 233. 1754.

Perennial or rarely annual herbs, shrubs [or rarely trees, sometimes climbing or prostrate], mostly armed with prickles. Leaves bipinnate (in some species with very short rachides, the pinnae appearing digitate) [rarely absent or reduced to phyllodes], often sensitive, petiolar nectaries absent [or rarely present], secondary rachides mostly 2-stipellate, the pinnae with few to numerous leaflets; stipules usually small and subulate, never spinescent. Inflorescences of spikes, racemes or ovoid globose heads, pedunculate, the peduncles solitary or more often fascicled, axillary, ebracteate. Flowers small, sessile, generally perfect, andromonoecious [or sterile in some species with the staminodia becoming subpetaloid at the apex]; perianth (3–)4–5(–6)-merous. Calyx usually minute, gamosepalous, sometimes paleaceous, with small lobes, ciliate [or irregularly laciniate]. Corolla sympetalous, tubular, the lobes often short, pubescent. Stamens the same number as or twice as many as the petals, free, exserted; anthers minute, dorsifixed, introrse, eglandular; pollen shed in tetrads [octads, or in a few species 12-grained polyads.] Stigma in a minute terminal pore; style filiform, usually exceeding the stamens; ovary generally short and sessile, ovules 2 to many. Fruit oblong to linear, usually plano-compressed, straight or curved, sometimes contorted, membranaceous to coriaceous, indehiscent or dehiscent, valves two, separating from the persistent margins, divided transversely into 1-seeded segments (or rarely entire), continuous or subseptate within, often pubescent and armed with prickles. Seeds ovoid, ovate to orbicular, plano-compressed, seed coat hard, lustrous, with a distinct pleurogram, generally transverse, endosperm present; embryo straight, the cotyledons flat. Base chromosome number probably 13. (*Lomoplis* Raf., *Sensitiva* Raf., *Pteromimosa* Britton, *Neomimosa* Britton & Rose, *Mimosopsis* Britton & Rose, *Acanthopteron* Britton, *Haitimimosa* Britton). LECTOTYPE SPECIES: *M. sensitiva* L.; see Britton & Millspaugh, Bahama Flora 161. 1920. (Name from Latin, *mimus*, a mimic, from the sensitive leaves that imitate the movement of an animal [cf. Tournefort, Inst. Rei Herb. 1: 606. 1700, "Mimosa a mimo, cujus motus imitari videtur] or, according to Greene, derived from Spanish *yerba mimosa*, sensitive plant, the name given it by C. Acosta, the first European to write about it [1578].)

A genus of some 400 to 450 species, mainly of South America, but of pantropical distribution and with a few species in mild-temperate regions of the world. The genus has two principal areas of diversification, the main one extending from the grasslands of southern Brazil southward, and the second from the drier grasslands or scrub vegetation in Mexico north into the southwestern United States. A few species of *Mimosa* occur throughout northern South America and Central America. Fifty-six species of *Mimosa* were recorded from Argentina by Burkart (1948) as compared to ten species of *Mimosa* in Texas (Correll & Johnston, 1970). On the basis of number of stamens per flower, *Mimosa* can be divided into two sections, one, or perhaps both, represented in our range by one species.

Section HABBASIA DC. (sect. *Bataucaulo* DC., sect. *Ameria* Bentham), distributed in both hemispheres, is distinguished by flowers with twice as many stamens as petals. Most species of this section shed their pollen grains in 8- or 16-grained polyads, although in some (e.g., *M. strigillosa*) the pollen is in tetrads. Section HABBASIA is represented in the southeastern United States by *M. strigillosa* Torrey & Gray, a native perennial herb that occurs from Florida and Georgia to southern Arkansas, Oklahoma, eastern and southeastern Texas, and Tamaulipas. It is disjunct in Argentina. It is found in meadows, woodlands, hammocks, pinelands and clearings, generally on sandy soils. In addition to the sectional characters, *M. strigillosa* can be recognized by the leaves with 4–8 pairs of pinnae, the peduncles as long as or longer than the leaves, the fruits uniformly spinescent-bristly and not strongly constricted between the seeds.

Section MIMOSA (sect. *Eumimosa* DC.), characterized by flowers with the same number of stamens as petals (generally 4) and restricted to the New World, includes approximately half of the known species of *Mimosa*. Although incompletely sampled, species of this section appear to shed their pollen in tetrads. Section MIMOSA includes the common neotropical *M. pudica* L., sensitive plant, $2n = 52$, which has been introduced as a greenhouse plant in the United States and is possibly incipiently naturalized in the southernmost part of our range. Small reported *M. pudica* as occurring on the Coastal Plain from Florida to Texas, but the lack of verified herbarium specimens fails to support his assertion (see also Ward). *Mimosa pudica* is native to South and Central America and the West Indies, and it has apparently been introduced in many parts of the tropics, presumably for the novelty of the sensitive leaves.

In tropical America, the pink-flowered *Mimosa pudica* can be found in such disturbed situations as roadsides and abandoned fields. It is easily distinguished from *M. strigillosa* by its annual habit and by leaves with one to two pairs of subdigitately arranged pinnae, peduncles shorter than the leaves, stamens as many as the corolla lobes, and fruits strongly constricted between the seeds and with spinescent bristles on the margin.

The leaves of *Mimosa pudica*, as well as most, if not all, other legumes, are nyctinastic, the leaflets folding together at night and the entire leaf dropping from a near horizontal to a more vertical position. The leaves are also sensitive to touch and various other stimuli, the same sort of movement often occurring quite rapidly. In both nyctinastic and thigmonastic responses movement is brought about by differential changes in the volume (turgidity) of motor cells in the pulvinus and the pulvinules. Differences in turgidity between the cells of the upper (adaxial) half of the pulvinus and those of the lower (abaxial) half create tensions in the tissues that, in turn, cause movement. As with *Albizia* (*q.v.*), which is not sensitive to touch, light-dark transition, endogenous circadian rhythms, and phytochrome seem to be involved in the nyctinastic movements. Fondeville *et al.* showed that leaflet-closure is controlled by phytochrome and is evident as few as five minutes after irradiation with red or far-red light. It has been proposed that phytochrome controls membrane properties, and it has been shown that the photoreceptor is in the pulvinus and the pulvinules. Fondeville *et al.* found that the action spectrum for the opening response was most effective in the 710 and 480 nm. ranges, which is similar to the action spectrum for high-energy response affecting morphogenesis in many plants. It appears that a second, as yet unknown pigment (or pigments) is involved.

The rapid response to touch is incompletely understood, but membrane permeability undoubtedly is involved, and, as in nyctinastic responses in *Albizia*, leaflet movement is associated with potassium flux into and out of the motor cells (see Satter & Galston). Calcium flux has been reported during thigmonastic movement in *Mimosa pudica* (Toriyama & Jaffe). The motor cells have many small vacuoles that disappear as cell volume decreases and reappear as turgidity is regained. Some of the vacuoles contain tannin deposits that are reported to have a regulatory function in both thigmonastic (Toriyama & Jaffe) and phytochrome-controlled (Setty & Jaffe) leaflet movements. The actual triggering mechanism of thigmonastic responses has not been accurately determined, but the rapidity of the response indicates that the system depends upon membrane permeability, rather than on enzyme action or gene activation, both of which would elicit slower reactions.

The palynological studies of Sorsa and of Guinet have firmly established the occurrence of three main pollen types in *Mimosa*. In the first, the tetrads of grains range in size from 6.3 μm. to 27μm. on the long axis of the tetrad. In the second common type, the pollen is shed in octads ranging in size from 11.5 μm. to 30 μm. on the long axis of the polyad. The third type, 12-grained polyads, is known in only a few species (perhaps confined to sect. HABBASIA); the polyad varies from 13.8 μm. to 20 μm. on the long axis. The individual grains of the tetrads, octads, and polyads are 3- to 6-porate or the apertures are indistinct. It is notable that *Mimosa* species have the smallest tetrads known in the Leguminosae.

Very little is known about the floral biology and breeding systems of species of *Mimosa*. Although outbreeding is suspected because the pollen is in polyads, self pollination apparently occurs in several species. Circumstantial evidence for self pollination is the lack of floral nectaries in species investigated by Ancibor (1969). Unlike certain species of *Albizia*, *Calliandra*, and *Neptunia*, most or all of the flowers of an inflorescence are generally perfect and capable of producing fruit.

The genus is poorly known cytologically. Chromosome numbers have been reported for only about two per cent of the species. According to Bolkhovskikh *et al.* (1969), six species have $2n = 26$, three species $2n = 52$, one species $2n = 28$, and one $2n = 40$.

Although of limited importance, species of *Mimosa*, when abundant, provide food for wildlife. The leaves are good forage, but the spines deter larger mammals from grazing. The pods and seeds are used by small mammals and by birds, especially quail. The bark is used locally in some regions of Mexico in tanning skins. Because of the short, often branched growth habit of the plants, the wood is not used to any extent in construction or for implements, but is an excellent fuel. The delicate appearance of the bipinnately compound leaves, together with the fragrant flowers makes some species desirable as ornamentals in warm, semiarid regions.

REFERENCES:

Under subfamily references see: BELL; BERGER, WITKUS & MCMAHON; BOLKHOVSKIKH *et al.*, p. 310; BRENAN; COMPTON, p. 6; GRAHAM; GUIGNARD; GUINET; RECORD & HESS, pp. 293, 294; SORSA; VINES, pp. 507–514; and WARD.

AIMI, R. Studies on the mechanism of seismonastic leaf movement in *Mimosa pudica* L. 1. Existence of irritability in the upper half of the main pulvinus. Bot. Mag. Tokyo **73**: 412–416. 1960.

ASANA, J. J. A preliminary report on the cytoplasmic inclusions in the pulvini of *Mimosa*, *Neptunia* and bean plants. Proc. Indian Sci. Congr. **17**: 291. 1930.

ASPREY, G. F., & J. H. PALMER. A new interpretation of the mechanics of pulvinar movement. Nature **175**: 1122. 1955. [Experiments with *Mimosa pudica* and *Samanea Saman*.]

BHATTACHARYYA, B. K., & J. DUTTA. Sitosterols from *Mimosa pudica* L. Proc. Indian Sci. Congr. **42**(3): 141. 1955.

BOUHARMONT, J. Mitose et polysomatie chez *Mimosa invisa* Mart. Cellule **61**: 5–17. 1960.

BRENAN, J. P. M. Notes on the Mimosoideae: I. Kew Bull. **10**: 161–192. 1955. [Typification of *M. pudica*, 184; restricts var. *pudica* to the lectotype specimen and recognizes var. *hispida* Brenan, var. *tetrandra* (Humb. & Bonpl. ex Willd.) DC., and var. *unijuga* (Duchass. & Walp.) Griseb.]

Brown, W. H. The mechanism of curvature in the pulvini of *Mimosa pudica.* Philip. Jour. Sci. **7:** 37–40. 1912.

Burge, W. E., & G. C. Wickwire. The effect of the performance of physical work on *Mimosa.* Science **82:** 304, 305. 1935.

Burkart, A. Las especies de *Mimosa* de la flora Argentina. Darwiniana **8:** 9–231. *pls. 1–26.* 1948.

———. Sinopsis de las especies de *Mimosa* de la serie *Lepidotae. Ibid.* **13:** 343–427. 1964.

Burkholder, P. R., & R. Pratt. Leaf-movements of *Mimosa pudica* in relation to light. Am. Jour. Bot. **23:** 46–52. 1936.

Buvat, R. Sur les chondriosomes des organes moteurs des feuilles de *Mimosa pudica* L. Compt. Rend. Acad. Sci. Paris **223:** 1017–1019. 1946.

Datta, M., & A. Chatterjee. Diurnal and nocturnal changes undergone by chloroplasts in motor cells of *Mimosa pudica* Linn. Sci. Cult. **24:** 426–428. 1959.*

Dnyansagar, V. R. Embryological studies in the Leguminosae. X. Supplementary observations on the development of the endosperm and embryo in *Leucaena glauca* Benth. and *Mimosa hamata* Willd. Jour. Indian Bot. Soc. **33:** 433–442. 1954.

Dutt, A. K. Vacuoles and movement in the pulvinus of *Mimosa pudica.* Vacuoles of the pulvinus and the mechanism of movement. Nature **179:** 254. 1957.

Dutt, S. M. The structural basis of sensitivity in *Mimosa pudica* Linn. (Abstr.) Proc. Indian Sci. Congr. **36**(3): 144. 1949.

Fondeville, J. C., M. J. Schneider, H. A. Borthwick & S. B. Hendricks. Photocontrol of *Mimosa pudica* L. leaf movement. Planta **75:** 228–238. 1967. [See also *ibid.* **69:** 357–364. 1966.]

Gernand, K., & H. Ehrig. Untersuchungen über die elektrische Reizbarkeit von *Mimosa pudica.* I. Mitteilung: Die Reizzeit-Spannungskurve. Biol. Zentralbl. **76:** 181–185. 1957. II. Die Summation unterschwelliger Reize. *Ibid.* 429–436.

Greene, E. L. Derivation of *Mimosa.* Pl. World **4:** 95, 96. 1901.

Henbest, O. J. A preliminary report on the legumes of the Arkansas uplands. Proc. Arkansas Acad. Sci. **1:** 21–23. 1941. [Includes *M. strigillosa*; see also D. M. Moore, *ibid.* **4:** 62. 1951.]

Hulyalkar, R. K., T. R. Ingle, & B. V. Bhide. Studies in carbohydrates. VI. Composition of the mucilage from seeds of *Mimosa pudica.* Jour. Indian Chem. Soc. **33:** 864–866. 1956.

Isely, D. Legumes of the United States. IV. *Mimosa.* Am. Midl. Nat. **85:** 410–424. 1971. [15 taxa including 13 species.]

Lima-de-Faria, A. The effect of gama radiation upon *Mimosa pudica* L. Portug. Acta Biol. A. **1:** 95–109. 1945.

Mulay, B. N., & B. S. Dhami. Microsporangium, microsporogenesis and male gametophyte of *Mimosa rubicaulis* Lamb. (Abstr.) Proc. Indian Sci. Congr. **42**(3): 227. 1955. [See also *ibid.* 241.]

Narasimhachar, S. G. An embryological study of *Mimosa pudica* Linn. Proc. Indian Acad. Sci. B. **33:** 192–198. 1951.

Robinson, B. L. Contributions from the Gray Herbarium of Harvard University XIII. I. Revision of the North American and Mexican species of Mimosa. Proc. Am. Acad. Arts Sci. **33:** 305–331. 1898.

Rudd, V. E. *Mimosa albida* and its varieties. Phytologia **16:** 435–441. 1968.

———. *Mimosa bahamensis*, A. Bahama-Yucatán disjunct. *Ibid.* **18:** 143–146. 1969. [*M. hemiendyta* Rose & Robinson, of Yucatán *M. bahamensis* Bentham, of the Bahamas.]

Satter, R. L., & A. W. Galston. Leaf movements: Rosetta stone of plant behavior? BioScience **23:** 407–416. 1973. [Review of research to date, especially on *Albizia* and *Mimosa*; numerous references.]

Setty, S. L., & M. J. Jaffe. Phytochrome controlled contraction and recovery of contractile vacuoles in the motor cells of *Mimosa pudica* L. as an intracellular correlate of nyctinasty. Planta **108:** 121–132. 1972.

Sibaoka, T. Action potential and conduction of excitation in the leaf of *Mimosa pudica.* Sci. Rep. Tôhoku Univ. Biol. **18:** 362–369. 1950.

———. Nature of conduction of excitation in the petiole of *Mimosa pudica. Ibid.* 370–376.

———. On a factor affecting the velocity of excitatory conduction in the petiole of *Mimosa pudica. Ibid.* 521–526.

———. Some aspects on the slow conduction of stimuli in the leaf of *Mimosa pudica. Ibid.* **20:** 72–88. 1953.

———. Excitable cells in *Mimosa.* Science **137:** 226. 1962.

Singh, T. C. N., & S. Ponniah. On the effect of musical sound of violin on the growth of *Mimosa pudica* L. (Abstr.) Am. Jour. Bot. **41:** 161. 1954.

Small, J. K. The Mimosaceae of the southeastern United States. Bull. N. Y. Bot. Gard. **2:** 89–101. 1901.

Toriyama, H. Observational and experimental studies of sensitive plants. I. The structure of parenchymatous cells of pulvinus. Cytologia **18:** 283–292. 1953; II. On the changes in motor cells of diurnal and nocturnal condition. *Ibid.* **19:** 29–40. 1954; III. On the epidermal system of the pulvinus and leaflet. *Ibid.* 286–298. 1954; IV. Some findings on the structure of the epidermal system and the cortex of the petiole. *Ibid.* **20:** 237–246. 1955; V. The development of the tannin vacuole in the motor cell of the pulvinus. Bot. Mag. Tokyo. **68:** 203–208. 1955; VI. The migration of potassium in the primary pulvinus. Cytologia **20:** 367–377. 1955; VII. Vital staining of the threadlike apparatus. *Ibid.* **22:** 60–68. 1957; X. On the fixation of threadlike apparatus in cortex of petiole. Bot. Mag. Tokyo **71:** 309–317. 1958; XI. On the threadlike apparatus and the chloroplasts in the parenchymatous cells of the petiole of *Mimosa pudica.* Cytologia **25:** 267–279. 1960; XIV. On the changes in a new cellular element of *Mimosa pudica* in diurnal and nocturnal conditions. *Ibid.* **27:** 276–284. 1962.

———. Preliminary note on the migration of a colloidal substance in the motor tissue of *Mimosa pudica.* Bot. Mag. Tokyo **70:** 16–18. 1957.

———. Changes in the lacunal parenchyma of *Mimosa pudica* in diurnal and nocturnal conditions. Nature **184:** 737, 738. 1959.

———. Behaviour of a thread-like apparatus in the petiole of *Mimosa pudica. Ibid.* **187:** 709, 710. 1960.

——— & M. J. Jaffe. Migration of calcium and its role in the regulation of seismonasty in the motor cell of *Mimosa pudica* L. Pl. Physiol. **49:** 72–81. 1972.

Weintraub, M. Leaf movements in *Mimosa pudica* L. New Phytol. **50:** 357–382. 1952.

WITKUS, E. R., & C. A. BERGER. Polyploid mitosis in the normal development of *Mimosa pudica.* Bull. Torrey Bot. Club **74**: 279–282. 1947.

3. **Schrankia** Willdenow, Linn. Sp. Pl. ed. 4. **4**: 1041. 1806, nom. cons.

Perennial herbs or undershrubs, often prostrate or decumbent, subscandent, or weakly ascending; branches terete to conspicuously angulate, often sulcate, armed with numerous short, recurved, internodal prickles. Leaves usually deciduous, with 1–8 pairs of pinnae, the pinnae when numerous with small leaflets and when few with larger leaflets, the rachis angulate, prickly eglandular, glabrous; leaflets generally small, subsessile to sessile, asymmetrical; stipules subulate, usually setaceous. Inflorescences pedunculate congested spikes or globose heads, axillary, solitary or rarely in pairs. Flowers perfect or polygamous, sessile, pale to bright pink, (4–)5(–6)-parted. Calyx minute, campanulate, with scarcely visible lobes. Corolla tubular to funnel-shaped, connate to about the middle, the lobes narrowly ovate, acute at the apex. Stamens (8–)10(–13), free, long exserted; filaments filiform; anthers minute, eglandular, subdorsifixed; pollen in tetrads. Stigma terminal, minute, invaginated and concave; style filiform; ovary sessile to subsessile, ovules about 16. Fruit linear to narrowly oblong, short to elongate, usually tetragonal, rarely subcompressed, acute to long-acuminate at apex, usually conspicuously prickly (prickles sometimes lacking), nonseptate, dehiscent, both margins splitting away from the sides, producing the effect of four valves. Seeds oriented longitudinally, oblong, subtetragonal to rhomboid, the hilum subapical, the funiculus short; seed coat thick, dark, the pleurogram large, U-shaped; endosperm present; embryo straight. Base chromosome number probably 13. (*Leptoglottis* DC., *Morongia* Britton; not *Schranckia* J. F. Gmelin, 1791, Celastraceae, nom. rejic.) LECTOTYPE SPECIES: *S. aculeata* Willd., nom. illeg. = *Mimosa quadrivalvis* L., *Schrankia quadrivalvis* (L.) Merrill; see ICBN 314. 1972; Isely, Sida **4**: 234. 1971. (Name commemorating Franz von Paula von Schrank, 1747–1835, German botanist and professor of botany at Munich.) — SENSITIVE BRIAR.

A small American genus of perhaps 16–18 species occurring mainly in the southern United States and Mexico, but distributed southward to Argentina. Beard (1963) concluded that all the described species are really a single one that is, in turn, a *Mimosa* (*M. quadrivalvis* L.). Isely (1971) did not accept these arguments and returned to the more traditional concepts within this genus, although he pointed out that problems of specific delimitation still exist.

Turner (1959) treated six species of *Schrankia* in his work on the legumes of Texas, and Isely's account of the genus in the United States closely followed Turner's, although he considered *S. Nuttallii* to be distinct from *S. uncinata.* Four of the seven species recognized by Isely occur in the southeastern United States; *S. Roemeriana* (Scheele) Blankinship and *S. latidens* (Small) Schum. are restricted to Texas and *S. occidentalis* (Wooton & Standley) Standley to Texas and adjoining New

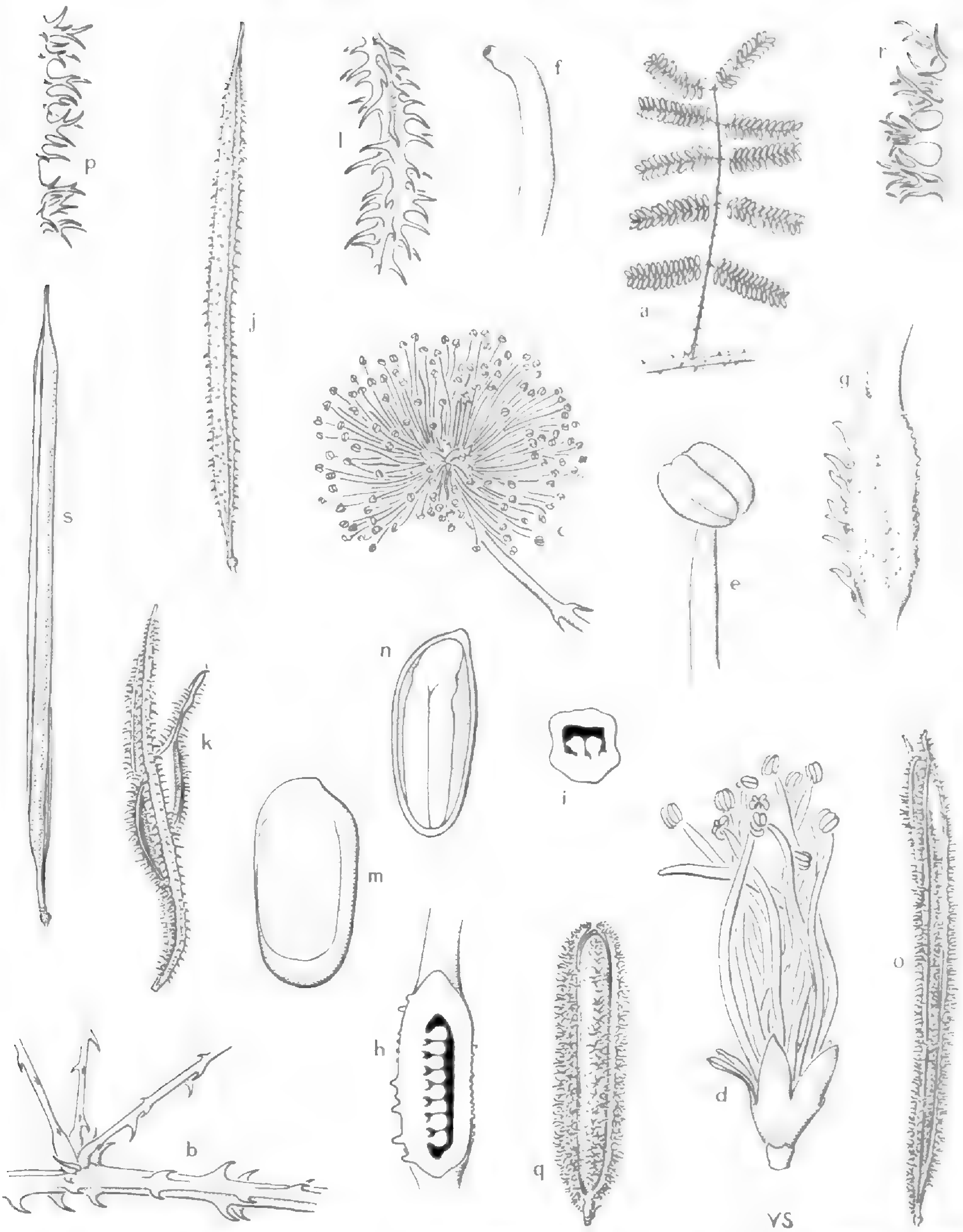


FIGURE 2. **Schrankia.** a–n, *S. microphylla*: a, leaf, × 1/2; b, nodal area, showing petiole (right oblique), two nearly upright peduncles, and the paired stipules, × 2; c, inflorescence at anthesis, × 2; d, perfect flower, × 6; e, anther and upper part of filament, × 20; f, upper part of style terminated by the porelike stigma, × 20; g, ovary, showing the beginning of development of prickles, × 20; h, ovary, in semidiagrammatic longitudinal section, showing ovules, × 25; i, ovary, in semidiagrammatic cross section, showing ovules in two ranks, × 25; j, mature fruit, × 3/4; k, mature fruit after dehiscence, × 3/4; l, prickles from part of one valve of fruit, × 3; m, seed showing pleurogram, × 6; n, seed, semidiagrammatic longitudinal section, showing cotyledons, radicle and endosperm (stippled), × 6. o, p, *S. Nuttallii*: o, mature fruit at dehiscence, × 3/4; p, prickles on mature fruit, side view, × 3. q, r, *S. hystricina*: q, mature fruit, × 1, r, prickles on mature fruit, side view, × 3. s, *S. uncinata*: mature fruit, extreme form (lacking prickles), × 3/4.

Mexico. The species are often poorly defined, with intergrading forms, and identifications should be made with caution. The present treatment closely follows Turner and Isely.

Restricted to southeastern Texas and southern Louisiana, *Schrankia hystricina* (Small ex Britton & Rose) Standley (*Leptoglottis hystricina* Small ex Britton & Rose), $2n = 26$, is distinguished by leaflets with conspicuously raised reticulate veins on the lower surface, bracts generally longer than the flower buds, a long peduncle, and a short, oblong fruit that is very prickly and rounded at the apex. It occurs in pine or oak woods and in disturbed areas, usually in sandy soils. Flowering is mostly from March through June.

The most widespread species, *Schrankia Nuttallii* (Britton & Rose) Standley (*Leptoglottis Nuttallii* DC. ex Britton & Rose; *S. uncinata* sensu many authors, not Willd.), $2n = 26$, is characterized by leaflets that are strongly reticulate beneath, bracts shorter than the flower buds, peduncles usually shorter than in *S. hystricina,* and an oblong-linear fruit that is densely prickly and tapers at the apex. Isely restricts the range of *S. Nuttallii* to an area from South Dakota to Texas and Louisiana, but Fernald (Gray's Man. Bot. ed. 8) included Alabama and North Carolina. Wilbur (1963) maintains that the Carolinian specimens are *S. microphylla,* an acceptable decision. Although Isely maintains this species as distinct from *S. uncinata* Willd., others (e.g., Turner and Gleason & Cronquist) have reduced *S. Nuttallii* to its synonymy.

Closely related to the two preceding species, *Schrankia uncinata* Willd. (*S. floridana* Chapman) is restricted to an area from southernmost Georgia to central peninsular Florida. It is separated by Isely from the other two species by its leaflets, which are hardly or not at all cuspidate. The fruits are linear-oblong and are very similar to those of *S. Nuttallii,* although they appear to be less prickly. *Schrankia uncinata* also has conspicuously veined leaflets. This species is found in disturbed habitats, pine or scrub woods, especially in sandy soils. It is a poorly known plant, and, until more is known about its biology, its taxonomic status will remain uncertain.

The fourth species in our range, *Schrankia microphylla* (Solander ex Sm.) Macbride[4] (*Mimosa microphylla* Solander ex Sm.; *S. angustata* Torrey & Gray; *Morongia angustata* (Torrey & Gray) Britton; *M. microphylla* (Solander ex Sm.) Britton ex Britton & Brown; *Leptoglottis microphylla* (Solander ex Sm.) Britton & Rose; *L. angustisiliqua* Britton & Rose; *S. angustisiliqua* (Britton & Rose) Hermann), $2n = 16$, lacks the conspicuous leaflet venation and usually has 6–8 pairs of pinnae per leaf. This species has an oblong-linear fruit that is usually very prickly and tapering at the apex. It occurs mainly on the Coastal Plain from southern Virginia to Florida, west to eastern Louisiana and eastern Texas.

Isely concluded that *Schrankia microphylla* includes two variants, al-

---

[4] Isely (1971) cited this name as *S. microphylla* (Dryander) Macbride, but Britten's arguments (Jour. Bot. **48**: 89, 90. 1920) for citing it as above appear to be correct.

though he did not give them a taxonomic rank. One, consisting of populations throughout the entire range, has shorter fruits that are very prickly and with little or no beak. The second, found only in Florida, is characterized by having four or five pairs of pinnae, smaller leaflets and flower heads, and a linear fruit that is slightly or moderately prickly. The two variant phenotypes intergrade with each other and with the more characteristic ones to form a variable species, the intra- and interspecific limits of which are questionable.

Schrankia is closely related to and probably derived from *Mimosa*. The distinguishing characters are found in the shape of the fruits, and their dehiscence, the shape of the seeds, and the abundance of prickles over most of the plant. The monotypic *Schrankiastrum* Hassler, of Paraguay, is closely allied to both genera and possibly has evolved from some of the highly variable and diverse species of *Mimosa*.

Palynologically *Schrankia* is very similar to *Mimosa*. In both genera the pollen is shed in rhomboidal tetrads. In *Schrankia* the tetrads are approximately 30 μm. in diameter, while in *Mimosa* they range from about 6 to 27 μm. The larger-sized tetrads of *Schrankia* suggest that it is slightly more specialized than *Mimosa*. The individual pollen grains in *Schrankia* are 4–6-porate. The tetrads of the South American *Schrankiastrum insigne* Hassler are approximately 25 μm. in diameter and are almost identical to those found in *Schrankia* and *Mimosa*.

The base chromosome number of *Schrankia* cannot be accurately determined at this time because of the differences in reported numbers. Three species were reported by Turner & Fearing (1960) to have $2n = 26$, while *S. latidens* (Small) Schum. had $2n = 22$. Turner & Beaman (1953) reported $2n = 24$ for *S. occidentalis*. It is not known whether these two instances represent descending aneuploidy. Only *S. leptocarpa* DC., of South America, has been reported to be tetraploid, $2n = 52$. An early report of $2n = 16$ for *S. angustata* (= *S. microphylla*) should be verified. This highly variable assemblage of poorly separated species might be understood better through a thorough cytotaxonomic study.

Data concerning the floral biology and breeding systems are very scanty. Insect pollination is suspected, but self pollination may also occur. Apparently all of the species are sensitive to touch.

Like many of the other genera, *Schrankia* is of no economic importance. The seeds are eaten by small wildlife, especially quail. The leaves are occasionally eaten, but the numerous prickles appear to be an effective deterrent.

REFERENCES:

Under subfamily references see ATCHISON, 1950; BERGER, WITKUS & MCMAHON; GRAHAM; GUIGNARD; GUINET; HUTCHINSON; ISELY, 1957; MAHLER, p. 70; RICKETT; SORSA; TURNER, pp. 43–47.

BEARD, L. S. A taxonomic study of *Mimosa quadrivalvis* L. (*Schrankia* Willd. nom. cons.). Unpublished thesis, Univ. North Carolina. 1963.*

BELL, E. A., & P. B. NUNN. Occurrence of diaminopropionic acid and derivatives in the genus *Schrankia*. Phytochemistry **9**: 924. 1970.

BIBB, L. B. Summation of dissimilar stimuli applied to leaflets of sensitive brier (*Schrankia*). Jour. Gen. Physiol. **3**: 523–526. 1921.*

BRITTEN, J. *Schrankia microphylla*. Jour. Bot. **58**: 89, 90. 1920.

BRITTON, N. L., & J. N. ROSE. *Leptoglottis*. N. Am. Fl. **23**: 138–144. 1928. [*Schrankia*.]

FRAHM-LELIVELD, J. A. Observations cytologiques sur quelques Légumineuses tropicales et subtropicales. Revue Cytol. Biol. Vég. **18**: 273–287. 1957.* [Includes *Schrankia leptocarpa*, $2n = 52$.]

HERMANN, F. J. Notes on North American Leguminosae. Jour. Wash. Acad. Sci. **38**: 236–238. 1948. [Includes *Schrankia angustisiliqua* and *S. Chapmanii* as comb. nov.]

ISELY, D. Legumes of the United States: III. *Schrankia*. Sida **4**: 232–245. 1971. [Recognizes 7 species.]

4. **Desmanthus** Willdenow, Linn. Sp. Pl. ed. 4. **4**: 1044. 1806, nom. cons.

Perennial herbs [subshrubs to small trees] of generally dry and often disturbed habitats; branches prostrate to erect, often angulate and striate, glabrous to pubescent, becoming woody, especially at the base, with a large tap root. Leaves with 1 to 15 pairs of pinnae, a nectary usually present between the insertion of the lowest pair of pinnae [rarely with one or more sessile nectaries between the insertion of the upper pairs of pinnae], the rachis angled, glabrous to pubescent, with a setaceous tip; rachis of pinnae narrowly winged, apiculate, the leaflets [4–8] 10–30 pairs per pinna, narrowly linear to oblong, obtuse to acute at the apex, mucronulate, asymmetrical, often ciliolate, glabrous to pubescent, lacking stipels; stipules usually persistent, filiform, setaceous [rarely auriculate]. Inflorescences congested, ovoid to ellipsoid pedunculate spikes, the peduncles solitary and axillary, bracteate. Flowers 5-merous, largely perfect, but the lower flowers of the spike staminate or neutral, or apetalous and with staminodia. Calyx campanulate, with short acute lobes, light green to white. Corolla valvate in aestivation, the petals distinct or connate only at the base, white. Stamens 10 or 5, free, usually exserted; filaments inserted near base of ovary, filiform; anthers bilocular, subdorsifixed, eglandular; pollen shed as 3-colporate or 3-colporoidate single grains. Stigma concave, terminal; style filiform, exceeding the stamens; ovary sessile to subsessile, the ovules numerous. Fruit plano-compressed to subterete, generally linear to oblong, straight to falcate, bivalved, marginally dehiscent, continuous within or subseptate between the seeds. Seeds oriented obliquely to lengthwise in the fruit, ovate to ellipsoid, slightly compressed; embryo inclosed by a horny endosperm; radicle slightly exserted. Base chromosome number 14. (*Acuan* Medicus, 1786, nom. rejic.; *Darlingtonia* DC.; *Acuania* Kuntze). LECTOTYPE SPECIES: *D. virgatus* (L.) Willd. (*Mimosa virgata* L.); Britton & Brown, ed. 2. **2**: 331. 1913; ICBN 314. 1972. (Name from Greek *desme*, a bundle, and *anthos*, flower.)

A small genus of approximately 30 species occurring primarily in tropical and subtropical regions of the New World, a few species largely temperate in distribution. Some 16 species occur in Mexico (Turner, 1950), while nine are reported from Texas (Correll & Johnston). Isely recognized nine species in the United States, three of them in our area.

The herbaceous or suffrutescent *Desmanthus illinoensis* (Michx.) Macmillan ex Robinson & Fern. (*D. brachylobus* (Willd.) Bentham), $2n = 28$, grows in ditches, field margins and open low ground from North Dakota and Minnesota, south to New Mexico and Texas, east to Ohio, and southward to Florida. Its distinguishing characters are the five stamens and the broadly oblong, falcate, and relatively short fruits (ca. 2–5 times as long as broad). The white flowers are first produced from early May to early June, and the plant continues to flower into the summer months. Individual flowers apparently are very short-lived, and the anthers fall within a few hours after the flowers open (Latting). Latting suspects that cross pollination may occur but that selfing is more likely. The legumes, like those of many other genera, are often infested by bruchid beetles. Seeds that are not destroyed by beetles are capable of germinating soon after maturity with no dormancy period required. As in other legumes, the leaves close at night but are not noticeably sensitive to touch.

The more western *Desmanthus leptolobus* Torrey & Gray (*Acuan leptolobum* (Torrey & Gray) Kuntze), $2n = 28$, is reported to occur in our range in Arkansas (Correll & Johnston), its main distribution being from central and southwestern Kansas and southwestern Missouri, south to south-central Texas. Steyermark notes collections from central and eastern Missouri as introductions. Beyond its five stamens per flower, *D. leptolobus* is characterized by few-flowered inflorescences, legumes 5 to 10 times as long as broad and constricted between the seeds, and seeds positioned lengthwise in the fruit. It has adapted to disturbed habitats, such as roadsides and vacant sites, and these may have allowed migration into Missouri and Arkansas. It is also found on calcareous soils, prairies, and sandy or rocky areas.

Our third species, *Desmanthus virgatus* (L.) Willd., $2n = 28$, is widespread in the tropical and subtropical portions of the New World and is naturalized in tropical Asia. It extends into the United States in southern Florida (via the West Indies) and into Texas and Arizona (via Mexico). Its diagnostic features are few-flowered inflorescences, flowers with ten stamens, fruits not constricted between the seeds, seeds oriented obliquely in the fruit, and leaves with relatively few pinnae and with well-developed stipules. Isely recognizes four varieties in the United States. Two occur in Florida: var. *virgatus* (*Acuan texanum* Britton & Rose, *A. Tracyi* Britton & Rose), from the Florida Keys and possibly from Tampa, and the more common var. *depressus* (Willd.) Turner, of southern peninsular Florida and the Keys. According to Isely, var. *virgatus* is an erect or ascending plant in Florida, while var. *depressus* is prostrate or low (in Texas var. *depressus* may also be erect.) The other varieties of the United

States are var. *glandulosus* Turner, of western Texas and adjacent Mexico, and var. *acuminatus* (Benth.) Isely (*D. acuminatus* Benth.), of eastern Texas. The distinctions between the subspecific taxa of *D. virgatus* are at best tenuous and will remain so until a careful biosystematic study of this variable species is made throughout its range.

The strongest relationship of *Desmanthus* is with *Neptunia*. Supporting morphological evidence was given by Windler in his revision of *Neptunia* and this was re-emphasized by Isely. Although Hutchinson places *Desmanthus* in the tribe Mimoseae and *Neptunia* in the tribe Adenanthereae (solely on the presence or absence of glandular anthers) the great similarity of the inflorescences, flowers, fruits, and seeds overwhelmingly supports the placement of these two closely related genera in the same tribe. Additional evidence for their relationship is seen in their pollen, which in both is shed as single grains that are basically 3-colporate, subspheroidal, and medium to large in size. The pollen of *Neptunia* is generally larger than that of *Desmanthus*, has better developed colpi and orae and is occasionally syncolpate or 4-colporate, characters that suggest that *Desmanthus* is perhaps less specialized than *Neptunia*. This interpretation would be further supported by the more specialized inflorescences found in some species of *Neptunia*. Turner & Beaman concluded that *Desmanthus* is more closely related to genera of the Adenanthereae, especially *Dichrostachys*, than to members of the Mimoseae.

Somatic polyploidy has been observed in five species of *Desmanthus* (Turner & Beaman). In all cases the tetraploid cells, $2n = 56$, occurred in the cortical regions of the root tip, while in the undifferentiated apical portion of the root tip only diploid cells, $2n = 28$, were present. According to Bolkhovskikh *et al.* (1969) all six species for which chromosome counts have been reported have $2n = 28$. Most genera of mimosoid legumes have a base chromosome number of 13, but both *Desmanthus* and *Neptunia* have the base number of 14, perhaps a further indication of their close relationship.

Little is known of the biology of the species of *Desmanthus*, except for the study of Latting, who investigated various autecological and biological aspects of *D. illinoensis*. Further studies of this kind are needed for a better understanding of evolutionary relationships within the mimosoid legumes.

The genus is of virtually no economic importance. Graham cited *Desmanthus Cooleyi* (Eaton) Trel. as an erosion-control plant because of its ability to grow on bare areas such as road cuts. The leaves have some forage value, and the seeds have been found in the crops of several species of quail. *Desmanthus illinoensis* was cited similarly.

REFERENCES:

Under subfamily references see BOLKHOVSKIKH *et al.*; GRAHAM; HUTCHINSON; RICKETT; STEYERMARK; TURNER, 1959, p. 54–59; VINES, pp. 502, 503.

DNYANSAGAR, V. R. A contribution to the embryology of *Prosopis spicigera*

Linn. and *Desmanthus virgatus* Willd. (Abstr.) Proc. Indian Sci. Congr. **40**(1953): 103. 1954.

Isely, D. Legumes of the United States. II. *Desmanthus* and *Neptunia*. Iowa State Jour. Sci. **44**: 495–511. 1970.

Latting, L. The biology of *Desmanthus illinoensis*. Ecology **42**: 487–493. 1961.

Rudd, V. E. Another Mexican Desmanthus? Leafl. West. Bot. **10**: 243, 244. 1966. [*D. nervosus* (Britton & Rose) Rudd, comb. nov.]

Turner, B. L. Vegetative key to Texas *Desmanthus* (Leguminosae) and similar genera. Field Lab. **18**: 51–54. 1950a.

———. Texas species of *Desmanthus* (Leguminosae). *Ibid.* 54–65. 1950b. [Nine species recognized.]

———. Mexican species of *Desmanthus* (Leguminosae). *Ibid.* 119–129. 1950c. [16 species, including 6 new taxa.]

——— & J. H. Beaman. Chromosome complements in *Desmanthus* (Leguminosae). Field Lab. **21**: 47–50. 1953.

5. **Neptunia** Loureiro, Fl. Cochinch. 2: 653. 1790.

Perennial herbs of various habitats [including aquatic], generally with a large tap root, the stems generally prostrate [to ascending], sometimes woody near the base, terete, angulate when young, unbranched to variously branched, glabrous to variously pubescent. Leaves stipulate, with (2–)3–6(–11) pairs of pinnae, petiolar nectaries absent [or 1 or 2 present, sometimes borne at the insertions of the lowest pair of pinnae] the rachis angled, glabrous to pubescent, lacking nectaries [or with small nectaries present between the insertion of each pair of pinnae], the rachis apiculately tipped; rachis of the pinnae distinctly winged, apiculate at tip, the leaflets [6–]8–43 pairs per pinna, oblong, obtuse to broadly acute at the apex, asymmetrical, often ciliolate, glabrous to pubescent; stipules paired, lanceolate to lanceolate-acuminate, obliquely cordate at the base, usually membranaceous, persistent [to deciduous]; stipels [present or] absent. Inflorescences pedunculate congested spikes borne singly or in pairs in leaf axils, usually bracteate, the bracts paired [rarely absent]. Upper flowers perfect; calyx campanulate, 5-merous, sessile, green, rarely yellow; corolla 5-merous, green or yellow; stamens 5 or 10, free, the filaments filiform, attached near the base of the corolla tube, exserted, the anthers bilocular, basifixed, usually terminated by a small stipitate gland, yellow; pollen shed as 3(4)-colporate or occasionally syncolpate monads; stigma concave, terminal, the style filiform, usually exceeding the stamens, the ovary stipitate, ovules many, anatropous. Lower flowers of the spike staminate, calyx campanulate, 5-merous, sessile; corolla 5-merous, yellow; stamens 5 or 10, fertile and like those of the perfect flowers or some or all of them becoming sterile and petaloid; gynoecium lacking. Fruit a legume, plano-compressed, usually oblong, marginally dehiscent by two valves, subseptate between the seeds [or rarely 1-seeded]; seeds transverse, ovate, compressed, funiculus filiform. Base chromosome number 14. (*Hemidesmas* Raf.) Type species: *N. oleracea* Lour. (Name Latin, *Neptunia*, of or belonging to Neptune, god of the sea and other waters, because of the aquatic habit of the type species.)

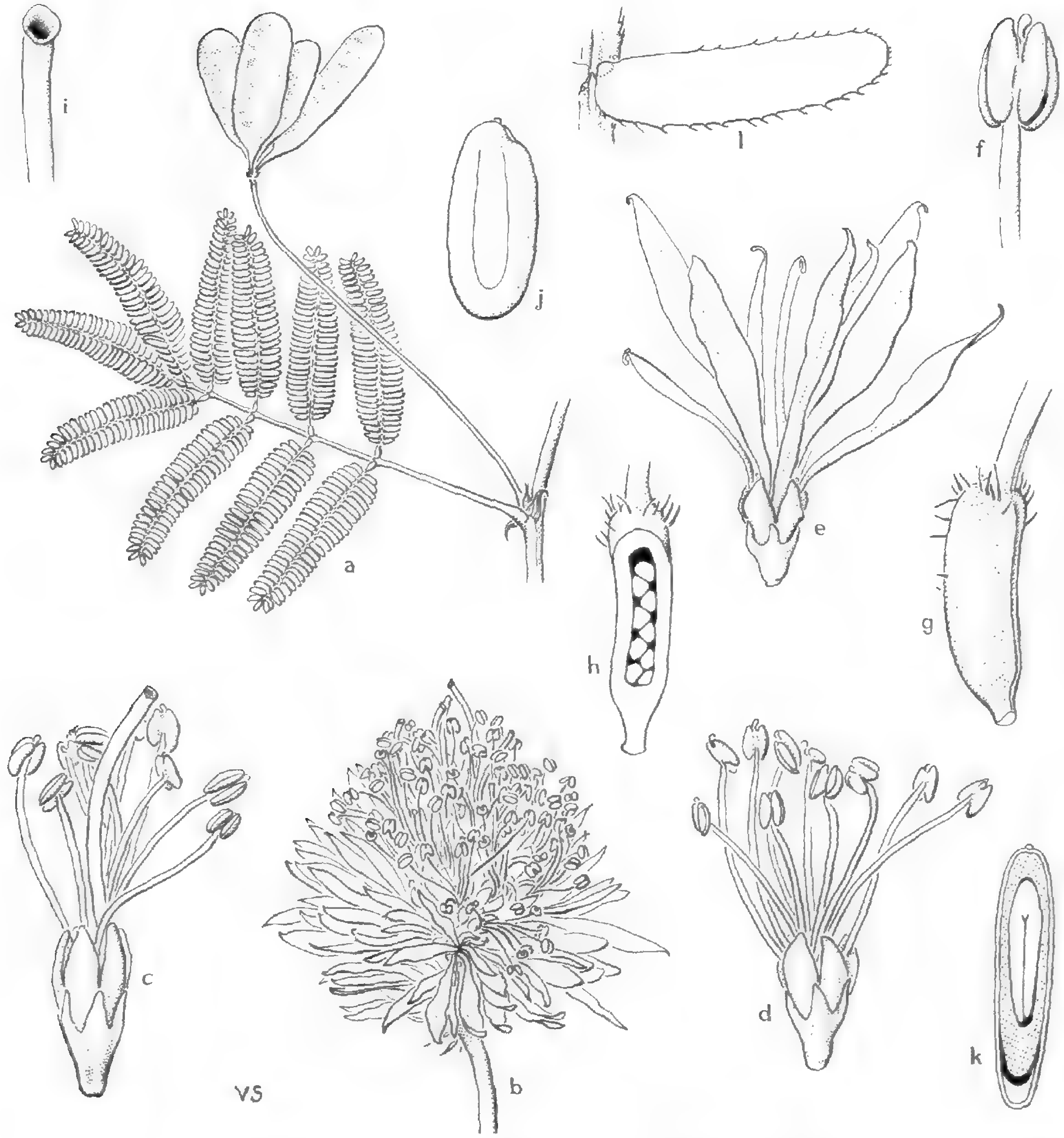


FIGURE 3. **Neptunia.** a–l, *N. pubescens*: a, habit, showing leaf and infructescence, × 1/2; b, inflorescence with perfect flowers at apex, neutral flowers with filaments modified as staminodia below, and staminate flowers in between, × 3; c, perfect flower, × 6; d, staminate flower, × 6; e, neutral flower, showing conspicuous staminodia, × 6; f, anther with apical gland, × 15; g, ovary, × 15; h, ovary in semidiagrammatic longitudinal section, showing the two-ranked ovules, from below, × 15; i, upper part of style showing concave stigma, × 15; j, seed, lateral view showing pleurogram, × 8; k, seed in semidiagrammatic longitudinal section showing embryo and endosperm (stippled), × 8; l, leaflet, × 8.

A small genus of 11 perennial species of tropical to subtropical regions with some penetration into mild temperate areas. Members of the genus are distributed from the southern United States, to Central America, the West Indies, and South America, and in the Old World representatives can be found in tropical Africa, India, southeastern Asia, and most of northern and northeastern Australia. *Neptunia lutea* (Leavenw.) Bentham and *N. pubescens* Bentham, occur in the southeastern United States.

A third species, *N. plena* (L.) Bentham, of coastal areas of Mexico, the West Indies, Central America, northern South America, and tropical Asia, extends into the United States in Texas.

Section NEPTUNIA, characterized by flowers with 10 stamens, occurs in both hemispheres. This section contains six species including the two in our range. The prostrate *Neptunia lutea* (*N. tenuis* Bentham, *N. lutea* var. *multipinnatifida* Turner), $2n = 28$, occurs largely in the eastern halves of Texas and Oklahoma but also extends eastward into Louisiana, Arkansas, southern Mississippi, and Alabama. It appears to be most frequent in fields, prairies, and roadsides. This species is distinguished from *N. pubescens* by the lack of staminodia in the lower flowers of the spike and by the 30- to 60-flowered spike that is cylindrical in bud, the stipules up to 4 mm. long, the fruiting stipe longer than 5 mm., and the white-ciliolate ovary. Although staminodia are lacking, the lower flowers of a spike are functionally staminate. *Neptunia lutea* is the only species of the genus that is endemic to the United States.

The more widespread *Neptunia pubescens* Benth., $2n = 28$, has staminodia present in the lower flowers of a spike, usually fewer than 30 flowers per spike, the spike ellipsoid in bud, the stipules 4–10 mm. long, the fruiting stipe less than 5 mm. long, and the ovary usually glabrous. Varietas *pubescens* (*N. floridana* Small, *N. Lindheimeri* Robinson, *N. pubescens* var. *floridana* (Small) Turner, *N. pubescens* var. *Lindheimeri* (Robinson) Turner), with the fruiting stipe longer than the calyx, the legume tapering toward the stipe and with 3–6 pairs of pinnae per leaf, occurs along the coastal area of the Gulf of Mexico from southern Florida to Mexico and the coastal regions of Central America, in the West Indies, and southward in South America to Argentina. In var. *microcarpa* (Rose) Windler (*N. microcarpa* Rose, *N. Palmeri* Britton & Rose) the fruiting stipe is shorter than the persistent calyx, the legume usually is rounded toward the stipe, and the leaves have 2 or 3 pairs of pinnae. This variety occurs more inland on dry, calcareous soils from southern Texas into Mexico (Coahuila, Nuevo León, Jalisco).

Two species of sect. NEPTUNIA, *N. acinaciformis* (Span.) Miquel and *N. triquetra* (Vahl) Bentham, $2n = 36$, are indigenous to southeastern Asia and India, respectively. The other species of this section, *N. plena* (L.) Bentham, $2n = 78$, and *N. oleracea* Lour. (*N. prostrata* (Lam.) Baillon), $2n = 56$, occur in both hemispheres. An aquatic rarity in the Leguminosae, *N. oleracea* typically has swollen floating stems buoyed by internodal aerenchyma, which Metcalfe (1931) considers homologous with cork, since the aerenchyma cells arise from a phellogen in the same manner as cork cells. The plants, growing in shallow water or near the edges of water, are anchored by a thick tap root, and adventitious roots are produced at the nodes. It seems possible that the aerenchyma may provide aeration for the roots, in addition to being the flotation tissue. The inflorescences, fruits, and most of the leaves extend above the surface of the water. *Neptunia plena* is either terrestrial or aquatic; when aquatic the stems develop aerenchyma, and such plants may be mistaken for

N. oleracea (cf. Fassett). The leaves of at least *N. lutea, N. pubescens, N. plena,* and *N. oleracea* are sensitive to touch.

Section PENTANTHERA Windler is composed of five species that have flowers with only five (rarely three) stamens. Fruit size and seed number per fruit are also reduced. Except for two collections from the Philippines, all five are restricted to Australia. In *N. monosperma* F. Mueller and *N. dimorphantha* Domin the legumes have only one seed (or rarely two). Although these two species are diploids, $2n = 28$, *N. gracilis*, Bentham, also of this section, is reported to be tetraploid, $2n = 56$.

Observations on four species of *Neptunia* show the plants to be self compatible and capable of producing viable seed (Windler). The inflorescences may be nodding, a position that would promote self pollination. Although specific pollinators have not been identified, various flower-visiting insects are suspected. It is not known whether any of the species hybridize or are capable of doing so. In spite of some questionable and conflicting reports, the base chromosome number of the genus appears to be 14, and one or perhaps two polyploid series are present.

Hutchinson's placement of *Neptunia* in the tribe Adenanthereae solely on the basis of stipitate glands on the anthers can hardly be correct, since in at least *N. acinaciformis* and *N. oleracea* the glands are lacking. Field observations to determine whether glands are initially present but are deciduous are obviously desirable. The true affinities of *Neptunia* appear to be with the tribe Mimoseae and *Desmanthus*, the principal difference between the two genera being the orientation of the seeds within the fruit.

REFERENCES:

Under subfamily references see BERGER, WITKUS & MCMAHON; BOLKHOVSKIKH *et al.*, p. 311; BRENAN; FRAHM-LELIVELD, 1953; GRAHAM; GUINET; HUTCHINSON, pp. 291, 292; RICKETT; SORSA.

ASANA, J. J. A preliminary report on the cytoplasmic inclusions in the pulvini of *Mimosa*, *Neptunia* and bean plants. Proc. Indian Sci. Congr. **17**: 291. 1930.*

BECK VON MANAGETTA, G. Über die Entwickelung und den Bau der Schwimmorgane von *Neptunia oleracea* Lour. Bot. Jahrb. **11**(Lit-ber.): 78. 1890.

DNYANSAGAR, V. R. Embryological studies in the Leguminosae. IV. A contribution to the embryology of *Neptunia triquetra* Benth. Proc. Indian Acad. Sci. B. **36**: 1–11. 1952.

———. Embryological studies in the Leguminosae. VII. Endosperm and embryo development in *Neptunia triquetra* Benth. and *Prosopis spicigera* Linn. Jour. Indian Bot. Soc. **33**: 247–253. 1954.

FASSETT, N. C. A deceiving aquatic *Neptunia* (Leguminosae) in Central America. Sida **1**: 382, 383. 1964. [*N. plena* (L.) Bentham forma *lumbricoides*, f. nov., aquatic form that simulates *N. oleracea*.]

GEITLER, L. Zur Morphologie der Infloreszenzen und Blüten von *Neptunia oleracea*. Ber. Deutsch. Bot. Ges. **45**: 36–39. 1927.

ISELY, D. Legumes of the United States II. *Desmanthus* and *Neptunia.* Iowa State Jour. Sci. **44**: 495–511. 1970.

METCALFE, C. R. The "aerenchyma" of *Sesbania* and *Neptunia.* Bull. Misc. Inf. Bot. Gard. Kew **1931**: 151–154. 1931. [*N. oleracea.*]

ROBINSON, B. L. Revision of the North American species of *Neptunia.* Proc. Am. Acad. Arts Sci. **33**: 332–334. 1898. [II in Contr. Gray Herb. 13.]

ROSANOFF, S. Ueber den Bau der Schwimmorgane von *Desmanthus natans* Willd. Bot. Zeit. **29**: 829–838. *pl. 10.* 1871. [*N. oleracea.*]

SINGH, B., & T. N. SHIVAPURI. The gametophyte of *Neptunia oleracea* Lour. Proc. Indian Acad. Sci. B. **1**: 423–434. *pl. 44.* 1935.

TURNER, B. L. Revision of the United States species of *Neptunia* (Leguminosae). Am. Midl. Nat. **46**: 82–92. 1951.

TURNER, B. L. & O. S. FEARING. The basic chromosome number of the genus *Neptunia* (Leguminosae-Mimosoideae). Madroño **15**: 184–187. 1960.

WINDLER, D. R. A revision of the genus *Neptunia* (Leguminosae). Austral. Jour. Bot. **14**: 379–420. 1966.

———. Notes on Leguminosae I. (*Neptunia* and *Cassia*). Southwest. Nat. **12**: 336, 337. 1967.

Tribe ACACIEAE Endlicher[5]

6. **Acacia** Miller, Gard. Dict. Abridged Ed. 4. 1: ord. alph. 1754.

Trees or shrubs [sometimes climbers] of various habitats; sapwood generally light in color, distinct or merging with the hard, durable, brownish heartwood, often irregularly grained; branches unarmed or armed with spinescent stipules or infrastipular spines. Leaves often appearing fascicled on short shoots, bipinnate [or modified to phyllodes], persistent or deciduous, petiolate, a nectary usually present on the adaxial side of petiole and/or often present on the rachis at the insertion of the pinnae, each pinna with one to many pairs of usually small, opposite leaflets; stipules small and caducous to large, persistent spines. Inflorescences pedunculate globose heads, pseudoumbels, cylindric spikes, or racemes, solitary and axillary or fasciculate on short leafless shoots and thus appearing paniculate. Flowers largely perfect, the lower flowers of an inflo-

---

[5] Endlicher (Enchiridion Botanicum 682. 1841) seems to have been the first to use this name at the rank of tribe, and, unfortunately, as a tribal name it appears to be superfluous and illegitimate. In 1834, Wight & Arnott used Acacieae for the name of a subtribe (Prodr. Fl. Penin. Indiae Orient. 1: 267. 1834) that included *Mimosa* L., and Endlicher also recognized this subtribe in his *Genera Plantarum* (p. 1324) in 1840. In 1841, in his *Enchiridion,* Endlicher used Acacieae as a tribe, again including *Mimosa*, which is the type genus of the earlier tribal name Mimoseae Bronn (1822). Although there is no description in the *Enchiridion* and no reference to the earlier *Genera Plantarum* it is impossible to say that there is no connection between the two works by the same author, and one can only say that Endlicher was raising the subtribe to tribal rank. As a subtribal name Acacieae (correctly Acaciinae) is legitimate, but when raised to tribal rank (still including *Mimosa*) it is superfluous and illegitimate. Bentham (London Jour. Bot. 1: 318. 1842) apparently was the first to use Acacieae to include only *Acacia,* and it has mostly been used in that sense to the present. There does not seem to be another tribal name based on any of the segregates of *Acacia,* and there seems to be no way short of conservation tc retain this name as a legitimate one. — C. E. WOOD, JR.

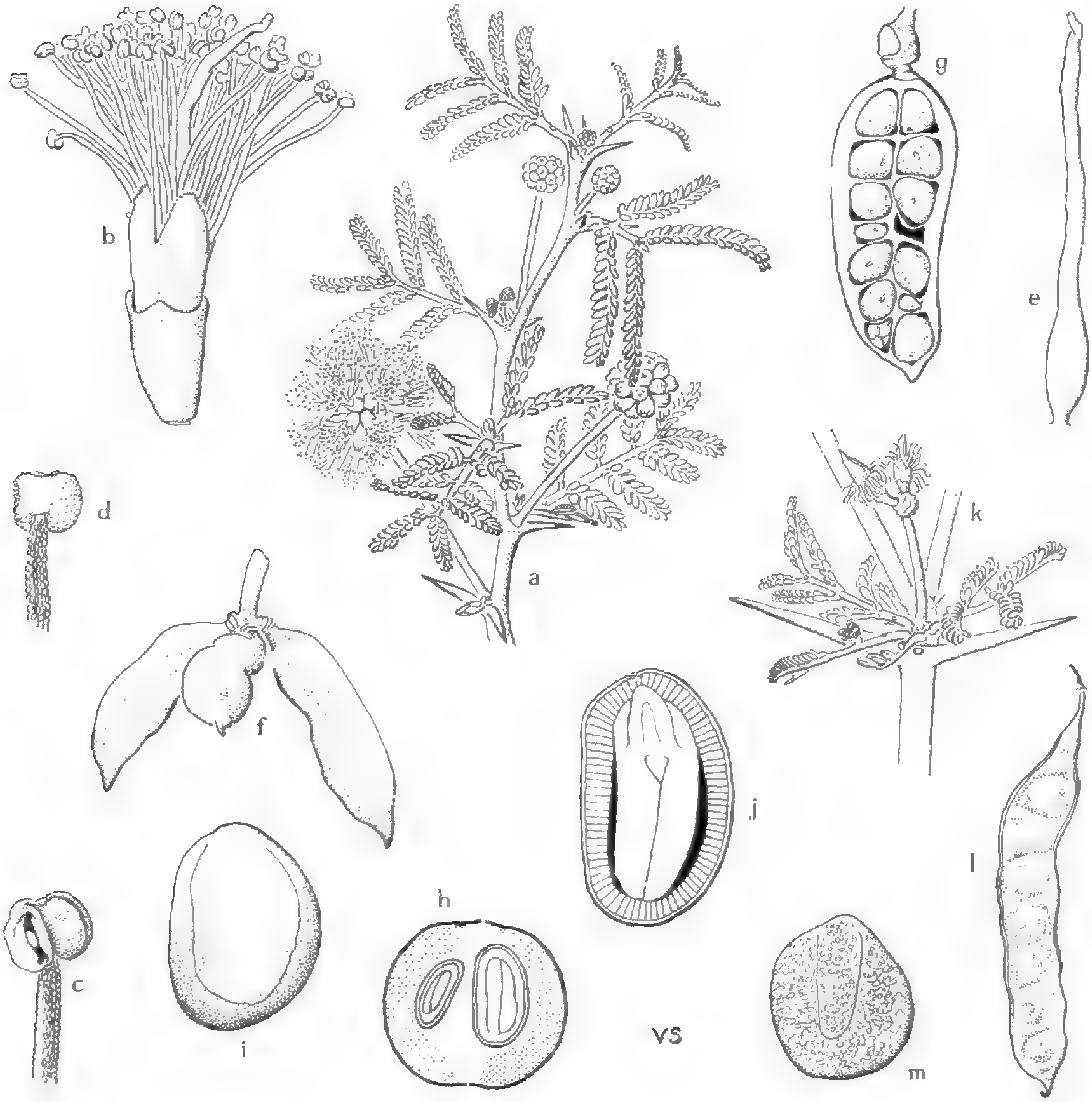


FIGURE 4. **Acacia.** a–k, *A. pinetorum*: a, habit, showing axillary inflorescences, × 2; b, flower, showing numerous stamens and single gynoecium, × 12; c, d, two views of anther, × 40; e, gynoecium, × 12; f, infructescence with three fruits, × 3/4; g, mature fruit with one side removed to show partitions separating seeds, × 1; h, mature fruit in semidiagrammatic cross section showing two seeds slightly superposed, × 2; i, seed, lateral view showing pleurogram, × 4; j, seed in semidiagrammatic longitudinal section showing large embryo and thick seed coat, × 4; k, nodal area showing paired spines, young leaves, and post anthesin inflorescence, × 2. l, m, *A. angustissima*: l, mature fruit, × 3/4; m, seed, lateral view, × 4.

rescence occasionally staminate, (4–)5–6(–7)-merous, sessile to pedicellate; subtending bract small, spathulate to linear and often dilated and peltate at apex, generally caducous. Calyx usually campanulate, with short lobes. Corolla typically funnel shaped, with as many lobes as the calyx, these more or less united [rarely absent]. Stamens usually more than 50, fertile, exserted, free or slightly and irregularly united at base, inserted under or just above base of ovary; filaments filiform; anthers small, eglandular or glandular at apex in some species, dorsifixed, versatile; pollen usually shed in 16- (or less frequently 12-) grained polyads. Stigma minute, terminal; style slender, filiform, exceeding the stamens; ovary elongate, sessile to stipitate, glabrous to puberulous, 1-locular, the ovules numerous. Fruit very variable, compressed, flat, or sometimes cylindric, continuous or moniliform, straight, curved [spiral or contorted], membranaceous to woody, dehiscent or sometimes indehiscent; seeds oriented transversely or longitudinally. Seed generally plano-compressed, usually ovate in outline, without endosperm, with an oval pleurogram on each face; funiculus filiform to thick, variously folded, often surrounding the seed and forming an aril; embryo with flat, oval cotyledons, the radicle straight, included or slightly exserted. Base chromosome number 13. (*Vachellia* Wight & Arn., *Poponax* Raf., *Senegalia* Raf., *Tauroceras* Britton & Rose, *Bahamia* Britton & Rose, *Feracacia* Britton & León, *Lucaya* Britton & Rose, *Fishlockia* Britton & Rose, *Myrmecodendron* Britton & Rose, *Acaciopsis* Britton & Rose; see Hutchinson, 1964, p. 280, for a more complete synonymy.) LECTOTYPE SPECIES: *Acacia vera* [Bauhin] Miller, 1754, nom. invalid. = *Mimosa nilotica* L., *Acacia nilotica* (L.) Delile; see Britton, N. Am. Trees 522. 1908, and Isely, 1969. (Name from Greek, *akakia* [in turn from *akis*, thorn], an Egyptian tree supposedly belonging to this genus.)

The largest genus of the Mimosoideae, with perhaps 700 species very widely distributed in tropical and subtropical regions of the world. Particularly abundant in Australia, the genus also occurs in Africa, southeastern Asia, the Pacific islands, Mexico, South and Central America, the West Indies, and the southern United States. Isely included 15 species in his treatment of the genus in the continental United States, with the largest number of species occurring in Texas. Five or six indigenous species occur in the southeastern United States (all but one in southern Florida), and one or two appear to have escaped from cultivation in Florida.

Bentham (1865) divided *Acacia* into six series based mainly on geographical distribution and on characters of the leaves and the type of inflorescence and its placement. He was unable to use floral or fruiting characters to support these groupings. This classification was adopted by Taubert (1894), and various modifications of the scheme have been used for regional treatments of the genus. The narrow generic concepts used by Britton & Rose (1928) and the resulting segregate genera are highly questionable, the amount of variation found within a single species often being greater than that between the genera established by them. Accordingly, *Acacia* is maintained here in the broad sense.

Of the species of *Acacia* in the southeastern United States, only *A. angustissima* (Miller) Kuntze, $2n = 26$, lacks the glands on petiole or rachis and the stipular spines that are so often associated with the genus. The white to pinkish or yellowish pedicellate flowers are borne in globose heads from summer to fall. The great infraspecific variation in *A. angustissima* has led to a variety of taxonomic treatments, in the most recent of which seven varieties, six of which are represented in the United States, are recognized (Isely). Our representative is var. *hirta* (Nutt. ex Torrey & Gray) Robinson (*Acaciella hirta* (Nutt. ex Torrey & Gray) Britton & Rose), which is an herbaceous to barely suffrutescent plant of prairies, roadsides, open woods, bluffs, and outcrops of shale or limestone from Louisiana and eastern Texas to southern Kansas and Missouri and northern Arkansas. The populations of peninsular Florida apparently are disjunct by several hundred miles. In Isely's circumscription, var. *hirta* intergrades with var. *texensis* (Torrey & Gray) Isely in western Texas. Other variants occur westward to New Mexico and Arizona and southward to Central America. Further study of this complex appears to be needed, since many of the varietal characters seem to be associated with various edaphic factors.

The highly variable *Acacia farnesiana* (L.) Willd. (*Vachellia farnesiana* (L.) Wight & Arn., $2n = 52, 104$, is perhaps the most common and widely distributed species of the genus in the New World. In our range it is primarily a plant of pinelands, hammocks, and disturbed areas, but it extends northward to Tampa and, as an introduction, into southern Georgia (cf. Isely). Beyond the Southeast, it occurs from the West Indies, Mexico, and Central America to South America. It is also found in the Old World, where some occurrences are introductions, while others may possibly be indigenous. The plant is a shrub or a small, spreading tree with generally conspicuous stipular spines, leaves with 4 or 5 pairs of pinnae, leaflets 4–5(–6) mm. long with prominent reticulate venation beneath, and terete obtuse to acute-tipped fruit with the two lateral sutures forming low ridges. The seeds are usually heavily preyed upon by bruchid weevils. There is considerable variation in the development of the stipular spines. The plant is frequently cultivated for its fragrant, bright yellow flowers.

A second species of this complex, *Acacia Smallii* Isely (*Vachellia densiflora* Alexander ex Small) occurs from the western panhandle of Florida to western Texas and sporadically to California and Mexico (fide Isely). A shrub or small tree of scrub areas, roadsides, grasslands, and various disturbed habitats, this plant is characterized by leaflets that are hardly reticulate beneath, by short, stout fruit, and by peduncles that are only 1–1.5 cm. long (*vs.* 2–3 cm. in *A. farnesiana*).

Restricted to southern peninsular Florida and the Keys in our area but perhaps extending into the West Indies, *Acacia pinetorum* Hermann (*Vachellia peninsularis* Small, *V. insularis* Small) is a shrub or small tree found in clearings, coastal scrub vegetation, or pinelands. It is closely related to *A. farnesiana* but can be distinguished by the smaller leaflets that have very obscure or absent lateral veins and by the sharply tapering or beaked fruits that lack protruding sutures. The two species may occur together (e.g., on Big Pine Key, Monroe County), and under these conditions are usually easily distinguished. Some herbarium specimens are difficult to place, however, and further study of the variation in the whole *A. farnesiana* complex is desirable.

The South American *Acacia macracantha* Humb. & Bonpl. ex Willd., $2n = 26$, extends into the West Indies and Mexico and has only recently been reported from Florida. A population on Ramrod Key may possibly be indigenous, but the single tree on Key Vaca (also in Monroe County), which is persistent after cultivation, does not appear to be reproducing. A population on Terra Ceia Island, Manatee County, is spreading from a single old tree that presumably was planted there. This species is distinguished by leaves with 14–20 pairs of pinnae and large, sword-shaped flat stipular spines, by the presence of nectaries between the terminal pair or pairs of pinnae, and by the laterally compressed fruits. (Cf. Ward, 1967, 1968.)

Acacia tortuosa (L.) Willd., $2n = 26$, also discovered recently in Florida, is reported from two localities, both on shell mounds in Collier County (Ward, 1968). As delimited by Isely, this species is West Indian; specimens from Mexico and Texas that have been referred to it are considered by Isely to be *A. Schaffneri* (Watson) Hermann. A small tree with a flat crown, *A. tortuosa* has leaves with 4–8 pairs of pinnae, an inconspicuous nectary present on the rachis between the uppermost pinnae pair, and nearly terete fruits 8–10 cm. long with more or less conspicuous constrictions between the seeds. *Acacia choriophylla* Bentham (*Lucaya choriophylla* (Bentham) Britton & Rose), a plant of the Bahamas and eastern Cuba, has been found wild on Key Largo, Monroe County (cf. Alexander, 1969). This plant is a small, unarmed tree with leaves with minute stipules, 1–3 pairs of pinnae, a nectar gland on the rachis between the two uppermost pinnae pairs, and compressed, oblong, tardily dehiscent legumes.

Ward (1972) has also recorded *Acacia sphaerocephala* Schlecht. & Cham. as sparingly escaped from cultivation in southern Florida. This is one of a Central American group of three to five species of bull-horn or swollen-thorn acacias that includes *A. cornigera* L. Acacias of this group produce leaves the year around and have long-persistent, enlarged, woody stipules with a soft pith, much-enlarged foliar nectaries, and leaflet-, pinna-, and rachis-tips constricted and modified into Beltian bodies. In their native areas, the stipular spines of these plants usually are inhabited by biting and stinging ants of the genus *Pseudomyrmex* that enter the spine by a hole cut near the tip and hollow out the pith. The ants, which live almost entirely on foliar nectar and on the Beltian bodies (a source of protein), attack any other insects on the plant and usually drive them off. They also attack any living plants that touch the foliage of the *Acacia* or that grow below it in an area 10–150 cm. in diameter, so that the acacia grows in a space free from other plants (Janzen).

Approximately 10 per cent of the species of *Acacia* have been investigated cytologically, and several levels of polyploidy have been found. Most of the species for which chromosome numbers have been reported have $2n = 26$, but there are several with $2n = 52$ and $2n = 104$. Sharma & Bhattacharyya investigated the structure and behavior of chromosomes in some species and suggested that polyploidy originated by allopolyploidy.

The inflorescences of *Acacia* are either globose or cylindrical, and the flowers are of varying shades of yellow to orange, rarely white, cream, or pinkish. Although the flowers of a single inflorescence are largely synchronous in anthesis, the inflorescences of a compound floral branch are not. The lowermost inflorescence will flower first, followed centrifugally by succeeding inflorescences. The flowers are often very fragrant, and pollination is mainly by insects. The floral and reproductive biology are very poorly known.

The pollen is generally shed in 16-grained polyads, although pollen in units of 32, 12, 8, or 4 grains is also known in the genus. The polyads are usually radially symmetrical, flattened, and are mostly 40–50 μm. across, although there are occasional species with polyads 90 μm. in diameter and others with polyads as small as 30. Guinet has proposed that *Acacia*, sensu lato, be divided into three large genera based on the number of pores, presence or absence and nature of the individual pollen grain furrows, and the presence or absence of stipular spines. The pores of the individual grains are paraisopolar and may be indistinct. The shape of the grains is variable, but most are pyramidal or cuboidal. In a comparison of 28 South African species with 31 from Australia, Coetzee found that the two groups could easily be separated on the basis of furrow configuration in the exine of the polyads. Within the South African group, the pollen fell into two categories that were somewhat correlated with the type of inflorescence (capitate *vs.* spicate or racemose).

Many species of *Acacia* are cultivated in the United States in greenhouses or in the Southwestern States (including California) and in southern Florida. The majority of the species in cultivation have been introduced from Australia and have leaves that are reduced to phyllodes in the mature plant; compound leaves are produced immediately after the cotyledons in seedlings. One of the most commonly cultivated species is *A. auriculiformis* Cunn., which in southern Florida shows signs of escaping to pine-palmetto woodland.

Species beyond our range are the source of valuable gums, tannins, and dyes. The wood is used locally for firewood and for fence posts. The Australian *A. melanoxylon* R. Br. is used in California as an erosion-control plant on slopes. Various species have been used for hedges and shelterbelts. They provide cover for small wildlife, and the fruits are highly sought after by animals. Deer, horses, and cattle are known to browse on the foliage, bark, and fruit.

REFERENCES:

Under subfamily references see BENTHAM & HOOKER, 1865; BERGER, WITKUS & MCMAHON; BLAGOVESCHENSKII & ALEKSANDROVA; BOLKHOVSKIKH *et al.*; BRENAN; COMPTON; FRAHM-LELIVELD, 1960; GRAHAM; GUIGNARD; GUI-

NET; Isely, 1957, 1961; Little, pp. 31–33; Little & Wadsworth; Record & Hess; Ridley; Sargent; Sorsa; Taubert; USDA Forest Service; Vines, pp. 491–500; and Ward.

Alexander, T. R. *Acacia choriophylla*, a tree new to Florida. Quart. Jour. Florida Acad. Sci. **31:** 197, 198. 1968 [1969].

Atchison, E. Studies in the Leguminosae. II. Cytogeography of *Acacia* (Tourn.) L. Am. Jour. Bot. **35:** 651–655. 1948.

Baker, J. G. *Acacia choriophylla.* Hooker Icones **19:** *pl. 1804.* 1889.

Barth, O. M. Feinstruktur des Sporoderms einiger brasilianischer Mimosoiden-Polyaden. (French summary.) Pollen Spores **7:** 429–441. 1965.

Benson, L. Revisions of status of southwestern desert trees and shrubs. Am. Jour. Bot. **30:** 230–240. 1943. [Includes *A. angustissima* var. *cuspidata*, and *A. constricta* var. *vernicosa*, comb. nov.]

Boke, N. H. Histogenesis and morphology of the phyllode in certain species of *Acacia.* Am. Jour. Bot. **27:** 75–90. 1940.

Brenan, J. P. M., & A. W. Exell. *Acacia pennata* (L.) Willd. and its relatives in tropical Africa. Bol. Soc. Brot. **31:** 99–140. 1957. [An example of taxonomic difficulties in this genus.]

——— & R. Melville. The Latin name of the Black Wattle. Kew Bull. **14:** 37–39. *pls. 1, 2.* 1960. [*A. Mearnsi* De Wild. (*A. mollissima* sensu many authors, not Willd.), an important economic plant.]

Bresinsky, A. Bau, Entwicklungsgeschichte und Inhaltsstoffe der Elaisomen. Bibliot. Bot. **126.** 54 pp. 1963.

Buscalioni, L., & G. Catalano. Morfologia ed anatomia dei fillodi di *Acacia.* Giorn. Sci. Nat. Econ. II. **6:** 66–70. 1924.*

Carlos, S. Acácieas Argentinas. Bol. Acad. Nac. Ci. Córdoba **26:** 7–334. 1923.

Coetzee, J. A. The morphology of *Acacia* pollen. S. Afr. Jour. Sci. **52:** 23–27. 1955.

Cookson, I. C. The Cainozoic occurrence of *Acacia* in Australia. Austral. Jour. Bot. **2:** 52–59. *1 pl.* 1954.

Cope, J. M. Response to carbon monoxide by geographic variants in *Acacia farnesiana.* Am. Jour. Bot. **56:** 600–602. 1969.

Dnyansagar, V. R. Embryological studies in the Leguminosae. VIII. *Acacia auriculaeformis* A. Cunn., *Adenanthera pavonina* Linn., *Calliandra haematocephala* Hassk., and *Calliandra grandiflora* Benth. Lloydia **21:** 1–25. 1958.

Fahn, A. Xylem structure and annual rhythm of development in trees and shrubs of the desert. II. *Acacia tortilis* and *A. Raddiana.* Bull. Res. Council Israel. D. **7:** 23–28. 1959.

Ghimpu, V. Contribution à l'étude chromosomique des *Acacia.* Compt. Rend. Acad. Sci. Paris **188:** 1429–1431. 1929.

———. Sur l'existence simultanée des mitoses diploïdes, didiploïdes et tétraploïdes chez les *Acacia.* Compt. Rend. Soc. Biol. Paris **101:** 1122, 1123. 1929.

Hill, A. F. Some nomenclatorial problems in *Acacia.* Harvard Univ. Bot. Mus. Leafl. **8:** 93–105. 1940.

Isely, D. Legumes of the United States: 1. Native *Acacia.* Sida **3:** 365–386. 1969.

Janzen, D. H. Coevolution of mutualism between ants and acacias in Central America. Evolution **20:** 249–275. 1966.

———. Interaction of the bull's-horn acacia (*Acacia cornigera* L.) with an ant inhabitant (*Pseudomyrmex ferruginea* F. Smith) in eastern Mexico. Univ. Kansas Sci. Bull. **47:** 315–558. 1967.

KHAN, M. I. R. Study of somatic chromosomes in some *Acacia* species and hybrids. Pakistan Jour. Sci. Res. **3:** 89–100. 1951. [Also in Pakistan Jour. Forestry **1:** 326–341. 1951.]

LARUE, C. D. The extraordinary funiculus of *Acacia confusa* Merrill. Rhodora **56:** 229–231. 1954.

LEMESLE, M. R. Particularités histologiques des phyllodes aciculaires chez quelques espèces d'*Acacia.* Compt. Rend. Acad. Sci. Paris **252:** 4180–4182. 1961.

———. Structure des phyllodes de forme oblongue, lancéolée ou linéaire chez diverses espèces australiennes d'*Acacia.* *Ibid.* **253:** 1479–1481. 1961.

———. Essai de classification des *Acacia* à phyllodes ovales, oblongs, lancéolés ou linéaires d'après leurs particularités histologiques. *Ibid.* 1722–1724.

NARASIMHACHAR, S. G. A contribution to the embryology of *Acacia farnesiana* L. (Willd.) Proc. Indian Acad. Sci. B. **28:** 144–149. 1948.

PEACOCK, J. T., & C. MCMILLAN. The photoperiodic response of American *Prosopis* and *Acacia* from a broad latitudinal distribution. Am. Jour. Bot. **55:** 153–159. 1968.

PRESTON, C. E. Peculiar stages of foliage in the genus *Acacia.* Am. Nat. **36:** 727–734. 1902.

RICKSON, F. R. Histochemistry and ultrastructure of Beltian bodies. (Abstr.) Am. Jour. Bot. **55:** 713. 1968.

RUDD, V. E. Nomenclatural problems in the *Acacia cornigera* complex. Madroño **17:** 198–201. 1964.

SAFFORD, W. E. *Acacia cornigera* and its allies. Jour. Wash. Acad. Sci. **4:** 356–368. 1914.

———. New or imperfectly known species of bullhorn acacias. *Ibid.* **5:** 355–360. 1915.

———. Ant acacias and *Acacia* ants of Mexico and Central America. Rep. Smithson. Inst. **1921:** 381–394. 1923.

SCHENK, H. Die myrmekophilen *Acacia*-Arten. Bot. Jahrb. **50**(Suppl.): 449–487. 1914.

SENEVIRATNE, A. S., & L. FOWDEN. The amino acids of the genus *Acacia.* Phytochemistry **7:** 1039–1045. 1968.

SHARMA, A. K., & N. K. BHATTACHARYYA. Structure and behaviour of chromosomes of species of *Acacia.* Phyton (Buenos Aires) **10:** 111–122. 1958.

SHINN, C. H. An economic study of Acacias. U. S. Dep. Agr. Bull. **9:** 1–38. *pls. 1–11.* 1913.

VASSAL, J. Intérêt taxonomique de la morphologie des graines dans le genre *Acacia.* Bull. Soc. Hist. Nat. Toulouse **98:** 341–371. 1963.

WARD, D. B. *Acacia macracantha,* a tree new to Florida and the United States. Brittonia **19:** 283, 284. 1967.

———. *Acacia tortuosa* (Leguminosae) new to Florida. Sida **3:** 279, 280. 1968. [Includes key to native Floridian species of *Acacia.*]

WIGGINS, I. L. *Acacia angustissima* (Mill.) Kuntze and its near relatives. Contr. Dudley Herb. **3:** 227–239. 1942.

WOOD, J. G. The phytogeography of Australia (in relation to radiation of *Eucalyptus, Acacia,* etc.). Monogr. Biol. **8:** 291–302. 1959.

Tribe INGEAE Bentham & Hooker

7. **Lysiloma** Bentham, London Jour. Bot. 3: 82. 1844.

Shrubs or more often trees of moderate to large size, the bark smooth but separating in plate-like scales on older trees, the wood heavy, hard, strong, and close-grained; branches stout, spreading, forming a rounded or flat-topped tree; lenticels numerous, conspicuous. Leaves deciduous [to persistent], pinnae 1 to many pairs, with numerous small leaflets or rarely with few large leaflets, petiolate, a petiolar nectary present just below the lowest pair of pinnae; stipules usually large, foliaceous, deciduous to subpersistent. Inflorescences of pedunculate, many-flowered, globose heads [or cylindrical spikes], solitary or fascicled, usually axillary or terminal. Flowers largely perfect, 5-merous, white, the lower flowers of the inflorescence occasionally staminate, usually sessile. Calyx campanulate [to tubular], the lobes short, equal [to unequal], usually more pubescent than the tube, valvate in aestivation. Corolla tube exceeding the calyx, the lobes approximately 1/4 to 1/3 the length of the tube, ovate, acute at the apex, usually densely pubescent, valvate in aestivation. Stamens generally 12 to 30, united at the base, inserted near the base of the ovary, exserted; filaments filiform; anthers minute, oblong, glabrous, eglandular, peltate; pollen shed in radially symmetric, flattened 16-grained polyads. Stigma terminal, minute, invaginated and concave, style filiform, ovary sessile to short stipitate, ovules numerous. Legume usually 8–12-seeded, straight or slightly falcate, often broad, plano-compressed, oblong, chartaceous, the valves separating at maturity from the persistent margins, continuous within, the exocarp thin, chartaceous, dark colored, separating from the endocarp, the endocarp usually thicker, yellowish. Seeds oriented transversely, plano-compressed, ovate, hard, lustrous, with a small U-shaped pleurogram on each side; funiculus long, slender hilum subbasal; endosperm absent; embryo with flat, oval cotyledons; radicle straight, slightly exserted. Base chromosome number 13. LECTOTYPE SPECIES: *L. bahamense* Bentham; see Britton N. Am. Trees 521. 1908.[6] (Name probably from Greek *lysis*, loose, and *loma*, border, in reference to the separation of valves of the fruit from the persistent margins.)

A small genus of about 35 species distributed in tropical America. Bentham established *Lysiloma* with some reservations (see footnote 6),

---

[6] Hutchinson (1964, p. 296) argues that *L. bahamense* can not be taken as the type species "because the fruit of that species was unknown to Bentham, who says: 'The generic character lies in the combination of the pod of a *Mimosa* with the monadelphous stamens of the *Ingoid* genera.'" Hutchinson's choice of *L. Schiedeanum,* however, is hardly any better, for Bentham had immature fruit of that species ["Legumen (nondum maturum) 5-pollicare, 8–9 lin. latum, stipitatum, apice longiuscule cuspidatum"], and it appears that he did not have both flowers and mature fruit of *any* of the seven species that he referred to *Lysiloma*. Bentham says, "The species I have collected under this generic name are evidently closely allied to each other, although there can be no certainty of their being truly congeners until the fruit of more species shall be known."

using as the unifying characters the combination of the numerous stamens united to form a tube and the fruit with valves that separate from the persistent margins. Because of its monadelphous stamens, *Lysiloma* has been placed in the tribe Ingeae, within which it is perhaps most closely related to *Albizia*.

Three species, two in the Southwest, occur in the United States. The Mexican *Lysiloma microphyllum* Bentham, which extends into southern Arizona, and *L. Thornberi* Britton & Rose, which is confined to the Rincon Mountains of southern Arizona, have been considered to be conspecific by Isely, who reduced *L. Thornberi* to a variety of *L. microphyllum*. The third, *L. bahamense*, $2n = 26$, is a West Indian species that reaches the United States only in southernmost Florida. It is common on some of the upper Keys and in southernmost peninsular Florida it behaves both as a weed tree and as a component of hammocks (cf. Alexander, Craighead). The tree reaches a maximum of 20 meters. The leaves are deciduous. The small white flowers of an inflorescence can appear from October through June. The fruits ripen by fall but remain on the tree until flowering begins the following year.

Palynologically similar to other mimosoid genera, *Lysiloma* has pollen in 16-grained, flattened symmetrical polyads that range in diameter from 53 to 100 μm. The individual grains are pyramidal in shape, (3–6–)8-porate (fide Sorsa) or 4-porate (fide Guinet), and each circular pore is covered by a membrane.

Data on the floral biology of *Lysiloma* species are almost completely lacking. The conspicuous inflorescences of tiny, fragrant, white flowers suggest cross fertilization by insect pollinators. The size of the polyads may however restrict the effective pollinators to the stronger insects such as bees.

Craighead considers the hammocks of southern Florida to be composed primarily of tropical hardwoods with *Lysiloma bahamense* being one of the more characteristic trees in the hammocks of the Pineland Ridge. Alexander found that in the absence of fire over a twenty-five year period, the pinelands surrounding the hammocks would be invaded by *L. bahamense*, which would persist until another fire at which time the area would revert to a pineland community.

Although the wood is easily worked, durable, and suitable for furniture and interior trim, the trees are generally not very abundant and are often too poorly formed to be of commercial importance as timber. *Lysiloma bahamense* is considered to be a valuable tree in the West Indies, where the wood is used in general construction. Graham listed *L. Thornberi* as a possible erosion-control shrub and roadside ornamental in the southwestern United States.

REFERENCES:

Under subfamily references see ATCHISON, 1951, p. 542; BOLKHOVSKIKH *et al.*, p. 307; GRAHAM; GUINET; HUTCHINSON; ISELY, 1970; LITTLE, pp. 229, 230;

RECORD & HESS, pp. 289, 290; RIDLEY; SARGENT, p. 127; SORSA; WEST & ARNOLD, p. 88.

ALEXANDER, T. R. A tropical hammock of the Miami (Florida) limestone — a twenty-five-year study. Ecology **48:** 863–867. 1967. [Ecology of pine forest invaded by *L. bahamense.*]

BRITTON, N. L., & J. N. ROSE. *Lysiloma.* N. Am. Fl. **23:** 76–84. 1928.

CRAIGHEAD, F. C. The trees of South Florida. Vol. 1. The natural environments and their succession. xvi + 212 pp. Coral Gables, Florida. 1971. [Includes several references to *Lysiloma.*]

WIT, H. C. D. DE. Typification and correct names of *Acacia villosa* Willd. and *Leucaena glauca* (L.) Bth. Taxon **10:** 50–54. 1961. [Includes discussion of *Lysiloma.*]

8. **Albizia** Durazzini, Magazz. Toscano 3(4) (vol. 12): 10, 13. *pl.* 1772.

Trees or shrubs, small to medium-sized, spreading and often with a flat crown [or large trees]; heartwood pale yellowish brown to brownish, sapwood yellowish; branches unarmed, the branchlets terete to angulate, generally puberulent, becoming glabrate with age, striate. Leaves deciduous; a petiolar nectary usually present; pinnae few to many [a nectary occasionally present between the insertion of each pair of pinnae], with [one to] many pairs of leaflets, the leaflets small and numerous or large and few; stipules usually caducous and setaceous [or rarely large, foliaceous and membranaceous]. Inflorescences of spikes, racemes, or heads, pedunculate, the peduncles solitary or more often fascicled, axillary or generally aggregated on short shoots and appearing paniculate. Flowers largely perfect, (4)5(6)-merous, the lower flowers of the inflorescence often staminate, the central one or two flowers with the corolla tube about 1.5 times longer than the other flowers and the staminal tube exserted, the remaining flowers with the calyx campanulate to short tubular, usually pubescent, short-lobed. Corolla generally infundibuliform, the lobes short (usually about 1/4 the tube length). Stamens 20 to 50, fertile, the filaments united into a staminal tube, the tube included to equalling the corolla tube, inserted near the base of the ovary; filaments filiform; anthers small, eglandular or glandular in bud, peltate; pollen in 16-grained polyads. Stigma terminal, minute, concave; style slender, filiform, slightly exceeding the stamens; ovary elongate, sessile to stipitate, glabrous, 1-locular, ovules ca. 12–18. Legume oblong, flattened, straight, tapering at base and apex, nonseptate, chartaceous to coriaceous, dry, indehiscent to tardily dehiscent, the valves thin, slightly thickened at the margins. Seeds transverse, plano-compressed, hard, lustrous, with a narrow, U-shaped pleurogram on each face, without endosperm; embryo filling the seed cavity, the cotyledons flat, oval, the radicle straight. Base chromosome number 13. (*Sericandra* Raf.) TYPE SPECIES: *A. Julibrissin* Durazz. (Named in honor of "Il Sig. Cavalier Filippo degl' Albizzi," an Italian nobleman who introduced *A. Julibrissin* into Tuscany in 1749. Although the Albizzi family spelled their name with two *z*'s, Durazzini

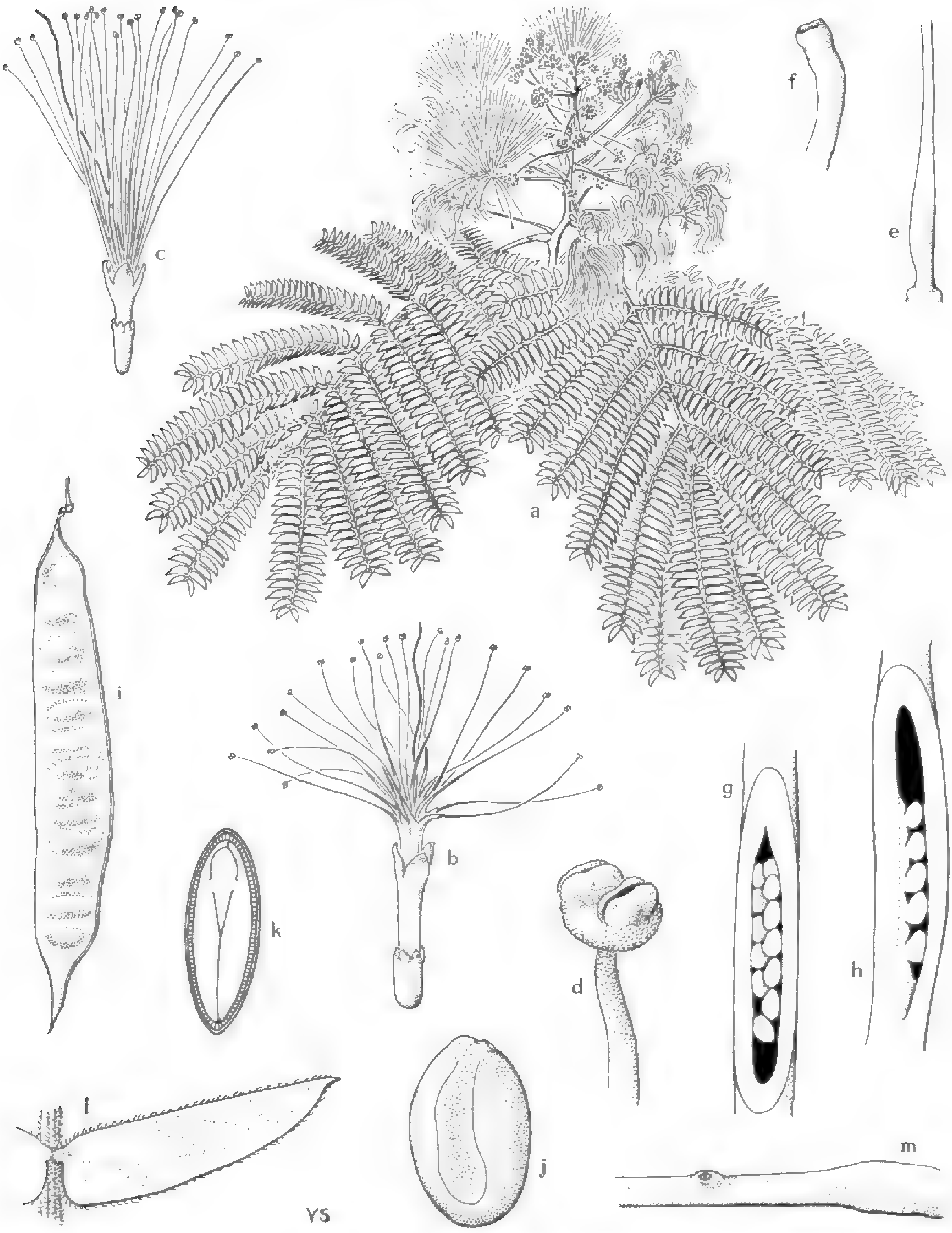


FIGURE 5. **Albizia.** a–l, *A. Julibrissin*: a, habit with compound inflorescence in various stages of flowering, × 1/4; b, perfect central flower of an individual inflorescence showing elongated corolla tube and exserted staminal tube, × 1 1/2; c, nonapical flower of an inflorescence, often functionally staminate, × 1 1/2; d, anther, showing peltate attachment, × 30; e, ovary and lower part of style, × 6; f, upper part of style and terminal concave stigma, × 25; g, ovary in semidiagrammatic longitudinal section from below to show two-ranked ovules, × 20; h, ovary in semidiagrammatic longitudinal section (lateral view) to show ovules, × 20; i, mature fruit, × 1/2; j, seed, lateral view showing pleurogram, × 4; k, seed in semidiagrammatic longitudinal section showing large embryo, × 4; l, leaflet, × 3; m, base of petiole, showing pulvinus and petiolar nectary, × 2.

was consistent in his use of only one in the generic name, and that spelling must be taken as correct. Cf. Little, 1945.)

A genus of approximately a hundred species distributed in tropical and subtropical Asia, Africa, Australia, and the Americas. Fosberg recognized two sections (SPICIFLORAE Bentham and PLATYSPERMAE (Bentham) Fosberg) for Old World species with flowers borne in cylindrical spikes (ca. 15 spp.). (Most previous authors have treated the two together under sect. LOPHANTHA Walpers ex Fournier, a superfluous name.) Section ALBIZIA, with the flowers borne in heads, is represented in both hemispheres, and two species of this section have become naturalized in the southeastern United States.

Native to tropical and subtropical Asia and possibly Africa, *Albizia Lebbeck* (L.) Bentham, $2n = 26$, was introduced first into the West Indies, then into Central and South America, and finally into southern Florida, where it has become naturalized. The tree is medium-sized, with a spreading crown, and is deciduous. The staminal filaments are yellow to white, unlike the pink to reddish ones of *A. Julibrissin*. The rather large fruits, which are produced in prodigious quantities, are long persistent on the tree. As they dry the seeds become loose inside the pods and rattle in a breeze, hence the West Indian vernacular name "woman's tongue." This species can grow in dry areas and in situations of moderate salt spray. It is propagated from seed.

Indigenous to temperate and tropical Asia from Iran to China, Korea, and Japan, *Albizia Julibrissin*, mimosa, silk-tree, $2n = 26$, has long been in cultivation. It has been planted as an ornamental tree throughout most of the eastern United States and over a broad area, from Maryland and West Virginia to Indiana and Kentucky, southward to Louisiana and Florida, has escaped from cultivation, in some areas becoming a conspicuous element along roadsides and woodland margins. It is a small to large flat-topped deciduous tree. The plant flowers from June to mid-September (in New England).

Maturation of the individual inflorescences on a short shoot is acropetal (see FIGURE 5a). Flowering in a single capitate inflorescence is usually more or less synchronous, although the apical flowers generally are the first to reach anthesis. The flowers are short-lived, rarely lasting longer than a day. Relatively few of the 16-grained polyads are produced in each anther, but the transfer of one of these can fertilize most or all of the seeds in a single ovary. The fragrant flowers are visited by numerous insects and by hummingbirds, but bumblebees appear to be the principal pollinators of *A. Julibrissin* in the United States. The upper halves of the filaments are pink to reddish and give the capitate inflorescences their striking "powder-puff" appearance. The plant can be propagated from either seeds or root cuttings.

The leaves of *Albizia Julibrissin* show the "sleep" movements typical of Leguminosae. These movements result from changes in the volume (as much as 3–4-fold) of motor cells in the pulvinus at the base of the petiole, the pulvinus at the base of each pinna, and the pulvinule at the base of each leaflet. Movement is accompanied by potassium flux into and out of the motor cells. Movements are controlled by light-dark transition, phytochrome, and endogenous circadian rhythms. Since it has been shown that the photoreceptors for leaflet movement, the "clock" controlling the rhythmic changes, and the energy substrate (as well as the motor cells) are all located in the pulvini and pulvinules, leaflets of *Albizia Julibrissin* have been used extensively by a number of investigators to study the interaction of these factors. (See Satter & Galston, 1973, for a review and for numerous references; also see *Mimosa.*)

Like those of many other legumes, seeds of *Albizia Julibrissin* are remarkable for their longevity. During an air raid and subsequent fire at the British Museum (Natural History) in 1940 seeds of this species got wet and when examined two months later were found to have germinated after 147 years of storage (Anonymous, 1942). Crocker (1938) notes seeds of this species giving 3.3 per cent germination after 70 years of storage.

At least two other species are known to be under cultivation in the United States. *Albizia Kalkora* (Roxb.) Prain, a small tree with whitish flowers that is native to central and eastern China, Indochina, and India, is only rarely encountered, and *A. lophantha* (Willd.) Bentham, native to Western Australia, is planted in California and Arizona, as well as other warm-temperate (and tropical) parts of the world.

Albizia is questionably distinguished from the other genera of the tribe Ingeae by its thin, straight, flattened fruit that is either indehiscent or tardily dehiscent only along the sutures. It was recognized as a distinct genus by Bentham in both 1844 and in his revision of the subfamily in 1875, but was reduced by Von Mueller (1872) and by Kurz (Jour. Asiat. Soc. Bengal **45**: 129. 1876) to synonymy under *Pithecellobium*. Mohlenbrock placed it between *Havardia* Small (fruits thin, papery, promptly dehiscent) and *Pseudalbizzia* Britton & Rose (fruits indehiscent but breaking transversely between the seeds), both segregates from *Pithecellobium* (q.v.).

Guinet examined the pollen of thirty species of *Albizia* in his survey of the palynology of the Mimosoideae. In all the species the pollen is in flattened, radially symmetrical 16-grained polyads that range in diameter from approximately 65 μm. to 98 μm. The individual pollen grains are 4–6(–8)-porate (the pores usually circular), paraisopolar to heteropolar, and pyramidal in shape.

In a study of the amino acids of the seeds of 29 species of *Albizia* Krauss & Reinbothe separated 36 protein and nonprotein amino acids. Twenty-three contained large amounts of albizzine. *Albizia polyphylla* and *A. polymorpha* were unique in containing mimosine, 5-hydroxypipecolic acid, and dichrosrachic acid.

Beyond the horticultural merits of some species of *Albizia*, notably *A. Julibrissin*, the genus is of limited economic importance. In the Old World some of the species are trees large enough to produce useful timber. The wood of the smaller trees is often used for fuel, fence posts, small furniture, paneling, and general construction. The bark has been used in tanning and for medicinal purposes. It has been used in various decoctions as an anthelmintic.

REFERENCES:

Under subfamily references see ATCHISON, 1951, p. 542; BENTHAM, 1844, pp. 84–92, & 1875; BERGER, WITKUS, & MCMAHON; BLAGOVESHCHENSKII & ALEKSANDROVA; BOLKHOVSKIKH *et al.*, p. 281; BRENAN; COMPTON, p. 7; GRAHAM; CROCKER; GUINET; HUTCHINSON; ISELY, 1970; KURZ & GODFREY, pp. 174–176; LITTLE, p. 48; RECORD & HESS, p. 230; SORSA; USDA FOREST SERVICE; VINES, p. 500.

ANONYMOUS. Duration of viability in seeds. Gard. Chron. III. **1942**(1): 234. 1942. [Seeds of *A. Julibrissin* 147 years old.]

BERGER, C. A., & E. R. WITKUS. Naturally occurring polyploidy in the development of *Albizzia Julibrissin* Durazz. Bot. Gaz. **111**: 312, 313. 1950.

CODD, L. E. The *Albizia* species of South Africa. Bothalia **7**: 67–82. 1958.

DEWOLF, G. P., JR. *Albizia Julibrissin* and its cultivar 'Ernest Wilson.' Arnoldia **28**: 29–35. 1968. [A hardy form from Korea.]

DUNCAN, W. H. Preliminary reports on the flora of Georgia. 2. Distribution of 87 trees. Am. Midl. Nat. **43**: 742–761. 1950. [Includes *A. Julibrissin.*]

EVANS, L. T., & W. G. ALLAWAY. Action spectrum for the opening of *Albizia Julibrissin* pinnules, and the role of phytochrome in the closing movements of pinnules and of stomata of *Vicia Faba*. Austral. Jour. Biol. Sci. **25**: 885–893. 1972.

FOGG, J. M., JR., & H. L. LI. *Albizzia*. Morris Arb. Bull. **7**: 40, 41. 1956.

FORDHAM, A. J. Propagation of *Albizia Julibrissin*. Arnoldia **28**: 36–40. 1968. [By seeds and root-cuttings.]

FOSBERG, F. R. Revision of *Albizia* sect. *Pachysperma* (Leguminosae-Mimosoideae). Reinwardtia **7**: 71–90. 1965.

GILL, D. L. Wilt-resistant mimosa trees. Natl. Hort. Mag. **38**: 105–107. 1959. [*A. Julibrissin.*]

GORDON, S., & W. L. KOUKKARI. The effect of cytokinins and auxins on phytochrome mediated nyctinasty in *Albizzia Julibrissin*. Pl. Physiol. **49**(Suppl.): 299. 1972.

HEPTING, G. H., & E. R. TOOLE. *Mimosa* wilt, a major problem. Proc. Natl. Shade Tree Conf. **18**: 254–258. 1942.

HILLMAN, W. S., & W. L. KOUKKARI. Phytochrome effects in the nyctinastic movements of *Albizzia julibrissin* and some other legumes. Plant Physiol. **42**: 1413–1418. 1967.

JAFFE, M. J. Rapid phytochrome responses. XI Int. Bot. Congr. Abstr. 11. 1969. [Includes *A. Julibrissin.*]

——— & A. W. GALSTON. Phytochrome control of rapid nyctinastic movements and membrane permeability in *Albizzia Julibrissin*. Planta **77**: 135–141. 1967.

KOUKKARI, W. L., & W. S. HILLMAN. Pulvini as the photoreceptors in the phytochrome effect of nyctinasty in *Albizzia Julibrissin*. Pl. Physiol. **43**: 698–704. 1968.

———, B. D. SOTHERN, & F. HALBERG. Nyctinastic movements of *Albizzia*

Julibrissin — quantification and phase-shifting of circadian parameters. XI Int. Bot. Congr. Abstr. 115. 1969.

KRAUSS, G. J., & H. REINBOTHE. Die Aminosauren der Gattung *Albizia* Durazz. (Mimosaceae). Biochem. Physiol. Pflanzen **161:** 243–265. 1970.

LITTLE, E. L., JR. Miscellaneous notes on nomenclature of United States trees. Am. Midl. Nat. **33:** 495–513. 1945. [*Albizia*, 510.]

——— & F. H. WADSWORTH. Common Trees of Puerto Rico and the Virgin Islands. U. S. Dep. Agr. Agr. Handb. **249.** 1964. [*A. Lebbeck*, 146–148; *A. procera*, 148–150.]

MAHESHWARI, P. Contribution to the morphology of *Albizzia Lebbek*. Jour. Indian Bot. Soc. **10:** 241–264. 1931.

MARIAN, M. Observations of growth in *Albizia* seedlings of the same generation. Proc. Okla. Acad. Sci. **35:** 4–5. 1954.

MORGAN, O. D. Mimosa (*Albizzia Julibrissin*) wilt spreading in southern Maryland. Pl. Disease Rep. **41:** 51, 52. 1957.*

MUELLER, C. *Albizia*. Ann. Bot. Syst. **4:** 630–634. 1857.

MUELLER, F. VON. The genus *Albizzia*: its origin and systematic limits considered. Jour. Bot. **10:** 7–11. 1872.

REED, R. M. The mimosa as an escape in West Virginia and Kentucky. Castanea **24:** 55, 56. 1959. [*A. Julibrissin*.]

SANNIE, C., H. LAPIN, & I. P. VARSHNEY. Sur les sapogénines d'*Albizzia Lebbek* Benth. Bull. Soc. Chim. France **11/12:** 1440–1444. 1957.*

SATTER, R. L., & A. W. GALSTON. Potassium flux: a common feature of *Albizzia* leaflet movement controlled by phytochrome or endogenous rhythm. Science **174:** 518–520. 1971a.

——— & ———. Phytochrome controlled nyctinasty in *Albizzia Julibrissin*. III. Interactions between an endogenous rhythm and phytochrome in control of potassium flux and leaflet movement. Pl. Physiol. **48:** 740–746. 1971b.

——— & ———. Leaf movements: Rosetta stone of plant behavior? BioScience **23:** 407–416. 1973. [Endogenous rhythms, phytochromes, potassium flux and *A. Julibrissin*, *Mimosa*, & *Samanea*; review to date; numerous references.]

———, P. B. APPLEWHITE, & A. W. GALSTON. Phytochrome-controlled nyctinasty in *Albizzia Julibrissin*. V. Evidence against acetylcholine participation. Pl. Physiol. **50:** 523–525. 1972.

———, P. MARINOFF, & A. W. GALSTON. Phytochrome controlled nyctinasty in *Albizzia Julibrissin*. II. Potassium flux as a basis for leaflet movement. Am. Jour. Bot. **57:** 916–926. 1970.

———, ———, & ———. Phytochrome controlled nyctinasty in *Albizzia Julibrissin*. IV. Auxin effects on leaflet movement and K flux. Pl. Physiol. **50:** 235–241. 1972.

———, D. D. SABNIS, & A. W. GALSTON. Phytochrome controlled nyctinasty in *Albizzia Julibrissin*. I. Anatomy and fine structure of the pulvinule. Am. Jour. Bot. **57:** 374–381. 1970.

SHAH, C. S., & A. R. BATTACHARYYA. Pharmacognostic study of *Albizzia Lebbek* Benth. bark. Jour. Sci. Industr. Res. **19C:** 199–203. 1960.*

TOOLE, E. R., & G. H. HEPTING. Selection and propagation of *Albizzia* for resistance to Fusarium wilt. Phytopathology **39:** 63–70. 1949.

WEBER, G. F. Vascular wilt of mimosa in Florida. Pl. Disease Rep. **41:** 640–642. 1957. [*Fusarium oxysporium* f. *perniciosum* on *A. Julibrissin*.]

9. **Pithecellobium** C. F. P. von Martius, Flora 20(2)(Beibl. 8): 114. 1837,[7] "Pithecollobium," nom. et orth. cons.

Trees or shrubs; bark smooth, often becoming rough in old trees, usually gray; sapwood often pungent, heartwood yellow to brown or almost to black; branches terete to angulate, unarmed or armed with persistent spinescent stipules, the branchlets with conspicuous, small pale lenticels. Leaves bipinnate [or rarely once-pinnate], petiolate [the pulvinus rarely subtended by large nectaries], the pinnae few to many-foliolate, a nectary usually present between the insertion of each pair of pinnae and often between the insertion of each pair of leaflets, the leaflets opposite [although the lower ones tend to be subalternate to alternate, occasionally the inner leaflet of the lowest pair absent]; stipules persistent and becoming spinescent [or large and foliaceous] or early caducous. Inflorescences of oblong spikes or racemes, globose heads, or pseudoumbels, pedunculate, the peduncles in terminal panicles or fascicled and axillary or fascicled and ramiflorous, the bracts minute, generally caducous. Flowers largely perfect [rarely the lower flowers functionally staminate], 5-(6)-merous, sessile to pedicellate. Calyx campanulate, with short lobes, glabrous to variously pubescent. Corolla infundibular, exceeding [or rarely equalling the calyx], the lobes short to long (up to 1/2 the length of the tube). Stamens numerous; filaments united into a tube generally equalling corolla tube, inserted near base of ovary; anthers minute, dorsifixed and versatile, eglandular; pollen in flattened, symmetrical 16-grained polyads. Stigma minute, terminal; style slender, filiform, exceeding stamens; ovary elongate, generally stipitate [rarely reduced or aborted], ovules numerous. Legume straight or curved, flattened to terete, 2-valved, dehiscent [or indehiscent], the valves continuous or interrupted within, dehiscence occurring along both sutures at the same time or proceeding from on the adaxial suture to the abaxial suture (usually incomplete), the valves becoming contorted after dehiscence. Seeds slightly to distinctly plano-compressed, oriented transversely in the fruit, the funiculus filiform or expanded into a conspicuous fleshy aril (in our species the aril red to white and the seeds hanging by the funiculus upon dehiscence of fruit); hilum subbasal; seed coat thick to thin, with a faint oval pleurogram; endosperm lacking, the embryo filling seed cavity, the radicle included or slightly exserted. Base chromosome number 13. (Including *Spiroloba* Raf.; *Siderocarpus* Small, not Pierre, 1888; *Havardia* Small; *Jupunba* Britton & Rose; *Cojoba* Britton & Rose; *Ebenopsis* Britton & Rose; *Painteria* Britton & Rose; *Chloroleucon* (Bentham) Britton & Rose; *Pseudalbizzia* Britton & Rose; *Abarema* Pittier; *Macrosamanea* Britton & Rose; *Klugiodendron* Britton & Rose; *Arthrosamanea* Britton & Rose; *Marmaroxylon* Killip; *Ortholobium* Gagnepain). LECTOTYPE SPECIES:

---

[7] The initial publication for *Pithecellobium* has often been cited as Martius, Hort. Reg. Monac. 188. 1829, but neither a description nor an illustration is given there. See Rickett & Stafleu, Taxon **8**: 288. 1959.

P. Unguis-cati (L.) Bentham (*Mimosa Unguis-cati* L.), typ. cons.; see ICBN 314. 1972, and Britton, N. Am. Trees 514. 1908. (Name from Greek, *pithekos*, ape, and *ellobion*, earring, from a Brazilian name [given by Martius as *brincos de sahoy*, monkey's earring] for one of the species, apparently in reference to the twisted fruit.)

The genus includes some 90 species distributed in tropical and subtropical habitats in both hemispheres, from southern Florida and Texas, the West Indies, Central and South America, and from tropical Asia, to Malesia and Australia. Of the five species that reach the southern United States, three, all of sect. PITHECELLOBIUM (sect. *Unguis-cati* Bentham), occur in southern Florida. *Pithecellobium flexicaule* (Bentham) Coulter and *P. pallens* (Bentham) Standley extend from Mexico northward into southern Texas. Our species are closely related and, as members of sect. PITHECELLOBIUM are characterized by spinescent stipules (except in *P. guadalupense*), leaves with (1 or) 2 to several pinnae and several pairs of leaflets, fruits with valves that are contorted after dehiscence, and arillate seeds.

A small, flat-topped shrub or tree, *Pithecellobium guadalupense* (Pers.) Chapman (*P. keyense* Britton), $2n = 26$, Guadeloupe blackbead, is characterized by leaves that generally lack spinescent stipules and have persistent, coriaceous, obovate to nearly orbicular leaflets. The pattern of branching is irregular, like that of many other species of the genus. The plant occurs in rocky or sandy soil in pine woods, in hammocks, and on open sand dunes of southern Florida, including the Keys. It is widely distributed in the West Indies and occurs in the Yucatán Peninsula. Flowering usually is from October through March. The flowers are aggregated in dense globose heads that are, in turn, borne in terminal panicles. The pink upper halves of the filaments produce an over-all effect of pink flowers.

A shrub or small tree, *Pithecellobium Unguis-cati*, catclaw blackbead, has angulate branchlets and leaves with stipular spines and persistent, chartaceous, obliquely obovate to oblong leaflets. In our area this species is restricted to southern peninsular Florida, including the Keys; its distribution elsewhere has been difficult to determine because it has been confused with other species, but Little (1953) included the West Indies, Mexico, Central America, and northern South America. As in *P. guadalupense*, the flowers are borne in globose heads, and the filaments give the inflorescences their pinkish to yellow color. The terminal panicle of inflorescences of both these species is more compact than in *P. dulce*. The black seeds of both this and the preceding species have a bright red aril.

The third species, *Pithecellobium dulce* (Roxb.) Bentham (*Mimosa dulcis* Roxb., *Feuilleea dulcis* (Roxb.) Kuntze), $2n = 26$, is a small to medium-sized tree with leaves with stipular spines and persistent, chartaceous to subcoriaceous, strongly oblique oblong leaflets. The whitish heads of flowers are borne on short peduncles in a narrow panicle. The arils of the black seeds are white to pink, acidulous, and edible (cf. Standley). Indigenous from Baja California to northern South America, *P. dulce* is widely planted elsewhere, and it was an early introduction into the Philippines. Lakela & Craighead and Long & Lakela have reported it as occurring in Collier County, Florida, and several presumably wild individuals have been found in Dade County, as well. It is presumably an escape from cultivation in our area.

The generic limits of *Pithecellobium* have been interpreted quite variously. Bentham at first (1844) recognized 75 species in eight sections but he later (1875) placed 108 species in seven sections. Britton & Rose's narrow concept of *Pithecellobium* (1928) led to the description of a number of new genera based mainly on fruit characters, and, to a lesser extent, on the position of the inflorescence. Students of neotropical plants have largely rejected these segregate genera as artificial, but Kostermans (1954) has split the Old World species into 11 genera, describing six of them as new and restricting *Pithecellobium* to the New World. He relied heavily on fruit and seed characters, the presence or absence of spines, and, to a lesser degree, on the position of the inflorescence. Mohlenbrock (1963a, b), employing a broader generic concept, although maintaining a number of the segregates (e.g., *Havardia*, *Pseudalbizzia*), reduced the Old World *Archidendron* to sectional rank under *Pithecellobium* and recognized five additional sections in the genus. In his concept *Pithecellobium* includes all those species in which the valves of the fruit become spirally contorted after dehiscence. Since the splintering of this large and loose assemblage into numerous seemingly artificial segregate genera does not solve the taxonomic problems, it seems better for the present to treat *Pithecellobium* in the broad sense.

Most species of *Pithecellobium* are plants of the margins of forests and waterways in tropical and subtropical areas. They are also found in developing secondary forest. The species found in pioneer vegetation and in unstable habitats typically have dehiscent pods with dangling seeds and conspicuous arils, adaptations for bird dispersal. Species that are restricted to the secondary tree element of mature rain forest usually have indehiscent, somewhat fleshy fruits that are dispersed by mammals. Van der Pijl (1956) has also cited water as a dispersal agent for those species that occur along waterways and that also have dry fruits and seeds that lack an aril. In the three species that occur in the southeastern United States the pods twist and coil in a loose spiral during dehiscence. The seeds have a conspicuous aril, are shiny black, and hang free by the funiculus. The seeds of all three presumably are dispersed by birds (cf. Ridley, 1930; van der Pijl, 1956).

Palynologically, *Pithecellobium* is specialized, with its pollen arranged in flattened, radially symmetrical 16- or 32-grained polyads similar to those of *Inga*, *Affonsea*, *Lysiloma*, and most species of *Calliandra*. The individual grains are usually pyramidal to oval in shape, generally 6–8-porate, and paraisopolar to heteropolar.

Apparently the chromosome numbers of only eight species of *Pithecel-*

lobium have been reported. Seven of these are diploids, $2n = 26$, and *P. polycephalum* is reported to be a tetraploid, $2n = 52$.

The wood is of very limited use, since plants of most species of the genus are small, often much-branched trees. The wood is hard, heavy, and strong, but brittle, and it is used mainly for fence posts and for fuel. The bark yields a yellow dye that has been used in tropical America for tanning skins (Record & Hess, 1943). Record & Hess also report that the bark is used in decoctions for its astringent properties.

REFERENCES:

Under subfamily references see ATCHISON, 1951, p. 542; BENTHAM, 1844, p. 195, and 1875, p. 570; BERGER, WITKUS & MCMAHON; BOLKHOVSKIKH *et al.*, p. 314; BRENAN; COMPTON, pp. 8, 9; GRAHAM; GUINET; HUTCHINSON; LITTLE, pp. 275–277; LITTLE & WADSWORTH; RECORD & HESS, p. 308; SCHERY, p. 211; SORSA; VINES, p. 514.

BRITTON, N. L. The genus *Pithecellobium* in Cuba. *In*: Studies of West Indian plants — V. Bull. Torrey Bot. Club **41**: 1–24. 1914. [*Pithecellobium*, 2–8; recognizes 19 spp., 7 of them new.]

ELIAS, T. S. Morphology and anatomy of foliar nectaries of *Inga* and *Pithecellobium* (Leguminosae). (Abstr.) Am. Jour. Bot. **57**: 744. 1970. [Includes *P. macradenium*.]

GOVINDARAJALU, E., & B. G. L. SWAMY. Size variations of septate wood fibers in *Pithecellobium dulce* Benth. Nature **176**: 315. 1955.

KOSTERMANS, A. J. G. H. A monograph of the Asiatic, Malaysian, Australian, and Pacific species of the Mimosaceae formerly included in *Pithecellobium* Mart. Bull. Organ. Sci. Res. Indonesia **20**: 1–122. 1954. [11 genera, 6 new, are distinguished.]

LAKELA, O., & F. C. CRAIGHEAD. Annotated checklist of the vascular plants of Collier, Dade, and Monroe counties, Florida. vii + 95 pp. Coral Gables, Florida. 1965. [*Pithecellobium*, 47.]

MERRILL, E. D. The systematic position of the "rain tree," *Pithecellobium Saman*. Jour. Washington Acad. Sci. **6**: 42–48. 1916. [*Samanea Saman* (Jacq.) Merr.]

SMALL, J. K. *Pithecellobium guadalupense*. Addisonia **1**: 51, 52. *pl. 26*. 1916.

SPRAGUE, T. A. The correct spelling of certain generic names: V. Bull. Misc. Inf. Bot. Gard. Kew **1929**: 241–243. 1929. [*Pithecellobium*, 243.]

STANDLEY, P. C. Mimosaceae *in* Trees and shrubs of Mexico. Contr. U. S. Natl. Herb. **23**: 348–400. 1922. [*Pithecellobium*, 391–397; includes the 3 spp. of our area.]

ARNOLD ARBORETUM
HARVARD UNIVERSITY
CAMBRIDGE, MASSACHUSETTS 02138

Present address:
CARY ARBORETUM
NEW YORK BOTANICAL GARDEN
MILLBROOK, NEW YORK 12545

THE SECONDARY PHLOEM OF AMENTOTAXUS

R. W. DEN OUTER and E. TOES

THE SYSTEMATIC POSITION of *Amentotaxus* is uncertain (Keng, 1969). It is placed either in the Taxaceae, Cephalotaxaceae, or in a separate family, the Amentotaxaceae (Kudo & Yamamoto, 1931; Li, 1963). The genus is held to represent only one species, i.e. *A. argotaenia* (Hance) Pilger (Kudo & Yamamoto), or four species, i.e. *A. argotaenia* (Hance) Pilger, *A. cathayensis* Li, *A. formosana* Li, and *A. yunnanensis* Li (Li, 1952), or three species, i.e. *A. argotaenia* (Hance) Pilger, *A. formosana* Li, and *A. yunnanensis* Li (Hu, 1964). Finally Chuang & Hu (1963) identify *A. formosana* Li with *A. argotaenia* (Hance) Pilger.

Because of all these different opinions, further investigations seem advisable. Although hampered by the lack of suitable material, Miller (1973) made a comparative study of the secondary xylem. He concluded that a) at the specific level taxonomic evaluation is not possible, or that b) *Amentotaxus* is monotypic. A comparative study of the secondary phloem is even more difficult, because fresh material is preferable for this purpose. The present investigation deals with the comparison of *A. argotaenia* (Hance) Pilger *sensu stricto* with some other representatives of the Taxaceae and Cephalotaxaceae.

MATERIAL

Twig material of *A. argotaenia* (Hance) Pilger *sensu stricto* was obtained from Hong Kong (Lantao Peak, Lantao Island) via Dr. D. K. Ferguson of the University of Antwerp. Using an increment borer with a diameter of 5 mm., fresh samples were taken from trees of *Taxus baccata* L., *Torreya grandis* Fortune, and *Cephalotaxus harringtonia* (Forbes) K. Koch. These trees in the Arboretum "De Dreyen" at Wageningen, had a diameter of approximately 15 cm. at breast height. Two stem samples of *Austrotaxus spicata* Compt. were obtained via Dr. A. M. W. Mennega and H. J. Miller from Sweden (Stockholm nr. *233*) and Australia (D. F. P. *32.479*).

RESULTS

The results of the investigation are shown in the following table.

TABLE 1. A comparison of Amentotaxus argotaenia with some genera of the Taxaceae and Cephalotaxaceae.

	TAXUS BACCATA	TORREYA GRANDIS	CEPHALOTAXUS HARRINGTONIA	AUSTROTAXUS SPICATA	AMENTOTAXUS ARGOTAENIA
Sequence of alternating tg. layers of cells	sieve cells–crystal cells–sieve cells–parenchyma cells–etc.	sieve cells–parenchyma cells–etc.	sieve cells–1 (to 3) layers parenchyma cells–etc.	sieve cells–parenchyma cells–etc.	1 to 10 (often 5) layers of sieve cells–parenchyma cells–etc.
Growth ring boundary	inconspicuous	inconspicuous	indistinct	indistinct	indistinct
Sieve cells:					
shape	fiber; rectangular in cross section	as in *Taxus*	as in *Taxus*	as in *Taxus*	as in *Taxus*
measurements	8–15 μm rd. 10–25 μm tg. ± 1250 μm lg.	as in *Taxus* as in *Taxus* ± 800 μm lg.	as in *Taxus* as in *Taxus* ± 900 μm lg.	as in *Taxus* as in *Taxus* ?	6–12 μm rd. 10–30 μm tg. ± 1600 μm lg.
sieve areas	in rd. walls; round to oval; 10–15 μm	as in *Taxus*; rounded to angular; as in *Taxus*	as in *Taxus*; rounded to angular; as in *Taxus*	as in *Taxus*; rounded to angular; as in *Taxus*	as in *Taxus*; rounded to oval; as in *Taxus*
collapsed from	third period	as in *Taxus*	as in *Taxus*	second period	second period
Albuminous cells	in the layers of phloem-parenchyma cells, mostly in lg. strands	as in *Taxus*	as in *Taxus*	?	?
Phloem-parenchyma cells:					
shape in conducting phloem	fiber; rectangular in cross section 10–20 μm rd. 20–25 μm tg.	as in *Taxus* as in *Taxus* as in *Taxus*	as in *Taxus* as in *Taxus* as in *Taxus*	as in *Taxus* as in *Taxus* as in *Taxus*	as in *Taxus* 8–15 μm rd. 10–30 μm tg.
shape in nonconducting phloem	fiber; oval to round in cross section; 30–40 μm rd.	as in *Taxus*	as in *Taxus*	as in *Taxus*	fiber; oval in cross section; 25–45 μm rd. 15–30 μm tg.
number of cells per fiber	6–16	5–18	6–16	5–20	5–20
lg. measurements of cells	50–200 μm	70–180 μm	50–200 μm	50–200 μm	80–200 μm
pits	mainly in radial and transverse walls	as in *Taxus*	as in *Taxus*	as in *Taxus*	as in *Taxus*
transverse walls	nodular	nodular	almost smooth	smooth	nodular
Sclereids:					
shape	fiber; bone-shaped in cross section	fiber; round to rectangular in cross section	fiber; round to rectangular in cross section	fiber; round to oval in cross section	irregular; oval in cross section; almost no lumen
measurements	1250–3000 μm lg.	1000–2000 μm. lg.	1000–1750 μm lg.	up to 1 cm. lg.	1000–1750 μm lg.
crystals	in outer cell wall	in outer cell wall	absent	absent	in outer cell wall
arrangement	irregular in tg. layers; every 3 or 4 [2 – ∞] period	irregular in tg. layers; every 1 or 2 period	in tg. layers, sometimes 4 cells wide; every 3 or 4 period	in long tg. layers, every 2 period	scattered, single
pits	mainly in radial walls	as in *Taxus*	as in *Taxus*	as in *Taxus*	as in *Taxus*
first present from	the 4 period on	the 2 period on	the 3 period on	the 2 period on	the 4 period on
originated from	crystal cells	crystal cells	phloem-parenchyma cells	phloem-parenchyma cells	crystal cells
Crystal cells	present	present	absent	absent	present
Phloem rays:					
direction	first oblique, afterwards radial	radial	radial	almost radial	first oblique, afterwards radial
width	uniseriate	uniseriate	uniseriate, sometimes biseriate	uniseriate	uniseriate
height in cells	1–16	1–13	1–15	1–10	[illegible]
measurements	35–50 μm rd. 15–30 μm tg. 15–35 μm lg.	20–60 μm rd. 15–50 μm tg. 15–50 μm lg.	35–65 μm rd. 13–30 μm tg. 13–40 μm lg.	10–50 μm rd. 13–30 μm tg. 15–35 μm lg.	[illegible] rd. [illegible] tg. 15–40 μm lg.

Abbreviations used in TABLE 1: rd. = radial, tg. = tangential, lg. = longitudinal; μm = micrometer [replaces "micron"]

CONCLUSIONS

Amentotaxus argotaenia (Hance) Pilger *sensu stricto* differs from the other investigated species in the following characteristic features: the axial system is, for the greater part, composed of sieve cells. They constitute tangential bands 1 to 10 (often 5) cells wide, alternating regularly with tangential layers of phloem-parenchyma cells 1 cell wide; sclereids, originated from either phloem-parenchyma cells or crystal cells, lie scattered in the nonconducting phloem, irregular, thus not in tangential layers; the rays are 1 to 4 cells high; the sieve cells are rather long. These differences in the characteristics of the secondary phloem are not sufficient to decide whether *Amentotaxus* should be placed in the Taxaceae or in the Cephalotaxaceae, or even in a separate family, the Amentotaxaceae.

Additional investigations are advisable, but only if and when fresh material is available.

ACKNOWLEDGMENTS

Our sincere thanks to Dr. D. K. Ferguson of the University of Antwerp and to Dr. A. M. W. Mennega and H. J. Miller of the State University of Utrecht, for providing the valuable bark samples.

REFERENCES:

CHUANG, T. I., & W. W. L. HU. 1963. Study of *Amentotaxus argotaenia* (Hance) Pilger. Bot. Bull. Acad. Sin. **4**(1): 10–14.

HU, S. Y. 1964. Notes on the flora of China IV. Gymnospermae. Taiwania, **10**(1): 13–62.

KENG, H. 1969. Aspects of morphology of *Amentotaxus formosana* with a note on the taxonomic position of the genus. Jour. Arnold Arb. **50**: 432–445.

KUDO, Y., & Y. YAMAMOTO. 1931. Amentotaxaceae. *In*: KUDO, Y., Materials for a flora of Formosa, IV. Jour. Soc. Trop. Agric. (Taihoku) 3(2): 110, 111.

LI, H. L. 1952. The genus *Amentotaxus*. Jour. Arnold Arb. **33**: 192–198.

———. 1963. Woody flora of Taiwan. Livingstone Publ. Co., Narberth, Pennsylvania, Pp. 36, 37.

MILLER, H. J. 1973. The wood of*Amentotaxus*. Jour. Arnold Arb. **54**(1): 111–119.

DEPARTMENT OF BOTANY
AGRICULTURAL UNIVERSITY, WAGENINGEN
THE NETHERLANDS

U S POSTAL SERVICE

STATEMENT OF OWNERSHIP, MANAGEMENT AND CIRCULATION

(Act of August 12, 1970 Section 3685 Title 39 United States Code.

SEE INSTRUCTIONS ON PAGE 2 (REVERSE)

1. TITLE OF PUBLICATION
Journal of the Arnold Arboretum

2. DATE OF FILING
October 1, 1973

3. FREQUENCY OF ISSUE
Quarterly (January, April, July, October)

4. LOCATION OF KNOWN OFFICE OF PUBLICATION *(Street city, county, state ZIP code) (Not printers*
22 Divinity Avenue, Cambridge, Massachusetts 02138

5. LOCATION OF THE HEADQUARTERS OR GENERAL BUSINESS OFFICES OF THE PUBLISHERS *(Not printers*
22 Divinity Avenue, Cambridge, Massachusetts 02138

6. NAMES AND ADDRESSES OF PUBLISHER, EDITOR, AND MANAGING EDITOR

PUBLISHER *(Name and address)*
The Arnold Arboretum of Harvard Univ., 22 Divinity Ave., Cambridge, Mass. 02138

EDITOR *(Name and address)*
Bernice G. Schubert, 22 Divinity Avenue, Cambridge, Mass. 02138

MANAGER EDITOR *(Name and address)*
Kathleen A. Clagett, 22 Divinity Avenue, Cambridge, Mass. 02138

7. OWNER *(If owned by a corporation, its name and address must be stated and also immediately thereunder the names and addresses of stockholders owning or holding 1 percent or more of total amount of stock. If not owned by a corporation, the names and addresses of the individual owners must be given. If owned by a partnership or other unincorporated firm, its name and address, as well as that of each individual must be given.)*

NAME	ADDRESS
The Arnold Arboretum of Harvard University	22 Divinity Avenue Cambridge, Massachusetts 02138

8. KNOWN BONDHOLDERS, MORTGAGEES, AND OTHER SECURITY HOLDERS OWNING OR HOLDING 1 PERCENT OR MORE OF TOTAL AMOUNT OF BONDS, MORTGAGES OR OTHER SECURITIES *(If there are none, so state)*

NAME	ADDRESS
The President and Fellows of Harvard University	Cambridge, Massachusetts 02138

9. FOR OPTIONAL COMPLETION BY PUBLISHERS MAILING AT THE REGULAR RATES (Section 132.121, Postal Service Manual)

39 U. S. C. 3626 provides in pertinent part. "No person who would have been entitled to mail matter under former section 4359 of this title shall mail such matter at the rates provided under this subsection unless he files annually with the Postal Service a written request for permission to mail matter at such rates."

In accordance with the provisions of this statute I hereby request permission to mail the publication named in Item 1 at the reduced postage rates presently authorized by 39 U. S. C. 3626.

(Signature and title of editor, publisher, business manager, or owner)
Bernice G. Schubert, Editor

10. FOR COMPLETION BY NONPROFIT ORGANIZATIONS AUTHORIZED TO MAIL AT SPECIAL RATES *(Section 132.122 Postal Manual)*

(Check one)

The purpose, function, and nonprofit status of this organization and the exempt status for Federal income tax purposes ☑ Have not changed during preceding 12 months ☐ Have changed during preceding 12 months *(If changed, publisher must submit explanation of change with this statement.)*

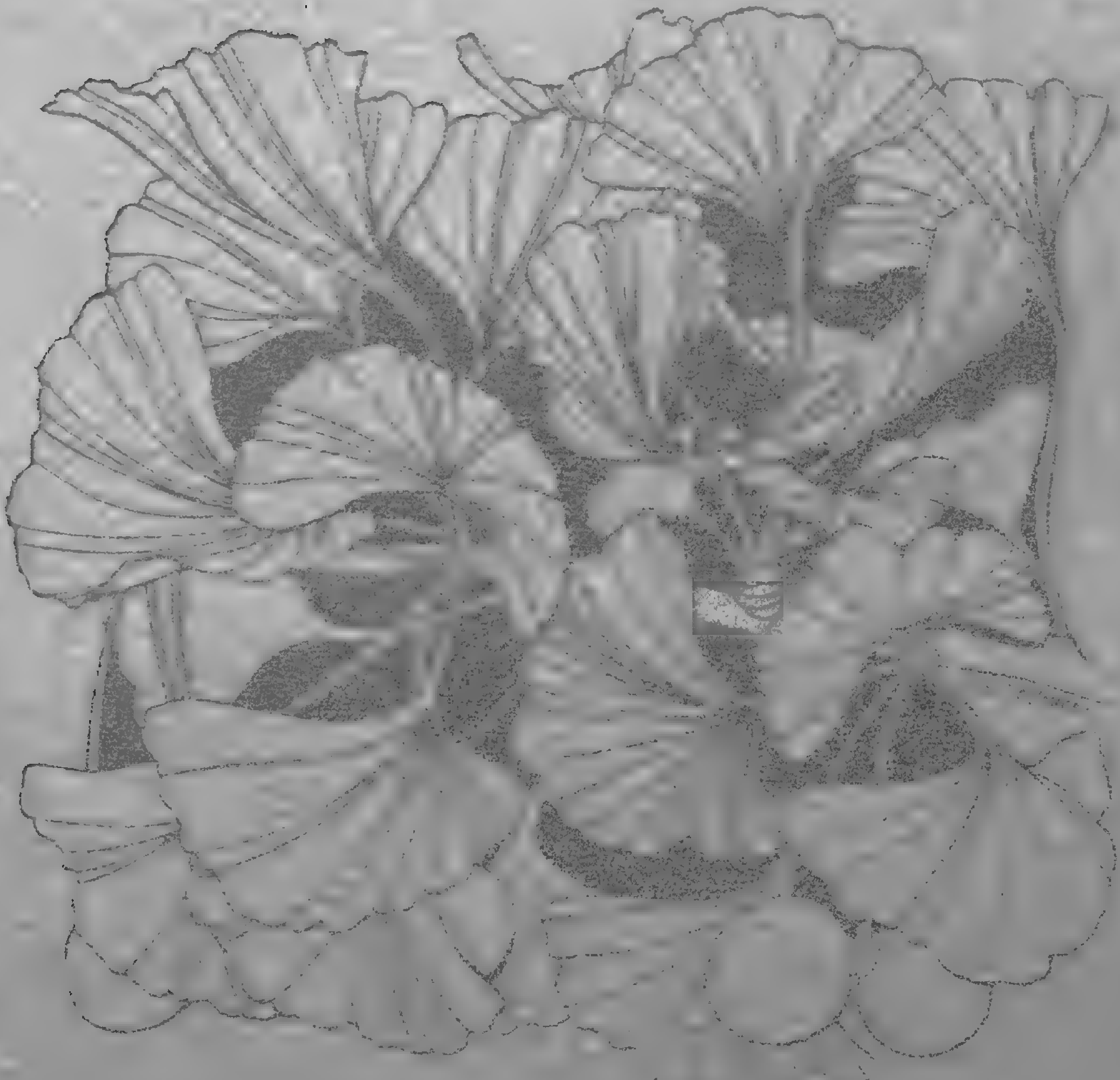
11. EXTENT AND NATURE OF CIRCULATION	AVERAGE NO. COPIES EACH ISSUE DURING PRECEDING 12 MONTHS	ACTUAL NUMBER OF COPIES OF SINGLE ISSUE PUBLISHED NEAREST TO FILING DATE
A. TOTAL NO. COPIES PRINTED *(Net Press Run)*	750	750
B. PAID CIRCULATION 1. SALES THROUGH DEALERS AND CARRIERS, STREET VENDORS AND COUNTER SALES	none	none
2. MAIL SUBSCRIPTIONS	620	635
C. TOTAL PAID CIRCULATION	620	635
D. FREE DISTRIBUTION BY MAIL, CARRIER OR OTHER MEANS 1. SAMPLES, COMPLIMENTARY, AND OTHER FREE COPIES	2	3
2. COPIES DISTRIBUTED TO NEWS AGENTS, BUT NOT SOLD	none	none
E. TOTAL DISTRIBUTION *(Sum of C and D)*	622	638
F. OFFICE USE, LEFT-OVER, UNACCOUNTED, SPOILED AFTER PRINTING	128	112
G. TOTAL *(Sum of E & F—should equal net press run shown in A)*	750	750

I certify that the statements made by me above are correct and complete

(Signature of editor, publisher, business manager, or owner)
Bernice G. Schubert

PS Form 3526 July 1971

JOURNAL OF THE ARNOLD ARBORETUM



Volume 55 HARVARD UNIVERSITY Number 2

MISSOURI BOTANICAL

JUN 11 1974

GARDEN LIBRARY

ISSN 0004-2625

Journal of the Arnold Arboretum

Published quarterly in January, April, July, and October by the Arnold Arboretum, Harvard University.

Subscription price $16.00 per year.

Subscriptions and remittances should be sent to Ms. Kathleen Clagett, Arnold Arboretum, 22 Divinity Avenue, Cambridge, Massachusetts 02138, U.S.A. Claims will not be accepted after six months from the date of issue.

Volumes I-XLV, reprinted, and some back numbers of volumes 46-50 are available from the Kraus Reprint Corporation, Route 100, Millwood, New York 10546, U.S.A.

EDITORIAL STAFF

B. G. Schubert, Editor

C. E. Wood, Jr.

S. A. Spongberg

CIRCULATION

K. Clagett

Printed at the Harvard University Printing Office, Boston, Massachusetts

COVER: *Ginkgo biloba* L., the maidenhair tree, so-called from the fancied resemblance of its leaves to those of the maidenhair fern. In China it has also been called the silver apricot, from the hard inner seed coat which is silvery when cleaned and vaguely resembles an apricot pit, and the duck-foot tree, from the resemblance of the leaves to the webbed feet of ducks.

The drawing for the cover and the devices for the back cover and reprints were planned and drawn by Karen Stoutsenberger Velmure from specimens taken from a tree cultivated in the Arnold Arboretum of Harvard University.

We want to assure the purists among our readers that our *Ginkgo* does not have leaves with open parallel venation. We think, however, that an exact reproduction of the dense dichotomous veins would have produced a much less dramatic design.

Second-class postage paid at Boston, Massachusetts

JOURNAL
OF THE
ARNOLD ARBORETUM

VOL. 55 APRIL 1974 NUMBER 2

THE STEM-NODE-LEAF CONTINUUM OF THE DICOTYLEDONEAE

RICHARD A. HOWARD

ALTHOUGH THE STEM, the node, and the leaf are treated as individual structures in many textbooks of general botany or plant anatomy, an understanding of the internal structure of any one of these is associated with information from the adjacent structure. The stem-node-leaf is a continuum of cells and tissues. An excellent article by Wetmore and Steeves (1971) considers the continuum from the developmental point of view and was written for the physiologically oriented reader.

The present study is derived from a survey of the structure of the node and the petiole to be contributed to a new edition of Metcalfe and Chalk's *Anatomy of the Dicotyledons*. Stems and leaves of representatives of every family of the Dicotyledoneae have been examined. For each family of the Takhtajan system to be followed in the new edition of *Anatomy of the Dicotyledons* (Metcalfe 1972) a description will be given there of the patterns of vascular tissue found in the internode, the node, the petiole, and the leaf blade to its apex, as revealed in a series of sections.

The material following here is a summary of the considerations needed in order to obtain a proper interpretation of the vascular patterns seen at the various levels of the stem-node-leaf continuum.

LEAF DEVELOPMENT

The development of the foliage leaf has been considered in detail for a relatively few dicotyledons, when one considers the number of taxa recognized in the class. Yet morphologists suggest that there is a basic pattern of development which is common to leaves in general, and that the difference in final form of the mature leaf can be explained in variations on one morphogenetic theme (Wetmore & Steeves 1971).

Upon and within the apex of the stem, a primordium of a leaf is distinguishable in a definite relationship to other primordia, which is expressed eventually as the phyllotaxy of leaves on a stem. This arrangement may be established as alternate, opposite, whorled, or orixiate

(Maekawa 1948). A distichous arrangement is considered to be superimposed.

Wetmore and Steeves (1971) reviewed the experimental work that has been done on leaf primordia, and Wetmore and Garrison (1966) are among the recent authors to state that "incontrovertible evidence now exists that primordia when produced on the apex are uncommitted. It is their natural biochemical milieu which determines their developmental destiny whether leaf or bud." Surgical isolation allows young leaf primordia to appear as buds.

The leaf primordium undergoes a period of growth, establishing a foliar axis, and perhaps, by basal elongation, the stem. The existence of recognizable areas within the primordium, variously termed soubassement, leaf buttress, leaf base, Unterblatt, and Oberblatt, has been suggested by some authors and denied by others.

The axis of the foliar primordium develops an adaxial meristem responsible for the thickening of a midrib region. An apical meristematic zone of the primordium may continue temporarily the elongation of the primordium. Marginal meristems along the foliar axis develop either the lamina of a simple leaf or the leaflets of a pinnately compound leaf. Divisions at the apex of the primordium develop the leaflets of a palmately compound leaf. Multidirectional expansion of an apical meristematic area produces the ascidiate or peltate leaf blade. Subsequent intercalary growth may be responsible for the petiolar area or the regions of the rachis between blade lobes or pinnae of compound leaves. The timing and relative development of each of these meristematic potentials can explain the form and size of the ultimate leaf (Kaplan 1970a, 1970b).

During its development, meristematic activity of cells within the leaf may be restricted and finally cease, with the subsequent enlargement being caused only by increase in cell size. The dicotyledonous leaf is generally assumed to have limited terminal growth. Examples of continued apical growth have been reported in the Meliaceae (Skutch 1946), while variable development of laminar portions of the blade and the axis of simple leaves is evident in tendrils of *Mutis* spp., *Triphyllophyllum*, and interrupted blade development in *Nepenthes* and *Codiaeum*. Residual meristematic activity of other cells is evident in the production of "leaf-plantlet meristems" (Warden 1971–72) normally in *Bryophyllum* spp. and in *Tolmeia menziesii*, or in the vegetative "leaf cutting" reproduction of many Gesneriaceae, Begoniaceae, etc. Limitation of expansion of the leaf may be due, in part, to the maturation of tissues, that is, the production of xylem and the development of a cambium and secondary tissues, and even the maturation of the mesophyll cells. However, the pulvinal areas may never develop sufficient quantities of xylem tissue to be considered incapable of further elongation or meristematic development.

Vegetative propagation of dicotyledons from leaf cuttings indicates a residual meristematic potential in some herbaceous plants. No woody plants are known to be reproduced from leaf or petiole cuttings alone. *Saintpaulia*, *Begonia*, *Peperomia*, are examples of plants which can be reproduced with ease from petiole plus blade cuttings. Reproduction from portions of the leaf blade are considered practical by the nurseryman only when they involve a portion of the midvein or a lateral vein. Regeneration is believed to come from dedifferentiation of some mature cells or from callus.

As the primordium develops into a recognizable leaf form, the vascular system is differentiated in stages, first as a procambial stage, and subsequently as xylem and phloem. The differentiation of the procambium is generally described as acropetal, taking place while the primordium is still undergoing cell division and even elongation. Differentiation of the phloem from the procambium is acropetal into the leaf primordium. Later, differentiation of xylem begins at the base of the leaf primordium and develops acropetally into the leaf and basipetally into the stem. The continuity of conducting tissue from the stem into the leaf is thus established and recognized as the primary vascular system.

In general, developmental studies have been concerned with primordia and very immature leaves. No literature seems to concern the development of the many varied and complex patterns of arrangement of mature vascular tissues in the petiole of the mature leaf, or how such complexities are established in an interpolated organ. The independence of bundle development is specified in a few ontogenetic studies. Although it appears from most studies that the median bundle extends into the developing leaf at a faster rate than lateral traces, Kaplan has shown (1970a) examples of the more rapid acropetal development of the primary lateral traces. The need for later stage developmental studies represents a serious lack of information when one considers that the leaf primordium may: interpolate a petiole; separate the rachis with or without articulations in the development of pinnate compound leaves; develop one to many pulvini; and form accessory foliage organs or appendages as stipules, stipels, thorns or glands.

THE PRIMARY VASCULAR SYSTEM

Shortly below the apical meristem of most shoots of the dicotyledons the primary body can be recognized as the vascular tissue, the pith, and the cortex. In cross sections the vascular tissue may be a continuous ring; that is, a siphonostele, or a series of discrete bundles, a eustele. Whether or not all of the vascular tissue is to be regarded as of leaf origin remains a matter of dispute. Some authors refer to the discrete bundles of the stem as traces, noting the ultimate departure of the tissue into the leaves. Other authors, noting the identity of the bundle for several internodes, refer to some bundles either as "stelar" or "cauline" bundles (Dormer 1972), thus distinguishing them from their branches or leaf traces, or as sympodia, indicating their multiple nature as branched or fused units. The primary vascular tissue can be recognized as occurring in many patterns until the development of metaxylem or secondary tissues makes the patterns obscure (Esau 1965). The patterns which have been described as "vascular systems" are based on a study of the path of the leaf traces down the stem. Individual traces, upon association with others in the stem, may join with them in entirety or by bifurcation to establish the vascular continuity. This may occur immediately below the node or at a greater distance involving several internodes. Generally the path downward is helical and associated with a spiral phyllotaxy, but in distichous or decussate leaves the path may be straight.

The studies of "eustelic" systems have been dominant in the literature, primarily due to the ease of obtaining these from seedlings or herbaceous plants. Dormer (1945) classified the vascular systems as "open" or "closed." The closed system is essentially a reticulum or network of bundles which branch or anastomose, depending on the direction the author accepts for his terminology, to or from the leaves. The open system is characterized by bundles which branch, but only exceptionally rejoin. Dormer did recognize that there were intermediates, or that both types could occur in the same vascular system. The "branches" from either system are the traces which enter the leaves, and the vascular tissue from which the branch originated is termed a stem bundle or a sympodium.

Most authors now attempt to illustrate diagrammatically the primary vascular system by assuming that the stem could be slit along one side and flattened. The vascular system is then shown in two dimensions, and the sympodia or cauline bundles are usually illustrated as heavier lines, the traces to leaves as lighter lines. The number of sympodia may be of descriptive value (e.g., the symmetrical six-fold to symmetrical twelve-fold systems, Slade 1971), as well as the nature of the branch trace pattern as cathodic or anodic into the meshes or interstices. The diagrams show the open system as unconnected vertical paths of vascular tissue, and the closed system as a reticulum of anastomosing tissues. Opposite, decussate, distichous, alternate or whorled-leaf arrangements can be correlated with unilacunar, trilacunar, or multilacunar nodes. Cortical or medullary bundles can be superimposed on such a diagram (Balfour & Philipson 1962). The vascular supply to axillary buds or branches has been generally neglected in such studies, although Dormer (1972) illustrates by diagrams some of the patterns previously reported.

Philipson and Balfour (1963) reviewed and illustrated the primary vascular system patterns recognized to that time. Subsequently Jensen's (1968) study of the Crassulaceae, which recognized sixteen patterns within one family, indicates that the survey is far from complete.

Benzing (1967a, 1967b) studied the primary xylem of the "woody Ranales," in which a pseudosiphonostele (Bailey & Nast, 1948) is present rather than the eustele studied by other authors. In a pseudosiphonostele there is a continuous ring of procambium and primary phloem near the stem apex, but the protoxylem is circumferentially discontinuous. What appears to be a single leaf trace to a unilacunar node or the individual traces of a trilacunar node may be, in fact, one or several strands of protoxylem exhibiting both "open" and "closed" systems in a variation of the application of those terms from that used by Dormer and others. By following the path of a protoxylem in species with unilacunar, trilacunar, and multilacunar nodes, additional diverse protoxylem strand patterns were recognized.

Benzing concluded from his evidence that the primitive node in the Angiospermae was a one-trace node (one protoxylem strand), either unilacunar or trilacunar in nature. He suggested that the two-trace unilacunar node of the *Clerodendrum* type (Marsden & Bailey 1955) is derived.

The descriptive value of the primary vascular system and/or the protoxylem patterns has been demonstrated. In the eustelic type of vascular system, the primary vascular pattern may be retained in the mature plant. In most woody plants, however, the primary vascular pattern is evident only in the upper few immature nodes and internodal portions of the shoot, due to the obscuring effect of cambial activity.

BUDS AND BRANCHES

By factors still unknown at the present time, the products of the apical meristem may be variable in regular or irregular sequences. One can consider as a unit of seasonal growth the stem and associated appendages produced during a growth interval, a season for example. The terminal bud of a temperate area woody plant extends in length until another terminal bud is formed, and this amount of growth is here termed a seasonal-unit, for Wetmore and Steeves (1971) have accepted the internode as the "growth unit." The appendages produced on this seasonal-unit may vary in size from scales such as prophylls or cataphylls, to eophylls, or to full foliage leaves. The seasonal-unit may have the smaller appendages at the base, larger ones in the middle, and either a gradual reduction in appendage size near the apex, or an abrupt reduction in size to the protective bud scales and the stem apex within the terminal bud. The mature foliage leaves may be largest at the base of the seasonal-unit, at the middle, or at the upper end.

Internodal elongation may be negligible at the base of the seasonal-unit, evident almost as in short shoots, and also at the apex of the seasonal-unit by the approximation of the foliage leaves below the terminal bud. In contrast, the basal internodes of the seasonal-unit may be greatly extended to form a hypopodium with cataphylls in great size contrast to the other nodes and internodes.

By the time a fourth leaf primordium has been differentiated at the stem apex, there may be evidence of an axillary bud in *Syringa* (Garrison 1949, Wetmore & Garrison 1966). The time of axillary bud initiation appears to vary in different taxa, although it is fairly consistent within the taxon (Wetmore & Steeves 1971). Buds are usually produced singly in the axils of foliage leaves, but they may be in multiples arranged horizontally or vertically or even extra-axillary in position. Buds may be sunken in stem tissue and covered by cortical tissue or protected by a sheath or by a concave petiole base.

The buds along a seasonal-unit may be vegetative buds or floral buds, or both may be present in the axil of a given leaf. Leaves at the basal nodes of a seasonal-unit may have the buds reduced in size, or they may be completely lacking. The production of vegetative or flower buds and the conversion of one type to the other have been demonstrated in the literature (Wetmore & Steeves 1971). No studies appear to have been made of the occurrence of both types of buds in axillary positions in many flowering plants. When two or more vertically arranged buds are present in the axil of the foliage leaf, either the upper or the lower bud alone may develop, or neither or several in apparently characteristic patterns. Thimann (1961, 1972) attributes the lack of bud formation in some nodes to the inhibiting effect of the leaves present, while the elongation of buds can be controlled by the balance between auxin and kinetin. Axillary vegetative buds may develop in a given growth period of (sylleptic) shoots, or be retarded, as in many temperate plants (proleptic), and develop only during the second year. In some genera the development of an axillary vegetative bud may be restricted by the conversion of the apex to a spine by the abrupt reduction of the apical meristem.

Flower buds are also produced in characteristic patterns of terminal, axillary, or extra-axillary positions. Within the seasonal-unit the flowers may be produced in all leaf axils, only in the lower leaf axils, at the middle, or in the upper leaf axils. If the lower leaf axils of the seasonal-unit characteristically produce the flower buds, these nodes are without vegetative branches in succeeding years, producing the appearance of separated units of leaves.

Cutter (1961) and others have noted that in some members of the Nymphaeaceae, sites in the genetic spiral have alternate developmental potentialities. Leaf and flower primordia in the same spiral may be formed consecutively on the apical meristem; that is, the physiological conditions conducive to flower formation must be followed immediately in a different sector of the apical meristem by those favoring leaf inception, and then again, flower formation. Occasionally flowers will occupy leaf positions in such a spiral. Cutter (1966) also reported the condition in many plants with opposite leaves where the vegetative and floral axillary buds occur in either sectorial or helicoidal patterns.

Wetmore et al. (1964) noted that "any of the young potential leaf primordia may become buds if isolation of the very young primordia is effected adequately soon after their appearance." These studies suggest that the original primordia are uncommitted and undifferentiated protuberances of cells as they are initiated.

The vascular supply of the axillary bud is usually associated with tissue on one or both sides of a gap within the vascular cylinder. Dormer (1972) illustrates examples of the vascular supply of the axillary bud being derived from the leaf traces themselves. In unilacunar nodes, the bud traces are associated with the single gap. In trilacunar nodes all cases reported to the present reveal the bud traces to be developed only from the central gap (Garrison 1949). Ogura (1964) reported multilacunar nodes with vascular supply to the axillary buds developed from several of the gaps in the Araliaceae, Compositae, Plumbaginaceae, and Ranunculaceae. No literature has been located describing the vascular supply to serial buds, whether arranged vertically or horizontally. Croizat (1960) has reported a node of *Chaenomeles* in which buds or branches were formed within the axil of the foliage leaf and each of the adjacent stipules, but he gave no anatomical details. Nast and Bailey (1946), and Garrison (1949) also reported the intermingling of bud and leaf traces in *Euptelea.*

Recently Bounaga (1973) has reported experiments in which an axillary bud was excised and the portion of the stem from which the bud was removed was grown in culture media. The study involved material of *Cestrum parquii, Dianthus barbatus,* and *Matthiola annua,* all of which have unilacunar nodes; and *Eryngium tricuspidatum* and *Bupleurum plantagineum,* both of which have multilacunar nodes. When grown in culture, the stem pieces developed new buds at the area of excision. Buds developed with connections to vascular tissue on either side of the leaf-gap or from only one side in the unilacunar nodal types. A variable number of buds, not exceeding the number of traces, developed in the cultured material of *Eryngium* and *Bupleurum.* Bounaga concluded that the production of neobuds was "inscribed" in the bud trace, and that the stems in the taxa studied were not caulogenic.

If the growth of the apical meristem in any given season is determined by the development of a terminal bud, this bud can be a flower bud, producing an inflorescence, or a vegetative shoot. In some plants the termination of apical growth results from the gradual reduction in size of the apex meristem and its appendages to the form of a spine. Subsequent elongation of the axis occurs through the elongation of a lateral bud. Growth may also terminate by the abortion of the shoot apex, a conspicuous failure of shoot development. Apical growth may be limited, too, by cladoptosis, the abscission of a portion of the shoot, a part or all of the seasonal-unit (Garrison & Wetmore 1961).

The onset of dormancy is often indicated by the lessening of the length of the internodes, and the closer association of the upper leaves or their reduction in size. The abrupt cessation of production of leaves in a seasonal-unit, followed by the development of bud scales, must be under hormonal control. Dostal (1959) showed that the removal of shoot leaves would delay the production of bud scales and cause the production of more leaflike organs.

With the onset of new growth, either as lammas shoots or following a seasonal dormant period, the bud internodes begin to increase in length. The outer bud scales usually abscise, and internodal elongation is lacking in the area of the bud scales. Some plants evidently enlarge in a given seasonal-unit only those leaf primordia found in the resting bud. Even this development may show transitional forms characterized successively as cataphylls, eophylls, or transitional leaves and characteristic foliage leaves. Bud scales and cataphylls commonly lack petioles, and may lack photosynthetic potential or have this reduced. Eophylls may or may not have a full petiole development comparable to that of the later leaves. The vascular supply or nodal type for each of these appendages may be different. Lammas shoots commonly have larger cataphylls and eophylls than comparable appendages developed from a true resting bud, and such appendages may be long lasting. Some plants with determinate growth and terminal buds may not only develop the leaf primordia included within the bud as "early leaves," but may continue to develop additional leaves, as "late leaves" (Critchfield 1960) before forming a terminal resting bud.

Plants with indeterminate growth, that is, those that do not form a resting terminal bud, may continue to produce standard foliage leaves until stopped by adverse weather in temperate regions. When a die back of tissue occurs, subsequent elongation of the stem takes place through the growth of an axillary bud in a lower position.

THE NODE

The node is commonly defined as the position on the stem at which leaves occur — a superficial topographic orientation. Variations within this definition allow for the node to have one leaf, two or opposite leaves, and several or whorled leaves associated with a single node.

When the leaf has abscised, a leaf-scar remains visible, commonly revealing cross sections of one or more vascular bundles, referred to as traces, which are the paths of conduction between the leaf and the vascular system of the stem. When the traces enter (or depart, depending on the point of view) the vascular system, a gap or gaps can be found in the higher plants. This area of gaps has also been accepted as a "node," permitting two contrasting considerations for descriptive purposes. The widely accepted classification, attributed to Sinnott (1914) although recognized much earlier, established three nodal types, unilacunar, trilacunar or multilacunar, depending on the number of gaps. Pant and Mehra (1964) have suggested the nodal classification of alacunar, unilacunar and multilacunar when the number of gaps is more than one. Independently in Europe emphasis was placed on the number of traces instead of the number of gaps. Pierre (1896) suggested the Monoxylées or Monophalangoxylées and the Trixylées or Triphalangoxylées for one or three traces entering the stem; while Hasselberg (1937) established the terminology "Unifaszikulärer insertion," "Trifaszikulärer insertion," and "Multifaszikulärer insertion." Later Marsden and Bailey (1955) combined the number of traces and gaps, recognizing a "fourth type of nodal anatomy" when the traces were two at one gap; and Takhtajan (1969) proposed a hypothetical but comparable "fifth type" with two traces to a median gap and single traces to each of two lateral gaps.

Arnal (1962) discussed alternative characteristics for a node, suggesting that it has been defined either as a zone of insertion on the stem of a leaf-axillary bud complex, or as the zone of non-elongation of the stem.

He acknowledged that the presence or absence of buds, including the formation of axillary and adventitious buds, was extremely variable; that leaves may be present or absent, and that internodes might also be lacking; and concluded that the only criterion for a node was that of non-elongation.

Croizat (1960), by contrast, has called attention to the variety of structures that could be produced and be present superficially in an area which he called a "nodal torus," such as buds, shoots, flowers, inflorescences, scales, cataphylls, eophylls, leaves, stipules, trichimoids, spines, glands, and meristematic tissue. He recognized that the nodal torus could occupy a considerable portion of the stem, far exceeding the leaf-scar area and the gap region of the stele. He pointed out that these products of the nodal torus are found completely surrounding the axis, sometimes extending a distance above the leaf-scar or occurring below the leaf-scar.

Boke (1961), noting that areole meristems of the Cactaceae produce new spines seasonally for many years, considers these to be dwarf shoots rather than simple buds, thus a single nodal torus.

No survey paper has yet considered, in the definition of a node, the presence of a cortical and/or medullary vascular system which may or may not contribute to the principal vascular cylinder and/or the leaf. Neither has attention been paid to accessory conducting-secreting systems as latex or resin canals and their role in the leaf-stem relationship.

Ideally all of these characteristics should be incorporated in any description of a node, but most important is the recognition of the nodal area in three dimensions. The interpretation of the single section usually drawn or illustrated is dependent on an understanding of the areas below and above that section.

The internode is generally defined as the area between two nodes, again a topographical definition. The internode is the result of both cell division and cell elongation (Wetmore & Garrison 1966), and the amount of tissue between the topographic nodes is obviously variable. If no elongation occurs and the leaves are close together, the growth form is either that of a rosette or of a short shoot. The rosette growth form is often altered with the induction of flowering and the subsequent production of internodes, especially in biennials (Wetmore & Garrison 1961). Lateral short shoots may remain as closely associated nodes for many years in flowering trees, but short shoots of terminal growth have been shown to be under hormonal control for shorter periods of time (Gunckel & Wetmore 1946, Gunckel, Thimann & Wetmore 1949, Titman & Wetmore 1955). A peculiar condition of double nodes has been reported in the genus *Anacharis* (Jacobs 1946), where occasionally an internodal area of the stem fails to elongate, and two leaf-bearing nodes are close together.

Surprisingly, the actual method of internodal elongation, with its initiation and cessation, has received little attention. Wetmore and Garrison (1961) studied the elongation of internodes in *Helianthus* and *Syringa*, and noted that in *Helianthus* elongation began at the base of the internodal area and proceeded acropetally into the supra-adjacent node, whereupon the next internode developed in a similar fashion. In *Syringa* several internodes did develop simultaneously though overlapping in timing. In *Helianthus*, cell enlargement is the dominant factor in internodal growth; whereas in *Syringa*, cell division is the more prominent of the two processes, although in both taxa mitosis and elongation are involved. In many members of the Gramineae and Liliaceae, as well as in *Equisetum*, elongation and maturation occur in the opposite direction, with the basal area of the internode the last area to mature, often remaining meristematic for some time. Although uninvestigated to the present, a similar situation may prevail in the Chloranthaceae and other plants primarily with opposite leaves, in which dried specimens show a shrunken or collapsed zone just above a pair of leaves or at the base of the internodal area. Although the processes of cell division and cell elongation are presumably under biochemical control, there is no explanation why they cease within the internodal area, causing the internode to be considered mature.

The amount of elongation, i.e. the length of the internode, may vary considerably on a given shoot or on one plant. Within a given flush of growth or development of a shoot from a bud of a woody plant, the basal portion of the stem and the apical portion may have the nodes close together, and the middle portion have the nodes well spaced. An explanation is possible if the growth hormones causing the internodal elongation are related to the appendage of the node. Thus, the lower internodes associated with bud scales, cataphylls, or eophylls are shorter than those associated with larger foliage leaves. The comparative lesser length of the upper internodes still associated with full-sized leaves immediately preceding the abrupt transition to bud scales of a terminal bud remains unexplained, as does the hypopodium development at the base of some branch systems where only cataphylls are present.

ANATOMICAL DESCRIPTION OF THE NODE

The continuity of the vascular tissue from the stem through the petiole to the apex of the leaf is evident, yet the nature of its path and the variations of pattern of bundle arrangement and position along its length have not received much consideration. A three-dimensional interpretation is desirable, yet extremely difficult to depict. Single sections in leaf-bearing regions, therefore, have generally been used to describe the node, and these remain useful. The usual single section will allow the description of the epidermis, hypodermis, and even some periderm; the cortex and its included vascular bundles in those species possessing a cortical vascular system, and sclerenchymatous tissue such as caps, rings or isolated idioblasts, and often laticiferous cells and resin cells, and the principal vascular system of secondary and/or primary phloem, cambium and secondary and/or primary xylem. The latter may be distinguishable as discrete bundles or continuous tissue being either collateral or bicollateral. The central portion of the section may be distinguishable as a pith of parenchymatous tissue of varying size and shape, but often with complete or incomplete medullary bundles, occasionally plates of sclerenchyma, idioblasts, and canals or cells of latex or resin. In some instances the pith area may be hollow in a characteristic fashion. Needless to say, any and all of the tissues and cells may have descriptive value of a comparative nature.

The traces are generally considered to have originated in the principal vascular system, and to have "departed," leaving a gap in the vascular cylinder before entering the petiole. They may be seen in the cortical areas in cross section or in a horizontal longitudinal section. During their transit through the cortex, associated sclerenchymatous cells are usually lacking.

The descriptions of three nodal types, unilacunar, trilacunar, and multilacunar, dominate the literature (PLATE I). The fourth type of nodal structure (Marsden & Bailey 1955) indicated a condition where two traces were associated in a single gap of a unilacunar node. Nast and Bailey (1946) did not name or number the nodal condition of *Euptelea* where the bud and leaf traces were intermingled in the node, nor has such numbering been applied to the split lateral or common gap condition reviewed by Howard (1970). Takhtajan (1969) proposed a theoretical "fifth type" of nodal structure which he speculated was the primitive type, a trilacunar node with two traces in the median gap.

Added to the basic four types of nodal structures must be the stems where a cortical vascular system is present which may or may not contribute to the vascular supply of the leaf (PLATE I). This has been described for *Calycanthus*, *Chimonanthus*, and *Nyctanthes* (Lignier 1887, Fahn & Bailey 1957, Balfour & Philipson 1962, Kundu & De 1968) where the cortical system forms a girdling bundle at the node, in addition to having branches entering the leaf. Acqua (1887) illustrated but did not comment on the cortical bundles of *Buxus*. The recently described *Idiospermum australiensis*, Idiospermaceae (Blake 1972) also has a cortical system in the stem. Ogura (1937) noted that some species of *Blahdia* (*Ardisia*) of the Myrsinaceae have a cortical vascular system while others do not. A cortical system was reported for *Rhynchopetalum* (*Lobelia*) (Bower 1884) without indication of its role in the leaf vascular supply. A special study is needed of cortical vascular systems, but to the present ample material has not been available. The general pattern of the relationships of the cortical vascular system to the leaf vascular supply seems to include these variations: 1. A cortical system may run the length of the stem without association with the main vascular supply of the leaf: 2. The cortical system may run the length of the stem, giving rise to girdling branches at each node, while other branches enter the petiole; 3. The cortical system may originate just above the node and enter the leaf at the next node.

The only developmental study of cortical vascular systems appears to be that of Balfour and Philipson (1962) who studied *Chimonanthus*. They reported that the cortical system developed independently and later than the principal vascular system in the shoot apex. The cortical sympodia are connected laterally and below the node, and each bundle gives off a branch which goes to the leaf as a lateral trace. Buds in *Chimonanthus* are vascularized both by the main system and the cortical system. One branch from each adjacent cortical bundle divides in the bud to form the two side cortical bundles of the bud vascular systems.

Medullary bundles have a varied role in their relationship to the principal vascular system of the stem and in their contributions to the vascular supply of the leaf. Metcalfe and Chalk (1950) list 55 families of dicotyledons in which cortical and/or medulary bundles are known. Lignier (1887) described the path of medullary bundles in many taxa of the Melastomataceae. Col (1904), Wilson (1924), Maheshwari (1929, 1930), Davis (1961), and Pant and Mehra (1963) all indicate the complexities of the medullary bundles in the Amaranthaceae, Chenopdiaceae, Nyctaginaceae, and Polygonaceae.

Medullary bundles may be complete bundles with xylem and phloem present, or incomplete, in which case they generally consist of phloem tissue alone. Sclerenchyma has not been found in association with medullary bundles. The medullary bundles of the Piperaceae (De Candolle 1866) may divide and anastomose with each other, and they may enter the principal vascular system of the stem or depart from it. Medullary bundles which enter the principal vascular system before entering the leaf may be indistinguishable from bundles of the usual leaf traces. In the Melastomataceae, many medullary bundles often enter the petiole independent of the bundles of the principal vascular system and retain a medullary position in the petiole (PLATE V, FIGURE 4).

In general, leaf trace bundles depart from the principal vascular system within the length of the stem that is represented superficially by the leaf base or leaf scar; i.e., the bundles make an abrupt angle. Lateral traces depart from the vascular cylinder and run horizontally around the stem in the cortex before entering the leaf. On the other hand, the traces may depart from the the vascular system a considerable distance below the leaf scar area of the stem and proceed upward in the cortex before entering the leaf. The terms cathodic and anodic traces have been applied to the traces to the left and right of the median trace; i.e., those away from or toward the direction of the spiral of the phyllotaxy. The idea of the consistent precocious departure of the cathodic trace is not substantiated. Attempts have also been made in the literature to characterize nodes of various plants on the basis of the number of bundles which are between the lateral traces or the lateral and the median trace (Record 1936). In general, the median trace is precocious in relation to the departure of the lateral traces. The fact that the traces may depart from a principal vascular system and be free in the cortex can often be determined by a superficial examination of the stem immediately below the leaf base. By far the most extreme example of early departure of a leaf trace is the example given by Johnston and Truscott (1956) of *Serjania*, where lateral traces may run in the cortex for 17 internodes before entering the leaf with the median trace.

Stems which have an opposite phyllotaxy may have the sets of traces associated with each leaf depart at the same level, or one leaf may be higher than the other in terms of trace departure. Opposite leaves may be unilacunar as to their vascular supply, or trilacunar. Opposite or whorled multilacunar nodes have not been encountered. Whorled leaves may also be unilacunar or trilacunar. Carlquist (1955) has described a member of the Compositae with whorled leaves in which traces branch and a bundle enters the base of each of the adjacent leaves. This occurrence of a split lateral or a common gap has been reported for a number of families (Howard 1970).

The presence of stipules requires a special descriptive consideration to be given later. It is possible for stipules to be vascularized by free bundles, by branches of a single lateral, or by laterals which run horizontally from their point of origin to the leaf base, fusing en route, and/or supplying branches which enter the stipules (Ozenda 1948).

Nodal sections may also give some information on the continuity of latex and resin systems between the cortex and the leaf. The number of resin canals in the internodal area or in the petiole may be several times the number of traces, but at the point of departure of the traces from the stem, only those resin canals associated with the traces persist, and the number of resin canals at the level of the abscission layer is usually equal to the number of traces (Artschweger 1943). The nature of the disappearance or the appearance of the intervening resin or latex canals has not been studied. In general, sclerenchyma caps to individual bundles will be less conspicuous in the node section than in the internodal or petiolar section.

Evidence of vascular supply to glands may also be present in the nodal section.

VARIATIONS ON NODAL PATTERNS

Sinnott (1914) considered the node as a section through the area of the leaf-trace gap, and gave a list of families of dicotyledons with unilacunar, trilacunar, or multilacunar nodes. In most cases Sinnott reported but one nodal type per family. A few corrections of interpretation and a few reports of variations have been published to Sinnott's much cited work. Sinnott considered the trilacunar node to be primitive. Subsequently Bailey (1956), Ozenda (1948), Canright (1955), Takhtajan (1969), Pant and Mehra (1964), and Benzing (1967) have arrived at differing conclusions. Trace number variation has been reported frequently in studies of seedlings where the mature nodal pattern is established three or four leaves after the cotyledonary node. Other authors have shown a variation in mature nodes of the trilacunar and multilacunar types as an inconsistency in the number of lateral traces on either side of the median trace. Kato (1966, 1967) reported such variation in *Citrus*, *Malus*, *Quercus*, and *Sorbus*, and Philipson and Philipson (1968) found a variation in ***Rhododendron***.

Post (1958) studied nodes at successive levels in plants of *Swertia* and *Frasera* where traces varied from 1 to 7 per node with a comparable number of gaps. This work may be subject to some interpretation in the nature of the almost rosette-like base with the stem leaves transitional to bracts of an inflorescence. Personal studies of other Gentianaceae failed to produce the variation described by Post.

Swamy and Bailey (1949) reported a difference in the node and trace number between leaves of *Cercidiphyllum* produced on long shoots (trilacunar) and those produced on short shoots (three-trace unilacunar). Their observations cannot be repeated on material from the same tree where recent studies showed all nodes on short shoots had regular trilacunar nodes.

Variations in unilacunar nodes may be encountered when sections are not examined from a sequence of levels. The double leaf trace found in many of the cultivated herbaceous Labiatae may show a fusion of the two traces above or below the level where a double trace is evident. A third trace may be present, weakly developed between two strong traces, and may fuse with one or the other of the double-trace bundles or simply disappear (Swamy & Bailey 1950, Nakazawa 1956, Yamazaki 1965). In many herbaceous plants with a single gap, the interpretation of the number of traces is difficult when vascular development is weak. A single, broad arc-like trace may be interpreted as 2 to 5 separate bundles.

Much nodal variation was reported by Howard (1970) in the case of the split lateral traces of *Alloplectus ambiguus*. From originally wild plants the pattern was altered from a clear-cut split-lateral trace, supplying vascular tissue to opposite leaves, to a situation of two trilacunar nodes when the plants were cultivated in a greenhouse. Such material was returned to native conditions in Puerto Rico where it has since been reexamined; in all stems studied the original split-lateral trace was again present.

Slade's (1952) study of cladode anatomy in New Zealand brooms showed a variation in the number of traces in successive leaves produced in a developing seedling. The earliest leaves may have three traces from three gaps. Later leaves may have pentalacunar or septalacunar nodes, either by the occurrence of flanking traces outside of the lateral traces, or by the incidence of interpolating traces inserted between the median and the lateral traces of extremely flattened stems. A few species showed both flanking and interpolating traces. Unfortunately, this work does not show the continuity of traces through the internodes, nor are developmental studies reported.

In the course of the present study, many possible sources of variation were considered in leaves of mature stems. At an early stage in the study, 500 leaves and nodes were examined from single trees, involving crown and base leaves, sun leaves and shade leaves, those of vigorous shoots, and of short shoots or slow-growing shoots. Leaves were also obtained from single species, e.g., *Acer rubrum*, *Acer negundo*, from plants growing in states from Maine to Florida, and west to Colorado. No significant variation was found in any instance. Many commonly cultivated tropical species, e.g., *Hibiscus rosa-sinensis*, *Lantana camara*, *Nerium oleander*, were obtained from wild material or cultivated plants from temperate area greenhouses or from botanical gardens around the world, and again vascular patterns proved to be consistent. Ecotypes were also considered, and no significant variation was encountered.

The patterns of traces and gaps accepted by Sinnott remain a good descriptive tool of anatomy and morphology. Supplemented with the accessory data on the vascular supplies of cortical and medullary bundles when these are present, a section through the node of comparable materials will yield information of descriptive value.

THE LEAF

A simple definition of a leaf proves to be a difficult exercise, due to the extreme diversity of morphology. Leaves are generally described as axillary appendages to the stem, dorsiventrally flattened, with a restricted terminal growth, an interpolated petiole, and primarily a photosynthetic function. There are many exceptions to all of these descriptive phrases. Even the relationship of the leaf to the stem remains a philosophic question, unanswered morphologically. Are the leaf and stem independent structures? Are leaves of common phylogenetic origin, or do leaves of the major taxa of the plant kingdom have diverse origins? Foster (1949) stated, and many authors have repeated the statement that "it is difficult on both theoretical as well as practical grounds to demarcate the leaf from the stem." Leaves and stems are actually integrated portions of the shoot system without sharp boundaries.

The mature leaf may be simple or compound. Pinnate and palmate compound leaves are recognized in several degrees of division and modification. Leaf blades may be entire, lobed, diplophyllous, or peltate. The distinction between a pinnately compound leaf and a pinnately lobed leaf may be extremely difficult to ascertain.

The leaf may be sessile or with a petiole of varying lengths. The leaf may have a pulvinus at the base of the petiole, and also one at the apex of the petiole. The leaf base may subtend a bud, or nearly or completely surround the bud. The base may be extended laterally and thus be sheathing in nature.

Abscission of the leaf may be by means of a layer or layers of cells developed at the base of the pulvinus, within the pulvinus, or at the apex of the pulvinus. In simple leaves the lamina may abscise, leaving the petiole to abscise later, or the whole leaf may be abscised at one time. In pinnately compound leaves the leaflets may abscise and later the petiole or rachis, or all may fall as a unit. Decompound leaves may abscise in successive parts, the ultimate divisions falling first, then successively proximate divisions, until finally the basal petiolar portion abscises from the stem. The nature of these "units" of the leaf has received little practical or theoretical consideration beyond the original definition of them by

De Candolle (1868), who classified leaves as unimerous, dimerous, trimerous, etc., to polymerous. The areas of articulation, joints or pulvini, have been noted and classified by Funcke (1929). Needless to say, the pattern of vascular tissue may be distinctive in these zones. No consideration of the pulvinus development appears in ontogenetic literature.

Although most leaves are recognized as dorsiventrally flattened, i.e., bifacial with different morphological characteristics in the cuticle, stomata, or pubescence, many examples of terete or flattened leaves have been reported and described as unifacial. A classification of unifacial leaves was proposed by Flachs (1916).

DURATION OF LEAVES

Kraus (1880) offers one of the early references to the persistence of leaves. Some conifers he reported retained their needles as long as 12 years. Dicotyledons often retained their leaves for 2 to 3 years in many species of *Ilex*, *Fagus*, and *Rhododendron*, with persistence of five years in *Buxus* and *Hakea*. Hallé (1966) reported the tropical *Schumanniophyton* with a leaf retention of 4 years, while Howard (1969) observed *Trichilia* (Meliaceae) having pinnate leaves of 4-years' duration. Pease (1917) found that the relatively smaller leaves of *Chimaphila* and *Pachystima* were retained in some cases for 8 years.

The petioles of leaves more than one year old usually show secondary xylem, with some evidence of annual increments. Attempts to estimate the volume of annual xylem production, or to correlate the amount of xylem in leaves of comparable age, were not successful.

Samantarai and Kabi (1953) observed the development of secondary xylem in the petioles of rooted leaves of *Amaranthus gangeticus*, *Chenopodium album*, and *Ipomoea batatas*. Secondary growth in *Amaranthus* was initiated outside of the original vascular bundles by accessory cambia formed in distinct arcs.

LEAF AS A CONTINUUM

There is a continuity of the vascular supply from the stem to the apex of the leaf. The nature of its variations, as revealed in transverse sections, within the length, is presented in the existing literature in a very few papers (Acqua 1887, Swamy & Bailey 1950, Nakazawa 1956, Yamazaki 1965, Schofield 1968, Sugiyama 1972).

For convenience one may consider the traces as departing from the stem and entering the leaf. The individual traces may separate ordinarily from the principal vascular system, and be seen in the cortex only immediately below the leaf gap or, in some species, in many varying numbers of internodes below the leaf gap. In the initial sub leaf-base internodal section descriptive information may include the nature and number of the traces; the presence or absence of resin canals or latex systems; the presence or absence of cortical bundles and/or medullary bundles as well as fibers or sclereids.

At the node in the classical anatomical sense, that is, the area of leaf gaps, one determines the size and nature of the traces, cathodic or anodic precocity, and the attitude or path of departure of all traces which may be on a gradual slope or abruptly at right angles to the axis. Only occasionally will traces depart from above the petiole base and curve backward, even running down the stem cortex (De Fraine 1913, Fahn 1967). Lateral traces, if present, usually run an abrupt nearly horizontal path and, when sheathing stipules are present, may produce branch traces which enter the stipular sheath.

The leaf base in the mature leaf may be of restricted development, or large and sheathing. Most leaves have a kidney-shaped scar with the axillary bud in the sinus. The leaf base may completely surround the bud, or a protuberance of unattached tissue may complete the circular protection of the axillary bud.

A pulvinus may be present at the base of the leaf and vary greatly in size and shape. Normally, the pulvinus is of greater diameter than the petiole above it. The pulvinus is regarded as an area of flexibility, as is evident in the "pouring out" leaves of tropical plants or those with nastic movements (Satter & Galston 1973). The pulvinus has a large amount of cortical tissue, a relatively small amount of vascular or supportive tissue, and appears to lack completely cambial activity or the development of sclerenchyma.

The petiole may be present or absent. If a leaf is sessile, that is, without a petiole, the basal area of the leaf often shows the same arrangement of bundles as does the pulvinus. The petiole is understood to be an area interpolated between the blade and the leaf base in development. The word pulvinus is applied arbitrarily to simple leaves as well as compound leaves. In pinnately compound leaves, the petiole is between the leaf base and the first leaflet or pair of leaflets. The remainder of the axis which bears leaflets in a pinnately compound leaf is referred to as the rachis.

In palmately compound leaves, the petiole is between the leaf base and the area of origin of the leaflets. Leaflets of pinnately or palmately compound leaves may have petiolules.

Transverse sections, taken successively from the base of the petiole to its apex, reveal the variations in number, position, and arrangement of the traces (PLATES II–VII). The lower end of the petiole is supplied with a characteristic number of traces, but successive sections reveal that these may remain independent, fuse, divide, or be rearranged, with changes in orientation. The petiole vasculature is most complex at the geographic middle of the petiole where there is the greatest amount of secondary tissue if a cambium has developed, and the greatest amount of collenchyma or sclerenchyma in the cortex and the pith of the petiole. Near the upper end of the petiole, the vascular pattern which has developed from the basal orientation may be undone in an exact reversal of its formation. Thus, in some simple leaves an upper pulvinus is present with a vascular pattern comparable to that of the lower pulvinus. In other leaves without an upper pulvinus, the vascular pattern of the petiole continues into the midrib until interrupted by the departure of primary veins.

Dormer (1972) concluded that a common feature of leaves in which separate strands exist in the petiole is that these should be linked by a massive collar or bridge of vascular tissue in the leaf base. This collar is often situated at the upper end of a stipular or sheathing region. He added that "in many compound leaves a similar type of cross connection may be associated with the attachment of each pinna."

Palmately compound leaves usually have such a plexus of tissues at the apex of the petiole, and it appears that each petiolule receives a supply of vascular tissue from each of the original traces. Palmately compound leaves have been associated with unilacunar, trilacunar, or multilacunar nodes.

Peltate leaves may have a relatively simple vascular pattern at the apex of the petiole, or one of great complexity.

Within the base of the leaf blade, the vascular pattern of the midrib is re-established in complexity if the petiole pattern was simplified in the upper pulvinus. The pattern of vascular tissues in the midrib is interrupted by the departure of the primary veins in a palmate or pinnate fashion.

The distinctions between deeply lobed leaves and pinnately compound or palmately compound leaves are arbitrary. Normally, if a leaflet is attenuated at the base to a petiolule which develops an abscission layer, the leaf is considered as compound. Compound leaves may be associated with unilacunar nodes, although most appear to be associated with trilacunar nodes. In general, a leaflet of a pinnately compound leaf receives its vascular supply from branches of the median and one lateral trace.

Diplophyllous leaves may vary considerably in the amount of vascular tissue which enters the secondary laminae.

The amount of vascular tissue in the midrib of the leaf or leaflet is greatest at the base of the blade, and is progressively diminished as veins are produced. Normally, some vascular tissue, usually from the median trace, continues to the ultimate apex of the leaf blade. In some pinnately compound leaves the ultimate terminal leaflet may abort, yet a vascular supply is evident in the rudiment. The mucro of the fused leaflets of *Bauhinia* is vascularized by the median trace.

THE PETIOLE

The petiole is interpolated in the development of the leaf. Studies of its elongation are relatively few. Masuda (1933) studied this extension in woody and herbaceous plants in the botanical garden at Tokyo. He divided young petioles into equal portions with India ink marks, and followed the elongation of each section. Three types of patterns of elongation were revealed in his studies, but no attention was given to the leaf base or the pulvinal areas. Type "a" had each zone elongate almost equally. In type "b" the upper zone of the petiole showed a conspicuous elongation; and in type "c" the lower zone showed a greater amount of elongation. Most of the study was made in May or June, although one report is for a study conducted during October. Growth was completed in as few as 6 days, or over a period of 51 days. Type "b" was regarded as the most common type with elongation ceasing from the base upward in a time sequence. Tchoun (1923) has shown that the petiole in the majority of plants completes its elongation before the lamina reaches its maximum size.

Studies were made in Boston, Massachusetts, of woody plants in the Arnold Arboretum, and revealed additional growth patterns that cannot be associated with the data given by Masuda. Using plants growing out of doors, young petioles were marked as closely as possible with India ink from the axil of the leaf base to the base of the lamina. With the exception of *Liriodendron tulipifera*, all leaves completed the elongation of the petiole in a period of 12 to 15 days. In general, the petioles appeared to increase in length in such a way that the middle of the total length of the petiole increased fastest in length and stopped its growth earliest. The expansion and cessation proceeded in a wave from the middle of the petiole to each end. The apex of the petiole, especially if a pulvinus was present, and the base of the petiole increase in length the least or not at all. *Liriodendron tulipifera* in the Boston area continues to produce leaves until growth and development are stopped by frost. The upper quarter of the petiole seemed to continue elongation as in the type "b" described by Masuda for *Liriodendron* and *Firmiana*.

The geographical middle of the petiole of leaves of most plants in the Boston area appears to increase in size first and reach maturity the earliest. This is shown internally by the amount of lignified tissue revealed by a phloroglucinol stain. A cambium may develop first at the middle of the petiole, and sequentially toward each end, being absent in the pulvinus areas. Comparable developmental patterns of sclerenchyma were observed. The pulvinal areas show the least elongation and no development of secondary tissues or of sclerenchyma.

Further support for Masuda's type "b" may be found in the statement of Funcke (1929) that some petioles are able, if necessary, to elongate themselves even after the adult stage is reached. Yin (1941) recorded growth in the length of the petioles of *Carica papaya* associated with diurnal movements of the leaves from a flexed to an upright position. The petiole was shown to grow on the lower side during the morning hours, and on the upper side during the evening hours, thus changing the attitude or position of the leaves.

Within a seasonal-unit such as occurs in a temperate tree, the lowest leaves may have shorter petioles than those of the middle of the growth unit, and the upper leaves may also have petioles comparatively reduced in length. Anisophylly of leaves and of petioles of many plants with decussate leaves has been reported by Heinricher (1910), Cook (1911), Sinnott and Durham (1923), and Howard (1970). Thus in most species of *Acer*, the leaves borne in the horizontal plane have petioles of equal length, but those of the vertical pair have a longer petiole in the lower leaf than in the upper leaf of the pair. Anisophylly of opposite leaves in such families as the Gesneriaceae and Urticaceae is characteristic of the family and reveals leaves and petioles of different sizes in the pair. No structural differences between the leaves or in the petioles of such plants have been reported. Leaves of two different morphological forms have been reported for single plants as heterophylly. Transitions from juvenile leaves to mature leaves may be gradual or abrupt. There appear to be no differences in the anatomical structure of such variants.

Superficial observations on the petiole are of descriptive and taxonomic value. These may include the length, color, presence or absence of upper and lower pulvini, presence or absence of stipules, glands, thorns, collators, pubescence, etc. The adaxial surface of the petiole may be grooved for various distances, and the petiole may be slightly ridged to strongly winged along the groove. Sections of the petiole reveal a characteristic outline which will vary from the base to the apex of the petiole.

DESCRIPTIONS OF VASCULAR PATTERNS IN THE PETIOLE

The earliest known recognition that a section of a petiole would reveal different patterns of vascular bundles was made by Grew in 1675 when he illustrated ten schematic cross sections of petioles.

In 1868 De Candolle had proposed a theory of a leaf, likening the structure to that of a stem. The first comprehensive survey of petiole anatomy was that published by Casimir de Candolle in 1879. His survey of twenty "families" led him to describe several fundamental concepts of the vascular structure he encountered. De Candolle proposed the terminology of an open system (système ouvert) versus a closed system (système fermé). In the open system the bundles, as seen in cross section, were arranged in an arc. In the closed system the bundles formed a circle comparable to that of the stem. The bundles could be free or united. The system was invariably open at the base of the petiole, and could become closed in the petiole and again open in the midrib or in the petiolule of a leaflet. De Candolle also recognized a principal system (système principal, système essentiel), and an accessory system (faisceaux detachés), the latter composed of "faisceaux intracorticaux" and/or "faisceaux intramédullaires." The medullary bundles could have the same orientation as those of the principal system or be inverted. It should be noted that the cortical and medullary systems of De Candolle referred to the petiole alone, and were not correlated with such systems or bundles in the stem. De Candolle classified the bundle arrangement in the families he studied. He noted that groups of species in *Acer*, *Alnus*, *Aesculus*, *Mallotus* and others might have one system or the other. His division of species of *Fagus*, for example, would today represent the differences between *Fagus* and *Nothofagus*. Noting the variation in pattern encountered in a series of sections from the base of the petiole to the apex of the blade, De Candolle suggested that the most reliable comparative section could be obtained at the first "meriphylle," that is, the interval of the midrib between the departure of the first and second primary veins.

In the decade that followed, Vesque (1885), Petit (1886, 1887, 1889), Lignier (1888) and Acqua (1887–88) added examples, ideas, and variations in terminology to the knowledge of petiole vascular patterns.

Vesque (1881, 1885) appears to be the first worker to suggest that the most reliable single section for comparative purposes be taken from the middle of the petiole. He studied a number of families and used the petiole anatomy to separate genera and families formerly united.

Petit (1886), working in France, and Acqua (1887), working in Italy, conducted broad studies of petiole vascular patterns and published their studies competitively. Petit's study involved five hundred species in three hundred genera of forty-eight families. He recognized differences in patterns along the length of the petiole and stated: "it is in a terminal section that there will be presented for each plant the disposition most complicated and most regular which offers from one plant to another the greatest differences. It is, of consequence, the section most instructive. I have given this the name of the characteristic, for in many cases it will be sufficient, in order to recognize the family of the plants, and in some cases, its genus." The names "coupe initiale" for the basal section and "coupe caractéristique" for the apical section are attributable to Petit. His work included as a resumé a key to the principal families of dicotyledons he studied on the basis of petiole vascular structure. Petit proposed a variation on the use of "open" and "closed" systems from that suggested by De Candolle. To Petit a closed system was one in which the bundles were fused; and an open system, one in which the bundles were distinct or separated. Petit felt that herbaceous plants showed distinct bundles (open) in the "coupe caractéristique," while in shrubby or woody plants the bundles were fused (closed) in an arc or a ring. He noted that sclerenchyma was generally lacking in herbaceous plants and present in woody plants, and placed value for classification on this tissue.

Acqua's study was published in full before Petit's, but following Petit's brief note indicating what he was doing. Acqua studied 19 families and proposed a classification of 13 patterns of vascular distribution in petioles. He correlated the position of the leaves with the vascular patterns; recognized unilacunar, trilacunar, pentalacunar, septalacunar, and nodes with a variable but greater number of bundles. His unit number 2 was the double leaf trace of *Phlomis* and *Lamium*, later described as the fourth type of nodal anatomy by Marsden and Bailey. Acqua also found in the Compositae examples of bundles from opposite leaves being associated with a single node, the "split lateral" or "common gap" (Howard 1970).

Lignier (1887) published an extensive monograph describing the stem, petiole, and leaf vasculature in the Calycanthaceae, Melastomataceae, and Myrtaceae where cortical and medullary bundles of the stem are involved in the vascular supply to the leaf. Three-dimensional drawings are used, and the complexities of the vascular system are described in detail. This was followed in 1888 by an essay on the vascular system of the leaf and the stem of the phanerogams. Lignier stressed the fact that a single section of the petiole was inadequate for an understanding of the complex pattern developed in the length of the petiole. He felt that the most common pattern to be found in petioles was the arrangement of the bundles in a vascular arc. This arc could be a single broad bundle or several bundles. The arc could be expanded or divided, with extra bundles appearing at the ends of the arc. He designated the extra bundles as "surnumeraires" which were called "surnumeraires intérieurs" if they assumed a medullary position, and "surnumeraires extérieurs" if they assumed a position in the cortex of the petiole. He noted that these corresponded only in some cases to comparable terms used by De Candolle.

Lignier proposed the idea that as the vascular arc increased in size within the petiole, it would be forced into folds (plis) as the animal brain is convoluted to increase the surface area. Folds could be to the interior (pli interne) or the exterior (pli externe), and if portions were separated from the vascular arc, these would be medullary or cortical bundles of the petiole. If the vascular arc had been a complete circle, and if an arc was cut off, by foldings, toward the adaxial side, one or more vascular crowns would be recognized. Foldings with the separation of portions of vascular tissue could be recognized at the secondary and tertiary level.

Morvillez (1919) accepted the idea of foldings as a descriptive approach in his study of petiole vascular patterns. He referred to the vascular bundle pattern seen in a cross section of the petiole as a "chaine foliaire" which could be a continuous arc of tissue or composed of separate bundles. As the arc curved inward at the adaxial ends, a crosier could be formed, and if portions of the crosier became isolated, internal bundles or plates of tissue were established in a medullary position. Dehay (1935 et seq.) and his students have used this descriptive vocabulary. Dehay chose for his illustrations the "section basilaire de la nervure médiane."

An extensive survey of vascular structure of the petiole and the leaf has been published by Watari (1934, 1936, 1939) for the Leguminosae, *Acer*, and the Saxifragaceae. Watari considered the entire length of the vascular tissue from the node through the petiole and the lamina. His detailed work concerned the many branchings of the traces and their interconnections, and is presented with sectional diagrams and complex three-dimensional reconstructions. For each group Watari proposed a classification based on the petiole structure.

Hare (1943), in a symposium on the taxonomic value of anatomical characteristics, proposed a simple classification of the vascular structure of the petioles as U-shaped, I-shaped, or O-shaped, the latter being the hollow cylinder of the petiolar vascular system. Hare related the structure to the mechanical stress of the weight of the lamina and the lateral movements of the leaf, and thought that the distinctive features of patterns should be regarded as mainly adaptive and functional, and of little phylogenetic significance. He concluded that "characters derived from the petiole, therefore, can be used with confidence, but their value for purposes of classification varies widely at different taxonomic levels." The proposals of Hare were incorporated in the first edition of the *Anatomy of the Dicotyledons* (Metcalfe & Chalk 1950) as 12 diagrammatic outlines.

Howard (1963) proposed a preliminary classification relating the nodal structure at the level of the leaf gaps to the vascular patterns obtained in the petiole as follows:

Node 1–1, simple trace, flat, slightly curved or "U"-shaped.

1. Trace continuous:
   a. Without rib traces — *Allamanda* (PLATE II, FIGURE 1a).
   b. With rib traces — *Graptophyllum* (PLATE II, FIGURE 1b).
   c. Trace split longitudinally, later fusing — *Eugenia* (PLATE II, FIGURE 1c).
2. Trace forming open or closed siphonostele:
   a. Vascular system open, with terminal rib traces — *Ilex* (PLATE II, FIGURE 1d).
   b. Vascular system open with lateral rib traces — *Actinidia* (PLATE II, FIGURE 1e).
   c. Vascular system open, without rib traces — *Celastrus* (PLATE II, FIGURE 1f).
   d. Vascular system closed, without rib traces — *Terminalia* (PLATE II, FIGURE 1g).
3. Trace invaginating at ends:
   a. Ends inroll — *Lyonia* (PLATE II, FIGURE 1h).
   b. Forming siphonostele with medullary plate — *Cordia* (PLATE II, FIGURE 1i).
   c. Inverted plate or simple arc — *Capparis* (PLATE II, FIGURE 1j).

Node 2 or more traces from one gap.

1. Trace bipartite:
   a. In petiole — *Clerodendron* (PLATE II, FIGURE 2a).
   b. Below petiole — *Calycanthus* (PLATE II, FIGURE 2b).
2. Trace tripartite or more:
   a. Bundles free, forming an arc — *Bougainvillea* (PLATE II, FIGURE 2c).
   b. Bundles fused in an arc — *Solandra* (PLATE II, FIGURE 2d).
   c. Bundles free, in ring — *Hernandia* (PLATE II, FIGURE 2e).

Node 3–3, bundles free.

1. Three bundles throughout the petiole — *Pedilanthus* (PLATE III, FIGURE 3a).
2. Lateral traces divide:
   a. Petiole with five free traces — *Pittosporum* (PLATE III, FIGURE 3b).
   b. Petiole with many traces in "U"-shaped pattern — *Miconia* (PLATE III, FIGURE 3c).
   c. Free traces in a ring with medullary bundles — *Aesculus* (PLATE III, FIGURE 3d).
   d. Free traces in a ring without medullary bundles — *Sambucus* (PLATE III, FIGURE 3e).
3. Median trace divides and the division products assume a dorsal position — *Hibiscus* (PLATE III, FIGURE 3f).

Node 3–3, bundles fuse to form an arc.

1. Bundles fuse and form an arc, flat or variously curved — *Lonicera, Betula* (PLATE III, FIGURE 3g).
2. Bundles fuse and form a flat arc with dorsal free traces — *Cornus* (PLATE III, FIGURE 3h).
3. Bundles fuse and invaginate at ends — *Congea* (PLATE III, FIGURE 3i).

Node 3–3, bundles fuse to form a siphonostele.

1. Vascular system simple:
   a. Formed by the simple fusion of traces — *Cotinus* (PLATE III, FIGURE 3j).
   b. Formed subsequent to division of the median, the branches of which form dorsal bundles — *Acer* (PLATE III, FIGURE 3k).
2. Vascular system with accessory bundles:
   a. One accessory large bundle situated dorsally — *Hamamelis* (PLATE III, FIGURE 3l).
   b. Small multiple accessory bundles dorsal in position — *Carya* (PLATE III, FIGURE 3m).
   c. Accessory bundles in medullary position — *Bauhinia* (PLATE III, FIGURE 3n).

Node 3–3, bundles fuse to form more complex patterns.

1. By invagination forming one or many medullary bundles or plates — *Quercus, Tilia* (PLATE IV, FIGURE 4a).
2. Siphonostele invaginating forming included or dorsal accessory bundles — *Fagus* (PLATE IV, FIGURE 4b).
3. Siphonostele formed, then lateral invaginations giving rise to dorsal, smaller siphonostele or plate over "U"-shaped arc — *Carpinus* (PLATE IV, FIGURE 4c).
4. Polystelic types:
   a. Axillary bud included, petiole not compressed — *Platanus* type.
   b. Axillary bud not included, petiole compressed — *Populus* type (PLATE IV, FIGURE 4d).

Nodes multilacunar, many traces from equal number of gaps.

1. Traces remain free:
   a. Bundles form ring or "U" — *Ricinus* (PLATE IV, FIGURE 5a).
   b. Bundle pattern invaginates — *Rhizophora* (PLATE IV, FIGURE 5b).
   c. By anastomosis forming concentric rings — *Coccoloba* (PLATE IV, FIGURE 5c).
2. Traces fuse:
   a. Ring simple — *Dendropanax* (PLATE IV, FIGURE 5d).
   b. Ring with included bundles — *Macaranga* (PLATE IV, FIGURE 5e).

Subsequent work has shown that this classification covers the majority of vascular system patterns found in the dicotyledons, but not all of the possible combinations with other characteristics. Variations have been found in genera suggesting that the use of family or generic names for the various patterns is not desirable, and the use of serial numbers would soon become unwieldy. Even the terminology used presents difficulties. In a single section the vascular tissue of a petiole may exhibit a complete cylinder, but this is not a eustele at that level, nor a siphonostele in relation to other sections. Invagination and inrolling are terms of motion visually descriptive, but confusing if considered developmentally.

Although previous workers have differed in their opinions on the taxonomic value of the anatomy of the node and the petiole in the recognition of taxa, it is possible to use a combination of characteristics to devise a key to sterile material of a local flora and probably to families and genera of dicotyledons. Such a dichotomous key would involve a great many characteristics, and some of these would be repeated in several categories. For example, a simple flat arc in the petiole might arise from a unilacunar node or a trilacunar node, while the relatively simple "U"-shaped pattern of vascular tissue in the middle of a petiole could be associated with a unilacunar, trilacunar, or multilacunar node (PLATES II–IV). The same characteristics are involved in compiling a description of the vascular system extending from the internode to the leaf tip.

The following characteristics are a few of many that would be useful descriptively:

INTERNODAL AREA: Cortical or medullary bundles present or absent.

NODAL AREA PER LEAF: Leaf gaps one (unilacunar), three (trilacunar), or five or more (multilacunar) with additional consideration to the number of traces in each gap as represented either by protoxylem strands or metaxylem.

LEAF POSITION: Opposite, alternate, orixiate, whorled; distichous or decussate.

LEAF FORM: Simple, compound including sub-units for pinnate or palmate with bi- or tri-compound as well as unifoliate types. Leaves entire or lobed. Venation equally pinnate or pli-nerved or palmately veined.

STIPULES: Present or absent; type and position.

PULVINUS: Present at the base or apex of the petiole, or both, or neither.

PETIOLE: Length; characteristics such as terete, flattened, grooved, winged, or decurrent.

PETIOLE STRUCTURE: Basal or apical vascular cross-zone networks present or absent. Traces free or united; branched or unbranched, reticulate equally or unequally. Bundles collateral or bicollateral, complete or incomplete. Traces in arc, ring, with accessory bundles to the petiole stele as rib bundles adaxial plate or stele; or as medullary bundles.

A great many individual papers over the years have illustrated the vascular pattern of the petiole by diagrams, camera lucida drawings, or photographs. In interpreting any one of these publications, it is necessary to determine where the section was taken; i.e., as a "coupe initiale," the middle of the petiole, a "coupe caractéristique," or a section in the "meriphylle."

When diagrams are given indicating the relationship of the vascular bundles, the method of indicating various traces is fairly standard with variations only in the language or abbreviation used. Thus, traces seen in cross section are usually distinguished as median, lateral, and ventral, and commonly indicated as M for the median and M^1 for branches of the median; L, Lg or Ld for the laterals as "gauche" or "droit" with branches of the laterals being L1, L2, L3, etc. Bundles in an adaxial position relative to the median and laterals may be designated as A, Ad, or V (ventral) without specific reference to their origin, which may be from independent gaps as distant laterals, as branches of the median, or of the laterals.

THE ROLE OF THE TRACES

In most herbaceous dicotyledons and in some families considered woody (Euphorbiaceae, Urticaceae, Saxifragaceae, Ranunculaceae) the principal traces which enter the base of the petiole remain distinct until they reach the blade. Interconnecting branching may be present but is minimal. Even when the individual traces are broadened by the development of a cambium and the addition of secondary tissue, careful observation of the points of primary xylem will permit the identification of the traces.

In general, the median trace is either unbranched in the petiole or may produce branches which move to a medullary or adaxial position, the latter remaining free, or fusing to form a single adaxial trace, or being incorporated in the vascular ring of the petiole. The median trace of a trilacunar or higher type of node does not generally contribute to the vascularization of veins of the lower part of the blade. Often the median trace and its adaxial branches may extend and be recognized to the apex of the lamina (Sugiyama 1972).

In a trilacunar node the lateral traces may remain independent of the median trace or become intimately associated with it. If the median trace formed branches which are seen in an adaxial position, the lateral traces will be interpolated into the interstices of the vascular pattern formed by the median trace (PLATE III, FIGURE 3k). In a trilacunar node of a plant having stipules, the lateral traces may enter the stipules or supply only a branch which enters the stipules. Within the lamina the lateral traces tend to supply the vascular tissue of the basal veins, the basal lobes, or the vascular system from 1/3 to 2/3 of the basal portion of the lamina, while the median trace supplies all of the vascular tissue of the upper portion of the lamina. In pentalacunar or septalacunar nodes the outer lateral traces supply the lower veins or the lower lobes of the lamina successively.

Although the median trace is usually the dominant trace in the petiole, it may also be the first eliminated. Swamy and Bailey (1950), Nakazawa (1956), and Yamazaki (1965) describe the median trace in *Sarcandra* and *Chloranthus* as an unbranched trace which becomes progressively indistinct in the costa and ultimately disappears before reaching the apex. Yamazaki (1965) pointed out that in *Liriodendron* the median trace had little relationship to the lateral venation of the leaf. Bailey and Swamy (1949) described a double trace condition in the petiole and blade of *Austrobaileya*. The traces originated from different parts of the "eustele" and remained independent to the apex of the blade. Each bundle supplied lateral branches as veins for the leaf. *Trimenia* (Money et al. 1950) also had a double trace in the petiole, while *Piptocalyx* (Monimiaceae) exhibited two traces at one gap and four at the other of a pair of opposite leaves. The two middle traces of the four fused so that the leaf received three traces. In *Ascarina* of the Chloranthaceae (Swamy 1953), two traces occur at the base of the petiole and remain distinct for most of the length of the leaf blade. The two traces present in the gap area of *Clerodendrum* (Marsden & Bailey 1955) divide in the petiole several times, and the middle ones fuse to form a single strand within the blade.

Some attention has been given by various authors to the orientation of the bundles within the petiole and the leaf blade. In general, the position of the phloem relative to the xylem, i.e., peripheral or toward the center, is of little value in single sections of the petiole. In a series of sections the changes in orientation are successive, so that a bundle with normal phloem orientation can be reversed in position a few sections later. The bundles obviously do not twist in development, but the position of the xylem and the phloem results from special paths of differentiation of these tissues in the procambial state.

In multilacunar nodes the distant trace or traces may enter only the sheathing stipules, contributing nothing to the petiole or the leaf blade, or may enter the edges of the sheathing leaf base.

METHODS OF STUDY OF PETIOLE ANATOMY

The vascular pattern of the petiole is of value as a taxonomic character useful in the identification of taxa. The systematic level of the taxonomic value does vary from one taxon to another. In some cases families can be recognized; in other cases genera, species, or varieties can be distinguished on the basis of the petiole vascular patterns.

The second edition of Metcalfe and Chalk's *Anatomy of the Dicotyledons* will contain descriptive information of petiole vascular patterns, and illustrations of these for all of the families recognized. Most of the patterns have been obtained from fresh material or material collected and preserved in alcohol.

To obtain the vascular pattern in three dimensions, a mature leaf is selected, and sections are made progressively from the internode and then through the node, the petiole, and the blade. The first series of sections taken at random intervals along the axis will determine where the critical areas of pattern change occur, although these can be expected at the node, immediately above the basal pulvinus, at the upper pulvinus or the base of the blade, at the point of attachment of leaflets, or at the departure of veins. Sections can be cut freehand with a straight razor or a single-edged razor blade, and stained in phloroglucinol and hydrochloric acid. This temporary stain does not work well on material preserved in any amount of formalin including FAA. No permanent slides are obtained by this method.

Phloroglucin stains lignified tissues, but often does so differentially. Srivastava (1966) has indicated the nature of the variation of this staining. Some plants such as members of the Thymelaeaceae assume a weak coloration with phloroglucinol or none at all.

In many cases neither fresh nor preserved material was available, and herbarium specimens were used. This obviously restricted the amount of material available for study, and required critical initial sectioning. The herbarium material was softened in boiling water or by soaking in sodium hydroxide. Woody portions often required softening in hydrofluoric acid. The standard technique of embedding, sectioning, and staining for permanent slides was also employed, especially for material difficult to obtain, to process by hand, or to interpret. Occasionally longitudinal sections are necessary for one or several angles of approach. Clearing and selective staining methods were also used.

Although this work has been in progress for twenty years and has involved a great many technicians, the number of species studied has been a relatively small proportion of the dicotyledons. I do appreciate the assistance of many people in preparing nodal-petiole patterns, and of many individuals who supplied material; and also the cooperation of innumerable directors and curators of botanical gardens and herbaria, who gave permission for me to obtain living material or fragments from herbarium specimens.

More problems are evident in the data presented. Hopefully, individuals with access to abundant material and with sufficient time will undertake the clarification of such problems. For all who attempt to use this type of information, I can only stress again the need to visualize in three dimensions what is illustrated most frequently in only two.

STIPULES

Although the presence or absence of the stipules, as well as their form, has long been used as a diagnostic character in plant taxonomy, the morphological nature and the origin of the stipule remain obscure. The stipule is commonly defined as an appendage or pair of appendages at the base of the leaf. The stipules may be paired or single, equal or unequal in size, large, foliaceous, and persistent or reduced to a mere protuberance or a small, readily deciduous scale. Some stipules have been modified to thorns or tendrils. Stipules are often represented as a stipular sheath, and may be below the point of attachment of the leaf, well above the point of attachment of the leaf, associated with the leaf, or free from it, being axillary (Philipson 1968) to the leaf, on both sides of the leaf attached to the stem, opposite the leaf, or at varying levels of the pulvinus or the petiole. Sinnott and Bailey (1914) believed that the stipules were primarily associated with trilacunar nodes, and many authors have indicated that most stipules are vascularized from the lateral traces of a trilacunar node.

A fundamental question, unresolved to the present, is whether the stipules are part of the leaf, or independent structures. Guédès (1972) apparently believes the stipules are comparable to portions of the leaf blade or leaflets, for he stated: "a petiole generally occurs because of intense intercalary growth either below the lowest pair of leaflets and the leaf is exstipulate or between the first pair of leaflets from below and the second one. The lower pair (of leaflets) is then isolated near the leaf insertion and becomes a pair of protostipules. It rises to the state of true stipules when proleptic development is obtained. . . . The petiole can also develop above several pairs of leaflets and there are then several pairs of stipules."

Regel (1843), Agardh (1850), Clos (1879), and Tyler (1897) have all suggested the independence of stipules from the foliage leaf in nature as well as in development. More recently Croizat (1940) proposed that the two stipules are basic structures, and between them a "dab" of meristem is found. Croizat refers to this meristem as a primary nerving center which may develop into a foliage leaf.

Examples of the seemingly independent development of stipules and the foliar leaf are many. A shoot developing from a dormant bud may produce successively cataphylls, lobed stipule-like structures, similar lobed structures with a nonpetioled lamina, and finally a normal petiolate leaf with basal stipules (Furuya 1953). Many authors have used the illustration of *Ribes* showing the retarded development of the leaf blade in successive stem appendages. Here the bud scales are clearly stipules, with the petiole and abortive leaf blade represented by a ridge, or a ridge and a small appendage. Fahn (1967, p. 194) gives an illustration of bud scales of *Vitis vinifera* where each pair of stipular scales has an included leaf. Large stipules with a rudiment of a leaf attached protect the buds in species of *Magnolia*. Large foliaceous stipules are often precociously developed in the Leguminosae. The seasonal growth of *Ilex laevigata* ends abruptly in transition from the normal foliage leaves with two minute gland-like basal stipules to an organ of three structures, the outer two comparable in size and shape to the stipules of the preceding leaf, and the middle one no larger in size and of the same shape, but in theory the primordium of the foliage leaf.

Traces which vascularize the stipules may be the complete lateral traces (Furuya 1953) or branches of the lateral traces of a trilacunar node (Bailey & Sinnott 1914). When the leaves are opposite at the node, e.g., in many Rubiaceae, the stipules of adjoining sides of the opposite leaves may be variously united, sometimes with a bifid apex or tapering to a single point (Howard 1970). The vascular supply to these conspicuous interpetiolar stipules may come from the sides of the single arc-like trace of each leaf. The branch bundles run horizontally or at an angle into the stipules, and may remain independent. In multilacunar nodes the leaf may be vascularized primarily by the centrally located vascular bundles, with small traces departing from the lateral nodes, running horizontally to the leaf base while giving rise to vertical bundles which vascularize the stipules. In some sheathing stipules (Ozenda 1948, Sugiyama 1972), the bundle or bundles most distant from the median trace may enter the stipules without connections with other bundles or with the leaf itself (Plate I, figure 1i). Sugiyama (1972) reports the bundle opposite the median trace in *Magnolia virginiana* may branch while remaining free and be noncontributory to the leaf itself.

The bundles of stipular sheaths which are above and free from the leaf, as in *Platanus*, may be vascularized by traces completely unassociated with any vascular supply to the leaf. So, too, with stipules which are borne on the side of the stem opposite the leaf scar (*Ricinus*), or borne below the leaf (Cunoniaceae).

GLANDS

The presence and nature of foliar glands has been recognized as a useful taxonomic character (Gregory 1915, Dorsey & Weiss 1920). Zimmerman (1932) has given an extensive systematic survey and classification of extra-floral nectaries. Schnell, Cusset, and Quenum (1963) also supplied a broad survey of foliar glands with a classification, with suggestions on the phylogenetic origin of glands, and with some anatomical details.

Glands can occur on the pulvinus, stipules, petiole, or blade in various positions. They can be sessile or stalked, and with or without vascular tissue. Bernhard (1964) found the petiolar glands in certain Euphorbiaceae to be present in the primordium, and compared the glands to other lobes of the lamina. Dorsey and Weiss (1920) also considered the gland to be the equivalent of a portion of the blade, and Messager (1886) earlier had proposed the origin of the gland as an abortive laminar structure. Schnell and Cusset (1963) regard the glands as nonfoliarized "elements foliaires," or the homologues of lobes of the lamina. Cusset (1965) later proposed the term "metamere" for the "article foliaire" in a connotation differing from that used earlier by De Candolle. He suggested the primitive leaf was a single metamere glandularized at the apex, while the foliar leaf of most plants is to be regarded as a compound product of several metameres with the glands persisting or lost in the evolutionary process.

The petiolar glands may be associated with simple or complex petiolar vascular patterns arising from unilacunar or trilacunar nodes. The majority of vascularized glands receive their vascular supply from the lateral traces or their derivatives, as sequential lateral traces or rib traces. The very large glands of *Pithecellobium* obtained a vascular supply from the adaxial bundles of the complex petiole vasculature (Elias 1972).

PHYLLODES

The term phyllode literally means leaflike, and has been applied in plant morphology in a variety of ways to flattened photosynthetic petioles; to rachides of compound leaves which have lost their leaflets; and to a quantity of dissected leaves with terete segments. A flattened leaflike stem may be termed a platyclade, a phylloclade, or a cladode.

The phyllodes of species of *Acacia* may be genetically without leaflets, or in maturation fail to develop leaflets, or lose the leaflets by abscission at various stages of development. Boke's (1940) study of the laterally (vertically) flattened phyllodes of several species of *Acacia* revealed fundamental differences in development, including the dominance of the adaxial meristem in producing the flattened organ. A short pulvinus was present, as were stipules. The orientation of the vascular bundles simulated the pattern present in the petiole of other leaves. Boke concluded that the phyllode was homologous to a petiole-rachis of a pinnately compound leaf. The initial three vascular traces in the phyllode are supplemented with interpolated bundles. Slade (1952) reported a similar interpolation of traces in cladodes of several New Zealand brooms. Peters (1912) recognized three types of phyllodes in *Acacia* which he termed "Platentypus," "Binsentypus" (rushlike), and "Übergangstypus" (transitional types). Phyllodes in species of *Oxalis*, e.g., *O. fruticosa*, *O. ptychochala*, represent the petiole of a palmately compound leaf which has lost the leaflets in development.

Articulated leaves have been described and illustrated for several families (Troll 1939). The "Gelenkknoten" of *Polyscias* species are clearly in the position of leaflets lost phylogenetically or ontogenetically from terete rachides, since one or more foliage leaflets are present. Species of *Citrus* occasionally show a similar articulated form. Troll (1939) illustrated the articulated phyllode of *Phyllarthron* (Bignoniaceae). Saha (1952) studied *Phyllarthron commorense* and concluded the "leaves are simple, petiolate with segmented blades." He denied the existence of articulation within a leaf, ignoring the frequent occurrence of such segments in the Bignoniaceae. *Phyllarthron* should be re-examined to determine if it is not a compound leaf which has lost or not developed pinnae.

Kaplan (1970b) has studied the development of the "rachis-leaves" in two genera of the Umbelliferae, and concluded that these terete leaves with septae are the equivalent of the rachis of a pinnately compound leaf with the appendages reduced, transformed pinnae which function as hydathodes.

Terete leaves have often been described as unifacial leaves. A cross section of the leaf may reveal the bundles are arranged in a circle with the phloem of each trace oriented to the periphery. Stomata may have a uniform distribution around the leaf surface, rather than be limited to the abaxial surface as in most dorsiventrally flattened leaves. Flachs (1916) proposed a classification for leaves of plants in the Australian flora which are terete or nearly so, and recognized "äquifacial" (laterally flattened), "unifacial," "bifacial," and "transitional" types. The classification was based mainly on the orientation of the bundles. The abrupt transition from a laminar leaf of *Hakea* (Proteaceae) to the dissected leaf with terete segments is shown by Troll (1939). *Franklandia fucifolia* (Proteaceae) is commonly cited as an example of foliar dichotomous divisions in terete or unifacial leaves.

EPIPHYLLOUS INFLORESCENCES

Flowers may be borne on leaves as single flowers or in inflorescences, and have been described as epipetiolous, epiphyllous, or hypophyllous according to their position; an epiracheal type should be recognized for compound leaves (PLATE VIII). Johnson (1958) has supplied a modern listing of 20 genera in 10 families, to which the Chailletiaceae should be added.

Payer (1890) concluded that the leaf and its axillary flowering branch were fused when flowers were borne epiphyllously. De Candolle (1890), after studying the vascular structure of the petiole and the blade, concluded instead that the epiphyllous inflorescence was of foliar origin. Stork (1956) debated whether the flattened structures bearing flowers might be considered "cladophylls." Melville (1962) regarded the epiphyllous inflorescence as evidence of his proposed primitive "gonophyll."

The hypophyllous inflorescence of *Erythrochiton hypophyllanthus* (Rutaceae) is apparently unique in the Angiospermae in bearing a flower on the lower side of the lamina (Engler 1897). Melville (1962) stated that "above the insertion of the inflorescence there is nothing unusual in the structure of the midrib. Below the flowers, the midrib bundle lies above and quite distinct from the vascular strands supplying the inflorescence. It is evident that in *Erythrochiton* the inflorescence is truly adnate to the lower surface of the leaf." No specimens are available to me for further examination of the vascular supply within the petiole to determine the origin of the traces supplying the inflorescence. Whether these are axillary to the leaf bearing the inflorescence or are from the subjacent node is not known.

Epipetiolar inflorescences are reported at the base of the petiole, along the petiole, or at the apex of the petiole. Johnson (1958) has shown that the epipetiolar inflorescence of *Turnera ulmifolia* originates as a branch trace and becomes associated in the petiole, but is not fused with the vascular supply of the leaf. He concluded that "the epiphyllous inflorescence in *Turnera* is axillary in origin, and through subsequent growth in the foliar buttress is displaced to a petiolar position . . . 10 out of 13 species of *Turnera* examined have epiphyllous inflorescences which originated in the axil of a foliar primordium." Prance (1972) described the vascular patterns in the petiole of several taxa of the Dichapetalaceae in which the inflorescence is borne at various positions on the petiole or well up on the midrib. He recognized "floral bundles" or "inflorescence trace" as distinguishable from "leaf bundles" or "leaf traces" in both sterile and fertile leaves. Although he stated "the floral bundles definitely arise from the leaf bundle within the petiole rather than in the stem" (p. 9), he stated later (p. 12) that "the presence of floral bundles in some sterile petioles, and the separate nature of the floral bundle, demonstrate that the position of the inflorescence has arisen by a gradual fusion of the peduncle with the petiole rather than being a true epiphyllous inflorescence."

Hallé and Delmotte (1973) have illustrated the difference in vascular patterns within the inflorescence axis and the petiole from which the inflorescence arose in the epipetiolar member of the Gesneriacae, *Epithema tenue*. Regrettably they do not show the relationships of individual bundles, or the origin of the vascular tissue supplying an axillary bud present between the inflorescence axis and the petiole.

Van Steenis (1961) described the "flowers serially bursting forth almost the entire length of the hypocotyl (petiole)" in *Moultonia singularis* (Gesneriaceae), and Letouzey et al. (1969) show several inflorescences arising from the long petioles of *Mocquerysia multiflora* (Flacourtiaceae). No data are given in either case for the vascular structure of the petiole.

Barth (1896) studied various species of the Dichapetalaceae in which petiole-borne inflorescences were present ("fertile leaves") or absent ("sterile leaves"). In the petioles of "fertile leaves" he found a stem-like vascular structure, the adaxial portions of which formed the vascular supply to the inflorescence. Such leaves may also have an axillary bud. In some "sterile leaves" the petioles also had an adaxial vascular supply comparable to that of the "fertile leaves." In others, the petiole had only a simple arc of xylem and a bud in the axil. Additional species were intermediate between the two extremes. Barth accepted the idea that the epiphyllous inflorescence was a congenital accrescence of the petiole with the floral peduncle; and although the bundles were of a foliar origin, concluded that the inflorescence is nothing more than one bud of several which might be produced in the axil. Stork (1956) concluded from his studies that "various degrees of coalescence prevail in species of Dichapetalaceae where inflorescences are borne on the petioles." To Melville (1962) "the sequence of vascular structures to be observed in the Chailletiaceae provides no evidence for adnation . . . but rather, it shows the last stages in the disengagement of the fertile branch from its leaf."

All of the inflorescences borne on leaf blades have been reported for simple leaves with the sole exception of *Chisocheton pohlianus* (Meliaceae), which may bear clusters of flowers in the axils of the pinnae of a pinnately compound leaf. Another species of *Chisocheton* is now known in which a simple or branched racemose inflorescence develops from the rachis of the compound leaf (Peter Stevens, pers. comm.). Harms (1917) illustrated a specimen with flowers borne in the axils of three pairs of leaflets. The illustration also shows an axillary bud at the base of the leaf, and immature pinnae at the apex. Contrasting is another shoot illustrated with an axillary racemose inflorescence and a separate pinnately compound leaf. No anatomical data are offered by Harms on the relationship of the vascular supply of the epirachial inflorescence to that of the rachis and the leaf blades. Melville (1962) refers to a "new species of Chisocheton" in which sections of the rachis were cut to reveal a "stem-like structure below the insertion of the inflorescence and leaf-like structure above." Considering the complex vascular patterns found in the rachis of leaves of the Meliaceae, this statement by Melville is unrevealing.

Flowers that are borne on the simple leaf blade are generally associated with the midrib or proliferations of it in pinnately veined leaves. Possible exceptions are found in *Peperomia foliiflora,* in which the inflorescences arise from the base of diverging palmate venation. No material is available for anatomical investigation. Data are also wanting for the epiphyllous palmately veined leaves of *Begonia prolifera* and *Begonia sinuata* cited by Johnson (1958).

The flowers may be at one of several positions along the blade, being near the middle of the length of the blade or along the extreme portions of it, even at the ultimate apex. Letouzey et al. (1969) concluded that the relative position of the inflorescence may vary and is without taxonomic significance. They further explain the presence of a large bract subtending the epiphyllous inflorescence of *Phylloclinium bracteatum* as an example of hyperfoliarization.

De Candolle's (1890) study of the vascular supply to the epiphyllous inflorescences of *Polycardia* (Celastraceae), *Phyllonoma* (Dulongiaceae) and *Helwingia* (Cornaceae) formed the basis for his conclusion that the inflorescences were foliar in origin and not concrescent branches. Melville (1962) stated: "in all of these the vascular system of the petiole, where it left the branch, was an open arc which, further up, arched round and formed a complete circle, as in a stem. . . . In all of these examples where the midrib extends beyond the inflorescence, its trace in section has the open arc appearance, which is very common in angiosperm leaves." Johnson (1958) reached the same conclusion. Watari (1939) was not aware of De Candolle's work, and supported the contrasting idea of Thouvenin (1890) that the traces for the flowering branch were fused with the petiole and the lamina. He cited species of *Saxifraga, Chrysosplenium,* and *Vahlia* in which branch traces fuse with the foliar traces in a comparable manner.

With the exception of the study by Johnson (1958) on *Turnera* and *Helwingia*, the majority of the anatomical data available in the literature does not consider the nodal origin of the vascular supply of the epiphyllous inflorescences.

The Dichapetalaceae, Turneraceae, and Flacourtiaceae have trilacunar nodes. The Celastraceae has a unilacunar node. *Helwingia,* variously assigned to the Cornaceae, Helwingiaceae, or Araliaceae, has a unilacunar node, an exceptional pattern in the Cornaceae and most unusual in the Araliaceae where Melville (1962) associates the genus. *Phyllonoma* has been placed in the Saxifragaceae, which has trilacunar or unilacunar nodes, but it is now associated with the Escalloniaceae (Melville 1962) with unilacunar nodes, or as the monotypic Dulongiaceae (Willis 1966). *Phyllonoma* is reported by Stork (1956) to have stipules, and is the only genus with stipules and an epiphyllous inflorescence.

SUMMARY AND CONCLUSIONS

The extreme morphological diversity represented in the photosynthetic organ of extant plants makes impossible a simple yet inclusive and satisfactory definition of either a leaf or a node. The search for this simple definition has resulted in the undesirable distinction made of a leaf and of a stem when these must be recognized, developmentally and morphologically, as a continuous system. The existing statements on the primitive type of leaf or the primitive type of node are equally futile exercises in semantics. The ancestral forms of the modern "leaf" are either lacking or have not been recognized.

The two basic theories proposed for the origin of the leaf recognize a stem as a primary structure, and the leaf as (1) an enation or protuberance from a stem, which has attained a vascular supply from the stem, or (2) the modification in various ways of a stem or a stem system. Casimir de Candolle (1868) proposed that the leaf was a flattened stem, a stem in which the adaxial portion had atrophied. Agnes Arber (1941) concluded that the "leaf is a partial-shoot . . . revealing an inherent urge toward becoming a whole-shoot, but never actually attaining this goal, since radial symmetry and the power of apical growth and self-reproduction are curtailed or inhibited." The telome theory (Wilson 1942) also proposed a primitive stem system of terete axes with dichotomous branching, from which a flattened leaflike structure could be derived by the fusion of axes (see Croizat 1973, footnote 84) or by the broadening of an individual axis. Such broadening and expansion has been called foliarization, planification, hyperfoliarization, or hypocladification. Melville's gonophyll hypotheses (1962) are but variations on this theme.

Sinnott and Bailey (1915) concluded that the primitive angiospermous leaf was simple, palmately veined, probably three lobed, and associated with a trilacunar node, but did not consider how this originated. Corner (1949) also begged the question by suggesting that the primitive leaf was a pinnately compound massive structure. He derived smaller and simple or palmate leaf types by reduction.

Some contrasting theories of the origin of the leaf place emphasis on the potential development of portions of a meristematic zone. Primordia in such an area can develop individually, or several can develop in association. The segmentation of the developmental area can produce either a vascular cylinder and a "leaf-skin," or contrastingly a "leaf base" and an apical region (Unterblatt *versus* Oberblatt), with each area of the two approaches having a potential for subsequent recognizable and different diversification.

The primitive node from the trace-gap point of consideration has been proposed variously as trilacunar with single traces (Sinnott 1914); trilacunar with a double trace in the median gap (Takhtajan 1969); unilacunar with a single trace (Benzing 1967); unilacunar with a double trace (Marsden & Bailey 1955), or multilacunar (Ozenda 1948). Associations of these nodal types with floral or other familial characteristics do not reveal any substantial correlation. The so-called primitive floral types may be found with either the proposed most advanced or the proposed most primitive nodal types, while advanced floral types have a preponderance of advanced nodal types but may also be associated with the proposed primitive nodal types.

The general tenet (Smith 1967) that primitive leaves are simple and advanced types of leaves are variously compound also lacks substantiation. The distinctions between a simple and a compound leaf, whether pinnate or palmate, are either difficult or arbitrary. Gradients do exist also between microphylls and megaphylls, and between sessile and petiolate leaves. The internal structure of any one type can be simple or complex. The proper phylogenetic position of the characteristics of cortical vascular systems and medullary vascular systems has not been determined, but in the majority of cases these unusual anatomical characteristics are associated with simple leaf types.

The evolutionary progress from alternate and spirally arranged leaves to opposite or whorled leaves has become established as a dictum in most botanical publications (Smith 1967, Cronquist 1968) without any real evidence. Only Croizat (1960) has proposed the alternate point of view that "what was originally verticillate of the foliation has tended to be dirempted into sets of leaves, and finally the sets themselves of leaves have . . . been dirempted again into single leaves in accordance with alternate and spiral modes of foliation."

A solution to the problem of what is primitive and what is advanced may well necessitate the abandonment of modern botanical semantics, and especially the current concepts of the leaf as a fundamental structure or a unit of the plant. The "leaf" of our current thinking may well have multiple possibilities of origin.

Croizat (1973) has proposed seven possible means of origin of the "leaf," and recognizes that there may be more. He suggests the following: 1. A simple scale (leaf *sensu stricto* of *Asparagus*). 2. An inflorescence adapted and imperfectly developed (leaf-cladode of the Asparagae). 3. An inflorescence adapted and imperfectly developed and joined with abundant fused fibers (*Washingtonia*). 4. A "rama-stem" of second or third order with characters more or less foliaceous (*Phyllanthus*, *Schumanniophyton* and *Guarea*, *Chisocheton*, *Schizolobium*). 5. A scale ("Unterblatt") associated with a primordium which is the origin of the typical "rama" or petiole ("Oberblatt"). This, Croizat remarks, is the typical leaf of the Angiospermae. 6. A leaf formed of fused leaflets (*Bauhinia*). 7. A spathe without a spadix (Araceae). He concluded "these examples do not pretend to be complete, irreproachable, etc. Finally they serve only for orientation and to give a very general idea of the different origins of the leaf. In total the leaf is an organ of complex morphogenetic and phylogenetic origin."

Various authors (Lignier 1888, Morvillez 1919, Maekawa 1952, Croizat 1960) have in the past suggested that the modern leaf is a compound structure, an assembly of components, and not necessarily derived by simple modification of a branch or a stem. Further support of this possibility is in the information on the node and the petiole just presented.

Three aspects of the foliage of the modern dicotyledonous angiosperm require consideration basic to any speculation on the origin of the "leaf."

1. The "node" of the modern dicotyledonous angiosperm is a locus of meristematic activity capable of producing one or more products. These products can be variously associated in development, and each is capable of achieving various degrees of specialization.

The nodal locus may extend around the stem at a given level and have, as well, varying degrees of vertical extension. The evolutionary progress of the nodal locus has been one of spatial restriction in toto as well as in the specialization of its derivative products. The products of the meristematic activity of the nodal locus, as has been pointed out, may be the leaf, occurring alternatively as a scale, a prophyll or an eophyll; stipules; vegetative or floral buds; vascularized or unvascularized glands, etc.

Applicable here are the studies of sheathing stipules which suggest that the nodal locus, as a meristematic zone, is capable of development completely around the stem, with a portion of the derivative tissue specialized into a foliage leaf, and the other portions existing as the sheathing stipule. It should be noted that the stipular portion may be free of the leaf in a lateral position, adaxial to the leaf, opposing the leaf, or located above or below the leaf. Since there are examples of the vascular independence of the leaf and the stipule, the stipule should be considered, in some cases at least, not a portion of the leaf, but phylogenetically a structure equivalent to the leaf where both may be developed from the same nodal locus meristem.

2. The leaf may well be a compound structure assembled by the lateral association of primordia from the nodal locus meristem developing individually or collectively. It has been pointed out that within the petiole and/or the complete leaf the several vascular bundles may be independent. It is possible to recognize the individuality of vascular bundles in many leaves. The median trace, for example, is most easily recognized and may extend undivided and unbranched to the uppermost portion of the leaf blade before developing secondary venation: i.e., the median trace, when more than one trace is present, vascularizes the upper portion of the leaf blade. Likewise, the median trace may be present only in the base of the petiole, and may deteriorate or be lost in the petiole or the blade. The lower portion of the entire leaf blade, or in some cases the lateral basal lobes of the simple leaf may be vascularized only or primarily by traces which enter the stem as lateral traces.

In many dicotyledons the median trace may give rise in the base of the petiole to two branches which assume an adaxial position. These adaxial branches of the median trace may fuse or remain independent to the tip of the blade. Lateral traces from the stem may then be interpolated in the petiolar vascular tissue between the median trace and its derivative adaxial branches. The secondary venation of the lower portion of the leaf blade may be derived only from these lateral trace components, and the lateral traces may be completely used up in the lower portion of the leaf blade, with the upper portion of the blade being supplied vascular tissue from the median trace and its adaxially located branches.

The path of derivative bundles from the cortical vascular system or the medullary vascular system of the stem within the petiole and the leaf blade also suggests the "leaf" is an assembly. The cortical vascular system within the stem may at times be associated with the principal vascular system or be completely independent of it. Within the leaf, the derivatives of the stem cortical vascular system may contribute the bundles normally called "laterals" in the petiole, and these extend, clearly recognizable and independent, into the lower portion of the leaf blade.

The medullary vascular system of the stem may also be associated at times, or in some plants, with the principal vascular system, or be independent of it. The medullary bundles of the stem may contribute to the vascular supply of the leaf completely independent of the vascular tissue derived from the principal vascular system of the stem. Within the leaf, the bundles derived from the medullary vascular system of the stem remain in a medullary position in the petiole or the midrib, and do not appear to contribute to the vascularization of the lamina.

The double leaf trace of *Ascarina* described by Swamy (1953) was said to have the two bundles associated with independent parts of the "eustele" of the stem. Within the leaf, each bundle was associated with one half of the lamina by branching only in one direction. Neither Bailey nor Swamy speculated that this might be the fusion product of two ancestral primordia.

Although many examples of interconnections between traces within the petiole, the rachis, or the lamina are known, still the independence and individuality of the trace predominates, and is discernible until secondary activity may obscure the condition. Thus there is much evidence that the leaf is a compound structure, assembled from parts represented today by the distinctive traces.

3. The "leaf" may be compound in the sense of a serially articulated structure, but the significance of the evidence is still not clear.

De Candolle (1868) suggested that the leaf was composed of a linear series of "metameres," and evidence for this is found in the pulvinal areas of the leaf. In compound leaves, one to many pulvinal areas may be present within the length of the leaf, and these may or may not be zones of abscission or articulation. In simple leaves, the pulvinal area may be at the base of the petiole or at the apex of the petiole, or in both locations. Whether or not abscission occurs in the pulvinal area, there is an alteration of the pattern of vascular tissue contrasting with that of the intervening zones. Leaves which lack obvious pulvini may have internal areas of vascular tissue specialized as cross zones at the apex or the base of the petiole, separating otherwise distinctive and characteristic areas of vascular organization.

Strey (1973) has recently described the leaves of *Cussonia spicata* (Araliaceae) where a palmately compound leaf has the segments pinnately compound. He used the terminology of Mirbel (1815) in referring to these leaves as "vertebrate," recognizing the ultimate abscission of each portion of these serially articulated segments. The presence of an apical gland (Cusset 1965) or food body, the so-called Beltian bodies, may also represent examples of metameres and the serial articulation of the leaf. Developmental studies of the serially articulated leaf appear to be completely lacking.

The origin of the modern leaf is to be sought in a small terete structure, probably an enation, with a single vascular strand. The primitive leaf may have developed laterally subsequently in some cases through the action of a marginal meristem. In other cases several of these enations developed as a single unit, the leaf, from the many enations present in the primitive broad nodal plexus of meristematic activity. The primitive leaf was probably borne in whorls or even vertically grouped clusters, and progress was the reduction, enlargement, and isolation of the derivative products. The primitive large nodal plexus has become restricted to the modern leaf scar. Vertical restriction, division, or isolation is recognizable by the development of the internode. Specialization of the derivative products is revealed as stipules, buds, glands, and leaves. It is suggested that areas within the primitive nodal plexus retained a meristematic potential for growth and differentiation, while other areas lost this potential to varying degrees. The multilacunar node of modern plants with a sheathing stipule may well be the residual expression of the primitive meristematic nodal plexus.

Two morphogenetic trends from this nodal plexus should be recognized as rameal and foliar, occurring simultaneously or in varying sequences, thus accounting for the modern pulvinus, petiole, rachis or serial articulations. The number of primitive enations may be represented in the modern leaf by the number of bundles present either in the gap-trace area or in the petiole.

Attempts to place in a single phylogenetic sequence the nodal gap-trace area; alternate, opposite, or whorled leaves; simple or compound leaves; sessile or petiolate leaves; stipulate or exstipulate leaves, etc., are fundamentally useless. Such characteristics of modern plants must be recognized as mid-points in the evolution of the modern leaf. The chances are that such morphological expressions are not sequential, but parallel developments from a very simple ancestral type. The success of the "leaf" as a photosynthetic organ has permitted if not contributed to the great diversification of form in modern foliage leaves.

BIBLIOGRAPHY

Acqua, C. Sulla distribuzione dei fasci fibrovascolari nel loro passaggio dal fusto alla foglia. Malpighia **1**: 277–282. 1887.

———. Sulla distribuzione dei fasci fibrovascolari nel loro descorso dal fusto alla foglia del dott. Ann. Inst. Bot. Roma **3**: 43–75. *pls. 6–8.* 1887–1888.

Agardh, J. G. Ueber die Nebenblätter (stipulae) der Pflanzen. Flora **33**: 758–761. 1850.

Arber, A. The interpretation of leaf and root in the angiosperms. Biol. Rev. **16**: 81–105. 1941.

Arnal, C. La notion de noeud. Bull. Soc. Bot. Fr. Mém. **41**: 104–111. 1962.

Artschwager, E. Contribution to the morphology and anatomy of guayule (*Parthenium argentatum*). U.S.D.A. Tech. Bull. 842. 33 pp. 1943.

Bailey, I. W. Nodal anatomy in retrospect. Jour. Arnold Arb. **37**: 269–287. 1956.

——— & C. G. NAST. Morphology and relationships of *Illicium*, *Schisandra* and *Kadsura*. I. Stem and leaf. Jour. Arnold Arb. **29**: 77–89. 1948.

——— & B. G. L. SWAMY. The morphology and relationships of *Austrobaileya*. Jour. Arnold Arb. **30**: 211–226. 1949.

BALFOUR, E. E., & W. R. PHILIPSON. The development of the primary vascular system in certain dicotyledons. Phytomorphology **12**: 110–153. 1962.

BARTH, F. Anatomie comparée de la tige et de la feuille des Trigoniacées et des Chailletiacées (Dichapétalées). Bull. Herb. Boiss. **4**: 481–520. 1896.

BENZING, D. H., Developmental patterns in stem primary xylem of woody Ranales. I. Species with unilacunar nodes. Am. Jour. Bot. **54**: 805–813. 1967a.

———. Developmental patterns in stem primary xylem of woody Ranales. II. Species with trilacunar and multilacunar nodes. *Ibid.* 813–820. 1967b.

BERNHARD, F. Les glandes pétiolaires de certaines Euphorbiacées dérivent de méristèmes identiques a ceux des lobes foliaires. Compt. Rend. Acad. Sci. Paris **258**: 6213–6215. 1964.

BLAKE, S. T. *Idiospermum* (Idiospermaceae), a new genus and family for *Calycanthus australiensis*. Contr. Queensl. Herb. No. 12. 37 pp. 1972.

BOKE, N. H. Histogenesis and morphology of the phyllode in certain species of *Acacia*. Am. Jour. Bot. **27**: 73–89. 1940.

———. Determinate shoot meristems in the Cactaceae. Pp. 759–761 *in* Recent advances in Botany, vol. I. (From lectures and symposia presented to the IX Int. Bot. Congr., Montreal, 1959.) xvi + 947 pp. Toronto. 1961.

BOUNAGA, D. Noeuds, traces gemmaires et morphogenèse. Ann. Sci. Nat. Bot. Paris 12ᵉ ser. **14**: 1–32. 1973.

BOWER, F. O. On the structure of the stem of *Rhynchopetalum montanum* (Fresen.). Jour. Linn. Soc. Bot. **20**: 440–446. *pls. 36–38.* 1884.

CANDOLLE, C. DE. Mémoire sur la famille des Pipéracées. Mém. Soc. Phys. Hist. Nat. Genève **18**: 1–32. 1866.

———. Théorie de la feuille. 35 pp. *pls. 1, 2.* Genève. 1868. [Reprinted from Arch. Sci. Bibl. Univer. **32**: 32–64. 1868.]

———. Anatomie comparée des feuilles chez quelques familles de dicotylédones. Mém. Soc. Phys. Hist. Nat. Genève **26**: 427–480. *2 pls.* 1879.

———. Recherches sur les inflorescences épiphylles. Mém. Soc. Phys. Hist. Nat. Genève, vol. suppl. (celebrating the Centennial of the foundation of the Society) No. 6. 33 pp. *2 pls.* 1890.

CANRIGHT, J. E. The comparative morphology and relationships of the Magnoliaceae IV. Wood and nodal anatomy. Jour. Arnold Arb. **36**: 119–140. *pls. 1–3.* 1955.

CARLQUIST, S. Leaf anatomy and ontogeny in *Argyroxiphium* and *Wilkesia* (Compositae). Am. Jour. Bot. **44**: 696–705. 1955.

CLOS, D. Indépendance, développement, anomalies des stipules; bourgeons a écailles stipulaires. Bull. Soc. Bot. France **26**: 189–193. 1879.

COL, A. Recherches sur la disposition des faisceaux dans la tige et les feuilles de quelques dicotylédones. Ann. Sci. Nat. Bot. VIII. **20**: 1–288. 1904.

COOK, O. F. Dimorphic leaves of cotton and allied plants in relation to heredity. U.S.D.A. Bur. Pl. Ind. Bull. 221. 59 pp. 1911.

CORNER, E. J. H. The durian theory or the origin of the modern tree. Ann. Bot. **52**: 367–414. 1949.

CRITCHFIELD, W. B. Leaf dimorphism in *Populus trichocarpa*. Am. Jour. Bot. **47**: 699–711. 1960.

CROIZAT, L. A comment on current notions concerning the leaf, stipule and budscale of the angiosperms. Lingnan Jour. Sci. **19:** 49–66. 1940.

———. Principia botanica. 1821 pp. Publ. by author, Caracas, Venezuela. 1960.

———. En torno al concepto de hoja, ensayo de botanica analitica y sintetica. Biblioteca Acad. Cien. Fis. Math. Nat. (Caracas) **12:** 5–196. 1973.

CRONQUIST, A. The evolution and classification of flowering plants. x + 396 pp. Boston. 1968.

CUSSET, G. Les nectaires extra-floraux et la valeur de la feuille des Passifloracées. Rev. Gén. Bot. **72:** 145–216. *pls. 1–18.* 1965.

CUTTER, E. G. Formation of the lateral members of the shoot. Pp. 820–823 *in* Recent advances in botany, vol. I. (From lectures and symposia presented to the IX Int. Bot. Congr., Montreal, 1959.) xvi + 947 pp. Toronto. 1961.

———. Patterns of organogenesis in the shoot. Pp. 220–234 *in* E. G. CUTTER, ed. Trends in plant morphogenesis. xvi + 329 pp. *frontisp.* + *8 pls.* London. 1966.

DAVIS, E. L. Medullary bundles in the genus *Dahlia* and their possible origin. Am. Jour. Bot. **48:** 108–113. 1961.

DEHAY, C. L'appareil libéro-ligneux foliaire des Euphorbiacées. Ann. Sci. Nat. Bot. X. **17:** 147–295. *pls. 1–4.* 1935.

———. Les affinités entre les Euphorbiales, les Morales et les Malvales, d'après l'appareil libéro-ligneux foliaire. Bull. Soc. Bot. France **85:** 23–31. 1938.

———. L'appareil libéro-ligneux foliaire des Sterculiacées. Ann. Sci. Nat. Bot. XI. **2:** 45–130. 1941.

———. Notice sûr les titres et travaux scientifiques de Charles Dehay. 1–57. Arras. 1942.

DORMER, K. J. An investigation of the taxonomic value of shoot structure in angiosperms with especial reference to Leguminosae. Ann. Bot. N.S. **9:** 141–153. 1945.

———. Shoot organization in vascular plants. 240 pp. London. 1972.

DORSEY, J. J., & F. WEISS. Petiolar glands in the plum. Bot. Gaz. **69:** 391–405. 1920.

DOSTAL, R. Versuche zur apikalen Dominanz in der Planzenmorphogenese. Acta Acad. Sci. Cechoslov. Basis Brunensis. **31:** 1–75. 1959.

ELIAS, T. S. Morphology and anatomy of foliar nectaries of *Pithecellobium macradenium.* Bot. Gaz. **133:** 38–42. 1972.

ENGLER, A. Rutaceae. *In*: A. ENGLER & K. PRANTL, Nat. Pflanzenfam. III. **4:** 95–201. 1896.

ESAU, K. Vascular differentiation in plants. ix + 160 pp. New York. 1965.

FAHN, A. The fleshy cortex of articulated Chenopodiaceae. Jour. Ind. Bot. Soc. (Maheshwari commemoration volume) **42 A:** 39–45. *1 pl.* 1963.

———. Plant anatomy. viii + 534 pp. Oxford. 1967.

——— & I. W. BAILEY. The nodal anatomy and the primary vascular cylinder of the Calycanthaceae. Jour. Arnold Arb. **38:** 107–117. 1957.

FLACHS, K. Über die Verbreitung des äquifazialen Blattsbaues in der australischen flora. Thesis. Kgl. Bayer. Ludwig-Maximilians Univ. Munich. 1–68. 1916.

FOSTER, A. Practical plant anatomy. ed. 2. 228 pp. New York. 1949.

FRAINE, E. DE. The anatomy of the genus *Salicornia.* Jour. Bot. Linn. Soc. [London] **41:** 317–348. *pls. 15, 16.* 1913.

FUNKE, G. L. On the biology and anatomy of some tropical leaf joints. Ann. Jard. Bot. Buitenzorg **40:** 45–74. *pls. 11–21.* 1929.

FURUYA, M. Problèmes de l'organogénèse dans rameau axillaire végétatif de dicotylédones. Jour. Fac. Sci. Univ. Tokyo III. Bot. **6**: 159–207. 1953.

GARRISON, R. Origin and development of axillary buds: *Betula papyrifera* and *Euptelea polyandra*. Am. Jour. Bot. **36**: 379–389. 1949.

——— & R. H. WETMORE. Studies in shoot-tip abortion: *Syringa vulgaris*. Am. Jour. Bot. **48**: 789–795. 1961.

GREGORY, C. T. The taxonomic value and structure of the peach leaf glands. Cornell Univ. Agric. Exp. Station Bull. **365**: 183–224. 1915.

GREW, N. Anatomie des plantes qui contient une description exacte de leurs parties et de leurs usages, et qui fait voir comment elles se forment, et comment elles croissent. 227 pp. Paris. 1675.

GUÉDÈS, M. Leaf morphology in some *Lachemilla*, with a reassessment of leaf architecture. Adv. Front. Pl. Sci. **29**: 183–221. 1972.

GUNCKEL, J. E., & R. H. WETMORE. Studies of development in long shoots and short shoots of *Ginkgo biloba* L. I. The origin and pattern of development of cortex, pith and procambium. Am. Jour. Bot. **33**: 285–295. 1946.

———, K. V. THIMANN, & R. H. WETMORE. Studies of development in long shoots and short shoots of *Ginkgo biloba* L. IV. Growth habit, shoot expression and the mechanism of its control. Am. Jour. Bot. **36**: 309–316. 1949.

HALLÉ, F. Étude biologique et morphologique de la tribu des Gardéniées (Rubiacées). Mem. O.R.S.T.O.M., Abidjan. **22**: 146 pp. 1966.

——— & A. DELMOTTE. Croissance et floraison de la Gesnériacée africaine *Epithema tenue* C. B. Clarke. Adansonia II. **13** (3): 273–287. 1973.

HARE, C. L. The anatomy of the petiole and its taxonomic value. Proc. Linn. Soc. London **155**: 223–229. 1943.

HARMS, H. Ueber eine Meliacee mit blattbürtigen Blüten. Bericht. Deutsch. Bot. Gesellsch. **35**: 338–348. 1917.

HASSELBERG, G. B. E. Zur morphologie des vegetativen sprosses der Loganiaceen. Symbol. Bot. Upsal. **2**(3): vii + 170 pp. 1937.

HEINRICHER, E. Beiträge zur Kenntnis der Anisophyllie. Ann. Jard. Bot. Buitenzorg Suppl. **3**: 649–664. *pls. 20–25.* 1910.

HOWARD, R. A. The vascular structure of the petiole as a taxonomic character. Adv. Hort. Sci. **3**: 7–13. 1963.

———. The ecology of an elfin forest in Puerto Rico. 8. Studies of stem growth and form and of leaf structure. Jour. Arnold Arb. **50**: 225–262. 1969.

———. Some observations on the nodes of woody plants with special reference to the problem of the "split-lateral" versus the "common gap." Pp. 195–214 *in* N. K. B. ROBSON, D. F. CUTLER, & M. GREGORY, *eds.* New research in plant anatomy. xii + 250 pp. *46 pls.* (Suppl. 1, Bot. Jour. Linn. Soc. **63**.) 1970.

JACOBS, D. L. Shoot segmentation in *Anacharis densa*. Am. Midl. Nat. **35**: 283–286. 1946.

JENSEN, L. C. W. Primary stem vascular patterns in three sub-families of the Crassulaceae. Am. Jour. Bot. **55**: 553–563. 1968.

JOHNSON, M. A. The epiphyllous flowers of *Turnera* and *Helwingia*. Bull. Torrey Bot. Club **85**: 313–323. 1958.

——— & F. H. TRUSCOTT. On the anatomy of *Serjania*. I. Path of the bundles. Am. Jour. Bot. **43**: 509–518. 1956.

KAPLAN, D. R. Comparative foliar histogenesis in *Acorus calamus* and its bearing on the phyllode theory of monocotyledonous leaves. Am. Jour. Bot. **57**: 331–361. 1970a.

———. Comparative development and morphological interpretation of 'rachis-leaves' in Umbelliferae. Pp. 101–125 + *6 pls. in* N. K. B. Robson, D. F. Cutler, & M. Gregory, *eds.* New research in plant anatomy. xii + 250 pp. *46 pls.* (Suppl. 1, Bot. Jour. Linn. Soc. **63.**) 1970b.

Kato, N. On the variation of nodal types in woody plants. I. Jour. Jap. Bot. **41:** 101–107. 1966; II. *Ibid.* **42:** 161–168. 1967.

Kraus. Die Lebensdauer der immergrünen Blätter. Sitzungsbericht. Naturf. Ges. zu Halle 1–15. 1880.

Kundu, B. C., & A. De. Taxonomic position of the genus *Nyctanthes.* Bull. Bot. Surv. India **10:** 397–408. 1968.

Letouzey, R., N. Hallé, & G. Cusset. Phyllobotryae (Flacourtiaceae) d'Afrique Centrale; variations morphologiques et biologiques conséquences taxonomiques. Adansonia II. **9:** 515–527. 1969.

Lignier, M. O. Recherches sur l'anatomie comparées des Calycanthées, des Mélastomacées et des Myrtacées. Arch. Sci. Nord France **4:** 455. 1887.

———. De la forme du systems libère-ligneux foliare chez les phanerogames. Bull. Soc. Linn. Normandie IV. **2:** 81–92. 1888.

Maekawa, F. Folia orixata, a new type of phyllotaxis and its significance to phyllotaxis evolution. Bot. Mag. Tokyo **61:** 7–10. 1948.

———. Topo-morphological investigations on the relation between stem and leaves and their bearing on the phylogenetic systematics of vascular plants. Part I. Jour. Fac. Sci. Univ. Tokyo, III. Bot. **6:** 1–28. 1952.

Maheshwari, P. Origin and development of internal bundles in the stem of *Rumex crispus.* Jour. Indian Bot. Soc. **8:** 89–117. 1929.

———. Contributions to the morphology of *Boerhaavia diffusa* II. *Ibid.* **9:** 42–61. 1930.

Marsden, M., & I. W. Bailey. A fourth type of nodal anatomy in dicotyledons, illustrated by *Clerodendron trichotomum* Thunb. Jour. Arnold Arb. **36:** 1–51. 1955.

Masuda, T. Studies on the elongation of petioles in some dicotyledons. Bot. Mag. Tokyo **47:** 347–370. 1933.

Melville, R. A new theory of the angiosperm flower. I. The gynoecium. Kew Bull. **16:** 1–50. 1962.

Messager, A. Les glandes du pétiole. Rev. Hort. **1886:** 367, 368. 1886.

Metcalfe, C. R. Metcalfe and Chalk's Anatomy of the Dicotyledons and its revision. Notes Jodrell Lab. **7:** 20–29. 1972.

Metcalfe, C. R., & L. Chalk. Anatomy of the Dicotyledons, vol. I. lxiv + pp. 1–724. *frontisp.*; vol. II. pp. 725–1500. *frontisp.* Oxford. 1950.

Mirbel, C. F. B. de. Élémens de physiologie végétale et de botanique. vol. I. viii + pp. 1–470; vol. II. pp. 471–924 + *explanation of plates & index*; vol. III. *pls. 1–72.* Paris. 1815.

Money, L. L., I. W. Bailey, & B. G. L. Swamy. The morphology and relationships of the Monimiaceae. Jour. Arnold Arb. **31:** 372–404. 1950.

Morvillez, F. Recherches sur l'appareil conducteur foliaire des Rosacées, des Chrysobalanées et des Légumineuses. Thèse, Fac. Sci. Lille, 181 pp. 1919.

Nakazawa, K. The vascular course of Piperales. I. Chloranthaceae. Jap. Jour. Bot. **15:** 199–207. 1956.

Nast, C. G., & I. W. Bailey. Morphology of *Euptelea* and comparison with *Trochodendron.* Jour. Arnold Arb. **27:** 186–192. *pls. 1–4.* 1946.

Ogura, E. Y. Comparative morphology and classification of plants. Phytomorphology **14:** 240–247. 1964.

Ogura, Y. Disarticulation of the branches in *Bladhia* (Myrsinaceae). Bot. Mag. Tokyo **51:** 158–167. 1937.

Ozenda, P. Recherches sur les Dicotylédones apocarpiques. Contribution à l'étude des Angiospermes dites primitives. Thèse Univ. Paris Série A, No. 2263; No. d'ordre 3134. 1948.

Pant, D. D., & B. Mehra. Nodal anatomy of *Mirabilis* and *Oxybaphus*. Proc. Nat. Inst. Sci. India **29:** 41–76. 1963.

——— & ———. Nodal anatomy in retrospect. Phytomorphology **14:** 384–387. 1964.

Payer, J. B. Traité d'organogénie végétale comparée de la fleur. vol. 1. viii + 748 pp.; vol. 2. viii + *pls. 1–154*. Paris. 1857.

Pease, V. A. Duration of leaves in evergreens. Am. Jour. Bot. **4:** 145–160. 1917.

Peters, T. Zur anatomie des phyllodiums von *Acacia*. Inaug. Diss. 46 pp. *1 pl.* Kiel (Braunschweig). 1912.

Petit, L. Sur l'importance taxonomique du pétiole. Compt. Rend. Acad. Sci. Paris **103:** 767–769. 1886.

———. Le pétiole des dicotylédones au point de vue de l'anatomie comparée et de la taxonomie. Mém. Soc. Sci. Phys. Nat. Bordeaux III. **3:** 217–404. *pls. 1–6.* 1887.

———. Nouvelles recherches sur le pétiole des phanérogames. Act. Soc. Linn. Bordeaux **43:** 11–60. *pls. 1–4.* 1889.

Philipson, W. R. The abaxial stipules of *Plagianthus divaricatus* J. R. C. Forst. New Zealand Jour. Bot. **6:** 518–521. 1968.

———. & E. E. Balfour. Vascular patterns in dicotyledons. Bot. Rev. **29:** 382–404. 1963.

——— & M. N. Philipson. Diverse nodal types in *Rhododendron*. Jour. Arnold Arb. **49:** 193–217. 1968.

Pierre, L. Plantes du Gabon. Bull. Mens. Soc. Linn. Paris **2:** 1249–1256. 1896.

Post, D. M. Studies in Gentianaceae. I. Nodal anatomy of *Frasera* and *Swertia perennis*. Bot. Gaz. **120:** 1–14. 1958.

Prance, G. T. Dichapetalaceae. Flora Neotropica, Monog. **10:** 3–84. Hafner Publ. Co., New York. 1972.

Record, S. J. Classification of various anatomical features of dicotyledonous woods. Trop. Woods **47:** 12–27. 1936.

Regel, E. Beobachtungen über den Ursprung und Zweck der Stipeln. Linnaea **17:** 193–234. *pls. 7, 8.* 1843.

Saha, B. Morphology of the leaves of *Phyllarthron commorense* DC. Bull. Bot. Soc. Bengal **6:** 25–31. 1952.

Samantarai, B., & T. Kabi. Secondary growth in petioles and the partial shoot theory of the leaf. Nature **172** (4366): 37. 1953.

Satter, R. L., & A. W. Galston. Leaf movements: Rosetta stone of plant behavior? BioScience **23:** 407–416. 1973.

Schnell, R., & G. Cusset. Glandularisation et foliarisation. Bull. Jard. Bot. État Bruxelles **33:** 525–530. 1963.

———, ———, & M. Quenum. Contribution à l'étude des glandes extraflorales chez quelques groupes de plantes tropicales. Rev. Gén. Bot. **70:** 269–342. 1963.

Schofield, E. K. Petiole anatomy of the Guttiferae and related families. Mem. N.Y. Bot. Gard. **18:** 1–55. 1968.

Sinnott, E. W. The anatomy of the node as an aid in the classification of angiosperms. Am. Jour. Bot. **1:** 303–322. 1914.

——— & I. W. Bailey. Investigations on the phylogeny of the angiosperms. 3. Nodal anatomy and the morphology of stipules. Am. Jour. Bot. **1:** 441–453. 1914.

——— & G. B. Durham. A quantitative study of anisophylly in *Acer*. Am. Jour. Bot. **10:** 278–287. 1923.

Skutch, A. F. A compound leaf with annual increments of growth. Bull. Torrey Bot. Club **73:** 542–546. 1946.

Slade, B. F. Cladode anatomy and leaf trace systems in New Zealand brooms. Trans. Roy. Soc. New Zealand **80:** 81–96. 1952.

———. Stelar evolution in vascular plants. New Phytologist **70:** 879–884. 1971.

Smith, A. C. The presence of primitive angiosperms in the Amazon Basin and the significance in indicating migrational routes. *In*: H. Lint, *ed.* Atas do Sympósio sôbre a Biota Amazônica **4:** 37–59. 1967.

Srivastava, L. M. Histochemical studies on lignin. Tappi **49** (4): 173–183. 1966.

Steenis, C. G. G. J. van. A second collection of *Moultonia singularis* Balf. f. & W. W. Sm. Blumea **11:** 133, 134. 1961.

Stork, H. E. Epiphyllous flowers. Bull. Torrey Bot. Club **83:** 338–341. 1956.

Strey, R. G. Notes on the genus *Cussonia* in South Africa. Bothalia **11:** 191–201. 1973.

Sugiyama, M. A vascular system of "node to leaf" in *Magnolia virginiana* L. Jour. Jap. Bot. **47:** 313–320. 1972.

Swamy, B. G. L. The morphology and relationships of the Chloranthaceae. Jour. Arnold Arb. **34:** 375–408. 1953.

——— & I. W. Bailey. The morphology and relationships of *Cercidiphyllum*. Jour. Arnold Arb. **30:** 187–210. 1949.

——— & ———. *Sarcandra*, a vesselless genus of the Chloranthaceae. *Ibid.* **31:** 117–129. 1950.

Takhtajan, A. Flowering plants: origin and dispersal. (Transl. C. Jeffrey.) x + 310 pp. Edinburgh. 1969.

Tchoun, Y. T. Morphologie comparative des feuilles à l'état jeune et à l'état adulte. Univ. de Nancy, Thèse #80. 217 pp. 1923.

Thimann, K. V. Correlative aspects. Pp. 832–837 *in* Recent advances in botany, vol. I. (From lectures and symposia presented to the IX Int. Bot. Congr., Montreal, 1959.) xvi + 947 pp. Toronto. 1961.

———. The natural plant hormones. Pp. 3–365 *in*: F. C. Steward, *ed.* Plant physiology: A treatise. vol. 6B. xviii + 365 pp. New York. 1972.

Thouvenin, M. Recherches sur la structure des Saxifragacées. Ann. Sci. Nat. Bot. VII. **12:** 1–174. *pls. 1–22.* 1890.

Titman, P. W., & R. H. Wetmore. The growth of long and short shoots in *Cercidiphyllum*. Am. Jour. Bot. **42:** 364–372. 1955.

Troll, W. Vergleichende Morphologie der höheren Pflanzen. Band 1. Vegetationsorgane. Berlin. 1939.

Tyler, A. A. The nature and origin of stipules. Ann. N.Y. Acad. Sci. **10:** 1–49. 1897.

Vesque, J. De l'anatomie des tissue appliquée a la classification des plantes. Nouv. Arch. Mus. Hist. Nat. II. **4:** 1–56. 1881.

———. Essai d'une monographie anatomique et descriptive de la tribu des Capparées. Ann. Sci. Nat. VI. **13:** 47–135. *pls. 1, 2.* 1882.

———. Charactères des principales familles gamopétales tirés de l'anatomie de la feuille. Ann. Sci. Nat. VII. **1:** 183–360. *pls. 9–15.* 1885.

WARDEN, J. Leaf-plantlet meristems (= "Leaf-embryos") of *Bryophyllum*, revision of terminology. Portugalliae Acta Biol. A. **12**: 97–100. 1971–72.

WATARI, S. Anatomical studies on some leguminous leaves with special reference to the vascular system in petioles and rachises. Jour. Fac. Sci. Univ. Tokyo Sec. III. **4**: 225–365. 1934.

———. Anatomical studies on the vascular system in the petioles of some species of *Acer*, with notes on the external morphological features. *Ibid*. **5**: 1–73. 1936.

———. Anatomical studies on the leaves of some saxifragaceous plants, with special reference to the vascular system. *Ibid*. **5**: 195–316. 1939.

WETMORE. R. H., A. E. DEMAGGIO, & J. E. RIER. Contemporary outlook on the differentiation of vascular tissues. Phytomorphology **14**: 203–217. 1964.

——— & R. GARRISON. The growth and organization of internodes. Pp. 827–832 *in* Recent advances in botany, vol. I. (From lectures and symposia presented to the IX Int. Bot. Congr., Montreal, 1959.) xvi + 947 pp. Toronto. 1961.

——— & ———. The morphological ontogeny of the leafy shoot. Pp. 187–199 *in* E. G. CUTTER, *ed*. Trends in plant morphogenesis. xvi + 329 pp. *frontisp*. + *8 pls*. London. 1966.

——— & T. A. STEEVES. Morphological introduction to growth and development. Pp. 3 — 166 *in*: F. C. STEWARD, *ed*. Plant physiology: A treatise. vol. 6A. xviii + 541 pp. New York. 1971.

WILLIS, J. C. A dictionary of the flowering plants and ferns. 7th ed. *rev*. by H. K. AIRY SHAW, xxii + 1214 pp. + liii. Cambridge Univ. Press. 1966.

WILSON, C. L. Medullary bundle in relation to the primary vascular system in Chenopodiaceae and Amaranthaceae. Bot. Gaz. **78**: 175–199. 1924.

———. The telome theory and the origin of the stamen. Am. Jour. Bot. **29**: 759–764. 1942.

YAMAZAKI, T. Phylogeny of the leaf in dicotyledons. Bot. Mag. Tokyo **78**: 332–343. 1965.

YIN, H. C. Studies on the nyctinastic movement of the leaves of *Carica papaya*. Am. Jour. Bot. **28**: 250–261. 1941.

ZIMMERMAN, J. G. Über die extrafloralen Nektarien der Angiospermen. Beih. Bot. Centralbl. **49**: 99–196. 1932.

ARNOLD ARBORETUM
HARVARD UNIVERSITY
CAMBRIDGE, MASSACHUSETTS 02138

EXPLANATION OF PLATES

PLATE I

Examples of nodal patterns. FIGURE 1. a–i. Leaves alternate: a. one trace; b. two traces from one gap; c. three or more traces from one gap; d. alternating traces to the leaf and an axillary bud in *Euptelea*; e. single trace showing vascular supply to stipules; f. three traces from three gaps; g. lateral traces of a trilacunar node with vascular supply to stipules; h. multilacunar node without stipules; i. multilacunar node with lateral traces showing vascular supply to the sheathing stipule.

FIGURE 2. a–f. Leaves opposite: a. one trace from each gap; b. two traces from each gap; c. three (or more) traces from each gap; d. opposite trilacunar nodes; e. "common gap" or "split lateral" condition where vascular supply of lateral traces to each of opposite leaves is supplied from a single lateral gap; f. a "split lateral" condition with two traces in each of the median gaps.

FIGURE 3. a, b. Leaves whorled: a. one trace from each gap; b. trilacunar condition with three traces from three gaps to each of three whorled leaves.

FIGURE 4. a–h. Examples of cortical bundles: a, c, e, g are internodal sections; b. the cortical bundle enters the leaf and is replaced in the suprajacent internode by a bundle derived from the central vascular cylinder; d. a "split lateral" with divided cortical bundles, of which one portion enters the leaf and the other continues in the stem; f. stem cortical bundles divide with portions of each entering the leaf and a portion continuing in the stem (a girdling nodal trace may also connect the cortical bundles); h. alternate leaf arrangement with two of the cortical bundles dividing to supply vascular tissue to each leaf.

PLATES II–IV

Diagrams of selected petiole vascular patterns. Successive sections were taken at the leaf base, the middle of the length of the petiole, and at the apex of the petiole or the base of the blade before the departure of the secondary veins. In FIGURES 1 to 4, the leaves may be alternate, opposite or whorled, simple or compound, with or without stipules. The stem may have, or lack, cortical and/or medullary vascular systems. See text pp. 144–150 for further explanation.

PLATE II

FIGURE 1. a–j. Nodes with one trace from one gap. FIGURE 2. a–e. Nodes with two or three traces from one gap.

PLATE III

FIGURE 3. a–n. Nodes with three traces from three gaps.

PLATE IV

FIGURE 4. a–d. Nodes with three traces from three gaps. FIGURE 5. a–e. Multilacunar nodal types with five or more traces from an equal number of gaps; leaves alternate only, but stipules may be present or absent.

PLATES V–VII

Examples of selected sections of stems, petioles, and laminae showing the continuous vascular patterns of different taxa. Diagrams produced from camera lucida drawings and, excluding the outline drawings of the leaf, the nodal and petiole sections for each taxon are on the same scale. Sclerenchyma tissue is shown in heavy black lines.

PLATE V

FIGURE 1. a. leaf of *Banksia serrata* (Proteaceae); b. section of trilacunar node; c. middle section of short petiole, median trace has produced two adaxial bundles while laterals divided many times, first veins depart from center of series of branches of the laterals; d. base of blade, similar organization of bundles but each surrounded by ring of sclerenchyma.

FIGURE 2. *Hakea dactyloides* (Proteaceae): a. leaf; b. node; c. petiole lacking adaxial derivatives of median trace and single division of lateral traces, all embedded in heavy sclerenchymatous tissue; d. section of leaf, veins are the lateral traces, and median trace has divided for the first time.

FIGURE 3. *Coccoloba rugosa* (Polygonaceae): a. leaf with sheathing stipule; b. subjacent nodal section showing precocious origin of traces; c. nodal section, upper traces enter stipular sheath, median and laterals enter petiole; d. basal section of petiole showing divergent trace branches in the "cross zone," note the absence of sclerenchyma in the lower pulvinal area; e. midpetiole section showing the organization of vascular bundles in several concentric rings; f. base of leaf blade with the organization of an adaxial plate from several lateral bundles.

FIGURE 4. *Amphilemma cymosum* (Melastomataceae): a. leaf; b. internodal section showing medullary bundles; c. nodal sectioning showing path of medullary bundles or their branches into the leaf base; d. mid-petiole section with medullary bundles from the stem in a medullary position; e. section through midrib with medullary bundles still present.

PLATE VI

FIGURE 1. *Symplocos glauca* (Symplocaceae): a. leaf; b. nodal section; c. section at base of petiole; d. section in middle of petiole, the rib-traces having arisen from the ends of the vascular tissue; e. midrib section.

FIGURE 2. *Peperomia hernandiifolia* (Piperaceae): a. peltate leaf; b. nodal section showing "herbaceous" pattern of scattered bundles, three traces from three "gaps"; c. base of petiole, lines separate the products of the three traces; d. upper end of petiole at attachment to peltate blade, bundle in medullary position supplies central veins descending from midrib, upper two bundles on each side supply basal veins of leaf, median and its branches supply vascular tissue for the upper portion of the blade.

FIGURE 3. *Melicoccus bijugatus* (Sapindaceae): a. leaf showing broadened rachis below upper leaflets; b. nodal section; c. base of petiole; d. terete portion of petiole below first pair of leaflets; e. section at the point of attachment of basal pair of leaflets; f. section at point of attachment of upper pair of leaflets; g. section of petiole of a leaflet.

FIGURE 4. *Aesculus hippocastanum* (Hippocastanaceae): a. palmately compound leaf; b. base of petiole, bundles may have originated from tri- or pentalacunar node; c. pulvinal section of petiole; d. just above the pulvinus two branches from median trace assume a medullary position; e. middle of petiole; f. apex of petiole at point of attachment of leaflets, medullary bundles of previous section have resumed association with median trace and its branches; g. section of petiole of leaflet.

PLATE VII

FIGURE 1. *Sloanea dentata* (Elaeocarpaceae): a. leaf showing upper and lower pulvini of petiole; b. nodal section; c. supranodal section showing dorsal association of lateral traces; d. section of lower pulvinus; e. section from middle of petiole, invagination and foldings have produced a medullary ring shown with a surrounding layer of sclerenchymatous tissue and dorsal small bundles each with ring of sclerenchyma; f. dissociation of heavy vascular rings in the

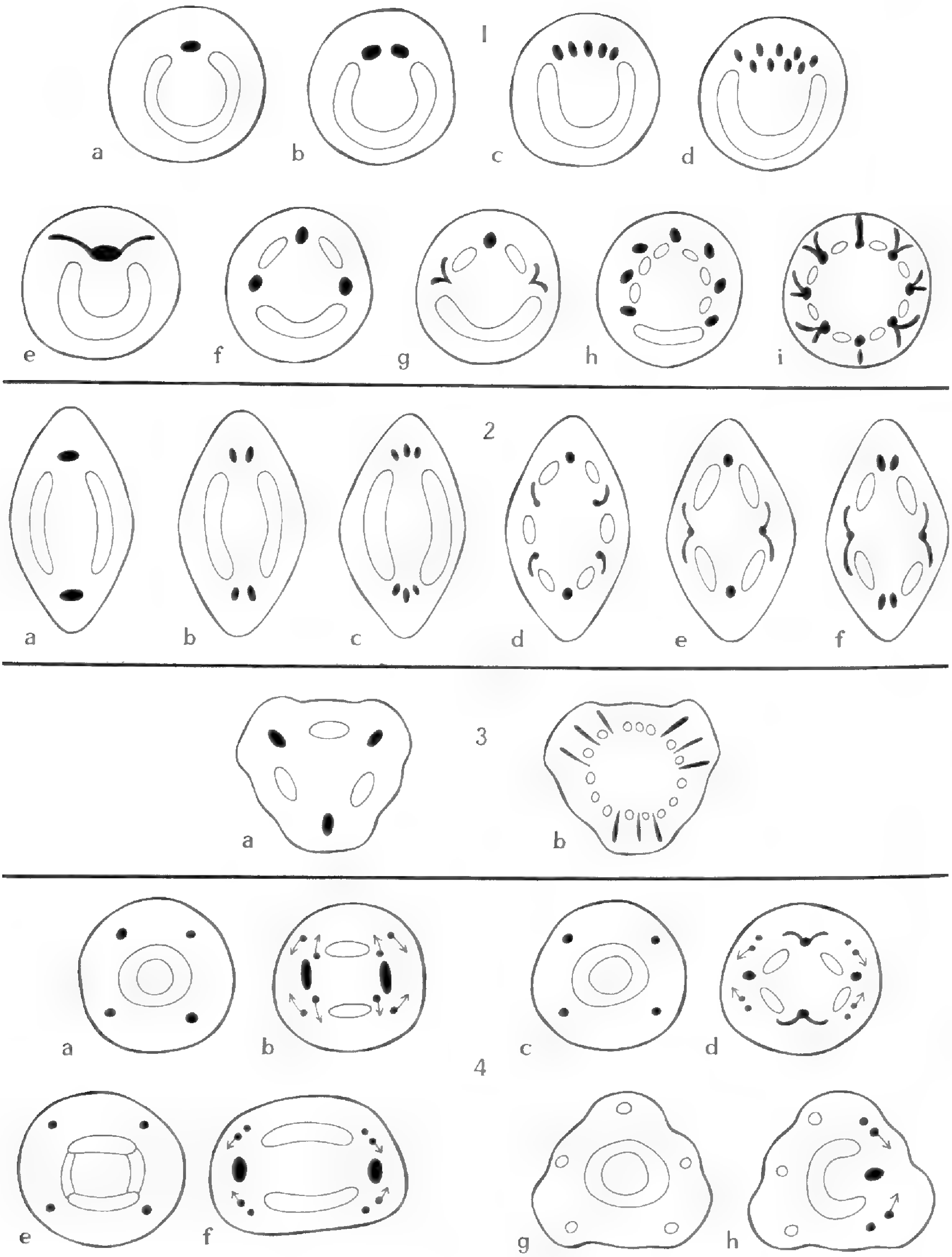
upper pulvinus, dorsal bundles have departed to lower veins; g. midrib section at point of first strong secondary veins.

FIGURE 2. *Populus tremuloides*: a. leaf, flattened petiole not well depicted; b. nodal section showing patches of scattered sclerenchyma; c. base of petiole; d. lower portion of petiole; e. middle of the petiole showing the organization of the vascular supply into a series of "rings"; f. apex of the petiole; g. base of the blade, middle bundles of the flattened portion of the previous section supply the basal secondary veins.

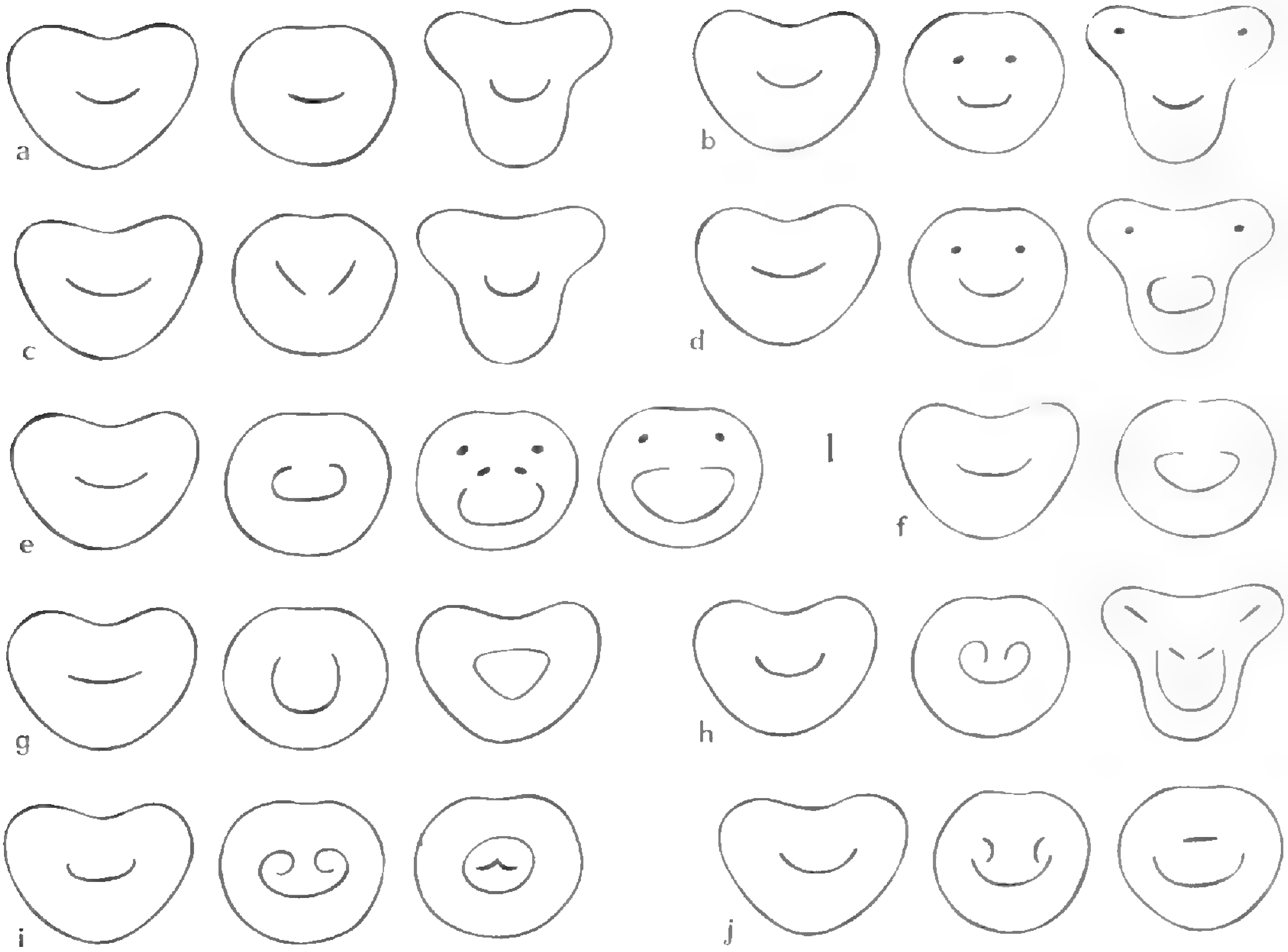
FIGURE 3. *Aristolochia esperanzae* (Aristolochiaceae): a. leaf; b. nodal section showing the distinct bundles of the stem; c. middle of the petiole showing the median bundle, two division products of each lateral trace, and the heavy sclerenchyma layer; d. base of leaf blade with the departure of the basal veins.

PLATE VIII

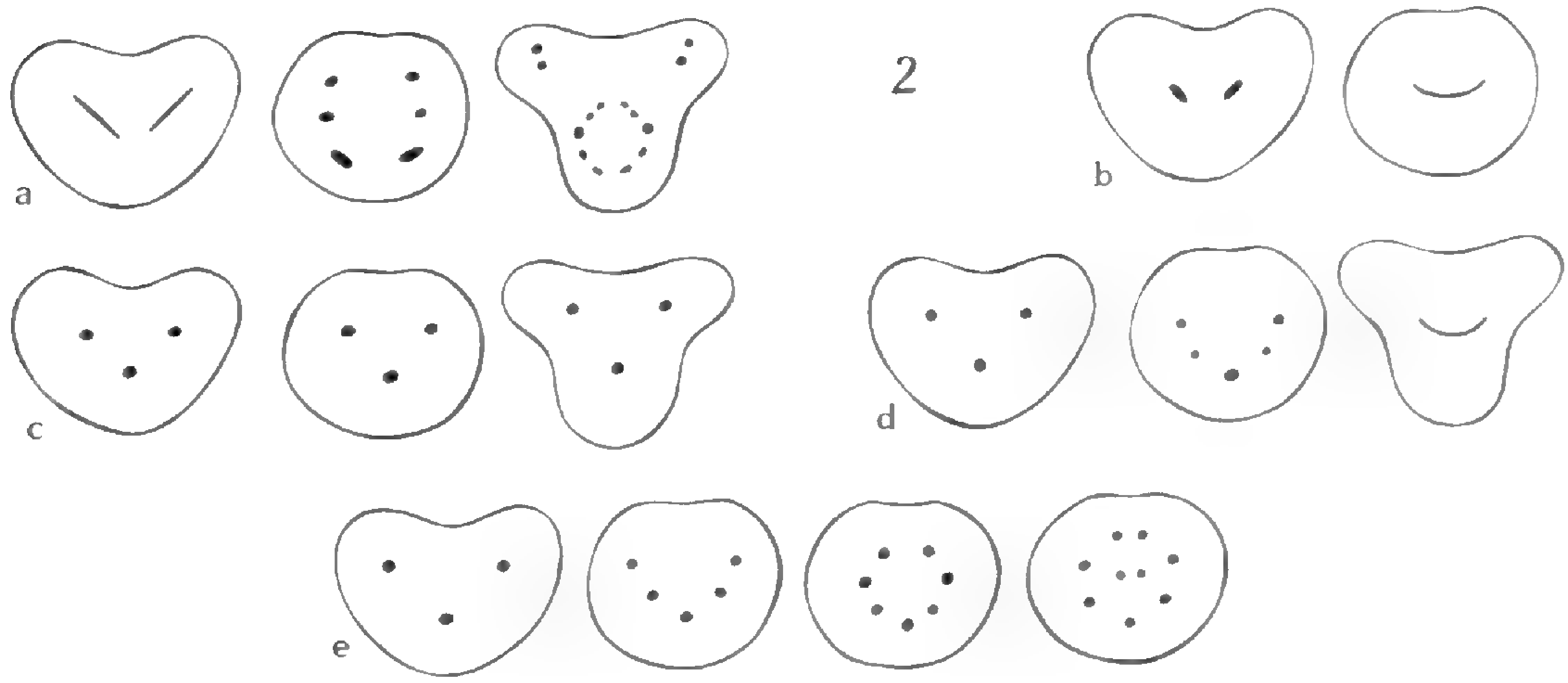
Examples of epipetiolar, epiphyllous, epirachial, and hypophyllous inflorescences. Scale marker is 1 cm. a. *Dichapetalum latifolium* (Dichapetalaceae), inflorescences from petiole; b. *Helwingia japonica* (Cornaceae), epiphyllous cluster of flowers, plants dioecious; c. *Phyllonoma laticuspis* (Dulongiaceae), epiphyllous inflorescences; d. *Turnera ulmifolia* (Turneraceae), single flower with bracts borne on the petiole; e. *Chisocheton pohlianus* (Meliaceae), epirachial flowers and racemes from single pinnately compound leaf; f. *Polycardia phyllanthoides* (Celastraceae), terminal epiphyllous flowers; g. *Phyllobotryum spathulatum* (Flacourtiaceae) [redrawn from Hooker's Icones **14**: *Plate 1353*. 1881, and herbarium material], flowers borne on upper surface of midrib, (epiphyllous); h. *Tapura latifolia* (Dichapetalaceae), flowers borne here at apex of petiole, but may also be on the lamina; i. *Erythrochiton hypophyllanthus* (Rutaceae) [redrawn from Engler, Engler & Prantl, Nat. Pflanzenfam. III. **4**: 96. *fig. 96 F*. 1896], flower borne on abaxial surface of lamina (hypophyllous).



Howard, Stem-Node-Leaf Continuum



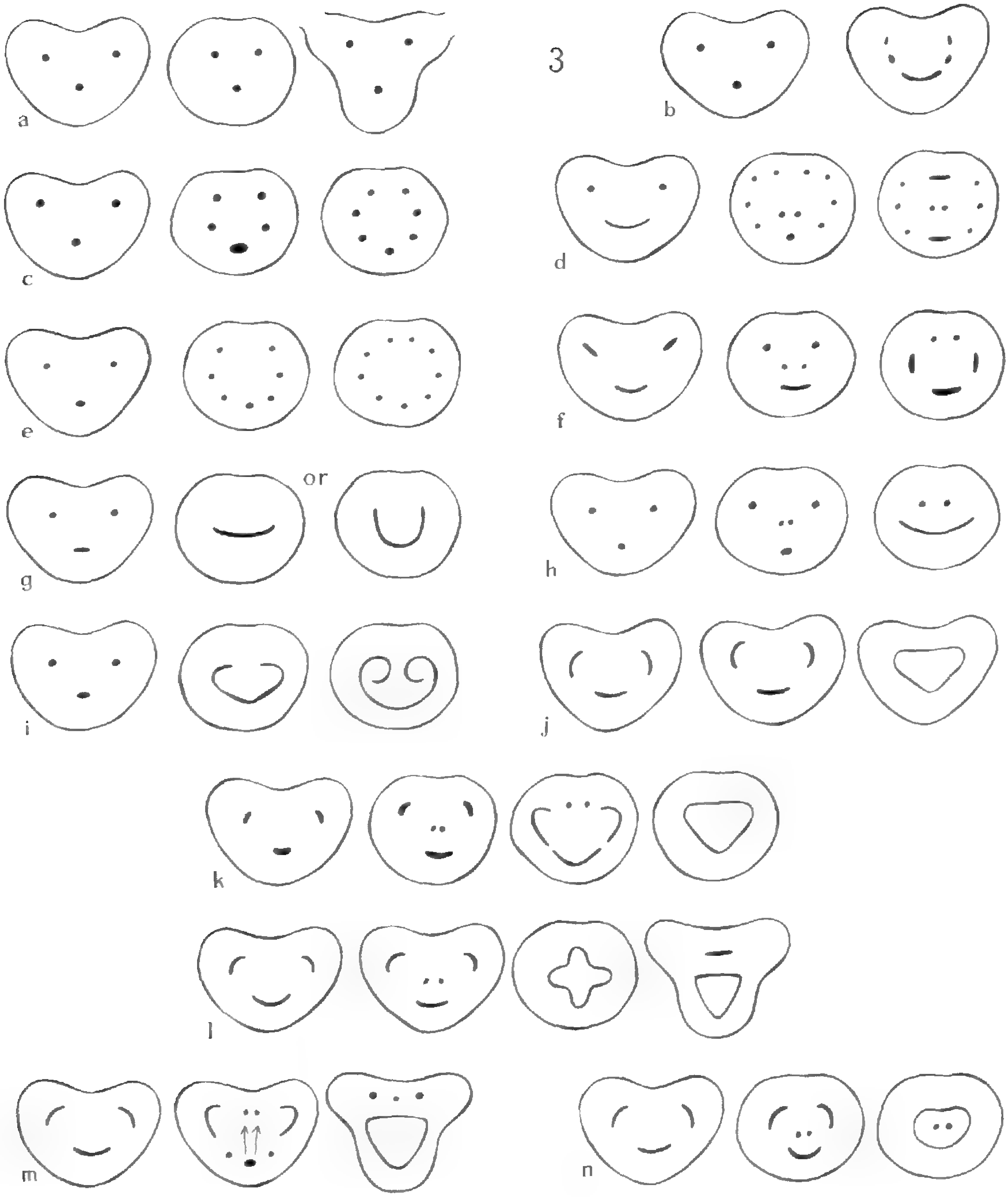
1



2

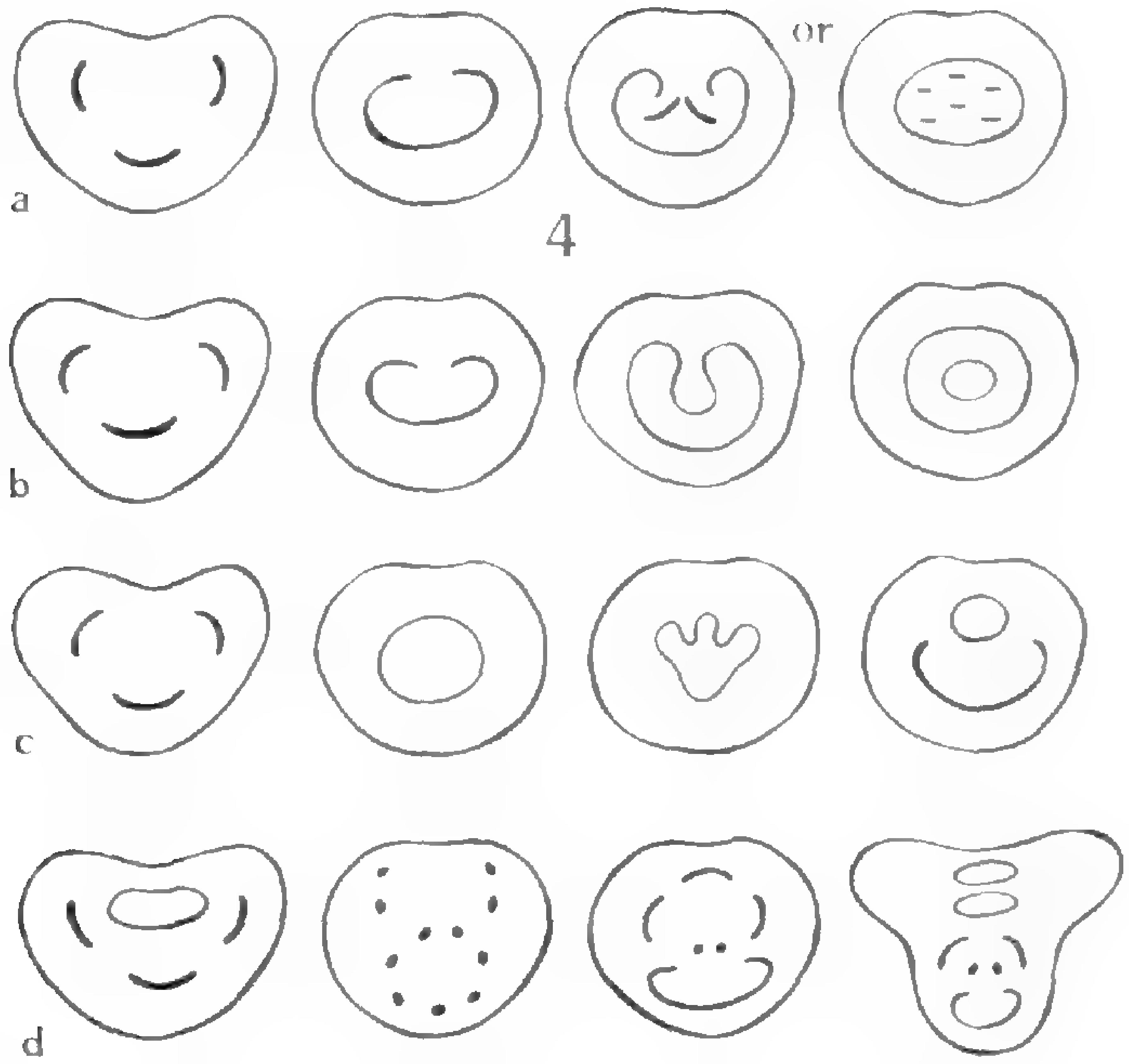
HOWARD, STEM-NODE-LEAF CONTINUUM

PLATE III

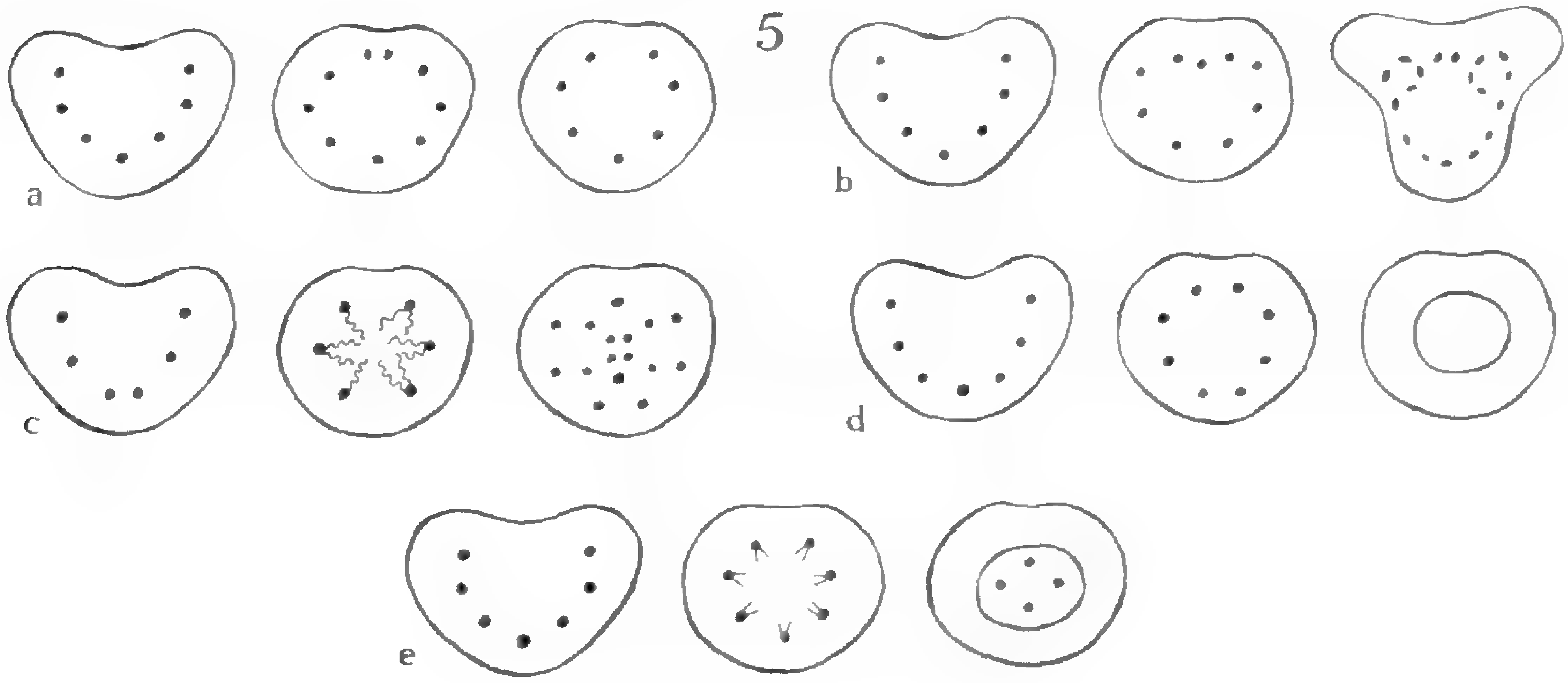


HOWARD, STEM-NODE-LEAF CONTINUUM

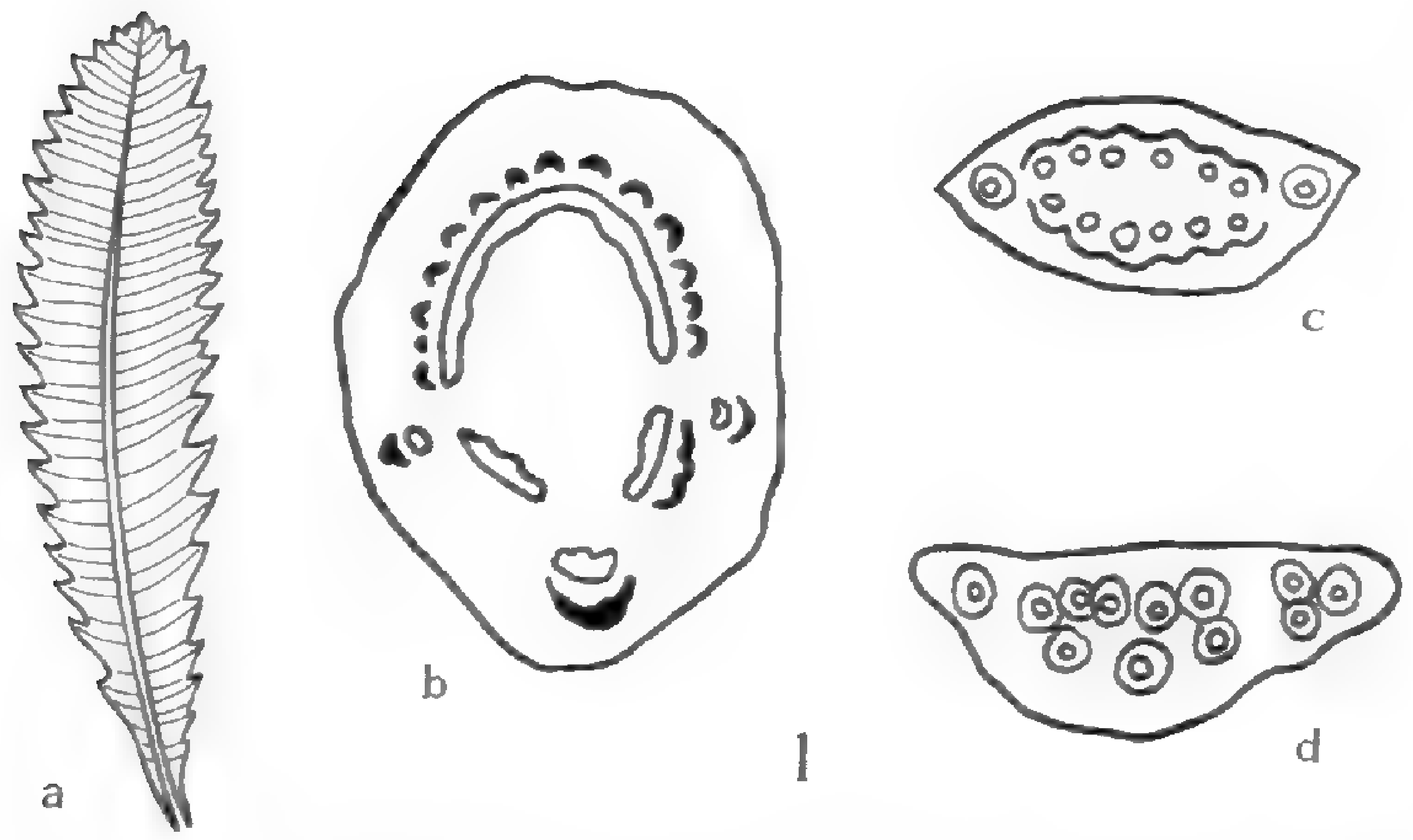
4



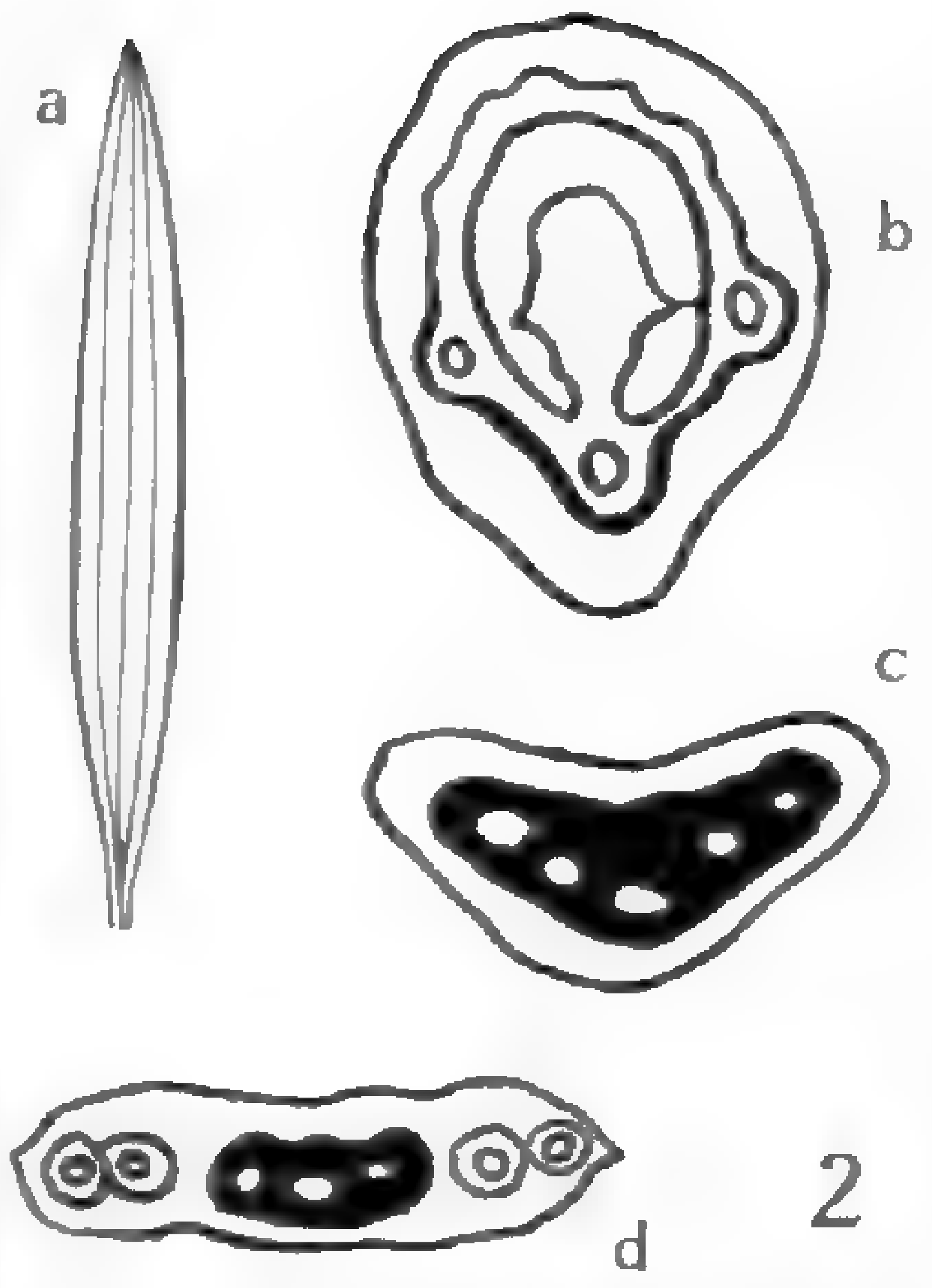
5



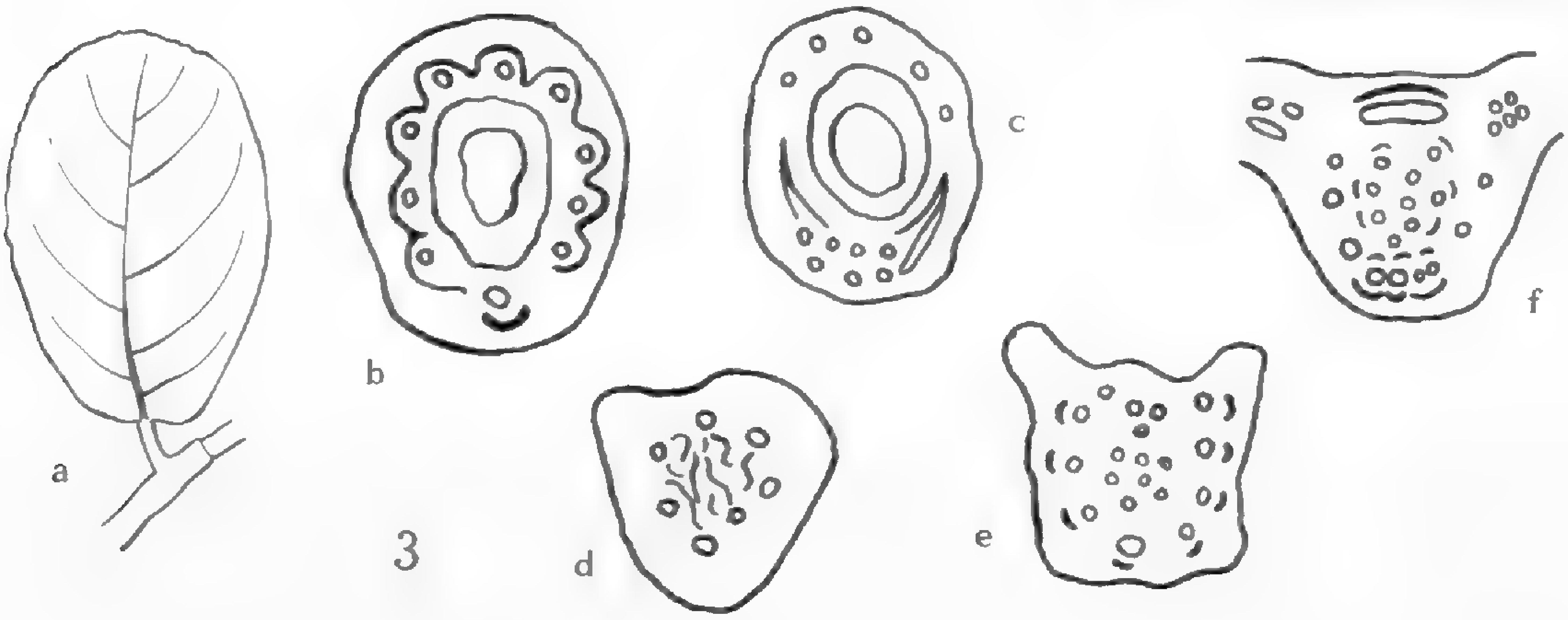
HOWARD, STEM-NODE-LEAF CONTINUUM



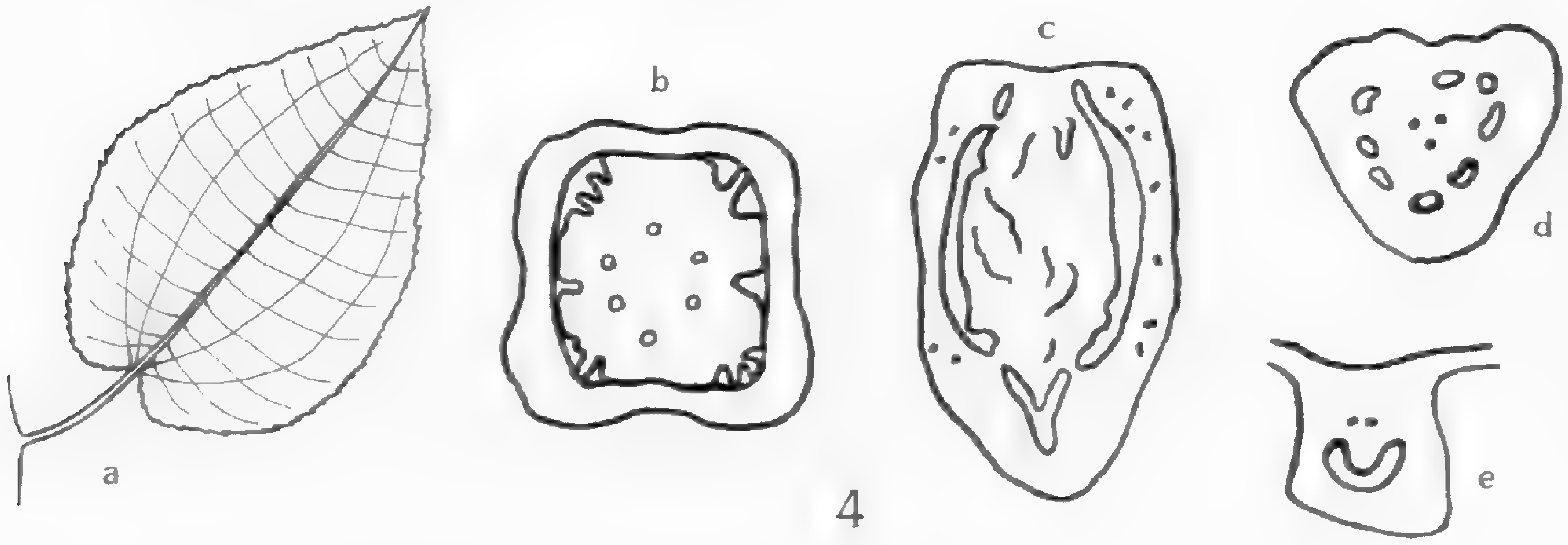
1



2

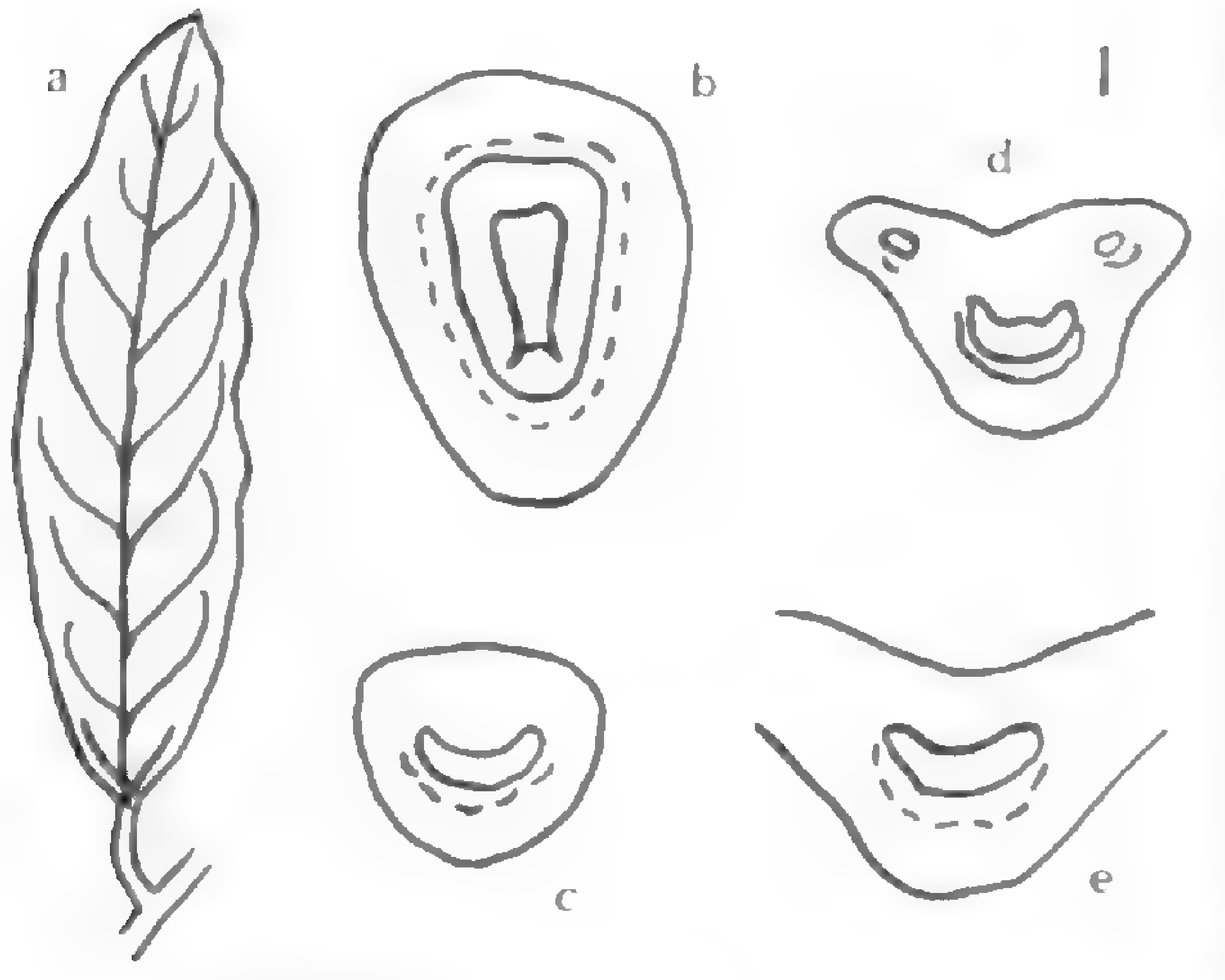


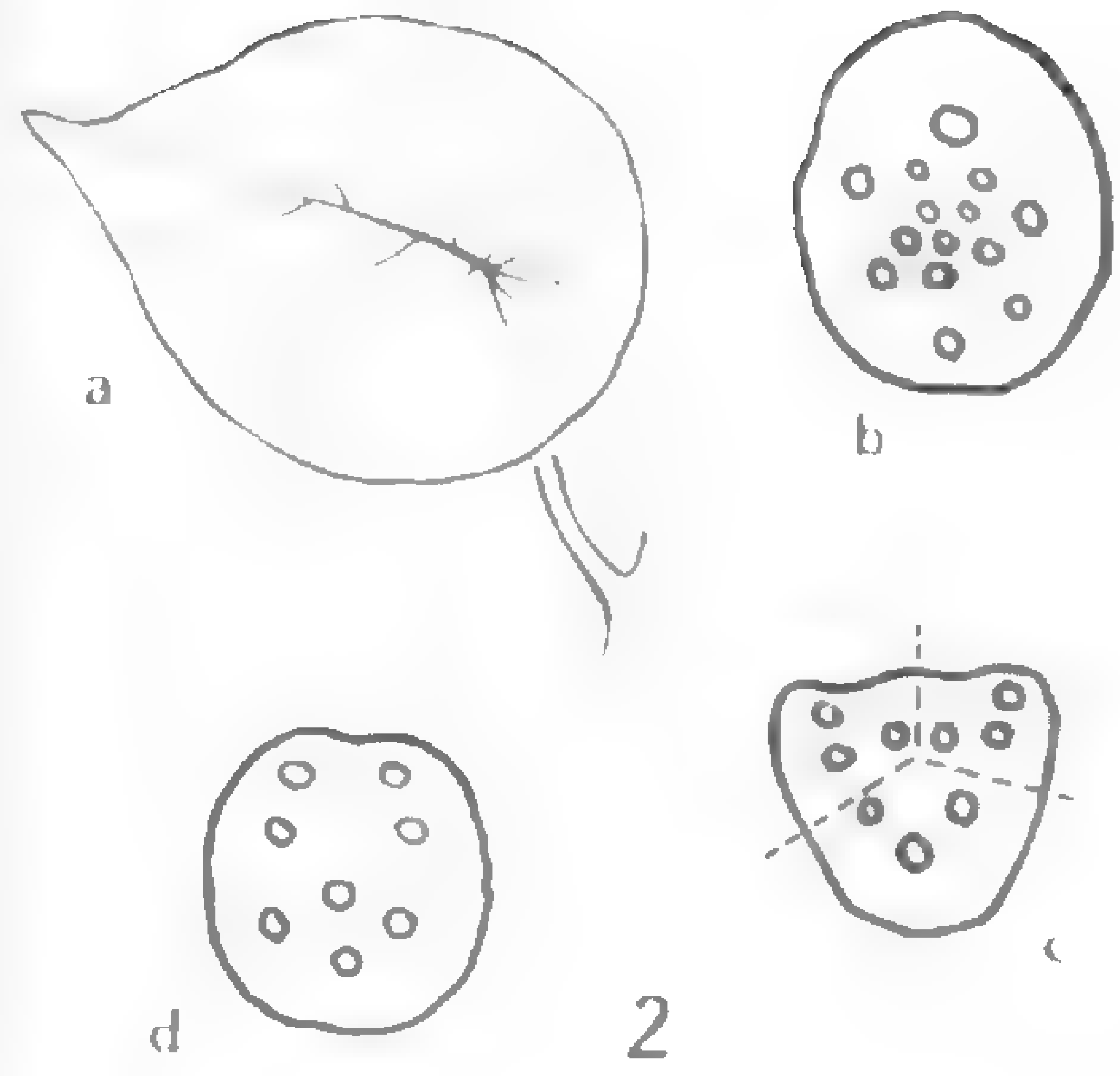
3

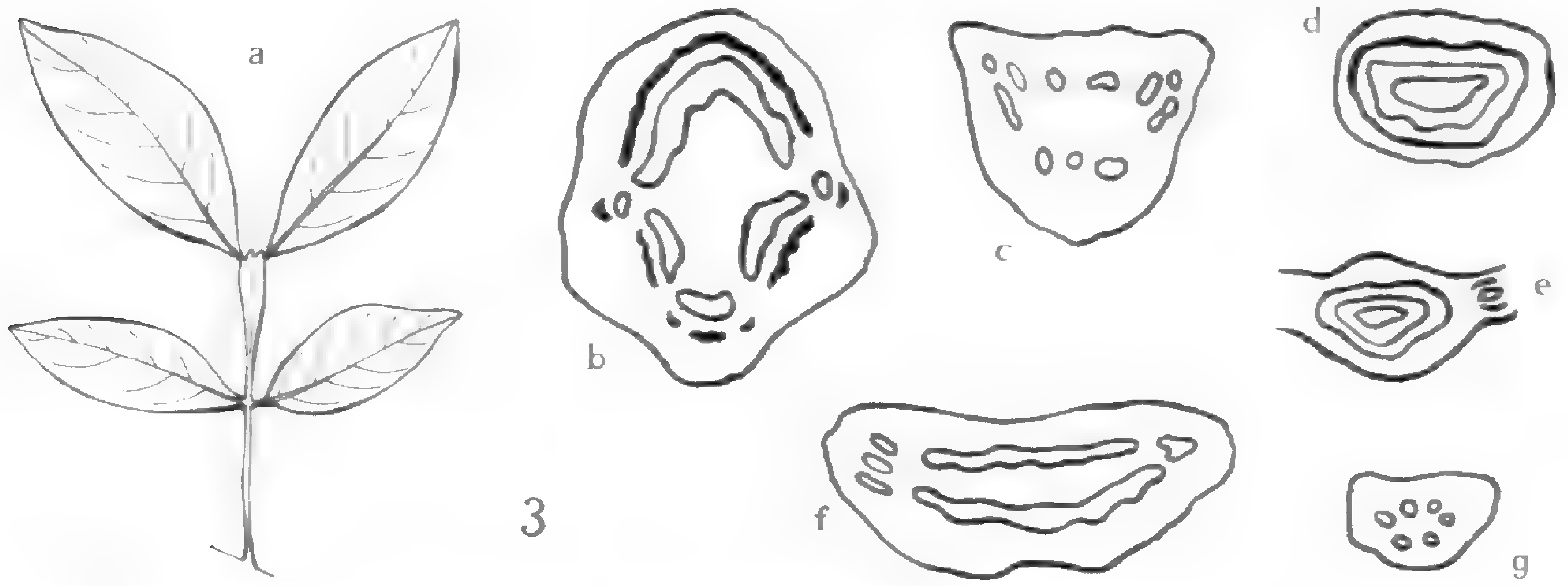


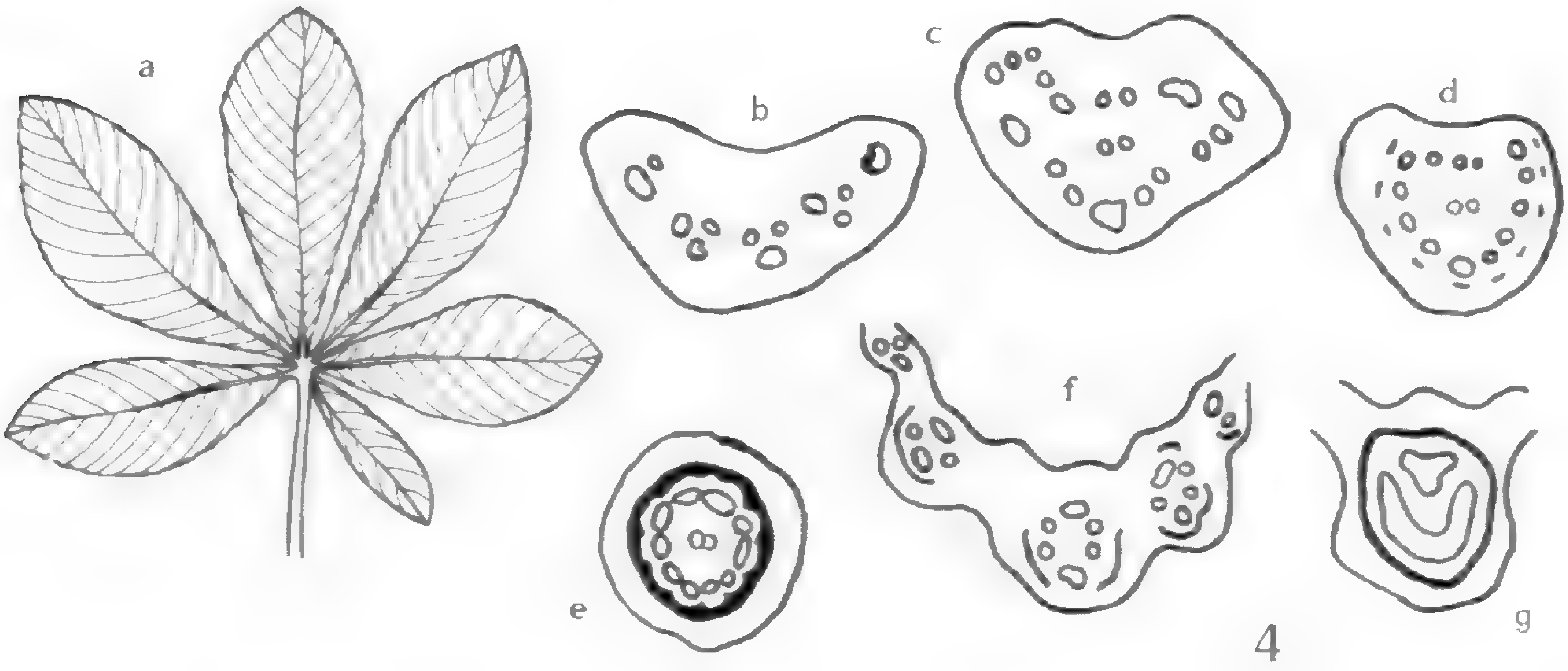
4

HOWARD, STEM-NODE-LEAF CONTINUUM


1

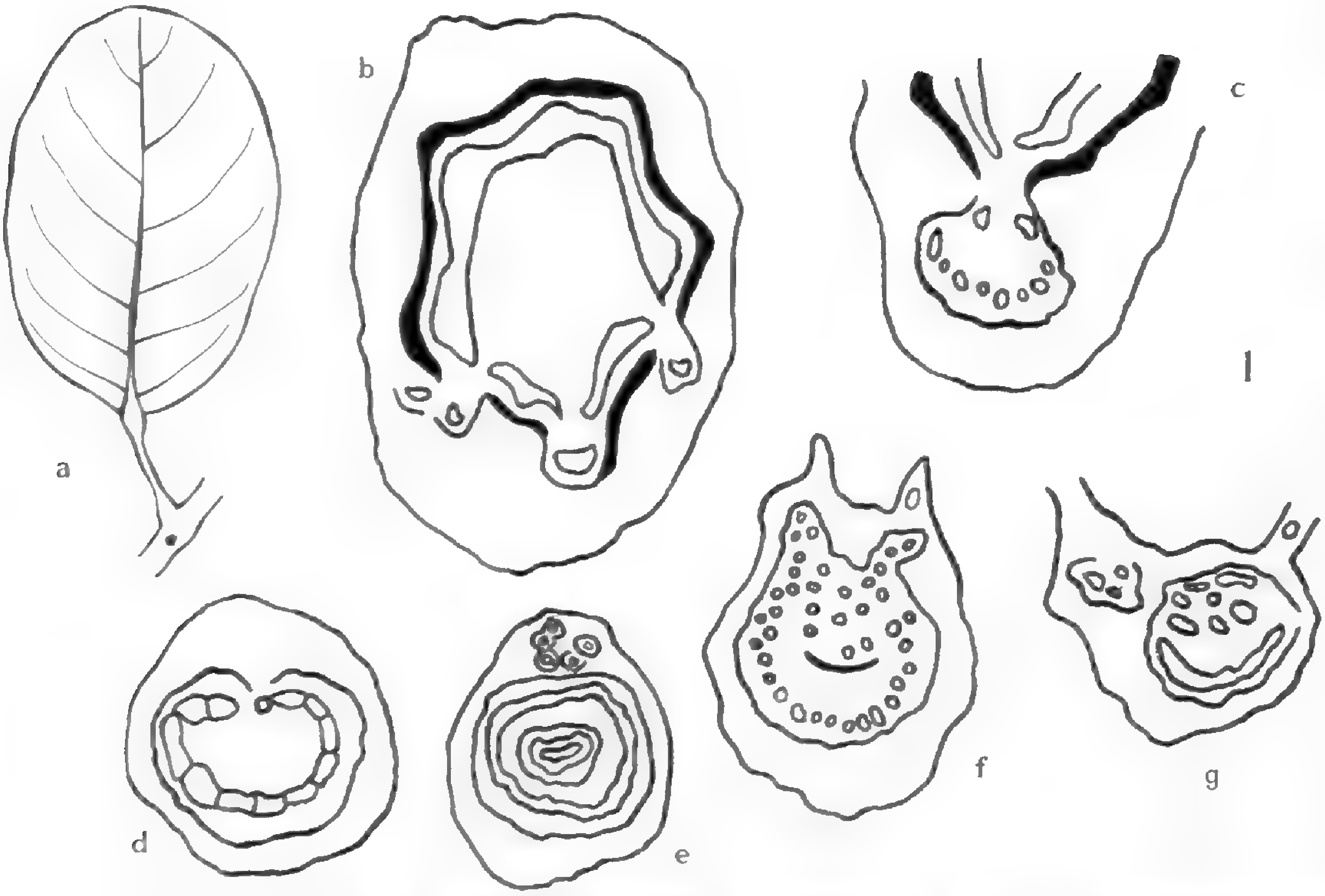

2


3

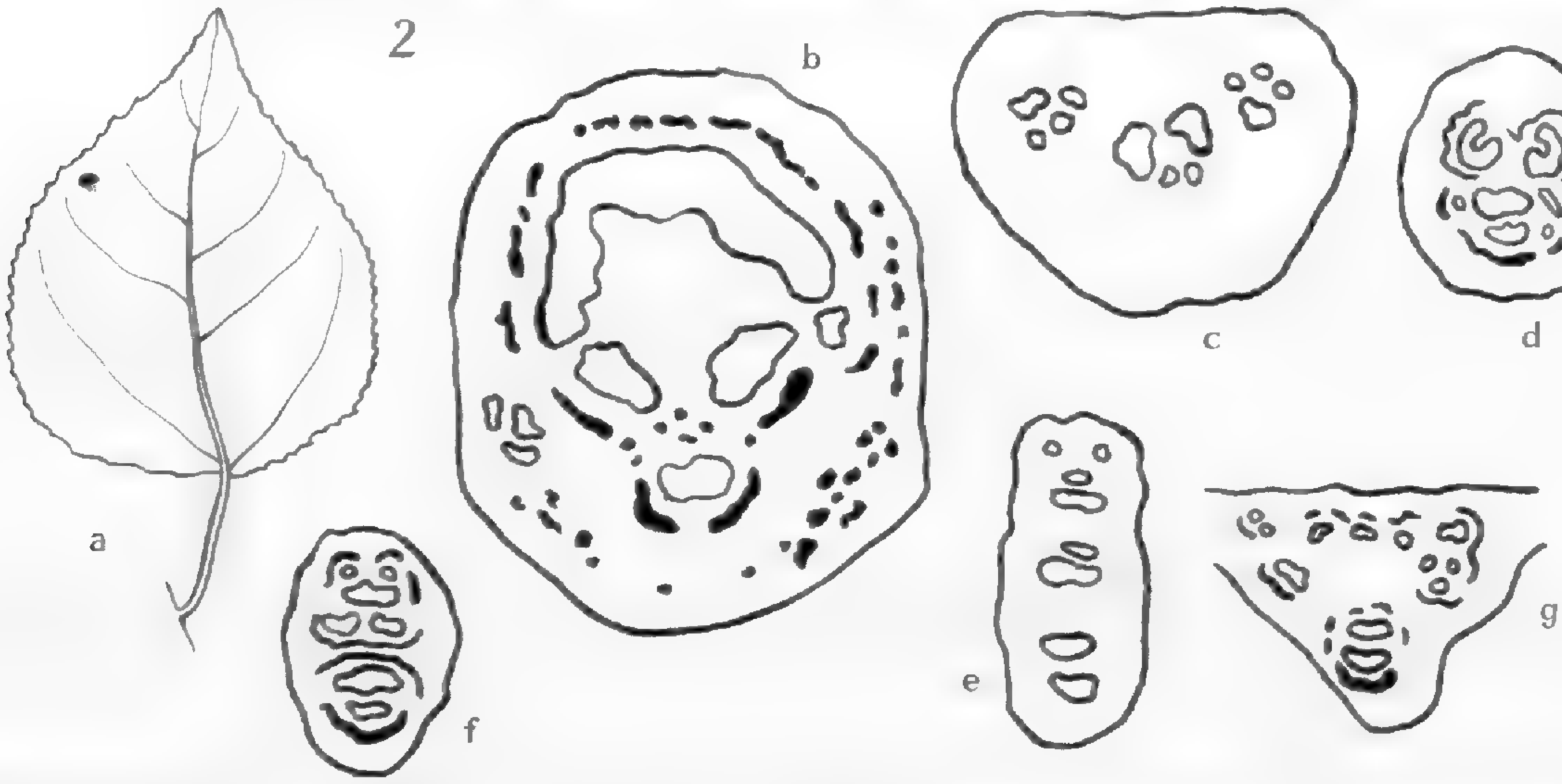

4

HOWARD, STEM-NODE-LEAF CONTINUUM

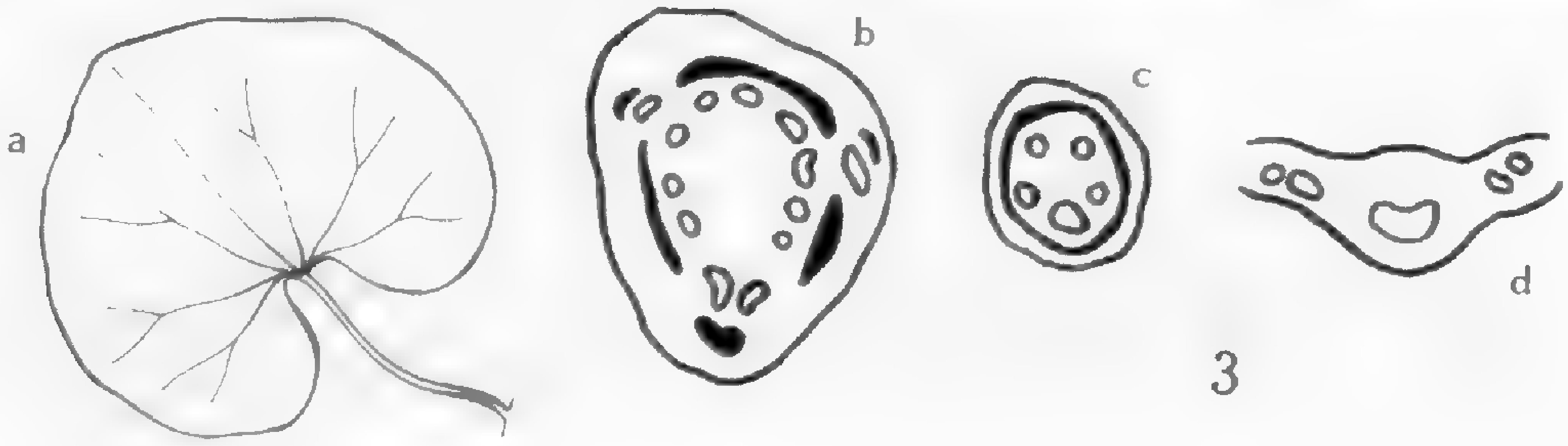
1



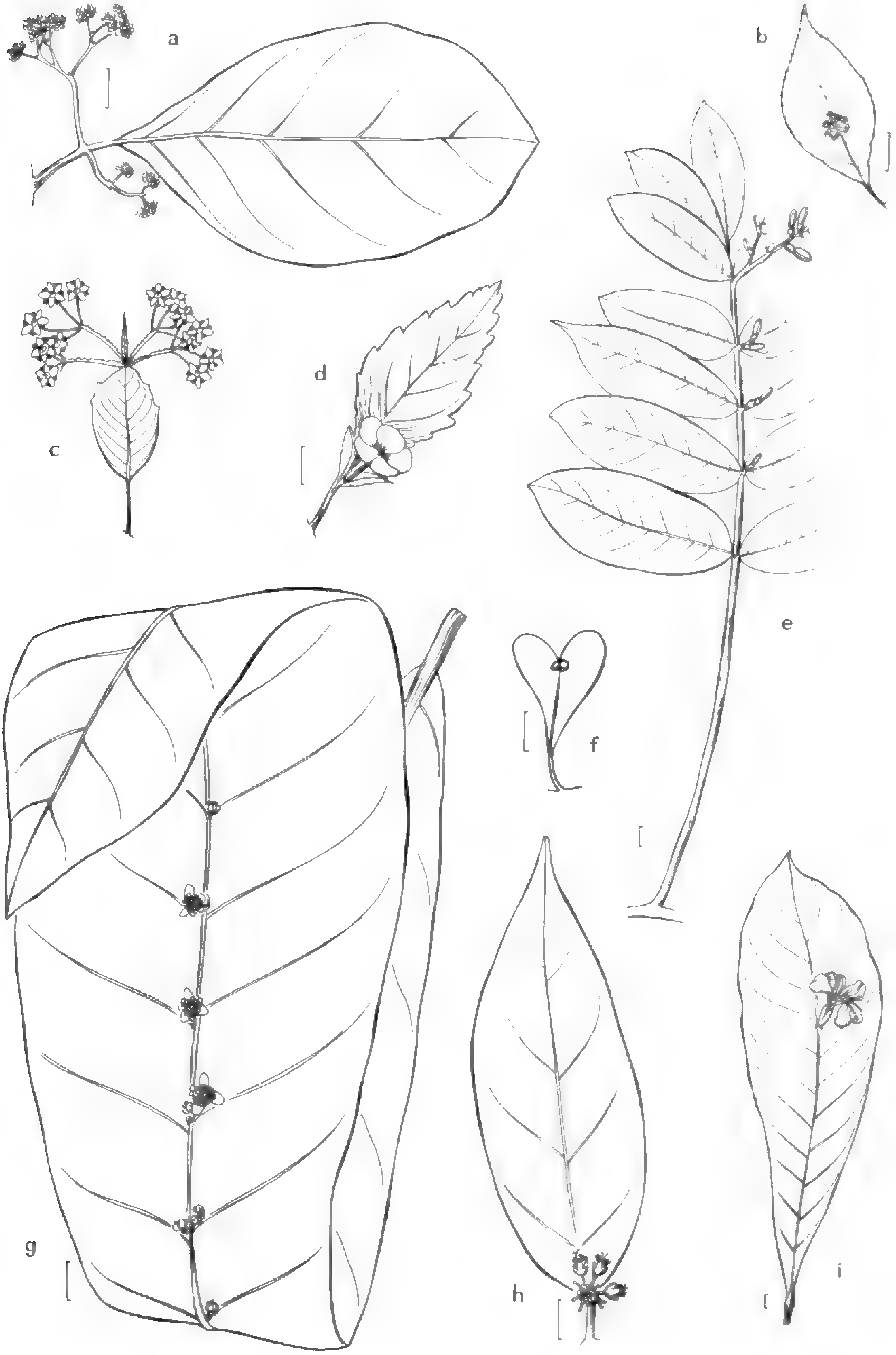
2



3



HOWARD, STEM-NODE-LEAF CONTINUUM



HOWARD, STEM-NODE-LEAF CONTINUUM

A REVIEW OF DECIDUOUS-LEAVED SPECIES OF STEWARTIA (THEACEAE)

STEPHEN A. SPONGBERG

As WITH MOST GENERA restricted in distribution to eastern and southeastern Asia and eastern North America, the theaceous genus *Stewartia* was based on an eastern North American plant, in this instance one known to eighteenth century European botanists and horticulturists, from Virginia. In fact, it was not until after the recognition of the second species indigenous to North America that an Asiatic species of *Stewartia* was discovered and described, and the genus could be added to the list of genera illustrating the floristic affinities of these two regions. Concomitant with the discovery of the species of *Stewartia*, the plants have been valued as garden ornamentals, and most of the taxa described have become prominent horticultural subjects in American and European gardens and arboreta.

Despite the long and continued horticultural interest in these late spring and summer flowering trees and shrubs, recent attempts to validate the identifications of *Stewartia* in the herbarium and in cultivation at the Arnold Arboretum led to some unexpected confusion that indicated need for a review of the genus. The present study is, therefore, an attempt to evaluate and reappraise the taxonomic status and relationships of the genus and its species, and this paper reports progress to date.

EARLY RECOGNITION OF THE GENUS

Baldwin (1969) has pointed out that the first reference to the plants now referred to *Stewartia* undoubtedly appears in the Reverend Mr. John Clayton's early "Account of Virginia," which Clayton (1657–1725) included in a letter he wrote to Robert Boyle in 1687. The plants that Clayton described and distinguished from the dogwood (*Cornus florida* L.) were from a population near Williamsburg, Virginia, on Archers Hope Creek. It is evident from his characterization of the flowers and fruit that Clayton was describing a shrub having flowers with five petals and a gynoecium that develops into a strongly five-ribbed capsule. Furthermore, the Archers Hope Creek population is still extant (Grimes, 1922) and represents a disjunct Coastal Plain population of what is otherwise primarily a montane species in the southeastern United States.

Fifty-five years after the Reverend Mr. John Clayton had described the plants from the Archers Hope Creek population, Mark Catesby, the English traveler and naturalist, received a new shrub for his garden at Fulham from another John Clayton (1686–1773), an English naturalist in Virginia who was apparently unrelated to the Reverend Mr. John Clayton. The plants flowered in May of 1742, and it is suspected that Catesby, recognizing their potential ornamental value as well as their botanical interest, gave plants of the new shrub to John Stuart, the third Earl of Bute, for the botanical garden he was helping to establish at Kew.

In addition to his gift of living plants to Catesby, the younger Clayton sent dried specimens of the new shrub to Gronovius at Leiden, one of which Gronovius forwarded to Linnaeus. The name *Stewartia*,[1] honoring John Stuart, was applied to the new genus by Linnaeus and was first published in 1746 (in the Acta Upsal. for the year 1741). Linnaeus stated that the description was based on Clayton's specimen as well as on the illustration (published with the description) drawn by George Ehret from plants in Stuart's garden and sent to Linnaeus by Isaac Lawson, a London physician.

Catesby himself included a plate of *Stewartia* in the *Appendix* to his *Natural History of Carolina, Florida, and the Bahama Islands* in the year following Linnaeus's publication.[2] Other than a few notes on the origin of his plants from Clayton, the text that accompanies the plate consists of a letter from John Mitchell (1680–1768), an English physician who had also traveled and collected in Virginia. In his letter to Catesby, Mitchell addresses himself to Linnaeus's description of the new genus.

Among other criticisms, Mitchell stated that *Malachodendron*, the name he used for the new genus, is characterized by five styles, not one, and that the strongly five-angled fruits dehisce apically. Mitchell also pointed out that the numerous stamens are united at the base and that, as a result, the genus properly belonged in class *Monadelphia Polyandria* where it formed a new tribe or order, *Pentagynia*, that separated it from malvaceous plants. The genus, appearing under the name *Malachodendron* and characterized in this manner, was later included by Mitchell in his *Dissertatio Brevis* of 1748.[3] Linnaeus, however, was unwilling to accept all of Mitchell's refinements, and in the *Species Plantarum* (1753) and *Genera Plantarum* ed. 5 (1754) complied only to the extent of including *Stewartia* in the class *Monadelphia Polyandria*. For the single species

---

[1] The spelling of the generic name consistently employed by Linnaeus is *Stewartia*, not *Stuartia*. Because of this invariance, it cannot be maintained under Art. 73 of the International Code of Botanical Nomenclature that Linnaeus's spelling contains an unintentional orthographic error, and the original spelling must be maintained. Cf. T. A. Sprague, Kew Bull. **1928**: 362. 1928 for the opposing viewpoint. Additional variant spellings include *Steuartia* and *Stevartia*.

[2] It is of interest to note that Stevenson [*Catalogue of Botanical Books in the Collection of Rachel McMasters Miller Hunt* 2(2): 144. 1961] attributes all but three plates in the *Natural History* to Catesby himself. The plate of *Stewartia* that was published by Linnaeus in 1746 and both attributed to and signed by Ehret is a small portion of the plate published by Catesby. If Catesby was indeed responsible for the plate appearing in the *Appendix*, as is indicated by his initials in the lower right-hand corner of the plate, it would seem that he enlarged upon the Ehret drawing.

[3] Mitchell's *Dissertatio Brevis*, republished in 1769, is acceptable as a valid publication for generic names. *Malachodendron*, as a genus, is usually attributed to Cavanilles, Diss. Bot. **5**: 302. *t. 158, fig. 2.* 1788, but is correctly attributed to Mitchell.

then known to him, he employed the binomial *Stewartia Malacodendron.*

It appears conclusive on the basis of the distributional and historical evidence summarized by Baldwin that Mitchell based his criticisms of Linnaeus's description on his observations of the plant that the Reverend Mr. John Clayton had discovered a half century earlier. Linnaeus based *Stewartia* on a second plant, a species that is essentially confined in distribution to the Atlantic Coastal Plain. Furthermore, both Clayton and Mitchell specimens of *Stewartia* are preserved at the British Museum, and it is clear that two taxa are represented. It is somewhat ironic that the first discovered species, known from a disjunct population, was rediscovered and described by Mitchell but was not accepted as distinct from *S. Malacodendron* until Cavanilles named the second species *Malachodendron ovatum* in 1788. Furthermore, according to Rees (1816), *S.* (*Malachodendron*) *ovata* essentially replaced *S. Malacodendron* as a favored ornamental in English gardens soon after its introduction in about 1785. Although some authors throughout the nineteenth century continued to accept *Malachodendron* as distinct from *Stewartia*, L'Héritier (1791) treated *M. ovatum* as a species of *Stewartia* (*S. pentagyna*), and there was a gradual acceptance of a single genus comprised of two species.

GENERIC RELATIONSHIPS

As subfamilial classifications and groupings of theaceous taxa were proposed periodically during the nineteenth century, *Stewartia* was generally associated with the superficially similar genus *Gordonia* Ellis. De Candolle (1824), recognizing both *Stewartia* and *Malachodendron* in the Ternstroemiaceae, aligned these genera with *Gordonia* in tribe Gordonieae DC., while *Camellia* L. and *Thea* L. were placed in a separate family, Camelliaceae. Choisy (1855), also recognizing two separate families, removed *Gordonia*, *Stewartia*, and *Malachodendron* to the Camelliaceae where *Stewartia* and *Malachodendron* were placed in a separate tribe, Stewartieae Choisy, on the basis of their gynoecia with ascending ovules, seeds with copious endosperm, and embryos with fleshy cotyledons. *Gordonia*, along with *Schima* Reinw. ex Bl. and *Laplacea* Kunth, was maintained in the Gordonieae, characterized by gynoecia with pendent ovules, seeds lacking endosperm, and embryos with foliaceous cotyledons.

Additional classifications were proposed as the genera comprising the Theaceae (as recognized today) were aligned with one another; these include the systems of Bentham & Hooker (1862), Szyszylowicz (1895), and Melchior (1925). The larger group of genera allied with *Stewartia* was recognized as forming a natural alliance, variously recognized as tribe Camellieae (DC.) Melchior or subfamily Camellioideae Airy-Shaw. The arrangement of genera within the tribe or subfamily, however, has been subject to debate, chiefly because of the criteria used in circumscribing the taxa. Fruit characters and those of the floral bracts, calyx, and corolla have been used in various combinations, resulting in numerous arrangements of the genera (cf. Keng, 1962, for a comparison of the more recent classifications).

Airy-Shaw (1937) initially pointed out the potential significance of the use of anatomical criteria for definition of subfamilies in the Theaceae, which encouraged several re-evaluations of existing classifications (Airy-Shaw, 1936; Sealy, 1958). The most recent scheme, proposed by Keng (1962), combines a morphological approach with the results of his considerable anatomical investigations of theaceous genera. The synoptic key to the tribes and subtribes of the Camellioideae which follows serves to distinguish *Stewartia* from its allies as well as to illustrate the basic alignment of the subfamily proposed by Keng.

KEY TO THE TRIBES & SUBTRIBES OF THE CAMELLIOIDEAE

A. Capsules lacking a persistent central columella; seeds wingless or narrowly winged; endosperm copious, embryos small, straight, with spatulate, flat cotyledons. STEWARTIEAE. (*Stewartia*, incl. *Hartia*).

A. Capsules with a persistent central columella; seeds conspicuously winged or wingless; endosperm lacking or confined to a thin layer, embryos large, straight or slightly curved, with flat or longitudinally undulate cotyledons. GORDONIEAE. .... B.

  B. Capsules woody, dehiscent, elongate or rounded; seeds winged (only rudimentary in *Franklinia*); endosperm forming a thin layer. C.

    C. Capsules elongate, ovoid to elliptic; seeds ellipsoid, with an oblong wing at the upper end. GORDONIINAE. (*Gordonia*, *Laplacea*).

    C. Capsules globose or subglobose; seeds rounded, flattened, with a conspicuous thin marginal wing, or the wing rudimentary. SCHIMIINAE. (*Schima*, *Franklinia*).

  B. Capsules woody, or sometimes coriaceous or drupaceous, indehiscent, more or less rounded; seeds wingless; endosperm absent. CAMELLIEAE. .... D.

    D. Seeds usually 1 (rarely 2 or more) per locule, rounded or rounded-cuneate; cotyledons thick. CAMELLIINAE. (*Camellia*, sensu lato).

    D. Seeds usually 2 or 2–4 per locule, ellipsoid, mutually compressed; cotyledons thin. PYRENARIINAE. (*Pyrenaria*, *Tucheria*).

The relationship between *Stewartia* and *Hartia*, a genus proposed by Dunn in 1902 to accomodate a plant from Yunnan Province in southwestern China and included in tribe Stewartieae by Keng, has been the subject of periodic discussions. The similarities of the two genera were commented upon by Dunn, and more recently the integrity of *Hartia* has been debated by Cheng (1934), Chun (1934), Airy-Shaw (1936), Merrill (1938), Wu (1940), and Sealy (1958). Dunn asserted that *Hartia* is distinct from *Stewartia* on the basis of the greater connation of its anther filaments into a tube at the base of the androecium and by its more numerous seeds. Wu (1940), who supported maintaining *Hartia*, emphasized in addition that the foliage of *Hartia* is persistent and that the conspicuously winged or inflated petioles successively enclose the terminal buds of the shoots.

Except for the difference of evergreen versus deciduous foliage, the reputed generic distinctions between *Stewartia* and *Hartia* fail to hold on even a cursory examination of the supposed differences in *Stewartia* sensu stricto. The number of seeds (ovules) per locule in *Stewartia* is either two or four (or fewer through abortion), while in *Hartia* the number is four. Connation of the anther filaments into a tube is at best a variable qualitative character, yet in *S. rostrata* a tube up to 9 mm. long is present that equals or surpasses, both in length and in relative amount of connation, any found in species assigned to *Hartia*. Furthermore, the petiole character mentioned by Wu occurs also in a deciduous species; all species of *Stewartia* have narrowly winged, shallowly grooved petioles, but in *S. ovata* the groove is deeper and the wings are enlarged, resulting in the concealment of the axillary and terminal buds.

Moreover, Keng's studies of *Stewartia* and *Hartia* have shown a consistent anatomical coincidence between the species, several aspects of which distinguish these from other theaceous genera. All genera of the Camellioideae, with the exception of *Stewartia* and *Hartia*, have capsules with persistent central columellae; while the nearly basal axile placentation, ascending ovules, and seeds with copious endosperm characteristic of *Stewartia* and *Hartia* also set these genera apart. The distribution of sclereids within the leaves of *Stewartia* species is unique in the Camellioideae since the sclereids are restricted to the petiole and petiolar-wing region. The same distribution pattern and the same type of sclereid are also found in leaves of species of *Hartia*. The wood anatomy of both genera is also similar. Both develop distinct growth rings, have a tendency towards ring porosity with the numerous pores solitary or in pairs, and the phellogen arises in the pericycle or adjacent layers.

Considering the breakdown of the originally proposed generic characters and the additional evidence of close or identical anatomical structure, it seems only logical to include *Hartia* within *Stewartia*. There is precedent for this proposal, since *H. sinensis* Dunn has been treated as a species of *Stewartia* (as *S. pteropetiolata* Cheng). Although a review of the taxonomy and nomenclature of the evergreen species is currently in progress, and they have been taken into account in preparing the generic description, only the deciduous species of *Stewartia* sensu stricto are considered in the taxonomic treatment of the present paper.

That *Stewartia* in this broad sense is relatively isolated within the Camellioideae is indicated by its segregation in a separate monotypic tribe. Its isolation could be a function of its relatively great age; fossil flowers attributable to the genus have been recorded from amber deposits of middle Oligocene in Central Europe, while fossil leaves that match well the leaves of present-day *S. monadelpha* have been found in Japan (Schenk, 1890). Moreover, the present-day distribution of *Stewartia* in eastern North America and eastern Asia along with the fossil evidence points to a former wider distribution and consideration of *Stewartia* as an Arcto-Tertiary relict.

SUBGENERIC CLASSIFICATION

Several authors have proposed subgeneric classifications of *Stewartia* sensu stricto. Wu (1940) divided *Hartia* into sect. HARTIA (sect. *Euhartia* Wu, flowers solitary, axillary) and sect. RACEMOSA Wu (inflorescence a few-flowered axillary raceme). Cheng (1934), in transferring *H. sinensis* to *Stewartia*, recognized two sections in *Stewartia* (sects. STEWARTIA and HARTIA (Dunn) Cheng) having limits that coincide with the old generic boundaries; while Keng (1962), in anticipation of the transfer of additional species of *Hartia* to *Stewartia*, also advocated two sections defined along former generic lines. The obstacle preventing my recognition of two subgenera or sections based on the former generic lines is the dearth of characters supplementing the one consistent distinction between the two proposed taxa, viz. persistent foliage versus deciduous foliage. Other characters seem to be reticulate within the genus and fail to coincide with this single difference.

Within *Stewartia* sensu stricto generic subdivisions have been delimited primarily on the basis of characters of the gynoecium and those of the calyx and its subtending bracts. Gray (1849), following Endlicher (1840, 1842) (who failed to designate the rank of his subdivisions), divided the genus into subg. STEWARTIA (styles united, capsules subglobose, not rostrate, seeds smooth, wingless; including sect. *Adelphonema* Endl.[4]) and subg. MALACODENDRON (Mitchell) Gray (styles 5, distinct, capsules ovate, acuminate, seeds with wrinkled epidermis, winged) using as criteria the generic boundaries that had separated *Malachodendron* from *Stewartia*. Szyszylowicz (1895) employed the same criteria in establishing sect. DIALYSTYLA, to include *S. ovata*, and sect. SYSTYLA (sect. *Cavanilla* (Salisbury) O. Kuntze), comprised of *S. Malacodendron* and the Asiatic species, all with united styles. Nakai (1950), treating the Japanese-Korean species, established two additional sections, sect. PSEUDOCAMELLIAE Nakai to include *S. pseudocamellia* (bracts shorter than the calyx) and sect. SERRATAE Nakai (bracts and sepals subequal) for the remaining species of that region.

All of the proposed generic subdivisions of *Stewartia* sensu stricto isolate one species from the remainder of the genus, and the resulting classification only serves to indicate the uniqueness of particular species. Conceivably, each species could be distinguished from the remainder of the genus by inclusion in a separate subgenus or section. In part, this situation has resulted from the examination of species of a limited area, but my examination of the entire genus convinces me that relationships among the taxa (including species of *Hartia*) are reticulate. Moreover, the species fail to fall into distinct subgeneric categories based on coherent groups of characters worthy of taxonomic recognition.

[4] The rank of Endlicher's subdivision was assigned by Gray.

ACKNOWLEDGMENTS

I should like to express my gratitude to the curators of the institutions from which herbarium materials have been borrowed for this study. These herbaria are cited according to the abbreviations found in J. Lanjouw & F. A. Stafleu, *Index Herbariorum*, ed. 5. 1965.

Particular thanks are extended to Drs. B. G. Schubert, C. E. Wood, Jr., G. P. DeWolf, Jr., K. R. Robertson, R. E. Weaver, Jr., Mr. R. S. Hebb, and Miss M. Gilmore, all of the Arboretum staff, for their freely given time and advice with numerous questions and problems. Special thanks are also extended to Dr. W. T. Gillis for his efforts on my behalf at the herbarium of the Linnean Society, London, and at the Royal Botanic Gardens, Kew, and to Mrs. F. Givens for providing preserved specimens from the living collections of the Henry Foundation for Botanical Research, Gladwyne, Pennsylvania.

FIGURE 1 is the exacting work of the late Dorothy H. Marsh, prepared for the *Generic Flora of the Southeastern United States*, a joint project of the Arnold Arboretum and Gray Herbarium of Harvard University made possible through the support of the National Science Foundation (Grant GB–6459X, principal investigator, Carroll E. Wood, Jr.) and reproduced here with the kind permission of Dr. Wood. FIGURE 2 was prepared by Virginia Savage, drawn for the most part from materials collected from living plants grown at the Arnold Arboretum, Jamaica Plain.

TAXONOMY

Stewartia Linnaeus, Sp. Pl. **2**: 698. 1753; Gen. Pl. ed. 5. 311. 1754.

Malachodendron Mitchell, Diss. Brev. Bot. Zool. 38. 1769.
Stuartia L'Héritier, Stirp. Nov. 153. 1791.
Cavanilla Salisbury, Prodr. Stirp. Chapel Allerton 385. 1796, non J. F. Gmelin, 1791, nec Thunberg, 1795.
Hartia Dunn, Hooker's Icones Pl. **28**: *t. 2727*. 1902.

Evergreen or deciduous trees or shrubs with closely fissured non-exfoliating or smooth, mottled, exfoliating bark; winter buds laterally compressed with 1 to several imbricate scales. Leaves alternate, chartaceous to coriaceous, short-petiolate, the petioles narrowly to widely winged, the wings sometimes enclosing and concealing the axillary and terminal buds; leaf blades ovate to lanceolate or elliptic with cuneate to rounded bases, serrulate to serrate margins, and acuminate, acute, or apiculate apices; venation pinnate, the midvein usually prominent and elevated on the adaxial surface; nodes unilacunar. Flowers perfect, solitary or occasionally 2 or 3 together, sometimes in a short, few-flowered axillary raceme, axillary or rarely terminal, pedicellate, with 1 or 2 persistent or rarely caducous bracts subtending the calyx. Sepals 5 (or 6), imbricate in bud and with overlapping margins at anthesis (quincuncial), subequal, persistent, connate and becoming lignified at the base. Petals 5, rarely 6–8, white, connate at the base forming a very shallow tube; blades obovate with wavy, finely erose margins, the abaxial surfaces silky pubescent. Stamens numerous, the filaments basally connate and adnate to the base of the corolla, otherwise free or coherent for part of their length and forming a tube; filaments white, purplish, or yellowish; anthers versatile, yellow or bluish. Gynoecium (4) 5 (or 6)-carpellate, the styles connate or free, partially persistent in fruit, terminating in (4), 5, (or 6) stigmatic arms or a single crenate stigma; ovary syncarpous, superior, (4) 5 (or 6)-loculate, each locule with 2 or 4 erect ovules on nearly basal axile placentae. Fruit a woody, globose to ovoid, often strongly rostrate capsule, lacking a persistent central columella, loculicidally dehiscent from the apex or by the outward folding of the valve margins; capsules maturing in a single season, often remaining on the branches for 2 or more seasons. Seeds 2 or 4 per locule (or fewer through abortion), angular and wingless or planoconvex with a narrow marginal wing, obovate to subovate in outline, the testa crustaceous and shining or chartaceous and dull with a finely rugose or puncticulate surface; embryo small, straight, the cotyledons subrounded, clasping, embedded in copious fleshy endosperm; germination epigeal. Base chromosome number 15. TYPE SPECIES: *S. Malacodendron* L.

KEY TO THE DECIDUOUS SPECIES OF STEWARTIA

A. Styles 5, distinct; petioles widely winged, enclosing the lateral and terminal buds; floral bract 1. .... 1. *S. ovata.*

A. Styles united, terminating in 5 or 6 stigmatic crests or arms; petioles narrowly winged, not enclosing the lateral and terminal buds; floral bracts 2. .... B.

  B. Stamens with purplish filaments and bluish anthers; capsules dehiscent by the outward folding of the valve margins, the apices of the valves ± coherent; seeds angular. .... 2. *S. Malacodendron.*

  B. Stamens with whitish filaments and yellow or orange anthers; capsules apically dehiscent, the valves spreading apart from the apex; seeds planoconvex. .... C.

    C. Floral bracts about equalling or longer than the calyx; small or large trees or shrubs with smooth or fissured bark; young branches usually terete, not zigzagged. .... D.

      D. Ovaries and/or capsules subglobose, completely glabrous or pubescent only at the very base. .... E.

        E. Ovaries and/or capsules completely glabrous; 2 ovules or seeds per locule; bark on older branches smooth and mottled. .... 3. *S. serrata.*

        E. Ovaries and/or capsules pubescent only at the very base; 4 ovules or seeds per locule; bark on older branches finely fissured. .... 4. *S. rostrata.*

      D. Ovaries and/or capsules conical, pilose or appressed-pubescent over the entire surface. .... F.

        F. Sepals oblong or ovate with acute apices. .... G.

          G. Floral bracts ovate, subequal to the sepals; styles 6–8 mm. long; seeds 7–9 mm. long. .... 5. *S. sinensis.*

G. Floral bracts oblong, conspicuously longer than the sepals; styles 3–4 mm. long; seeds 5–6 mm. long. .... 6. *S. monadelpha.*

F. Sepals ovoid with rounded, ciliate apices. .. 7. *S.* × *Henryae.*

C. Floral bracts conspicuously shorter than the calyx; small trees with smooth, mottled bark; young branches usually compressed and zigzagged, rarely terete. .... 8. *S. pseudocamellia.*

1. **Stewartia ovata** (Cavanilles) Weatherby, Rhodora **41**: 198. 1939. FIGURE 1.

Malachodendron ovatum Cavanilles, Diss. Bot. **5**: 302. *t. 158*, *fig. 2*. 1788. TYPE: presumably at MA, but not seen.
Stewartia pentagyna L'Héritier, Stirp. Nov. 155. *t. 74*. 1791.
Stewartia montana Bartram, Travels 334. 1791.
Malachodendron pentagynum (L'Héritier) Dumont-Courset, Bot. Cult. ed. 2. **5**: 107. 1811.

Shrubs or small trees to 6 m., usually with several limbs from the base; periderm on young shoots silvery gray-brown, with long, longitudinal fissures, the bark non-exfoliating, grayish-brown, tight, with close, shallow fissures; winter buds small, 2–5 mm. long, with one pubescent scale en-

FIGURE 1. **Stewartia ovata.** a, flowering branchlet of forma *grandiflora* × 1/2; b, flower of forma *ovata*, × 1/2; c, apically dehiscent capsule with 5 persistent styles and persistent calyx, × 1 1/2; d, seed with winged margin and finely rugose surface, × 3.

closing the silvery-pubescent embryonic leaves. Leaf petioles 4–14 mm. long with winged margins, the margins enclosing and concealing the axillary and terminal buds; leaf blades ovate to ovate-lanceolate, (3–)7–15 cm. long, (2–)4.5–7(8.5) cm. wide, with acute to shortly acuminate apices, rounded bases, and ciliate, obscurely serrulate margins with apiculate teeth; upper surface of the blades glabrous, lower surfaces finely pubescent, particularly along the veins. Flowers axillary, pedicels short and stout, 3–4 mm. long; one bract subtending the calyx, foliaceous, 11–14 mm. long, 3.5–4.5 mm. wide, oblong with an acute apex, persistent. Sepals 5 (or occasionally 4), connate at base, 14–17 mm. long, 6–9 mm. wide, the free lobes lanceolate-oblong with acute apices and ciliate margins; sepals erect in bud, persistent, spreading-erect in fruit. Petals 5, free to the base, 2.8–4.2 cm. long, 2.2–3 cm. wide, obovate to suborbicular, margins erose and wavy. Stamens numerous, the filaments united into a short tube at base, 3–4 mm. long, adnate to the corolla, the free portions 10–12 mm. long above, white, yellowish, or rose; anthers yellow. Ovary conical, 5–6 mm. long at anthesis, irregularly 5-lobed, densely sericeous, particularly toward the base of the styles; styles 5, distinct, subequal, 12–14 mm. long, each terminating in a small capitate stigma. Capsules reddish brown, finely pubescent, particularly along the margins of the locules, ovoid with truncate apices (the styles persistent at varying lengths) and strongly 4- or 5-angled, 18–22 mm. long, 14–16 mm. broad, apically dehiscent into 4 or 5 locules, the locule walls 6–7 mm. wide. Seeds 2 per locule, reddish brown, 8–10 mm. long, 5–7 mm. wide, plano-convex, obovate to oblong in outline, narrowly winged, the apex rounded or sometimes emarginate, the raised central portion finely rugose. $2n = 30$.

DISTRIBUTION: Known from the mountains and adjacent Piedmont of Kentucky, Tennessee, North and South Carolina, Georgia, and Alabama; occurring in two disjunct populations on the Coastal Plain of Virginia.

Representative specimens. **Alabama.** CHILTON Co.: Sand Mountain, *T. G. Harbison, s.n.* 20 VI 1905 (A); same locality, *T. G. Harbison, s.n.* 20 VI 1913 (A). CULMAN Co.: St. Bernard, *W. Wolf, s.n.* 25 VI 1934 (GH). DEKALB Co.: gorge of Town Creek, *R. M. Harper 4043* 12 IX 1947 (GH). FRANKLIN Co.: edge of sandstone gorge along Dismal Branch, *R. M. Harper 3398* 17 VI 1935 (A, GH). **Georgia.** FULTON Co.: West Paces Ferry Road over the Chattahoochee River, *H. Bookout, Jr. 35* 20 VI 1957 (GH); ravine slope near Sandy Springs, *E. T. Wherry, s.n.* 7 IX 1934 (A). MADISON Co.: S slope of Mill Shoal Creek, 1 mi. SE of Colbert at ca. 600 ft., *W. H. Duncan 11595* 4 VIII 1950 (GH). OCONEE Co.: slopes of wooded ravine ca. 3 1/2 mi. SE of Farmington, *W. H. Duncan 3794* 4 VIII 1941 (GH). RABUN Co.: rocky stream bank, 7 mi. S of Highlands, N.C., *T. G. Harbison 52 & 53* 1 VII 1918 (A, two sheets); canyon at Tallulah Falls at 1600 ft., *J. K. Small, s.n.* 15 VIII 1893 (A, GH). STEPHENS Co.: southern slope of Lee Mountain, *H. Bookout, Jr. 21* 8 VII 1956 (GH); bank of stream, Toccoa, *T. G. Harbison 10* 20 VI 1918 (A, two sheets). TOWNS Co.: near Hiawassee, *C. S. Sargent, s.n.* 28 IX 1885 (A). Without locality: C. *Wright, s.n.* 1875 (GH). **Kentucky.** BELL Co.: Clear Creek, *E. L. Braun 1580* 15 VII 1937 (A); along the Cumberland River, *T. H. Kearney 322* IX 1893 (A, GH). MCCREARY Co.: Yahoo Ridge, western edge of Cumberland Plateau, *E.*

L. Braun, s.n. 18 VI 1935 (GH). Pulaski Co.: Rockcastle Springs, *J. D. Smith, s.n.* 18 VIII 1883 (GH). **North Carolina.** Macon Co.: southern exposures of the Blue Ridge Mountains, *Biltmore Herb. 886b* 3 VII & 9 VIII 1897 (A, BM, GH, P); Highlands, *T. G. Harbison, s.n.* VI 1903 (GH). Stokes Co.: north-facing bluff of the Dan River N of Moore Springs, *W. B. Fox 5500* 30 IX 1951 (GH); same locality, *S. W. Leonard & D. B. Russ 2554* 1 VII 1969 (BM, GH, P). Without locality: *S. B. Buckley, s.n.* (BM, GH); *F. Rugel, s.n.* 1841 (BM); *C. S. Sargent, s.n.* 26 IX 1885 (A). **South Carolina.** Oconee Co.: E side of W fork of Little River, 3 mi. SW of Salem at ca. 900 ft., *W. H. Duncan 11259* 8 VII 1950 (GH). **Tennessee.** Blount Co.: Abrams Falls Trail, Cades Cove, *R. E. Shanks & A. J. Sharp 13184* 25 VI 1949 (GH). Cumberland Co.: Cumberland Mountain, *A. Gattinger 408* (A, BM, GH). Grundy Co.: along stream below Altamont, *H. K. Svenson 7306* 9 VII 1935 (GH). Knox Co.: Clinch Mountain above Lea Lakes near Blane, *H. M. Jennison, s.n.* 6 VII 1929 (GH). Marion Co.: Cumberland Plateau ca. 5 mi. SE of Sewanee at 1800 ft., *H. K. Svenson 8913* 22 VI 1938 (GH). Monroe Co.: Cherokee Natl. Forest, 1 mi. up North River Road toward Beech Gap, *M. H. Berry 16444* 29 VI 1952 (GH). Polk Co.: banks of the Ocoee River, *Biltmore Herb. 886c* 26 VIII 1897 (A, GH). Rhea Co.: near Rockwood, *D. M. Coffman, s.n.* 15 VI 1890 (A). Sequatchie Co.: Eagle, *J. H. H. Boyd, s.n.* VII 1891 (A). Sevier Co.: along road to Indian Gap and along Fightin' Creek Road, Lower Sugarlands Valley at 500 m., *H. M. Jennison & J. G. Smith, s.n.* 29 VI 1937 (GH); between Pitman's Center and Greenbrier, *A. J. Sharp, et al. 1963* 15 VII 1934 (BM). Union Co.: near The Gourd, *Kelley 2105* 10 VII 1934 (GH). Without locality: *A. Gattinger, s.n.* 1879 (A, two sheets); *F. Rugel, s.n.* VI 1842 (BM); *A. Ruth 239* (GH); *C. S. Sargent, s.n.* 21 IX 1888 (A). **Virginia.** James City Co.: Williamsburg, bluff above College Creek, $2n = 34$, *J. T. Baldwin 14951* 19 VI 1954 (GH); moist or dry hillsides, 1 1/2 mi. SE of Williamsburg, *E. J. Grimes 3818* 24 VI 1921 (GH). Lancaster Co.: bank of John Creek, Merry Point, *W. J. Harley 2265* 18 VI 1960 (GH); same locality, *W. J. Harley 2272* 25 VIII 1960 (GH). Without locality: *J. Mitchell, s.n.* (BM); *Michaux, s.n.* (P).

Cultivated. **England.** Surrey: Royal Botanic Gardens, Kew, Richmond, *no collector* (BM). Without locality: Hortus Dickens, 14 IX 1916 (BM). **United States.** Massachusetts: Arnold Arboretum, plant from seed from Germantown, Pa., 1928, Acc. # 637–28, *E. J. Palmer, s.n.* 21 VI 1938 (AAH); plant grown from seed from New York Botanical Garden, 1933, Acc. # 313–34, *E. J. Palmer, s.n.* 11 X 1938 (AAH); plant from T. G. Harbison, Highlands, N.C., 1925, Acc. # 18244, *C. E. Kobuski, s.n.* 17 VII 1933 (AAH), *E. Murray 318* 7 IV 1965 (AAH); plant from H. F. Kelsey, Boxford, Mass., 1922, Acc. # 18847, *S. Kreps, s.n.* 10 VII 1964 (AAH), *G. P. DeWolf & P. Bruns 2175* (AAH); without data, 14 VII 1911 (AAH). Brookline: Hortus H. H. Richardson, *A. Rehder, s.n.* 13 VII 1921 (AAH, two sheets). Jamaica Plain: Hortus Dixwell, 25 IX 1882 (AAH); same locality, VIII 1885 (GH); Hortus F. Parkman, 18 VII 1889 & 25 III 1896 (AAH, two sheets). South Lancaster: Hortus Mrs. Bayard Thayer, *E. H. Wilson, s.n.* 24 VII 1927 (AAH, two sheets). New York: Pecks Mill, *L. Lundquist, s.n.* 17 VII 1937 (AAH). North Carolina: Shortia Gardens, Highlands, *T. G. Harbison, s.n.*, V 1903 (GH). Pennsylvania: Morris Arboretum, Acc. # 62–116, *J. M. Fogg, Jr., s.n.* 29 VI 1967 (AAH).

Stewartia ovata is easily distinguished from other deciduous species of *Stewartia* by its winged petioles that enclose and conceal the terminal and lateral buds. In this respect, *S. ovata* is more closely allied to the evergreen Asiatic species that have been treated as species of *Hartia* than are other deciduous species. This taxon is also unique within the genus due to its gynoecium with five distinct styles and its one floral bract that subtends the calyx.

Plants with flowers having purple rather than yellowish-white stamen filaments and with five to eight petals have been recognized as forma *grandiflora* (Bean) Kobuski. Baldwin (1969, 1970), however, reported flowers with stamen filaments ranging in color from white through rose to purple from the James City County population on the Virginia Coastal Plain and questioned whether this variation was a result of introgressive hybridization between *S. ovata* and *S. Malacodendron*, the flowers of which normally have purple stamen filaments. Wood (1957) and Kobuski (1959) commented on this color variation and noted the range from white to light purple in the same and in different flowers of a single plant of *S. ovata* from Highlands, North Carolina, cultivated at the Arnold Arboretum. They attributed the variation to genetic instability similar to that known in some *Camellia* cultivars. Inasmuch as additional evidence supporting introgression is lacking, somatic mutation seems to be the most plausible explanation.

In the citation of herbarium specimens, sheets of forma *grandiflora* have been included with sheets of forma *ovata* since stamen filament color does not preserve well and the number of petals in flowers of forma *grandiflora* is variable and often difficult to determine in pressed specimens. A presentation of the nomenclature and synonymy of forma *grandiflora*, which is of some importance horticulturally, follows this discussion.

Although *Stewartia ovata* was first described by Mitchell as the basis for the genus *Malachodendron*, the combination *M. ovatum* was first made by Cavanilles. The specimen on which this name is based is presumably preserved at Madrid. However, in his protologue Cavanilles refers only to living plants he observed at Trianon Palace and cites Mitchell's publication. If a specimen studied by Cavanilles is not preserved at Madrid the plate published by him might be designated as lectotype. Before this problem can be resolved, however, the collections at Madrid must be examined.

1a. **Stewartia ovata** (Cavanilles) Weatherby forma **grandiflora** (Bean) Kobuski, Jour. Arnold Arb. **40**: 419. 1959.

Stewartia ovata (Cavanilles) Weatherby var. *grandiflora* (Bean) Weatherby, Rhodora **41**: 198. 1939.
Stewartia pentagyna L'Héritier var. *grandiflora* Bean, Trees & Shrubs Hardy Brit. Isles ed. 1. **2**: 555. 1914.
Malachodendron pentagynum (L'Héritier) Dumont-Courset var. *grandiflorum* (Bean) Ashe, Torreya **31**: 41. 1931.

Differs from forma *ovata* in its corolla comprised of 5 to 8 petals and in its purple stamen filaments.

2. **Stewartia Malacodendron** Linnaeus, Sp. Pl. **2**: 698. 1753. Holotype: *Clayton 734* (LINN, No. 876.1; IDC 177. 469: III. 2.); isotypes (BM, two sheets!).

Stewartia virginica Cavanilles, Diss. Bot. **5**: 303. *t. 159, fig. 2.* 1787.
Cavanilla florida Salisbury, Prodr. Stirp. Chap. Allerton 385. 1796.
Stuartia nobilis Salisbury, *Ibid.* 386.
Stewartia marilandica Donn ex Haworth, Andr. Bot. Repos. **6**: *t. 397.* 1804.
Malachodendron monogynum Dumont-Courset, Bot. Cult. ed. *2.* **5**: 106. 1811.

Shrubs or small trees to 7 m.; young branches pubescent, the periderm reddish brown, flaking in irregular longitudinal strips; bark tight, close, silvery gray, non-exfoliating; winter buds compressed, 5–9 mm. long, with 2 densely silvery-pubescent imbricate scales. Leaf petioles 2–4 mm. long, shallowly grooved on the adaxial surface; leaf blades (2.5–)5.5–11 cm. long, (1.1–)2.5–5 cm. wide, ovate to elliptical with acute or acuminate apices, cuneate to attenuate bases, and finely serrulate, obscurely ciliate margins; upper surfaces of the blades glabrous, the lower surfaces finely appressed-pubescent, particularly along the midveins. Flowers axillary, the pedicels short, up to 5 mm. long; bracts subtending the calyx 2, ovate to suborbicular, 2–4 mm. long, 2–4 mm. wide, with short apiculate apices, persistent. Sepals 5, connate at base, 8–11 mm. long, 5–9 mm. wide, the free lobes suborbicular to obovate with ciliate margins and apiculate apices, persistent and reflexed in fruit. Petals 5, connate at base, (3–) 4–5 cm. long, 3–4(–4.9) cm. wide, obovate to suborbicular in outline with entire or erose, wavy margins, the abaxial surfaces sericeous toward the base. Stamens numerous, the filaments purple, connate at base forming an ill-defined tube ca. 1 mm. long, the tube entirely adnate to the base of the corolla; free portions of the filaments up to 10 mm. long, pubescent at base; anthers bluish. Ovary ca. 5 mm. long at anthesis, subglobose, 4- or 5-angled, densely sericeous, the style glabrous, 3–5 mm. long, terminated by 4 or 5 stigmatic crests. Capsules woody, reddish brown, finely appressed pubescent, subglobose, 4- or 5-angled, often broader than long, 12–16 mm. long, 12–18 mm. broad, with apiculate apices, the base of the deciduous style projecting 1–1.5 mm. from the apex of the capsule; capsule dehiscing into 4 or 5 locules, by the outward and backward folding of the lateral margins of the valve walls, the apices of the valves remaining coherent or only slightly separated, one or two of the valves rarely deciduous. Seeds 2 or 4 per locule (or fewer through abortion), 5–7 mm. long, 4–6 mm. wide, angular, ovate to subovoid in outline, wingless, lustrous purplish or reddish brown. $2n = 30$.

Distribution: Occurring in scattered localities on the Coastal Plain and Piedmont in the southeastern United States from Virginia to Florida and west to Mississippi, Louisiana, and Arkansas; known from two localities in the mountains of North Carolina and recently discovered in Newton County in eastern Texas.

Representative specimens. **Alabama.** Butler Co.: 3 mi. SW of Greenville, *R. M. Harper 98* 20 VI 1906 (GH). Tuscaloosa Co.: Tuscaloosa, *E. A. Smith, s.n. 22* V 1884 (A). **Arkansas.** Ouachita Co.: Camden, *A. Fendler, s.n.* 19 V 1850 (GH). **Florida.** Calhoun Co.: Chipola River, E of Clarksville, *R. K. Godfrey 56339* 3 IV 1958 (GH); 7 mi. S of Alta, *R. K. Godfrey 62701* 7 IV 1963 (GH). Escambia Co.: Pensacola, *Clifton, s.n.* (BM). Gadsden Co.: Rocky Comfort Creek N of Lake Talquin, *R. K. Godfrey & W. D. Reese 54724* 7 V 1956 (GH); same locality, *R. K. Godfrey & R. Kral 54969* 7 VII 1956 (GH). Jackson Co.: Round Lakes, *T. G. Harbison, s.n.* 27 V 1916 (A). Liberty Co.: Apalachicola River near Allum Bluff, *E. J. Palmer 38546* 11 IV 1931 (A). Okaloosa Co.: Big Creek, W of Laurel Hill, *R. K. Godfrey 61291* 2 VIII 1961 (GH). Santa Rosa Co.: Escambia River slope W of Jay, *R. K. Godfrey & H. Kurz 54758* 10 V 1956 (GH). Walton Co.: deep ravines and steep hillsides near Eucheeanna, *E. J. Palmer 38605* 14 IV 1931 (A); 14 mi. NE of DeFuniak Springs, *D. Plank, E. West, & L. E. Arnold, s.n.* 6 V 1948 (GH); same locality, *D. Plank & E. West, s.n.* XII 1948 (GH); 8 1/2 mi. S of DeFuniak Springs, *R. R. Smith 2337* 7 V 1968 (GH); 8 mi. W of Portland, *E. L. Tyson, s.n.* 26 V 1952 (GH). Without locality: *W. Baldwin, s.n.* (GH); *A. W. Chapman, s.n.* 1845 (BM, GH). **Georgia.** Bulloch Co.: Lott's Creek, 7 1/2 mi. SW of Statesboro, *G. P. DeWolf & J. A. Boole 1674* 22 VIII 1961 (GH); Lower Lott's Creek, *K. Ussery 192* 5 V 1962 (GH). Calhoun Co.: along Ichawaynochaway Creek 3 mi. W of Leary, *R. F. Thorne & W. C. Muenscher 7990* 5 IV 1948 (GH). Candler Co.: ca. 3 mi. E of Metter, *W. H. & M. B. Duncan 3964* 24 VIII 1941 (A, GH); open woods, Salem Church, 2 mi. NE of Metter, *E. T. Wherry, s.n.* 4,5 VII 1936 (GH). Hancock Co.: Spring Creek, 9.1 mi. E of Milledgeville, *W. H. Duncan 11024* 2 VI 1950 (GH). Screven Co.: SE portion of county, *D. Eyles 6936* 12 V 1940 (GH). Without locality: *T. G. Harbison 1150* 13 V 1913 (A, two sheets). **Louisiana.** Orleans Parish: New Orleans, *T. Drummond 204* 1832 (BM). St. Tammany Parish: Covington, *R. S. Cocks, s.n.* IV 1900 (A). Without locality: *S. B. Buckley, s.n.* (BM); *M. Carpenter, s.n.* (GH); *J. Hale, s.n.* (GH). **Mississippi.** Forrest Co.: Hattiesburg, *T. G. Harbison 10* 19 V 1915 (A). George Co.: plant 10 ft. tall, University of Mississippi Forest land near Benndale, *D. Demaree 34934* 25 IV 1954 (GH). Perry Co.: woods along Tallahala Creek near Runnelstown, *S. B. Jones, Jr. 5195* 4 V 1966 (GH). **North Carolina.** Craven Co.: W of New Bern, *T. G. Harbison, s.n.* 20 IV 1919 (A). Duplin Co.: Coshen Swamp, 3 mi. SW of Kornegay, *H. E. Ahles & G. Ramseur 24063* 27 IV 1957 (GH). Hertford Co.: pine-hardwood forest 2 mi. W of Camp P-D, *F. W. Woods & D. E. Moreland 731* 26 VIII 1948 (GH). Jones Co.: hardwood forest on Island Creek, *A. E. Radford 6649* 30 VIII 1952 (GH). Onslow Co.: near New River 2 mi. SW of Green Branch, *D. E. Moreland, s.n. 22* V 1948 (GH). Pasquotank Co.: 1 mi. S of Elizabeth City, *K. M. Wiegand & W. E. Manning 1977* 17 VI 1927 (GH). **South Carolina.** Beaufort Co.: SW of Middleton Gardens, ca. 15 mi. NW of Charleston, *W. H. Duncan 6024* 11 V 1944 (GH); near Bluffton, *J. H. Mellichamp, s.n.* (A, three sheets). Dorchester Co.: near Dorchester, *J. H. Mellichamp, s.n.* 1889 (A). Georgetown Co.: shady woods near Andrews, *T. G. Harbison, s.n.* 26 IV 1918 (A). **Texas.** Newton Co.: Little Cow Creek E of Old Hemphill Road, ca. 15 mi. NW of Burkeville, *D. S. Correll, et al. 29632* 16 V 1964 (GH). **Virginia.** Accomac Co.: Messongo Creek, *E. Mears, s.n.* V 1886 (GH). Norfolk Co.: rich woods near Gertie, *M. L. Fernald & L. Griscom 4455* 7 V 1935 (A, GH); Great Dismal Swamp W of Yadkin, *M. L. Fernald & B. Long 11078* (GH); same locality, *M. L. Fernald & B. Long 12131* 11 VI 1940 (GH); 10 mi. S of Norfolk, *E. B. Harger 419* 28 V 1900 (GH). PRINCESS ANN CO.: wet woods near Pungo, *M. L. Fernald & B. Long 10726* 22 VII 1939 (GH). Without locality: *J. Clayton, s.n.* (BM, two sheets, LINN); *Michaux, s.n.* (P).

Cultivated. **New York:** Oyster Bay, Long Island, Hortus H. de Forest, *A. Rehder, s.n.* 9 IX 1921 (AAH, two sheets). **Pennsylvania:** Germantown, Hortus W. J. Campbell, *W. J. Campbell, s.n.* 6 VI 1935 (AAH). **South Carolina:** Hartsville, Hortus W. C. Coker, *E. J. Palmer 42378* 18 V 1934 (AAH). **Virginia:** Wachapreague, Hortus Mrs. J. M. Durbin, *J. M. Durbin, s.n.* 14 IX 1967 (AAH).

Stewartia Malacodendron appears isolated within the genus and is remarkably uniform throughout its range. It is recognized in flower by its androecium with purplish stamen filaments and bluish anthers. The capsules of *S. Malacodendron* are distinct in their dehiscence which occurs by the outward and backward folding of the lateral margins of the valves at the sutures between the valves. Seeds of *S. Malacodendron* are also diagnostic; their angular shape and the dark, smooth, and shining seed coat are not repeated elsewhere in the genus.

Although primarily a species of the Coastal Plain in the southeastern United States, where it inhabits low rich woodlands, usually along stream banks and on ravine slopes, *Stewartia Malacodendron* is also known from a few localities on the Piedmont and in the mountains of North Carolina in Avery and Macon Counties. Its range overlaps that of *S. ovata*, but sympatric populations are not known.

Of the specimens that Clayton sent to Gronovius, one, sent by Gronovius to Linnaeus, is in the Linnaean Herbarium in London, while two additional specimens are preserved at the British Museum.

3. **Stewartia serrata** Maximowicz, Bull. Acad. Sci. St.-Pétersb. III. **11**: 430. 1867; Mél. Biol. Acad. Sci. St.-Pétersb. **6**: 201. 1867, "*Stuartia*." HOLOTYPE: presumably at LE, but not seen.

Stewartia serrata var. *sericea* Nakai, Bull. Natl. Sci. Mus. Tokyo **29**: 93. 1950. HOLOTYPE: *S. Okuyama, s.n.* (TNS, sheet #80681!).

Stewartia serrata forma *sericea* (Nakai) Hara, Enum. Spermatophytarum Japon. **3**: 169. 1954.

Stewartia epitricha Nakai, Bull. Natl. Sci. Mus. Tokyo **29**: 92. 1950. HOLOTYPE: *Z. Tashiro, s.n.* (TNS, sheet #18654!).

Stewartia serrata var. *epitricha* (Nakai) Ohwi, Bull. Natl. Sci. Mus. Tokyo **33**: 79. 1953; Fl. Jap. 775. 1953, invalid, basionym not cited.

Stewartia serrata forma *epitricha* (Nakai) Ohwi, Fl. Jap. English ed. 629. 1965, invalid, basionym not cited.

Small trees to 10 m. (?); periderm on young shoots exfoliating in thin strips or flakes, the young branchlets finely pubescent, slender, grayish and reddish brown; bark on older limbs smooth, reddish brown, exfoliating; winter buds compressed, 4–6 mm. long with 2 reddish-brown, marginally ciliate, imbricated scales. Petioles (2–)5–12 mm. long, shallowly grooved on the adaxial surface; leaf blades ovate to lanceolate or oblanceolate, (1.7–)2.5–7.5 cm. long, (1–)1.4–2.6 cm. wide, with acuminate apices, serrulate and often ciliate margins with inwardly curved teeth, and cuneate to attenuate bases; upper surfaces of the blades glabrous or with few scattered hairs, lower surfaces glabrous or with hairs along the midvein, sometimes with tufts of hairs in the axils of the midvein and lateral veins. Flowers axillary, pedicels 4–5(–7) mm. long; bracts subtending the calyx 2, foliaceous, often flushed with red, subopposite, lanceolate with acute apices and undulating, finely serrulate margins, 13–17 mm. long, 7–9 mm. wide, eventually deciduous in fruit. Calyx of 5 basally connate sepals, often suffused with reddish pigment, the free lobes essentially like the bracts in outline, erect or spreading in bud, lanceolate with acute to apiculate apices and undulating, serrulate margins, (12–)19–25 mm. long, 8–10 mm. wide; calyx becoming lignified at base, erect to spreading in fruit, eventually deciduous. Petals 5, connate at the base, obovate to suborbicular with erose margins and cuneate bases, (25–)30–33 mm. long, 20–25 mm. wide, the abaxial surface finely sericeous and sometimes (?) suffused with reddish pigment at the base. Stamens numerous, the filaments up to 25 mm. long, connate at the base, forming a tube 7–8 mm. long, the entire tube adnate to the base of the corolla, the free portions of the filaments finely pubescent at the base; anthers yellow. Ovary subglobose, 5-angled, glabrous, 3–4 mm. long at anthesis, tapering into a glabrous style, 17–20 mm. long, terminating in 5 very short stigmatic arms 0.5–1 mm. long, the arms marginally ciliate and often appearing connate. Capsules reddish brown, (13–)16–18 mm. long, (12–)14–17 mm. wide, completely glabrous, subglobose, 5-angled, with short rostrate apices, the style deciduous nearly at the apex of the ovary; capsule dehiscing into 5 locules, the locule walls 6–9 mm. wide. Seeds 2 per locule, 9–12 mm. long, 5–7 mm. wide, planoconvex, obovate in outline, oblique at the notched base with a narrow wing surrounding the raised central portion, reddish brown, the surface finely puncticulate. $2n = 30$.

DISTRIBUTION: Known from scattered localities in mountainous areas of southcentral Honshu, Shikoku, and Kyushu Islands, Japan; cultivated in western gardens.

Representative specimens. **Honshu.** PREF. KANAGAWA: Mt. Tanzawa, *Y. Hayashi, s.n.* 20 VII 1956 (TNS); Mt. Kamiyama, *I. Hurusawa 1479* 22 X 1951 (A); Yokohama, *Maximowicz, s.n.* 1862 (GH, P, a mixed collection with *S. monadelpha*); Mt. Kamiyama, in *Fagus* forest, *M. Mizushima 706* 28 XI 1950 (A); same locality, rather common in forest, *M. Mizushima 1617* 22 X 1951 (A); Mt. Tanzawa, *S. Okuyama 20189* IX 1962 (TNS); Mt. Komagatare (?), *K. Sakurai, s.n.* 9 VII 1910 (A); Mt. Kozukayama, *T. Sawada 2177* 20 VI 1927 (A); Mt. Komagatake, *E. H. Wilson, s.n.* (A). PREF. SHIZUOKA: Mt. Amagi, *G. Hashimoto, s.n.* 18 VIII 1932 (TNS); same locality, *Y. Hayashi, s.n.* 7 VII 1951 (TNS); same locality, in summer-green forest, *M. Mizushima 2453* 22 X 1953 (A); Abe-tôge, *S. Okuyama, s.n.* 22 VII 1939 (TNS); Mt. Amagi, *T. Sawada 2219* 2 VIII 1927 (A). **Kyushu.** PREF. FUKUOKA: Mt. Hiko at 1000 m., *J. Ohuchi, s.n.* 24 VI 1951 (TNS). PREF. KUMAMOTO: Mt. Ichifusa, *T. Suzuki, s.n.* 14 VII 1957 (TNS); same locality, *Z. Tashiro, s.n.* 29 VIII 1908 (TNS). PREF. MIYAZAKI: Shiiba-mura, Higashiusuki-gun, *D. Shimizu 116280* (TNS). PREF.

NAGASAKI (or Pref. Fukuoka ?): Mt. Hikosan, *Maximowicz, s.n.* 1863 (BM, two sheets, K, P, US). **Shikoku.** PREF. TOKUSHIMA: Mt. Tsurugi, *K. Abe, s.n.* 19 VIII 1930 (TNS); same locality, *K. Abe, s.n.* 25 VII 1947 (TNS); same locality, *J. Nikai, s.n.* 13 VIII 1904 (TNS); same locality, no collector, VIII 1909 (E).

Cultivated. **England.** SUSSEX: Borde Hill, *A. B. Jackson, s.n.* 19 VI 1939 (BM); Horsham, Hortus E. G. Loder, Leonardslee, *E. G. Loder, s.n.* 23 VI 1915 (K); same locality, *E. G. Loder, s.n.* 12 VI 1917 (K). SURREY: Royal Botanic Gardens, Kew, Acc. # 130–98–13001, *W. T. Gillis, s.n.* VI 1973 (AAH). **United States.** CONNECTICUT: The Conde Nast Garden, Greenwich, no collector, 21 VI 1938 (AAH, two sheets). MASSACHUSETTS: Arnold Arboretum, plant from Royal Botanic Gardens, Kew, 1938, Acc. # 615–38, *E. J. Palmer, s.n.* 21 VI 1938 (AAH). PENNSYLVANIA: Morris Arboretum, plant from F. D. Moore & Sons, Acc. # 62–96, *J. M. Fogg, Jr., s.n.* 11 VII 1962 (MOAR).

Maximowicz based *Stewartia serrata* on a collection from Mt. Hikosan on the island of Kyushu, Japan, and the holotype is presumably in Maximowicz's herbarium at Leningrad. Included in the collections examined in the present study are four sheets of *S. serrata*, one each at K and US, and two at BM, which were collected at the type locality by Maximowicz in 1863. These sheets are undoubtedly authentic material, presumably isotypes, but such designation must await examination of the Leningrad collections.

Variable in foliage indumentum, *Stewartia serrata* is otherwise relatively invariable in other foliage and floral characters. Nakai, studying the Japanese and Korean representatives of the genus, segregated *S. epitricha* from *S. serrata* on the basis of a finely pilose indumentum on the surfaces of the leaves and along the veins. Furthermore, he recognized as var. *sericea* of *S. serrata* those plants with sericeous pubescence along the veins on the lower surfaces of the leaves. Leaves of *S. serrata* are, however, generally glabrescent; the young leaves are usually characterized by a sericeous-pilose indumentum, and the species and variety recognized by Nakai appear to be artificial segregates based on differences that are probably environmentally induced and within the genetic potentiality of *S. serrata*.

Stewartia serrata is most closely related to the Chinese *S. rostrata*, from which it differs in its smooth, exfoliating bark, its completely glabrous gynoecium and capsules, and its 5-loculate ovary with two ovules and/or seeds per locule. From *S. monadelpha*, the only other Japanese species with which it might be confused, *S. serrata* differs in its small winter buds with two overlapping scales, its larger flowers with the subtending floral bracts and sepals similar in size and shape, and in its subglobose, entirely glabrous gynoecium and capsules.

4. **Stewartia rostrata** Spongberg, sp. nov. FIGURE 2, a–e.

Species distincta, *Stewartiae serratae*, *S. monadelphae*, et *S. sinensi* affinis, sed ex his speciebus facile distinguenda periderma non exfoliata, et cortice arcto cum fissuris approximatis et non profundis. Differt a *S. serrata* pubescentia sericea basi ovario capsulaque et quattuor ovulis vel seminibus in loculis omnibus; a *S. monadelpha* et *S. sinense* ovario subgloboso vel globoso sericeo non nisi in basi vera et capsula globosa vel subglobosa basi sericea apice valde rostrata.

Shrubs or small trees with ascending branches to ca. 10 m., usually with several branches from the base; periderm on young growth non-exfoliating, the bark slate-gray, tight with close shallow fissures; winter buds compressed, ca. 5 mm. long with 2 or 3 finely pubescent imbricated scales. Petioles (2–)4–6(–9) mm. long, shallowly grooved on the adaxial surface; leaf blades ovate to elliptic, (2–)6–10.5 cm. long, (1.2–)2.5–4.5 cm. wide,

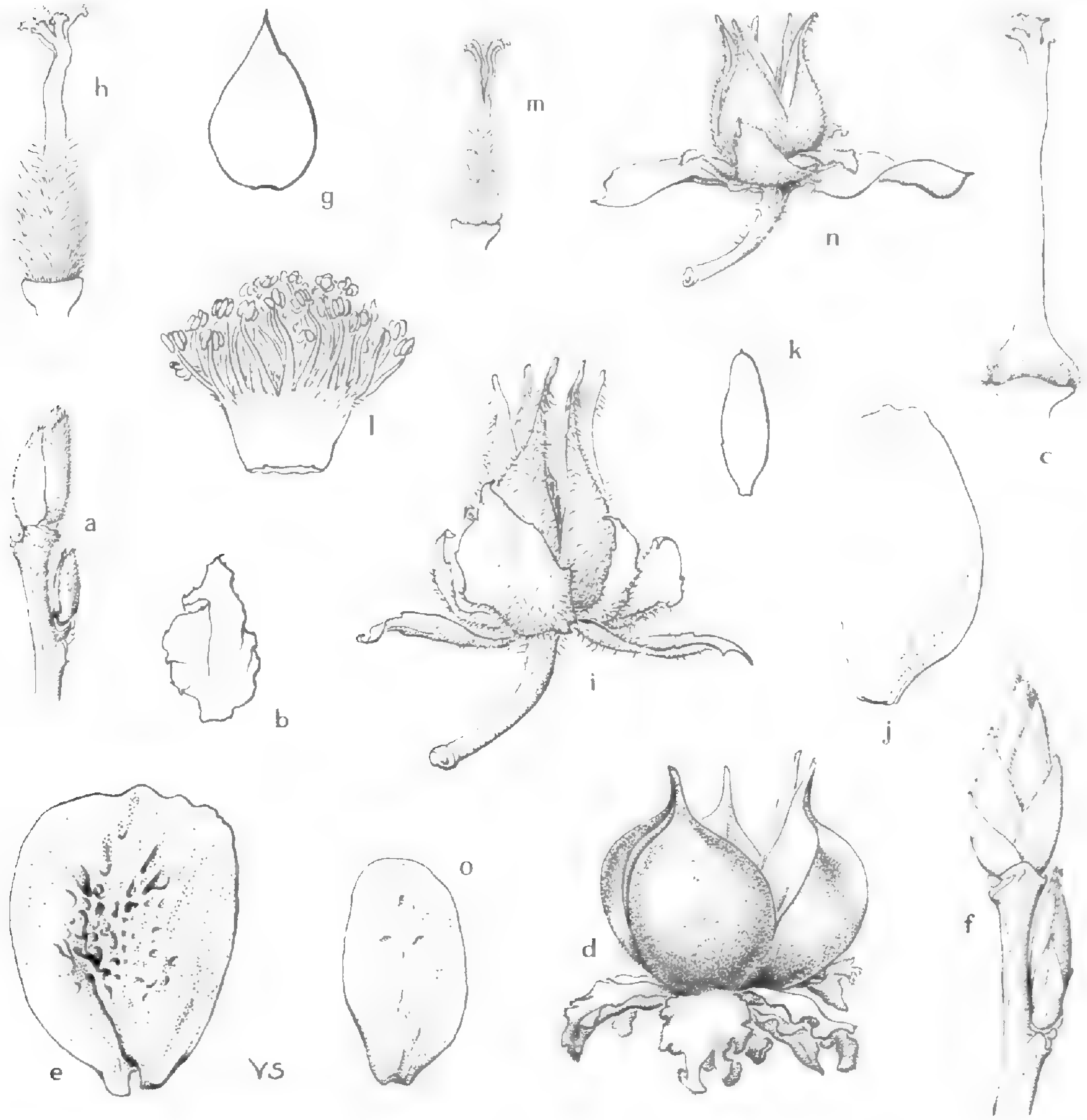


FIGURE 2. **Stewartia.** a–e, *S. rostrata*: a, dormant winter buds, × 2; b, floral bract, × 2; c, gynoecium with pubescence only at base of ovary, × 2; d, dehisced capsule with persistent floral bracts and calyx, × 1 1/2; e, seed, × 4. f–j, *S. sinensis*: f, dormant winter buds, × 2; g, floral bract, × 2; h, gynoecium, × 2; i, dehisced capsule with persistent floral bracts and calyx, × 1 1/2; j, seed, × 4. k–o, *S. monadelpha*: k, floral bract, × 2; l, androecium, × 2; m, gynoecium, × 2; n, capsule with persistent floral bracts and calyx, × 1 1/2; o, seed, × 4.

with acuminate apices, rounded bases, and serrate margins, the teeth with apiculate tips; lower surfaces of the blades with scattered long hairs, particularly on the elevated midvein, and with tufts of short hairs in the axils of the midvein and lateral veins. Flowers axillary, pedicels 5–7 mm. long; bracts subtending the calyx foliaceous, subopposite, (12–) 15–20 mm. long, (6–)8–12 mm. wide, ovate with a acuminate apices and irregularly undulating margins, persistent. Sepals 5, connate at the base, the free lobes similar to the bracts in outline, ovate to obovate or orbicular with acute or sometimes rounded apices and irregularly undulating margins, 12–18 mm. long, 7–10 mm. wide; sepals persistent, the calyx becoming lignified at the base, in fruit spreading or strongly reflexed beneath the capsule, often clasping the twig below. Petals 5, connate at the base, 2.8–3.8 cm. long, 2–3 cm. wide, obovate to suborbicular with erose margins and cuneate bases, the abaxial surfaces finely sericeous. Stamens numerous, the filaments up to 25 mm. long, connate at the base into a tube 6–9 mm. long, the tube adnate to the corolla; free portions of the filaments finely pubescent at base; anthers yellow. Ovary subglobose or globose, 5- or 6-angled, densely sericeous at the base, glabrous above, ca. 3 mm. long at anthesis, tapering into a glabrous style; styles 16–18 mm. long, terminating in 5 or 6 marginally ciliate stigmatic arms, each arm ca. 1.5 mm. long. Capsules subglobose or globose with a rostrate apex, strongly 5- or 6-angled, the body of the capsule 12–16 mm. long, 14–16 mm. broad with the persistent portion of the style projecting 5–8(–10) mm. above; capsule finely and obscurely pubescent at the base, brownish with a purplish red apex at maturity, becoming dark, blackish brown with age, dehiscing apically into 5 or 6 locules, the locule walls 7–9 mm. wide. Seeds 4 per locule, planoconvex, 8–10 mm. long, 6–7 mm. wide, obovate in outline, notched at the base and narrowly winged, the wing ca. 2 mm. wide at the apex; raised central portion finely rugose, yellowish brown, becoming reddish- or chestnut-brown.

HOLOTYPE: rare tree in thicket near stream, Niushiung-an, Mo-fou-shan, Hunan Province, China, 10 September 1947, *Y. K. Hsiung 05819* (A).

DISTRIBUTION: Moderate elevations in the mountains of Chekiang, eastern Hunan, and Kiangsi Provinces, China; cultivated in western gardens.

Representative specimens. **China.** CHEKIANG PROVINCE: Tien Tai Shan, tree 40 ft. along stream side, *C. Y. Chiao, s.n.* 22 VII 1927 (A, E, US); no definite locality, tree at side of stream to 8 m. with brownish green bark, *R. C. Ching 5177* 23 VIII 1924 (A); Tien-moo-shan, shrub to 6 m., bark dim gray, *R. C. Ching 5059* 18 VIII 1924 (A); Tihtaishan, at 600 to 1200 m., *R. C. Ching 1533* 5–18 V 1924 (P). KIANGSI PROVINCE: Hushan, Forest Station, *R. C. Ching 4795* (A, K); Lushan Mountains at 700–800 m., *H. H. Chung & S. C. Sun 574* 17 VII 1933 (A); Lushan Mountains, *H. H. Hu 2654* VIII 1934 (A); roadside, Russian Valley, *A. N. Steward 2735* (A, US); Kuling, *E. H. Wilson 1722, in part* 31 VII 1907 (A, two sheets, BM, E, two sheets, GH, US).

Cultivated. **United States.** MASSACHUSETTS: Arnold Arboretum, plant grown from seed received from Lu Shan Arboretum, Kiukiang, China, 1936, Acc. # 769–36, *A. C. Gibson 769* 16 VI 1969 (AAH), *W. Judd, s.n.* 9 IV 1937 (AAH), *E. Murray 314* 7 IV 1965 (AAH, MOAR), *E. J. Palmer, s.n.* 12 VI 1939, 3 X 1940 (AAH). PENNSYLVANIA: Barnes Arboretum, Merion, *J. M. Fogg, Jr., s.n.* 22 VI 1962 (MOAR), *J. M. Fogg, Jr., s.n.* 6 VIII 1962 (MOAR), *J. M. Fogg, Jr., s.n.* 3 VII 1967 (MOAR); Morris Arboretum, Acc. # 57–544, *J. M. Fogg, Jr., s.n.* 11 VII 1962 (MOAR), *J. M. Fogg, Jr., s.n.* 1 IX 1964 (MOAR).

It seems appropriate that the specific epithet of this previously unrecognized species of *Stewartia* emphasize its strongly rostrate capsules that often remain on the branchlets for more than a year after maturation and dehiscence. First collected by E. H. Wilson in Kiangsi Province, China, under his number 1722, specimens of *S. rostrata* became mixed with specimens of *S. sinensis* collected by Wilson under the same number. This collection was cited by Rehder and Wilson when they described *S. sinensis*, and their circumscription included some elements of *S. rostrata*. Additional details of the taxonomic and nomenclatural confusion are discussed under *S. sinensis*.

TABLE 1. **Comparison of characters of three species of Stewartia.**

	S. ROSTRATA	S. SINENSIS	S. SERRATA
CHARACTER			
bark	non-exfoliating, close with shallow fissures	exfoliating, smooth, & mottled	exfoliating, smooth, & mottled
winter buds	ca. 5 mm. long, 2 or 3 imbricated scales	ca. 1 cm. long, 4 or 5 imbricated scales	4–6 mm. long, 2 imbricated scales
ovary shape	subglobose or globose, 5- or 6-angled	cylindrical, faintly 5- or 6-angled	globose, 5-angled
ovary surface	densely sericeous at the very base, glabrous above	densely pilose over the entire surface	completely glabrous
style length	1.6–1.8 cm.	0.6–0.8 cm.	1.7–2.0 cm.
ovule/ seed no. per locule	4	2	2
capsule shape & surface	subglobose, 5- or 6-angled & rostrate, finely pubescent at base	ovoid, 5- or 6-angled & rostrate, finely pilose	subglobose, 5-angled & shortly rostrate, glabrous
seed length, surface	8–10 mm., finely rugose	7–9 mm., finely puncticulate	9–12 mm., finely puncticulate

Stewartia rostrata is readily distinguished from *S. sinensis* and its closest ally, the Japanese *S. serrata*, by a number of characters, several of which are listed in TABLE 1, while some morphological details of *S. rostrata* and *S. sinensis* are illustrated in FIGURE 2.

In the horticultural trade plants of *Stewartia rostrata* may be listed and sold as *S. sinensis*. The one living specimen of *S. rostrata* at the Arnold Arboretum was grown from seed obtained from the Lu-Shan Arboretum in China in 1936, and seeds and propagating material from this large shrub, now about 4 m. tall, have undoubtedly been distributed as *S. sinensis*.

5. **Stewartia sinensis** Rehder & Wilson, Pl. Wilsonianae **2**: 395. 1915. HOLOTYPE: *Wilson 2148* (A!); isotypes (A! E! K, two sheets!). FIGURE 2, f–j.

Stewartia gemmata Chien & Cheng, Contr. Biol. Lab. Sci. Soc. China, Bot. Ser. **6**: 66. 1931. SYNTYPES: *Chien 737*, *Ching 3006* (Herb. Biol. Lab. Sci. Soc. China, Nanking, not seen); ISOSYNTYPES: *Chien 737* (A! K!), *Ching 3006* (A, two sheets! K, two sheets!).

Stewartia monadelpha sensu Bean, Trees & Shrubs Hardy Brit. Isles, ed. 1. **2**: 553. 1914, non Siebold & Zuccarini.

Ascending shrubs with several branches from the base or small trees to ca. 20 m. (?); periderm on young shoots flaking or exfoliating in thin strips, the bark becoming smooth and mottled with alternating reddish-brown and lighter buff-colored areas, exfoliating in thin sheets; winter buds compressed, relatively large, ca. 1 cm. long with 4 or 5 silvery-pubescent imbricated scales. Leaves with petioles 3–10 mm. long, shallowly grooved on the adaxial surface; blades ovate, elliptical, or oblanceolate, 3–10.5 cm. long, 1.4–4.5 cm. wide, with acuminate apices, serrate margins, and rounded or cuneate bases, both surfaces sparsely but finely sericeous, becoming glabrous. Flowers axillary, the pedicels (3–)10–16(–29) mm. long; bracts subtending the calyx often appearing articulated on the base of the calyx, foliaceous, subopposite, ovate with acuminate apices and irregularly serrate margins, (9–)11–19 mm. long, 7–11 mm. wide, persistent. Sepals 5, erect in bud, finely pubescent on the abaxial surface at the base, an outer pair resembling the bracts in outline and size, (9–)11–20 mm. long, 7–11 mm. wide, the 3 inner sepals ovate to lanceolate in outline, 11–20 mm. long, 3–5 mm. wide; sepals persistent, becoming lignified at the base, in fruit spreading slightly, or erect and appressed to the dehisced capsule. Petals 5, connate at the base, obovate to suborbicular with slightly erose margins and cuneate bases, 2.5–3.2 cm. long, 1.5–2.5 mm. wide, the abaxial surface sericeous. Stamens numerous, the filaments up to 20 mm. long, connate at the base into a tube 5 or 6 mm. long, the tube adnate to the base of the corolla, the free portions of the filaments glabrous or with scattered hairs at their bases; anthers yellow. Ovary cylindrical, 6–7 mm. long during anthesis, densely pilose over the entire surface, tapering into a glabrous style; style 6–8 mm. long, terminating in 5 or 6 marginally ciliate stigmatic arms, each arm ca. 2 mm. long.

Capsules grayish brown, finely pubescent, particularly at the rostrate apices, ovoid and 5- or 6-ribbed, 14–19 mm. long, 9–12 mm. broad, the styles deciduous at apex, dehiscing into 5 or 6 locules, the locule walls 3–5 mm. wide. Seeds 2 per locule, 7–9 mm. long, 4 mm. wide, planoconvex, obovate in outline, obtuse at the base with a very narrow wing surrounding the raised central portion, the wing often emarginate at apex, the surface finely puncticulate, grayish brown.

Distribution: Moderate elevations in the mountainous regions of east-central China; infrequently cultivated in western gardens.

Representative specimens. **China.** Anhwei Province: Wangshan, southern Anhwei, *R. C. Ching 3006* 15 VII 1925 (A, two sheets, K, two sheets); same locality, *R. C. Ching 3023* 15 VII 1925 (A, two sheets, E); same locality, *W. C. Cheng 4203* 21 X 1933 (BM, P, US). Chekiang Province: western Tien-mu-shan, *S. S. Chien 737* 11 VIII 1929 (A, K); Tihtaishan at 3,500 ft., *R. C. Ching 1533* 10 V 1924 (A, E, US); near Siachu at 300–1000 m., *R. C. Ching 1644* 24 V 1924 (A, two sheets, US); no locality or date, *R. C. Ching 4584* (A); west Tienmu at 3,000 ft., *H. H. Hu 1643* 22 VI 1927 (A); Tien-tai-shan at 2,400 ft., *Y. L. Keng 1083* 13 VIII 1927 (A); no localities or collectors, Lingnan University Nos. *78228*, *78229*, *78230* (A, three sheets). Hupeh Province: no locality, *A. Henry 6166* 1885–88 (A, BM, GH, US, paratypes); western Hupeh, *E. H. Wilson 2148* VII 1901 (A, two sheets, E, K, two sheets). Kiangsi Province: near Kuling, *W. Y. Chun 4288* 26 X 1922 (A); Chuen Yuen, *Z. S. Chung 81971* 14 VI 1937 (A); Lushan Mountains at 700–800 ft., *H. H. Chung & S. C. Sun 164* 28 VI 1933 (A); same locality, *H. H. Chung & S. C. Sun 578* 19 VII 1933 (A); same locality, *H. H. Hu 2363* VIII 1934 (A); Land's End *A. N. Steward 2687* 31 VIII 1922 (A, E); Huang Ai Sze, *A. N. Steward 4665* 26 VIII 1923 (A, US); Kuling, at 4,000 ft., *E. H. Wilson 1722* 29 VII 1907 (A, paratype); same locality, *E. H. Wilson 1722* 31 VII 1907 (E, GH, US, paratypes, all mixed collections with *S. rostrata*). Szechwan Province: no locality, *A. Henry 7392* 1885–88 (BM, GH, P, paratypes); Mushan [Hsien], *A. Henry 7392a* 1885–88 (A, US, paratypes).

Cultivated: **England.** Devon: Cann House, Crown Hill, *H. W. Grigg, s.n.* (K). Cornwall: garden of G. H. Johnstone, Grampound Road, 12 VII 1934 (K). Surrey: Royal Botanic Gardens, Kew, Acc. # 641–10–64102, *W. T. Gillis, s.n.* VI 1973 (AAH). Without locality: (BM, two sheets). **United States.** District of Columbia: U.S. Natl. Arboretum, Acc. # 912, *P. M. Mazzeo, s.n.* 23 VI 1965 (MOAR). Massachusetts: Arnold Arboretum, plant grown from seed received from Sun Yat Sen Memorial Park, Nanking, China, 1934, Acc. # 531–34–C, *E. Murray 316* 7 IV 1965 (AAH); same Acc. #, *A. C. Gibson 783* 20 VI 1969 (AAH); same locality, no Acc. #, *T. R. Dudley, s.n.* 18 VIII 1960 (AAH).

In the protologue accompanying the description of *Stewartia sinensis*, Rehder and Wilson cite two of Wilson's Chinese collections (and one of seed) from western Hupeh and Kiangsi Provinces, as well as three collections by Augustine Henry from Hupeh and Szechuan Provinces. Wilson's number 2148 is designated as the type. In the herbarium of the Arnold Arboretum, Cambridge, Wilson's number 2148 is represented by two sheets, one of which has, above the label, in Wilson's hand, "Type." This sheet, therefore, is the holotype of the name *Stewartia sinensis*.

Careful examination of the paratypes reveals that two taxa are present. All of the Henry collections (including one flowering and two fruiting collections) correspond with the holotype, but the remaining Wilson collection (number 1722) consists of fruiting material of *Stewartia rostrata* and on some sheets of this collection, foliage of *S. sinensis* as well. It is apparent that Rehder and Wilson inadvertently assumed that the fruiting specimens of *S. rostrata* represented the same taxon as the flowering collections. Moreover, although their description of *S. sinensis* encompasses some aspects of *S. rostrata*, vegetative, floral, and fruit characters evident in the holotype and paratypes indicate differences sufficient for maintaining the two taxa as distinct.

The periderm on young branches of the holotype of *Stewartia sinensis* is a rich reddish-brown color, very smooth and, in places, exfoliating in thin, irregular patches. On young branches of *S. rostrata* the periderm is grayish brown, closely and finely fissured, and tends to exfoliate in long, very thin strips. The terminal and lateral buds of *S. sinensis* are relatively large (ca. 1 cm. long) and consist of 4 or 5 imbricated scales, while those of *S. rostrata* are half as long (ca. 5 mm.) and consist of 2 or rarely 3 imbricated scales. Finally, the ovaries of the flowering specimens of *S. sinensis* are pilose over the entire surface, as are the capsules of the fruiting Henry collections (numbers 7392 and 7392a). The capsules of *S. rostrata* present in Wilson's collection 1722, however, are glabrous except at the very base.

In describing *Stewartia gemmata*, here reduced to synonymy under *S. sinensis*, Chien and Cheng contrasted *S. gemmata* with *S. sinensis*, from which *S. gemmata* was stated to differ in its variable pedicel length, its completely pubescent ovary, its pale-brown, smooth bark, and its distinct winter buds. An examination of type material of *S. sinensis* and comparisons between these collections and the isosyntypes and paratypes of *S. gemmata* indicate that Chien and Cheng inadvertently redescribed plants corresponding to *S. sinensis*. Although Chien and Cheng were apparently aware that two elements were passing under the name *S. sinensis*, they did not know which of the two elements corresponded with the holotype of that species. As a result of this situation, the unnamed taxon is described here as the new species, *S. rostrata*.

Stewartia sinensis and *S. monadelpha* of Japan are very closely related taxa, here treated as distinct species. All the floral parts of *S. sinensis* are larger; in addition, its ovoid floral bracts are subequal to the five calyx lobes. In *S. monadelpha* on the other hand, the oblong floral bracts are longer than the small, ovoid-deltoid calyx lobes. Styles of *S. sinensis* are 6–8 mm. long, and the seeds range in length from 7 to 9 mm., while in *S. monadelpha* the styles are 3–4 mm. and the seeds 5–6 mm. long. Further studies, particularly genetic and breeding investigations, may indicate a relationship between the two species best expressed by treating *S. sinensis* as a subspecies of *S. monadelpha*.

6. **Stewartia monadelpha** Siebold & Zuccarini, Fl. Japonica **1**: 181. *t. 96.* 1841. HOLOTYPE: *H. Bürger*, presumably at LE, but not seen. FIGURES 2, k–o, and 3.

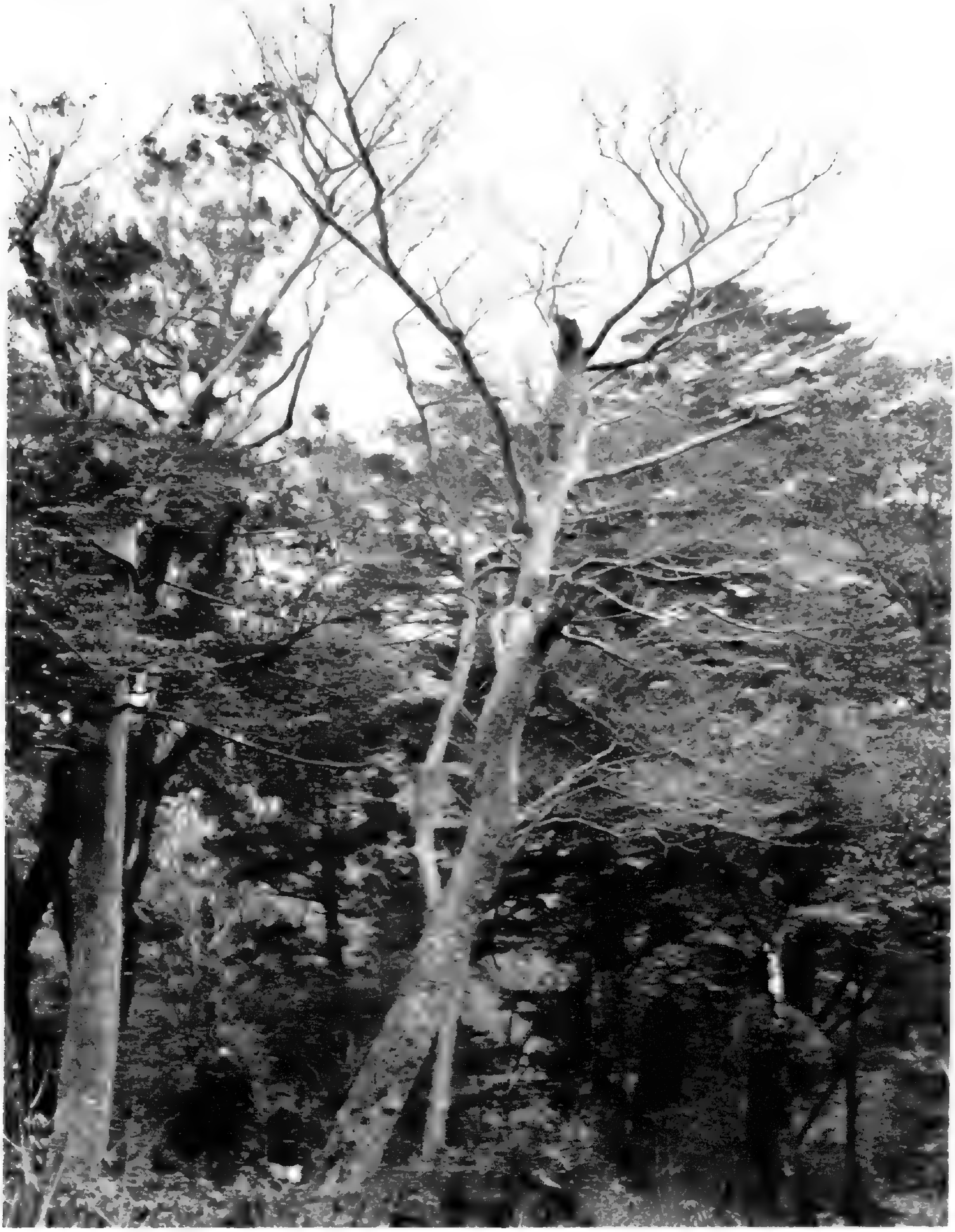


FIGURE 3. **Stewartia monadelpha.** Photograph by E. H. Wilson (negative #4739) of several large trees of *S. monadelpha* at 780 m. in a *Trochodendron-Abies* forest on the Japanese island of Yakushima in February, 1914. The large tree in the center foreground measured 17 m. in height and ca. 2.5 m. d.b.h.; for scale, note the man in white pants standing to the left of this center tree.

Stewartia sericea Nakai, Bull. Natl. Sci. Mus. Tokyo **29:** 92. 1950. HOLOTYPE: *Y. Hayashi, s.n.* (TNS, sheet #80767!).

Stewartia monadelpha Siebold & Zuccarini forma *sericea* (Nakai) Hara, Enum. Spermatophytarum Jap. **3:** 169. 1954.

Shrubs with several branches from the base or trees to 25 m.; periderm on young shoots exfoliating in thin strips or flakes, the young branches pubescent, becoming smooth and reddish brown; bark smooth and mottled with alternating reddish-brown and lighter buff-colored areas, exfoliating in thin sheets; winter buds compressed, ca. 7 mm. long with 3–5(–7) finely pubescent, imbricated scales. Petioles 4–15 mm. long, shallowly grooved on the adaxial surface; leaf blades ovate, elliptical to lanceolate, 4.2–10 cm. long, 1.6–3.4 cm. wide, with finely crenate-serrulate margins ciliate when young and with incurved teeth, acuminate apices, and broadly to narrowly cuneate or attenuate bases; upper and lower surfaces of the blades finely appressed-pubescent, primarily along the veins, often with axillary tufts of hairs in the axils of the midvein and lateral veins beneath. Flowers axillary, very rarely 2 together, the pedicels (5–)7–10(–16) mm. long; the persistent bracts subtending the calyx foliaceous, subopposite, oblong to oblong-ovate, 9–17 mm. long, 4–7 mm. wide, with acuminate to obtuse apices and finely serrulate margins. Sepals 5, connate at the base, the free lobes subequal, ovate to suborbicular, 5–7 mm. long, 3–4 mm. wide, with acute to acuminate apices; calyx persistent, appressed to the lower portion of the maturing capsule, in fruit the lobes erect or slightly reflexed. Petals 5, connate at base, obovate to suborbicular with slightly erose margins and cuneate bases, 11–15 mm. long, 8–12 mm. wide, the abaxial surface sericeous. Stamens numerous, the filaments connate at the base into a tube ca. 4 mm. high, the tube adnate to the base of the corolla; free portions of the filaments finely pubescent, up to 10 mm. long. Ovary conical, 5-angled, 3–5 mm. long at anthesis, densely pilose and tapering into the basally pilose style; style glabrous above, 3–4 mm. long, terminating in 5 stigmatic arms, the arms 1–2 mm. long. Capsules 11–14 mm. long, 7–11 mm. broad, ovoid, reddish brown, finely pubescent, particularly at the rostrate apices, 5- or occasionally 6-ribbed, dehiscing apically into 5 or 6 locules, the valve walls 4–5 mm. wide. Seeds 2 per locule, 5–6 mm. long, 3–4 mm. wide, planoconvex, irregularly obovate in outline, reddish brown, the base often shallowly notched, the raised central portion surrounded by a very narrow wing; surface finely puncticulate. $2n = 30$.

DISTRIBUTION: Known from a few collections from mountainous regions of south-central Honshu, Kyushu, and Shikoku Islands, Japan; cultivated in western gardens.

Representative specimens. **Honshu.** PREF. KANAGAWA: Hakone, *K. Hisauchi, s.n.* 19 X 1950 (TNS); Yokohama (Hakone), *Maximowicz, s.n.* 1862 (BM, GH, P, a mixed collection with *S. serrata*); Hakone, bark orange-brown, smooth and glossy, *M. Mizushima 765* 28 XI 1950 (A); Hakone, *T. Sawada 2175* 21 VI 1927 (A). PREF. SHIZUOKA: Mt. Tochu, Misakubo-cho, Shûchi-gun at 1000 m., *Y. Hayashi, s.n.* 20 X 1949 (TNS); Mt. Ashitaka, *J. Sugimoto, s.n.* 7 VIII 1962

(TNS). **Kyushu.** PREF. KAGOSHIMA: Mt. Kirishima at 100–1000 m., *Z. Tashiro, s.n.* 19 VIII 1917 (A); Island of Yaku or Yakushima, in mountains, *U. Faurie 3801* 1900 (BM); Island of Yaku, Mt. Nagata, *Z. Tashiro, s.n.* 9 VIII 1923 (TNS); Island of Yaku at 300–1500 m., tree with pale brown bark, 15–25 m. tall, 2–4 m. in diameter, *E. H. Wilson 6024* 20 II 1914 (A, three sheets, BM, GH). Without definite locality: Herb. Zuccarinii, *H. Bürger, s.n.* (K); Herb. Zuccarinii, *Siebold, s.n.* 1842 (GH); Herb. Zuccarinii, *Siebold, s.n.* 1843 (K); *M. Blume, s.n.* (P).

Cultivated. **England.** SUSSEX: Nymans Gardens, Handcross, *no collector* 5 VIII 1965 (K, two sheets). **Germany.** Hortus H. A. Hesse, Weener, *O. Luyken, s.n.* 1931 (AAH). **New Zealand.** Botanical Garden, Christchurch, South Island, *W. R. Sykes 124914* 1 XI 1962 (AAH). **United States.** CONNECTICUT: Stamford, lot W of Stamford Hospital, *R. P. Marshall, s.n.* 19 IX 1933 (AAH). DISTRICT OF COLUMBIA: U.S. Natl. Arboretum, *P. Mazzeo, s.n.* 23 VI 1965 (MOAR). MASSACHUSETTS: Arnold Arboretum, plant from seed from F. M. Ellis, Griffin, Ga. Acc. # 22392–A, *E. J. Palmer, s.n.* 5 VII 1938 (AAH, MOAR). NEW YORK: New York Botanical Garden, *H. Teuscher, s.n.* 20 VI 1935 (AAH). PENNSYLVANIA: Barnes Arboretum, *J. M. Fogg, Jr., s.n.* 22 VI 1962 (AAH, two sheets, MOAR, three sheets), 6 VIII 1962 (MOAR), 28 VI 1963 (MOAR), 3 VII 1967 (MOAR); Ellis School Arboretum, Newton Square, *J. M. Fogg, Jr., s.n.* 13 VII 1962 (MOAR, four sheets); Morris Arboretum Acc. # 58–186A, *J. M. Fogg, Jr., s.n.* 26 VI 1962 (A, MOAR), Acc. # 54–965, *J. M. Fogg, Jr., s.n.* 1 IX 1964 (MOAR), Acc. # 57–251A, *J. M. Fogg, Jr., s.n.* 1 IX 1964 (MOAR); Ker Feal, Chester County, *J. M. Fogg, Jr., s.n.* 2 VI 1962 (MOAR), 11 VII 1968 (AAH, MOAR); F. D. Moore & Sons Nurseries, Penn Valley, *J. M. Fogg, Jr., 22331* 7 VII 1965 (MOAR).

Siebold and Zuccarini based *Stewartia monadelpha* on a collection made by Dr. Heinrich Bürger from the mountains on the island of Shikoku, Japan. Presumably, the holotype is among the 800–1000 Japanese types and 850 drawings in the Siebold and Zuccarini collection that, according to A. P. de Candolle, are at Leningrad. Among the specimens I have seen is a Bürger collection of *S. monadelpha* preserved at Kew. This is undoubtedly authentic material, probably an isotype, but such designation cannot be made until the collections at Leningrad are examined. If, however, my supposition is correct, the Bürger collection, which lacks locality data, would be the only sheet of this taxon examined from Shikoku Island.

The relations of *Stewartia monadelpha* are with *S. sinensis* and are discussed under that species.

Stewartia sericea, segregated from *S. monadelpha* by Nakai on the basis of purported differences in pubescence of the foliage and branchlets, differs in no way from the majority of specimens of *S. monadelpha* examined during this study. As a result, *S. sericea* is reduced to the synonymy of *S. monadelpha*.

7. **Stewartia × Henryae** Li, Morris Arb. Bull. **15**: 15. 1964. HOLOTYPE: *H. L. Li, s.n.* 9 June 1963 (MOAR!); isotypes (MOAR, two sheets!).

[*Stewartia pseudocamellia* Maxim. (as *S. koreana* Rehder) × *S. monadelpha* Sieb. & Zucc.]

Small trees to ca. 10 m. with smooth, exfoliating bark; young branches mostly zigzagged and slightly compressed; winter buds compressed, ovoid and pointed at the apex, 6–7 mm. long with 3 or 4 silky, imbricated scales. Petioles 7–14 mm. long, shallowly grooved on the adaxial surface; leaf blades ovate to elliptical, (3.5–)5.8–8 cm. long, (2.5–)3–3.5(–5.5) cm. wide, the margins ciliate and finely rounded-serrulate with very short apiculate teeth; apices acuminate, the bases cuneate; blades finely appressed-pubescent on both surfaces, particularly along the veins of the lower surface. Flowers axillary, pedicels 13–20 mm. long; persistent bracts subtending the calyx, foliaceous, subopposite, oblong to oblong-ovate, 12–13 mm. long, 7 mm. wide, with acute or rarely obtuse apices and finely serrulate margins. Sepals 5, connate at base, the free lobes subequal, suborbicular, 8–9 mm. long, 6–7 mm. wide, with rounded apices, irregularly and finely serrulate margins, silky-sericeous on the abaxial surfaces; sepals persistent, appressed to the lower half of the maturing capsule, the lobes erect or slightly reflexed in fruit, eventually deciduous. Petals 5, connate at the base, obovate to suborbicular, 2.5–2.8 cm. long, 2.1–2.7 cm. wide, with finely erose margins, the abaxial surfaces sericeous. Stamens numerous, the filaments connate at the base into a tube ca. 5 mm. long, the tube adnate to the base of the corolla, free portions of the filaments ca. 10 mm. long, the bases of the filaments finely pubescent. Ovary conical, 5-lined, ca. 9 mm. long at anthesis, pilose, the glabrous style ca. 4 mm. long above, terminating in 5 stigmatic arms, each arm ca. 1 mm. long. Capsules 13–23 mm. long, 10–16 mm. broad, ovoid, reddish brown, finely appressed-pubescent, 5-ribbed, dehiscing apically into 5 locules, the valve walls 5–6 mm. wide. Seeds 2 per locule, 6–7 mm. long, 5–6 mm. wide, planoconvex, irregularly subovate in outline, the base and the winged apex shallowly notched, reddish brown, the raised central portion finely rugose.

DISTRIBUTION: Occurring spontaneously, known from several small trees and seedlings in cultivation at the Henry Foundation for Botanical Research, Gladwyne, Pennsylvania. In addition to the types, it is represented by the following two collections.

United States. PENNSYLVANIA: Henry Foundation, *H. L. Li, s.n.* 12 I 1964 (MOAR, paratype), *S. A. & H. C. Spongberg 73–184* 8 V 1973 (AAH).

Stewartia × *Henryae* differs only slightly from *S. pseudocamellia* (*S. koreana*), and most of the characters by which Li establishes the position of *S.* × *Henryae* between *S. pseudocamellia* and *S. monadelpha* are open to modification. Examination of a series of preserved specimens of both putative parents from the Henry Foundation indicates that in most instances the measurements and character states listed as differing between *S.* × *Henryae* and *S. pseudocamellia*, the putative seed parent, can be revised reducing the differences between the two taxa. Data listed under bract number and branchlet pubescence for *S.* (*koreana*) *pseudocamellia* are incorrect on the basis of my studies. Young branchlets of *S. pseudo-*

camellia may be slightly pilose, at least to the degree exhibited by branchlets of *S.* × *Henryae.* Furthermore, I have not seen flowers of *S. pseudocamellia* subtended by more than two bracts, whereas Li lists the usual numbers as four or five. The only differences found to support the putative hybrid status of *S.* × *Henryae* are the decidedly greater length and shape of the floral bracts, the smaller petal dimension (resulting in a smaller flower diameter), and the presence of two ovules and/or seeds per ovary locule. All three of these characters, as exhibited by flowers of *S.* × *Henryae*, are suggestive of flowers of *S. monadelpha*, but until cytological investigations and controlled hybridization experiments can be conducted, the status of *S.* × *Henryae* must, in my opinion, remain tentative.

8. **Stewartia pseudocamellia** Maximowicz, Bull. Acad. Sci. St.-Pétersb. III. **11**: 429. 1867; Mél. Biol. Acad. Sci. St.-Pétersb. **6**: 201. 1867, "*Stuartia.*" HOLOTYPE: cultivated at Tokyo, presumably at LE, but not seen.

Stewartia grandiflora Carrière, Rev. Hort. **1874**: 399. 1874.
Stuartia grandiflora Siebold ex Briot, Rev. Hort. **1879**: 430. 1879.
Stuartia japonica Hort. ex Nicholson, Kew Handb. Trees & Shrubs **1**: 41. 1894, pro. syn.
Stewartia koreana Nakai ex Rehder, Jour. Arnold Arb. **7**: 242. 1926; emend. Rehder, *Ibid.* **9**: 31. 1928. HOLOTYPE: *E. H. Wilson 9596* (A!); isotypes (A! BM! US!).
Stewartia pseudocamellia var. *koreana* (Nakai ex Rehder) Sealy, Bot. Mag. **165**: *t. 20.* 1948.

Small trees to 20 m., usually with several limbs from a short trunk; periderm on young branches exfoliating in thin strips or flakes, the branchlets dark blackish- or silvery-gray, often zigzagged and compressed; bark smooth and mottled with alternating pinkish, brownish, and grayish areas; winter buds compressed, 7–11 mm. long, with 2–4 finely pubescent imbricated scales. Petioles 4–10(–15) mm. long, shallowly grooved on the adaxial surface; leaf blades broadly ovate to elliptical, (1.5–)3.5–11.5 cm. long, (1.5–)2.5–6(–8) cm. wide, with acute to acuminate apices, shallowly serrate margins, the teeth with short, blackish points, and rounded to cuneate bases. Flowers axillary, rarely terminal, pedicels (0.8–)1–4 cm. long, seemingly increasing in length after anthesis; bracts subtending the calyx subopposite to distinctly alternate, much smaller than and closely appressed to the sepals, broadly reniform to oblong in outline with ciliate margins, sometimes with an acute apex, 4–8 mm. wide, 5–8 mm. long, the margins often overlapping laterally, persistent. Sepals 5, enclosing the flower in bud, thickened and connate at base, the free lobes subequal, suborbicular, 7–13 mm. long, (7–)9–11 mm. wide, with rounded or occasionally acute apices, densely silky sericeous abaxial surfaces, and entire or ciliate margins; calyx persistent, almost totally enclosing the maturing capsule, remaining erect or often reflexed or partially deciduous in fruit. Petals 5, densely silky sericeous on the abaxial surface, connate at the base, suborbicular or scallop-shaped, 3–4.6 cm. long, (1.5–)2–4 cm. wide, the margins wavy and erose. Stamens numerous, the filaments up to 20 mm. long, connate at the base into a tube ca. 5 mm. long, the tube adnate to the base of the corolla, the free filaments glabrous. Ovary conical, basally 5- or 6-lobed and densely pilose, 5–8 mm. long at anthesis, tapering into a glabrous 5- or 6-ribbed style 8–11 mm. long, the style terminating in 5 or 6 marginally ciliate stigmatic arms, the arms 1–2 mm. long. Capsules light to dark reddish brown, finely appressed-pubescent, ovoid with rostrate apices and strongly 5- or 6-angled, variable in size, (13–)15–24 mm. long, (9–)11–18 mm. broad, dehiscing into 5 or 6 locules, the locule walls 6–8 mm. wide. Seeds 4 per locule, 2 often aborted, 5–8 mm. long, (3.5–)4–5 mm. wide, reddish brown or purplish, ovate, obovate, or oblong in outline with an obtuse apex, essentially wingless, the surface of the raised central portion puncticulate or often finely rugose. $2n = 30$.

DISTRIBUTION: Mountainous regions of Northern and Central Honshu, Kyushu, and Shikoku Islands, Japan, and in mountainous areas of the southern Korean peninsula; widely cultivated in western gardens.

Representative specimens. Japan. **Kyushu.** PREF. KAGOSHIMA: Mt. Ônamicke at 1400 m., *T. Tanaka 100183* 4 VIII 1924 (A); Mt. Kirishima at 100–1000 m., *Q. Tashiro, s.n.* 24 VII 1917 (A). Without locality: small tree 4–8 m. high, at 600–1000 m. *E. H. Wilson 6231* 8 III 1914 (A). **Honshu.** PREF. CHIBA: near Usui (?) at 4,000 m., *P. H. Dorsett & W. J. Morse 985* VIII 1929 (A, US). PREF. GIFU: no locality, *K. Shiota 90* 17 VIII 1927 (A), *K. Shiota 7598* 10 VII 1934 (A), *K. Shiota 3860* 3 VII 1928 (A), *K. Shiota 112* 28 VII 1929 (A). PREF. GUMMA: Mt. Myôgi, *N. Ishii, s.n.* 20 VIII 1961 (TNS); same locality, *M. Mizushima 11653* 5 IX 1953 (A); Mt. Akagi-san at 1300 m., *M. Nishida 2687* 10 VIII 1950 (A); Mt. Haruna, *S. Okuyama 9234* 11 VII 1937 (TNS); Mt. Akagi, *T. Wakana, s.n.* 1 VII 1968 (TNS). PREF. HYOGO: Hyôgoken, *K. Uno 24145* 17 VIII 1939 (A). PREF. KANAGAWA: Yokohama, *Maximowicz, s.n.* 1862 (BM). PREF. KYOTO: Sirakawa, *H. Muroi 2762* 25 VI 1955 (A). PREF. MIYAGI: Hanaizumi, *H. Muroi 4700* 15 VIII 1955 (A). PREF. NARA: Ōdaigaharasan, *M. Kume, s.n.* 26, 27 VIII 1943 (A). PREF. NAGANO: Kutsukake-Kose at 100 m., *M. Mizushima 10165* 15 VIII 1951 (A); without locality, *R. Yatabe, s.n.* 19 VII 1880 (A). PREF. NIIGATA: Mt. Yahiko, *S. Togasi 1774* 3 VII 1958 (A, E, TNS, US). PREF. SAITAMA: Nishitama-gun at 1120 m., *M. Mizushima 2573* 14 VIII 1954 (A). PREF. SHIGA: en route from Yakumoga-hara to summit of Bunagatake in Hira Mountains at ca. 1000 m., *K. Seto 5913* 4 VIII 1955 (TNS). PREF. TOCHIGI: Nikko, Urami-ga-taki, *J. Bisset 4210* VIII 1887 (BM, E, two sheets); Nikko, *J. Bisset 4232* VIII 1887 (BM, E); Nikko Mountains, *L. Boehmer, s.n.* (A); Hanaishi, Urami, Nikko, *M. Mizushima 2114* 12 VIII 1952 (A); shores of Lake Chuzenji, in forest, large tree, *M. Mizushima 2294* 5 VII 1952 (A); same locality, *M. Mizushima 2312* 5 VII 1952 (A); Mt. Hikosan, *K. Sakurai, s.n.* 15 VII 1909 (A); Nikko, *H. Sakurai, s.n.* 2 VIII 1909 (E); shores of Lake Chuzenji, tree 40–50 ft. × 2 ft., *C. S. Sargent, s.n.* 3 IX 1892 (A, two sheets); same locality, *S. Suzuki 348* 23 VII 1939 (A); Nikko, Yokohama Nursery Co., Ltd. VIII 1904, 1906 (E, two sheets); without locality, *E. H. Wilson 7677* 21 X 1914 (A, US). PREF. TOYAMA: Arimine, Kaminiikawa-gun, *T. Yamazaki 9781* 4 VIII 1965 (A). PREF. YAMANASHI: Mitsu-tôge, *S. Okuyama 15379* 7, 8 IX 1955 (TNS); same locality, tree 10 m. high, 12 cm. d.b.h., *S. Suzuki 91* 15 VII 1952 (A). **Shikoku.** PREF. EHIME: Futatsuno, Iyo, *K. Watanabe, s.n.* 5 VIII 1888 (GH). Without locality: *U. Faurie 6125* VIII 1904 (A, two sheets, BM, P); *N. Mochizuki, s.n.* V 1912 (E); *N. Mochizuki, s.n.* IX 1910 (E); *T. Takemoto 113* (A); *Tschonoski, s.n.* 1864 (BM, GH, P, US). **Korea.** PROV. S. KEISHO: Mt. Kirishan, *R. K. Smith 654* 9 VIII 1934 (A, US); same locality, *K. Uno 23356* 7 VIII 1938 (A); same locality, *K. Uno 23421* 7 VIII 1938 (A); tree, 15–40 ft. × 1–3 ft., common in woods, Mt. Kirishan, *E. H. Wilson 9596* 14 XI 1917 (A, two sheets, BM, US). Province uncertain: Mt. Kaya, Kyongsang-Pukdo, *C. In-Cho 1145* 13 VI 1947 (MICH); Mt. Songni, Chung-chong, *C. In-Cho 3371* 27 V 1948 (MICH); Zennan, no collector, 7 VIII 1935 & 17 VII 1936 (TNS, two sheets).

Cultivated. **England.** CORNWALL: Trebah, *Hext, s.n.* IV 1938 (BM). HAMPSHIRE: Exbury, Southampton, Hortus Major Rothschild, *A. B. Jackson, s.n.* 2 VII 1945 (BM). SURREY: Royal Botanic Gardens, Kew, Acc. # 071:42, *W. T. Gillis, s.n.* VI 1973 (AAH); same locality, no collector, 10 VII 1947 (K). SUSSEX: Borde Hill, *A. B. Jackson, s.n.* 15 VI 1940 (BM). **France.** Hortus Vilmorin, *R. L. de Vilmorin, s.n.* 30 VI 1927 (AAH). **Japan.** PREF. TOKYO: gardens in Yedo, *R. Fortune, s.n.* VI 1861 (BM). **New Zealand.** South Island, Botanic Garden, Christchurch, *W. R. Sykes 1069* 29 XI 1962 (AAH). **Scotland.** Edinburgh, Royal Botanic Garden VI 1956 (E). **United States.** DELAWARE: Greenville, Mt. Cuba Botanical Park, *R. C. Bauman 168* 30 IX 1969 (AAH); same locality, *S. L. Kelsey 158* (AAH). DISTRICT OF COLUMBIA: U.S. National Arboretum, *F. G. Meyer & P. Mazzeo, s.n.* 23 VI 1965 (MOAR). MASSACHUSETTS: Arnold Arboretum, Acc. #11440–A & B, plants grown from seed collected by E. H. Wilson in Korea, 1918, *A. C. Gibson 268* 22 VII 1968 (AAH), *M. Holland & N. Payne, s.n.* (AAH, two sheets), *E. J. Palmer, s.n.* 29 VI 1942 (MICH), *A. Rehder, s.n.* 21 IX 1922 (AAH), *A. Rehder, s.n.* 2 XI 1926 (AAH, two sheets), *A. Rehder, s.n.* 22 IX 1927 (AAH, two sheets), *A. Rehder, s.n.* 27 IX 1927 (AAH); Acc. #405–42A, plant from F. W. Schumacher, Jamaica Plain, 1882, *J. M. Fogg, Jr., 22404* 7 X 1965 (MOAR), *S. Kreps, s.n.* 10 VII 1965 (AAH); Northampton, Smith College Botanic Garden, *M. Campbell, s.n.* 1965 (AAH, five sheets). NEW YORK: Glen Cove, Hortus C. A. Dana, 4 VII 1888 (AAH). NORTH CAROLINA: Biltmore, *Biltmore Herb. 5761* 14 VII 1897 (AAH). PENNSYLVANIA: Merion, Barnes Arboretum, *J. M. Fogg, Jr., s.n. 22* VI 1962 (AAH); Morris Arboretum, Acc. # 64–659, *J. M. Fogg, Jr., s.n.* 29 VI 1967 (AAH); Swarthmore, Scott Foundation, *J. M. Fogg, Jr., s.n.* 29 VI 1962 (AAH, two sheets).

The most widely cultivated *Stewartia* in western gardens, *S. pseudocamellia* was described by Maximowicz from specimens collected in Japanese gardens in Tokyo. The type is presumably among Maximowicz's collections at Leningrad, yet specimens at BM, GH, P, and US collected in 1864 by Tschonoski, Maximowicz's Japanese assistant, may constitute part of the type material. In addition, there is an 1862 Maximowicz collection from Yokohama at the British Museum which may also be type material.

Stewartia pseudocamellia is readily distinguished from other deciduous species of the genus by its small broadly reniform to suborbicular floral bracts that are conspicuously shorter than the calyx, the densely sericeous abaxial surfaces of the sepals, and its usually compressed and often zigzagged branchlets. As a distinct taxon, the affinities of *S. pseudocamellia* with other deciduous species are obscure and may rather be with the evergreen species that have been treated as members of the genus *Hartia*.

Rehder based *Stewartia koreana* on fruiting specimens collected by E. H. Wilson in Korea and on plants grown at the Arnold Arboretum from seeds from Wilson's collection. He distinguished the new taxon from *S. pseudocamellia* on the basis of sepal shape and a combination of leaf characters including shape, margin, indument, texture, and autumn coloration. He also stated that branchlets of *S. koreana* tend to be compressed and zigzagged, while in *S. pseudocamellia* they are terete and relatively straight. In 1928, after the plants grown from Wilson's seeds had flowered, he amended the description with details of floral morphology but concluded that flowers of *S. koreana* were not different from those of *S. pseudocamellia* except that the corolla is slightly larger and flatter, resulting in a more showy, open flower in *S. koreana*.

According to Sealy (1948), who reduced *Stewartia koreana* to a variety of *S. pseudocamellia*, the morphological characters stated by Rehder as distinguishing the two taxa "do not exist . . . whilst others break down." Sealy's contention that *S. koreana* was deserving of varietal rank, however, was based on its flatter, saucer-shaped corolla; in addition he observed that in var. *koreana* the leaves are slightly smaller, more oval in outline, and the pedicels are shorter.

Examination of herbarium specimens and plants of both taxa cultivated at the Arnold Arboretum has led me to conclude that there are no reliable morphological distinctions that separate plants of the two taxa. Sealy's observations that the leaves and pedicels of var. *koreana* are slightly smaller than those of var. *pseudocamellia* are in general true, yet the size and length variation in these two characters within his var. *koreana* is as great as that within var. *pseudocamellia*. As a result, *Stewartia koreana* is treated here as conspecific with *S. pseudocamellia*.

Observations that plants from Korea differ from those of *Stewartia pseudocamellia* from Japan in autumn coloration, saucer-shaped flowers, and a prolonged blooming period appear to be correct for Korean plants I know of in cultivation. It should be pointed out, however, that most of the Korean plants in cultivation at the Arnold Arboretum represent plants derived from Wilson's original seed collection and are, as a result, plants of one or perhaps a few clones. If these variations are to be recognized, particularly in the horticultural trade, recognition as a named cultivar would be desirable.

REFERENCES

AIRY-SHAW, H. K. Notes on the genus *Schima* and on the classification of the Theaceae–Camellioideae. Kew Bull. **1936**: 496–500. 1936.

BALDWIN, J. T., JR. A seventeenth century record for *Stewartia*. Rhodora **71**: 434–438. 1969.

———. *Stewartia ovata* on the Coastal Plain of Virginia. Am. Hort. Mag. **49:** 88–90. 1970.

Bentham, G. Notes on Ternstroemiaceae. Jour. Linn. Soc. Bot. **5:** 53–65. 1860.

——— & J. D. Hooker. Ternstroemiaceae. Gen. Pl. **1:** 177–189. 1862.

Candolle, A. P. de. Ternstroemiaceae and Camellieae. Prodr. **1:** 523–530. 1824.

Catesby, M. The natural history of Carolina, Florida, and the Bahama Islands. Vol. 2, Appendix. *pls. 1–20.* London. 1747.

Cheng, W. C. Notes on ligneous plants of China. Contr. Biol. Lab. Sci. Soc. China Bot. Ser. **9:** 189–205. 1934.

Choisy, J. D. Mémoire sur les familles des Ternstroemiacées et Camelliacées. Mém. Soc. Phys. Hist. Nat. Genève **14:** 115–184. *pls. 1–3.* 1855.

Chun, W. Y. Additions to the flora of Kwangtung and south-eastern China (2). Sunyatsenia **2:** 49–87. *pls. 15–20.* 1934.

DeWolf, G. P., Jr. The introduction of our hardy Stewartias. Arnoldia **29:** 41–48. 1969. [The labeling of the illustrations should be corrected as follows: *S. monadelpha* = *S. sinensis*; *S. koreana* = *S. pseudocamellia*; *S. sinensis* = *S. rostrata*.]

Endlicher, S. Ternströmiaceae. Gen. Pl. 1017–1024. 1840; Suppl. **2:** 81. 1842.

Fogg, J. M., Jr. *Stewartia* in the Philadelphia area. Morris Arb. Bull. **15:** 43–48. 1964. [*Fig. 63* is *S. rostrata*, not *S. sinensis*.]

Gray, A. The genera of the plants of the United States. Vol. 2. 229 pp. + *pls. 101–186.* New York. 1849. [*Stewartia*, 97–100, *pls. 138, 139.*]

Grimes, E. J. Some interesting plants of the Virginia Coastal Plain. Rhodora **24:** 148–152. 1922.

Henry, M. G. Stewartias. Natl. Hort. Mag. **17:** 117–121. 1938. [Reprinted, *Ibid.* **34:** 218–221. 1955.]

Keng, H. Comparative morphological studies in Theaceae. Univ. Calif. Publ. Bot. **33:** 269–384. *pls. 1–7.* 1962.

Kobuski, C. E. Studies in the Theaceae, XXI. The species of Theaceae indigenous to the United States. Jour. Arnold Arb. **32:** 123–138. 1951. [Includes distribution maps for *S. ovata* and *S. Malacodendron*.]

———. Footnote, p. 419 *in* C. E. Wood, Jr., 1959.

Linnaeus, C. Decem plantarum genera. Acta Soc. Reg. Sci. Upsal. **2:** 77–84. *pl.* 2. 1746. [Published for the year 1741.]

Melchior, H. Theaceae. Nat. Pflanzenfam. ed. 2. **21:** 109–154. 1925.

Merrill, E. D. New or noteworthy Indo-Chinese plants. Jour. Arnold Arb. **19:** 21–70. 1938.

Mitchell, J. Dissertatio brevis de principiis botanicorum et zoologorum. 46 pp. Nürnberg. 1769. [Original publication: Acta Nat. Cur. Ephemerides **8**(App.): 187–224. 1748.]

Nakai, T. Contributions to the knowledge of flowering plants. Bull. Natl. Sci. Mus. Tokyo **29:** 71–98. 1950.

Prain, D. *Stewartia serrata.* Bot. Mag. **144:** *t. 8771.* 1918; *Stewartia sinensis. Ibid. t. 8778.* 1918.

Rees, A. *Stuartia.* Cyclopedia Universal Dict. Arts, Sci. Lit. Vol. 34. 1816.

Santamour, F. S., Jr. Cytological studies in the Theaceae. Morris Arb. Bull. **14:** 51–53. 1963. [Reports $2n = 30$ for *S. ovata*, *S. Malacodendron*, *S. serrata*, *S. pseudocamellia*, *S. monadelpha*, and *S. sinensis*.]

Schenk, A. Palaeophytologie, Cistiflorae. In: K. A. Zittel, Handb. Palaeontol. Abth. II. **6:** 515–518. 1890.

SEALY, J. R. A revision of the genus *Camellia*. viii + 239 pp. *frontisp*. London. 1958.

SZYSZYLOWICZ, I. VON. Theaceae. Nat. Pflanzenfam. III. **6:** 175–192. 1893.

WOOD, C. E., JR. Some cultivated relatives of the *Camellia*. Arnoldia **17:** 1–12. 1957.

———. The genera of Theaceae of the southeastern United States. Jour. Arnold Arb. **40:** 413–419. 1959.

WU, Y. C. Beiträge zur Kenntnis der Flora Süd-Chinas. Bot. Jahrb. **71:** 169–199. 1940.

ARNOLD ARBORETUM
HARVARD UNIVERSITY
CAMBRIDGE, MASSACHUSETTS 02138

ADDENDUM

Since this paper was sent to the printers, an additional name, *Stewartia rubiginosa* Chang, has been located in the literature (p. 23, *fig. 6*, *in*: H. T. CHANG, Notulae Plantarum Austro-Sinicarum. Zhongshan Daxue Xuebao. Ziran Kexue. [Bull. Sunyatsen Univ., Nat. Sci.] **2:** 19–48. 1959). *Stewartia rubiginosa* was allied to *S. gemmata* (= *S. sinensis*) by Chang. but judging from the Latin description it is perhaps closer to *S. pseudocamellia*. This new species is a deciduous tree to ca. 15 m. with smooth. reddish-brown bark and short-petiolate, elliptic-ovate leaves 9–13 cm. long, 5–6.5 cm. wide. The flowers are subtended by two reniform bracts about half as long as the sepals. The ovaries are hirsute, and the corollas are comprised of large petals, 3.5–4 cm. long. Capsules are unknown. The type, *H. Fung & P. Tsang 10722*, was collected in Kwangtung Province, China, at Yingtak on Mt. Wat-shui-shan; it is presumably in the herbarium of Sunyatsen University. I have neither seen any specimens that could be referred to *S. rubiginosa*, nor have I seen any reference to this species except in the obscure original publication. If duplicates of the type collection were at one time distributed to western herbaria, Dr. S. Y. Hu of the Arnold Arboretum (whom I thank for translating the Chinese) suggests that the collection might appear under a Lingnan University number. S.A.S.

STUDIES OF PACIFIC ISLAND PLANTS, XXVIII. THE GUTTIFERAE OF THE FIJIAN REGION [1]

ALBERT C. SMITH and STEVEN P. DARWIN

THE MOST COMPREHENSIVE REVIEWS of the large and complex family Guttiferae (Clusiaceae) have been those of Vesque (1889, 1893) and Engler (1925), but the family remains taxonomically difficult in many parts of its pantropical range. With the primary aim of clarifying the taxonomy and nomenclature of the Fijian components, we have reviewed much of the herbarium material available from the Fijian Region, the area extending from the Santa Cruz Islands and the New Hebrides to Tonga and Samoa. Only three genera are indigenous in this area: *Calophyllum*, with nine species, *Mammea*, with two species, and *Garcinia*, with five species. Of the 16 species here treated, four are described as new. Generic classifications in the Guttiferae are still unsatisfactory, Vesque having followed Planchon & Triana (1860–62) in utilizing certain anatomical characters that are of questionable taxonomic utility. For instance, it is not feasible readily to determine whether the cotyledons are large and the radicle minute, as in *Calophyllum*, or whether the cotyledons are small and the bulk of the seed composed of a tigellus, as indicated for *Garcinia* by Vesque and Engler but questioned by Kostermans (1956). The genera of our area are readily recognized by the gross characters used in the key below, although such a key may not reflect the entire composition of the genera.

We express our appreciation to the administrators of the following institutions who have made their herbarium collections available to us: Arnold Arboretum of Harvard University (A); Bernice P. Bishop Museum (BISH); British Museum (Natural History) (BM); Gray Herbarium of Harvard University (GH); Royal Botanic Gardens, Kew (K); Department of Botany, University of Massachusetts (MASS); New York Botanical Garden (NY); Muséum National d'Histoire Naturelle, Paris (P); Departments of Agriculture and Forestry, Suva, Fiji (SUVA); University of California, Berkeley (UC); and U. S. National Herbarium (US).

KEY TO GENERA INDIGENOUS IN THE FIJIAN REGION

Plants polygamo-dioecious or with consistently hermaphrodite flowers; stamens free or essentially so, with filiform filaments; ovary unilocular or (in our

---

[1] This paper is based on research partially supported by a grant from the National Science Foundation. No. XXV of this series was published in Jour. Arnold Arb. **54**: 1–41, 228–292. 1973; no. XXVI in Am. Jour. Bot. **60**: 479–490. 1973; and no. XXVII in Am. Jour. Bot. **61**: 109–128. 1974. Dr. B. C. Stone has kindly permitted us to utilize a preliminary draft of a study of Guttiferae that he undertook some years ago, and we have also profited from discussions with Dr. P. F. Stevens bearing on his study of *Calophyllum* in Papuasia. The taxonomic and nomenclatural conclusions here presented, however, are those of the present authors.

species of *Mammea*) 4-locular and soon becoming unilocular by abortion; fruits with a single seed; leaf-blades with regular venation composed of closely parallel secondary and tertiary nerves.

Leaf-blades with veinlets not forming a conspicuous reticulum, the ultimate areoles not conspicuous nor with a central gland; inflorescences appearing racemose (or reduced and more obviously cymose), the flowers hermaphrodite; calyx composed of 4 decussate sepals; style obvious. .... 1. *Calophyllum.*

Leaf-blades with veinlets forming a conspicuous reticulum, the ultimate areoles depressed in dried leaves and with a raised gland in the center; inflorescences fasciculate, the flowers ♂ or ☿ on different trees; calyx composed of 2 sepals completely fused in bud but separating at anthesis; style short or essentially none. .... 2. *Mammea.*

Plants dioecious; androecium diverse, the stamens aggregated into one or more phalanges; ovary with 2 or more developing ovules and fruits with 2 or more seeds; leaf-blades often with comparatively spaced secondary nerves, or the secondaries, if crowded, not regularly paralleled by conspicuous tertiaries; inflorescences (in our species) cymose or fasciculate or glomerulate, the flowers with 4–8 decussate perianth-segments. .... 3. *Garcinia.*

1. **Calophyllum** L. Sp. Pl. 513. 1753; Seem. Fl. Vit. 11. 1865.

The sections of *Calophyllum* recognized by Vesque (1889, 1893), Lauterbach (1922), and Engler (1925) seem artificial and scarcely useful, since inter-relationships among species are probably too complex to permit meaningful infra-generic classification at our present state of knowledge. It seems possible that in the western Pacific a single highly vagile strand species, *C. inophyllum* L., has locally given rise to many inland derivatives. These local forms are often superficially similar in different regions (e.g., in Melanesia, Papuasia, Malesia, etc.), but one may doubt that they are genetically closely related among themselves. For instance, the Solomon Island specimens that have been identified as *C. vitiense* and *C. cerasiferum* are now considered to represent distinct taxa (P. F. Stevens, personal communication). Among species of the Fijian Region, it seems likely that *C. inophyllum* and perhaps *C. samoense* have fruits with a specific gravity that permits them to be successfully dispersed by ocean currents. Other species would appear to have heavier fruits in proportion to their size, and the transport of such fruits over significant water barriers is questionable.

The species of our region are trees, sometimes among the larger of the forests and sometimes locally abundant, with pale yellow or white latex. Vegetative and inflorescence parts are characteristically glabrous, but the terminal buds are usually closely and evanescently puberulent (FIGURE 4); the indument is obvious and subpersistent in only one of our species (FIGURE 1). The branchlets are subquadrangular or slightly flattened in the distal internodes, soon becoming terete, and brownish to gray in color. The opposite leaves have distinct petioles that broaden into often thick-textured and glossy leaf-blades, these drying dark green to olive-brown and usually paler beneath, with very close, parallel, spreading secondary nerves that terminate in the thickened and usually narrowly revolute margin. The inflorescences are solitary, axillary, pseudo-racemose but sometimes reduced and obviously cymose, few- to many-flowered, and with a short peduncle and a rachis that are bluntly angular and soon subterete. The flower-subtending bracts are small and caducous in very young bud, leaving transversely narrow scars on inconspicuous swellings. The flowers are pedicellate, opposite or subopposite, and hermaphrodite, with 4 papyraceous decussate sepals with numerous and obvious parallel nerves (FIGURES 7, 14). The petals in some of our species are lacking, in others 4 and decussate (FIGURES 8, 15), and in still others more numerous and imbricate; when present they resemble the sepals in texture and venation or may be somewhat more membranous. The stamens (FIGURES 12, 21) are numerous, 2–several-seriate, essentially free but with slender, filiform filaments that are subcoherent toward the base; the anthers are basifixed, oblong, and rounded at both ends, dehiscing by lateral clefts. The ovary (FIGURES 8, 12, 15) is essentially globose, unilocular, with a single, erect, anatropous ovule; the style is terete, often filiform but sometimes comparatively carnose, with a peltate or shallowly infundibular stigma. The fruit (FIGURE 2) is an indehiscent drupe, subglobose to ellipsoid, usually rounded at base and apex, sometimes with subpersistent perianth-segments and stamens at base, and often surmounted by the base of the subpersistent style. The exocarp is thin, drying to a somewhat brittle texture; the mesocarp is sometimes fibrous and compact (FIGURES 3, 20) and not much altered in drying, but sometimes spongy and greatly shrinking in drying (FIGURES 10, 13), leaving air-spaces between the exocarp and endocarp; the endocarp is bony or crustaceous and is usually very durable. The single seed is erect, the testa being 2-layered and variable. The inner layer remains thin and fragile, but the outer integument develops into a spongy layer closely adherent to the endocarp. In occasional sterile fruits this spongy layer fills the cavity except for a small central opening (FIGURE 11), but normally it is compressed by the developing cotyledons (FIGURES 10, 13, 19), remaining conspicuous in mature fruits, among our species, only in *Calophyllum inophyllum* (FIGURE 6).

The above characters being more or less generic in nature, they are not repeated in the following descriptions unless especially significant. Although *Calophyllum* is a notoriously difficult genus in which to express taxonomic distinctions, we find that the species of the Fijian Region are reasonably well characterized. Flower size and the number (or absence) of petals seem dependable within limits, but most available collections have been prepared in fruiting condition. Usable fruiting characters refer to size and color, the thickness and texture of the mature mesocarp and endocarp, and the nature of the outer integument of the seed at maturity. Vegetative characters, although variable, seem useful in respect to the robustness of branchlets and petioles, and in respect to the leaf-blades as to texture, size, proportions, apex, and, within very broad limits, the number of secondary nerves.

In the Fijian Region we now recognize nine species of *Calophyllum*, of which three are here described as new. The circumscriptions of others are altered by study of types and many recent collections; only *C. inophyllum* has a broad distribution outside our area.

KEY TO SPECIES

Petals none; flowers small, 6–10 mm. in diameter at anthesis, the sepals not more than 4 mm. long; stamens 40–60; inflorescences cymose or pseudoracemose, congested, less than 4.5 cm. long in fruit; fruits comparatively small, 9–17 × 9–15 mm. at maturity and apparently white, the mesocarp compactly fibrous and thin, the endocarp thin, 0.2–0.8 mm. thick; slender inland plants, the branchlets 1–2 mm. in diameter toward apex, the petioles not exceeding 15 mm. in length, the leaf-blades rarely exceeding 9 × 3 cm.; Fiji.

Indument of buds, young branchlets, young petioles, and peduncles conspicuous, the hairs copious, spreading, 0.3–0.5 mm. long; pedicels not exceeding 5 mm. long in fruit; stamens 40–45; apparently mature fruits 9–12 mm. in diameter, the endocarp 0.2–0.3 mm. thick. .... 1. *C. leucocarpum.*

Indument of buds and young parts minutely and evanescently sericeous-puberulent; pedicels 4–13 mm. long; stamens about 60; mature fruits 12–17 mm. in diameter, the endocarp 0.4–0.8 mm. thick. .... 2. *C. leptocladum.*

Petals present; flowers larger, at least 10 mm. in diameter at anthesis, the sepals at least 4 mm. long; stamens at least 80; inflorescences appearing racemose and comparatively extended; fruits at maturity usually larger than 17 × 15 mm. and glaucous to purple or black; comparatively robust plants, the branchlets usually more than 2 mm. in diameter toward apex.

Leaves variable in size but usually with petioles 6–35 mm. long and blades 5–30 × 2–11 cm.; pedicels usually 8–42 mm. long; flowers 10–30 mm. in diameter at anthesis, the sepals 4–15 × 4–12 mm., the petals always 4 (in our observation), 5–16 × 3–10 mm.; mature fruits usually 22–50 × 15–40 mm., the pericarp variable, the mesocarp compactly fibrous or spongy, the endocarp 0.4–3.5 mm. thick.

Trees of the strand, rarely occurring inland; mature fruits 32–50 × 27–40 mm., buoyant in sea water, the outer layer of the seed-testa spongy, 1–12 mm. thick, not much compressed by the developing cotyledons; leaf-blades elliptic- to ovate-oblong, 10–23 × 5–11 cm., about twice as long as broad, usually obtuse to rounded at apex, the secondary nerves usually 10–16 per centimeter; flowers 15–30 mm. in diameter at anthesis; a widespread and vagile species. .... 3. *C. inophyllum.*

Trees of inland forests, if occurring at sea-level not typical of the strand; mature fruits not exceeding 40 × 30 mm., not buoyant in sea water (except perhaps in no. 5), the outer layer of the seed-testa compressed by the developing cotyledons and not exceeding 4 mm. in thickness; leaf-blades lanceolate to oblong-elliptic, rarely exceeding 7.5 cm. in width, usually 2.5–4 times as long as broad; flowers 10–23 mm. in diameter at anthesis.

Flowers comparatively large, 20–23 mm. in diameter at anthesis, the sepals 7–15 × 7–12 mm., the petals 9–16 × 7–10 mm.; mature fruits with a fibrous-spongy mesocarp 2–5.5 mm. thick, this often shrinking or collapsing in drying, the endocarp (1.8–) 2–3.5 mm. thick; leaf-blades lanceolate or narrowly elliptic, 3–4 times as long as broad, usually 13–30 × 3–7.5 cm. and acuminate to acute at apex, the secondary nerves usually 11–20 per centimeter; Fiji. . . . . 4. *C. vitiense.*

Flowers smaller, 10–18 mm. in diameter at anthesis, the sepals 4–10.5 × 4–7.5 mm., the petals 5–11 × 3–6.5 mm.; mature fruits with an endocarp 0.4–1.5 mm. thick; leaf-blades often smaller and 2–3 times as long as broad, infrequently exceeding 17 × 7 cm., the secondary nerves 12–30 (or more) per centimeter.

Mature fruits with a fibrous-spongy mesocarp 3.5–6 mm. thick, this often shrinking or collapsing in drying; leaf-blades ovate- to oblong-elliptic, usually 6.5–17 × 2–7 cm., obtuse to short-acuminate at apex; Samoa, Horne Islands, and eastern (Lau) group of Fiji. . . . . 5. *C. samoense.*

Mature fruits with a compactly fibrous mesocarp 1–4 mm. thick; leaf-blades elliptic to lanceolate or narrowly ovate-oblong, usually 5–17 × 2–5.5 cm.

Petioles slender, 1–1.8 mm. in diameter, the leaf-blades obtuse to obtusely cuspidate at apex; flowers 10–16 mm. in diameter at anthesis; mature fruits 17–35 × 13–28 mm., the endocarp 0.4–1 mm. thick; New Hebrides. . . . . 6. *C. neo-ebudicum.*

Petioles comparatively robust, often 3.5 (–5) mm. in diameter, the leaf-blades rounded to obtuse at apex or occasionally obtusely short-cuspidate; flowers 12–18 mm. in diameter at anthesis; mature fruits 25–40 × 20–30 mm., the endocarp 0.5–1.5 mm. thick; Fiji, Tonga, and Niue. 7. *C. amblyphyllum.*

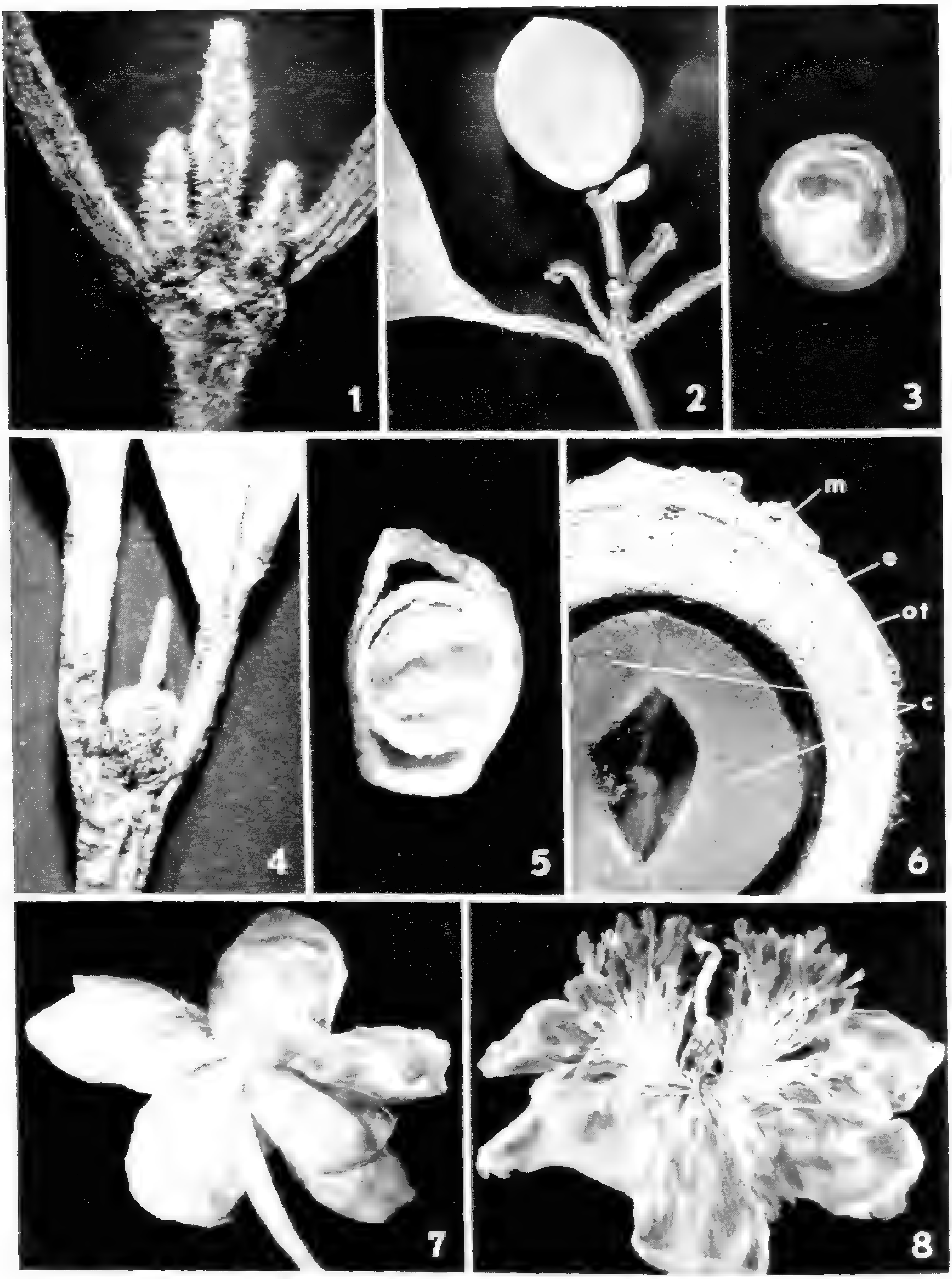
Leaves comparatively small, the petioles 3–16 mm. long, the blades not exceeding 10 × 5 cm. and usually smaller; pedicels not exceeding 13 mm. in length even in fruit; flowers 12–20 mm. in diameter at anthesis, the sepals not much exceeding 9 × 6 mm., the petals often more than 4, sometimes as many as 10, not exceeding 10 × 6 mm.; mature fruits not exceeding 25 mm. in diameter, the pericarp 1.5–4 mm. thick, the mesocarp thin and compactly fibrous, less than 3 mm. thick, the endocarp 1–1.5 mm. thick; Fiji.

Leaf-blades elliptic-oblong to ovate or obovate, 3.5–8 × 1.3–5 cm., usually less than twice as long as broad; young parts and buds essentially glabrous, sometimes obscurely glandular-puberulent; petals often 4 but frequently as many as 10; fruits subglobose, the mesocarp 1–3 mm. thick. . . . . 8. *C. cerasiferum.*

Leaf-blades narrowly elliptic to lanceolate-oblong, 5–10 × 2–3.5 cm., usually about 3 times as long as broad; young parts and buds copiously but minutely tomentellous with glandular hairs, soon glabrate; petals 4–6 (as far as known); fruits ovoid-ellipsoid, obviously longer than broad, the mesocarp negligible, 0.2–0.5 mm. thick. . . . . 9. *C. tenuicrustosum.*

1. **Calophyllum leucocarpum** A. C. Sm. in Jour. Arnold Arb. 31: 314. 1950; J. W. Parham, Pl. Fiji Isl. 134. 1964. FIGURES 1–3.

Slender tree to 4 m. high, the young parts and terminal buds copiously hispidulous with hairs 0.3–0.5 mm. long, the indument subpersistent on



FIGURES 1–3. *Calophyllum leucocarpum*: all from *Smith 6820*. 1, tip of branchlet, showing petiole-bases, terminal bud, and axillary buds, × 5; 2, fruiting inflorescence, × 2; 3, cross section of fruit, × 2. FIGURES 4, 5. *Calophyllum leptocladum*: 4 from *Smith 7538*, 5 from *Smith 7874*. 4, tip of branchlet, showing petioles and terminal bud, × 5; 5, cross section of fruit, × 2. FIGURES 6–8. *Calophyllum inophyllum*: 6 from *Smith 7944*, 7 from *O. & I. Degener 32219*, 8 from *Smith 8101*. 6, cross section of fruit, × 2; 7, proximal surface of flower, × 2; 8, open flower, × 2. m = mesocarp; e = endocarp; ot = outer layer of testa; c = cotyledons.

the young branchlets, young petioles, and peduncles, the branchlets slender, 1–1.5 mm. in diameter toward apex, at length glabrate; petioles slender, canaliculate, (8–) 10–15 mm. long, at length glabrate; leaf-blades coriaceous, oblong-lanceolate, (4–) 5–7.5 cm. long, (1.5–) 2–3 cm. broad, attenuate at base and obviously decurrent on the petiole, obtusely cuspidate at apex, the costa sharply elevated on both sides, somewhat hispidulous beneath when young, the secondary nerves 12–22 per centimeter, slightly impressed above and prominulous beneath; inflorescences congested, once- or twice-branched, 3–5-flowered, about 1 cm. long at anthesis and to 2 cm. long in fruit, glabrous except for the subpersistently pilose peduncle, the pedicels 0.5–3 mm. long at anthesis, to 5 mm. long in fruit; flowers 8–10 mm. in diameter at anthesis, the sepals suborbicular to obovate, obscurely ciliolate, the outer ones about 2.5 × 3.5 mm., the inner ones to 4 mm. long; petals none; stamens 40–45, more or less biseriate, the filaments about 2 mm. long at anthesis, the anthers 0.6–0.8 mm. long; style about 1 mm. long, the stigma peltate; apparently mature fruits subglobose to ellipsoid, 9–12 × 9–10 mm., the mesocarp densely fibrous, 0.6–1.2 mm. thick, the endocarp crustaceous, 0.2–0.3 mm. thick.

TYPE LOCALITY: Seanggangga Plateau, Mathuata Province, Vanua Levu, Fiji; the type is *Smith 6820*.

DISTRIBUTION: Known only from the type collection, occurring in patches of forest in open rolling country at an elevation of 100–200 m., as a slender tree 4 m. high; the sepals and filaments are white, the anthers yellow, and the fruit white. It is surprising that no additional collections of this plant have been obtained, although the area has been visited by other collectors. Nevertheless, the drainage basin of the Ndreketi River in Vanua Levu requires further field work; another example of this unexpectedly local endemism is seen in the rubiaceous *Gardenia candida* (Smith, 1974: 120), represented only by its type collection from the same locality.

Fiji. VANUA LEVU: MATHUATA: Seanggangga Plateau, in drainage of Korovuli River, vicinity of Natua, Dec. 4, 1947, *Smith 6820* (A holotype; isotypes at BISH, K, NY, US).

The present species and the following novelty are the only taxa of *Calophyllum* in the Fijian Region to lack petals; additionally they are characterized by their slender habit, small leaves and flowers, comparatively few stamens, and small, white fruits with a thin and fibrous mesocarp and a thin endocarp.

2. **Calophyllum leptocladum** A. C. Sm. & S. Darwin, sp. nov.

FIGURES 4, 5.

Calophyllum neo-ebudicum sensu J. W. Parham, Pl. Fiji Isl. ed. 2. 192. p. p. 1972; non Guillaumin.

Arbor ad 21 m. alta praeter partes juveniles et gemmam terminalem minute et evanescenter sericeo-puberulas ubique glabra, ramulis gracilibus apicem versus 1–2 mm. diametro; petiolis gracilibus leviter canaliculatis 4–13 (–15) mm. longis; foliorum laminis tenui-coriaceis lanceolatis vel oblanceolatis vel anguste oblongo-ellipticis, 3–9 (–11.5) cm. longis, 1–3.2 cm. latis, basi acutis vel attenuatis et in petiolum longe decurrentibus, apice obtuse brevi-cuspidatis, costa supra vadose canaliculata vel subplana subtus peracute elevata, nervis secundariis (16–) 22–36 (–40) per centimetrum utrinque subplanis vel paullo prominulis; inflorescentiis pauciramosis 3–7-floris sub anthesi 1.5–2.5 cm. sub fructu ad 4.5 cm. longis pedunculo sub anthesi ad 6 mm. sub fructu ad 15 mm. longo ut rhachidi gracili; bracteis sub floribus lineari-lanceolatis 1.5–2 mm. longis obscure puberulis glabratis evanescentibus, pedicellis gracilibus sub anthesi 4–9 mm. sub fructu ad 13 mm. longis; floribus sub anthesi 6–8 mm. diametro, sepalis ellipticis vel orbicularibus, exterioribus circiter 3 × 2 mm., interioribus ad 4 mm. longis; petalis nullis; staminibus circiter 60, filamentis sub anthesi circiter 2 mm. longis, antheris ad 1 mm. longis; stylo circiter 1.5 mm. longo, stigmate peltato; fructibus subglobosis vel ellipsoideis 15–17 × 12–15 mm., pericarpio 1–2.5 mm. crasso, mesocarpio dense fibroso 0.5–2 mm. crasso, endocarpio crustaceo 0.4–0.8 mm. crasso.

TYPE LOCALITY: Slopes of Mt. Ndelaitho, Ngau, Fiji; the type is *Smith 7874.*

DISTRIBUTION: Endemic to Fiji and known from several of the high islands at elevations of 150–670 m., occurring in dense forest or in the forest-grassland demarcation zone. It has been recorded as a tree 9–21 m. high, sometimes slender, with a trunk to 50 cm. in diameter; the fruit is noted as pale green, becoming nearly white at maturity. Among the available specimens, flowers have been obtained in December and January and fruits between May and July.

LOCAL NAMES AND USE: The generally recorded name is ***ndamanu***, but Fijian collectors have also noted ***ndamanu ndraulailai*** and ***ndamanu ndilondilo*** on Viti Levu. It is considered a good hardwood timber tree.

Fiji. VITI LEVU: NANDRONGA & NAVOSA: Nausori Highlands, *O. & I. Degener 32165* (BISH, NY). SERUA: Inland from Ngaloa, *Berry 111* (BISH, SUVA). NAMOSI: Nambukavesi Creek, *Fiji Dept. For. 489* (MASS, SUVA). NAITASIRI: Vicinity of upper Navatuvula village, *Fiji Dept. Agr. 15694* (BISH, SUVA); Prince's Road, *Fiji Dept. Agr. 142* (A, SUVA, US). RA: Vicinity of Naivotho village, *Damanu K273* (K, US). OVALAU: Hills west of Lovoni Valley, on ridge south of Mt. Korolevu, ***Smith 7538*** (BISH, GH, K, NY, SUVA, UC, US). NGAU: Slopes of Mt. Ndelaitho, on northern spur, toward Navukailangi, alt. 350–500 m., June 22, 1953, ***Smith 7874*** (US 2190685 holotype; isotypes at BISH, GH, K, NY, UC). VANUA LEVU: THAKAUNDROVE: Mt. Kasi, *Fiji Dept. Agr. 15733* (SUVA, US); vicinity of Valeni, *Fiji Dept. Agr. 15722* (BISH, SUVA); valley of Navonu Creek, ***Howard 104*** (BISH, SUVA, US), *Berry 4* (SUVA). FIJI, without further locality: *G. W. Cottle*, Dec. 1950 (BISH, SUVA).

Unfortunately the only available mature flowers are on the Cottle specimen, without detailed locality, and even those flowers are insect-damaged. Two other specimens, *O. & I. Degener 32165* and *Fiji Dept. For. 489,* bear immature inflorescences. However, these three collections adequately permit an understanding of the floral characters. As the type we have preferred to designate a fruiting collection with numerous duplicates. In our area this new species, without petals, is closely related only to *Calophyllum leucocarpum*, differing primarily in the very different and evanescent indument of its young parts; it also has comparatively obvious pedicels, more numerous stamens, and a larger fruit with a thicker endocarp.

3. **Calophyllum inophyllum** L. Sp. Pl. 513. 1753; A. Gray, Bot. U. S. Expl. Exped. **1**: 218. 1854; Seem. in Bonplandia **9**: 254. 1861, in op. cit. **10**: 296. 1862, Viti, 433. 1862, in Jour. Bot. **2**: 71. 1864, Fl. Vit. 12. 1865; Horne, A Year in Fiji, 258. 1881; Vesque in DC. Monogr. Phan. **8**: 544. 1893; Reinecke in Bot. Jahrb. **25**: 656. 1898; Burkill in Jour. Linn. Soc. Bot. **35**: 27. 1901; Rechinger in Denkschr. Akad. Wiss. Wien **81**: 313. 1910; Guillaumin in Bull. Soc. Bot. France **66**: 268. 1919; Setchell in Carnegie Inst. Wash. Publ. **341**: 68. 1924; Guillaumin in Bull. Soc. Bot. France **74**: 694. 1928, in Jour. Arnold Arb. **12**: 227. 1931; Christophersen in Bishop Mus. Bull. **128**: 147. 1935; Yuncker in op. cit. **178**: 85. 1943, in op. cit. **184**: 52. 1945; J. W. Parham in Agr. Jour. Dept. Agr. Fiji **19**: 98. 1948, in op. cit. **29**: 32. 1959; Yuncker in Bishop Mus. Bull. **220**: 187. 1959; J. W. Parham, Pl. Fiji Isl. 134. *fig. 52*. 1964, ed. 2. 192. *fig. 57*. 1972; Sykes in New Zealand Dept. Sci. Indust. Res. Bull. **200**: 100. 1970; St. John & A. C. Sm. in Pacific Sci. **25**: 326. 1971; B. E. V. Parham in New Zealand Dept. Sci. Indust. Res. Inform. Ser. **85**: 32. 1972. FIGURES 6–8.

Spreading tree to 25 m. high, often with a massive trunk, glabrous throughout except the young parts and terminal buds minutely but copiously brown-puberulent, the branchlets stout, 3–7 mm. in diameter toward apex; petioles stout, flattened above or canaliculate, 12–30 mm. long; leaf-blades thick-coriaceous, elliptic- to ovate-oblong, 10–23 cm. long, 5–11 cm. broad, obtuse to rounded at base and abruptly decurrent on the petiole, obtuse to rounded or emarginate at apex, rarely subacute, the costa conspicuous, slightly or prominently elevated above and sometimes canaliculate, prominent beneath, the secondary nerves (8–) 10–16 per centimeter, prominulous on both surfaces; inflorescences appearing racemose, rarely paniculate with 1 or 2 short lateral branches, 7–27-flowered, 4–13 cm. long or slightly longer in fruit, the peduncle stout, 3–20 mm. long; flower-subtending bracts papyraceous, broadly ovate, 3–4 × 2–3 mm., rounded at apex, minutely glandular-ciliolate, evanescent, leaving conspicuous transversely oblong scars, the pedicels slender, 10–42 mm. long; flowers 15–30 mm. in diameter at anthesis, the sepals elliptic to suborbicular, broadly obtuse or rounded, the outer ones 6–10 × 5–8 mm., the inner ones 9–15 × 7.5–10 mm.; petals 4 (sometimes stated as 3–5 or even 8), elliptic or obovate, 8–14 mm. long, 5–9 mm. broad, rounded and entire, often irregularly involute; stamens usually 150–200, the filaments 4–8 mm. long at anthesis, the anthers 1.3–2 mm. long; style conspicuous, 2.5–5 mm. long, the stigma subpeltate, 0.7–1.5 mm. in diameter; fruits drying coriaceous and rugulose, subglobose to subobovoid, 32–50 × 27–40 mm., obtuse to rounded at base, the pericarp 2–4 mm. thick, the mesocarp fibrous, 1–3 mm. thick and adhering to the endocarp, this bony, 0.5–1.5 mm. thick; testa of seed with a spongy outer layer 1–12 mm. thick and often conspicuous, the cotyledons oily and dark, not completely filling the locule nor conspicuously compressing the spongy outer layer of the testa.

TYPE LOCALITY: Linnaeus based his species on three prior references, and it is probable that the lectotype should be the plant described in his *Flora Zeylanica*, 201. 1747. We refrain from formally proposing this lectotypification because we lack access to the basic materials that require study, and we may have overlooked some pertinent earlier discussion. However, it is evident that the common Old World species so widespread on beaches is correctly placed under this binomial.

DISTRIBUTION: Eastern Africa and India throughout Malesia and into eastern Polynesia; in Hawaii it is probably a Polynesian introduction that is now thoroughly naturalized. In our area it occurs abundantly on beaches, in coastal thickets or sea-level forests, or along streams near the coast. Its occurrence at elevations of more than a few meters (i.e. near Namosi village in Fiji; on Alofi, Horne Islands; on Ofu, Samoa) doubtless reflects deliberate inland introductions of a useful and ornamental plant. *Calophyllum inophyllum* is a striking and often massive tree, to 25 m. or more in height and with a trunk sometimes 1.5 m. in diameter; its fragrant flowers have white or waxy sepals and petals and yellow anthers; its large fruits, fragrant when ripe, then become yellow to purplish or blackish. In our area it may be found in flower and fruit at all seasons.

LOCAL NAMES AND USES: As one of the best known Pacific trees, this species has quite stabilized local names: *ndilo* (Fiji); *fifau* (Rotuma); *tsilo* or *tilo* (Horne Islands); *fetau* (Wallis Islands, Tonga, Niue, Samoa). In Samoa and possibly in Fiji it sometimes passes as *Alexandrian laurel* or *beach mahogany*. The uses of this beautiful tree are legion, and one can scarcely add to Seemann's 1865 discussion in his "Flora Vitiensis." Its wood is prized for canoe-making and boat-knees, for paddles, house-beams, drums, and bowls. Oil expressed from the fragrant fruits is used extensively as a medicinal liniment and to scent coconut oil; and an infusion of the leaves is used for medicinal purposes ranging from eye-washes to cures for chicken pox.

New Hebrides. VANUA LAVA, Banks Group: *Kajewski 431* (A, NY). TANA: Port Resolution, *Kajewski 69* (A, NY). ANEITYUM: Anelgauhat Bay, *Kajewski 783* (A, BISH, K, NY, US).

Fiji. YASAWAS: WAYA: Yalombi, *St. John 18903* (BISH). MAMANUTHAS: MALOLO GROUP: Nggalito Island, *O. & I. Degener 32219* (BISH, NY). VITI LEVU: MBA: Lautoka, *Greenwood 351* (K). NANDRONGA & NAVOSA: Vatukarasa, *Fiji Dept. Agr. 9287* (*McKee 2857*) (BISH, SUVA). SERUA: Namboutini, *Fiji Dept. For. 969* (SUVA); Korovisilou, *Fiji Dept. For. 281* (*Damanu 9*) (K, SUVA); Vunimanggo, *Fiji Dept. For. 914* (SUVA); Ndeumba, *Fiji Dept. Agr. 12461* (SUVA); Navua, *Livingston*, in 1945 (US), *Fiji Dept. For. 989* (SUVA). NAMOSI: Waindina valley near Namosi village, *Gillespie 2811* (A, BISH, UC). RA: Waindawa, near Vaileka, *Degener 15420* (A, BISH, K, NY, UC, US); Ellington, *Parks 20853* (BISH, UC). TAILEVU: *Fiji Dept. Agr. 13591* (SUVA); Matavatathou, *Fiji Dept. Agr. 9231* (SUVA); Nausori, *Fiji Dept. Agr. 141* (A, SUVA). NAITASIRI: Vunindawa, *Fiji Dept. Agr. 10011* (SUVA). REWA: Suva, *Meebold 16426* (SUVA). KANDAVU: Namalata Isthmus region, *Smith 177* (BISH, GH, K, NY, UC, US). OVALAU: *Graeffe* (NY); Thawathi, *Smith 8101* (BISH, GH, K, NY, SUVA, UC, US); Levuka, *Degener & Ordonez 13786* (A, NY). KORO: Nambosovi, *Fiji Dept. Agr. 1033* (SUVA). NAIRAI: *Milne*, Nov. 1855 (K). NGAU: Shore of Herald Bay, near Sawaieke, *Smith 7944* (BISH, GH, K, NY, SUVA, UC, US). VANUA LEVU: MATHUATA: Nakuthi Island, *Fiji Dept. Agr. 15279* (BISH, SUVA). THAKAUNDROVE: Ndawara, lower Yanawai River, *Fiji Dept. Agr. 15737* (SUVA); west of Valethi, *Bierhorst F114* (MASS); east of Savusavu, *Bierhorst F187* (MASS); Korotasere, *Fiji Dept. Agr.*, Nov. 26, 1949 (SUVA). "TAVEUNI and LAKEMBA": *Seemann 48* (BM, GH, K). TAVEUNI: Nggeleni Road, *Fiji Dept. Agr. 15873* (SUVA); Waiyevo, *Gillespie 4633* (BISH). YATHATA: Navakathuru, *Fiji Dept. Agr. 15557* (SUVA), *16197* (MASS, SUVA). VANUA MBALAVU: Lomaloma, *Fiji Dept. Agr. 10206* (SUVA). NAVUTU-I-LOMA: *Bryan 463* (A, UC, US). FIJI, without further locality: *U. S. Expl. Exped.* (GH, NY), *Storck 873* (BM), *Howard 31* (SUVA).

Horne Islands. FUTUNA: *Burrows 14* (BISH). ALOFI: Mt. Vaisei, *Yen X58* (BISH).

Wallis Islands. UVEA: *Graeffe 33* (BM), *Burrows W16* (BISH).

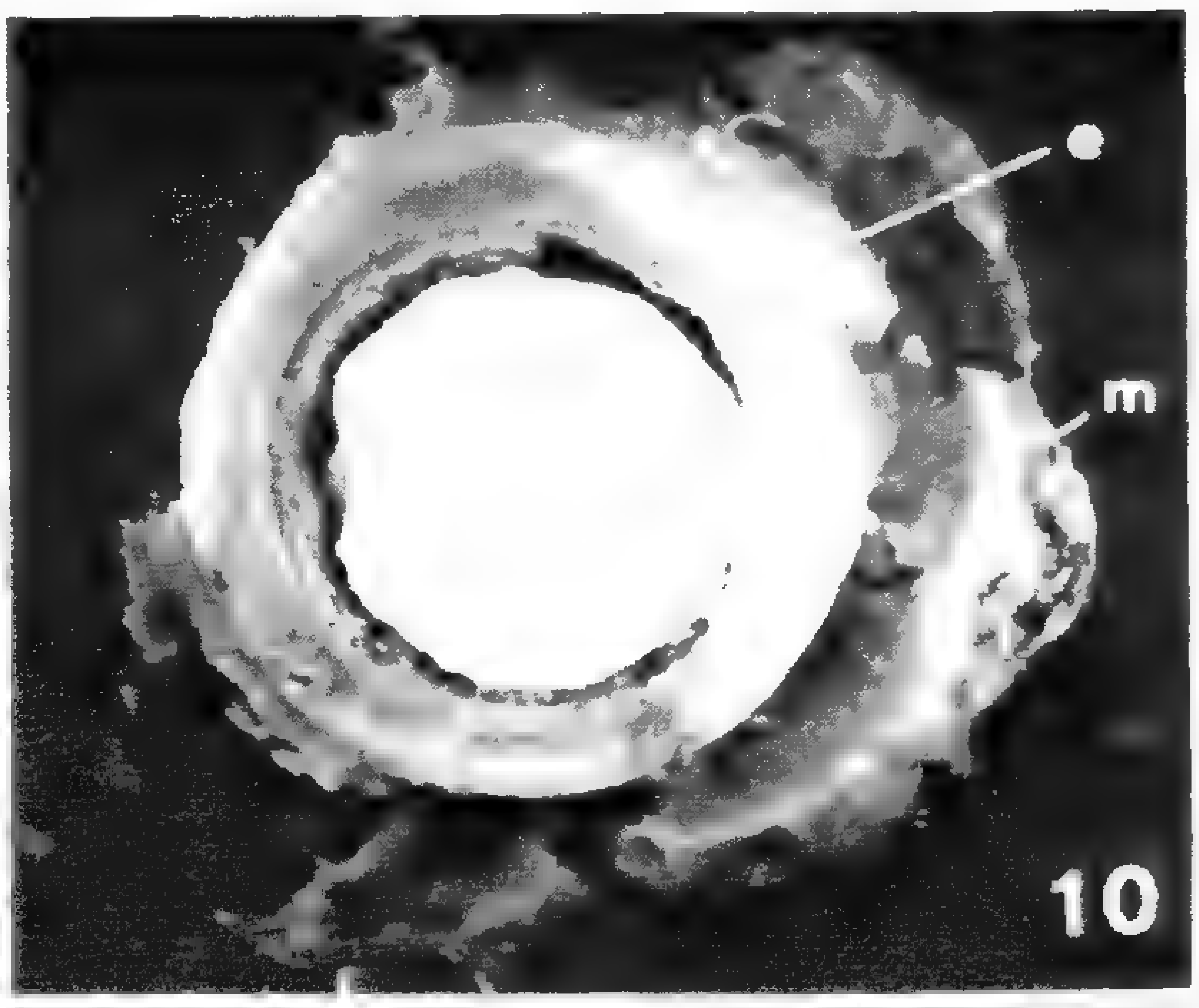
Tonga. LIFUKA: Toward southern end of island, *Yuncker 15792* (BISH, BM, US). TONGATAPU: Ha'avakatolo, *Setchell & Parks 15595* (UC); Sopo, *Yuncker 15024* (BISH, BM, GH, US); Nuku'alofa, *Soakai 476* (BISH, K); Hihifo, *Setchell & Parks 15515* (UC); Kolonga Point, *Setchell & Parks 15387* (UC). 'EUA: *Moore 427* (US); Ohonua, *Parks 16383* (BISH, UC), *Yuncker 15638* (BISH, BM, GH, US). TONGA, without further locality: *Cook's 3rd Voyage* (BM), *McKern 37* (BISH).

Niue. Near Alofi, *Yuncker 9738* (A, BISH, UC), *10059* (BISH, UC, US), *Sykes 353* (BISH).

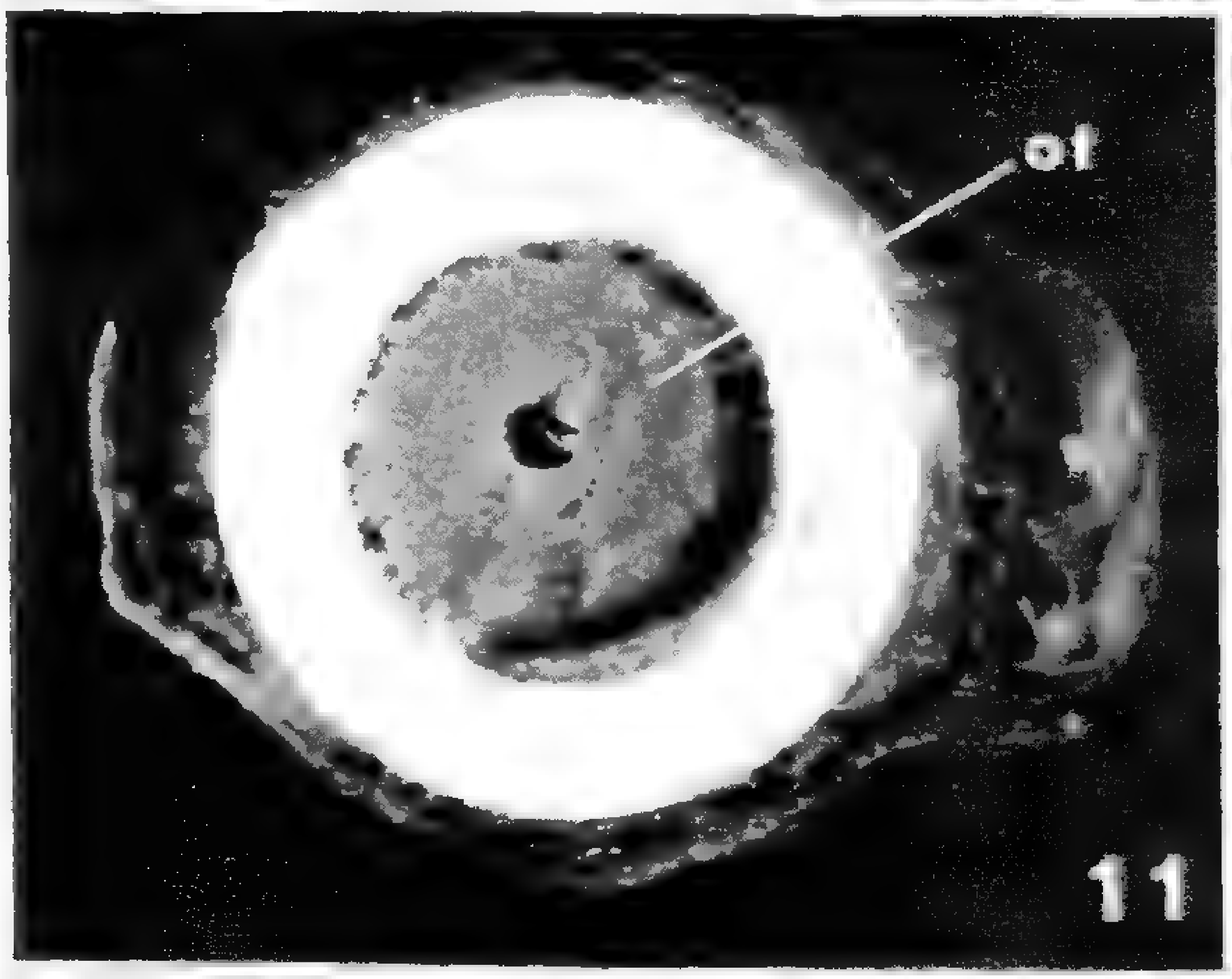
Samoa. SAVAII: Asau Harbor, *Hocking*, Nov. 24, 1968 (BISH), *Walker*, Dec. 27, 1968 (BISH); Matautu Bay, *Reinecke 506a* (BISH); Lelepa, *Christophersen & Hume 1941* (BISH); Sale'aula, *Bristol 2347* (BISH); between Salailua and Lataitai, *Christophersen 2870* (BISH, NY). UPOLU: Leulumoega, *Rechinger 571* (BM, US); between Mata'utu and Salamumu, *Bristol 2368* (BISH). TUTUILA: Pago Pago, *Setchell 99* (UC); Fagatoga, *Wisner 111* (BISH). OFU: On ridge back of Ofu village, *Yuncker 9468* (BISH). TAU: Luma, *Garber 704* (BISH, UC); Siufaga, *Yuncker 9194* (BISH). SAMOA, without further locality: *Whitmee* (GH).

Calophyllum inophyllum is readily distinguished from the other species of our area in being a tree of the seashore (unless introduced inland), in its large, comparatively broad, and characteristically rounded leaf-blades, and in its large flowers and fruits, the latter with the outer integument of the seed spongy and very thick even when the cotyledons are fully developed. This last characteristic gives the fruits great buoyancy and permits them to become established along the strand.

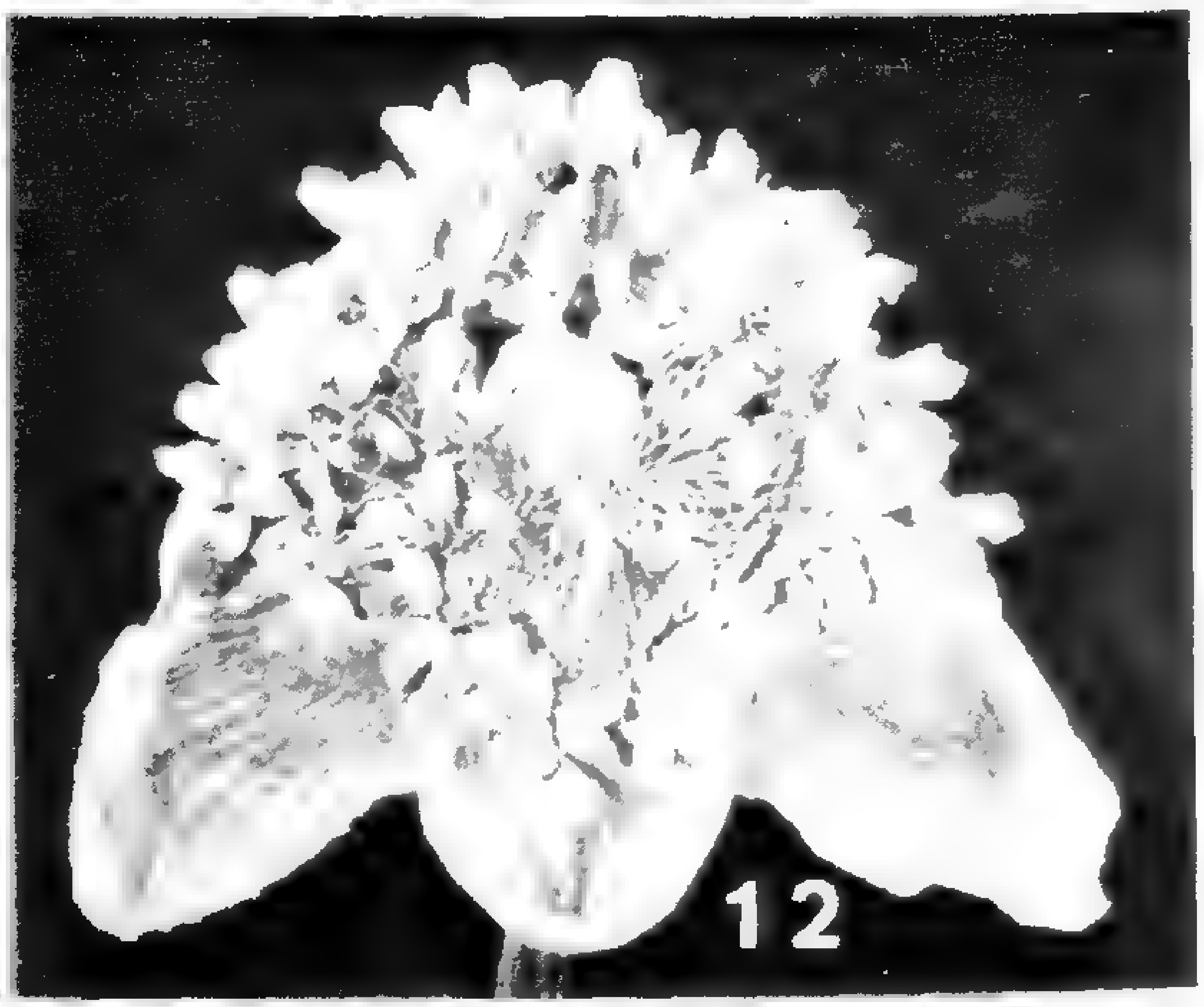

9

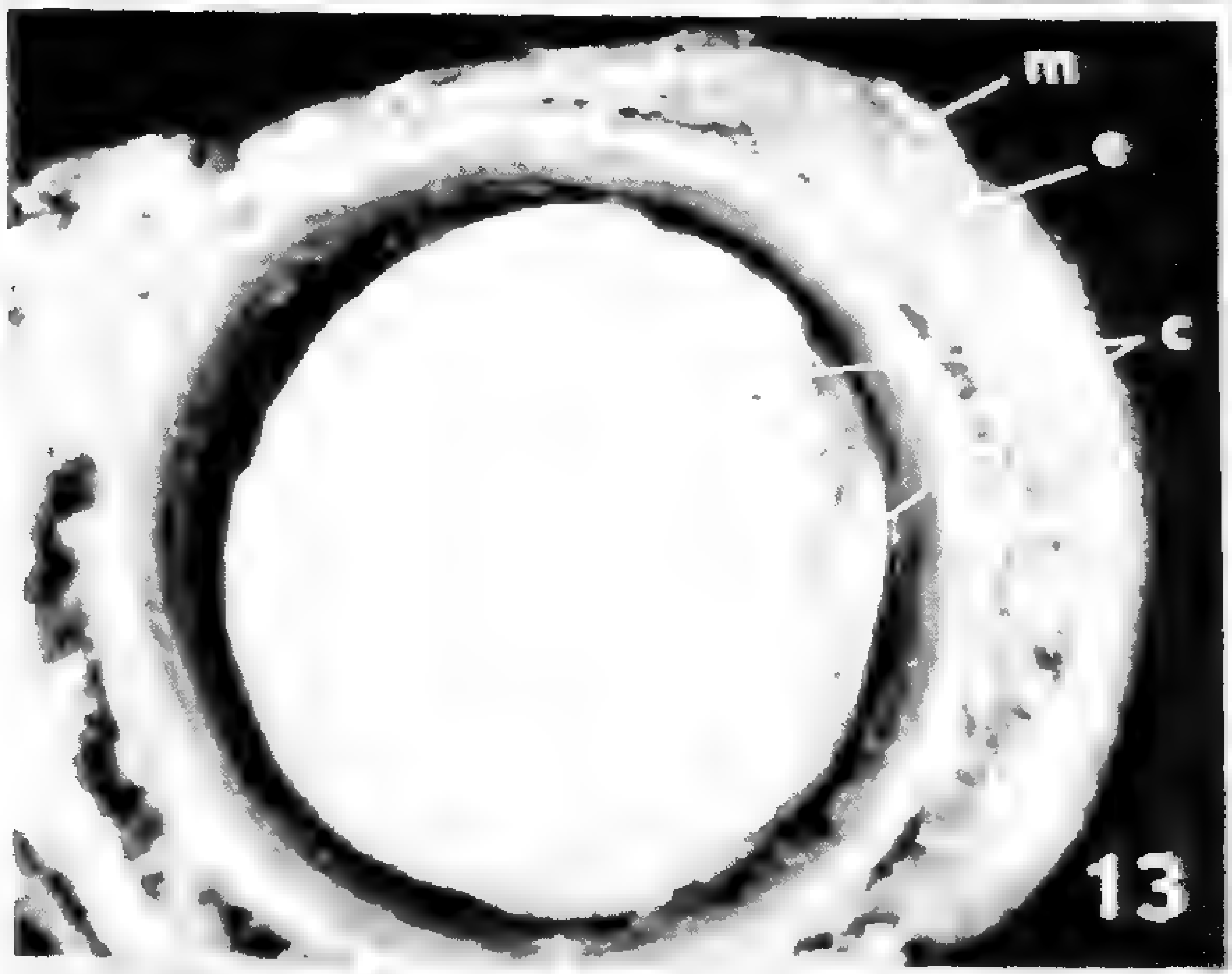


10



11

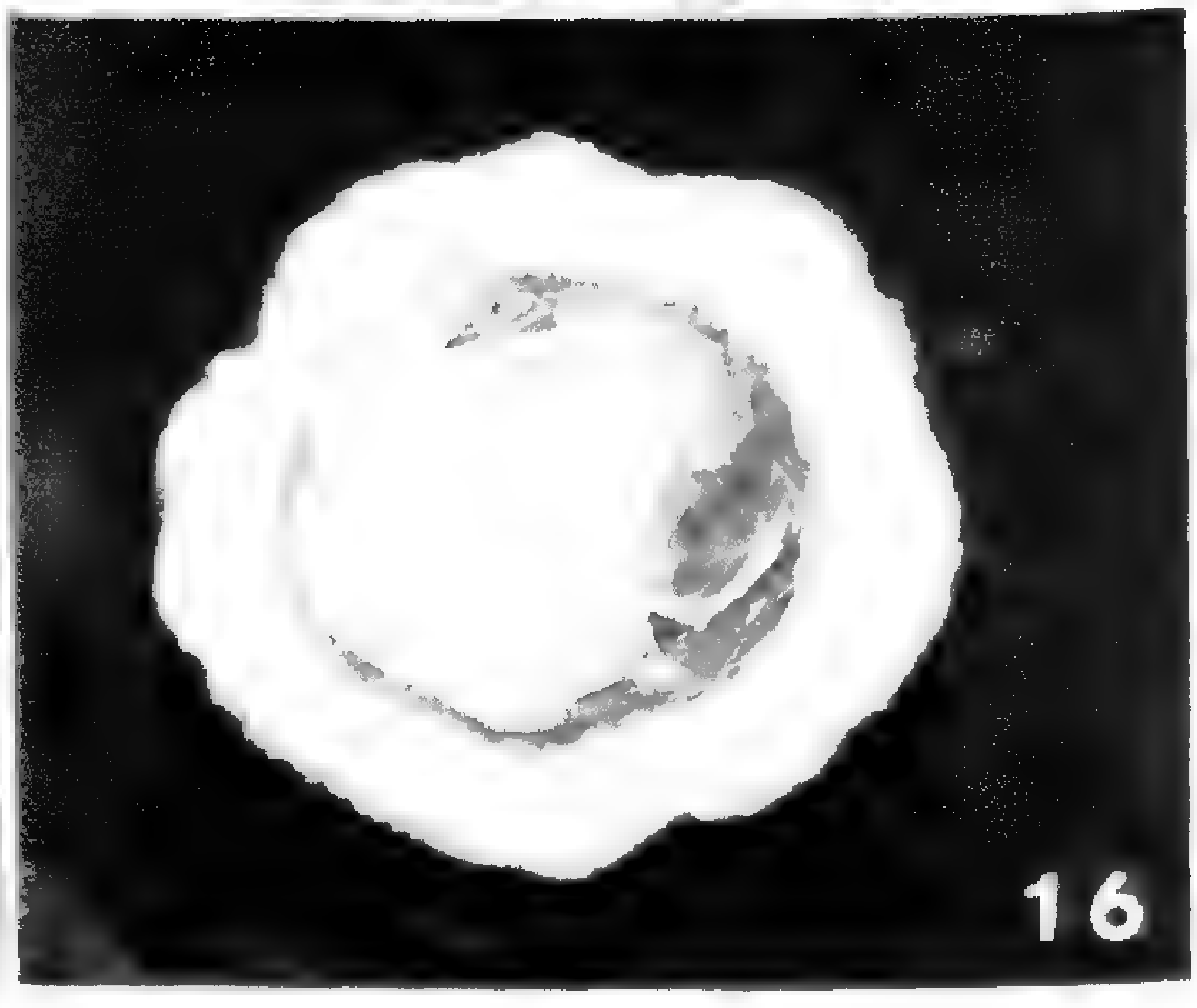

12



13


14


15


16

4. **Calophyllum vitiense** Turrill in Jour. Linn. Soc. Bot. **43**: 17. 1915; Watkins in Agr. Jour. Dept. Agr. Fiji **31**: 15. *fig.* 1961; J. W. Parham, Pl. Fiji Isl. 134. 1964, ed. 2. 192. 1972. FIGURES 9–11.

Calophyllum spectabile sensu A. Gray, Bot. U. S. Expl. Exped. **1**: 218, p. p. 1854, in Proc. Am. Acad. Arts **5**: 315. 1862, in Bonplandia **10**: 34. 1862; Seem. Fl. Vit. 11. 1865; Horne, A Year in Fiji, 258. 1881; non Willd.

Calophyllum polyanthum sensu Seem. in Bonplandia **9**: 254. 1861, Viti. 433. 1862; non Wall.

Calophyllum lanceolatum sensu Seem. Viti. 433. 1862; non auct.

Tree to 30 m. high, glabrous throughout except the young parts and terminal buds copiously but minutely ferruginous-tomentellous-puberulent, the branchlets stout, 2–5 mm. in diameter toward apex; petioles stout, semiterete or canaliculate, (5–) 15–35 mm. long; leaf-blades coriaceous, lanceolate or narrowly elliptic, (7–) 13–30 cm. long, (2–) 3–7.5 cm. broad, acute to attenuate at base and long-decurrent on the petiole, acuminate to acute at apex (tip to 10 mm. long, rounded or obtuse), rarely subobtuse, the costa plane or slightly raised above and often shallowly canaliculate, prominent beneath, the secondary nerves (8–) 11–20 (–24) per centimeter, prominulous on both surfaces; inflorescences appearing long-racemose, infrequently reduced, (3–) 7–15-flowered, (2–) 8–14 cm. long or slightly longer in fruit, the peduncle (0.5–) 1–6 cm. long, with the rachis and pedicels very obscurely puberulent but soon glabrate; flower-subtending bracts oblong-lanceolate, 5–7 mm. long, about 2 mm. broad, soon caducous, the pedicels slender, terete, 9–30 (–35) mm. long; flowers 20–23 mm. in diameter at anthesis, the sepals orbicular to obovate, conspicuously nerved, the outer ones 7–10 mm. in diameter, the inner ones 12–15 × 10–12 mm.; petals 4, papyraceous, elliptic, 9–16 mm. long, 7–10 mm. broad, rounded and often obscurely erosulous distally, nerved like the sepals; stamens about 200, the filaments 3–7 mm. long at anthesis, the anthers 0.9–1.2 mm. long; style conspicuous, 3–6 mm. long, the stigma peltate, about 1.5 mm. in diameter; fruits ellipsoid or subglobose, 22–30 × 15–26 mm., the pericarp 4–9 mm. thick, the mesocarp fibrous-spongy, greatly shrinking or collapsing in drying, 2–5.5 mm. thick, the endocarp bony, (1.8–) 2–3.5 mm. thick; testa of seed with a fibrous outer layer, this at first (and in sterile fruits) 2–4 mm. thick, usually compressed to 0.2–0.6 mm. thick by the developing cotyledons.

TYPE LOCALITY: Turrill cited two collections, *Seemann 47* and *im Thurn 297*; although the two are certainly conspecific, the first is sterile,

---

FIGURES 9–11. *Calophyllum vitiense*: 9 from *Smith 6362*, 10 from *Greenwood 907*, 11 from *Howard 187*. 9, flower, with one petal and a few stamens removed, × 3; 10, cross section of fruit, the outer layer of the testa compressed by the developing cotyledons, × 2; 11, cross section of sterile fruit without cotyledons, the outer layer of the testa thickened, × 2. FIGURES 12, 13. *Calophyllum samoense*: 12 from *Christophersen 720*, 13 from *Bristol 2248*. 12, open flower, × 3; 13, cross section of fruit, × 2. FIGURES 14–16. *Calophyllum neoebudicum*: 14 and 15 from *Kajewski 705*, 16 from *Kajewski 399*. 14, proximal surface of flower, × 3; 15, open flower, × 3; 16, cross section of fruit, × 2. m = mesocarp; e = endocarp; ot = outer layer of testa; c = cotyledons.

and obviously the second was the principal basis of the original description. We therefore designate as the lectotype the three complementary sheets (at Kew) of *im Thurn 297*, from the vicinity of Nandarivatu, Mba Province, Viti Levu, Fiji.

DISTRIBUTION: Endemic to Fiji and known from several of the high islands at elevations of 100–950 m., occurring in dense forest as a tree 5–30 m. high and with a trunk diameter up to (and doubtless exceeding) 50 cm. The sepals, petals, filaments, and style are white; the anthers are yellow; the fruit is at first green but when mature becomes dark purple. Flowers have been noted between October and January, but fruits seem to persist throughout the year.

LOCAL NAMES AND USES: In addition to *ndamanu* (used by Fijians for any inland species of the genus), the name *ndamanu ndilondilo* has been noted. Foresters and timber-cutters in Fiji do not differentiate among the forest species of *Calophyllum*, considering any tree of *ndamanu*, if sufficiently large, to produce a valuable and durable timber suitable for general construction, furniture, etc.

Fiji. VITI LEVU: MBA: Mountains near Lautoka, *Greenwood 907* (A); Mt. Evans Range, *Greenwood 1232* (US); vicinity of Nandarivatu, Dec. 2, 1906, *im Thurn 297* (K lectotype; isolectotype at BM), *Tothill 24* (K), *Mead 1972* (K), *Gillespie 4003* (UC), *4055* (BISH, GH, UC), *4229* (A, BISH, GH, NY, UC, US), *Vaughan 3431* (BM, K). NAMOSI: *Fiji Dept. Agr. 14236* (A, NY, SUVA). TAILEVU: Hills east of Wainimbuka River, near Ndakuivuna, *Smith 7201* (BISH, GH, K, NY, SUVA, UC, US). NAITASIRI: Wainiveimbalambala Creek, *Fiji Dept. Agr. 5833* (BISH, SUVA); Tholo-i-suva, *Fiji Dept. Agr. 12448* (*Watkins 751*) (K, MASS, SUVA); Tamavua, *Gillespie 2407* (BISH, GH, NY, UC, US); Kalambo, *Fiji Dept. Agr. 16410* (BISH, MASS, SUVA), *16411* (SUVA); Nasinu, *Gillespie 3647* (BISH, UC). VITI LEVU, without further locality: *M'Gillivray 38* (K), *M'Gillivray & Milne 67* (K), *Seemann 47* (GH, K). OVALAU: *Graeffe* (NY); Mt. Korotolutolu, west of Thawathi, *Smith 8021* (BISH, GH, K, NY, SUVA, UC, US); west of Lovoni valley, on ridge south of Mt. Korolevu, *Smith 7542* (BISH, GH, K, NY, SUVA, UC, US); hills east of Lovoni valley, *Smith 7269* (BISH, GH, K, NY, SUVA, UC, US). KORO: Main ridge, *Smith 1047* (BISH, GH, K, NY, UC, US). VANUA LEVU: MATHUATA: Vicinity of Lambasa, *Greenwood 507* (K), *515* (K); Mt. Numbuiloa, east of Lambasa, *Smith 6362* (A, K, US). VANUA LEVU, without further locality: *Milne 244* (K), *Howard 187* (SUVA, US). FIJI, without further locality: *U. S. Expl. Exped.* (GH), *Horne 192* (GH).

Among the inland species of our area with 4 petals, *Calophyllum vitiense* is readily distinguished by its large and comparatively narrow leaf-blades and its elongate inflorescences with large flowers. Its fruits characteristically have a fibrous-spongy mesocarp that shrinks or collapses in drying; *C. samoense*, which occurs in the Lau Group of Fiji, has a similar mesocarp but there the endocarp is seldom more than 1 mm. thick, whereas the endocarp of the fruits of *C. vitiense* is usually 2–3.5 mm. thick, more solid and durable than those of any other *Calophyllum* of the Fijian Region.

In our present opinion *Calophyllum vitiense* is endemic to the high islands of Fiji. References to its occurrence in the Solomon and Santa Cruz Islands (Smith, 1941: 347; Whitmore, 1966: 78; 1967: 12) seem unwarranted, in view of the superficial similarities among forest *Calophylla* of different southwestern Pacific archipelagoes and their presumably independent origins from coastal species. *Calophyllum vitiense* has also been mentioned as occurring in Samoa and Tonga and on Niue; such usages are cited in the synonymies to follow.

5. **Calophyllum samoense** Christophersen in Bishop Mus. Bull. **128**: 147. *fig. 20.* 1935; Yuncker in Bishop Mus. Bull. **184**: 52. 1943; B. E. V. Parham in New Zealand Dept. Sci. Indust. Res. Info. Ser. **85**: 121. 1972. FIGURES 12, 13.

Calophyllum spectabile sensu Reinecke in Bot. Jahrb. **25**: 656. 1898; Rechinger in Denkschr. Akad. Wiss. Wien **81**: 313. 1910; non Willd.

Calophyllum vitiense sensu Setchell in Carnegie Inst. Wash. Publ. **341**: 69. 1924; non Turrill.

Calophyllum neo-ebudicum sensu St. John & A. C. Sm. in Pacific Sci. **25**: 326. 1971; non Guillaumin.

Tree to 25 m. high, glabrous throughout except the young parts and terminal buds copiously but minutely ferruginous-tomentellous-puberulent, the branchlets 1.5–3.5 mm. in diameter toward apex; petioles slender, semiterete or shallowly canaliculate, 10–25 mm. long; leaf-blades subcoriaceous, ovate- to oblong-elliptic, (4–) 6.5–17 cm. long, (1.5–) 2–7 cm. broad, attenuate to acute at base and long-decurrent on the petiole, obtuse to obtusely cuspidate or short-acuminate at apex (tip to 7 mm. long), the costa nearly plane but shallowly canaliculate above, prominent beneath, the secondary nerves 14–30 per centimeter, prominulous on both sides; inflorescences pseudo-racemose, 7–13-flowered, (2.5–) 5–11 cm. long, the peduncle (0.5–) 1–3.3 cm. long, slender like the rachis; pedicels slender, terete, (8–) 10–22 mm. long; flowers 13–16 mm. in diameter at anthesis, the sepals orbicular to elliptic, rounded and often involute, the outer ones 4.5–8 × 4–7 mm., the inner ones 5.5–10.5 × 4–5.5 mm.; petals 4, obovate-elliptic, 5–11 mm. long, 3.5–5 mm. broad, rounded and sometimes inconspicuously erosulous distally; stamens about 150, the filaments (1–) 3–4.5 mm. long at anthesis, the anthers 0.8–1.1 mm. long; style 2–3 mm. long at anthesis, the stigma peltate, 0.8–1 mm. in diameter; fruits ovoid or subglobose, (22–) 25–30 × (20–) 23–30 mm., the pericarp 4–7 mm. thick at maturity, the mesocarp fibrous-spongy, 3.5–6 mm. thick, the endocarp 0.5–1.2 mm. thick; testa of seed with a fibrous outer layer, this compressed by the developing cotyledons and at maturity not exceeding 1 mm. thick.

TYPE LOCALITY: Between Vaipouli and Manase, Savaii, Samoa; the type is *Christophersen 720.*

DISTRIBUTION: Samoa, and also occurring in the Horne Islands and in the Lau Group of Fiji. It has been obtained at elevations close to sea-level and up to 650 m. in dry or humid forest or in secondary forest, often growing on limestone. Collectors indicate it as a tree 5–25 m. high, with a trunk diameter of up to 60 cm.; the sepals and petals are white; and the fruits at maturity become purple or black. Flowers have been obtained between September and December, but fruits persist through much of the year.

LOCAL NAMES AND USES: In Samoa and the Horne Islands *tamanu* is commonly used; in Samoa *malili* has also been noted, and on Moala, Fiji, *ndamanu kula*. The timber is used for canoes, house-building, and bowls in both Samoa and the Horne Islands; no such uses were recorded in Lau, although practically any hardwood of this size is prized in Fiji.

Fiji. MOALA: *Bryan*, July 11, 1924 (BISH); near Maloku, *Smith 1334* (BISH, GH, K, NY, UC, US). NAITAMBA: *Fiji Dept. For. L.12384* (BISH). MANGO: On limestone, *Bryan 569* (A, BISH).

Horne Islands. FUTUNA: Upland forests, *Burrows 18* (BISH); slopes south of Mt. Puke, *McKee 19850* (P). ALOFI: On limestone, *McKee 19810* (BISH, P).

Samoa. SAVAII: Neiafu, *Bristol 2209* (BISH); vicinity of Manase, *Vaupel 214* (BISH, K, NY, US), *Christophersen & Hume 2417* (BISH, NY, UC); between Vaipouli and Manase, alt. 100 m., Sept. 21, 1929, *Christophersen 720* (BISH holotype; isotypes at A, BISH, K, UC, US); inland from Vaipouli, *Christophersen & Hume 1916* (BISH, NY, UC, US); Matavanu lava field, *Christophersen & Hume 1871* (A, BISH); Salailua, *Christophersen 2991* (A, BISH, NY, UC, US); inland from Gataivai, *Bristol 2248* (BISH, GH). UPOLU: Inland from Apia, *Reinecke 204* (BISH); ridge above and vicinity of Malololelei, *Christophersen 162a* (BISH), *305* (BISH, US). TUTUILA: Trail to Vatia, *Setchell 334* (BISH, UC); Aua-Aofono Pass, *Setchell 221* (UC). SAMOA, without further locality: *Whitmee 9* (K), *Powell 335* (K).

Although the *Calophylla* of our area with 4 petals are confusingly similar when sterile, we believe that the present taxon cannot be referred to either *C. vitiense* or *C. neo-ebudicum*. It differs from the former in its differently proportioned leaf-blades and its smaller flowers, and most markedly in the comparatively thin endocarp of its fruits. From *C. neo-ebudicum* it is less readily separated in floral characters, but its fruits are quite different; those of the New Hebridean species are definitely longer than broad and have a firmly fibrous mesocarp 1–4 mm. thick that does not fall away from the endocarp and leave air-cavities, as does the thicker, spongy mesocarp of *C. samoense*. Proportions of the leaf-blades of the two taxa also differ slightly. Dr. M. Corbasson, of the Centre Technique Forestier Tropical in Noumea, on the basis of his field observation points out to us (in litt.) that the two taxa differ in their habit, general aspect, bark, wood, and even habitat; although zones of coralline limestone occur in the New Hebrides, they are not occupied by *C. neo-ebudicum*. The comparatively broad distribution of *C. samoense* may be due to the buoyancy of its fruits in sea water imparted by their spongy mesocarp.

6. **Calophyllum neo-ebudicum** Guillaumin in Jour. Arnold Arb. 12: 227. 1931. FIGURES 14–16.

Calophyllum inophyllum ? Guillaumin in Jour. Arnold Arb. 12: 227. 1931.

Tree to 30 m. high, glabrous throughout except for the obscurely puberulent young parts and terminal buds, the branchlets slender, 1.7–2 mm. in diameter toward apex; petioles slender, semiterete or shallowly canaliculate, (12–) 14–25 mm. long; leaf-blades subcoriaceous, elliptic-lanceolate or narrowly ovate-oblong, (3.5–) 5–10 cm. long, (1.5–) 2.3–4.2 cm. broad, attenuate to acute at base and long-decurrent on the petiole, obtuse to obtusely cuspidate at apex (tip rarely as much as 5 mm. long), the costa slightly raised above and shallowly canaliculate, sharply raised beneath, the secondary nerves 15–30 per centimeter, slightly prominulous on both sides; inflorescences pseudo-racemose, (3–) 7–13-flowered, (2.5–) 5–7 cm. long, the peduncle 1–3 cm. long, slender like the rachis; pedicels slender, 10–25 mm. long; flowers 10–16 mm. in diameter at anthesis, the sepals orbicular to elliptic, the outer ones 5.5–7 (–7.5) × 4–6 mm., the inner ones 5.5–7.5 (–9) × 5–7 mm.; petals 4, elliptic or obovate, 6.5–8 (–11) mm. long, 3–4.5 mm. broad, rounded and often involute; stamens 150–225, the filaments 3–4 (–4.5) mm. long at anthesis, the anthers 0.6–0.9 mm. long; style 2–2.5 mm. long at anthesis, the stigma peltate or shallowly infundibular, 0.7–1 mm. in diameter; fruits obovoid or ellipsoid, 17–35 × 13–28 mm., the pericarp 2–5 mm. thick at maturity, the mesocarp firmly fibrous, adhering to the endocarp, not spongy, 1–4 mm. thick, the endocarp 0.4–1 mm. thick; testa of seed with an outer layer compressed by the developing cotyledons at maturity and less than 1.5 mm. thick.

Type locality: Anelgauhat Bay, Aneityum, New Hebrides; as the lectotype we herewith designate *Kajewski 705*. In describing this species Guillaumin cited three of Kajewski's collections, nos. *288* and *399* from Eromanga as well as no. *705*. The only flowering specimen of the three seems the most appropriate lectotype.

Distribution: Apparently endemic to the Santa Cruz Islands and the New Hebrides, where it occurs at elevations of 25–300 m. in dense or disturbed forest, as a tree 20–30 m. high with a trunk diameter up to 1 m. The sepals and petals are white and the anthers yellow; the fruit becomes brown or blackish at maturity. Flowers have been collected in November and February, and fruits between May and September.

Local names and uses: Kajewski has noted the names *keoli* (Vanikoro), *pork-cull* or *porkgudi* (Eromanga), and *inpece* (Aneityum). The species produces light, strong wood that is locally used for canoe-building and for spears; the timber is also a valuable export. The tree is said to be one of the largest and most common trees of the New Hebrides forest.

Santa Cruz Islands. Vanikoro: *Kajewski 642* (A, UC, US).

New Hebrides. Eromanga: Dillon Bay, *Kajewski 288* (A, NY), *399* (A, BISH, K, NY); South River watershed, *Johnson 13* (A, K). Aneityum: Anelgauhat Bay, alt. 25 m., Feb. 4, 1929, *Kajewski 705* (A lectotype; isolectotypes at BISH, K, NY, P, US), *Wilson* (in *Kajewski*) *953* (A, BISH, NY, US).

Among described species, *Calophyllum neo-ebudicum* seems suggestive only of *C. samoense*. As discussed above under the latter species, the two taxa have quite different fruits; they have probably evolved independently from coastal forbears. Whitmore (1967: 14) cites *Kajewski 705* (K) as an isotype without explanation, but this can scarcely be considered adequate lectotypification; he also mentions *Kajewski 642* as intermediate between *C. neo-ebudicum* and *C. paludosum* C. T. White, although to us it appears entirely typical of the former. The reference of other collections from the Santa Cruz Islands (Whitmore, 1967: 13) to *C. vitiense* should be examined with *C. neo-ebudicum* in mind.

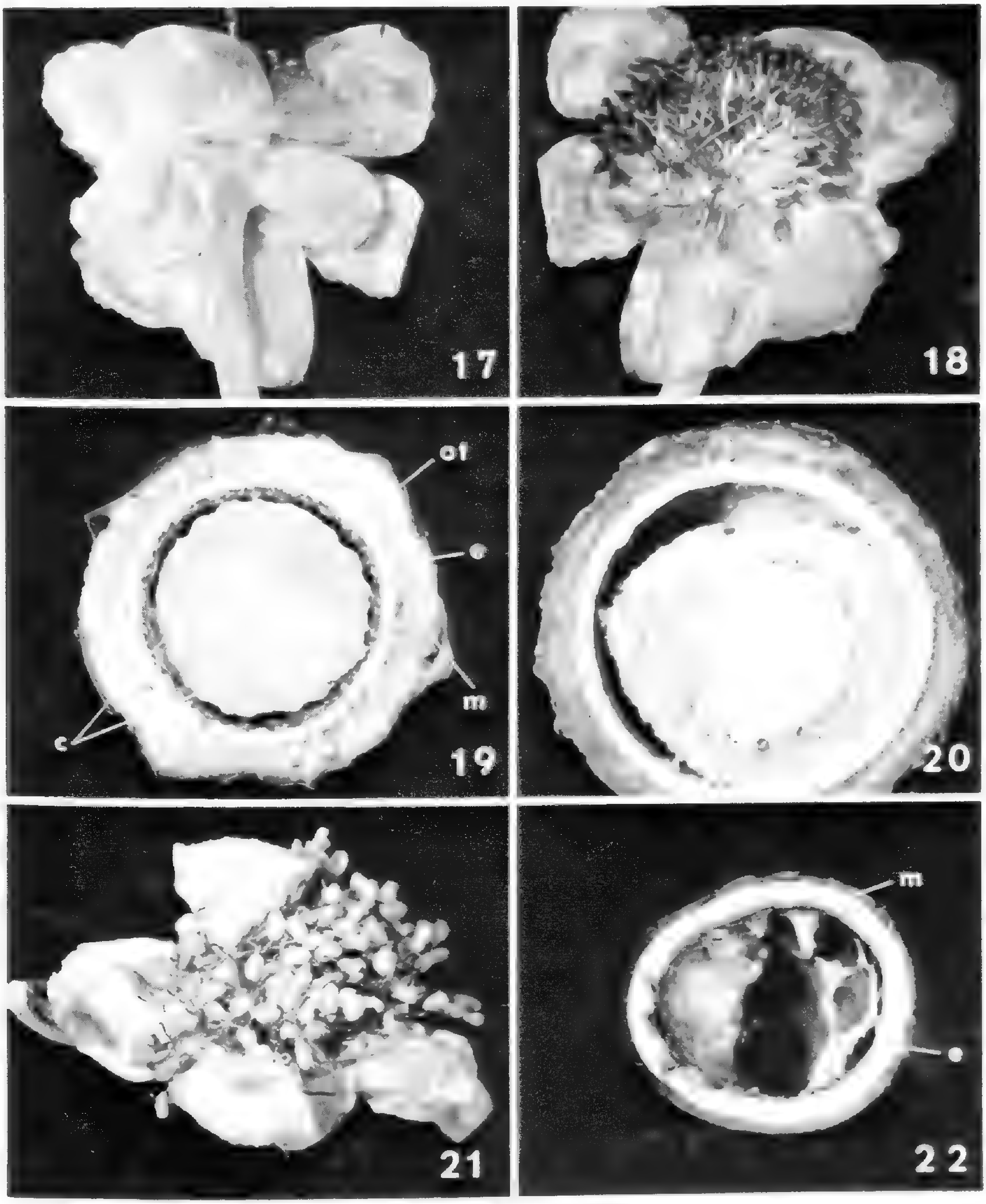
7. **Calophyllum amblyphyllum** A. C. Sm. & S. Darwin, sp. nov.

FIGURES 17–19.

Calophyllum sp. n. Horne, A Year in Fiji, 258. 1881.
Calophyllum spectabile sensu Hemsl. in Jour. Linn. Soc. Bot. **30**: 169. 1894; non Willd.
Calophyllum sp. Burkill in Jour. Linn. Soc. Bot. **35**: 27. 1901.
Calophyllum vitiense sensu Yuncker in Bishop Mus. Bull. **220**: 188. 1959; Sykes in New Zealand Dept. Sci. Indust. Res. Bull. **200**: 100. *fig. 9.* 1970; non Turrill.
Calophyllum neo-ebudicum sensu J. W. Parham, Pl. Fiji Isl. ed. 2. 192, p. p. 1972; non Guillaumin.

Arbor ad 25 m. alta partibus juvenilibus et gemma terminali copiose sed minute ferrugineo-puberulis mox glabratis, ramulis comparate robustis apicem versus 2–4.5 (–7) mm. diametro; petiolis crassis semiteretibus vel leviter canaliculatis 6–35 mm. longis; foliorum laminis coriaceis ellipticis vel ovato-ellipticis vel lanceolatis, (5–) 6–17 (–25) cm. longis, (1.5–) 2–5.5 (–8) cm. latis, basi acutis vel obtusis et in petiolum decurrentibus, apice obtusis vel rotundatis interdum obtuse brevi-cuspidatis, margine anguste recurvatis vel interdum manifeste revolutis, costa supra leviter vel peracute canaliculata subtus prominenti, nervis secundariis 12–30 (–50) per centimetrum utrinque prominulis vel supra subplanis; inflorescentiis ficte racemosis (3–) 5–13-floris sub anthesi 3–7 cm. et interdum sub fructu ad 17 cm. longis, pedunculo 0.2–3 (–7) cm. longo; pedicellis gracilibus sub anthesi (5–) 8–20 mm. et interdum sub fructu ad 45 mm. longis; floribus sub anthesi 12–18 mm. diametro, sepalis suborbicularibus vel ellipticis, exterioribus 5–8 × 5–7.5 mm., interioribus 6–9.5 × 4.5–7.5 mm., saepe anguste involutis; petalis 4 ellipticis 6–10 mm. longis 3–6.5 mm. latis integris vel obscure erosulis; staminibus 150–200, filamentis sub anthesi 2–6 mm. longis, antheris 0.7–1.1 mm. longis; stylo sub anthesi circiter 2 mm. longo, stigmate peltato 0.6–1.2 mm. diametro; fructibus ellipsoideis vel subglobosis 18–40 × 15–30 mm., in sicco coriaceis, pericarpio maturitate 1.5–5 mm. crasso, mesocarpio dense fibroso compacto non spongioso ad endocarpium adhaerenti 1–4 mm. crasso, endocarpio osseo 0.5–1.5 mm. crasso; testae seminis strato externo cotyledonibus evolutis compresso maturitate raro plus quam 2 mm. crasso.

TYPE LOCALITY: Hills west of Waivunu Creek, Serua Province, Viti Levu, Fiji; as type we designate *Smith 9243*, a flowering specimen.



FIGURES 17–19. *Calophyllum amblyphyllum*: 17 and 18 from *Smith 9243*. 19 from *Smith 6449*. 17, proximal surface of flower, × 3; 18, open flower, × 3; 19, cross section of fruit, × 2. FIGURES 20, 21. *Calophyllum cerasiferum*: 20 from *Berry 79*, 21 from *Berry 48*. 20, cross section of fruit, × 2; 21, open flower, × 3. FIGURE 22. *Calophyllum tenuicrustosum*: cross section of fruit, from *Smith 4058*, × 2. m = mesocarp; e = endocarp; ot = outer layer of testa; c = cotyledons.

DISTRIBUTION: Fiji, Tonga, and Niue, occurring at elevations of 50–970 m. in dense or dry forest, on rocky forested slopes, or in crest thickets. It has been recorded as a tree 5–25 m. high, with a trunk diameter up to 60 cm.; the sepals are white or sometimes pink-tinged, the petals and filaments white, and the anthers yellow; the fruit, at first green, becomes reddish-tinged and at length black. Flowers and fruits have been obtained more or less throughout the year.

LOCAL NAMES AND USE: *Ndamanu* (Fiji); *tamanu* (Niue). Like other forest species of *Calophyllum*, this new species is considered an important timber tree, producing a durable wood.

Fiji. VITI LEVU: MBA: Southern slopes of Mt. Ndelainathovu, on the escarpment west of Nandarivatu, *Smith 4944* (A, BISH, K, NY, US); Sovutawambu, near Nandarivatu, *Degener 14664* (A, K, NY). NANDRONGA & NAVOSA: Northern portion of Rairaimatuku Plateau, between Nandrau and Nanga, *Smith 5461* (A, BISH, K, NY, US). SERUA: Nambukelevu, upper Navua River, *Fiji Dept. Agr. 15654* (BISH, MASS, SUVA); inland from Namboutini, *Fiji Dept. For. 573* (or *797*, or *Damanu R-22*) (BISH, K, SUVA); hills west of Waivunu Creek, between Ngaloa and Korovou, alt. 50–150 m., Nov. 23, 1953, *Smith 9243* (US 2191735 holotype; isotypes at BISH, GH, K, NY, SUVA, UC); inland from Ngaloa, *Fiji Dept. For. 574* (or *798*, or *Damanu G-22*) (BISH, K, NY, SUVA); vicinity of Taunovo Creek, east of Wainiyambia, *Smith 9576* (BISH, GH, K, NY, SUVA, UC, US). NAMOSI: Hills bordering Wainavindrau Creek, vicinity of Wainimakutu, *Smith 8525, 8553* (both BISH, GH, K, NY, SUVA, UC, US); hills near Navua River, *Greenwood 1036* (A, BISH, K). REWA: Nggoya Forest Reserve, *Fiji Dept. Agr. 13764* (*Damanu 124*) (BISH, SUVA). VITI LEVU, without further locality: *Milne 65* (K), *89* (K). OVALAU: *Horne 43* (K); summit of Mt. Ndelaiovalau and adjacent ridge, *Smith 7617* (BISH, GH, K, NY, SUVA, UC, US); vicinity of Levuka, *Gillespie 4480* (BISH). VANUA LEVU: MATHUATA: Mt. Numbuiloa, east of Lambasa, *Smith 6449* (A, BISH, K, NY, US). THAKAUNDROVE: Mt. Kasi, Yanawai River region, *Smith 1789* (BISH, GH, K, NY, UC, US). TAVEUNI: Near crater lake east of Somosomo, *Smith 8378* (BISH, GH, K, NY, SUVA, UC, US); valley between Mt. Manuka and Mt. Koroturanga, east of Wairiki, *Smith 8286* (BISH, GH, NY, UC, US). FIJI, without further locality: *Horne* (GH), *732* (K).

Tonga. VAVA'U: *Crosby 204* (K). KAO: *Yuncker 15883* (BISH, BM, US). 'EUA: *Lister*, Dec. 1889 (K); near center of island, *Yuncker 15326* (BISH, BM, US); near summit of eastern ridge, *Yuncker 15435* (BISH, BM, GH, US). TONGA, without further locality: *Capt. Cook's 3rd Voyage* (BM).

Niue. Ana, near Hakapu-Liku Road, *Sykes 821A* (BISH), *823* (BISH).

Among the inland species of our region with 4 petals, the taxon here described has been confused with *Calophyllum vitiense*, *C. samoense*, and *C. neo-ebudicum*. However, examination of a now extensive suite of specimens shows that it should be excluded from each of these, differing from all three in its somewhat thicker leaf-blades with rounded or obtuse, only occasionally obtusely short-cuspidate, apices. It further differs from *C. vitiense* in its smaller flowers, different mesocarp, and thinner exocarp; from *C. samoense* in its quite different fruits; and from *C. neo-ebudicum* in its comparatively robust facies and somewhat larger fruits with a generally thicker endocarp. The absence of *C. amblyphyllum* from the Lau Group of Fiji and its reappearance in Tonga and Niue, while *C. samoense* occurs in Lau, disturbs the geographic pattern; but this may be explicable by the adaptation of the former to dense inland forests and the latter primarily to limestone areas. Or, of course, the actual geographic and ecological situation may remain to be clarified by future collecting.

Whitmore (1967: 14) cites *Horne 732* and other Fijian collections as *Calophyllum cerasiferum*, a species with very different foliage, flowers, and fruits than the present taxon.

8. **Calophyllum cerasiferum** Vesque, Epharmosis 2: 10. *pl. 32.* 1889, in DC. Monogr. Phan. 8: 540, 585. 1893; J. W. Parham, Pl. Fiji Isl. ed. 2. 192. 1972. FIGURES 20, 21.

Calophyllum burmanni sensu Seem. in Bonplandia 9: 254. 1861, Viti, 433. 1862; Horne, A Year in Fiji, 258. 1881; non Wight.

Calophyllum burmanni var. *parvifolium* sensu Seem. Fl. Vit. 11. 1865; non Wight.

Tree to 15 m. high, the young parts obscurely glandular-puberulent, the terminal buds often somewhat vernicose, the branchlets comparatively stout and with short distal internodes, 2–4 mm. in diameter toward apex; petioles stout, semiterete or dorsiventrally flattened, 3–16 mm. long; leaf-blades coriaceous, ovate to obovate or elliptic-oblong, 3.5–8 cm. long, 1.3–5 cm. broad, acute to attenuate at base and decurrent on the petiole, rounded to subacute at apex or often short-cuspidate, the costa shallowly canaliculate above, prominent beneath, the secondary nerves 22–44 per centimeter, subplane above, prominulous beneath; inflorescences appearing racemose, 3–7-flowered, 1.2–5 cm. long at anthesis, to 7 cm. long in fruit, the peduncle stout, 0.4–1.8 cm. long; pedicels stout, 5–13 mm. long; flowers 12–20 mm. in diameter, the sepals ovate to elliptic, the outer ones 4.5–6 mm. in diameter, the inner ones 8–9 × 4.5–5.2 mm.; petals sometimes 4 but often 5–9 and frequently 10, elliptic, 6–10 mm. long, 4–6 mm. broad, rounded and sometimes faintly erosulous distally; stamens usually 80–120, perhaps sometimes as many as 250, the filaments 3–5.5 mm. long at anthesis, sometimes distally divided, the anthers 0.8–1.3 mm. long; style 1–1.6 mm. long, the stigma peltate, 0.6–0.8 mm. in diameter; fruits subglobose, at maturity 18–25 mm. in diameter, coriaceous when dried, the pericarp 2–4 mm. thick, the mesocarp compactly fibrous, 1–3 mm. thick, adherent to the endocarp, this bony, 1–1.5 mm. thick; testa of seed with an outer spongy layer 2–3.5 mm. thick in young fruits, becoming compressed by the developing cotyledons.

TYPE LOCALITY: Mt. Voma, Namosi Province, Viti Levu, Fiji; the type is *Seemann 49*, a fruiting specimen. Although the presumed holotype is clearly marked "Voma peak," Seemann erroneously cited the number in 1865 as from Kandavu.

DISTRIBUTION: Endemic to Fiji and thus far known only from the uplands of Viti Levu at elevations of 600–1150 m., where it occurs in montane or hill forest often on ridges, or occasionally in secondary forest. It has been noted as a tree 2–15 m. high, with a trunk diameter up to 40 cm., often being stunted on exposed ridges; the sepals, petals, and filaments are white or cream-colored. Flowers, not previously described, have been collected in March and November, and fruits between August and November.

LOCAL NAMES AND USE: *Ndamanu* (as other species of the genus) or *ndamanu ndilondilo*. It has been noted as a useful timber, although since it is smaller than most Fijian *Calophylla*, such use must be limited.

Fiji. VITI LEVU: MBA: Waimongge Creek and vicinity, south of Nandarivatu, *Berry 82* (BISH, MASS, SUVA, US), *85* (BISH, SUVA), *88* (BISH, MASS, SUVA, US). NANDRONGA & NAVOSA: South of Mt. Tomanivi, *Fiji Dept. Agr. 14292* (BISH, K, SUVA); track to Vanualevu village, *Berry 79* (MASS, SUVA). NAMOSI: Mt. Vakarongasiu, *Gillespie 3267* (BISH); Mt. Voma, Aug. 24, 1860, *Seemann 49* (K presumed holotype; isotypes at BM, GH); Mt. Voma track, *Fiji Dept. Agr. 604* (SUVA). NAMOSI-NAITASIRI boundary: Summit of Mt. Naitarandamu, *Gillespie 3232* (BISH, GH, UC). NAITASIRI: Vicinity of Rewasau, *Howard 308* (BISH, SUVA, US); summit of Mendrausuthu Range, *Fiji Dept. Agr. 15463* (MASS, SUVA), *15471* (BISH, SUVA).

This apparently rare and local species has become adequately known only through recent collecting. It is readily distinguished from other described Fijian *Calophylla* by its numerous petals; although occasional flowers are found to have only 4 petals, others in the same collection are seen to have 5–10 petals. Even in the absence of flowers, *C. cerasiferum* is sharply characterized by its robust, quadrangular branchlets with short distal internodes, its small, thick leaf-blades that are usually less than twice as long as broad, and its comparatively small, subglobose fruits with a compactly fibrous mesocarp and a bony, comparatively sturdy endocarp. The reference of Solomon Island specimens to *C. cerasiferum* (Whitmore, 1966: 77; 1967: 13) seems unjustified.

9. **Calophyllum tenuicrustosum** A. C. Sm. & S. Darwin, sp. nov.

FIGURE 22.

Arbor ad 20 m. alta, praeter partes juveniles et gemmam terminalem pilis glandulosis copiose sed minute ferrugineo-tomentellas plerumque mox glabrata, ramulis apicem versus 1.5–3 mm. diametro; petiolis 5–16 mm. longis sub anthesi interdum subpersistenter puberulis; foliorum laminis coriaceis anguste ellipticis vel lanceolatis vel lanceolato-oblongis, 5–10 cm. longis, 2–3.5 cm. latis, basi acutis et in petiolum decurrentibus, ad apicem acutum vel obtuse cuspidatum gradatim angustatis, costa supra leviter canaliculata subtus prominenti, nervis secundariis 15–35 per centimetrum utrinque subtiliter prominulis; inflorescentiis ficte racemosis vel interdum reductis (1–) 3–15-floris sub anthesi ad 6 cm. et sub fructu ad 11 cm. longis, pedunculo comparate crasso subnullo vel ad 3 cm. longo interdum ut partibus juvenilibus puberulo plerumque glabrato; bracteis sub floribus papyraceis ovatis ad 3 × 2 mm. apice subacutis mox caducis, pedicellis ante anthesin 5–10 mm. sub fructu 8–12 mm. longis; floribus ante anthesin 12–16 mm. diametro, sepalis suborbicularibus circiter 6 mm. diametro saepe involutis; petalis 4–6 ellipticis 7–9 mm. longis 3.5–5 mm. latis, superne rotundatis et obscure erosulis; staminibus in alabastro vetusto circiter 200; fructibus ovoideo-ellipsoideis in sicco coriaceis et subrugulosis ad 22 × 18 mm., pericarpio 1.5–1.8 mm. crasso, mesocarpio compacte fibroso 0.2–0.5 mm. crasso ad endocarpium adhaerenti, hoc osseo 1–1.3 mm. crasso; testae seminis strato externo fibroso cotyledonibus evolutis endocarpium arcte adpresso.

TYPE LOCALITY: Mt. Evans Range, Mba Province, Viti Levu, Fiji; the type is *Smith 4058.*

DISTRIBUTION: Endemic to Fiji and thus far known from only a few collections on Viti Levu and Vanua Levu, these occurring in dense forest at elevations from near sea-level to 1,050 m. It has been noted as a tree 9–20 m. high, with a trunk to 50 cm. in diameter; the sepals and petals are white and the fruit green. Advanced flower buds were collected in September and November and fruits in April.

LOCAL NAME: Like other Fijian species of the genus, this is locally known as *ndamanu.*

Fiji. VITI LEVU: MBA: Natua Levu, Mt. Evans Range, *Fiji Dept. Agr. 14053* (BISH, SUVA); slopes of Mt. Nairosa, eastern flank of Mt. Evans Range, alt. 700–1,050 m., April 28, 1947, *Smith 4058* (A holotype; isotypes at BISH, K, NY, US). SERUA: Queen's Road, *Fiji Dept. Agr. 7036* (BISH, SUVA). VANUA LEVU: MATHUATA: Sasa Tikina (without other locality), *Howard 195* (MASS, SUVA).

Since good differentiating characters are found in the foliage and fruit, the best fruiting collection and one with several duplicates is designated as the type. The known distribution of this novelty is erratic both as to geography and altitude, but the cited specimens seem definitely conspecific. The best flowers are found on *Fiji Dept. Agr. 14053*, but even these are not quite mature. *Howard 195* has still younger inflorescences. However, the presence of four, five, or six petals in the flowers of the latter two collections indicates the relationship of this taxon to *Calophyllum cerasiferum*, a position confirmed by the general facies and the thin, fibrous mesocarp. From *C. cerasiferum* the new species differs in having its leaf-blades narrowly elliptic to lanceolate-oblong and usually about three times as long as broad, in the more obvious indument of its young parts and terminal buds, and in its proportionately narrower fruits with a distinctly thinner, almost negligible, mesocarp.

2. **Mammea** L. Sp. Pl. 512. 1753; Kosterm. Mammea and Ochrocarpos, For. Serv. Indones., Div. Plann. 11. 1956, in Commun. For. Res. Inst. Indones. 72: 2. 1961.

Calysaccion Wight, Illustr. Ind. Bot. 130. 1831; Seem. Fl. Vit. 13. 1865.

The taxonomic status of *Ochrocarpos* Thou. has puzzled students of the family, but the solution proposed by Kostermans (1956, 1961) seems logical and is here accepted. *Ochrocarpos* is typified by *O. madagascariensis* Thou. ex DC. and, in the interpretation of Kostermans, is limited to certain Madagascan taxa. *Mammea* L., typified by *M. americana* L., includes some 26 species in Asia, Malesia, and the Pacific, with a secondary center in Madagascar, a few species in tropical Africa, and only *M. americana* in America. In this interpretation, *Mammea* is characterized by the conspicuous and glanduliferous areoles of its leaf-blades and by the essentially free filaments, while *Ochrocarpos* has leaf-blades with bands of secretory canals crossing the secondary nerves and the filaments fascicled.

One widespread species and one Samoan endemic represent *Mammea* in our area. They are polygamo-dioecious trees, glabrous throughout; the branchlets are slightly flattened or subquadrangular in the distal internodes, turning from pale brown to grayish, with sparse, oval, slightly protruding lenticels. The opposite leaves have inconspicuously short-excavate petioles, the excavation at first enclosing the terminal bud, the petioles soon diverging to leave an interpetiolar pseudostipular line. The leaf-blades are coriaceous and entire, with spreading secondary nerves prominulous on both surfaces and interspersed with many less conspicuous ones; the principal nerves anastomose well within the margin but also continue outward to merge into an irregular collecting nerve close to the margin. The veinlets form a conspicuous reticulum (FIGURES 27, 28, 30, 31), resulting in areoles that in dried leaves are depressed on both surfaces and have a dark raised gland in the center. The inflorescences are axillary, often to scars of fallen leaves, fasciculate, and with 2–5 flowers, of which only one seems to mature. The flowers (FIGURES 24, 25) are pedicellate and subtended by closely imbricate bracts, with a calyx composed of 2 sepals that are completely fused in bud but separate at anthesis. The petals are usually 4 in *Mammea*, but in *M. odorata* they appear to be uniformly 6. The androecium of ♂ and ☿ flowers appears similar, composed of numerous essentially free stamens (FIGURE 25), of which the 2-celled anthers dehisce longitudinally. The gynoecium is lacking in ♂ flowers; in ☿ flowers it consists of a sessile, 4-locular ovary which soon becomes unilocular by abortion; the single ovule is basal and anatropous. The fruits, carnose when fresh, become coriaceous in drying; they are borne on branchlets below the leaves and are oblique or curved, with a single basally attached seed. The sepals are caducous and the stigma persistent. The pericarp (FIGURE 26) consists of a thin exocarp, a mesocarp that dries dense and hard, and a fibrous endocarp. The seed appears embedded in pulp when fresh, but the amount of this apparently varies with the species, and consequently a conspicuous or negligible air-space surrounds the seed in old fruits.

KEY TO SPECIES

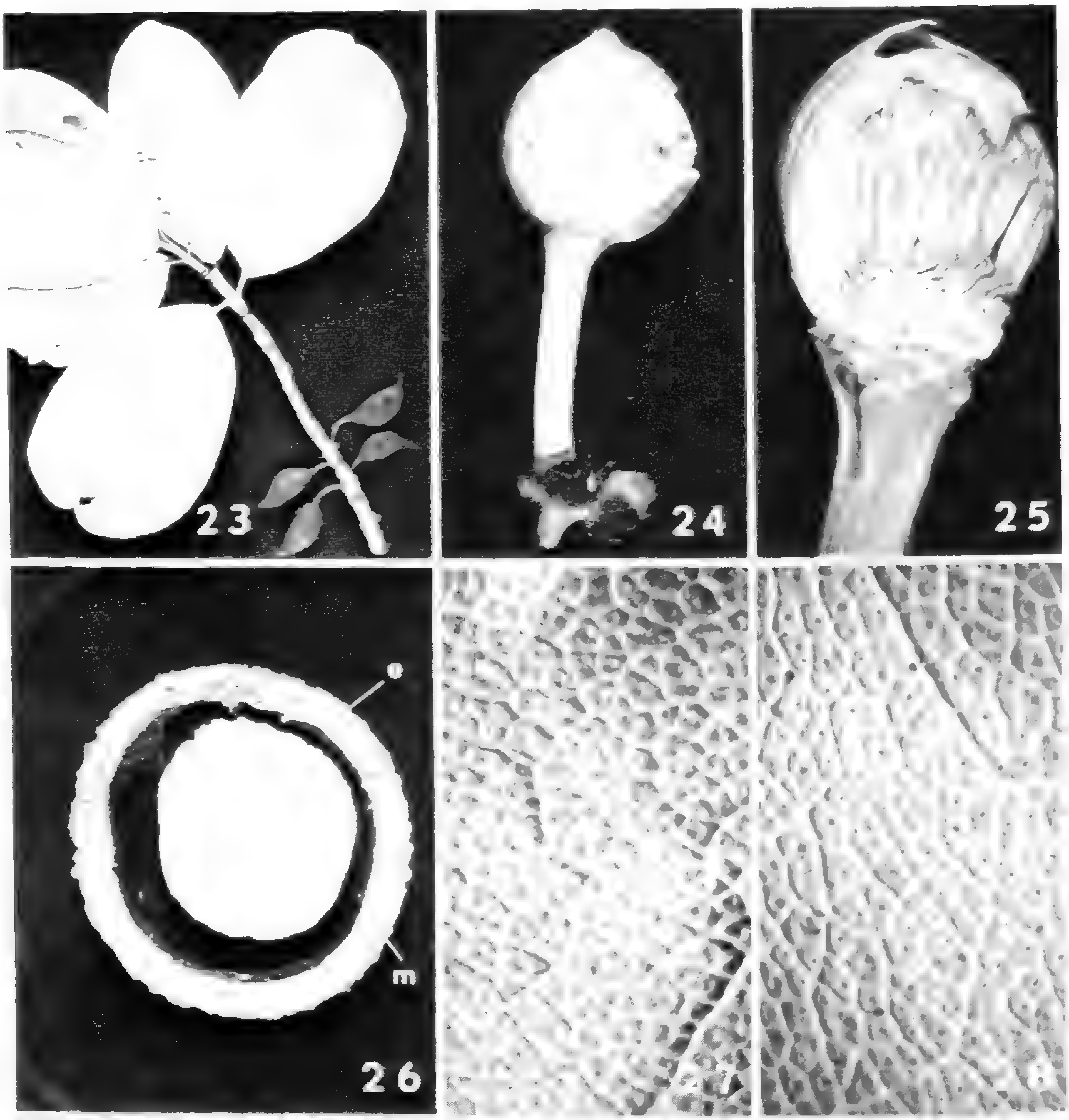
Branchlets and petioles robust, the former 4–6 mm. in diameter toward apex, the latter 3–5 mm. in diameter; leaf-blades concolorous, obovate or elliptic, usually 11–20 × 7–11 cm., the outer collecting nerve 1–3 mm. within margin; fruiting pedicels 7–17 mm. long, the fruit tapering to a manifest style about 2 mm. long, the stigma about 3 mm. in diameter, the endocarp 2–4 mm. thick, the seed embedded in pulp when fresh, this evanescent and leaving a conspicuous air-space in dried fruit. . . . . 1. *M. odorata*.

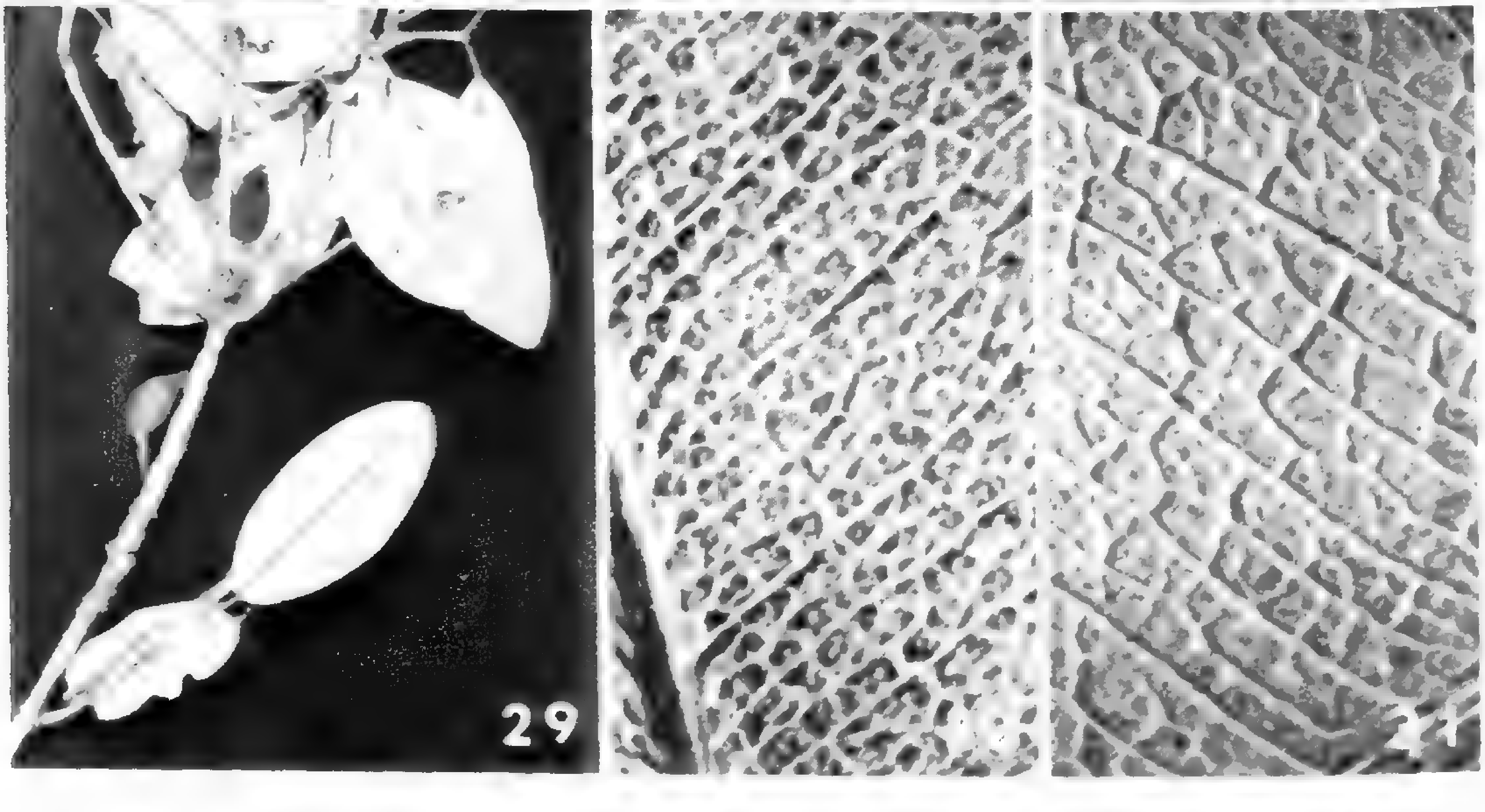
Branchlets and petioles comparatively slender, the former 2–3 mm. in diameter toward apex, the latter 1.5–2.5 mm. in diameter; leaf-blades paler and glaucous beneath, elliptic to oblong, usually 7–14 × 3–5.5 cm. (juvenile up to 22 × 8.5 cm.), the outer collecting nerve 0.3–1 mm. within margin: fruiting pedicels 20–30 mm. long, the fruit tapering to a sessile stigma, this 3.5–4 mm. in diameter, the endocarp 0.5–1 mm. thick, the seed apparently appressed to the endocarp and not leaving a conspicuous air-space in dried fruit. . . . . 2. *M. glauca.*

1. **Mammea odorata** (Raf.) Kosterm. Mammea and Ochrocarpos, For. Serv. Indones., Div. Plann. 13. 1956, in Commun. For. Res. Inst. Indones. 72: 15. *fig. 9, 10.* 1961; J. W. Parham, Pl. Fiji Isl. ed. 2. 195. 1972. FIGURES 23–28.

Lignum clavorum Rumph. Herb. Amb. **3:** 97. *t. 64.* 1743.
Lolanara odorata Raf. Fl. Tellur. **1:** 16, *nom. nud.* 1837, op. cit. **2:** 34. 1837.
Calophyllum excelsum Zoll. & Mor. Nat. Geneesk. Arch. Ind. **2:** 582. 1845.
Calysaccion obovale Miq. Fl. Ind. Bat. Suppl. 500. 1861; Seem. in Bonplandia **9:** 254. 1861; A. Gray in Proc. Am. Acad. Arts **5:** 315. 1862; Seem. Viti. 433. 1862.
Calysaccion tinctorium Seem. Fl. Vit. 13. *pl. 9.* 1865.
"*Calyaccion tinctorum*" Horne, A Year in Fiji, 258. 1881.
Ochrocarpus tinctorius Drake, Ill. Fl. Ins. Mar. Pac. 116. 1890.
Ochrocarpus excelsus Vesque in DC. Monogr. Phan. **8:** 525. 1893; Engl. in Engl. & Prantl, Nat. Pflanzenfam. ed. 2. **21:** 192. *fig. 80, A–H.* 1925.
Ochrocarpos odoratus Merr. in Jour. Arnold Arb. **26:** 94. 1945.
Ochrocarpus odoratus Merr. ex J. W. Parham, Pl. Fiji Isl. 136. 1964.

Tree to 12 m. high, the branchlets stout, 4–6 mm. in diameter toward apex, soon thickening; leaves often distally congested, the petioles robust (3–5 mm. in diameter), semiterete or canaliculate, 8–20 mm. long; leaf-blades drying brown to dull green, concolorous, obovate or elliptic, (9–) 11–20 cm. long, (6–) 7–11 cm. broad, broadly obtuse to acute at base and decurrent on the petiole, rounded or retuse or abruptly cuspidate at apex (tip to 3 mm. long, obtuse or acute), recurved at margin, the costa stout, broadly flattened and often shallowly canaliculate above, prominent beneath, the principal secondary nerves 10–15 per side, irregularly anastomosing 5–10 mm. within margin and also forming an irregular outer collecting nerve 1–3 mm. within margin, the ultimate areoles often subquadrangular or pentagonal, 0.5–1 mm. in diameter; flowers borne on inconspicuous irregularly rounded protuberances 3–5 mm. broad, each subtended by 4–8 closely imbricate bracts, these chartaceous, broadly ovate, 1–2 × 2–3 mm., obtuse, entire or obscurely erosulous; pedicels terete, 7–15 mm. long (to 17 mm. in fruit); flowers ellipsoid in bud, spreading at anthesis to 15–25 mm. in diameter; sepals papyraceous, elliptic, 7–9 × 5–7 mm., obtuse or subacute at apex, with 15–18 parallel nerves; petals 6, broadly imbricate in bud, at length spreading, submembranaceous, obovate, at anthesis 10–17 × 4–7 mm., obtuse to rounded at apex, entire or faintly erosulous at margin, with 10–15 ascending nerves dichotomously branched distally; androecium of ♂ flowers composed of about 200 stamens, the filaments filiform, 4–8 mm. long at anthesis, free or weakly connate in the basal 0.5 mm., the anthers oblong, 1.5–2 mm. long, the thecae





FIGURES 23–28. *Mammea odorata*: 23 from *Smith 1263*, 24 and 25 from *Smith 1190*, 26–28 from *Fiji Dept. Agr. 16818*. 23, branchlet with half-grown fruits, × 1/5; 24, ♂ flower bud, × 2 1/2; 25, ☿ flower bud with sepals and 4

slightly exceeded by the obtuse connective; ☿ flowers similar to the ♂ but with a central gynoecium, the ovary ellipsoid, 2–2.5 mm. in diameter at anthesis, the style terete, about 2 mm. long, the stigma peltate, inconspicuously 2-lobed, about 2 mm. in diameter; fruits obliquely ellipsoid to ovoid, up to 100 × 50 mm. at maturity, obtuse at base, narrowed distally to the persistent style and stigma, the stigma slightly accrescent, the pericarp 2–5 mm. thick, the mesocarp 0.5–1 mm. thick, the endocarp 2–4 mm. thick, the seed embedded in pulp when fresh, this evanescent, leaving a conspicuous air-space around the seed.

TYPE LOCALITY: Presumably Amboina; *Lolanara odorata* Raf. is based solely on *Lignum clavorum* Rumph., which may be considered typified by the Rumphian description and plate. The synonymy given above is incomplete, but as far as noted the nomenclatural usages and basionyms pertinent to the Fijian Region have been included. The complex synonymy of this much named species is more fully discussed by Merrill (1945) and Kostermans (1956, 1961). Of the basionyms involved, only *Calysaccion tinctorium* Seem. is typified by a plant from our area: *Seemann 46*, from Taveuni, Fiji, cited below. There are two sheets of this at Kew, on one of which the Taveuni locality is noted, with a comment: "In Mbau there was only one tree." This implies that Seemann saw the species on the islet of Mbau (Tailevu Province, Viti Levu) but not necessarily that any of his preserved material was obtained there.

DISTRIBUTION: Coastal areas throughout Malesia from Java and the Philippines, thence eastward to Micronesia and Fiji. Specimens from the New Hebrides have not been seen, but the species may be expected there. *Mammea odorata* seems not to have been recorded from Tonga, and the Samoan records probably all refer to *M. glauca*. In Fiji *M. odorata* is strictly littoral, occurring in beach thickets, often on limestone, or on the inner edge of mangrove swamps. It is a spreading tree 4–12 m. high, with white petals, filaments, and ovary, and with yellow anthers; as far as noted the fruits are green. Flowers and fruits do not seem seasonal.

LOCAL NAMES AND USES: *Vetao* or *vetau* are the usual Fijian names, but *uvitao* is also recorded. The close-grained wood is considered useful, and the latex was sometimes used by Fijians to dye their hair orange-brown.

Fiji. VITI LEVU: MBA: Namaka, *Fiji Dept. Agr. 11734* (BISH, SUVA). TAILEVU: Mokani, *Fiji Dept. Agr. 656* (SUVA); between Mokani and Ndravo, *Fiji Dept. Agr. 629* (A, SUVA), *15458* (SUVA). MBENGGA: Ndakuni, *Fiji Dept. Agr. 2075* (BISH, SUVA). KORO: Uthu ni Vanua, *Fiji Dept. Agr. 15831* (BISH, MASS, SUVA). VANUA LEVU: THAKAUNDROVE: Ndromoninuku, *Fiji Dept. Agr. 16818* (BISH, MASS, SUVA). TAVEUNI: Vicinity of Somosomo, May 1860, *Seemann 46* (K holotype of *Calysaccion tinctorium*; isotypes at BM, GH). KATAFANGA: *Fiji Dept. Agr.*, May 5, 1947 (BISH, SUVA). NAYAU: *Tothill 22* (K). KAMBARA: Lime-

---

petals removed, × 5; 26, cross section of fruit, × 1; 27, upper surface of leaf-blade, × 5; 28, lower surface of leaf-blade, × 5. FIGURES 29–31. *Mammea glauca*: all from *Christophersen & Hume 2029*. 29, branchlet with fruits, × 1/4; 30, upper surface of leaf-blade, × 5; 31, lower surface of leaf-blade, × 5. m = mesocarp; e = endocarp.

stone formation, *Smith 1263* (BISH, K, NY). FULANGA: Limestone formation, *Smith 1190* (BISH, GH, K, NY, UC, US). FIJI, without further locality: *Howard 133* (SUVA).

In the Kostermans revision of 1961, *Mammea odorata* would appear to be a taxonomically isolated species, but perhaps one may assume that from its forbear such local species as *M. papuana* (Lauterb.) Kosterm. and the Samoan *M. glauca* have been derived. As suggested by Merrill (1945), its fruits are probably dispersible by sea-water flotation.

2. **Mammea glauca** (Merr.) Kosterm. Mammea and Ochrocarpos, For. Serv. Indones., Div. Plann. 12. 1956, in Commun. For. Res. Inst. Indones. 72: 27. *fig. 24.* 1961. FIGURES 29–31.

Ochrocarpus excelsus sensu Christophersen in Bishop Mus. Bull. **128**: 147. 1935; non Vesque.

Ochrocarpos glaucus Merr. in Jour. Arnold Arb. **26**: 95. *fig. 1.* 1945.

Mammea sp. Kosterm. in Commun. For. Res. Inst. Indones. **72**: 31. 1961.

Mammea odorata sensu B. E. V. Parham in New Zealand Dept. Sci. Indust. Res. Inform. Ser. **85**: 73. 1972; non Kosterm.

Tree to 18 m. high, the branchlets comparatively slender, 2–3 mm. in diameter toward apex; petioles comparatively slender (1.5–2.5 mm. in diameter), canaliculate, 10–17 mm. long (to 30 mm. on juvenile leaves); leaf-blades drying dull green above, paler and glaucous (in mature leaves) beneath with a thin waxy coating, elliptic to oblong, (4–) 7–14 cm. long, (2–) 3–5.5 cm. broad (up to 22 × 8.5 cm. in juvenile leaves), obtuse at base and short-decurrent on the petiole, acute to obtuse or emarginate at apex (or on juvenile leaves cuspidate to short-acuminate), the costa stout, flattened or shallowly canaliculate above, prominent beneath, the principal secondary nerves 10–15 per side, irregularly anastomosing 3–7 mm. within margin (to 10 mm. in juvenile leaves) and also forming an irregular outer collecting nerve usually 0.3–1 mm. within margin, the ultimate areoles irregularly 3–5-sided, 0.3–1 mm. in diameter; flowers not seen, the flower-subtending bracts caducous in fruit but presumably several and imbricate; pedicels in fruit stout, subterete, 20–30 mm. long, slightly swollen at apex; fruits curved-ovoid, up to 25 × 15 mm. (not fully mature), obtuse at base, narrowed distally to the persistent stigma, the sepals caducous, the style essentially none, the stigma peltate-bilobed, 3.5–4 mm. in diameter, recurved at margin, the pericarp 1–2 mm. thick, the mesocarp 0.5–1 mm. thick, the endocarp 0.5–1 mm. thick, the seed apparently appressed to the endocarp and not leaving a conspicuous air-space in drying.

TYPE LOCALITY: Medium wet forest above Matavanu, Savaii, Samoa; the type is *Christophersen & Hume 2029*, cited below.

DISTRIBUTION: Endemic to Samoa and thus far known only from Savaii, occurring in coastal and inland forest at elevations from near sea-level to 900 m. It has been recorded as a tree 15–18 m. high, with a trunk to 40 cm. in diameter and lacking latex (note on type collection), with green fruits; the fruiting material available to us has been obtained in July, but Kostermans (1961) also cites *Vaupel 566* from Falealupo as bearing fruits in December.

LOCAL NAMES AND USES: In upland Savaii the names *mamalava* and *taipoipo* have been noted, and in lowland forest the name *manapau*. B. E. V. Parham, recording the species as *Mammea odorata*, indicates that the timber is heavy and has been used for making clubs.

Samoa. SAVAII: Vicinity of Falealupo, *Christophersen* (coll. *Stehlin*) *2664* (BISH), *Christophersen 3318* (BISH, NY, UC); above Matavanu, July 15, 1931, *Christophersen & Hume 2029* (A holotype; isotypes at BISH, K, NY, P, UC, US), *2053* (BISH).

This Samoan endemic was presumably derived from the inland movement of a population of *Mammea odorata*, although in its typical form the latter seems now to be lacking from Samoa. While *M. odorata* is strictly a strand plant or is associated with mangroves, the lowland representatives of the genus in Samoa occupy a forest niche. The two such collections that we have seen, those from the vicinity of Falealupo, are sterile and apparently from juvenile plants; their leaves are more robust than those of the montane specimens, but in shape and other characteristics they definitely represent *M. glauca* rather than *M. odorata*. Lacking flowers of *M. glauca*, we may still point to reproductive differences between it and *M. odorata*. In the Samoan endemic, the fruits have a negligible style and a comparatively large, recurved, distinctly bilobed stigma, and it seems probable that the seed is embedded in comparatively sparse pulp, so that a minimal air-space is left within the fruit at maturity.

In his 1961 revision, Kostermans (p. 31) lists *Christophersen 3318* as an undescribed Samoan species, overlooking the fact that he had (p. 28) also cited this collection as *Mammea glauca*, a disposition that seems correct to us.

3. **Garcinia** L. Sp. Pl. 443. 1753; Seem. Fl. Vit. 10. 1865.

In his voluminous work on the forest flora of Cochinchina (1879–1907), Pierre (1883: 1: I–XL. *pl. 54–92*) discusses *Garcinia* at length, providing excellent illustrations of many species, and comments on several from our area. Many of his sections have been retained by Engler (1925), but only three of them appear to extend eastward into the Fijian Region, where the diversity of this complex genus, of more than 200 species, has become greatly attenuated.

The species of our area are dioecious trees, often copiously laticiferous and with secretory canals in the foliage and flowers, glabrous throughout. The branchlets are subquadrangular or slightly flattened in the distal internodes and there brownish or purplish, soon becoming subterete and grayish, with sparse, small, oval lenticels. The opposite leaves have petioles that are semiterete or shallowly canaliculate, excavate basally around the terminal bud, soon diverging and leaving an interpetiolar pseudostipular line (FIGURE 40) or scar (FIGURE 48); the excavation may be distally produced into a conspicuous ligule (FIGURE 38) or not. The leaf-blades are coriaceous to chartaceous or membranaceous, drying dull green or brownish, with secondary nerves spreading or subascending from a curved base. The inflorescences in our species are terminal at inception and cymose, or axillary (often to caducous leaves) and fasciculate or glomerulate, with small but usually obvious flower-subtending bracts. The flowers are pedicellate or sessile, the 4, 6, or 8 decussate perianth-segments with obscure nerves or more obvious longitudinal secretory canals. The androecium is highly diverse in the ♂ flowers, providing a basis for sectional recognition. An androecial rudiment may be present or absent in ♀ flowers, which have a superior sessile ovary with 2 or several (FIGURE 37) or many locules. The ovules are solitary in each locule, axile (FIGURE 55) or subascending, and anatropous; in our species the stigma is sessile or nearly so. The fruit is baccate or drupaceous, carnose when fresh but drying either smooth or costate, depending upon the texture of the endocarp.

The following key is based only on the species of our area and does not incorporate the full range of variation present in the three sections represented. We here recognize five species, one of which is described as new.

KEY TO SPECIES

Petioles with the proximal excavation distally produced into a conspicuous ligule 1.5–4 mm. long; leaf-blades with secondary nerves 6–16 per centimeter; inflorescences terminal at inception, cymose, with paired bracts at the nodes; sepals and petals each 4; ♂ flowers with the androecium composed of 60–100 stamens aggregated into 4 phalanges opposite the petals, a sterile central gynoecium present; ovary of ♀ flowers with (4–) 5 or 6 locules; fruits ovoid to obovoid, often apiculate with the persistent short style and accrescent stigma, with (4–) 5 or 6 seeds, the dissepiments thin, the sepals persistent (Sect. MANGOSTANA); New Hebrides, Fiji, and Tonga. .... 1. *G. pseudoguttifera.*

Petioles with the proximal excavation not produced into a ligule; leaf-blades with 1–3 (–8) secondary nerves per centimeter; inflorescences axillary, often to caducous leaves, fasciculate or glomerulate, the flowers arising from a pulvinate or irregularly subglobose or short-cylindric peduncle; sepals and petals often each 4, sometimes fewer; fruits ellipsoid, the stigma strictly sessile, persistent, pulvinate-discoid.

  Pedicels obvious, 3–12 (–15) mm. long, distally swollen into an inconspicuous flattened receptacle; androecium of ♂ flowers composed of numerous (up to 700) stamens aggregated into 4 phalanges opposite the petals, a sterile central gynoecium present; ovary of ♀ flowers with 2 locules; fruits smooth in drying, the seeds 2, the dissepiment thin, the sepals caducous, the stigma conspicuously accrescent (Sect. DISCOSTIGMA).

    Flowers comparatively small, the sepals 1.5–3.5 × 1.5–4 mm., the petals 3–4.5 × 2.5–3.5 mm., the androecium in ♀ flowers lacking or forming an obscure annulus hardly 0.1 mm. high; mature fruits 13–16 × 12–14 mm.; petioles 2–10 mm. long; leaf-blades 4–11 × 1.2–5 cm., attenuate at base and long-decurrent on the petiole; New Hebrides and Fiji. . . . . 2. *G. vitiensis.*

Flowers larger, the sepals 3–5 × 4–7 mm., the petals 3–6 × 3–7 mm., the androecium in ♀ flowers composed of short-oblong phalanges 0.5–0.7 mm. high; mature fruits 20–45 × 15–30 mm.; petioles 4–20 (–25) mm. long; leaf-blades usually 7–17 × 4–11 cm., obtuse at base and short-decurrent on the petiole; Fiji and Tonga. . . . . 3. *G. myrtifolia.*

Pedicels lacking or minute, rarely as long as 2.5 mm., imperceptibly enlarging into the calyx; androecium of ♂ flowers central, composed of 7–30 stamens fused into a carnose stalk, the anthers sessile or essentially so, a gynoecium lacking; ovary of ♀ flowers with 5–13 locules; fruits costate in drying, the seeds 5–13, enclosed in pyrenes separated by air-chambers or pulp, the endocarp of each pyrene bony or horny, the sepals persistent, the stigma only slightly accrescent (Sect. MUNGOTIA).

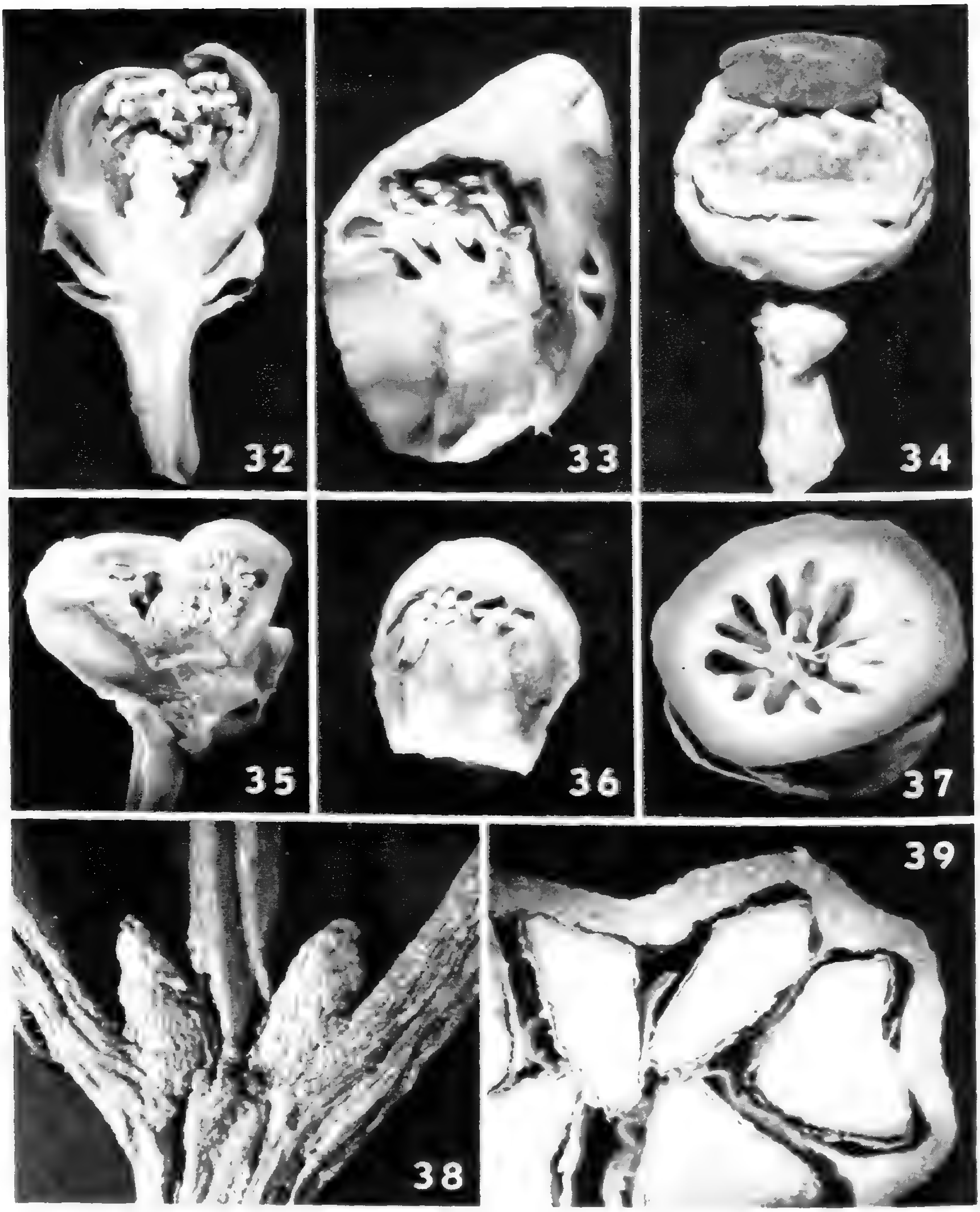
Corolla composed of 4 petals, these very early becoming marginally imbricate and soon conspicuously so; inflorescences composed of 3–9 flowers, the flower-subtending bracts usually 2 per flower; fruits with a mesocarp 0.5–1.5 mm. thick, sharply (6–) 10–13-costate when dried, the pyprenes (6–) 10–13, with bony endocarps 0.2–1 mm. thick, obtuse to narrowly rounded on the dorsal face; leaf-blades usually chartaceous to membranaceous, obtuse to acute at base; Santa Cruz Islands, Fiji, Tonga, and Samoa. . . . . 4. *G. sessilis.*

Corolla composed of 2 valvate petals, these with thick margins broadly appressed to each other; ♂ inflorescences usually composed of 15–40 flowers, rarely of 3–7 flowers in distal inflorescences, the flower-subtending bracts often more than 2 per flower; fruits with a mesocarp 2–3 mm. thick, obtusely 5–8-costate when dried, the pyrenes 5–8, with horny endocarps 1–4 mm. thick, broadly rounded on the dorsal face; leaf-blades subcoriaceous to chartaceous, acute to attenuate at base; Fiji. . . . . 5. *G. adinantha.*

1. **Garcinia pseudoguttifera** Seem. Fl. Vit. 11. 1865; Horne, A Year in Fiji, 262. 1881; Pierre, Fl. For. Cochinch. 1: XL. 1883; Vesque in DC. Monogr. Phan. 8: 483. 1893; Yuncker in Bishop Mus. Bull. 220: 188. 1959; J. W. Parham, Pl. Fiji Isl. 134. 1964, ed. 2. 194. 1972. FIGURES 32–39.

Garcinia echinocarpa sensu Seem. in Bonplandia 9: 254. 1861; non Thw.
Garcinia pedicellata Seem. Viti, 433, quoad spec. vit., non sensu typi. 1862.
Garcinia sp. n. Horne, A Year in Fiji, 262. 1881.
Garcinia pancheri sensu Guillaumin in Jour. Arnold Arb. 12: 226. 1931; non Pierre.

Tree to 25 m. high, the branchlets 1.5–4.5 mm. in diameter toward apex; petioles slender to robust, 10–35 mm. long, conspicuously excavate, the excavation distally produced into a conspicuous ligule, this coriaceous, oblong-ovate, rounded distally, free from petiole in the ultimate 1.5–4 mm.; leaf-blades coriaceous, ovate to oblong-elliptic or slightly obovate, (4–) 6–17 cm. long, (2.5–) 3.5–12 cm. broad, obtuse to attenuate at base and decurrent on the petiole, obtusely cuspidate to rounded or sometimes retuse at apex, entire and often narrowly recurved at margin, the costa



FIGURES 32–39. *Garcinia pseudoguttifera*: 32 from *Yuncker 16204*, 33 from *Kajewski 831*, 34 from *Smith 4464*, 35 from *Fiji Dept. Agr. 13936*, 36 from *Smith 997*, 37 from *Smith 7143*, 38 from *Smith 6308*, 39 from *Smith 217*. 32, section of ♂ flower, showing 2 phalanges and sterile gynoecium, × 3; 33, petal and phalange of ♂ flower, × 4; 34, developing gynoecium, with persistent sepals, × 3; 35, section of ♂ flower, showing 2 phalanges, × 3; 36, petal and phalange of ♂ flower, × 4; 37, cross section of developing gynoecium, × 3; 38, petiole-bases, showing the conspicuous ligules, × 5; 39, cross section of fruit, × 2.

stout, plane or slightly raised above, prominent beneath, the secondary nerves 6–16 per centimeter, spreading, irregularly anastomosing, prominulous on both surfaces, joined in a collecting nerve 0.2–1 mm. within margin, the veinlet-reticulation sparse, immersed or prominulous on both surfaces, sometimes parallel to secondaries; inflorescences terminal at inception, sometimes on short lateral branchlets, cymose, the ♂ 3–5-times branched, 5–40-flowered, up to 6 cm. long and 10 cm. broad, the ♀ usually 2- or 3-times branched, 1–7-flowered (flower often solitary and terminal), up to 3 × 3 cm. at anthesis and to 7 cm. long in fruit, the peduncle stout, usually 3–15 mm. long but sometimes lacking; bracts at inflorescence-nodes paired, subcoriaceous, ovate or oblong, obtuse, 2–5 mm. long, the flower-subtending bracts similar or semi-orbicular, to 1 × 2 mm.; pedicels (above ultimate articulation) inconspicuous, 1–6 mm. long, in ♀ flowers scarcely exceeding 4 mm., becoming stout and often sulcate in fruit; flowers in ultimate groups of 2 or 3, but usually solitary in ♀ and sometimes ♂ inflorescences, 10–17 mm. in diameter at anthesis, the perianth-segments often with immersed opaque glands; sepals 4, decussate, thick-carnose, broadly ovate or suborbicular, rounded at apex, entire or undulate, the outer ones 3–4 × 4–8 mm., the inner ones 4–5 × 5–9 mm.; petals 4, broadly imbricate, thick-carnose, orbicular to broadly obovate, 6–10 mm. long, 5–9 mm. broad, rounded, entire; androecium of ♂ flowers cupuliform, composed of 60–100 stamens aggregated into 4 phalanges opposite the petals, each phalange carnose, 3–7 mm. long, irregularly divided at margin, the anthers single or in small clusters, basifixed, ovoid or ellipsoid, 0.5–1 mm. long, laterally dehiscing, the gynoecium in ♂ flowers minute or oblong, irregular, solid, to 3 mm. long; ♀ flowers with a subglobose ovary 3–4 mm. in diameter at anthesis, the wall thick-carnose, with copious longitudinal mucilage-canals, the dissepiments thin, the locules (4–) 5 or 6, often bilobed on the extrorse face, the style none or stout and very short, the stigma peltate to rounded, 2–3 mm. in diameter at anthesis, minutely tuberculate, often becoming inconspicuously 4–9-lobed, the androecium in ♀ flowers composed of 4 dendroid phalanges adnate to petals and bearing small irregular staminodia; fruits carnose at maturity, becoming coriaceous in drying, ovoid to obovoid, to 50 × 40 mm. (but perhaps sometimes larger), often apiculate with the persistent short style and enlarged stigma to 8 mm. in diameter, the pericarp variable in thickness, 1.5–10 mm. thick, the dissepiments persistent, the locules (4–) 5 or 6; seeds curved-ellipsoid, angled on inner edge, convex or bilobed on extrorse face, to 20 mm. long and 10 mm. broad.

TYPE LOCALITY: In his protologue Seemann mentions "Kandavu, in mountainous woods," but the holotype bears the inscription "Wood about Navua." Seemann (1862) visited the lower Navua River on three occasions, in July, August, and September, 1860, and Kandavu twice, in August and September. As his material was doubtless sorted after his return to England, it is likely that the data with the specimens are the more accurate. The type, *Seemann 50,* is cited below as from the vicinity of Navua, Serua Province, Viti Levu.

Distribution: New Hebrides, Fiji, and Tonga, occurring with some frequency in the first two archipelagoes but apparently collected only once in Tonga. It has been noted at elevations from near sea-level to 450 m. (New Hebrides) or 1,150 m. (Fiji), in dense or thin forest or sometimes in beach thickets, as a tree 4–25 m. high with a trunk diameter up to 30 cm. (which is probably exceeded) and with abundant yellow or pale latex. The petals are yellowish white, becoming pale pink to red; the fruit is usually noted as green, but becomes red or perhaps darker at maturity. Flowers and fruits have been obtained throughout the year.

Local names and uses: *Neyaheven* has been recorded in the New Hebrides and *mo'onia* in Tonga. In Fiji the frequently used names are *kau yalewa*, *mbulu*, *mbuluwai*, or *mbuliwai*, but also noted are *sueri*, *mali*, *sarosaro*, *mbulumangayalewa*, *mbulumanga*, and *nambulinomati*. The fruit is considered edible in both the New Hebrides and Fiji; and in the latter archipelago the plant is sometimes used for timber, an extract of the leaves is used to relieve pain, and oil from the fruit is used as a perfume.

New Hebrides. Vanua Lava, Banks Group: *Kajewski 414* (A), *415* (A, NY). Epi: Mont Alembe, *Aubert de la Rüe*, Nov. 21, 1935 (A, P). Eromanga: Inland from Dillon Bay, *Kajewski 342* (A, BISH, NY, US), *389* (A, NY); Ulenarap, S. River, *Johnson 19* (A, K). Aneityum: Anelgauhat Bay, *Kajewski 831* (A, BISH, NY, US).

Fiji. Yasawas: Waya: Along Wailevu Creek, *St. John 18072* (BISH, SUVA, US); vicinity of Nangua, *St. John 18153* (BISH, SUVA, US). Viti Levu: Mba: Mountains near Lautoka, *Greenwood 507A* (A, BISH); vicinity of Nalotawa, eastern base of Mt. Evans Range, *Smith 4464* (A, BISH, K, NY, US); Naloto Range, *Fiji Dept. Agr. 14761* (BISH, SUVA), *14775* (SUVA); vicinity of Nandarivatu, *Tothill* (K), *Gillespie 3881*, *4194* (both BISH, GH, UC); Mt. Nanggaranambuluta, *Smith 6308* (A, US); slopes of Mt. Tomanivi, *Gillespie 4077* (BISH, GH, NY, UC), *Smith 5216* (A, BISH, K, NY, US). Nandronga & Navosa: Vicinity of Nandrau, *Berry 70* (BISH, MASS, SUVA), *Fiji Dept. For. 1178* (BISH, SUVA); northern portion of Rairaimatuku Plateau, between Nandrau and Nanga, *Smith 5498*, *5552* (both A, BISH, K, NY, US). Serua: Rovondrau Bay, *Fiji Dept. Agr. 7199* (SUVA), *7203* (SUVA); Ndeumba, *Fiji Dept. Agr. 16977* (SUVA); Koromba Beach, *Fiji Dept. Agr. 15277* (MASS, SUVA); vicinity of Navua, July–Sept. 1860, *Seemann 50* (K holotype; isotypes at BM, GH). Namosi: Northern slopes of Korombasambasanga Range, in drainage of Wainavindrau Creek, *Smith 8753* (BISH, GH, US). Ra: Vicinity of Rewasa, near Vaileka, *Degener 15392* (A, BISH, K, NY, P, UC, US), *15495* (A, BISH, NY, US). Naitasiri: Between Viria and Namuamua, *Fiji Dept. Agr. 68* (SUVA); Waindrandra Creek, *Fiji Dept. Agr. 795* (SUVA); between Nawangasua and Nanduna, *Fiji Dept. Agr. 639* (SUVA); vicinity of Tamavua, *Gillespie 2196* (BISH). Tailevu: East of Wainimbuka River, vicinity of Ndakuivuna, *Smith 7143* (BISH, GH, K, NY, SUVA, UC, US). Kandavu: Mt. Mbuke Levu, *Smith 217* (BISH, GH, K, NY, UC, US); Lutumatavoro, *Fiji Dept. Agr. 14925* (A, NY, SUVA). Ovalau: West of Lovoni Valley, on ridge south of Mt. Korolevu, *Smith 7544*, *7637* (both BISH, GH, K, NY, SUVA, UC, US); hills above Levuka, *Gillespie 4438* (BISH), *4510* (BISH, UC). Makongai: *Tothill 23* (K). Koro: Eastern slope of main ridge, *Smith 997* (BISH, GH, K, NY, UC, US). Vanua Levu: Mbua: Southern portion of Seatovo Range, *Smith 1557* (BISH, NY); Wainunu

Valley, *Fiji Dept. Agr. 15761* (SUVA), *15794* (SUVA). MATHUATA: Above Nasingasinga, *Berry 51* (SUVA); Mt. Ndrandramea, *Fiji Dept. Agr. 15386* (SUVA); Nanduri, *Tothill F435* (BISH, K); Seanggangga Plateau, *Smith 6894* (A, BISH, NY, US), *Fiji Dept. Agr. 13936* (BISH, SUVA); Tambia River area, *Howard 410* (SUVA); Mt. Numbuiloa, east of Lambasa, *Smith 6552* (A, BISH, NY, US). THAKAUNDROVE: Mt. Kasi, Yanawai River region, *Smith 1801* (BISH, GH, K, NY, UC, US); Tuvamila, Natewa Peninsula, *Howard 73* (SUVA). RAMBI: *Horne 450* (GH, K). TAVEUNI: Vicinity of Waiyevo, *Gillespie 4633* (BISH); Mt. Manuka, east of Wairiki, *Smith 8319* (BISH, GH, NY, US). MOALA: Near Maloku, *Smith 1335* (BISH, GH, K, NY, UC, US). VANUA MBALAVU: *Tothill 23a* (K); northern limestone section, *Smith 1471* (BISH, GH, K, NY, UC, US). FIJI, without further locality: *U. S. Expl. Exped.* (GH).

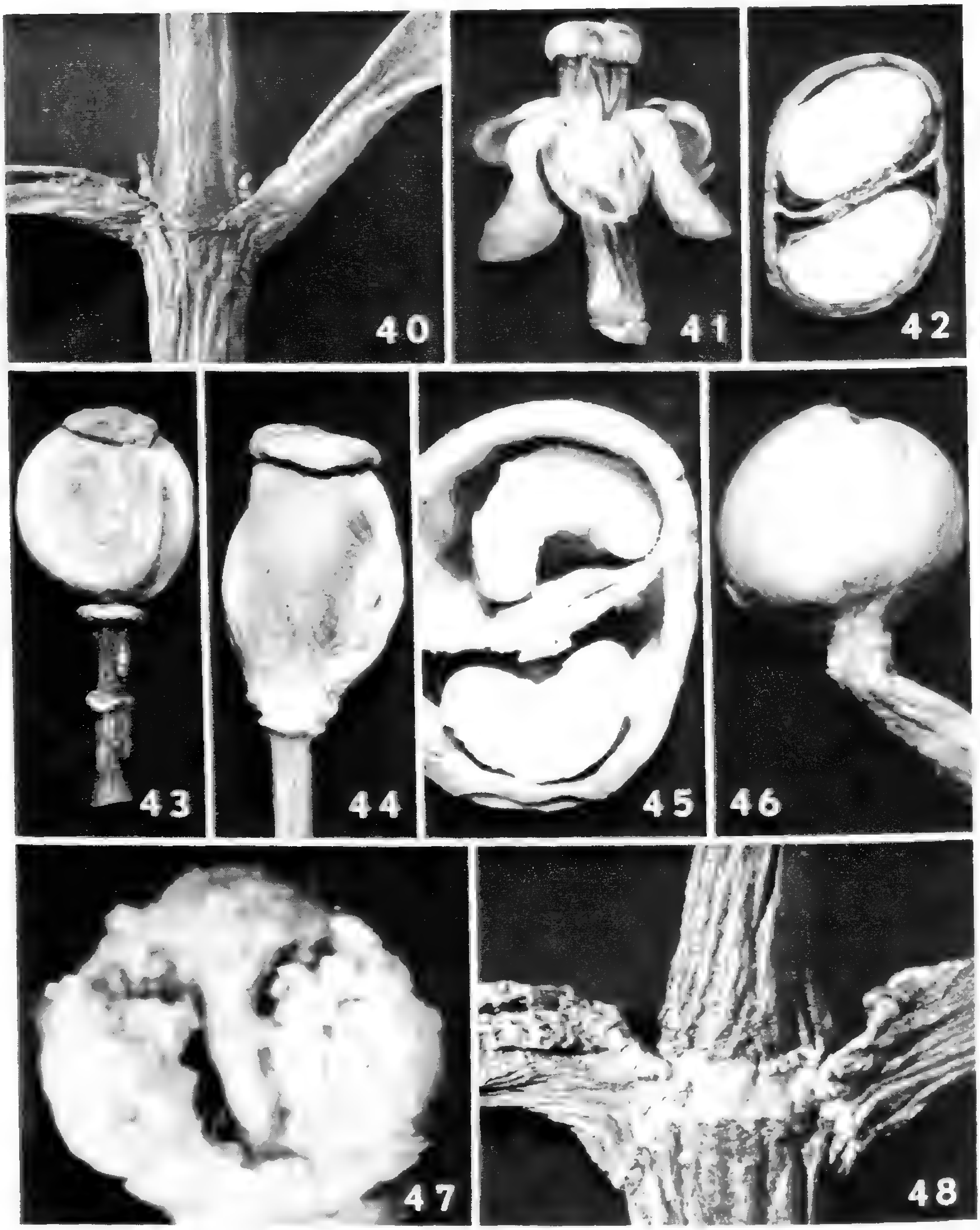
Tonga. VAVA'U: Near Mataika, north of Neiafu, *Yuncker 16204* (BISH, GH, US).

The New Hebridean specimens cited above, including those listed by Guillaumin in 1931 as *Garcinia pancheri*, are clearly referable to *G. pseudoguttifera*. They are scarcely distinguishable in facies and foliage from many Fijian collections; their androecia have phalanges (FIGURE 33) inclined to be distally divided into branches composed of several filaments, whereas in Fiji the phalanges (FIGURE 36) are often irregular and bear individual anthers, but throughout the taxon the form of phalange is highly variable as to the degree of filament-fusion. *Garcinia pancheri* Pierre (1883: **1**: XXV. *pl. 89, D*), apparently a New Caledonian endemic, differs superficially from *G. pseudoguttifera* in its smaller leaf-blades with fewer secondary nerves, its less complex and fewer-flowered ♂ inflorescences, and its smaller sepals and petals. Pierre placed his species in Sect. MUNGOTIA, the stamens being 26–32 in number and aggregated on the convex summit of a tetragonal axis. The species is not mentioned by Engler (1925), but in his treatment it would seem correctly placed in Sect. MUNGOTIA, although Vesque (1893: 274, 435) referred it to Sect. CAMBOGIA. In either case it is only remotely related to *G. pseudoguttifera*, which seems best placed in Sect. MANGOSTANA.

Seemann (1862: 433) correctly proposed the binomial *Garcinia pedicellata* for *Clusia pedicellata* Forst. f. (Fl. Ins. Austr. Prodr. 74. 1786), erroneously referring to it his no. *50*. In 1865 Seemann clarified the matter by describing *G. pseudoguttifera* and amplifying his concept of *G. pedicellata* as a presumable New Caledonian endemic. Neither Pierre (1883: **1**: XL) nor Vesque (1893: 483) has further elaborated the status of *G. pedicellata*.

2. **Garcinia vitiensis** (A. Gray) Seem. Fl. Vit. 10. 1865; Horne, A Year in Fiji, 262. 1881; Pierre, Fl. For. Cochinch. **1**: XXXVI. 1883; Vesque in DC. Monogr. Phan. **8**: 365. 1893; Engl. in Engl. & Prantl, Nat. Pflanzenfam. ed. 2. **21**: 223. 1925; Guillaumin in Jour. Arnold Arb. **12**: 227. 1931; J. W. Parham, Pl. Fiji Isl. 136. 1964, ed. 2. 195. 1972. FIGURES 40–43.

Discostigma vitiense A. Gray, Bot. U. S. Expl. Exped. **1**: 216. 1854, Atlas



FIGURES 40–43. *Garcinia vitiensis*: 40 from *Smith 9420*, 41 from *Fiji Dept. Agr. 15482*, 42 from *Smith 6818*, 43 from *Smith 5066*. 40, young branchlet and petioles, × 5; 41, ♀ flower, × 5; 42, cross section of fruit, × 2; 43, developing gynoecium, × 3. FIGURES 44–48. *Garcinia myrtifolia*: 44 from *Smith 4573*, 45 from *Parks 16260*, 46 and 47 from *Hürlimann 258*, 48 from *Degener 14651*. 44, developing gynoecium, × 3; 45, cross section of fruit, × 2; 46, ♂ flower bud, × 5; 47, androecium of ♂ flower, with phalange removed to show sterile gynoecium, × 10; 48, young branchlet and petiole-bases, × 5.

pl. 16, A. 1856; Seem. Viti, 433. 1862.
Garcinia sp. n. Horne, A Year in Fiji, 262. 1881.

Tree to 25 m. high, the branchlets 1–2.5 mm. in diameter toward apex; petioles often slender, 2–10 mm. long; leaf-blades coriaceous or thick-chartaceous, elliptic to lanceolate, 4–11 cm. long, 1.2–5 cm. broad, attenuate at base and long-decurrent on the petiole, obtuse to obtusely acuminate at apex (acumen to 10 mm. long), entire and thickened-recurved at margin, the costa plane or sharply elevated above, subprominent beneath, the secondary nerves 2–8 per centimeter, ascending or subspreading, prominulous on both sides or immersed above and plane beneath, inconspicuously joined in a collecting nerve 0.5–1 mm. within margin, obscurely interconnected by a veinlet-reticulation, this usually immersed or sometimes faintly prominulous beneath; ♂ inflorescences not seen; ♀ inflorescences axillary, fasciculate, composed of 1–4 flowers arising from an inconspicuous pulvinate peduncle, the flower-subtending bracts subcoriaceous, ovate-deltoid, 0.5–1 mm. long and broad, obtuse; pedicels subterete or subquadrangular, 4–10 mm. long, sometimes articulate near middle and there bibracteolate (bracteoles slightly smaller than bracts), distally swollen into an inconspicuously flattened receptacle; perianth composed of 3 or 4 decussate pairs of segments, 5–8 mm. in diameter at anthesis; sepals 4, rounded, the outer ones papyraceous, ovate, 1.5–3 × 1.5–2.5 mm., entire and sometimes inflexed at margin, with immersed nerves, the inner ones submembranaceous or papyraceous, suborbicular, 3–3.5 × 3–4 mm., entire or faintly erosulous at margin, with about 12 inconspicuous ascending nerves; petals 2 or 4, broadly imbricate, submembranaceous, elliptic or suborbicular, 3–4.5 mm. long, 2.5–3.5 mm. broad, rounded, entire or faintly erosulous at margin, with 12–15 inconspicuous ascending nerves; ♀ flowers with a carnose, ovoid to obovoid ovary 1–1.5 mm. long and in diameter at anthesis, the wall thick-carnose, the dissepiment thin, the locules 2, the stigma strictly sessile, carnose, pulvinate-discoid, 2–2.5 mm. in diameter, smooth or faintly tuberculate, the androecium in ♀ flowers often lacking but sometimes forming an obscure 4-lobed annulus less than 0.1 mm. high; fruits carnose at maturity, becoming coriaceous in drying, ellipsoid, 13–16 mm. long, 12–14 mm. broad, often cicatricose at base with scars of caducous perianth-segments, surmounted by the persistent stigma, this accrescent to 6 mm. in diameter, the pericarp about 0.5 mm. thick, the dissepiment persistent, thin, chartaceous, the locules 2; seeds semi-ellipsoid, filling the locules.

TYPE LOCALITY: Ovalau, Fiji; the type is a U. S. Exploring Expedition specimen, cited below.

DISTRIBUTION: The New Hebrides and Fiji, apparently rare in the former archipelago, but occasional on high islands in the second. The species occurs at elevations from near sea-level to 1,050 m., in dense, open, or rocky forest, or on forested ridges. It is a tree 3–25 m. high, sometimes compact or slender, and with pale latex; the sepals are pale green, the petals cream-colored, the stigma yellow, and the fruit turning from green to reddish purple and becoming black at maturity. No staminate flowers have been seen, but pistillate flowers have been obtained in March and April; fruits in various stages seem to persist throughout the year.

LOCAL NAME AND USE: The name *asivula* has been recorded in Mba Province, Fiji; Kajewski notes that the tree is common on Aneityum, New Hebrides, and that the wood is durable.

New Hebrides. EROMANGA: Southeastern part of island, *Schmid 3207* (P). ANEITYUM: Anelgauhat Bay, *Kajewski 840* (A, BISH, NY).

Fiji. VITI LEVU: MBA: Mt. Ndelaiyoö, west of Nandarivatu, *Smith 5066* (A, BISH, K, NY, US); vicinity of Nandarivatu, *Tothill 150* (K). SERUA: Inland from Yarawa, *Fiji Dept. For. 1048* (A, K); north of Ngaloa, in drainage of Wainінggere Creek, *Smith 9420* (BISH, GH, K, NY, UC, US). NAMOSI: Mt. Vakarongasiu, *Fiji Dept. Agr. 16130* (BISH, SUVA). NAITASIRI: Mendrausuthu Range, *Fiji Dept. Agr. 15482* (MASS, SUVA); Tholo-i-suva, *Fiji Dept. Agr. 117* (SUVA); Prince's Road, *Fiji Dept. Agr. 1621* (SUVA). REWA: Mt. Korombamba, *Fiji Dept. Agr. 16504* (BISH, MASS, SUVA), *Webster & Hildreth 14085* (MASS). OVALAU: In 1840, *U. S. Expl. Exped.* (US 11515 holotype; isotype at GH). NGAU: East of Herald Bay, inland from Sawaieke, *Smith 7760, 7761* (both BISH, GH, K, NY, SUVA, UC, US). VANUA LEVU: MATHUATA: Seanggangga Plateau, in drainage of Korovuli River, vicinity of Natua, *Smith 6690* (A, BISH, K, NY, US), *6818* (A, BISH, US); Mt. Numbuiloa, east of Lambasa, *Smith 6440* (A, US), *6577* (A, BISH, K, US); Wainikoro River, *Greenwood 700* (A, K). THAKAUNDROVE: Between Waiwai and Lumaloma, *Horne 630* (GH, K). FIJI, without further locality: *Horne 1095* (GH, K).

Although represented by many specimens with fruits in various stages, and by a few with ♀ flowers, *Garcinia vitiensis* seems still unknown as to its ♂ flowers. Nevertheless, it is certainly correctly referred to Sect. DISCOSTIGMA by Pierre, Vesque, and Engler. Most available ♀ flowers have no trace of an androecium, but sometimes a minute, 4-lobed annulus is present as a vestige.

3. **Garcinia myrtifolia** A. C. Sm. in Jour. Arnold Arb. **31**: 315. 1950; Yuncker in Bishop Mus. Bull. **220**: 188. 1959; J. W. Parham, Pl. Fiji Isl. 134. 1964, ed. 2. 194. *fig. 58.* 1972. FIGURES 44–48.

Tree to 28 m. high, the branchlets 1.5–3 mm. in diameter toward apex; petioles 4–20 (–25) mm. long; leaf-blades thin-coriaceous, oblong-ovate to elliptic, (5–) 7–17 cm. long, (3–) 4–11 cm. broad, obtuse at base and short-decurrent on the petiole, obtuse at apex or broadly cuspidate and often emarginate, entire and slightly thickened-recurved at margin, the costa stout, plane or broadly elevated and sometimes shallowly canaliculate above, prominent beneath, the secondary nerves usually 2 or 3 per centimeter, spreading, with lesser ones sometimes interspersed, usually obvious and prominulous on both sides, rarely subimmersed, inconspicuously joined in a collecting nerve 0.5–1 mm. within margin, interconnected by an irregular but often obvious veinlet-reticulation; inflorescences axillary, often to caducous leaves, fasciculate, composed of 1–5 (usually 1 or

2) flowers arising from a pulvinate peduncle, this rarely irregularly terete and to 5 mm. long, the flower-subtending bracts subcoriaceous, oblong, 1–2 mm. long and broad, obtuse, caducous; pedicels subterete, 3–12 mm. long at anthesis and to 15 mm. long in fruit, ebracteolate or sometimes bearing a pair of bracteoles resembling the bracts below middle, distally swollen into an inconspicuously flattened receptacle; flower buds subglobose, 5–7 mm. in diameter just prior to anthesis, the perianth composed of 2, 3, or 4 decussate pairs of segments; sepals usually 4, rarely 2, broadly imbricate, thin-coriaceous, suborbicular, 3–5 × 4–7 mm., rounded and entire, with 12–15 freely branching veins, these immersed or inconspicuous, the inner sepals (if present) slightly smaller; petals 2 or 4, subcarnose or submembranaceous, suborbicular or obovate, 3–6 × 3–7 mm., rounded, undulate or faintly erosulous, flabellinerved with 12–25 irregularly dichotomously branched veins, these sometimes obscure or subimmersed; ♂ flowers with an androecium composed of 500–700 anthers aggregated into 4 phalanges opposite the petals, these dendroid, irregularly several-times branched, the anthers borne on both inner and outer surfaces, subglobose, 0.2–0.3 mm. long and broad, the gynoecium present as a slender, terete, sterile ovary sometimes with a capitate-discoid stigma 2–2.5 mm. in diameter; ♀ flowers with a carnose oblong-subglobose ovary 1.5–2 mm. in diameter at anthesis, the dissepiment thin, the locules 2, the stigma strictly sessile, carnose, pulvinate-discoid, 1.5–2.5 mm. in diameter, often obscurely scrobiculate, the androecium in ♀ flowers composed of 2 or 4 carnose short-oblong phalanges, these 0.5–0.7 mm. long, about 2 mm. broad, marginally bearing a few minute sessile staminodia; fruits carnose at maturity, oblong-ellipsoid, 20–45 mm. long, 15–30 mm. broad, surmounted by the persistent stigma, this accrescent to 7 mm. in diameter, the pericarp 0.5–2 mm. thick, often becoming brittle in drying, the dissepiment persistent, the locules 2; seeds oblong, filling the locules, the testa brittle.

TYPE LOCALITY: Southern slopes of Nausori Highlands, Nandronga & Navosa Province, Viti Levu, Fiji; the type is *Smith 4573*, cited below.

DISTRIBUTION: Fiji and Tonga, now known to occur with some frequency on high islands of the former group, but known only on Kao and 'Eua in the latter. In both archipelagoes the species is found at elevations above 50 m., in Fiji up to 915 m. and in Tonga up to 400 m., in primary, secondary, open, or rocky forest, sometimes on limestone. It has been recorded as a tree 3–28 m. high, sometimes spreading or slender, with a trunk up to 41 cm. in diameter and with yellow or brownish latex; the flowers are white or greenish white, and the fruit turns greenish white to dull yellow, red-tinged, or purple at maturity. Flowers and fruits may be anticipated in any season.

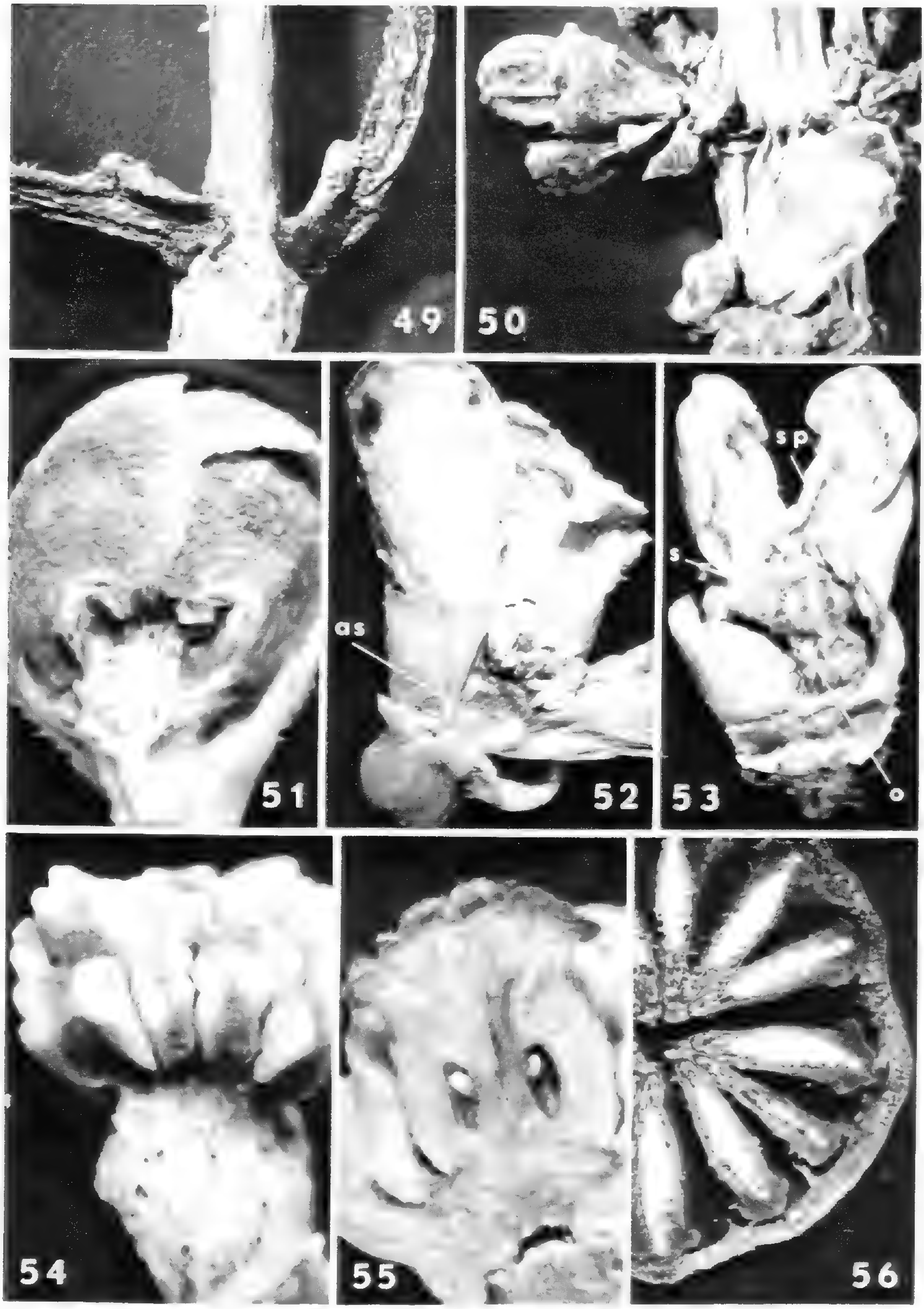
LOCAL NAMES AND USES: The species is uniformly known in Fiji as *laumbu*, and it is considered a timber tree, often used as posts for houses and other buildings. In Tonga a local name is *feto'omaka*, and the bark is said to be used for scenting oil.

Fiji. VITI LEVU: MBA: Mt. Evans Range, *Greeenwood 1152* (A, BISH, K, UC, US), *1215* (BISH, UC, US); vicinity of Nandarivatu, *Mead 1990* (K), *Gillespie 3397* (BISH, GH, UC), *4401.2* (BISH); Sovutawambu, near Nandarivatu, *Degener 14651* (A, BISH, NY); Mt. Tomanivi, *Smith 5128* (A, BISH, K, NY, US). NANDRONGA & NAVOSA: *Fiji Dept. Agr. 14298* (MASS, SUVA); Nausori Highlands, *Fiji Dept. For. 1140* (K, SUVA), *1141* (K), *Fiji Dept. Agr. 15607* (SUVA), *15631* (MASS, SUVA); southern slopes of Nausori Highlands, in drainage of Namosi Creek above Tumbenasolo, May 29, 1947, *Smith 4573* (A holotype; isotypes at BISH, K, NY, US); near Vanualevu Village, *Berry 81* (SUVA). SERUA: Upper Navua River, Vunamaravu, *Fiji Dept. Agr. 15503* (SUVA); Navutulevu, *Fiji Dept. For. 653* (SUVA); inland from Namboutini, *Fiji Dept. For. R–40* (K), *816* (or *592*) (BISH, SUVA), *1127* (K, SUVA), *1130* (K, SUVA), *Berry 77* (SUVA); inland from Korovou, *Nasoqiri 12* (K); inland from Ngaloa, *Fiji Dept. For. G–13* (K), *817* (or *593*) (BISH, SUVA), *1137* (K, SUVA), *1139* (K, SUVA), *Fiji Dept. Agr. 13778* (BISH, SUVA). NAMOSI: Between Korombasambasanga Range and Mt. Naitarandamu, *Smith 8459* (BISH, GH, K, NY, SUVA, UC, US); northern base of Korombasambasanga Range, *Smith 8683* (BISH, GH, K, NY, SUVA, UC, US); Saliandrau, *Fiji Dept. Agr. 14244* (SUVA); Wairoro Creek, *Fiji Dept. Agr. 13812* (BISH, SUVA); Nambukavesi Creek, *Damanu NI–26* (K), *Fiji Dept. For. 488* (SUVA), *652* (SUVA); Wainandoi River, *Vaisewa 17* (K). NAITASIRI: Navolau Forest, *Fiji Dept. Agr. 118* (SUVA); Navuakethe district, *Fiji Dept. Agr. 235* (SUVA), *236* (SUVA); Waimanu River, *Fiji Dept. Agr. 15680* (SUVA), *15836* (SUVA); Tholo-i-suva, *Fiji Dept. Agr. 12196* (SUVA), *14610* (BISH, SUVA), *16490* (BISH, MASS, SUVA); vicinity of Nasinu, *Gillespie 3667* (BISH, GH, UC, US). KANDAVU: *Fiji Dept. Agr. 11938* (SUVA); Naikorokoro, *Fiji Dept. For. 651* (SUVA). VANUA LEVU: MATHUATA: Ndongotuki Tikina, *Howard 149* (SUVA, US); Vunivia River, *Howard 401* (SUVA). FIJI, without further locality: *Fiji Dept. Agr. 684* (SUVA), *16495* (SUVA), *L.12633* (SUVA), *Bola 46* (K), *Howard 65* (SUVA).

Tonga. KAO: In rocky or open forest, *Yuncker 15908* (BISH, US), *15955* (BISH, GH, US). 'EUA: *Parks 16318* (BISH, UC); near center of island, *Yuncker 15381* (BISH, UC, US), *Parks 16260* (BISH, GH, UC); east of Pangai, *Hürlimann 151* (US); Powell Plantation, *Parks 16005* (BISH, UC); between Fuai and eastern ridge, *Hürlimann 174* (US); top of eastern ridge, *Hürlimann 258* (US).

Garcinia myrtifolia, originally described from two ♀ specimens, is now well known from abundant material obtained in Fiji and Tonga. Its relationship is definitely with *G. vitiensis*, from which only differences of degree distinguish it. However, it is usually recognizable even when sterile by its comparatively large, obtuse, more obviously nerved, and longer-petiolate leaves. Its flowers and fruits are larger than those of *G. vitiensis*, and its androecia are more obvious in the ♀ flowers. Staminate flowers are not yet known for *G. vitiensis*, but one may anticipate that they also will show slight androecial differences.

4. **Garcinia sessilis** (Forst. f.) Seem. Viti, 433. 1862, Fl. Vit. 10. 1865; Horne, A Year in Fiji, 262. 1881; Pierre, Fl. For. Cochinch. 1: XXVII. 1883; Hemsl. in Jour. Linn. Soc. Bot. **30**: 169. 1894; Engl. in Engl. & Prantl, Nat. Pflanzenfam. ed. 2. **21**: 226. 1925; Christophersen in Bishop Mus. Bull. **128**: 149. 1935; Yuncker in op. cit. **220**: 189. 1959; J. W. Parham, Pl. Fiji Isl. 135. 1964, ed. 2. 195.



FIGURES 49–56. *Garcinia sessilis*: 49 from *Kajewski 564*, 50 from *Smith 8588*, 51 and 54 from *Yuncker 16118*, 52, 53, and 55 from *Setchell & Parks 15560a*, 56 from *Greenwood 936*. 49, young branchlet and petiole-bases, × 5; 50, young ♂ inflorescences, × 5; 51, ♂ flower bud, with sepals and 1 petal removed, × 10; 52, ♂ flower, with 2 sepals and 1 petal removed, × 5; 53, ♀ flower, with

1972; B. E. V. Parham in New Zealand Dept. Sci. Indust. Res. Inform. Ser. **85**: 111. 1972. FIGURES 49–56.

Clusia sessilis Forst. f. Fl. Ins. Austr. Prodr. 74. 1786.
Garcinia roxburghii sensu Seem. in Bonplandia **9**: 254. 1861; non Wight.
Garcinia sp. n. Horne, A Year in Fiji, 262. 1881.

Tree to 20 m. high, the branchlets 1–2.5 mm. in diameter toward apex; petioles slender, 5–20 mm. long, the basal cavity remaining obvious and sometimes distally cucullate; leaf-blades chartaceous to membranaceous, infrequently thin-coriaceous, elliptic to ovate- or obovate-elliptic, (4–) 6–15 cm. long, (1.5–) 3–7.5 cm. broad, obtuse to acute at base and decurrent on the petiole, cuspidate to acuminate at apex (tip to 15 mm. long, obtuse to acute, sometimes slender), entire and narrowly recurved at margin, often with apparent secretory canals sinuously parallel to the secondary nerves, the costa shallowly canaliculate to slightly raised above, prominent beneath, the secondary nerves 1–3 per centimeter, subascending, prominulous on both sides, irregularly anastomosing toward margin but not joined by a symmetrical collecting nerve, interconnected by a lax veinlet-reticulation; inflorescences axillary, often to caducous leaves, glomerulate-fasciculate, usually composed of 3–9 flowers arising from an irregularly subglobose or short-cylindric peduncle, this 1–5 mm. long and 1–3 mm. in diameter, the flower-subtending bracts subcoriaceous, ovate or deltoid, 1–1.5 × 1–2 mm., obtuse, usually paired at base of each flower; flowers essentially sessile or borne on pedicels rarely as long as 2.5 mm., these becoming stout in fruit but remaining inconspicuous, ebracteolate or sometimes bearing a pair of bracteoles slightly larger than the bracts; flowers ellipsoid in bud and 3–5 mm. in diameter, at anthesis spreading to 16 mm. in diameter, the perianth composed of 4 decussate pairs of segments; calyx cupuliform, the sepals 4, broadly imbricate, chartaceous or thin-carnose, longitudinally traversed by numerous parallel subsinuous secretory canals, broadly orbicular or reniform, 1.7–4 × 2–5 mm., rounded, entire, persistent in fruit; petals 4, appearing subvalvate in very young bud but soon becoming marginally imbricate and then broadly imbricate, centrally thick-carnose, thin-margined, cruciate and spreading at anthesis, oblong or obovate, 5–8 × 3–6 mm., rounded at apex, obscurely erosulous, with longitudinal sinuously parallel secretory canals; ♂ flowers with a central androecium 2–3 mm. long, this composed of 7–30 stamens fused into a carnose subquadrangular stalk 1–2 mm. long and broad, the anthers sessile or essentially so on apex of androecial stalk, oblong-obovoid, 0.6–1.2 mm. long, 0.4–0.7 mm. broad, the thecae 2, longitudinal, subequal to the truncate connective, the gynoecium none; ♀ flowers with a thick-carnose oblong gynoecium about 3 mm. long at anthesis, the ovary ellipsoid-cylindric, the locules (6–) 10–13, the stigma sessile, pulvinate-discoid, about 2.5 mm. in diameter, copiously and conspicuously tuberculate with

---

2 sepals and 2 petals removed, × 5; 54, androecium, × 20; 55, section through gynoecium, × 10; 56, cross section of fruit, × 2. as = androecium-stalk; sp = sterile phalange; s = stigma; o = ovary.

projections 0.2–0.4 mm. long, marginally irregularly (6–) 10–13-lobed, the androecium in ♀ flowers composed of 4–7 phalanges adherent to the petals but irregular in respect to them, each phalange 2–3 mm. long and with 1–4 terminal anthers, these resembling those of ♂ flowers but sterile; fruits carnose at maturity but drying strongly (6–) 10–13-costate, subglobose to ellipsoid, sometimes imperfectly developed and oblique, up to 50 mm. long and broad, surmounted by the persistent stigma, this slightly accrescent to 4 mm. in diameter, the exocarp thin, the mesocarp carnose when fresh, drying subcoriaceous, 0.5–1.5 mm. thick, becoming spongy inward between the (6–) 10–13 pyrenes and there dissipating into air-chambers, the pyrenes narrowly oblong and laterally compressed or lunate, up to 30 × 10 × 4 mm., acute to obtuse on the inner edge, obtuse to narrowly rounded dorsally, separated by air-chambers in dried fruits, the endocarp of each pyrene bony, 0.2–1 mm. thick, usually distinct but sometimes interconnected by lateral protrusions toward the outer edge, the seeds laterally compressed and lunate, the outer layer of the testa spongy and resiniferous, compressed by the developing seeds.

TYPE LOCALITY: Tongatapu Island, Tonga; the type material was obtained by the Forsters on Cook's Second Voyage. The BM specimen, cited below, may be taken as the lectotype.

DISTRIBUTION: Santa Cruz Islands, Fiji, Tonga, and Samoa; now known from many collections in Fiji and Tonga, occurring from sea-level to (in Fiji) 1,150 m., in dense or dry forest, open thickets, and on edges of mangrove swamps. It has been noted as a tree 4–20 m. high, with a trunk diameter of 30 cm. and with abundant yellowish latex. The petals are pale yellow and pink-tinged to coral-red or carmine; the ovary and stigma are green at anthesis; the fruits are yellowish white to red at maturity, the pyrenes being embedded in white pulp. Flowers and fruits have been noted throughout the year in Fiji. The species is known to us from only single collections in both the Santa Cruz Islands and Samoa. The material from Vanikoro is sterile, with old glomerulate inflorescences from which the flowers have fallen, but there seems no reason to doubt its identity or its indigenousness. The occurrence of *Garcinia sessilis* in the Solomon Islands is indicated by Whitmore (1966: 183), but such specimens have not been examined. The Samoan collection certainly represents the species and was obtained from hillside forest near Apia. Because the species is rare in Samoa, and because of the similarity to Tongan collections in its local name and uses, one may question the indigenous occurrence of the species in Samoa; it may have become sparingly naturalized there from a cultivated introduction.

LOCAL NAMES AND USES: The usual names for this taxon in Fiji are *mbuluwai* or *laumbu*, but also recorded are *mbulumangayalewa* and *elala*, the last from Kambara and perhaps reflecting Tongan influence. The species is considered a timber tree in Fiji and is used in house construction. In Tonga the staminate plant is known as *heilala* and the pistillate as *bulu*; the faintly fragrant flowers are there used in necklaces and the leaves are said to be used medicinally. Eames reports the Samoan name as *seilala* and states that the bark is used medicinally. In both Tonga and Samoa the flowers are used to scent oil.

Santa Cruz Islands. VANIKORO: *Kajewski 564* (A).

Fiji. VITI LEVU: MBA: Mountains near Lautoka, *Greenwood 936* (A, BISH, K), *936A* (A, BISH, K, P); slopes of escarpment north of Nandarivatu, *Smith 6268* (A, BISH, K, NY, US); vicinity of Nandarivatu, *Parks 20661* (BISH, SUVA, UC), *Gillespie 4331* (BISH, GH, UC, US); Waimongge Creek, Nandrau track, *Berry 86* (BISH, MASS, SUVA). NANDRONGA & NAVOSA: North of Komave, *St. John 18951* (BISH, US). SERUA: Between Navua River and Wainiyavu Creek, near Namuamua, *Smith 9020* (BISH, GH, K, NY, SUVA, UC, US); inland from Ngaloa, *Smith 9205, 9411* (both BISH, GH, K, NY, SUVA, UC, US), *Fiji Dept. Agr. 14118* (SUVA). NAMOSI: Vicinity of Wainimakutu, Wainavindrau Creek, *Smith 8588* (BISH, GH, K, NY, SUVA, UC, US); vicinity of Namosi, *Seemann 51* (BM, GH, K, P); vicinity of Namuamua, *Gillespie 3021* (BISH, GH, UC), *3055* (BISH, GH, NY, UC, US). NAMOSI-NAITASIRI boundary: Mt. Naitarandamu, *Gillespie 3245* (BISH, UC). RA: Vicinity of Nasukamai, *Gillespie 4692.3* (BISH, GH, UC). NAITASIRI: Vicinity of Viria, *Meebold 17065* (K), *18501* (K); Central Road, *Tothill 401* (K); vicinity of Nasinu, *Gillespie 3636* (BISH), *3665* (BISH, GH, NY, UC, US). OVALAU: Lovoni Valley, *Horne 185* (GH, K), *Fiji Dept. Agr. 13297* (SUVA). VANUA LEVU: MATHUATA: Near Mt. Ndrandramea, *Fiji Dept. Agr. 15387* (A, SUVA). TAVEUNI: Vicinity of Wairiki, *Gillespie 4757* (BISH, GH, NY, UC). VANUA MBALAVU: Northern limestone section, *Smith 1482* (BISH, GH, K, NY, UC, US). KAMBARA: On limestone, *Smith 1274* (BISH, GH, K, NY, UC, US).

Tonga. VAVA'U: *Wilder*, June 28, 1925 (BISH); near Houma, *Yuncker 16118* (BISH, GH, US). NOMUKA: Between sea and central lake, *Yuncker 15864* (BISH, US). TONGATAPU: *J. R. & G. Forster* (BM lectotype); Vaikele, experimental gardens, loose ♂ and ♀ flowers from different plants, *Setchell & Parks 15560a* (UC); vicinity of Nuku'alofa, *Setchell & Parks 15178* (NY, UC), *15235* (BISH, GH, UC, US); near Bea, *Setchell & Parks 15560* (UC), *15600* (UC); near Haake, *Setchell & Parks 15347* (UC); below Lavagatoga, *Yuncker 15177* (BISH, US). 'EUA: Near Pangai, *Yuncker 15464* (BISH, US); plantation area, M'ua, *Bristol 1912* (BISH). TONGA, without further locality: *McKern 33* (BISH), *78* (BISH).

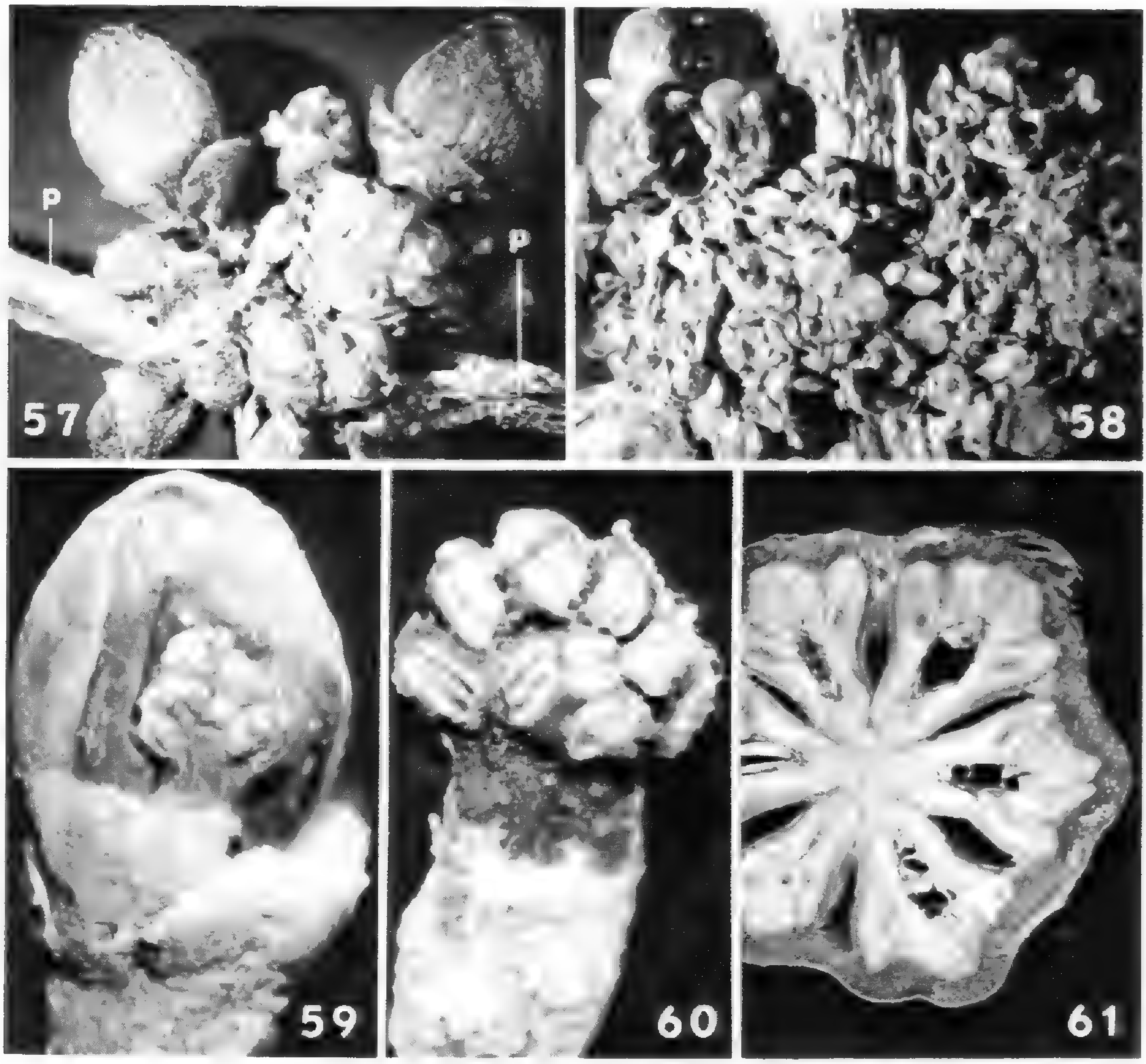
Samoa. UPOLU: Vicinity of Apia, *Eames 71* (BISH, NY).

The androecium (FIGURE 54) of *Garcinia sessilis* is composed of a central stalk bearing sessile or essentially sessile anthers on its summit, the anthers not being appreciably grouped into four short fascicles. In the ♀ flowers, the sterile androecium (FIGURE 53) is indeed composed of separate fascicles appressed to the petals, but apparently Pierre's 1883 treatment was based entirely on *Seemann 51*, a ♂ collection. In that treatment Sect. TETRACLINIA was described on the sole basis of *G. sessilis*. This section now seems unnecessary; in Engler's (1925) system *G. sessilis* seems in all respects to fall into Sect. MUNGOTIA.

5. **Garcinia adinantha** A. C. Sm. & S. Darwin, sp. nov. FIGURES 57–61.

Garcinia sp. n. Horne, A Year in Fiji, 262. 1881.

Arbor ad 20 m. alta, ramulis apicem versus 1.5–4 mm. diametro; petiolis (2–) 7–25 mm. longis, foliorum laminis subcoriaceis vel chartaceis, ellipti-



Figures 57–61. *Garcinia adinantha*: 57, 59, and 60 from *Smith 1827*, 58 from *Smith 9372*, 61 from *Smith 1644*. 57, ♂ inflorescences at distal node, × 5; 58, ♂ inflorescences from older branchlet, × 5; 59, ♂ flower, with 1 petal removed, × 10; 60, androecium, × 20; 61, cross section of fruit, × 2. p = petiole.

cis vel ovato- vel elliptico-lanceolatis, (4–) 7–19 cm. longis, (1.5–) 3–7.5 cm. latis, basi acutis vel attenuatis et in petiolum longe decurrentibus, apice breviter cuspidatis (raro late obtusis) vel gradatim acuminatis (apice ipso obtuso, 5–20 mm. longo), integris, canalibus secretoriis manifestis inter nervos secundarios sinuose parallelis interdum ornatis, costa crassa supra elevata vel plana et interdum vadose canaliculata subtus prominenti, nervis secundariis 1–3 per centimetrum subadscendentibus utrinque prominulis marginem versus irregulariter anastomosantibus rete venularum obscure reticulato immerso vel interdum subtus leviter prominulo interconnexis; inflorescentiis axillaribus vel supra cicatrices foliorum caducorum enatis, glomerulato-fasciculatis, plerumque 15–40(raro distalibus 3–7)-floris, floribus e pedunculo semigloboso cicatricibus florum caducorum verruculoso orientibus, flore ipso bracteis 2 vel pluribus congestis late deltoideis 0.5–2 × 1–2 mm. obtusis caducis subtento; floribus subsessilibus vel pedicellis ebracteolatis 1–1.5 mm. longis et diametro; floribus ♂ solum visis in alabastro vetere ellipsoideis 4–5 mm. diametro; calyce vadose cupuliformi, sepalis 4 decussatis subcarnosis orbicularibus vel late ovatis, 1.5–2 × 1.5–3 mm., apice rotundatis vel late obtusis, minute erosulis, sub fructu persistentibus; corollae alabastro inconspicue carinato, petalis 2 carnosis valvatis ellipticis 5–6 × 4–5.5 mm. apice rotundatis lateraliter inter se late adpressis; androecio simplici 1–2.5 mm. longo, staminibus 8–20, stipite carnoso subtereti 0.6–2 mm. longo basim petalorum adpresso, antheris sessilibus subquadrato-ellipsoideis, 0.4–0.7 mm. longis, 0.3–0.5 mm. latis, thecis 2 longitudinalibus connectivo truncato subaequalibus, gynoecio nullo; fructibus in vivo carnosis in sicco obtuse 5–8-costatis ellipsoideis interdum inaequilateralibus, maximis visis ad 35 × 25 mm. stigmate persistenti ornatis, eo sessili discoideo 2–3 mm. diametro conspicue tuberculato margine 5–8-crenato, endocarpio tenui, mesocarpio in vivo 2–3 mm. crasso et canalibus resiniferis perducto demum spongioso et in cavernulas aerias inter pyrenas 5–8 dissipato, pyrenis oblongo-cuneiformibus ad 25 × 10 × 8 mm. margine interiore obtusis exteriore irregulariter rotundatis in sicco cavernulis aeriis separatis, endocarpio pyrenae omnis corneo 1–4 mm. crasso, seminibus complanato-lunatis, testae strato exteriore spongioso resinifero semine crescenti compresso.

TYPE LOCALITY: Mt. Kasi, Yanawai River region, Thakaundrove Province, Vanua Levu, Fiji; the type is *Smith 1827*, cited below.

DISTRIBUTION: Endemic to Fiji and thus far known only from Viti Levu and Vanua Levu, occurring at elevations of 50–1,050 m. in dense or dry forest. It has been recorded as a tree 3–20 m. high, with yellow latex; the young petals vary from salmon-pink to dull red. Flower buds have been obtained throughout the year, and fruits in April and May.

LOCAL NAMES AND USE: Names recorded from Vanua Levu are *raumba*, *mbulu*, *mbulumanga*, and *mbulumangayalewa*. Like the related *Garcinia sessilis*, it is considered a useful timber tree.

Fiji. VITI LEVU: MBA: Nandende Levu, Mt. Evans Range, *Fiji Dept. Agr. 14835* (BISH, SUVA); northern portion of Mt. Evans Range, between Mt. Vatuyanitu and Mt. Natondra, *Smith 4379* (A, BISH, K, NY, US). SERUA: Hills between Wainినggere and Waisese Creeks, between Ngaloa and Wainiyambia, *Smith 9372* (BISH, GH, K, NY, SUVA, UC, US). NAMOSI: Mt. Vakarongasiu, *Gillespie 3256* (BISH, GH, UC), *Fiji Dept. Agr. 14704* (BISH, SUVA), *16129* (SUVA). NAITASIRI: Vicinity of Navuso, *Fiji Dept. Agr. 12595* (MASS, SUVA); vicinity of Tamavua, *Gillespie 2042* (BISH, UC). REWA: Vicinity of Na Vasi, *Horne 734* (GH, K). VANUA LEVU: MBUA: Navotuvotu, summit of Mt. Seatura, *Smith 1644* (BISH, GH, K, NY, UC, US); Tambulotu, Wainunu Valley, *Fiji Dept. Agr. 15754* (SUVA); vicinity of Thongea, Wainunu River, *Fiji Dept. Agr. 15768* (SUVA), *15771* (BISH, SUVA, US). MATHUATA: Vicinity of Nasingasinga, *Berry 53* (SUVA), *54* (SUVA). THAKAUNDROVE: Mt. Kasi, Yanawai River region, May 11, 1934, *Smith 1827* (BISH holotype; isotypes at GH, K, NY, UC, US). FIJI, without further locality: *Berry 30* (SUVA).

This new taxon is proposed with a certain amount of diffidence, but we believe it unwise to expand the concept of *Garcinia sessilis* to include it.

Several of the cited specimens bear young ♂ flowers, the most advanced being those of the type collection. All flowers examined have only two petals, whereas all flowers of specimens included by us in *G. sessilis* have four petals. In *G. vitiensis* and *G. myrtifolia*, as noted above, we have included in our concepts both 2-petalled and 4-petalled plants, but there the petals are similarly imbricate in both instances. The two petals of *G. adinantha*, however, are valvate and with tightly appressed thick margins (FIGURE 59), at least in advanced bud, whereas the four petals of *G. sessilis* in a similar stage of development (FIGURE 51) are already broadly imbricate and thin-margined. The two taxa have otherwise different facies, *G. adinantha* having comparatively thick-textured leaf-blades that tend in general to be more gradually narrowed at the base and long-decurrent on the petiole, whereas those of typical *G. sessilis* are thinner in texture and less tapering basally. The ♂ flowers of the new species are the more numerous (FIGURE 58), usually 15–40 per congested, multibracteate inflorescence, while those of *G. sessilis* are fewer in number (FIGURE 50) and rarely with more than two subtending bracts per flower. On the basis of the fruits now available there are also differences between the two taxa. Of *G. adinantha*, only *Smith 1644* and *4379* bear fruits, but several fruiting collections of *G. sessilis* are available. The fruits of *G. sessilis* (FIGURE 56) typically have a mesocarp 0.5–1.5 mm. thick and dry to a sharply 10–13-costate (rarely 6-costate) form; the 10–13 (rarely as few as 6) pyrenes have bony endocarps 0.2–1 mm. thick and are obtuse to narrowly rounded dorsally. The fruits of *G. adinantha* (FIGURE 61), in contrast, have a mesocarp 2–3 mm. thick and dry to an obtusely 5–8-costate form; the 5–8 pyrenes are comparatively broad and rounded on the dorsal face and have horny endocarps 1–4 mm. thick.

Of the cited collections, *Gillespie 2042* and *3256* and *Fiji Dept. Agr. 14704* are extreme in their small, short-petiolate leaves with very conspicuous secretory canals, but in other respects, including flower buds with two petals, they agree with the concept here outlined.

CULTIVATED SPECIES

Garcinia dulcis (Roxb.) Kurz in Jour. Asiat. Soc. Bengal 43(2): 88. 1874.

Xanthochymus dulcis Roxb. Pl. Coromand. 3: 66. *t. 270.* 1820.

No herbarium record supports the occurrence in our area of this Malesian tree, but it has been observed in the Botanical Gardens in Suva, Fiji.

Garcinia mangostana L. Sp. Pl. 443. 1753; J. W. Parham, Pl. Fiji Isl. 134. 1964, ed. 2. 192. 1972.

Fiji. VANUA MBALAVU: Lomaloma Botanical Gardens, *Fiji Dept. Agr. 10212* (SUVA).

The Malesian *mangosteen*, while not easy to establish outside its native area, was successfully introduced in Fiji in the 1880's and a few trees are still to be seen there.

Garcinia xanthochymus Hook. f. Fl. Brit. Ind. 1: 269. 1874; J. W. Parham, Pl. Fiji Isl. ed. 2. 195. 1972.

Fiji. VANUA LEVU: MATHUATA: Lambasa, *Fiji Dept. Agr. L.11589* (SUVA). **Samoa.** Without definite locality: *Guest 8* (BISH).

The *sour mangosteen*, a native of southeastern Asia, is probably moderately common in cultivation in Fiji.

Mammea americana L. Sp. Pl. 512. 1753; J. W. Parham in Agr. J. Dept. Agr. Fiji **19**: 102. 1948, Pl. Fiji Isl. ed. 2. 195. 1972.

Fiji. VITI LEVU: REWA: Suva, *Fiji Dept. Agr. 3126* (SUVA). **Samoa.** Without definite locality: *Guest 1* (BISH), *4* (BISH).

The American *mammey apple* or *mammee apple* is now widely cultivated throughout the tropics as an ornamental tree.

Mesua ferrea L. Sp. Pl. 515. 1753.

Fiji. VITI LEVU: NAITASIRI: Nanduruloulou, *Fiji Dept. Agr. 5523* (SUVA).

This Indo-Malesian tree, with many uses in its native area, was probably experimentally introduced into Fiji, but it may no longer occur there in cultivation.

REFERENCES

ENGLER, A. Guttiferae. *In*: ENGLER, A., & K. PRANTL. Nat. Pflanzenfam. ed. 2. **21**: 154–237. 1925.

KOSTERMANS, A. J. G. H. The genera *Mammea* L. and *Ochrocarpos* Thou. For. Serv. Indones., Div. Plann. (Djawatan Kehutanan Indonesia, Bagian Planologi Kehutanan), 9–15. 1956.

———. A monograph of the Asiatic and Pacific species of *Mammea* L. (Guttiferae). Commun. For. Res. Inst. Indones. (Pengumaman Lembaga Pusat Penjelidikan Kehutanan, Indonesia) **72**: 1–63. 1961.

LAUTERBACH, C. Beiträge zur Flora von Papuasien. IX. Die Guttiferen Papuasiens. Bot. Jahrb. **58**: 1–49. 1922.

MERRILL, E. D. *Ochrocarpos odoratus* (Rafinesque) Merrill, a new name for a much named species, with a new species from Samoa. Jour. Arnold Arb. **26**: 93–96. 1945.

PIERRE, L. Flore forestière de la Cochinchine. 5 vols. (and Register) in 26 fascicles. *pl. 1–400.* 1879–1907.

PLANCHON, J. E., & J. TRIANA. Mémoire sur la famille des Guttifères. Ann. Sci. Nat. IV Bot. **13**: 306–376; **14**: 226–367; **15**: 240–319; **16**: 263–308. 1860–62.

SEEMANN, B. Viti: An account of a government mission to the Vitian or Fijian Islands in the years 1860–61. 447 pp. 1862.

SMITH, A. C. Studies of Papuasian plants, III. Jour. Arnold Arb. **22**: 343–374. 1941.

———. Studies of Pacific Island plants. XXVII. The genus *Gardenia* (Rubiaceae) in the Fijian Region. Am. Jour. Bot. **61**: 109–128. 1974.

VESQUE, J. Epharmosis, sive materiae ad instruendam anatomiam systematis naturalis. Pars secunda. Genitalia foliaque Garciniearium et Calophyllearum. 1–30. *tab. I–CLXII.* 1889.

———. Guttiferae. DC. Monogr. Phan. **8**: 1–669. 1893.

Whitmore, T. C. Guide to the forests of the British Solomon Islands. For. Record No. 2, For. Dept. Brit. Solomon Islands Protectorate. 208 pp. 1966.

———. Notes on the systematy of Solomon Island's plants and some of their New Guinea relatives, IV. Guttiferae. Gard. Bull. Singapore **22**: 9–16. 1967.

Department of Botany
University of Massachusetts
Amherst, Massachusetts 01002

THREE NEW SPECIES OF PHALERIA (THYMELAEACEAE) FROM PAPUASIA

P. F. STEVENS

IN THE LAST TEN YEARS quite extensive collections have been made in the highlands of Papua New Guinea, and these collections have included several numbers of the genus *Phaleria* Jack (Thymelaeaceae). The few specimens of *Phaleria* from the highlands known to Ding Hou in his account of the genus in the *Flora Malesiana* (Hou 1960a, b) were named by him as *P. coccinea* (Gaud.) F. Muell., *P. macrocarpa* (Scheff.) Boerl., *P. nisidai* Kan., and *P. perrottetiana* (Decne.) F.-Vill. Highland specimens determined as *P. nisidai* and *P. macrocarpa* represent two hitherto undescribed species, *P. okapensis* and *P. pilistyla*, and a third previously undescribed species, *P. longituba*, is also represented in these new collections.

Phaleria coccinea and *P. perrottetiana*, the two other species reported from the highlands, are not common there, although the latter species has given rise to a local highland race discussed below. However, both these species, as well as the other six species of *Phaleria* recognized by Hou (1960b) as occurring in the area from Malaya to New Guinea, grow in the lowlands of Papuasia. The identification of some of the lowland species is difficult, and it is possible that too many names are being used in Papuasia for these lowland taxa. Careful collections are needed to assess the significance of the variation in the characters of inflorescence position and size, floral tube length and pubescence, and ovary pubescence, all of which are used to distinguish the species. The three new taxa described here are, by contrast, very distinct and cannot be confused either with the other Malesian species or with those from the Fijian area, an important center of distribution of the genus (Smith 1942). The island of New Guinea appears to be another center of the genus, both in the number of species present and in their diversity.

The new species can be determined easily with little disruption of the key in Ding Hou's treatment (Hou 1960b). If couplet 5 in that key is removed, *P. nisidai*, the species identified in that couplet, and the new species described in this paper may be keyed out in a series of introductory couplets as follows.

1. Flowers 8–8.5 cm. long; lamina 5.2–9 × 2.5–3.2 cm. .... *P. longituba* sp. nov.
1. Flowers less than 4.5 cm. long; lamina usually larger.
    2. Anthers included, ± sessile; stigma included.
        3. Inflorescences borne on twigs, 2–5-flowered; flowers with erect calyx lobes. .... *P. okapensis* sp. nov.
        3. Inflorescences usually terminal and/or in the axils of the uppermost or adjacent leaves, 8–20-flowered; flowers with reflexed calyx lobes.

4. Inflorescences 9–20-flowered, involucral bracts 2, ca. 4 × 2 mm.; style with short crisped hairs along its entire length. . . . . *P. pilistyla* sp. nov.
4. Inflorescences 8–12-flowered, involucral bracts 4, 7–10 × 4–6 mm.; style with long hairs only at the base. *P. nisidai* Kan.

2. Anthers and stigma usually exserted, if included then anthers with prominent filaments and floral tube more than 1 cm. in diameter at the throat.
5. As in lead 1 in Hou (1960b, p. 16).

Phaleria longituba P. F. Stevens, sp. nov.

A ceteris speciebus *Phaleriae Malesianae* in tubo florali duplo longiore differt.

Arbor ca. 18 m. alta, trunco recto, cortice griseo. Petiolus 5–6 mm. longus; lamina elliptica vel plus minusve obovalis, 5.2–9 × 2.5–3.5 cm., apice acuminata (acumine usque ad 1.5 cm. longo), basi acuta, glabra, tenuiter coriacea, costa supra plus minusve plana, infra elevata, venatione brochidodroma, nervis lateralibus 6–9-jugis, rete venularum supra inconspicuo, infra elevato. Inflorescentiae capitatae terminales vel in axillis summis crescentes; pedunculus 0.7–1.7 cm. longus 5–9 flores gerens, basi bracteis paucis parvis decussatis praeditus; bracteae involucrales non cognitae. Flos fragrans, 8–8.5 cm. longus, tubo florali apicem versus aliquantum dilatato, apice 3.5–4 mm. in diametro, glabro vel intus pilis perpaucis praedito, rubro-albo, lobis calycibus 4, patentibus, 7–8 × 5–6.5 mm., apicibus rotundatis, intus pilis brevibus praeditis; squamae petalae obscurae; stamina 8 leviter exserta antheris 1–1.6 mm. longis; stamina antisepala ad orificium tubi inserta cum filamentis ca. 2.8–3.5 mm. longis; stamina alternisepala 4.5–5.5 mm. infra orificium tubi inserta cum filamentis 6–8 mm. longis; ovarium ca. 1.3 mm. longum, glabrum, disco ca. 1 mm. alto margine fimbriato; stylus 7–7.5 cm. longus, glaber; stigma clavatum 2.5–3 × 0.8 mm. Fructus immaturus solus cognitus, subsphaericus, ca. 6 × 6 mm.

TYPE: Papua New Guinea, Western Highlands District, Kuna, ca. 2135 m., 17.v.1966, *NGF 27699* coll. *Streimann & Kairo* (holotype LAE; isotypes A, CANB, NSW; further duplicates sent from LAE to L, K, BO, BRI, SING, PNH, and BISH).

The length of the floral tube, together with the small, prominently acuminate lamina, makes *Phaleria longituba* a very easily recognized species; other Malesian species of *Phaleria* have floral tubes less than 4.5 cm. long. *P. longituba* is perhaps closest to *P. acuminata* (A. Gray) Gilg, from Samoa, Tonga, and Fiji, but the floral tube in the latter species is pubescent within and less than 6 cm. long; the ovary and style base usually have long hairs.

The type of *Phaleria longituba* was collected in *Nothofagus*-dominated montane forest.

Phaleria okapensis P. F. Stevens, sp. nov.

A ceteris speciebus *Phaleriae Malesianae* in inflorescentiis parvis rami-floris, lobis calycibus erectis, et staminibus styloque non exsertis differt.

Frutex usque ad 3 m. altus. Petiolus 4–6 mm. longus; lamina oblanceolata vel obovata, raro plus minusve elliptica, 7–15.5 × 1.5–5.7 cm., apices acuminata, basi acuta vel decurrenti, glabra, subchartacea, costa supra plana vel leviter elevata infra elevata, venatione brochidodroma, nervis lateralibus 6–11-jugis, rete venularum utrinque elevato. Inflorescentiae capitatae (interdum 2 vel 3 simul) ex axillis infimis foliatis vel in axillis defoliatis crescentes; pedunculus 0.5–3.5 mm. longus 2–5 flores gerens, basi bracteis parvis decussatis praeditus; bracteae involucrales 4 vel 5, plus minusve obovatae, ca. 3 mm. longae, caducae. Flos 1.6–2.4 cm. longus, tubo florali infundibulari apice 4–6 mm. in diametro, albo, intus roseo, glabro, lobis calycibus 4, raro 5, erectis, 3–5 × 3–4 mm., apicibus rotundatis, intus indumento denso puberulo praeditis; stamina 8, raro 10, ad orificium tubi inserta (stamina alternisepala 0.5–1 mm. infra stamina antisepala inserta), filamentis 0.5–1 mm. longis, antheris 0.5–1.1 mm. longis; ovarium ca. 1.3 mm. longum, glabrum, disco ca. 0.5 mm. alto margine fimbriato; stylus 1.2–1.9 cm. longus, glaber; stigma capitatum 0.5–1 mm. longum. Fructus ruber, subsphaericus (in spiritu servatus), 1.5 × 1.5 cm., apice mucronatus, pericarpio tenui, seminibus duobus.

TYPE: Papua New Guinea, Eastern Highlands District, near Waisa, ca. 24 km. SW of Okapa, 1525 m., 25.xi.1964, *Hartley 13119* (holotype LAE, isotype A).

Additional specimens seen. **Papua New Guinea.** EASTERN HIGHLANDS: base of Kratke Range ca. 19 km. S of Aiyura, ca. 1830 m., *Hartley 12173* (A, LAE); Kini Creek, NE of Mt. Michael, 1980 m., *NGF 11389* coll. *Womersley* (LAE); near Okapa Patrol Post, 1980 m., *NGF 9564* coll. *White* (LAE); near Okapa, ca. 1830 m., *Hornabrook 41* (LAE); Okapa Road, 1920 m., *Robbins 954* (CANB, LAE); behind village of Nemuka, near Kainantu, *Sayers 178* (CANB); 16 km. SE of Obura, 2104 m., *Hays 82* (LAE); *ibid.*, 1954 m., *Hays 282* (LAE); limestone near Chuave, *Anonymous* (LAE).

Phaleria okapensis has ramiflorous inflorescences like those of *P. macrocarpa* (Scheff.) Boerl. but is otherwise very different from that species: it has monomorphic flowers with erect calyx lobes (in *P. macrocarpa* the flowers are heteromorphic and the calyx lobes are reflexed) and small fruits (the fruits of *P. macrocarpa* are at least 3 × 3 cm. and the pericarp is thick). *NGF 9564* was cited under *P. macrocarpa* by Hou (1960b), but its inclusion in that species may have been an error; see the discussion under *P. pilistyla.*

The collection cited above made from "limestone near Chuave" consists of material preserved in spirit, viz. inflorescences with fully opened flowers on twigs and a single fruit also attached to a twig. The description of the fruit was made from this collection.

The leaves of *Hartley 12173* were tested for alkaloids but gave no reaction in the field test used (Hartley *et al.* 1973). This specimen was identified as *Phaleria sogerensis* S. Moore. *P. okapensis* differs from *P. sogerensis* in its inflorescences that are borne on the twigs rather than terminally or in the upper leaf axils; in its erect, rather than reflexed, calyx lobes; and in its included, rather than exserted, anthers and stigma.

Phaleria perrottetiana (Decne.) F.-Vill.

A group of specimens collected at 1400 to 1675 meters altitude in the Bulolo-Wau-Aseki area of the Morobe District, Papua New Guinea, although close to *P. perrottetiana*, may eventually deserve formal taxonomic recognition. *NGF 8364*, from Skindewai on the Wau to Mabo road, was determined as *P. perrottetiana* by Ding Hou (1960a), but both it and the other specimens cited here differ from that species in having inflorescences with fewer than ten flowers; these flowers are densely pubescent outside. The other specimens are *NGF 39057*, *39064*, *47751*, and *47674*.

Phaleria pilistyla P. F. Stevens, sp. nov.

A ceteris speciebus *Phaleriae Malesianae* in stylo cum pilis parvis pro tota longitudine praedito differt.

Frutex erectus vel arborescens vel arbor parva usque ad 8 m. alta, cortice brunneo pustulis praedito. Petiolus 5–7 mm. longus; lamina ovata, (2–)4–8 × (0.9–)2–3.5 cm., apice acuta vel acuminata, basi acuta vel rotundata, glabra, subcoriacea, costa supra plana vel leviter elevata infra elevata, venatione brochidodroma, nervis lateralibus 4–8-jugis, rete venularum utrinque obscuro vel leviter elevato. Inflorescentiae capitatae terminales vel in axillis summis raro inferioribus crescentes; pedunculus 0.6–1.3 cm. longus, basi (raro secus pedunculum) bracteis parvis decussatis praeditus, interdum bracteis duabus usque ad 2 mm. longis medio pedunculi ortis, 9–20 flores gerens; bracteae involucrales plerumque 2, ovatae, ca. 4 × 2 mm., caducae. Flos 2.5–2.8 cm. longus, tubo florali roseo apice ca. 2 mm. in diametro, extus glabro, intus indumento puberulo praedito, lobis calycibus 4, patentibus vel recurvatis, intus albis et cum indumento puberulo praeditis; stamina 8, inclusa, antheris ovoideis ca. 0.7 mm. longis; stamina antisepala ad orificium tubi inserta cum filamentis ca. 0.5 mm. longis; stamina alternisepala ca. 3 mm. infra orificium tubi inserta cum filamentis ca. 1 mm. longis; ovarium 1–1.5 mm. longum apice puberulum, disco ca. 0.7 mm. alto margine fimbriato; stylus 1.4–1.6 cm. longus pilis parvis densis praeditus; stigma clavatum 2–3 mm. longum. Fructus niger, subsphaericus, ca. 1.4 × 1.2 cm., apice basique acutus, pericarpio tenui ca. 0.5 mm. crasso, seminibus duobus.

TYPE: Papua New Guinea, Eastern Highlands District, Goroka Subdistrict, Fatima River bank, 2350 m., 28.v.1965, *NGF 22581* coll. *Millar* (holotype LAE, isotype CANB, further duplicates sent from LAE to L, A, K, BO, BRI, and SING).

Additional specimens seen. **Papua New Guinea.** WESTERN HIGHLANDS: Porget logging area ca. 19 km. N of Wabag, ca. 2285 m., *NGF 11317* coll. *Womersley* (A, LAE); Yobobos grassland area, Laiagam Subdistrict, ca. 2590 m., *Hoogland & Schodde 7554* (A, CANB, LAE); near Lake Inim, Wabag, 2530 m., *ANU 2771* coll. *Flenley* (LAE); ca. 6 km. NW of Kupalis, near Wabag, 2560 m., *ANU 2334* coll. *Flenley* (A, LAE); Lagaip-Kandep Divide near Kiskau, 2338 m., *Rob-*

bins 3227 (CANB). EASTERN HIGHLANDS: Fatima River, Marafunga, 2350 m., *NGF 24557* coll. *Womersley* (A, LAE); *ibid.*, 2340 m., *NGF 40637* coll. *Millar* (LAE); Mt. Wilhelm, ca. 2600 m., *Borgmann 293* (LAE).

Phaleria pilistyla has been confused with *P. nisidai* Kan. (*NGF 9564* & *11317*, see Hou, 1960a, b) from which it may be distinguished by its often relatively broader lamina, its inflorescence with more numerous flowers (there are less than twelve flowers per inflorescence in *P. nisidai*), its fewer and smaller involucral bracts, and also by its style that has short hairs along its entire length. Those species of *Phaleria* with hairy styles have longer hairs only at the very base. *P. pilistyla* also has 4-merous flowers and a clavate stigma, while *P. nisidai* has flowers predominantly 5-merous and a capitate stigma only ca. 1 mm. long.

Pronounced transverse cracks develop on older twigs of *P. pilistyla*. Similar cracks occur on twigs of other members of the Thymelaeaceae, e.g., *Phaleria capitata* Jack, *Wikstroemia indica* (L.) C. A. Mey, and *W. venosa* Merr. & Perry.

The field label of *ANU 2334* records that the bark was used as a source of fiber, presumably for the Enga people, and was used with *Eleocharis* (*E. dulcis* (Burm. f.) Henschel is probably the species involved) in the manufacture of "grass" skirts. The Enga name given for *Phaleria pilistyla* is "Worapi."

ACKNOWLEDGMENTS

The Directors of the herbaria cited are thanked for their permission to examine material of *Phaleria*; thanks are also due to Dr. B. G. Schubert for helpful comments on the manuscript.

LITERATURE CITED

HARTLEY, T. G., E. A. DUNSTONE, J. S. FITZGERALD, S. R. JOHNS, & J. A. LAMBERTON. 1973. A survey of New Guinea plants for alkaloids. Lloydia **36**: 217–319.

HOU, D. 1960a. Identification lists of Malesian specimens 9. Thymelaeaceae. Flora Malesiana Foundation, Leyden.

———. 1960b. "Thymelaeaceae" in Flora Malesiana 1. **6**(1): 1–48.

SMITH, A. C. (& collaborators). 1942. Fijian plant studies, II. Botanical results of the 1940–41 cruise of the "Cheng Ho." Sargentia **1**: 1–148.

ARNOLD ARBORETUM
HARVARD UNIVERSITY
CAMBRIDGE, MASSACHUSETTS 02138

BREEDING MECHANISMS IN TREES NATIVE TO TROPICAL FLORIDA — A MORPHOLOGICAL ASSESSMENT *

P. B. Tomlinson

Some recent discussion of probable speciation processes in tropical rain forest trees has centered on breeding mechanisms (Fedorov, 1966; Ashton, 1969) and has served to draw attention to our ignorance of the topic. There are no extended observations on breeding mechanisms in a wide range of tropical trees, so the subject has been discussed largely at a hypothetical level. One assumption is that since individuals of the same species tend to be widely separated in tropical rain forests, self-fertilization (autogamy) must be the rule (Federov, 1966). Ashton (1969), on the other hand, on the basis of observation suggests that outcrossing (xenogamy) is the rule. An extended assessment by Bawa (1973), based on controlled pollinations in a lowland semideciduous forest in Costa Rica, demonstrates a high degree of outcrossing, chiefly on the basis of a high incidence (52 per cent) of self-incompatible species. Bawa estimates that at least 75 per cent of the species have an obligate xenogamous mode of reproduction. Whether it is safe to regard these results as typical of other communities is uncertain, but they indicate interesting trends. In this context also, the ability of some bees to travel long distances in tropical environments (Janzen, 1971) is suggestive of an agent assisting outcrossing, although experimental evidence that bees cover these distances in transferring pollen has not yet been provided, nor is it likely to be done easily.

Bawa provides a lengthy discussion of the kinds of problems encountered in work of this sort. Since it is necessary to make extended observations on sizable populations of a great variety of tree species in natural environments, progress is likely to be slow. In this sense Bawa's observations represent only a pioneering venture. The practical importance of this type of work is not in doubt. For example, cultivation of avocado (*Persea americana*) is scarcely possible without a knowledge of its complex pollination mechanism, one of the few examples of the breeding mechanisms of a tropical tree which has been studied in detail. The floral mechanism of avocado is outlined by Wood (1958, p. 331) and involves dianthesis, that is, two periods of opening on successive days with an intermediate period when the flower is closed. The stage of flower development is synchronous throughout a single tree. Two types of tree, "A" and "B," are recognized whose periods of flowering are staggered

---

* "Tree" is used in a rather generous sense. I include a number of native woody plants which mostly occur as tall shrubs. The selection of species is undeniably arbitrary, but certainly includes all species which would conform to a forester's definition of a tree, excluding only a few very rare species which have not been investigated.

so that cross-pollination is possible. Flowers are protogynous; in type "A" the stigmas are receptive on the morning of the first day, the flowers close in the afternoon to re-open on the afternoon of the second day; in type "B" the carpellate stage is in the afternoon of the first day, the staminate phase is in the morning of the second day. Avocado cultivation requires that cultivars in one orchard should be of both "A" and "B" type in order to permit fruit set.

The present account represents only a superficial and elementary contribution to this field, using a part of the native woody flora of South Florida. It is a preliminary assessment of kinds of breeding mechanisms of the trees of this area, based solely on floral morphology and without the complementary experiments that Bawa (1973) demonstrates are essential for a more reliable analysis. However, since I am unlikely to have the opportunity to extend this study in the required direction, the information is presented with the hope that botanists in South Florida will continue the work. Although South Florida is wholly extratropical, this study is relevant to students of tropical biology because the species represented are predominantly West Indian or circum-Caribbean in their distribution, are within their natural range, and grow in natural habitats. The uniqueness of this tree flora in the continental United States has been emphasized previously (e.g., Sargent, 1905); it represents an outlier of tropical vegetation surrounded by, and to a certain extent penetrated by, temperate tree-species of the flora of the eastern United States. Nevertheless the biological potential of this area for extended investigation goes largely unrecognized by American scientists.

Quite elementary observations are still to be made on this flora. The existence of dioecism in the genus *Coccoloba* (150 species, Polygonaceae) was not recognized clearly until described by Howard (1949) in West Indian species. Previously Lindau, a monographer of the genus, had, in ignorance of the dioecious condition in certain dried collections, based separate species on staminate and carpellate flowers of what is now known to be a single species. Two species of *Coccoloba* (*C. diversifolia* and *C. uvifera*) are native to South Florida, and quite casual observation demonstrates the essentially dioecious condition readily, albeit with the recognition that there is some additional polymorphism which requires further study.

The existence of monoecism in the commercially valuable West Indian mahogany (*Swietenia mahagoni*) seems not to have been recognized generally until described by Lee (1967) from specimens cultivated in Taiwan. Previously *Swietenia* had been described as having perfect flowers. *Swietenia mahagoni*, native in South Florida, shows monoecism clearly, in confirmation of the earlier record. The implication of this simple observation in an understanding of the breeding mechanism of *Swietenia* is significant, although the functions of the two kinds of flowers in the pollination "strategy" are (as in most monoecious species) not clear. The special case of *Swietenia* is only one example in the Meliaceae, a family which now seems to be generally diclinous, although this fact again was not generally recognized until 1963 (see Styles, 1972).

Dioecism in populations of *Citharexylum fruticosum* native to South Florida was first described by Tomlinson and Fawcett (1972), and it is possible that again we have a large genus in which dioecism is more widespread than has hitherto been appreciated (Arechavaleta, 1902; Tomlinson, 1973).

Other examples of floral polymorphism which have been previously overlooked or neglected are described in this article. Undoubtedly yet others will be brought to light. These examples serve to demonstrate the value of the woody flora of South Florida as a potential source of information about growth characteristics of tropical trees, which is of general value to biologists (cf. also Gill & Tomlinson, 1971; Tomlinson & Craighead, 1972).

THE WOODY FLORA OF SOUTH FLORIDA

The area considered is that covered by Long and Lakela's "Flora" (1971), including the Florida Keys, South Florida south of Lake Okeechobee, plus a coastal strip on each side of the peninsula whose limits correspond approximately to the 50° F. January isotherm (Tomlinson & Craighead, 1972). Treating this woody flora in a somewhat general sense to include a number of low shrubs which only exceptionally reach any marked stature, I include 114 species. The great majority of these (98) can be described as "tropical," since they represent species with a wider distribution in tropical America, but are, in South Florida, at the northern limit of their range. The remaining 16 species are, in contrast, "temperate," with a wider range in the eastern United States, so that in South Florida they are almost at their southern limit. These northern species are indicated by the letter N in subsequent lists.

METHODS

Observations have been made on fresh specimens collected mainly in the wild at flowering times, supplemented by collections from trees in cultivation (mainly at Fairchild Tropical Garden). No attempt has been made to establish the incidence of self-incompatibility by experimental procedures. Dissections of fresh flowers have been examined under a Wild M-5 stereomicroscope. Representative black-and-white illustrations of all species in the flora have been made to form the basis of a more extended publication. The illustrations which accompany the present article are, however, original.

RESULTS

A preliminary subdivision is made between species that show dioecism or monoecism (dicliny) and species with perfect flowers (monocliny). In some instances the distinction is not absolute, and one group of species is best discussed under the separate category of polymorphic flowers, since perfect and imperfect flowers are found on the same tree. Within the general group of species with perfect flowers morphological or functional subcategories can be recognized, notably heterostyly and dichogamy, where there is strong indication of an outcrossing mechanism.

Within each group certain species are discussed in greater detail to supplement or substantiate the categorization. It is appreciated that my observations are based only on limited samples and may be incorrect when larger populations are sampled both within South Florida and elsewhere. It seems evident, as for example with *Acer rubrum*, that there can be differences in breeding mechanisms in different parts of the range of one species.

1. **Species dioecious** (with separate staminate[1] and carpellate[1] flowers, each kind of flower restricted to a particular individual; i.e. separate staminate and carpellate trees).

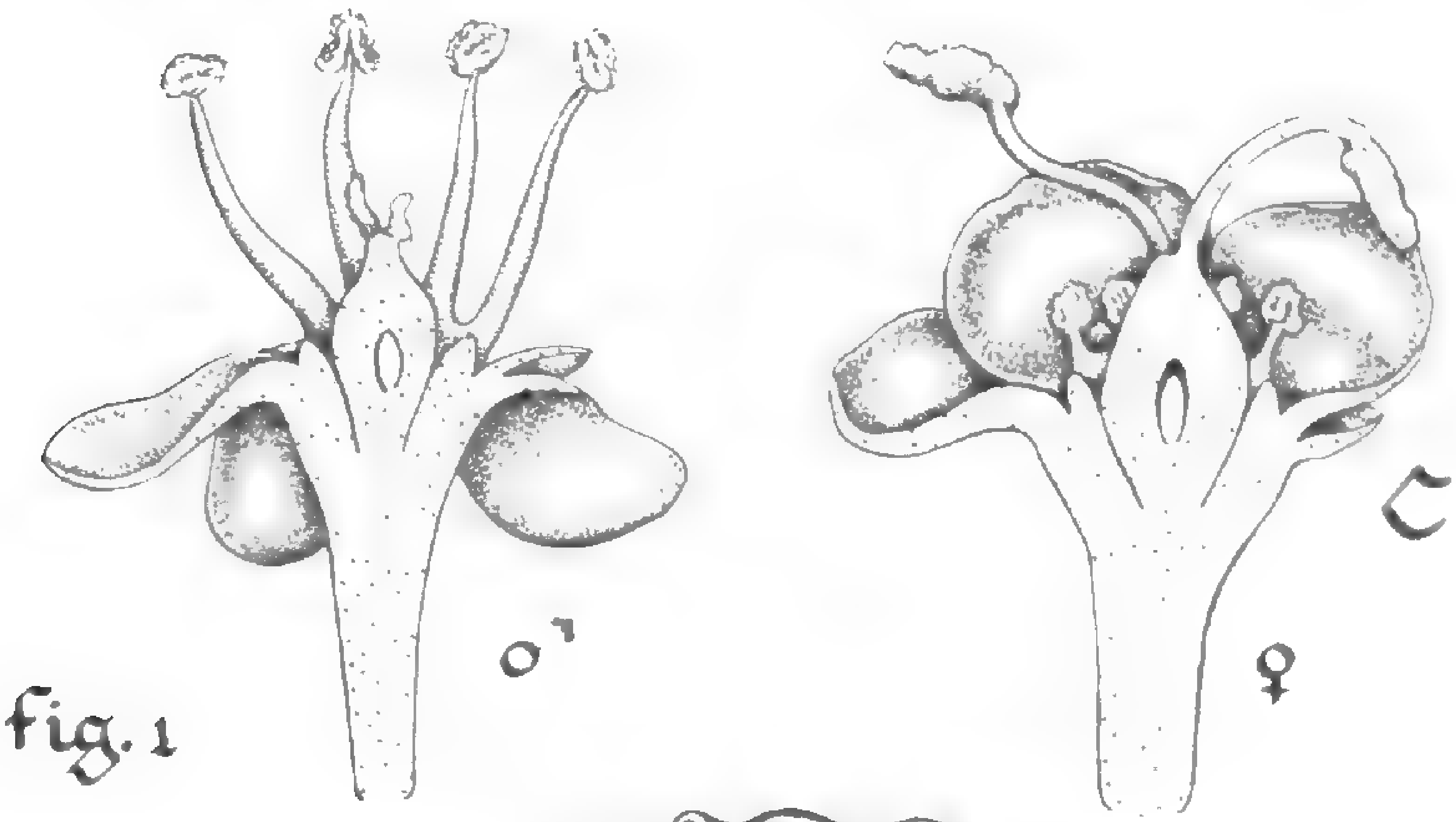
Alvaradoa amorphoides *
Baccharis glomeruliflora * N
Baccharis halimifolia * N
Casasia clusiifolia (Figure 2)
Citharexylum fruticosum
Clusia rosea
Coccoloba laurifolia
Coccoloba uvifera (Figure 1)
Conocarpus erectus *
Diospyros virginiana N
Dodonaea viscosa (see p. 281).
Drypetes diversifolia *
Drypetes lateriflora *
Exothea paniculata (see p. 281)
Forestiera segregata *
Fraxinus caroliniana * N
Gyminda latifolia
Ilex cassine
Ilex krugiana
Laguncularia racemosa *
Metopium toxiferum
Myrica cerifera * N
Picramnia pentandra *
Pisonia rotundata
Rhus copallina N
Salix caroliniana N
Savia bahamensis
Schaefferia frutescens
Simarouba glauca
Torrubia (Guapira) longifolia
Zanthoxylum fagara

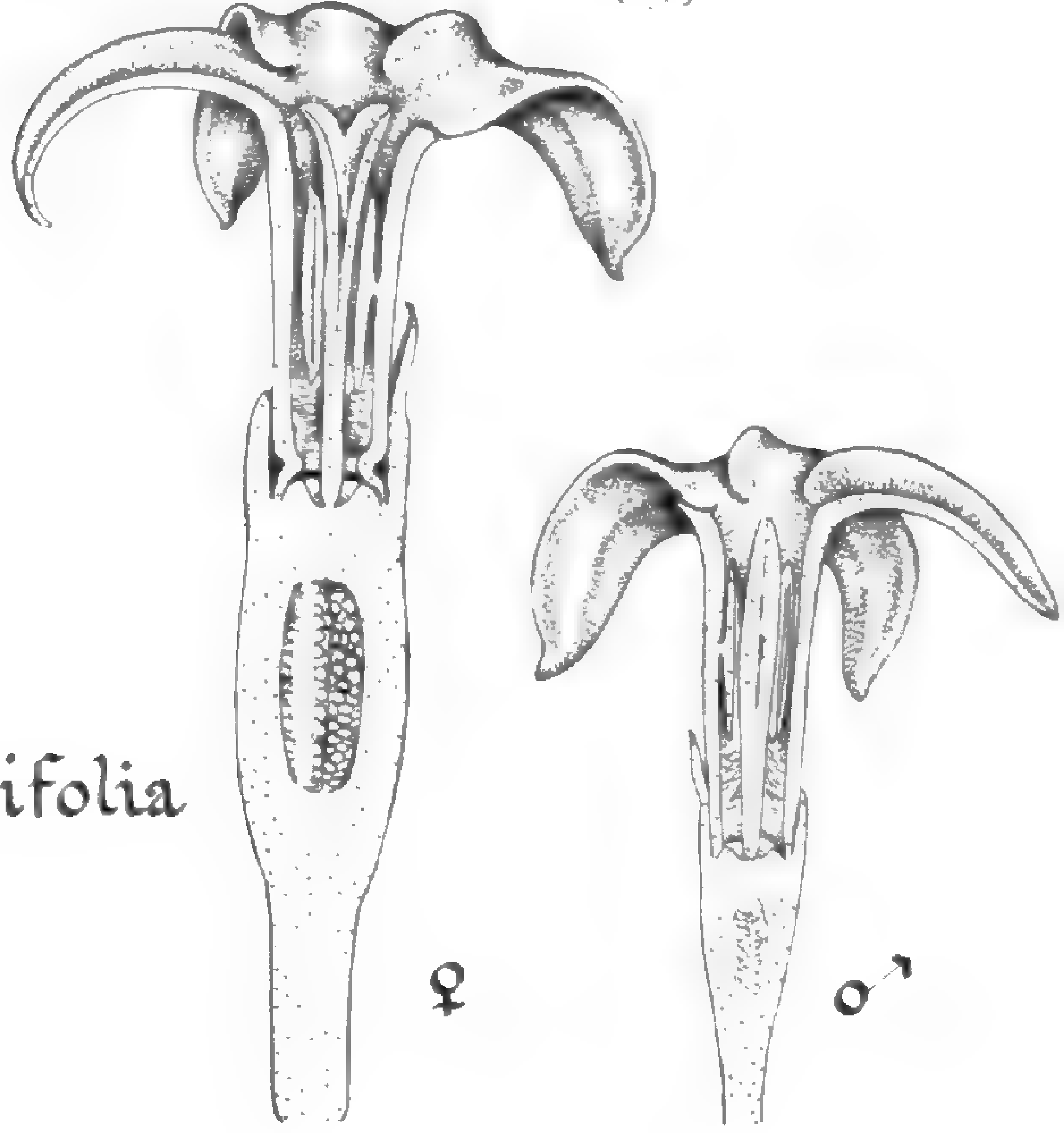
* Probably wind-pollinated (see p. 287).
N North temperate distribution.

Most of the species in this list show evident dioecism, although in some the distinction between staminate and carpellate flowers has been overlooked until recently. *Coccoloba* species have already been mentioned. Representative staminate and carpellate flowers of *Coccoloba uvifera* are shown in Figure 1. The dioecious condition in *Casasia clusiifolia* (Rubiaceae) is not usually recognized, since staminate flowers may have a quite well-developed ovary (Figure 2). The distinction between staminate trees (without fruit) and carpellate trees (with fruit) in the field seems abso-

---

[1] The terms "male" and "female" are avoided because of the ambiguities pointed out by Thieret (1973); "staminate" and "carpellate" are used at the suggestion of Dr. C. E. Wood, Jr.





FIGURES 1 and 2. EXAMPLES OF DIOECISM; flowers in longitudinal section: 1, **Coccoloba uvifera,** × 6, staminate flower to the left, carpellate flower to the right; 2, **Casasia clusiifolia,** × 1 1/2, carpellate flower to the left, staminate flower to the right.

lute. Furthermore, staminate flowers are borne in groups; carpellate flowers are solitary and usually larger.

The dioecious condition in *Citharexylum fruticosum* is described by Tomlinson and Fawcett (1972).

Clusia rosea (Guttiferae) represents a peculiar situation. I have seen no staminate flowers, and trees (mainly in cultivation) seem to be wholly carpellate, their flowers being without functional stamens. Nevertheless, the tree produces fruit with viable seeds by which it can be propagated. Presumably we are dealing here with an example of apomixis, although this needs to be verified. Some circumstantial evidence for apomixis is the observation by Dr. C. E. Wood, Jr. (pers. comm.) that *Clusia rosea* is polyembryonic.

For some species in this list there are records of perfect flowers, as in *Conocarpus* and *Simarouba*, but in my experience staminate and carpellate flowers and trees are quite distinct. In some trees of *Laguncularia* the carpellate flowers may well have functional stamens, but this has not been verified.

The correlation between dioecism and wind-pollination will be commented upon later.

2. **Species monoecious** (with separate staminate and carpellate flowers, but these borne on the same individual; i.e. trees all of one kind).

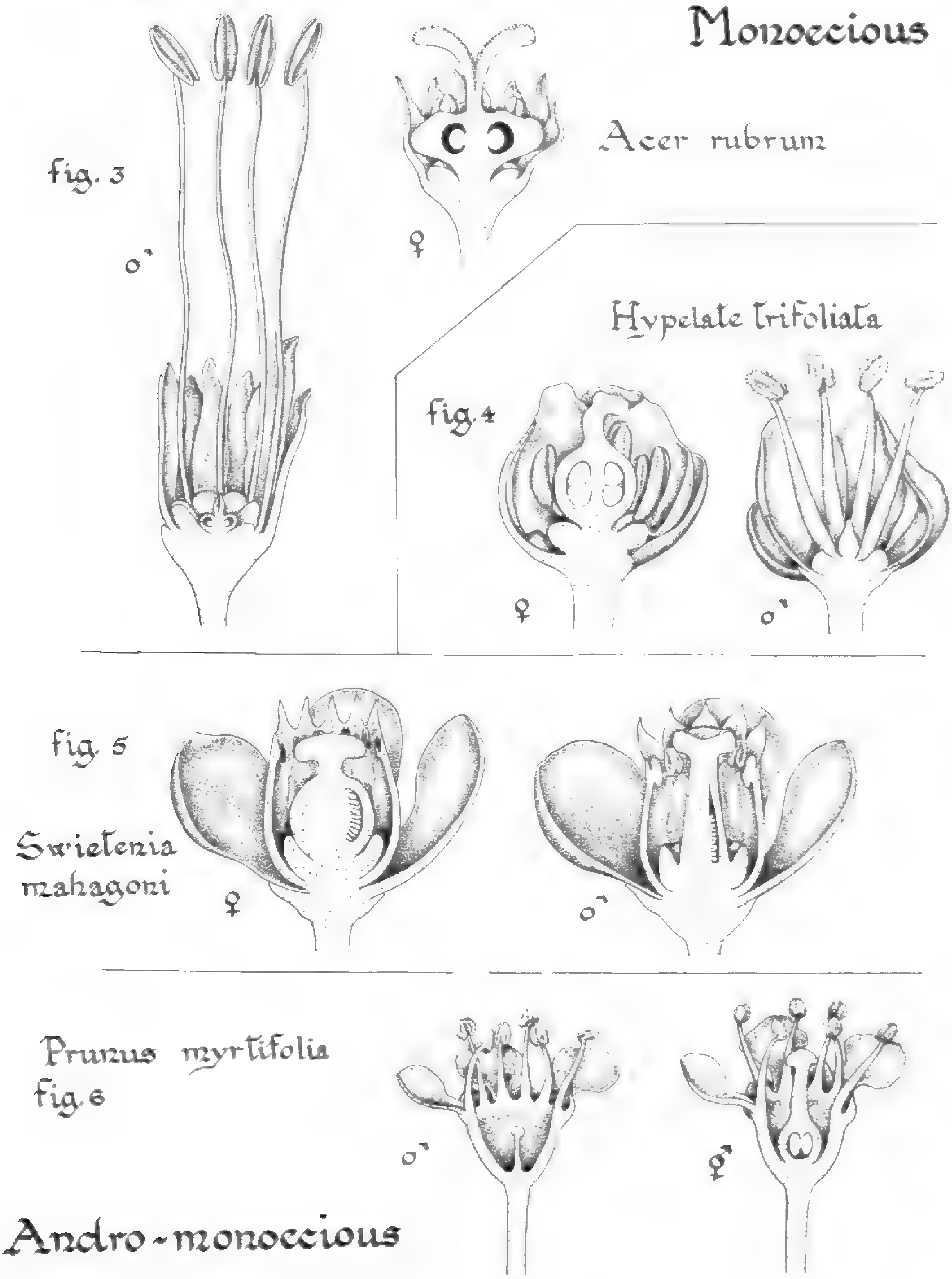
Acer rubrum * N (Figure 3)
Celtis laevigata * N
Cupania glabra
Ficus aurea
Ficus citrifolia
Gymnanthes (Ateramnus) lucida
Hippomane mancinella
Hypelate trifoliata (Figure 4)
Morus rubra * N
Quercus virginiana * N
Sapindus saponaria
Swietenia mahagoni (Figure 5)
Trema micrantha
Trema lamarckiana

* Probably wind-pollinated.
N North temperate distribution.

Acer rubrum (Aceraceae) is included unequivocally in this category. In much of its range *Acer rubrum* is regarded as dioecious (Dr. C. E. Wood, Jr., pers. comm.), but in South Florida I have seen flowers as different as those illustrated in Figure 3 on one individual. There is nevertheless a strong tendency toward the development of flowers which appear to be perfect. However, though well-developed stamens may seemingly be formed, one cannot be too sure that their pollen is functional. In view of the proven demonstration of physiological races in *Acer rubrum* (Perry & Wang Chi Wu,1960), it would be unwise to generalize about its floral mechanism on the basis of a limited sample from one locality. This description of polymorphic flowers applies equally well to the two sapindaceous representatives, *Hypelate* (e.g., Figure 4) and *Sapindus*, which tend toward the polygamous condition of the Sapindaceae generally, often producing perfect as well as staminate and carpellate flowers. *Cupania glabra*, in the same family, is monoecious, but dioecism may be suggested where flowers of one sex predominate. Further field study might indicate that *Hypelate* and *Sapindus* would be better included in the polymorphic group where I have included two other members of the family (p. 281). *Trema* (Ulmaceae) also requires further extended observation. Trees are dioecious superficially, since they bear a preponderance of one flower type at a particular time and some trees seem to fruit more heavily than others. Incipient dioecism seems to exist here.

The remaining examples are more familiar and clear cut. The situation with regard to *Swietenia* has been described in the introduction, and representative staminate and carpellate flowers are illustrated in Figure 5.

The special case of monoecism in *Ficus* is discussed separately (p. 283).



FIGURES 3–6. EXAMPLES OF MONOECISM AND ANDRO-MONOECISM; flowers in longitudinal section: 3. **Acer rubrum,** × 5. staminate flower to the left, carpellate flower to the right; 4. **Hypelate trifoliata,** × 6. carpellate flower to the left, staminate flower to the right; 5. **Swietenia mahagoni,** × 8. carpellate flower to the left, staminate flower to the right; 6. **Prunus myrtifolia,** × 6. staminate flower to the left, perfect flower to the right.

3. Species with perfect (hermaphrodite) flowers (all flowers and individuals apparently with functional stamens and ovaries).

Acacia farnesiana *
Acacia pinetorum *
Amyris elemifera
Annona glabra
Ardisia escallonioides
Avicennia germinans
Bourreria cassinifolia
Bourreria ovata
Bourreria succulenta
Bumelia celastrina
Bumelia reclinata N
Bumelia (Dipholis) salicifolia
Byrsonima lucida
Calyptranthes pallens
Calyptranthes zuzygium
Canella alba (= winterana)
Capparis cynophallophora
Capparis flexuosa
Cassia bahamensis
Cephalanthus occidentalis N
Chiococca alba
Chrysobalanus icaco
Chrysophyllum oliviforme
Colubrina arborescens
Colubrina cubensis
Colubrina elliptica
Crossopetalum rhacoma
Erithalis fruticosa
Erythrina herbacea
Eugenia axillaris
Eugenia confusa
Eugenia foetida
Exostema caribaeum
Gossypium hirsutum
Guaiacum officinale
Hamelia patens
Hibiscus tiliaceus
Jacquinia keyensis
Krugiodendron ferreum
Licaria triandra
Lysiloma bahamensis
Magnolia virginiana N
Manilkara bahamensis
Mastichodendron foetidissimum
Myrcianthes fragrans
Nectandra coriacea
Persea borbonia N
Piscidia piscipula
Pithecellobium guadelupense *
Pithecellobium unguis-cati *
Psidium (Myrtus) longipes
Rhizophora mangle †
Sambucus canadensis
(simpsonii) N
Solanum bahamense
Solanum erianthum
Sophora tomentosa
Suriana maritima
Tetrazygia bicolor
Thespesia populnea
Ximenia americana
Vallesia antillana

N North temperate distribution.

* In some Mimosoideae, e.g., *Pithecellobium* (*Samanea*) *saman* and *Albizia lebleck* (the latter a weedy tree of South Florida), the terminal flower of each inflorescence is different from the others. The native South Florida representatives of this subfamily show no such variation.

† See Footnote p. 288.

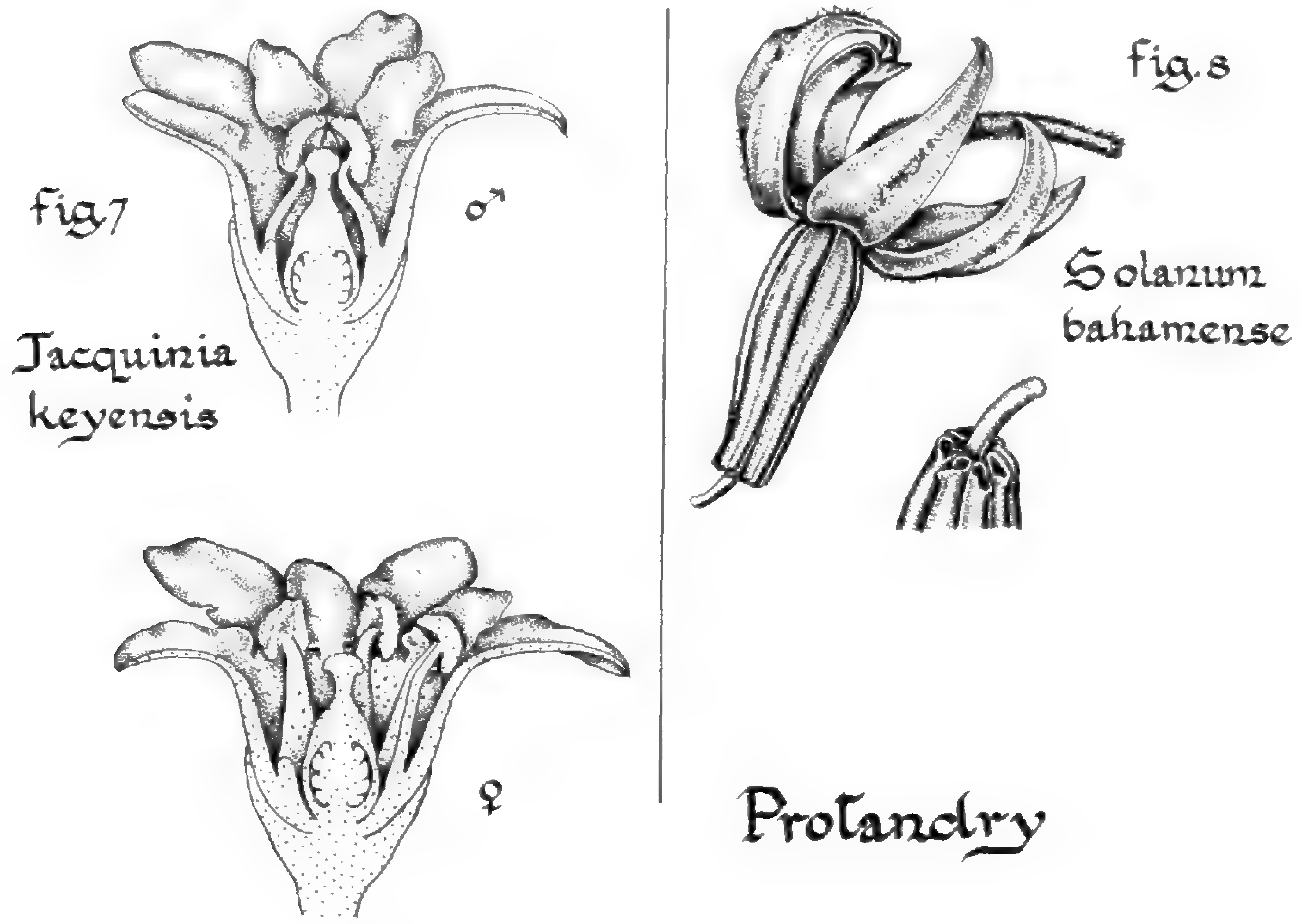
Despite the common character of perfect flowers, this group evidently includes a heterogeneous assemblage in terms of possible breeding mechanisms. Outbreeding is suggested in a number of examples by several sorts of dichogamy, with both protandry and protogyny evident in different species. Known examples where dichogamy is pronounced are listed and discussed briefly below. Field studies in other species with hermaphrodite flowers may reveal additional examples. Dichogamy itself, of course, only prevents self-pollination within individual flowers, not between the flowers of a whole plant.

3a. *Species showing dichogamy* (anthers and stigmas of the flower maturing at different times).

(i) Protandry (stamens maturing first).

Cephalanthus occidentalis
Chrysophyllum oliviforme
Crossopetalum rhacoma
Jacquinia keyensis (Figure 7)
Solanum bahamense (Figure 8)

Jacquinia keyensis (Theophrastaceae) shows pronounced protandry (Figure 7). In the early "male" phase, when the flower first opens, the stamens remain at the center of the flower, forming a small cavity within which the stigma is completely enclosed. At this time the anthers dehisce extrorsely so that pollen is displayed remote from the stigma of the same flower. In the later "female" phase the stamens bend away from the stigma which is so exposed. The same mechanism has been described by Janzen (1970) for *Jacquinia pungens*. In *Solanum bahamense* the stamens are aggregated to form a conspicuous column. Dehiscence, which is by pores, occurs while the style is short and still included within the staminal column. Subsequently the stigma is exserted by late elongation of the style. The close juxtaposition of stigma and anther pores is such that self-pollination is likely (Figure 8). In *Chrysophyllum* and *Crossopetalum* protandry is evident because the stigmas do not diverge until



Figures 7 and 8. Examples of protandry; flowers in longitudinal section and from the side: 7, **Jacquinia keyensis,** × 4 1/2, staminate phase above, carpellate phase below; 8, **Solanum bahamense,** × 3, flower in late "carpellate" phase with stigma protruding, detail to right, × 6, showing apical pores of anther.

well after the stamens have dehisced. *Chrysophyllum* (Sapotaceae) has a very simple flower structure and should be contrasted with the complex protogynous sapotaceous flowers described below.

(ii) Protogyny (stigmas maturing first).

ANNONA GLABRA
ARDISIA ESCALLONIOIDES (FIGURE 11)
AVICENNIA GERMINANS
BUMELIA SALICIFOLIA (FIGURE 10)
CANELLA ALBA (FIGURE 9)
FICUS AUREA
FICUS CITRIFOLIA
MAGNOLIA VIRGINIANA
MANILKARA BAHAMENSIS
NECTANDRA CORIACEA
PERSEA BORBONIA
SOPHORA TOMENTOSA
TETRAZYGIA BICOLOR

The flowers of *Ardisia escallonioides* (Myrsinaceae) suggest a mechanism for promoting outcrossing that may occur in other unrelated trees in South Florida with similar general floral structure (FIGURE 11). Before the flower is fully opened the corolla lobes are rolled together to form a tube. The tip of the style protrudes through this tube and is apparently receptive; therefore, functionally the flower is carpellate. Subsequently the flower opens and pollen is presented; it is not known if the stigma continues to be receptive in this later stage. *Sophora tomentosa* seems to be essentially of this type. *Sophora* flowers are relatively unspecialized in the Faboideae (having free stamens), and their pollination mechanism seems also unspecialized compared with that of many other Leguminosae.

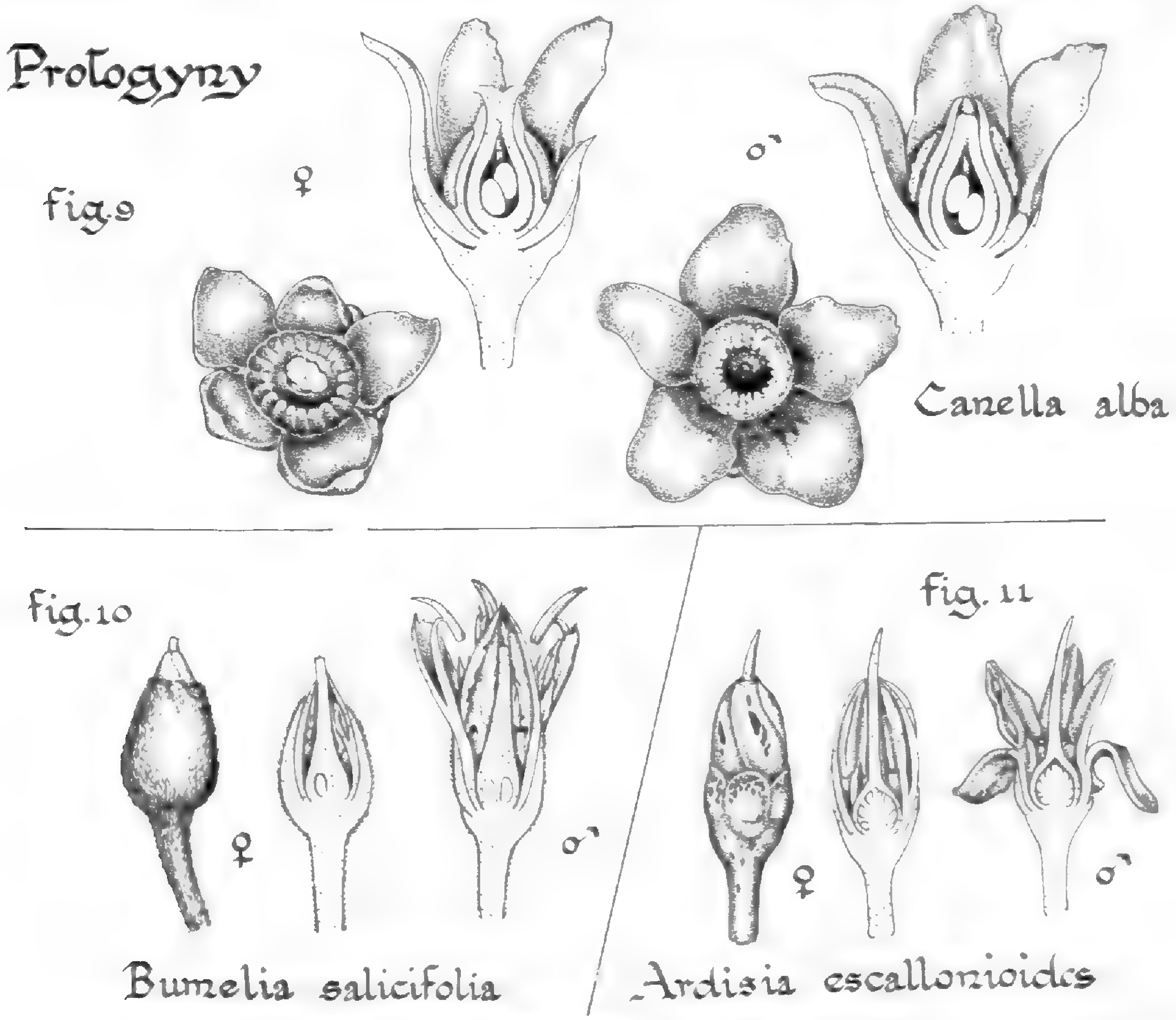
The Sapotaceae in South Florida show a wide range of floral mechanisms. Floral structure in some species is complicated by the existence of one or more kinds of scales on the corolla tube (either staminodes or stamen appendages). The morphology of these scales has been much discussed, but their function has been little considered. *Bumelia* (*Dipholis*) *salicifolia* is protogynous and the early carpellate phase is represented by FIGURE 10 (left), with the style protruding through the mouth of the yet unexpanded corolla tube. (This should not be confused with the late stage when the corolla has fallen and the style persists on the young fruit enclosed by the calyx.) Subsequently the corolla expands (FIGURE 10, right), but the scales bend over to form a canopy which would seem to prevent access of pollen to the stigma. Self-pollination is further minimized because the anthers dehisce extrorsely.

Manilkara bahamensis (Sapotaceae) is clearly protogynous, and its flowers behave much as those of *Bumelia salicifolia*, with the long style protruding from the flower essentially before it is open. This is succeeded by a staminate phase when the flower opens widely and the stamens dehisce.

Protogyny in Lauraceae is likely to be complex in view of the known situation in avocado, as outlined earlier. Both common native species of *Nectandra* and *Persea* have essentially the same floral structure as *Persea americana* and are evidently protogynous, with the carpellate phase (stigma erect – receptive; stamens depressed – undehisced) followed by one or two staminate phases (stigma shrivelled; stamens erect and dehisced via pores). There may be two distinct staminate phases, with the inner series of stamens dehiscing before the 2 outer series. Wood (1958; p. 331) has observed the same precise method of dianthesis in *Persea borbonia* (near Brooksville, Hernando County) as has been described for *P. americana.* In South Florida the mechanism seems less precise, as flowers at both staminate and carpellate phases have been observed on a single tree. However, the mechanism is known to be influenced by the weather, and detailed observation is needed.

Annona glabra and *Magnolia virginiana* (Magnoliaceae) are both clearly protogynous, a feature common in the magnolialian families (Wood, 1958).

Canella alba (Canellaceae) shows the protogynous condition very clearly. When the flower first opens, the stamens, which form a continuous cylinder, remain undehisced while the stigma protrudes and is receptive (FIGURE 9, left). Later the stigma shrivels and is retracted while the



FIGURES 9–11. EXAMPLES OF PROTOGYNY: 9, **Canella alba,** × 4 1/2, flowers from above and in longitudinal section, left-hand pair at early (carpellate) phase, right-hand pair at later (staminate) phase; 10, **Bumelia salicifolia,** × 4 1/2, flowers from the side and in longitudinal section, left-hand pair at early (carpellate) phase, right-hand flower at later (staminate) phase; 11, **Ardisia escallonioides,** × 3, flowers from the side and in longitudinal section, left-hand pair at early (carpellate) phase, right-hand flower at later (staminate) phase.

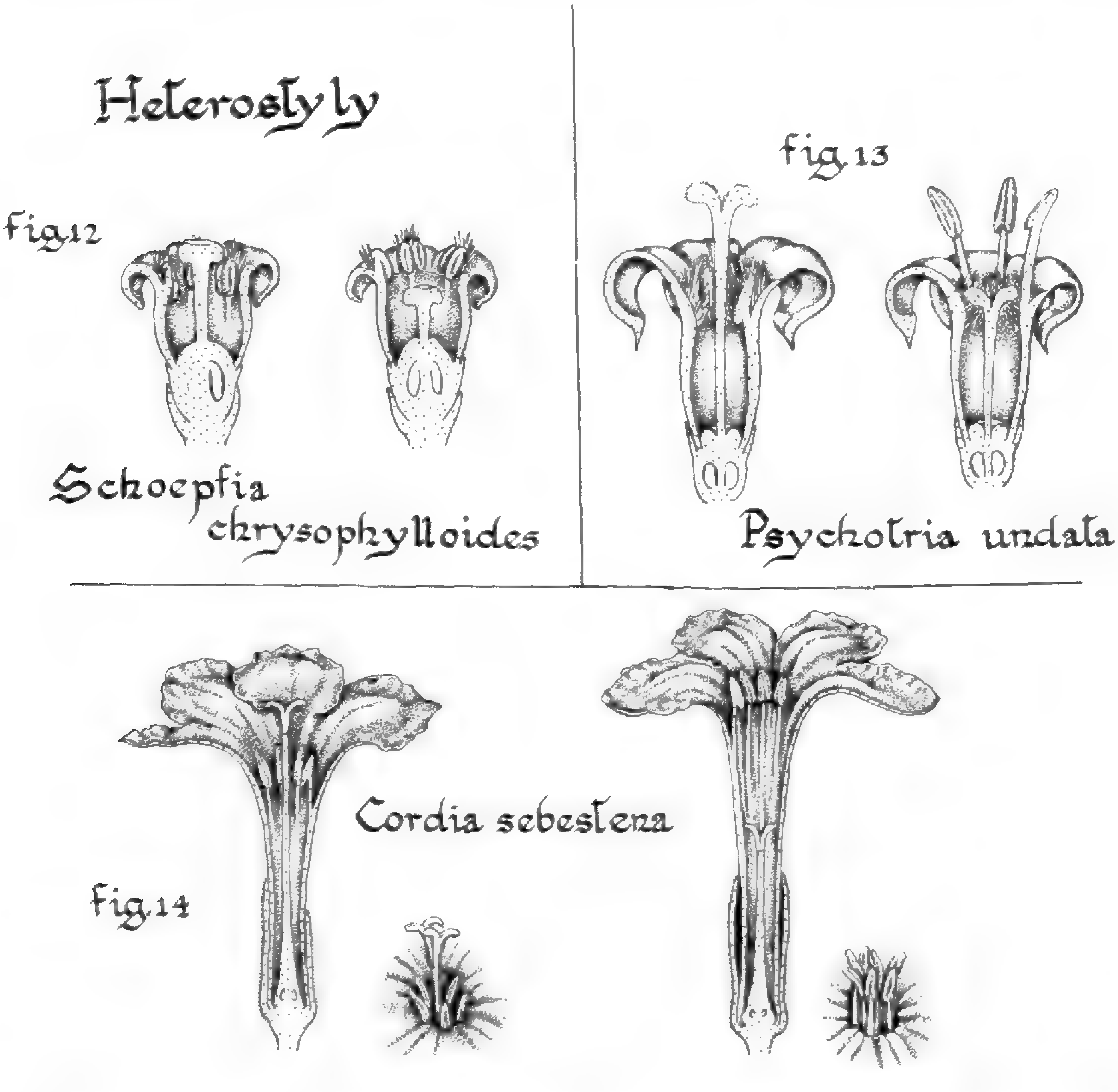
anthers dehisce extrorsely (FIGURE 10, right). Since the pollen, when released, is conspicuous on the stamen cylinder, the distinction between the early (carpellate) and the later (staminate) phase is easily recognized. Protogyny in *Avicennia* and *Tetrazygia* is less obvious but seems distinct. The complex protogyny of *Ficus* is described in detail later (p. 283).

3b. *Species with dimorphic* (*heterostylous*) *flowers* (only one kind of flower on a particular individual).

CORDIA SEBESTENA (FIGURE 14)
PSYCHOTRIA SULZNERI
PSYCHOTRIA UNDATA (FIGURE 13)
SCHOEPFIA CHRYSOPHYLLOIDES (FIGURE 12)

These species all represent clear-cut examples of morphological flower dimorphism, but it is not known if this dimorphism is correlated with self-incompatibility.

Schoepfia chrysophylloides (Olacaceae) provides a clear-cut example of heterostyly (FIGURE 12). Previous descriptions of this species in South



FIGURES 12–14. EXAMPLES OF HETEROSTYLY; flowers in longitudinal section with long-styled form to left, short-styled form to right in each example: 12, **Schoepfia chrysophylloides**, × 4 1/2, left-hand flower tricarpellate; 13, **Psycho-**

Florida have not recorded it as heterostylous and, indeed, heterostyly was not recorded for the family Olacaceae by Vuilleumier (1967). However, Adams (1972) records heterostyly in *Schoepfia chrysophylloides* in Jamaica, which suggests that it is a feature of the species throughout its range.

Psychotria in South Florida shows heterostyly of the classical type, which is well known in the genus and in other members of the Rubiaceae. Here the floral dimorphism is always clear cut (e.g., FIGURE 13). In some other Rubiaceae in South Florida flowers are polymorphic, suggesting incipient heterostyly. These examples are included in the next category.

Heterostyly is known in species of *Cordia* (Vuilleumier, 1967). Its existence in populations of *Cordia sebestena* may account for the low fruit set of this species, which tends to occur infrequently and as isolated individuals. Distinct "pin" (long-styled) and "thrum" (short-styled) forms are here illustrated (FIGURE 14), but there is some variation in style length among individual trees of the same flower type.

4. **Species with polymorphic flowers, including polygamo-monoecious or -dioecious** (usually more than one kind of flower occurring on a single individual).

BURSERA SIMARUBA (FIGURE 16)
DODONAEA VISCOSA
EXOTHEA PANICULATA
GUETTARDA SCABRA (FIGURE 17)
MAYTENUS PHYLLANTHOIDES
MYRSINE FLORIDANA
PRUNUS MYRTIFOLIA (FIGURE 6)
RANDIA ACULEATA (FIGURE 15)

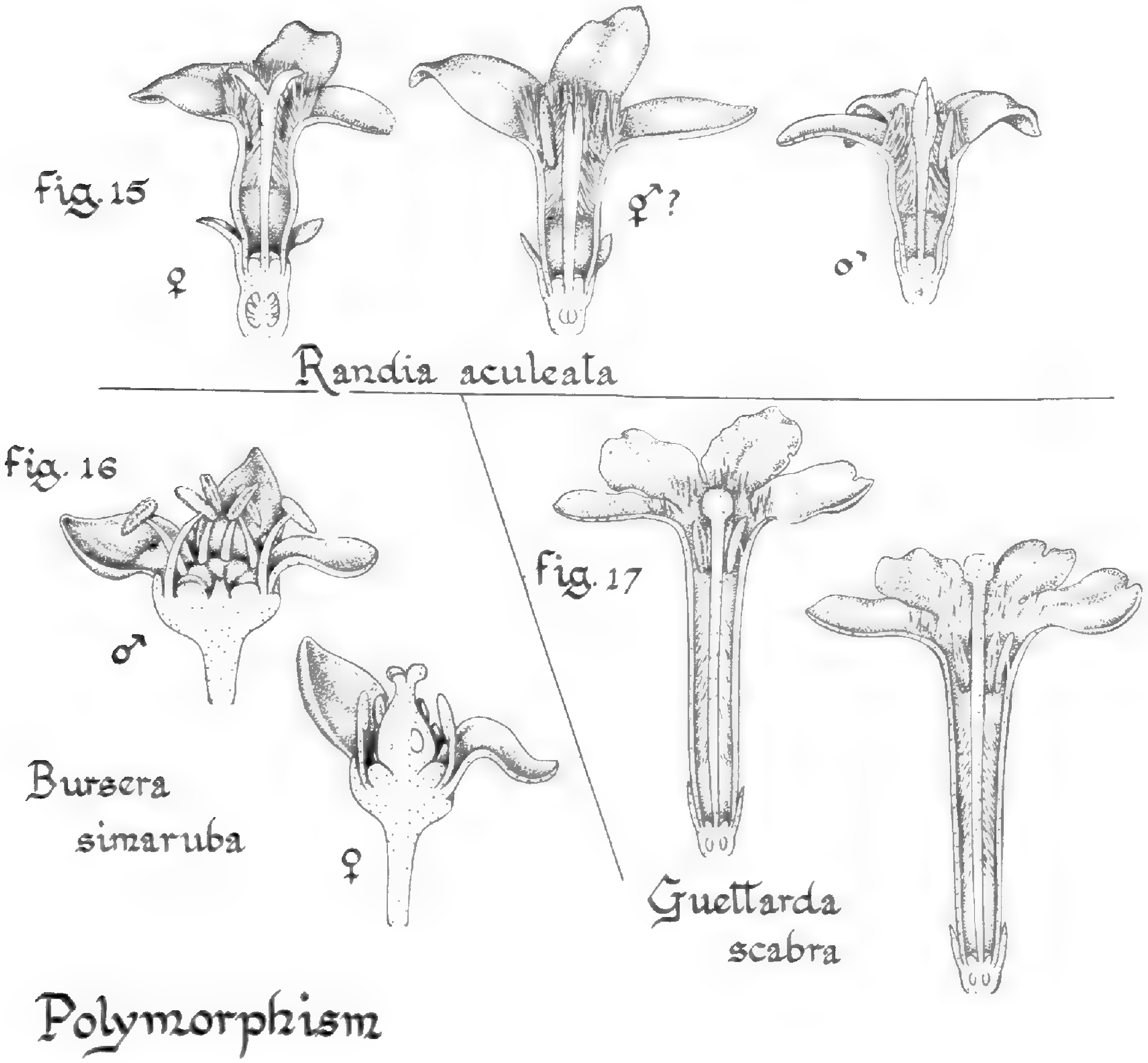
This is a rather artificial category, in which various kinds of floral variation are included.

Species listed in other categories but which show some degree of morphological variation might well be included in this list, such as *Acer rubrum* and especially other members of the Sapindaceae, a family in which floral polymorphism is well known (Radlkofer, 1933). The inclusion in this category of the South Florida members of the family (*Dodonaea*, *Exothea*) is undoubtedly quite arbitrary and further field study is needed. The significance of such polymorphism in pollination and breeding mechanisms is not known.

Bursera simaruba (Burseraceae) is similar. Staminate and carpellate flowers are illustrated in FIGURE 16. The species is usually described as dioecious. However, I have seen no trees which seem incapable of forming fruit, as would be the case if there were staminate trees. This might reflect the limited size of my sample, since Dr. K. J. Bawa has informed me of fruitless trees of *Bursera simaruba* in Costa Rica. Perfect flowers can be found. Dr. Carroll E. Wood, Jr., has made observations which suggest that there are at least staminate and carpellate inflorescences, but

---

tria undata, × 1; 14, **Cordia sebestena,** × 1, insets show mouth of corolla tube from above in each type of flower.



FIGURES 15–17. EXAMPLES OF FLORAL POLYMORPHISM; flowers in longitudinal section: 15, **Randia aculeata,** × 3, carpellate flower to the left, staminate flower to the right, central flower apparently perfect, but ovules probably not functional; 16, **Bursera simaruba,** × 6, staminate and carpellate flowers representing the extreme forms; intermediates which may be described as "perfect" can occur; 17, **Guettarda scabra,** × 3, two examples of flowers with different style lengths; this may represent incipient heterostyly.

that each staminate inflorescence usually has one perfect flower. The situation deserves more critical study.

Maytenus phyllanthoides (Celastraceae) has essentially perfect flowers in South Florida, but by abortion unisexual flowers are commonly produced on a single individual. It is commonly described as either monoecious or dioecious (Brizicky, 1964). The distribution and function of these flowers require further study.

The two rubiaceous species in the above list are polymorphic but not heterostylous. In *Randia aculeata* dioecism seems to predominate, since flowers on a single plant are chiefly unisexual by abortion (FIGURE 15, left and right), but the details of distribution of different flower types remain unknown. Flowers which possibly are perfect exist; these include apparently functional stamens and a partially developed ovary with some ovules (FIGURE 15, center). Whether these flowers can set fruit is not known. In *Guettarda scabra* most of the variation is in the length of the style, without any obvious variation in the structure of the ovary (FIGURE 17). As illustrated, this variation might suggest different stages in the elongation of the style, but style length is constant for an individual flower. Number of floral parts also varies widely with whorls of four to eight members.

Myrsine floridana (*Rapanea guianensis* sensu most authors) resembles *Randia* in that it seems to be essentially dioecious, but apparently perfect flowers can occur. The dioecious state is best demonstrated by the observation that trees are either heavy fruit bearers, or not, but the distinction is not sharp.

Prunus myrtifolia (Rosaceae) represents a species which is easy to categorize, since it is essentially andromonoecious (FIGURE 6) with separate perfect and staminate flowers on the same tree and indeed in the same spike. The basal flowers of one spike are staminate and the distal ones perfect; consequently fruits always appear toward the ends of the inflorescences.

THE SPECIAL POLLINATION MECHANISM OF FICUS SPECIES NATIVE TO FLORIDA (FIGURES 18 and 19).

The general complexity of pollination in *Ficus* is well known, and the distinctive symbiosis with species of wasps has been investigated in some detail. However, *Ficus* is one of the largest genera of flowering plants and the variations on the basic theme are many. Galil and Eisikowitch (1968) have most recently described the special mechanism in certain African species which seems to correspond to that in the two species of *Ficus* native to South Florida, *F. aurea* and *F. citrifolia*. The process is apparently the same in both species, but since different species of wasps are associated with each *Ficus* species (Galil, pers. comm.), there is no hybridization between them. The following account refers to *F. citrifolia*; *F. aurea* seems to be the same and is not described further. The general structure of the fig inflorescence and details of the flowers are shown in FIGURE 18. The mechanism is represented diagrammatically in FIGURE 19, with illustrations of male and female wasps.

The young figs (syconia) originate in pairs in the axil of a leaf on the new growth and always with a vegetative bud between them (FIGURE 18a–b). They develop within the terminal bud and are exposed by the fall of the surrounding stipules. The flowers are each subtended by a narrow bract and scattered without apparent order over the inner surface of the fig (FIGURE 18c). Carpellate flowers are either long-stalked with a short style or short-stalked with a long style in such a way that the feathery, unequal two-lobed stigmas of flowers are all at the same height (FIGURE 19a). The staminate flower consists of a single anther (FIGURE 18d). All flowers are at first enclosed in a membranaceous "perianth," which is ruptured as the flower enlarges (FIGURE 18d, right). Carpellate

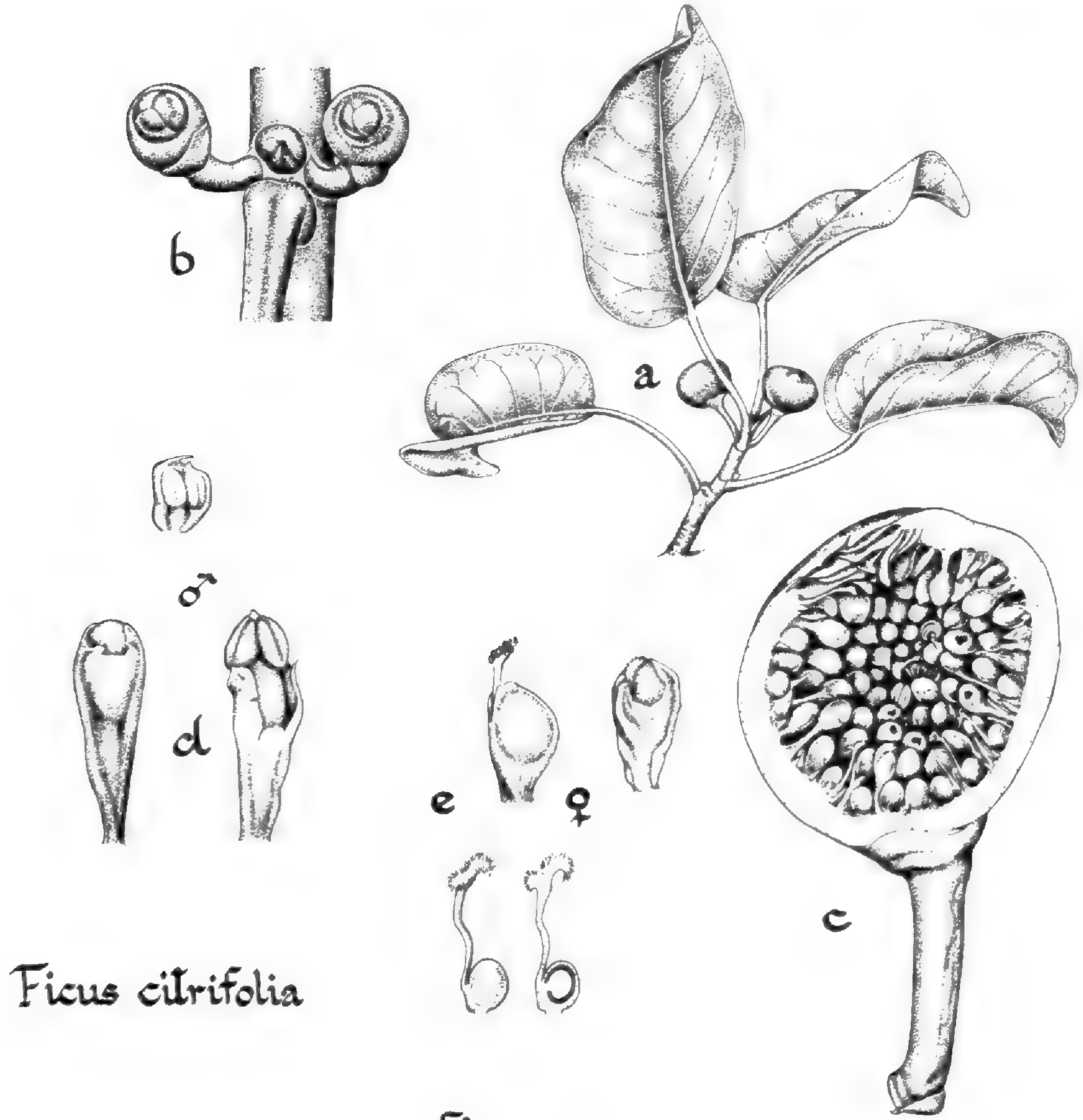


Fig.18

FIGURE 18a–e. **Ficus citrifolia,** inflorescence and flower morphology: a, leafy branch with figs, × 2/3; b, young fig-pair with intervening vegetative bud in axil of leaf. × 4; c, fig in vertical section at stage with grubs hatching, × 4; d, individual staminate flowers, × 12, various ages, oldest flower (lower right) with ruptured perianth; e, individual carpellate flowers, × 12, various ages, lower flower with perianth removed and in longitudinal section.

flowers function much earlier than staminate flowers in a way which is closely related to the method of pollination.

Female flowers expand their stigmas within the young green fig. At this stage winged female wasps (*Blastophaga* sp.), bearing fertile eggs, fly to the figs, which they penetrate via scales at the mouth that loosen slightly (FIGURE 19a). It is not known what attracts the wasps to a fig, but a chemical substance is probably involved. To enter a fig is a difficult task for such a small insect and the wasp usually loses its wings (and even its antennae) in wriggling between the scales. The remains of wasp wings among the scales will indicate that a young fig contains wasps. Once inside the fig the female wasp serves her own ends by laying fertile eggs within the female fig flowers by inserting her ovipositor down the style of the flower. At the same time she actively pollinates the flower, transferring pollen to each stigma as she lays an egg. The pollen is carried in a pair of small pollen sacs, one on each side of the thorax (arrows in FIGURE 19g, h). Once egg-laying and pollination are completed the wasp dies, being unable to escape from the fig.

Female flowers, now pollinated, develop over a period of a few weeks (FIGURE 19b). Some flowers develop normally and produce a single seed; others, known as gall-flowers, produce a wasp-grub which lives on the developing ovule of the female flower. This ovule fails to become a seed. Whether a flower develops a fruit or becomes a gall-flower is determined simply by the length of its style. In short-styled flowers the ovipositor of the wasp can reach the ovule and the wasp egg develops within nutritive tissue. In long-styled flowers the wasp's ovipositor is too short to lay the wasp egg in the correct position near the base of the flower, so the egg dies. Pollination has been performed by the wasp, however, and seed development proceeds normally. It seems necessary for both types of flower to be pollinated, even the gall-flower, since the development of the ovule must take place in order that the wasp-grub may be nourished.

Figs enlarge but remain green as seeds ripen and grubs mature (FIGURE 19c). The male flower then expands, rupturing its perianth, and the stamen dehisces (FIGURE 19d). At the same time the grubs (presumably after suitable metamorphosis) hatch from the gall-flowers to produce male and female wasps (FIGURE 19f–h). The male wasp is strikingly different from the female; it is larger, wingless, and brown rather than black (FIGURE 19f). It shows evidence of paedomorphism. Nevertheless it has two important functions. First it impregnates the adult female within the flower, subsequently assisting the escape from the flower of the delicately winged female by chewing a hole in the gall-flower. Since grubs are likely to be the progeny of several different parental wasps which all entered the same fig, outcrossing between wasps can take place. Secondly, the male wasp provides a further escape tunnel for the impregnated females by eating a hole through the wall of the fig using its well-developed mouth parts. The males may themselves escape through these holes, but since they are wingless they fall to the ground and die. The females, now egg-bearing, have one important function before they leave a fig. They load their pollen sacs from the pollen provided by the ripe anthers. Details of how this is done are still unknown, and it seems (FIGURE 19g, h) that the anther does not dehisce but is bitten into by the wasp. Once pollen-loading is accomplished the females make their escape via the holes provided by the males, fly to a young fig, and begin a new cycle (FIGURE 19d). The deliberate transfer of pollen by female wasps is a peculiarly instinctive action, but one on which the whole process is dependent. Of interest is the method of survival of wasp populations during a long period in winter when *Ficus* is inactive and produces few figs. This has not been investigated.

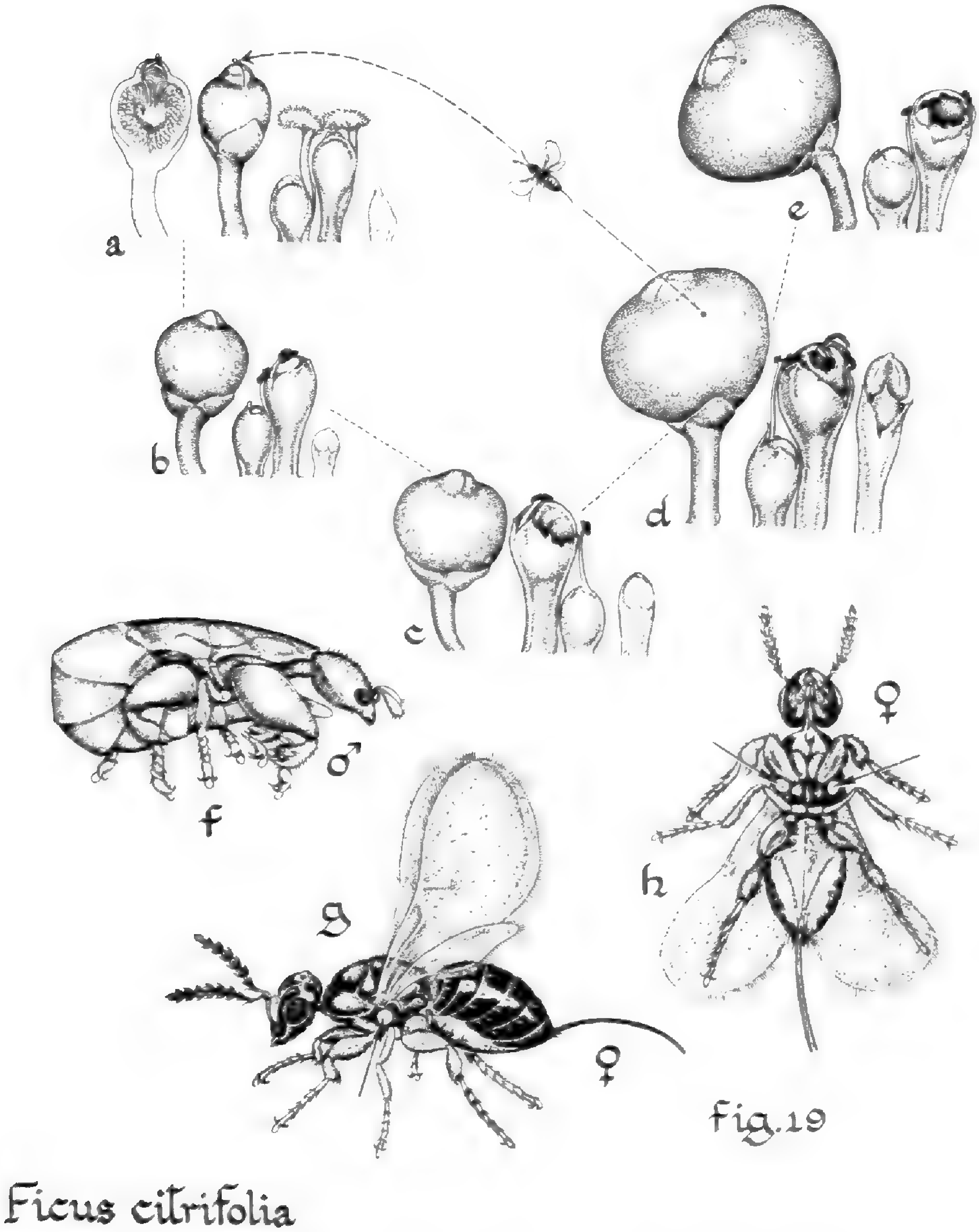


FIGURE 19a–e. **Ficus citrifolia,** diagram of pollination mechanism. Sequence of events, each illustration showing a fig to the left and an enlarged diagram of a carpellate and staminate flower to the right as they appear at this phase of development: a, fig recently occupied by a female wasp, carpellate flowers ready for pollination and oviposition; b, development of seed (left) and gall (right) flower from two kinds of carpellate flowers; c, ripening of seed and gall-flower; d, hatching of gall-flower and maturation of staminate flower, release of winged female insects; e, fruit ripening, empty gall-flowers. f–h. **Blastophaga** sp., male and female pollinating wasps: f, *B.* sp. male, × 45; g, *B.* sp. female from the side, × 40; h, *B.* sp. female from below, × 40, arrows indicating position of pollen-bearing pouches.

Unfortunately the situation is complicated by a number of other insects which parasitize the fig-wasp environment. Commonly there are male and female wasps of a second species in the figs. The female of this species has a long ovipositor and it may lay its eggs in female flowers without ever entering the fig so that it is of no value to the fig in pollen transfer. Additional large galls are also common in these figs, and they are probably made by an insect which enters and leaves a flower without ever going into the cavity of the fig at all.

DISCUSSION

Distribution of Breeding Mechanisms

The possibility that many South Florida trees are self-incompatible without there being any marked floral dimorphism is very likely in view of the high incidence recorded by Bawa (1973) in Costa Rica. Bawa records self-incompatibility for species in the genera *Manilkara*, *Piscidia*, and *Pithecellobium*, which are represented in South Florida.

In contrast *Byrsonima crassifolia* is recorded by Bawa as self-compatible. *Byrsonima lucida* in South Florida has conspicuous flowers which pass through several color phases as they develop. Assuming that this species is also self-compatible, outbreeding here may be dependent on specialized pollinator behavior but remains uninvestigated.

Since the flora of South Florida has been examined neither in detail nor experimentally, the only suggestion we presently have for outcrossing mechanisms comes from a knowledge of flower structure alone. Morphologically, out of 114 species 31 (27 per cent) are dioecious where outcrossing is obligate. Monoecism, which may promote outcrossing, occurs in 14 species (12 per cent). Heterostyly is distinct in 4 species (3.5 per cent), dichogamy is suggested in 18 species (16 per cent), and floral polymorphism, which may presage dioecism or monoecism, is evident in 8 species (7 per cent). Whether these structural differences in fact do reflect a tendency toward outcrossing can only be determined by further study. Even at the morphological level our records are very incomplete.

A further example will show that self-incompatibility and outcrossing may be more widespread than is currently evident. In the family Rhamnaceae, Galil and Zeroni (1967) have demonstrated a type of dichogamy in *Zizyphus spina-christi* which bears comparison with that in *Persea americana*, except that the flowers are protandrous, not protogynous. In *Zizyphus* Galil and Zeroni recognized 6 distinct flower phases (A–F) through which each flower passes. Pollen is presented in the earlier (staminate) phases B–C; the stigma becomes receptive in the carpellate phases D–E when all pollen is dispersed. All flowers on a single tree are in phase with each other. Outcrossing is obligate because the flowers are self-incompatible. Crossing is possible because there are two kinds of trees, staggered with respect to flower phase so that there are some trees with flowers in the male phase and other trees with flowers in the female phase.

Colubrina species in South Florida have flowers very similar to those of *Zizyphus*, and certain of the phases described by Galil and Zeroni can be recognized. It will be of interest to see if further work demonstrates a *Zizyphus* type of mechanism in *Colubrina*, or indeed in other Rhamnaceae.

POLLINATION MECHANISMS

The preceding outline has been presented, except in *Ficus*, without any consideration of the probable mechanism of pollen transfer itself. Initially one can make a rather subjective distinction between wind- and insect-pollinated flowers. Probable wind-pollinated species are marked with an asterisk in the preceding tables, based largely on flower structure and pollen texture. Most doubt can be cast upon my claim for wind pollination in the tropical level. However, even at this subjective level the incidence of wind-pollinated species is low. Furthermore, wind-pollination is strongly correlated with dicliny, on the one hand, and a temperate distribution, on the other. Of the 45 species included in the dioecious and monoecious category, I estimate that 15 (33 per cent) are wind-pollinated, whereas probably no species[2] with perfect flowers is wind-pollinated (0 per cent). A proportion of species with a generally temperate distribution (marked * N in the above tables) are wind-pollinated (4 out of 7 of the dioecious species; 4 out of 4 of the monoecious species). This confirms the higher incidence of wind-pollination in temperate tree floras which is generally appreciated and has been discussed recently by Daubenmire (1972), Janzen (1967), and Whitehead (1969) in relation to such factors as availability of pollinators, deciduousness, and the distribution of angiosperm families.

PHENOLOGY

Interaction between flowering trees and pollinators implies a close dependence on their respective seasonal behavior, as had been emphasized by Janzen (1967). It is perhaps not justifiable to comment upon seasonal flowering behavior of trees in South Florida, since the subject is scarcely investigated and my own phenological records are too incomplete to indicate more than general trends. However, the subject is of major importance in a discussion of breeding mechanisms in trees. Observations made so far show that many trees have distinctive (though often extended) flowering periods and that published records of trees as "everflowering" are often misleading, in part because they are based on early literature which was produced by observers who had little opportunity to make continuous records. The subject needs long, continued field investigation.

Diurnal variation in flower function is also an important factor in the study of pollination and breeding mechanisms. In certain trees in South Florida the flowers open only at night (e.g., *Capparis* species) or become scented at night, notably *Mastichodendron foetidissimum*. The pollinating agents here are not known.

These brief comments serve to indicate the several directions from which the observer may proceed once a more complete morphological assessment has been made.

---

[2] Recent field observations by John W. Kress (Harvard undergraduate) suggests that *Rhizophora mangle* is wind-pollinated and that populations of this species include male sterile plants. Statements about this species may have to be modified.

ACKNOWLEDGMENTS

I am indebted to Dr. K. S. Bawa for access to his unpublished manuscript and to Professor J. Galil of the Hebrew University, Jerusalem, for helpful clarification of the *Ficus* situation. Dr. Carroll E. Wood, Jr., and Dr. W. T. Gillis have both reviewed the manuscript and made helpful comments. The illustrations are the work of Priscilla Fawcett, Botanical Illustrator at Fairchild Tropical Garden, Miami, Florida, whose general assistance is much appreciated.

BIBLIOGRAPHY

ADAMS, C. D. 1972. Flowering plants of Jamaica. Glasgow Univ. Press. Glasgow.

ARECHAVALETA, J. 1902. *Citharexylon barbinerve* Cham. et Schlecht., tendencia hacia la unisexualidad de sus flores. Anal. Mus. Nac. Montevideo **4**: 149–152.

ASHTON, P. S. 1969. Speciation among tropical forest trees: some deductions in the light of recent evidence. Biol. Jour. Linn. Soc. **1**: 155–196.

BAWA, K. S. 1973. Breeding systems of tree species of a lowland tropical community. Evolution **27**: in press.

BRIZICKY, G. K. 1964. The genera of Celastrales in the Southeastern United States. Jour. Arnold Arb. **45**: 206–234.

DAUBENMIRE, R. 1972. Phenology and other characteristics of tropical semideciduous forest in north-western Costa Rica. Jour. Ecol. **60**: 147–170.

FEDOROV, A. A. 1966. The structure of the tropical rain forest and speciation in the humid tropics. Jour. Ecol. **54**: 1–11.

GALIL, J., & D. EISIKOWITCH. 1968. On the pollination ecology of *Ficus religiosa* in Israel. Phytomorphology **18**: 356–363.

——— & M. ZERONI. 1967. Pollination of *Zizyphus spina-christi*. Israel Jour. Bot. **16**: 71–77.

GILL, A. M., & P. B. TOMLINSON. 1971. Studies on the growth of red mangrove (*Rhizophora mangle* L.) 3. Phenology of the shoot. Biotropica **3**: 109–124.

HOWARD, R. A. 1949. The genus *Coccoloba* in Cuba. Jour. Arnold Arb. **30**: 388–424.

JANZEN, D. H. 1967. Synchronization of sexual reproduction of trees within the dry season in Central America. Evolution **21**: 620–637.

———. 1970. *Jacquinia pungens*, a heliophile from the understory of tropical deciduous forest.. Biotropica **2**: 112–119.

———. 1971. Euglossine bees as long distance pollinators of tropical plants. Science **171**: 203–205.

LEE, H. Y. 1967. Study of *Swietenia* (Meliaceae) — an observation on the sexuality of flowers. Jour. Arnold Arb. **48**: 101–104.

LONG, R. W., & O. LAKELA. 1971. A flora of tropical Florida. University of Miami Press. Coral Gables.

PERRY, T. O., & WANG CHI WU. 1960. Genetic variation in the winter chilling requirement for date of dormancy break for *Acer rubrum*. Ecology **41**: 790–794.

RADLKOFER, L. 1933. Sapindaceae. *In*: A. ENGLER, Das Pflanzenreich. IV. (Heft 98a) 165(1).

SARGENT, C. S. 1905. Manual of the trees of North America (exclusive of Mexico). Houghton Mifflin Co., Cambridge.

STYLES, B. T. 1972. The flower biology of the Meliaceae and its bearing on tree breeding. Silvae Genetica **21**: 170–182.

THIERET, J. W. 1973. Sex and the angiosperms. Sida **5**: 59, 60.

TOMLINSON, P. B. 1973. Dioecism in *Citharexylum* (Verbenaceae): an addendum. Jour. Arnold Arb. **54**: 120.

——— & F. C. CRAIGHEAD. 1972. Growth ring studies on the native trees of sub-tropical Florida. Pp. 39–51. *In*: Research trends in plant anatomy. K. A. Chowdhury Commemoration volume. Tata McGraw-Hill. New Delhi.

——— & P. FAWCETT. 1972. Dioecism in *Citharexylum* (Verbenaceae). Jour. Arnold Arb. **53**: 386–389.

VUILLEUMIER, B. S. 1967. The origin and evolutionary development of heterostyly in the angiosperms. Evolution **21**: 210–226.

WHITEHEAD, D. R. 1969. Wind pollination in the angiosperms: evolutionary and environmental considerations. Evolution **23**: 28–35.

WOOD, C. E., JR. 1958. The genera of the woody Ranales in the southeastern United States. Jour. Arnold Arb. **39**: 296–346.

HARVARD FOREST
PETERSHAM, MASSACHUSETTS 01366

SISYRINCHIUM SOLSTITIALE (IRIDACEAE): A FLORIDA ENDEMIC

Daniel F. Austin and Royce L. Oliver

Numerous species of *Sisyrinchium* from the southeastern United States were described by Bicknell (1899). Many of these have been placed in synonymy or ignored because of their uncertain status. Included among these is *S. solstitiale*, which is similar to, and usually included within, *S. xerophyllum* Greene. In the original publication of the former species, Bicknell emphasized the different flowering times of these species (autumnal in *S. solstitiale*, vernal in *S. xerophyllum*) and later (1903) stated that in *S. xerophyllum* the tufts of plants are densely fibrous at the base, while in *S. solstitiale* such fibers are lacking. The amount and condition of fibers depends on the age of the plant, fires, and microhabitat and does not distinguish these species. We believe that not recognizing this has led to the inclusion of *Sisyrinchium solstitiale* in *S. xerophyllum* in recent treatments of the genus in Florida (Lakela & Craighead, 1965; Ward, 1968; Long & Lakela, 1971).

After two years of observing living populations of *Sisyrinchium* in peninsular Florida, of collecting data on pollinators, phenology, habitat, cytology, and of examining numerous herbarium specimens, it became apparent that the entity called "*S. xerophyllum*" in recent literature was composed of two distinct, yet closely related, taxa. Historically, few infraspecific taxa of *Sisyrinchium* have been recognized in North America. Until a clear species concept can be established through detailed population and biosystematic studies, we prefer to follow the present system and maintain *S. xerophyllum* and *S. solstitiale* as distinct species. Table I lists the characters that may be used to distinguish them.

The genus *Sisyrinchium* is taxonomically difficult; species limits are often vague, and many variants have been described as distinct. Numerous collections in herbaria are undetermined or misdetermined. Taxonomic studies on the genus are few and based mostly on herbarium material. They are mostly regional in coverage or concerned with small species groups. A modern revision is needed.

ECOLOGY

Sisyrinchium solstitiale and *S. xerophyllum* are closely allied species which were probably derived relatively recently from a common ancestor. *Sisyrinchium solstitiale* is adapted to the xeric conditions of the Scrub Pinelands, and *S. xerophyllum* to the comparatively mesic conditions of the High Pinelands. The distribution of these species (Figure 5) apparently reflects the Pleistocene insulation and inundation described

TABLE I. **Criteria for distinguishing Sisyrinchium solstitiale from S. xerophyllum.**

	S. SOLSTITIALE	S. XEROPHYLLUM
1.	Scapes 30–54 cm. long.	Scapes 7–25(–30) cm. long.
2.	Inflorescences 12.5–23 cm. long; 3.5–9.5 cm. longer than the leafy bract.	Inflorescences 4–8 cm. long; up to 3 cm. longer than the leafy bract.
3.	Spathes ± terete at base, gradually broadening.	Spathes flattened, abruptly expanding from base.
4.	Outer bract gradually tapering to a point.	Outer bract abruptly narrowing from point of attachment.
5.	Inner bract not gibbous.	Inner bract slightly gibbous.
6.	Pedicels (0–)5–7(–10) mm. longer than spathes.	Pedicels (0–)2(–6) mm. longer than spathes.
7.	Roots commonly pilose (root hairs?).	Roots commonly smooth.
8.	Habitat: Scrub.	Habitat: High Pine and Flatwoods.
9.	Flowering July to December.	Flowering March to April.
10.	Leaves evergreen, persistent throughout year.	Leaves dying in the fall.

by Neill (1957) for numerous species of plants and animals. *Sisyrinchium solstitiale* now grows on the Ocala Ridge from Marion County south to Highlands County and southeast on the Scrub Pine sand dunes to Dade County. Where the species occurs in Pine Flatwoods it has been our observation that a "relic" of Scrub Pinewoods is always closely associated.

With the exception of the collection *Nash 133*, *S. xerophyllum* occurs north of the Suwanee Straits from Alachua and Putnam counties north to Duval County. It appears to be absent from the Suwanee River basin, but reappears in the panhandle from Leon to Walton counties. This absence from the Suwanee River basin is probably a result of the inundation of this region during the Pleistocene. Neill (1957) described in detail the effect of the embayment on local biogeography and noted that many species of plants and animals have not yet reinhabited the area.

Sisyrinchium solstitiale is constantly associated with the white St. Lucie and associated cross-bedded sands of the Pleistocene (Cook, 1945). Vegetation growing on this sand complex is usually called Scrub or Scrub Pine (Carr, 1940; Davis, 1943; Long & Lakela, 1971) and is characterized by the dominant plants *Pinus clausa*, *Ceratiola ericoides*, and several species of *Quercus*. In *Pinus clausa* stands having a closed canopy and thick shrub layers, *S. solstitiale* is not apparent even after fires. Conversely, scrub pine stands with an open canopy are common sites of large *Sisyrinchium* populations. Following fires that do not kill the scrub pine, large *Sisyrinchium* populations are abundant in open areas. Roads and trails leading through or near such populations allow the spread of a few plants into nearby High Pinelands or Flatwoods. *Sisyrinchium solstitiale* appears unable to compete with *Serenoa repens* (saw palmetto), ericaceous shrubs, and grasses common in the High Pinelands and Flatwoods. In southern Florida *S. solstitiale* is found only in young Flatwoods and their disturbed margins, and only then when there is a Scrub area nearby. When the lower pine forest layers begin to mature *Sisyrinchium* becomes rare or absent.

This perennial *Sisyrinchium* may not be adapted to fire in the same ways that *Serenoa*, *Quercus*, *Lyonia*, and *Ilex* are adapted, but, as with many Florida plants, it benefits from reduced competition, release of nutrients, and the preparation of the proper habitat for growth and reproduction. The species possibly exists marginally for long periods of time until fire reduces competition and thus opens and maintains a suitable habitat.

The genus *Sisyrinchium* is largely one of temperate regions, although some species extend into tropical zones. Those species in the tropics usually occur at higher altitudes where conditions are functionally temperate. Most species of the north temperate area flower in the spring and early summer.

Sisyrinchium solstitiale rarely produces flowers in the spring; of the several hundred living plants examined in March, 1972, only two plants had one flower each. These same plants had flowering stalks with capsules that had already dispersed their seed. Observations during three seasons of one population in Palm Beach County and another in Martin County, plus data from herbarium material indicate that the majority of *S. solstitiale* flowers are produced from July to December.

From greenhouse studies it has been determined that flowering is initiated by photoperiod in some *Sisyrinchium* species (Oliver, unpublished). This photoperiod sensitivity undoubtedly has partially dictated the time of year when *S. solstitiale* produces flowers. Spring and fall flowering appear to reach their peak near the equinoxes when there are about twelve hours of light. The production of occasional flowers by *S. solstitiale* in the spring suggests that flowering is at least partially triggered by photoperiod.

However important photoperiod might be in initiating flowering, moisture seems to be one of the main factors affecting the change from spring to late summer and fall flowering. Spring is almost always dry in peninsular Florida, while fall terminates the wet season. Since the spring drought is augmented by the very porous well-drained sand soils where *S. solstitiale* occurs, this may have become a factor limiting spring flowering of this species. Spring flowering for *S. solstitiale* must have become an evolutionary handicap, and selection caused a shift to fall flowering. A similar fall flowering tendency is exhibited by numerous Mexican species of the genus that begin flowering in July and August. This also corresponds with the rainy season.

POLLINATION

Two widely separated populations of *S. solstitiale* have been observed for insect visitors. Although several kinds of insects were seen in the vicinity of the populations, only three species of Hymenoptera visited *Sisyrinchium*.

In the Boca Raton, Palm Beach County population, flowers opened from 2:30 to 3:00 p.m. E.S.T. and remained open until after dark. The afternoon flowering appears to be a unique characteristic of *S. solstitiale*; other species of the genus flower in the morning. Bees were not apparent until the flowers opened. Shortly after opening the flowers were visited by *Augochlorella gratiosa* Smith and *Anthidiellum notatum rufimaculatum* Schwarz. *Augochlorella* was a regular visitor for the next few hours, at least one bee visiting the flowers at all times. The body of *Augochlorella* was positioned across or around the staminal column for gathering nectar (FIGURES 3 and 4). Pollen was collected with the anterior pair of legs after nectar had been taken, and then stored in scopae on the posterior legs.

Anthidiellum, a larger bee, landed across the staminal column to take nectar at the flower base while gathering pollen at the same time with the posterior legs. This bee stores pollen on ventral abdominal scopae. Although there is no detectable fragrance, these bees always approach the flowers from down-wind.

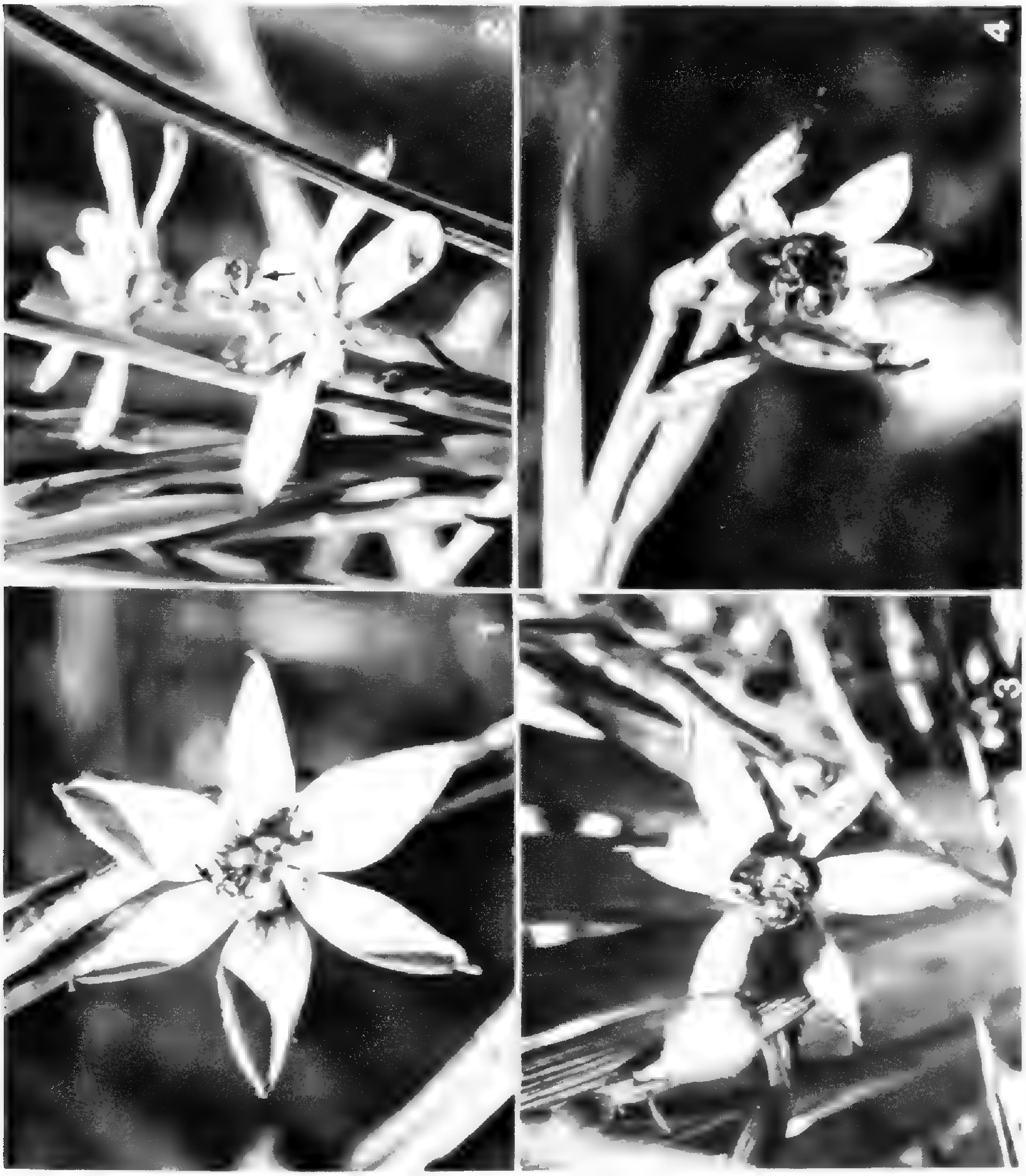
The second population was studied in Jonathan Dickenson State Park, Martin County. *Augochlorella* was not observed and few *Anthidiellum* visited the flowers. The *Anthidiellum* was the same species visiting the Palm Beach County population and exhibited the same behavior. The major difference in behavior was that the individuals in Martin County were extremely nervous.

The common visitor to this population was *Dialictus nymphalis* Smith. These small bees were numerous, and several were usually active at the same time. Because of their small size they landed on the tepals, then climbed onto the staminal column (FIGURES 1 and 2). The bees were observed gathering pollen only; however, visits to nearby *Polygonella gracilis* were apparently for nectar. As with *Augochlorella*, pollen was stored on the scopae of the posterior legs.

The details here described were obtained in 1970. Subsequent observations in 1971 and 1972 substantiate the original data. No other species have been observed visiting the flowers of this population of *Sisyrinchium solstitiale*.

All the data indicate that these three bee species are effective pollinators. Each exhibits a different behavior while on the flowers, but all contact stamens and stigmas on every flower visited. It was not unusual for bees to fly from plant to plant and cross-pollination could easily have been accomplished.

In the spring of 1971 several populations of various species of *Sisyrinchium* were studied. These populations ranged from Alachua County



FIGURES 1 and 2. **Dialictus nymphalis:** 1, bee climbing from the tepals of *Sisyrinchium solstitiale* onto the staminal column; 2. bee collecting pollen on the staminal column of *S. solstitiale*. FIGURES 3 and 4. **Augochlorella gratiosa:** 3. bee gathering pollen from *S. solstitiale*; 4. bee taking nectar from *S. solstitiale*.

south to Broward County. In only one of these spring flowering populations was a common visitor shared with the fall populations. A population of *S. miamiense* Bicknell (*S. atlanticum* sensu Long & Lakela, 1971) in Broward County was visited by *Augochlorella gratiosa*; pollination was apparently accomplished but only one individual was seen. The plants were also visited briefly on two days by *Anthidiellum notatum rufimaculatum*; on neither occasion was the bee observed to land on the flowers. The visit by *Anthidiellum* appeared to be only an inspection of the blue flowers.

CYTOLOGY

Both *Sisyrinchium solstitiale* and *S. xerophyllum* belong to *Sisyrinchium* section BERMUDIANA, which has blue and white flowers associated with an undivided staminal column. Species presently studied in this section have a base chromosome number of $x = 8$ (Bowden, 1945; Böcher & Larson, 1950; Lewis & Oliver, 1961; Oliver & Lewis, 1962; Böcher, 1966; Oliver, 1966; Ingram, 1967; Taylor & Mulligan, 1968; Mosquin, 1970). Polyploids and a single diploid have been reported; the majority of the species are tetraploids.

Plants of *S. solstitiale* were grown in St. Louis, Missouri, from seed collected in Florida. Root tips were pretreated with low temperatures (18 hours at 1–4° C) before chromosome squashes were made. The chromosome number for *S. solstitiale* is $2n = 32$. Voucher: **Florida.** Palm Beach Co., Boca Raton, *Austin 4276* (FAU).

Mosquin (1970) reported compatibility and selfing in a bagging experiment on what we assume to be a 12-ploid population of *S. montanum* Greene. In contrast to this we found *S. solstitiale* to be self-incompatible. Seed set could be accomplished only by cross pollination. Self-incompatibility is also common in other tetraploid *Sisyrinchium* species from the Pacific Northwestern United States (Douglas Henderson, pers. comm.). We have not seen evidence of gene exchange between this species and any other.

DISCUSSION

We suggest that the ancestral form of the two species of *Sisyrinchium* we have studied occurred in the lower southeastern United States at the beginning of the Pleistocene. During the changing sea levels of the glacial and interglacial stages, various populations of the ancestral form became isolated. Each of the modern species resulted from evolutionary shifts in preference to habitat, flowering season, flowering time of day, pollinators, etc. *Sisyrinchium xerophyllum* maintained a more conservative biology by retaining the temperate spring flowering characteristics and living in relatively mesic conditions in the High Pinelands.

Sisyrinchium solstitiale was perhaps isolated from the other forms on the Pleistocene islands. The Scrub forests of the Ocala Ridge and farther south have been considered the sites of evolution for several plant and animal species (Carr, 1940; Neill, 1957). Since *S. solstitiale* now prefers this habitat, it seems reasonable to assume that this species may also have evolved with the other Scrub species. Because conditions are xeric in the Scrub, spring flowering plants were probably at a disadvantage since the spring is usually dry. A selection toward flowering in the late summer and early fall, when rain is more abundant, would have resulted in survival and reproduction being more easily accomplished. This shift to late flowering parallels similar shifts in Mexico.

If this interpretation is correct, *Sisyrinchium solstitiale* can be considered a recently evolved species. Almost certainly its closest relative is *S. xerophyllum*. Because their habitat and flowering seasons rarely overlap, there is a strong tendency to consider the populations as two separate gene pools.

ACKNOWLEDGMENTS

For this study we have examined materials from the herbaria at A, FAU, FLAS, FSU, GH, MO, SMU, UNC, USF, and US (abbreviations follow Index Herbariorum, Ed. 5, Reg. Veg. 31. 1964). We are grateful for the assistance given by curators and staff members of these herbaria. W. H. Mahler graciously furnished space at the Southern Methodist University for this study during most of the summer of 1972. B. G. Schubert and K. R. Robertson gave many helpful suggestions on the original manuscript.

5

FIGURE 5. Distribution of *Sisyrinchium solstitiale* (solid dots) and *S. xerophyllum* (stars).

DOCUMENTATION

1. **Sisyrinchium xerophyllum** Greene, Pittonia **4**: 32. 1899. HOLOTYPE: *Nash 133* (ND–G); (GH, MO, NY, US, isotypes).

REPRESENTATIVE SPECIMENS:

Florida. CALHOUN CO.: 10 May 1964, *McDaniels 4428* (FSU). FRANKLIN CO.: 24 Mar. 1970, *Godfrey 69316* (FSU); 23 Mar. 1961, *Kral 118313B* (FSU); *Godfrey 53124* (NY). GADSON CO.: 19 Mar. 1966, *McDaniels 7286* (FSU). HERNANDO CO.: 19 Mar. 1958, *Cooley & Monachino 5659* (FSU). LAKE CO.: 20 Mar. 1894, *Nash 133* (MO, ND–G, NY, US). LEON CO.: 28 Apr. 1964, *Godfrey 63578* (FSU); 30 Mar. 1957, *Kral 4747* (SMU). PUTNAM CO.: Apr. 1961, *Gillis 4348* (FSU). WAKULLA CO.: 1 Apr. 1934, *Hunnewell 13094* (GH). WALTON CO.: 17 Apr. 1958, *Godfrey 56629* (FSU, SMU); 6 Apr. 1957, *Godfrey 55491* (FSU, GH, NY, SMU).

2. **Sisyrinchium solstitiale** Bicknell, Bull. Torrey Bot. Club **26**: 219. 1899. TYPE: *Nash.* ". . . high pine land at Eustis, Lake Co., Florida, Aug. 10, 1894, the first flowers just opened. Type in herbarium Geo. V. Nash" (presumably NY, not located).

REPRESENTATIVE SPECIMENS:

Florida. BREVARD CO.: 15 Jan. 1903, *Fredholm 5698* (GH, US). BROWARD CO.: 19–25 Nov. 1903, *Small & Carter 1228* (NY). DADE CO.: 30 Nov. 1912, *Small 4008* (NY); 30 Jan. 1930, *Moldenke 300A* (NY). HIGHLANDS CO.: 17 Oct. 1967, *Beckner 788* (FSU, GH, USF); 22 Aug. 1971, *Godfrey 70805* (FSU); 20 Sept. 1964, *Kral 22893* (SMU); 27 Dec. 1924, *Small 11573* (NY); 4–5 Sept. 1934, *Small & West s.n.* (NY); 28 Nov. 1959, *Ray 9628* (FSU, GH, USF); 7 Oct. 1960, *Ray et al. 10348* (USF); 2 Sept. 1954, *Shanks et al. 17959* (SMU); 7 Dec. 1925, *Small 12728* (NY, UNC, USF). INDIAN RIVER CO.: 26 June 1957, *Kral 5073* (SMU). MARION CO.: 12 Sept. 1929, *O'Neill 7828* (FSU, US); 12 Oct. 1964, *Ward 4192* (FLAS, FSU, GH, USF). MARTIN CO.: 23 July 1959, *Ward & Ward 1575* (FLAS, FSU). ORANGE CO.: 26 Oct. 1959, *Craighead s.n.* (FSU); 20 Dec. 1949, *Shallert 5442* (SMU). OSCEOLA CO.: 14 Oct. 1960, *Putnam s.n.* (USF); 14 Oct. 1960, *Ray et al. 10462* (USF). PALM BEACH CO.: 25 Oct. 1970, *Austin 4276* (FAU); 20 Dec. 1968, *Churchill s.n.* (SMU). POLK CO.: 11 Nov. 1960, *Lakela 23592* (FSU). ST. LUCIE CO.: 7 Dec. 1920, *Small & DeWinkler 9728* (GH, SMU, UNC, US). COUNTY UNKNOWN: S. Florida, *Binney s.n.* (GH) [annotated by Bicknell in 1899; the only specimen of this species annotated by the original author that we have seen.]

LITERATURE CITED

BICKNELL, E. P. Studies in *Sisyrinchium* — I: Sixteen new species from the southern states. Bull. Torrey Bot. Club **26**: 217–231. 1899.

———. *Sisyrinchium*. *In*: J. K. SMALL, Flora of the Southeastern United States, 293–304. 1903.

BÖCHER, T. W. Experimental and cytological studies on plant species. X. *Sisyrinchium* with special reference to the Greenland representative. Bot. Tidsskr. **61**: 273–290. 1966.

——— & K. Larsen. Chromosome numbers of some arctic or boreal flowering plants. Medd. Grønl. **147**(6): 1–32. 1950.

Bowden, W. M. A list of chromosome numbers in higher plants. I. Acanthaceae to Myrtaceae. Am. Jour. Bot. **32**: 81–92. 1945.

Carr, A. F. A contribution to the herpetology of Florida. Univ. Florida Publ. Biol. **3**: 1–118. 1940.

Cook, C. W. Geology of Florida. Florida Geol. Surv. Geol. Bull. **29**: 1–339. 1945.

Davis, J. H., Jr. The natural features of southern Florida. Florida Geol. Surv. Geol. Bull. **25**: 311 pp. 3 maps. 1943.

Ingram, R. On the identity of the Irish populations of *Sisyrinchium*. Watsonia **6**: 283–289. 1967.

Lakela, O., & F. C. Craighead. Annotated checklist of the vascular plants of Collier, Dade and Monroe Counties, Florida. viii + 95 pp. Fairchild Trop. Gard. & Univ. Miami Press, Coral Gables. 1965.

Lewis, W. H., & R. L. Oliver. Meiotic chromosomes in six Texas and Mexican *Nemastylis* and *Sisyrinchium* (Iridaceae). Southwest. Nat. **6**: 45, 46. 1961.

Long, R. W., & O. Lakela. A Flora of Tropical Florida. xviii + 962 pp. Univ. Miami Press, Coral Gables. 1971.

Mosquin, T. M. Chromosome numbers and a proposal for classification in *Sisyrinchium* (Iridaceae). Madroño **20**: 269–275. 1970.

Neill, W. T. Historical biogeography of present-day Florida. Bull. Florida State Mus. **2**: 175–220. 1957.

Oliver, R. L. Chromosome numbers in phanerogams. I. Ann. Missouri Bot. Gard. **53**: 100–103. 1966.

——— & W. H. Lewis. Chromosome numbers of *Sisyrinchium* (Iridaceae) in Eastern North America. Sida **1**: 43–48. 1962.

Taylor, R. L., & G. A. Mulligan. Flora of the Queen Charlotte Islands. Part 2. Cytological aspects of the vascular plants. Canada, Dept. Agric. Monogr. 4(2). x + 148 pp. 1968.

Ward, D. B. Checklist of the Vascular Flora of Florida. I. Bull. Florida Agric. Exper. Sta. **762**: 1–72. 1968.

D. F. A.
Department of Biological Sciences
Florida Atlantic University
Boca Raton, Florida 33432

R. L. O.
Department of Biology
Washington University
and
Missouri Botanical Garden

Present address:
Department of Botany
Smithsonian Institution
Washington, D.C. 20560

THE REDUCTION OF RUSBYANTHUS AND THE TRIBE RUSBYANTHEAE (GENTIANACEAE)

RICHARD E. WEAVER, JR.

THE SYSTEM FOLLOWED by most taxonomists for the classification of the Gentianaceae is that of Gilg (1895). In this system five tribes of the Gentianoideae are recognized, all distinguished on the basis of pollen grain characters: Gentianeae Gilg (40 genera), Rusbyantheae Gilg (1 genus), Helieae Gilg (15 genera), Voyrieae Gilg (1 genus), and Leiphaimeae Gilg (2 genera). With more adequate collections since Gilg's time, better equipment for the study of pollen grains, and utilization of a broader spectrum of characters, several of these tribes have been shown to be either unnatural or unnecessary. For example, *Voyriella* Miq., one of the two genera in Gilg's Leiphaimeae is certainly more correctly classified among the Gentianeae; the other genus, *Leiphaimos* Cham. & Schlecht., is probably congeneric with *Voyria* Aublet, therefore completely eliminating the tribe. In this paper, the elimination of the Rusbyantheae is proposed in addition.

Macrocarpaea cinchonifolia (Gilg) Weaver, comb. nov.

Rusbyanthus cinchonifolius Gilg in Engler & Prantl, Nat. Pflanzenfam. **4**(2): 95. 1895. LECTOTYPE: **Bolivia:** Mapiri, *Rusby 1173* (NY).

M. pachystyla sensu Ewan, Contr. U.S. Natl. Herb. **29**: 245. 1948.

To judge from the few available collections, the distribution of this species ranges from 1000 to 1800 meters in the Andes of the Peruvian Departments of Huanuco and Puno and the Bolivian Department of La Paz. It is closely related to *Macrocarpaea viscosa* (R. & P.) Gilg, *M. corymbosa* (R. & P.) Ewan, and *M. pachystyla* Gilg, the three species found by Nilsson (1968) to have pollen of what he called the "*M. corymbosa*-type."

Gilg proposed the tribe Rusbyantheae to accommodate *Rusbyanthus cinchonifolius* Gilg, the pollen grains of which were supposedly unique in the family. He described them as lacking furrows but with three equatorial pores and with the exine beset with numerous large processes standing apart from each other at regular intervals. However, Nilsson (1968, 1970) recently described the pollen of *Rusbyanthus* as being 3-colporate (with 3 aperturate furrows), the normal condition in the family, and he noted a fine reticulum between the large, wartlike processes. In addition, he found that three species of *Macrocarpaea* (Griseb.) Gilg, the genus closest to *Rusbyanthus* in Gilg's treatment, but in the Gentianeae-Tachiinae, possessed pollen of the same type.

In *Macrocarpaea* the exine pattern of the pollen grains is typically a coarse reticulum, the muri of which are 0.7–2 μm. broad. Nilsson noted that in transverse section the muri of these are similar to the processes of *Rusbyanthus* and that a reduction of the muri would lead to pollen of the *Rusbyanthus*-type. He suggested that the two genera might be combined.

Ewan (1948) considered *Macrocarpaea* and *Rusbyanthus* to be closely allied, and he listed the diagnostic features separating them as follows: *Rusbyanthus* with calyx lobes distinctly unequal, a berrylike capsule that dehisces irregularly, and large, lunate to reniform seeds 3–4 mm. long; and *Macrocarpaea* with calyx lobes essentially equal, a capsule dehiscent into 2 regular longitudinal valves, and small or minute seeds less than 2 mm. long. The calyx character, however, is not constant, many species of *Macrocarpaea* having distinctly unequal calyx lobes. Ewan badly misinterpreted the seeds and capsules of *Rusbyanthus*, his description undoubtedly based on fragments of a solanaceous plant mounted with several specimens of *R. cinchonifolius* (*Rusby 1173*, PH, US). A Miguel Bang collection, without number (NY), shows the capsule of *Rusbyanthus* to be a typical gentianaceous one, larger than but similar to that of many species of *Macrocarpaea*. The seeds, minute and flat with an elongate wing at each end, are also similar to those of many species of that genus.

Morphologically *Rusbyanthus cinchonifolius* fits perfectly well within *Macrocarpaea*; and since the pollen of the two is basically similar, there is no reason to recognize *Rusbyanthus* as a distinct genus, let alone the Rusbyantheae as a valid tribe. The date of publication is the same for both genera (Gilg, 1895), but since *Macrocarpaea* is by far the larger it is the logical choice as the name to be retained when the two are combined.

The nomenclatural history of *Macrocarpaea cinchonifolia* is somewhat confused. N. L. Britton annotated two specimens of this taxon (*Rusby 1173*, NY) as "*Lisianthus cinchonaefolius* (Britton, n. sp.)," at an unknown date, but the name was never published. Gilg (1895), in describing *Rusbyanthus* as a new genus, mentioned "*R. cinchonifolius* (Britt.) Gilg" as its sole species, evidently intending to make a new combination. But since neither the name nor the description of Britton's new species was ever published, the name *Rusbyanthus cinchonifolius* must be attributed to Gilg alone.

Gilg did not cite any specimens when he inadvertently described *Rusbyanthus cinchonifolius*; any specimens that may have been among the collections at Berlin, where he worked at that time, were destroyed during World War II. Therefore, a lectotype must be chosen.

By 1895 *Rusby 1173* and a Bang collection without number were the only known collections of this taxon. Two specimens of the latter are preserved at the New York Botanical Garden. One is in fruit and the other consists of a vegetative branch. Since Bang's collections were distributed by Britton, these probably represent the first set. Therefore, it is assumed that this collection did not include flowering material. Gilg did not mention the capsule in his description of *Rusbyanthus*, so it is likely that he did not examine the Bang collections at least by the time of publication. The Rusby collection consists of flowering material and is well distributed. One of the three specimens at the New York Botanical Garden was annotated by Gilg as "*Rusbyanthus cinchonifolius* Gilg n. gen." in 1896. This specimen is designated the lectotype of that name. Although Gilg's annotation was made the year after the name appeared in print, there is little doubt that this is the collection on which he based his description.

LITERATURE CITED

EWAN, J. 1948. A revision of *Macrocarpaea*, a neotropical genus of shrubby gentians. Contr. U.S. Natl. Herb. **29**(5): 209–249.

GILG, E. 1895. Gentianaceae. *In*: A. ENGLER & K. PRANTL, Die Natürlichen Pflanzenfamilian **4**(2): 50–108.

NILSSON, S. 1968. Pollen morphology in the genus *Macrocarpaea* (Gentianaceae) and its taxonomical significance. Sv. Bot. Tidskr. **62**: 338–364.

———. 1970. Pollen morphological contributions to the taxonomy of *Lisianthus* L. s. lat. (Gentianaceae). *Ibid.* **64**: 1–43.

ARNOLD ARBORETUM
HARVARD UNIVERSITY
JAMAICA PLAIN
MASSACHUSETTS 02130

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

KENNETH R. ROBERTSON

ROSACEAE A. L. de Jussieu, Gen. Pl. 334. 1789, nom. cons.

(ROSE FAMILY)

Trees, shrubs, perennial herbs, or, infrequently, annuals, sometimes armed with thorns or prickles; indumentum of simple and/or stellate or glandular trichomes; plants often increasing vegetatively by rhizomes, runners, creeping stems, or suckers. Leaves alternate [very rarely opposite], simple to palmately or pinnately compound, cauline and/or basal, sometimes clustered on short shoots, short to long petiolate, the blades commonly toothed and lobed; stomata ranunculaceous; stipules present (absent in some Spiraeoideae), paired, inconspicuous to foliaceous, often adnate to the petioles. Inflorescences terminal or axillary cymes, corymbs, umbels, racemes, spikes, or panicles, infrequently reduced to a single flower; bracts subtending the inflorescences and their branches. Flowers perfect, rarely imperfect and the plants then dioecious or monoecious, regular or rarely slightly irregular by displacement, 5-merous (or rarely 4-merous), the insertion of the perianth and androecium perigynous to epigynous, seldom nearly hypogenous. Calyx lobes 5 (rarely 4), often with an equal number of alternating epicalyx lobes, appearing to arise from the rim of the floral cup, nearly always persistent in fruit, valvate (quincuncial in *Rosa*) in aestivation; floral tube (cup) various: flat, cup-shaped, cylindric, campanulate, turbinate, or urceolate, free from or adnate to the carpels, often enlarging in fruit, a nectar ring usually inside the rim of the cup or lining it. Petals the same number as the calyx lobes, rarely absent or "doubled," white, yellow, pink, purple, or orange, never

---

[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. Part of this research has been supported by 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 the plants in this area, with additional information from extraterritorial taxa in brackets. References that I have not seen are marked by an asterisk.

This paper has been scrutinized by Professor Wood, and I am most grateful for his numerous suggestions and corrections. Appreciation is also extended to Nancy Dunkly and Judi Hanhisalo for checking many of the references and typing parts of the manuscript. The illustrations of *Aruncus*, *Porteranthus*, *Fragaria* and *Duchesnea*, *Potentilla*, *Prunus*, *Pyrus* subg. *Aronia*, and *Rosa* are by Karen Stoutsenberger Velmure; those of *Neviusia* and *Physocarpus* by Rachel A. Wheeler; that of *Amelanchier* by Arnold D. Clapman.

blue or truly red, often shortly clawed below, caducous, imbricate or rarely contorted in bud, inserted at the upper edge of the floral cup. Androecium most frequently of 15 or more centripetally developing stamens in several series (whorls) with the inner ones shorter than the outer, or often 10 (8) in one series, or infrequently 5 (4), or rarely reduced to 1 or 2, inserted on the rim of, or rarely on the adaxial wall of, the floral cup; filaments free or basally united to the nectar ring, commonly persistent; anthers small, ± versatile (or infrequently basifixed), 2-loculate at anthesis, dehiscing introrsely [or extrorsely] by longitudinal slits [very rarely by subterminal pores], the locules sometimes separated by broad connectives; pollen 2-celled when shed, basically tricolporate, the sexine striate. Gynoecium of 1 to many spirally or cyclically arranged carpels inserted at the base of, on the sides of, or inclosed by the floral cup, the receptacle flat, concave, or convex to hemispheric or cylindric, the carpels or receptacles infrequently stipitate, the carpels apocarpous [rarely syncarpous], although sometimes ± laterally connate and abaxially adnate to the floral cup, the ovaries superior to partly or completely inferior; styles as many as the carpels, free or connate below, terminal, lateral, or nearly basal, deciduous or persistent; stigmas terminal, punctiform, discoid, or in bands decurrent on the styles; each carpel with 1 or 2 (or more in the Spiraeoideae) anatropous (rarely orthotropous) ovules basal, lateral, or pendulous from the adaxial wall, the micropyles abaxial. Fruits very diverse: follicles (sometimes dehiscing along both adaxial and abaxial sutures), achenes exposed or inclosed within the floral cup, pomes, drupes, or aggregate or accessory with drupelets or achenes [or very rarely capsules]. Seeds very small to large, variously textured [winged in tribe Quillajeae]; endosperm usually absent or sparse (abundant in some Spiraeoideae); embryo spathulate, the cotyledons fleshy, plano-convex [rarely foliaceous, convolute, or folded], the radicle straight to slightly bent, superior or inferior. Base chromosome numbers 7, 8, or 9. (Including Spiraeaceae D. Don, Malaceae J. K. Small, and Amgydalaceae D. Don; excluding Chrysobalanaceae R. Brown [see Prance]). TYPE GENUS: *Rosa* L.

About 100 genera and 3000 species (not including "microspecies" of apomictic genera) in four subfamilies and 13 tribes. Members of the family can be found in nearly every region of the world where vascular plants occur, but Rosaceae are most abundant, both in numbers of individuals and of diverse forms, in the North Temperate regions, particularly western North America and eastern Asia. No genus is restricted to Europe and no tribe to the Old World; tribe Quillajeae is limited to the New World. With the exception of the Kerrieae (Rosoideae), all tribes are represented in western North America. Twenty-two genera (three introduced from the Old World) of all four subfamilies and 10 tribes occur in the southeastern United States; an additional eight genera (including five that have escaped from cultivation) are found in northeastern North America. *Porteranthus*, *Neviusia*, and *Dalibarda* are endemics of eastern North America. Twenty-three more genera grow in western North America, and of these 20 (or 21 if *Heteromeles* is considered distinct from *Photinia*) are essentially restricted to that area. Five genera (six if *Hesperomeles* is separated from *Osteomeles*) do not occur outside of Central and South America. Forty-five genera have species indigenous to North America, and there are 42 with species restricted to that region.

Although diverse in vegetative and fruit morphology, the family is a natural one. There has long been rather general agreement about the supraspecific taxa that are related to one another, but the taxonomic rank given these groups varies greatly. Perhaps as few as 80 or as many as 130 genera can be recognized. The genera, in turn, have been grouped variously into subtribes, tribes, or subfamilies, and several tribes and/or subfamilies are often given familial status. The information available at present indicates that *Chrysobalanus* and its relatives should be considered as a separate family, Chrysobalanaceae (see Prance), and that *Neurada*, *Neuradopsis*, and *Grielum* are best segregated as Neuradaceae. The remaining genera of Rosaceae can be assigned to four subfamilies: Spiraeoideae (with tribes Neillieae, Spiraeeae, Sorbarieae, Quillajeae, and Exochordeae), Rosoideae (with tribes Kerrieae, Fragarieae, Dryadeae, Ulmarieae, Sanguisorbeae, Adenostomateae, Roseae, and Rubeae), Amygdaloideae, and Maloideae. On the basis of morphological, cytological, and chemical data, it seems that Spiraeoideae and Amygdaloideae are the basic stocks of the family, the Rosoideae being derived from the Spiraeoideae by reduction in the number of ovules per carpel with a concomitant increase in the number of carpels per flower (the fruits becoming indehiscent), a dramatic multiplication or reduction in the number of stamens in many cases, a decrease in the base chromosome number, the loss of flavonols and sorbitol, and the acquisition of ellagic acid. Maloideae perhaps arose through hybridization between some ancient species of Spiraeoideae and Amygdaloideae (see discussion under Maloideae).

In the Englerian scheme of classification, Rosaceae are placed along with Platanaceae, Crossosomataceae, Connaraceae, and Leguminosae in suborder Rosineae of the Rosales. Most recent phylogenists group Platanaceae with Hamamelidaceae and Crossosomataceae with Dilleniaceae, and there is rather general agreement that Rosaceae, Saxifragaceae, Leguminosae, and Connaraceae are allied, although various taxonomic ranks are recognized. Hutchinson included Dichapetalaceae and Calycanthaceae in his Rosales.

Flowers of Rosaceae vary greatly in size, from very small, as in species of *Alchemilla*, *Aruncus*, and *Spiraea*, to large and showy, as in *Rosa* and *Rubus*. Flower color ranges from white and cream to yellow, pink, purple or orange; blues are totally absent (see below), and true red flowers occur rarely, if ever. Rosaceae do not seem to have undergone a series of extensive adaptations related to different pollination mechanisms such as those found in Ranunculaceae. Most species of Rosaceae have rather generalized perfect, regular, flat or shallowly cup-shaped flowers with a prominent nectar ring at the apex of the floral cup. Flies and shorttongued bees are the commonest pollinators of small flowers, while long-tongued bees, other Hymenoptera, Coleoptera, and Lepidoptera visit large-flowered species. Some species of *Sanguisorba* lack petals and are wind pollinated. Homogamy and, to a lesser extent, proterogyny are common in the family. Should cross pollination not take place, many species are automatically self pollinated and are self compatible. Imperfect flowers regularly occur in some species of *Aruncus*, *Bencomia*, *Cliffortia*, *Dryas*, *Hagenia*, *Kageneckia*, *Osmaronia*, *Rubus*, and *Sanguisorba*, and the plants are then dioecious or variously monoecious.

Many fruit types occur in Rosaceae, and fruit morphology is used as a prime character in the subdivision of the family. The fruits of most Spiraeoideae are follicles (legumes?) that may split along both adaxial and abaxial sutures. *Holodiscus* is the only member of the Spiraeoideae with achenes. In *Exochorda* the carpels become connate at maturity, and the fruit is capsular. *Lindleya* and *Vauquelinia* have loculicidal capsules. Rosoideae have achenes or drupelets, these sometimes aggregated, or inclosed by the dry to fleshy floral cup, or borne on the fleshy receptacle. All Maloideae have pomes (see discussion under that subfamily), while drupes are produced by members of the Amygdaloideae.

The family seems to have undergone an extensive series of adaptations evidently tied to dispersal by various means. Mechanisms for dispersal by wind are found in tribe Quillajeae (winged seeds), some Spiraeoideae (small seeds with loose, membranaceous seed coats), many Dryadeae (plumose styles), and some Sanguisorbeae (winged floral cups that inclose the seeds). Adaptations for transport by attachment to animals are found in Dryadeae (hooked styles), some species of *Rosa* (prickles on the floral cups), and some Sanguisorbeae (hooked bristles or spines with retrorse barbs on the floral cups). Certain species of *Potentilla* that have achenes with elaiosomes are dispersed by ants. Many Rosaceae have fleshy fruits and are eaten by mammals, birds, and reptiles, the seeds passing through the digestive tracts. In *Prunus* and *Rubus*, the outer carpel walls become fleshy, in *Fragaria* and *Duchesnea*, the receptacles, and in *Rosa* and all Maloideae, the floral cups.

Chromosome numbers have been reported from species representing over 60 genera. Unfortunately, many of these counts are old, undocumented, and/or from cultivated materials of unknown origin, and some widespread genera, as well as some commonly cultivated (at least in botanical gardens), have not been examined cytologically. A concentrated effort to obtain counts for as many Rosaceae as possible would be most worthwhile, even if tedious. Subfamily Spiraeoideae has a base chromosome number of 9, with only a few occurrences of 8 or 10. *Quillaja brasiliensis* is anomalous in that it is thus far the only known species of Rosaceae outside the subfamily Maloideae with a chromosome number $2n = 34$. Except for some populations of *Aruncus dioicus*, only diploids and tetraploids occur in Spiraeoideae. Subfamily Rosoideae has base numbers of 7 and 9, rarely 8. A base number of 9 occurs mostly in tribes Kerrieae, Adenostomateae, and some New World genera of Dryadeae.

Many genera of Rosoideae have polyploid series, and the highest chromosome number known for the family is $2n=$ ca. 224 in *Alchemilla faroënsis*. The base chromosome number of subfamily Amygdaloideae is 8, and most species are either diploid or tetraploid. All members of subfamily Maloideae have a base number of 17; see the discussion under that subfamily for several hypotheses on the possible origin of this number.

Many Rosaceae have been rather extensively studied for their chemical constituents, especially phenolics. Cyanidin is the common petal pigment, with pelargonidin rarely occurring; delphinidin is absent (hence no blue-flowered Rosaceae). Leucocyanidin occurs in the leaves of all species; leucodelphinidin is known only from *Potentilla anserina* (but it regularly occurs in Chrysobalanaceae). The flavonols kaempferol and quercetin are ubiquitous, while the family (with the exception of *Potentilla anserina*) lacks trihydroxy flavonoid compounds that are found in Chrysobalanaceae. Dihydrochalkones have been isolated from species of *Malus* and *Docynia* (Maloideae), *Adenostoma* (Rosoideae), and *Sorbaria* (Spiraeoideae). Flavone glycosides are present in all four subfamilies, but in Rosoideae are restricted to tribe Kerrieae. Ellagic acid is found in all Rosoideae, except the Kerrieae, but is lacking in the other subfamilies. Sorbitol occurs throughout the Maloideae, Amygdaloideae, Spiraeoideae, and tribe Kerrieae of the Rosoideae; it is absent from other Rosoideae. Arbutin is known from *Sorbaria* and *Exochorda* (Spiraeoideae), *Adenostoma* (Rosoideae), and *Pyrus* (Maloideae). Alkaloids seem to occur only rarely in the family.

Some members of Rosaceae are often confused with Ranunculaceae and Saxifragaceae. Rosaceae can be distinguished from the former by the flowers with floral cups, by the perigynous to epigynous insertion of the petals and stamens, and by the whorled stamens. Rosaceae differ from Saxifragaceae by the mostly alternate, stipulate leaves, the apocarpous gynoecium, and the more numerous stamens and carpels. Fruits of Rosaceae are diverse but are never berries as in some Ranunculaceae and Saxifragaceae, or are very rarely capsules as in most Saxifragaceae; seeds of Rosaceae lack endosperm (except for some Spiraeoideae).

Rosaceae are among the more economically important families of plants. Although no species is a staple food item, the diets of many peoples of the world are enriched by fruits of Rosaceae. From species of *Pyrus* come pears and apples; from *Prunus*, plums, cherries, peaches, nectarines, apricots, and almonds; from *Rubus*, blackberries and raspberries; from *Fragaria*, strawberries; from *Eriobotrya*, loquats; from *Amelanchier*, service berries; from *Cydonia*, quinces; from *Mespilus*, medlars; and from *Rosa*, rose hips. Rosaceae with fleshy fruits are important wildlife foods, and the foliage of *Purshia* and *Cowania* is eaten by game and livestock in southwestern North America. Many species of Rosaceae are used in home medicines for a variety of ailments; this is unusual for a family in which alkaloids are rare. Otto (or attar) of roses, an essential oil used in perfumery, is distilled from the petals of *Rosa*

Damascena. Wood from species of *Prunus*, *Pyrus*, *Crataegus*, and *Amelanchier* goes into the manufacture of furniture, musical instruments, and other items. Most genera of Rosaceae are cultivated to a limited degree, with *Crataegus*, *Prunus*, *Pyracantha*, *Pyrus*, *Rosa*, and *Spiraea* furnishing important ornamental plants in the Northern Hemisphere. Several states have designated members of Rosaceae as their state flowers or trees.

REFERENCES:

See also subfamily references. The following authors deal with most or all of the genera in our area and are not referred to again under the generic references: BAILLON, BENTHAM & HOOKER, BOLKHOVSKIKH *et al.*, DE CANDOLLE, CHITTENDEN, DAVIS, FOCKE, HUTCHINSON, JUEL, KANIA, KOMAROV, A. C. MARTIN, PRODINGER, REITSMA, RYDBERG, SCHULZE-MENZ, and VALENTINE & CHATER.

BAILLON, H. Monographie des Rosacées. Hist. Pl. **1**: 345–483. 1869. [English transl. M. M. HARTOG, The natural history of plants. **1**: 335–471. 1871.]

BALDWIN, J. T., JR. Chromosomes of *Spiraea* and of certain other genera of Rosaceae. Rhodora **53**: 203–206. 1951. [*Cowania*, *Fallugia*, *Neviusia*, *Physocarpus*, *Spiraea*.]

BATE-SMITH, E. C. Chromatography and taxonomy in the Rosaceae, with special reference to *Potentilla* and *Prunus*. Jour. Linn. Soc. Bot. **58**: 39–54. 1961. [Also 14 other genera.]

BEAN, W. J. Trees and shrubs hardy in the British Isles, ed. 7. Vol. 3. viii + 664 pp. *pls. 1–41.* London. 1951 [*Rosa*, *Rubus*, *Spiraea*, *Sorbus*]; ed. 8, G. TAYLOR, ed. Vol. 1. xx + 845 pp. *77 pls. on 48 pp.* 1970 [*Amelanchier*, *Aronia*, *Crataegus*]; Vol. 2. xvi + 784 pp. *106 pls. on 64 pp.* 1973. [*Malus*.]

BENTHAM, G., & J. D. HOOKER. Rosaceae. Gen. Pl. **1**: 600–629. 1865. [Treatment by HOOKER; family divided into 10 tribes.]

BOLKHOVSKIKH, Z., V. GRIF, T. MATVEJEVA, & O. ZAKHARYEVA. Chromosome numbers of flowering plants. Ed. by A. A. FEDOROV. (Russian and English prefaces.) 926 pp. Leningrad. 1969. [Rosaceae, 617–642; includes literature to 1967, but does not include indices of plant chromosome numbers for 1965 (Regnum Veg. **50**) or 1966 (Regnum Veg. **55**).]

BONNE, G. Recherches sur le pédicelle et la fleur des Rosacées. 380 pp. *10 pls.* Paris. 1928.*

BOUTINEAU, E. De la fleur des Rosacées. Contribution à l'étude des ovaires infères. 44 pp. *4 pls.* Paris. 1883. [Including *Agrimonia*, *Alchemilla*, *Crataegus*, *Filipendula*, *Geum*, *Potentilla*, *Prunus*, *Pyrus*, *Rosa*, and *Sanguisorba*.]

BUNTING, M. The structure of the cork tissues in roots of some rosaceous genera. Contr. Bot. Lab. Univ. Penna. **2**: 54–65. *pl. 10.* 1898. [Including *Agrimonia*, *Alchemilla*, *Duchesnea*, *Filipendula*, *Geum*, *Potentilla*, *Prunus*, *Pyrus*, *Rosa*, *Rubus*, *Sanguisorba*, and *Waldsteinia*.]

CANDOLLE, A. P. DE. Rosaceae. Prodr. **2**: 525–639. 1825. [8 tribes recognized.]

CEJP, K. Einige Bemerkungen über die Diagrammatik der Rosaceen. Österr. Bot. Zeitschr. **73**: 48–58. 1924.

CHITTENDEN, F. J., ed. Royal Horticultural Society Dictionary of Gardening. Ed. 2 by P. M. SYNGE. 4 vols. 2316 pp. Genera arranged alphabetically. London. 1956. Supplement, ed. 2. xii + 555 pp. 1969. [Contains important treatments, sometimes contributed by specialists, on the cultivated members of the family.]

CLARK, R. C. The woody plants of Alabama. Ann. Missouri Bot. Gard. **58**: 99–242. 1971. [Rosaceae, 172–185; keys to genera and species, distribution maps; also see editor's note, 266.]

CHUTE, H. M. The morphology and anatomy of the achene. Am. Jour. Bot. **17**: 703–723. *pls. 42–44.* 1930. [Including *Agrimonia*, *Dalibarda*, *Duchesnea*, *Fragaria*, *Geum*, *Potentilla*, *Rubus*, *Waldsteinia*.]

CROCKER, W., & L. V. BARTON. After-ripening, germination, and storage of certain rosaceous seeds. Contr. Boyce Thompson Inst. **3**: 385–404. [*Amelanchier*, *Prunus*, *Pyrus*, *Rosa*.]

DAVIS, G. L. Systematic embryology of the angiosperms. x + 528 pp. New York. 1966. [Rosaceae, 228, 229.]

DEVADAS, C., & C. B. BECK. Development and morphology of stelar components in the stems of some members of the Leguminosae and Rosaceae. Am. Jour. Bot. **58**: 432–446. 1971. [Including *Geum*, *Physocarpus*, *Potentilla*, *Prunus*, *Rubus*.]

——— & ———. Comparative morphology of the primary vascular systems in some species of Rosaceae and Leguminosae. *Ibid.* **59**: 557–567. 1972. [Including *Geum*, *Physocarpus*, *Potentilla*, *Prunus*, *Rubus*.]

DIPPEL, L. Handbuch der Laubholzkunde. Vol. 3. viii + 752 pp. Berlin. 1893. [Rosiflorae, 355–650; consult for all woody genera.]

EICHLER, A. W. Rosaceae. Blüthendiagramme **2**: 495–514. 1878.

EVANS, G., D. P. WATSON, & H. DAVIDSON. Initial evaluation of grafting some species of the Rosaceae. Proc. Am. Soc. Hort. Sci. **78**: 580–585. 1961.*

FOCKE, W. O. Rosaceae. Nat. Pflanzenfam. III. 3: 1–61. 1888; Nachträge II–IV: 186–189. 1897; Ergänzungsheft. I: 29. 1900.

FREE, J. B. Insect pollination of crops. xi + 544 pp. London & New York. 1970. [*Prunus* and *Pyrus*, chapter 34; *Fragaria*, chapter 35; *Rubus*, chapter 36.]

GERSTNER, E., V. MÄTZKE, & E. PFEIL. Zur chemischen und biologischen Systematik der Rosaceen. Untersuchung des Flavinsystems D-Oxynitrilase. Naturwissenschaften **55**: 561–563. 1968. [Compound absent in all Spiraeoideae and Rosoideae tested, present in most Maloideae and Amygdaloideae.]

GUSTAFSSON, Å. Apomixis in higher plants. Part I. The mechanism of apomixis. Acta Univ. Lund. II. Afd. 2. **42**(3): 1–68. 1946; Part II. The causal aspect of apomixis. *Ibid.* **43**(2): 69–180. 1947; Part III. Biotype and species formation. *Ibid.* **43**(12): 181–370. 1947.

HARA, H. Contributions to the study of variations in the Japanese plants closely related to those of Europe or America. I. Jour. Fac. Sci. Univ. Tokyo Bot. **6**: 29–96. 1952. [*Aruncus*, *Dryas*, *Geum*, *Potentilla*, *Rosa*, *Rubus*, *Sanguisorba*, *Sibbaldia*, *Spiraea*.]

HARBORNE, J. B. Comparative biochemistry of the flavonoids. viii + 383 pp. London and New York. 1967. [Flavonoids of the Rosaceae, 154–160.]

HEGI, G. Rosaceae. Illus. Fl. Mittel-Europa **4**(2): 662–908. *pls. 145–151.* 1922; 909–1112b. *pls. 152–157.* 1923. [*Agrimonia*, *Alchemilla*, *Amelanchier*, *Aruncus*, *Crataegus*, *Filipendula*, *Fragaria*, *Geum*, *Potentilla*, *Prunus*, *Pyrus*, *Rosa*, *Rubus*, *Waldsteinia*; also see HUBER.]

HESS, H. E., E. LANDOLT, & R. HIRZEL. Flora der Schweiz. Vol. 2. 965 pp. Basel & Stuttgart. 1970. [Rosaceae, 309–480; *Agrimonia*, *Alchemilla*, *Amelanchier*, *Aruncus*, *Crataegus*, *Filipendula*, *Fragaria*, *Geum*, *Potentilla*, *Prunus*, *Rosa*, *Rubus*, *Sanguisorba*, *Spiraea*.]

Hilton, R. J., A. S. Jaswal, B. J. E. Teskey, & B. Barabas. Rest period studies on seeds of *Amelanchier*, *Prunus*, and *Sorbus*. Canad. Jour. Pl. Sci. **45**: 79–85. 1965.

Hitchcock, C. L., A. Cronquist, M. Ownbey, & J. W. Thompson. Vascular plants of the Pacific Northwest. Part 3: Saxifragraceae to Ericaceae. 614 pp. Seattle. 1961. [Rosaceae, 89–195.]

Huber, H. Die Verwandtschaftsverhältnisse der Rosifloren. Mitt. Bot. Staatssam. München **5**: 1–48. 1963.

———. Rosaceae. *In*: G. Hegi, Illus. Fl. Mittel-Europa, ed. 2. **4**(2a): 231–438. *pls. 145, 146.* 1961–1966. [Conspectus of family with descriptions of 15 tribes and most genera; detailed accounts of ***Aruncus***, ***Dryas***, ***Filipendula***, *Geum*, *Rubus*, *Spiraea*, *Waldsteinia*; Amygdalaceae, Chrysobalanaceae, Mespilaceae, and Neuradaceae recognized.]

Hultén, E. The amphi-Atlantic plants and their phytogeographical connections. Sv. Vet. Akad. Handl. IV. **7**(1): 1–340. 1958. [*Alchemilla*, *Fragaria*, *Geum*, *Potentilla*, *Rubus*.]

———. The circumpolar plants. II. Dicotyledons. *Ibid.* **13**(1): 1–463. 1971. [*Aruncus*, *Geum*, *Potentilla*, *Pyrus* subgen. *Sorbus*, *Rosa*, *Rubus*.]

Hutchinson, J. The genera of flowering plants. Vol. 1. xii + 516 pp. London. 1964. [Rosaceae, 174–216; 20 tribes recognized.]

———. Evolution and phylogeny of flowering plants. Dicotyledons: facts and theory. xxvi + 717 pp. *2 charts.* London & New York. 1969. [Rosaceae, 48–64.]

Ikuse, M. Pollen grains of Japan. xii + 303 pp. *Frontisp., 76 pls.* Tokyo. 1956. [Rosaceae, 86–91, *pl. 18*.]

Jacobsson-Stlasny, E. Versuch einer embryologisch-phylogenetischen Bearbeitung der Rosaceae. Sitz-ber. Akad. Wiss. Berlin, Abt. 1. **123**: 763–800. 1914.*

Jessen, K. The structure and biology of arctic flowering plants. II. 8. Rosaceae. Medd. Grønl. **37**: 1–126. 1913. [Including *Alchemilla*, *Potentilla*, *Pyrus* subgen. *Sorbus*, *Rubus*.]

Juel, H. O. Beiträge zur Blütenanatomie und zur Systematik der Rosaceen. Sv. Vet. Akad. Handl. II. **58**(5): 1–81. 1918. [50 genera examined.]

———. Über die Blütenanatomie einiger Rosaceen. Nova Acta Soc. Sci. Upsal. Extra Vol. 1927. 31 pp. *1 pl.* 1927. [15 additional genera.]

Kaden, N. N. Evolution of fruit in Rosales. (In Russian; English summary.) Bull. Soc. Nat. Moscou Biol. **73**(2): 127–135. 1968.

Kania, W. Entwicklungsgeschichtliche Untersuchungen an Rosaceenblüten. Bot. Jahrb. **93**: 175–246. 1973. [52 spp. from all 4 subfam. examined.]

Kirchheimer, F. Rosaceae. *In*: W. Jongmans, ed., Fossil. Catal. II. **25**: i–xxxi + 1–259. 1942.

Knobloch, I. W. Intergeneric hybridization in flowering plants. Taxon **21**: 97–103. 1972. [Rosaceae, 102; 1478 interspecific and intergeneric hybrids reported in family, incomplete list of intergeneric hybrids.]

Knuth, P. Handbook of flower pollination. Vol. 2. Transl. J. R. A. Davis. viii + 703 pp. London. 1908. [Rosaceae, 342–395. In German ed. cf. **2**(1): 345–396; **3**(1): 334–347.]

Komarov, V. L., ed. Rosaceae: Spiraeoideae, Pomoideae. Fl. URSS **9**: xv–xix + 279–468, 489–510. 1939 [In Russian; English transl., L. Behrman, Fl. USSR **9**: xv–xix + 215–356, 375–396. Jerusalem. 1971]; Rosaceae: Rosoideae, Prunoideae. *Ibid.* **10**: xxiii + 673 pp. 1941 [English transl., R. Lavoott, *Ibid.* **10**: xii + 512 pp. 1971].

LEBÈGUE, A. Recherches embryogéniques sur quelques dicotyledones dialypetales. Ann. Sci. Nat. Bot. XI. **13:** 1–160. 1952.

LI, H. L. Floristic relationships between eastern Asia and eastern North America. Trans. Am. Philos. Soc. II. **42:** 371–429. 1952. [Reprinted, with a new foreword and additional references, by the Morris Arboretum. Philadelphia. 1971.]

LÖVE, Á., & D. LÖVE. Cytotaxonomy of the alpine vascular plants of Mount Washington. Univ. Colorado Stud. Biol. **24.** 74 pp. 1966. [*Amelanchier, Fragaria, Geum, Potentilla, Pyrus, Rubus, Spiraea.*]

LUBBOCK, J. A contribution to our knowledge of seedlings. Vol. 1. viii + 608 pp. London. 1892. [Rosaceae, 476–502; including *Agrimonia, Alchemilla, Crataegus, Geum, Potentilla, Pyrus, Rosa, Rubus, Sanguisorba, Spiraea.*]

MARTIN, A. C. The comparative internal morphology of seeds. Am. Midl. Nat. **36:** 513–660. 1946. [Rosaceae (Malaceae and Amygdalaceae), 620–623, 627, 636, 638, 644, 646.]

MARTIN, P. S., & C. M. DREW. Additional scanning electron photomicrographs of Southwestern pollen grains. Jour. Arizona Acad. Sci. **6:** 140–161. 1970. [*Coleogyne, Fallugia, Holodiscus, Vauquelinia.*]

METCALFE, C. R., & L. CHALK. Rosaceae (excluding Chrysobalanoideae). Anat. Dicot. **1:** 539–550. 1950.

MOORE, R. J. Index to plant chromosome numbers 1967–1971. Regnum Veg. **90:** 1–539. 1973.

MÜLLER, H. The fertilization of flowers. (English transl. D. W. THOMPSON, preface by CHARLES DARWIN.) xii + 669 pp. London. 1883. [Rosaceae, 221–243.]

MURBECK, S. Untersuchungen über das Androeceum der Rosaceen. Lunds Univ. Årsskr. II. Sect. 2. **37**(7): 1–56. 1941.

PÉCHOUTRE, F. Contributions à l'étude du développement de l'ovule et de la graine des Rosacées. Ann. Sci. Nat. Bot. VIII. **16:** 1–158. 1902.

PLOUVIER, V. Contribution à l'étude biochimique des quelques Rosacées. Thèse. Fac. Sci. Univ. Paris. 234 pp. Paris. 1941.

PRANCE, G. T. The genera of Chrysobalanaceae in the southeastern United States. Jour. Arnold Arb. **51:** 521–528. 1970.

PRODINGER, M. Das Periderm der Rosaceen in systematischer Beziehung. Denkschr. Akad. Wien Math. Naturw. **84:** 329–383. *pls. 1–4.* 1908. [Includes all genera in our area.]

REHDER, A. Manual of cultivated trees and shrubs hardy in North America exclusive of the subtropical and warmer temperate regions, ed. 2. xxx + 996 pp. *map.* New York. 1940. [Rosaceae, 322–482; *Amelanchier, Crataegus, Neviusia, Physocarpus, Potentilla, Prunus, Pyracantha, Pyrus, Rosa, Rubus, Spiraea.*]

REITSMA, R. Pollen morphology of some European Rosaceae. Acta Bot. Neerl. **15:** 290–307. *pls. 1–3.* 1966. [46 spp. in 15 genera.]

RICKETT, H. W. Wildflowers of the United States. Vol. 2. The Southeastern States. Part 1. x + 322 pp. *pls. 1–116.* New York. 1966. [Rosaceae, 183–196, *pls. 66–70.*]

ROBERTSON, C. Flowers and insects — Rosaceae and Compositae. Trans. Acad. Sci. St. Louis **6:** 435–480. 1894. [*Agrimonia, Amelanchier, Crataegus, Fragaria, Geum, Potentilla, Prunus, Pyrus, Rosa, Rubus, Spiraea.*]

———. Flowers and insects. Lists of visitors of four hundred and fifty-three flowers. 221 pp. Carlinville, Illinois. 1928. [Rosaceae, 164–175; same genera as preceding paper plus *Aruncus* and *Porteranthus* (as *Gillenia*).]

Rodriguez-Barrueco, C. The occurrence of nitrogen-fixing root nodules on non-leguminous plants. Bot. Jour. Linn. Soc. London **62:** 77–84. *1 pl.* 1969. [*Cercocarpus*, *Dryas*, *Purshia*.]

Roemer, T., & W. Rudorf. Handbuch der Pflanzenzüchtung, ed. 2. Vol. 6. Züchtung von Gemüse, Obst, Reben und Forstpflanzen. xxxvii + 913 pp. Berlin & Hamburg. 1962. [Rosaceae, 477–509, 514–722; *Fragaria*, *Prunus*, *Pyrus*, *Rubus*.]

Ross-Craig, S. Drawings of British plants. VIII. Rosaceae (1). *40 pls.* London. 1955. [*Dryas*, *Filipendula*, *Fragaria*, *Geum*, *Potentilla*, *Prunus*, *Rubus*, *Sibbaldia*.] IX. Rosaceae (2). *39 pls.* 1956. [*Agrimonia*, *Alchemilla*, *Cotoneaster*, *Crataegus*, *Mespilus*, *Pyrus*, *Rosa*, *Sanguisorba*.]

Rouane, M. L. Intérêt taxinomique des plantules de Rosacées. Bull. Soc. Hist. Nat. Toulouse **102:** 429–435. 1966.

Rouffa, A. S., & J. E. Gunckel. A comparative study of vegetative shoot apices in the Rosaceae. Am. Jour. Bot. **38:** 290–300. 1951.

——— & ———. Leaf initiation, origin, and pattern of pith development in the Rosaceae. *Ibid.* 301–307.

Rydberg, P. A. Rosaceae. N. Am. Fl. **22:** 239–388. 1908; 389–480. 1913; 481–533. 1918. [Also see series of 14 articles entitled "Notes on Rosaceae" in Bull. Torrey Bot. Club, vols. 35–50. 1908–1923; Malaceae and Amygdalaceae not treated.]

Sargent, C. S. Rosaceae to Saxifragaceae. Silva N. Am. **4:** 1–141. *pls. 148–197.* 1892. [Includes *Amelanchier*, *Crataegus*, *Prunus*, *Pyrus*.]

———. Manual of the trees of North America (exclusive of Mexico). ed. 2. xxvi + 910 pp. *map.* Boston & New York. 1922. [Rosaceae, 376–585; very complete descriptions.]

Saunders, E. R. Perigyny and carpel polymorphism in some Rosaceae. New Phytol. **24:** 206–224. 1925.

———. On carpel polymorphism. I. Ann. Bot. **39:** 123–167. 1925; II. *Ibid.* **41:** 569–627. 1927.

Schneider, C. K. Illustriertes Handbuch der Laubholzkunde. Vol. 1. x + 810 pp. 1904–1906. [Spiraeaceae, 440–499. 1905; Rosaceae, 499–802. 1905, 1906.]

Schulze-Menz, G. K. Rosaceae. *In*: H. Melchior, A. Engler's Syllabus der Pflanzenfamilien. ed. 12. **2:** 209–218. 1964. [17 tribes in 4 subfamilies; Chrysobalanaceae and Neuradaceae recognized.]

Stephens, H. A. Trees, shrubs, and woody vines in Kansas. vi + 250 pp. Lawrence, Kansas. 1969. [*Amelanchier*, *Crataegus*, *Prunus*, *Pyrus*, *Rosa*, *Rubus*; includes photographs of leaves, bark, buds, flowers, and fruits.]

Sterling, C. Comparative morphology of the carpel in the Rosaceae. I. Prunoideae: *Prunus*, Am. Jour. Bot. **51:** 36–44. 1964; II. *Maddenia*, *Pygeum*, *Osmaronia*. *Ibid.* 354–360; III. Pomoideae: *Crataegus*, *Hesperomeles*, *Mespilus*, *Osteomeles*. *Ibid.* 705–712; IV. *Chamaemeles*, *Cotoneaster*, *Dichotomanthes*, *Pyracantha*. *Ibid.* **52:** 47–54. 1965; V. *Amelanchier*, *Aronia*, *Malacomeles*, *Malus*, *Peraphyllum*, *Pyrus*, *Sorbus*. *Ibid.* 418–426; VI. *Eriobotrya*, *Heteromeles*, *Photina*, *Pourthiaea*, *Raphiolepis*, *Stranvaesia*. *Ibid.* 938–946; VII. *Chaenomeles*, *Cydonia*, *Docynia*. *Ibid.* **53:** 225–231. 1966; VIII. Spiraeoideae: Holodisceae, Neillieae, Spiraeeae, Ulmarieae. *Ibid.* 521–530; IX. Quillajeae, Sorbarieae. *Ibid.* 951–960; X. Evaluation and summary. Österr. Bot. Zeitschr. **116:** 46–54. 1969.

Tarchi, A. M. F. Micrographic comparison of the wood of some Rosaceae. (In Italian.) Ann. Accad. Ital. Sci. Forest. Florence **9:** 57–115. 1960.*

TAYLOR, L. A. Plants used as curatives by certain southeastern tribes. Part I. Plants used medicinally. xi + 88 pp. Botanical Museum, Harvard University. 1940. [*Amelanchier*, *Porteranthus* (as *Gillenia*) *Prunus*, *Pyrus*, *Rosa*, *Rubus*.]

TAYLOR, T. M. C. The rose family of British Columbia. British Columbia Prov. Mus. Victoria Bull. **30.** 223 pp. 1973.

TEPPNER, H. Zur Kenntnis der Gattung *Waldsteinia*, I. Schlüssel zum Bestimmen von Rosaceen-Pollen einschliesslich ähnlicher Pollenformen aus anderen Familien. Phyton Austria **11:** 224–238. 1966.

VALENTINE, D. H., & A. O. CHATER, eds. Rosaceae. *In*: T. G. TUTIN, V. H. HEYWOOD, *et al.*, eds., Fl. Europaea **2:** 3–80. 1968.

VINES, R. A. Trees, shrubs and woody vines of the Southwest. xii + 1104 pp. Austin, Texas. 1960. [Rosaceae, 329–490; includes species of *Amelanchier*, *Crataegus*, *Physocarpus*, *Potentilla*, *Prunus*, *Pyracantha*, *Pyrus*, *Rosa*, *Rubus*, and *Spiraea* that occur in Arkansas and Louisiana.]

WILLIS, J. C. A dictionary of the flowering plants and ferns. Ed. 8. (Revised by H. K. Airy Shaw.) xxii + 1245 pp. + lxvi pp. (Key to the families of flowering plants.) Cambridge, England. 1973. [Rosaceae, 1004, 1005; 4 subfamilies and 11 tribes recognized; genera alphabetically arranged.]

WOOD, C. E., JR. Some floristic relationships between the southern Appalachians and western North America. Pp. 331–404 *in* P. C. HOLT, ed. The distributional history of the biota of the southern Appalachians. II. Flora. Research Div. Monogr. **2.** Virginia Polytech. Inst. State Univ. 1971. [*Aruncus*, *Sanguisorba*, *Spiraea*, 377; *Filipendula*, 378; *Physocarpus*, *Rubus*, *Waldsteinia*, 390.]

KEY TO THE SUBFAMILIES, TRIBES, AND GENERA OF ROSACEAE IN THE SOUTHEASTERN UNITED STATES

A. Gynoecium of 2 to many carpels (rarely one); fruit a follicle, pome, or achene, or fruit aggregate or accessory with drupelets or achenes; insertion perigynous to epigynous, the ovaries superior to inferior; ovules various; styles terminal to nearly basal.

  B. Carpels free from the floral cup, although sometimes surrounded by it, the ovaries superior; fruits follicles, achenes, or drupelets; shrubs or herbs, unarmed or with prickles.

    C. Fruits follicles, sometimes opening on both abaxial and adaxial sutures; ovules 2 or more per carpel; endosperm often present; stipules sometimes absent (subfam. SPIRAEOIDEAE).

      D. Seed coat hard, shining; fruits inflated; endosperm abundant; carpels united at least basally; stipules present (NEILLIEAE). .... 1. *Physocarpus*.

      D. Seed coat membranaceous or roughened, not hard and shiny; fruits not inflated; endosperm sparse or abundant; carpels free or basally united; stipules present or absent.

        E. Stipules absent; carpels antepetalous, when 5; seeds small, tapering at each end, the coat membranaceous; endosperm sparse (SPIRAEEAE).

          F. Plants shrubs; leaves simple; flowers perfect; carpels 5. .... 2. *Spiraea*.

          F. Plants herbaceous; leaves several times pinnately compound;

flowers mostly imperfect, the plants dioecious; carpels usually 3(2–5). 3. *Aruncus.*

E. Stipules prominent, persistent; carpels 5, antesepalous; seeds about 5 mm. long, not tapering, the coat hard, roughened; endosperm thick, fleshy (Sorbarieae). 4. *Porteranthus.*

C. Fruits indehiscent, a solitary achene or aggregate or accessory with several to numerous drupelets or achenes; ovules 1 or 2 per carpel; endosperm nearly always absent; stipules present, infrequently caducous (subfam. ROSOIDEAE).

G. Carpels several to many, becoming achenes or drupelets on a dry to fleshy receptacle; floral cup short, not inclosing the fruits.

H. Receptacle flat, with 4–10 carpels in one whorl; fruits large 1-seeded achenes.

I. Plants shrubs with simple leaves; flowers large; carpels usually 4 or 5 (Kerrieae).

J. Leaves opposite; flowers 4-merous; petals white. [*Rhodotypos.*]

J. Leaves alternate; flowers 5-merous.

K. Petals absent; flowers in few-flowered corymbs; calyx lobes large, foliaceous, deeply toothed. 5. *Neviusia.*

K. Petals present, yellow; flowers solitary; calyx lobes short, entire. [*Kerria.*]

I. Plants perennial herbs with pinnately compound leaves; flowers small; carpels 5–15 (Ulmarieae). 6. *Filipendula.*

H. Receptacle convex, with many carpels in several series (rarely 5–10, the plants then with both petaliferous and apetalous flowers); fruits small achenes or drupelets, in some aggregate or accessory.

L. Plants shrubs with or without prickles, rarely woody vines or perennial herbs; leaves of the herbaceous forms palmately veined and cordate at base; fruits aggregate, of fleshy or rarely dryish, 1-seeded drupelets; each carpel with 2 ovules; calyx ebracteate (Rubeae).

M. Plants shrubs with erect, arching, or trailing stems; leaves compound or simple and palmately lobed; carpels numerous, becoming juicy drupelets; flowers petaliferous. 7. *Rubus.*

M. Plants low, creeping evergreen, perennial herbs; leaves simple, with crenate margins and cordate bases; carpels 5–10, becoming achene-like drupelets; flowers of 2 types, petaliferous and apetalous. 8. *Dalibarda.*

L. Perennial herbs with pinnately or palmately compound leaves; fruits small achenes; carpels with one ovule; calyx usually with an epicalyx.

N. Styles basal to subterminal, deciduous, or if persistent, the insertion lateral, not geniculate or plumose above; ovules anatropous and pendulous, ascending, or descending; receptacle dry or fleshy in fruit (Fragarieae).

O. Receptacle enlarging, red and fleshy in fruit; leaves trifoliolate.

P. Flowers white; epicalyx lobes entire; mature receptacle juicy, flavorful; styles persistent. .... 9. *Fragaria*.

P. Flowers yellow; epicalyx lobes apically 3–5 toothed; mature receptacles spongy, insipid; styles deciduous. ...... 10. *Duchesnea*.

O. Receptacle not enlarging, dry; leaves digitate, trifoliolate, or imparipinnate. ...... 11. *Potentilla*.

N. Styles terminal, wholly deciduous and terete or at least the lower part persistent and the upper part geniculate or plumose; ovules basal and upright-apotropous; receptacle dry in fruit (Dryadeae).

Q. Styles geniculate or plumose above, at least the lower part persistent in fruit; lower leaves imparipinnate (rarely appearing simple). ...... 12. *Geum*.

Q. Styles straight, deciduous at base; leaves trifoliolate. .... 13. *Waldsteinia*.

G. Carpels 1 to many, becoming achenes inclosed by the dry or fleshy floral cup.

R. Plants herbaceous; petals small or absent; carpels 1–4; floral cup dry in fruit (Sanguisorbeae).

S. Floral cup armed with hooked bristles; petals present; leaves imparipinnate with large leaflets interspersed with smaller ones. .... 14. *Agrimonia*.

S. Floral cup not armed; petals absent; leaves simple or imparipinnate with ± equal leaflets.

T. Plants tiny annuals; leaves simple, palmately lobed or dissected; stamen one; flowers perfect, in few-flowered sessile cymules. .... 15. *Alchemilla*.

T. Plants perennials or moderate-sized, erect annuals; leaves imparipinnate; stamens 4–12; flowers often imperfect, crowded in dense heads or spikes at the tips of long peduncles. .... 16. *Sanguisorba*.

R. Plants shrubs with prickles; flowers showy; carpels usually numerous, lining the base or sides of the fleshy floral cup (Roseae). .... 17. *Rosa*.

B. Carpels surrounded by and adnate to the floral cup, the ovaries partly to completely inferior; fruit a pome; shrubs or trees, often armed with thorns (subfam. MALOIDEAE).

U. Endocarps becoming hard in fruit, the pomes usually with 5 stones (endocarps); thorns commonly numerous.

V. Shrubs with crenate-margined leaves; stipules caducous; stones often 2-seeded. .... 18. *Pyracantha*.

V. Shrubs or trees with lobed and/or toothed leaves; stipules persistent; stones 1-seeded. .... 19. *Crataegus*.

U. Endocarps becoming cartilaginous, membranaceous, or leathery in fruit, the pomes with 5–10 seeds; unarmed or rarely with a few thorns.

W. Flowers in rather elongated racemes; petals obovate to lanceolate, not clawed; pomes juicy, berry-like, appearing to be 10-locular; leaves serrate-margined or rarely entire. ...... 20. *Amelanchier*.

W. Flowers in umbel-like racemes or few- to many-flowered corymbs;

petals subcircular, clawed; pomes fleshy, 5-locular; leaves toothed and often lobed, or pinnately compound. .... 21. *Pyrus.*

A. Gynoecium of one carpel; fruit a drupe; insertion perigynous, the ovaries superior; ovules 2, pendulous; styles terminal (subfam. AMYGDALOIDEAE). .... 22. *Prunus.*

Subfam. SPIRAEOIDEAE Endlicher, "Subordo Spiraeaceae"

About 20 genera in five tribes; in our area four genera representing three tribes. Most genera of Spiraeoideae are small and of limited geographical distribution; only *Physocarpus*, *Spiraea*, and *Aruncus* occur in both the Old and New worlds. *Spiraea* is the largest genus with about 50 species. None of the other genera exceeds 15 species, and eight are either monotypic or have only two species. *Porteranthus* is endemic to eastern North America, seven genera are confined to western North America, two are South American, and six are Asiatic. The two tribes that do not occur in the southeastern United States are Quillajeae, with *Quillaja* Molina (3–6 spp. of South America), *Kageneckia* Ruiz & Pavon (3–6 spp. of temperate South America), and *Vauquelinia* Corrêa ex HBK. (8–10 spp. of the southwestern United States and Mexico); and Exochordeae, with *Exochorda* Lindley (about 5 spp. of central and eastern Asia) and *Lindleya* HBK. (2 spp. of Mexico). The relationships of *Holodiscus* (K. Koch) Maxim. (about 6 spp., British Columbia to Bolivia) are unclear; the genus has been placed in the Spiraeeae, in a distinct tribe of Spiraeoideae or Rosoideae, or considered to be transitional between the two subfamilies. *Lyonothamnus floribundus* Gray, $2n = 54$, of four offshore islands of southern California, has been included in tribes Sorbarieae and Quillajeae.

REFERENCES FOR SPIRAEOIDEAE:

CAMBESSÈDES, J. Monographie du genre *Spiraea*; précédée de quelques considérations sur la famille des Rosacées. Ann. Sci. Nat. **1:** 225–243. 1824; Monographie des Spirées. *Ibid.* 352–392. *pls. 15–17, 25–28.* Reprinted with continuous pagination 1–58 + *pls. 15–17, 25–28.* Paris. 1824.

MAXIMOWICZ, C. J. Adnotationes de Spiraeaceis. Acta Horti Petrop. **6:** xi + 105–261. 1879.

ZABEL, H. Die strauchigen Spiräen unserer Gärten. iv + 128 pp. Berlin. 1893.

Tribe NEILLIEAE Maximowicz

1. **Physocarpus** (Cambessèdes) Rafinesque, New Fl. N. Am. 3: 73. 1838 (Jan.-Mar.), "*Physocarpa*"; corr. Maximowicz, Acta Horti Petrop. **6:** 219. 1879, nom. cons.[2]

---

[2] *Epicostorus* Rafinesque (Atlantic Jour. **1:** 144. 1832; type species *E. montanus* Raf. = *Physocarpus monogynus* (Torrey) Coulter) is earlier than *Physocarpus* (Camb.) Raf. When the two genera are united, as in current practice, *Epicostorus* would be the correct name, even though *Physocarpus* is conserved. In the interest of nomenclatural stability, it has been proposed that *Epicostorus* Raf. be added to the

Deciduous shrubs with erect or spreading principal branches and terete or slightly 5-angled short lateral branches; bark in several layers, the outer peeling off in longitudinal strips; buds small, solitary, sessile; indumentum of stellate trichomes, very variable in density. Leaves simple, alternate, distinctly petiolate; blades dentate, palmately 3–5-lobed, with the center lobe usually larger than the lateral ones, the blades of vegetative branches longer and more strongly divided than those of flowering branches, the blades of immature leaves often unlobed; leaf scars elevated, semielliptic and ± 3-lobed with 5 bundle traces; stipules linear, deciduous. Inflorescences many-flowered, bracteate, umbel-like corymbs [panicles, or racemes] terminating lateral branches of the current year. Calyx ebracteolate, the 5 lobes spreading to reflexed, persistent, valvate in aestivation; floral cup hemispheric, free of the carpels. Petals 5, white to pinkish, spreading, deciduous, suborbicular, perigynous at the edge of the floral cup. Androecium of 20–40 exserted stamens; filaments long, filiform, equal [or alternate filaments shorter], arising from a nectar ring that surrounds the mouth of the floral cup, some persistent; anthers small. Gynoecium of 3–5 [1], shortly stipitate carpels, antepetalous when 5, united at the bases [or for more than half their length]; styles terminal, elongated, the lower part persistent as a beak on the fruit; stigmas subcapitate; each carpel with 2–4 superposed ovules on an adaxial placenta, the upper ascending, with the micropyle inferior, the lower pendulous, with the micropyle superior. Fruits firm-walled, ± inflated, few-seeded follicles, often dehiscent along both adaxial and abaxial sutures. Seeds obliquely pyriform, the seed coat hard, shining; endosperm copious; embryo spatulate, the cotyledons plano-convex, the radicle inferior or superior. Base chromosome number 9. (*Spiraea* sect. *Physocarpos* Camb., *Opulaster* Medicus ex Schneider; including *Epicostorus* Raf.) TYPE SPECIES: *Spiraea opulifolia* L. = *P. opulifolius* (L.) Raf.[3] (Name from Greek, *physa*, a bladder or pair of bellows, and *karpos*, a fruit, in referto the inflated follicles.) — NINEBARK.

Six or more species with an Arcto-Tertiary distribution: *Physocarpus opulifolius* (L.) Raf. in eastern North America, about four species in the Cordillera of western North America, and *P. amurensis* Maxim. in Manchuria and Korea. Most species occur in moist, rocky habitats in foothills or mountains.

Although five species (three supposedly endemic) have been reported from our area, there appears to be only a single, more or less polymorphic species, *Physocarpus opulifolius*, $2n = 18$, that ranges from extreme northern Florida and adjacent Georgia, northward to Maine, Nova Scotia, and

---

nomina generica rejicienda as a taxonomic synonym of *Physocarpus* (Taxon **21**: 211, 212. 1972), and this proposal has been approved by the Committee for Spermatophyta (Taxon **22**: 156. 1973).

[3] Abrams (Illus. Fl. Pacific States **2**: 409. 1944) incorrectly gives the type species as *P. amurensis* Maxim.; lectotypification is unnecessary, since *S. opulifolia* L. was the only species referred by Cambessèdes to his section *Physocarpos*.

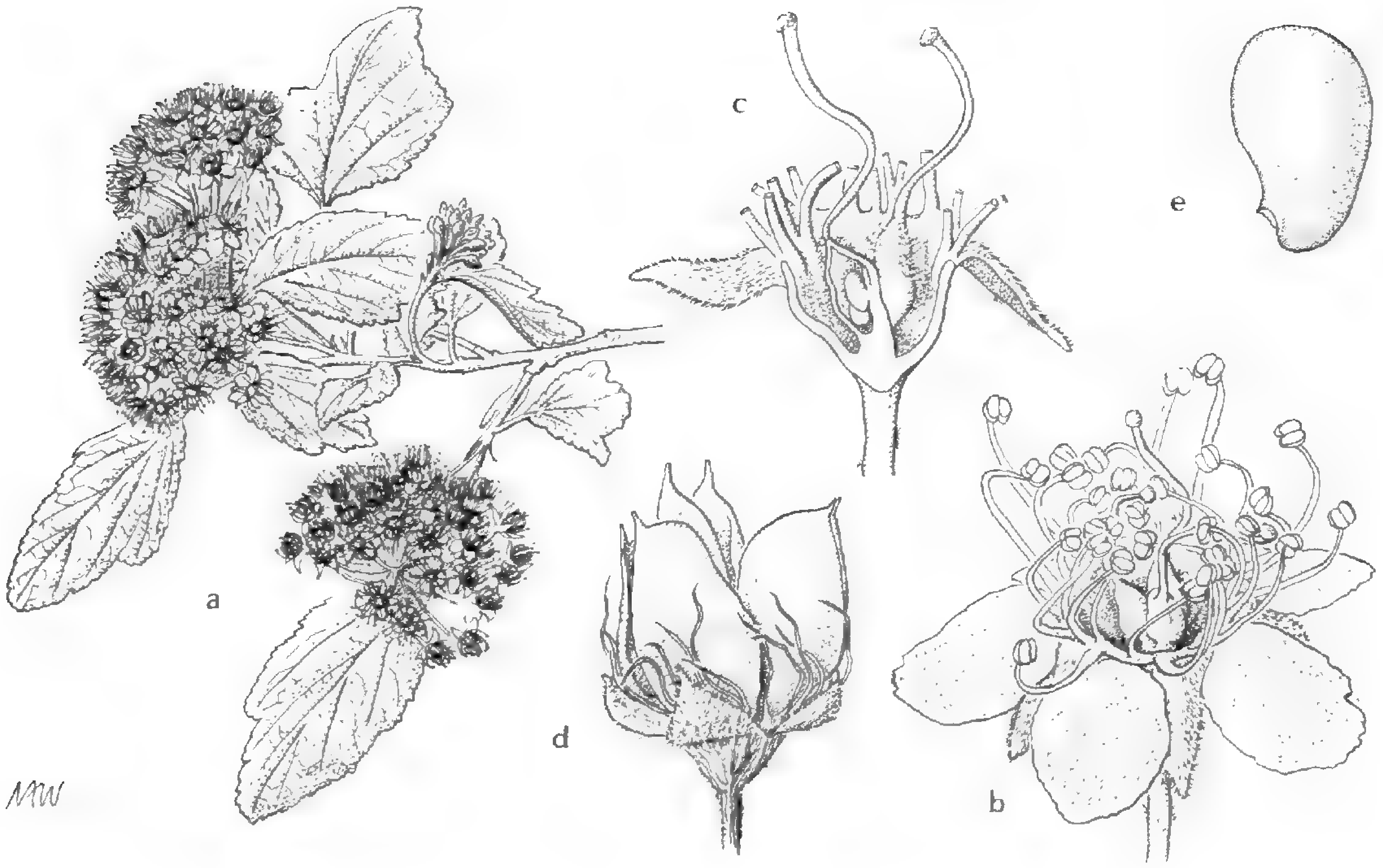


FIGURE 1. **Physocarpus.** a–e, *P. opulifolius*: a, flowering branchlet, × 1/2; b, flower, the stamens (not fully expanded) inserted on nectar ring, × 5; c, flower in vertical section to show placentation and floral cup, most of staminal filaments removed, × 6; d, mature fruit after dehiscence, the follicles open, × 3; e, seed, × 12.

James Bay, westward to Arkansas, southeastern Kansas, Missouri, Iowa, and Minnesota, and that also occurs disjunctly in the Black Hills of South Dakota and in central Colorado. This species is particularly variable in indumentum density and persistence, and certain variations are to some degree geographically restricted. Almost glabrous plants are most common in the northeastern United States and adjacent Canada and occur west to Minnesota and south to Georgia but are absent in the Midwest. Plants with pubescent pedicels and sepals and glabrous follicles are the commonest form in most of the eastern United States. Toward the Midwest and South, pubescence of leaves, young branches, pedicels, sepals, and follicles increases in density. Plants with varying degrees of pubescence have been segregated as *P. intermedius* (Rydb.) Schneider (*P. opulifolius* var. *intermedius* (Rydb.) Robinson = ? var. *tomentellus* (Seringe ex DC.) Boivin), *Opulaster alabamensis* Rydb., and *P. stellatus* (Rydb.) Rehder. The mature follicles are variable in shape and size; Rydberg distinguished those plants with small, abruptly acute follicles as *Opulaster australis* (*P. australis* (Rydb.) Rehder).

Characteristic plants of *Physocarpus opulifolius* in the eastern United States have obtuse to acute or rarely acuminate leaf dentation (leaves of the vegetative branches generally have sharper teeth than those of the flowering stems). Toward the west, and to some degree toward the south, the teeth are more acute or (commonly) acuminate. All Twentieth

Century floras and treatments of the genus recognize as distinct the western *P. capitatus* (Pursh) Kuntze (southern Alaska to coastal southern California; mostly west of the Cascade Mountains, but disjunct in northern Idaho), $2n = 18$, which differs from *P. opulifolius* in the consistently acute or acuminate leaf toothing and slightly larger flowers, follicles, and seeds. The Asian *P. amurensis* also differs from *P. opulifolius* by virtually the same characteristics. It needs to be ascertained whether these three taxa are actually conspecific. Evidently much could be learned from biometric studies of the variations found in species of *Physocarpus*.

Other generic names have been applied to this genus. *Physocarpus* was considered by Bentham & Hooker to be congeneric with *Neillia*, and this interpretation was followed by both Greene and Jones. Today however, these two genera are recognized as distinct. *Opulaster* Medicus (Pfl. Anat. 109. 1799) was adopted by Schneider and by Rydberg and used in several subsequent floras, but this name was a nomen nudum that was validated by Schneider. In addition to *Physocarpus*, Rafinesque published two other generic names that involve this genus, *Icotorus* (Bull. Bot. Seringe 1: 216. 1830), a nomen nudum, and *Epicostorus* (see footnote 2).

The genus is separable into two more or less distinct groups. *Physocarpus opulifolius*, *P. capitatus*, and *P. amurensis* comprise one group with the carpels usually numbering three to five (rarely fewer) and united only at the bases. Members of the other group, including *P. alternans* (M. E. Jones) J. T. Howell, *P. monogynus* (Torrey) Coulter, and *P. malvaceus* (Greene) Kuntze, all of western North America, have either solitary carpels or two (rarely to five) carpels united at least half their lengths. The species in both groups are variable and sometimes difficult to distinguish; numerous segregate species have been proposed.

Physocarpus, *Neillia* D. Don (10 to 13 species of the Himalayas to eastern Asia and Java and Sumatra), and *Stephanandra* Sieb. & Zucc. (4 or 5 species of eastern Asia) comprise the tribe Neillieae, characterized by the presence of stipules, carpels (when more than one) united at least basally, hard and shining seed coats, and abundant endosperm. Hutchinson included *Guamatela* Donn. Sm. (monotypic; Guatemala) in this tribe, although it differs from the other three genera in the free carpels and absence of endosperm.

Species of *Physocarpus* are cultivated as ornamentals under the name "Ninebark," in reference to the layered, peeling bark, and there are several named cultivars of *P. opulifolius*. The plants are attractive, although not very showy, and are grown primarily in botanic gardens, in parks, and on campuses. *Physocarpus opulifolius* has become naturalized in parts of Europe.

REFERENCES:

See subfamily references. Under family references see BALDWIN, DEVADAS & BECK, DIPPEL, HUBER, LI, REHDER, SCHNEIDER, STERLING (VIII), VINES, and WOOD.

CULLEN, J. The genus *Neillia* (Rosaceae) in mainland Asia and in cultivation. Jour. Arnold Arb. **52:** 137–158. 1971. [*Physocarpus* included in key; multiple buds absent in *Physocarpus.*]

GREENE, E. L. The North American *Neilliae*. Pittonia **2:** 25–31. 1889. [*Physocarpus* and *Neillia* considered congeneric.]

HOWELL, J. T. A Great Basin species of *Physocarpus*. Proc. Calif. Acad. Sci. IV. **22:** 129–134. 1931. [3 varieties of *P. alternans.*]

JONES, M. E. Contributions to western botany 4. Zoë **4:** 22–54. *pl. 25.* 1893. [*Neillia,* 38–44; retort to Greene's paper.]

LEIBERG, J. B. On the carpels of *Opulaster malvacea* (Greene). Bull. Torrey Bot. Club **22:** 271, 272. 1895.

TURRILL, W. B. *Physocarpus opulifolius* f. *luteus*. Bot. Mag. **175:** *pl. 459.* 1964.

VIDAL, J. Le genre *Neillia* (Rosaceae). Adansonia II. **3:** 142–166. 1963. [*Physocarpus* included in key.]

Tribe SPIRAEEAE Jussieu [4]

2. **Spiraea** Linnaeus, Sp. Pl. 1: 489. 1753; Gen. Pl. ed. 5. 216. 1754.

Deciduous shrubs with numerous erect, reclining, or ascending stems, mostly unbranched below the inflorescence to diffusely branched; branches terete, sometimes angled from the nodes, with a small, round, continuous pith; buds small, solitary [or collaterally multiplied], sessile, with 2–8 exposed scales; indumentum of simple trichomes, variable in density. Leaves simple, alternate, shortly petiolate to subsessile; blades ovate, elliptic, or obovate with dentate, entire [or lobed] margins; leaf scars minute, strongly elevated, semicircular or crescent shaped with 1 bundle trace; stipules generally absent. Inflorescences many-flowered, bracteate, compact panicles, compound [or simple] corymbs [racemes or umbels] terminal on branches of the current year [or lateral from buds of the preceding year's growth]. Flowers small, perfect [rarely imperfect, the plants polygamous]. Calyx ebracteolate, the 5 lobes short, triangular, erect or spreading, deciduous in fruit or persistent, valvate or slightly imbricate in aestivation; floral cup hemispheric, campanulate, or turbinate, free from the carpels. Petals white to rose, widely spreading, equal, suborbicular to obovate with slightly undulate or uneven margins, very shortly clawed, deciduous, imbricate or contorted, inserted at the outer edge of the nectar ring. Androecium of 15 to many exserted stamens; filaments slender, unequal in length, free except at the base, inserted in one to several series at the edge of the floral cup between the perianth and a usually prominent, fleshy nectar ring that surrounds the mouth of the floral cup. Gynoecium usually of 5, free, antepetalous, superior carpels; styles terminal or subterminal, elongated, forming a beak on the fruit; stigmas capitate-discoid; each carpel with 2 to several anatropous ovules pendulous from an adaxial placenta, the micropyle superior. Fruits firm-walled, few-seeded follicles completely dehiscent along the adaxial suture and apically on the abaxial suture. Seeds small, linear or oblong, tapered at each end; seed coat mem-

---

[4] Rank assigned by Cambessèdes, Monogr. *Spiraea*, 5. 1824.

branaceous, areolate-scalariform; endosperm absent or scarce; embryo elongate, the cotyledons oblong, the radicle superior. LECTOTYPE SPECIES: *S. salicifolia* L.; see P. A. Rydberg, N. Am. Fl. 22: 245. 1908. (Name from Greek *speiraia*, used by Theophrastus for a shrub [apparently privet, *Ligustrum vulgare*] and applied by Clusius, Tournefort, and Linnaeus to this rosaceous genus.) — SPIREA.

Largely restricted to the North Temperate Zone and widespread in North America, eastern Europe (absent in western and middle Europe), and Asia. Probably fewer than 50 species are currently recognized, although recent estimates range from 70 to 120 species. About ten indigenous and six or more naturalized species occur in North America; six (including one introduced) occur in our area. *Spiraea Hartwegiana* Rydberg (*S. parvifolia* Bentham non Raf.), endemic to the highlands of south-central Mexico, is quite different from other species of the genus, and its relationships are obscure.

Section SPIRAEA (*Spiraria* Seringe in DC.) (inflorescence an elongate panicle or raceme terminating a long shoot) is represented in our area by three species. *Spiraea tomentosa* L., hardhack or steeple bush, $2n = 24$, occurs in low, moist, open, usually infertile habitats with acidic soils such as bogs, low meadows, and woodland borders from Prince Edward Island, Nova Scotia, and New Brunswick to Ontario, Manitoba, Michigan, and Minnesota southward to the Carolinas, northern Georgia, Tennessee, southeastern Missouri, Arkansas, and Kansas. The characteristically abaxially densely tomentose leaves and large, spirelike inflorescences give most individuals of this species a striking appearance. The flowers have reflexed calyx lobes, lack nectar rings, and are usually rose colored, although a white-flowered form is known. Plants occurring inland with the flowers loosely clustered on the inflorescence branches have been segregated as var. *rosea* (Raf.) Fernald, but there is complete intergradation with the typical variety. *Spiraea subcanescens* Rydb., described from South Carolina, is evidently a spontaneous hybrid between *S. tomentosa* and *S. alba*. Artificial hybrids between *S. tomentosa* and the *S. Douglasii*-*S. Menziesii* group of western North America are known.

Spiraea alba DuRoi and *S. latifolia* (Aiton) Borkh., both commonly called meadowsweet, are distinguished from *S. tomentosa* by their nearly glabrous leaves, usually white flowers, spreading calyx lobes, and the presence of a prominent nectar ring at the base of the filaments. *Spiraea alba*, $2n = 36$, occurs in moist open habitats, primarily to the west of the Appalachian Mountains, from extreme northwestern Vermont, western New York and southern Quebec to Michigan and Alberta, south to western North Carolina, Missouri, and South Dakota. This species is set off from *S. latifolia* by its yellowish-brown, rather than reddish, stems; finely serrate and rather narrow leaves, instead of coarsely-toothed broader ones; thyrsoid, instead of open-pyramidal, inflorescences; and strongly pubescent, rather than mostly glabrous, inflorescence branches. Also preferring moist conditions, but occurring primarily in and east of the Appalachians, *S.*

latifolia (*S. alba* var. *latifolia* (Aiton) Ahles), $2n = 36$, ranges from Newfoundland to North Carolina. Low plants with dense, cylindric to ovoid inflorescences lacking elongate lower branches and occurring in subarctic and alpine regions from Newfoundland, southern Labrador, and the Ungava district, south to the New England mountains, have been distinguished as var. *septentrionalis* Fernald (*S. septentrionalis* (Fernald) Löve & Löve). This variety has also been reported from the Keweenaw Peninsula of Michigan and the mountains of northern Virginia. A chromosome number of $2n = 54$ is known from populations on Mt. Washington, New Hampshire, and Hawksbill Mountain, Page Co., Virginia. The voucher specimen from Virginia (*Baldwin 5601*, GH) is, however, quite different in appearance from northern plants of this variety. In a study of variation in *S. alba* and *S. latifolia*, Kugel concluded that the two represent distinct species that hybridize extensively, especially in the region between the Straits of Mackinac and Lake Abitibi, and introgress toward both extremes.

Spiraea salicifolia L., $2n = 36$, is a Eurasian member of this section reportedly escaping from cultivation in the eastern United States and differing from the very similar *S. alba* by its usually pink flowers and its leaves broadest below, rather than above, the middle. The variations found in *S. tomentosa*, *S. alba*, and *S. latifolia* are paralleled to some degree in *S. Douglasii* Hooker, $2n = 36$, of western North America, in its vars. *Douglasii*, *roseata* (Rydb.) C. L. Hitchc., and *Menziesii* (Hooker) Presl.

Section CALOSPIRA K. Koch (inflorescence a compound corymb terminating a long shoot) is represented in our area by two indigenous and one introduced species. *Spiraea virginiana* Britton is a rare species of rocky stream banks endemic to the mountains of West Virginia, western North Carolina, and eastern Tennessee. This distinctive species is a much-branched shrub with nearly entire, obovate leaves and glaucous pedicels and floral cups.

Spiraea betulifolia Pallas var. *corymbosa* (Raf.) Wenzig, $2n = 27, 36$, a low, often rhizomatous shrub with simple or seldom-branched erect stems, coarsely serrate, broadly ovate or elliptic leaves, and often pubescent pedicels, occurs along stream banks and in rocky places in the mountains from northern New Jersey and Pennsylvania to West Virginia, Kentucky, North Carolina, Alabama, and Georgia. Plants with larger, apically truncate leaves and pink flowers have been recognized as f. *Campii* Fosberg. Varietas *lucida* (Douglas ex Greene) C. L. Hitchcock (*S. lucida* Douglas ex Greene; *S. betulifolia* sensu Hultén), $2n = 36$, ranges from British Columbia and Saskatchewan, south to Oregon, Wyoming, and North Dakota, and var. *betulifolia* occurs in eastern Siberia, Kamchatka, northeastern China, and Japan. The affinities of these three taxa have long been known, although they are often recognized at ranks other than that of variety (see discussions in Fosberg, Greene, Hitchcock *et al.*, Hultén, and Komarov). Most characters used to distinguish the three such as indumentum density, sepals reflexed or erect in fruit, and the position of the stylar beak on the follicles, are too variable to be diagnostic. However, the North American varieties are rhizomatous (var. *lucida* more strongly so than var. *corymbosa*), and the plants usually are larger than those of var. *betulifolia*, the branches of which are said to arise from dense, globose crowns. *Spiraea Stevenii* (Schneider) Rydb. (*S. Beauverdiana* auct., non Schneider, see Uttal, Bull. Torrey Bot. Club **100**: 236, 237. 1973), $2n = 18$, is evidently a closely related, but distinct, species distributed from eastern Siberia and Kamchatka to Alaska and the Yukon.

Spiraea japonica L. f., $2n = 18, 36$, characterized by long-acuminate and sharply serrate leaves and conspicuously pubescent pedicels and floral cups, is locally naturalized from New England to Georgia. Among other species assigned to sect. CALOSPIRA are *S. densiflora* Nutt. ex T. & G. (northwestern North America), $2n = 18$, *S. decumbens* Koch in Röhling (southeastern Alps), and *S. Baldschuanica* B. Fedtsch. (Central Asia); Rehder lists 17 additional species that are mostly of China and the Himalayas.

The twenty or more species of sect. CHAMAEDRYON Seringe in DC. (subg. *Nothospiraea* Zabel) (inflorescence a simple corymb or umbel terminating a short, lateral shoot or sessile on a long shoot) are native to central and eastern Europe and Asia. A number of them, including *Spiraea chamaedryfolia* L., $2n = 18, 36$, *S. prunifolia* Sieb. & Zucc., $2n = 18$, *S. Thunbergii* Sieb., and *S.* × *Vanhouttei* (Briot) Zabel, are commonly cultivated in the eastern States and sometimes persist afterward.

Tribe Spiraeeae, delimited by the usual absence of stipules and by free or basally united, antepetalous (when 5) carpels, wingless seeds, membranaceous seed coats, and the sparse development of endosperm, is composed of six genera: ***Spiraea***, ***Aruncus*** L., ***Petrophytum*** (Nutt. ex T. & G.) Rydb. (three species of western North America), ***Kelseya*** (Watson) Rydb. (*K. uniflora* (Watson) Rydb., of Montana, Idaho, and Wyoming), ***Luetkea*** Bongard (*L. pectinata* (Pursh) Kuntze, of northwestern North America), and ***Sibiraea*** Maxim. (two to six species of northwestern Europe and Asia). ***Apopetalum*** Pax (one species of Bolivia), sometimes referred to this tribe, is a synonym of ***Brunellia*** Ruiz & Pavon, of the Brunelliaceae.

The basic taxonomic works on *Spiraea* are by Cambessèdes (1824), Maximowicz (1879), Zabel (1893), and Schneider (1905). All are quite out of date, and a modern revision using biosystematic, as well as classical, methodology is needed. Huber has recently indicated that the customary division of the genus into three sections does not show true infrageneric relationships, and he assigns the indigenous or naturalized species of Central Europe to nine species groups.

Reported sporophytic chromosome numbers in *Spiraea, sensu stricto*, are 10, 18, 27, 36, and 54, with a basic number of 9. All species of sect. SPIRAEA are tetraploid ($2n = 36$) except for the hexaploid *S. latifolia* var. *septentrionalis*. The Old World members of sect. CALOSPIRA are mostly diploids, while the New World species are predominantly tetraploids. Plants of *S. Stevenii* (eastern Russia) and the very closely related *S. densiflora* (northwestern North America) are diploid. Both diploid and tetraploid plants are known in *S. japonica*. Sax reported a triploid cultivated plant of *S. betulifolia* var. *corymbosa*, and Baldwin found two tetraploid populations of this variety in Virginia. Most species of sect. CHAMAEDRYON are diploid, although *S. myrtilloides* Rehder is hexaploid, *S. chamaedryfolia* var. *ulmifolia* is tetraploid, and *S. media* has been reported as $2n = 10$ and 18.

Sterility barriers are not well developed in the genus, and artificial crosses have been made between both species belonging to different sections and species native to the Old and New worlds. Rehder (1940) listed hybrids involving all species in our area, except *S. virginiana*. Hybridization in nature, however, is infrequent, since the species are often geographically, ecologically, or phenologically isolated. Evidence has recently been presented by Hess that shows rather conclusively the hybrid origin of *S. pyramidata* Greene (*S. Douglasii* var. *Menziesii* × *S. betulifolia* var. *lucida*). As previously mentioned, *S. alba* and *S. latifolia* are thought to hybridize extensively toward the northern limits of their ranges.

REFERENCES:

See subfamily references. Under family references see BALDWIN, BEAN, DIPPEL, HARA, HESS *et al.*, HITCHCOCK *et al.*, HUBER, LÖVE & LÖVE, LUBBOCK, REHDER, RICKETT, ROBERTSON, SCHNEIDER, STERLING (VIII), VINES, and WOOD.

BALDWIN, J. T., JR. *Spiraea latifolia* var. *septentrionalis* in Virginia. Rhodora **48**: 112. 1946.

———. Chromosomes of *Spiraea* and of certain other genera of Rosaceae. *Ibid.* **53**: 203–206. 1951.

CLARKSON, R. B. The West Virginia *Spiraea*. Castanea **24**: 143–146. 1959. [*S. virginiana*.]

CRUTCHFIELD, P. J. Taxa collected from Roanoke Island new to the flora of North Carolina. Castanea **29**: 129–137. 1964. [*S. cantoniensis*, *S. prunifolia*, *S.* × *Vanhouttei*.]

FERNALD, M. L. The inland variety of *Spiraea tomentosa*. Rhodora **14**: 188–190. 1912. [Var. *rosea* (Raf.) Fernald.]

FOSBERG, F. R. Observations on Virginia plants, Part I. Virginia Jour. Sci. **2**: 106–111. 1941. [*Spiraea*, 109.]

GILLE, A. Le *Spiraea tomentosa* L. dans la région de Granby (Comté de Shefford, Québec, Canada): étude écologique et phytosociologique. (In French; English summary.) Vegetatio **2**: 166–196. *Map 1.* 1949.

GOTO, G., K. SASAKI, N. SAKABE, & Y. HIRATA. The alkaloids obtained from *Spiraea japonica* L. fil. Tetrahedron Lett. **11**: 1369–1373. 1968.

GREENE, E. L. On certain Spiraeaceae. Pittonia **2**: 219–222. 1892. [*S. betulifolia*, *S. corymbosa*, *S. lucida*, *S. pyramidata*.]

HARRIS, J. A. On the distribution of abnormalities in the inflorescence of *Spiraea Vanhouttei*. Am. Jour. Bot. **4**: 624–636. *pls. 30, 31.* 1917.

HÉLYE, D. Étude sur les Spirées. Bull. Soc. Dendrol. France **1935**: 17–24. 1935.

HESS, W. J. A taxonomic study of *Spiraea pyramidata* Greene (Rosaceae). Sida **3**: 298–308. 1969. [A species of hybrid origin; includes chromosome numbers for four taxa.]

HÖRHAMMER, L., R. HÄNSEL, & W. ENDRES. Über die Flavonglykoside der Gattungen *Filipendula* und *Spiraea*. Arch. Pharm. **289**: 133–140. 1956.*

HULTÉN, E. Flora of Kamtchatka and the adjacent islands. Vol. **3**. Sv. Vet. Acad. Handl. III [V] **8**(1): 1–213. *pls. 1–3.* 1929. [*Spiraea*, 38–43.]

KUGEL, A. R. Variation in the *Spiraea alba–latifolia* complex. vi + 124 pp. Ph.D. Thesis, University of Michigan, Ann Arbor. 1958. [Unpublished. Cf. Diss. Abstr. **19**(6): 1183, 1184. 1958.]

NASH, G. V. *Spiraea Thunbergii.* Addisonia **3**: 63, 64. *pl. 112.* 1918.

REHDER, A. Webb's "Study of *Spiraea*." Bot. Gaz. **34**: 246. 1902. [Refers to article by J. E. WEBB, who studied *Astilbe japonica*, not *Spiraea japonica*, and *Aruncus astilboides* instead of *Spiraea astilboides*.]

SALAMUN, P. J. A population study of the variation in the inflorescence of *Spiraea tomentosa*. Rhodora **53**: 280–292. 1951.

SAX, K. Polyploidy and geographic distribution in *Spiraea*. Jour. Arnold Arb. **17**: 352–356. 1936. [19 taxa in 3 sections.]

SCHAEPPI, H., & K. FRANK. Vergleichend-morphologische Untersuchungen an der Blütenachse und am Gynoecum einiger Spiraeoideen (Spierstrauchgewächse). Mitt. Naturw. Ges. Winterthur **32**: 73–104. 1967.*

SCHNEIDER, C. K. Uebersicht über die spontanen Arten und Formen der Gattung *Spiraea* (*Euspiraea*). Bull. Herb. Boiss. II. **5**: 335–350. 1905. [Recognizes 57 species, of which 11 are North American.]

SVIAZEVA, O. A. The geography of the genus *Spiraea* L. in the U.S.S.R. (In Russian.) Bot. Zhur. **51**: 1500–1506. 1966. [25 spp.; maps.]

WEBB, J. E. A morphological study of the flower and embryo of *Spiraea*. Bot. Gaz. **33**: 451–460. 1901. [Plants misidentified; see REHDER.]

WIEGAND, K. M. Some varieties of *Potamogeton* and *Spiraea*. Rhodora **2**: 102–104. 1900. [*S. salicifolia* and var. *latifolia*.]

ZHUNGIETU, I. I. Morphogenesis of shrub *Spiraea japonica* L. f. (In Russian.) Biull. Glavn. Bot. Sada Moskova **75**: 71–74. 1970.

3. **Aruncus** Linnaeus, Opera Varia 259. 1758.[5]

Perennial herbs with several tall stems, largely unbranched below the inflorescence, arising from crowns on a thick, woody, branched rhizome; cortex fibrous with the vascular bundles forming a ± continuous, tough ring that surrounds a large, whitish, soft, spongy pith; indumentum of simple, recurved trichomes, variable in density. Leaves alternate, large, compound, irregularly ternate, imparibipinnate, or imparitripinnate, usually long petiolate, the petiolar bases half sheathing the stems; leaflets doubly serrate and sometimes lobed or subdivided, long petiolulate; stip-

---

[5] The generic name was published in the part of *Opera Varia* that is a reprint of the second edition of *Systema Naturae*, originally published in 1740. Although Linnaeus recognized *Aruncus* as a genus in his early publications, he considered it a synonym of *Spiraea* in all post-1753 works. In an analogous situation with *Dalea* L. (Leguminosae), Barneby (Taxon **14**: 163. 1965) argued that "the adoption by means of a pirated edition of an opinion which Linnaeus had roundly and repeatedly rejected in his mature judgment cannot be tolerated; or if tolerated it cannot be attributed to Linnaeus." However, such complications are unavoidable with an arbitrary starting point for botanical nomenclature, and it seems that we are obliged to attribute the name *Aruncus* to Linnaeus, since there is nothing in *Opera Varia* to indicate that he did not accept it.

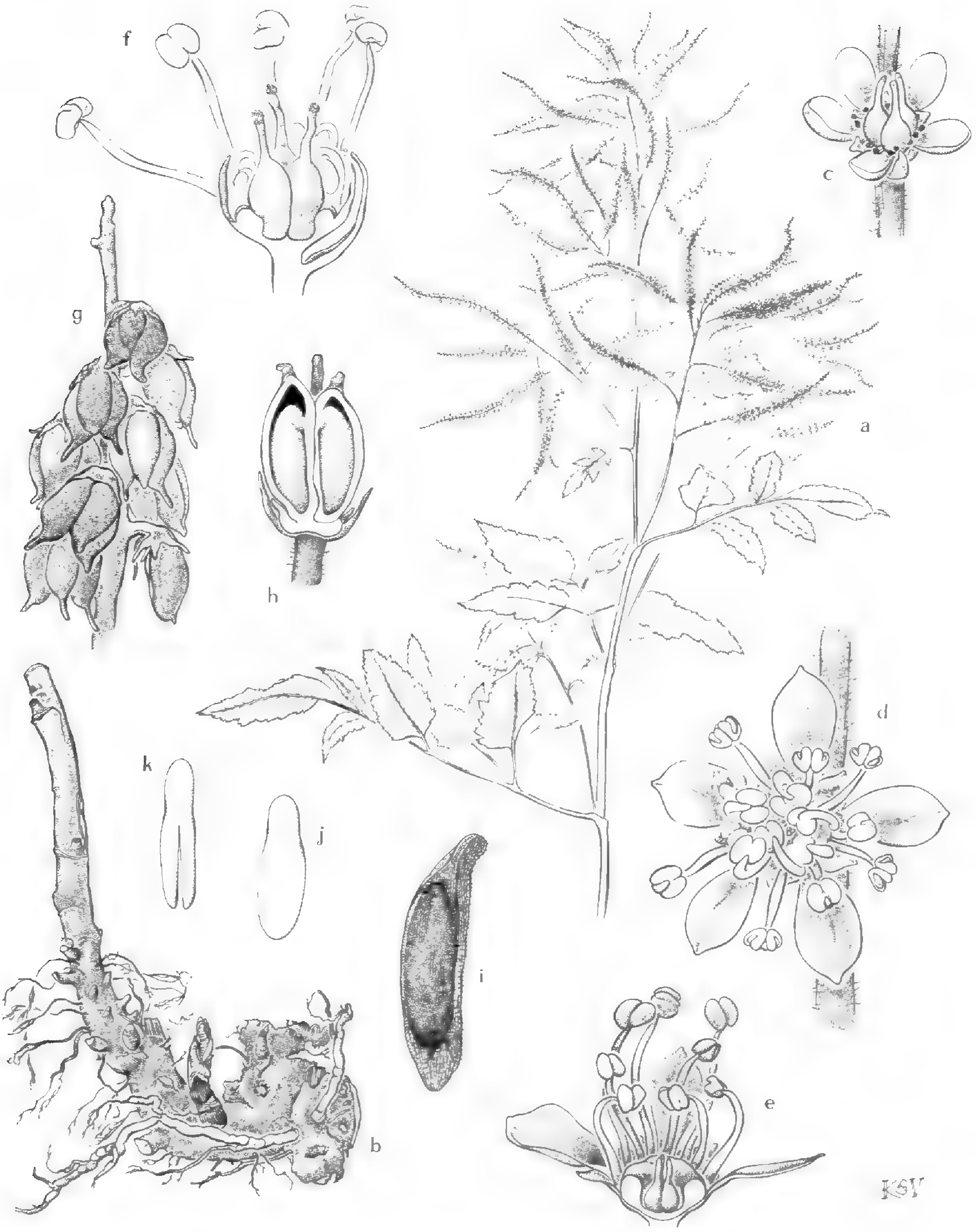


FIGURE 2. **Aruncus.** a–k, *A. dioicus*: a, upper part of flowering stem, staminate plant, × 1/4; b, portion of rhizome with stem base, vegetative buds, and adventitious roots, × 1/2; c, carpellate flower — note rudimentary stamens, × 12; d, staminate flower, stamens not fully expanded, 3 stigmas of rudimentary carpels in center, × 12; e, staminate flower in vertical section to show nectar ring, rudimentary carpels, and insertion of stamens and petals, × 12; f, perfect flower from inflorescence of "staminate" plant in vertical section, not all stamens expanded, petals removed, × 12; g, portion of infructescence, showing reflexed fruits, × 5; h, developing fruit in section to show pendulous ovules, the micropyle superior, × 12; i, seed with loose, membranaceous seed coat, × 20; j, embryo, oriented as in "i," × 20; k, same, side view, × 20.

ules absent. Inflorescences of numerous racemes organized in large, terminal panicles, bracteate, each pedicel with a bracteole. Flowers white or greenish, quite small, imperfect or rarely perfect and the plants dioecious to polygamodioecious. Calyx lobes 5, short, triangular, spreading, persistent in fruit, valvate in aestivation; floral cup shallow, basin shaped. Petals 5, obovate to elliptic, narrowed or shortly clawed at the bases, the apices obtuse, imbricate or contorted, inserted at the edge of the floral cup. Staminate flowers with an androecium of usually 20 (15–30) exserted stamens; filaments slender, unequal in length, free, inserted in a single series at the edge of the floral cup between the calyx and a fleshy nectar ring that surrounds the mouth of the cup; anthers small; several vestigial carpels present. Carpellate flowers smaller, with a gynoecium of 3 (2–5, antepetalous when 5) free carpels; styles short, terminal, forming a beak on the fruit; stigmas capitate-discoid; each carpel with few anatropous ovules pendulous from an adaxial ventral placenta, the micropyle superior; rudimentary stamens present; nectar ring scarcely developed. Follicles as numerous as the carpels, shining, completely dehiscent along the adaxial suture and apically along the abaxial one, the pedicels recurving and inverting the fruits. Seeds 2–4, small, the seed coat loose, membranaceous, caudate at both ends, scalariform-reticulate; endosperm scanty; embryo spathulate. TYPE SPECIES: *Spiraea Aruncus* L. = *A. dioicus* (Walter) Fernald. (Latin name from Greek, *aryngos*, goat's beard, first used by Pliny; pre-Linnaean authors called the genus *Barba caprae.*) — GOAT'S BEARD.

A single polymorphic species disjunct in mountainous regions of the North Temperate and Subarctic zones, occuring in the eastern United States, Pacific North America, Alaska and the Aleutian Islands, central and eastern Europe, eastern Siberia to Kamchatka, eastern China, and Japan.

In eastern North America, *Aruncus dioicus* is found in or along the margins of rich woods, moist or rocky woodlands, bluffs, and ravines in mountainous or hilly terrain from Pennsylvania, west to Illinois, Iowa, and Missouri, and south to the Carolinas, northern Georgia, Alabama, Arkansas, and Oklahoma. In the eastern part of its range, most plants have rather lustrous foliage, glabrous or scarcely pubescent lower leaf surfaces and rather broad, ovoid follicles; these plants represent var. *dioicus* (*A. allegheniensis* Rydb.). Varietas *pubescens* (Rydb.) Fernald, with dull foliage, mostly pubescent lower leaf surfaces, and narrower, subcylindric follicles, is the predominant form in the Midwest, particularly in the Ozark Mountains, but such plants occur as far east as West Virginia. These two varieties intergrade completely, and it is questionable whether they should be maintained.

The variability within the genus is reflected by the number of segregate species that have been proposed. Rydberg recognized five in North America, and, in the Flora of the USSR, Pojarkova (see Komarov) distinguished four species. More recently, Hara (1955) and Tutin (1967) have considered *Aruncus* to be composed of a single, polymorphic species, Hara recognizing thirteen varieties, one of which he subsequently elevated to subspecific status. Varietas *acuminatus* (Rydb.) Hara, ranging from northwestern California to Alaska and differing from vars. *dioicus* and *pubescens* by the shorter stylar beaks and larger follicles and seeds, is very similar to var. *vulgaris* (Raf. ex Maxim.) Hara (*A. vulgaris* Raf. ex Maxim.; *A. Aruncus* (L.) Karst.; *A. sylvester* Kostel., nom. nud.), of Central Europe.

In our area, *Aruncus dioicus* and *Astilbe biternata* (Saxifragaceae) are examples of convergent evolution, both species having a remarkably similar aspect and being especially alike in habit and leaf and inflorescence morphology. Both occur in the same habitats and can grow side by side, although *Astilbe biternata* has a more restricted range (Virginia and West Virginia to Georgia and Tennessee). This strong resemblance is superficial, however, and *Astilbe biternata* differs from *Aruncus dioicus* by its glandular, rather than simple, trichomes; ten, rather than twenty, stamens; two partly united, rather than three or four free, carpels; and many-seeded follicles about 4 mm. long, rather than two- to four-seeded follicles less than 2.5 mm. long. Like *Aruncus*, *Astilbe* is particularly variable in Asia, and over twenty species have been described from China, Japan, and the Himalayas. The degree of convergence between Asiatic species of *Astilbe* and varieties of *Aruncus dioicus* has not yet been studied.

The flowers of *Aruncus dioicus* are mostly functionally imperfect and the plants dioecious. Carpellate flowers have rudimentary stamens, while staminate flowers have vestigial carpels that occasionally develop fully in certain flowers of a staminate inflorescence and set fruit. Bond found that perfect flowers occur together in groups toward the apices of the racemes or that entire secondary panicles sometimes contain only perfect flowers. Seeds from fruit developing from perfect flowers give rise to staminate plants that always produce some perfect flowers. Observations on a living plant in the Arnold Arboretum indicate that plants with perfect flowers are self compatible. Thus far, perfect flowers are not known to occur in carpellate inflorescences. Hara reports that subsp. *triternatus* (Wall.) Hara, of the Himalayas, tends to have perfect flowers.

Reported chromosome numbers for *Aruncus* are $2n = 14, 16, 18, 36$, and 42, with 18 the most common. Polyploidy is evidently very infrequent. The only counts from North American plants (from British Columbia) are $2n = 18$.

Aruncus dioicus is commonly grown for its showy inflorescences (because of their larger flowers, staminate plants are the better suited for cultivation). The leaves and flowers have been used as fever-reducing agents. A cyanogenic glucoside is supposedly present in all parts of the plant.

REFERENCES:

Consult subfamily references. Under family references see HARA, HEGI, HESS *et al.*, Hitchcock *et al.*, Huber, Hultén (1971), Knuth, Rickett, Robertson, Sterling (VIII), and Wood.

Abraham, E. P., N. G. Heatley, R. Rolt, & E. M. Osborn. An antibiotic from *Spiraea Aruncus* L. Nature **157**: 511. 1946. [Active ingredient isolated in crystalline form and its chemical properties discussed.]

Bond, T. E. T. On bisexual flowers in *Aruncus sylvester*. Baileya **10**: 89–91. 1962.

Fernald, M. L. Contr. Gray Herb. No. 113. V. Memoranda on *Aruncus*. Rhodora **38**: 179–182. *pl. 416.* 1936. (Reprinted in Contr. Gray Herb. **113.**)

———. Contr. Gray Herb. No. 126. IV. New species, varieties and transfers. Rhodora **41**: 423–461. *pls. 559–569.* 1939. [*Aruncus*, 423, 424.] (Reprinted in Contr. Gray Herb. **126.**)

Hara, H. Miscellaneous notes on the nomenclature of Asiatic plants (II). (In Japanese.) Jour. Jap. Bot. **13**: 381–389. 1937. [*Aruncus*, 386–389.]

———. Critical notes on some type specimens of East-Asiatic plants in foreign herbaria (2). *Ibid.* **30**: 65–72. 1955. [*A. sylvester* and *A. dioicus*, 65–69.]

Meusel, H. Verbreitungskarten mitteldeutscher Leitpflanzen. 2 Reihe. Hercynia **1**: 309–326. 1938. [*Aruncus*, 314–318.]

Porsch, O. Geschichtliche Lebenswertung der Kastanienblüte. Österr. Bot. Zeitschr. **97**: 269–321. 1950. [*Aruncus*, 289, 290; genus has "beetle-flowers."]

Schaeppi, H. Untersuchungen über den Habitus von *Aruncus*. *Astilbe* und einiger ähnlicher Pflanzen. Beitr. Biol. Pflanzen **46**: 371–387. 1970.

Tutin, T. G. *Aruncus*. *In*: V. H. Heywood, ed., Notulae systematicae ad Floram Europaeam spectantes. Repert. Sp. Nov. **74**: 25. 1967. [Genus has but one variable species, *A. dioicus*.]

Webb, J. E. A morphological study of the flower and embryo of *Spiraea*. Bot. Gaz. **33**: 451–460. 1901. [*S. astilboides planiflora* is *Aruncus*; see A. Rehder, Bot. Gaz. **34**: 246. 1902.]

Tribe Sorbarieae Rydberg

4. **Porteranthus** Britton, Mem. Torrey Bot. Club **4**: 115. *pls. 76, 77.* 1894.

Perennial herbs with one or more principal stems arising from woody horizontal rhizomes, lateral branches none or few below the inflorescence; roots with thick periderm, the larger ones often helical; indumentum of simple, glandular, and (on the sepals) stellate trichomes. Leaves alternate, trifoliolate or simple (in the inflorescence), sessile or shortly petiolate; leaflets subsessile, serrate with glandular-tipped teeth (leaflets of the lower leaves pinnately dentate or divided in *P. stipulatus*); stipules persistent, subulate or foliaceous and easily mistaken for 2 extra leaflets. Inflorescences terminal, loose, long-pedicellate, several-flowered panicles. Flowers white to pinkish, slightly irregular. Calyx ebracteolate, the 5 lobes erect, persistent, imbricate in aestivation; floral tube cylindric to slightly campanulate or urceolate, 10-nerved, free from the carpels, nectar ring not evident. Petals spreading somewhat, slightly unequal, linear to narrowly oblanceolate, clawed, deciduous, convolute in bud, perigynously inserted at the edge of the floral tube. Androecium of 20 (rarely more or

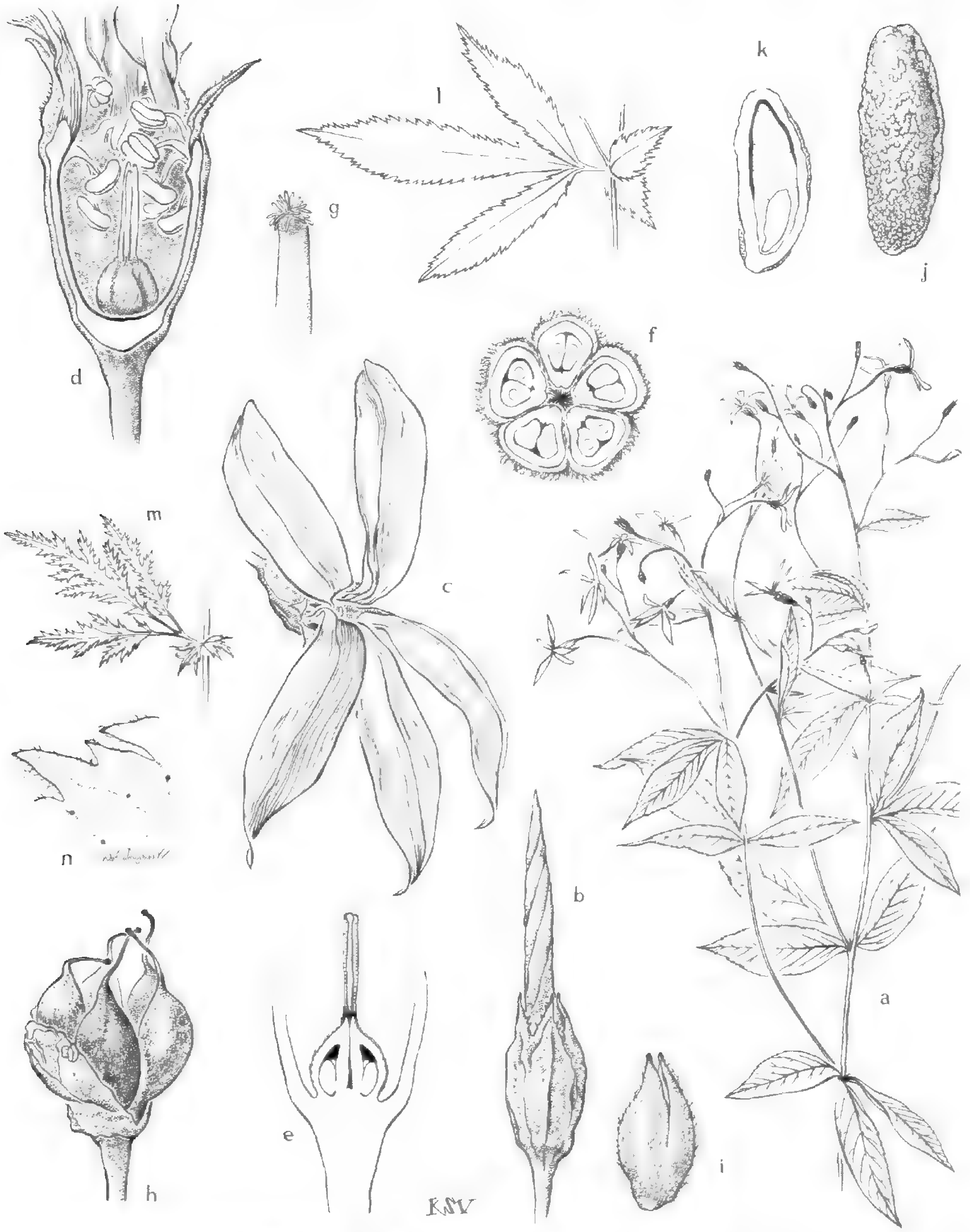


FIGURE 3. **Porteranthus.** a–k, *P. trifoliatus*: a, upper part of flowering plant — note small stipules, × 1/4; b, flower bud, petals contorted, × 3; c, flower, petal-arrangement somewhat zygomorphic by lateral displacement, × 2; d, slightly off-center vertical section of floral tube to show attachment of petals and stamens, × 5; e, base of floral cup and gynoecium in diagrammatic vertical section to show ovules, the micropyle inferior, × 6; f, gynoecium in semidiagrammatic cross section showing the 5 adpressed, but distinct, carpels, each with 2 ovules, × 12; g, tip of style with stigmatic papillae, × 25; h, mature, undehisced follicles, × 3; i, abaxial surface of an open follicle, abaxial suture partly split, × 3; j, seed, × 6; k, seed in vertical section, seed coat thick (white), endosperm abundant (stippled), embryo small (unshaded), × 6. l–n, *P. stipulatus*: l, leaf from near base of inflorescence, stipules foliaceous, × 1/2; m, leaf from near base of plant, × 1/2; n, detail of lower leaf surface — note both simple and glandular, sessile trichomes, × 10.

fewer) included or scarcely exserted stamens, ten in the upper whorl, 5 in the middle, antepetalous whorl, and 5 in the lower, antesepalous whorl; filaments short, incurved, free, perigynous on the floral tube; anthers rather large. Gynoecium superior, of 5 antesepalous carpels, ± connate at first, becoming distinct in fruit; styles terminal, punctiform; each carpel with 2–4 ascending anatropous ovules on a single adaxial and basal placenta, the micropyle inferior. Follicles rupturing the floral tube, 1 to few seeded, dehiscing completely on the adaxial suture and partially on the abaxial one. Seeds ovoid or ellipsoid, rugulose or verruculose, endosperm thick, fleshy; embryo spathulate, the cotyledons linear-oblong, flat, the radicle inferior. (*Gillenia* Moench, 1802, non *Gillena* Adanson, 1763).[6] TYPE SPECIES: *P. trifoliatus* (L.) Britton. (Name commemorating T. C. Porter, 1822–1901, botanist at Lafayette College.) — INDIAN PHYSIC.

Two very distinct species restricted to eastern North America, *Porteranthus trifoliatus* (*Gillenia trifoliata* (L.) Moench) and *P. stipulatus* (Muhl. ex Willd.) Britton (*G. stipulata* (Muhl. ex Willd.) Baillon; *Spiraea stipulacea* Pursh, sphalm).

Porteranthus trifoliatus, $2n = 18$, bowman's root, occurs primarily in the mountains and Upper Piedmont of the Appalachian mountain system from northern Alabama to western New York and southern Ontario at altitudes often above 3000 feet; the collections reported from Missouri by Steyermark (Fl. Missouri, 796) probably represent plants introduced along a railroad right-of-way. Characterized by small, linear stipules; sparse indumentum with glandular trichomes largely confined to leaflet dentation tips; monomorphic cauline leaves with leaflets of the lowermost slightly smaller and broader than the upper; pubescent, scarcely wrinkled, shortly beaked follicles; and ellipsoid seeds ca. 5 mm. long. *P. trifoliatus* is most frequently collected in rich woods, but also occurs in open, dry, rocky woods and along highway cuts. There are indications that this species prefers acidic soils.

Porteranthus stipulatus, American ipecac, usually occurs in dry, open upland woods, ranging from northeastern West Virginia, Ohio, Indiana, Illinois, and Missouri south to the Lower Piedmont of North Carolina, Louisiana, northeastern Texas, eastern Oklahoma, and southeastern Kansas. This species is distinguished by large foliaceous stipules that superficially resemble two extra leaflets; glandular trichomes abundant on the lower surfaces of the leaflets; dimorphic cauline leaves with the lowermost having pinnatifid leaflets; nearly glabrous, prominently wrinkled and veined, long-beaked follicles; and ovoid seeds ca. 3.5 mm. long. Rad-

---

[6] *Gillenia* Moench is a later homonym and an orthographic variant of *Gillena* Adanson (= *Clethra* L.), both names commemorating Arnold Gille (latinized as Gillenius), who, according to Stearn, was a medical man with a botanical garden at Kassel in 1627. It does not seem worthwhile to propose *Gillenia* Moench for conservation, since *Porteranthus* has been in limited use, the nomenclatural combinations have already been made, and there are only two species of limited geographical distribution and economic use.

ford *et al.* (Man. Vasc. Fl. Carolinas, 554) state that this species occurs primarily in basic soils in the Carolinas, while Steyermark (*loc. cit.*) indicates that it prefers acidic soils in Missouri.

Porteranthus; *Spiraeanthus Schrenckianus* (Fisch. & Mey.) Maxim., of central Asia; *Chamaebatiaria Millefolium* (Torrey) Maxim., of the western United States; and *Sorbaria* (Ser. in DC.) A. Braun, 10 to 15 spp. of temperate Asia, comprise the tribe Sorbarieae, which is characterized by persistent basally connate stipules, antesepalous carpels, and wingless seeds. Only *Porteranthus* is herbaceous; the other three genera are shrubs or subshrubs. *Porteranthus* (as *Gillenia*) and *Spiraeanthus* were segregated as tribe Gillenieae Maxim. by Schulze-Menz.

The red young stems and buds, white to pinkish flowers, reddish-brown fruits, and neat habit give plants of both species an attractive, though not spectacular, appearance, and they are grown to some extent as perennials and rock garden plants in the United States and Europe. The American Indians apparently used the rhizome of both species in medicinal preparations, particularly as an emetic.

REFERENCES:

See subfamily references. Under family references see BALDWIN, RICKETT, ROBERTSON, STERLING (IX), and L. A. TAYLOR.

BABB, G. F. *Gillenia* or bowman's root. Bull. Am. Rock Gard. Soc. **15**: 118, 119. 1957. [*P. trifoliatus*.]

BARTON, W. P. C. Vegetable materia medica of the United States; or medical botany. Vol. 1. 273 pp. *pls. 1–24.* Philadelphia. 1817. [*P. trifoliatus*, 65–70, *pl. 5*, the root system well illustrated; *P. stipulatus*, 71–76, *pl. 6*.]

BIGELOW, J. American Medical Botany. Vol. 3. x + 198 pp. *pls. 41–60.* Boston 1820. [*P. trifoliatus*, 11–18, *pl. 41*; plant an effective emetic.]

GRIFFITH, R. E. On *Gillenia trifoliata.* Jour. Phila. Coll. Pharm. **4**: 177–184. *col. pl.* 1833.*

HOLM, T. Medicinal plants of North America. 19. *Gillenia trifoliata* Moench. Merck's Rep. **17**: 234–236. 1908.* [See Bot. Centralbl. **110**: 31, 32. 1909.]

———. Observations on seedlings of North American phaenogamous plants. Ottawa Nat. **22**: 235–244. *pls. 7, 8.* 1909. [*P. trifoliatus*, 238, *pl. 8*.]

MOTTA, J. DE LA. An investigation of the properties and effects of the *Spiraea trifoliata* of Linnaeus, or Indian Physic. 44 pp. Philadelphia. 1810. [Discussion of medicinal properties.]

SIMS, J. *Spiraea trifoliata.* Three-leaved Spiraea. Bot. Mag. **14**: *pl. 489.* 1800.

SOPER, J. H. Some genera of restricted range in the Carolinian flora of Canada. Trans. Roy. Canad. Inst. **34**(1): 3–56. *pl. 1.* 1962. [*P. trifoliatus*, 19, 20, southern Ontario.]

STEARN, W. T. Early Marburg botany. Pp. I–XIX. *In*: C. MOENCH, Methodus plantas horti botanici et agri marburgensis. viii + 780 pp. + [20]. Marburg. 1794. Facsimile ed. Koenigstein-Taunus. 1966. [*Gillenia* and *Porteranthus*, XV.]

(*To be continued*)

JOURNAL OF THE
ARNOLD ARBORETUM

Volume 55 HARVARD UNIVERSITY Number 3

MISSOURI BOTANICAL
OCT 1 - 1974
GARDEN LIBRARY

US ISSN 0004-2625

Journal of the Arnold Arboretum

Published quarterly in January, April, July, and October by the Arnold Arboretum, Harvard University.

Subscription price $16.00 per year.

Subscriptions and remittances should be sent to Ms. Kathleen Clagett, Arnold Arboretum, 22 Divinity Avenue, Cambridge, Massachusetts 02138, U.S.A. Claims will not be accepted after six months from the date of issue.

Volumes I–XLV, reprinted, and some back numbers of volumes 46–50 are available from the Kraus Reprint Corporation, Route 100, Millwood, New York 10546, U.S.A.

EDITORIAL STAFF

B. G. Schubert, Editor

C. E. Wood, Jr.

S. A. Spongberg

CIRCULATION

K. Clagett

Printed at the Harvard University Printing Office, Boston, Massachusetts

COVER: *Ginkgo biloba* L., the maidenhair tree, so-called from the fancied resemblance of its leaves to those of the maidenhair fern. In China it has also been called the silver apricot, from the hard inner seed coat which is silvery when cleaned and vaguely resembles an apricot pit, and the duck-foot tree, from the resemblance of the leaves to the webbed feet of ducks.

The drawing for the cover and the devices for the back cover and reprints were planned and drawn by Karen Stoutsenberger Velmure from specimens taken from a tree cultivated in the Arnold Arboretum of Harvard University.

We want to assure the purists among our readers that our *Ginkgo* does not have leaves with open parallel venation. We think, however, that an exact reproduction of the dense dichotomous veins would have produced a much less dramatic design.

Second-class postage paid at Boston, Massachusetts

Karl Sax

JOURNAL
OF THE
ARNOLD ARBORETUM

VOL. 55 JULY 1974 NUMBER 3

KARL SAX, 1892–1973

RICHARD A. HOWARD

With portrait *

KARL SAX, PROFESSOR OF BIOLOGY at Harvard and the third director of the Arnold Arboretum, was born in Spokane, Washington, November 2, 1892, and died in Media, Pennsylvania, October 8, 1973. His parents were William L. Sax, a school teacher, superintendent of County Schools, and one-time Mayor of Colville, Washington, and Minnie A. Morgan Sax, an artist and amateur botanist. After completing high school, Sax took a year of business training, then entered Washington State College and received a B.S. degree in agriculture in 1916. He came to the Bussey Institution of Harvard University, in Jamaica Plain, Massachusetts, and was awarded an M.S. degree in 1917; after which he served in the United States Army, at first as a private and later, from 1918 to 1919, as a second lieutenant at Fort Amador in the Canal Zone. His early professional employment was first as an instructor in genetics at the University of California at Berkeley, then as a plant breeder for the Riverbank Laboratory at Geneva, Illinois. Subsequently he joined the staff of the Agricultural Experiment Station, University of Maine, Orono, Maine, where he worked from 1920 until 1928, during which time he also earned a D.Sc. (1922) from the Bussey Institution. In 1928 Sax was appointed Associate Professor of Plant Cytology at the Arnold Arboretum, with a faculty appointment on the staff of the Bussey Institution as well. He was promoted to a full professorship in 1936, and during the reorganization of the Bussey Institution he moved his office, research laboratories, and students to the Biological Laboratories of Harvard University in Cambridge.

With the retirement of Dr. Elmer D. Merrill as director of the Arnold Arboretum, Sax was appointed acting director in 1946, and then director the following year. Sax's administrative role at the Arnold Arboretum was terminated in 1954, but he remained as Professor of Biology until 1959.

Sax had planned on his retirement to continue his work in plant breeding in the area of Media, Pennsylvania; yet for part of each year between 1959 and 1966 he accepted appointments as visiting professor at the Uni-

---

* Portrait courtesy Harvard University News Office; taken in 1959.

versity of Florida, Yale University, North Carolina State College, the University of California, the University of Tennessee, Cornell University, and the University of Georgia, thus avoiding the cold and the dormant growing seasons of Pennsylvania. Also, at the age of sixty-nine, he received a Guggenheim Fellowship which he used at Oxford, England.

Sax was a national lecturer for the American Institute of Biological Sciences (1957) and for The Society of the Sigma Xi (1962), and he presented the Lowell Lectures in Boston in 1951 on the subject, "Population Problems of the World." He was elected to membership in the American Academy of Arts and Sciences and the National Academy of Sciences (1951); and he became an honorary member of Phi Beta Kappa (1941), an honorary member of the Japanese Genetics Society (1956), and a foreign correspondent of the French Academy of Agriculture (1946). In 1956 he received the Certificate of Merit from the Botanical Society of America. His horticultural work was recognized by the award of the Jackson Dawson Memorial Medal of the Massachusetts Horticultural Society in 1959 and the Norman J. Colman Award of the American Association of Nurserymen in 1961. He was named horticulturist of the year by the University of Massachusetts Student Horticultural Club (1959), and later the University of Massachusetts awarded him an honorary Doctor of Science degree (1965). His own college, Washington State University, named Sax a "distinguished alumnus" in 1966. He belonged to many professional societies and served as president of the Genetics Society of America (1958) and of the Planned Parenthood League (1958).

Sax's research and publications were primarily in three fields, cytology and genetics, horticulture, and demography, and in each he left his mark. His first scientific paper, in 1916, concerned fertilization in *Fritillaria*, and began a long study of the behavior of chromosomes in pollen and of fertilization and seed production. At that time the number of chromosomes in most taxa of flowering plants was unknown, and over a period of years he and his students contributed systematic studies of chromosome numbers in various families and genera. Many of these studies were based on the extensive collections at the Arnold Arboretum. His observations on the behavior of chromosomes led to extensive studies and initial contributions on chromosome structure and the mechanism of crossing over. Since much of his employment was with stations interested in agriculture, he worked on wheat, beans, corn, and apples as significant crop plants. Sax's most important early contribution was the demonstration and publication of the fact that alloploidy existed in the cultivated wheats, and that basic series of 7, 14, and 21 chromosome numbers existed. Although the fact was published a few months earlier by a Japanese botanist, Sax's work was independent, and he is usually credited with this contribution.

The failure of chromosomes to pair and resultant sterility are often associated with chromosome breakage. The methods of chromosome breakage were the object of Sax's research for many years, during which he used experimental exposures to X-rays and other types of radiation, as well as variations in temperature, age, and chemicals. His classic paper in 1938, dealing with X-ray induced chromosomal aberrations in *Tradescantia*, opened up a new area of investigation subsequently exploited by others. Several grants from the National Institutes of Health, in his post-retirement period, supported his study of the radio-mimetic effects of common products such as coffee, cola beverages, drugs, and food additives.

Sax's contributions in the field of horticultural plant breeding produced many hybrid plants which he named. Perhaps the best known are a hybrid cherry, *Prunus* 'Hally Jolivette,' named for his wife, and *Magnolia* 'Dr. Merrill,' named for his predecessor as director of the Arnold Arboretum. His interest in improving *Forsythia* resulted in the tetraploid *Forsythia* 'Arnold Giant,' and *Forsythia* 'Karl Sax' (later named for him by Dr. Joab Thomas), which have proved better plants than the *Forsythia* 'Arnold Dwarf' or the problematic triploid *Forsythia* 'Beatrix Farrand.' Numerous crabapples, selected from deliberate crosses or open pollinations, include *Malus* 'Henrietta Crosby,' *M*. 'Beatrix Potter,' and *M*. 'Henry DuPont,' all named for Friends of the Arnold Arboretum, many of whom sponsored his research.

At the University of Maine, Sax began a study of apples that was continued throughout his life. It involved production, propagation, breeding, and selection, as well as methods for producing dwarf trees through the use of understocks, interstocks, and bark inversions. By inverting a ring of bark on apple trees, Sax was able to demonstrate a control of tree growth. Although the technique was known in nearly ancient horticultural literature, its modern application has been adopted, with Sax's techniques, by many nurserymen who now produce small trees for the home garden. Sax demonstrated the nutritional blocking effect of this bark inversion by the use of radioactive compounds in studies of phloem transport. Another of his inventive recommendations, the use of weed killers and insecticides in a grease base for the control of poison ivy and bark borers, was much used before environmental concerns restricted the general use of such chemicals.

While at the Bussey Institution, and later in the Biological Laboratories in Cambridge, Sax was in close association with the distinguished geneticist, Edward M. East, who was concerned with the expanding world population and the problems of feeding an ever-increasing number of people. After East's death, Sax developed his own interest in demographic problems and was a spokesman for the Planned Parenthood program. His book, *Standing Room Only*, recently reprinted as a paperback, and his many lectures, newspaper reports and special articles on the subject of birth control brought criticism from the Catholic community of Boston. In fact, for a period he was subjected to embarrassing harassment for his views.

His tenacity in his beliefs also showed up in his opposition to a proposal by botanists at Harvard that the resources of the Arnold Arboretum be used for the general benefit of botany as a whole. A University committee had recommended that portions of the collections of books and specimens of the Arnold Arboretum be moved to Cambridge, closer to the students, and be combined with other comparable collections maintained by Harvard.

The funds of the Arboretum were to be used within the Department of Biology, and the interest in horticulture and the living collections was to be lessened. Sax did not approve of this plan; he opposed it in principle and then in implementation. As the director he would not carry out the proposal until it was submitted to judicial review and approved legally. Therefore, the Harvard Corporation relieved him of his responsibilities as director of the Arnold Arboretum and supervisor of the Bussey Institution. As Professor of Biology, however, he continued his teaching and research until he reached the normal retirement age of 66. Sax contributed a great deal of information to the group which fought this move through the courts of Massachusetts in a suit against the Harvard Corporation. He was a worthy opponent. An associate, Mrs. Beatrix Farrand, a distinguished landscape architect, always deliberately mispronounced his name as "Dr. Pax." Karl Sax accepted this graciously and wrote that this was his personality and the role he wished to pursue in his life; but he was never able to do so because of the firmness of his belief in individual integrity.

During his active years at Harvard, Karl Sax supervised the work of five successful candidates for the degree of Master of Arts, and twenty-one for the Doctor of Philosophy in Biology. Numerous postdoctoral scholars worked with him in his laboratories. This is an enviable record of excellent teaching rarely exceeded.

Karl Sax is survived by his widow, Hally Mary Delilia Jolivette Sax, whom he married in 1915 when he was an undergraduate student. Their happy marriage of fifty-eight years produced three sons, Karl Jolivette Sax, William Peter Sax, and Edward A. Sax.

ARNOLD ARBORETUM OF HARVARD UNIVERSITY
CAMBRIDGE, MASSACHUSETTS 02138

BIBLIOGRAPHY *

— 1916 —

Fertilization in *Fritillaria pudica*. Bull. Torrey Bot. Club **43**: 505–522.

— 1918 —

The inheritance of doubleness in *Chelidonium majus*, L. Genetics **3**: 300–307.

The behavior of the chromosomes in fertilization. *Ibid*. 309–327.

— 1921 —

Sterility in wheat hybrids. I. Sterility relationships and endosperm development. Genetics **6**: 399–416.

A simple device for weighing seeds. Bot. Gaz. **71**: 399.

Productive and unproductive types of apple trees. (With J. W. Gowen.) Jour. Hered. **12**: 291–300.

Studies in orchard management. II. Factors influencing fruit development of the apple. Bull. Maine Agr. Expt. Sta. **298**: 53–84.

Chromosome relationships in wheat. Science **54**: 413–415.

---

* Compiled by Ida Hay Burch, The Arnold Arboretum of Harvard University, Jamaica Plain, Massachusetts 02130.

— 1922 —

The relation of tree type to productivity in the apple. (With J. W. Gowen.) Bull. Maine Agr. Expt. Sta. **305**: 1–20.

Sterility relationships in Maine apple varieties. *Ibid*. **307**: 61–76.

Sterility in wheat hybrids. II. Chromosome behavior in partially sterile hybrids. Genetics **7**: 513–552.

Sterility in wheat hybrids. III. Endosperm development and F_2 sterility. *Ibid*. 553–558.

— 1923 —

Color factors in bean hybrids. (With H. C. McPhee.) Jour. Hered. **14**: 205–208.

The cause and permanence of size differences in apple trees. (With J. W. Gowen.) Bull. Maine Agr. Expt. Sta. **310**: 1–8.

Permanence of tree performance in a clonal variety and a critique of the theory of bud mutation. (With J. W. Gowen.) Genetics **8**: 179–211.

The association of size differences with seed-coat pattern and pigmentation in *Phaseolus vulgaris*. *Ibid*. 552–560.

Bud and root selection in the propagation of the apple. Proc. Am. Soc. Hort. Sci. **20**: 244–250.

The place of stocks in the propagation of clonal varieties of apples. (With J. W. Gowen.) Genetics **8**: 458–465.

The relation between chromosome number, morphological characters and rust resistance in segregates of partially sterile wheat hybrids. *Ibid*. 301–321.

— 1924 —

The nature of size inheritance. Proc. Natl. Acad. Sci. **10**: 224–227.

A genetic and cytological study of certain hybrids of wheat species. (With E. F. Gaines.) Jour. Agr. Res. **28**: 1017–1032.

Chromosome behavior in a genus cross. (With Hally Jolivette Sax.) Genetics **9**: 454–464.

The "probable error" in horticultural experiments. Proc. Am. Soc. Hort. Sci. **21**: 252–256.

Nursery stock investigations. *Ibid*. 310–312

— 1925 —

Fertilization of apple orchards in Maine. Bull. Maine Agr. Expt. Sta. **322**: 1–8.

— 1926 —

Varieties of ensilage corn for Maine. (With Iva M. Burgess.) Bull. Maine Agr. Expt. Sta. **330**: 49–56.

Sweet-corn breeding experiments. *Ibid*. **332**: 113–144.

Quantitative inheritance in *Phaseolus*. Jour. Agr. Res. **33**: 349–354.

A genetical interpretation of ecological adaptation. Bot. Gaz. **82**: 223–227.

Statistical methods in horticulture. Proc. Am. Soc. Hort. Sci. **23**: 141–149.

— 1928 —

Bud and root selection in the apple. Bull. Maine Agr. Expt. Sta. **344**: 21–32.

Chromosome behavior in *Triticum* hybrids. Zeitschr. Indukt. Abstammungs-Vererbungsl. Suppl. II. Verhandl. V. Internat. Kongresses Vererbungswissenschaft. Berlin 1927. Pp. 1267–1284.

— 1929 —

Chromosome counts in *Vitis* and related genera. Proc. Am. Soc. Hort. Sci. **26:** 32, 33.

Chromosome behavior in *Sorbopyrus* and *Sorbaronia*. Proc. Natl. Acad. Sci. **15:** 844, 845.

— 1930 —

Chromosome number and behavior in the genus *Syringa*. Jour. Arnold Arb. **11:** 7–14.

Chromosomes and phylogeny in the Caprifoliaceae. (With D. A. Kribs.) *Ibid.* 147–153.

Chromosome structure and the mechanism of crossing over. *Ibid.* 193–220.

Arnold Arboretum cytological laboratory report 1929–1930. *Ibid.* 237, 238.

Chromosome stability in the genus *Rhododendron*. Am. Jour. Bot. **17:** 247–251.

— 1931 —

The origin and relationships of the Pomoideae. Jour. Arnold Arb. **12:** 3–22.

Chromosome numbers in the ligneous Saxifragaceae. *Ibid.* 198–206.

Arnold Arboretum cytology laboratory report 1930–1931. *Ibid.* 299.

The smear technique in plant cytology. Stain Tech. **6:** 117–122.

Chromosome ring formation in *Rhoeo discolor*. Cytologia **3:** 36–53.

Crossing over and mutation. Proc. Natl. Acad. Sci. **17:** 601–603.

Plant hybrids. Arnold Arb. Bull. Pop. Inf. **5:** 17–20.

— 1932 —

Chromosome numbers and the anatomy of the secondary xylem in the Oleaceae. (With E. C. Abbe.) Jour. Arnold Arb. **13:** 37–48.

The cytological mechanism of crossing over. *Ibid.* 180–212.

Chromosome relationships in the Pomoideae. *Ibid.* 363–367.

Arnold Arboretum cytological laboratory report 1931–1932. *Ibid.* 450, 451.

Meiosis and chiasma formation in *Paeonia suffruticosa*. *Ibid.* 375–384.

The cytological mechanism for crossing over. Proc. 6th Int. Genetics Cong. **1:** 256–273.

Flowering habits of trees and shrubs. Arnold Arb. Bull. Pop. Inf. **6:** 14–16.

Review: Recent advances in cytology, by C. D. Darlington. Collecting Net **7:** 201–203.

— 1933 —

Segmental interchange in chromosomes of *Tradescantia*. (With Edgar Anderson.) Genetics **18:** 53–67.

Chromosome number and morphology in the Conifers. (With Hally Jolivette Sax.) Jour. Arnold Arb. **14:** 356–375.

Development of the male gametophyte in Tradescantia. (With H. W. Edmonds.) Bot. Gaz. **95:** 156–163.

Species hybrids in *Platanus* and *Campsis*. Jour. Arnold Arb. **14:** 274–278.

Chromosome behavior in *Calycanthus*. *Ibid.* 279–281.

The origin of the Pomoideae. Proc. Am. Soc. Hort. Sci. **30:** 147–150.

Chromosome numbers in *Ulmus* and related genera. Jour. Arnold Arb. **14:** 82–84.

Taxonomic and cytological relationships of *Yucca* and *Agave*. (With Susan Delano McKelvey.) *Ibid.* 76–81.

— 1934 —

Interlocking as a "demonstration" of the occurrence of crossing over. Am. Nat. **68:** 95, 96.

A cytological analysis of self-sterility in *Tradescantia.* (With Edgar Anderson.) Bot. Gaz. **95:** 609–621.

Chromosomes of the Cycadales. (With J. M. Beal.) Jour. Arnold Arb. **15:** 255–258.

Interlocking of bivalent chromosomes in *Tradescantia.* (With Edgar Anderson.) Genetics **19:** 157–166.

Structure of meiotic chromosomes in microsporogenesis of *Tradescantia.* (With L. M. Humphrey.) Bot. Gaz. **96:** 353–362.

Cytology for students. (Review of "Introduction to cytology" by L. W. Sharp.) Science **80:** 407.

— 1935 —

Chromosome numbers in the Hamamelidaceae and their phylogenetic significance. (With Edgar Anderson.) Jour. Arnold Arb. **16:** 210–215.

Chromosome structure in the meiotic chromosomes of *Rhoeo discolor* Hance. Jour. Arnold Arb. **16:** 216–224.

The cytological analysis of species-hybrids. Bot. Rev. **1:** 100–117. 1935.

Variation in chiasma frequency in *Secale, Vicia* and *Tradescantia.* Cytologia **6:** 289–293.

The effect of temperature on nuclear differentiation in microspore development. Jour. Arnold Arb. **16:** 301–310.

Chromosome structure and behavior in mitosis and meiosis. (With Hally Jolivette Sax.) *Ibid.* 423–439.

— 1936 —

The experimental production of polyploidy. *Ibid.* **17:** 153–159.

Polarity and differentiation in microspore development. (With Ladley Husted.) Am. Jour. Bot. **23:** 606–609.

Polyploidy and geographic distribution in *Spiraea.* Jour. Arnold Arb. **17:** 352–356.

Chromosome coiling in relation to meiosis and crossing over. Genetics **21:** 324–338.

— 1937 —

Effect of variations in temperature on nuclear and cell division in *Tradescantia.* Am. Jour. Bot. **24:** 218–225.

Chromosome inversions in *Paeonia suffruticosa.* Cytologia, Fujii Jub. Vol. 108–114.

Stomata size and distribution in diploid and polyploid plants. (With Hally Jolivette Sax.) Jour. Arnold Arb. **18:** 164–172.

Chromosome behavior and nuclear development in *Tradescantia.* Genetics **22:** 523–533.

Review: Recent advances in cytology, by C. D. Darlington. Jour. Hered. **28:** 217–219.

— 1938 —

The relation between stomata counts and chromosome number. Jour. Arnold Arb. **19:** 437–441.

Chromosome aberrations induced by X-rays. Genetics **23:** 494–516.

— 1939 —

The time factor in X-ray production of chromosome aberrations. Proc. Natl. Acad. Sci. **25:** 225–233.

An X-ray analysis of progressive chromosome splitting. (With K. Mather.) Jour. Genet. **37:** 483–490.

The effect of temperature on X-ray induced chromosome aberrations. (With E. V. Enzmann.) Proc. Natl. Acad. Sci. **25:** 397–405.

— 1940 —

An analysis of X-ray induced chromosomal aberrations in *Tradescantia*. Genetics **25:** 41–68.

The effect of radiation on chromosome structure. Am. Philos. Soc. Yearb. **1940:** 240, 241.

— 1941 —

Mechanism of mitosis in pollen tubes. (With J. G. O'Mara.) Bot. Gaz. **102:** 629–636.

Differential sensitivity of cells to X-rays. (With C. P. Swanson.) Am. Jour. Bot. **28:** 52–59.

The behavior of X-ray induced chromosomal aberrations in *Allium* root tip cells. Genetics **26:** 418–425.

Types and frequencies of chromosomal aberrations induced by X-rays. Cold Spring Harbor Symposium of Quantitative Biology **9:** 93–101.

— 1942 —

The distribution of X-ray induced chromosomal aberrations. Proc. Natl. Acad. Sci. **28:** 229–233.

The mechanisms of X-ray effects on cells. Jour. Gen. Physiol. **25:** 533–537.

— 1943 —

The effect of centrifuging upon the production of X-ray induced chromosomal aberrations. Proc. Natl. Acad. Sci. **29:** 18–21.

The relation between X-ray dosage and the frequency of chromosomal aberrations. (With Robert T. Brumfield.) Am. Jour. Bot. **30:** 564–570.

— 1944 —

Population problems of a new world order. Sci. Monthly **58:** 66–71.

Soviet Biology. Science **99:** 298, 299.

— 1945 —

The demographic dilemma. Science **101:** 325, 326.

Lilac species hybrids. Jour. Arnold Arb. **26:** 79–84.

"Population problems," *in* RALPH LINTON, *ed.*, The science of man in the world crisis. Columbia Univ. Press, New York. Pp. 258–281.

— 1947 —

How new plants are made. Horticulture **25**(n.s.): 127, 128.

Mechanism of heredity. Am. Fruit Grower **67:** 16, 28, 29.

Plant breeding at the Arnold Arboretum. Arnoldia **7:** 9–12.

Temperature effects on X-ray induced chromosome aberrations. Genetics **32:** 75–78.

Soviet science and political philosophy. Sci. Month. **65:** 43–47.

The Arnold Arboretum during the fiscal year ended June 30, 1947. Jour. Arnold Arb. **28:** 447–452.

The Arnold Arboretum of Harvard University. Arb. Bull. **10**(3): 9, 10, 24.

The Bussey Institution. Arnoldia **7:** 13–16.

The cytogenetics of generic hybrids of *Sorbus*. (With Hally Jolivette Sax.) Jour. Arnold Arb. **28:** 137–140.

— 1948 —

The Arnold Arboretum during the fiscal year ended June 30, 1948. Jour. Arnold Arb. **29:** 422–428.

— 1949 —

The Arnold Arboretum during the fiscal year ended June 30, 1949. Jour. Arnold Arb. **30:** 450–455.

John George Jack, 1861–1949. *Ibid.* 345–347.

— 1950 —

Rootstocks for lilacs. Arnoldia **10:** 57–60.

The cytological effects of low intensity radiation. Science **112:** 332, 333.

Dwarf trees. Arnoldia **10:** 73–79.

Oakes Ames, 1874–1950. Jour. Arnold Arb. **31:** 335–349.

The effect of X-rays on chromosome structure. Jour. Cell. & Comp. Physiol. **35** (Suppl. 1): 71–81.

The Arnold Arboretum during the fiscal year ended June 30, 1950. Jour. Arnold Arb. **31:** 430–434.

The effect of the rootstock on the growth of seedling trees & shrubs. Proc. Am. Soc. Hort. Sci. **56:** 166–168.

"Population and agriculture," *in* GLEN HOOVER, *ed.*, Twentieth century economic thought. Philosophical Library, N.Y. Pp. 647–668.

— 1951 —

Biological resources as a factor in international understanding. Sci. Monthly **72:** 300–305.

Can the earth feed its millions? United Nations World **5:** 22–25.

Photosynthetic energy via agriculture. Proc. Am. Acad. Arts Sci. **79:** 205–211.

The Arnold Arboretum during the fiscal year ended June 30, 1951. Jour. Arnold Arb. **32:** 412–416.

Food resources and population growth. Bull. Atomic Scientists **7:** 105–107.

"Population problems in world development," *in* Social progress through technology: the human conditions of economic growth. A week-end conference in four panels. M. I. T. foreign student summer project. Pp. 4–6.

— 1952 —

The effect of fractional X-ray dosage on the frequency of chromosome aberrations. (With Henry Luippold.) Heredity **6:** 127–131.

The effects of CO and O on the frequency of X-ray induced chromosome aberrations in *Tradescantia*. (With E. D. King and H. A. Schneiderman.) Proc. Natl. Acad. Sci. **38:** 34–43.

The Arnold Arboretum during the fiscal year ended June 30, 1952. Jour. Arnold Arb. **33:** 403–409.

— 1953 —

Interstock effects in dwarfing fruit trees. Proc. Am. Soc. Hort. Sci. **62:** 201–204.

Enough for all? (Review of "The Road to Abundance" by J. Rosin & M. Eastman.) Jour. Hered. **44:** 203, 204.

The Arnold Arboretum during the fiscal year ended June 30, 1953. Jour. Arnold Arb. **34:** 412–416.

Review: Symposium on chromosome breakage. Science **118:** 658, 659.

— 1954 —

The control of tree growth by phloem blocks. Jour. Arnold Arb. **35:** 251–258.

Here's an easy way to dwarf trees. Better Fruit **49:** 9, 10.

Population problems of Central America. Ceiba **4:** 153–164.

Stock and scion relationship in graft incompatibility. Proc. Am. Soc. Hort. Sci. **64:** 156–158.

— 1955 —

An X-ray analysis of chromosome duplication. (With E. D. King.) Proc. Natl. Acad. Sci. **41:** 150–155.

The effect of ionizing radiation on plant growth. Am. Jour. Bot. **42:** 360–364.

The effect of fractionated X-ray dosage on the frequency of chromatid and chromosome aberrations. (With E. D. King and H. Luippold.) Radiation Res. **2:** 171–179.

Evaluation of the recombination theory. Jour. Cell. & Comp. Physiol. **45**(Suppl. 2): 243–247.

Plant breeding at the Arnold Arboretum. Arnoldia **15:** 5–12.

Induction of early flowering of ornamental apple trees. (With A. G. Johnson.) Jour. Arnold Arb. **36:** 110–114.

Dwarf trees with bark inversion. Am. Fruit Grower **75**(3): 38, 39.

Standing room only; the challenge of overpopulation. Beacon Press, Boston. 206 pp.

Pflanzenzüchtung im Arnold Arboretum. Deutsche Baumschule **7:** 177–183.

— 1956 —

What's new in plant propagation? Natl. Hort. Mag. **35:** 116–118.

Phloem polarity in bark regeneration. (With Alan Q. Dickson.) Jour. Arnold Arb. **37:** 173–179.

Paste the poison ivy. Arnoldia **16:** 5–8.

The story behind dwarf fruits. Horticulture **34**(n.s.): 203, 233.

The population explosion. Headline Series, Foreign Policy Assoc. No. **120:** 3–61.

Review: Chromosome Botany, by C. D. Darlington. Science **124:** 688.

— 1957 —

The control of vegetative growth and the induction of early fruiting of apple trees. Proc. Am. Soc. Hort. Sci. **69:** 68–74.

The effect of ionizing radiation on chromosomes. Quart. Rev. Biol. **32:** 15–26.

Dwarf ornamental and fruit trees. Proc. Plant Propagators Soc. **7:** 146–155.

— 1958 —

The juvenile characters of trees and shrubs. Arnoldia **18:** 1–6.

"The genetic future of man," *in* ROY G. FRANCIS, *ed.*, The population ahead. Univ. Minn. Press, Minneapolis. Pp. 87–97.

"Experimental control of tree growth and reproduction," *in* K. THIMANN, *ed.*, The physiology of forest trees. Ronald Press, New York. Pp. 601–610.

Forsythia 'Beatrix Farrand'. Natl. Hort. Mag. **37:** 112, 113.

Breeding ornamental trees & shrubs. Proc. Plant Propagators Soc. **8:** 120–126.

— 1959 —

The cytogenetics of facultative apomixis in *Malus* species. Jour. Arnold Arb. **40:** 289–297.

— 1960 —

Meiosis in interspecific pine hybrids. Forest Sci. **6:** 135–138.

Standing room only: the world's exploding population. Beacon Press. (Revised edit. pap.)

— 1961 —

The effect of age of seed on the frequency of spontaneous and gamma ray induced chromosome aberrations. (With Hally Jolivette Sax.) Radiation Bot. **1:** 80–83.

Radiation sensitivity of *Tradescantia* microspore chromosomes to a second exposure of X-rays. Radiation Res. **14:** 667–673.

— 1962 —

The effect of X-rays on the aging of seeds. (With Hally Jolivette Sax.) Nature **194:** 459, 460.

Aspects of aging in plants. Ann. Rev. Plant Physiol. **13:** 489–506.

— 1963 —

The stimulation of plant growth by ionizing radiation. Radiation Bot. **3:** 179–186.

The effect of chronic gamma irradiation on apical dominance of trees. (With Lloyd A. Schairer.) *Ibid.* 283–285.

— 1964 —

The world's exploding population. Perspectives in Biology and Medicine **7:** 321–330.

The effect of chronological and physiological aging of onion seeds on the frequency of spontaneous and X-ray induced chromosome aberrations. (With Hally Jolivette Sax.) Radiation Bot. **4:** 37–41.

Population problems. Topic **8:** 5–19.

— 1965 —

Cycasin: radiomimetic effects. (With H. J. Teas and Hally Jolivette Sax.) Science **149:** 541, 542.

— 1966 —

Biological problems of the age of science. Washington State Rev. **10:** 5–9.

The Bussey Institute: Harvard University's Graduate School of Applied Biology. Jour. Hered. **57:** 175–178.

Radiomimetic beverages, drugs and mutagens. Proc. Natl. Acad. Sci. **55:** 1431–1435.

Radiomimetic effects of beverages, drugs and insecticides. Cranbrook Inst. Sci. News Letter **36:** 46–49.

— 1968 —

Possible mutagenic hazards of some food additives, beverages and insecticides. Jap. Jour. Genet. **43:** 89–94.

THE GENERA OF ROSACEAE IN THE SOUTHEASTERN UNITED STATES *

KENNETH R. ROBERTSON

Subfam. ROSOIDEAE

About 520 species (excluding the apomictic complexes of *Alchemilla, Potentilla,* and *Rubus*) in 41 genera and eight tribes. Eleven genera representing seven tribes occur in the southeastern United States. Two, *Alchemilla* and *Duchesnea,* are introduced. *Kerria* and *Rhodotypos* may possibly be established locally in our area and are included in the key to genera (see discussion under *Neviusia*). Two genera, *Dalibarda* and *Neviusia,* are restricted to eastern North America, eleven to western North America, seven to Eurasia, four to Africa and Macaronesia, and three to South America. Twelve genera are largely of the North Temperate region; *Acaena* is circum-Antarctic. Tribe Adenostomateae includes a single genus with two species, *Adenostoma fasciculatum* Hooker & Arn., $2n = 18$, and *A. sparsifolium* Torrey, $2n = 18$, both from the Upper Sonoran Zone of California and Baja California (see Anderson, subfamily references, for a study of introgression in *A. fasciculatum*).

Base chromosome numbers in the tribes of Rosoideae are nine in the Kerrieae (*Neviusia* has counts of $2n = 14, 16, 18$); seven in the Ulmarieae (some aneuploidy); seven in the Rubeae; seven in the Fragarieae; seven in *Geum, Waldsteinia,* and *Coluria* and nine in the other genera of Dryadeae; eight in *Alchemilla* and seven in the remaining genera of Sanguisorbeae that have been examined cytologically; nine in the Adenostomateae; and seven in the Roseae.

SUBFAMILY REFERENCES:

ANDERSON, E. Introgression in *Adenostoma.* Ann. Missouri Bot. Gard. **41:** 339–350. 1954.

BESSEY, E. A. The comparative morphology of the pistils of the Ranunculaceae, Alismaceae and Rosaceae. Bot. Gaz. **26:** 297–313. *pl. 25.* 1898.

BRESINSKY, A. Bau, Entwicklungsgeschichte und Inhaltsstoffe der Elaisomen. Studien zur myrmekochoren Verbreitung von Samen und Früchten. Bibliot. Bot. **126:** 1–54. 1963.

CHOAY, E. Recherches anatomiques et physiologiques sur les Dryadées. 128 pp. *4 pls.* Paris. 1888.*

JACKSON, G. The morphology of the flowers of *Rosa* and certain closely related genera. Am. Jour. Bot. **21:** 453–466. 1934. [*Dalibarda, Dryas, Geum Rubus,* and *Waldsteinia.*]

---

* Continued from volume 55, p. 332.

Nestler, C. G. Monographia de *Potentilla*. 81 pp. + *11 pls.* Paris and Strasbourg. 1816. [Also *Dalibarda* and *Waldsteinia*.]

Rydberg, P. A. A monograph of the North American Potentilleae. Mem. Dept. Bot. Columbia Univ. **2:** 1–221. *pls. 1–112.* 1898.

Schaeppi, H., & F. Steindl. Vergleichend-morphologische Untersuchungen am Gynoeceum der Rosoideen. Bull. Soc. Bot. Suisse **60:** 15–50. 1950.

Tribe Kerrieae Focke

5. **Neviusia** A. Gray, Mem. Am. Acad. Arts Sci. II. **6:** 374. *pl. 30.* 1858.

Deciduous shrubs with numerous slender, arching primary stems and short lateral branches; twigs terete, decurrently ridged from the nodes; buds small, solitary, sessile; leaf scars round-cordate to crescent-shaped, slightly elevated with 3, ± doubled bundle scars; indumentum of simple and, on the lower leaf surfaces, multicellular glandular trichomes. Leaves alternate, petiolate; blades simple, ovate with rounded or rarely cordate bases, acute to acuminate-attenuate apices, and usually doubly serrate margins; stipules free, setaceous, the lower part persistent as a small scale. Inflorescences few flowered, open, subumbellate corymbs terminating growth of the current season, flowering as the leaves expand; bracts small, linear. Flowers apetalous, about 2.5 cm. in diameter, perfect. Calyx without an epicalyx, the 5–7 lobes large, green, foliaceous, deeply toothed above the middle, reflexed at anthesis, persistent and enlarged somewhat in fruit, quincuncial in aestivation; floral cup flat, very short. Petals absent. Androecium of numerous stamens (usually more than 100) inserted in several whorls on the flat floral cup area; filaments white, long, slender, free to the bases, persistent, the inner shorter than the outer; nectar ring not discernible; anthers yellow, small, basifixed. Gynoecium of 2–5 superior and free carpels (opposite the calyx lobes when 5); styles as many as the carpels, free, terminal on the adaxial margins of the carpels, the lower part persistent on the fruit; stigmatic region a narrow vertical band on the adaxial surface of the styles; each carpel with a single anatropous ovule pendulous from an adaxial placenta, the micropyle superior. Fruit a greenish, drupaceous achene, the epicarp slightly fleshy, thin, the endocarp crustaceous. Seeds one per carpel, completely filling the achene; testa smooth, thin; embryo descending, completely surrounded by a layer of endosperm, the cotyledons plano-convex, the radicle superior, inflexed-accumbent. Type species: *N. alabamensis* A. Gray. (Named in honor of one of the original collectors, the Rev. Reuben Denton Nevius, 1827–1913.) — Snow-wreath.

One of our rarest shrubs, *Neviusia alabamensis*, the only species of the genus, was known for a long time only from the cliffs along the Black Warrior River above Tuscaloosa, Alabama; this species is now known from Tuscaloosa, Jackson, Madison, and Morgan counties, Alabama; Conway and Faulkner counties, Arkansas; and Butler County, Missouri. The type locality was evidently destroyed by blasting operations about the turn of

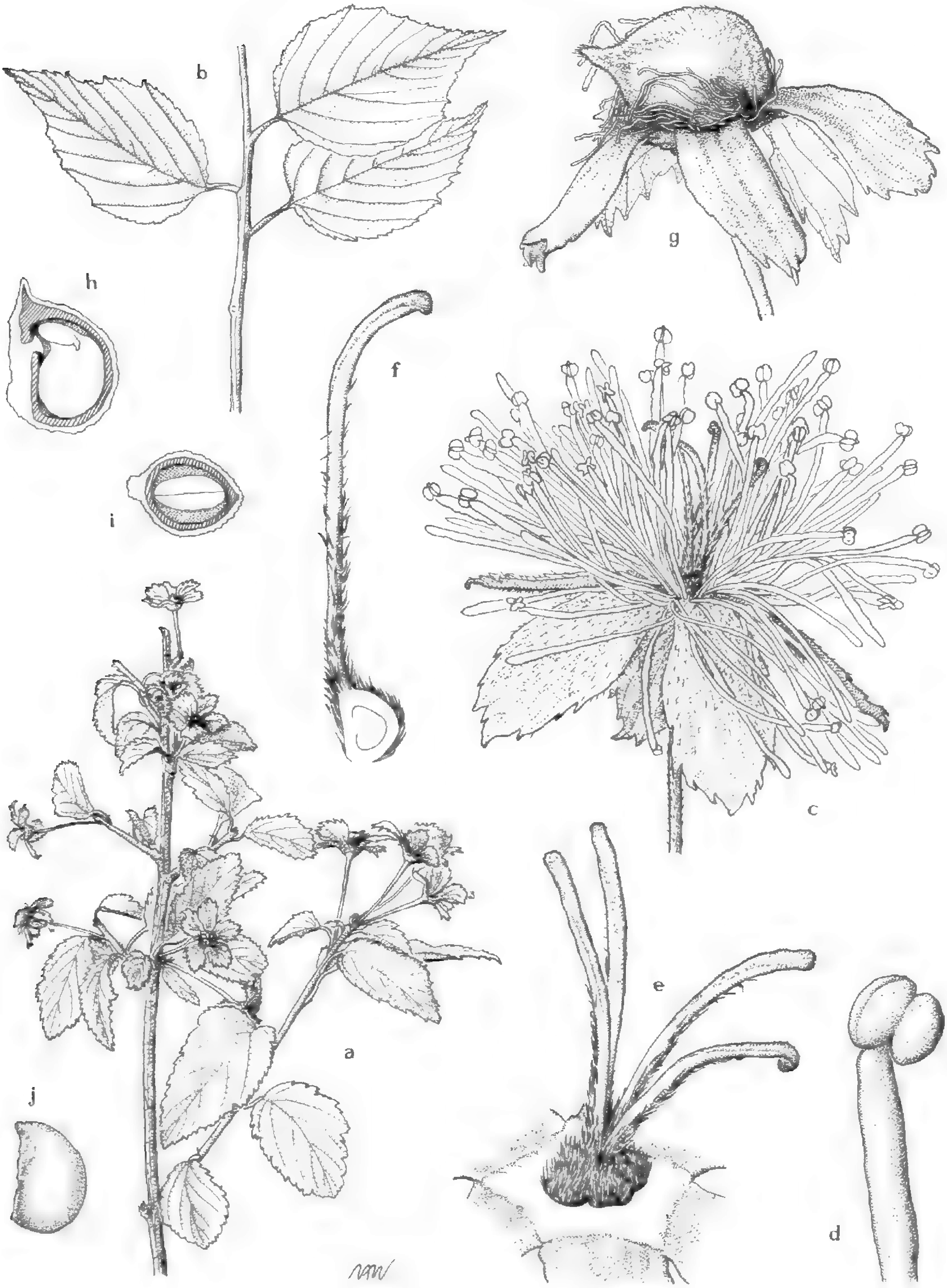


FIGURE 4. **Neviusia.** a–j, *N. alabamensis*: a, tip of long shoot with several lateral shoots in fruit, × 1/2; b, leaves of long shoot, × 1/2; c, flower — note numerous stamens, × 4; d, tip of stamen, × 20; e, central part of flower, stamens removed, to show gynoecium, × 8; f, carpel, ovary in vertical section (ovule nearly pendulous, micropyle superior) — note stigmatic band on adaxial surface of style, × 10; g, fruit, calyx lobes and filaments persistent, × 4; h, vertical section of fruit, epicarp (unshaded) slightly fleshy, endocarp (hatched) crustaceous, embryo surrounded by endosperm (stippled), × 4; i, same, in cross section, × 4; j, seed, × 4.

the present century, but populations still occur along both sides of the river in that vicinity. The Missouri record by Uphof seems certain, although later attempts to relocate his stations have been unsuccessful.

The substrata on which *Neviusia* has been reported are shale, limestone, and sandstone in Alabama, sandstone in Arkansas, and sandy loam in Missouri. All these are Carboniferous or sub-Carboniferous formations. Moore points out that all the known localities for *Neviusia* lie at the periphery of the Mississippi embayment of the old Gulf Coastal Plain and suggests that since this area has been above sea level since the late Paleozoic or early Mesozoic, *Neviusia alabamensis* might be an epibiotic, relatively old relict species, rather than a strict endemic of recent origin.

The chromosome number of *Neviusia* was first reported by Sax (1931) as $2n = 16$; he corrected this the next year to $2n = 18$, stating that the earlier count was an error since the chromosomes tend to clump. Baldwin confirmed Sax's later count, but Thomas & Deramus give the chromosome number of this species as $2n = 14$. The supposed relatives of *Neviusia*, *Kerria japonica*, and *Rhodotypos scandens*, have a reported chromosome number of $2n = 18$.

Tribe Kerrieae is composed of three monotypic genera, *Kerria* DC., *Rhodotypos* Sieb. & Zucc., and *Neviusia*. *Kerria japonica* (L.) DC. (flowers 5-merous, petals yellow, carpels 5–8) is native to central and western China and Kyushu, Shikoku, and Honshu islands, Japan. Commonly grown in North American gardens, this species perhaps has escaped locally from cultivation; Small reports *K. japonica* from eastern South Carolina, but Radford, Ahles, & Bell do not include the species in their *Flora of the Carolinas*. *Rhodotypos scandens* (Thunb.) Makino (*R. kerrioides* Sieb. & Zucc.) (leaves opposite, flowers 4-merous, petals white, carpels 4 and developing into shining, black, dryish drupes) is native to eastern Asia. Although *Rhodotypos* is commonly cultivated and is locally adventive in North America, the only possible record of this species in our area is from a single, supposedly wild plant, near the Guntersville Dam, Marshall County, Alabama, collected and communicated in 1969 by J. E. Butler, of New Hope, Alabama, to J. L. Thomas, who, in turn, relayed the information to us.

The phenolic constituents of the members of tribe Kerrieae are fairly well known (see Bate-Smith and Harborne, family references; Challice [1973], Maloideae references). Within subfam. Rosoideae, flavones are restricted to tribe Kerrieae. Ellagic acid, a compound universal in other Rosoideae, is lacking in *Neviusia*, *Kerria*, *Rhodotypos*, and *Coleogyne ramosissima* Torrey (southwestern North America; included in tribe Kerrieae by Schulze-Menz). Sorbitol, found throughout the Maloideae, Amygdaloideae, and Spiraeoideae, is restricted to tribe Kerrieae within subfam. Rosoideae. *Rhodotypos* differs from *Kerria* and *Neviusia* by the absence of leuco-anthocyanins. Thus, on chemical grounds a strong argument could be made for removing tribe Kerrieae from the Rosoideae. Morphologically, these three genera occupy a position somewhere between the Spiraeoideae and Rosoideae. Since detailed comparative studies have not been made, it seems best for now to follow Gray's alignment of these genera with the Rosoideae.

Neviusia alabamensis is hardy far to the north of its native range, and plants have survived in the coldest part of the Arnold Arboretum for many years. Although usually cultivated only as a novelty and rarely listed in nursery catalogues, the white stamens give plants of *Neviusia* in full bloom much the attractive aspect of *Fothergilla*, of the Hamamelidaceae. It deserves more horticultural attention. Unless carefully pruned, the plants can assume an unkempt appearance similar to their wild relatives growing on densely vegetated cliffs. Evidently, all plants in cultivation are derived from the populations along the Black Warrior River; it is quite possible that the other natural populations could produce more horticulturally desirable forms.

Information on pollination mechanisms is lacking, but the plants are evidently partly self-compatible since the sole plant of the species in cultivation at the Arnold Arboretum produces some fruit each year.

REFERENCES:

Under family references see BALDWIN, BATE-SMITH, BEAN, DIPPEL, REHDER, and SCHNEIDER.

ALEXANDER, E. J. *Rhodotypos kerrioides*. Addisonia **23**: 45, 46. *pl. 759*. 1958.

BEAN, W. J. Trees and Shrubs. Gard. Chron. III. **35**: 229, 230. 1904. [Good illustration of *N. alabamensis*; also see *Ibid.* **41**: 40, 41. *photo opposite 41*. 1907.]

FERNALD, M. L. Specific segregations and identities in some floras of eastern North America and the Old World. Rhodora **33**: 25–63. *pl. 204*. 1931. [*Neviusia*, 29.]

FOCKE, W. O. Die Keimung von *Kerria* und die natürliche Gruppe der Kerriae. Abh. Naturw. Ver. Bremen **12**: 343–345. 1892.

GRAY, A. *Neviusia*, a new genus of Rosaceae. Mem. Am. Acad. Arts Sci. II. **6**: 373–376. *pl. 30*. 1858.

HARPER, R. M. Notes on the distribution of some Alabama plants. Bull. Torrey Bot. Club **33**: 523–540. 1906. [*Neviusia*, 532.]

———. Economic botany of Alabama. Part 2. Catalogue of the trees, shrubs and vines of Alabama, with their economic properties and local distribution. Geol. Surv. Alabama Monogr. **9**. 357 pp. University, Alabama. 1928. [*Neviusia*, 194–196; photographs.]

HOOKER, J. D. *Neviusa* [sic] *alabamensis*. Bot. Mag. **111**: *pl. 6806*. 1885.

MOHR, C. Rare and little known trees and shrubs of Alabama. Trans. Mississippi Valley Hort. Soc. **2**: 216–219. 1884? *

———. Plant life of Alabama. Alabama ed. xii + 921 pp. *pls. 1–13*; *A, B*. Montgomery, Alabama. 1901. [Reprinted from Contr. U.S. Natl. Herb. **4**, with added letter, biography, and *pls. A, B*; *Neviusia*, 539, *pl. 4*.]

MOORE, D. M. *Neviusia alabamensis* in Arkansas. Rhodora **58**: 187–191. 1956.

MURBECK, S. Über staminale Pseudapetalie und deren Bedeutung für die Frage nach der Herkunft der Blütenkrone. Acta Univ. Lund. II. Sect. 2. **14**(25): 1–59. 1918. [*Neviusia*, 6–8, 50, 51, 58; illustration of staminal insertion of *Neviusia*, *Kerria*, *Rhodotypos*.]

POLLARD, C. L. A visit to the home of *Neviusia*. Pl. World **3**: 136, 137. 1900.

THOMAS, J. L., & R. DERAMUS. The chromosome number of *Neviusia alabamensis* Gray. Rhodora **66:** 274. 1964.

UPHOF, J. C. T. Das Vorkommen von *Neviusia alabamensis* Gray in Süden von Missouri. Mitt. Deutsch. Dendrol. Ges. **31:** 282, 283. 1921. [Illustration.]

———. Ecological relations of plants in southeastern Missouri. Am. Jour. Bot. **9:** 1–17. *pls. 1, 2.* 1922. [*Neviusia*, 7.]

Tribe ULMARIEAE Focke

6. **Filipendula** Miller, Gard. Dict. Abr. ed. 4. alph. ord. 1754.

Tall, rhizomatous, glabrous [or pubescent], perennial herbs; stems erect, hollow [or solid], grooved [angled or rounded], mostly unbranched below the inflorescences, the nodes somewhat swollen. Leaves aromatic, the basal ones quite large, imparipinnately compound, the leaflets incised and sharply toothed, the terminal leaflets palmately cleft, larger than the reduced or nearly absent lower leaflets, small leaflets frequently interspersed with larger leaflets along the rachis; cauline leaves similar, but becoming smaller and less compound toward the stem apices; stipules of the basal leaves adnate to the petioles, those of the cauline leaves free, large, asymmetrically reniform, clasping, incised. Inflorescences ebracteate, many flowered, ascending, paniculate corymbs terminating erect stems, the lateral inflorescence branches exceeding, and flowering after, the central ones; pedicels pink [or green]. Flowers small, 5-merous, perfect [or imperfect, the plants then dioecious]. Calyx without an epicalyx, often colored as the petals, deeply lobed, the segments reflexed at anthesis, persistent, valvate in aestivation; floral cup shallow [to nearly flat], free of the carpels, the upper part slightly thickened and fleshy. Petals pink [white, yellowish, or purple], spreading at anthesis, deciduous, about twice as long as the calyx lobes, shortly clawed [or not], the blades orbicular [to ovate] with slightly erose [or entire] margins, the bases auriculate [rounded or tapering]. Androecium of 10–40 (usually 15–20) stamens; filaments slender, equaling or exceeding the petals, deciduous, nearly hypogynous and inserted in several series on the short floral tube; anthers medifixed, deep pink [yellow or white], the anther sacs slightly separated, the connectives enlarged on the abaxial side. Gynoecium of 5–15 free, sessile or stipitate carpels in one whorl [the carpels sometimes spirally imbricated]; styles short, terminal on the adaxial margins of the carpels, bent above so the stigmas face outward laterally; stigmas comparatively large, capitate-discoid, terminal; each carpel with 2 anatropous ovules pendulous from the upper adaxial part of the wall, the micropyle superior. Fruit elongate, flattened, indehiscent, one-seeded, few [to all] carpels of a flower developing into fruit; seed not filling fruit, the seed coat thin, the radicle superior. (Including *Ulmaria* Miller, 1754; *Filipendula* and *Ulmaria* first united, under the former name, by Adanson, Fam. Pl. 2: 295. 1763.) LECTOTYPE SPECIES: *Spiraea Filipendula* L. = *F. vulgaris* Moench; see B. L. Robinson, Rhodora **8**: 204. 1906; also see P. A. Rydberg, N. Am. Fl. 22: 266. 1908. (Name from Latin, *filum*, a thread, and *pendulus*, hanging, after the tuberous roots of *F. vulgaris* that seem suspended from thin roots.)

A small genus of North Temperate and Subarctic regions composed, according to Shimizu, of 15 species in three subgenera and four sections. *Filipendula rubra* (Hill) Robinson occurs in eastern North America, *F. occidentalis* (S. Watson) Howell in northwestern Oregon, two species in Eurasia, and the remaining species primarily in eastern Asia.

Filipendula rubra (*F. lobata* (Jacquin) Murray), queen-of-the-prairie, had an aboriginal distribution from Pennsylvania to Minnesota, southward to North Carolina, Georgia, Kentucky, Illinois, and Missouri, but has escaped from cultivation northward and eastward to New York, New England, and Nova Scotia. This plant, a tall perennial herb with hollow stems, large leaves, palmately lobed leaflets, showy inflorescences of pink flowers, and glabrous, short-stipitate, straight carpels, prefers moist habitats such as meadows, wet prairies, low woods, and bogs. Shimizu places this species, along with seven species of northeastern Asia, in subg. ULMARIA (Miller) Juz. sect. SCHALAMEYA Juz. and notes that *F. rubra* and *F. palmata* (Pall.) Maxim. are geographically vicarious species. *Filipendula occidentalis* is quite different and belongs to the monotypic subg. HYPOGYNA Shimizu. Two European species, *F. vulgaris* (*F. hexapetala* Gilib., nom. illegit.), dropwort, of subg. FILIPENDULA, and *F. Ulmaria* (L.) Maxim., queen-of-the-meadow, have escaped from cultivation to the north of our area.

Because of the general aspect of plants of *Filipendula* species, their small flowers with several free carpels in one whorl on a flat receptacle, and the fruits resembling follicles (although they are indehiscent), this genus was referred by early authors to the Spiraeoideae. However, interruptedly compound leaves (the basal ones with the stipules adnate to the petioles), such as those of *Filipendula*, are common in tribes Dryadeae and Sanguisorbeae of subfam. Rosoideae but do not occur in the Spiraeoideae. The fruits are one-seeded and indehiscent, as in most Rosoideae. The base chromosome number of seven in *Filipendula* is common in the Rosoideae, but is virtually absent from the Spiraeoideae. A glucoside, spiraeoside (quercetin-4′ glucoside) occurs in *F. vulgaris* and *F. Ulmaria* but not in species of *Spiraea*; its possible occurrence in other Rosoideae has evidently not been checked. *Thriphragmium filipendulae*, a rust fungus of tribe Phragmideae, parasitizes *F. vulgaris*; related fungi are known from numerous Rosoideae but few Spiraeoideae. All these data indicate that *Filipendula* is best placed in the Rosoideae.

Reported chromosome numbers in the genus are *Filipendula kamtschatica* (Pall.) Maxim., $2n = 14–18, 28, 28–42$; *F. palmata*, $2n = 14, 15$; and *F. yezoensis* Hara (as *F. koreana*), $2n = 16$. Such disparities in base chromosome numbers and ploidy levels both within and between species suggest that a cytotaxonomic study of the genus would be illuminating. An odd-diploid chromosome number of 15 was listed by Maude for English horticultural material of *F. vulgaris* (as *Spiraea Filipendula*). Darlington inferred that the situation in this species paralleled that experimentally observed in *Campanula persicifolia* in which a metacentric or acrocentric chromosome misdivided through the centromere producing two telocentric chromosomes; "in *Spiraea Filipendula* in England it [the odd-diploid number] is found in every individual. The species has become a true-breeding hybrid in respect of a structural change in the chromosomes. . . ." Baker & Baker, however, dispute this hypothesis on the basis of their observation of $n = 7$ and $2n = 14$ in numerous plants of *F. vulgaris*.

REFERENCES:

Under subfamily references see SCHAEPPI & STEINDL; under family references see BATE-SMITH, BOUTINEAU, BUNTING, CHITTENDEN, HEGI, HUBER (1961–1966), RICKETT, ROSS-CRAIG, and WOOD.

BAKER, H. G., & I. BAKER. The cytotaxonomy of *Filipendula* (Rosaceae) and its implications. Am. Jour. Bot. **54**: 1027–1034. 1967. [*F. vulgaris* and *F. Ulmaria*, both $2n = 14$.]

BARANOV, A. I. Contributions to the study of *Filipendula palmata* (Pall.) Maxim. and similar Far Eastern species. Bot. Jahrb. **79**: 521–525. 1960.

DARLINGTON, C. D. Chromosome botany and the origins of cultivated plants. ed. 2. xvi + 232 pp. London. 1963. [*Filipendula*, 14, 49.]

HÖRHAMMER, L., R. HÄNSEL, & W. ENDRES. Über die Flavonglykoside der Gattungen *Filipendula* und *Spiraea*. Arch. Pharm. **289**: 133–140. 1956. [*F. Ulmaria*, *F. vulgaris*, and 58 spp. of *Spiraea*.]

LEBÈGUE, A. Embryogénie des Rosacées. Développement de l'embryon chez le *Spiraea Ulmaria* L. Compt. Rend. Acad. Sci. Paris **228**: 1243–1245. 1949. [= *F. Ulmaria*; development of the embryo similar to that of *Geum urbanum*.]

MAUDE, P. F. Chromosome numbers in some British plants. New Phytol. **39**: 17–32. 1940. [*Filipendula*, 31, *fig. 21*.]

MEEHAN, T. *Spiraea lobata*. Meehans' Monthly **2**: 145, 146. *pl. 10*. 1892. [= *F. rubra*; colored plate.]

MOREVA, T. A. Dynamics of growth of the green stuff and accumulation of tannins of meadowsweet, *Filipendula Ulmaria* (L.) Max. (In Russian.) Acta Inst. Bot. Acad. Sci. URSS. 5. Mater. Rudes Pl. **4**: 269–285. 1956.

ROBINSON, B. L. *Filipendula rubra*, a new binomial. Rhodora **8**: 202–204. 1906.

SAUNDERS, E. R. On the gynaecium of *Filipendula Ulmaria* Maxim. and *Filipendula hexapetala* Gillib.: A correction. Ann. Bot. **49**: 848–852. 1935. [Refutes an earlier conclusion (Ann. Bot. **41**: 609, 610. 1927) that each ovary is composed of 2 carpels, one sterile and one fertile.]

SAVILE, D. B. O. Parasite relationships and disposition of *Filipendula*. Brittonia **20**: 230, 231. 1968. [The rust fungus found on *F. vulgaris* is closely related to those restricted to Rosoideae.]

SERGIEVSKAYA, E. V. Subgenus *Ulmaria* Moench of genus *Filipendula* Adans. on USSR territory and distribution of its species. 178 pp. Israel Program for Scientific Translations, Jerusalem. 1968.* [Translated from the Russian original of 1965.]

SHIMIZU, T. Taxonomical notes on the genus *Filipendula* Adans. (Rosaceae). Jour. Fac. Textile Sci. Tech. Shinshu Univ. **26**: Ser. A. 10: 1–31. 1961. [Complete taxonomic treatment of genus.]

YAPP, R. H. *Spiraea Ulmaria* L., and its bearing on the problem of xeromorphy in marsh plants. Ann. Bot. **26**: 815–870. *pls. 81–83*. 1912. [= *F. Ulmaria*; a study of the spatial and temporal distribution of foliar indumentum.]

Tribe RUBEAE Dumort.

7. **Rubus** Linnaeus, Sp. Pl. 1: 492. 1753; Gen. Pl. ed. 5. 218. 1754.

Mostly armed erect to trailing shrubs or scramblers from rootstocks or creeping stems, rarely herbaceous; shoots mostly biennial, those of the first year's growth (primocanes or, in older American and in European literature, turions) from buds at or below ground level, bearing leaves along their length, buds in the axils of these leaves producing lateral branches with leaves and flowers the next year, the cane usually dying after fruit matures (the whole second-year stem called a floricane); reproducing vegetatively by root or stem suckers or rooting stem tips; armature of the stems, inflorescence branches, petioles, and calyx lobes of variously shaped and sized prickles or bristles (acicles) or absent; indumentum of simple and/or sessile or stalked glandular trichomes, the density variable. Leaves deciduous or persistent through winter, those of the first and second year's growth often quite different, simple (mostly lobed), ternately trifoliolate, palmately compound with 5–7 leaflets, imparipinnate with 5–7 [or more] leaflets [or bipinnate or partly tripinnate]; leaflets toothed and often lobed, sessile to short or long petiolulate, the central leaflet often larger than the others; stipules linear, small to conspicuous, free or adnate to the base of the petiole, persistent or caducous. Flowers solitary or inflorescences determinate, simple or compound cymes, "racemes," or "panicles." Flowers usually showy, 5-merous, perfect [or imperfect, the plants then dioecious]. Calyx without an epicalyx, the lobes elongate, with acute or tapering-acuminate apices, ascending to reflexed at anthesis and in fruit, valvate in aestivation, persistent; floral cup short, nearly flat; nectar ring usually prominent. Petals white or rarely pink, elliptic to spathulate or orbicular, shorter than to exceeding the calyx lobes [or absent]. Androecium of many stamens inserted at the edge of the floral cup, the outer longer than and dehiscing before the inner ones; filaments slender; anthers sometimes pubescent. Gynoecium of numerous free carpels on a nearly flat to cylindrical receptacle; styles slender or somewhat clavate, terminal, commonly deciduous; stigmas discoid or slightly 2-lobed; each carpel with 2 collateral or superposed, anatropous ovules pendulous from an adaxial placenta, the micropyle superior. Fruit of many red to black (rarely white, yellow, or orange) 1-seeded drupelets on a dry or spongy, often elongated receptacle, the drupelets falling individually or coalescent and either falling from the receptacle as a unit or with it; stones hard, variously textured; seeds filling the stones; embryo small, the radicle superior. Base chromosome number 7. (Including *Rubacer* Rydb. and *Oreobatus* Rydb.) LECTOTYPE SPECIES: *R. fruticosus* L.; see N. L. Britton & A. Brown, Illus. Fl. No. U.S. Canada ed. 2. **2**: 275. 1913.[5] — BLACKBERRY, DEWBERRY, RASPBERRY.

---

[5] Later the same year, Rydberg (N. Am. Fl. **22**: 429) listed *R. idaeus* L. as the type species. Hitchcock & Green (Int. Bot. Congr. Cambridge Nomencl. Prop. Brit. Bot. 1929) say: "The type-species of the genus *Rubus* is undoubtedly *R. fruticosus*, but this name has fallen into disuse as it has been used in different senses by different authors. It therefore seems preferable to choose *R. caesius* L. as the standard species."

Perhaps 700 or more species found nearly throughout the range of the family, the taxonomy of some subdivisions of the genus notoriously difficult. *Rubus* is particularly diverse morphologically in eastern Asia and South America and, to a lesser degree, in North America. Major concentrations of species (mostly the abundant forms of subg. RUBUS) occur in North America and Europe. Basic taxonomic works on *Rubus* are those of Sudre (1908–1913, Europe), Focke (1911–1914, world-wide revision), and Bailey (1941–1949, North America); unfortunately, the subgeneric classification and nomenclature of each of these works are largely independent of the others. Gustafsson's account of the European blackberries is a major contribution toward an understanding of that group.

Eleven subgenera, excluding *Dalibarda*, can be recognized; five widespread ones occur in eastern North America (three in our area). Three subgenera are confined to Asia and the western parts of the Americas, two are essentially restricted to South America, and subg. DALIBARDASTRUM is of eastern Asia.

Subgenus ANOPLOBATUS Focke (stems erect, unarmed; bark peeling or flaking; leaves entire, palmately lobed; styles somewhat clavate; receptacle nearly flat) is represented with us by *Rubus odoratus* L., $2n = 14$, flowering raspberry. This species occurs in shaded areas such as along the edges of woods, stream banks, and roadsides from Quebec and Nova Scotia to Michigan and Wisconsin, southward to New England, New York, Pennsylvania, the Virginias, Ohio, and Indiana, and in the mountains to North Carolina, Tennessee, and Georgia. The plant is a handsome shrub with large leaves (often 30 cm. wide) and rose-like, magenta flowers. The drupelets are reddish, densely pubescent apically and abaxially, only slightly fleshy, and scarcely edible; they fall from the receptacle either individually or in groups. The length of glandular trichomes on the pedicels and veins of the lower leaf surfaces and the density of nonglandular trichomes on the leaf blades is variable; Fassett distinguished seven forms based largely on these characters. Similar patterns of variation are found in the closely related, white-flowered *R. parviflorus* Nutt., $2n = 14$, thimbleberry, which occurs in western North America from Alaska to New Mexico and northern Mexico and disjunctly in the regions around the northern Great Lakes (northeastern Minnesota and adjacent Ontario, northern Wisconsin, northern Michigan and the Keweenaw Peninsula, and the Bruce Peninsula). *Rubus odoratus* and *R. parviflorus* evidently do not occur sympatrically. Other related species occur in western North America, Central America, and Japan.

Subgenus IDAEOBATUS Focke (stems erect, often arching, armed with prickles; petals [in ours] scarcely or not exceeding the calyx lobes; drupelets separating from the receptacle), raspberries, is primarily of temperate

---

Most European authors today use *R. fruticosus* L. only in an aggregate sense for practically all of sect. *Rubus*, indicating that the name is based on two elements (*R. plicatus* Weihe & Nees and *R. ulmifolius* Schott f.) that belong to different subsections (see Heslop-Harrison in Valentine *et al.*, family references). Watson (1958) takes *R. ulmifolius* as the type species.

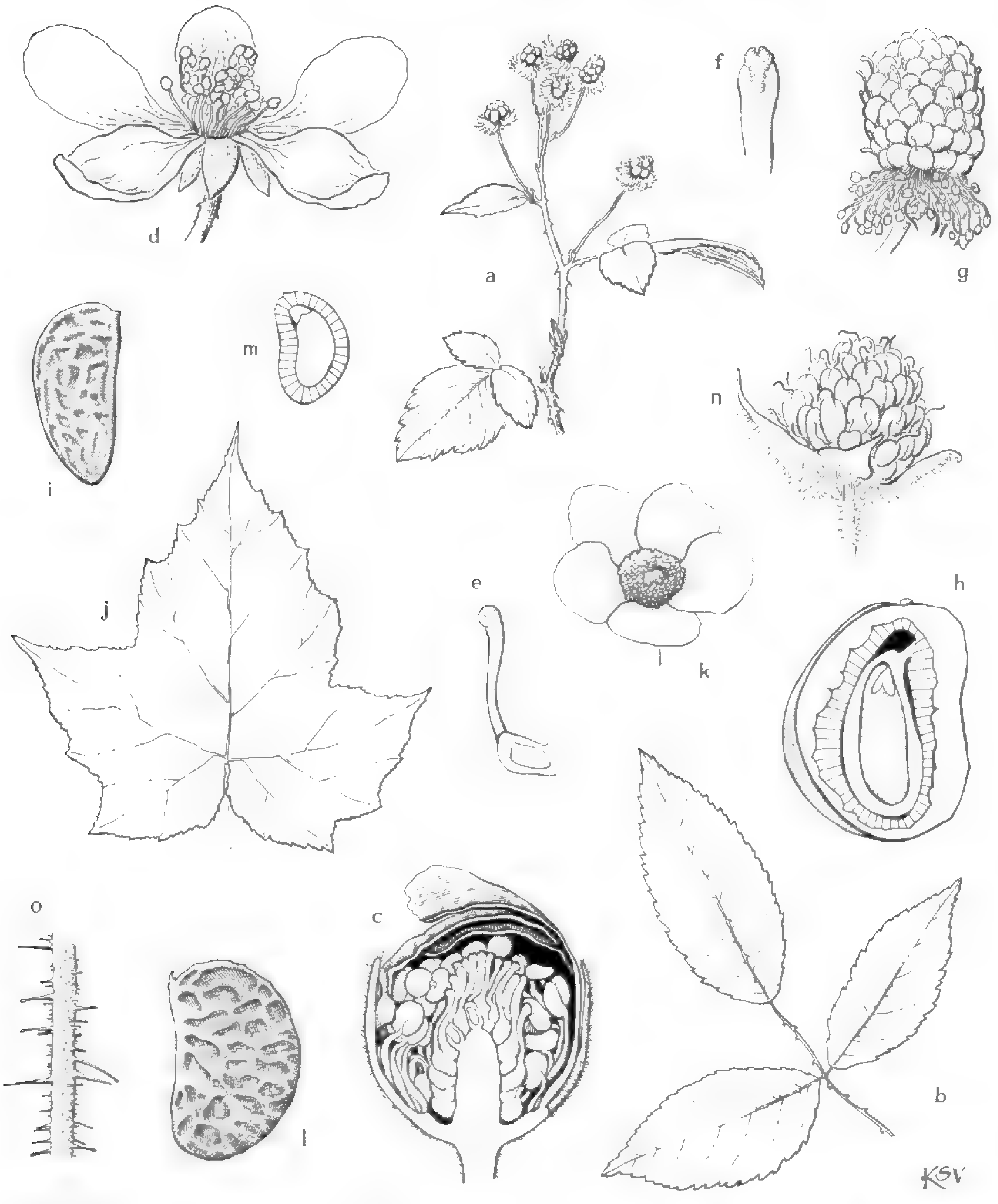


FIGURE 5. **Rubus** subg. **Rubus** (a–i), subg. **Anaplobatus** (j–m), and subg. **Idaeobatus** (n, o). a–i, *R. betulifolius*: a, tip of floricane with young infructescence, × 1/2; b, leaf of primocane, × 1/2; c, vertical section of flower bud, calyx lobes, petals, and stamens inserted at edge of nearly flat floral cup, carpels borne on cylindrical receptacle, × 6; d, open flower, × 2; e, carpel, ovule in section to show pendulous ovule, × 12; f, tip of style with stigma, × 25; g, nearly mature fruit, note persistent stamens, × 2; h, developing drupelet in section, fleshy outer layer unshaded, hard endocarp wall hatched, endosperm even-stippled, embryo sac unshaded [endosperm absorbed and embryo filling nutlet at maturity], × 12; i, endocarp from mature fruit, × 10. j–m, *R. odoratus*: j, leaf of floricane, × 1/2; k, flower at anthesis, × 1/2; l, endocarp from mature fruit, × 12; m, endocarp in vertical section, wall hatched, radicle unshaded, cotyledon stippled, × 6. n, o, *R. idaeus* subsp. *melanotrachys* (*R. strigosus*): n, mature fruit, × 2; o, detail of pedicel to show bristles and simple and glandular trichomes, × 6.

and subtropical Asia, and to a lesser degree, East and South Africa. Relatively few species occur in Europe, North America, and Australia. Bailey (Sp. Batorum, 859) says "Taxonomically the raspberries are the most difficult group of North American brambles."

Rubus idaeus L. (drupelets red; canes erect, not rooting at the tips; petals about equaling the calyx lobes), red raspberry, $2n = 14$ (polyploid in some cultivars), is variable particularly in the shape and size of the leaflets and calyx lobes and in the presence or absence, distribution, and size of prickles, bristles, stipitate-glandular trichomes, and eglandular trichomes. Several segregate species are sometimes recognized (see Hara, Hitchcock *et al.*, and Hultén [family references], Fernald, and Rozanova). The taxonomic treatment of Hara, who recognized one circumpolar species with several subspecies is followed here. Subspecies *idaeus* (inflorescences without glandular trichomes and bristles; drupelets coherent and falling as a unit) is a taxon of Europe and western Asia which Fernald contended is indigenous to the Dakotas and the Magdalen islands of Minnesota. It is commonly cultivated in much of North America and has escaped locally in some areas. Plants native to North America (Labrador to Alaska, southward to New England, Pennsylvania, the mountains of Virginia and North Carolina, Ohio, Indiana, Missouri, Nebraska, Wyoming, and Arizona) and much of eastern Asia have prominent stipitate-glandular trichomes on the young canes and inflorescence branches and drupelets that fall individually; these are distinguished as subsp. *melanolasius* Focke (including *R. strigosus* Michx., *R. sachalinensis* Lévl., *R. idaeus* var. *aculeatissimus* Regel & Tiling). Fernald distinguished five varieties in eastern North America; plants in our area correspond to var. *canadensis* Richardson. Varieties of the red raspberry of commerce are derived from either *R. idaeus* subsp. *idaeus* or subsp. *melanolasius*, or from hybrids between them (see Roemer & Rudorf, family references).

Rubus occidentalis L., black raspberry, $2n = 14$, a shrub with glaucous, arching canes that root at the tips, purple-black (rarely yellowish) drupelets, and petals shorter than the calyx lobes, has a broad distribution, Quebec to North Dakota and eastern Colorado south to Georgia, Arkansas, and Oklahoma. This species and *R. idaeus* subsp. *melanolasius* occasionally hybridize (*R.* × *neglectus* Peck) when they are sympatric. *Rubus leucodermis* Douglas ex Torrey & Gray, $2n = 14$, is a related species of Pacific North America. The various forms of the cultivated black raspberry are derived from *R. occidentalis*. Two species of eastern Asia are locally naturalized in our area: *R. phoenicolasius* Maxim. (canes, petioles, pedicels, and calyx lobes densely covered with long-stalked glandular trichomes; calyx lobes connivent around the red fruit), wineberry, $2n = 14$, and *R. illecebrosus* Focke (flowers and fruits quite large; canes annual), strawberry-raspberry, $2n = 14$.

Subgenus Rubus (subg. *Eubatus*) (petals longer than calyx lobes; drupelets retained on the deciduous or persistent receptacle), blackberries and dewberries, is one of the taxonomically more difficult groups in the North Temperate Zone. The European blackberries have been studied extensively (see particularly Gustafsson and Haskell). It is hypothesized that during the interglacial period of the late Pliocene or early Pleistocene there were a number of diploid, sexually reproducing species in Europe. As the glaciers moved southward, these self-incompatible species were at a disadvantage as the numbers of individuals became smaller and physically isolated from one another. Self-compatible, auto- or allopolyploids that were much better adapted to conditions during and after glaciation arose. Most of the diploid species became extinct. Recessive genes for apomixis were brought together by polyploidy and segregation, and as the glaciers retreated, the apomicts proliferated in the newly opened, barren habitats. It is these apomictic plants of hybrid origins and unknown parentage that are the dominant brambles in Europe today. Since apomixis in *Rubus* is facultative and pseudogamous, variation can result from the production of occasional sexual hybrids and, at least with respect to germination and seedling growth, from pseudogamously produced endosperm.

Detailed studies of North American species are lacking, but the situation here may be somewhat analogous to that in Europe. Some species are diploid or tetraploid and sexually reproducing, while others are polyploid and apomictic. The effect of Pleistocene glaciation on variability in subg. RUBUS in North America is unknown, but much of the variation may be of rather recent origin. As the lands were cleared for cultivation, species that were previously isolated perhaps came together and hybridized, as is presumably the case in *Crataegus* and *Amelanchier*. The taxonomic confusion within subg. RUBUS in North America will remain until a study that integrates gross morphology, cytology, embryology, and genetics is made.

Plants of subg. RUBUS in eastern North America are variable, particularly in growth habit; the number, disposition, and shape of leaflets; the morphology and distribution of spines, bristles, and glands; the pubescence of the leaves; and the type of inflorescence. In the preparation of herbarium specimens, it is necessary to collect both floricanes and primocanes and to take notes on the habit of the plant and whether the canes root at the tip or not. Taxonomic treatments of the subgenus vary widely: Bailey recognized about 400 species in America north of Mexico; Davis *et al.*, just under 200 in eastern North America; Fernald (Gray's Manual, ed. 8), nearly 200 in northeastern North America; Gleason (New Britton & Brown Illus. Fl. No. U.S. Canada), 15, including "collective species"; and Radford *et al.* (Man. Vasc. Fl. Carolinas), 15 in North and South Carolina. It is beyond the scope of this paper (or any other at present) to sort out the taxonomic problems in our area, but a few comments are in order.

All species of this subgenus in eastern North America belong to sect. MORIFERI sensu Focke (1910–1914). American botanists prefer to divide this group into numerous sections. Bailey recognized nine sections with species indigenous to North America; eight of these are largely confined to eastern North America, while sect. URSINI is restricted to the western United States. The sections in our area are: sect. HISPIDI Rydb. (rank assigned by Bailey), groundberries, dewberries, represented with us only by *R. hispidus* L. in the mountains and Coastal Plain of North and South

Carolina; sect. VEROTRIVIALES Bailey, southern dewberries, nearly confined to the Southeast; sect. FLAGELLARES Bailey, dewberries, widespread and taxonomically complex, the collective species *R. Enslenii* sensu Gleason mostly southern in distribution; sect. CUNEIFOLII Bailey, sand blackberries, mostly of the Coastal Plain and Outer Piedmont from Connecticut to Florida; sect. CANADENSES Bailey, smooth blackberries (a glandless and nearly thornless counterpart of the next section), mostly northern in distribution, occurring southward in the mountains to Georgia; sect. ALLEGHENIENSES Bailey, high bush blackberries, including many blackberries of northeastern North America, mostly in the mountains in our area; and sect. ARGUTI Rydb. (rank assigned by Bailey), high bush blackberries, widespread, exceedingly variable, and including the commonest southeastern blackberries.

The base chromsome number in *Rubus* is seven. Most species of subg. IDAEOBATUS are diploid and polyploidy (mostly autoploidy) has evidently played only a minor role in the evolution of this group. Most European species of subg. RUBUS are tetraploid, with relatively few diploids or hexaploids; triploids and pentaploids are quite rare. The North American species are more complex cytologically. All ploidy levels from diploid to 12-ploid occur; diploids, triploids, tetraploids, and hexaploids occur most commonly. Some species evidently have several ploidy levels. *Rubus ursinus* Cham. & Schlecht., of the Pacific Northwest, has reported chromosome numbers of $2n = 42, 56, 63, 70, 77$, and 84, the last the highest number known in the genus.

REFERENCES:

Under subfamily see JACKSON and SCHAEPPI & STEINDL. Under family references see BEAN, BUNTING, CHUTE, DEVADAS & BECK, DIPPLE, FREE, GUSTAFSSON, HARA, HEGI, HUBER (1961–1966), HULTÉN (1958, 1971), JESSEN, LÖVE & LÖVE, LUBBOCK, REHDER, ROBERTSON, ROEMER & RUDORF, ROSS-CRAIG, SCHNEIDER, STEPHENS, TAYLOR, VINES, and WOOD. Because of the great number of papers dealing with the breeding and commercial cultivation of *Rubus*, many references have been omitted; this list contains primarily basic taxonomic works, summary papers, and recently published titles.

AALDERS, L. E., & I. V. HALL. A cytotaxonomic survey of the native blackberries of Nova Scotia. Canad. Jour. Genet. Cytol. **8**: 528–532. 1966.

ALDOUS, S. E. Food habits of chipmunks. Jour. Mammol. **22**: 18–24. 1941. [Raspberries and thimbleberries important foods.]

BAILEY, L. H. Species batorum. The genus *Rubus* in North America (north of Mexico). I. Gentes Herb. **5**: 1–65. 1941; II. *Hispidi. Ibid.* 66–125; III. *Setosi. Ibid.* 128–198; IV. *Verotriviales. Ibid.* 200–228; V. *Flagellares. Ibid.* 230–422. 1943; VI. *Cuneifolii. Ibid.* 424–461; VII. *Canadenses. Ibid.* 464–503. 1944; VIII. *Allegheniense. Ibid.* 506–588; IX. *Arguti*, European species introduced. *Ibid.* 590–856. 1945; X. *Idaeobatus, Anoplobatus. Ibid.* 858–918. Index to volume 5, 919–932. Addendum I. Chromosome studies in *Rubus* (by J. EINSET). *Ibid.* **7**: 181–192. 1947; Species studies in *Rubus. Ibid.* 193–349. Addendum II. *Rubus* studies — review and additions. *Ibid.* 480–526. 1949.

BAMMI, R. K., & H. P. OLMO. Cytogenetics of *Rubus*. V. Natural hybridization between *R. procerus* P. J. Muell. and *R. laciniatus* Willd. Evolution **20:** 617–633. 1966.

BARNOLA, P. Recherches sur le déterminisme de la basitonie chez le ronce (*Rubus fruticosus*). (English summary.) Beitr. Biol. Pflanzen **47:** 469–480. 1971.

BERGER, A. The systematic botany of edible brambles. Pp. 23–85. *In*: U. P. HEDRICK, *et al.*, The small fruits of New York. xi + 614 pp. *Frontisp. 94 pls.* 33rd Annual Rep. New York State Agr. Exper. Sta. Albany. 1925.

BERGER, X. Untersuchungen über die Embryologie apomiktischer *Rubus*bastarde. Bull. Soc. Bot. Suisse **63:** 224–266. *pls. 4, 5.* 1953.

BLANCHARD, W. H. *Rubus* of eastern North America. Bull. Torrey Bot. Club **38:** 425–439. 1911. [Concludes that 8 spp. include perhaps 90% of the blackberries.]

BOIVIN, B. Études batologiques. II. Sous-genre *Idaeobatus* Focke. Bull. Soc. Bot. France **102:** 237, 238. 1955.

BRITTON, D. M., & J. W. HULL. Mitotic instability in *Rubus*. Jour. Hered. **47:** 205–210. 1956.

CHRISTEN, H. R. Untersuchungen über die Embryologie pseudogamer und sexueller *Rubus*arten. Bull. Soc. Bot. Suisse **60:** 153–198. *pls. 1, 2.* 1950.

CLAUSEN, J., D. D. KECK, & W. M. HIESEY. Experimental studies on the nature of species. II. Plant evolution through amphiploidy and autoploidy, with examples from the Madiinae. Carnegie Inst. Wash. Publ. **564:** vii + 1–174. *4 unnumbered pls.* 1945. [Amphiploids in the genus *Rubus*, 104–116.]

CRAIG, D. L. Studies on the cytology and the breeding behavior of *Rubus canadensis* L. Canad. Jour. Genet. Cytol **2:** 96–102. 1960.

CRANE, M. B. Reproductive versatility in *Rubus*. I. Morphology and inheritance. Jour. Genet. **40:** 109–118. 1940. [For part II, see THOMAS.]

———. The origin of new forms in *Rubus*. II. The loganberry, *R. loganobaccus* Bailey. *Ibid.* **40:** 129–140. *pl. 5.* 1940. [For part I, see below; for part III, see THOMAS.]

——— & C. D. DARLINGTON. The origin of new forms in *Rubus*. I. Genetica **9:** 241–277. 1927.

——— & P. T. THOMAS. Reproductive versatility in *Rubus*. III. Raspberry-blackberry hybrids. (With an appendix by C. D. DARLINGTON.) Heredity **3:** 99–107. *figs. 1, 2.* 1949. [For part I, see CRANE; for part II, see THOMAS.]

DAVIS, H. A., & MRS. H. A. DAVIS. Collecting *Rubus* in the Upper South. Castanea **20:** 32, 33. 1955.

DAVIS, H. A., A. M. FULLER, & T. DAVIS. Contributions toward the revision of the *Eubati* of eastern North America. I. Castanea **32:** 20–37. 1967. II. *Setosi. Ibid.* **33:** 50–76. 1968. III. *Flagellares. Ibid.* 206–241. IV. [*Verotriviales, Canadenses, Alleghenienses.*] *Ibid.* **34:** 157–179. 1969. V. *Arguti. Ibid.* 235–266. VI. *Cuneifolii. Ibid.* **35:** 176–194. 1970.

DAVIS, W. H. Apomixis, hybridization, and speciation in *Rubus*. Castanea **23:** 52–55. 1958.

DOWRICK, G. J. Biology of reproduction in *Rubus*. *Nature* **191:** 680–682. 1961. [". . . apomixis in its commonly accepted sense, is not an important reproductive mechanism in tetraploid forms of *Rubus*. The production of maternal-like progeny, though superficially simulating apomixis, depends solely on the formation of reduced egg cells."

———. Breeding systems in tetraploid *Rubus* species. Genet. Res. **7:** 245–253. *pls. 1, 2.* 1966.

Einset, J. Chromosome studies in *Rubus*. Gentes Herb. **7**: 181–192. 1947.

———. Apomixis in American polyploid blackberries. Am. Jour. Bot. **38**: 768–772. 1951.

Fassett, N. C. Mass collections: *Rubus odoratus* and *R. parviflorus*. Ann. Missouri Bot. Gard. **28**: 299–368. *pls. 9–12.* 1941.

Fernald, M. L. *Rubus idaeus* and some of its variations in North America. Rhodora **21**: 89–98. 1919.

———. Critical plants of the upper Great Lakes region of Ontario and Michigan. Rhodora **37**: 272–301. *pls. 363–375.* 1935. [Includes *R. parviflorus*.]

Focke, W. O. Species Ruborum. Monographie generis *Rubi* prodromus. Bibliot. Bot. **72**: 1–223. 1910, 1911; **83**: 1–274. 1914. [The basic taxonomic work for the genus.]

Gerlach, D. Befruchtung und Autogamie bei *Rubus caesius*. (English summary.) Biol. Zentralbl. **84**: 611–633. 1965.

Gustafsson, Å. The origin and properties of the European blackberry flora. Hereditas **28**: 249–277. 1942.

———. The genesis of the European blackberry flora. Lunds Univ. Årssk. II. Sect. 2. **39**(6): 1–200. 1943.

Haskell, G. The history, taxonomy and breeding system of apomictic British *Rubi*. Pp. 141–151. *In*: J. G. Hawkes, ed., Reproductive biology and taxonomy of vascular plants. 183 pp. *Frontisp.* Oxford. 1966. [Includes references to earlier papers.]

Heslop-Harrison, Y. Natural and induced rooting of the stem apex in *Rubus*. Ann. Bot. II. **23**: 307–318. 1959.

Hodgdon, A. R., & F. Steele. Glandularity in *Rubus allegheniensis* Porter. Rhodora **64**: 161–168. 1962.

——— & ———. *Rubus* subgenus *Eubatus* in New England: a conspectus. Rhodora **68**: 474–514. 1966.

Hudson, J. P. Effects of environment on *Rubus idaeus* L. I. Morphology and development of the red raspberry plant. Jour. Hort. Sci. **34**: 163–169. 1959. [Good review of the vegetative life history; for part II, see Williams.]

Jennings, D. L. Some genetic factors affecting fruit development in raspberries. New Phytol. **70**: 361–370. *pl. 1.* 1971.

———. Some genetic factors affecting the development of endocarp, endosperm and embryo in raspberries. *Ibid.* **70**: 885–895. 1971.

Kato, N. On the variation of nodal types in the woody plants. 2. A contribution to the nodal anatomy. 2. Jour. Jap. Bot. **42**: 161–168. 1967. [Includes *R. Sieboldii*, 165–167.]

Keep, E. Accessory buds in the genus *Rubus* with particular reference to *R. idaeus* L. Ann. Bot. II. **33**: 191–204. *pls. 1–3.* 1969.

Larsson, E. G. K. Experimental taxonomy as a base for breeding in northern *Rubi*. Hereditas **63**: 283–351. 1969.

Mandrik, V. Y., & Y. P. Petrus. Differentiation of seedbud, development of female gametophyte and embryogenesis in *Rubus idaeus* L. and *Rubus caesius* L. (In Ukranian; English summary.) Ukrain. Bot. Zhur. **28**: 469–476. 1971.

Markarian, D., & H. P. Olmo. Cytogenetics of *Rubus*. I. Reproductive behavior of *R. procerus* Muell. Jour. Hered. **50**: 131–136. 1959.

Oredsson, A. Drawings of Scandinavian plants. *17–20.* *Rubus* L. subg. *Rubus*. Bot. Not. **122**: 1–8. 1969; *21–24.* *Ibid.* 153–159; *25–28.* *Ibid.* 316–321;

29–32. Ibid. 449–456; *33–36. Ibid.* **123:** 1–7. 1970; *37–40. Ibid.* 213–219; *41–44. Ibid.* 363–370; *17–44.* Key to *Rubus* subg. *Rubus. Ibid.* 447–454.

PERCIVAL, M. S. Observations on the flowering and nectar secretion of *Rubus fruticosus* (agg.). New Phytol. **45:** 111–123. 1946.

PETRAKHILEV, I. M. Intergeneric hybrids of raspberries. (In Russian.) Priroda **1958**(8): 109–111. 1958.

PRATT, C., & J. EINSET. Development of the embryo sac in some American blackberries. Am. Jour. Bot. **42:** 637–645. 1955.

———, ——— & R. T. CLAUSEN. Embryology, breeding behavior and morphological characteristics of apomictic, triploid *Rubus idaeus* L. Bull. Torrey Bot. Club. **85:** 242–254. 1958.

REEVE, R. M. Fruit histogenesis in *Rubus strigosus*. I. Outer epidermis, parenchyma, and receptacle. Am. Jour. Bot. **41:** 152–160. 1954. II. Endocarp tissues. *Ibid.* 173–181.

ROUSI, A. Variation among populations of *Rubus idaeus* in Finland. Ann. Agr. Fenniae **4:** 49–58. 1965.*

ROYEN, P. VAN. The genus *Rubus* (Rosaceae) in New Guinea (Sertulum Papuanum XV). Phanerogamarum Monographiae 2. 126 pp. Lehre. 1969.

STEELE, F., & A. R. HODGDON. Hybridization of *Rubus hispidus* and *R. setosus.* Rhodora **65:** 262–270. 1963.

——— & ———. Hybrids in *Rubus* subgenus *Eubatus* in New England. *Ibid.* **72:** 240–250. 1970. [See correction on p. 547.]

SUDRE, H. *Rubi* Europae vel monographia iconibus illustrata Ruborum Europae. 305 pp. *215 pls.* Paris. 1908–1913.

TAMMISOLA, J., & A. RYYNÄNEN. Incompatibility in *Rubus arcticus* L. Hereditas **66:** 269–277. 1970.

THOMAS, P. T. Reproductive versatility in *Rubus*. II. The chromosomes and development. Jour. Genet. **40:** 119–128. 1940. [For part I, see CRANE.]

———. The origin of new forms in *Rubus*. III. The chromosome constitution of *R. loganobaccus* Bailey, its parents and derivatives. *Ibid.* **40:** 141–155. *pl. 6.* 1940. [For part II, see CRANE.]

THOMPSON, M. M. Cytogenetics of *Rubus*. II. Cytological studies of the varieties "Young," "Boysen," and related forms. Am. Jour. Bot. **48:** 667–673. 1961. III. Meiotic instability in some higher polyploids. *Ibid.* **49:** 575–582 1962.

TOPHAM, P. B. Fertility in crosses involving diploid and autotetraploid raspberries. I. The embryo. Ann. Bot. II. **31:** 673–686. 1967. II. Fruit and seed development. *Ibid.* 687–697.

VAARAMA, A. Cytology of hybrids between Pacific *Rubi ursini* types and an eastern blackberry. Am. Jour. Bot. **40:** 565–570. 1953.

VIRDI, B. V., & G. W. EATON. Embryo sac and early embryo development in the salmonberry (*Rubus spectabilis*). Canad. Jour. Bot. **47:** 1891–1893. 1969.

WALDO, G. F., & G. M. DARROW. Origin of the Logan and the Mammoth blackberries. Jour. Hered. **39:** 98–107. 1948.

WATSON, W. C. R. Handbook of the *Rubi* of Great Britain and Ireland. xi + 274 pp. Cambridge, England. 1958.

WEBER, H. E. Die Gattung *Rubus* L. (Rosaceae) im nordwestlichen Europa. Phanerogamarum Monographiae **7.** vii + 504 pp. Lehre. 1972.

WILLIAMS, I. H. Effects of environment on *Rubus idaeus* L. II. Field observations on the variety Malling Promise. Jour. Hort. Sci. **34:** 170–175. 1959. [For part I, see HUDSON.]

8. **Dalibarda** Linnaeus, Sp. Pl. 1: 491. 1753; Gen. Pl. ed. 5. 217. 1754.

Low, unarmed perennial herbs with the aspect of a stoloniferous *Viola*; rhizomes slender, with internodal roots. Leaves often evergreen, borne along the length of the rhizomes and sometimes in lax to ± condensed rootstocks on the rhizomes, simple, long petiolate, the blade rounded-cordate with crenate margins; stipules small, linear, deeply divided, free. Flowers solitary on axillary pedicels, heteromorphic: petaliferous, morphologically perfect flowers that rarely set fruit, and apetalous, "cleistogamous," fertile ones. Petaliferous flowers in the axils of leaves; calyx lobes 5, rarely 6, divergent, unequal, at least the outer ones apically 3-toothed; floral cup short; petals 5, white, elliptic, spreading, slightly exceeding the calyx lobes; androecium of ca. 50 exserted stamens inserted in several series at the apex of the floral cup, the filaments slender, white, the anthers about 5 mm. long; gynoecium of 5–10 villous carpels, usually not setting fruit. Apetalous flowers produced mostly from rosettes and from tips of rhizomes; pedicels not exceeding the petioles; calyx lobes 5, erect, inclosing the stamens and carpels, the outer ones apically 3-toothed; floral cup short; petals absent; androecium of 5–10 stamens, the anthers about 3 mm. long; gynoecium of 5–10 villous carpels on a flat receptacle, the styles terminal on the adaxial margin of the carpels, deciduous, the stigmatic region a band decurrent on the adaxial surface of the style, each carpel with 2 anatropous ovules pendulous from an adaxial placenta. Fruits of 5–10 nearly dry, light-colored drupelets inclosed by the calyx lobes; the exocarp slightly fleshy, pubescent, the mesocarp hard, slightly wrinkled longitudinally; seed nearly filling the carpel wall, the coat thin; embryo spathulate, the radicle superior, slightly bent. TYPE SPECIES: *D. repens* L. (Name commemorating Thomas François Dalibard, 1705–1799, French botanist.) — DEW DROP, FALSE VIOLET, ROBIN-RUN-AWAY.

A monotypic genus of eastern North America. *Dalibarda repens*, a distinctive species of moist or dry woods, bogs, and swamps, ranges from Quebec, Ontario, northern Ohio, Michigan, and Minnesota, south to New England, New Jersey, and Pennsylvania and in the mountains to West Virginia and North Carolina. In our area it is known only from bogs in Transylvania Co., North Carolina, where it is probably a relict from the last glacial period. Surprisingly little is known about this interesting plant; not even its chromosome number has been determined. The apetalous flowers appear to develop mostly before the petaliferous ones. The carpels of the petaliferous flowers seem to be normal, but they rarely set fruit; pollen of these flowers is evidently viable.

Linnaeus (Gen. Pl. ed. 5) allied this species with *Rubus Chamaemorus* L. and later (Sp. Pl. ed. 2. 708. 1762) included it in *Rubus* as *R. Dalibarda* (L.) L. Focke established *Rubus* subg. DALIBARDA for *R. Dalibarda*, also including *R. lasiococcus* A. Gray (British Columbia to California), *R. pedatus* J. E. Sm. (northwestern North America), *R. Fockeanus* S. Kurz (China and the Himalayas), and *R. Gunnianus* Hooker (Tasmania). Bailey maintained the genus *Dalibarda* and referred *R. lasiococcus*, *R. peda-*

tus, and six other species to *Rubus* subg. CYLACTIS, a somewhat heterogeneous group of mostly semiherbaceous northern species.

REFERENCES:

Under subfamily references see JACKSON and NESTLER; under family references see CHITTENDEN, CHUTE, and RICKETT.

BAILEY, L. H. The standard cyclopedia of horticulture. ed. 2. vol. 1. xxiv + 1200 pp. *frontisp.* New York. 1928. [*Dalibarda*, 961.]

———. Species Batorum. The genus *Rubus* in North America (north of Mexico). I. Gentes Herb. 5: 1–64. 1941. [*Dalibarda*, 25.]

FOCKE, W. O. Species Ruborum. Monographie generis Rubi prodromus. Bibliot. Bot. **72:** 1–223. 1910, 1911; **83:** 1–274. 1914. [*Rubus* subg. *Dalibarda*, 13–17.]

SMITH, J. E. Plantarum icones hactenus ineditae. vi + 75 pp. *pls. 1–75.* 1789–1791. [*Rubus Dalibarda, pl. 20.*]

Tribe FRAGARIEAE Dumort.

9. **Fragaria** Linnaeus, Sp. Pl. 1: 494. 1753; Gen. Pl. ed. 5. 218. 1754.

Perennial, rosulate herbs with simple [or compound], scaly crowns terminating underground rhizomes, spreading and forming colonies by stolons that root and produce plantlets at the nodes; principal roots several, coarse, the secondary roots fibrous and numerous. Leaves radical, with 2/5 phyllotaxy, trifoliolate or simple in the inflorescence [rarely all simple], long petiolate; leaflets deeply serrate at least apically, sessile to short petiolulate; stipules adnate to the bases of the petioles, membranaceous, persistent and forming scales on the crowns. Inflorescences usually one to few per crown, of rather loose, long pedunculate, few to several-flowered cymes, sometimes becoming racemiform; bracts conspicuous, the larger ones often foliaceous. Flowers perfect or partly to wholly imperfect and the plants then variously polygamodioecious. Calyx with an epicalyx, the epicalyx lobes narrower than the calyx lobes, both erect or reflexed at anthesis, persistent, valvate in aestivation; floral cup saucer-shaped, free of the carpels, a nectar ring absent. Petals 5 [to 9], white to pinkish, spreading, deciduous, orbicular to obovate, the margins slightly erose or undulate, the bases shortly clawed, inserted at the edge of the floral cup, imbricate. Androecium of usually 20–35 stamens in multiples of 5 and in 3 whorls, sometimes some or all reduced to staminodia; filaments unequal in length, basally dilated and fused to form a disk that lines the floral cup; anthers yellow, sometimes opening under tension throwing pollen onto the stigmas. Gynoecium of many free carpels on a hemispheric to conical receptacle that enlarges in fruit; styles inserted adaxially near the bases of the carpels, persistent; stigmas terminal, discoid; each carpel with one anatropous ovule ascending from the middle of the locule, the micropyle inferior. Accessory fruits red (infrequently white), fleshy, juicy, sweet and fragrant, subtended by the calyx and epicalyx, the entire fruits falling from the plants. Achenes brownish, minute, numerous, dry, crustaceous, superficial or sunken into

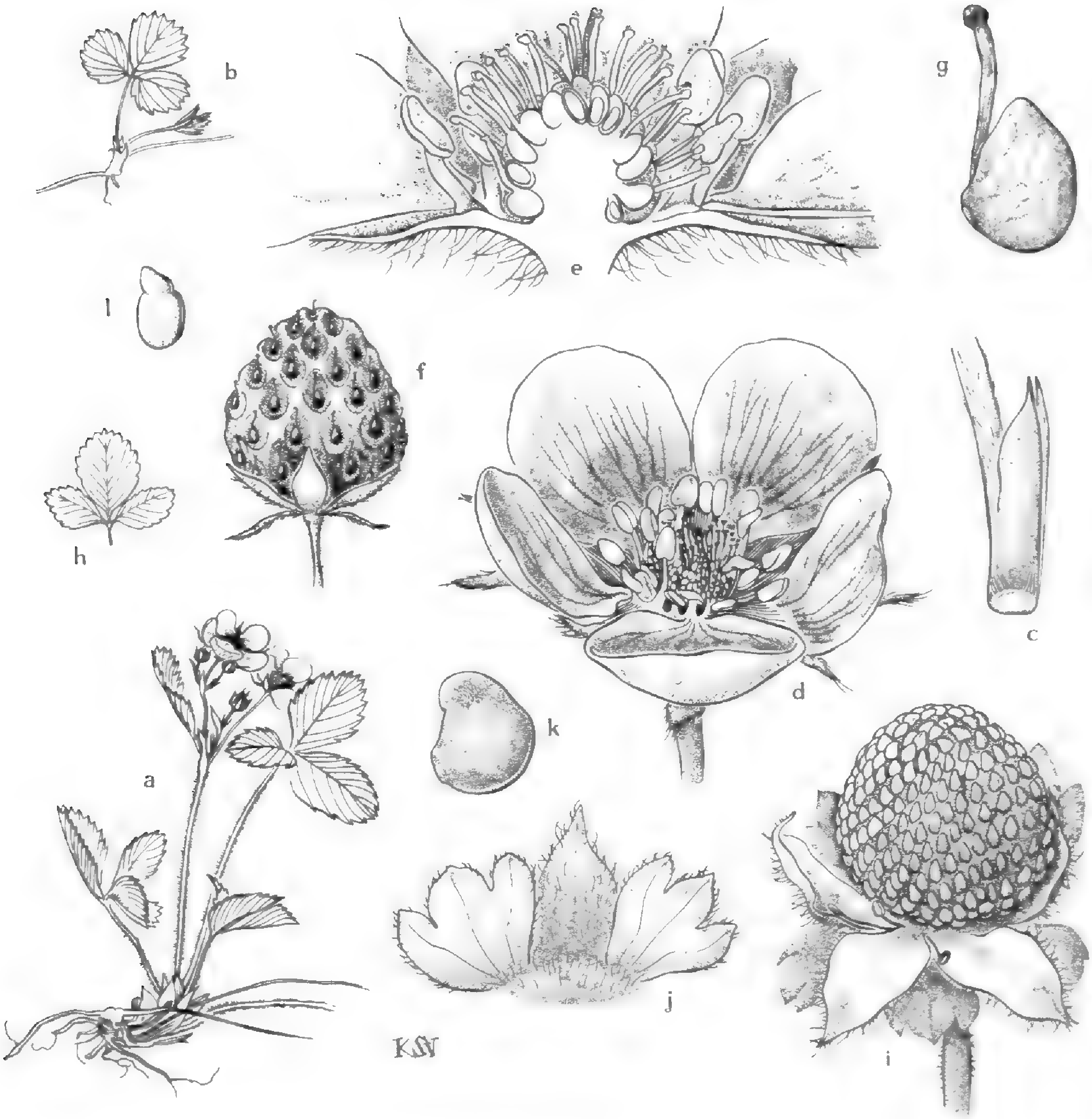


FIGURE 6. **Fragaria** and **Duchesnea.** a–g, *F. virginiana*: a, flowering plant, a stolon (pubescent) to right of crown, × 1/2; b, young plantlet on stolon, × 1/2; c, base of petiole showing adnate stipules, × 3; d, perfect flower, × 3; e, vertical section of flower, petals and stamens attached at edge of nearly flat floral cup, carpels on an elongated receptacle, × 6; f, accessory fruit, achenes in pits on fleshy, enlarged receptacle, × 1; g, side view of achene, style nearly basal, persistent, × 12. h–l, *D. indica*: h, leaf, × 1/2; i, fruit, calyx and epicalyx lobes persistent, styles deciduous, × 2; j, portion of floral cup with 2 trilobed epicalyx lobes and one entire calyx lobe, × 3; k, achene, attachment point of style (deciduous) at notch to upper left, × 12; l, embryo, oriented as in the achene, × 12.

shallow pits, persistent on the enlarged receptacles; embryo nearly filling the achene, spathulate, the radicle inferior, straight. Base chromosome number 7. LECTOTYPE SPECIES: *F. vesca* L.; see P. A. Rydberg, N. Am. Fl. 22: 356. 1908. (Name from *fraga*, the Latin name for the strawberry; the adjectival form was used by Linnaeus in reference to the fruit's fragrance.) — STRAWBERRY.

A natural assemblage of more than a dozen species primarily of the North Temperate Zone, but also indigenous (mostly at higher elevations) to Mexico, Central America, South America from central Chile southward to Patagonia, and Hawaii. Species and cultivars have been introduced into most of the world's temperate regions. Three species (and nine subspecies) occur in North America, two in our area. The species, often difficult to distinguish, can be placed in four groups that largely correspond to chromosomal ploidy level and geographical distribution. There are about nine diploid species ($2n = 14$) (all except *Fragaria vesca* confined to the Old World), with *F. vesca* and *F. viridis* Duchesne distributed throughout most of Europe, three species in Japan, and four species in the Himalayas. There are only two tetraploid species ($2n = 28$), *F. moupinensis* (Franchet) Cardot and *F. orientalis* Losinsk., both of eastern Asia, and only *F. moschata* Duchesne, of Europe, is hexaploid ($2n = 42$). *Fragaria virginiana* Duchesne (North America), *F. chiloënsis* (L.) Duchesne (California to the Aleutians; Chile and Argentina; Hawaii), and *F. iturupensis* Staudt (Iturup, Kuril Islands) are octoploid species with $2n - 56$. The nomenclature used below is based on that of Staudt (1962), in an important and rather widely accepted paper that unfortunately does not give descriptions, synonymy, or complete geographical ranges for the subspecific taxa.

Fragaria vesca L. (inflorescence often racemiform with unequal primary branches; calyx lobes spreading or reflexed after flowering; achenes superficial on the fruit), $2n = 14$, is circumboreal in distribution, occurring throughout Europe, in northern Asia, northern Africa, eastern and western North America, and Mexico. This species evidently is represented with us only by the occurrence of *F. vesca* subsp. *americana* (Porter) Staudt (*F. americana* Porter) in the rich woodlands of Watauga County, North Carolina. This subspecies, which differs from the typical form by its more slender habit, thinner, pale green leaves, and sparser, more or less appressed indumentum, is found in eastern North America from the Gaspé Peninsula southward to upland Virginia and northwestern North Carolina, and along the northern edges of the prairies to British Columbia. The primary range of subsp. *vesca* is Eurasian, but it is supposedly indigenous to Newfoundland and eastern Quebec, and it has been introduced into the northeastern United States. Staudt (1962) recognized two subspecies of *F. vesca* in the western United States, subsp. *bracteata* (Heller) Staudt and subsp. *californica* (Cham. & Schlecht.) Staudt. He suggested that the Mexican and Guatemalan populations (often called F. *mexicana* Schlecht. or *F. Gillmanii* Clinton) may conform to *F. vesca* subsp. *vesca* f. *semperflorens*

(Duchesne) Staudt. It appears that subsp. *americana* is more closely related to subsp. *vesca* than to either subsp. *bracteata* or *californica*.

Fragaria virginiana Duchesne has a very wide range: Newfoundland and the Hudson Bay region, to British Columbia, the Yukon, and Alaska, southward in the west to Montana, Colorado, New Mexico, and California, and in the east to Georgia, Alabama, Texas, and the midwestern states. This variable species, set apart by its low, slender habit, usually symmetrical umbellate cymes, small flowers and fruits, connivent calyx lobes, and achenes that are in pits on the accrescent receptacle, is an octoploid with $2n = 56$. Several subspecies, varieties, and segregate species, based largely on pubescence differences, have been proposed; further study of the variations and how they can be reflected best in a taxonomic scheme is needed. Four subspecies, two of which occur in the southeastern United States, were proposed by Staudt. Subspecies *virginiana* (including *F. australis* Rydb.), with loosely spreading trichomes on the petioles and also often on the peduncles, occurs mostly in open sites from Newfoundland westward to Alberta and southward to Georgia and Texas; it is found only infrequently on the Coastal Plain or in prairies. Plants with pinkish flowers have been distinguished as forma *maliflora* Haynie. Fernald described *F. multicipita* to include populations of the Gaspé Peninsula that have many crowns on much branched rhizomes; Reed (in Darrow, 1966) postulated that these may be virus-infected plants. Subspecies *Grayana* (Vilmorin) Staudt (*F. Grayana* Vilmorin; var. *illinoënsis* (Prince) Gray) is coarser throughout, with denser, widely spreading trichomes on the petioles and peduncles; it ranges from New York to Minnesota, south to Alabama, Louisiana, and Kansas. Subspecies *platypetala* (Rydb.) Staudt and subsp. *glauca* (Watson) Staudt occur in western North America.

The cultivated strawberry, *Fragaria* × *ananassa* Duchesne (*F. grandiflora* Ehrhart), is a hybrid between *F. virginiana* and *F. chiloënsis* that originally arose spontaneously in European gardens in the mid-18th Century; it was first recorded and illustrated by Philip Miller in 1759. The strawberry is grown commercially and in private gardens nearly throughout our area, and cultivars have persisted or escaped from cultivation in some areas. It is possible that part of the variation in *F. virginiana* may be the result of introgression with cultivated or escaped plants of *F.* × *ananassa*. In the coastal areas of Washington and British Columbia, the distributions of *F. virginiana* and *F. chiloënsis* overlap and putative natural hybrid populations occur; Staudt called these plants *F.* × *ananassa* nothomorph *cuneifolia* (Nutt. ex Howell) Staudt. Almost since its discovery, *F.* × *ananassa* has been the subject of intensive breeding and selection programs that have resulted in thousands of cultivars, practically all octoploid. Numerous strains of both parental species from throughout their native ranges have been tested for traits desirable in new cultivars. Recently, other species of *Fragaria* have been hybridized with *F.* × *ananassa* in attempts, for example, to introduce the distinctive flavors and aromas of *F. moschata* and *F. vesca* into cultivated strawberries.

Hypotheses about the relationships and evolution of the species have come from the multitudinous genetical and cytological studies and from recent chemical and intergeneric hybridization analyses. The diploid species are quite different from each other morphologically and are difficult to hybridize, with the exception of the closely related *Fragaria nubicola* and *F. viridis* Duchesne. Hybrids between diploids are usually weak and largely sterile, although meiosis is nearly regular, suggesting that the genomes are mostly homologous with merely cryptic structural or plasmatic differences. The tetraploid species are interfertile, and it has been suggested that *F. orientalis* is an autopolyploid of *F. vesca*. The hexaploid *F. moschata* has perhaps two *F. viridis* or *F. nubicola* genomes and one genome of *F. vesca*. The octoploids *F. virginiana* and *F. chiloënsis* are of complex and probable polyphyletic origins, although they can be hybridized readily. Staudt (1959) believes that the octoploids could not have been derived from the American populations of *F. vesca*, but that they share characters with eastern Asiatic diploid species such as *F. Iinumae* and *F. Daltoniana* J. Gay. Bringhurst and his associates think that *F. chiloënsis* is derived from *F. viridis* and American *F. vesca*, while *F. viridis*, *F. Iinumae*, and European and American *F. vesca* are in the genealogy of *F. virginiana*.

Bringhurst and his associates have studied extensively natural hybrid populations between *Fragaria vesca* and *F. chiloënsis* in coastal California. Numerous novel ploidy groups were observed. These, and the postulated origins of their parental gametes are: pentaploid ($2n = 35$; reduced diploid + reduced octoploid), hexaploid ($2n = 42$; unreduced diploid + reduced octoploid), enneaploid ($2n = 63$; reduced diploid + unreduced octoploid), decaploid ($2n = 70$; unreduced pentaploid + unreduced pentaploid), decaploid (reduced octoploid + unreduced hexaploid hybrid), 12-ploid ($2n = 84$; unreduced octoploid + reduced octoploid), and 14-ploid ($2n = 98$; double-unreduced pentaploid + reduced octoploid). Instances of unreduced and double-unreduced gametes in *Fragaria*, particularly in polyploid hybrids, also have been reported by several other investigators, and it is now thought that such gametes may have played a significant role in the evolution of polyploid *Fragaria* species. Although apomixis has been reported in *Fragaria*, it does not seem to have been a major evolutionary force in the genus.

The flowers of diploid species of *Fragaria* are perfect, except in *F. vesca* subsp. *bracteata*, while perfect and imperfect flowers occur in polyploid species; *F. chiloënsis* subsp. *sandwicensis* and *F. chiloënsis* f. *chiloënsis* among the polyploids have perfect flowers only. The expression of staminate or carpellate flowers is evidently the result of a single gene with multiple alleles. The allele that prevents the formation of functional stamens (abbreviated by Staudt as Su^F) is dominant over the allele that blocks the development of normal carpels (Su^M), and both these alleles are dominant over the factor for the production of perfect flowers (Su^+). In the hexaploid *F. moschata*, one Su^F takes precedence over five Su^M or Su^+ factors and one Su^M is dominant over five Su^+ factors. While such polymorphism assures a high degree of cross-fertilization in polyploid species, some outcrossing is obligatory in perfect-flowered plants, since the stigmas toward the center of the receptacle are receptive before the anthers of that flower dehisce.

At least four different intergeneric hybrids have resulted from crosses between *Fragaria* (carpellate) and *Potentilla* (staminate). A pentaploid hybrid arose from the cross *F.* × *ananassa* ($2n = 56$) × *P. fruticosa* var. *grandiflora* ($2n = 14$); a 7-ploid hybrid from *F.* × *ananassa* × *P. palustris* ($2n = 42$); a hexaploid hybrid from [*F. vesca* × *F.* × *ananassa*, $2n = 70$] × *P. fruticosa* var. *grandiflora*; and a triploid hybrid from autotetraploid *F. vesca* ($2n = 28$) × *P. fruticosa* var. *grandiflora*. Pollen of *P. anserina*, *P. anglica*, *P. erecta*, *P, reptans*, *P. rupestris*, and *P. nepalensis* will stimulate the production of normal fruit with large achenes on plants of *F. vesca*. A hybrid has been reported between *F. vesca* (carpellate) and *Duchesnea indica* (staminate). Knobloch (see family references) lists three hybrids between *Rubus* cultivars and an unnamed species of *Fragaria*.

Generic lines are difficult to draw in tribe Fragarieae, and arguments can be presented for the recognition of only one genus or for as many as 17. *Potentilla* is treated here in a broad sense to include *Argentina* Hill, *Comarum* L., *Pentaphylloides* Duhamel, *Dasiphora* Raf., and *Sibbaldiopsis* Rydb.; *Fragaria* L. and *Duchesnea* J. E. Sm. are maintained. Other members of this tribe are *Horkelia* Cham. & Schlecht. (17 spp. mostly of California), *Ivesia* Torrey & Gray (22 spp., western North America), *Purpusia* Brandegee (2 spp. of Nevada, Arizona, California, and Baja California), *Stellariopsis santalinoides* (Gray) Rydb. (California), *Chamaerhodos* Bunge (5 spp. of eastern Asia, especially Siberia, and northwestern North America), and *Sibbaldia* L. (a complex of 6 to 20 species of boreal, arctic, and alpine regions of the Northern Hemisphere).

REFERENCES:

A large number of references, many containing biologically important information, have had to be omitted because of limitations of space. In the following list those works that have extensive bibliographies are noted in the annotations. Consult *Horticultural Abstracts* for current horticultural references. Under subfamily references see BESSEY, BRESINSKY, RYDBERG, and SCHAEPPI & STEINDL; under family references see BATE-SMITH, CHUTE, FREE, HEGI, HULTÉN (1958), LÖVE & LÖVE, RICKETT, ROBERTSON, ROEMER & RUDORF, and ROSS-CRAIG.

AALDERS, L. E. Production of maternal-type plants through crosses to apomictic species. Nature **204:** 101, 102. 1964. [Diploid and octoploid *Fragaria* cultivars can set seed apogamously.]

ANDERSON, W. The strawberry, a world bibliography, 1920–1966. 731 pp. Metuchen, New Jersey. 1969. [An invaluable key to the literature on strawberries.]

ARNEY, S. E. Studies of growth and development in the genus *Fragaria*. I. Factors affecting the rate of leaf production in 'Royal Sovereign' strawberry. Jour. Hort. Sci. **28:** 73–84. 1953; * II. The initiation, growth, and emergence of leaf primordia in *Fragaria*. Ann. Bot. II. **17:** 477–492. 1953; III. The growth of leaves and shoot. *Ibid.* **18:** 349–365. 1954; IV. Winter growth. *Ibid.* **19**: 265–276. 1955; V. Spring growth. *Ibid.* 277–287; VI. The effect of photoperiod and temperature in leaf size. Jour. Exper. Bot. **7**: 65–79. 1956; VII. The effect of defoliation on leaf growth. Phyton Buenos Aires **5**: 93–105. 1955; VIII. The effect of defoliation on leaf initiation and early growth of the leaf initials. *Ibid.* **6**: 109–120. 1956; IX. An investigation of floral initiation under natural conditions. *Ibid.* **7**: 89–102. 1956.

Asker, S. An intergeneric *Fragaria* × *Potentilla* hybrid. Hereditas **64**: 135–139. 1970. [*F. moschata* ♀ × *P. fruticosa* ♂.]

———. Some viewpoints on *Fragaria* × *Potentilla* intergeneric hybridization. *Ibid.* **67**: 181–190. 1971.

Berezenko, N. P. On studying microsporogenesis, male gametophyte and embryogenesis in *Fragaria grandiflora* Ehrh. (In Ukrainian; Russian and English summaries.) Ukrain. Bot. Zhur. **26**(4): 82–89. 1969.

Beridze, R. K. Phylogenetic relations and evolution of the genus *Fragaria* in the light of the new experimental data. X Int. Bot. Congr. Abstr. 332, 333. 1964.

Bringhurst, R. S., & T. S. Gill. Unreduced and double-unreduced gametes in the evolution of polyploid *Fragaria* species. XI Int. Bot. Congr. Abstr. 22. 1969.

——— & ———. Origin of *Fragaria* polyploids. II. Unreduced and double-unreduced gametes. Am. Jour. Bot. **57**: 969–976. 1970. [For Part I, see Senanayake & Bringhurst.]

——— & D. A. Khan. Natural pentaploid *Fragaria chiloënsis* — *F. vesca* hybrids in coastal California and their significance in polyploid *Fragaria* evolution. *Ibid.* **50**: 658–661. 1963.

———, ——— & V. Voth. Biochemical relationships among *Fragaria* species. (Abstr.) *Ibid.* **51**: 688. 1964. [Phylogenetic relationships previously determined by cytology (see Senanayake & Bringhurst) confirmed.]

——— & Y. D. A. Senanayake. The evolutionary significance of natural *Fragaria chiloënsis* × *F. vesca* hybrids resulting from unreduced gametes. *Ibid.* **53**: 1000–1006. 1966.

———, ——— & D. A. Khan. *Fragaria* polyploids, chromatographic analysis. (Abstr.) *Ibid.* **53**: 638. 1966. [Relationships of 9 species.]

Brown, T., & P. F. Wareing. The genetical control of the everbearing habit and three other characters in varieties of *Fragaria vesca*. Euphytica **14**: 97–112. 1965. [Also runner production and fruit color.]

Bumagina, S. I., & E. Mesarosh. The evaluation of the results of interspecific hybridization in strawberry species *Fragaria vesca* L., *Fragaria viridis* Duch., *Fragaria moschata* Duch. based on the seed formation set in the hybrids and on the viability of the hybrid seeds. (In Russian; English summary.) Genetika Moscow **5**(5): 32–38. 1969.

Comstock, R. E., T. Kelleher, & E. B. Morrow. Genetic variation in an asexual species, the garden strawberry. Genetics **43**: 634–646. 1958.

Dahlgren, K. V. O. Die Lösung des *micrantha*-Problems bei *Fragaria vesca*. (English summary.) Bot. Not. **115**: 288–292. 1962. [The *micrantha* characters are the result of a periclinal chimera.]

Darrow, G. M. The strawberry: history, breeding and physiology. xiv + 447 pp. *frontisp. 52 col. pls.* New York. 1966. [A useful, up-to-date book that covers many topics; extensive references.]

Dogadkina, N. A. A contribution to the question of genome relations in some species of *Fragaria*. Compt. Rend. Acad. Sci. URSS II. **30**: 166–168. 1941. [*F. vesca* × *F.* × *ananassa; F. orientalis* × *F. moschata.*]

Duchesne, A. N. Histoire naturelle des fraisiers, xii + 324 pp. Chart + 118 pp. (Remarques particulières.) Paris. 1766. [A remarkable work that still is the basis for modern studies; see Guédès.]

———. Fraisier, *Fragaria*. *In*: J. B. Lamarck, Encycl. Méthod. Bot. **2**: 527–540. 1788.

Ellis, J. R. The allopolyploid hybrid between *Fragaria vesca* and *F. moschata*. (Abstr.) Proc. XI Int. Congr. Genet. **1**: 209, 210. 1963.

———. Cytogenetic studies in the genera *Fragaria* and *Potentilla*. Ph.D. Thesis. Univ. Manchester. 263 pp. 1958.*

———. *Fragaria-Potentilla* intergeneric hybridization and evolution in *Fragaria*. Proc. Linn. Soc. London **173**: 99–106. *pls. 1, 2.* 1962.

Evans, W. D., & J. K. Jones. Incompatibility in *Fragaria*. Canad. Jour. Genet. Cytol. **9**: 831–836. 1967. [*F. vesca, F. viridis, F. nubicola, F. nilgerrensis.*]

Fadeeva, T. S. Problems of comparative plant genetics. 1. Principles of the genome analysis on the example of the genus *Fragaria*. Genetika Moscow **1966**(1): 12–28. 1966; 2. Genetics of characters and mutations in the strawberry. *Ibid.* **1966**(7): 100–117. 1966; 3. The study of intraspecific variability of the natural species forms in *Fragaria vesca* L. Vestn. Leningrad. Univ. **1966**(21): 126–135. 1966; 4. The potential of genetic variability of species as exemplified by the genus *Fragaria*. Genetika Moscow **1966**(12): 36–45. 1966. [All articles in Russian with English summaries.]

——— & A. I. Dyatlova. Dynamics of germination of achenes of the reciprocal hybrids of strawberry. (In Russian.) Bot. Zhur. **47**: 1190–1194. 1962.

——— & V. N. Migalovskaya. Cytogenetical study of hybrids between three species in the genus *Fragaria* L. (In Russian; English summary.) Vestn. Leningrad. Univ. **1966**(2): 119–131. 1966. [*F. vesca, F. viridis, F. moschata.*]

Federova, N. J. Crossability and phylogenetic relations in the main European species of *Fragaria*. Compt. Rend. Acad. Sci. URSS II. **52**: 545–547. 1946.

Gupta, B. K. Chromosome survey in strawberries of Kashmir. Cytologia **35**: 107–110. 1970.

Guédès, M. Notules de bibliographie botanique V — VIII. Jour. Soc. Bibliogr. Nat. Hist. **6**: 174–180. 1972. [VII. Un exemplaire de l'essai sur l'histoire naturelle des fraisiers de Duchesne annoté par l'auteur, 177.]

Guttridge, C. G. Evidence for a flower inhibitor and vegetative growth promoter in the strawberry. Ann. Bot. II. **23**: 351–360. 1959. [See also *ibid.* 612–621.]

Haskell, G., & H. Williams. Biometrical variation in flowers of a polyploid series of strawberries. Jour. Genet. **52**: 620–630. 1954. [Diploid, hexaploid, and octoploid spp.; cultivars.]

Hedrick, U. P., *ed.* Sturtevant's notes on edible plants. vii + 686 pp. *frontisp.* Vol. 2(2), 27th Annual Rep. N.Y. State Agr. Exper. Sta. Albany. 1919. [*Fragaria*, 273–282; includes discussion on the strawberry in classical and pre-Linnaean literature; also see Sturtevant, Trans. Mass. Hort. Soc. **1888**: 191–204. 1888.]

Hylander, N. Linnaeus, Duchesne and the strawberries. Sv. Linné-Sällsk. Årsskr. **28**: 17–40. 1945. [Reviews correspondence between Linnaeus and Duchesne; in Swedish with English summary on pp. 95, 96.]

ISLAM, A. S. Possible role of unreduced gametes in the origin of polyploid *Fragaria*. Biologia Lahore **6**: 189–192. 1960.

———. Reinvestigation into the reported instances of paternal and maternal inheritance in *Fragaria*. *Ibid*. 241–251. [Includes mention of a haploid *F. vesca* derived by parthenogenesis from a cross between a diploid *F. vesca* and an octoploid.]

JAHN, O. L., & M. N. DANA. Crown and inflorescence development in the strawberry, *Fragaria ananassa*. Am. Jour. Bot. **57**: 606–612. 1970.

——— & ———. Effects of cultivar and plant age on vegetative growth of the strawberry, *Fragaria ananassa*. *Ibid*. 993–999.

JONES, J. K. Cytogenetical studies in genera *Fragaria* and *Potentilla*. Ph.D. Thesis, Univ. Manchester. 1955.*

KALKMAN, C. *Potentilla*, *Duchesnea*, and *Fragaria* in Malesia (Rosaceae). Blumea **16**: 325–354. 1968. [Notes on generic delimitation.]

KAHN, D. A. Cytogenetics and inheritance of certain morphological and biochemical characters in *Fragaria* hybrids involving species of different ploidy levels. 151 pp. Ph.D. Thesis, Univ. California, Davis. 1964.* [Diss. Abstr. **26**(4): 1873B. 1965.]

KLIMSTRA, W. D., & F. NEWSOME. Some observations on the food coactions of the common box turtle, *Terrapene c. carolinae*. Ecology **41**: 637–647. 1960. [*Fragaria* fruits eaten.]

LEBEGUE, A. Recherches sur la polyembryonie chez les Rosacées (g. *Fragaria* et *Alchemilla*). Bull. Soc. Bot. France **99**: 273–275. 1952. [*F. vesca*.]

LOSINA-LOSINSKAJA, A. S. Révision critique du genre *Fragaria*. (In Russian; Latin diagnoses; French résumé.) Izv. Glavn. Bot. Sada SSSR **25**: 47–88. 1926.

MCFADDEN, W. H., R. TERANISHI, J. CORSE, D. R. BLACK, & T. R. MON. Volatives from strawberries. II. Combined mass spectrometry and gas chromatography on complex mixtures. Jour. Chromatography **18**: 10–19. 1965. [Over 150 components found, most of them identified.]

NÜRNBERG-KRÜGER, U. Genetische Untersuchungen an diploiden *Fragaria*-Arten. I. Die Kreuzung zwischen *Fr. vesca* und *Fr. nilgerrensis*, ihre Auswirkung auf die Morphologie der Pflanzen und die Ausbildung des Geschlechts. Zeitschr. Vererbungslehre **89**: 747–773. 1958.

SATTLER, R. Organogenesis of flowers. xxvi + 207 pp. Toronto. 1973. [*F. vesca*, 72–77; excellent photographs of floral development.]

SENANAYAKE, Y. D. A. Morphological, cytological and biochemical studies on *Fragaria* interspecific hybrids and on *Fragaria-Potentilla* intergeneric hybrids. 179 pp. Ph.D. Thesis, Univ. California Davis. 1966.* [Diss. Abstr. **27**: 698B. 1966.]

———& R. S. BRINGHURST. Origin of *Fragaria* polyploids. I. Cytological analysis. Am. Jour. Bot. **54**: 221–228. 1967.

SMEETS, L. Runner formation on strawberry plants in autumn and winter. I. Euphytica **4**: 53–59. 1955; II. Influence of the light intensity on the photoperiodic behavior. *Ibid*. 240–244.

———. Influence of the temperature on runner production in five strawberry varieties. *Ibid*. **5**: 13–17. 1956.

SONDHEIMER, E., & C. B. KARASH. The major anthocyanin pigments of the wild strawberry (*Fragaria* vesca). Nature **178**: 648, 649. 1956.

SOUÈGES, R. Observations embryologiques sur quelques *Fragaria* de culture. Bull. Soc. Bot. France **82**: 458–461. 1935.

Staudt, G. Über Fragen der phylogenetischen Entwicklung einiger Arten der Gattung *Fragaria.* Züchter **21:** 222–232. 1951. [Includes distribution maps of the spp.]

———. Cytogenetische Untersuchungen an *Fragaria orientalis* Los. und ihre Bedeutung für Artbildung und Geschlechts-differenzierung in der Gattung *Fragaria* L. Zeitschr. Indukt. Abst. Vererbungslehre **84:** 361–416. 1952.

———. Die geographische Verbreitung der Gattung *Fragaria* und die Bedeutung für die Phylogenie der Gattung. Ber. Deutsch. Bot. Ges. **66:** 236–238. 1953.

———. Die Vererbung des Geschlechts beider tetraploiden, diözischen *Fragaria orientalis* Los. *Ibid.* **67:** 384–387. 1954.

———. Cytotaxonomy and phylogenetic relationships in the genus *Fragaria.* (Abstr.) Proc. IX Int. Bot. Congr. **2:** 377. 1959.

———. Die Entstehung und Geschichte der grossfrüchtigen Gartenerdbeeren *Fragaria* × *ananassa* Duch. Züchter **31:** 212–218. 1961.

———. Taxonomic studies in the genus *Fragaria*; typification of *Fragaria* species known at the time of Linnaeus. Canad. Jour. Bot. **40:** 869–886. *pls. 1, 2.* 1962. [The best modern survey of the genus, although it is difficult to ascertain Staudt's delimitation of New World subspecific taxa since descriptions and synonyms are not given.]

———. Die Genetik und Evolution der Heterözie in der Gattung *Fragaria.* I. Untersuchungen an *Fragaria orientalis.* Zeitschr. Pflanzenz. **58:** 245–277. 1967; II. Die Artkreuzungen *F. vesca* × *F. orientalis* und *F. viridis* × *F. orientalis. Ibid.* 309–322; III. Untersuchungen an hexa- und oktoploiden Arten. *Ibid.* **59:** 83–102. 1968. [All with English summaries.]

———. Tests for apomixis in strawberries. Hort. Res. Edinburgh **10**(2): 148–150. 1970.*

———. *Fragaria iturupensis*, eine neue Erdbeerart aus Ostasien. Willdenowia **7:** 101–104. 1973. [The only octoploid known from outside the New World.]

Thompson, P. A. The development of embryo, endosperm, and nucellus tissues in relation to receptacle growth in the strawberry. Ann. Bot. II. **27:** 589–605. *pl. 1.* 1963.

Watkins, R., & L. P. S. Spangelo. Components of genetic variance in the cultivated strawberry. Genetics **59:** 93–103. 1968.

———, ——— & A. T. Bolton. Genetic variance components in cultivated strawberry. Canad. Jour. Genet. Cytol. **12:** 52–59. 1970.

Westergaard, M. The mechanism of sex determination in dioecious flowering plants. Adv. Genet. **9:** 217–281. 1958. [*Fragaria*, 232–235.]

Winter, M., & B. Willhalm. Sur l'arôme des fraises fraîches. Analyse des composés carbonylés, esters et alcools volatils. Helvet. Chim. Acta **47:** 1215–1227. 1964.

10. **Duchesnea** J. E. Smith, Trans. Linn. Soc. London 10: 372. 1811.

Herbaceous perennials with rosettes of leaves on short, vertical rootstocks and long, prostrate, leafy, sympodially branching stems; adventitious plants produced frequently at nodes along the prostrate stems. Leaves radical and cauline, trifoliolate (infrequently simple), long petiolate; leaflets nearly equal in size, serrate at least in the upper parts, short petiolulate; stipules of the rosette leaves adnate for half their length to the petiole, those of the cauline leaves ± free. Inflorescences 1-flowered, arising from the rosettes and also axillary along the prostrate stems; evidently ebracteate. Flowers perfect, borne on long pedicels. Calyx lobes 5, equaling or exceeding the petals, valvate in aestivation, entire, narrowly triangular, alternate with the 5 obovate, apically 3–5-toothed epicalyx lobes, both epicalyx and calyx lobes enlarging with the fruit and becoming reflexed; floral cup short, saucer-shaped, free of the carpels, a nectar ring scarcely evident. Petals 5, yellow, spreading, deciduous, narrowly obovate with ± entire margins, inserted at edge of floral cup, imbricate. Androecium of 15–25 stamens in multiples of 5, some persistent; filaments of 3 lengths, free, perigynous at edge of floral cup; anthers yellow. Gynoecium of many free carpels on an elevated, ± hemispheric receptacle that enlarges in fruit; styles inserted adaxially above the middle of the carpels, promptly caducous; stigmas terminal, discoid; each carpel with one pendulous and anatropous ovule, the micropyle superior. Accrescent receptacle red, much like that of *Fragaria*, subcarnose, neither aromatic nor flavorful, subtended by the persistent calyx and epicalyx, the entire fruits sometimes falling from the plants. Achenes red, numerous, minute, superficial, with an adaxial appendage, falling from the enlarged receptacle; embryo filling the achene, the radicle superior, slightly bent. Base chromosome number 7. (Not *Duchnesia* Cass., 1817). TYPE SPECIES: *D. fragiformis* J. E. Sm., nom. illegit. = *D. indica* (Andrews) Focke. (In commemoration of Antoine Nicolas Duchesne, 1747–1827, author of an early, quite remarkable monograph on *Fragaria*.) — INDIAN STRAWBERRY.

Probably two species of the Old World, with *Duchesnea indica* (*Fragaria indica* Andrews; *Potentilla indica* (Andrews) Wolf), $2n = 84$, indigenous from Afghanistan and India to China, Laos, Vietnam, Korea, Japan, Taiwan, and the Philippine Islands (introduced into Malesia, Europe, and the New World), and *D. chrysantha* (Zoll. & Moritzi) Miquel, $2n = 14$, 28?, ranging from Japan to southern China, India, Taiwan, the Philippines, Sumatra, and Java.

Duchesnea indica is naturalized, mostly in open areas such as waste ground, lawns, roadsides, and pastures, in the eastern United States from northern Florida westward to eastern Texas and northward to southern Connecticut and New York, Ohio, Indiana, Illinois, Iowa, Arkansas, and Oklahoma; it is also found occasionally on the Pacific Coast, primarily east of the Cascade Mountains. This species is cultivated as a ground cover or basket plant or as a low climber.

Plants of *Duchesnea indica* and *D. chrysantha* have a great resemblance, particularly when in fruit, to *Fragaria* species and are sometimes included within that genus. However, this similarity is probably the result of parallel evolution. *Duchesnea* is perhaps more closely related to *Potentilla*, and both Wolf (cf. *Potentilla*) and Kalkman alluded to affinities with *P. reptans*. Artificial intergeneric hybrids are *D. indica* × *P. reptans* and *F. vesca* × *D. indica*. The F_1 hybrids of the first cross are quite vigorous and produce numerous flowers but no fruit, while those of the second cross are weak and do not flower.

The achenes of *Duchesnea indica* sometimes have an adaxial appendage similar to the elaiosomes of *Potentilla* sect. FRAGARIASTRUM; the function of such appendages in *Duchesnea* is not known, but in *Potentilla* sect. FRAGARIASTRUM they evidently aid in the distribution of the achenes by ants. It has been reported that birds may eat the fruits of *D. indica*.

REFERENCES:

Under subfamily references see RYDBERG; under family references see BATE-SMITH, BUNTING, CHUTE, RICKETT.

ANDREWS, H. *Fragaria indica*, Indian strawberry. Bot. Repos. **7**: *pl. 479*. 1807.

HARA, H., & S. KUROSAWA. On the *Duchesnea indica* group. Jour. Jap. Bot. **34**: 161–166. 1959. [The only modern world-wide taxonomic revision.]

HASKELL, G., & H. WILLIAMS. Biometrical variation in flowers of a polyploid series of strawberries. Jour. Genet. **52**: 620–630. 1954. [Includes *D. indica*.]

HSU, C. C. Preliminary chromosome studies on the vascular plants of Taiwan (II). Taiwania **14**: 11–27. 1968. [*D. chrysantha*, $2n = 28$.]

KALKMAN, C. *Potentilla*, *Duchesnea*, and *Fragaria* in Malesia (Rosaceae). Blumea **16**: 325–354. 1968. [Notes on generic delimitation; *D. indica* placed in *Potentilla*.]

KER-GAWLER, J. B. *Fragaria indica*. Yellow-flowered strawberry. Bot. Regist. **1**: *pl. 61*. 1815.

MANGELSDORF, A. J., & E. M. EAST. Studies on the genetics of *Fragaria*. Genetics **12**: 307–339. 1927. [Includes mention of a hybrid between *D. indica* and *F. vesca*.]

WIGHT, R. G. *Fragaria indica*. Ic. Pl. Indiae Orient. **3**: *pl. 989*. 1845.

11. **Potentilla** Linnaeus, Sp. Pl. 1: 495. 1753; Gen. Pl. ed. 5. 219. 1754.

Perennial or infrequently annual or biennial herbs, rarely shrubs, often with long rhizomes covered with persistent leaf bases, the plants rosulate, caespitose, or with creeping stems rooting at nodes, sometimes with true stolons. Leaves basal and/or cauline, digitate, trifoliolate, or imparipinnate, the lower leaves long petiolate; leaflets toothed to dissected, sessile or shortly petiolulate; stipules of the basal leaves adnate for most of their length to the petioles and forming membranaceous wings, those of the cauline leaves mostly free, entire, linear or deeply parted. Inflorescences lax cymes or single flowered, arising from the crowns and/or creeping stems, long pedunculate; bracts often foliaceous, deeply divided. Flowers pale to bright yellow or white [or reddish-purple], usually perfect. Calyx with an epicalyx, the epicalyx lobes 5 (4), alternate with and usually equaling, but narrower than, the 5 (4) calyx lobes, both spreading at anthesis, valvate in aestivation; floral cup saucer-shaped or hemispheric, free of the carpels, a nectar ring often prominent. Petals 5 (4), spreading, deciduous, imbricate, orbicular, obovate, or cuneate, the apices often emarginate, the bases rounded, seldom clawed, inserted at the edge of the floral cup. Androecium of 10–30, usually 20, stamens, infrequently fewer or more, sometimes in fascicles; filaments tapering-filiform, free to the base, perigynous at the inside margin of the nectar ring; anthers yellow, basifixed,

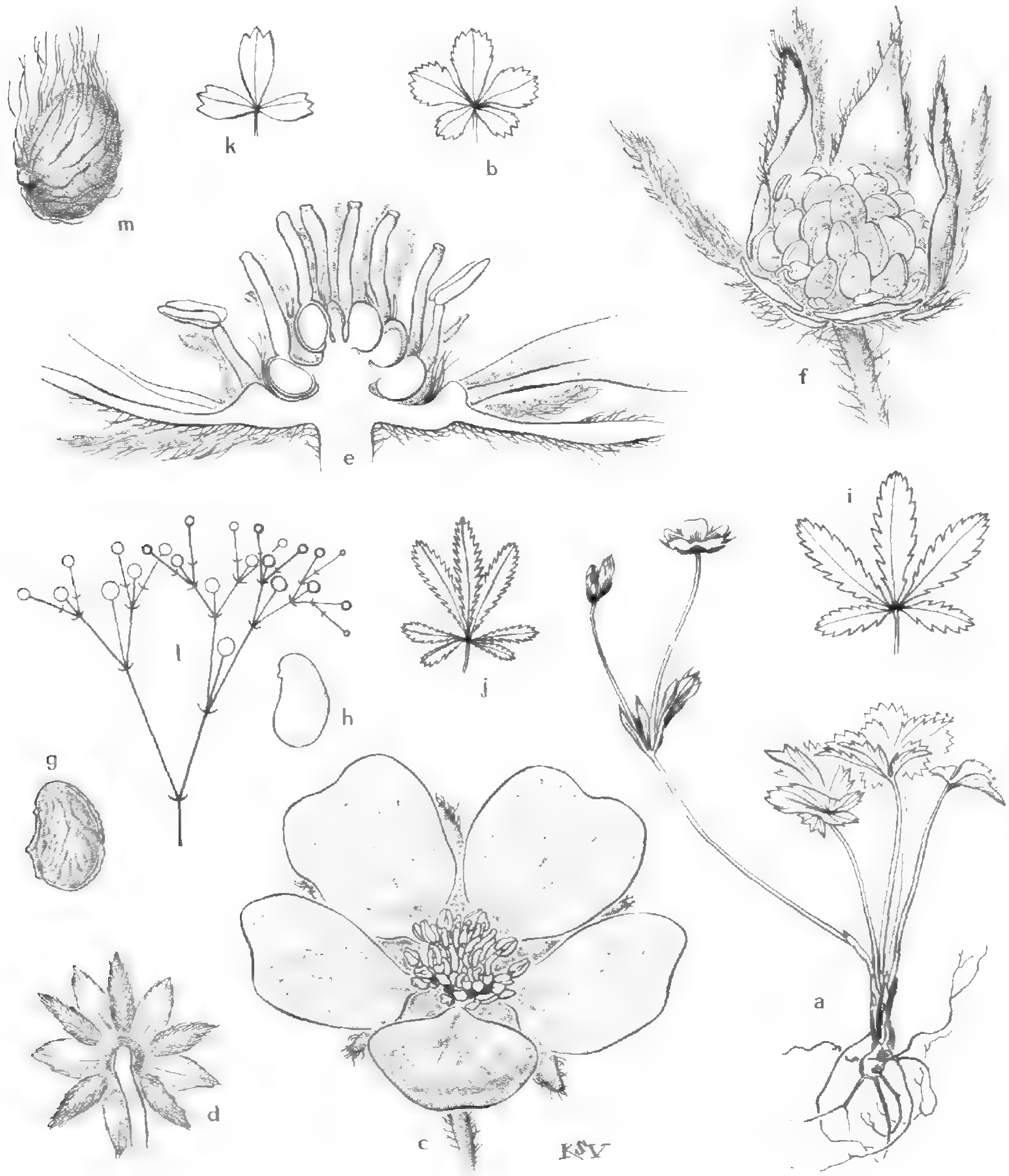


FIGURE 7. **Potentilla.** a–h, *P. canadensis*: a, young plant with first flowers of season, × 1; b, basal leaf, × 1/2; c, flower, × 5; d, lower side of flower showing epicalyx and calyx lobes, petals not shown, × 3; e, vertical section of flower, petals inserted at the edge of floral cup, stamens inserted at inside margin of nectar ring, carpels on a hemispherical receptacle, × 12; f, fruit, 2 epicalyx and 2 calyx lobes removed, × 3; g, achene, × 12; h, seed, × 12. i, *P. simplex*: leaf, × 1/2. j, *P. recta*: leaf, × 1/4. k–m, *P. tridentata*: k, leaf, × 1/2; l, diagrammatic sketch of inflorescence, × 1/2; m, achene, × 12.

didymous. Gynoecium of many [rarely only 5 or 10] simple, free carpels on a hemispherical or conical receptacle; style terminal or lateral to nearly basal on the adaxial side of the carpel, basally articulated, deciduous, filiform or short and basally thickened; stigma terminal, discoid; each carpel with a single, anatropous and pendulous, ascending, or descending ovule, the micropyle adaxial or abaxial. Accessory fruits dry, surrounded or inclosed by the persistent, often accrescent calyx, the receptacle seldom enlarging. Achenes smooth or variously textured, pubescent or not, sometimes appendaged, at maturity detaching from the receptacle; embryo filling the achene, the radicle inferior or superior. Base chromosome number 7. (Including *Argentina* Hill, *Comarum* L., *Dasiphora* Raf., and *Drymocallis* Fourreau ex Rydb.) LECTOTYPE SPECIES: *P. reptans* L., see P. A. Rydberg, N. Am. Fl. 27: 293. 1908. (Name the diminutive of Latin *potens*, powerful; originally applied to *P. anserina* for its reputed medicinal powers.) — CINQUEFOIL, FIVE-FINGER.

A taxonomically complex genus of perhaps 300 species of the North Temperate Zone. The frequent occurrence of polyploidy, hybridization, apomixis, and ecotype formation makes the number of biological species impossible to determine at present. The genus is most diverse in northern Eurasia, and many species are of arctic or montane regions. Not many species are common to both the Eastern and Western hemispheres, and there are very few indigenous species south of the equator. In North America, the genus is particularly well developed in the western Cordillera. Eleven species (four introduced from Europe) representing three infrageneric categories occur in our area.

The classification of the genus is based largely on the treatments of the North American species by Rydberg (1898, 1908), who divided *Potentilla*, sensu lato, into several segregate genera (with his restricted *Potentilla* including 176 species in 31 groups of undesignated rank), and the worldwide revision of Wolf (1908) who assigned the 305 recognized species to 2 sections, 6 subsections, and 31 greges. (Citations of infrageneric categories need to be checked carefully, since many names are not validly published, several nonhomologous systems of classification have been used, and many ranks are incorrectly given.) The numerous biosystematic investigations since 1908 show clearly that these basic classifications need extensive reconstruction before true intrageneric relationships can be reflected.

Subgenus POTENTILLA is represented in our area by nine species in two "groups." *Potentilla simplex* Michx. (*P. canadensis* auct., non L.; *P. caroliniana* Poiret) and *P. canadensis* L. (*P. pumila* Poiret; *P. caroliniana* auct., non Poiret) belong to the "Tomentillae." Both of these native species are perennial herbs with arching, nodally rooting stems that arise from basal rosettes, digitate leaves, solitary flowers, glabrous carpels (although the receptacle may be pubescent), and obliquely terminal, slender styles. Their chromosome numbers are unknown. In *P. simplex*, the rhizome is elongated and irregularly enlarged, the cauline leaves are well expanded when the flowers in their axils are at anthesis, the leaflets of mature leaves are usually less than half as wide as long and toothed nearly to the bases, and the first flower of the season is usually produced in the axil of the second fully developed cauline leaf. This species occurs in dry moist pastures, fields, thickets, open woodlands, and lawns from Newfoundland, Nova Scotia, and southern Ontario to Minnesota southward to Georgia, Louisiana, Oklahoma, and Texas. The plants characteristically have spreading-strigose stems, petioles, and peduncles. Nearly glabrous individuals have been separated as var. *calvescens* Fern. (from the northern limits of the species to South Carolina, Illinois, Missouri, and Oklahoma), while plants with the leaves silvery-sericeous beneath may be called var. *argyrisma* Fern. (Pennsylvania and Indiana to Tennessee, Illinois, Missouri, Kansas, and Arkansas). *Potentilla canadensis* differs in that the rhizome is shorter and thicker than in *P. simplex*, the cauline leaves are only partly expanded at anthesis, the leaflets of mature leaves are usually more than half as wide as long and toothed only in the upper half, and the first flower of the season is usually produced in the axil of the first fully developed cauline leaf. This species ranges from western Nova Scotia and southern Maine to southwestern Ontario and northern Ohio southward to Georgia, Alabama, and southeastern Missouri and is found mostly in dry habitats such as rocky open woods, borders, pastures, fields, and lawns. Two varieties are sometimes recognized: var. *canadensis* with the petioles, stems, peduncles, lower leaf surfaces, and calyces silky-pilose with appressed or loosely ascending, soft trichomes (from the northern limits of the species to Long Island, South Carolina, and Ohio), and var. *villosissima* Fern. with long villous, loosely spreading to reflexed indumentum (Maryland and Ohio to the southern limits of the species); Steyermark notes that the latter variety occurs on acidic soils in Missouri.

Species of the "Supinae" group (including the "Rivales," "Argenteae," and "Rectae" of Rydberg and Wolf) are annual to perennial herbs with cymose, many-flowered, leafy inflorescences terminating mostly unbranched stems that arise from the rosettes; pale to light yellow flowers; glabrous carpels; and subterminal, basally thickened styles. This group is primarily of western North America and Europe; two indigenous, one possibly circumpolar, and four introduced species occur with us. The European *Potentilla argentea* is readily recognized by the digitate leaves with narrow, deeply toothed, revolute leaflets that are densely white-tomentose beneath. Plants are usually diploid and commonly reproduce apogamously. In North America it is naturalized from Newfoundland to Washington southward to North Carolina, Tennessee, Ohio, Indiana, and Illinois. *Potentilla recta* L. (including *P. sulphurea* Lam.), erect, hirsute perennial herbs with nearly leafless cymes standing above the principal foliage; characteristic digitate leaves with 5 to 7 oblanceolate, deltoid-toothed leaflets; petals that much exceed the calyx lobes; and 30 stamens, is naturalized from Europe in grassy or ruderal areas from Newfoundland, Quebec, Ontario, and Minnesota to Georgia, Alabama, and Texas, as well as in Washington and Montana. This species shows much less variation in North America than in Europe. The only species of the "Supinae' in our area with pinnate leaves and a large, wedge-shaped appendage on the adaxial side of the achene is *P. paradoxa* Nuttall ex Torrey & Gray, which is most abundant in the Mississippi River valley, but ranges from Ontario to British Columbia southward to Pennsylvania, Ohio, Illinois, Missouri, Kansas, Louisiana, Texas, New Mexico, and northern Mexico; it evidently occurs also in eastern Asia. Allied species are *P. Nicolletii* (S. Watson) E. Sheldon of the midwestern United States (often included within *P. paradoxa*) and *P. supina* L., of Europe.

Potentilla pentandra Engelm. is a variable species with digitately quinate or ternate basal leaves (the lower leaflets deeply divided), 5 stamens, and smooth achenes. It is a plant mostly of sandy bottomlands and prairies from Minnesota to Alberta, southward to Arkansas, Kansas, and Oklahoma. The closely related *P. millegrana* Engelm. differs in the ternate leaves, petals much shorter than the calyx lobes, and 10 or 15 stamens. Not yet reported from our area, this species could occur in Arkansas, since its known range is from Manitoba and Washington to Illinois, southern Missouri, Kansas, Oklahoma, New Mexico, and California. Both *P. pentandra* and *P. millegrana* are frequently merged with *P. rivalis* Nutt. ex Torrey & Gray either at the varietal level or without taxonomic recognition; these taxa may represent an apomictic complex.

Potentilla norvegica L. (*P. monspeliensis* L.), $2n = 70$ (42, 56), is widespread in the Northern Hemisphere, occurring in North America from Greenland and Labrador to Alaska, southward to Georgia, Alabama, California, and northern Mexico; it is uncertain whether this species is indigenous to the New World. The lower leaves are digitate, with three elliptic to broadly elliptic leaflets; the calyx is accrescent in fruit; there are usually 15 or 20 stamens; and the achenes are prominently ribbed. Swedish plants of this species reproduce primarily by apomixis, which is assumed to be the common method of reproduction throughout its range. The European *Potentilla intermedia* L., $2n = 56$, which differs from *P. norvegica* by the mostly digitately basal leaves, has become naturalized from Newfoundland, Quebec, and Michigan, southward to Virginia and North Carolina. Apparently an obligate apomict, *P. intermedia* has morphological features of both *P. norvegica* and *P. argentea*, and, consequently, is thought to be of hybrid origin, although this remains to be proven. *Potentilla inclinata* Vill. (*P. canescens* Bess.) is much like the two preceding taxa, but the leaves are more densely pubescent, and the petals noticeably exceed the calyx lobes. Indigenous to Europe, *P. inclinata* may be of hybrid origin (*P. recta* × *P. argentea*); in North America it occurs from southwestern Quebec and Ontario to North Carolina, Indiana, and Michigan.

Potentilla anserina L. (*Argentina anserina* (L.) Rydb.) has been reported recently from Sevier County, Tennessee (Roger & Bosers, Castanea **34**: 395. 1969). Characterized by pinnate leaves with numerous leaflets, solitary flowers axillary along elongated stolons, glabrous carpels, and lateral, filiform styles, this species is one of the most widely distributed members of the genus, occurring from the arctic regions of North America, Europe, and Asia, to California, New Mexico, the Mediterranean area, and southeastern Asia. It occurs also in western South America from central Chile to Patagonia, and it is naturalized in Australia, Tasmania, and New Zealand. Plants from most of the eastern United States belong to subsp. *anserina* (lower leaflets silvery-sericeous beneath with straight trichomes; achenes dorsally grooved; bractlets usually toothed or lobed), $2n = 28$, 42, a variable, self-incompatible subspecies found in most parts of temperate Eurasia and North America. In the eastern United States and Europe, subsp. *anserina* grows mostly in disturbed sites, where it is often a troublesome weed, while, in the western United States, it is rarely seen except in natural, unspoiled habitats. *Potentilla anserina*, sensu lato, has been variously treated taxonomically; Rydberg divided the North American representatives into 8 species, placing them in the segregate genus *Argentina* Lam. *Potentilla anserina* is the only species of Rosaceae known to produce the trihydroxyflavonoids myricetin and leucodelphinidin, compounds that are also known from the Chrysobalanaceae.

The apomictic *Potentilla arguta* Pursh, $2n = 14$, (plant erect, glandular-villous; petals whitish; leaves pinnate; stamens 25 to 30, in 5 festoons on a thick, glandular disc; style subbasal; receptacle distinctly enlarging in fruit), was reported from the vicinity of Nashville, Tennessee, by Gattinger (Fl. Tennessee, 1901), but evidently has not been seen again in our area. Its range is from New Brunswick and Quebec to Mackenzie and British Columbia, southward to the District of Columbia, West Virginia, Ohio, Indiana, Illinois, Missouri, Oklahoma, Colorado, and Arizona. It has been placed in the segregate genus *Drymocallis* Fourr. (as *D. agrimonioides* (Pursh) Rydb.) along with related species of Eurasia and western North America, including *P. glandulosa* Lindley, one of the best studied flowering plants of North America in terms of experimental taxonomy (Clausen, Keck, & Hiesey).

Gattinger also reported *Potentilla fruticosa* L., shrubby cinquefoil, golden-hardhack, of subg. TRICHOTHALAMUS (Lehm.) Reichenb. (shrubs with pinnate leaves, the leaflets entire; style clavate, subbasal; carpels pubescent) from Cherokee County, North Carolina. Elkington recognized two subspecies: subsp. *fruticosa* (tetraploid; plants dioecious) that ranges from Ireland and northern Europe to Asia, and subsp. *floribunda* (Pursh) Elkington (diploid; flowers perfect) that occurs in southern Europe, Turkey, the Caucasus Mountains, Asia to Japan and the Kamchatkan Peninsula, and North America from Labrador to Alaska southward to Pennsylvania, Ohio, Indiana, Illinois, Iowa, South Dakota, Arizona, New Mexico, and California. The other species of subg. TRICHOTHALAMUS are from eastern Asia. This group has been treated at the generic level as *Dasiphora* Raf. or *Pentaphylloides* Duhamel.

Potentilla tridentata Aiton (*Sibbaldiopsis tridentata* (Aiton) Rydb., $2n = 28$, three-toothed cinquefoil, of subg. SIBBALDIOPSIS (Rydb.) Boivin, a low perennial with creeping, woody stems from a caudex; ternately compound leaves with evergreen, coriaceous, apically 3- or 5-toothed leaflets; white petals; filiform, basal styles; and pubescent carpels is primarily of subarctic regions, occurring from Greenland, Labrador, and Mackenzie to New England, New York, Michigan, Wisconsin, Iowa, and North Dakota, and southward in scattered localities in the Appalachian Mountains to northern Georgia. *Potentilla ambigua* Camb., of the Himalayas, and *P. Miyabei* Makino, of Japan, are possibly close relatives.

Several types of breeding systems occur in *Potentilla*. Some species are diploid (*P. fruticosa* subsp. *floribunda*) or polyploid (*P. anserina*, *P. recta*, *P. tridentata*) and sexually reproducing, often with extensive ecotype formation; others are apomictic diploids (*P. argentea*, *P. arguta*), a situation very rare among the flowering plants; and many are part of polyploid-agamic complexes (*P. canescens*, *P. intermedia*, *P. norvegica*). The type of reproduction, and often even the chromosome number, is not known for most of the common species indigenous to eastern North America (e.g., *P. canadensis*, *P. paradoxa*, *P. pentandra*, *P. rivalis*, and *P. simplex*). Apomixis occurs most commonly in sect. GYMNOCARPAE subsects. *Conostylae* and *Gomphostylae*, of Wolf. Unreduced embryo sacs of apomictic *Potentilla* species usually are produced aposporously, although both diospory and diplospory occur in the British *P. Tabernaemontani*. Since the archesporangium is multicellular, the distinction between the two types of embryo sac development is difficult to determine and may not be indicative of any fundamental difference in *Potentilla*. The apomicts are pseudogamous, and fertilization of the polar nuclei is necessary for seed development; pollen of even distantly related species often functions, although seed set is reduced. All transitions occur between complete sexuality, facultative apomixis, and obligate apomixis. Even in the last case, unreduced egg cells can occasionally be fertilized. Throughout the genus, aneuploidy and odd-level polyploids are very rare; chromosome numbers range from $2n = 14$ to 112; no triploid apomicts are known from nature. The genetic control of apomixis is still poorly known but is believed to involve several genes. Asker (1966, 1970–71) has shown that sexual tetraploids resulted from colchicine treatment of apomictic diploids, and he also has evidence that polyploidization and hybridization between apomicts may interfere with the production of unreduced embryo sacs. "In *Potentilla*, facultative apomicts may have arisen on the diploid level, later giving rise to polyploids with stabilized obligate apospory; but . . . an independent origin of apomixis in polyploids is also possible, at least where the *argentea* complex is concerned" (Asker, 1970–71, III).

REFERENCES:

Under subfamily references see BESSEY, BRESINSKY, NESTLER, RYDBERG, and SCHAEPPI & STEINDL; under family references see BATE-SMITH, BOUTINEAU, BUNTING, CHUTE, DEVADAS & BECK, DIPPLE, GUSTAFSSON, HARA, HEGI, HULTÉN (1958, 1971), JESSON, LUBBOCK, REHDER, RICKETT, ROBERTSON, ROSS-CRAIG, SCHNEIDER, and VINES.

ASKER, S. Induced sexuality after chromosome doubling in an apomictic *Potentilla argentea*-biotype. Hereditas **57**: 339–342. 1967.

———. Apomictic biotypes in *Potentilla intermedia* and *P. norvegica*. *Ibid.* **66**: 101–108. 1970.

———. Apomixis and sexuality in the *Potentilla argentea* complex. I. Crosses with other species. *Ibid.* 127–144. II. Crosses within the complex. *Ibid.* 189–204. III. Euploid and aneuploid derivatives (including trisomics) of some apomictic biotypes. *Ibid.* **67**: 111–142. 1971.

———. Some viewpoints on *Fragaria* × *Potentilla* intergeneric hybridization. *Ibid.* 181–190. [Good review paper.]

———. Studies in apomictic and sexual *Potentilla* L. 7 pp. Lund, Sweden. 1971.

[Abstract of papers submitted as a doctoral thesis to the University of Lund.]

——— J. & S. FRÖST. Chromatographic studies in *Potentilla argentea* L. Hereditas **62**: 426–429. 1969.

——— & ———. Chromatographic studies of phenolic compounds in apomictic *Potentilla* L. *Ibid.* **65**: 241–250. 1970.

——— & ———. Plant age and chromatographic pattern in *Potentilla. Ibid.* **72**: 149–152. 1972. [*P. argentea, P. canescens, P. norvegica.*]

BORHIDI, A., & I. ISÉPY. Statistical studies on *Potentilla* species. Acta Bot. Acad. Sci. Hungar. **12**: 221–239. 1966.*

BOWDEN, W. M. Cytotaxonomy of *Potentilla fruticosa,* allied species and cultivars. Jour. Arnold Arb. **38**: 381–388. 1957.

CARLBLOM, C. Premeiotic reduction in *Agrostis* L., *Potentilla* L. and *Triticum* L. Hereditas **61**: 421–423. 1969. [*P. argentea.*]

CLAUSEN, J., D. D. KECK, & W. M. HIESEY. Experimental studies on the nature of species. I. Effect of varied environments on western North American plants. Carnegie Inst. Publ. **520**: vii + 452 pp. 1940. [*P. glandulosa* and its allies. 26–124; *P. gracilis* and its allies, 125–175; *P. Drummondii* and *P. Breweri,* 176–195.]

DANSEREAU, P. Studies in *Potentillae* of high latitudes and altitudes. Trans. Roy. Soc. Canada III. Sect. 5. **49**: 11–23. 1955. [Includes list of arctic and alpine spp.; discussion of important characteristics of genus.]

ELKINGTON, T. T. Cytotaxonomic variation in *Potentilla fruticosa* L. New Phytol. **68**: 151–160. 1969.

——— & S. R. J. WOODELL. Biological flora of the British Isles: *Potentilla fruticosa* L. Jour. Ecol. **51**: 769–781. 1963.

FERNALD, M. L. The representatives of *Potentilla anserina* in eastern America. Rhodora **11**: 1–9. 1909. [3 spp. recognized.]

———. *Potentilla canadensis* and *P. simplex.* Rhodora **33**: 180–191. *pls. 214, 215.* 1931.

GENTSCHEFF, G., & Å. GUSTAFSSON. Parthenogenesis and pseudogamy in *Potentilla.* Bot. Not. **1940**: 109–132. 1940.

GREWAL, M. S., & J. R. ELLIS. Sex determination in *Potentilla fruticosa.* Heredity **29**: 359–362. 1972.

GUÉDÈS, M. Premières observations sur la stipule ligulaire de quelques dicotylédons. Beitr. Biol. Pflanzen **45**: 313–327. 1968. [*P. anserina, P. fruticosa, P. reptans, P. rupestris.*]

HÅKANSSON, A. Untersuchungen über die Embryologie einiger *Potentilla*-Formen. (English summary.) Lunds Univ. Årsskr. II. **42**(5): 1–70. 1946.

HARPER, R. M. A southern outpost for *Potentilla tridentata.* Rhodora **31**: 221–223. 1929. [Blood Mt., Union Co., Georgia.]

HOLM, T. Contributions to the knowledge of the germination of some North American plants. Mem. Torrey Bot. Club **2**: 57–108. *pls. 5–19.* 1891. [*P. canadensis,* 70.]

HUNZIKER, H. R. Beitrag zur Aposporie und ihrer Genetik bei *Potentilla.* (English summary.) Arch. Julius Klaus-Stiftung **29**: 135–222. *pl. 1.* 1954.

KALKMAN, C. *Potentilla, Duchesnea,* and *Fragaria* in Malesia (Rosaceae). Blumea **16**: 325–354. 1968.

KECK, D. D. Revision of *Horkelia* and *Ivesia.* Lloydia **1**: 75–142. 1938. [Includes discussion on generic delimitation of *Potentilla.*]

KELLEY, W. R. Study of seed identification and seed germination of *Potentilla* spp. and *Veronica* spp. N.Y. State Agr. Exper. Sta. Mem. **317.** 31 pp. 1953.*

LEBÈGUE, A. Polyembryonie chez le *Potentilla aurea* L. Bull. Soc. Bot. France **97:** 199–201. 1950. [See also SOUÈGES, *ibid.* **82:** 381–384. 1935, for polyembryony in *P. reptans.*]

LISTOWSKI, A. Observations on plant development (IX). The development of *Potentilla supina.* (In English; Polish summary.) Acta Soc. Bot. Polon. **34:** 1–26. *1 table.* 1965. (XIV). Interactions between seedling time, age of plant, vernalization length and florescence of *Potentilla supina. Ibid.* **36:** 449–458. 1967.

LÖVE, Á. Cytotaxonomical remarks on some American species of circumpolar taxa. Sv. Bot. Tidskr. **48:** 211–232. 1954. [*P. fruticosa,* sensu lato, segregated as *Pentaphylloides,* N. Am. form called *P. floribunda* (Pursh) Á. Löve; *P. norvegica.*]

MATFIELD, B., & J. R. ELLIS. The allopolyploid origin and genomic constitution of *Potentilla anglica.* Heredity **29:** 315–327. *pl. 1.* 1972. [A segmental allopolyploid between *P. reptans* and *P. erecta.*]

———, J. K. JONES, & J. R. ELLIS. Natural and experimental hybridization in *Potentilla.* New Phytol. **69:** 171–186. 1970.

MÜNTZING, A. The balance between sexual and apomictic reproduction in some hybrids of *Potentilla.* Hereditas **44:** 145–160. 1958. [*P. argentea* complex.]

———. Heteroploidy and polymorphism in some apomictic species of *Potentilla. Ibid.* 280–329.

———. Further studies on intraspecific polyploidy in *Potentilla argentea* (coll.) Bot. Not. **111:** 209–227. 1958.

PAWLOWSKI, B. De generis *Potentilla* L. serie *Crassinerviae* (Th. Wolf) B. Pawl. nec non de taxis affinibus. (In Latin; Polish summary.) Frag. Fl. Geobot. **11:** 53–91. *figs. 19–22.* 1965.

POPESCU, A. Consideratii taxonomice si filogenetice asupra sectiei *Rectae* (Th. Wolf) Juz. a genului *Potentilla* L. Stud. Cercet. Biol. Bucuresti Bot. **20**(1): 39–46. 1968.*

ROUSI, A. Biosystematic studies on the species aggregate *Potentilla anserina* L. Ann. Bot. Fenn. **2:** 47–112. 1965. [3 subspp. recognized.]

RUTISHAUSER, A. Fortpflanzungsmodus und Meiose apomiktischer Blütenpflanzen. 245 pp. Springer-Verlag, Vienna & New York. 1967. [Includes material from, and references to, the author's earlier work on *Potentilla.*]

SHAFRANOVA, L. M. The anatomical structure of shoots in *Potentilla fruticosa* L., *P. parvifolia* Fisch. and *P. bifurca* L., associated with the transformation of shrubs into herbs in *Potentilla* L. (*s.l.*). (In Russian; English summary.) Biull. Moskov. Obshch. Ips. Pri. Biol. II. **73**(1): 140–154. 1968.

SMITH, G. L. Studies in *Potentilla* L. I. Embryological investigations into the mechanisms of agamospermy in British *P. Tabernaemontani* Aschers. New Phytol. **62:** 264–282. *pl. 6.* 1963. II. Cytological aspects of apomixis in *P. Crantzii* (Cr.) Beck ex Fritsch. *Ibid.* 283–300. *pl. 7.* III. Variation in British *P. Tabernaemontani* Aschers. and *P. Crantzii* (Cr.) Beck ex Fritsch. *Ibid.* **70:** 607–618. *pls. 1, 2.* 1971. [Part III published posthumously, prepared and augmented by V. G. BOZMAN and S. M. WALTERS.]

SOJÁK, J. Nomenklatorische Anmerkungen zur Gattung *Potentilla.* Folia Geobot. Phytotax. Bohemoslov. **4:** 205–209. 1969. [*P. supina* subsp. *paradoxa* (Nutt. ex T. & G.) Soják.]

SOUÈGES, R. Embryogénie des Rosacées. Développement de l'embryon chez le *Potentilla reptans* L. Compt. Rend. Acad. Sci. Paris **200**: 1972–1974. 1935.

TANSLEY, A. G. The nature and range of variation in the floral symmetry of *Potentilla erecta* (L.) Hampe. New Phytol. **47**: 95–110. 1948. [Flowers typically 4-merous, but 3-, 5-, and 6-merous flowers occur.]

WATSON, P. J. Evolution in closely adjacent plant populations. 6. An entomophilous species, *Potentilla erecta*, in two contrasting habitats. Heredity **24**: 407–422. 1969.

WOLF, T. Monographie der Gattung *Potentilla*. Bibliot. Bot. **16**: 1–715. *pls. 1–20. maps 1, 2.* 1908.

Tribe DRYADEAE DC.

12. **Geum** Linnaeus, Sp. Pl. 1: 500. 1753; Gen. Pl. ed. 5. 200. 1754.

Perennial herbs with rosettes terminating short, vertical rootstocks or elongated, horizontal rhizomes covered with persistent leaf bases. Basal leaves long petiolate, imparipinnately compound, mostly lyrate in outline, the terminal leaflet usually larger than the lower ones, the latter of varying sizes, some usually greatly reduced or absent, the shape and degree of division sometimes markedly different on the same plant; cauline leaves similar to basal ones, but less compound and with shorter petioles, often simple in the inflorescences; stipules of the basal leaves adnate for their entire length to the petioles and forming membranaceous wings, those of the cauline leaves free. Inflorescences terminating stems arising from the rosettes, the flowers in several- to many-flowered open cymes [rarely solitary]. Flowers white, yellow or pinkish [to orange or purple], perfect, mostly 5-merous. Calyx with an epicalyx, rarely without; calyx lobes erect, spreading, or reflexed at anthesis, commonly reflexed in fruit, green [or reddish]; floral cup saucer-shaped [to campanulate or short-cylindric], free from carpels, a small to prominent nectar ring surrounding mouth of floral cup or at base of carpels. Petals spreading [or erect] at anthesis, deciduous, shorter than to exceeding calyx lobes, narrowly to broadly elliptic, nearly circular or spathulate, the apices rounded to emarginate, the bases rounded, narrowed, or rarely distinctly clawed, inserted at outer edge of floral cup, imbricate. Androecium of 20 to many stamens in several series; filaments glabrous [or pubescent], usually persistent, perigynous on floral cup at outer edge of nectar ring [or on the sides of the floral cup]; anthers yellow. Gynoecium of several to very many free, glabrous, or pubescent, sessile [or stalked] carpels on a hemispheric to nearly globose or cylindric, glabrous or hirsute, sometimes stipitate receptacle; styles terminal, entire and wholly persistent or jointed and geniculate near or above the middle with the apical part deciduous, leaving a hooked rostrum on the fruit; stigmas terminal, punctiform; each carpel with a single, basal, upright-apotropous ovule, the micropyle inferior. Fruit an aggregation of achenes with long, straight or hooked glabrous or plumose persistent styles, the receptacle not enlarging but sometimes elevated above the calyx on an elongated stipe; seeds erect, the radicle inferior, the seed coat membranaceous. Base chromosome number 7. (Including *Acomastylis* E. L. Greene, *Stylipus* Raf., and *Sieversia* Willd.) LECTOTYPE SPECIES: *G. urbanum* L.; see Britton & Brown, Fl. No. U.S. Canada ed. 2. 2: 269. 1913. (A name used by Pliny, perhaps for *G. urbanum.*) — AVENS.

About 60 species in eleven subgenera, primarily of the Northern Hemisphere, with many species of arctic or alpine regions or moist boreal forests; a few species in the mountains of South America and in southern Africa, Tasmania, New Zealand, and the Auckland Islands. Approximately 17 species in six subgenera are found in North America, all except *Geum urbanum* indigenous, and ten of them are restricted to that area; twelve species occur in eastern North America, seven in the southeastern United States. Generic delimitation and subgeneric classification are still problematical, and numerous segregate genera and several systems of division have been proposed. Important treatments of the genus are those by Rydberg (1913), Bolle, Gajewski, and Huber in Hegi.

Four species of subg. GEUM (styles geniculate and jointed near the middle or above, the upper part deciduous, leaving a hooked rostrum on the achenes; epicalyx present) occur with us. *Geum canadense* Jacq., $2n = 42$, is a variable plant with flowers with white petals that equal or exceed the calyx lobes, densely pubescent receptacles, and sharply toothed cauline leaves that only gradually become smaller and less compound toward the stem apices. The terminal portion of the basal leaves varies from simple and merely toothed to lobed, ternate, or pinnately compound. The range of this species is from Nova Scotia to North Dakota, south to Georgia, Alabama, and eastern Texas. The plant usually occurs in moist, shaded habitats, such as woods, ravines, coves, stream banks, and thickets. Fernald & Weatherby noted six recognizable trends (four varieties and two forms) with differences in the type, distribution, and density of trichomes, number of carpels per flower, and leaf morphology. Character correlations, however, are quite weak, and subspecific categories probably are unwarranted.

The closely related *Geum laciniatum* Murray, $2n = 42$ (*G. virginianum* auct. not L.), has stouter pedicels, smaller petals that rarely exceed the calyx lobes, and mostly glabrous receptacles. This species occurs only in moist places, such as meadows, rich woodlands, and the margins of ponds, streams, and ditches, from Nova Scotia and southern Ontario to Minnesota, south to North Carolina, Alabama, Illinois, Missouri, and Kansas. Plants, mostly from the southern part of the range, with sparsely hirsute, rather than glabrous, achenes have been distinguished as var. *trichocarpum* Fern. The artificial hybrid between this and the preceding species is vigorous and quite fertile. Gajewski (1957) noted that in *G. laciniatum* the achenes do not readily become detached from the receptacle, but instead the entire fruiting head is easily broken off at the base and dispersed as a unit.

Geum aleppicum Jacq., $2n = 42$, has the widest distribution of any species of *Geum*, occurring in northern Eurasia from Kamchatka and Japan to Poland, Czechoslovakia, Hungary, and Albania, and in North

America from Newfoundland and the Gaspé Peninsula to Mackenzie and British Columbia, southward to North Carolina, Ohio, Indiana, Illinois, Iowa, Nebraska, New Mexico, California, and northern Mexico. New World plants have been called var. *strictum* Fern., but the great range of variation in this species makes the recognition of subspecific taxa futile. *Geum aleppicum* can be recognized by its deep yellow to orange petals that exceed the calyx lobes, hirsute receptacles, and pinnate basal, lower, and middle leaves.

Geum virginianum L. (*G. flavum* (Porter) Bickn.; *G. hirsutum* Muhl.), $2n = 42$, is very similar to *G. canadense*, but differs in the cream-colored to pale yellow petals that are shorter than the calyx lobes and in the larger stipules. This species occurs in dry to moist upland woods and thickets from Massachusetts to Indiana, south to South Carolina, Tennessee, and Kentucky. Raynor and Gajewski indicate that *G. virginianum* may have originated by hybridization between *G. canadense* and *G. aleppicum*. Plants of true *G. virginianum* are quite fertile and show no segregation in subsequent generations. The artificial F_1 hybrid between *G. canadense* and *G. aleppicum*, while morphologically similar to *G. virginianum*, is highly sterile. Some herbarium specimens assignable to *G. virginianum* have mostly aborted pollen and may represent natural hybrids; these are mostly from north of our area where *G. canadense* and *G. aleppicum* are sympatric.

Geum geniculatum Michaux is a poorly known species restricted to balds, shaded coves, and moist woods on the upper slopes of Roan and Grandfather mountains in western North Carolina and eastern Tennessee, where it is locally abundant. Nodding flowers, spathulate petals that are truncate or emarginate above and clawed below, and plumose styles that exceed the calyx lobes at or soon after anthesis (the terminal stylar portion as long as or longer than the beak portion) characterize this species, which is quite similar to the circumpolar *G. rivale* L., $2n = 42$, but which differs from it by the spreading (not strongly ascending) perianth, greenish (not purple) floral cups, and hemispheric and sessile (instead of globose and stipitate) fruiting aggregates. Gajewski (1957) thinks that *G. geniculatum* is a hybrid, with *G. rivale* being one parent. It cannot, however, be a first generation hybrid, since the nearest station for *G. rivale* is in West Virginia. The percentage of pollen stainability of *G. geniculatum* is very high.

The only species of subg. STYLIPUS (Raf.) Torrey & Gray is *Geum vernum* (Raf.) Torrey & Gray (*Stylipus vernus* Raf.), $2n = 42$, which occurs in moist, rich woods, swamp forests, and shaded valleys from New York and southern Ontario to Michigan and Iowa, southward to North Carolina, Tennessee, Kentucky, Arkansas, and eastern Texas. This species has very small flowers with cream-colored to yellow petals, a floral cup that lacks an epicalyx, sepals that are strongly reflexed at anthesis, and an aggregation of achenes that is elevated on a stipe above the calyx.

Subgenus MICRACOMASTYLIS (F. Bolle) K. R. Robertson[6] (styles

---

[6] *Geum* subgenus **Micracomastylis** (F. Bolle) K. R. Robertson, comb. nov. *Acomastylis* E. L. Greene subg. *Micracomastylis* F. Bolle, Repert. Sp. Nov. Beih. 72: 85. 1933; including *Acomastylis* subg. *Megacomastylis* F. Bolle. LECTOTYPE SPECIES:

straight, not jointed, basally pubescent, wholly persistent in fruit) is represented with us by *Geum radiatum* Michaux (*Sieversia radiata* (Michaux) Greene; *Acomastylis radiata* (Michaux) F. Bolle; *Parageum radiatum* (Michaux) Hara), $2n = 42$, that is endemic to balds on the high mountains of western North Carolina and eastern Tennessee. This species is easily recognized by the basal leaves with a large, reniform terminal lobe. The cauline leaves are few and much reduced in size. Its relatives are *G. Peckii* Pursh (White Mountains, of New Hampshire, and Brier Island, western Nova Scotia), $2n = 42$; *G. Schofieldii* Calder & Taylor (Queen Charlotte Islands, British Columbia), $2n = 112$; *G. calthifolium* Smith (Japan and Kamchatka to Alaska and British Columbia), $2n = 42$; and two species of China and the Himalayas.

Geum, *Waldsteinia*, and *Coluria* R. Br. (5 spp. of China and southern Siberia) are closely related and form a distinctive unit ("Geinae" of Schulze-Menz in Melchior; tribe Geeae sensu Gajewski) of tribe Dryadeae DC. (mostly shrubs and perennial herbs; styles terminal, elongated; each carpel with one (exceptionally two) basal, erect-apotropous ovule; fruit an aggregation of achenes). Other members of this tribe are *Dryas* (Holarctic; 3 or more species [numerous local forms have been given specific status]), *Cowania* D. Don (about six species of the southwestern United States and Mexico), *Fallugia paradoxa* (D. Don) Endl. (southwestern North America), *Chamaebatia* Bentham (2 spp. of California and Baja California), *Purshia* DC. (two spp.; Oregon to Wyoming and Colorado, California, and Mexico), and *Cercocarpus* HBK. (10 or more species; Oregon to western Kansas southward to Mexico). The ovule type of these genera was used by Juel to segregate them as a distinct subfamily, Dryadoideae (DC.) Juel.

Within tribe Dryadeae are found adaptations that evidently resulted from a change from insect to wind pollination. Most species of *Geum* and *Waldsteinia* have complete perianth whorls and punctiform stigmas and are insect pollinated. The flowers of *Cercocarpus* species are apetalous, with the stigmatic area forming a crest on the styles, and are presumably anemophilous. Some other genera of the tribe are intermediate between these extremes. Several dispersal mechanisms also occur in the tribe. Species of *Geum* subg. GEUM and STYLIPUS have an achene surmounted by a hooked rostrum that catches in the fur of mammals (and the clothing of botanists). In *G. heterocarpum* Boiss., $2n = 28$ (Spain and northern Africa and disjunct in Asia Minor and Central Asia) the rostrum is straight and bears many retrorse, apical bristles. Other species of *Geum*, and members of *Dryas*, *Cowania*, *Fallugia*, and *Cercocarpus*, are wind dispersed by their elongated, persistent, plumose styles. The achenes of *Waldsteinia*, *Chamaebatia*, *Coluria*, and *Purshia* have no obvious dispersal mechanisms and are perhaps eaten by birds and small mammals or carried by ants. Some (or all?) species of *Cercocarpus*, *Dryas*, and *Purshia* have nitrogen-fixing root nodules (see Rodriguez-Barrueco, family ref.).

G. Rossii (R. Br.) Ser. in DC.; see P. A. Rydberg, N. Am. Fl. 22: 401. 1913. Gajewski's use of *Acomastylis* Greene at the subgeneric level under *Geum* is superfluous.

The base chromosome number in *Geum*, *Waldsteinia*, and *Coluria* is 7. In the other genera of Dryadeae it is 9, and only diploids are known. Most species of *Geum* thus far known cytologically are hexaploid with $2n = 42$. Relatively few species are tetraploid, octoploid, decaploid, or 12-ploid, and no diploids have been reported. The highest chromosome number reported for the genus is $2n = 112$ for *G. Schofieldii*. The chromosomes of *Geum* species are mostly small and uniform in size and shape.

The species of *Geum* are mostly quite distinct and show considerable differentiation in gross morphology, degree of polyploidy, and geographic distribution; yet barriers to artificial hybridization are nearly nonexistent in subg. Geum, and many intersubgeneric crosses can be made. Gajewski's extensive studies indicate that the ability of two species to hybridize generally does not appear to be correlated with systematic relationship, chromosome number, direction of the cross, or biotypes used. There is, however, considerable variation in the viability and fertility of the interspecific hybrids.

The inheritance of certain morphological traits has also been studied by Gajewski. The presence of anthocyanin pigments in *Geum rivale* is due to a single dominant gene. Perhaps three allelomorphic genes determine petal color: one gene either allows the expression of the other genes or suppresses them (the petals are then white), another gene determines cream-colored petals, and the remaining gene red petals. Yellow petals occur when the genes for "color," "red," and "cream" are homozygous in the same plant. Petal apices are controlled by one gene, with "emarginate" dominant over "rounded." In F_1 hybrids between *G. montanum* L. $2n = 28$ (styles straight, pinnately plumose, entirely persistent), and species of subg. Geum, a variety of stylar types occurs in the same individual or flower. In the second generation, most plants have hooked styles, but "montanum" and intermediate type styles occur infrequently. (Gajewski postulates that subg. Geum is of amphiploid origin between species related to *G. montanum* and *Waldsteinia*.)

References:

Under subfamily references see Jackson and Schaeppi & Steindl; under family references see Boutineau, Bunting, Chute, Devadas & Beck, Hara, Hegi, Huber (1961–1966), Hultén (1958, 1971), Löve & Löve, Lubbock, Rickett, Robertson, and Ross-Craig.

Bolle, F. Eine Übersicht über die Gattung *Geum* L. und die ihr nahestehenden Gattungen. Repert. Sp. Nov. Beih. **72:** 1–119. 1933.

Bucherer, E. Ueber Prolification und Phyllodie bei *Geum rivale*. Ber. Deutsch. Bot. Ges. **10:** 571–576. *pl. 29.* 1892.

Cheymol, J. Variations dans la composition glucidique de la racine de Benoîte (*Geum urbanum* L.) au cours de la végétation d'une année. Bull. Soc. Chim. Biol. **13:** 470–476. 1931.

Fernald, M. L. Critical plants of the upper Great Lakes region of Ontario and Michigan (continued). Rhodora **37:** 273–301. *pls. 363–375.* 1935. [*Geum,* 292–295, *pls. 368–370.*]

——— & C. A. Weatherby. Varieties of *Geum canadense. Ibid.* **24:** 47–50. 1922. [6 recognizable, morphological trends; 4 vars., 2 forms.]

Gajewski, W. A cytogenetic study on the genus *Geum* L. Monogr. Bot. **4:** 3–416. *pls. 1–4.* 1957. [Major taxonomic and cytogenetic paper on *Geum*; many subgeneric names invalidly published.]

———. Evolution in the genus *Geum*. Evolution **13:** 378–388. 1959. [Morphological, geographical, cytological, hybridization, and genetical data used to trace evolutionary history of genus.]

———. The heredity of seed-dispersing mechanisms in *Geum*. Genetics today, Proc. 11th Int. Congr. Genet. 1963. **2:** 423–430. 1965. [*G. rivale, G. montanum*, and their hybrids.]

Grigorescu, E. Pharmakognostiche Studie über das Rhizom von *Geum urbanum* und Bestimmung der Gerbstoffe. Farmacia **4:** 226 +. 1956.* [Also see **6:** 441. 1960.*]

Hooker, W. J. *Sieversia Peckii.* Mr. Peck's Sieversia. Bot. Mag. **55:** *pl. 2863.* 1828. [= *G. Peckii.*]

Iltis, H. Über das Gynophor und die Fruchtausbildung bei der Gattung *Geum*. Sitz-ber. Akad. Wiss. Math.-Naturw. Wien. Abt. I. **122:** 1177–1212. *pls. 1, 2.* 1913.

Juguet, M. Polyembryonie chez le *Geum rivale* L. Bull. Soc. Bot. France **113:** 133–137. 1966.

——— & A. Lebègue. Développement de l'embryon chez les *Geum rivale* et *Geum reptans*. Compt. Rend. Acad. Sci. Paris **261:** 4814–4817. 1965.*

Kowal, T., & A. Krupińska. The diagnostic characters of fruits and seeds of *Geum* L. species. (In Polish; extensive English summary.) Monogr. Bot. **29:** 69–120. 1969. [26 spp.; key to species using fruit and seed characters; illustrations.]

Král, M. Die Begrenzung der Gattung *Parageum* Nakai et Hara. Preslia **38:** 151–153. 1966. [2 subgenera, 2 sects., and 2 series recognized.]

Marsden-Jones, E. M. The genetics of *Geum intermedium* Willd. haud Ehrh., and its back-crosses. Jour. Genet. **23:** 377–395. *pls. 12–15.* 1930.

McArthur, I. C. S., & T. A. Steeves. An experimental study of vascular differentiation in *Geum chiloënse* Balbis. Bot. Gaz. **133:** 276–287. 1972. [= *Geum* 'Mrs. Bradshaw.']

Phelouzat, R. Morphologie, phyllotaxie, ontogénie de trois Rosacées: *Agrimonia Eupatoria* L., *Poterium Sanguisorba* L., *Geum urbanum* L. Revue Cytol. Biol. Vég. **26:** 101–362. 1963.*

Pšenák, M., A. Jindra, P. Kovács, & H. Dulovcová. Biochemical study on *Geum urbanum*. Pl. Med. **19:** 154–159. 1970.

Raynor, L. A. Cytotaxonomic studies of *Geum*. Am. Jour. Bot. **39:** 713–719. 1952. [Based on a doctoral dissertation submitted to Cornell Univ. in 1945.]

Schneider, G. H., Jr. *Geum canadense*, a study of its seasonal periodicity in New Jersey. Castanea **17:** 117–128. 1952.

Schulthess, H. Pharmakognostisch-anatomische und chemische Untersuchungen von Drogen des Genera *Geum, Sieversia* und *Dryas*. Thesis, Zurich. 114 pp. 1945.*

Souèges, R. Embryogénie des Rosacées. Les premiers stades du développement de l'embryon chez le *Geum urbanum* L. Compt. Rend. Acad. Sci. Paris **174:** 1070–1072. 1922; Les derniers stades du développement de l'embryon chez le *Geum urbanum* L. *Ibid.* 1197–1199.

———. Développement de l'embryon chez le *Geum urbanum* L. Bull. Soc. Bot. France **70:** 645–660. 1923.

13. **Waldsteinia** Willdenow, Neue Schr. Ges. Naturf. Freunde Berlin **2:** 105. *pl 4, fig. 1.* 1799.

Low, perennial, colonial herbs with the aspect of strawberry plants, the leaves in basal rosettes from crowns on slender subterranean rhizomes at the time of flowering, but (at least in *W. fragarioides*) the rosettes later elongating and the leaves cauline by autumn; roots adventitious along monopodially branching rhizomes; indumentum of long and short, simple as well as multicellular-glandular trichomes. Leaves ternately compound or palmately 3-5-lobed, long petiolate, the leaf blades or leaflets variously toothed and incised; stipules adnate to petiole for nearly their entire length, forming membranaceous, reddish wings at base of petiole; lower part of petioles and stipules persistent on the rhizomes. Inflorescences loose, long pedunculate, few-flowered cymes arising from the rosettes; bracts small, deltoid, entire to slightly 3-lobed [or foliaceous]. Flowers light to bright yellow, the centers often more intensely colored, perfect. Calyx with or without an epicalyx; calyx lobes 5, triangular-lanceolate, persistent, valvate in aestivation; floral tube obconic, free of the carpels, a lobed nectar ring nearly covering the mouth of the floral tube. Petals 5, spreading, deciduous, narrowly to broadly ovate, very short clawed with 2 basal auricles in *W. geoides*, inserted at the edge of the floral tube, quincuncial cochlear. Androecium of 25–80 stamens; filaments slender, in several series, persistent, perigynous around the periphery of the floral tube; anthers yellow. Gynoecium of 2–6 (rarely more) free, pubescent, distinctly stalked, superior carpels; styles terminal, articulated at the bases and wholly caducous; stigmas terminal, punctiform; each carpel with a single, basal, erect-apotropous ovule. Accessory fruits dry, surrounded by the persistent calyx and filaments, the receptacle not enlarging. Achenes dry, pubescent, plump, obovoid; embryo erect, the radicle inferior. Base chromosome number 7. TYPE SPECIES: *W. geoides* Willd. (Named in honor of Graf Franz de Paula Adam von Waldstein-Wartenberg, 1759–1823.) — BARREN STRAWBERRY.

Five species distributed in an Arcto-Tertiary relict pattern with *Waldsteinia geoides*, $2n = 14$, the only species of subg. WALDSTEINIA, in Bulgaria, Yugoslavia, Rumania, southwestern Ukraine, Czechoslovakia, and Hungary; *W. fragarioides* (Michx.) Tratt. in the eastern, and *W. lobata* (Baldwin in Elliott) Torrey & Gray in the southeastern United States; *W. idahoënsis* Piper in west-central Idaho; and *W. ternata* (Stephen) Firsch in three widely separated areas: subsp. *ternata* along the southeastern shore of Lake Baikal in eastern Siberia; subsp. *Maximowicziana* Teppner, $2n = 42$, in Sakhalin, the Amur and Ussuri river regions, Manchuria, North Korea, and Japan; and subsp. *trifolia* (Rochel ex Koch) Teppner, $2n = 28, 35, 42$, in Austria, Rumania, and Czechoslovakia. The last four species comprise subg. COMAROPSIS (Richard in Nestler) Teppner. The taxonomy used here is that adopted by Teppner in his recent revision of the genus.

Waldsteinia fragarioides (leaves ternately compound, epicalyx lobes either absent or small and occurring only between some calyx lobes, pedicels with red-capped glandular trichomes of two lengths) ranges from New Brunswick and Maine to Ontario and Minnesota, southward to Georgia, Alabama, and Missouri. A northern and a southern subspecies can be distinguished. Subspecies *fragarioides,* with the petals broadly obovate or elliptic and greatly exceeding the calyx lobes, occurs in woods, thickets, and clearings from the northern limit of the species to southwestern Virginia, Ohio, Indiana, and southern Missouri; this taxon probably enters our area in the mountains of northwestern North Carolina. Two chromosomal races are known, diploid ($2n = 14$), reported from Ontario and Pennsylvania, and triploid ($2n = 21$), known from localities in Quebec, Ontario, New York, and Pennsylvania. The southern subsp. *Doniana* (Tratt.) Teppner (*W. Doniana* Tratt., *W. parviflora* Small, *W. fragarioides* var. *parviflora* (Small) Fernald) has petals that are narrower and shorter than the calyx lobes. It is restricted to the mountains and Piedmont of North and South Carolina, southern Kentucky, Tennessee, and northern Alabama and Georgia. *Waldsteinia fragarioides* and *W. ternata* are quite similar morphologically and form a pair of closely related vicarious species, as noted by Gajewski.

Waldsteinia lobata is a very poorly known species endemic to the Piedmont of Georgia and adjacent South Carolina. Both *W. lobata* and its close relative *W. idahoënsis,* an endemic of the Bitter Root Mountains in Idaho, have three- to five-lobed leaves and calyces that lack epicalyx lobes; in *W. lobata* the petals are about the same length as and narrower than the calyx lobes, while in *W. idahoënsis* the petals much exceed the calyx lobes in both length and width. Chromosome counts are lacking for these two species, but Teppner (1968) notes that the larger pollen grains frequently with four instead of three colpi in *W. idahoënsis* suggest a higher ploidy level in that species than in *W. lobata.* Gajewski thought that *W. lobata* and *W. geoides* were allied vicarious species. However, although both species have lobed rather than compound leaves, they differ in numerous floral details, and Teppner placed them in distinct subgenera.

The only confirmed interspecific hybrid is *Waldsteinia* × *Vranyi* Hendrych (*W. geoides* × *W. ternata* subsp. *trifolia*).

The genus is of little economic importance. Some species, particularly *Waldsteinia ternata* and *W. fragarioides*, are cultivated as ground covers, used in edging borders, or grown in rock gardens.

REFERENCES:

Under subfamily references see JACKSON and NESTLER; under family references see BUNTING, CHITTENDEN, CHUTE, HUBER (1961–1966), RICKETT, and WOOD.

FERNALD, M. L. Critical plants of the upper Great Lakes region of Ontario and

Michigan (cont.). Rhodora **37:** 272–301. *pls. 363–375.* 1935. [*Waldsteinia,* 285, 286.]

GAJEWSKI, W. A cytogenetic study on the genus *Geum* L. Monogr. Bot. **4:** 1–416. 1957. [Includes review of related genera; for *Waldsteinia* see particularly pp. 7–15, 99–105, 115, 116.]

———. Evolution in the genus *Geum.* Evolution **13:** 378–388. 1959. [Includes *Waldsteinia.*]

HOOKER, W. J. *Dalibarda lobata.* Hooker's Ic. Pl. **1:** *pl. 76.* 1837. [= *W. lobata.*]

MULLIGAN, G. A., & B. R. BAUM. *In:* Á. Löve, IOPB chromosome number reports XXVIII. Taxon **19:** 608–610. 1970. [*W. fragarioides,* $2n = 14$ (Ontario and Pennsylvania) and $2n = 21$ (Quebec, Ontario, and Pennsylvania).]

SIMS, J. *Dalibarda fragarioides.* Strawberry-leaved Dalibarda. Bot. Mag. **38:** *pl. 1567.* 1813. [= *W. fragarioides* subsp. *Doniana.*]

TEPPNER, H. Zur Kenntnis der Gattung *Waldsteinia.* 1. Schlüsel zum Bestimmen von Rosaceen-Pollen einschliesslich ähnlicher Pollenformen aus anderen Familien. Phyton Austria **11:** 224–238. 1966.

———. Zur Kenntnis der Gattung *Waldsteinia.* Inaug. Diss., Karl-Franzens-Univ., Graz. 129 pp. + *39 pl.* Graz. 1968. [World-wide revision.]

WALDSTEIN, F. P. A. VON, & P. KITAIBEL. *Waldsteinia geoides.* Descr. Ic. Pl. Hungariae **1:** 79. *pl.* 77. 1801 or 1802.

Tribe SANGUISORBEAE Juss. [rank assigned by DC. Prodr. 2: 588. 1825].

14. **Agrimonia** Linnaeus, Sp. Pl. 1: 448. 1753; Gen. Pl. ed. 5. 206. 1754.

Perennial herbs with erect stems arising from stout horizontal rhizomes, stems mostly unbranched below the inflorescences; roots coarse, fibrous, sometimes with fusiform thickenings; indumentum of simple and/or glandular trichomes, the density various. Leaves imparipinnate, the basal leaves rather small, not persistent, the cauline ones with small leaflets interspersed between large leaflets, the leaflets sharply toothed or lobed; stipules of the basal leaves elongate, adnate to either side of the petiole and forming a dilated wing, the apices free, acuminate, the margins with few or no teeth, those of the cauline leaves larger and broader, only basally adnate to the petiole, the margins deeply toothed or divided. Inflorescences several elongate racemes terminating the main stems, the flowers nearly sessile, the pedicels ascending in flower, spreading or descending in fruit, subtended by a small bract, the floral cup with 2 small bractlets beneath. Flowers small, 5-merous. Calyx without an epicalyx, the lobes spreading at anthesis, becoming incurved and forming a beak on the fruit; floral cup turbinate to hemispheric, the throat constricted, the outer rim of the cup with numerous hooked bristles that elongate and stiffen in fruit; nectar ring prominent, conical, nearly closing the mouth of the floral cup. Petals yellow, small, oval to orbicular, without claws, caducous. Androecium of 5–15 stamens; filaments slender, inserted at the outer edge of the nectar ring; anther locules somewhat separated by the broad connectives. Gynoecium of 2 separate carpels inserted at the base of, and free from, the floral cup; styles terminal; stigmas terminal, somewhat 2-lobed; each carpel with a solitary, anatropous ovule pendulous from an adaxial placenta, the micropyle superior. Fruit accessory, of 2 achenes inclosed within the enlarged, hardened, usually 10-grooved floral cup, the bristles stiff, hooked, reflexed to ascending; each achene with a single seed, the seed coat membranaceous, the radicle superior. Base chromosome number 7. TYPE SPECIES: *A. Eupatoria* L.; see Linnaeus, Gen. Pl. ed. 5. 206. 1754.[7] — AGRIMONY.

About 18 species with ten in North America (seven in our area), two in eastern South America, two confined to eastern Asia, *A. repens* L., $2n = 28$, in Anatolia (naturalized in other parts of Europe), *A. procera* Wallroth (*A. odorata* auct.), $2n = 56$, in Europe, *A. Eupatoria* L., $2n = 28$, with three subspecies extending from Europe to central and southwestern Asia, and *A. pilosa* Ledeb., $2n = 56$, that ranges from eastern Europe to the Himalayas, China, Siberia, and Japan. The genus is being revised by Vladimír Skalický, who groups the species into five series and several subseries.

Agrimonia gryposepala Wallroth, $2n = 56$, the only member of series *Procerae* Skalický in our area, ranges from Prince Edward Island to Ontario, northern Michigan and North Dakota, southward to New Jersey, Pennsylvania, Indiana, Missouri, eastern Kansas, and Louisiana, and in the mountains of eastern Tennessee and western North and South Carolina. This species, readily distinguished from others in the Southeast by its larger fruits (to 8 mm. long) and the minutely glandular inflorescence branches, prefers moist habitats, such as thickets, woodlands, and the borders of woods; with us it is found mostly in bogs, meadows, and low pastures. *Agrimonia macrocarpa* Rydb., of Mexico, and *A. procera*, of western, central, and southern Europe, are allied species.

Series *Tuberosae* Skalický, named for the fusiform-thickened roots, is strictly American, and all four species are found with us. *Agrimonia pubescens* Wallroth (*A. mollis* (Torrey & Gray) Britton), with cauline indumentum of long, incurving, eglandular trichomes, lower leaves with mostly 5 to 7 (rarely 9), elliptical leaflets, and mature fruits 2.5–5 mm. long, ranges from New England, southern Ontario, Michigan, and Minnesota to the Carolinas, Tennessee, Georgia, Alabama, Mississippi, Missouri, Arkansas, eastern Kansas, and Oklahoma, occurring in rather dry, often calcareous habitats. The very similar *A. Bicknellii* (Kearney) Rydb. (Massachusetts, New York, Michigan, and Illinois, to New Jersey, Pennsylvania, North Carolina, Tennessee, and Georgia) is often merged with *A. pubescens*. It differs from *A. pubescens* in the greater number of leaflets (usually 7 to

---

[7] In the *Species Plantarum*, Linnaeus distinguished two species, *A. Eupatoria* and *A. Agrimonoides*, and in the *Genera Plantarum* two subgeneric categories, *Agrimoniae* and *Agrimonoidis*. According to Article 22 of the International Code of Botanical Nomenclature, "when the epithet of a subdivision of a genus is identical with or derived from the epithet of one of its constituent species, this species is the type of the name of the subdivision of the genus . . . ." The subgeneric category *Agrimonoidis* is based on *A. Agrimonoides*, which is thus its type. Therefore, *A. Eupatoria* is the type of the subgeneric taxon *Agrimoniae* and the genus *Agrimonia*. De Candolle (Prodr. 2: 588. 1825) later removed *A. Agrimonoides* to the genus *Aremonia* Necker ex Nestler.

13) and in the spreading instead of ascending bristles on the fruit. *Agrimonia microcarpa* Wallroth (*A. pubescens* var. *microcarpa* (Wallroth) Ahles; including *A. platycarpa* Wallroth and *A. pumila* (Muhl.) Bicknell) is a woodland species with a more southern distribution (Pennsylvania, New Jersey, southward to the Virginias and Carolinas, Kentucky, Tennessee, Georgia, and Florida, and westward to eastern Texas). It is distinguished by the longer, more spreading trichomes on the stems, the fewer leaflets per leaf (3 to 5 or rarely 7), and the smaller fruits (1.5 to 3 mm. long). These three species are grouped by Skalický in his subseries *Tuberosae.* The only species of subseries *Rostellatae* Skalický is *A. rostellata* Wallroth (*A. striata* sensu Bicknell), which occurs in open woods from southern New England, New York, Ohio, Indiana, Illinois, Missouri, and eastern Kansas, southward to the Carolinas, Georgia, Oklahoma and eastern Texas. It is characterized by an indumentum of glandular trichomes and small fruits with the calyx lobes exceeding the short ascending or spreading bristles.

Series *Parviflorae* Skalický has an unusual geographical distribution: two species in eastern North America and two poorly known species, *A. villosa* Cham. & Schlecht. and *A. hirsuta* Bongard in Meyer in southeastern Brazil. *Agrimonia parviflora* Aiton, a plant of moist, open areas, is found from Florida to Texas north to Connecticut, New York, southern Ontario, Michigan, Illinois, Iowa, and Nebraska. It occurs disjunctly on Hispaniola. This is a rather coarse plant with spreading, long-villous stems, and leaves that have 11 to 15 abaxially glandular-dotted, lanceolate large leaflets and numerous small leaflets per leaf. *Agrimonia incisa* Torrey & Gray, quite similar but with deeply incised leaflets only 1 to 3 cm. long, is restricted to pine woods from South Carolina to Florida, and Mississippi. This series is supposed to lack fusiform-thickened roots, but at least one collection (*Curtiss 753* [GH], dry pine woods near the Santee Canal, South Carolina), definitely has such roots.

Fourteen genera comprise tribe Sanguisorbeae (carpels one to four, rarely to ten, inclosed by, but not adnate to, the urceolate floral cup; fruits achenes inclosed by the usually dry and hardened floral cups that frequently have spines or marginal wings; ovules solitary; stamens 15 or fewer, rarely to ca. 50; leaves mostly imparipinnate); the tribe is particularly diverse south of the Tropic of Cancer in South America and Africa. The genera can be placed in three groups (variously treated as tribes or subtribes: *Agrimonia* and related genera; *Alchemilla*; and *Sanguisorba* and congeners. Genera allied to *Agrimonia* are *Aremonia* Necker ex Nestler, nom. cons. (*A. agrimonoides* (L.) DC., central and southern Europe); *Spenceria* Trimen (two species, China); *Hagenia* J. F. Gmelin (*H. abyssinica* (Bruce) J. F. Gmelin, tropical Africa); and *Leucosidea* Ecklon & Zeyher (*L. sericea* Ecklon & Zeyher, South Africa).

REFERENCES:

Under subfamily references see SCHAEPPI & STEINDL; under family references

see BATE-SMITH, BOUTINEAU, BUNTING, CHUTE, HEGI, LUBBOCK, RICKETT, ROBERTSON, and ROSS-CRAIG.

ALEXANDER, E. J. *Agrimonia gryposepala.* Addisonia **17:** 19, 20. *pl. 554.* 1932.

BICKNELL, E. P. The North American species of *Agrimonia.* Bull. Torrey Bot. Club **23:** 508–523. *pls. 282, 283.* 1896. [Comments by B. L. ROBINSON on the nomenclature used by Bicknell are found in Rhodora **2:** 235–238. 1900, and Bull. Torrey Bot. Club **28:** 295–300. 1901; retorts by BICKNELL in Bull. Torrey Bot. Club **28:** 102–108, 514–518. 1901.]

BRITTAN, N. H. Cytotaxonomy of some species of *Agrimonia* L. (Abstract.) Proc. VII Int. Bot. Congr. **1950:** 278. 1953.*

GAMS, H. *Agrimonia. In:* G. HEGI, Ill. Fl. Mittel-Europa, ed. 1. **4**(2): 930–935. 1922.

HARA, H., & S. KUROSAWA. Cytotaxonomical notes on some Asiatic species of *Agrimonia.* Jour. Jap. Bot. **43:** 392–400. *pls. 20, 21.* 1968.

MADAN, C. L., & B. C. KUNDU. Pharmacognosy of the root of *Agrimonia Eupatoria* Linn. Jour. Sci. Industr. Res. C. **20**(12): 348–350. 1961.*

PHELOUZAT, R. Le méristème apical d'*Agrimonia Eupatoria* L. dans l'ontogénie de la pousse végétative et de l'inflorescence. Compt. Rend. Acad. Sci. Paris **245:** 2525–2528. 1957.

———. Morphologie, phyllotaxie et ontogénie de trois Rosacées: *Agrimonia Eupatoria* L., *Poterium Sanguisorba* L., *Geum urbanum* L. Revue Cytol. Biol. Vég. **26:** 101–362. 1963.*

SKALICKÝ, V. Ein Beitrag zur Erkenntnis der europäischen Arten der Gattung *Agrimonia* L. Acta Horti Bot. Pragensis **1962:** 87–108. 1962.

———. Amerikanische Odermennige *Agrimonia* L. ser. *Parviflorae* ser.n. Novit. Bot. Univ. Carolinae Pragensis **1970:** 9–16. 1971. [*A. incisa* and *A. parviflora.*]

———. Diagnoses, conspectus et claves analyticae taxorum infragenericorum novorum generis *Agrimonia* L. adhusca rite non publicatorum. *Ibid.* **1971:** 13–22. 1972.

———. Miscellanea taxonomica et nomenclatorica ad generis *Agrimonia* L. investigationem pertinentia. *Ibid.* **1972:** 11–18. 1973.

———. Amerikanische Arten der Gattung *Agrimonia* L. ser. *Tuberosae* ser. nova. Folia Geobot. Phytotax. **8:** 95–104. 1973. [Includes *A. Bicknellii, A. microcarpa, A. pubescens, A. rostellata.*]

SVENSON, H. K. Report of the Local Flora Committee. II. *Agrimonia;* III. *Quercus;* IV. *Ranunculus;* V. *Viola.* Torreya **41:** 3–7. 1941. [With plate illustrating the differences between 6 spp. of *Agrimonia.*]

WALLROTH, F. W. Monographischer Versuch über die Gewächs-Gattung *Agrimonia* Celsi. Beiträge zur Botanik. Leipzig **1:** 1–61. *pl. 1.* 1842.

15. **Alchemilla** Linnaeus, Sp. Pl. 1: 123. 1753; Gen. Pl. ed. 5. 59. 1754.

Small, much branched annual [or, more commonly, moderate sized, rhizomatous, or cespitose perennial] herbs. Leaves simple [rarely compound], orbicular in outline, palmately [very rarely pinnately] lobed or dissected, short [to long] petiolate, all cauline [or also basal in rosettes]; stipules deeply divided, adnate to the bases of the petioles, those of each leaf connate, clasping the stems and inflorescences, with the appearance of a multifid perfoliate leaf [or the basal leaves with adnate but not connate stipules]. Inflorescences few flowered, sessile cymules in the axils of the leaves [or flowers rarely solitary or cymules arranged in elongate, compound panicles or corymbs]. Flowers very small, perfect, apetalous, usually 4-merous. Calyx with or rarely without an epicalyx, the epicalyx lobes minute [to larger than the calyx lobes], the calyx lobes green [yellowish] slightly spreading at anthesis, persistent, valvate in aestivation; floral tube urceolate [turbinate or campanulate], free of the carpels, the throat nearly closed by a fleshy nectar ring. Petals absent. Stamen 1 [or stamens 2–5], opposite [or alternate with] a calyx lobe; anther extrorse [or introrse]; filament short, inserted at the inner [or outer] edge of the nectar ring. Gynoecium of 1 carpel [or as many as 10], carpel(s) sessile [or short stipitate] at the base of the floral tube and included within it; style inserted at the base of the ovary, protruding above the throat of the floral tube; stigma discoid; each carpel with a single, ascending, orthotropous ovule. Fruit an achene enclosed within the dry, thin floral tube that does not greatly elongate; seed coat thin; embryo filling the seed, the radicle superior, straight, the cotyledons flattened, broadly ovoid. Base chromosome number 8. (Including *Aphanes* L., *Lachemilla* (Focke) Rydb., and *Zygalchemilla* Rydb.) LECTOTYPE SPECIES: *A. vulgaris* L.; see P. A. Rydberg, N. Am. Fl. **22**: 377. 1908. (Name adopted, with a change in spelling, from Tournefort, the word evidently of Arabic origin; there have been various attempts to link the name with the possible use of plants of this genus in alchemy.)

Estimates of the number of species vary from 100 to over 1000, depending on how apomictic complexes are treated. Three subgenera can be recognized. Subgenus ALCHEMILLA (perennials; stamens 4, inserted on the outer edge of the nectar ring, alternate with the calyx lobes; anthers introrse) is primarily of the northern and alpine regions of Eurasia, but it also occurs in East Africa, Madagascar, India, Ceylon, and southeastern Asia. A few species are amphi-Atlantic, reaching Greenland, Labrador, Newfoundland, and the Maritime Provinces of Canada. Perhaps three other species are introduced into eastern North America, but none occurs in our area. Subgenus APHANES (L.) Reichenb. (annuals of low elevations, often weedy; stamen solitary, rarely paired, opposite a calyx lobe and on the inner margin of the nectar ring; anther extrorse) has been said to include 20 species and to have a disjunct distribution with species described from Europe, the Mediterranean region, eastern North America, western North America, southwestern South America, the eastern coast of South America, and Australia. However, most or perhaps even all of the "species" found outside Europe may be introductions of the European *A. arvensis* (L.) Scop. and/or *A. microcarpa* Boiss. & Reuter. The latter is found with us. This subgenus probably was confined to Europe before western man began his explorations of the world. Subgenus LACHEMILLA (Focke) Langerh. (perennials; stamens 2, rarely 3 or 4, opposite calyx lobes and inserted at the inner edge of the nectar ring; anthers extrorse), confined to high elevations in the western cordilleras of the Americas, includes about 50 species occurring from Mexico to Chile, Bolivia, and Argentina; *A. domingensis*

Urban is restricted to the Dominican Republic. These three subgenera are often given generic status, particularly in European floras, and, when only members of subg. ALCHEMILLA and APHANES are considered, such a treatment has merit. This position is less tenable when subg. LACHEMILLA is examined, since its diverse members largely bridge the discontinuities between the first two subgenera. Dr. Lily Perry monographed *Lachemilla* in 1929, treating it as a section of *Alchemilla*; she now thinks that it is generically distinct.

Alchemilla microcarpa (*Aphanes microcarpa* (Boiss. & Reuter) Rothmaler; *Aphanes australis* Rydb.), $2n = 16$, parsley-piert, a tiny winter annual of western Europe and the Mediterranean region, is naturalized in the United States from Delaware and the District of Columbia along the Piedmont and inner Coastal Plain to North Carolina, Tennessee, Georgia, Florida, Alabama, Mississippi, and eastern Texas. This species, usually occurring in open, disturbed areas and sometimes becoming a troublesome lawn weed, supposedly reproduces sexually, although it is closely allied to the facultatively apomictic *A. arvensis*, $2n = 48$.

All of the European species of subg. ALCHEMILLA (except *A. pentaphyllea* L. and a few others) are obligate apomicts, but many of them are no more difficult to delimit than sexually reproducing species in other genera. Some are very widely distributed and, although often quite variable, retain morphological distinctions; a large number have very local or disjunct distributions, but likewise present no taxonomic difficulties. These species are high-level polyploids (to $2n =$ ca. 220, ca. 224 in *A. faroënsis* (Lange) Burser), and it has been suggested that they are complex hybrids involving now extinct sexually reproducing species.

Because of its apetalous flowers, urceolate floral tubes inclosing the solitary or few carpels, and fruits with achenes inclosed by the floral cup, *Alchemilla* is often included in tribe Sanguisorbeae Juss., along with *Agrimonia* L., *Sanguisorba* L., and about ten other genera. *Alchemilla* differs from these, however, in its palmate leaves, basal styles, basal, orthotropous ovules, and base chromosome number of 8. It is sometimes placed in its own tribe; Schulze-Menz in Melchior considered it a subtribe of his Potentilleae.

REFERENCES:

Under subfamily references see SCHAEPPI & STEINDL; under family references see BATE-SMITH, BOUTINEAU, BUNTING, GUSTAFSSON, HEGI, HULTÉN (1958), JESSEN, LUBBOCK, RICKETT, and ROSS-CRAIG.

BÖÖS, G. Über parthenogenesis in der Gruppe *Aphanes* der Gattung *Alchemilla* nebst einigen im Zusammenhang damit stehenden Fragen. Lunds Univ. Årsskr. II. Sect. 2. **13**(4): 1–37. 1917.

———. Neue embryologische Studien über *Alchemilla arvensis* (L.) Scop. Bot. Not. **124**: 209–250. 1924.

FERNALD, M. L. Noteworthy plants of southeastern Virginia (continued). Rhodora **40**: 434–459. *pls. 521–530.* 1938. [*Alchemilla*, 435, 436; eastern North American plants are *A. microcarpa*, not *A. arvensis*.]

HJELMQVIST, H. Studien über Embryologie und Variabilität bei einigen *Aphanes*-Arten. (English summary.) Bot. Not. **112:** 17–64. 1959. [*A. arvensis*, *A. microcarpa*, *A. floribunda*.]

KERSHAW, K. A. Cyclic and pattern phenomena as exhibited by *Alchemilla alpina*. Jour. Ecology **48:** 443–453. 1960.

MURBECK, S. Parthenogenetische Embryobildung in der Gattung *Alchemilla*. Lunds Univ. Årsskr. Sect. 2 **36**(7): 1–46. *pls. 1–6.* 1901.

———. Über das Verhalten des Pollenschlauches bei *Alchemilla arvensis* (L.) Scop. und das Wesen der Chalazogamie. *Ibid.* **36**(9): 1–20. *pls. 1, 2.* 1901.

———. Zur Morphologie und Systematik der Gattung *Alchemilla*. *Ibid.* II. Sect. 2. **11**(8): 1–16. 1915.

PERRY, L. M. A tentative revision of *Alchemilla* § *Lachemilla*. Contr. Gray Herb. **84:** 1–57. 1929.

REICHGELT, T. *Aphanes microcarpa* in the Netherlands. Acta Bot. Neerl. **1:** 115–121. 1952. [Discusses distinctions between *A. microcarpa* and *A. arvensis*; also reasons for generic status of *Aphanes*.]

ROTHMALER, W. Systematische Vorarbeiten zu einer Monographie du Gattung *Alchemilla* (L.) Scop. emend. III. Notizen uber das Subgenus Aphanes (L.). Repert. Sp. Nov. **38:** 36–43. 1935. VII. Aufteilung der Gattung und Nomenklatur. *Ibid.* **42:** 164–173. 1937. [*Alphanes* recognized at generic level, list of species and their distributions.]

———. Aufforderung zur Mitarbeit an einer Flora von Europa. (Introduction à une Flore d'Europe). Repert. Sp. Nov. **53:** 254–270. 1944. [Textbeispiel eines Manuskripte für die "Flora Europaea." (Exemple de manuscript pour la "Flora Europaea"); *Aphanes*, 265–270.]

TURESSON, G. Variation in the apomictic microspecies *Alchemilla vulgaria* L. Bot. Not. **1943:** 413–427. 1943. II. Progeny tests in agamotypes with regard to morphological characters. *Ibid.* **109:** 400–404. 1956. III. Geographical distribution and chromosome number. *Ibid.* **110:** 413–422. 1957.

WALTERS, S. M. The taxonomic implications of apomixis. Pp. 162–168. *In*: J. G. HAWKES, *ed.*, Reproductive biology and taxonomy of flowering plants. 183 pp. *Frontisp.* Oxford. 1966.

———. Endemism in the genus *Alchemilla* in Europe. Pp. 301–305. *In*: D. H. VALENTINE, *ed.*, Taxonomy, phytogeography and evolution. xi + 431 pp. London and New York. 1972.

16. **Sanguisorba** Linnaeus, Sp. Pl. 1: 116. 1753; Gen. Pl. ed. 5. 53. 1754.

Branched perennial herbs from stout rhizomes, rarely short-lived perennials or annuals from tap-roots [or shrubs]; indumentum of unicellular, multicellular, and/or glandular trichomes. Leaves basal and cauline, imparipinnately compound, long petiolate, the leaflets sessile or shortly petiolulate, toothed or deeply dissected; stipules partly sheathing the stems, those of the basal leaves adnate for their entire length to the petioles and forming membranaceous wings, those of the cauline leaves basally adnate to the petioles, the apices free and leaflet-like. Inflorescences compact to dense, long pedunculate, many flowered, indeterminate [or determinate] spikes or heads, several inflorescences terminating each stem, each flower nearly sessile, subtended by 1 bract and 2 bractlets (sometimes reduced). Flowers small, perfect or imperfect, the plants then variously monoecious.

Calyx lobes 4, somewhat petaloid, white, green, or reddish, at length deciduous; floral tube urceolate, ± 4-angled, variously textured, a nectar ring nearly closing the mouth of the tube or absent. Petals absent. Androecium of 2, 4, or to ca. 48, included or exserted stamens; filaments white or green, filiform or flattened above, long or short, not persistent; anthers didymous; pollen 6- or 3-colporate. Gynoecium of 1, 2, or rarely more carpels inclosed by, but free from, the floral tube; styles terminal, slightly or greatly exserted beyond the throat of the floral tube; stigmas much branched, the branches short to filiform; each carpel with a solitary, anatropous ovule pendulous from an adaxial placenta, the micropyle superior. Fruit accessory, of 1 or 2 hard-walled achenes inclosed within and filling the enlarged, 4-angled or 4-winged, dry, chartaceous floral tube. Seed coat thin, membranaceous; radicle superior. Base chromosome number 7. (Including *Poterium* L., 1753, and *Poteridium* Spach; *Sanguisorba* and *Poterium* first united, under the former name, by Scopoli, Fl. Carniolica ed. 2. 1: 110. 1772.) LECTOTYPE SPECIES: *S officinalis* L.; see P. A. Rydberg, N. Am. Fl. 22: 386. 1908. (Name from the Latin *sanguis*, blood, and *sobere*, to absorb, from the use of the type species as an astringent.) — BURNET.

Eighteen or more often variable species in four subgenera of the Northern Hemisphere. The genus has been studied in detail by Nordborg, and the classification used here is based on her work. Subgenus SANGUISORBA (flowers all perfect, leaflets crenate or serrate, stamens 12 or fewer) is nearly circumpolar in distribution but is absent from Greenland. Nordborg (1966) recognized two sections and five "species groups." Members of sect. SANGUISORBA (pollen 6-colporate, floral tube ± 4-angled and winged) include *S. canadensis* L., which occurs in our area, and *S. officinalis*, a broadly distributed species (circumpolar except for eastern North America and Greenland). Subgenus POTERIUM (L.) A. Br. & Bouché (flowers perfect and imperfect, the plants variously monoecious, floral tube sculptured in fruit) ranges from Europe, northern Africa, and southwestern Asia to the Himalayas; *S. minor* Scop. is naturalized in North America. Subgenus POTERIDIUM (Spach) A. Br. & Bouché (leaflets pinnatifid, stamens 4 or 2) is composed of one or two species of the south-central United States and western North America. Subgenus DENDRIOPOTERIUM (Svent.) Nordborg (shrubs, all flowers imperfect) has three species restricted to the Canary Islands and Madeira.

Sanguisorba canadensis, American burnet, a tall perennial herb with large pinnate leaves, white flowers in cylindrical, indeterminate spikes, four long-exserted stamens, and one smooth carpel per flower, occurs in moist areas frequently underlaid by peat, such as marshes, meadows, bogs, and prairies from Labrador and Newfoundland to Manitoba and Michigan, southward to New Jersey, Delaware, Ohio, Indiana, and Illinois and in the Appalachians to North Carolina. Plants with broader and shorter leaflets and sepals tinged with red and purple are found in subarctic or montane regions from Alaska to northeastern Oregon and central Idaho; these are variously recognized as a distinct species, *S. stipulata* Raf.[8] (*S. sitchensis* C. A. Meyer) or under *S. canadensis* as subsp. *latifolia* (Hooker) Calder & Taylor or var. *latifolia* Hooker.

There are similar plants in Japan, extreme eastern USSR, Siberia, Mongolia, central Asia, and Iran and Turkey. Some of these populations may be conspecific with *S. canadensis*, while others perhaps represent distinct species; see the discussions in Calder & Taylor (Fl. Queen Charlotte Islands Pt. 1. 410, 411. 1968), Fernald (Rhodora **48**: 12. 1946), Hara (Jour. Jap. Bot. **23**: 31. 1949), Hitchcock *et al.* (fam. ref.), and Nordborg (1966). *Sanguisorba canadensis* has also been reported from several localities in central Scotland from the Firth of Clyde to the Firth of Tay (see Lennie). Reported chromosome numbers for *S. canadensis*, sensu lato, are $2n = 28$ (eastern Canada, British Columbia, Alaska, Sakhalin Island, Mongolia) and $2n = 56$ (eastern Canada). It had been thought that plants from eastern North America were octoploid (and thus specifically distinct), while those from western North America and eastern Asia were tetraploid. Mulligan & Cody found, however, only tetraploids ($2n = 28$) in samples from 41 localities in Nova Scotia, New Brunswick, Quebec, and British Columbia. *Sanguisorba Menziesii* Rydb. (Alaska to the Olympic Peninsula of Washington) is somewhat intermediate between *S. canadensis* subsp. *latifolia* and *S. officinialis* and may be of hybrid origin, being either a chance hybrid or perhaps even an established amphiploid. Nordborg (1966) mentions that *S. albanica* Andr. & Jáv. from Albania is also intermediate between these same species.

Sanguisorba minor Scop. (*Poterium Sanguisorba* L.), salad or garden burnet, $2n = 28, 56$, a variable species of the Old World, is naturalized from Nova Scotia to Ontario south to North Carolina and Kentucky; it is locally adventive in Washington, Oregon, and California. Plants of this species are smaller than those of *S. canadensis*; the inflorescences are greenish, globose or slightly ovoid, and composed of both perfect (below) and functionally carpellate (above) flowers; the stamens of the perfect flowers droop and number 12 or more; there are two carpels per flower; and in fruit the floral cups are roughened between the angles. Its indigenous range is from Scandinavia to northern Africa and the Canary Islands, eastward to southwestern and central Asia. There are both tetraploid and octoploid races, the latter restricted to the Mediterranean area. Numerous segregate and allied species have been proposed. Primarily on the basis of fruit morphology (which is usually not correlated with other characters), Nordborg (1967a) recognized 5 subspecies and several "form series" of *S. minor*. Plants found in eastern North America seem to correspond to subsp. *muricata* (Spach) Nordborg. In an embryological study of this species, Nordborg (1967b) found that while only reduced embryo sacs are functional in spontaneous tetraploid and octoploid plants, there is a strong

---

[8] Nordborg's neotypification (Op. Bot. **11**: 54. 1966) of this name by a specimen from Japan is quite improper; Rafinesque clearly indicated that his material was from the "Oregon Mountains and territory." Also, the name was first published in Herb. Raf. 43. 1833, not in Autik. Bot. **3**: 171. 1840.)

tendency toward apospory. Both amphimixis and apomixis were found in artifical tetraploid and hexaploid hybrids.

Sanguisorba annua (Nutt. ex Hooker) Torrey & Gray, $2n = 14$, of subg. POTERIDIUM is a short-lived tap-rooted perennial or annual herb with pectinately dissected leaflets, short-cylindric inflorescences of perfect flowers, and four stamens. It occurs in disturbed habitats in the south-central United States (Arkansas, Kansas, Oklahoma, and Texas). It is locally adventive in South Carolina and Massachusetts. Clearly related plants with two stamens and with the floral cups merely four-angled at maturity, rather than four-winged, occur in the Pacific Northwest (British Columbia to California, Idaho, and Montana); these are either included in *S. annua* or recognized as a distinct species.

Pollen grains of the tetraploid and octoploid races of *Sanguisorba officinalis* differ in size and shape, and both kinds are often preserved in late-glacial deposits of northwestern Europe; fossil fruits of the species are known from the British Isles. The fossil evidence suggests that *S. officinalis* was common and widely distributed during late-glacial times, with disjunction occurring in the post-glacial period.

Sanguisorba is unusual among Rosaceae in that within the genus is found a series of morphological changes that evidently have resulted from a shift from insect to wind pollination. In the entomophilous *S. officinalis* all flowers are perfect, the inflorescences are red-purple, the stamens are short and stiff, the stigmatic branches are short and compact, and a prominent nectar ring surrounds the mouth of the floral tube. *Sanguisorba minor* is wind pollinated, as are all species of subg. POTERIUM, and the inflorescences are greenish, the stamens filiform and long exserted, the stigmatic branches quite elongate (penicillate), and a nectar ring is nearly lacking; the lower flowers of the inflorescence are perfect, while the upper ones are carpellate. Other species can have different combinations of floral characters. Both *S. canadensis* and *S. annua* have perfect flowers with long filaments and moderately long, tufted stigmatic branches. All the flowers are imperfect in the closely related anemophilous genera *Sarcopoterium* Spach (*S. spinosum* (L.) Spach, eastern Mediterranean area) and *Bencomia* Webb & Berth. (four species of the Canary Islands and Madeira); plants of the former are monoecious, those of the latter dioecious.

Sanguisorba, *Sarcopoterium*, and *Bencomia* constitute the "*Sanguisorba* group" of Nordborg. Allied genera are *Margyricarpus* Ruiz & Pavon (two or more species of Andean South America and the Juan Fernández Islands); *Tetraglochin* Poeppig (possibly eight species of the Andes, often included in the preceding genus); *Acaena* L. (about 40 species, circum-Antarctic: Australia, Tasmania, New Zealand, islands of the southern Indian and Atlantic Oceans, South Africa, Hawaii, Patagonian and Andean South America northward to California); *Polylepis* Ruiz & Pavon (about 20 species, Andean South America); and *Cliffortia* L. (80 species of South Africa with one in East Africa, Nyassaland, and Angola). A natural intergeneric hybrid is × *Margyracaena Skottsbergii* Bitter (*Acaena argentea* Ruiz & Pavon × *Margyricarpus digynus* (Bitter ex Skottsb.) Skottsb.)

from the Juan Fernández Islands. These genera are of particular interest because of their geographical distribution, often bizarre growth habits, frequent occurrence of imperfect flowers and wind pollination, and adaptations for dispersal by animals or wind.

REFERENCES:

Under family references see BATE-SMITH, BOUTINEAU, BUNTING, CHITTENDEN, HEGI, LUBBOCK, RICKETT, ROSS-CRAIG, and WOOD.

BERGLUND, B. E. Late-Quaternary records of *Sanguisorba officinalis* in southeastern Sweden. Bot. Not. **116:** 289–292. 1963.

BÖCHER, T. W., & K. LARSEN. Cytotaxonomical studies in the *Sanguisorba minor* complex. Bot. Tidsskr. **53:** 284–290. 1957.

ERDTMAN, G., & G. NORDBORG. Über Möglichkeiten die Geschichte verschiedener Chromosomenzahlenrassen von *Sanguisorba officinalis* und *S. minor* pollenanalytisch zu beleuchten. Bot. Not. **114:** 19–21. 1961.

GODWIN, H. The history of the British flora. A factual basis for phytogeography. viii + 384 pp. *26 pls. Chart.* Cambridge, England. 1956. [*Poterium* and *Sanguisorba*, 118, *pl. 23*; fossil fruit and pollen remains.]

LARSEN, K. Chromosome studies in some Mediterranean and South European flowering plants. Bot. Not. **109:** 293–307. 1956. [*Bencomia, Dendriopoterium, Marcetella,* discussion of Sanguisorbeae.]

———. Cytology of the genus *Sanguisorba*. Nature **184:** 743, 744. 1959.

LENNIE, J. M. *Sanguisorba canadensis* at Castle Semple Loch. Glasgow Nat. **18:** 522. 1967. [Also see the editor's note that follows.]

LINDENBEIN, W. Beiträge zur Kenntnis der Samen und Früchte. I. *Sanguisorba minor* Scop. und *S. muricata* (Spach) Greml. Ang. Bot. **30:** 107–119. 1956.*

MULLIGAN, G. A., & W. J. CODY. A clarification of the chromosome number situation in *Sanguisorba canadensis*. Canad. Jour. Bot. **51:** 2075–2077. 1973.

——— & ———. Rosaceae, p. 194. *In:* Á LÖVE, IOPB Chromosome number reports XLIII. Taxon **23:** 193–196. 1974. [*S. minor*, $2n = 56$; *S. occidentalis*, $2n = 14$; *S. officinalis* subsp. *microcephala*, $2n = 28$.]

NORDBORG, G. Studies in *Sanguisorba officinalis* L. Bot. Not. **116:** 267–288. 1963.

———. *Sanguisorba* L., *Sarcopoterium* Spach, and *Bencomia* Webb et Berth. Delimitation and subdivision of the genera. Op. Bot. **11**(2): 1–103. *pls. 1–6.* 1966.

———. The genus *Sanguisorba* section *Poterium*. Experimental studies and taxonomy. *Ibid.* **16:** 1–166. 1967a.

———. Embryological studies in the *Sanguisorba minor* complex (Rosaceae). Bot. Not. **120:** 109–119. 1967b.

———. Pubescence in the *Sanguisorba* group (Rosaceae). *Ibid.* **121:** 641–651. 1969.

PHELOUZAT, R. Ontogénie de la pousse aérienne chez le *Poterium Sanguisorba* L. Compt. Rend. Acad. Sci. Paris **255:** 153–155. 1962.

———. Morphologie, phyllotaxie, ontogénie de trois Rosacées: *Agrimonia Eupatoria* L., *Poterium Sanguisorba* L., *Geum urbanum* L. Revue Cytol. Biol. Vég. **26:** 101–362. 1963.*

———. La gamétogénèse et la fertilité dans les fleurs femelles et les fleurs hermaphrodites du *Poterium Sanguisorba* L. Bull. Soc. Bot. France **112:** 370–378. *pls. 1, 2.* 1965.

PIROLA, A. Ricerche su *Sanguisorba dodecandra* Moretti. (English summary.) Ist. Bot. Univ. Lab. Crittog. Pavia Atti V. **21**: 69–103. 1964. [Includes photographs and good illustrations.]

REITSMA, T. Some aspects of the pollen morphology of the genus *Sanguisorba* L. (Rosaceae). Rev. Paleobot. Palynol. **4**: 305–310. 1967. [Reprinted as Meded. Bot. Mus. Herb. Rijksuniv. Utrecht **293**. 1967.]

VAHL, I. On germination inhibitors. III. Germination inhibitors in the fruits of *Poterium spinosum* L. Palestine Jour. Bot. Jerusalem **2**: 28–32. 1940.

WEIMARCK, H. Monograph of the genus *Cliffortia*. 233 pp. Lund. 1934. [Discussion of relationships of *Cliffortia* and its relatives, 176–186.]

(*To be concluded*)

VASCULAR PATTERNS IN PALM STEMS: VARIATIONS OF THE RHAPIS PRINCIPLE

Martin H. Zimmermann and P. B. Tomlinson

Some years ago, we published our first joint paper on the vascular pattern in the stem of *Rhapis excelsa*, a small ornamental palm of South Florida, native of eastern Asia (Zimmermann & Tomlinson, 1965). *Rhapis* was chosen for our first analyses for quite practical reasons. The plant is not too big and is available in quantity. Its stem contains only about 1000 vascular bundles in a transverse section, and it is relatively easily sectioned. Anyone who has ever attempted to section palm stem tissues knows that most species are notoriously difficult to handle, because their hard resistant fibrous vascular bundles are surrounded by soft, yielding parenchyma.

The choice of *Rhapis* proved very fortunate because the vascular pattern of its stem is relatively simple. Ever since its discovery this pattern has served us as a model for the understanding of the more complicated vascular patterns of other monocotyledonous species.

As soon as the study of *Rhapis excelsa* was well on its way we began to look both at other species of palms and at other families of monocotyledons. So far we have studied, in greater or lesser detail, about 30 species of palms in addition to plants of other families (e.g., *Prionium* (Juncaceae), Zimmermann & Tomlinson, 1968; *Dracaena* (Agavaceae), Zimmermann & Tomlinson, 1969; Pandanaceae, Zimmermann *et al.*, 1974; and others as yet unpublished, members of the Araceae, Bromeliaceae, Cyperaceae, Dioscoreaceae, Flagellariaceae, Smilacaceae, Strelitziaceae, Xanthorrhoeaceae). From a taxonomic point of view this is indeed a small number, but from an anatomical point of view it is an amount of information which could not, with conventional anatomical methods, have been gathered by us within our whole lifetimes. We have so far analyzed, and can at any time review again, over 300,000 transverse images.

During the course of our study a number of basic anatomical principles have emerged, the discussion of which is the purpose of this paper. Some of these principles may have physiological, others developmental significance. At the moment we have too little information to comment at length on the taxonomic significance, although in at least one instance it is clear (Pandanaceae; Zimmermann *et al.*, 1974). For the time being, we merely want to describe the variability of the three-dimensional vascular anatomy of the palm family which we have found so far.

METHODS

A motion-picture technique has been used throughout this study. An overall view is obtained by surface methods, whereby transversely cut surfaces of the stem or parts of stem are photographed while held in the microtome, usually at axial intervals of 0.1–1 mm. (depending upon the species) over a length of up to 100 cm. (Zimmermann & Tomlinson, 1967b). One m. is the distance from the laboratory floor to the top of the microtome on the bench. Our instrumentation is steadily improving. Specially constructed microtome clamps permit the continuous advance of the specimen itself rather than the clamp, in contrast to most commercially available sliding microtomes. Focusing of the camera is rather difficult and critical because of the very shallow depth of field in close-up photography. Previously two microscope lamps were used, but this does not give sufficiently bright illumination to allow the camera lens to be stopped down appreciably. A brighter light source was found in an electronic flash, constructed for us by the Electronics Design Center of Harvard University. It is used in conjunction with a synchronized Bolex H 16 REX camera and has several special features. A recycling time of 0.5 sec. enables us to work at a normal rate. A long-life flash lamp is necessary because a single film requires the firing of 4,000 flashes. Ordinary electrolyte condensers failed after several thousand flashes; therefore, large storage condensers were necessary. When the light and depth-of-field problems were finally solved, we found ourselves with too much light! As the camera lens is stopped down, theoretical resolution deteriorates. Resolution limits have been calculated for a number of typical settings and we are now careful to balance the light in such a way that we can stop down far enough for maximum depth of field but still make use of the full resolving power of the 16 mm. film, which is of the order of 20–60 lines per millimeter (50–15 μm.), depending on contrast.

In order to analyze large palms (such as *Cocos*) a piece of stem was quarter cut into a (radial) board with a circular saw. This was further subdivided into two to six "sticks" (or positions) (FIGURE 1). Each of these positions was analyzed separately. The resulting films were studied by projection onto a white sheet of paper on a table via a mirror, where plots could be made by taking positional measurements of individual vascular strands. Radial and longitudinal magnifications were determined in each case by the appearance, on the screen, of a ruler photographed on the first frame of each sequence, and by the number of frames of each sequence and the sectioned length of stem.

Microscopic details were obtained from sequential photography through the microscope of section series cut on a sliding microtome. Most microphotography was done with our shuttle microscope (Zimmermann & Tomlinson, 1966). Since the lowest magnification of the M20 shuttle is limited to a width of ca. 5 mm. on the microslide, and we often needed lower magnification for the larger plants, analyses have also been made with the older drawing method (cf. Zimmermann & Tomlinson, 1965) and a specially adapted M5 Wild stereomicroscope. Since the drawing method is a much slower procedure than the shuttle method, we therefore developed, in collaboration with the Brookfield Machine Company, West Brookfield, Massachusetts, a low-magnification shuttle which now enables us to photo-

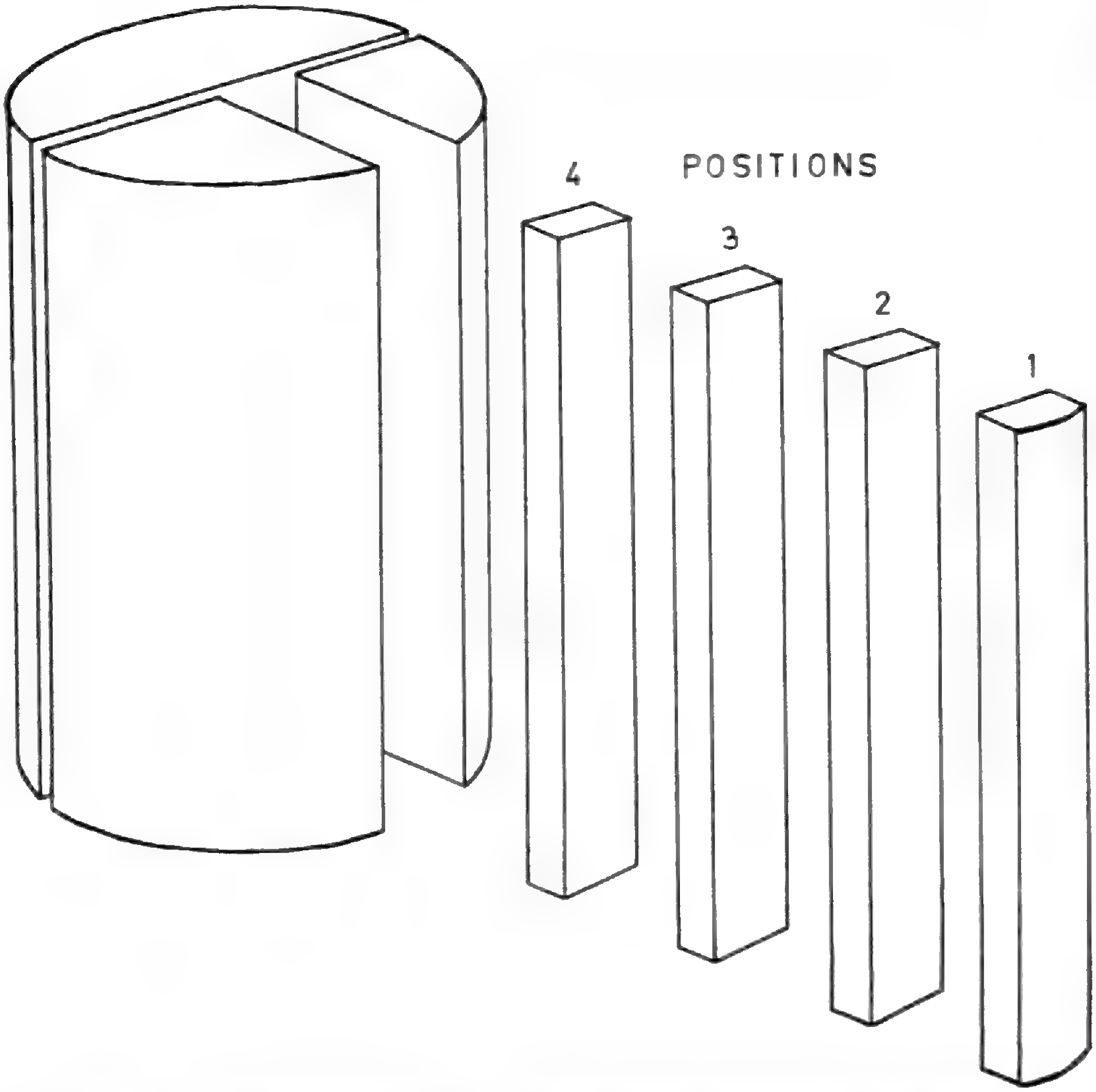


FIGURE 1. Method of dividing a large palm stem into "positions" which are analyzed separately by surface photography.

graph sections up to 24 mm. wide. (This instrument is illustrated on p. 12 in Zimmermann, 1971).

TERMINOLOGY OF THE VASCULAR SYSTEM

It is perhaps useful if we start out with a brief summary of our terminology as we have used it in our earlier papers. Longitudinally running stem bundles are now called *axial bundles* (a term we have substituted for "vertical bundles," which was used in our earliest papers, because axial bundles are horizontally oriented in rhizomes). As we follow an axial bundle distally, it approaches the center of the stem and then reaches a point where it turns out toward the stem periphery and finally enters a leaf. This point of deepest penetration into the stem is regarded as the most distal point of the bundle. Arbitrarily from this point to the level of entry into the leaf, the bundle is referred to as a *leaf trace*. *Major*, *intermediate*, and *minor* leaf traces (bundles) are distinguished which differ not only in diameter (major ones being the widest), but also in degree of penetration from surface towards the stem center. Axial-bundle length is measured by number of internodes from one leaf trace to the next, the *leaf-contact distance*, and is usually longest in major bundles.

Structurally the most important feature of monocotyledonous vascular anatomy is the upward-branching of each leaf trace. Normally, one axial bundle is among these branches, though there may be none or more than one. Thus the stem maintains a more or less constant number of vascular bundles as it grows taller. Other types of bundle branch upward from the leaf trace. *Bridges*, up to as many as six, connect the leaf trace with neighboring axial bundles. In the presence of an axillary bud or branch, either vegetative or reproductive, and even if the branch is aborted early during development, there are additional branches of the leaf trace, called *satellite bundles*, or simply *satellites*, connecting the leaf trace with the axillary axis (Zimmermann & Tomlinson, 1972; Tomlinson, 1973).

In addition to the vascular system of the central cylinder which we refer to as the *inner system*, there is a system of fibrous cortical traces which we refer to as the *outer system*. The developmental significance of the two has been discussed recently (Zimmermann & Tomlinson, 1972). Additional fibrous strands are present in certain species among the regular vascular bundles of the central cylinder; these are described under the heading "Fibrous bridges."

We would like to emphasize again at this point that in our descriptions we use a terminology which is descriptive of what one can see in analytical films. We speak of "leaf-trace departure," of bundles that "move," "give off branches," are "borrowed," etc. It does not imply developmental events, or movement, but merely describes what one can see in the projected films.

THE THREE-DIMENSIONAL BUNDLE ARRANGEMENTS

From the outset we were faced with the problem of representing for publication three-dimensional bundle paths in two dimensions. We usually do this by showing all bundles in a single radial plane, regardless of their relative compass orientations within the stem. Description in the text or a complementary plot on a transverse plane was used to help the reader to reconstruct the three-dimensional image in his mind. FIGURE 2 shows the plots of two bundles of *Geonoma* in the conventional radial and transverse views.

In stems of many palms, as one watches surface motion-picture sequences, one can see the central bundles all following a helical path, i.e., they describe a rotating motion clockwise or counterclockwise on the projection screen. This helical path of axial bundles is established early during development (*cf. Figure 1* in Zimmermann & Tomlinson, 1967a) and goes in the same direction as the phyllotactic spiral of the stem. The helical path may be more or less distinct, and in some cases there may be two helices rotating in opposite directions in the central and subperipheral areas of the

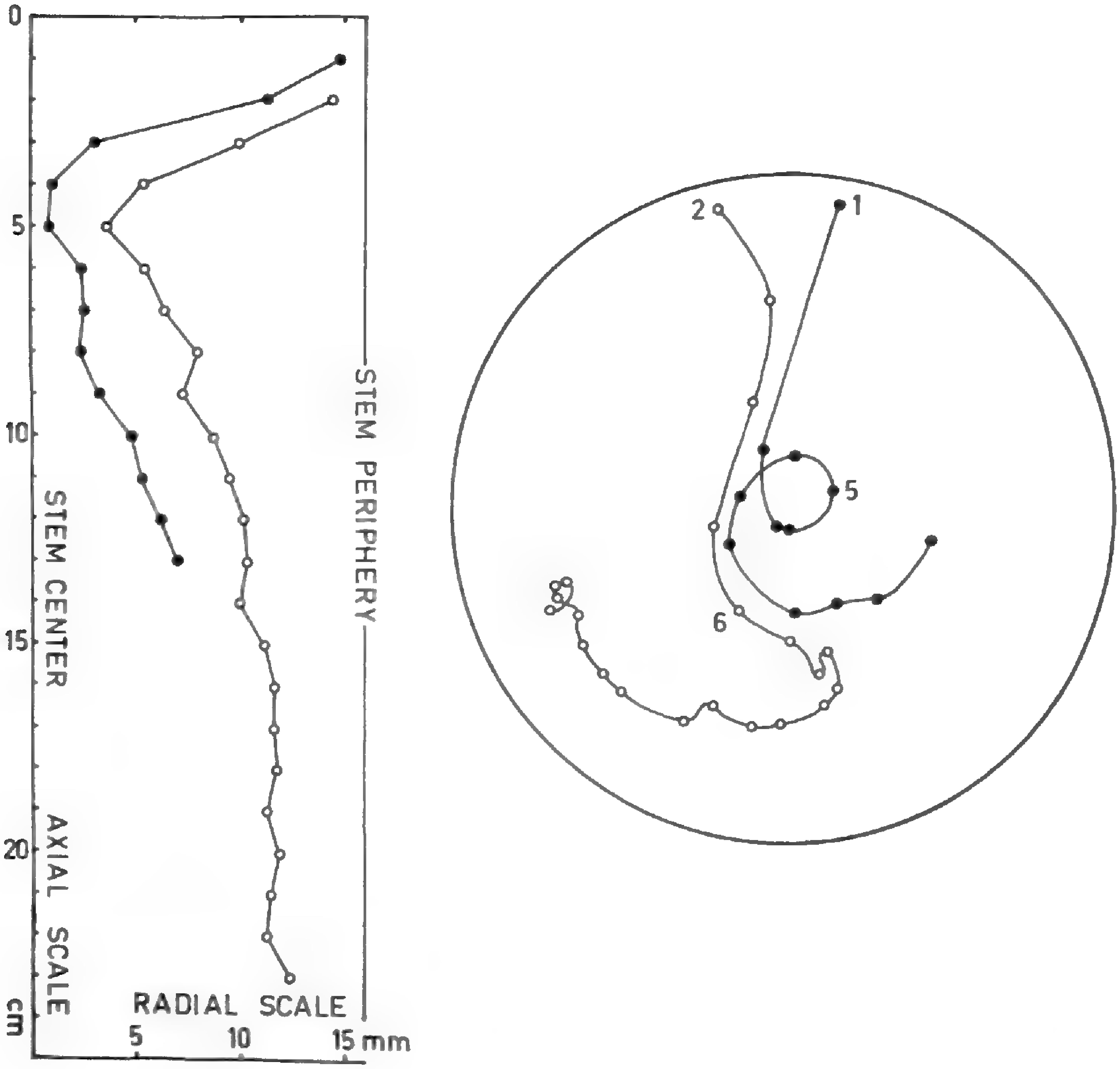


FIGURE 2. The three-dimensional course of two bundles of *Geonoma*. On the left Von Mohl's "double curve" of two vascular bundles along the stem is shown in a radial plane. The plot on the right shows the same bundles and the same points of measurement in axial view, i.e. projected onto a transverse plane. The numbers indicate centimeters on the axial scale. The bundle indicated with dots described two full turns along the inner helix before it left the field of view. The bundle indicated by the circles described a half turn along the inner helix, then a fourth of a turn along the outer (counter-running) helix before nearing the periphery of the central cylinder. Note that the axial scale in the left-hand figure is about 5 times foreshortened.

stem respectively, with only one of them corresponding to the phyllotactic spiral. This is so in *Geonoma* and can be recognized in FIGURE 2.

For reasons of clarity we ordinarily ignore the helical-bundle path and use our conventional two dimensional illustrations in which all bundle positions within the stem are rotated into a single radial plane. In other words positions are given as distances from stem center (or periphery) regardless of compass orientation.

AXIAL BUNDLE CONTINUITY

Perhaps the most important single aspect of monocotyledonous stem anatomy is the pattern that provides the continuity of vascular bundles along the stem. When we started our work with *Rhapis* the question we asked ourselves was why is the stem not depleted of vascular bundles, if of the 1,000 axial bundles in a single transverse section 100 "depart" as leaf traces into each leaf? The answer for *Rhapis* and many other plants, as is now well known, is the fact that each departing leaf trace branches upwardly and thus gives rise to a continuing axial bundle. However, we have subsequently found that this is not the only answer. Furthermore, bundle continuity must be looked at from a functional as well as developmental point of view.

One could regard the continuing axial bundle of the *Rhapis* stem as a single structure from which, at certain intervals, leaf traces branch off, as has been done for dicotyledons (cf. Devadas & Beck, 1972). This makes sense functionally because the continuing bundle consists of metaphloem and metaxylem whereas the leaf trace portion contains only protophloem and protoxylem. Functionally even more important than the axial-bundle branch, at least in a quantitative respect, are the bridges which provide, from each leaf trace, half a dozen or so alternate translocation pathways (Zimmermann, 1973). During later maturation of the stem the axial-bundle branch is often obliterated by weathering of the stem surface if it is located near the stem periphery, and bridges thus provide the only axial continuity because they are more centrally located (cf. FIGURE 3, Type C).

However, from a developmental point of view, the continuing axial bundle cannot be regarded as a continuous unit with leaf traces attached at intervals, because vascular strands differentiate in distinct stages. The leaf trace branches at the periphery of the cap, and as the stem apex grows distally away from the leaf trace, the axial bundle elongates with its proximal end attached to the leaf trace and its distal, growing end in the cap. This elongation continues until the distal end of the axial bundle in the cap is connected with a newly arising leaf trace into a growing leaf primordium. Thus the developing unit is a vascular bundle consisting of an axial bundle and its upper leaf-trace end (Z-Y-X in *Figure 3* in Zimmermann & Tomlinson, 1972). This unit remains discrete for a number of plastrochrones until its distal leaf-trace end branches as it reaches the cap periphery.

SMALL-PALM TYPES

The vascular patterns of small palms so far examined (with stems up to a diameter of about 3 cm.) are all similar to the *Rhapis* type; they differ merely in the position of the axial bundle branch, which can be located anywhere between the stem center and the periphery (FIGURE 3).

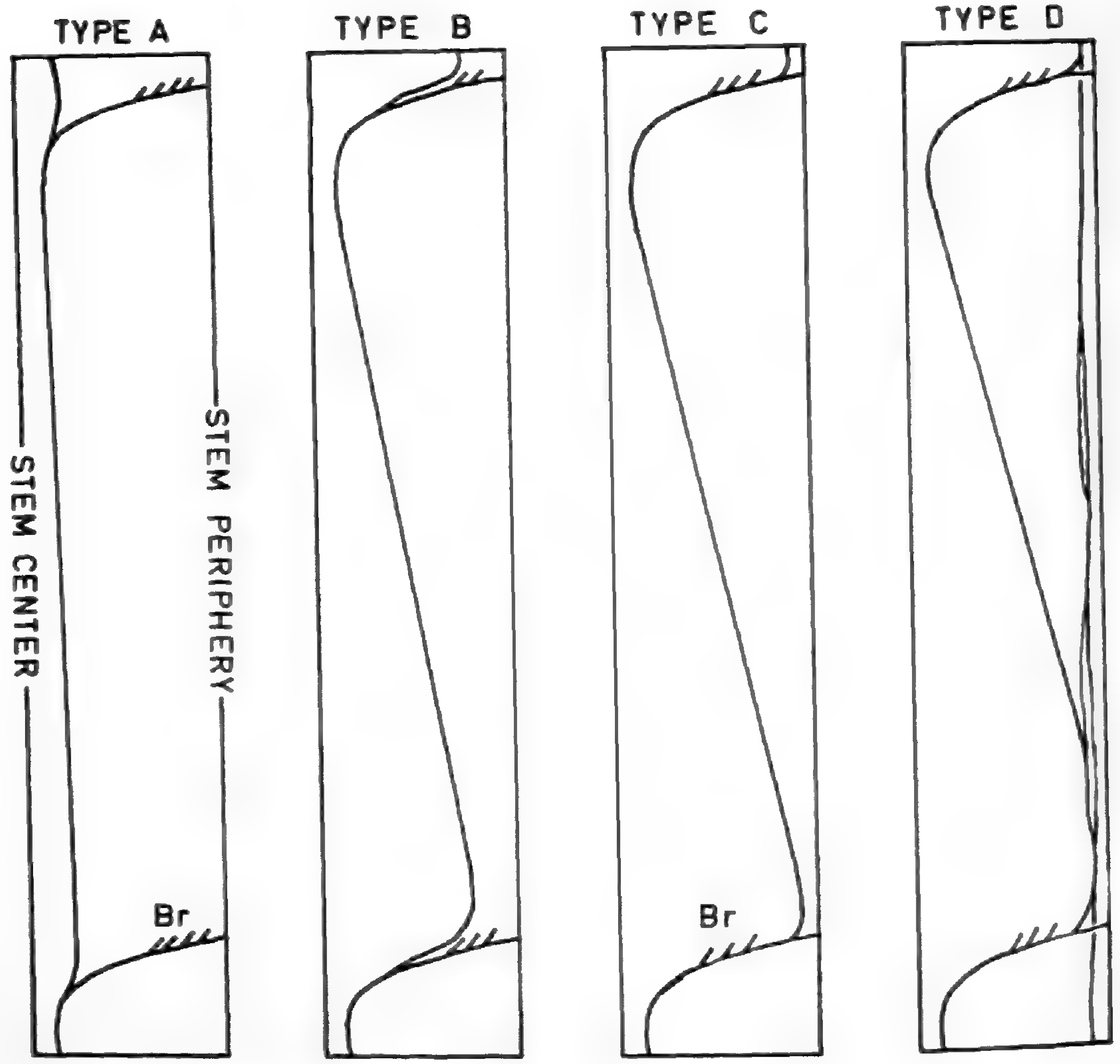


FIGURE 3. Diagrammatic representation of the path of vascular bundles in some small palms. The helical path is ignored, bundle positions are all shown in a single radial plane.

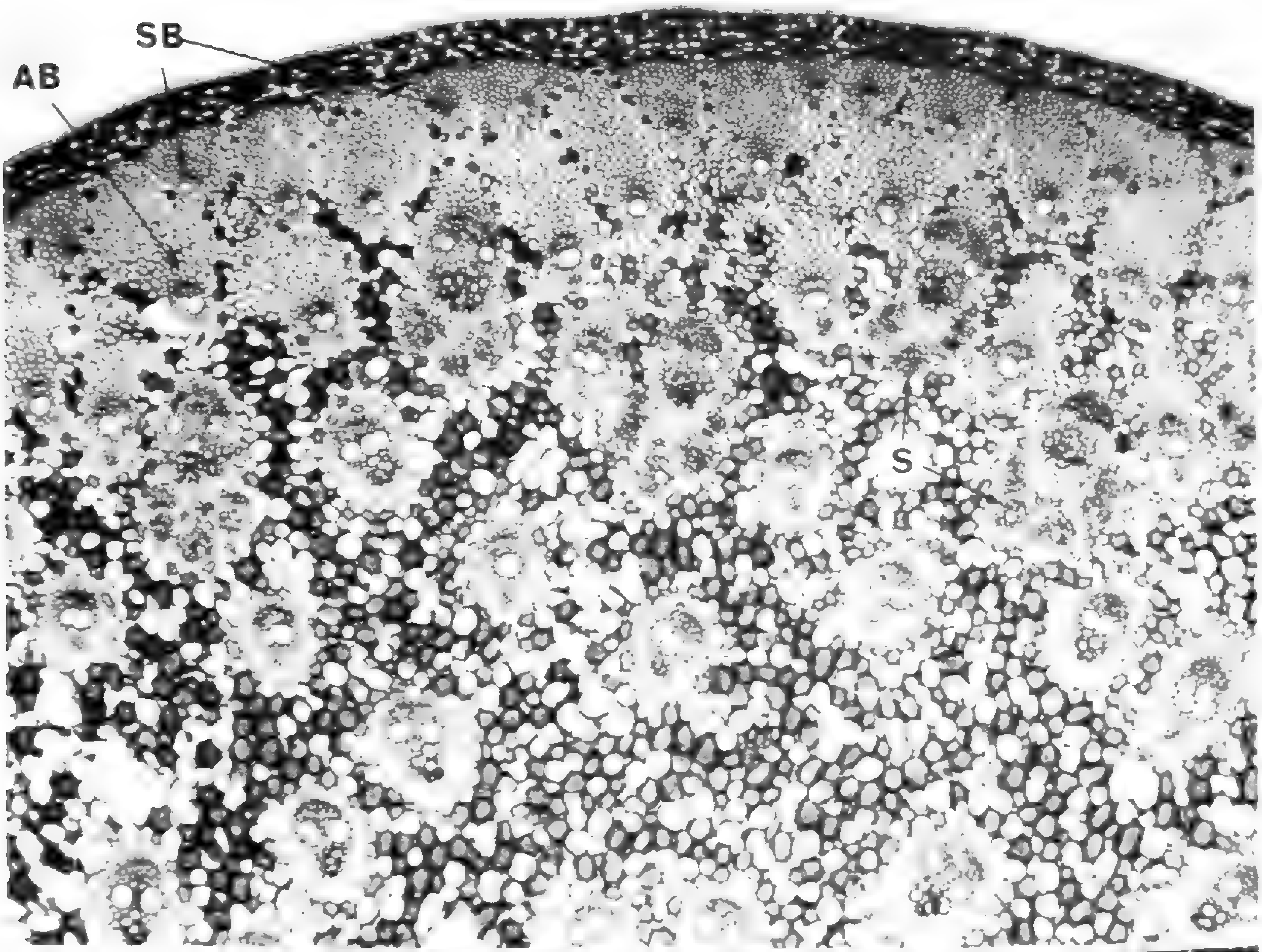
The Rhapis-Rhizome Type (FIGURE 3, Type A). This pattern was first found in the *Rhapis* rhizome and has been illustrated before (*Figure 4* in Tomlinson & Zimmermann, 1966a). The illusion that the leaf trace is merely a branch of the axial bundle is most pronounced in this example because the axial bundle maintains an almost perfectly axial path even in the region of leaf-trace departure. However, even here the developmental sequence indicates that the axial bundle with its distal leaf-trace end develops six plastochrones before the axial-bundle branch (the continuing axial bundle) is initiated (*Figure 3* in Zimmermann & Tomlinson, 1967a). The seeming redundancy of a vascular system in an organ like the scale leaf, which neither assimilates nor has any storage function, underscores the importance of the developmental events which lead to the establishment of the vascular system of the axis.

The Rhapis-Aërial-Stem Type (FIGURE 3, Type B). This pattern has received sufficient attention in numerous publications that we need not describe it further. As in the previous type, the axial bundle is usually developmentally the first, and in the mature stem the most proximal, leaf-trace branch. In a motion picture of transverse sections it can be seen to follow the leaf trace on its way toward the periphery, while numerous additional branches are given off from the leaf trace. These branches are mostly bridges, but at the level where the stem has become reproductive many are also satellites. The axial bundle is left behind near the periphery of the central cylinder; from there it resumes its course up the stem and repeats the cycle. *Bactris major*, *Chrysalidocarpus lutescens*, and *Hyospathe elegans* are of this type, although they are somewhat different from *Rhapis* in other respects.

The Geonoma Type (FIGURE 3, Type C) differs from the previous one in that the axial-bundle branch is one of the most distal (peripheral) to come from the leaf trace, very near the periphery of the central cylinder. The distinction between Types B and C is somewhat arbitrary; the patterns of *Rhapis* and *Geonoma* are quite similar. The juvenile axis of *Iriartea exorrhiza* is of this type. *Iriartea* is a stilt palm; the diameter of its stem increases from less than one to some 20 cm. over a height of 1–2 meters (see *Figure 6* in Tomlinson, 1961). We have not yet looked at a large-diameter stem.

The Chamaedorea Type (FIGURE 3, Type D). *Chamaedorea* was one of the first genera that we investigated after we had studied *Rhapis*, because the genus contains a number of small, easily obtainable species. It resembles *Geonoma* in that each leaf trace often gives off one, or occasionally two axial bundles near the periphery of the central cylinder. On the other hand, many outgoing leaf traces can be observed in motion-picture sequences, which give off only bridges and no discrete axial bundle. *Chamaedorea* has practically no cortical (fibrous) bundle system. However, the periphery of the central cylinder consists of numerous crowded, small vascular bundles which are quite freely anastomosing (FIGURE 4). As one follows a transverse section series upwards, one can observe that departing leaf traces contribute bridges to this peripheral small "bundle-pool" and that larger, discrete (i.e. nonanastomosing) vascular bundles emerge from this "pool" and continue to repeat the cycle at a higher level. This behavior has also been found in *Desmoncus* and *Ptychosperma*. It has been described before for *Dracaena fragrans* (*Figure 10* in Zimmermann & Tomlinson, 1969).

It should be stressed that there is no sharp distinction between the four types shown in FIGURE 3 and described above. There is a continuous range of patterns from A to D, and any one palm may either resemble a given type closely or be intermediate between two of them. Furthermore, it is possible that the pattern gradually changes with increasing height within a single stem, as is described below in a special section. So far at least, this



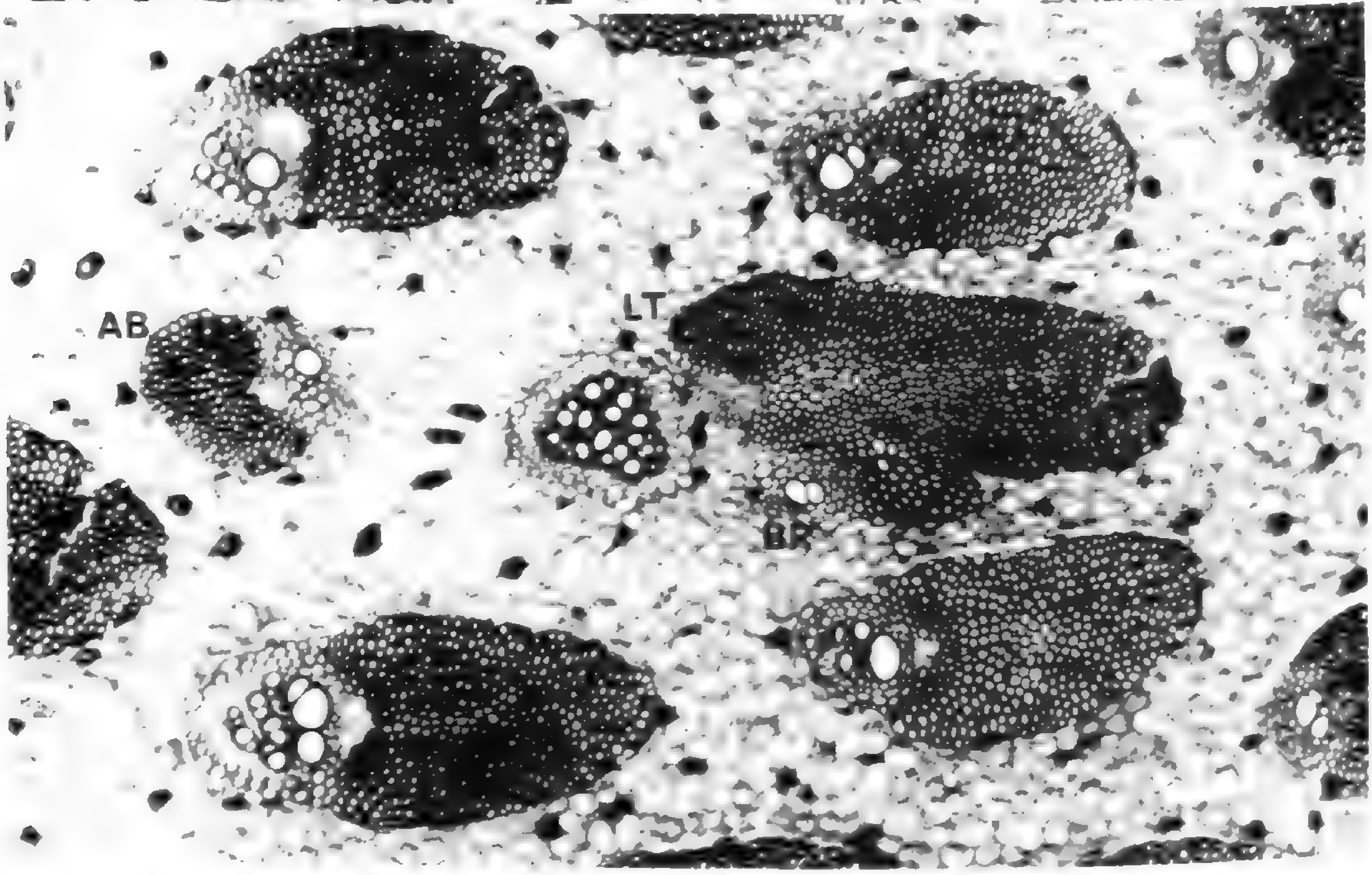


FIGURE 4 (above). Stem transverse section of *Chamaedorea* sp., showing axial bundles (AB) and peripheral, small, anastomosing bundles (SB). Deeply-inserted satellites (S) are seen associated with leaf traces.

FIGURE 5 (below). Detail from stem transverse section of *Nannorrhops ritchiana*. From a single section it is impossible to know whether an axial bundle (AB) associated with a leaf trace (LT) is either a branch of this leaf trace or merely "borrowed." A presumed bridge (BR) can be seen splitting off the leaf trace (LT).

classification of patterns serves the purpose of allowing us to describe the vascular pattern in each new species we investigate.

LARGE-PALM TYPES

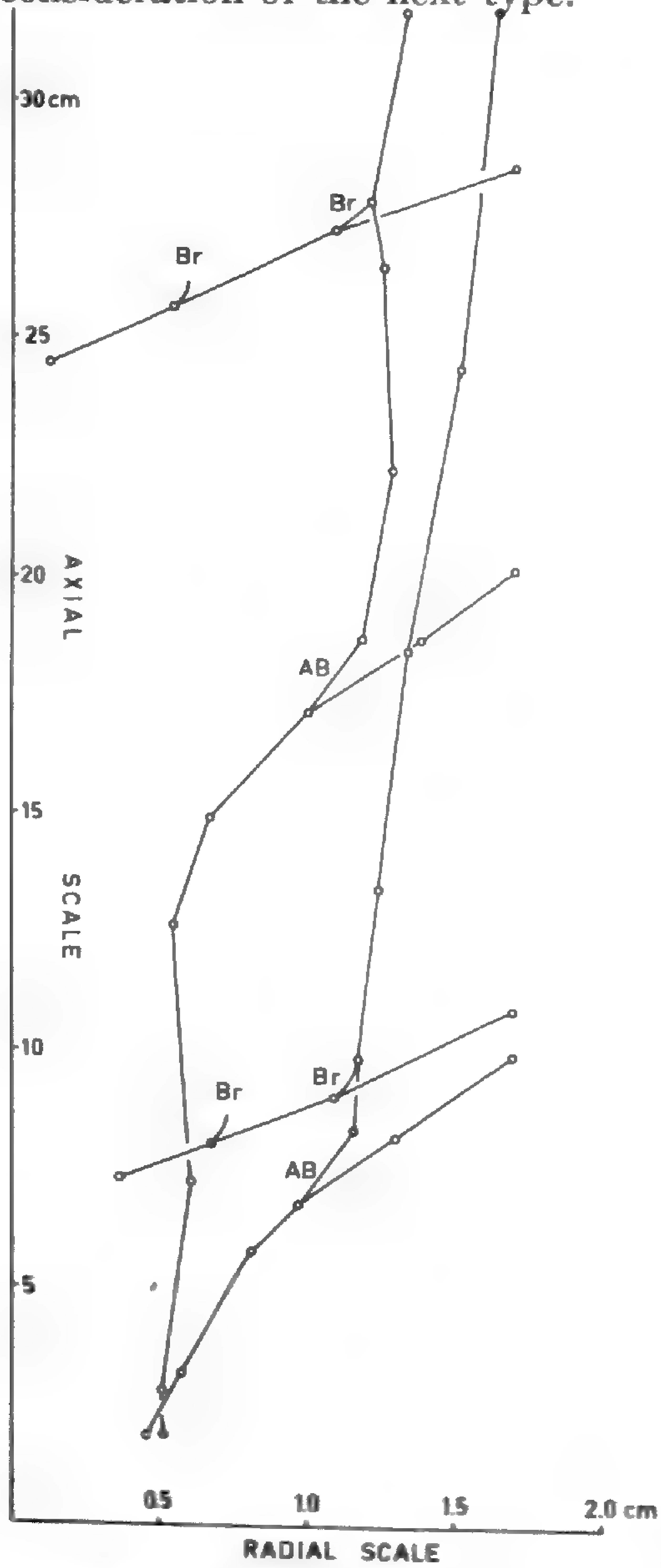
While the patterns in small palm species resemble each other, larger palms (with stems well above a diameter of 3 cm.) do not merely show the *Rhapis* principle in bigger dimensions; their patterns are considerably more complicated. The reason for this is probably functional: the apical region of a large palm could not receive nutrients in as straightforward a way as in small palms simply because the direct distance from mature photosynthesizing leaves to meristem is too great across the immature tissues of the crown region. Although we have not as yet analyzed the developmental pattern of a palm as large as a coconut, we believe that from our knowledge of the structure of a small apex we can make certain extrapolations to the larger ones. It remains to be seen whether this assumption will prove to be correct.

Large palms cannot be analyzed as completely as small ones. Sheer size makes it impossible to follow a bundle, particularly a major one, along its entire leaf-contact distance. With the surface method we can follow bundles over a maximum axial distance of 100 cm. (provided they are not lost to the field of view) as described in the METHODS section. We then have to piece together and intrapolate what we have seen. Even in a relatively small palm like *Chrysalidocarpus lutescens* where we have followed entire leaf-contact distances of minor bundles over distances of about 40 cm., plots of individual parts of major bundles indicate that leaf-contact distances of major bundles may be as long as 2 meters or more (FIGURE 7). Nevertheless, the necessarily incomplete analyses which we have so far carried out have provided a wealth of information for comparative purposes.

The Phoenix Type. The central part of aërial stems of a number of species show a vascular pattern of the Type A as illustrated in FIGURE 3. This was first found in the two *Phoenix* species we analyzed (*P. roebelenii* and *P. dactylifera*) and involved major as well as intermediate bundles (FIGURE 6). It was further found in a number of other palms, namely *Acoelorrhaphe* (*Paurotis*) *wrightii*, *Sabal palmetto*, *Washingtonia filifera*, and others, but here only in major bundles, i.e., only in the very center of the stem. The plotted course of some central (major) bundles of *Phoenix roebelenii* is shown in FIGURE 6. As a consequence of this branching pattern axial bundles run much more nearly axis-parallel than in the other types. A comparison of Type A with Types B–D (FIGURE 3) makes this clear.

It is interesting to note that Hilgeman (1951) had recognized this phenomenon in *Phoenix dactylifera* and therefore concluded that Von Mohl was incorrect in his classic description of a "double curve" for monocotyledonous stem bundles (i.e. the bundle path as shown in FIGURE 2). We know now that Von Mohl (1824) was not wrong. The double curve is practically always present as FIGURE 6 shows; it is merely less pronounced in the one species investigated by Hilgeman.

Although all leaf traces show numerous bridges, intermediate and minor bundles (in *Washingtonia* and *Sabal*) and minor bundles (in *Phoenix*) do not show any leaf-trace-axial-bundle branch. This observation leads to a consideration of the next type.



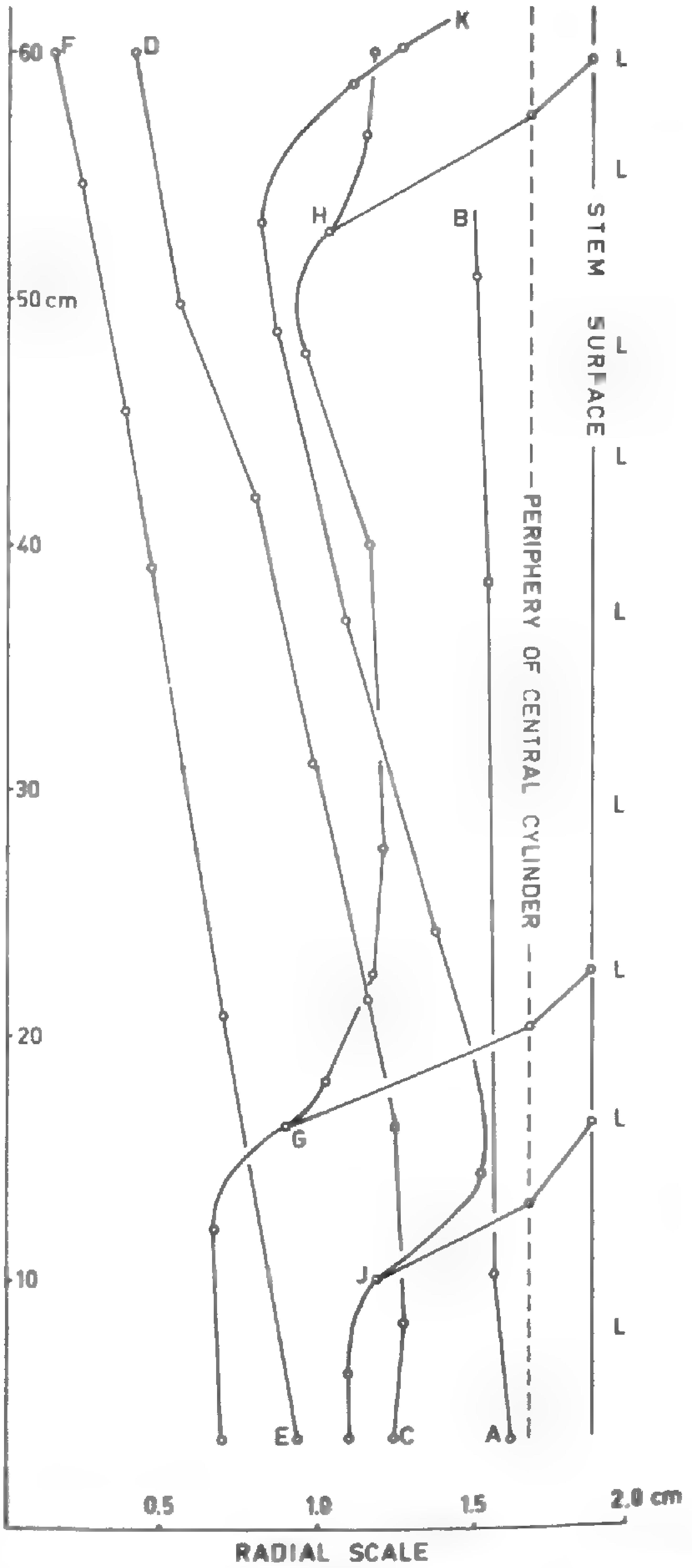


FIGURE 6 (left). Intermediate position in the stem of *Phoenix roebelenii* showing plots of two different leaf-trace-axial-bundle branches (at AB), and bridges to these axial bundles from other leaf traces (Br). Note that the position of the radial scale is arbitrary, neither periphery nor center of the stem are in the field of view. The axial scale is foreshortened about six times.

FIGURE 7 (right). The peripheral stem region of *Chrysalidocarpus lutescens*. Leaf insertions are indicated by (L) along the stem periphery. One complete leaf contact is shown for a minor bundle (G–H); it is six internodes long. Another minor leaf contact (J–K), eight internodes long, is almost complete. Axial-bundle portions A–B, C–D, and E–F indicate that the leaf-contact distance of major bundles must be very long (two or three meters). The stem center is outside the field of view. The axial scale is foreshortened about 12 times.

The Regeneration Type. Palms like *Phoenix* and *Sabal* puzzled us because we could not see any axial bundle branch off the intermediate and minor leaf traces. As one follows a transverse-sectional series up the stem, leaf traces continuously depart and bundles are thus lost from the stem. In careful study of the peripheral area in which, we were certain, must lie the answer to this puzzle, it was discovered that, going up, the axial bundles are continuously "replenished" by fibrous cortical bundles "drifting" from cortex to central cylinder and becoming vascular (axial) bundles. When followed on their way up, these replenishing bundles appear initially very small as they enter the central cylinder, but quickly enlarge into fully fledged vascular bundles as they receive bridges from departing leaf traces. We may define these cortical bundles as inner-system bundles (Zimmermann & Tomlinson, 1972). It took some time (and thousands of sections!) before the proximal ends of these fibrous bundles were found. The inner system seems to be regenerated from the outer one, in a manner comparable to the establishment-growth phase of *Dracaena fragrans* which we have already described (Zimmermann & Tomlinson, 1970). There is a regular network of outer fibrous (and phloem-containing) bundles (i.e. outer leaf traces) in the outer cortex with which axial bundles are in contact via inner fibrous cortical bundles (Figure 9). The Regeneration Type is very common in large palms such as *Cocos*, *Elaeis*, *Phoenix*, *Roystonea*, *Sabal*, *Washingtonia*, etc., but we have also observed it in the basal part of the stem of *Chrysalidocarpus lutescens*. In *Bismarckia* we found it in spite of the fact that almost all leaf traces (even minor ones) have an axial bundle branch. However, many of the peripheral axial bundles are lost to the inflorescence (see the section on Borrowed Axial Bundles).

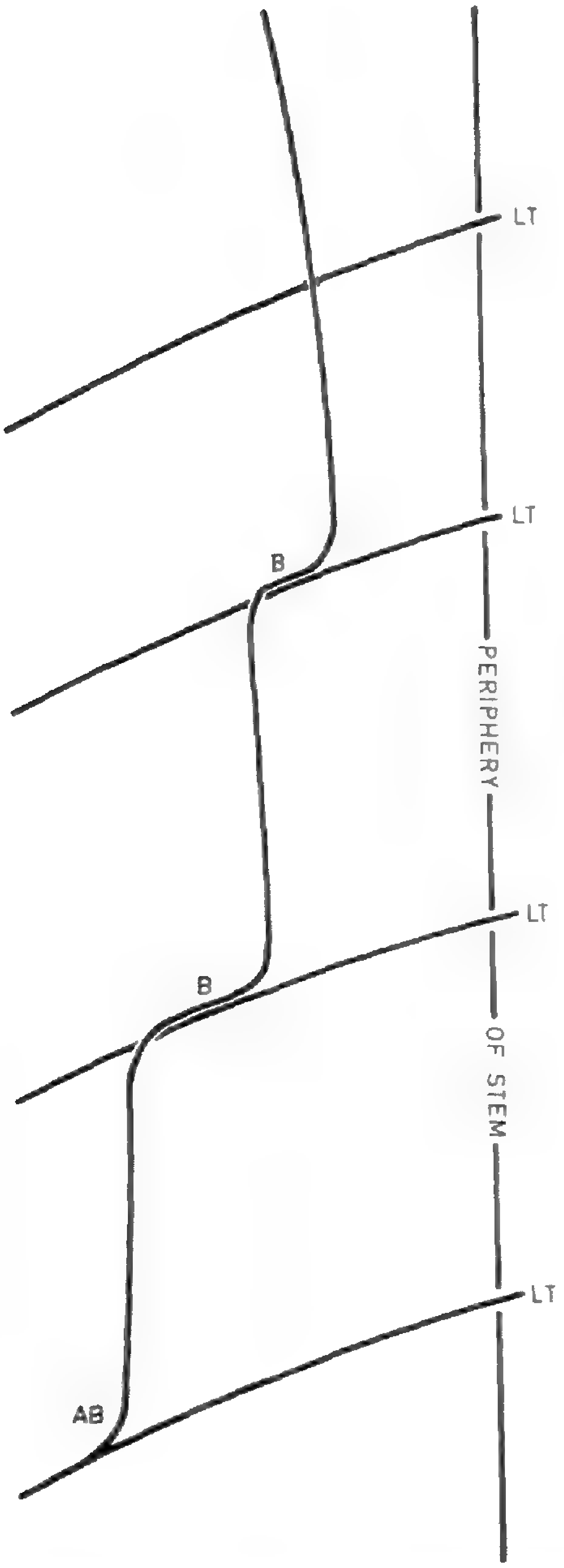
In *Chamaerops humilis*, *Elaeis guineensis*, and other palms, we have seen fibrous axial bundles branching from minor leaf traces in the inner cortical region, just outside the central cylinder. Followed in an upward direction these fibrous bundles enter the central cylinder where they become regular vascular axial bundles by receiving bridges from outgoing leaf traces (Figure 9, at C).

It must be emphasized that these axial-bundle origins which we have described are not very distinctly different from each other. In fact, there is a rather continuous range of ways in which the axial bundle can be derived from lower traces. The structural interrelationship may be expressed as follows, for descriptive, comparative purposes (Types A–D as illustrated in Figure 3, Regeneration Type in Figure 9):

$$\begin{tikzcd} & & & \text{Type D} \\ \text{Type A} \arrow[r, leftrightarrow] & \text{Type B} \arrow[r, leftrightarrow] & \text{Type C} \arrow[ur, leftrightarrow] \arrow[dr, leftrightarrow] & \\ & & & \text{Regeneration Type} \end{tikzcd}$$

This is intended to suggest that any one type can be regarded as a modification of another.

Any one palm can be assigned a region along this continuous range of possibilities. Thus *Chamaedorea* species, for example, are actually most often intermediate between the *Chamaedorea* (D) and the *Geonoma* Type



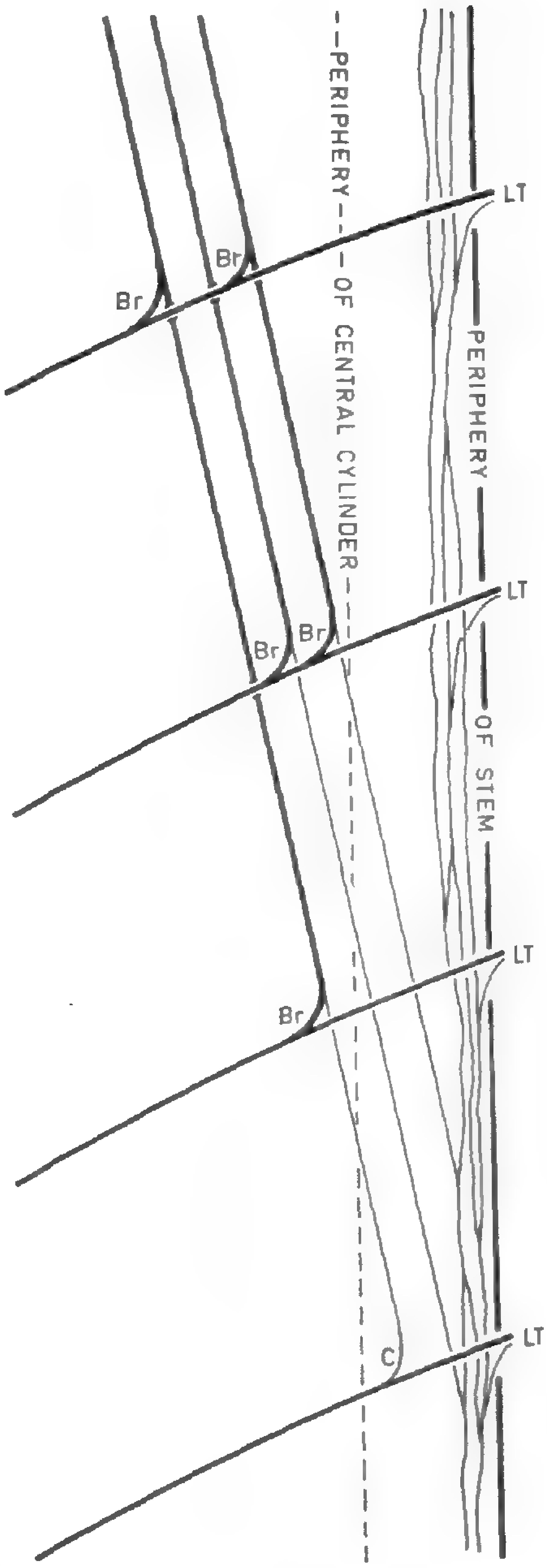


FIGURE 8 (left). The principle of a "borrowed" axial bundle shown in a radial plane. An axial bundle branches off a leaf trace (at AB). Higher up in the stem it closely follows other leaf traces on their path toward the stem periphery (at B). LT = leaf trace.

FIGURE 9 (right). The principle of regeneration of the inner from the outer system shown in a radial plane. From the network of fibrous bundles and fibrous leaf traces near the stem periphery (thin lines, the outer system), fibrous bundles enter the central cylinder in a distal direction. By receiving bridges from outgoing leaf traces (at Br), they become regular, xylem-containing axial bundles. In some cases fibrous axial bundles are given off the leaf trace in the cortical region (as indicated at C). These also enter the central cylinder and become axial bundles by receiving bridges from outgoing leaf traces. Each leaf insertion is shown with one inner and one outer leaf trace at LT.

(C). *Phoenix*, *Sabal*, and *Washingtonia* occupy two regions along this continuous scale. The stem center is of the *Rhapis* Rhizome Type (A), whereas the periphery is of the Regeneration Type.

Borrowed Axial Bundles. A further complication of the pattern of leaf-trace-axial-bundle branching is shown diagrammatically in FIGURE 8, a very common type in large palms. As one follows a leaf trace acropetally one can see the axial bundle branching off at the point where it begins to turn toward the periphery (FIGURE 8, AB). On its way up, the axial bundle can be seen to follow closely another, unrelated leaf trace for a short distance, but it is left behind again. It may do this repeatedly. Thus it may eventually reach a point nearer the periphery of the central cylinder whence it gradually regains the stem center again (upper part in FIGURE 8). In our working jargon, we call this a "borrowed" axial bundle. Axial bundles which are borrowed, i.e., follow unrelated leaf traces, have no vascular contact with them. In a single transverse section such grouping of a leaf trace and an axial bundle looks conspicuous (FIGURE 5) and only three-dimensional analysis shows whether the axial bundle is actually a branch of the leaf trace or is merely "borrowed." As an example, a plot of the paths of two "borrowed" axial bundles is shown in FIGURE 10. The possible developmental significance of borrowed bundles is discussed further below.

It may be added that the "borrowing" of axial bundles can take place to a variable degree. It is very pronounced in many palms such as *Cocos nucifera*, *Chamaerops humilis*, etc., or there may be only a slight tendency for it in smaller palms such as *Chrysalidocarpus lutescens* where it is easily overlooked.

BRIDGES

The presence of bridges, i.e. upwardly-directed branches of the leaf trace connecting with neighboring axial bundles, is one of the most constant features of monocotyledonous vasculature as we have observed it in representatives from a wide range of families (information largely unpublished). About 2 to 6 bridges usually come off each leaf trace. These are often very short, such as in *Dracaena fragrans* (Zimmermann & Tomlinson, 1969) or the peripheral region of *Geonoma*. A departing leaf trace in that case almost touches the neighboring axial bundle at the point where vascular contact is made via a bridge. Bridges are often longer, i.e. one to several millimeters, and then link bundles more remote from each other.

From a functional point of view, bridges are of considerable importance, because they provide alternate axial as well as lateral pathways of translocation (Zimmermann, 1973). In palms of the type described under the heading "Regeneration Type," where direct axial branches from leaf traces are missing, they are indeed the only means of providing axially continuous pathways. This is also true, as we have mentioned, in palms with very peripherally located axial bundle branches when the old stem periphery, as often happens, weathers away.

ANASTOMOSING BRIDGE SYSTEMS

In certain cases, bridges are quite long. As one watches such a bridge in a transverse-sectional series in acropetal direction, one gets the initial impression that one is following an axial bundle which has branched from the

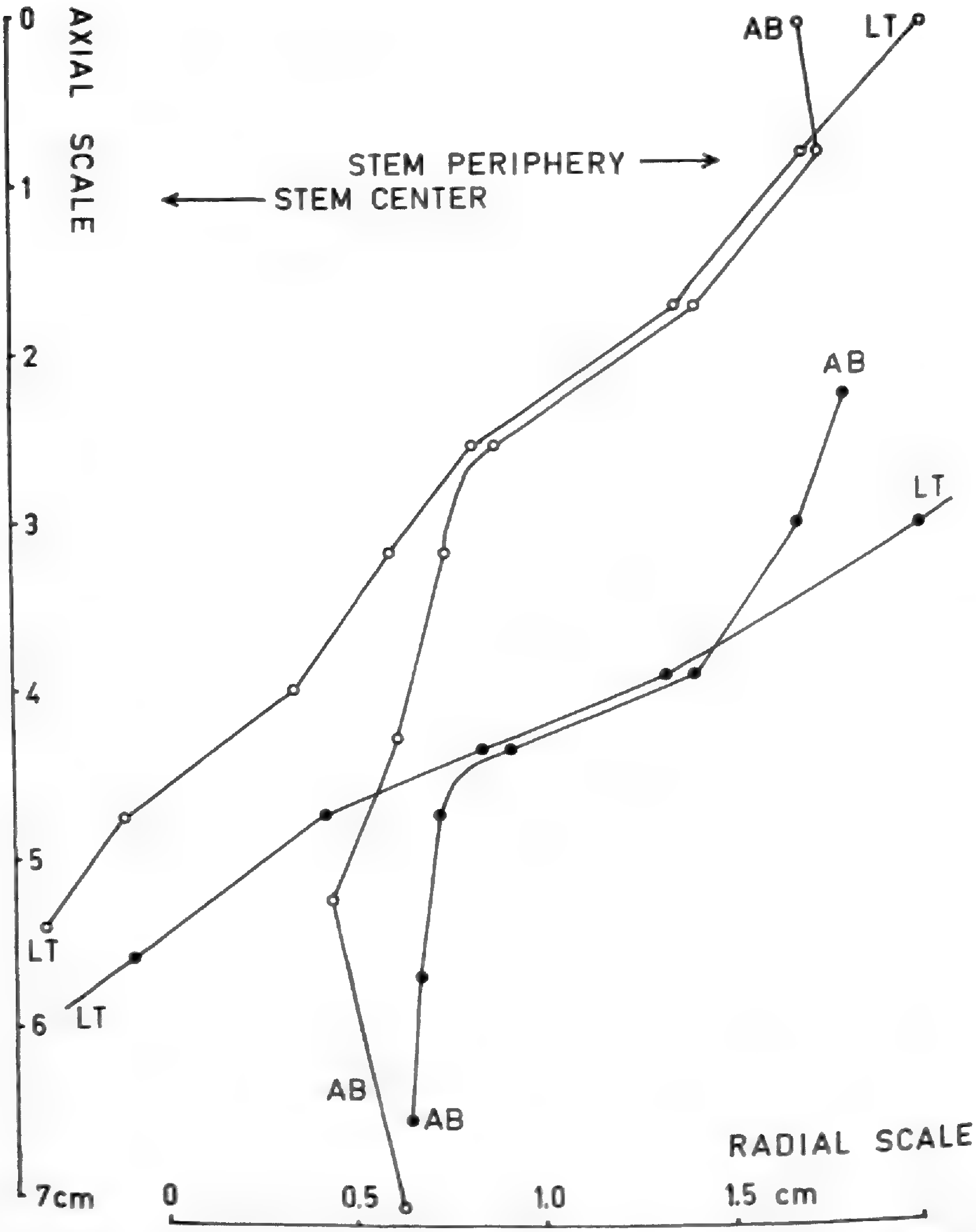


FIGURE 10. Parts of the paths of two leaf traces in an intermediate position of the stem of *Arecastrum romanzoffianum* plotted on a radial plane. Neither the stem periphery nor the stem center are in the field of view. The radial scale is in an arbitrary position. Along each leaf-trace path (LT) an unrelated axial bundle (AB) is shown to run closely parallel. This is referred to in the text as "borrowing." Note that the axial scale is foreshortened about two times.

leaf trace. As one continues to follow the course of this bundle further, it may then finally fuse with a neighboring axial bundle and thus manifest itself as a bridge. This has been found in the *Rhapis* rhizome (Tomlinson & Zimmermann, 1966a, p. 310). In other cases numerous long bridges come off the leaf trace and anastomose freely among each other; some of the branches fuse with neighboring axial bundles, others may become independent axial bundles. This was first found in the juvenile axis of *Rhapis* (Tomlinson & Zimmermann, 1966b). Anastomosing bridge systems are quite common in larger palms such as *Cocos* and *Nannorrhops*.

Fibrous bridges

Vascular tissues of bridges are usually similar in their appearance to those of vascular bundles, thus indicating that they are regular pathways of transport. The chief difference is mechanical, since axial bundles have a much greater development of fibrous sheathing tissue. Indeed the functional significance of bridges, i.e. their full transport capacity, has recently been confirmed in an experiment in which ^{14}C sugar has been found to move freely from bundle to bundle via bridges (Zimmermann, 1973).

In other cases, bridges are very small and consist only of a fibrous strand, sometimes with a phloem center. We interpret these fibrous bridges tentatively as vascular strands which are functional only during earlier stages of stem development and cease to function as transport channels as the stem matures. Such bridges are found occasionally in some species, but in others they are a regular feature. In the central part of the *Geonoma* stem, for example, there is a regular anastomosing fibrous bridge system. Some of these bridges have a central phloem core and it is not known whether these are still functional in sugar transport in the mature stem.

If, in a single stem transverse section, small fibrous strands are seen among the regular vascular bundles, these may be fibrous bridges as in the center of the stem of *Geonoma* and the basal part of *Cocos*. In other cases small fibrous strands, although continuous, do not seem to be connected with the vascular system of the stem. In *Bactris major*, for example, single stem transverse sections show numerous fibrous strands among the vascular bundles. In spite of considerable effort to elucidate their significance in analyses of the mature stem as well as the apical region, it has not yet been possible to find their relation to the vascular system of the stem.

VASCULAR CONNECTIONS BETWEEN STEM AND AXILLARY INFLORESCENCES

Satellites

Most palm species begin to produce axillary inflorescences only after they have reached a certain height (the "reproductive phase" of growth, Tomlinson, 1964). If one studies the vascular system of the stem in prior phases, one can see anatomical evidence of inflorescence vestiges at a height below the point where flowering actually begins. This evidence within the stem consists of many leaf-trace branches which are additional to the regular axial-bundle continuity and the bridges. These additional branches can be seen to follow the leaf trace to the stem periphery and then enter the axillary shoot (e.g., *Figure 6* in Zimmermann & Tomlinson, 1965). These are present even if the inflorescence does not continue to develop into an externally visible organ. Because these branches surround the leaf trace in the manner of a halo in section, we have called them satellite bundles (cf. *Figure 9* in Zimmermann & Tomlinson, 1965).

BORROWED SATELLITES, AND DEVIATION OF AXIAL BUNDLES

In many species, such as *Chamaerops humilis* in which borrowing of axial bundles is common, satellites are also borrowed. In ascending motion pictures of the stem one can see in the peripheral region satellites diverging from the leaf trace. Some of these may be left behind as the leaf trace enters the leaf, i.e., they do not irrigate the inflorescence in the axil of the supplied leaf, but they subsequently follow another leaf trace to the stem periphery, i.e., they enter a more distal inflorescence. This is a phenomenon very similar to the borrowing of axial bundles which has been described before in this paper.

In many cases, one can see a large number of peripheral axial bundles leaving the central cylinder to enter the axillary inflorescence, following a leaf trace in a satellitelike manner. This is well seen in *Serenoa repens*. These redirected axial bundles (minor bundles in all cases) must have been rerouted very early during development as a small portion of the meristematic cap of the main axis forming the cap of the axillary shoot. The developmental timing of these events has been explained and illustrated in one of our recent papers (*Figure 5*, region B, in Zimmermann & Tomlinson, 1972; illustrated also in Tomlinson, 1973).

DEEPLY INSERTED SATELLITES

As one follows leaf traces down into the stem in *Chamaedorea, Arecastrum romanzoffianum*, etc., one frequently sees that they are followed (on the inside) by a number of small satellites which do not fuse with the leaf trace until several internodes below the leaf insertion. In some cases, such as in *Bactris major*, and *Caryota mitis*, these are in part real satellites (i.e., attached to the leaf trace at their lowest extremity), and in part "demand-type" bundles which finally fuse with neighboring axial bundles (such as develop in region D, *Figure 5*, Zimmermann & Tomlinson, 1972). In *Geonoma* they are borrowed satellites, originating from the fibrous anastomosing bridge system of the stem center. In *Cocos* the borrowed satellites are regular bundles. These facts serve to illustrate the diversity of methods by which lateral inflorescences are irrigated in palms.

VARIATIONS OF STRUCTURE WITH HEIGHT IN STEM

To anyone familiar at all with the internal structure of the stems of palms, quantitative variation in gross anatomy at different heights in a single stem is obvious and considerable. Differences in vascular-bundle density, the average diameter of individual bundles, the extent of the fibrous sheath associated with each bundle, and the amount of cell wall lignification are evident when single transverse surfaces at different heights are compared. In *Chrysalidocarpus lutescens*, for example, the vascular-bundle diameter was found to be of the order of 0.8 mm. and the bundle density 50 per cm.^{2} at 20 cm. above ground, while near the top of the stem, at 120 cm. above ground level, bundle diameters were 0.4 mm. and the density 300 per cm.^{2}. The difference in bundle diameter appeared to be primarily due to a more fully developed fibrous sheath at the base, and the lesser bundle density at the base partly to a thickening of the stem by expansion of the ground parenchyma during stem maturation. Measurements of cell sizes also show differences at different heights. Vessel-element length shows distinct trends in *Sabal palmetto* (Tomlinson & Zimmermann, 1967) which are to a large extent paralleled by sieve-tube-element length (Parthasarathy & Tomlinson, 1967). This published work is supported by additional unpublished records for several species and other cell types (e.g., fiber length). In *Washingtonia*, for example, average vessel-element length at the base of the stem may be five times that in mature tissue close to the top of the tree. The question has already been asked — is it possible to find more than one vascular pattern in a single axis?

Some effort to provide an answer to this question has been made with *Cocos* by means of surface analyses of the stem of an eleven-meter-tall trunk at one and ten meters in height respectively. Considerable uniformity was found to be imposed on the more obvious dimensional trends. Thus, regeneration of the inner from the outer system, as well as anastomosing bridge systems were found at both heights. Satellites, expectedly absent at the base in view of the lack of inflorescences at the lower nodes, were numerous at ten meters in height, with bundle borrowing very common. One of the differences in stem transverse sections at different heights is the presence of numerous fibrous bundles among the vascular strands in the central cylinder at the base of the stem. These have been found to come off distally from every departing leaf trace and thus represent a fibrous bridge system. Their distal ends disappear from view on the surface film and will have to be followed in serial section in the shuttle microscope. We intend to publish these findings in detail elsewhere.

A difference in three dimensional structure at the two heights in *Chrysalidocarpus* has been mentioned before: 20 cm. above ground, the stem shows a distinct regeneration type (i.e. no axial-bundle branches), while in the distal part of the stem (50 cm. above ground and higher) a very distinct *Rhapis*-type structure is observed.

A systematic investigation of structural differences of different heights was not intended to be the topic for this paper; this may be done in greater detail in the future. However, at the present, we know enough to make us very cautious in attaching taxonomic significance to differences found in various species. It should also be a warning to paleobotanists dealing with palm stems. It is easy to assign fossil stem fragments to different species even if these fragments originated from a single individual stem!

DISCUSSION

Developmental inferences

In an earlier paper we introduced the concept of an inner and an outer vascular system in monocotyledons (Zimmermann & Tomlinson, 1970). This concept is based upon the pattern of development in the meristematic crown; it has been described in general terms in a more recent paper (Zimmermann & Tomlinson, 1972). According to this concept, all vascular bundles of the central cylinder in *Rhapis* are inner bundles, all fibrous cortical strands are outer bundles. This distinction can be made because the former develop from the meristematic cap, the latter outside the cap; the situation in *Rhapis* is relatively simple.

Results discussed in the present paper add a complication. When, as in *Chamaerops*, axial bundles branch off the leaf trace as fibrous bundles in the inner cortical region, we could consider this cortical fibrous-bundle region as belonging to the inner system. The same would have to be said for the Regeneration Type. In other words, only the very outermost cortical fibrous-bundle region would then be part of the outer system.

On the other hand, we could say that only vascular bundles, i.e. the xylem-containing bundles of the central cylinder, are derived from the cap. Since the question is one of defining the cap region in the meristematic crown, it is, therefore, really only a semantic one. Therefore we would like to leave it open until we know more about developmental patterns in larger palm crowns.

We have not yet investigated the Regeneration Type during its course of development. From the mature structure we infer that the inner, fibrous cortical bundles, originally procambial and then protophloem strands, regenerate the cap (the future central cylinder) from the outer system. Evidently their functional life terminates early during development, but not before their developmental and functional role has been taken over by bridges from developing leaf traces. It is hoped that the developmental pattern of this type can be studied in the future. It will not be an easy task because very large apical regions will have to be analyzed microscopically.

We do not yet know the developmental significance of "borrowing." However, there is some similarity of this structure with the arrangement of the inverted bundles in the Pandanaceae (Zimmermann *et al.*, 1974). In Pandanaceae it is the proximal parts of axial bundles which run closely parallel (and inverted) along more distal parts of other axial bundles. The overall pattern appears similar in "borrowed" bundles where proximal axial-bundle ends run parallel to other leaf traces. The "borrowed" bundle is often also inverted, but in a different way, depending on the species, the xylem of the borrowed bundle in some cases facing the xylem of the leaf trace (cf. FIGURE 5). The developmental pattern of bundle formation of the Pandanaceae has been worked out (Zimmermann *et al.*, 1974) and it remains to be seen whether the "bundle borrowing" in palms is due to a similar developmental sequence of events.

FUNCTIONAL INFERENCES

There may be a functional difference between the vascular patterns of the Type A and B–D respectively (FIGURE 3). The apical region of the aërial stem of *Rhapis* is almost certainly fed directly from the mature leaves, i.e., from the stem periphery near the apical region, whereas the rhizome apex must be fed axially from behind because the rhizome bears only non-photosynthesizing scale leaves. It is possible that vascular differentiation is influenced by the origin of nutrient supply. This would mean that the central apical region of larger stems (such as *Phoenix*, *Sabal*, and *Washingtonia*) is fed in an axial direction from below, while the peripheral regions are fed from current photosynthate of mature leaves in a more radial direction. This would make sense because in large stems the apical region of enclosed (i.e., unilluminated and therefore assimilate-importing) leaf primordia is separated from the green, photosynthesizing leaves by very large areas of meristematic tissue. Even though the path of movement across this meristematic tissue is the shortest, it may be useless because long-distance phloem transport can go only through mature vascular tissue. The central part of the apical region might, therefore, be fed not via the shortest, but rather via an indirect route from old leaves deeply down into the stem, and from there axially up via *Phoenix*-type major axial bundles.

TAXONOMIC SIGNIFICANCE

In view of the small number of species examined so far, it is appreciated that any comment about the taxonomic significance of our findings is likely to be premature. In addition, we have suggested that some of the patterns we have described relate to the size of the trunk; this is implied in the distinction we make between bundle types in large- and small-stemmed palms. In other cases (e.g., *Chrysalidocarpus*) we have found significant differences in a single stem at different heights.

However, we have shown elsewhere (Zimmermann *et al.*, 1974) that members of the family Pandanaceae do have diagnostically useful features of stem anatomy which are related directly to the 3-dimensional course of vascular bundles. We already have some indication that a similar construction may occur in certain Araceae and can suggest that the features which categorize the *Pandanus* type of vasculature may represent variants of developmental principles which operate in other large woody monocotyledons. Furthermore, we know that in Strelitziaceae and Zingiberaceae outer bundles contain xylem (cf. *Figure 6* in Zimmermann & Tomlinson, 1972). Within the Strelitziaceae, a very natural group, the same pattern of inner-bundle grouping is suggested by our preliminary examination of its three constituent genera, *Phenakospermum*, *Ravenala*, and *Strelitzia*. Thus the possibility exists that interfamily relationships may be revealed by this type of analysis.

In the Palmae itself we have suggested that the *Phoenix* Type (which occurs in several genera) may be related to the method of irrigation of the meristematic crown. Even so, within the genus *Phoenix*, in stems as divergent in size as those of *P. dactylifera* and *P. roebelenii*, the constructional pattern is identical. Furthermore, where we have examined several species of a genus, the range of variation seems small, e.g., several species of *Chamaedorea* show the *Chamaedorea* principle and several of *Geonoma*, the *Geonoma* principle.

Our present position can be summarized by saying that it is unlikely that this method of analysis will provide much evidence for taxonomic interrelationships, except where taxa of high rank are concerned. But information at this level may be very significant and the possibility of establishing interfamily relationships is continually borne in mind as further analyses are made.

SUMMARY

The variety of vascular patterns in stems of different palm species is described as a series of types. In the *Rhapis*-Rhizome Type the axial bundle branches off the leaf trace at the point of leaf-trace departure, in the *Geonoma* Type at the very periphery of the central cylinder. In the *Chamaedorea* Type only a few of the leaf traces give off a discrete axial bundle. At the same time all leaf traces contribute, via bridges, to a peripheral "pool" of small, anastomosing vascular bundles from which axial bundles come off distally toward the inside. Large palm stems are more complicated. In some cases (e.g., *Cocos*) axial bundles branch off the leaf trace at the point of leaf-trace departure. These axial bundles then follow other, unrelated leaf traces towards the periphery of the central cylinder ("borrowing") whence they resume their distal course, regaining the center. In *Phoenix*, *Sabal*, and *Washingtonia*, major bundles (i.e. those of the stem center) are *Rhapis*-rhizomelike, while minor bundles originate from the cortical fibrous strands. In many large palms the lower ends of most vascular bundles are continuous with fibrous cortical strands (Regeneration Type).

Bridges, i.e. upwardly-directed branches of the leaf trace, distally fusing with neighboring axial bundles, are the most constant feature of monocotyledonous vascular anatomy. Variations of the pattern of bridges, and the patterns of vascularization of the axillary inflorescence are described.

ACKNOWLEDGMENTS

These investigations, which have been carried out over a period of ten years, have been made in cooperation with the Fairchild Tropical Garden in Miami, Florida, where one of the authors (P.B.T.) had been a staff member for 12 years and still maintains a collaborative appointment. The research of one of us (P.B.T.) has been supported in Miami largely by a series of N.S.F. grants, currently GB-31844X. Most material has been obtained from the living collections of the Fairchild Garden and the Montgomery Foundation. Additional material has been obtained from palms in natural habitats in the New World Tropics. We wish to thank the many persons who, over the years, have given us invaluable technical assistance, in particular and most recently Miss Monika Mattmüller, who made many thousands of stem transverse sections and assisted with the photography of many surface films.

REFERENCES

DEVADAS, C., & C. B. BECK. 1972. Comparative morphology of the primary vascular systems in some species of Rosaceae and Leguminosae. Am. Jour. Bot. **59**: 557-567.

HILGEMAN, R. H. 1951. The anatomy and development of the leaf and stem of the date palm. 3 pp. Univ. of Arizona Citrus Expt. Sta.

PARTHASARATHY, M. V., & P. B. TOMLINSON. 1967. Anatomical features of metaphloem in stems of *Sabal*, *Cocos*, and two other palms. Am. Jour. Bot. **54**: 1143-1151.

TOMLINSON, P. B. 1961. Palmae. *In* C. R. METCALFE, *ed.* Anatomy of the Monocotyledons II. xv + 453 pp. Clarendon Press, Oxford.

———. 1964. Stem structure in arborescent monocotyledons. *In* M. H. ZIMMERMANN, *ed.* The formation of wood in forest trees. Academic Press, New York. Pp. 65-86.

———. 1973. Branching in Monocotyledons. Quart. Rev. Biol. **48**: 458-466.

——— & M. H. ZIMMERMANN. 1966a. Anatomy of the palm *Rhapis excelsa*, II. Rhizome. Jour. Arnold Arb. **47**: 248-261.

——— & ———. 1966b. Anatomy of the palm *Rhapis excelsa*, III. Juvenile phase. *Ibid.* 301-312.

——— & ———. 1967. The "wood" of monocotyledons. Bulletin of the International Association of Wood Anatomists. **1967**(2): 4-24.

VON MOHL, H. 1824. De palmarum structura. *In* K. F. P. VON MARTIUS, Historia naturalis palmarum **1**: I-LII. *16 pls.*

ZIMMERMANN, M. H. 1971. The Harvard Forest, Harvard University (Annual report 1970-71).

———. 1973. Transport problems in arborescent monocotyledons. Quart. Rev. Biol. **48**: 314-321.

——— & P. B. TOMLINSON. 1965. Anatomy of the palm *Rhapis excelsa*, I. Mature vegetative axis. Jour. Arnold Arb. **46**: 160-180.

——— & ———. 1966. Analysis of complex vascular systems in plants: Optical shuttle method. Science **152**: 72, 73.

——— & ———. 1967a. Anatomy of the palm *Rhapis excelsa*, IV. Vascular development in apex of vegetative aërial axis and rhizome. Jour. Arnold Arb. **48**: 122-142.

——— & ———. 1967b. A method for the analysis of the course of vessels in wood. Bull. Int. Assoc. Wood Anatomists **1967**(1): 2-6.

——— & ———. 1968. Vascular construction and development in the aerial stem of *Prionium* (Juncaceae). Am. Jour. Bot. **55**: 1100–1109.

——— & ———. 1969. The vascular system in the axis of *Dracaena fragrans* (Agavaceae), I. Distribution and development of primary strands. Jour. Arnold Arb. **50**: 370–383.

——— & ———. 1970. The vascular system in the axis of *Dracaena fragrans* (Agavaceae), II. Distribution and development of secondary vascular tissue. *Ibid.* **51**: 478–491.

——— & ———. 1972. The vascular system of monocotyledonous stems. Bot. Gaz. **133**: 141–155.

———, ——— & J. LECLAIRE. 1974. Vascular construction and development of certain Pandanaceae. Bot. Jour. Linn. Soc. **67**: 21–41.

HARVARD UNIVERSITY
HARVARD FOREST
PETERSHAM, MASSACHUSETTS 01366

CAESALPINIA SUBGENUS GUILANDINA IN THE BAHAMAS

William T. Gillis and George R. Proctor

When the authors were engaged in field collecting in the southern Bahama Islands early in 1973, pursuant to the preparation of a new Bahama Flora, they were especially interested in the reproductive biology of the nicker beans, *Caesalpinia spp.*[1] Drs. Carroll E. Wood, Jr. and Kenneth R. Robertson of the Arnold Arboretum had noted apparent dioecy in one species of this group of plants in South Florida [*C. bonduc* (L.) Roxb.]. Accordingly, we examined populations of the genus during our field work in Mayaguana and Inagua, and found that dioecy seems to be typical of this group, at least in all populations we saw. Dioecy was noted by Linnaeus (1754) but apparently was overlooked until relatively recently, probably because the carpellate flowers have well-developed anthers and appear to be perfect, yet no pollen is produced. The staminate flowers lack a gynoecium. In recent years, however, Wilczek (1952) for the Flora of the Congo and Brenan (1967) for the Flora of Tropical East Africa noted dioecy in *C. bonduc*.

The Caesalpinioideae, subtribe Caesalpinieae, the type of which is *Caesalpinia*, have been treated by different workers as a complex either comprised of a large number of genera or consolidated into few. Britton and Rose (1930) in their treatment for the North American Flora recognized 28 genera in North America, among them *Guilandina* L. (which would have to be considered as having perfect flowers in their key). Fifteen to 17 of these genera might well be considered *Caesalpinia*, *sensu lato*, not warranting segregation because of the relatively minor characters used for distinguishing them. *Guilandina* is one of these genera.

The *Guilandina* species comprise the only group within *Caesalpinia*, *sensu lato*, apparently having unisexual flowers. Moreover, these species have compressed, thick, rounded, rigidly chartaceous legumes, and an unusual scrambling habit. Most other *Caesalpinia* species are either trees or shrubs. A few, however, like *C. decapetala* (Roth) Alston in Trimen (frequently called *C. sepiaria* Roxb.), resemble species of the *Guilandina* group in their vinelike, scrambling shrubby habit. The *Guilandina* group inhabits chiefly the coastal regions of Central America, the Greater Antilles, the Bahamas, and Bermuda. Two vines of mountainous regions of Costa

---

[1] The nicker beans are also called nickels, probably a corruption of the name of a game played by the people of the West Indies. The game reportedly originated in Africa where it was played with stones in holes in the ground. Instead of stones, the playing "bits" or "nickels" in the West Indies were seeds of various species of *Caesalpinia* subg. Guilandina. The seeds were evidently used in place of coins and possibly represented one's winnings or losings. In the Bahamas, a wooden board was developed for table use in playing the game. Such a playing board with twelve depressions for the nickels is preserved and on display in the Bahamia Museum in Nassau.

Rica and Haiti are also placed here by Britton and Rose (1930). Little is known of *Guilandina* in the Old World except for the widespread species *C. crista* (L.) Roxb., which is often confused with the gray-seeded *C. bonduc* (L.) Roxb. of the New World (Dandy & Exell, 1938).

Because of the great diversity within subtribe Caesalpinieae, one could elect either to follow Britton and Rose by proliferating genera, or to take a more conservative generic view, resulting in a fairly inclusive *Caesalpinia*. Because data presently available for all *Caesalpinia* species are insufficient, we have chosen not to defend segregation of such genera as *Libidibia* Schlecht., *Erythrostemon* Klotzsch, *Tara* Molina, *Ticanto* Adans., *Nicarago* Britton & Rose, *Guaymasia* Britton & Rose, *Russellodendron* Britton & Rose, *Poincianella* Britton & Rose, and *Biancaea* Todaro. However, because of habit, distinctive fruit, and dioecy of *Guilandina*, we feel justified in treating it as a subgenus of *Caesalpinia*.

Caesalpinia subg. **Guilandina** (L.) Gillis & Proctor,[2] comb. & stat. nov.

Guilandina L. Sp. Pl. 381. 1753; Gen. Pl. ed. 5. 179. 1754, *pro gen.* Benth. & Hook. Gen. Pl. 1: 566. 1865, *pro sect.* TYPE: *Guilandina bonduc* L. = *Caesalpinia bonduc* (L.) Roxb.

Frutex volubilis, differt a subgeneribus aliis floribus unisexualibus, fructibus chartaceis, compressis rotundatis.

Britton and Millspaugh's *Bahama Flora* (1920) records three species of *Guilandina* in the Bahamas. One of these [*Guilandina crista* (L.) Small = *Caesalpinia bonduc* (L.) Roxb.] has flat, round, gray seeds, often with a depression in the center, while the two other species have yellow-orange or brownish seeds and lack the central depression [*Guilandina bonduc* L. = *Caesalpinia divergens* Urban and G. *ovalifolia* (Urban) Britton = *Caesalpinia ovalifolia* Urban]. While we were studying plants of these taxa on the island of Inagua in the vicinity of Matthew Town, we found two populations that were clearly different from the species listed by Britton and Millspaugh, one of which we are describing as new. The other remains, for the moment, anomalous.

The one new species of *Caesalpinia* subgenus GUILANDINA is distinct from the others indigenous to the Bahamas in its dusky, glabrous legume, its elongate, striate, brownish seeds, and its unarmed stems. An occasional individual was found with some recurved spines subtending the leaflets, but the spines were sparse. A number of such intermediate forms occurred suggesting that this new species, *Caesalpinia murifructa*, is interfertile with *C. ovalifolia*, with which it was growing intertwined. The style continues to elongate during development of the fruit, becoming curled and greatly resembling an animal's tail. The dusky, gray-brown color, its rounded shape, and the "tail" give the legume the appearance of a mouse, hence

---

[2] Although an adequate description of this taxon was published by Linnaeus (1754), we are emending it with a diagnosis indicating characters which segregate subg. GUILANDINA from its relatives.

FIGURE 1. Cluster of fruits of *Caesalpinia murifructa* from type locality, Matthew Town, Inagua, Bahama Islands.

the specific epithet *murifructa* (Latin, *mus*, *muris*, mouse, + *fructus*, fruit). (FIGURE 1).

Caesalpinia murifructa Gillis & Proctor, sp. nov. Frutex inermis adscendens saepius volubilis, foliis bipinnatim compositis, exstipulatis; foliolis ovalibus usque orbicularibus, inaequilateralibus, apicibus emarginatis, plerumque setaceo-mucronatis, mucrone usque ad 0.5 mm.; floribus unisexualibus; sepalis utrinque dense aureo-pubescentibus, petalis luteis, glabris vel glabratis; legumine glabro fusco-murino; stylo accrescente in caudam usque 2.2 cm.; seminibus sublateritiis, dilute horizontaliter striatis, 2–4 in fructu. Differt a *Caesalpinia culebra* et a *C. portoricense* seminibus sublateritiis, et a *C. caymanense* seminibus sublateritiis et caulis puberulis.

HOLOTYPE. Bahamas: Great Inagua Island, abandoned field, Matthew Town, in rocky roadside thicket. Scrambling shrub entirely lacking in spines. *Proctor 33371* (A); isotypes: (IJ, BM).

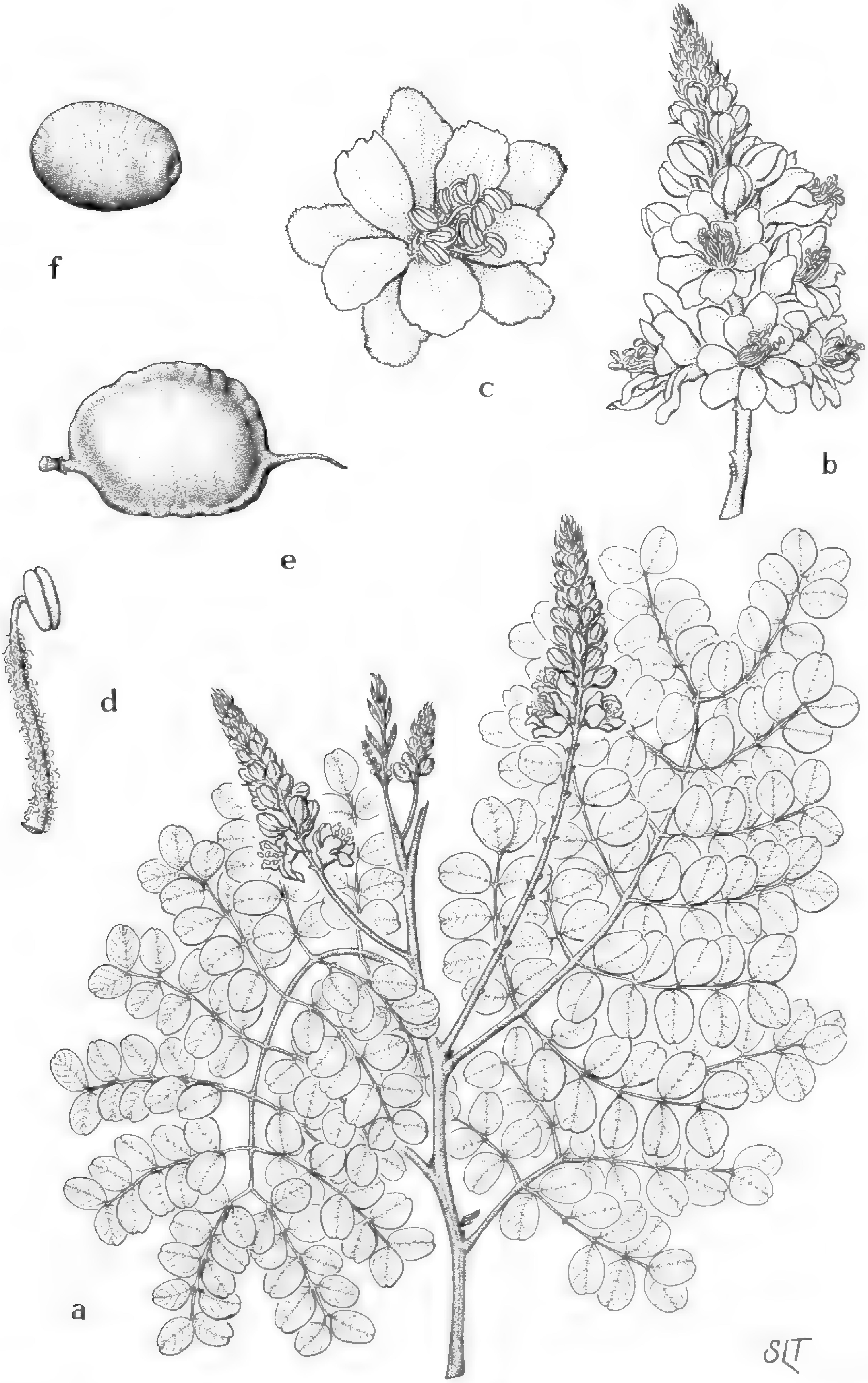


FIGURE 2. *Caesalpinia murifructa*. a, habit, note erect flowering stalks and pedicel bases of fallen staminate flowers, × 1/2; b, staminate inflorescence,

Vinelike, scrambling shrub, branches usually unarmed, puberulent; leaves bipinnately compound, 1.2–2.3 dm. long, stipules wanting; pinnules to 6 or 7 pairs, 4–8 cm. long, 1.5–2.5 cm. between pinnae; leaflets 4 or 5 pairs, generally without spines, 1–2 cm. long, oval to orbicular, 0.6–1.5 cm. broad, inequilateral, emarginate with bristle-tip, with aborted foliar flap at the tip of the pinnule, 1–1.5 mm. long; petiolule 1–1.5 mm. long. Inflorescence a raceme, 8–15+ cm. long, axis regular; subulate bract subtending each flower, 0.5 cm. long, the distal half an awn, the awn totally deciduous at anthesis. Flowers bright yellow; sepals ovate, 5, covered with a golden bronze puberulence on both surfaces, 1 cm. long; petals 5, deeper in hue than the sepals, short-clawed, erose, 0.8 cm. long, glabrous or with a few scattered hairs on the abaxial surface; pedicels 1–3 mm. long; staminate flowers with 10 stamens, anthers orange, filaments villous; carpels lacking. Carpellate flowers with 10 stamens, anthers orange, filaments villous, appearing as in staminate flowers but lacking pollen; carpels glabrous; receptacle densely golden puberulent. Fruit laterally compressed, dehiscent, dusky gray-brown, glabrous, rigid-chartaceous, 5 cm. long, 4 cm. broad, 1.5 cm. thick, style accrescent forming a tail-like beak up to 2.2 cm. long, usually curved or curled. Seeds brown-orange, ovoid, horizontally faintly striate, 2–4 per legume, 1.7 × 1.4 cm., usually with a slight depression on the surface nearest the other seeds. (FIGURE 2).

Additional specimen examined: Vacant lots in Matthew Town, Inagua, *Dunbar 352* (A).

The closest relatives of *Caesalpinia murifructa* appear to be the unarmed species *C. caymanensis* Millsp. with white-hairy branches and gray seeds; *C. culebrae*,[3] with orange-yellow seeds; and *C. portoricensis*,[4] with black seeds that are not striate.

Another population of *Caesalpinia* subgenus GUILANDINA was discovered in a field adjacent to the type locality of *C. murifructa*. Its flowers were one and one-half times the size of the flowers of any other Bahama species of subgenus GUILANDINA. The only flowers seen were staminate, yet one young, seemingly aborted, fruit was also found. The clone may represent a polyploid population. Until more material is known, it is considered an anomalous form of *C. ovalifolia*.

[3] **Caesalpinia culebrae** (Britton & Wilson ex Britton & Rose) Gillis & Proctor, comb. nov. *Guilandina culebrae* Britton & Wilson ex Britton & Rose, N. Am. Fl. **23**: 339. 1930. TYPE. Coast of Culebra I., Puerto Rico, *Britton & Wilson 79* (NY).

[4] **Caesalpinia portoricensis** (Britton & Wilson) Gillis & Proctor, comb, nov. *Guilandina portoricensis* Britton & Wilson, Sci. Surv. Porto Rico Virgin Is., **5**: 380. 1924. TYPE. Salinas de Guanicas, Puerto Rico, *Britton, Cowell, & Brown 4916* (NY).

---

with open flowers and buds subtended by awned bracts, × 1 1/2; c, staminate flower showing varying lengths of stamens, × 2; d, single stamen, note pubescence on filament, × 5; e, fruit, with remnant of calyx and accrescent stylar "tail," × 1/2; f, seed, showing faint striations, × 1.

ACKNOWLEDGMENTS

We are indebted to Miss Shari L. Trautz who made the drawing included herein. The Latin diagnoses were edited by Dr. Leslie A. Garay. The photograph was taken by the first author. Costs of the field work and other studies involved in this project were supported by a generous, anonymous grant to the Arnold Arboretum for work on the Bahama flora. Field assistance by Messrs. George N. Avery and Richard F. Leo is gratefully acknowledged. We appreciate the editorial assistance of Drs. Stephen Spongberg and Kenneth R. Robertson who read the manuscript and made constructive suggestions.

LITERATURE CITED

BRENAN, J. P. M. 1967. Leguminosae, subfamily Caesalpinioideae. E. MILNE-REDHEAD & R. M. POLHILL, *eds.* Fl. Trop. East Afr. Pp. 1–231. Publ. Crown Agents for Oversea Governments and Administrations.

BRITTON, N. L., & C. F. MILLSPAUGH. 1920. The Bahama flora. Privately published. Reprinted 1962, Hafner Publishing Co., New York, N.Y. 695 pp.

——— & J. N. ROSE. 1930. Caesalpiniaceae. North Am. Fl. **23**: 201–349.

DANDY, J. E., & A. W. EXELL. 1938. On the nomenclature of the species of *Caesalpinia*. Jour. Bot. **76**: 175–180.

LINNAEUS, C. VON. 1754. Genera Plantarum. Stockholm.

WILCZEK, R. 1952. Caesalpiniaceae. II. Eucaesalpinieae. Flore du Congo Belge et du Ruanda-Urundi. **3**: 247–264. Bruxelles.

W. T. G.

ARNOLD ARBORETUM OF HARVARD UNIVERSITY
22 DIVINITY AVENUE
CAMBRIDGE, MASSACHUSETTS 02138
AND
DEPARTMENT OF BIOLOGY
UNIVERSITY OF MIAMI
CORAL GABLES, FLORIDA 33124

G. R. P.

SCIENCE MUSEUM
INSTITUTE OF JAMAICA
KINGSTON, JAMAICA, B.W.I.

LENBRASSIA (GESNERIACEAE)
A NEW GENUS ENDEMIC TO NORTH QUEENSLAND

George W. Gillett *

The late C. T. White, in describing *Coronanthera australiana*, the sole Australian representative of *Coronanthera* and of the tribe Coronanthereae, remarked: "If when better known the plant is found to bear definitely fleshy, indehiscent fruit, then it may have to form the basis for a new genus." White confirmed this possibility by a collection made only a few months later (*White 10548*, Sept. 1936), showing that the species was indeed characterized by a fleshy fruit. In 1967, in the publication in this journal (**48**: 245) of a new species of *Coronanthera* indigenous to the Solomon Islands, I remarked that the genus was not to be considered indigenous to Australia because the alleged representative was, according to White, characterized by fleshy fruit. This situation would mandate the exclusion of *C. australiana* not only from the genus *Coronanthera*, but also from the tribe Coronanthereae, characterized by capsular fruit and wind-dispersed seed.

During August, 1973, it was possible for me to carry out field studies in the rain forest of North Queensland and to make an ample collection of *Coronanthera australiana*, at that time in flower and fruit. The field work confirms White's observation that this species (Figure 1) has a fleshy fruit. This character and the larger, cylindrical corolla, do indeed make it a strongly discordant element in the Coronanthereae.

A perhaps closer relationship for this monotypic Queensland endemic would be with the genus *Fieldia*, indigenous to South Queensland, New South Wales, and Victoria, and the Australian representative of the South American tribe Mitrarieae (*Sarmienta, Asteranthera, Mitraria*). At the same time, the coherent anthers, borne on twisted filaments, and the arborescent habit alienate it from *Fieldia*. It appears, therefore, that the most reasonable interpretation of this different, attractive element is as a separate genus in the tribe Mitrarieae. This lends emphasis to an interesting although not unusual pattern of phytogeographic relationship, with three genera of the tribe indigenous to southern South America and two genera in eastern Australia.

The name chosen for the new genus, *Lenbrassia*, is in commemoration of Leonard Brass, whose prodigious botanical explorations in the Southwest Pacific have played a significant role in the advancement of the botany of that area.

Lenbrassia G. W. Gillett, gen. nov.

Propter fructum carnosum et corollam majorem cylindricam Tribui Mitrariearum propter antheras cohaerentes generi Asteranthereae affinis. Type Species: *L. australiana*.

---

* Research supported by Grant GB 32094 National Science Foundation.

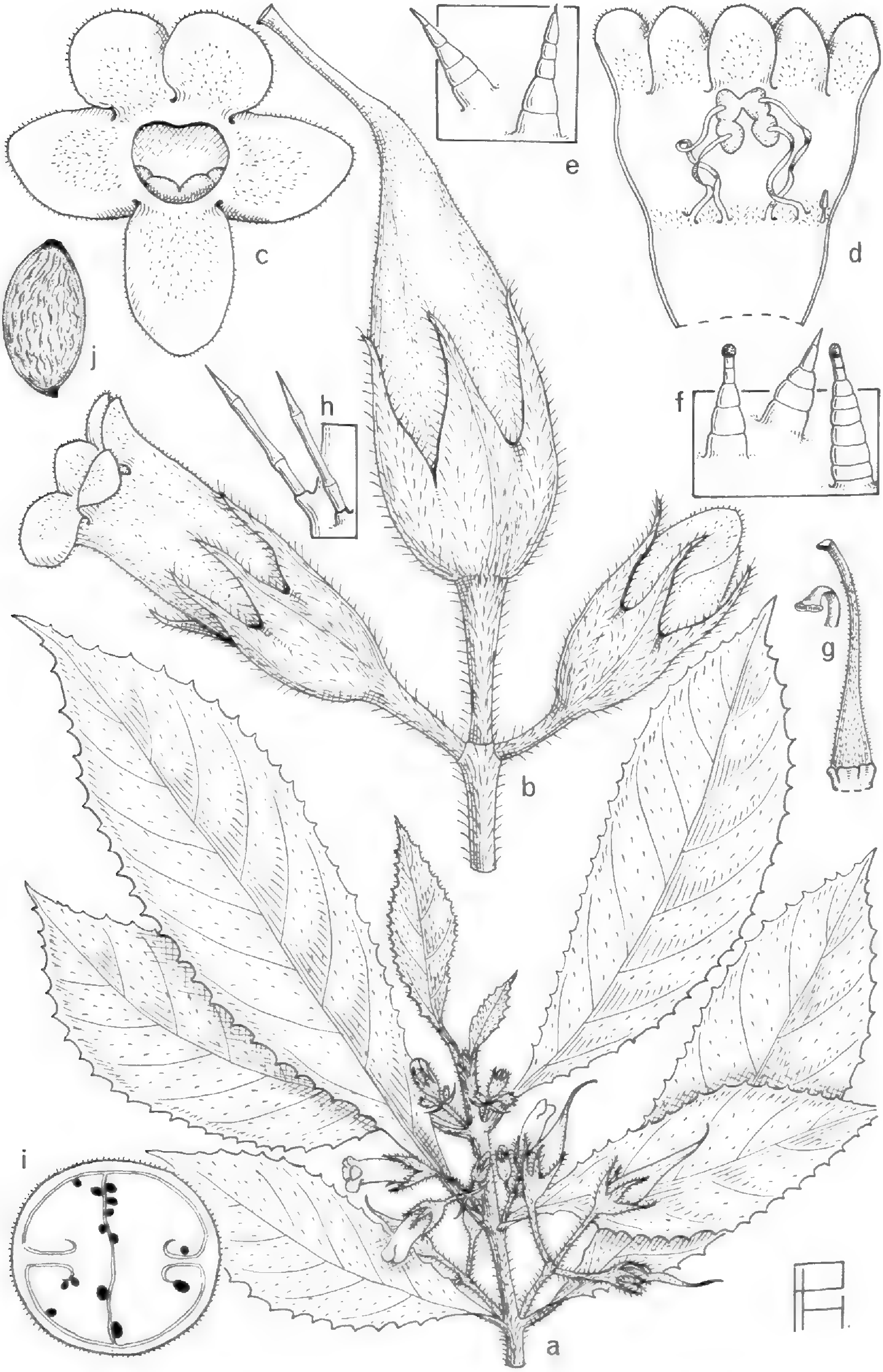


FIGURE 1. *Lenbrassia australiana*: a, habit, × 2/3; b, inflorescence, × 2; c, flower, × 3; d, opened corolla (anterior lobe in center), × 2; e, hairs from the outer surface of the corolla, × 60; f, hairs from the inner surface of the corolla.

Lenbrassia australiana (C. T. White) G. W. Gillett, comb. nov. FIGURE 1.

Coronanthera australiana C. T. White, Proc. Roy. Soc. Queensland **47**(5): 73. 1936.

Habit a branching tree up to 13 m. high, with hard, strong wood, the buds and young foliage purple, turning green with maturity. *Indument* of light brown, nonglandular hairs 50–100 μm. in basal diameter and 0.5–1.0 mm. long. *Leaves* opposite with a scabrous pubescence on the upper and lower surfaces, the petioles 0.5–2.0 cm. long, the blades lanceolate to oblanceolate, 2.5–5.5 cm. broad and 5–15 cm. long, the primary veins 7–9 per side and curved acropetally along the margins of the blade, the secondary and tertiary veins obscure above and below, the blades unequal and acute to cuneate at bases, acute to acuminate at apices, sharply serrate, with narrow, evenly spaced teeth about 1–1½ per cm. at margins. *Inflorescences* scabrous, cymose, of 1–3 flowers, the axillary peduncles 0.5 — 1.5 cm. long, terminated by a pair of deciduous, linear bracts 3–8 mm. long, the bracts subtending 1–3 pedicels 0.5–1.5 cm. long. *Calyx* persistent, the tube clasping the base of the mature fruit, the calyx 10–12 mm. long, cleft 2/3 of its length into 5 equal to subequal, subterete, linear-acuminate lobes, the calyx scabrous on the outer and inner surfaces with nonglandular hairs, the outer hairs erect, 50–100 μm. in basal diameter and 0.5–1.0 mm. long, the inner hairs much smaller, 20–30 μm. in basal diameter and 100–200 μm. long, acropetally inclined on the tube, erect on the lobes. *Corolla* tangerine orange, cylindrical, pubescent on the outer and inner surfaces with erect, nonglandular hairs 20–30 μm. in diameter and 100–150 μm. long, the corolla 18–20 mm. long, cleft 2–4 mm. into 5 unequal, rounded lobes, the 2 posterior lobes shorter. *Stamens* 4, borne as 2 lateral pairs, the 4 anthers coherent at apices, the filaments 9–10 mm. long, pubescent near apices with small, nonglandular hairs, the filaments twisted and curved, adnate to the corolla tube 5 mm. above its base and 12 mm. below the sinuses of each of the two lateral lobes, the 4 anthers at early anthesis raised to the posterior wall of the corolla tube, displaying the pollen prior to the elongation of the style, at late anthesis lowered against the anterior wall of the tube, concealing the pollen. *Staminode* glabrous, 2 mm. long, comprised of a short filament and rudimentary anther, the filament adnate to the corolla 6 mm. above the base of the tube and 11–12 mm. below the sinus of the posterior lobes. *Ovary and style* 15–16 mm. long at late anthesis, pubescent with small, erect, nonglandular hairs, the ovary tapering uniformly, concavely, into the style, the placentation parietal, the glabrous, cupulate annular disc wholly adnate to the base of the ovary as a swollen rim 0.5 mm. high. *Stigma* glabrous, spatulate, truncate, entire. ***Fruit*** fleshy, light green, shiny, pubescent, 2.0–2.5 cm. long, obclavate, tipped by 0.75–1.25 cm. of the persistent style base.

× 60; g, gynoecium, × 2; h, hairs from the style, × 40; i, cross section of fruit, × 3; j, seed, × 40. Drawn from *Gillett 2606*.

Seeds ovoid, brown, 0.6–0.7 mm. long, the coats with longitudinal striations.

TYPE LOCALITY. Mt. Demi, North Queensland, 760 m., in rain forest. Holotype collected by Brass, cited below.

DISTRIBUTION. Upland rain forest in North Queensland, between the latitudes of Mossman and Cape Tribulation, 760–1250 m.

Queensland: Mt. Spurgeon, *Merrotsy 27* (BRI, K), *C. T. White 10548* (BRI, K); Mt. Demi, *Brass 2087* (BRI–holotype); Mt. Misery, *Balgooy 1594* (BRI, K, UC); between Mt. Lewis and Mt. Demi, *Gillett 2606* (A, BRI, E, K, L, UC); Mt. Lewis, *L. S. Smith 10099* (BRI); Thornton Peak, *Brass & White 220* (BRI, K).

The population represented by *Gillett 2606* occurs as well dispersed, small trees in the understory of a very dense rain forest that grows on decomposed granite, on steep topography. The area is at 1050 m., northwest of Mt. Lewis and near the boundary between the South Mary and North Mary logging areas, along the Mt. Lewis logging road. The population occurs on the slopes above (west of) the road. This road joins the Mt. Malloy — Mossman road about 18 miles southwest of Mossman and 1–2 miles west of Julatten. This population, or possibly a series of disjunct populations, extend along the east side of the Great Dividing Range from Mt. Spurgeon to Mt. Lewis, for a distance of about 30 km. The genus also occurs in a second region, about 30 km. to the east, east of the Daintree River, in the Thornton Range. It is not known elsewhere.

Associated genera of the Mt. Lewis — Mt. Demi population (*Gillett 2606*) include: *Syzygium, Angophora, Flindersia, Bubbia, Pullea, Austrobaileya, Scaevola, Orania, Linospadix, Cyathea,* etc.

The orientation of the stamens in the flowers of *Lenbrassia* would promote outcrossing. The protandrous anthers display the pollen at early anthesis along the access route to the nectary and well above the nonreceptive stigma. At later anthesis, the thecae are depressed against the anterior wall of the corolla (FIGURE 1d), the residual pollen isolated and concealed from the elongating style and stigma, now displayed along the access route for the optimal reception of pollen from other flowers.

DEPARTMENT OF BIOLOGY
UNIVERSITY OF CALIFORNIA
RIVERSIDE, CALIFORNIA 92502

ILEX COLLINA, A SECOND SPECIES OF NEMOPANTHUS IN THE SOUTHERN APPALACHIANS *

Ross C. Clark

In his revision of North American Ilicineae and Celastraceae, Trelease (1892) described *Ilex longipes* and attributed it to A. W. Chapman. In his description Trelease noted that it was related to *Ilex decidua* Walter, and that its fruiting pedicels were about an inch long. Following the description, he referred to: "*Nemopanthes Canadensis*, Gattinger, Tennessee Flora, 31," as a synonym.

In his 1887 Tennessee Flora, Gattinger listed "*Nemopanthes Canadensis* DC." (now known as *Nemopanthus mucronatus* (L.) Trelease) from "Mts. at Cowan." His 1901 Flora of Tennessee does not include *Nemopanthes* in its catalogue (though the genus is included in the introduction, which is repeated *verbatim* from the 1887 Flora). Gattinger was apparently persuaded not to include *Nemopanthes* in his later edition by a letter to him from Chapman in May, 1887, which stated that the material received from Gattinger "is not [Nemopanthes], but a new species of Ilex (I. longipes S. fl. . . .)" (Oakes, 1932). Extant specimens of "Ilex longipes Chapm. ined." with undated labels in Gattinger's handwriting indicate that Gattinger accepted Chapman's correction, but the question of why *Ilex longipes* did not appear in Gattinger's 1901 Flora in place of *Nemopanthes* is unresolved.

Critical examination of type material indicates that *Ilex longipes* Chapman ex Trelease has been applied to plants within the circumscription of *Ilex decidua* Walter; therefore, the former name belongs in the synonymy of the latter. (Incidentally, a thorough study of the *Ilex decidua* complex would be a worthwhile contribution.)

Unfortunately, confusion over the application of the name *Ilex longipes* Chapman ex Trelease has become even more involved. Brooks (1920) attributed *Ilex longipes* to West Virginia, basing his report upon Sargent's correspondence with him in 1915. In 1936 Brooks found wild plants which were identified for him as *Ilex longipes*; he therefore reported its presence in West Virginia as certain. In the same report, Brooks (1936) included a drawing of the plant, presumably made from material he had collected. However, the plant he illustrated is not *Ilex longipes* Chapman ex Trelease, but is obviously referable to the taxon described later as *Ilex collina* Alexander (1941).

Apparently due to misdetermination, Brooks's association of *Ilex longipes* Chapman ex Trelease (= *Ilex decidua* Walter) with the illustration of putative *Ilex collina* Alexander has led to an habitual association of the

---

* Contribution No. 3, Spartanburg County Arboretum, Switzer, South Carolina, USA.

two. This occurs in the treatments of Fernald (1950), Gleason (1952), Edwin (1957), Gleason and Cronquist (1963), Stupka (1964), and James (1969), although Alexander (1941) and Woods (1951) have attempted to correct the misconception. Woods (1951), Ammons and Core (1945), and Strausbaugh and Core (1958) correctly realized that the plants in question should not be referred to *Ilex longipes* Chapman ex Trelease, while Massey (1961) was noncommittal.

Recent examination of specimens of plants referred to *Ilex collina* Alexander indicates that they should not even be included within *Ilex*, but within *Nemopanthus* instead. *Nemopanthus* Rafinesque is a genus characterized by obviously apopetalous corollas of narrow petals, stamens that are free from the corolla, inconspicuous calyx lobes in staminate flowers, and calyx lobes in pistillate flowers which are deciduous or semipersistent as the fruit matures. These characteristics are in contrast to the gamopetalous, rotate corollas with oblong-ovate lobes, stamens fused (if only slightly) to the corolla, and obvious, strongly persistent calyx lobes encountered in plants referable to *Ilex* (Loesener, 1942). There is sentiment at present among some North American workers toward abandoning *Nemopanthus* as a segregate of generic status. This writer feels that reassessment of generic concepts within the Aquifoliaceae is an issue that still awaits thorough investigation. However, on the basis of Loesener's (1942) treatment, it appears that if more than one genus is recognizable in the Aquifoliaceae, then *Nemopanthus* does merit recognition.

From examination of type and other material of *Ilex collina* Alexander and its yellow-fruited form, *I. collina* f. *van-trompii* (M. Brooks) Core & Davis, it is evident that plants commonly referred to these taxa meet criteria for their inclusion in the genus *Nemopanthus* as an additional species. This is reflected by the following treatment.

Nemopanthus Raf. Am. Monthly Mag. Crit. Rev. **4**: 357. 1819, nom. cons. (Int. Rules Bot. Nomencl. ed. 3. 102. 1935.)

Nemopanthes Raf. Jour. Phys. Chim. Hist. Nat. **89**: 96. 1819.
Ilicioides Dumont-Courset, Bot. Cult. ed. 1. **4**: 27, 28. 1802.
Nuttallia DC. Rapp. Jard. Genève 44. 1821.
Deweya Eaton, Man. Bot. ed. 7. 403, in obs. 1836.
Iliciodes O. Kuntze, Rev. Gen. Pl. **1**: 113. 1891.

Dioecious shrubs or small trees; stems glabrous, rarely puberulent or glaucous, with prominent lenticels and smooth, gray bark; bud scales ciliate. Leaves deciduous, simple, alternate, petiolate, glabrate, the upper surfaces sometimes rugose, stipules caducous. Flowers 1 to several at a node, radially symmetrical, pedicellate, essentially ebracteolate. Calyx lobes 0–5, ephemeral to semipersistent, glabrous, entire; corolla apopetalous, petals 3–4, linear or lanceolate, glabrous, entire; stamens 2–6, anthers dorsifixed, longitudinally and introrsely dehiscent, filaments alternate with petals, glabrous; carpels 4–5, stigma sessile, ovary superior, glabrous. Drupe enclosing 4 or 5 pyrenes, each enclosing a single seed. As presently known, the genus includes two species of eastern North America.

DIAGNOSTIC KEY TO THE SPECIES OF NEMOPANTHUS RAFINESQUE

Leaves acuminate and glandular at tip, with glandular-serrate margins; calyx lobes of staminate flowers (when present) subulate, 0.7–1.7 mm. long and 0.3–0.8 mm. wide, anthers 0.8–1.7 mm. long; calyx lobes of pistillate flowers subulate, 0.6–1 mm. wide, semipersistent on fruit; endocarps (pyrenes) 5.2–6.3 mm. long and 2.6–4 mm. broad, dorsally and usually laterally ribbed. . . . . 1. *Nemopanthus collinus* (Alex.) Clark.

Leaves obtuse and mucronate at tip, with entire to remotely serrate margins; calyx lobes of staminate flowers (when present) setaceous, 0.2–1 mm. long and 0.1 mm. or less wide, anthers 0.3–0.8 mm. long; calyx lobes of pistillate flowers setaceous, 0.1 mm. or less wide, deciduous on fruit; endocarps (pyrenes) 3.8–5.2 mm. long and 2.5–3.2 mm. broad, dorsally smooth or ribbed, laterally smooth. . . . . . . 2. *Nemopanthus mucronatus* (L.) Trelease.

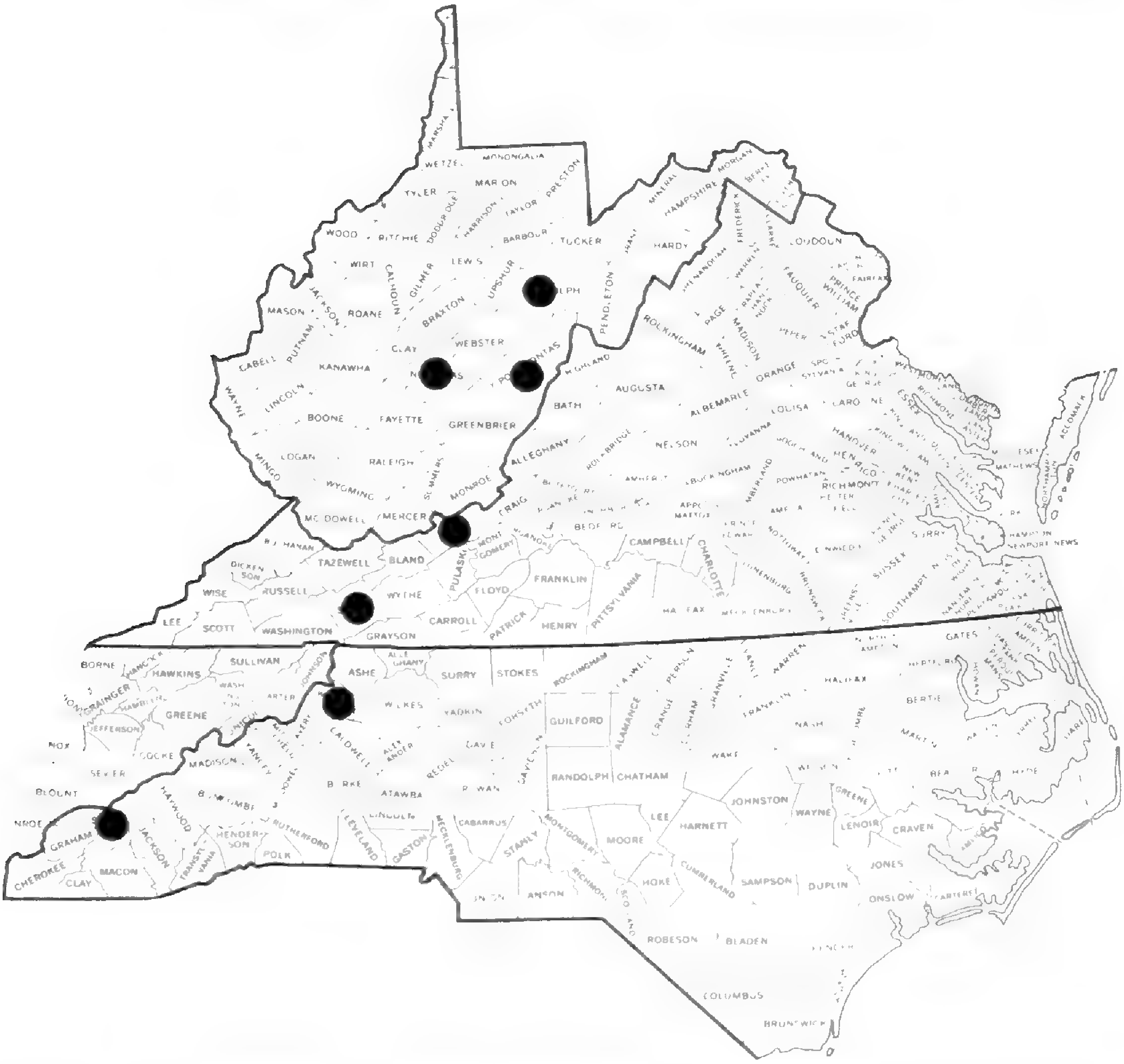
1. **Nemopanthus collinus** (Alexander) Clark, comb. nov. MAP 1.

Ilex collina Alexander, Castanea **6**: 30, 31. 1941.

Ilex longipes Chapman *sensu* Fernald (1950), Edwin (1957), Gleason & Cronquist (1963), Stupka (1964); Gleason (1952) and James (1969) in part, not Trelease (1892).

Shrubs or small trees to about 4 m. high. Leaf blades elliptic to oblanceolate or obovate (occasionally suborbicular), to 9.5 cm. long and 6.5 cm. wide, glabrous to pilose, apices acuminate with a sessile gland at the tip, margins glandular-serrate and occasionally sparsely ciliate proximally, bases cuneate to attenuate; petioles to 1.9 cm. long, glabrous, stipules linear. Pistillate flowers 1 (rarely 2) per node, staminate flowers pedicellate, 1–3 at a node. Pistillate flower: calyx lobes 4, subulate, acute to acuminate, 0.4–0.8 mm. long, 0.6–1 mm. wide, semipersistent in fruit; petals (only one specimen seen) 4, greenish-white, linear or narrowly lanceolate, 1.7–2.3 mm. long, 0.4–0.6 mm. wide; carpels 4; pedicels 7–34 mm. long, often reddish in fruit, glabrous, ebracteolate. Staminate flower: calyx lobes 0–5, ephemeral, lanceolate to ovate, acuminate, 0.7–1.7 mm. long, 0.3–0.8 mm. wide; petals 4, greenish-white, linear, to about 4 mm. long, 0.3–0.5 mm. wide; stamens 3–6, anthers 0.8–1.7 mm. long, 0.3–0.6 mm. broad; pedicels 4.5–13 mm. long, glabrous, ebracteolate or with occasional, minute, basal bracteoles. Drupe 7–10 mm. long and broad, red or yellow, enclosing 4 endocarps (pyrenes) (fewer by abortion), the endocarps 5.2–6.3 mm. long, 2.6–4 mm. broad, dorsally and usually laterally ribbed. Flowering May–June; fruiting August-February. Stream and bog margins, seepages and moist exposed slopes, in the mountains of West Virginia, Virginia, and North Carolina. TYPE (!): *Alexander, Everett & Pearson*, Whitetop Mtn., Va., Sept. 1, 1933 (NY!).

ILLUSTRATIONS. Castanea **1**: 84 (as *I. longipes* Chapm.); Castanea **10**: 58 (as *I. collina* Alex.); Gleason (1952), in the figure on p. 500 (vol. 2), shows staminate material of *Ilex decidua* Walter to the left and pistillate material of *Nemopanthus collinus* (Alex.) Clark to the right (as *I. longipes* Chapm.); Strausbaugh & Core (1958), p. 603 (as *Ilex collina* Alex.).



MAP 1. Distribution of *Nemopanthus collinus* (Alexander) Clark (map from U.S. Gov. Printing Office, stock no. 0301–1896).

With the transfer of *Ilex collina* Alexander into *Nemopanthus* Raf., its yellow-fruited form (TYPE!, WVA) becomes:

Nemopanthus collinus forma **van-trompii** (M. Brooks) Clark, comb. nov.

Ilex longipes f. *van trompi* M. Brooks, Castanea **5:** 15. 1940.
Ilex collina f. *Van Trompii* (M. Brooks) Core & Davis, Proc. W. Va. Acad. Sci. **16:** 39. 1944.

2. **Nemopanthus mucronatus** (L.) Trelease, Trans. Acad. Sci. St. Louis **5:** 349. 1892.

Vaccinium mucronatum L. Sp. Pl. 350. 1753.
Ilex canadensis Michx. Fl. Bor.-Am. **2:** 229. 1803.
Nemopanthes fascicularis Raf. Jour. Phys. **89:** 97. 1819.
Nemopanthes canadensis (Michx.) DC. Mém. Soc. Genève **1:** 450. 1823.
Ilicioides mucronata (L.) Britton, Mem. Torrey Bot. Club **5:** 217. 1894.

Shrubs or small trees. Leaf blades oblong, elliptic or ovate to sublanceolate or oblanceolate, to 6 cm. long and 3 cm. wide, upper and lower surfaces glabrous or rarely puberulous, apex obtuse to acute or abruptly acuminate and mucronate (or emarginate by abortion of the mucro), margin entire to remotely serrate (rarely remotely dentate), base cuneate, truncate, or obtuse; petioles to 2 cm. long, glabrous or puberulous, stipules setaceous. Pistillate flowers 1 (rarely 2) per node, staminate flowers 1–2 at a node. Pistillate flower: calyx lobes 0–4, ephemeral, setaceous, 0.5–1 mm. long, 0.1 mm. or less wide; petals 4, greenish-white, linear or narrowly lanceolate, 1.4–2.5 mm. long, 0.4–0.6 mm. wide; pedicels often reddish in fruit, 11–43 mm. long, occasionally with lenticels, glabrous or puberulous. Staminate flower: calyx lobes 0–4, fugacious, linear or setaceous, 0.2–1 mm. long, 0.1 mm. or less wide; petals greenish-white, linear, 1.5–2.1 mm. long, 0.2–0.4 mm. wide; stamens 2–5, anthers 0.3–0.6 mm. broad, 0.3–0.8 mm. long, filaments 1–2.8 mm. long; pedicels 7–23 mm. long, glabrous. Drupe 7–10 mm. long and broad, dark red, enclosing 4 or 5 endocarps (pyrenes) (fewer by abortion), the endocarps 3.8–5.2 mm. long, 2.5–3.2 mm. broad, dorsally smooth or ribbed, laterally unribbed. ($2n = 40$.) Flowers March–June; fruits July–November or later. Bogs, lake margins, low woods and open ground, moist slopes and ridges, from Newfoundland and Nova Scotia to Ontario, Minnesota, Indiana, Ohio, West Virginia, Virginia and Maryland, and attributed to Illinois by Fernald (1950). TYPE: *Kalm* (LINN); not seen.

ACKNOWLEDGMENTS

My gratitude is extended to the curators of the following herbaria for having made materials in their care available for examination: Gray Herbarium, Smithsonian Institution, U.S. National Arboretum, Missouri Botanical Garden, New York Botanical Garden, and the Universities of North Carolina, West Virginia, and Tennessee. I am also indebted to Ken Moore, whose collections led to this treatment, to J. R. Massey for his helpful interest, to A. E. Radford for critical reading of the manuscript, and to S. A. Spongberg for valuable bibliographic assistance.

REFERENCES CITED

ALEXANDER, E. J. 1941. Two new species from the southern Appalachians. Castanea **6**: 30–32.

AMMONS, N., & E. L. CORE. 1945. The hollies of West Virginia. Castanea **10**: 57–60.

BROOKS, A. B. 1920. West Virginia trees. W. Va. Exp. Sta. Bull. 175.

———. 1936. A new holly for West Virginia. Castanea **1**: 83–85.

EDWIN, G. 1957. Notes on *Ilex*. Rhodora **59**: 20–23.

FERNALD, M. L. 1950. Gray's manual of botany, 8th ed. [Corrected printing, 1970.] lxiv + 1632 pp. D. Van Nostrand Co., New York, New York.

GLEASON, H. A. 1952. The new Britton and Brown illustrated flora of the northeastern United States and adjacent Canada. Vol. 2. iv + 655 pp. New York Botanical Garden, New York, New York.

——— & A. CRONQUIST. 1963. Manual of vascular plants of northeastern United States and adjacent Canada. li + 810 pp. D. Van Nostrand Co., Princeton, New Jersey.

GATTINGER, A. 1887. The Tennessee flora; with special reference to the flora of Nashville. 109 pp. Published by the author, Nashville, Tennessee.

———. 1901. The flora of Tennessee and a philosophy of botany. 296 pp. Gospel Advocate Publ. Co., Nashville, Tennesee.

JAMES, F. C. 1969. The woody flora of Virginia. Ph.D. thesis (unpubl.), Department of Botany, Univ. North Carolina, Chapel Hill.

LOESENER, T. 1942. Aquifoliaceae. *In* A. ENGLER & K. PRANTL, Die natürlichen Pflanzenfamilien, 2nd ed. **20b:** 38–86. (Photocopied reprint ed. 1960.) W. Engelmann, Leipzig.

MASSEY, A. B. 1961. Virginia flora. Va. Agric. Exp. Sta. Bull. 155.

OAKES, H. N. 1932. A brief sketch of the life and works of Doctor Augustin Gattinger. 152 pp. Cullom & Ghertner Co., Nashville, Tennessee.

STRAUSBAUGH, P. D., & E. L. CORE. 1958. Flora of West Virginia, part III. W. Va. Univ. Bull. Ser. 58. No. 12–3.

STUPKA, A. 1964. Trees, shrubs and woody vines of Great Smoky Mountains National Park. ix + 186 pp. Univ. Tennessee Press, Knoxville.

TRELEASE, W. 1892. Revision of North American Ilicineae and Celastraceae. Trans. Acad. Sci. St. Louis **5:** 343–357.

WOODS, F. W. 1951. The status of *Ilex collina* Alexander. Castanea **16:** 126, 127.

ERSKINE COLLEGE
DUE WEST
SOUTH CAROLINA 29639

ADDITIONAL NEW TAXA AND NEW COMBINATIONS IN HYMENAEA (LEGUMINOSAE, CAESALPINIOIDEAE)

Y. T. Lee and J. H. Langenheim

The leguminous genus *Hymenaea* in the tribe Detarieae (Cynometreae sensu Léonard) has long been considered a neotropical genus. With the recent reinstatement of *Hymenaea* in the recorded African flora (Langenheim & Lee, 1974), the genus again has an amphi-Atlantic distribution. Although all species of *Hymenaea* but one are neotropical, evidence clearly supports an African origin for the genus with the Amazon Basin being a secondary center of distribution (Langenheim, 1973; Langenheim, Lee, & Martin, 1973; Langenheim & Lee, 1974). The African species *H. verrucosa* (formerly *Trachylobium verrucosum*) is restricted to the east tropical coast and adjacent offshore islands, occurring in seasonally dry lowland forests. In the New World, 17 species have been recognized to date (Lee & Langenheim, 1973) which span the tropics, occurring from 23°N to approximately 25° S and occupying all major ecosystem types from equatorial rain forest to thorn forest.

During the course of a systematic study of *Hymenaea* (Lee, 1973, unpublished thesis), one new species, two new varieties, and several new combinations were suggested which are discussed in the present paper.

Hymenaea maranhensis Y. T. Lee & Langenheim, sp. nov.

Figures 1 & 2.

Arbor parva usque ad 2–6 m. alta plerumque fruticosa cum ramulis prope terram. Foliola obovata vel oblonga, 8–10 × 4.0–5.5 cm., supra hebetata et sparse adpresso tomento praedita, infra tomento rubro-fusco implecto praedita, pilis maxime prominentibus secus venas et margines. Inflorescentia corymbosa racemis paucis paucifloribus composita, ramulis brevibus robustis indumento dense tomentoso praeditis, bracteolis ovatis vel obovatis 16–18 × 14–16 mm., plerumque per anthesin persistentibus. Hypanthium floris campanulatum, sessile; lobi calycis oblongi, 25–30 × 10–15 mm., indumento extus griseo-brunneo tomentoso intus aureo-tomentoso-sericeo praediti; petala spathulata, 28 × 12 mm., manifeste unguiculata (unguibus 6–7 mm. longis); ovarium longistipitatum (stipite circa 8 mm. longo), circa 10 × 4 mm., basi et secus margines indumento dense flavido-piloso praeditum, parte centrali plerumque nuda; ovula 8–12. Fructus maturus seminaque non cognita.

Type: **Brazil.** Maranhão: Municipio de Loreto, "Ilha de Balsas" region, between Balsas and Parnaiba River, ca. 20 km. south of Loreto, north of main house of Fazenda Trabalhosa, Apr. 8, 1962, *G. & L.T. Eiten*

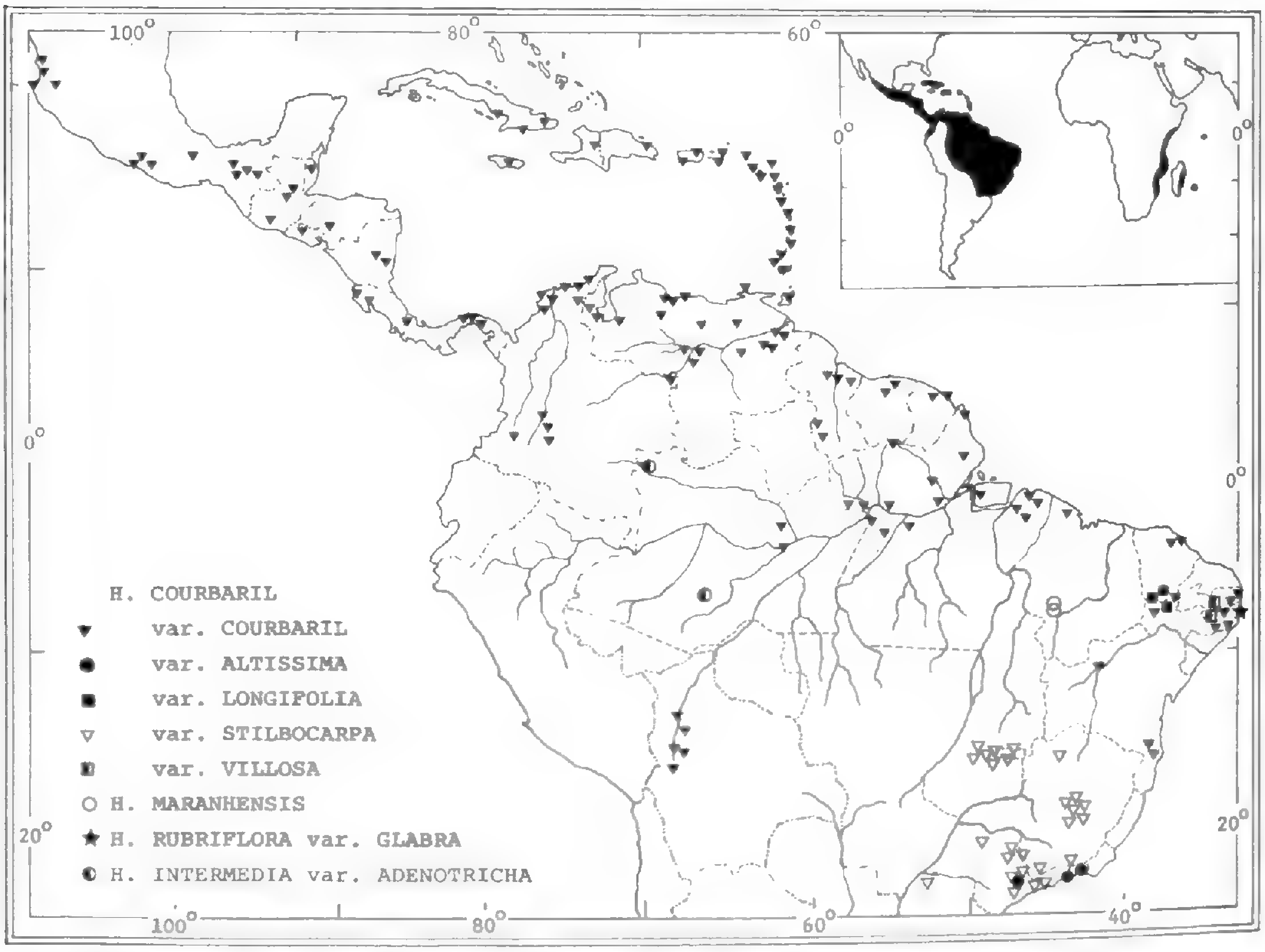


FIGURE 1. Distribution of some species and varieties of *Hymenaea.* Insert showing general distribution of the genus.

4183 (NY, holotype!; UB!, isotype; additional type material was sent to K, SP, and US from UB).

Small tree, usually shrubby and branched near base. Leaves bifoliolate and petiolate, the petiole 12–16 mm. long, densely puberulent, the leaflets with twisted petiolule ca. 3 mm. long, the lamina obovate to oblong, the inner half much narrower than the outer half, the apex obtuse, the base oblique, with one side acute and the other side rounded, the midrib and secondary veins prominent on both sides, elevated beneath. Inflorescence corymbose, composed of few racemes, each with relatively few flowers, the pedicels 8–14 mm. long, the bracts not seen, bracteoles ovate to obovate, usually persistent during anthesis. Flowers relatively large, the bud before opening ca. 28 × 14 mm.; hypanthium campanulate, subsessile; calyx lobes oblong, grayish-brown tomentose outside, yellowish-brown tomentose-sericeous within; petals creamy white, spatulate, early deciduous; stamens 10, the filaments 30–35 mm. long, the anthers ca. 8 mm. long; ovary long-stipitate, obliquely oblong, densely yellowish pilose at base and along the margins but usually glabrate in the central parts, the style ca. 25 mm. long, glabrous, the ovules 8–12.

HABITAT AND DISTRIBUTION. This species is restricted to southeastern Maranhão and has only been collected a few times. It grows in sandy xeromorphic woodland, a type of *cerrado* (regionally referred to as 'chapada'). The flowering season is from February to April.

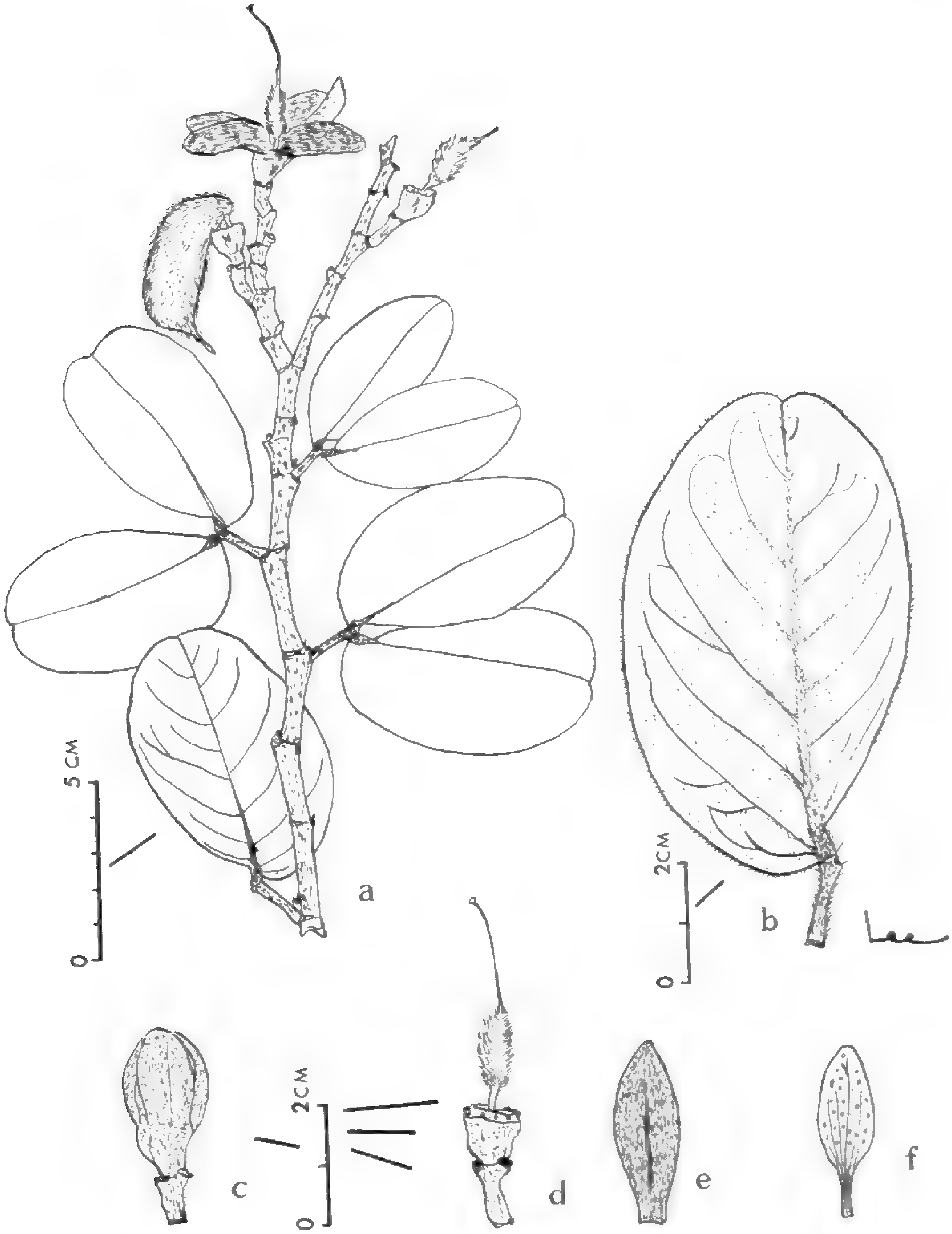


FIGURE 2. *Hymenaea maranhensis*. a, floral branch; b, leaflet (ventral side); c, flower bud; d, pedicel, hypanthium, and pistil; e, sepal (ventral side); f, petal.

Brazil. MARANHÃO. MUNICIPIO DE LORETO: "Ilha de Balsas" region between Balsas and Parnaiba River, Feb. 3, 1970, *G. & L.T. Eiten 10460* (NY, UB); ca. 1 km. north of Parnaiba River at Santa Barbara, Feb. 18, 1971, *10669* (UB); ca. 6 km. SE of Loreto, Feb. 28, 1970, *10809* (A, UB).

VERNACULAR NAMES. "Jatobá do vaqueiro" and "jatobá da quaresma," Maranhão.

Professors G. and L. T. Eiten of Dept. VEG-IB, Universidade de Brasilia, DF, Brazil, have kindly sent us their *Hymenaea* collections from Maranhão for study; from these the description of this new species was drawn. *Hymenaea maranhensis* is closely related to *H. eriogyne* and *H. aurea*, but can be separated from these species by (1) the vesture pattern of the ovary which is densely pilose at the base and along the margins but usually glabrate in the central parts, (2) the relatively large and usually persistent bracteoles, (3) the long pedicels, and (4) the sessile hypanthium. It can be distinguished from the other species of sect. HYMENAEA, to which it belongs, by its pubescent ovary. It differs from the species in sect. TRACHYLOBIUM in its corymbose inflorescence and large flowers.

The specific epithet is derived from the name of the state of Maranhão, Brazil.

Hymenaea maranhensis has a partially pubescent ovary and spatulate petals, both characters of species which we considered to be more primitive and which occur in the rain forest; these characters, as well as the proximity of its range to the Amazon Basin, suggest the relictual nature of this species. Several presumably adaptative characters, such as the large and usually persistent bracteoles, the thickly coriaceous leaves, and the shrubby habit, indicate an evolutionary trend toward a drier habitat. Its resemblance to the more common *cerrado* species *H. stigonocarpa* also suggests an intermediate position between that species and those of the Amazonian rain forests (Lee, 1973, unpublished thesis).

Hymenaea rubriflora var. **glabra** Y. T. Lee & Andrade-Lima, var. nov. FIGURES 1 & 3.

Varietatis *rubriflorae* similis sed in foliolis latioribus chartaceis utrinque glabris differt.

TYPE: **Brazil**. PERNAMBUCO: "Bonito, Mata secund., marg. estr. 1 km. além divisa Camocim de São Felix," Feb. 10, 1969, *D. de Andrade-Lima 67-4929* (IPA, holotype!; UC, isotype!).

Small tree 5–6 m. tall. Leaves bifoliolate and petiolate, the petiole slender, 12–20 mm. long, glabrous, the leaflets with twisted petiolule ca. 4 mm. long, the lamina oblong, 10–14 × 4–7 cm., the inner half much narrower than the outer half, chartaceous, glabrous and shining on both sides, the apex obtuse to apiculate, the base oblique, with one side acute and the other side rounded, the midrib and secondary veins prominent, elevated beneath, the veinlets finely reticulate and conspicuous on both sides. Inflorescence corymbose, composed of few racemes, its branches short and densely reddish-brown tomentose, the pedicels 4–6 mm. long, bracteoles ca. 10 × 8 mm. The hypanthium campanulate, sessile to subsessile; calyx lobes oblong, obtuse, 16–18 × 6–9 mm.; petals red, lanceolate, 14–22 × 5–8 mm., short unguiculate (claws 2–3 mm. long); stamens ca. 25 mm. long, the anthers 4–5 mm. long, the filaments red to pink; ovary long-stipitate (the stipe ca. 5 mm. long), obliquely oblong, 7–8 × 3.5 mm., the style ca. 20 mm. long, the ovules 6–10. Fruit and seeds not seen.

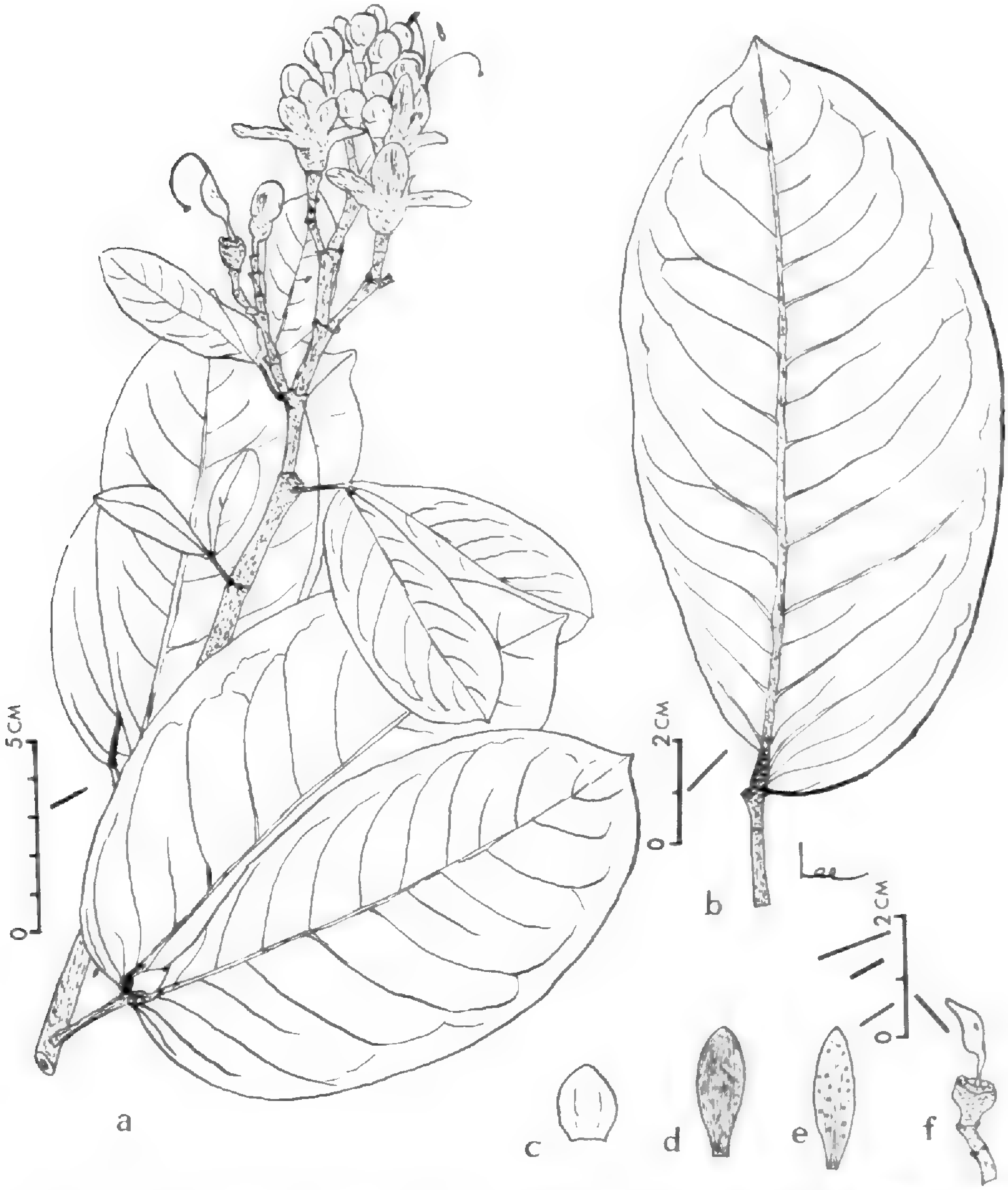


FIGURE 3. *Hymenaea rubriflora* var. *glabra*. a. floral branch; b, leaflet (dorsal side); c, bracteole (ventral side); d. sepal (ventral side); e. petal; f. pedicel, hypanthium, and pistil.

HABITAT AND DISTRIBUTION. This new variety is known solely from the type collection which was made in a secondary forest on a hilly range along the Atlantic coast. Flowering was in February.

VERNACULAR NAME. "Jatobá." This name is also used for other *Hymenaea* species.

Hymenaea rubriflora var. *glabra* may be easily separated from var. *rubriflora* by its broader, chartaceous, and glabrous leaflets.

The oblong, rather large (ca. 14 × 7 cm.), and glabrous leaflets are similar to those of *H. oblongifolia* var. *latifolia* which has been collected along Rio Gurjau, Pernambuco, and in southern coastal Bahia (Lee &

Langenheim, 1973). The two species, however, belong to different sections of the genus and can be separated by the type of inflorescence, vesture of the ovary, and the size of the flower.

Hymenaea courbaril L. Sp. Pl. 1192. 1753. var. **courbaril.** FIGURE 1.

> *Hymenaea courbaril* var. *obtusifolia* Ducke, syn. nov., Arch. Jard. Bot. Rio de Janeiro **4**: 47. 1925. Based upon a cultivated tree in Museu Goeldi, Belém, Pará, Brazil (from Ilha de Marajó?), *Ducke 16906* (MG, holotype!).

Hymenaea courbaril var. **villosa** Y.T. Lee & Andrade-Lima. FIGURES 1 & 4.

Varietatis *subsessilis* similis sed in foliolis supra sparse pubescentibus infra dense villosis (praesertim secus costam et venas secundarias), floribus minoribus et ovario cum stipite distincto differt.

TYPE: **Brazil.** PARAÍBA: Along roadside near Paquevira de Natuba, Oct. 27, 1971, *Lee & Andrade-Lima 83* (UC, holotype!; UC, isotype!).

Medium-sized tree 8–10 m. tall, the trunk ca. 35 cm. in diameter, the branchlets lightly puberulent to glabrous. Leaves bifoliolate and petiolate, the petiole slender, 12–18 mm. long, slightly to densely puberulent, the leaflets with twisted petiolule 2–3 mm. long, the lamina broadly to narrowly falcate, 6–9 × 3.5 cm., the inner half much narrower than the outer half, coriaceous, shining and glabrate above, lightly to densely pubescent beneath, occasionally conspicuously short-hairy on margins, the apex acute to short-acuminate, the base oblique, with one side acute and the other side rounded, the midrib and secondary veins elevated beneath and densely villous, the veinlets finely reticulate beneath and obscure above. Inflorescence branches, pedicels, and flowering buds lightly ochraceous to yellowish-brown, puberulent, the pedicels ca. 6 mm. long. Flowering buds before opening ca. 18 × 7 mm.; the hypanthium with a stalk-like base 6–7 mm. long; calyx lobes obovate, ca. 14 × 7 mm., ochraceous to subgolden-brown pubescent outside, densely golden-brown tomentose within; petals creamy white, obovate, obtuse, 12 × 7 mm., subsessile; stamens 22–25 mm. long, the anthers 5–6 mm. long; ovary short-stipitate (the stipe ca. 3 mm. long), obliquely oblong, ca. 5 × 3 mm., slightly pilose at one side of the base to glabrous, the ovules 8–12. Fruit oblong to cylindrical, 9–12 cm. long, 4.5–5.5 cm. wide, and 3.5–4.0 cm. thick, light to dark brown, subcompressed, the suture not prominent. Seeds 4–8, obovoid to ellipsoid, about 2.5 cm. long, 2 cm. wide, and 1.2 cm. thick, the testa dark brown, its intrusion in the cotyledon producing 2 shallow furrows.

HABITAT AND DISTRIBUTION. The type specimen was collected from a moist forest in hills (elevation ca. 500 m.) in inland Paraíba about 70 km. west of the Atlantic coast. Two other specimens were collected in the same location and one in the neighboring state of Pernambuco. The flowering time is December and January.

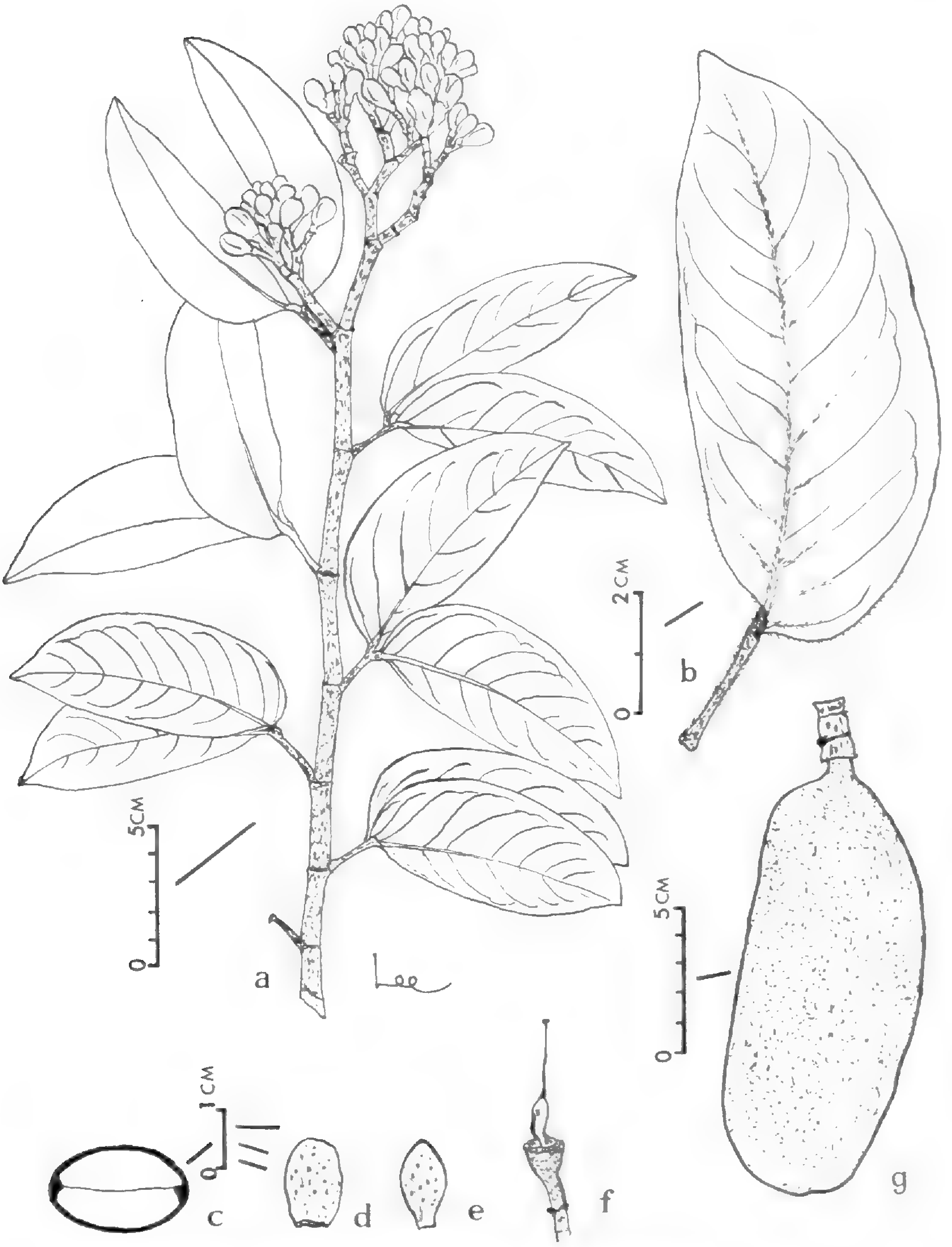


FIGURE 4. *Hymenaea courbaril* var. *villosa*. a, floral branch; b, leaflet (ventral side); c, seed (cross section) showing intrusions of testa; d, sepal (dorsal side); e, petal; f, pedicel, hypanthium, and pistil; g, mature fruit.

Brazil. PARAÍBA: in the vicinity of Natuba, Nov. 27, 1971, *Lee & Andrade-Lima 81 & 82* (UC); Alagoinha, Jan. 4, 1943, *L. Xavier 1183* (Herb., Univ. Federal de Paraíba). PERNAMBUCO: Tapera, Dec. 6, 1931, *D. B. Pickel 2853* (A, IPA).

VERNACULAR NAME. "Jatobá."

Hymenaea courbaril var. *villosa* is very similar to var. *subsessilis* but may be distinguished from it by (1) the lightly to densely villous lower surface of the leaflets, particularly the midrib and secondary veins, (2) the smaller flowers, and (3) the occasional pilosity at the inner side of the base of the ovary.

Because of its occasionally very densely hairy leaflets this variety has been confused with *Hymenaea martiana*, which is generally found in the drier habitats such as the thorn forests in northeastern Brazil and the savannah in central Brazil. However, *H. courbaril* var. *villosa* may be distinguished from *H. martiana* by its falcate leaflets, smaller flowers, and the vesture of the calyx.

Hymenaea courbaril var. **altissima** (Ducke) Y. T. Lee & Langenheim comb. & stat. nov. FIGURE 1.

Hymenaea altissima Ducke, Annaes Acad. Brasil. Sci. 7: 207. 1935.

TYPE: **Brazil.** STATE OF RIO DE JANEIRO: Aveller, Fazenda Posse, 1930, *A. Ducke RB 30306* (RB, lectotype!; MG!, R!, isotypes). Since Ducke merely listed six collections and did not indicate a type, one of these collections was designated by Egler (1963) as the "type."

HABITAT AND DISTRIBUTION. This variety has a very narrow distribution along the Atlantic coast. It has been collected in humid forests in the city of Rio de Janeiro, Guanabara, in Serra do Mar of the state of Rio de Janeiro, and in the city of São Paulo, São Paulo. Trees flower in November and December and have mature fruit in the following May.

VERNACULAR NAME. "Jatahy," commonly used for the entire genus in southern Brazil.

Hymenaea altissima was characterized by (1) small, short- or long-acuminate, and distinctly falcate leaflets on floral branches, (2) the highly reticulate venation of the leaflets conspicuous on both surfaces, (3) the relatively small flowers, and (4) the one- or many-seeded fruits.

The foliar characters and the relative size of flowers do not appear sufficiently significant to warrant specific status for this taxon. Of the two types of fruits described by Ducke, the one-seeded fruits are ovoid to obovoid and subcompressed, whereas the many-seeded fruits are oblong and strongly compressed, essentially similar to those of *H. courbaril* var. *courbaril*. Thus we conclude that the relationship of *H. altissima* is best expressed by varietal status under *H. courbaril*; the occurrence of two different types of fruits may be the result of factors controlling the availability of pollen during anthesis.

Hymenaea courbaril var. **longifolia** (Benth.) Y. T. Lee & Andrade-Lima, comb. nov. FIGURE 1.

Hymenaea splendida var. *longifolia* Benth., in Martius, Flora Brasiliensis **15**(2): 237. 1870.

TYPE: **Brazil.** BAHIA: Villada Barra, *Blanchet 3135* (R, holytype!; P, isotype!).

HABITAT AND DISTRIBUTION. Other than the type collection, this variety has been collected in Chapada do Araripe, in the border area of the states of Ceará, Piauí, and Pernambuco, which is surrounded by the thorn forest (*caatinga*), a vegetation type in northeastern Brazil. The vegetation of the *chapada* or highland is relatively dense, with scattered medium-sized trees and a thick ground cover (*cerrado* or *cerradão*). The difference of the highland vegetation from the surrounding areas probably results from its elevation (ca. 1000 m.) and more abundant annual rainfall. This variety flowers in November and December; the fruit usually falls in the following September.

VERNACULAR NAME. "Jatobá."

This taxon was originally described by Bentham (1870) as a variety of *H. splendida* and is known only from the type collection. It was brought to our attention by Professor D. de Andrade-Lima of the Instituto de Pesquisas Agronômicas, Recife, Pernambuco, Brazil. Additional material was collected during a trip to northeastern Brazil (*Lee & Andrade-Lima 95, 110, 111, & 112*) which enabled us to determine its present taxonomic status. *Hymenaea splendida* var. *splendida*, on the other hand, is considered to be synonymous with *H. courbaril* var. *stilbocarpa* (see below).

Hymenaea courbaril var. *longifolia* may be distinguished from other varieties of *H. courbaril* by the (1) large, rather long (ca. 12 × 7 cm.), glabrous, and usually obtuse leaflets, (2) medium-sized flowers (buds before opening ca. 30 × 12 mm.), (3) occasionally clawed petals, (4) externally ochraceous-puberulent and internally yellowish-tomentose calyx, and (5) unusual shape of the fruit, which is broadest at the distal end.

This variety may be separated from *H. stigonocarpa* var. *stigonocarpa*, which is characterized by glabrous leaflets and is commonly found in the *cerrado* of central Brazil, by its smaller flowers, long-stalked hypanthium (the stalk-like base is 6–7 mm. long), and the shape of the fruit.

Hymenaea courbaril var. **stilbocarpa** (Hayne) Y. T. Lee & Langenheim, comb. & stat. nov. FIGURE 1.

Hymenaea stilbocarpa Hayne, Arzneikunde gebräuchlichen Gewächses **11**: *pl. 11.* 1830 (Flora **10**: 740. 1827, nomen).

Hymenaea confertifolia Hayne, *ibid. pl. 9.* 1830 (Flora **10**: 740. 1827, nomen). Based upon *Sellow*, "Brasilia" (B, probably destroyed; photographs, A!, K!, NY!, US!).

Hymenaea splendida Vog., syn. nov. Linnaea **11**: 409. 1837. Based upon *Sellow 1025*, Bahia, Victoria, Brazil (B, probably destroyed; photographs, A!, K!, NY!, US!).

TYPE: **Brazil.** Ad Caldas in Minas Gerais, Sept. 1867, *Regnell 11–91* (K!). Hayne (1830) did not cite any specimens in his original description of this taxon. One of the four collections listed by Bentham (1870), the first set of specimens ever cited as this taxon, is chosen here as the representative specimen.

HABITAT AND DISTRIBUTION. This variety is native along rivers in relatively dry forests on the plateau of the state of São Paulo and in adjacent parts of Río de Janeiro and Minas Gerais. It has also been collected in southern Bahia, in the Federal District and southern Goiás. It is frequently cultivated in Belo Horizonte, Minas Gerais. It flowers from November to January; the fruit is usually mature in September.

VERNACULAR NAMES. "Jatobá"; "jatobá amarelo" (Minas Gerais); "jatobá mirim" (São Paulo); "jatobá miudo" (Ceará) and "jatobá de caatinga" (Bahia).

In describing this taxon, Hayne (1830) emphasized its dark-brown, sausage-shaped fruit. Although this variety has been confused with var. *altissima*, it is usually more like var. *courbaril*, and Bentham (1870) stated that fruit of the two could scarcely be distinguished. Ducke (1935) predicted that *H. stilbocarpa* would eventually be considered a subtropical variety of *H. courbaril*. The leaflets of var. *stilbocarpa* resemble those of certain populations of var. *courbaril* in western Mexico and the West Indies in shape, texture, and shiny surface, a similarity possibly explained by progressive radiation into adjacent subtropical regions. After evaluating all the characters, we agree with Ducke's view that the taxon is best considered as a variety of *H. courbaril*.

Hymenaea courbaril var. *stilbocarpa* is characterized by (1) calyx lobes rusty or dark brown and sericeous-velutinous externally, golden-brown sericeous internally, (2) fruit often dark brown and occasionally subterete, (3) flowers smaller than in var. *courbaril* and var. *subsessilis* but much larger than in var. *altissima*, and (4) medium-sized, subfalcate leaflets.

Hymenaea courbaril, therefore, is now considered to be a polymorphic species with six varieties — the five described here and the Amazonian variety *subsessilis*. The range of the species is essentially that of the genus. In the northern part of its distribution, *H. courbaril* var. *courbaril* has radiated into various ecosystems, whereas in the Amazon and south of it there is evidence of more morphological differentiation of *H. courbaril* in different geographical ranges characterized by distinctive habitats, leading to the recognition of these varieties.

Hymenaea intermedia var. **adenotricha** (Ducke) Y. T. Lee & Langenheim, comb. & stat. nov. FIGURE 1.

Hymenaea adenotricha Ducke, Bull. Mus. Hist. Nat. (Paris), ser. 2. 5: 727. 1932.

TYPE: **Brazil.** AMAZONAS: Habitat silva non inundabili prope São Paulo de Olivença, Aug. 19, 1929, *Ducke RB 23282* (RB, holotype!; K!, P!, US!, isotypes).

HABITAT AND DISTRIBUTION. This variety has hitherto been known solely from the type collection made in São Paulo de Olivença, close to the Peruvian border, where only a single tree occurs in *terra firma* forest. A recent collection from Rio Curuquetê, near Cachoeira Santo Antonio (*Prance et al. 14342*), appears to belong to this variety. This suggests that the taxon may have a wider range than previously indicated. Flowering of the type collection was in August. Fruit and seeds have not been collected.

VERNACULAR NAME. "Jutaí," a name commonly used for the genus in the Amazon Basin.

Ducke in the original description recognized the affinity of this taxon to *Hymenaea intermedia* but distinguished *H. adenotricha* from it by (1) thickly coriaceous leaflets with the base broadly expanded on one side, (2) leaflets and petioles pubescent beneath, and (3) the ovary with short stiff hairs on one side. After examining the type, we consider *H. adenotricha* to be a western Amazonian variant of the typical form of *H. intermedia.*

Ducke (1935) also noted that the young fruits of this variety resembled those of *Peltogyne*, a neotropical genus which has been considered by some the genus most closely related to *Hymenaea.* This similarity, however, is only superficial. Mature fruit of *Peltogyne* is dehiscent, subtriangular to obliquely orbicular, flat, without pulpy endocarp, and usually one-seeded. This kind of fruit is significantly different from the fruit of *Hymenaea*, which is indehiscent, ovoid to oblong, with pulpy endocarp surrounding the seed or seeds. The leaves of *Peltogyne* are bifoliolate; however, in most species, the petiolule is distinct and cylindrical. The petiolule of *Hymenaea*, on the other hand, is twisted, with the outer side covered by the lamina of the leaflet. Additional evidence against an immediate affinity of the two genera comes from seedling characters. The difference in shape and number of primary leaves, again may indicate a relatively remote relationship between the two genera.

ACKNOWLEDGMENTS

We wish to thank Professor D. de Andrade-Lima, who kindly invited the first author to join a collecting trip, sponsored by the Brazilian Academy of Science for the study of the flora of the thorn forests in northeastern Brazil, while he was collecting under the auspices of an NSF Dissertation Improvement Grant (GB–29278). We also appreciate his criticism of some of the descriptions of taxa from his area. We are grateful, too, to Professors G. & L. T. Eiten for sending their Maranhão collections to us for study and for their supplementary information on *H. maranhensis*. We appreciate help with the Latin descriptions and criticism of the manuscript by Drs. B. G. Schubert and P. F. Stevens. Our gratitude is also expressed to the curators of the herbaria listed in the text by standard abbreviations, who kindly loaned material or provided us facilities to examine specimens essential to this study. Grateful acknowledgment is made for funds granted to the second author for this study by the National Science Foundation (GB-5816, GB-13659, and GB-29278).

LITERATURE CITED

BENTHAM, G. 1870. Leguminosae II. Swartzieae et Caesalpinieae. *In*: MARTIUS, Flora brasiliensis **15**(2): 234-237.

DUCKE, A. 1935. As especies brasileiras de jatahy, jutahy ou jatobá (genero *Hymenaea* L., Leguminosas Caesalpiniaceas). Annaes Acad. Brasil, Sci. **7**: 203-211.

EGLER, W. 1963. Adolpho Ducke — Traços biográficos, viagens e trabalhos. Bol. Mus. Paraense Hist. Nat. **18**: 51.

HAYNE, F. G. 1827. Ueber die Gattungen *Hymenaea*, Vouapa und eine neue (*Trachylobium*) mit Hinsicht auf die Abstammung des aus Amerika kommenden Copals. Flora **10**: 737-746.

———. 1830. Arzneikunde gebräuchlichen Gewächses **11**: *pls. 6-12*. Berlin.

LANGENHEIM, J. H. 1973. Leguminous resin-producing trees in Africa and South America. *In*: MEGGARS, AYENSU & DUCKWORTH, Tropical forest ecosystems in Africa and South America: A comparative review. Smithsonian Press.

——— & Y. T. LEE. 1974. Reinstatement of the genus *Hymenaea* L. (Leguminosae, Caesalpinioideae) in Africa. Brittonia **26**(1): 3-21.

——— & S. S. MARTIN. 1973. An evolutionary and ecological perspective of the Amazonian hylaea species of *Hymenaea* (Leguminosae, Caesalpinioideae). Acta Amazonica **3**(1): 5-37.

LEE, Y. T. 1973. A systematic study of the genus *Hymenaea* L. (Leguminosae, Caesalpinioideae, Detarieae). Ph.D. thesis (unpubl.). University of California, Santa Cruz.

——— & J. H. LANGENHEIM. 1973. New taxa from Brazil and Guyana in the genus *Hymenaea* (Leguminosae, Caesalpinioideae). Jour. Arnold Arb. **54**(1): 94-104.

Y. T. LEE
ARNOLD ARBORETUM
HARVARD UNIVERSITY
CAMBRIDGE, MASSACHUSETTS 02138

J. H. LANGENHEIM
DIVISION OF NATURAL SCIENCES
UNIVERSITY OF CALIFORNIA
SANTA CRUZ, CALIFORNIA 95060

A CONTRIBUTION TO THE KNOWLEDGE OF CYTOLOGY IN MAGNOLIALES

PETER GOLDBLATT

RECENT INTEREST IN THE PHYLOGENY of the primitive angiosperms has resulted in the addition of considerable cytological data on the group (Raven & Kyhos, 1965; Ehrendorfer *et al.*, 1968; Raven, Kyhos & Cave, 1971). Nevertheless the cytology of two families, the Trimeniaceae and Gomortegaceae (Raven, 1974), has remained unknown and represents an important gap in our knowledge. The cytology of one species of the Trimeniaceae, *Trimenia papuana*, $2n = 16$, is described here as well as that for two other species, *Hortonia floribunda*, $2n = 38$ (Monimiaceae)[1] and *Austrobaileya cf. scandens*, $2n = 44$ (Austrobaileyaceae). While the chromosome count for *Hortonia* is the first report for this genus, the count for *Austrobaileya* cf. *scandens* is a confirmation of a previous count of $2n = 44$ for this plant published by Rüdenberg (1967) in this journal. A later record of $2n = 46$ for this species (Ehrendorfer *et al.*, 1968) which threw doubt on Rüdenberg's report must be viewed with misgiving.

MATERIALS AND METHODS

Mitotic counts were made from root tips of seedlings grown from seed collected in the wild in the case of *Trimenia* and *Hortonia*, while root tip material was obtained from *Austrobaileya cf. scandens* from a cutting of the same material originally studied by Rüdenberg. Root tips were pretreated on 0.1 per cent colchicine for five hours at ± 4°C., fixed in acetic: ethanol, 1:3, for three minutes, and then stored in 70 per cent ethanol. Root tips were hydrolized in 10 per cent HCl at 60°C. and then squashed in lacto-propionic orcein (Dyer, 1963).

OBSERVATIONS

1. TRIMENIACEAE
    Trimenia papuana Ridley, $2n = 16$, Mount Kaindi, Wau, New Guinea, *P. Katik 56376.*
2. MONIMIACEAE
    Hortonia floribunda Wight, $2n = 38$, Kruikles, 800 m., Ceylon. *Kostermans s.n.*
3. AUSTROBAILEYACEAE
    Austrobaileya cf. scandens C. T. White, $2n = 44$, Australia, Queensland, near Ravenshoe, *Webb & Tracy 6301.*

The record for *Trimenia papuana* represents the first count for the family Trimeniaceae. Chromosomes of this species are of medium size

---

[1] Recently Smith (1971) proposed the segregation of *Hortonia* in Hortoniaceae.

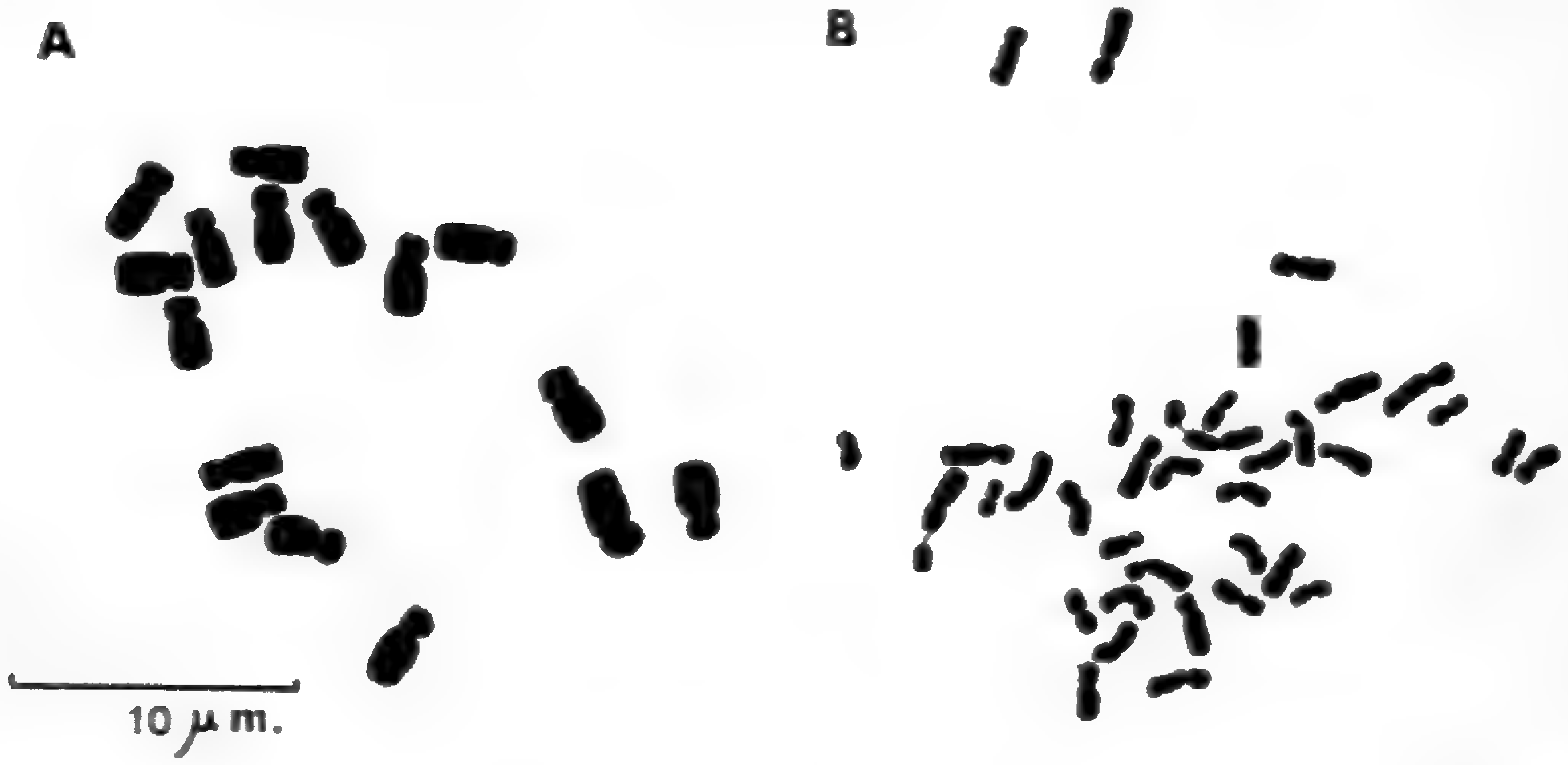


FIGURE 1. A, Chromosomes of *Trimenia papuana* Ridley, $2n = 16$; B, *Hortonia floribunda* Wight, $2n = 38$.

(FIGURE 1A), ranging from 2.5–3.5 µm. in length, and though they are somewhat smaller than those of *Austrobaileya,* as described and illustrated by Rüdenberg, they are of the same order. The karyotype of *Trimenia papuana* is, however, far more simple and comprises eight pairs of similarly sized submetacentric chromosomes.

The chromosomes of *Hortonia* are very small and although they range in size from about 3.0 to less than 1.8 µm. the mean size is only about 2 µm. (FIGURE 1B). Considerable difficulty was experienced in establishing the chromosome number with certainty as there are a pair of extremely large satellites on the longest pair of chromosomes, and in all but the best preparations a higher chromosome count was obtained.

The count of $2n = 44$ for *Austrobaileya* and every aspect of the karyotype reported by Rüdenberg is verified here. Of particular note in the karyotype are the two long pairs of chromosomes, the smaller of which bears a very large satellite. The conflicting count of $2n = 46$ by Ehrendorfer *et al.* (1968) cannot be explained, though it should be noted that the material examined by Rüdenberg is in fact from the same stock as that studied here.

DISCUSSION

The basic number of $x = 8$ found in *Trimenia* is remarkable for the Magnoliales, where much higher basic numbers are common, and the only other group with diploids is the distantly related Annonaceae (Raven, 1974). It is even more unusual in the group of families sometimes separated from the Magnoliales in the order Laurales (Takhtajan, 1969; Smith, 1971), and *Trimenia* stands out as the only diploid in this alliance. The cytology fully supports the segregation of Trimeniaceae from the Monimiaceae as proposed by Money, Bailey, and Swamy (1950) on the basis of morphological and anatomical differences. The cytological infor-

TABLE 1. **Chromosome numbers in Monimiaceae s.s.** (sensu Schodde, 1970).

SPECIES	CHROMOSOME NO. n (HAPLOID)	AUTHOR
PEUMOIDEAE		
Peumus boldus Mol.	39	Tschischow, 1956
MONIMIOIDEAE		
Kibara sp.	22	Borgmann, 1964
Tetrasynandra sp.	ca. 43	Ehrendorfer *et al.*, 1968
Hedycarya arborea Forst.	57	Hair & Beuzenberg, 1959
Hedycarya angustifolia R. Cunn.	19	Ehrendorfer *et al.*, 1968
Hedycarya loxocarya (Benth.) Francis	19	" " "
Hedycarya sp. 1	19	" " "
Hedycarya sp. 2	19	" " "
Levieria acuminata (F. V. Muell.) Park	19, ca. 19	" " "
Palmeria scandens F. V. Muell.	19, ca. 19	" " "
Palmeria sp.	ca. 19	" " "
Wilkiea macooraia (Baill.) Perk.	ca. 38	" " "
Mollinedia blumenavii Perk.	18	Gadella *et al.*, 1969
HORTONIOIDEAE		
Hortonia floribunda Wight	19	Goldblatt

mation would in fact suggest that this family is even more distinct than previously supposed, and cytological data for other species of *Trimenia* and especially of *Piptocalyx*, the only other genus in the Trimeniaceae, are eagerly sought.

The family Monimiaceae is comparatively well known cytologically. Work by Hair and Beuzenberg (1959) and by Ehrendorfer *et al.* (1968) has indicated a base number of $x = 19$ in nine species of four different genera of Monimioideae (TABLE 1). There are, however, other base numbers indicated even within Monimioideae sensu Money, Bailey, and Swamy: Borgman (1964) reported $2n = 44$ in *Kibara* sp.; Ehrendorfer *et al.* (1968) found $2n = \pm 86$ in *Tetrasynandra* sp.: and Gadella *et al.* (1969) obtained $2n = 36$ in *Mollinedia blumenavii*. *Peumus boldus*, believed to be only distantly allied to the main group of Monimioideae and placed in a separate subfamily (Schodde, 1970), has $2n = 78$ (Tschischow, 1956). It should also be noted that the two subfamilies of Monimiaceae, Atherospermatoideae and Siparunoideae, recently segregated as two distinct families (Schodde, 1970), both differ in their cytology from the bulk of the Monimiaceae with $x = 22$ in all species examined to date.

The chromosome number of $2n = 38$ for *Hortonia floribunda* is thus consistent with the majority of chromosome numbers known for the Monimiaceae — Monimioideae. The chromosomes of *Hortonia* are similar to those of Monimiaceae in size as far as this can be gauged from a photograph published by Hair and Beuzenberg (1959) for one species of Monimiaceae.

Unfortunately, although many other representatives of the Monimiaceae are known cytologically, no other report or illustration of chromosome size in the family is known. It is disappointing to note that in spite of the large number of chromosome counts that are known for the Magnoliales, there are very few instances where other characters of the karyotype are described. The author would like to make a general plea that cytologists recording chromosome number at least make some mention of general chromosome size if they do not give the size range and indication of method used in preparation. In this way, additional karyotypic information can be made available with very little effort.

If the chromosome size figured by Hair and Beuzenberg is consistent in the Monimiaceae, then both base number and size strongly link *Hortonia* with this family. This does not add weight to Smith's (1971) segregation of Hortoniaceae, while Money, Bailey, and Swamy's (1950) conclusion that *Hortonia* resembles the Monimioideae in many ways and that it is much more closely related to this family than *Trimenia* or *Piptocalyx* is clearly supported by the cytological evidence. On the other hand, information now known for *Trimenia* supports the segregation of this genus in a distinct family. Chromosome number alone might be seen to be consistent with suggestions that the Austrobaileyaceae is related to the Lauralean group of families. However, the great difference in size observed between *Austrobaileya* and the few representatives of the Monimiaceae where this character is known suggests that the relationship between these two families is not particularly close. Since $x = 7$ is accepted as the original base number for the Magnoliales, the Trimeniaceae would appear to be an ancient diploid and to be one of the few extant primitive diploid woody angiosperms. *Hortonia* is probably of palaeohexaploid origin.

ACKNOWLEDGMENTS

I should like to thank the following for providing the plant material used in this study: Mr. R. S. Womersley of the Department of Forests, New Guinea, for the seed of *Trimenia papuana*; Dr. R. A. Howard of the Arnold Arboretum for cuttings of *Austrobaileya*; and Dr. A. Kostermans, Dr. F. Popham, and Dr. R. Fosberg, who under the auspices of the Ceylon Flora project provided the seed of *Hortonia floribunda*. I should also like to thank Dr. Peter H. Raven, Director of the Missouri Botanical Garden for encouragement and advice in this study.

LITERATURE CITED

BORGMAN, E. 1964. Anteil der Polyploiden in der Flora des Bismarckgebirges von Ostneuguinea. Zeitschr. Bot. **52:** 118–172.

DYER, A. F. 1963. The use of lacto-propionic orcein in rapid squash methods. Stain Technol. **38:** 85–90.

EHRENDORFER, F., F. KRENDL, E. HABELER, & W. SAUER. 1968. Chromosome numbers and evolution in primitive Angiosperms. Taxon **17:** 337–353.

GADELLA, TH. W. J., E. KLIPHUIS, J. C. LINDEMAN, & E. A. MENNEGA. 1968. Chromosome numbers and seedling morphology of some Angiosperms collected in Brazil. Acta Bot. Neerl. **18:** 74–83.

HAIR, J. B., & E. J. BEUZENBERG. 1959. Contributions to a chromosome atlas of the New Zealand flora 2. New Zealand Jour. Sci. **2:** 148–156.

MONEY, L. L., I. W. BAILEY, & B. G. L. SWAMY. 1950. The morphology and relationships of the Monimiaceae. Jour. Arnold Arb. **31:** 372–404.

RAVEN, P. H. 1974. Cytology and the bases of Angiosperm phylogeny. Brittonia **26** (in press).

———, D. W. KYHOS, & M. S. CAVE. 1971. Chromosome numbers and relationships in Annoniflorae. Taxon **20:** 479–483.

RÜDENBERG, L. 1967. The chromosomes of *Austrobaileya*. Jour. Arnold Arb. **48:** 241–244.

SCHODDE, R. 1970. The new suprageneric taxa in the Monimiaceae alliance (Laurales). Taxon **19:** 324–328.

SMITH, A. C. 1971. An appraisal of the orders and families of primitive extant Angiosperms. Jour. Indian Bot. Soc. Golden Jubilee Vol. **50A:** 215–226.

TAKHTAJAN, A. 1969. Flowering Plants: Origin and Dispersal. (Transl. C. JEFFREY). Edinburgh.

TSCHISCHOW, N. T. DE, 1956. Numero de chromosomes de algunas plantas chilenas. Bol. Soc. Biol. Concepcion. Chile. **31:** 145–147.

MISSOURI BOTANICAL GARDEN
2315 TOWER GROVE AVENUE
ST. LOUIS, MISSOURI 63110

RHIZOME ORGANIZATION IN RELATION TO VEGETATIVE SPREAD IN MEDEOLA VIRGINIANA

ADRIAN D. BELL

THE INDIAN CUCUMBER, *Medeola virginiana* L., represents the only species of the genus *Medeola* (Trilliaceae). Plants develop above-ground parts and flowers during summer in rich woods, from Quebec south through the Eastern States and down into Florida, Alabama, and Louisiana. Each aërial shoot consists of a single slender stem averaging about 30 cm. in height, bearing two pseudo-whorls of simple leaves and a semi-umbel of small recurved flowers (Fernald, 1950) (FIGURE 1A). The aërial stem arises from an underground rhizome system of great uniformity from plant to plant. This consists of a single thin stem, swollen at its distal end to form a tuber, and normally producing just two branches during the summer, one at each end.

The only detailed study of the morphology of *Medeola* is presented in a paper by Berg (1962), where it is compared with that of *Trillium*. His material from three sites in North America (one of them Harvard Forest) was grown for study in Norway in cold frames. The present investigation is based on plants collected from natural sites and records their pattern of symmetrical growth from one year to the next. This shows a high degree of organization which is related to the method of vegetative spread. These plants showed much less diversity than those collected from Harvard Forest but cultivated in Norway.

Other references to *Medeola* contain scant information about the underground stems of the plants (e.g., Holm, 1925; Ker, 1810) or are concerned solely with taxonomy or cytology (e.g., Gates, 1917; Stewart & Bamford, 1942; Woodard, 1948). The present account confirms Berg's observations on rhizome morphology and is intended to draw attention to the remarkable degree of symmetry in the shoot system which permits a very efficient method of exploiting the substrate.

METHODS

Thirty individual plants were carefully exposed in the leaf litter of Harvard Forest, Massachusetts, 25 on May 14, 1973, and 5 on June 27, 1973. The following data were recorded for each plant.

1. Size and maturity of aërial shoot;
2. Dimensions of parent rhizome system;
3. State and orientation of branches;
4. Presence of injury or disease;
5. Depth of rhizome in soil.

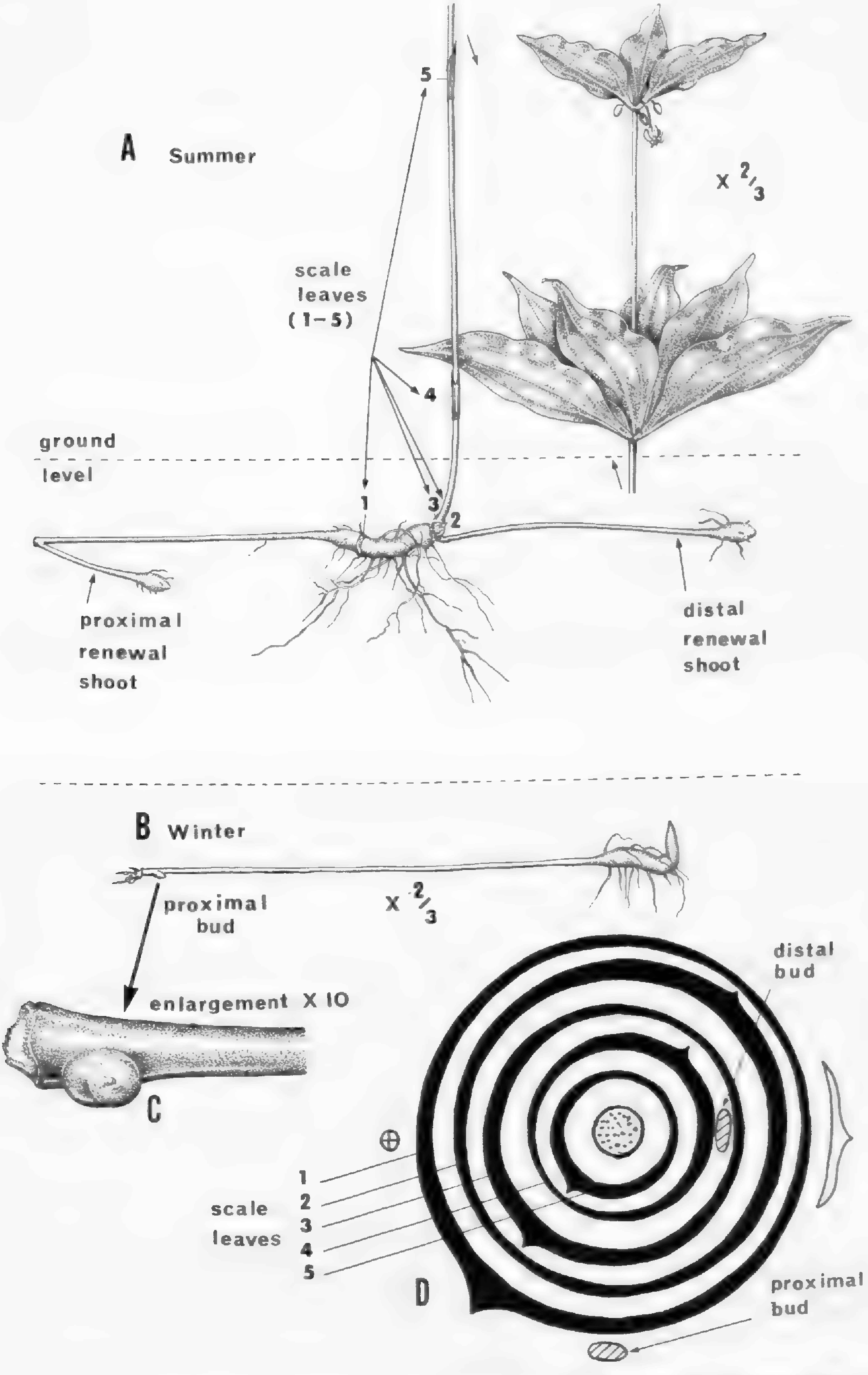


FIGURE 1. *Medeola virginiana* L.: A, entire plant in summer; B, entire plant in winter; C, proximal bud detail; D, plan of scale leaf, and bud, arrangement.

Each plant was located for subsequent study by means of a pair of small flags, and the litter replaced. Unfortunately two thirds of the flags were stolen during the summer. The remaining eleven plants were re-excavated on November 14, 1973. A total of twenty-five plants was fixed in formalin-acetic-alcohol (FAA) during May for further dissection in the laboratory. In addition, five clumps of *Medeola*, each containing about five plants embedded in litter, were transferred undisturbed to a greenhouse in May and excavated in November. Thus this survey is based on the study of about eighty individual plants overall.

OBSERVATIONS

The subterranean part of the plant consists of a long, thin, brittle stem about 3 mm. in diameter bearing neither roots nor leaves for most of its length but terminating in a swollen root-bearing tuber. The distal end of the tuber turns erect to form the aërial shoot. Forward extension of the sympodial system is continued by the development of a single vegetative bud (the distal bud) at the base of the aërial shoot. This is always associated with a scale leaf but is not necessarily opposite its mid-vein. A second vegetative bud (the proximal bud) appears close to the proximal end of the parent rhizome, entirely unconnected with any foliar appendage (FIGURE 1B). Further buds, which normally do not develop, may be present, subtended by other scale leaves. Each unit of the sympodium includes up to two whorls of foliage leaves on the aërial stem, six leaves on average in the lower, and three in the upper whorl. In addition there are five scale leaves, one on the tuber, two at the base of the aërial shoot, and two further up the aërial shoot. These may be numbered for convenience 1–5 (FIGURE 1, A and D). Scale leaf 3 always subtends the distal vegetative bud, except occasionally in small plants which may have only four scale leaves, lacking the one on the tuber (1). Berg (1962) distinguished between scale leaves (recording up to five on the tuber) and cataphylls — three or rarely four associated with the aërial shoot. His diagrams, however, indicate the condition I have recorded, i.e. five reduced leaves in all, with scale leaf 3 subtending the distal renewal shoot.

All plants show a remarkable uniformity of branching pattern despite a considerable range in overall size at maturity as follows:

	Average	*Range*
Height of aërial stem	29.2 cm.	15.0–54.0 cm.
Length of underground stem	11.0 cm.	3.0–27.0 cm.
Length of tuber	3.0 cm.	1.5– 5.0 cm.

Small tubers produce small aërial shoots. Generally speaking, tubers less than 3 cm. long develop aërial shoots with one whorl of leaves and no flowers; tubers greater than 3 cm. long produce two whorls of leaves with flowers. In an established population the size of plants can be related to their position of origin; small plants originate from proximal buds, large plants originate from the distal buds. Similarly the narrow rootless stem section is proportionally much shorter in small plants than in large plants. Rhizomes were found at an average depth in the soil of 5.5 cm., ranging from 3 cm. in compacted soil to 13 cm. in loose litter.

Annual sequence of growth and branching pattern. The dormant plant in late fall is shown in Figure 1B. It consists of a swollen distal end bearing roots and terminating in an upturned bud in which all the aërial grains. Scale leaf 3 of the upturned bud has a very small renewal bud in its organs of next year's growth are present. The tuber is packed with starch axil, usually oriented to point forward. The proximal end of the plant consists of the long thin stem bearing neither leaves nor roots. Within 2 to 3 mm. of the blunt end of this narrow stem, to which the remains of the parent axis may be attached, there is a second small bud situated horizontally either to the left or to the right (Figure 1C). The origin of this proximal bud is obscure; as was observed by Berg, it is not associated with a leaf. The plant in this winter dormant state is shown diagrammatically in Figure 2A.

In the spring (May in Massachusetts), the large upturned bud expands, raising a first whorl of vegetative leaves above the ground. About this time the forward pointing renewal bud grows horizontally through the soil. It bears no roots, and the only leaves are three leaf primordia at its apex. This state is represented diagrammatically in Figure 2B. During the summer the horizontal stem continues to extend forward for some 15 to 20 cm. and then its distal end swells, beginning in July. The developing tuber produces roots, thus arresting further growth. During this time also the aërial stem continues to grow, unfolding a second whorl of usually three small foliage leaves and the terminal inflorescence. Towards the end of the summer the proximal vegetative bud grows out horizontally for some 2 to 5 cm. at an angle of approximately 45° to the parent stem, and its advancing end also begins to swell, illustrated diagrammatically in Figure 2C. This branch has the same construction as the parent axis, but as has been noted, its dimensions are smaller. In the fall the aërial system dies and withers and the parent rhizome system entirely rots away. A distinct line of separation is developed, producing the blunt but rounded proximal end. Proximal vegetative buds develop on the two daughter plants as shown at *u* and *v* in Figure 2D. This sequence is repeated each year, theoretically producing four plants during the second year (Figure 2F), eight plants during the third year (Figure 3A), and sixteen plants during the fourth year (e.g., by the fifth winter the theoretical population would be represented by Figure 3B).

This potential doubling of the population each year in fact must occur very rarely since mortality of individuals during the summer and fall is high. Often the proximal vegetative bud is absent — the rear end of the parent rhizome either becoming rotten, or being eaten, or failing to develop. The same fates sometimes befall distal vegetative buds. In this manner the number of individuals in an area is restricted.

Organization and symmetry. The symmetry of the shoot system is very strict and seems well adapted to exploiting the forest floor. In every excavation in which the disposition of two successive seasons' growth could be determined, the proximal vegetative bud was on alternate sides from one year to the next. If it is on the right one year it will be on the left the next

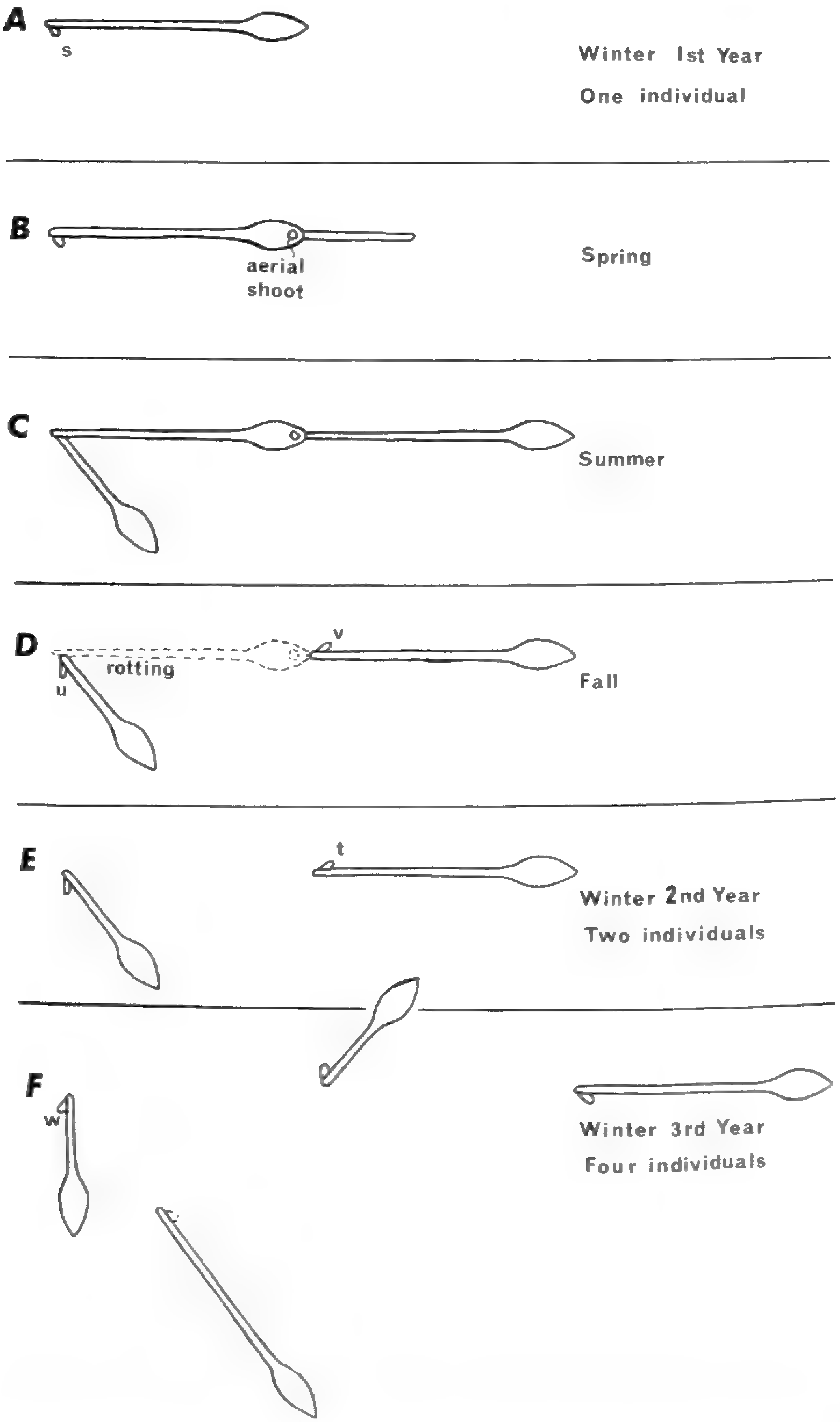


FIGURE 2. *Medeola* branching pattern. Diagrammatic plan view, 1st to 3rd years (s, t, u v, w, see text).

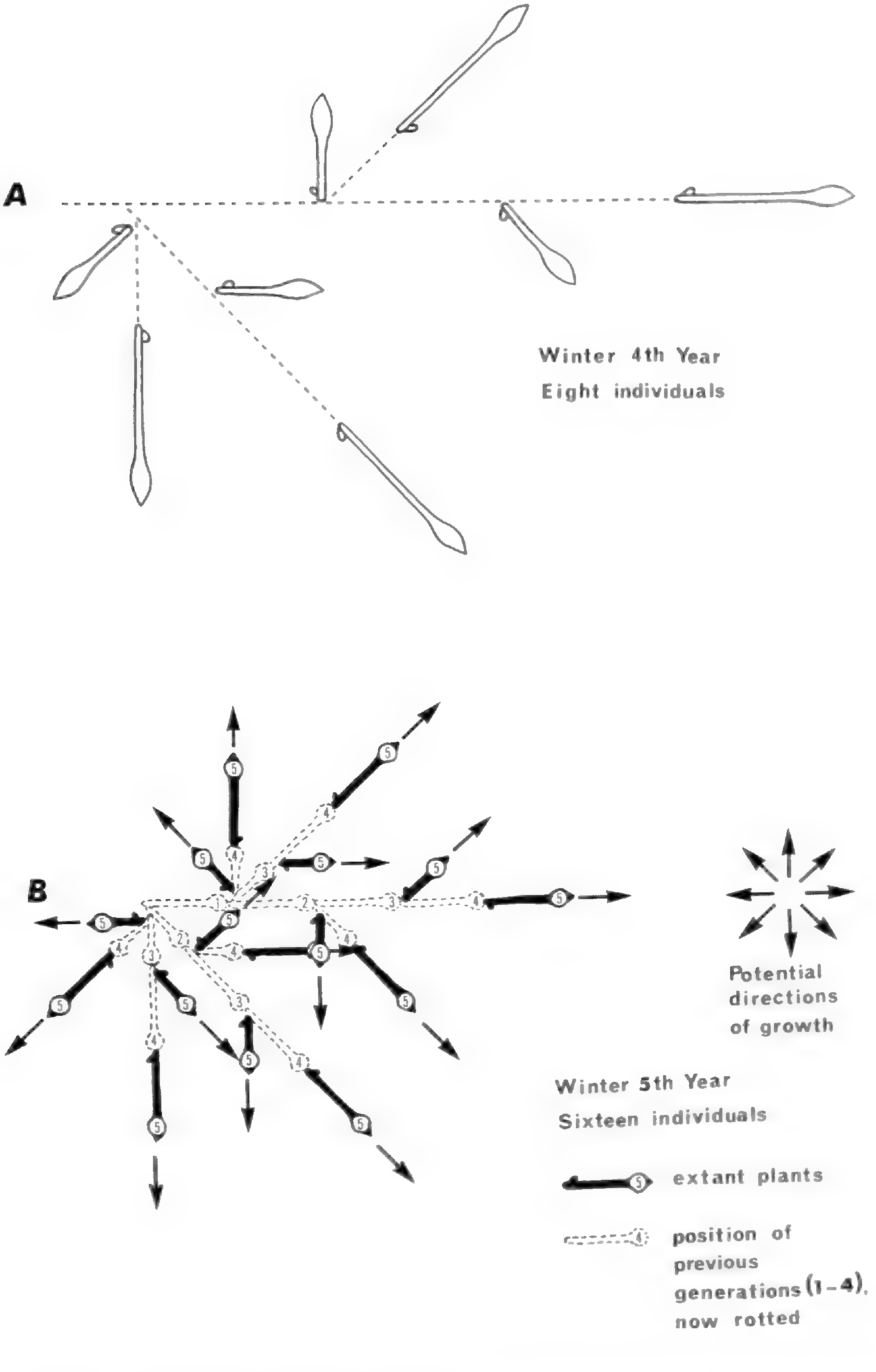


FIGURE 3. *Medeola* branching pattern. Diagrammatic plan view, 4th to 5th years.

year and *vice versa*. This is made evident by comparing FIGURES 2A and 2E; the right-hand bud (*s*) in A is on the left (*t*) in E. No deviations from this rule were found. Consequently as the rhizome system advances forward one unit each year, it leaves behind a second unit alternately to the left and right and thus initiates new lines of growth at 45° to the line of growth of the parent axis. This is evident in FIGURE 3A, where the lines of growth are drawn in. At the same time, the base of each line of growth continues as a generating center for a series of new lines whose orientation rotates 45° each year. The direction of rotation is constant because proximal buds are consistently to the same side — a right hand proximal bud always bears its proximal bud to the right and *vice versa*. Again no deviations from this rule have been observed (c.f. for example the buds *s*, *u*, and *w*, in FIGURE 2). Consequently, at the same time as the rhizome front advances, it leaves behind an increasing number of loci where proximal buds are developed. The appearance of the rhizome system after four years' growth is shown in FIGURE 3B. Sixteen dormant plants (solid black) are present representing lines of advance in eight directions at 45° intervals around the compass. The axes which generated these existing plants are represented in outline.

From an ecological standpoint this rigid organization results in the potential migration of the clone in all directions plus a constant restocking at all sites — the rear buds borne on rear buds rotating portions of the clone on the spot, so to speak.

Leaf orientation. Rather surprisingly the consistent positioning of the vegetative buds does not appear to be governed by a consistent orientation of the scale leaves on the rhizome. The first leaf along the stem (1) is the one borne at about the middle of the tuber. The dorsal side of this leaf may be located at any point on the circumference of the axis of the tuber, apparently at random and without reference to the dorsiventral symmetry of the rhizome. The remaining four scale leaves (2–5) are in a distichous order in relation to the first leaf (1). Again, the distal vegetative bud is positioned towards the advance side of the aërial shoot, in most cases regardless of the dorsiventral and encircling orientation of the subtending scale leaf (3) (FIGURE 1D).

Serial transverse sections reveal that the proximal vegetative bud is not associated with a leaf; nevertheless it inevitably develops in a position which correctly maintains the rigid organizational pattern of the rhizome system. This is one of the most distinctive and remarkable features of this shoot system and presents something of a morphogenetic puzzle.

Growth under greenhouse conditions. Five clumps of *Medeola* were dug up intact in May and maintained undisturbed in a greenhouse with ample light and water for the duration of the growing season. The result of this simple transplantation was quite dramatic and illustrated the further potential for vegetative propagation which is not manifest in natural populations.

Five of these plants are shown diagrammatically in FIGURE 4. The favorable growing conditions have resulted in the production of additional tubers in two ways. Firstly there is the precocious development of shoots which are normally the product of several years' growth, e.g., at *x* in FIGURE 4, where two generations (or orders) of branching develop in one year. Secondly, there is the emergence of branches associated with scale leaves other than scale leaf 3, e.g., at *y* in FIGURE 4. These branches sometimes bear precocious branches themselves, always to the same side consistently either to the left or right and thus behaving like proximal branches in the normal plant, e.g., *z* in FIGURE 4. If a single plant had produced all the variations represented by these five examples, it would have developed nine new plants in the one season compared with the maximum of two produced by a plant in the field.

In view of the results of this simple experiment, it is all the more remarkable that in spite of the potential for extra bud development, vegetative growth is constantly restricted to two buds at opposite ends of the plant.

DISCUSSION

The organized mobility of a clone of *Medeola* described in this account represents a relatively simple example of a widespread phenomenon. A great many plants are rhizomatous (or stoloniferous), only one major group, the Gymnosperms, apparently lacking examples of this ubiquitous mode of growth. However, precise details of rhizomatous growth patterns are infrequently recorded (e.g., N. Hallé, 1967, *Aframomum* and *Costus*; McClure, 1966, bamboos; Primack, 1973, *Lycopodium*; Smirnova, 1967, *Carex* and *Aegopodium*; Takenouchi, 1931, bamboos; Tomlinson, 1970, *Croomia* and *Thalassia*; Tomlinson & Esler, 1973, *Ripogonum*; and *Alpinia*, at present under study, Bell).

It appears that a limited number of basic pattern types reoccur in unrelated groups. *Trientalis borealis* Raf. (Primulaceae) growing in the same habitat as *Medeola* has a similar annual rhizome strategy, producing one (sometimes two) distal renewal shoot but lacking the proximal shoot (Anderson and Loucks, 1973). Invariably the addition of new units to the distal ends of the system is accompanied by the progressive rotting of the old proximal end, resulting in the "movement" of the plant through the soil (c.f. Holttum, 1955; Madison, 1970). *Medeola* is unusual in that an individual never consists of more than three orders of branching at a time — two mature and the third represented by buds, and particularly in that one branch arises at the proximal end of the parent. (A superficially similar sequence occurs in *Costus spectabilis*, which, however, has a vertical two-unit rhizome system; F. Hallé, 1972, personal communication.)

Individual ramets of most rhizomatous plants consist of more than three consecutive orders of branching (a ramet is a single vegetative member of a clone, the genet; Sarukhán & Harper, 1973). The extent of spread of a genet will depend on the details of rhizome pattern and durability.

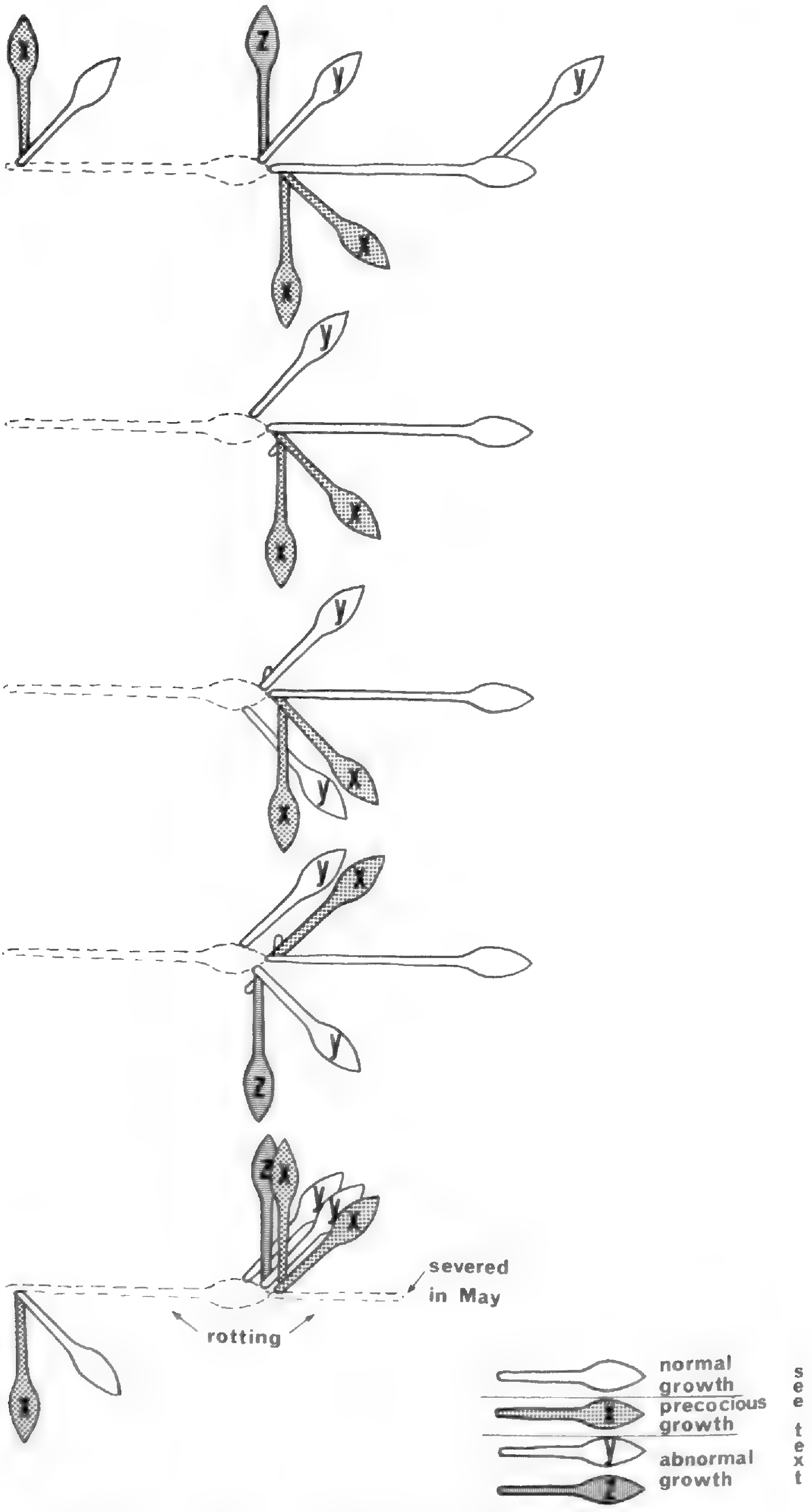


FIGURE 4. *Medeola.* Growth under greenhouse conditions.

The inevitable influence of rhizome symmetry on the location of plants in an ecological context is commonly ignored. It is not usually feasible to excavate an entire plot to determine the subterranean affinities of aërial "individuals," and the significance of the rhizomatous habit in a community is overlooked. However, the symmetrical organization of many of these plants allows quantitative data typifying specific patterns to be collected, and the future growth and spread of the plant can be simulated for many generations. This approach to population dynamics as governed by growth habit is at present being assessed by the author in the case of a ginger, *Alpinia speciosa* (Zingiberaceae). A computer linked to a graphic display screen can demonstrate the future spread of a population given the rules of branching determined by a detailed study of an actual population. The results are proving to be very interesting and allow considerable scope for further study.

SUMMARY

The rhizome of *Medeola virginiana* L. (Trilliaceae) is a simple but highly organized sympodial structure. Under natural growing conditions the rhizomes of individual plants vary in size but not in their quantitative construction. In its winter resting state each long thin rhizome, which is swollen at its distal end, bears five scale leaves and two branch buds. One of these buds (the distal bud) grows horizontally forward from the base of the developing aërial shoot during the following spring. A little later the second (proximal) bud extends horizontally sideways from the extreme proximal end of the parent rhizome and at an angle of 45° to it. This bud does not arise in the axil of a leaf. During the fall the parent unit completely rots away leaving the two dormant branch units now independent of each other. The process is then repeated, the potential annual doubling of the population being modified by a high mortality rate. The symmetrical pattern of events from year to year is recorded. The disposition of the proximal bud follows a very strict sequence alternately from left to right in successive generations. The overall result is a predictable spread of the clone in eight directions from distal buds, together with replacement at each site by proximal buds. The significance of predictable rhizome patterns in population ecology is briefly discussed.

ACKNOWLEDGMENTS

This study was conducted during tenure of a post-Doctoral fellowship from the Cabot Foundation, Harvard University. A stimulating atmosphere and help have been provided by all inhabitants at the Harvard Forest. Particular thanks are due to P. B. Tomlinson for encouragement and advice throughout and to Jenny Richards for enthusiastic assistance with excavations. Habit drawings are by Miss Priscilla Fawcett, Botanical Illustrator at the Fairchild Tropical Garden.

LITERATURE CITED

ANDERSON, R. C., & O. L. LOUCKS. 1973. Aspects of the biology of *Trientalis borealis* Raf. Ecology **54**: 798–808.

BERG, R. Y. 1962. Morphology and taxonomic position of *Medeola*, Liliaceae. Skr. Norske Vidensk-Akad. Oslo. 1. Mat-Naturv. Kl. Nyser. No. 3, 56 pp.

FERNALD, M. L. 1950. Gray's manual of botany. 8th ed. lxiv + 1632 pp. D. Van Nostrand Co. New York, New York.

GATES, R. R. 1917. A systematic study of the North American genus *Trillium*, its variability, and its relation to *Paris* and *Medeola*. Ann. Missouri Bot. Gard. **4**: 43–92.

HALLÉ, F. 1972. Field notes on *Costus spectabilis*. [Personal communication.]

HALLÉ, N. 1967. *Aframomum polyanthum* (K. Schum.) K. Schum. et *Costus Dinklagi* K. Schum. Deux Zingiberacées peu connues et nouvelles pour le Gabon, présentées avec leurs parties souterraines d'après des sujets vivants. Adansonia (sér. 2.) **7**(1): 73–80.

HOLM, T. 1925. Hibernation and rejuvenation exemplified by North American herbs. Am. Midl. Nat. **9**: 439–512.

HOLTTUM, R. E. 1955. Growth-habits of Monocotyledons — variations on a theme. Phytomorphology **5**: 399–413.

[KER-] Gawler, J. B. 1810. *Medeola virginiana*, Indian Cucumber. Curtis's Bot. Mag. **32**: *pl. 1316*. (Identified by "G." following the description.)

MADISON, J. H. 1970. An appreciation of monocotyledons. Notes Roy. Bot. Gard. Edinburgh. **30**(2): 377–390.

MCCLURE, F. A. 1966. The bamboos — a fresh perspective. xv + 347 pp. Harvard Univ. Press. Cambridge, Massachusetts.

PRIMACK, R. B. 1973. Growth patterns of five species of *Lycopodium*. Am. Fern Jour. **63**: 3–7.

SARUKHÁN, J., & J. L. HARPER. 1973. Studies on plant demography: *Ranunculus repens* L., *R. bulbosus* L. and *R. acris* L. I. Population flux and survivorship. Jour. Ecol. **61**: 675–716.

SMIRNOVA, O. B. 1967. Growth structure of *Carex pilosa* Scop. and *Aegopodium podagraria* L. *In*: A. A. URANOV, *ed*. Ontogenesis and the age composition of the populations of flowering plants. Moscow, U.S.S.R.

STEWART, R. N., & R. BAMFORD. 1942. The chromosomes and nucleoli of *Medeola virginiana*. Am. Jour. Bot. **29**: 301–303.

TAKENOUCHI, Y. 1931. Systematisch — vergleichende Morphologie und Anatomie der Vegetationorgane der Japanischen Bambus-Arten. Taihoku Imp. Univ. (Formosa) Fac. Sci. Mem. **3**: 1–60.

TOMLINSON, P. B. 1970. Monocotyledons — towards an understanding of their morphology and anatomy. *In*: R. D. PRESTON, *ed*. Advances in botanical research Vol. 3. Academic Press. London & New York. Pp. 207–292.

——— & A. E. ESLER. 1973. Establishment growth in woody monocotyledons native to New Zealand. New Zealand Jour. Bot. **11**: 627–644.

WOODARD, J. M., JR. 1948. Differences in form and reaction to cold in root-tip and apical bud chromosomes of *Medeola*. Bull. Torrey Bot. Club **75**: 250–255.

SCHOOL OF PLANT BIOLOGY
UNIVERSITY COLLEGE OF NORTH WALES
BANGOR, LL57 2UW, NORTH WALES

A REVISION OF THE GENUS ACRONYCHIA (RUTACEAE)*

THOMAS G. HARTLEY

THE GENUS *Acronychia* J. R. & G. Forster is known to occur naturally from India east to southwest China and Taiwan, southeast throughout Malesia to the Solomon Islands, New Caledonia and Lord Howe Island, and south in eastern Australia from Cape York Peninsula to eastern Victoria. Despite this rather wide distribution the genus is almost entirely eastern Australian and New Guinean, 15 of the 42 known species being endemic to the former area and 24 to the latter. Of the remaining species, *A. laevis* is common to Australia, Lord Howe Island, and New Caledonia (see MAP 4); *A. pedunculata* is distributed from mainland Asia throughout Malesia to New Guinea (see MAP 9); and *A. trifoliolata*, with three varieties, ranges from Java to the Solomon Islands (see MAPS 7 and 8).

Acronychia can be distinguished from the majority of genera of the Rutaceae in the Indo-Pacific region by its drupaceous fruit. Of the genera that share this characteristic, *Halfordia*, *Toddalia*, *Vepris*, and *Skimmia* differ in having alternate leaves; *Phellodendron* differs in having pinnately compound leaves; and *Bauerella*, a segregate of *Acronychia* which I recognize as being distinct, differs in having functionally unisexual flowers, valvate sepals, and persistent petals. Three species described from northwest Malesia and adjacent mainland Asia, *Acronychia obovata* Merr., *A. oligophlebia* Merr., and *A. porteri* Hook. f., also have drupaceous fruits (although these occasionally dehisce loculicidally near the apex) but are here considered distinct from *Acronychia* since they have functionally unisexual flowers and seeds with crustaceous outer testa. Their correct generic placement is not clear; in several respects they seem closest to *Melicope*.

Glycosmis, *Micromelum*, *Murraya*, and *Clausena*, all of the subfamily Aurantioideae,[1] have fruits which superficially resemble those of some acronychias. The leaves of these genera are alternate, however, and the fruits baccate, lacking the cartilaginous or pergamentaceous endocarp of *Acronychia*.

Although *Melicope* and *Euodia* are usually distinguishable from *Acronychia* by their follicular fruits, both of the former genera also include capsular-fruited species which have been confused with *Acronychia*. Species now placed in the genus *Evodiella* have also been confused with *Acronychia* because of their capsular fruits. Also, the type species of the closely re-

---

* This is the fifth of a series of studies on the Rutaceae of Malesia. See Jour. Arnold Arb. **47**: 171–221. 1966; *Ibid.* **48**: 460–475. 1967; *Ibid.* **50**: 481–526. 1969; and *Ibid.* **51**: 423–426. 1970.

[1] *Acronychia* was placed in the subfamily Toddalioideae by Engler (1896 & 1931) but is probably better placed in the subfamily Rutoideae in view of its close relationship to *Melicope, Euodia, Evodiella,* and *Medicosma.*

lated genus *Medicosma* was initially placed in *Acronychia.* The distinguishing characteristics of these four genera and *Acronychia* are given in the following key.

Fruits drupaceous (the carpels completely connate or more or less separated to the axis by septicidal fissures), not loculicidally dehiscent; seeds carunculate; testa smoothish to finely tuberculate, muricate or rugose, bony; stamens twice as many as petals; filaments without stalked glands, usually densely ciliate toward the base and densely retrorse-pilose at about the middle adaxially; flowers bisexual; petals valvate; indumentum of simple trichomes. .... *Acronychia.*

Fruits follicular or capsular, loculicidally dehiscent (at least apically); seeds ecarunculate; testa smooth or smoothish, bony or with crustaceous outer layer; stamens the same number or twice as many as petals; filaments with or without stalked glands, densely ciliate, ciliolate or eciliate, glabrous or loosely pubescent adaxially; flowers functionally unisexual or bisexual; petals valvate or imbricate; indumentum of simple or stellate trichomes.

  Filaments densely ciliate toward the base, with abundant stalked glands toward the apex; stamens twice as many as petals; flowers bisexual; petals imbricate; outer testa crustaceous; indumentum of stellate trichomes. .... *Medicosma.*

  Filaments ciliolate or eciliate, without stalked glands; stamens the same number or twice as many as petals; flowers functionally unisexual or bisexual; petals valvate or imbricate; testa bony or with crustaceous outer layer.

    Fruits capsular, locules inflated basally; testa dull, smoothish, more or less bony; filaments glabrous, geniculate; stamens the same number as petals; petals imbricate; indumentum of simple trichomes. .. *Evodiella.*

    Fruits follicular or capsular, locules usually not inflated basally; testa shiny, smooth, with crustaceous outer layer; filaments ciliolate or eciliolate, glabrous or loosely pubescent adaxially, geniculate or more or less straight; stamens the same number or twice as many as petals; petals imbricate or valvate; indumentum of simple or stellate trichomes.

      Stamens the same number as petals. .... *Euodia.*

      Stamens twice as many as petals. .... *Melicope.*

I have been able to collect and study in the field several of the New Guinean species of *Acronychia*, mostly while employed with the Australian Commonwealth Scientific and Industrial Research Organization Phytochemical Survey of New Guinea, 1961–1965.[2] This study is otherwise based on herbarium specimens. The contributing herbaria are listed below, with abbreviations 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

---

[2] Of nine species of *Acronychia* collected and tested for alkaloids during that survey (*A. murina, A. kaindiensis, A. brassii, A. smithii, A. montana, A. pullei, A. gurukorensis, A. trifoliolata,* and *A. ledermannii*), only one, *A. murina,* gave a positive test.

BRI	Queensland Herbarium, Brisbane
CANB	C.S.I.R.O. Herbarium Australiense, Canberra
G	Conservatoire et Jardin Botaniques, Genève
GH	Gray Herbarium of Harvard University, Cambridge
K	Royal Botanic Gardens, Kew
L	Rijksherbarium, Leiden
LAE	Department of Forests, Lae, Papua New Guinea
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
U	Botanical Museum and Herbarium, Utrecht
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 B. P. M. Hyland, of the Commonwealth of Australia Forest Research Institute, Atherton, Queensland, and A. G. Floyd, of the New South Wales Forestry Commission station at Coffs Harbour, for their efforts in obtaining additional material of some of the Australian species of *Acronychia*.

Acronychia J. R. & G. Forst. Char. Gen. Pl. ed. 1. *t. 27.* 1775 (cf. St. John, 1971); *Ibid.* ed. 2. 1776, *nom. cons.* Type species: *Acronychia laevis* J. R. & G. Forst.

Jambolifera L. Sp. Pl. **1**: 349. 1753; Fl. Zeyl. 58. 1747; Gen. Pl. ed. 5. 165. 1754. Type species: *Jambolifera pedunculata* L. [*Acronychia pedunculata* (L.) Miq.].

Cunto Adans. Fam. Pl. **2**: 446. 1763. Type: *Rheede*, Hort. Malab. **5**: *t. 15.* 1685 [= *Acronychia pedunculata* (L.) Miq.].

Jambolana Adans. *Ibid.* 508 ≡ *Jambolifera* L.

Koelpinia Scop. Introd. Hist. Nat. 231 & index. 1777 ≡ *Cunto* Adans.

Roelpinia Scop. *Ibid.* 231, *sphalm.*

Cyminosma Gaertn. Fruct. **1**: 280. 1788 ≡ *Jambolifera* L.

Gela Lour. Fl. Cochinch. 232. 1790. Type species: *Gela lanceolata* Lour. [= *Acronychia pedunculata* (L.) Miq.].

Laxmannia Schreb. Gen. **2**: 800. 1791 ≡ *Jambolifera* L.

Dorrienia Dennst. Schluess. Hort. Malab. 31. 1818 ≡ *Cunto* Adans.

Selas Spreng. Syst. Veg. **2**: 216. 1825 ≡ *Gela* Lour.

Huonia Montros. Mem. Acad. Roy. Sci. Lyon, Sect. Sci. Ser. 2. **10**: 185. 1860 ≡ *Acronychia* J. R. & G. Forst.

Pleiococca F. Muell. Frag. Phytogr. Austral. **9**: 117. 1875. Type species: *Pleiococca wilcoxiana* F. Muell. [*Acronychia wilcoxiana* (F. Muell.) Hartley].

Errerana O. Ktze. Rev. Gen. Pl. 937. 1891 ≡ *Pleiococca* F. Muell.

Trees, shrubs or rarely climbers; branchlets terete to tetragonous; indumentum of simple trichomes. Leaves opposite, trifoliolate or unifoliolate; leaflets pellucid-dotted, entire, pinnately veined, articulate at the base. Inflorescences axillary, paniculate, subcorymbose or reduced to one or a few flowers. Flowers bisexual; sepals 4, distinct or connate basally, usually imbricate, persistent or rarely deciduous; petals 4, distinct, valvate, white to cream or yellowish, pellucid-dotted, narrowly triangular to sublanceolate, becoming reflexed, deciduous or rarely semipersistent in fruit; stamens 8, nearly as long as the petals, the antesepalous slightly longer than the antepetalous, filaments flattened, gradually tapering from a rather broad base to a subulate apex, usually densely ciliate toward the base and retrorsely pilose at about the middle adaxially, gland dotted, becoming reflexed, anthers 2-celled, ovoid to ellipsoid, obtuse or obtusely apiculate, basifixed; disc intrastaminal, pulvinate, shallowly 8-lobed, persistent or obsolete in fruit; gynoecium a single, 4-carpellate, 4-loculate (rarely 4- to 8-carpellate and 4- to 8-loculate) pistil, at anthesis about one half the length of the petals, ovary with or without septicidal fissures, placentation axile, ovules superposed, 2 per locule, style twisted, about twice the length of the ovary, stigma shallowly 4-lobed, otherwise scarcely differentiated from the style. Fruit a 4-loculate (or rarely 4- to 8-loculate) drupe, with or without septicidal fissures; epicarp[3] semifleshy, spongy-crustaceous or woody when dry, with or without evident mesocarp; endocarp cartilaginous to pergamentaceous. Seeds narrowly ellipsoid to subpyriform, slightly bent, carunculate, 2 or occasionally (by abortion) 1 per locule; testa bony, dull to rather shiny, smoothish to finely tuberculate, muricate or rugose; endosperm fleshy; embryo straight or nearly so, ovate to subelliptic, cotyledons flattened, hypocotyl terminal.

The name *Acronychia* was conserved and listed in the Vienna Code, but only against the name *Cunto* Adanson (cf. Rickett & Stafleu, Taxon **8**: 301. 1959). It should also be conserved against *Jambolifera* L., the type species of which, *J. pedunculata*, is congeneric with *Acronychia laevis*, the type species of *Acronychia*. I have submitted a proposal to this effect to the International Bureau for Plant Taxonomy and Nomenclature, Committee for Spermatophyta (Taxon, in press).

Gela was previously placed in the synonymy of *Acronychia* by Merrill, 1935: 220.

My reasons for placing *Pleiococca* in synonymy are given below, following the description of *Acronychia wilcoxiana*.

Branchlets in the majority of the species vary in shape[4] from terete to

---

[3] Throughout this study the term epicarp is used to designate the two outer layers of the pericarp — the exocarp and the mesocarp.

[4] Branchlet shape, color of dried leaflets, persistence of sepals and petals, thickness of petals, carpel number, ovary shape, fruit surface features (other than indumentum), persistence of the disc, and surface characters of the testa are all features that are diagnostic for one or only a few species. Their variations in the genus as a whole are discussed here since in the body of the revision they are described only for those species for which they are diagnostic.

subterete, the latter type usually being more or less compressed and often slightly grooved on the flattened surfaces. In three species, however, they are more or less tetragonous: those of *Acronychia aberrans* are sharply tetragonous and concavely compressed in the internodes, and those of *A. murina* and *A. emarginata* are usually slightly tetragonous, the angles formed from decurrent petiole bases.

In the majority of species the color of the dried leaflets ranges from medium- to dark-green to various shades of brown, often with considerable intraspecific variation. Four species deviate from this: the dried leaflets of *Acronychia ledermannii* are pale green or greenish yellow when mature, those of *A. schistacea* are a rather metallic blue-gray above and olivaceous below, and those of *A. papuana* and *A. imperforata* are often slightly blue-gray above, especially when young.

In the genus as a whole, leaflet venation tends to be prominent and to have a characteristic reticulate appearance. The degree of prominence has not proved to be useful as a taxonomic character, however, since it varies considerably within species, probably with habitat, age of the leaves, and method of drying.

Flower color also varies in most or possibly all of the species and appears to be of no taxonomic value.

Sepals are persistent in fruit in all of the species but one, *Acronychia macrocalyx*.

Petals are typically deciduous in the genus, but in a few species — *Acronychia parviflora*, *A. brassii*, *A. pubescens*, *A. dimorphocalyx*, and *A. acronychioides* — they are semipersistent, i.e., they usually remain on the mature fruit but are easily removed.

The petals of *Acronychia crassipetala* are obviously fleshy and in dried state are about 0.7 mm. thick near the apex. In the other species of the genus they are consistently much thinner.

The staminal filaments are typically ciliate toward the base and retrorsely pilose at about the middle adaxially. There is considerable variation in the genus, however, and for the most part it correlates with flower size: the filaments of the larger flowers tend to be densely ciliate toward the base and densely retrorse-pilose adaxially, while those of the smaller flowers tend to be ciliolate toward the base or rarely eciliate and sparsely pubescent or rarely glabrous adaxially.[5]

The ovary and fruit are consistently four-carpellate in all of the species except *Acronychia wilcoxiana*, which varies from four- to eight-carpellate.

The ovary is typically globose or subglobose in the genus but varies to subcylindric in *Acronychia crassipetala* to ellipsoid in *A. murina*.

The fruit varies, in dry condition, from a type with entirely semifleshy epicarp (about the texture of a raisin) and no evident mesocarp to types with spongy-crustaceous or woody mesocarp. The latter two types may or may not have semifleshy exocarp.

---

[5] Descriptions of surface features of staminal filaments have been omitted from the descriptions of the species since there is this correlation with flower size. Omitted on the same basis are size measurements of the petals, stamens, and gynoecia.

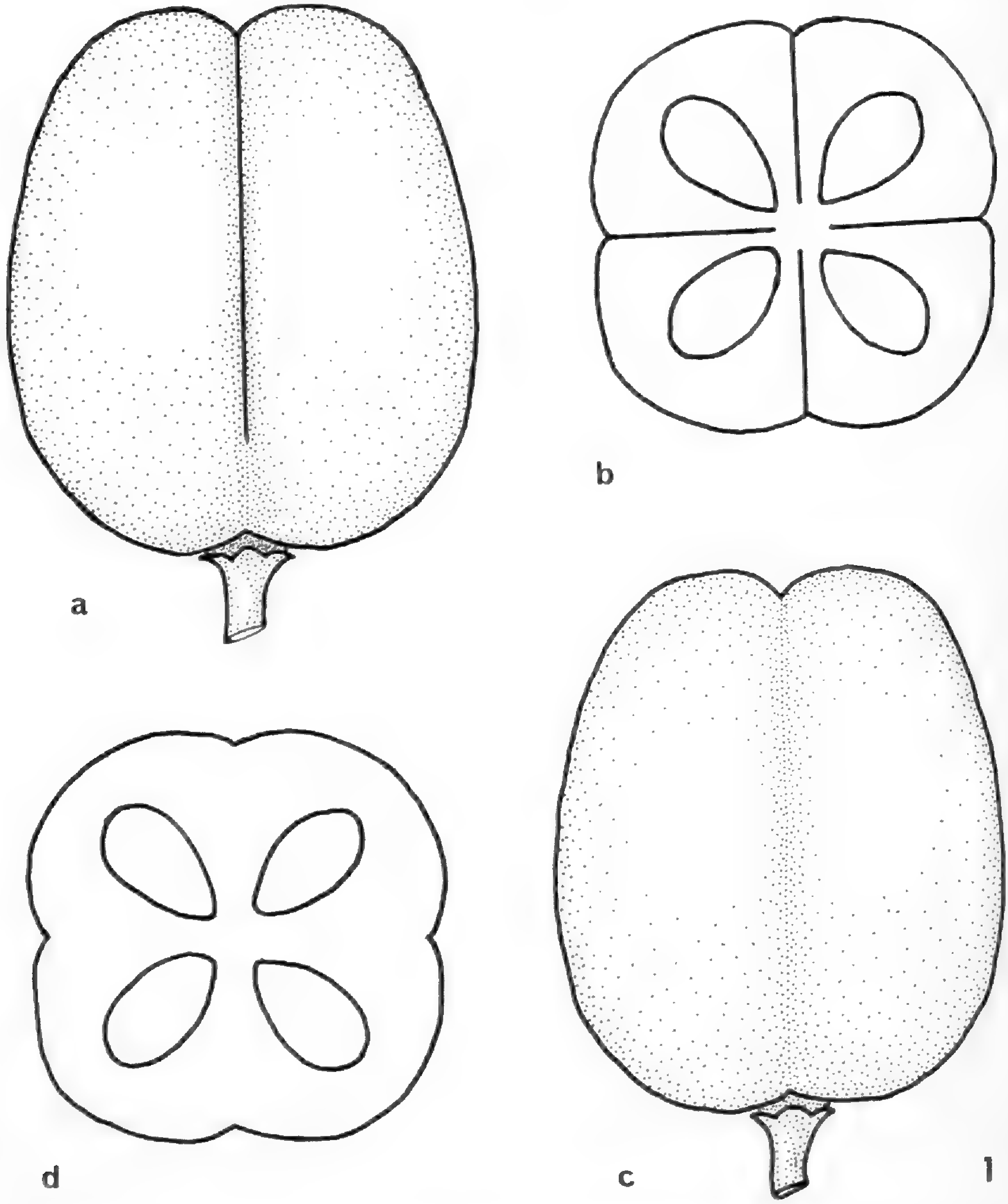


FIGURE 1. Fruit types in *Acronychia*. a, the primitive type with septicidal fissures extending for more than one half the length; b, transverse section of the primitive type; c, d, the derived type lacking septicidal fissures.

The surface of the fruit, apart from whether or not it is dissected by septicidal fissures, is smooth or only slightly roughened by oil glands in all but four of the species: it is fissured in *Acronychia goniocarpa*, roughened and often constricted and/or fissured in *A. vestita*, wrinkled in *A. rugosa*, and pitted in *A. foveata*.

The disc is generally obsolete in fruit but persists as an annular structure in *Acronychia foveata* and as a short stipe in *A. murina* and *A. emarginata*.

The testa is unusually thick and longitudinally wrinkled in *Acronychia baeuerlenii* and *A. aberrans*. In the remaining species it varies, often within species, from smoothish to finely tuberculate to muricate.

The septicidal fissures which occur in the ovary and fruit of many of the species of *Acronychia* appear to be vestigial and therefore may provide a clue to the phylogeny of the genus. Evidence for the vestigial nature of these fissures is that in a number of species they are represented only by small, apical slits or indentations, and also that they seem to be of no adaptive value. It is assumed that in the primitive condition the septicidal fissures extend from the apex to the base of the ovary and fruit, separating the carpels to the central axis, and that in the derived condition the ovary and fruit completely lack septicidal fissures, thus having completely connate carpels.[6] These fruit types are illustrated in FIGURE 1.

The texture of the epicarp appears to correlate, to some extent, with the amount of separation of the carpels by septicidal fissures and therefore may also be of phylogenetic significance. It seems most likely that the entirely semifleshy type represents a primitive condition from which the spongy-crustaceous and finally the woody types were derived. Evidence for this is that the semifleshy type predominates in those species that appear to be the most primitive on the basis of septicidal fissures whereas the woody type is found only in species that appear to be advanced in this regard.

It should be pointed out, however, that epicarp texture is probably an adaptive characteristic since the different types would almost certainly attract different species of animals and therefore would be subject to selection in seed dispersal. This could result in the supposed trend of semifleshy to woody being reversed.

In the following outline the species are divided into groups based primarily on the amount of separation of carpels by septicidal fissures and secondarily on the texture of the epicarp. Australian species are indicated by an asterisk.

GROUP I. Septicidal fissures extending to at least one half the length of the ovary and fruit.

GROUP Ia. Entire epicarp drying semifleshy or (rarely) soft-spongy; without evident mesocarp.

*1. *A. suberosa*
*2. *A. chooreechillum*
*4. *A. baeuerlenii*
*5. *A. pauciflora*
*21. *A. wilcoxiana*
*28. *A. pubescens*

---

[6] The main trend in most of the genera of the Rutaceae with subapocarpous species (for example, *Euodia, Melicope*, and *Zanthoxylum*) seems to be in the opposite direction, from a syncarpous condition to subapocarpous, evidenced by the fact that in most subapocarpous species the otherwise nearly separate carpels are joined by a common stigma.

GROUP Ib. Epicarp drying with spongy-crustaceous mesocarp.

- *3. *A. crassipetala*
- 29. *A. wabagensis*

GROUP II. Septicidal fissures extending from one fourth to one half the length of the ovary and fruit.

GROUP IIa. Entire epicarp drying semifleshy; without evident mesocarp.

- *6. *A. oblongifolia*
- *7. *A. acuminata*

GROUP IIb. Epicarp drying with spongy-crustaceous mesocarp.

- 8. *A. goniocarpa*
- 9. *A. rugosa*
- 30. *A. intermedia*
- 31. *A. montana*

GROUP III. Septicidal fissures apical or lacking.

GROUP IIIa. Entire epicarp drying semifleshy; without evident mesocarp.

- *10. *A. parviflora*
- *11. *A. laevis* (also in Lord Howe Island & New Caledonia)
- 12. *A. murina*
- 13. *A. emarginata*
- 14. *A. schistacea*
- 15. *A. papuana*
- 16. *A. arfakensis*
- 17. *A. similaris*
- 18. *A. kaindiensis*
- 19. *A. normanbiensis*
- 20. *A. brassii*
- *22. *A. acidula* (with some spongy-crustaceous mesocarp)
- *23. *A. aberrans*
- 25. *A. smithii*
- 32. *A. carrii*
- 33. *A. pullei*
- 34. *A. gurukorensis*
- 35. *A. macrocalyx*
- 36. *A. dimorphocalyx*
- 37c. *A. trifoliolata* var. *microcarpa*

GROUP IIIb. Epicarp drying with spongy-crustaceous mesocarp.

- 26. *A. foveata* (mesocarp grading to sub-woody)
- 27. *A. cartilaginea*
- 37b. *A. trifoliolata* var. *ampla*
- 38. *A. reticulata*
- 39. *A. ledermannii*

GROUP IIIc. Epicarp drying with woody or subwoody mesocarp.

*24. *A. vestita*
37a. *A. trifoliolata* var. *trifoliolata*
*40. *A. acronychioides*
*41. *A. imperforata*
42. *A. pedunculata*

From the above it is evident that the largest number of apparently primitive species exist in Australia. It seems probable, therefore, that New Guinea was initially colonized by Australian species[7] and that subsequent radiation has resulted in the comparatively large number of species on that island. Adaptive radiation appears still to be going on in New Guinea, especially in the species of Group IIIa. Most of the Australian species, on the other hand, appear to occur as relic populations,[8] probably as a result of the contraction and fragmentation of rain forest areas that is thought to have been going on there since the Tertiary (cf. Darlington, 1965: 100).

The numbers preceding the species in the above outline correspond with the arrangement of species in the body of the revision. That arrangement differs considerably from the sequence of species in the outline since the former is based on the assumption that there are four more or less independent lines of evolution in *Acronychia* (listed below). That these evolutionary lines appear to be independent is certainly the result of extinction of ancestral species. I know of no evidence that *Acronychia* is polyphyletic.

Evolutionary Line I
    Species 1 (*A. suberosa*) through species 3 (*A. crassipetala*).
Evolutionary Line II
    Species 4 (*A. baeuerlenii*) through species 20 (*A. laevis*).
Evolutionary Line III
    Species 21 (*A. wilcoxiana*) through species 27 (*A. cartilaginea*).
Evolutionary Line IV
    Species 28 (*A. pubescens*) through species 42 (*A. pedunculata*).

To my knowledge, chromosome counts have been published for only two species, *Acronychia oblongifolia* and *A. pedunculata*. In the former, according to Smith-White (1954: 295, 298), $2n = 36$, and in the latter, according to Mehra and Khosla (Taxon **18**: 215. 1969), $n = 18$. Smith-White published his count for *A. laevis*, but since the material was collected at Ourimbah, between Newcastle and Sydney, New South Wales, it is almost certainly *A. oblongifolia* (see MAPS 2 and 4).

---

[7] In view of the recently proposed theory of plate tectonics, Raven and Axelrod (1972) have suggested that several groups of Australian plants colonized New Guinea via late Tertiary land connections. Land connections (although probably more lowland than the above) also existed between the two areas during the Pleistocene with the fluctuations in sea level that occurred during that period.

[8] It is likely, however, that two of the Australian species, *Acronychia acronychioides* and *A. imperforata*, have originated from extra-Australian stock. Evidence for this is given below following the descriptions of those species.

KEY TO THE SPECIES
(based on flowering material [9])

1. Leaves unifoliolate (rarely with occasional trifoliolate leaves). . . . . 2.

2. Petioles of younger leaves glabrous or glabrate. . . . . 3.

3. Larger inflorescences not more than 2 cm. long. . . . . 4.

4. Leaflets acuminate at the apex, the acumen 1.5–2 cm. long; flowers 4 mm. long, ovary pubescent at the apex, otherwise glabrous, with septicidal fissures [10] extending to about one third the length. . . . . 7. *A. acuminata.*

4. Leaflets rounded, obtuse, acute or acuminate at the apex, acumen, when present, less than 1.5 cm. long. . . . . 5.

5. Ovary densely pubescent at the apex, otherwise glabrous; leaflets 7–13 cm. long; flowers 8.5–9 mm. long; petals puberulent abaxially. . . . . 26. *A. foveata.*

5. Ovary entirely glabrous or with a few hairs around the base of the style; leaflets 1.4–15 cm. long; flowers 3–6.5 mm. long; petals glabrous to puberulent abaxially. . . . . 6.

6. Flowers 5–6.5 mm. long; ovary with septicidal fissures extending to at least one half the length. . . 5. *A. pauciflora.*

6. Flowers 3–6 mm. long; septicidal fissures, if present, only at the apex of the ovary. . . . . 7.

7. Leaflets 3–15 cm. long, usually oblanceolate and often more than three times as long as wide, usually cuneate at the base and acuminate at the apex. . . 20. *A. brassii.*

7. Leaflets 1.4–9.5 cm. long, elliptic-oblong to ovate or suborbicular, usually less than three times as long as wide. . . . . 8.

8. Leaflets coriaceous, elliptic to obovate to suborbicular, 1.4–3 cm. long, acute to obtuse to rounded at the apex. . . . . 16. *A. arfakensis.*

8. Leaflets chartaceous to subcoriaceous, elliptic, elliptic-oblong or ovate, 2.5–9.5 cm. long, acuminate at the apex.

Flowers 3–3.5 mm. long; pedicels puberulent, 0.5–1 mm. long; leaflets chartaceous to subcoriaceous, 3.3–9.5 cm. long; inflorescences 0.6–0.8 cm. long. . . . . 10. *A. parviflora.*

Flowers about 4.5 mm. long; pedicels glabrous, 2–3.5 mm. long; leaflets subcoriaceous, 2.5–6 cm. long; inflorescences 0.7–1.3 cm. long. . . 15. *A. papuana.*

3. Larger inflorescences more than 2 cm. long. . . . . 9.

9. Internodes of younger branchlets concavely compressed, tetragonous. . . . . 23. *A. aberrans.*

9. Internodes of younger branchlets terete to slightly compressed or subtetragonous. . . . . 10.

10. Petioles 0.2–0.5 cm. long; leaflets coriaceous, broadly elliptic to suborbicular, 3.5–7 cm. long; ovary entirely pubescent. . . . . 19. *A. normanbiensis.*

---

[9] Flowers are not known for species 8 and 9, *A. goniocarpa* and *A. rugosa.*

[10] Septicidal fissures are generally not evident in dried flowers without boiling.

10\. Petioles usually longer; leaflets variable in shape but not suborbicular. . . . . 11.

  11\. Ovary entirely pubescent or, rarely, pubescent only at the apex; disc pubescent or glabrous; inflorescences often more than 10 cm. long. . . . . 42. *A. pedunculata.*

  11\. Ovary entirely glabrous or pubescent only at the apex; disc glabrous; inflorescences less than 10 cm. long . . . . 12.

    12\. Septicidal fissures extending for at least one third the length of the ovary. . . . . 13.

      13\. Flowers 5–7 mm. long; ovary densely ascending-pubescent at the apex, otherwise glabrous, with septicidal fissures extending to one third to one half the length; leaflets usually narrowly elliptic to oblanceolate, 4–12 cm. long. . . . . 6. *A. oblongifolia.*

      13\. Flowers 8.5–16 mm. long. . . . . 14.

        14\. Leaflets chartaceous, 6–11 cm. long; flowers 9–13 mm. long; pedicels 4–9 mm. long; sepals 0.6–1 mm. long, 1.4–2 mm. wide; petals glabrous. . . . . 4. *A. baeuerlenii.*

        14\. Leaflets chartaceous to subcoriaceous, 5.5–21 cm. long; flowers 8.5–16 mm. long; pedicels 0.5–7 mm. long; sepals more than 1 mm. long and usually more than 2 mm. wide; petals puberulent or glabrous abaxially. . . . . 15.

          15\. Petals obviously fleshy, in dry condition about 0.7 mm. thick near the apex. . . . . 3. *A. crassipetala.*

          15\. Petals not as obviously fleshy, in dry condition much thinner near the apex.

          Inflorescences usually many-flowered; flowers 8.5–10 mm. long; pedicels 0.5–3 mm. long; petals glabrous; ovary 4- to 8-carpellate. . . . . 21. *A. wilcoxiana.*

          Inflorescences few-flowered; flowers 12–16 mm. long; pedicels 3–7 mm. long; petals glabrous to puberulent abaxially; ovary 4-carpellate. . . . . 31. *A. montana.*

    12\. Septicidal fissures present only at the apex of the ovary, if at all. . . . . 16.

      16\. Petioles 2–7 cm. long; leaflets 8–23.5 cm. long, 4.3–12 cm. wide, base broadly rounded to acute or occasionally cuneate; flowers about 9.5 mm. long; pedicels 2–2.5 mm. long. . . 22. *A. acidula.*

      16\. Petioles 0.3–3.2 cm. long; leaflets 2.3–12 cm. long, 1–5.5 cm. wide, base narrowly rounded to attenuate; flowers 5–10 mm. long; pedicels 1.5–13 mm. long. . . . . 17.

17. Ovary ellipsoid; disc at anthesis 0.6–1 mm. high; internodes of younger branchlets often more or less tetragonous, the angles formed by narrow ridges or very thin wings of decurrent petiole bases; petals often puberulent abaxially; pedicels 3–12 mm. long; sepals 0.5–1.5 mm. long, 0.8–1.9 mm. wide. .... 12. *A. murina.*

17. Ovary globose or subglobose in outline; disc at anthesis 0.2–0.5 mm. high; internodes of younger branchlets terete or slightly compressed, petiole bases not decurrent into narrow ridges or wings; petals glabrous abaxially.

Sepals 0.7–1.3 mm. wide; pedicels 3.5–13 mm. long. .... 11. *A. laevis.*

Sepals 1.5–2.5 mm. wide; pedicels 1.5–4.5 mm. long. ...... 41. *A. imperforata.*

2. Petioles of younger leaves pubescent or puberulent, at least adaxially. 18.

18. Larger inflorescences not more than 3 cm. long. .... 19.

19. Ovary entirely pubescent.

Inflorescences about 9-flowered; flowers 3.5–4 mm. long; sepals 0.8 mm. long. .... 17. *A. similaris.*

Inflorescences 1- to 3-flowered; flowers 7–8.5 mm. long; sepals 1–1.4 mm. long. .... 18. *A. kaindiensis.*

19. Ovary entirely glabrous or pubescent only at the apex. ... 20.

20. Flowers 5–9 mm. long; leaflets 2–9.5 cm. long.

Ovary with septicidal fissures extending for at least one half its length; leaflets usually obovate or oblanceolate. .... 5. *A. pauciflora.*

Ovary without septicidal fissures; leaflets elliptic to elliptic-oblong. .... 14. *A. schistacea.*

20. Flowers 3–4.5 mm. long; leaflets 3–15 cm. long.

Flowers 3.5–4.5 mm. long; pedicels 1–2 mm. long; leaflets subcoriaceous to coriaceous, 3–15 cm. long, usually oblanceolate and often more than three times as long as wide; shrub to 3 m. .... 20. *A. brassii.*

Flowers 3–3.5 mm. long; pedicels 0.5–1 mm. long; leaflets chartaceous to subcoriaceous, 3.3–9.5 cm. long, elliptic or elliptic-oblong to ovate, usually not more than three times as long as wide; shrub or small tree to 8 m. .... 10. *A. parviflora.*

18. Larger inflorescences more than 3 cm. long. .... 21.

21. Septicidal fissures extending for about one half the length of the ovary. .... 28. *A. pubescens.*

21. Septicidal fissures present only at the apex of the ovary, if at all. .... 22.

22. Petioles puberulent to finely pubescent; leaflets glabrous; inflorescences often more than 8 cm. long; disc often pubescent; ovary usually pubescent throughout. .... 42. *A. pedunculata.*

22\. Petioles finely pubescent to tomentose; leaflets at least sparsely pubescent on the veins below; inflorescences less than 8 cm. long; disc glabrous.
  Leaflets subcoriaceous; flowers about 9 mm. long; pedicels 5–10 mm. long; sepals densely pubescent, about 2 mm. long; ovary pubescent throughout. .... 27. *A. cartilaginea.*
  Leaflets chartaceous; flowers 6.5–8 mm. long; pedicels 3–4.5 mm. long; sepals glabrous, 0.6–0.7 mm. long; ovary densely pubescent at the apex, otherwise glabrous. .... 24. *A. vestita.*

1\. Leaves trifoliolate (often with occasional unifoliolate leaves). .... 23.
23\. Sepals 4–5 mm. long.
  Leaflets elliptic-oblong to narrowly oblanceolate, 3.5–5.5 cm. wide; outer pair of sepals 4 mm. long and 4.5 mm. wide, inner pair 3.5 mm. long and 2.5 mm. wide; ovary pubescent throughout. .... 36. *A. dimorphocalyx.*
  Leaflets elliptic, 5–8.5 cm. wide; outer pair of sepals 4.5–5 mm. long, 4–5 mm. wide, inner pair only slightly smaller; ovary pubescent at the apex, otherwise glabrous. .... 35. *A. macrocalyx.*
23\. Sepals not more than 3 mm. long. .... 24.
24\. Flowers 3.5–4.5 mm. long; leaflets 0.7–2.8 cm. wide; internodes of younger branchlets often subtetragonous, the angles formed from narrow ridges or very thin wings of decurrent petiole bases. .... 13. *A. emarginata.*
24\. Flowers 4.5–17 mm. long; leaflets usually more than 3 cm. wide; internodes of younger branchlets terete or more or less compressed, petiole bases not decurrent into narrow ridges or wings. ...... 25.
25\. Septicidal fissures extending for at least one third the length of the ovary. .... 26.
26\. Sepals tomentose; leaflets usually pubescent below, at least on the veins. .... 28. *A. pubescens.*
26\. Sepals glabrous to finely pubescent; leaflets glabrous. 27.
27\. Ovary pubescent throughout; leaflets 7.5–15 cm. long; flowers 6.5–7 mm. long. .... 29. *A. wabagensis.*
27\. Ovary glabrous throughout or pubescent only at the apex. .... 28.
28\. Flowers 15–17 mm. long; leaflets 8–19 cm. long. .... 30. *A. intermedia.*
28\. Flowers 6.5–10 mm. long; leaflets 3.5–11.5 cm. long.
  Flowers 8–10 mm. long; sepals 2.8–3 mm. long; petals glabrous adaxially; petioles of younger leaves puberulent, at least adaxially; upper branches of inflorescences puberulent; leaflets usually oblanceolate. .... 1. *A. suberosa.*
  Flowers 6.5–8.5 mm. long; sepals 1.2–1.4 mm. long; petals rather densely pubescent adaxially; petioles and branches of inflorescences glabrous; leaflets usually elliptic or obovate. .... 2. *A. chooreechillum.*

25. Septicidal fissures, if present, not extending more than one third the length of the ovary. 29.

29. Younger leaflets densely pubescent on the midrib below; younger branchlets and petioles of younger leaves densely pubescent to tomentose. . . . . 38. *A. reticulata.*

29. Younger leaflets glabrous. . . . . 30.

30. Ovary and style entirely glabrous; pedicels 4–13 mm. long; flowers 9–13 mm. long; inflorescences usually many-flowered, 4.5–8.5 cm. long. . . . . . . 33. *A. pullei.*

30. Ovary and/or style at least partially pubescent; pedicels 1–7.5 mm. long. . . . . 31.

31. Flowers 9–14 mm. long; sepals 0.7–3 mm. long. . . . . 32.

32. Sepals 0.7–1.5 mm. long; leaflets drying dark reddish brown when young, pale green or yellowish green when older; inflorescences few-flowered, 4–10 cm. long; ovary sparsely pubescent at the apex, otherwise glabrous. 39. *A. ledermannii.*

32. Sepals 1.5–3 mm. long; leaflets drying more or less uniformly medium- or dark-green or brown. . . . . 33.

33. Ovary glabrous throughout. . . . . 32. *A. carrii.*

33. Ovary pubescent throughout or densely pubescent in the apical one third to one half.

Petals densely appressed-pubescent abaxially; inflorescences few-flowered, 1.5–5 cm. long . . . . 25. *A. smithii.*

Petals glabrous abaxially; inflorescences usually many-flowered, 3–9 cm. long. . . . . . 40. *A. acronychioides.*

31. Flowers 4.5–9 mm. long; sepals 0.3–1.5 mm. long.

Inflorescences 1- to few-flowered, 2.5–4 cm. long; flowers 7–8 mm. long; petals glabrous abaxially; disc glabrous; ovary pubescent throughout; leaflets chartaceous. . . . . 34. *A. gurukorensis.*

Inflorescences few- to many-flowered, 2–9 cm. long; flowers 4.5–9 cm. long; petals glabrous to pubescent abaxially; disc glabrous to pubescent; ovary pubescent throughout or only at the apex; leaflets chartaceous to subcoriaceous. . . . . 37. *A. trifoliolata.*

KEY TO THE SPECIES
(based on fruiting material)

1. **Leaves unifoliolate (rarely with occasional trifoliolate leaves).** . . . . 2.

2. **Petioles of younger leaves glabrous or glabrate.** . . . . 3.

3. Larger infructescences less than 2 cm. long. .... 4.
    4. Fruits broadly ovoid, about 12 mm. wide, heavily pitted; epicarp drying 2–3 mm. thick, with spongy-crustaceous or subwoody mesocarp; leaflets 7–13 cm. long. .... 26. *A. foveata.*
    4. Fruits ellipsoid or subglobose, 6–10 mm. wide, not heavily pitted; epicarp drying much thinner; leaflets 1.4–15 cm. long. .... 5.
        5. Fruits depressed at the apex, with narrow septicidal fissures extending for at least one half their length. .. 5. *A. pauciflora.*
        5. Fruits rounded to apiculate at the apex, septicidal fissures present only at the apex, if at all. .... 6.
            6. Leaflets 3–15 cm. long, usually oblanceolate and often more than three times as long as wide, usually cuneate at the base and acuminate at the apex. .... 20. *A. brassii.*
            6. Leaflets 1.4–9.5 cm. long, elliptic-oblong, ovate or suborbicular, usually less than three times as long as wide. .. 7.
                7. Leaflets coriaceous, elliptic to obovate to suborbicular, 1.4–3 cm. long, acute to obtuse to rounded at the apex. .... 16. *A. arfakensis.*
                7. Leaflets chartaceous to subcoriaceous, elliptic, elliptic-oblong or ovate, 2.5–9.5 cm. long, acuminate at the apex.
                    Leaflets chartaceous to subcoriaceous, 3.3–9.5 cm. long; infructescences, not including the lengths of the fruits, 0.5–1 cm. long; pedicels puberulent, 0.5–1 mm. long; fruits about 7 mm. wide with semipersistent petals. .... 10. *A. parviflora.*
                    Leaflets subcoriaceous, 2.5–6 cm. long; infructescences, not including the lengths of the fruits, 0.7–1.5 cm. long; pedicels glabrous, 2–3.5 mm. long; fruits about 6 mm. wide, without semipersistent petals. .... 15. *A. papuana.*

3. Larger infructescences more than 2 cm. long. .... 8.
    8. Internodes of younger branchlets concavely compressed, tetragonous; fruits 13–18 mm. wide. .... 23. *A. aberrans.*
    8. Internodes of younger branchlets terete to slightly compressed or subtetragonous; fruits 5–15 mm. wide. .... 9.
        9. Petioles 0.2–0.5 cm. long; leaflets coriaceous, broadly elliptic to suborbicular, 3.5–7 cm. long. .... 19. *A. normanbiensis.*
        9. Petioles usually longer; leaflets variable in shape, but not suborbicular. .... 10.
            10. Fruits usually pubescent throughout *and* with a ring of dense, appressed hairs at the base, occasionally glabrous throughout or pubescent only at the apex; epicarp drying with hard, more or less woody mesocarp; infructescences often more than 10 cm. long. ...... 42. *A. pedunculata.*
            10. Fruits glabrous throughout or pubescent only at the apex; drying semifleshy, spongy-crustaceous, or woody; infructescences less than 10 cm. long. .... 11.
                11. Leaflets acuminate at the apex, the acumen 1.5–2 cm. long; fruits sparsely pubescent at the apex, otherwise glabrous, with septicidal fissures extending for about one third the length, 10 mm. wide; epicarp drying thin

and semifleshy, without evident mesocarp. . . . . 7. *A. acuminata*.

11. Leaflets rounded, obtuse, acute or acuminate at the apex, the acumen, when present, less than 1.5 cm. long. . . . . 12.
    - 12. Fruits with a ring of dense pubescence around the base of the dehisced style, 6–8 mm. wide, with inconspicuous septicidal fissures extending for not more than one half the length; leaflets usually narrowly elliptic to oblanceolate, 4–12 cm. long. . . . . 6. *A. oblongifolia*.
    - 12. Fruits glabrous throughout or with a very few hairs at the apex, or if more densely pubescent apically, then larger and with conspicuous septicidal fissures. . . . . 13.
        - 13. Fruits 10–14 mm. wide, without septicidal fissures. . . . . 22. *A. acidula*.
        - 13. Fruits smaller, or if as large, then with septicidal fissures. . . . . 14.
            - 14. Epicarp drying with woody mesocarp. . . . . 41. *A. imperforata*.
            - 14. Epicarp drying thin and semifleshy or with spongy-crustaceous mesocarp. . 15.
                - 15. Septicidal fissures extending for at least one third the length of the fruit. . . . . 16.
                    - 16. Epicarp drying thin (less than 0.5 mm. thick) and semifleshy.
                        - Fruits 4-carpellate, about 9 mm. wide, with narrow, inconspicuous septicidal fissures; leaflets 6–11 cm. long; pedicels 4–9 mm. long; sepals about 1 mm. long. . . 4. *A. baeuerlenii*.
                        - Fruits 4- to 8-carpellate, 8–15 mm. wide, with conspicuous septicidal fissures; leaflets 7–21 cm. long; pedicels 0.5–3 mm. long; sepals 1.2–2.7 mm. long. . . . . . . 21. *A. wilcoxiana*.
                    - 16. Epicarp drying 0.5–1.5 mm. thick, with spongy-crustaceous mesocarp.
                        - Fruits strongly depressed at the apex; septicidal fissures about 3 mm. wide. . . . . . . 3. *A. crassipetala*.
                        - Fruits rounded to apiculate at the apex; septicidal fis-

sures to 2 mm. wide. . . . . 31. *A. montana.*

15. Septicidal fissures, if present, not extending for more than one third the length of the fruit. . . . . . . 17.
    17. Epicarp drying 1–1.5 mm. thick, with spongy-crustaceous mesocarp; leaflets 5.5–16 cm. long. . . . . . . 31. *A. montana.*
    17. Epicarp drying much thinner, semifleshy, without evident mesocarp; leaflets 2.3–9.5 cm. long.
        Fruits mitriform to subglobose, estipitate, apex usually depressed; internodes of younger branchlets terete, petiole bases not decurrent into narrow ridges or wings. . . . . 11. *A. laevis.*
        Fruits ellipsoid, usually on a stipe to about 1 mm. long, apex acute or short-apiculate or rounded; internodes of younger branchlets often more or less tetragonous, the angles formed by narrow ridges or very thin wings of decurrent petiole bases. . . . . 12. *A. murina.*

2. Petioles of younger leaves pubescent or puberulent, at least adaxially. 18.
    18. Larger infructescences not more than 3 cm. long. . . . . 19.
        19. Fruits pubescent (though often sparsely) throughout.
            Fruits subglobose, about 6 mm. wide; sepals 0.8 mm. long. . . . . 17. *A. similaris.*
            Fruits ellipsoid to subglobose, 6–10 mm. wide; sepals 1–1.4 mm. long. . . . . 18. *A. kaindiensis.*
        19. Fruits glabrous throughout or pubescent only at the apex. . . 20.
            20. Septicidal fissures extending for at least one half the length of the fruit. . . . . 5. *A. pauciflora.*
            20. Septicidal fissures, if present, only at the apex of the fruit. . . . . 21.
                21. Leaflets subcoriaceous to coriaceous, 3–15 cm. long, usually oblanceolate and often more than three times as long as wide. . . . . 20. *A. brassii.*
                21. Leaflets chartaceous to subcoriaceous, 3.3–9.5 cm. long, ovate to elliptic-oblong, usually less than three times as long as wide.
                    Younger leaflets drying brown or brownish green above; pedicels to about 1 mm. long; fruits about 7 mm.

wide, with semipersistent petals. .... 10. *A. parviflora*.

Younger leaflets drying blue-gray above; pedicels often more than 1 mm. long; fruits about 10 mm. wide, without semipersistent petals. . . 14. *A. schistacea*.

18. Larger infructescences more than 3 cm. long. .... 22.

22. Fruits with semipersistent petals; septicidal fissures extending for at least one third the length of the fruit. . . 28. *A. pubescens*.

22. Fruits without semipersistent petals; septicidal fissures, if present, only at the apex of the fruit. .... 23.

23. Petioles puberulent to finely pubescent; leaflets glabrous; infructescences often more than 10 cm. long. .... 42. *A. pedunculata*.

23. Petioles sparsely pubescent to tomentose; leaflets pubescent below, at least on the veins; infructescences less than 10 cm. long.

Leaflets chartaceous; fruits entirely glabrous or pubescent only at the apex, pyriform to subglobose, irregularly roughened and often deeply and irregularly constricted and/or fissured; epicarp drying 1–2 mm. thick. .... 24. *A. vestita*.

Leaflets subcoriaceous; fruits pubescent (though sparsely and minutely) throughout, broadly ellipsoid, not irregularly roughened or constricted or fissured; epicarp drying about 0.5 mm. thick. ...... 27. *A. cartilaginea*.

1. Leaves trifoliolate (often with occasional unifoliolate leaves). .... 24.

24. Fruits with septicidal fissures and also deeply and irregularly fissured or wrinkled.

Pedicels 10–18 mm. long; fruits ellipsoid to pyriform in outline, 8–11 mm. wide. .... 8. *A. goniocarpa*.

Pedicels 3–4.5 mm. long; fruits subglobose in outline, about 5 mm. wide. .... 9. *A. rugosa*.

24. Fruits with or without septicidal fissures, not otherwise fissured or wrinkled. .... 25.

25. Sepals 4–5 mm. long, persistent or deciduous in mature fruit; fruits about 19 mm. wide; epicarp drying semifleshy, without evident mesocarp.

Leaflets elliptic, 5–8.5 cm. wide; sepals and petals deciduous in fruit. .... 35. *A. macrocalyx*.

Leaflets elliptic-oblong to narrowly oblanceolate, 3.5–5.5 cm. wide; sepals persistent and petals semipersistent in fruit. .... 36. *A. dimorphocalyx*.

25. Sepals not more than 3 mm. long, persistent in mature fruit; fruits 4–23 mm. wide; epicarp drying semifleshy or with woody or spongy-crustaceous mesocarp. .... 26.

26. Septicidal fissures extending for at least one third the length of the fruit. .... 27.

27. Sepals tomentose; leaflets usually pubescent below, at least on the veins. .... 28. *A. pubescens*.

27. Sepals glabrous to finely pubescent; leaflets glabrous. 28.

28. Fruits pubescent (though rather sparsely) through-

out, with septicidal fissures extending nearly to the base; leaflets 7.5–15 cm. long, 3–6.3 cm. wide. . . . . 29. *A. wabagensis.*

28. Fruits entirely glabrous or pubescent only at the apex. . . . . 29.

29. Leaflets 8–19 cm. long; septicidal fissures extending for about one half the length of the fruit; epicarp drying about 2 mm. thick, with spongy-crustaceous mesocarp. . . . . . . 30. *A. intermedia.*

29. Leaflets 3.5–8.5 (–11.5) cm. long; epicarp drying about 0.5 mm. thick or less.

Petioles of younger leaves puberulent, at least adaxially; branches of inflorescences puberulent; petals semipersistent in fruit; septicidal fissures extending to the base of the fruit; leaflets usually oblanceolate. 1. *A. suberosa.*

Petioles and branches of inflorescences glabrous; petals deciduous in fruit; septicidal fissures extending for about one half the length of the fruit; leaflets usually elliptic or obovate. 2. *A. chooreechillum.*

26. Septicidal fissures, if present, not extending for more than one third the length of the fruit. . . . . .30.

30. Younger leaflets pubescent on the veins below; younger branchlets and petioles of younger leaves densely pubescent to tomentose; fruits subglobose, 12–16 mm. wide; epicarp drying 2–3 mm. thick, with spongy-crustaceous mesocarp. . . . . 38. *A. reticulata.*

30. Younger leaflets glabrous. . . . . 31.

31. Fruits about 20 mm. wide; epicarp drying thin (less than 0.5 mm. thick) and semifleshy. . . . . 34. *A. gurukorensis.*

31. Fruits smaller, or if as large, then with epicarp drying at least 1 mm. thick. . . . . 32.

32. Epicarp drying thin (less than 0.3 mm. thick) and semifleshy, without evident mesocarp; fruits 4–10 mm. wide. . . . . 33.

33. Fruits 9–10 mm. wide; sepals 1–2 mm. long; leaflets subcoriaceous to coriaceous, 4–20 cm. long.

Pedicels to about 14 mm. long; sepals 1–1.5 mm. long; leaflets subcoriaceous to coriaceous, 5.5–20 cm. long. . . . . 33. *A. pullei.*

Pedicels to about 4 mm. long; sepals 2 mm. long; leaflets subcoriaceous, 4–11.5 cm. long. . . . . 32. *A. carrii.*

33. Fruits 4–6 mm. wide; sepals 0.3–0.8 mm. long; leaflets chartaceous to subcoriaceous, 1.7–15 cm. long.

Leaflets 0.7–2.8 cm. wide; internodes of younger branchlets often subtetragonous, the angles formed from narrow ridges or very thin wings of decurrent petiole bases. . . . . . . 13. *A. emarginata.*

Leaflets 2.3–6 cm. wide; internodes of younger branchlets terete or slightly compressed, petiole bases not decurrent into narrow ridges or wings. . . . . 37. *A. trifoliolata.*

32. Epicarp drying thicker, with or without spongy-crustaceous or woody mesocarp; fruits 5–23 mm. wide. . . . . 34.

34. Sepals 1.5–3 mm. long; fruits 8–12 mm. wide; epicarp drying about 1 mm. thick, with semifleshy or woody mesocarp.

Fruits about 12 mm. wide, ovoid to subglobose; mesocarp drying semifleshy; infructescences 2–5 cm. long. . . . . 25. *A. smithii.*

Fruits 8–11 mm. wide, subpyriform or occasionally subglobose; mesocarp drying woody; infructescences 3–9 cm. long. . . . . 40. *A. acronychioides.*

34. Sepals 0.7–1.5 mm. long; fruits 5–23 mm. wide; epicarp drying 0.5–4 mm. thick, with woody or spongy-crustaceous mesocarp.

Leaflets drying more or less uniformly dark- to medium-green, brown or blackish; pedicels 0.5–7 mm. long; fruits 5–18 mm. wide; epicarp drying 0.3–4 mm. thick, with woody or spongy-crustaceous mesocarp. . . . . 37. *A. trifoliolata.*

Leaflets drying dark reddish brown when young, pale green or yellowish green when older; pedicels 1–3 mm. long; fruits 12–23 mm. wide; epicarp drying about 4 mm. thick, with spongy-crustaceous mesocarp. . . . 39. *A. ledermannii.*

1. **Acronychia suberosa** C. T. White, Proc. Roy. Soc. Queensl. 43: 47. 1932. LECTOTYPE: *Tryon & White*, January, 1921, Queensland, Moreton District. Lamington National Park.

Small to medium tree to about 20 m.; younger branchlets finely pubescent to glabrate. Leaves trifoliolate (occasional leaves unifoliolate); petiole puberulent, at least adaxially, becoming glabrous and cracking transversely with age, 1–4.5 cm. long; leaflets subcoriaceous to coriaceous, glabrous, oblanceolate or occasionally elliptic to elliptic-oblong 3.5–8.5 cm. long, 0.9–3 cm. wide, base cuneate or occasionally attenuate, main veins 7–9 on each side of the midrib, apex obtuse to acuminate, the acumen to 1 cm. long. Inflorescences few-flowered, 1.8–3.5 cm. long, axes and branches puberulent to glabrate. Flowers 8–10 mm. long; pedicels puberulent to finely pubescent, 1–3.5 mm. long; sepals glabrate to finely pubescent, broadly elliptic to suborbicular, 2.8–3 mm. long, 2.5–2.7 mm. wide; petals sparsely appressed-pubescent abaxially, glabrous adaxially, semipersistent in fruit; disc glabrous, 0.5–1 mm. high, 2.3–3 mm. wide; ovary sparsely pubescent at the apex, otherwise glabrous, with septicidal fissures extending to the base; style pubescent toward the base, otherwise glabrous. Fruits creamy yellow to whitish, drying reddish brown or blackish, sparsely pubescent at the apex, otherwise glabrous, with septicidal fissures extending to the base, subglobose to ellipsoid, 10–12 mm. wide, base rounded, apex rounded to obtuse; epicarp drying less than 0.5 mm. thick, semifleshy to soft-spongy, without evident mesocarp; endocarp subcartilaginous. Seeds reddish brown to blackish, about 4 mm. long.

DISTRIBUTION. Extreme southeast Queensland and adjacent New South Wales; primary and secondary rain forests and borders, 200–1000 meters.

Queensland. MORETON DISTRICT: Lamington National Park, *Fraser*, April 18, 1953 (NSW 127092), *Shirley*, May, 1918 (NSW 127093), *Smith & Webb 3599* (CANB), *Tryon & White*, January, 1921 (BRI, lectotype; A, K, isotypes), *T. & J. Whaite 3030* (NSW), *White 12082* (BRI); Springbrook, *Carroll 1194* (NSW), *Goy & Smith 190* (A, BRI), *White 6270* (BRI), *7055* (BRI). **New South Wales.** Gibberagunyah, *Jones 3429* (CANB); near Kyogle, *Jones*, June, 1943 (BRI, NSW); Whian Whian State Forest, *Constable*, January 14, 1953 (A, NSW 22352), *Johnson & Hayes*, June 10, 1957 (NSW 127094), *Jones 2708* (CANB), April 23, 1945 (NSW), *Jones (leg. Tracey) 950* (CANB), *Webb & Tracey*, 1953–1958 (BRI, CANB), *Webb & White 2135* (BRI).

The epithet *suberosa* refers to the corky outer bark of this plant. The diagnostic value of this feature is difficult to assess since bark characteristics are so seldom noted on herbarium labels of collections of *Acronychia*.

A narrow endemic of southeast Queensland and adjacent New South Wales, *Acronychia suberosa* appears to be closely related to *A. chooreechillum*, an endemic of northeast Queensland. The latter species is probably the more advanced of the two, having less separation of the carpels by septicidal fissures.

The lectotype is one of two collections (the other being *White 6270*) cited in the original description.

2. **Acronychia chooreechillum** (F. M. Bailey) C. T. White, Contr. Arnold Arb. Harvard Univ. No. 4: 49. 1933.

Melicope chooreechillum F. M. Bailey, Report Govt. Sci. Exped. Bellenden Ker Range 33. 1889. TYPE: *Bellenden Ker Expedition*, 1889. Queensland, Cook District, Mt. Bartle Frere.

Shrub or small tree to about 12 m.; branchlets glabrous. Leaves trifoliolate (or occasional or rather frequent leaves unifoliolate); petiole glabrous, 1.5–6 cm. long; leaflets coriaceous or occasionally subcoriaceous, glabrous, elliptic to obovate to oblanceolate, 4–7.5 (–11.5) cm. long, 1.6–3.5 (–5.8) cm. wide, base cuneate to attenuate, main veins 7–10 on each side of the midrib, apex rounded to obtuse or occasionally obtusely acuminate, the acumen to 0.4 cm. long. Inflorescences few-flowered, 2.5–6 cm. long, axes and branches glabrous. Flowers 6.5–8.5 mm. long; pedicels glabrous, 1.5–5 mm. long; sepals glabrous, broadly rounded, 1.2–1.4 mm. long, 1.3–2 mm. wide; petals glabrous abaxially, rather densely pubescent adaxially; disc glabrous, 0.4 mm. high, 1.3–2 mm. wide; ovary glabrous throughout or with a few hairs at the base of the style, with septicidal fissures extending for about one half the length; style with spreading or ascending pubescence toward the base, otherwise glabrous. Fruits drying greenish brown, glabrous throughout or with a few hairs at the apex, with septicidal fissures extending for about one half the length, elliptic in outline, usually 4-angled, 7–10 mm. wide, base rounded, apex acute; epicarp drying less than 0.5 mm. thick, semifleshy, without evident mesocarp; endocarp pergamentaceous. Seeds reddish black, about 4 mm. long.

DISTRIBUTION. Thornton Peak south to Mt. Bartle Frere, Cook District, Queensland; usually in stunted rain forests on mountain summits, 1200–1600 meters.

Queensland. COOK DISTRICT: Thornton Peak, *Brass 2296* (A, BISH, BRI), *Brass & White 205* (BRI), *Olsen 400* (BRI, NSW); Mt. Alexander (Alexandra), Daintree River, *Kajewski 1491* (A, BRI, NY); Mt. Spurgeon, *White 10668* (A, BM, BRI), *10714* (A, BRI); Mt. Bellenden Ker, *Sayer*, 1887 (BRI, MEL), *Smith 14619* (BRI), *14661a* (BRI); Mt. Bartle Frere, *Bellenden Ker Expedition*, 1889 (BRI, holotype of *Melicope chooreechillum* F. M. Bailey; K, isotype), *Johnson*, November, 1891 (MEL), *Martin & Hyland 1877* (BRI), *Palmerston* (MEL), *Scarth-Johnson 121(33)* (K).

The epithet *chooreechillum* is derived from an aboriginal name for Mt. Bartle Frere.

A collection from Mt. Spurgeon, *White 10714*, has unusually large leaflets up to 11.5 cm. long and 5.8 cm. wide. A second *White* collection from the same mountain, *10668*, is more or less intermediate with typical *A. chooreechillum*, however, indicating that there is clinal variation in this species between tall rain forest and stunted rain forest of mountain summit areas.

3. **Acronychia crassipetala** Hartley, sp. nov.

Arbor parva; ramulis glabris; foliis unifoliolatis; petiolo glabro, 0.9–2.5 cm. longo; foliolo subcoriaceo, glabro, elliptico vel elliptico-oblongo, 6.3–9.5 cm. longo, 2.5–5.3 cm. lato, basi acuto vel cuneato, venis primariis utrinsecus costa 8–11, apice subacuto vel obtuse acuminato, acumine usque ca. 0.5 cm. longo; inflorescentiis paucifloris, ca. 3 cm. longis, axi et ramulis glabris vel puberulis; floribus ca. 11 mm. longis, pedicellis puberulis, ca. 2 mm. longis; sepalis glabratis, rotundatis, 1.9–2.8 mm. longis, 2.2–2.8 mm. latis; petalis crasse carnosis prope apicem ca. 0.7 mm. crassis, basin versus abaxialiter puberulis, adaxialiter subtiliter adpresse pubescentibus; disco glabro, 0.6 mm. alto, 2.2 mm. lato; ovario apice sparse pubescenti, aliter glabro, subcylindrico, fissuris septicidalibus fere ad basin extensis; stylo basin versus patulo-pubescenti, aliter glabro; fructibus in sicco rubiginosis, glabris, fissuris septicidalibus latis saltem 1/2 longitudine extensis, ambitu subglobosis, valde 4-lobatis, ca. 10 mm. latis, basi truncatis, apice depressis; epicarpio in sicco 0.5–1 mm. crasso, mesocarpio spongioso-crustaceo; endocarpio subcartilagineo; seminibus rubiginosis, ca. 4 mm. longis. HOLOTYPUS: *T. Carr* (BRI). FIGURE 2.

DISTRIBUTION. Cook and North Kennedy Districts, Queensland; rain forests from 1080 to 1200 meters.

Queensland. COOK DISTRICT: Mt. Spurgeon, *T. Carr* (BRI, holotype). NORTH KENNEDY DISTRICT: State Forest Reserve 194, Lat. 17° 20′ S., Long. 145° 25′ E., *Hyland 4019* (BRI).

It might be suspected that the unusually thick petals of this plant are the result of the flowers having been stung by insects. There is no evidence that this is the case, however; the ovary and ovules appear normal.

The carpels of this and the preceding species may become completely separated apically in fully mature fruit. They are not separate in the ovary and young fruit, however, being at least axially connate for their entire length.

The relationships of *Acronychia crassipetala* are not particularly clear, but it seems closest to *A. chooreechillum*, differing mainly in having unifoliolate leaves, larger flowers, thicker petals, and a thicker epicarp.

4. **Acronychia baeuerlenii** Hartley, sp. nov.

Arbor parva usque 9 m. alta; ramulis glabris; foliis unifoliolatis; petiolo glabro, 0.8–1.8 cm. longo; foliolo chartaceo, glabro, elliptico vel elliptico-oblongo, 6–11 cm. longo, 2–4 cm. lato, basi cuneato vel anguste obtuso, venis primariis utrinsecus costa 10–12, apice obtuso vel obtuse acuminato, acumine usque 1 cm. longo; inflorescentiis paucifloris, 3–6.5 cm. longis, axi et ramulis glabris; floribus 9–13 mm. longis, pedicellis glabris, 4–9 mm. longis; sepalis glabris vel glabratis, late rotundatis, 0.6–1 mm. longis, 1.4–2 mm. latis; petalis glabris; disco glabro, 0.4–0.6 mm. alto, 1.7–1.8 mm. lato; ovario glabro, fissuris septicidalibus 1/2 vel 3/4 longitudine extensis; stylo basin versus sparse patulo-pubescenti, aliter glabro; fructibus in sicco brunneis, glabris, fissuris septicidalibus saltem 1/2 longitudine extensis, subglobosis, ca. 9 mm. latis, basi et apice rotundatis; epicarpio in sicco minus quam 0.5 mm. crasso, semicarnoso, mesocarpio non evidenti; endocarpio pergamentaceo; seminibus pallide rubiginosis, grosse et irregulariter rugosis, ca. 4 mm. longis. HOLOTYPUS: ***Forsyth***, October, 1898 (NSW). FIGURE 3.

2

3

FIGURE 2. *Acronychia crassipetala* Hartley, photograph of type (BRI). FIGURE 3. *Acronychia baeuerlenii* Hartley, photograph of type (NSW).

DISTRIBUTION. Extreme southeast Queensland and adjacent New South Wales; rain forests to about 800 meters.

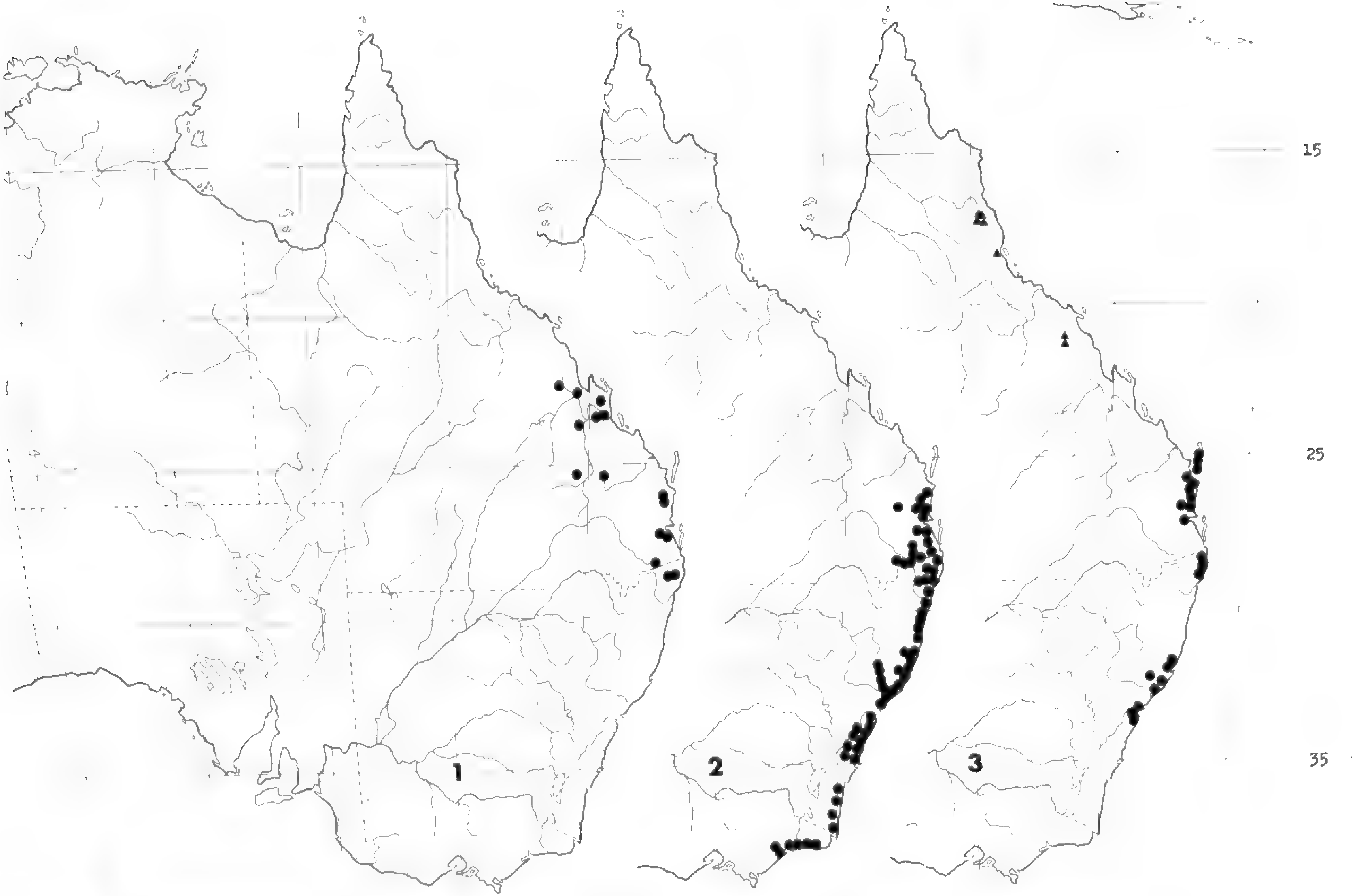
Queensland. MORETON DISTRICT: Lamington National Park, Macpherson Range, *White & Tryon*, March, 1920 (BRI). **New South Wales.** Mt. Warning, *Guilfoyle* (MEL); Toonumbar State Forest, 14 miles WNW of Kyogle, *Hayes*, 1947 (Herb. NSW Forestry Station, Coffs Harbour); Burringbar, *Forsyth*, October, 1898 (NSW 127033, holotype); Byron Bay, *Forsyth*, October, 1898 (UC, W); Lismore, *Baeuerlen*, November, 1892 (NSW 127035), April, 1894 (U); Wollongbar, *Manager Experimental Farm*, February, 1905 (NSW 127034); Alstonville, *Baeuerlen* 697 (MEL); Tintenbar, *Baeuerlen 641a* (NSW); Richmond River, *Baeuerlen 217* (MEL), *Fawcett* (MEL). Without definite locality: *Cunningham 34* (MEL).

Acronychia baeuerlenii appears to be the most primitive of a large group of related species (Evolutionary Line II), most of which have small, fleshy fruits and small flowers. On the basis of the dissection of the ovary and fruit by septicidal fissures it seems to be most closely related to *A. pauciflora*. On other characters, however, *A. oblongifolia* and *A. laevis* appear to be closer relatives.

The most recent collections of this species were made by Hayes, in 1947, and Tryon & White, in 1920. All of the remaining collections were made around the turn of this century or before. This rarity of modern collections is probably due to extensive clearing of rain forest areas in northeast New South Wales.

5. **Acronychia pauciflora** C. T. White, Proc. Roy. Soc. Queensl. **57**: 21. 1947. TYPE: *Clemens*, January, 1945, Queensland, Moreton District, Mt. Glorious.

Shrub or small tree to about 5 m.; younger branchlets finely pubescent to glabrate. Leaves unifoliolate; petiole finely pubescent to puberulent, at least adaxially, becoming glabrate and cracking transversely with age, 0.4–1.8 cm. long; leaflet subcoriaceous or occasionally chartaceous, glabrous throughout or rarely very sparsely short-pubescent below, obovate to oblanceolate or rarely elliptic, 2–9.5 cm. long, 1–4.8 cm. wide, base obtuse to cuneate, main veins 7–9 on each side of the midrib, apex obtuse to obtusely acuminate (the acumen to 1 cm. long) or occasionally rounded or subacute. Inflorescences few-flowered, 0.8–1.2 cm. long, axes and branches finely pubescent. Flowers 5–6.5 mm. long; pedicels glabrous to puberulent, 1–1.8 mm. long; sepals glabrous to puberulent, obtusely triangular to rounded, 0.8 mm. long, 0.9–1.1 mm. wide; petals glabrous or with scattered hairs abaxially, glabrous adaxially; disc glabrous, 0.5–1 mm. high, 1.5–2 mm. wide; ovary glabrous throughout or with a few hairs around the base of the style, with septicidal fissures extending for at least one half the length; style pubescent toward the base, otherwise glabrous. Fruits drying dark reddish brown, glabrous throughout or with a few hairs at the apex, with narrow septicidal fissures extending for at least one half



Maps 1–3. Distributions of *Acronychia* species: 1, *A. pauciflora* C. T. White; 2, *A. oblongifolia* (A. Cunn. ex Hook.) Endl. ex Heynh.; 3, *A. acidula* F. Muell. (triangles) and *A. wilcoxiana* (F. Muell.) Hartley (dots).

the length, subglobose, 7–9 mm. wide, base rounded, apex depressed; epicarp drying about 0.5 mm. thick, semifleshy to soft-spongy, without evident mesocarp; endocarp subcartilaginous. Seeds reddish black, about 4 mm. long.

DISTRIBUTION. Eastcentral Queensland south to northeast New South Wales; dry scrubs and rain forests at lower elevations. See MAP 1.

Queensland. LEICHHARDT DISTRICT: Croyden Homestead, *Jones 2813* (CANB); 4 miles ESE of Edungalba, *Johnson 1973* (BRI); Arcadia Creek in vicinity of Arcadia Homestead, *Story & Yapp 323* (CANB). PORT CURTIS DISTRICT: Marlborough Road, 80 mile, *Jones 3181* (CANB); N of Broad Sound, *Jones*, July, 1967 (CANB); Rockhampton, *Bowman* (K, MEL), *Dallachy*, July, 1863 (BM, BRI, MEL, W), *Dietrich 874* (MEL), *1585* (MEL), *1765* (MEL), *2116* (MEL, NY, P), *2197* (MEL), *O'Shanesy 118* (MEL); Capricorn, *Bowman*, May, 1861 (MEL); Gogango, *Thozet 773* (MEL). BURNETT DISTRICT: Eidsvold, *Bancroft*, April, 1913 (BRI). WIDE BAY DISTRICT: Kin Kin, *White*, January, 1916 (BRI); Imbil, *Clemens 43391* (A, NY, US), *43392* (A, BRI), *Smith & Webb 3141* (CANB). MORETON DISTRICT: Mt. Glorious, *Bray*, May, 1943 (BRI), ("rain forest near gully") *Clemens*, January, 1945 (BRI, holotype; GH, MICH, NY, UC, isotypes), ("forest road") *Clemens*, January, 1945 (AD, BISH, BRI, GH, MICH, NY, UC); Samford, *Webb & Tracey leg. Tracey 3395* (CANB); Samford Creek, *White 12638* (A, BRI); Brisbane River, *Mueller*, 1857 (K); Little Mt. Alford, *Michael 2227* (NY). **New South Wales.** Lismore, *Baeuerlen*, March, 1898 (NSW 127029); Richmond River, *Fawcett* (NSW 127030).

This species, *Acronychia pauciflora*, is the only species of *Acronychia* showing a tendency to adapt to the xeric conditions of the Australian interior, several of the collections having been made in the brigalow scrub (*Acacia harpophylla*) of eastcentral Queensland.

6. **Acronychia oblongifolia** (A. Cunn. ex Hook.) Endl. ex Heynh. Nomencl. Bot. Hort. **2**: 8. 1846.

Cyminosma oblongifolia A. Cunn. ex Hooker's Bot. Mag. **61**: *t. 3322.* 1834. TYPE: *Cunningham*, New South Wales, Port Jackson (Sydney).

Jambolifera oblongifolia (A. Cunn. ex Hook.) Steudel, Nomencl. ed. 2. **1**: 796. 1840.

Acronychia laurina F. Muell. 3rd Gen. Report Veg. Victoria 7. 1854; Frag. Phytogr. Austral. **1**: 27. 1858, *nomen illegit.*, based on *Cyminosma oblongifolia* A. Cunn. ex Hook.

Acronychia laevis J. R. & G. Forst. var. *leucocarpa* F. M. Bailey, Queensl. Dept. Agr. Bot. Bull. **14**: 7. 1896. TYPE: *F. M. Bailey*, Queensland, Moreton District, Eumundi.

Acronychia laevis J. R. & G. Forst. var. *dictyophleba* Domin, Bibliot. Bot. **22**(89): 294. 1927. TYPE: *Domin 5582*, March, 1910, Queensland, Moreton District, Tamborine Mt.

Shrub or small to large tree to about 27 m.; branchlets glabrous. Leaves unifoliolate (rarely occasional leaves trifoliolate); petiole glabrous, 0.7–3.2 cm. long; leaflet subcoriaceous or occasionally chartaceous, glabrous, elliptic to narrowly elliptic-oblong to oblanceolate, rarely obovate, 4–12 cm.

long, 1.4–4.5 cm. wide, base obtuse to attenuate, main veins 5–11 on each side of the midrib, apex obtuse to rounded. Inflorescences few-flowered, 2–6 cm. long, axes and branches glabrous. Flowers 5–7 mm. long; pedicels glabrous, 1.5–8 mm. long; sepals glabrous, obtusely triangular to broadly rounded, 0.5–1 mm. long, 0.9–1.5 mm. wide; petals glabrous; disc glabrous, 0.3–0.5 mm. high, 1.2–1.8 mm. wide; ovary densely ascending-pubescent at the apex, otherwise glabrous, with septicidal fissures extending for one third to one half the length; style densely pubescent basally, otherwise glabrous. Fruits white, drying reddish brown or blackish, with a ring of dense, short pubescence at the apex, otherwise glabrous, with inconspicuous septicidal fissures extending for not more than one half the length, subglobose to mitriform, 6–8 mm. wide, base rounded, apex rounded or slightly depressed; epicarp drying less than 0.5 mm. thick, semifleshy and with soft-spongy mesocarp differentiated between the locules; endocarp subcartilaginous. Seeds blackish, about 3.5 mm. long.

ILLUSTRATION. Cunningham, A. ex W. J. Hooker, *loc. cit.*

DISTRIBUTION. Southeast Queensland south to southeast Victoria; rain forests to 1100 meters. See MAP 2.

Queensland. WIDE BAY DISTRICT: Traveston, 12 miles SE of Gympie, *Francis*, July, 1921 (UC); Noosa, *Smith & McGillivray 3078* (NSW); Amamoor, *Swain*, October, 1912 (BRI). DARLING DOWNS DISTRICT: Forest Reserve 405, ca. 25 miles NE of Warwick, *Smith 11468* (BRI); Reserve 327, Warwick, *Spiden B 1* (BRI); near Emu Vale, Macpherson Range, *Francis*, November, 1920 (BRI); Killarney, *de Beuzeville*, April, 1935 (NSW 127118); Spring Creek, near Killarney, *Hubbard 5810* (A, BRI, K); Wilson's Peak, *Goy 406* (BRI). MORETON DISTRICT: Bunya Mts., *White*, October, 1919 (BRI); Eumundi, *Bailey* (BRI, holotype of *Acronychia laevis* J. R. & G. Forst. var. *leucocarpa* F. M. Bailey; BM, K, isotypes), *White*, June, 1912 (BRI); Blackall Range, *White*, December, 1916 (BRI); Conondale, *Williams*, March, 1967 (BRI); Mt. Glorious, *Clemens*, January, 1945 (MICH); Brisbane River, *Mueller* (BM); Mt. Mitchell, *White 6873* (A, BRI, NY); Mt. Mistake, *Bailey 4* (MEL); Logan River, *Scortechini* (MEL); Tamborine Mt., *Clemens*, March, 1947 (MICH, NY, UC), *Domin 5582* (PR, holotype of *Acronychia laevis* J. R. & G. Forst. var. *dictyophleba* Domin); near Lamington National Park along road to Moran's Falls, *Smith 14185* (BRI); Lamington National Park, *Smith & Webb 3596* (CANB), *3603* (CANB), *Webb 5010* (CANB). **New South Wales.** Acacia Creek, near Killarney, Queensland, *Dunn*, December, 1904 (NSW 127119), January, 1906 (NSW 127112), *Gray & Shaikh 4409* (CANB); Cudgen, *Guilfoyle*, 1871 (MEL); Toonumbar, *Constable*, May 18, 1949 (NSW 11186); Moore Park, near Kyogle, *White 12512* (A, BRI, UC, US); Whian Whian State Forest, *Webb & Tracey*, 1953–1958 (BRI); Lismore, *Fawcett*, June 27, 1867 (MEL); Richmond River, *Boorman*, March. 1909 (BISH), *Fawcett 108* (MEL, NSW), *Henderson 160* (MEL); Casino, *Irby*, March, 1917 (NSW 127115), *McAuliffe*, July, 1913 (NSW 127114), *McLean*, February, 1918 (NSW 127116), June 26, 1918 (NSW 127113); Ballina, *Baeuerlen*, June, 1892 (A); Clarence River, *Beckler* (GH, MEL, U, W), *Mueller* (NSW), *Wilcox*, November, 1875 (MEL); Ramornie to Orara River, *Blakely & Shiress*, July, 1922 (NSW 127120); Dorrigo, *Boorman*, 1909 (NSW 127120), *Fraser*, January 2, 1935 (NSW 127121), *Tindale*, April 3, 1944 (A, NSW, UC), *Vickery*, April 15, 1953 (NSW 23854), *White 7536* (A, BRI, NY); Pine Creek State Forest, *McGillivray 757* (NSW); Bellinger District, *Hewitt*, March 1, 1946 (NSW 127123); Raleigh, Bellinger River, *Boorman*, June, 1910 (NSW 127124), *Swain*, March, 1910 (NSW 127126); Nambucca Heads, *Boorman*, June, 1910 (W); Macleay River, *Beckler* (MEL), *McDonald*, 1889 (MEL); Port Macquarie to Kempsey, *Maiden*, July, 1895 (NSW 127127); Hastings River, *Beckler* (U), *Cunningham 48* (BM, K, MEL); Port Macquarie, *Evans*, August 22, 1927 (CANB), *Lilier*, September, 1938 (NSW 127129); between Port Macquarie and Tacking Point, *Todd*, January, 1966 (NSW 127130); Wauchope, *Maiden*, May, 1915 (NSW 127128, US); Comboyne Plateau ca. 1 mile W of Comboyne, *Schodde 5155* (CANB); Moorland, N of Taree, *McGrath*, June 29, 1953 (NSW 127131); Craven Plateau ca. 20 miles NW of Gloucester, *Briggs*, August 3, 1964 (NSW 64997); upper Williams River, *Fraser & Vickery*, January 10, 1934 (NSW 127132), *Rodway 1851* (NSW); Williams River, *Fraser & Vickery*, January 15, 1934 (NSW 127133); Bungwahl, *Rupp*, June, 1924 (NSW 127135); Myall River, *Rupp*, March, 1924 (NSW 127136), August 5, 1924 (NSW 127134); Dungog, *Rudder*, February 10, 1893 (NSW 127138), February 16, 1894 (NSW 127137); Ash Island, Hunter's River, *Scott* (MEL); Newcastle, *Oakman*, February 6, 1941 (NSW 137139); Belmont, *Dwyer 1091* (NSW); Hawkesbury River, *Brown 5330* (BM, K); Lisaroa, Gosford District, *Evans*, July 28, 1927 (CANB); Narara Creek, Narara, *McGillivray 714* (NSW); Gosford, *Fletcher*, February 25, 1888 (NSW 126998), *Maiden*, October, 1887 (MEL); Newport to Barranjoey, *Maiden*, July, 1905 (NSW 126999); Newport, *Maiden & Cambage*, July, 1905 (NSW 127031), *White 10337* (BRI); Blue Mts., *Atkinson 26* (MEL); Kogarah, *Camfield*, September, 1900 (NSW 127001); Manly, *Betche*, June, 1889 (NSW 127000); Sydney, *Brown* (MEL), *Cunningham* (K, holotype of *Cyminosma oblongifolia* A. Cunn. ex Hook.), *Macarthur*, 1854 (K); Hacking River, *Johnson*, 1947 (NSW 127002); Otford, ca. 13 miles S of Sutherland, *Coveny 1243* (BRI, NSW); Bulli, *Collie* (NSW 127007); Neplow River, Douglas Park, *McBarron 11841* (NSW); Mt. Keira, *Johnson 397x* (NSW), *Martensz 203* (NSW); Woonona, near Wollongong, *Maiden*, March 3, 1891 (GH); Wollongong, *Baeuerlen*, March 3, 1891 (MEL); West Dapto, *Cambage 404* (NSW); Minnamurra Falls, *Judd*, May, 1953 (NSW 127006), June, 1953 (NSW 127005); Cambewarra Range, *Rodway*, March, 1922 (NSW 127003); Broger's Creek, *Baeuerlen 27* (MEL); Kiama, *Harvey*, January, 1856 (K); Gerringong, *Fraser & Vickery*, April 20, 1934 (CANB); Foxground, *Hay*, November, 1906 (NSW 127004); Shoalhaven River *Baeuerlen 43* (MEL); Comerong Island, *Rodway 877* (NSW); Mt. Dromedary, Tilba Tilba, *Johnson & Constable*, September 9, 1960 (NSW 127008); Tantawangalo Mt., *Targett*, October, 1921 (NSW 127009); Jigamy Creek 2 miles N of Eden, *Webb & Tracey 3633* (BRI); Timbillica Crossing, *Allan & Taylor* (MEL). **Victoria.** Deep Creek near Bruthen, *Allender*, December 28, 1962 (MEL); Lake King, *Mueller*, February, 1855 (BM, K, MEL); Kalimna, near Lakes Entrance, *Willis*, August 15, 1944 (MEL); Mottle Gully about 14 miles NW of Orbost, *Elliott*, May 26, 1963 (MEL); Snowy River, *Pescott*, August, 1901 (NSW), *Rowe*, 1902 (NSW); Orbost, *Pescott*, April, 1901 (NSW); Brodribb River, *Pescott*, September, 1900 (MEL). **Cultivated.** VICTORIA: Melbourne Botanic Gardens, *Anonymous*, February 23, 1923 (A).

Acronychia oblongifolia has often been confused with *A. laevis*. The two species are readily distinguishable by the ring of dense pubescence at the apex of the ovary and fruit in the former.

7. **Acronychia acuminata** Hartley, sp. nov.

Arbor 8 m. alta; ramulis glabris; foliis unifoliolatis; petiolo glabro, 1.5–3.5 cm. longo; foliolo subcoriaceo, glabro, elliptico, 9–15 cm. longo, 3–5 cm. lato, basi cuneatis, venis primariis utrinsecus costa 8–10, apice acuminatis, acumine 1.5–2 cm. longo; inflorescentiis paucifloris, ca. 1.5 cm. longis, axi et ramulis glabratis; floribus 4 mm. longis, pedicellis glabratis, 1–2 mm. longis; sepalis glabris, triangularibus, 1 mm. longis, 1.2 mm. latis; petalis abaxialiter glabris, adaxialiter sparse pubescentibus; disco glabro, 0.3 mm. alto, 1.5 mm. lato; ovario apice pubescenti, aliter glabro, fissuris septicidalibus 1/3 longitudine extensis; stylo basin versus pubescenti, aliter glabro; fructibus in sicco rubiginosis, apice sparse pubescentibus, aliter glabris, fissuris septicidalibus 1/3 longitudine extensis, ovoideis, ca. 10 mm. latis, basi rotundatis, apice obtusis; epicarpio in sicco minus quam 0.5 mm. crasso, semicarnoso, mesocarpio non evidenti; endocarpio pergamentaceo; seminibus nigricantibus, ca. 4.5 mm. longis. HOLOTYPUS: *Webb & Tracey 10760* (CANB). FIGURE 4.

DISTRIBUTION. Known only from the type locality; rain forest border.

Queensland. COOK DISTRICT: MacDowall Range between Daintree River and Bloomfield River, Lat. 16° 30′ S., Long. 145° 17′ E., *Webb & Tracey 10760* (CANB, holotype).

This plant appears to be closely related to *Acronychia parviflora* but differs in having longer-acuminate leaflets, larger flowers, and larger fruits.

8. **Acronychia goniocarpa** Merr. & Perry, Jour. Arnold Arb. **22**: 57. 1941. TYPE: *Brass 12093*, West Irian, Idenburg River.

Tree 25 m.; branchlets glabrous. Leaves trifoliolate; petiole glabrous, 3–6 cm. long; leaflets subcoriaceous, glabrous, elliptic-oblong, 10–21 cm. long, 4.5–7 cm. wide, base obtuse to cuneate or attenuate, main veins 11–15 on each side of the midrib, apex obtuse to obtusely acuminate, the acumen to 1 cm. long. Infructescences 8–11 cm. long, axes and branches glabrous; fruiting pedicels glabrous, 10–18 mm. long; sepals glabrous, broadly rounded, 0.7 mm. long, 2 mm. wide. Fruits yellow, drying reddish black, with a few hairs at the apex, otherwise glabrous, with septicidal fissures extending for one fourth to one half the length and otherwise deeply and irregularly fissured with sharply angled intervening ridges, elliptic to pyriform in outline, 8–11 mm. wide, base subtruncate, apex usually short-apiculate; epicarp drying about 0.5 mm. thick, with spongy-crustaceous mesocarp; endocarp cartilaginous. Seeds reddish brown, about 4 mm. long. Flowers not seen.

DISTRIBUTION. Known only from the type locality; montane rain forests from 1750 to 1780 meters.

West Irian. Idenburg River, 15 km. SW of Bernhard Camp, *Brass 12093* (A, holotype; BRI, L, LAE, isotypes), *Brass & Versteegh 11926* (A, L, LAE).

FIGURE 4. *Acronychia acuminata* Hartley, photograph of type (CANB). FIGURE 5. *Acronychia rugosa* Hartley, photograph of type (A).

Although *Acronychia goniocarpa* and *A. rugosa* may be rather closely related, both having irregularly roughened fruits, their relationships to other species of the genus are not at all clear. Only *Acronychia vestita*, of north Queensland, shares the characteristic of irregularly roughened fruit, but it differs in lacking septicidal fissures and in having much larger, unifoliolate leaves.

9. **Acronychia rugosa** Hartley, sp. nov.

Arbor parva vel mediocris usque 25 m. alta; ramulis glabris; foliis trifoliolatis (foliis infrequentibus unifoliolatis); petiolo glabro, 1.5–4.5 cm. longo; foliolis subcoriaceis, glabris, elliptico-oblongis vel oblanceolatis, 6.5–11 cm. longis, 2–4.5 cm. latis, basi cuneatis vel attenuatis, venis primariis utrinsecus costa 11–12, apice rotundatis vel obtuse acuminatis, acumine usque 0.5 cm. longo; infructescentibus usque 6.5 cm. longis, axi et ramulis glabratis; pedicellis fructiferis glabratis vel puberulis, 3–4.5 mm. longis; sepalis puberulis, obtuse triangularibus vel rotundatis, 0.7 mm. longis, 1 mm. latis; fructibus albis, in sicco brunneis, glabris, profunde et irregulariter rugosis, fissuris septicidalibus ca. 1/2 longitudine extensis, subglobosis, ca. 5 mm. latis, basi truncatis, apice obtusis; epicarpio in sicco ca. 0.5 mm. crasso, mesocarpio spongioso; endocarpio cartilagineo; seminibus nigricantibus, ca. 2.5 mm. longis; floribus non visis. HOLOTYPUS: *Brass & Versteegh 11951* (A). FIGURE 5.

DISTRIBUTION. West Irian and Papua (Western District); montane rain forests from 1800 to 2480 meters.

West Irian. Mt. Doorman, *Lam 1933* (L); Idenburg River, 15 km. SW of Bernhard Camp, *Brass 12044* (A, L, LAE), *Brass & Versteegh 11951* (A, holotype; L, LAE, isotypes); Star Mts., Mt. Antares, *Kalkman 4319* (CANB). **Papua.** WESTERN DISTRICT: Kiunga Subdistrict, Berlin, Ok Tedi River, *Foreman & Galore NGF 45786* (CANB, LAE).

Acronychia rugosa differs from *A. goniocarpa*, which appears to be its closest relative, in having smaller fruits and leaves and shorter fruiting pedicels.

10. **Acronychia parviflora** C. T. White, Contr. Arnold Arb. Harvard Univ. No. 4: 51. 1933. TYPE: *Kajewski 1214*, Queensland, Cook District, Atherton Tableland.

Shrub or small tree to 8 m.; younger branchlets finely pubescent to glabrate. Leaves unifoliolate; petiole finely pubescent or occasionally glabrate, becoming glabrous with age, 0.5–1.5 cm. long; leaflet chartaceous to subcoriaceous, glabrous throughout or with a few scattered hairs on the midrib below, ovate to elliptic to elliptic-oblong, 3.3–9.5 cm. long, 1.4–4.5 cm. wide, base obtuse to cuneate, main veins 9–14 on each side of the midrib, apex acuminate, the acumen to about 1 cm. long. Inflorescences 1- to few-flowered, 0.6–0.8 cm. long, axes and branches finely pubescent. Flowers 3–3.5 mm. long; pedicels puberulent, 0.5–1 mm. long; sepals sparsely short-pubescent, obtusely triangular, 0.7–1 mm. high, 1–1.2 mm. wide; petals glabrate to sparsely puberulent abaxially, glabrous adaxially, semipersistent in fruit; disc glabrous, 0.3 mm. high, 1.3 mm. wide; ovary glabrous throughout or sparsely pubescent around the base of the style, with apical septicidal fissures; style glabrous throughout or sparsely pubescent only at the base. Fruits light purple, drying reddish brown, glabrous throughout or sparsely pubescent only at the apex, with narrow septicidal fissures at the apex, subglobose in outline, drying 4-lobed, about 7 mm. wide, base and apex rounded; epicarp drying less than 0.5 mm. thick, semi-fleshy, without evident mesocarp; endocarp subcartilaginous. Seeds reddish brown, about 3.8 mm. long.

Distribution. Northeast Queensland, Atherton Tableland south to Tully Falls; rain forests from 200 to 1350 meters.

Queensland. Cook District: Davies Creek, Lamb Range between Mareeba and Kuranda, *Webb & Tracey 7231* (bri); Glen Allyn, Malanda, *Hayes* (bri), *Kajewski 1214* (bri, holotype; k, ny, isotypes); Boonjee, near Malanda, *Blake 15181* (bri, mel); Mt. Bartle Frere, *Blake 9822* (bri); Tully Falls, *Fielding, North Queensland Naturalists Club 13333* (bri).

Acronychia parviflora is apparently closely related to *A. acuminata* (q.v.).

11. **Acronychia laevis** J. R. & G. Forst. Char. Gen. Pl. ed. 1. *t. 27.* 1775 (cf. St. John, 1971); *ibid.* ed. 2. 1776. Type: *J. R. & G. Forster*, New Caledonia.

Lawsonia acronychia L. f. Suppl. Pl. 219. 1781 (*nomen illegit.*, based on *Acronychia laevis* J. R. & G. Forst.).

Huonia laevis (J. R. & G. Forst.) Montrous. Mém. Acad. Roy. Soc. Lyon, Sec. Sci. II. **10:** 185. 1860.

Jambolifera laevis (J .R. & G. Forst.) O. Ktze. Rev. Gen. Pl. **1:** 102. 1891.

Acronychia laevis J. R. & G. Forst. var. *purpurea* F. M. Bailey, Queensl. Dept. Agr. Bot. Bull. **14:** 7. 1896. Type: not designated.

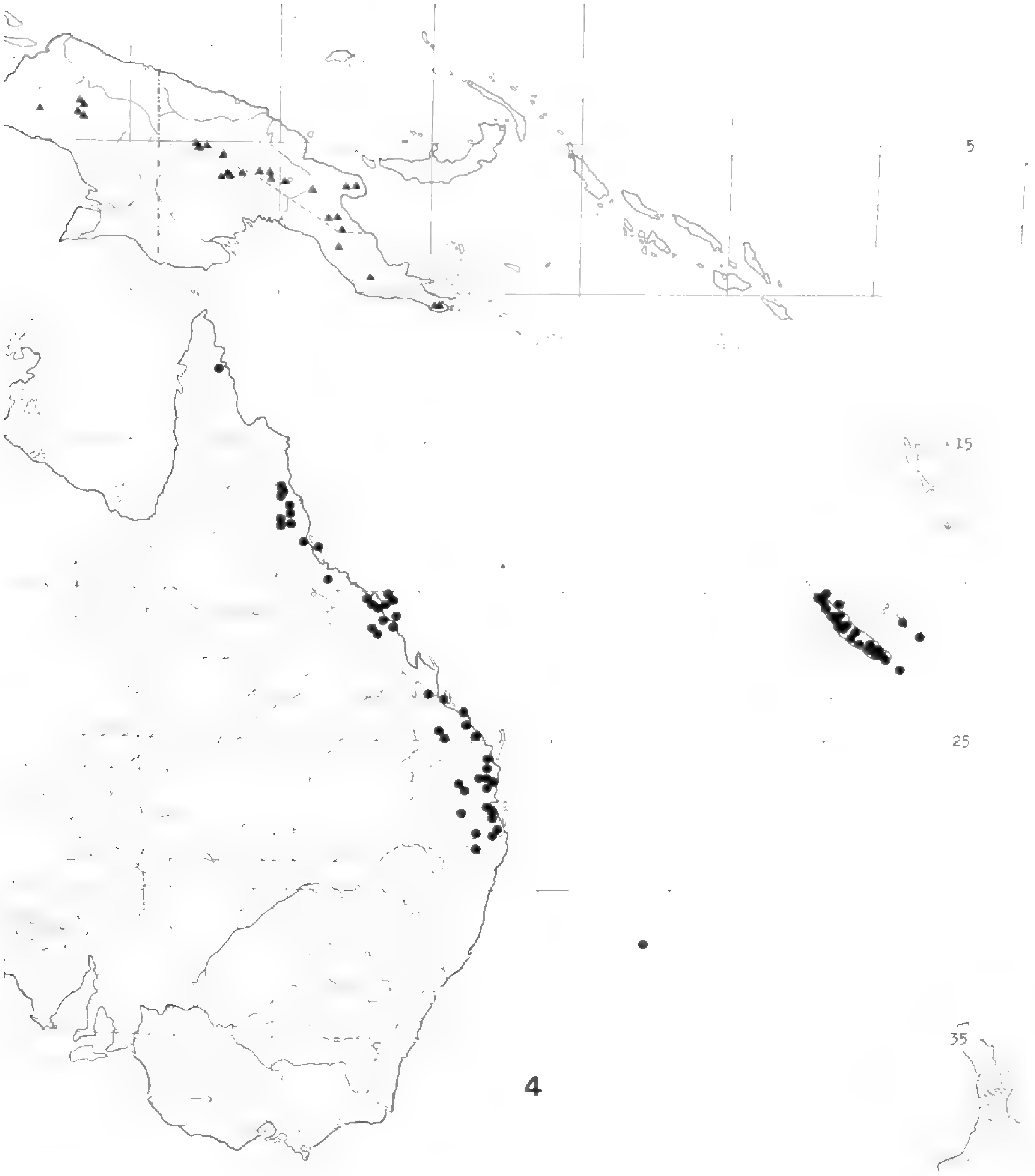
Acronychia laevis J. R. & G. Forst. var. *longiflora* Domin, Bibliot. Bot. **22**(89): 294. 1927. Syntypes: *Domin 5585*, December, 1909, Queensland, Port Curtis District, Gladstone; *Dietrich 648*, Queensland, Moreton District, Brisbane River.

Shrub or small tree to 12 m.; branchlets glabrous. Leaves unifoliolate; petiole glabrous or with a few hairs at the apex, 0.3–3 cm. long; leaflet chartaceous to subcoriaceous, glabrous, elliptic to elliptic-oblong or obovate to oblanceolate, 2.5–9.5 cm. long, 1–5 cm. wide, base cuneate to narrowly rounded, main veins 7–11 on each side of the midrib, apex rounded to obtuse or occasionally obtusely acuminate, the acumen to 0.8 cm. long. Inflorescences few- to many-flowered, 1.5–7 cm. long, axes and branches glabrous. Flowers 6–7 (–10) mm. long; pedicels glabrous, 3.5–13 mm. long; sepals glabrous, obtusely triangular to triangular, 0.7–2 mm. long, 0.7–1.3 mm. wide; petals glabrous abaxially, glabrous or occasionally sparsely appressed-pubescent toward the base adaxially; disc glabrous, 0.2–0.5 mm. high, 1–1.5 mm. wide; ovary glabrous, without septicidal fissures; style sparsely to rather densely pubescent toward the base, otherwise glabrous. Fruits white to purplish, drying reddish brown to blackish, glabrous, without septicidal fissures, mitriform or occasionally subglobose, 6–8 (–12) mm. wide, base obtuse to rounded, apex usually rather deeply depressed; epicarp drying less than 0.5 mm. thick, semifleshy, without evident mesocarp; endocarp subcartilaginous to pergamentaceous. Seeds dark reddish brown, 4–4.5 mm. long.

ILLUSTRATIONS: Banks, J., & D. Solander, Illustrations of the botany of Captain Cook's voyage 1: *t. 35.* 1900 (as *Jambolifera laevis*). Forster, J. R. & G., *loc. cit.*

DISTRIBUTION. Cape York Peninsula, Queensland, south to northeast New South Wales and east to New Caledonia (including the Loyalty Islands) and Lord Howe Island; rain forests and scrubs to 600 meters in Australia; rain forests, scrubs, and rather open rocky slopes to 750 meters in New Caledonia. See MAP 4.

Queensland. COOK DISTRICT: Tozer Gap, Tozer Range, *Brass 19438* (BRI, CANB); Mt. Fraser, *Brass 2435* (A, BISH, BRI); Mt. Malloy, *Brass 2454* (A, BISH, BRI, P); Boyle Creek NW of Mareeba, McKee *9138* (CANB); Forestry Reserve 185, Danbulla, *Volek QF 54/128* (BRI); Forestry Reserve 185, Juara Logging area, *Hyland 3098* (BRI); near Atherton, *Bailey* (BRI); Stannary Hills, *Bancroft*, September, 1909 (BRI); 40 miles W of Mount Garnet, *Brass & White 103* (BRI). NORTH KENNEDY DISTRICT: Mt. Macalister, *Dallachy*, April 9, 1869 (MEL); Stony Creek, Rockingham Bay, *Dallachy*, March, 1867 (BM, K, MEL); Palm Island, *Sommerville*, May, 1926 (BRI); Mt. Elliot, *Campbell*, June 14, 1959 (CANB); foothills of Mt. Elliot along Alligator Creek, *Macfarlane*, May 30, 1965 (BRI); Port Denison, *Fitzalan*, June 18, 1863 (MEL); Mt. Dryander, NE of Proserpine, *Webb & Tracey 7871* (BRI); Preston, near Proserpine, *Michael 1071* (BM, BRI, GH); Cannonvale to Proserpine, *Jones 3188* (CANB); Cannonvale, *Jones 1554* (CANB); Conway State Forest between Airlie and Shute Harbour, *Webb & Tracey 7622* (BRI); Shute Harbour, *Jones 2030* (CANB), *Webb & Tracey 7937* (BRI); Hayman Island, *White 10085* (A, BRI, NY); South Molle Island, *Scanlan 2b* (BRI); Whitsunday Island, *White 10086* (BRI, NY). SOUTH KENNEDY DISTRICT: Cawley State Forest W of Cathu between Mackay and Proserpine, *Webb & Tracey 7693* (BRI); Brampton Island, *Bardsley*, November 1, 1967 (BRI); Dalrymple Heights and vicinity, *Clemens*, July-September, 1947 (MICH, UC), July-November, 1947 (BRI), September-October, 1947 (BISH, BRI), September-November, 1947 (GH, MICH); Dalrymple Range near Broken River Bridge, *Haines 125* (K); Eungella Range, *Francis*, October 3–12, 1922 (BRI); Port Mackay, *Dietrich 2523* (MEL), *2630* (MEL). PORT CURTIS DISTRICT: Bay of Inlets (Broad Sound), *Banks & Solander*, 1770 (MEL, P, US, W); Fitzroy River, *O'Shanesy 88 ser. 9* (MEL); Rockhampton, *Dallachy 275* (MEL, U, W), April 13, 1863 (MEL), *O'Shanesy 194* (MEL), *Simmons*, 1903 (NSW 127036), *Thozet 27* (MEL, P); Keppel Bay, *Brown 5331* (BM, BRI, K, MEL); Gladstone, *Domin 5585* (PR, syntype of *Acronychia laevis* J. R. & G. Forst. var. *longifolia* Domin); Bustard Bay, *Jeffrey*, April 28, 1967 (BRI); Rosedale, *Dovey 73* (BRI), *198* (BRI). BURRETT DISTRICT: Callide Valley, *White 10808* (A, BRI); Coongarra Rock, Coalstoun Lakes, *White 7728* (A, BRI, NY). WIDE BAY DISTRICT: The



MAP 4. Distributions of *Acronychia murina* Ridley (triangles) and *A. laevis* J. R. & G. Forst. (dots).

Hummock, near Bundaberg, *Goy & Smith 610* (BRI); Mary River, *Young*, January, 1917 (UC); Mt. Bauple, *Clemens*, June 18–20, 1945 (GH); Glastonbury, *Swain*, April, 1917 (NSW); Gympie, *Kenny*, 1906 (BRI). DARLING DOWNS DISTRICT: Toowoomba, *Longman* (K). MORETON DISTRICT: Eumundi, *White*, 1911 (BRI); Buderim Mt., *White*, April, 1912 (BRI); Bunya Mts., *White*, October, 1919 (AD); Yarraman, *Cameron*, February, 1925 (A); Cedar Creek, ca. 20 miles NW of Brisbane, *Goy & Smith 45* (BRI); Samford, *White*, March, 1920 (A, BRI); Clear Mt., *White 6090* (A, BRI); Gold Creek, *White*, June 3, 1915 (NSW); Enoggera Creek, *Bailey* (US); Taylor's Range, *Bailey*, July, 1879 (BRI); Mt. Coot-tha, *Blake 3322* (BRI), *4739* (BRI), *Hubbard 3390* (A, BRI), *Williams*, June 20, 1970 (BRI); West Ithaca Creek, foot of Taylor Range, *Everist 2969* (BRI, CANB); Ithaca Creek E of Brisbane, *White*, July 15, 1916 (BRI, NSW); Goodna, *White 881* (BRI, UC); Brisbane, *Griffith* (MEL); Normans Creek, *Leichhardt*, 1845 (P); Brisbane River, *Cunningham 24* (BM, BRI, K, MEL), *Dietrich 648* (NY, P, isosyntypes of *Acronychia laevis* J. R. & G. Forst. var. *longiflora* Domin), 1863–1865 (BM, BRI, US, W), *Mueller* (K, MEL); Mount Edwards, *Everist 611* (BRI); Mt. Tamborine, *Clemens*, March, 1947 (AD, BISH, BRI, MICH); Lamington National Park, *Shirley*, February, 1918 (NSW 127032), *Smith 14192* (BRI). **New South Wales.** Rivertree Area, ca. 39 miles E of Liston, *Clark, Pickard & Coveny 1772* (NSW); Lord Howe Island, *Anonymous* (GH, K, W). **New Caledonia.** Poume, *Compton 2369* (BM), *Vieillard 289* (A, K); Îlot Mouac, *Virot 247* (A, P); Île Pam, *Balansa 3373* (A, BM, K, P, US); Col d'Amoss, *Thorne 28142* (P); Oubatche, *Schlechter 15501* (BM, NSW, W), *15555* (BM, NSW, W); Tiébaghi Mt., *Thorne 28102* (P); N of Hienghène, *Virot 775* (P); Gatope Island, *Vieillard 285 bis* (K), *2436* (BM); Voh, *Baumann-Bodenheim leg. Baas-Becking 5972* (P); Mt. Poindala, *Daeniker 1090* (P), *Guillaumin & Baumann-Bodenheim 9414* (P); Houaïloa, *Leenhardt 212* (P); Col Nékoro, *Guillaumin 13348* (P); Canala, *Deplanche 108* (P), *Lecard* (P); Bourail, *Balansa 1350* (BM, K, US), *1350a* (P), *LeRat 662* (P); road from Canala to La Foa, *McMillan 5171* (A, BISH, P, UC); Col d'Amieu, inland from La Foa, *Schodde 5221* (CANB); Plateau de Dogny, *LeRat*, July, 1910 (P); La Foa, *Leenhardt 455* (P); Mt. Bacon, *Daeniker 696* (P); lower Tontouta Valley, *McKee 3460* (A, P, US); Mt. Dzumac, *LeRat 2601* (A, P); Mt. Mou, *Compton 517* (BM, MEL), *White 2085* (A, BRI, P); St. Vincent, *Brousmiche 1130* (P), *Daeniker 413e* (P); Païta, *LeRat 35* (P), *Schlechter 15001* (BM, GH, K, NSW, P, W); Dumbea, *LeRat 2391*; Koghis Mts., *Godefroy*, 1910–1911 (P); Nouméa and vicinity, *Balansa 431* (BM, P), *Deplanche*, 1855–1860 (P), *Germain*, 1874–1876 (BM, P), *LeRat 1642* (P), *Virot 818* (A, P), *939* (P), *1165* (P), *1181* (P); Thi River N of St. Louis Mission, *Buchholz 1616* (A, BISH, P, UC, US); St. Louis Mission, *Taylor 5* (A); Mt. Dore, *Franc 1342* (A, BM, BRI, K, P, UC); Mt. Ouen Toro, *McKee 1022* (A, P). *2002* (BISH, P, UC, US), *2156* (A, P, US), *Virot 540* (A, P), *950* (A, P); Baie des Pirogues, *White 2268* (A, BRI, P); Prony, *Cribs 1555* (BRI, NSW, P), *1665* (P); Île des Pins, *Cribs 1155* (P), *LeRat 110* (P), *Pancher*, 1861 (MEL, P), *Virot 1063* (P); without definite locality, *Anderson*, 1774 (BM), *Aubreville-Heine 88* (P), *Banks* (W), *Baudouin 763* (P), *Baumann-Bodenheim 5144* (P), *14654* (P), *Brousmiche 1032* (P), *Caldwell*, 1868 (K), *Compton 661* (BM, NSW), *Cook*, 1774 (BM), *Cribs 1215* (P), *Deplanche 7* (A, W), *438* (P), *Forster* (K, holotype of *Acronychia laevis* J. R. & G. Forster; BM, P (photo), W, isotypes), *Guillaumin & Baumann-Bodenheim 7575* (P), *7582* (P), *7598* (P), *9196* (A), *9221* (P), *10040* (P), *13124* (P), *Hodgson*, 1887 (MEL), *Huerlimann 1169* (P), *1270* (P), *LeRat 1471* (P), *Pancher*, 1860 (P), *Roberts*, 1886 (MEL). **Loyalty Islands.** Lifou Island, *Daeniker 2975a* (P), *Bergeret 140* (P), *Whitmee* (BM); Maré Island, *Daeniker 2589a* (P).

The Australian collections of *Acronychia laevis* are rather variable in size of flower and fruit: two collections from southeast Queensland, *Dallachy 275* and *Dietrich 648*, have flowers about 10 mm. long, the usual size in the species being 6–7 mm. long; and three collections from northeast Queensland, *Brass 2435*, *2454*, and *19483*, and one from southeast Queensland, *Everist 611*, have fruits about 12 mm. wide, the usual size for the species being 6–8 mm. wide.

The New Caledonian collections are more homogeneous and as a whole differ only slightly from the majority of the Australian collections. (The leaves in the former tend to be somewhat less punctate and have slightly less-ascending main veins.) In view of this lack of differentiation between the two areas and the lack of much variation in New Caledonia, it seems probable that *Acronychia laevis* arrived in New Caledonia in relatively recent times via long distance dispersal.

12. **Acronychia murina** Ridley, Trans. Linn. Soc. Bot. II. **9**: 25. 1916. TYPE: *Kloss* (*Wollaston Expedition*), 1912–1913, West Irian, Mt. Carstensz.

Acronychia wichmannii Lauterb. Bot. Jahrb. **55**: 255. 1918; Nova Guinea (Bot.) **14**: 145. 1924. SYNTYPES: *Pulle 997*, *1015*, West Irian, Mt. Wichmann; *Versteeg 2417*, West Irian, Mt. Hubrecht.

Shrub or small to medium tree to 25 m.; branchlets glabrous, more or less tetragonous in younger growth, the angles formed by narrow ridges or very thin wings of decurrent petiole bases. Leaves unifoliolate (rarely occasional leaves trifoliolate); petiole glabrous, 0.4–2 cm. long; leaflet chartaceous to coriaceous, glabrous, elliptic to elliptic-oblong to obovate, 2.3–9.5 cm. long, 1.2–4 cm. wide, base narrowly rounded to attenuate, main veins 6–11 on each side of the midrib, apex rounded to obtuse. Inflorescences few-flowered, 1.4–7 cm. long, axes and branches glabrous. Flowers 6–8 mm. long; pedicels glabrous or occasionally finely puberulent, 3–12 mm. long; sepals glabrous or glabrate, rounded to obtusely deltoid, 0.5–1.5 mm. long, 0.8–1.9 mm. wide; petals glabrous to puberulent abaxially, glabrous adaxially; disc glabrous, 0.6–1 mm. high, 1–1.5 mm. wide; ovary glabrous throughout or pubescent only at the apex, ellipsoid, with or without apical septicidal fissures; style glabrous throughout or pubescent only in the basal one half to two thirds. Fruits whitish, drying brown to blackish, glabrous throughout or with a few hairs only at the apex, with or without apical septicidal fissures, elliptic in outline, often more or less four-angled, 4–6 mm. wide, base obtuse to subtruncate, usually on a stipe formed from the disc to about 1 mm. long, apex rounded to acute to short-apiculate; epicarp drying less than 0.5 mm. thick, semifleshy, without evident mesocarp; endocarp subcartilaginous. Seeds dark reddish brown, 3.5–4 mm. long.

DISTRIBUTION. West Irian, Territory of New Guinea and Papua; montane rain forests, cloud forests and subalpine shrubberies and borders; 1500–3260 meters. See MAP 4.

West Irian. Utakwa River to Mt. Carstensz, Camp 11–13, *Kloss* (*Wollaston Expedition*), 1912–1913 (BM, holotype of *Acronychia murina* Ridley; K, isotype); Mt. Doorman, *Lam 1728* (K, L); Lake Habbema, *Brass 9309* (A, L), *9537* (A, L), *10593* (A, L, LAE); Mt. Hubrecht, *Versteeg 2417* (K, L, U, isosyntypes of *Acronychia wichmannii* Lauterb.); Mt. Wichmann, *Pulle 997* (K, L, U, isosyntypes of *Acronychia wichmannii* Lauterb.), *1015* (K, L, U, isosyntypes of *Acronychia wichmannii* Lauterb.). **Territory of New Guinea.** WESTERN HIGH-

LANDS DISTRICT: McNicoll-Andabare Plateau SW of Laiagam, *Robbins 3327* (CANB); Wabag-Laiagam Road 1 mile SE of Sirunke Mission, *Womersley NGF 15230* (CANB); Ambum-Marimuni Divide, upper Ambum Valley, *Robbins 3075* (CANB); Mur Mur Pass, Lat. 5° 50′ S., Long. 143° 50′ E., *Vandenberg, Katik & Kairo NGF 39850* (BISH, L, LAE, NSW); Tambil-Tomba Road, Nebelyer Divide, *Robbins 473* (CANB); road below Tomba, upper Nebeleyer River, *Robbins 242* (CANB); Minj-Nona Divide, Kubor Range S of Minj, *Pullen 5198* (CANB), *5290* (CANB). EASTERN HIGHLANDS DISTRICT: Daulo, Goroka Subdistrict, *Saunders 853* (CANB); Mt. Elandora, Kratke Mts., *Brass & Collins 32158* (CANB, L, LAE, US). MOROBE DISTRICT: Mt. Sarawaket, *Clemens 5557* (A), *5596* (A), *5772* (A); Mannasat, Cromwell Mts., *Hoogland 9532* (CANB); Spreader Divide NW of Aseki, *Schodde & Craven 4896* (CANB), *4966* (CANB); Mt. Kaindi, *Brass 29584* (CANB, US), *29716* (CANB, US), *Coode et al. NGF 32860* (CANB), *Hartley 13659* (CANB), *Merava & Kairo NGF 17163* (CANB), *Millar NGF 23657* (CANB), *Millar & van Royen NGF 18749* (CANB, K, LAE), *Millar & Womersley NGF 12248* (LAE), *Szent-Ivany BMF 5* (BISH, LAE), *BMF 5A* (BISH, LAE), *Womersley & Sleumer NGF 13906* (L, LAE), *NGF 13918* (CANB, NSW); above Bakaia, about 15 miles SW of Garaina, *Hartley 12738* (CANB). **Papua.** SOUTHERN HIGHLANDS DISTRICT: Lei Camp, SE slope of Mt. Ambua, Lat. 5° 55′ S., Long. 143° 10′ E., *Frodin NGF 26990* (L, LAE, NSW), *NGF 28318* (CANB); Ibiwara & vicinity, *Gillison NGF 25121* (CANB), *NGF 25145* (CANB), *Vink 17198* (CANB); between Margarima River and Ibiwara River, *Vink 17512* (CANB); Mt. Ne, *Frodin NGF 26970* (CANB), *Kalkman 4910* (CANB, UC); Mt. Giluwe, *Schodde 2009* (CANB), *2112* (CANB). CENTRAL DISTRICT: Murray Pass & vicinity, Wharton Range, *Brass 4516* (A, K, L, NY, UC, US), *Foreman NGF 45559* (CANB), *Ridsdale NGF 36952* (CANB), *van Royen NGF 20452* (CANB); main range NW of The Gap, *Carr 15224* (A, L, NY). MILNE BAY DISTRICT: Mt. Mon, E of Bonenau village, Lat. 9° 53′ S., Long. 149° 20′ E., *Pullen 8030* (CANB); Mt. Wadimana, eastern Mt. Simpson Range, *Schodde 5473* (CANB).

The epithet *murina* refers to a mousy odor detected by Ridley from the freshly boiled flowers.

Collections from elevations above about 3000 meters tend to have more coriaceous and often smaller leaflets and larger flowers than those from lower elevations. Thus Lauterbach's syntypes of *Acronychia wichmannii*, all from 3000 meters or higher, appeared quite distinct when compared, as was the case, with only the description of the type of *A. murina*, collected from 2490 meters. Now, with collections available from elevations ranging from 1500 to 3260 meters, it is evident that the former cannot be maintained as a distinct species.

Acronychia emarginata is the closest relative of *A. murina*, the former differing in having predominantly trifoliolate leaves, smaller flowers, and thinner, usually shorter pedicels. There also appear to be different habitat preferences in the two species, the former being collected at elevations ranging from 1760 to 2370 meters compared to a range of 1500 to 3260 meters for the latter. At the only station where both species were collected, Mt. Ne, in the Southern Highlands of Papua, *A. emarginata* was found in *Nothofagus* forest at 2010 meters and *A. murina* in upper montane forest at 2790 meters.

13. **Acronychia emarginata** Lauterb. Bot. Jahrb. **55**: 250. 1917. NEOTYPE: *Pullen 520*, Territory of New Guinea, Eastern Highlands District.

Shrub or small tree to 12 m.; branchlets glabrous, often subtetragonous in younger growth, the angles formed from narrow ridges or very thin wings of decurrent petiole bases. Leaves trifoliolate (occasional leaves unifoliolate); petiole glabrous, 1–3 cm. long; leaflets chartaceous to subcoriaceous, glabrous, elliptic-oblong to obovate to oblanceolate, 1.7–7 cm. long, 0.7–2.8 cm. wide, base cuneate to attenuate, main veins 7–9 on each side of the midrib, apex rounded to obtuse or occasionally emarginate. Inflorescences few-flowered, 1–5.5 cm. long, axes and branches glabrous. Flowers 3.5–4.5 mm. long; pedicels glabrous to glabrate, 2–9 mm. long; sepals glabrous, rounded to obtusely triangular, 0.5 mm. long, 0.8 mm. wide; petals glabrous; disc glabrous, 0.5–1 mm. high, about 1 mm. wide; ovary glabrous, without septicidal fissures; style glabrous throughout or with a few hairs only at the base. Fruits yellowish white to white, drying reddish brown, glabrous, without septicidal fissures, subglobose to elliptic in outline, drying four-lobed, 4–5 mm. wide, base obtuse, often on a stipe about 0.5 mm. high formed from the disc, apex rounded; epicarp drying less than 0.5 mm. thick, semifleshy, without evident mesocarp; endocarp subcartilaginous. Seeds dark reddish brown, 3–4.5 mm. long.

DISTRIBUTION. West Irian, Territory of New Guinea and Papua; montane rain forests from 1760 to 2370 meters.

West Irian. Wissel Lakes & vicinity, *Eyma 5405* (L), *Vink & Schram BW 8674* (L), *BW 8991* (L). **Territory of New Guinea.** EASTERN HIGHLANDS DISTRICT: upper Asaro Valley about 4 miles E of Kwonggi, *Pullen 520* (CANB, neotype). **Papua.** WESTERN DISTRICT: Kiunga Subdistrict, headwaters of Ok Tedi River, *Henty, Foreman & Galore NGF 42824* (CANB). SOUTHERN HIGHLANDS DISTRICT: 6 miles W of Mt. Ne, Tari, *Frodin NGF 28399* (CANB).

Of the six collections at hand, the three from the Wissel Lakes area of West Irian seem to represent a minor variant, all being shrubs with inflorescences 1–2 cm. long, flowers 3.5 mm. long, and pedicels 2–3 mm. long. The three collections from eastern New Guinea are more typical of the species, all being small trees with inflorescences 2.5–5.5 cm. long, flowers 4.5 mm. long, and pedicels 4.5–9 mm. long.

Lauterbach's description, based on a single collection, matches closely the specimen chosen as a neotype. The type, *Ledermann 11845*, from 2070 meters on Schrader Mountain (Madang District, Territory of New Guinea), was apparently destroyed at Berlin during World War II. No isotypes have been seen.

A collection from the Northern District of Papua, *Pullen 5840*, seems closely related to this species but differs in having broader, long-acuminate leaflets. It has immature fruits only, however, and cannot be placed with certainty. In the INDEX TO EXSICCATAE it is listed as *Acronychia* aff. *emarginata*.

14. **Acronychia schistacea** Hartley, sp. nov.

Arbor gracilis usque 4 m. alta vel frutex scandens; ramulis novellis puberulis vel subtiliter pubescentibus; foliis unifoliolatis; petiolo subtiliter pubescenti vel puberulo, mox glabro, 0.6–2 cm. longo; foliolo chartaceo vel subcoriaceo, subtus puberulo vel glabrato, in sicco griseo-viridi vel olivaceo, supra glabro, in sicco schistaceo (saltem ubi novello), elliptico vel subcoriaceo, subtus puberulo vel glabrato, in sicco griseo-viridi vel cuneato, venis primariis utrinsecus costa 8–10, apice acuminato, acumine usque 1.3 cm. longo; inflorescentiis unifloris vel paucifloris, 1–2 cm. longis, axi et ramulis subtiliter pubescentibus; floribus 5–9 mm. longis, pedicellis puberulis vel subtiliter pubescentibus, 1–4 mm. longis; sepalis puberulis, rotundatis, 1–1.2 mm. longis, 1.5–2 mm. latis; petalis glabris; disco glabro, 0.5–0.6 mm. alto, 1.2–2 mm. lato; ovario glabro, sine fissuris septicidalibus; stylo omnino glabro vel tantum basin versus pubescenti; fructibus aurantiacis, in sicco rubiginosis, glabris, sine fissuris septicidalibus, subglobosis, ca. 10 mm. latis, basi et apice rotundatis; epicarpio in sicco minus quam 0.5 mm. crasso, semicarnoso, mesocarpio non evidenti; endocarpio pergamentaceo; seminibus rubiginosis vel nigricantibus, ca. 5 mm. longis. HOLOTYPUS: *Brass 24852* (CANB). FIGURE 6.

DISTRIBUTION. Papua, Milne Bay District; montane rain forests from 1550 to 1600 meters.

Papua. MILNE BAY DISTRICT: Maneau Range, Mt. Dayman, *Brass 22994* (A), *23204* (CANB, US); Goodenough Island, *Brass 24793* (A, LAE), *24828* (A, L, LAE), *24852* (CANB, holotype; US, isotype).

The collections from Mt. Dayman differ from those from Goodenough Island in being climbers with flowers about 5 mm. long and pedicels about 1 mm. long, while the plants of Goodenough Island are small trees with flowers 8–9 mm. long and pedicels about 4 mm. long.

Acronychia schistacea and the next six species, all narrow endemics in the mountains of New Guinea, have probably evolved from a common widespread ancestor. Their apparent interrelationships may seem unlikely, however, when their distributions are considered. Such is the case with *A. schistacea*, which, on morphological grounds, appears to be most closely allied to *A. papuana*, known only from the Vogelkop Peninsula at the opposite end of New Guinea. The former species differs from the latter in having glabrous petioles, smaller fruits, and generally smaller leaves. In both species the tendency for blue-gray leaves is apparent (in dried condition).

15. **Acronychia papuana** Gibbs, Contr. Phytogr. Fl. Arfak Mts. 144. 1917. TYPE: *Gibbs 5958*, West Irian, Arfak Mts.

Small tree; branchlets glabrous. Leaves unifoliolate; petiole glabrous, 0.35–0.8 cm. long; leaflet subcoriaceous, glabrous, usually drying somewhat blue-gray above, especially when young, elliptic, 2.5–6 cm. long,

FIGURE 6. *Acronychia schistacea* Hartley, photograph of type (CANB). FIGURE 7. *Acronychia similaris* Hartley, photograph of type (K).

1.2–2.6 cm. wide, base acute to cuneate, main veins 7–9 on each side of the midrib, apex acuminate, the acumen about 0.7 cm. long. Inflorescences 1- to few-flowered, 0.7–1.3 cm. long, axes and branches glabrous. Flowers about 4.5 mm. long; pedicels glabrous, 2–3.5 mm. long; sepals sparsely puberulent, obtusely deltoid, 0.4 mm. long, 0.8 mm. wide; petals glabrous; disc glabrous, 0.4 mm. high, 1.2 mm. wide; ovary glabrous throughout or with a few hairs only at the apex, without septicidal fissures; style with a few hairs toward the base, otherwise glabrous. Fruits drying dark brown, glabrous, without septicidal fissures, subglobose, about 6 mm. wide, base and apex rounded, epicarp drying less than 0.5 mm. thick, semifleshy, without evident mesocarp; endocarp pergamentaceous. Seeds dark reddish brown, about 4 mm. long.

DISTRIBUTION. Known only from the type collection.

West Irian. VOGELKOP PENINSULA: Arfak Mts., Angi Lakes, 2100 m., *Gibbs 5958* (BM, holotype; K, L, isotypes).

Acronychia papuana is apparently most closely related to *A. arfakensis*, from which it differs in habit and in having larger, acuminate leaflets. Possibly these differences are environmentally induced, but whether this is the case cannot be determined with the few collections at hand.

16. **Acronychia arfakensis** Gibbs, Contr. Phytogr. Fl. Arfak Mts. 144. 1917. TYPE: *Gibbs 5610*, West Irian, Arfak Mts.

Prostrate or erect shrub to 3 m.; branchlets glabrous. Leaves unifoliolate; petiole glabrous, 0.3–0.8 cm. long; leaflet coriaceous, glabrous, elliptic to obovate to suborbicular, 1.4–3 cm. long, 0.6–2.1 cm. wide, base acute to rounded, main veins 6–8 on each side of the midrib, apex acute to rounded. Inflorescences 1- to few-flowered, 0.4–1.2 cm. long, axes and branches glabrate. Flowers about 6 mm. long; pedicels glabrate, about 2 mm. long; sepals glabrate, rounded, 0.6 mm. long, 1 mm. wide; petals glabrous; disc glabrous, 0.5 mm. high, 1.7 mm. wide; ovary glabrous throughout or with a few hairs only at the apex, without septicidal fissures; style glabrous throughout or with a few hairs only at the base. Fruits drying dark reddish brown, glabrous throughout or with scattered hairs only at the apex, without septicidal fissures, subglobose to ellipsoid, about 7 mm. wide, base rounded, apex slightly apiculate; epicarp drying to less than 0.5 mm. thick, semifleshy, without evident mesocarp; endocarp pergamentaceous. Seeds reddish black, about 3.5 mm. long.

DISTRIBUTION. Known only from the type locality; open mountain summit area from 2300 to 2700 meters.

West Irian. VOGELKOP PENINSULA: Arfak Mts., Mt. Koebré, *Gibbs 5610* (BM, holotype), *Gjellerup 1205* (L), *Kanehira & Hatusima 13668* (A), *13721* (A).

17. **Acronychia similaris** Hartley, sp. nov.

Frutex interdum scandens ca. 1 m. altus; ramulis novellis subtiliter pubescentibus; foliis unifoliolatis; petiolo subtiliter pubescenti, mox glabro, 0.5–1.2 cm. longo; foliolo subcoriaceo, subtus subtiliter pubescenti vel glabrato, supra glabro, elliptico vel elliptico-oblongo, 3.5–8 cm. longo, 1.5–3.5 cm. lato, basi obtuso vel cuneato, venis primariis utrinsecus costa 9–10, apice obtuse acuminato, acumine 0.5–1 cm. longo; inflorescentiis paucifloris, ca. 2 cm. longis, axi et ramulis subtiliter pubescentibus; floribus 3.5–4 mm. longis, pedicellis subtiliter pubescentibus, 1–2.5 mm. longis; sepalis puberulis, triangularibus, 0.8 mm. longis, 0.9 mm. latis; petalis abaxialiter puberulis, adaxialiter glabris; disco glabro, ca. 0.5 mm. alto, ca. 1 mm. lato; ovario pubescenti, sine fissuris septicidalibus; stylo basin versus pubescenti, aliter glabro; fructibus albis, in sicco rubiginosis, sparse adpresse pubescentibus, sine fissuris septicidalibus, subglobosis, ca. 6 mm. latis, basi rotundatis, apice apiculatis, apiculo ca. 0.5 mm. longo; epicarpio in sicco minus quam 0.5 mm. crasso, semicarnoso, mesocarpio non evidenti; endocarpio pergamentaceo; seminibus atro-rubiginosis, ca. 3.5 mm. longis. HOLOTYPUS: *van Royen & Sleumer 7910* (K). FIGURE 7.

DISTRIBUTION. Known only from the type locality; primary and secondary montane rain forests at 1650 meters.

West Irian. VOGELKOP PENINSULA: Nettoti Range, Mt. Nettoti, *van Royen & Sleumer 7910* (K, holotype; CANB, isotype), *Versteegh BW 10398* (L).

The epithet *similaris* refers to the close relationship of this species to *Acronychia arfakensis.* The two are distinguishable by the larger leaflets, pubescent petioles, and pubescent ovary and fruit in the former.

The collection *van Royen & Sleumer 7085*, from the Aifat River Valley, Vogelkop Peninsula, appears to be closely related to this species, differing mainly in having trifoliolate leaves. A positive identification is not possible, however, since the flowers (in bud only) are stung and abnormal and there is no fruit.

18. **Acronychia kaindiensis** Hartley, sp. nov.

Arbor parva usque 6 m. alta vel frutex; ramulis novellis puberulis vel subtiliter pubescentibus; foliis unifoliolatis; petiolo puberulo vel subtiliter pubescenti, mox glabro, 0.3–1.5 cm. longo; foliolo subcoriaceo vel coriaceo, glabro (costa interdum puberulo), ovato vel elliptico-oblongo, 3–7 cm. longo, 1.2–3 cm. lato, basi acuto vel rotundato, venis primariis utrinsecus costa 9–11, apice obtuso vel obtuse vel subacute acuminato, acumine usque 0.7 cm. longo; inflorescentiis unifloris vel paucifloris, 0.7–2 cm. longis, axi et ramulis puberulis vel subtiliter pubescentibus; floribus 7–8.5 mm. longis, pedicellis puberulis vel subtiliter pubescentibus, 2–3.5 mm. longis; sepalis puberulis vel subtiliter adpresse pubescentibus, obtuse triangularibus, 1–1.4 mm. longis, 1.5 mm. latis; petalis abaxialiter subtiliter adpresse pubescentibus, adaxialiter sparse pubescentibus vel glabris; disco glabro, ca. 0.7 mm. alto, ca. 1.5 mm. lato; ovario dense pubescenti, sine fissuris septicidalibus; stylo basin versus dense pubescenti, aliter glabro; fructibus albis, in sicco rubiginosis, sparse pubescentibus, sine fissuris septicidalibus, ambitu ellipsoidalibus vel subglobosis, ± 4-lobatis, 6–10 mm. latis, basi truncatis vel rotundatis, apice rotundatis vel apiculatis, apiculo usque ca. 2.5 mm. longo; epicarpio in sicco minus quam 0.5 mm. crasso, semicarnoso, mesocarpio non evidenti; endocarpio subcartilagineo; seminibus atro-rubiginosis vel nigricantibus, 3.5–4 mm. longis. HOLOTYPUS: *Millar NGF 23669* (L). FIGURE 8.

DISTRIBUTION. Known only from the type locality; primary and secondary montane rain forests from 1800 to 2100 meters.

Territory of New Guinea. MOROBE DISTRICT: Edie Creek-Mt. Kaindi area, *Brass 29563* (CANB, US), *Hartley 11682* (CANB), *Hartley leg. Sayers 12610* (CANB), *Kairo & Streimann NGF 30851* (CANB), *Kanis & Coode NGF 40171* (L, LAE), *Millar NGF 23654* (L, LAE), *NGF 23669* (L, holotype; LAE, *isotype*), *Ridsdale NGF 30251* (L, LAE), *Sayers NGF 19939* (LAE), *Streimann NGF 30848* (BRI, CANB), *Womersley NGF 24501* (CANB), *Womersley & Sleumer NGF 13938* (LAE).

Acronychia kaindiensis is apparently closely related to *A. similaris*, but it differs in having larger fruits and flowers.

A flowering collection from Lake Trist about 35 miles southeast of Mt. Kaindi (*Henty NGF 29069*) may be best placed here, although differing in having glabrous petioles and smaller flowers with almost entirely glabrous ovaries. It is listed in the INDEX TO EXSICCATAE as *Acronychia* cf. *kaindiensis*.

19. **Acronychia normanbiensis** Hartley, sp. nov.

Arbor usque 10 m. alta; ramulis glabris; foliis unifoliolatis; petiolo glabro, 0.2–0.5 cm. longo; foliolo coriaceo, glabro, late elliptico vel obovato vel suborbiculari, 3.5–7 cm. longo, 2.5–5 cm. lato, basi obtuso vel rotundato, venis primariis utrinsecus costa 7–8, apice rotundato vel interdum obtuso; inflorescentiis paucifloris, 2–3 cm. longis, axi et ramulis glabratis; floribus ca. 6.5 mm. longis, pedicellis glabris vel puberulis, ca. 3 mm. longis; sepalis puberulis, late rotundatis, 0.8 mm. longis, 1.5 mm. latis; petalis abaxialiter subtiliter adpresse pubescentibus, adaxialiter glabris; disco glabro, ca. 0.5 mm. alto, ca. 1.5 mm. lato; ovario dense pubescenti, sine fissuris septicidalibus; stylo basin versus pubescenti, aliter glabro; fructibus luteis, in sicco rubiginosis, sparse pubescentibus, mox glabris, sine fissuris septicidalibus, subpyriformibus, ca. 8 mm. latis, basi obtusis, apice rotundatis; epicarpio in sicco minus quam 0.5 mm. crasso, semicarnoso, mesocarpio non evidenti; endocarpio subcartilagineo; seminibus nigricantibus, ca. 3.5 mm. longis. HOLOTYPUS: *Brass 25746* (US). FIGURE 9.

DISTRIBUTION. Known only from the type locality; stunted mountain summit rain forest; 820–950 meters.

Papua. MILNE BAY DISTRICT: Normanby Island, Mt. Pabinama, *Brass 25746* (US, holotype; A, L, LAE, isotypes), *25787* (A, L, LAE).

8

9

FIGURE 8. *Acronychia kaindiensis* Hartley, photograph of type (L). FIGURE 9. *Acronychia normanbiensis* Hartley, photograph of type (US).

Acronychia normanbiensis is probably quite closely related to *A. kaindiensis*, although the highly modified leaves of the former give that species a very different appearance. The flowers and fruits of the two plants are remarkably similar.

The collection *Brass 25759*, from the type locality, almost certainly belongs here but is listed in the INDEX TO EXSICCATAE as *Acronychia* cf. *normanbiensis* since the flowers are abnormal. Some of the leaflets in this collection are larger (to 10 cm. long) than in the collections of *A. normanbiensis* and have petioles to 2 cm. long.

20. **Acronychia brassii** Hartley, sp. nov.

Frutex usque 3 m. altus; ramulis novellis glabris vel subtiliter pubescentibus; foliis unifoliolatis; petiolo glabro vel subtiliter pubescenti, mox glabro, 0.5–2.5 cm. longo; foliolo subcoriaceo vel coriaceo, glabro, oblanceolato et 3–4 plo longiore quam lato vel interdum obovato vel elliptico, 3–15 cm. longo, 1.2–4.8 cm. lato, basi cuneato vel interdum acuto vel obtuso, venis primariis utrinsecus costa 8–15, apice obtuse vel acute acuminato (acumine usque ca. 1 cm. longo) vel interdum obtuso; inflorescentiis unifloris vel paucifloris, 0.7–1.5 cm. longis, axi et ramulis glabratis vel sparse adpresse pubescentibus; floribus 3.5–4.5 mm. longis, pedicellis glabratis vel sparse adpresse pubescentibus, 1–2 mm. longis; sepalis puberulis vel sparse adpresse pubescentibus, rotundatis vel obtuse triangularibus, 0.5–0.8 mm. longis, 0.8–1.3 mm. latis; petalis abaxialiter glabris vel puberulis, adaxialiter glabris, in fructu saepe semipersistentibus; disco glabro, 0.3–0.4 mm. alto, 1–1.2 mm. lato; ovario omnino glabro vel apice sparse pubescenti, sine fissuris septicidalibus; stylo omnino glabro vel tantum basi sparse pubescenti; fructibus albis, in sicco atro-rubiginosis, glabris, sine fissuris septicidalibus, ambitu subglobosis, ± 4-lobatis, 7–10 mm. latis, basi et apice rotundatis; epicarpio in sicco minus quam 0.5 mm. crasso, semicarnoso, mesocarpio non evidenti; endocarpio subcartilagineo; seminibus nigricantibus, ca. 3.5 mm. longis. HOLOTYPUS: *Robbins 924* (CANB). FIGURE 10.

DISTRIBUTION. Territory of New Guinea; montane rain forests from 1650 to 2280 meters.

Territory of New Guinea. WESTERN HIGHLANDS DISTRICT: Wankl village, about 5 km. SE of Mt. Hagen, *Hoogland & Pullen 5800* (CANB); Mt. Kum, near Mt. Hagen, *Womersley NFG 9427* (A, CANB); Jimmi Divide, *Robbins 599* (CANB); Nondugl & vicinity, *Womersley NGF 4364* (A, LAE), *NGF 4490* (A, LAE), *NGF 4873* (LAE); Kubor Ranges between Kuli and Minj, *Robbins 539* (CANB); Kubor Range, Uinba, Nona-Minj Divide, *Vink 16517* (CANB, P). EASTERN HIGHLANDS DISTRICT: Chuave-Chimbu Road near Kumul Mission, *Womersley NGF 14125* (LAE); Daulo-Chuave Road, *McKee & Floyd NGF 6340* (LAE); Mt. Michael, *Brass 31365* (CANB, US), *Womersley NGF 11383* (CANB); Purosa, Okapa area, *Brass 31633* (L, LAE, US), *31724* (LAE); near Wanatabi, about 15 miles SW of Okapa, *Hartley 13143* (CANB); Kainantu-

10

11

FIGURE 10. *Acronychia brassii* Hartley, photograph of type (CANB). FIGURE 11. *Acronychia aberrans* Hartley, photograph of type (BRI).

Okapa Road, *Stauffer & Sayers 5606* (L, LAE, NSW), *Womersley NGF 24642* (CANB), *NGF 37188* (L, LAE); Nemuka village, near Kainantu, *Sayers 167* (CANB); near Barola, Kainantu Road, *Robbins 924* (CANB, holotype); ridge above Noreikora Swamp, Kainantu Subdistrict, *Wheeler ANU 5881* (CANB); Saboa, Andandara village, Kainantu Subdistrict, *Streimann NGF 23987* (LAE); Aiyura, *McKee 1286* (L), *Womersley, van Royen & Versteegh NGF 5998* (A, L, LAE), *Womersley NGF 6026* (A, L, LAE); 10 miles SE of Obura, Lat. 6° 40′ S., Long. 146° E., *Hays 159* (LAE).

This species, *Acronychia brassii*, is probably most closely related to *A. kaindiensis*, but the two differ quite strongly in size and shape of leaves and pubescence of ovary and fruit.

21. **Acronychia wilcoxiana** (F. Muell.) Hartley, comb. nov.

Pleiococca wilcoxiana F. Muell. Frag. Phytogr. Austral. 9: 117. 1875. TYPE: *Anonymous* (*?Wilcox*), eastern Australia, between the Clarence and Brisbane Rivers.

Errerana wilcoxiana (F. Muell.) O. Ktze. Rev. Gen. Pl. 937. 1891 (*nomen illegit.*).

Small tree to about 9 m.; branchlets glabrous. Leaves unifoliolate; petiole glabrous, 0.6–3 cm. long; leaflet chartaceous to subcoriaceous, glabrous, elliptic to elliptic-oblong or occasionally suboblanceolate or subspatulate, 7–21 cm. long, 2.5–9 cm. wide, base narrowly cordate to obtuse to cuneate, main veins 11–14 on each side of the midrib, apex rounded to obtusely acuminate, the acumen to 0.5 cm. long. Inflorescences many-flowered, 4–6.5 cm. long, axes glabrous, branches glabrous to short-pubescent. Flowers 8.5–10 mm. long; pedicels glabrous, 0.5–3 mm. long; sepals glabrous, broadly elliptic to suborbicular, 1.2–2.7 mm. long, 1.6–3 mm. wide; petals glabrous; disc glabrous, about 0.6 mm. high, about 2 mm. wide; ovary glabrous throughout or with dense, ascending pubescence at the apex, 4- to 8-carpellate, with septicidal fissures extending for at least one half the length; style densely ascending pubescent toward the base, otherwise glabrous. Fruits maturing white, drying reddish brown or blackish, glabrous throughout or with a tuft of hairs at the apex, 4- to 8-carpellate, with broad septicidal fissures extending for at least one half the length, broadly ovate, conical or subglobose in outline, 4- to 8-lobed, 8–15 mm. wide, base truncate, apex obtuse to acute; epicarp drying less than 0.5 mm. thick, semifleshy, without evident mesocarp; endocarp cartilaginous or subcartilaginous. Seeds dark reddish brown, about 4.5 mm. long.

DISTRIBUTION. Fraser Island, Queensland, south to Gosford, New South Wales; coastal scrub except for a few inland localities in New South Wales. See MAP 3.

Queensland. WIDE BAY DISTRICT: Fraser Island, *Baxter 870* (BRI), *Petrie*, June, 1917 (BRI), *Webb & Tracey 6330* (BRI); Noosa River ca. 23 miles NE of Gympie, *Smith 12118* (BRI); Gympie, *Kenny*, 1905 (BRI), *Shirley* (BRI); Imbil, *McGillivray 499* (NSW); Kin Kin, *Smith*, April, 1944 (BRI); Lake Cootharaba, 11 miles NE of Cooroy, *Keys 67* (BRI); Tewantin Forestry Reserve, *Harrold*, April 1, 1964 (BRI). MORETON DISTRICT: Eumundi, *Bailey & Gunn*, June, 1895

(BRI); Blackall Range, *Field Naturalists Club Excursion*, April, 1918 (BRI, NSW); Yandina-Coolum Road, *Williams*, March, 1967 (BRI); One Mile Creek, Lawnton, *Blake 2323* (BRI), February 18, 1932 (BRI). **New South Wales.** Tweed Heads, *Kenny* (BRI); Murwillumbah, *Watts*, April, 1957 (NSW 127148); Myocum, Mullumbimby District, *Flowers*, July, 1964 (NSW 127149); mouth of Brunswick River, Brunswick Heads, *Schodde & Hayes 3555* (AD, CANB); Cape Byron, *Betche*, March, 1896 (NSW 127150); Richmond River, *Fawcett*, 1877 (MEL), 1878 (MEL), *Fletcher*, February 26, 1892 (NSW 127152); Port Macquarie, *Cunningham 49* (K); Hastings River, *Beckler* (K); Comboyne, *Chisholm*, June, 1934 (NSW 126979); Forster, *Rudder*, March 15, 1892 (NSW 127154), February, 1895 (NSW 127155); Tiona Park via Forster, *Monk*, July, 1933 (NSW 127156); upper Williams River, *Fraser & Vickery*, January 8, 1934 (NSW 127158), *Rodway*, August, 1935 (NSW); Seal Rocks, *Briggs*, August 1, 1964 (NSW 127157), *Rodd & Jones 684* (NSW); Wyong, *Boorman*, March, 1899 (NSW 127159); Ourimbah State Forest, *de Beuzeville*, March, 1918 (NSW 127160); Narara, near Gosford, *Froggatt*, June, 1910 (NSW 126991). **Cultivated.** NEW SOUTH WALES: Elizabeth Bay House, Sydney, *Joyce*, June, 1917 (NSW 127163); Sydney Botanic Gardens, *Boorman*, April, 1918 (NSW 127162), *Chippendale*, February 15, 1951 (NSW 127161). Without definite locality: between the Clarence and Brisbane Rivers, *Anonymous* (*?Wilcox*) (MEL, holotype of *Pleiococca wilcoxiana* F. Muell.; BRI, isotype).

The variable number of carpels in specimens of *Acronychia wilcoxiana*, the type species of the monotypic genus *Pleiococca*, is unique in *Acronychia*, all of the other species being consistently four-carpellate. There are no other differences between the two genera, however, and therefore it seems impractical to recognize *Pleiococca* as a distinct genus. Examination of the specimens at hand revealed that the carpel number generally varies in single collections from four to six, five to seven, or six to eight. The four-carpellate condition occurs most frequently. I have not seen the nine-carpellate condition mentioned by F. M. Bailey (Queensl. Fl. 1: 207, 208. 1899). Neither have I seen evidence that the carpels are tardily dehiscent in fruit, as is stated by Mueller in the original description. Whether they are or not, however, the seeds are still typical of *Acronychia*, lacking the shiny, crustaceous outer testa found in genera, such as *Euodia* and *Melicope*, with dehiscent carpels.

The relationship of *Acronychia wilcoxiana* to other species of the genus is difficult to determine. In the leaves and branchlets it seems rather close to *A. acidula*, but in the ovary and fruit the two are quite different, the latter species lacking septicidal fissures.

The distribution in New South Wales, with a disjunction between the Richmond River and Port Macquarie, is puzzling but does not appear to be taxonomically significant.

22. **Acronychia acidula** F. Muell. Phytogr. Austral. 4: 154. 1864. TYPE: *Dallachy*, Queensland, North Kennedy District, Rockingham Bay.

Jambolifera acidula (F. Muell.) O. Ktze. Rev. Gen. Pl. 1: 102. 1891.
Acronychia superba Domin, Bibliot. Bot. 22(89): 295. 1927. TYPE: *Domin 3406*, February, 1910, Queensland, Cook District, Allumbah (Yungaburra).

Medium to large tree to about 27 m.; branchlets glabrous. Leaves unifoliolate; petiole glabrous, 2–7 cm. long; leaflet chartaceous to subcoriaceous, glabrous, elliptic, 8–23.5 cm. long, 4.3–12 cm. wide, base rounded to acute or occasionally cuneate, main veins 10–14 on each side of the midrib, apex obtuse to obtusely acuminate, the acumen to 1 cm. long. Inflorescences several- to many-flowered, 5–9 cm. long, axes and branches glabrous. Flowers about 9.5 mm. long; pedicels glabrous, 2–2.5 mm. long; sepals glabrous, broadly rounded, 1.5 mm. long, 2.5 mm. wide; petals glabrous; disc glabrous, about 0.5 mm. high, about 3 mm. wide; ovary glabrous, without septicidal fissures; style densely pubescent toward the base, otherwise glabrous. Fruits white to cream, drying brown or blackish, glabrous, without septicidal fissures, subglobose to broadly conical in outline, 4-lobed when mature, 10–14 mm. wide, base usually truncate, apex rounded to acute; epicarp drying less than 0.5 mm. thick, semifieshy and with spongy-crustaceous mesocarp differentiated between the locules; endocarp cartilaginous, densely resin-dotted. Seeds blackish, about 4.5 mm. long.

DISTRIBUTION. Northeast Queensland from the Atherton Tableland south to the Eungella Range west of Mackay; upland rain forests to about 900 meters. See MAP 3.

Queensland. COOK DISTRICT (all on the Atherton Tableland): Danbulla, *Webb & Tracey 7222* (BRI); Tinaroo Range, Danbulla Road, *Moriarty 819* (BRI); Atherton, *Betche*, August, 1901 (NSW 127100); Wongabel, *Tardent x277* (BRI); Barron, *Webb 2088* (CANB); East Barron, *Webb 749* (CANB); Bromfield Crater, *Brass 33485* (BRI); Yungaburra, *Domin 3406* (PR, holotype of *Acronychia superba* Domin), *White*, January, 1918 (BRI); Lake Eacham, *Briggs 1925* (NSW), *Helms 1204* (A); Peeramon, *Horsey* (BRI); Gadgarra, *Francis*, March, 1932 (BRI), *Kajewski 1049* (BRI, NSW, NY), *White 1564* (A, BRI, NSW); Malanda, *Blake 15157* (BRI); Glen Allyn, Malanda, *Hayes* (BRI). NORTH KENNEDY DISTRICT: Rockingham Bay, *Dallachy* (MEL, holotype of *Acronychia acidula* F. Muell.; K, NSW, isotypes). SOUTH KENNEDY DISTRICT: Dalrymple Heights & vicinity, *Clemens*, July-November, 1947 (BRI, CANB), August-October, 1947 (BRI, MICH, NY, UC); Eungella Range via Mackay, *Francis*, October 3–12, 1922 (BRI). Without definite locality: *Webb 5043* (CANB).

A report of this species from New South Wales (Maiden & Betche, Census New South Wales Pl. 118. 1916) was probably based on misidentified *Acronychia wilcoxiana.*

Domin refers to *Acronychia acidula* in his description of *A. superba* but does not explain why he considers the two distinct. To me they are obviously conspecific.

23. **Acronychia aberrans** Hartley, sp. nov.

Arbor parva vel mediocris; ramulis glabris, internodiis novellis 4-angulatis et concave compressis; foliis unifoliolatis; petiolo glabro, 1.5–5.5 cm. longo; foliolo coriaceo, glabro, elliptico vel late oblanceolato, 6–23 cm. longo, 3–10.3 cm. lato, basi cuneato vel interdum obtuso, venis primariis utrinsecus costa 10–13, apice obtuso; inflorescentiis paucifloris, ca. 4 cm. longis, axi et ramulis glabris; floribus 8 mm. longis, pedicellis glabratis, ca. 5 mm. longis; sepalis glabratis, late triangularibus, 1.2 mm. longis, 1.5 mm. latis; petalis abaxialiter pubescentibus, apicem versus adaxialiter pubescentibus; disco glabro, 0.6 mm. alto, 2.3 mm. lato; ovario apice dense pubescenti, aliter glabro, sine fissuris septicidalibus; stylo basin versus dense pubescenti, aliter glabro; fructibus luteolis, in sicco brunneis, glabris, sine fissuris septicidalibus, subglobosis vel late pyriformibus, 13–18 mm. latis, basi anguste truncatis, apice rotundatis vel parum depressis; epicarpio in sicco 2.5–3.5 mm. crasso, mesocarpio semicarnoso; endocarpio cartilagineo; seminibus pallide rubiginosis, longitudinaliter rugosis, 6–7 mm. longis. HOLOTYPUS: *Hyland 998* (BRI). FIGURE 11.

DISTRIBUTION. Cook District, Queensland; rain forests from 720 to about 900 meters.

Queensland. COOK DISTRICT: Mt. Spurgeon, *White 10678* (A, BM, BRI, P, UC); Atherton Tableland, Forest Reserve 310, *Hyland 998* (BRI, holotype), *1996* (BRI), *2191* (BRI), *6703* (CANB).

The epithet *aberrans* refers to the unusual branchlets of this species, which, in the internodes, are concavely compressed and sharply tetragonous.

Acronychia acidula may be the closest relative of *A. aberrans*, having rather similar fruits and leaves, but the relationship does not appear to be particularly close.

24. **Acronychia vestita** F. Muell. Frag. Phytogr. Austral. **4**: 155. 1864. TYPE: *Dallachy*, June 1, 1864, Queensland, North Kennedy District, Rockingham Bay, Dalrymple Creek.

Jambolifera vestita (F. Muell.) O. Ktze. Rev. Gen. Pl. **1**: 102. 1891.

Tree to 21 m.; younger branchlets densely to rather sparsely short-pubescent. Leaves unifoliolate; petiole sparsely to densely pubescent, 1–4 cm. long; leaflet chartaceous, sparsely to rather densely pubescent below, glabrous above or with sparse hairs on the midrib, usually elliptic or elliptic-obovate but grading to elliptic-oblong or obovate, 8–23 cm. long, 3.8–11.5 cm. wide, base narrowly cordate to obtuse, main veins 10–16 on each side of the midrib, usually rather pronounced below and impressed above, apex rounded to obtusely acuminate, the acumen to 1 cm. long. Inflorescences many-flowered, 5–7 cm. long, axes and branches sparsely to rather densely short-pubescent. Flowers 6.5–8 mm. long; pedicels glabrate to sparsely short-pubescent, 3–4.5 mm. long; sepals glabrous, obtusely triangular to broadly rounded, 0.6–0.7 mm. long, 1.2–1.5 mm. wide; petals glabrous; disc glabrous, 0.3–0.5 mm. high, 1.2–1.4 mm. wide; ovary densely pubescent at the apex, otherwise glabrous, without septicidal fissures; style densely spreading-pubescent toward the base, otherwise glabrous. Fruits pale yellow, drying reddish brown or blackish brown, glabrous throughout or pubescent only at the apex, without septicidal fissures, irregularly roughened and often rather deeply and irregularly constricted and/or fissured, pyriform, subglobose or elliptic in outline, often slightly 4-lobed, about 15 mm. wide, base obtuse to truncate, apex acute to rounded, occasionally apiculate, the apiculum to 3 mm. long; epicarp drying 1-2 mm. thick, with subwoody mesocarp; endocarp cartilaginous. Seeds dark reddish brown, 5-5.5 mm. long.

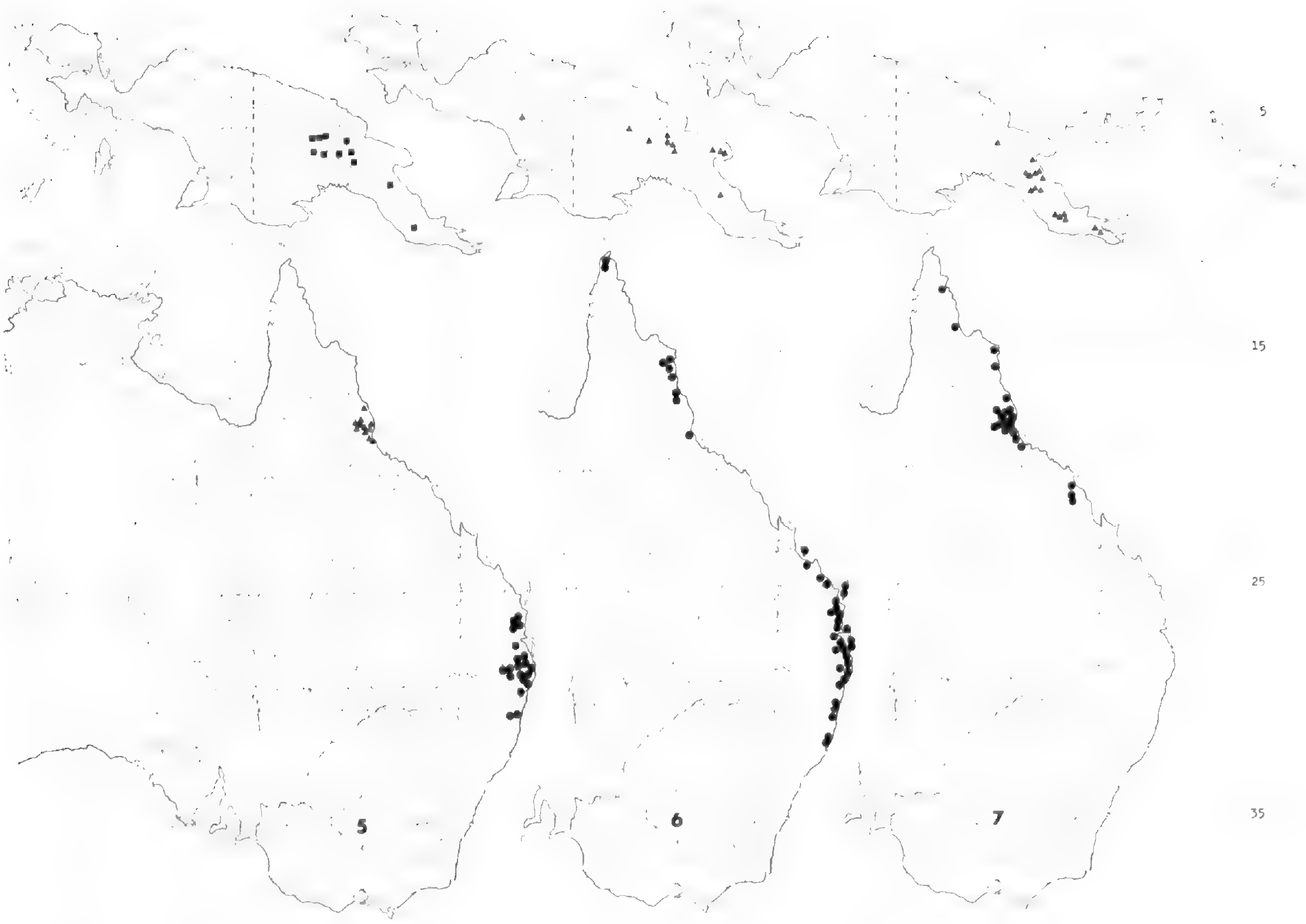
DISTRIBUTION. Northeast Queensland from Cairns south to Rockingham Bay; rain forests to about 900 meters. See MAP 5.

Queensland. COOK DISTRICT: Cairns, *Bailey* (NSW); Behana Creek, *Bailey, Meston's Bellenden Ker Expedition*, 1899 (BRI); Rocky Creek, Atherton District, *Bailey*, June 29, 1899 (BRI); Atherton, *Bailey* (BRI, NSW), *Webb 5052* (CANB); Barron River, *Cowley 49b* (BRI); Gadgarra, *Francis*, March, 1932 (BRI), *Forest Officer Fuller 42G* (BRI), *Jones 1507* (CANB), *White 1565* (A, BRI, NSW); Glen Allyn, Malanda, *Hayes* (BRI); Boonjie, *Jones 3880* (CANB), *Kajewski 1210* (A, BRI, NY); Miriwinni, near Mt. Bartle Frere, *Webb & Tracey 6678* (BRI); Russell River, *Sayer*, 1886 (MEL); Johnstone River, *Michael 150* (BRI); Berner Creek, via Innisfail, *Cumming 68* (A); Innisfail, *Michael 131* (GH); Gregory Falls, lower Palmerston via Innisfail, *Webb & Tracey 6835* (BRI); Lacey's Creek, El Arish, *Jones 1269* (CANB), *3193* (CANB). NORTH KENNEDY DISTRICT: Clump Point, near Cardwell, *White* (NSW 127097); Mission Beach, *McKean MB 1* (BRI, CANB); near Cardwell, *White* (NSW 127098); Flagstone Creek, Rockingham Bay, *Dallachy*, August 18, 1869 (MEL); Mackay (now Tully) River, Rockingham Bay, *Dallachy*, March 28, 1866 (MEL, W); Dalrymple Creek, Rockingham Bay, *Dallachy*, June 1, 1864 (MEL, holotype; BM, BRI, K, NSW, isotypes); Dalrymple Gap, Rockingham Bay, *Dallachy*, July 10, 1865 (MEL); Rockingham Bay, *Dallachy*, April 12, 1866 (MEL). Without definite locality: *Webb 2089* (CANB).

This species, *Acronychia vestita*, is probably most closely related to *A. acidula*, but differs strongly in having roughened and often constricted and/or fissured fruits. Also, the branchlets and leaves are pubescent in *A. vestita*, glabrous in *A. acidula*.

25. **Acronychia smithii** Hartley, sp. nov.

Arbor parva vel mediocris usque 15 m. alta; ramulis glabris; foliis trifoliolatis; petiolo glabro, 1.5-4 cm. longo; foliolis chartaceis vel subcoriaceis, glabris, ellipticis vel elliptico-oblongis vel oblanceolatis, 5.5-11 cm. longis, 1.8-4 cm. latis, basi cuneatis vel attenuatis, venis primariis utrinsecus costa 10-12, apice obtusis vel obtuse acuminatis, acumine usque 0.7 cm. longo; inflorescentiis paucifloris, 1.5-5 cm. longis, axi et ramulis puberulis; floribus ca. 9.5 mm. longis, pedicellis puberulis, 2.5-4 mm. longis; sepalis dense adpresse pubescentibus, late rotundatis vel orbicularibus, 2 mm. longis, 2.5-3.5 mm. latis; petalis abaxialiter dense adpresse pubescentibus, adaxialiter glabris; disco glabro, ca. 0.5 mm. alto, ca. 2 mm. lato; ovario omnino pubescenti vel tantum apicem versus pubescenti, sine fissuris septicidalibus; stylo basin versus pubescenti, aliter glabro; fructibus albis, in sicco rubiginosis, omnino adpresse pubescentibus vel tantum



MAPS 5–7. Distributions of *Acronychia* species: 5. *A. montana* Hartley (squares), *A. vestita* F. Muell. (triangles), and *A. pubescens* (F. M. Bailey) C. T. White (dots); 6. *A. pullei* Lauterb. (triangles) and *A. imperforata* F. Muell. (dots); 7. *A. trifoliolata* Zoll. & Mor. var. *microcarpa* Hartley (triangles) and *A. acronychioides* (F. Muell.) Hartley (dots).

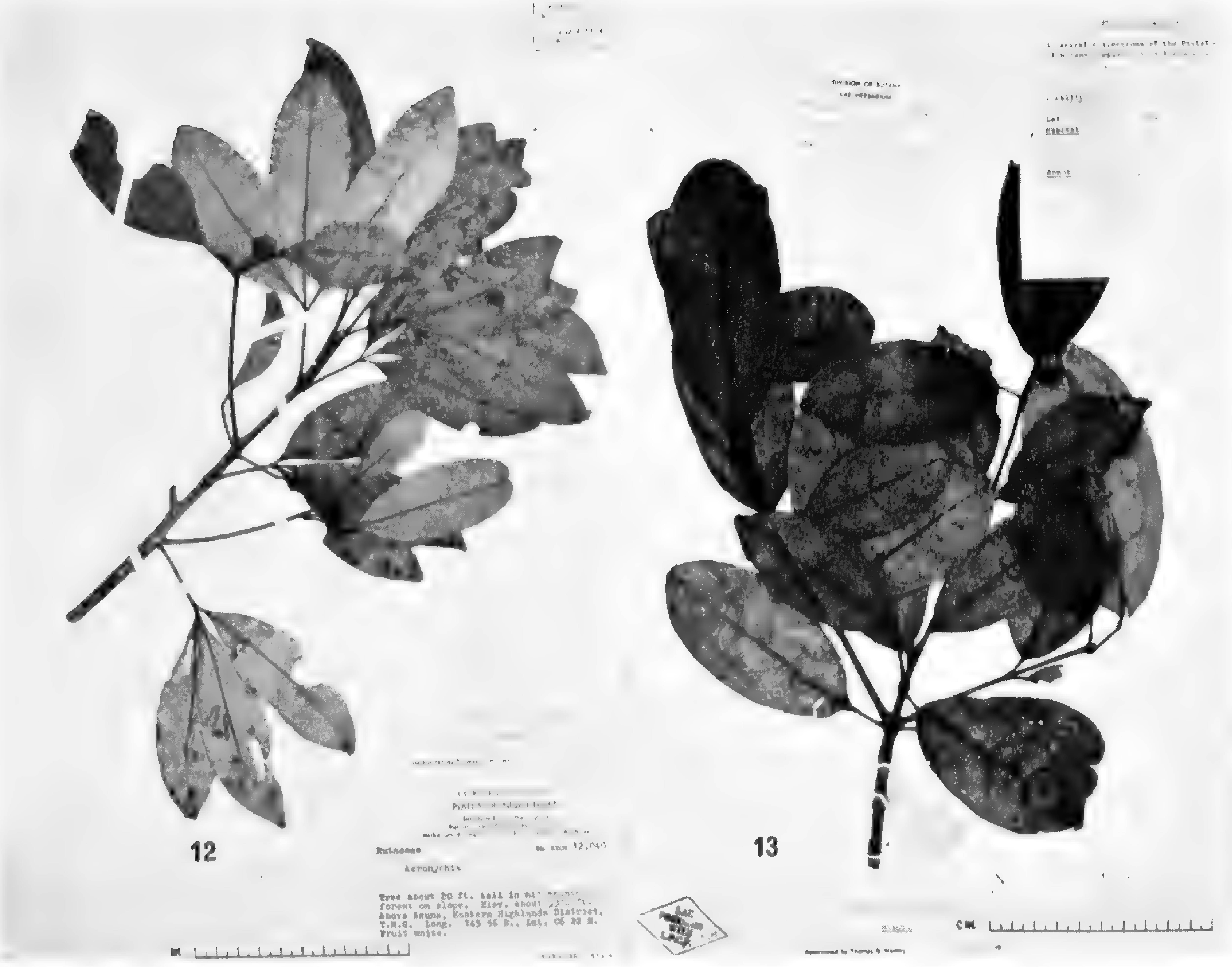


FIGURE 12. *Acronychia smithii* Hartley, photograph of type (CANB). FIGURE 13. *Acronychia foveata* Hartley, photograph of type (LAE).

apicem versus adpresse pubescentibus, sine fissuris septicidalibus, ovoideis vel subglobosis, ca. 12 mm. latis, basi rotundatis vel subtruncatis, apice obtusis vel acutis; epicarpio in sicco ca. 1 mm. crasso, mesocarpio semicarnoso; endocarpio cartilagineo; seminibus rubiginosis, ca. 3.5 mm. longis. HOLOTYPUS: *Hartley 12040* (CANB). FIGURE 12.

DISTRIBUTION. Eastern Highlands District, Territory of New Guinea; montane rain forests from 1560 to 1950 meters.

Territory of New Guinea. EASTERN HIGHLANDS DISTRICT: Kumul Mission, Chauve-Chimbu Road, *Womersley NGF 14127* (A, CANB, K); Mt. Michael, *Womersley NGF 11720* (CANB); Aiyura, *Smith NGF 1105* (BISH, BRI, LAE); Aiyura Range, *Womersley NGF 6049* (CANB); above Akuna, *Hartley 12040* (CANB, holotype).

On the basis of fruit structure, *Acronychia smithii* and *A. foveata*, which follows, appear to be rather closely related. They can easily be distinguished, however, the former having trifoliolate and the latter unifoliolate leaves.

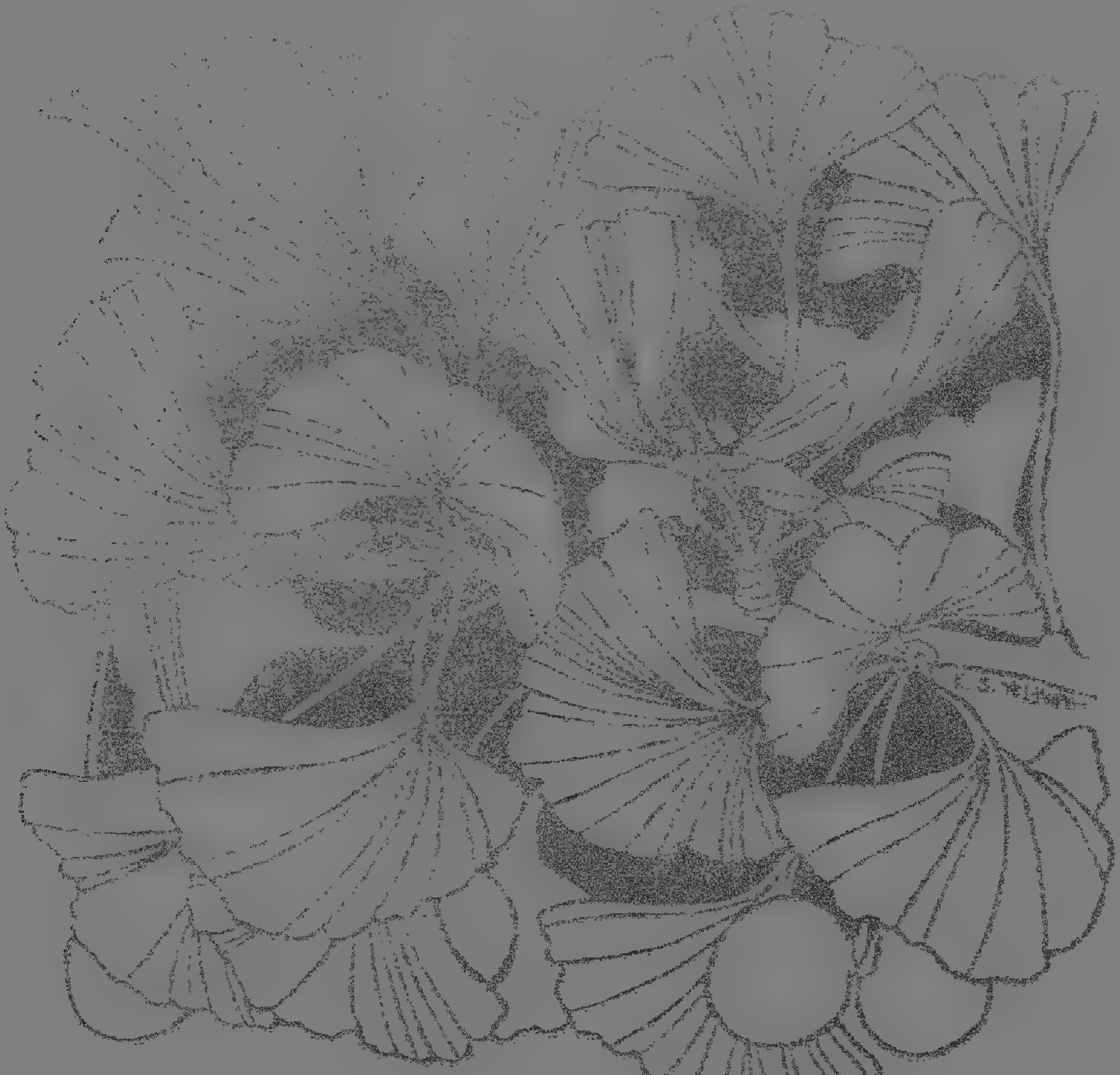
Acronychia smithii is named in honor of Lindsay S. Smith (1917-1970), Queensland and New Guinea rain forest botanist.

(*To be concluded*)

H32

JOURNAL OF THE

ARNOLD ARBORETUM



Volume 55 HARVARD UNIVERSITY Number 4

MISSOURI BOTANICAL
DEC 10 1974
GARDEN LIBRARY

US ISSN 0004-2625

Journal of the Arnold Arboretum

Published quarterly in January, April, July, and October by the Arnold Arboretum, Harvard University.

Subscription price $16.00 per year.

Subscriptions and remittances should be sent to Ms. Kathleen Clagett, Arnold Arboretum, 22 Divinity Avenue Cambridge, Massachusetts 02138, U.S.A. Claims will not be accepted after six months from the date of issue.

Volumes I-XLV, reprinted, and some back numbers of volumes 46-50 are available from the Kraus Reprint Corporation, Route 100, Millwood, New York 10546, U.S.A.

EDITORIAL STAFF
B. G. Schubert, Editor
C. E. Wood, Jr.
S. A. Spongberg

CIRCULATION
K. Clagett

Printed at the Harvard University Printing Office, Boston, Massachusetts

COVER: *Ginkgo biloba* L., the maidenhair tree, so-called from the fancied resemblance of its leaves to those of the maidenhair fern. In China it has also been called the silver apricot, from the hard inner seed coat which is silvery when cleaned and vaguely resembles an apricot pit, and the duck-foot tree, from the resemblance of the leaves to the webbed feet of ducks.

The drawing for the cover and the devices for the back cover and reprints were planned and drawn by Karen Stoutsenberger Velmure from specimens taken from a tree cultivated in the Arnold Arboretum of Harvard University.

We want to assure the purists among our readers that our *Ginkgo* does not have leaves with open parallel venation. We think, however, that an exact reproduction of the dense dichotomous veins would have produced a much less dramatic design.

Second-class postage paid at Boston, Massachusetts

JOURNAL
OF THE
ARNOLD ARBORETUM

VOL. 55 OCTOBER 1974 NUMBER 4

A REVISION OF THE GENUS ACRONYCHIA (RUTACEAE)*

THOMAS G. HARTLEY

26. **Acronychia foveata** Hartley, sp. nov.

Arbor parva usque 10 m. alta; ramulis novellis glabratis; foliis unifoliolatis; petiolo glabro vel glabrato, 1–2.5 cm. longo; foliolo chartaceo vel subcoriaceo, glabro, obovato vel elliptico vel elliptico-oblongo, 7–13 cm. longo, 3–6 cm. lato, basi rotundato vel obtuso vel cuneato, venis primariis utrinsecus costa 7–10, apice obtuso vel obtuse acuminato, acumine usque 0.5 cm. longo; inflorescentiis unifloris, ca. 1.5 cm. longis, axi glabratis; floribus 8.5–9 mm. longis, pedicellis glabratis, 1.5–2.5 mm. longis; sepalis puberulis, late rotundatis, 1 mm. longis, 2 mm. latis; petalis abaxialiter puberulis, adaxialiter glabris; disco glabro, 0.4 mm. alto, 1.2 mm. lato; ovario apice dense pubescenti, aliter glabro, sine fissuris septicidalibus; stylo basin versus dense pubescenti, aliter glabro; fructibus luteolis, in sicco rubiginosis, manifeste foveatis, apice sparse pubescentibus, aliter glabris, sine fissuris septicidalibus, late ovoideis, ca. 12 mm. latis, basi disco persistenti annulari 1.5 mm. alto, 6 mm. lato, apice obtusis vel acutis; epicarpio in sicco 2–3 mm. crasso, mesocarpio spongioso-crustaceo vel sublignoso; endocarpio subcartilagineo; seminibus nigricantibus, ca. 5 mm. longis. HOLOTYPUS: *Vandenberg, Katik & Kairo NGF 39820* (LAE). FIGURE 13.

DISTRIBUTION. Territory of New Guinea (Morobe District) and Papua (Southern Highlands District); montane rain forests from 1950 to 2400 meters.

Territory of New Guinea. MOROBE DISTRICT: Bulldog Track, Edie Creek, *Sayers NGF 21201* (CANB). **Papua.** SOUTHERN HIGHLANDS DISTRICT: 7 miles from Kagaba Camp toward Mendi, Lat. 6° 5′ S., Long. 143° 50′ E., *Vandenberg, Katik & Kairo NGF 39820* (LAE, holotype; L, isotype); Ialibu, *Womersley & Woolliams NGF 37080* (L, LAE), *NGF 37090* (LAE).

The outstanding characteristics of *Acronychia foveata* are the heavily pitted fruit and persistent, annular disc.

Acronychia aberrans and *A. vestita*, both endemics of north Queensland,

---

* Continued from volume 55, page 523.

have rather similar fruits to *A. smithii* and *A. foveata* and possibly are relicts of the ancestral stock from which the latter species evolved.

27. **Acronychia cartilaginea** Hartley, sp. nov.

Arbor 10 m. alta; ramulis novellis tomentosis; foliis unifoliolatis; petiolo tomentoso, 2.5–4.5 cm. longo; foliolo subcoriaceo, subtus dense pubescenti, supra praeter costa pubescenti glabro, elliptico, 12–20 cm. longo, 5–8 cm. lato, basi obtuso, venis primariis utrinsecus costa 15, subtus prominentibus, supra parum impressis, apice breviter acuminato, acumine usque ca. 0.8 cm. longo; inflorescentiis paucifloris, ca. 5.5 cm. longis, axi et ramulis tomentosis; floribus ca. 9 mm. longis, pedicellis dense pubescentibus, 5–10 mm. longis; sepalis dense pubescentibus, rotundatis, 2 mm. longis, 2 mm. latis; petalis apicem versus abaxialiter pubescentibus, adaxialiter sparse pubescentibus; disco glabro, 0.3 mm. alto, 1.5 mm. lato; ovario dense pubescenti, fissuris septicidalibus apicalibus; stylo basi pubescenti, aliter glabro; fructibus in sicco brunneis, sparse pubescentibus, fissuris septicidalibus apicalibus, ambitu late ellipticis, 4-angulatis, ca. 12 mm. latis, basi truncatis, apice rotundatis breviter apiculatis; epicarpio in sicco 0.5 mm. crasso, mesocarpio spongioso; endocarpio crasse cartilagineo; seminibus atro-rubiginosis, ca. 4.5 mm. longis. HOLOTYPUS: *Frodin NGF 28411* (LAE). FIGURE 14.

DISTRIBUTION. Known only from the type collection.

Papua. SOUTHERN HIGHLANDS DISTRICT: 6.5 miles W of Mt. Ne, mixed beech forest, 2010 m., *Frodin NGF 28411* (LAE, holotype; CANB, isotype).

I am at a loss to recognize the nearest relative of *Acronychia cartilaginea*, clearly marked by its pubescent leaves and unusually thick, cartilaginous endocarp. I have placed it here in the sequence because of its general similarity, in the fruit, to *Acronychia vestita*, *A. smithii*, and *A. foveata*. It could just as well, however, be placed next to *Acronychia reticulata*.

28. **Acronychia pubescens** (F. M. Bailey) C. T. White, Proc. Roy. Soc. Queensl. **50**: 68. 1939.

Acronychia melicopoides F. Muell. var. *lasiantha* F. Muell. Frag. Phytogr. Austral. **7**: 145. 1871. TYPE: *C. Moore*, New South Wales, Clarence River.
Melicope pubescens F. M. Bailey, Queensl. Dept. Agr. Bot. Bull. **9**: 9. 1891. LECTOTYPE: *Field Naturalists Club Excursion*, March 1, 1891, Queensland, Moreton District, Yandina.
Melicope pubescens F. M. Bailey var. *superba* Domin, Bibliot. Bot. **22**(89): 843. 1927. TYPE: *Domin 5638*, March, 1910, Queensland, Moreton District, Tamborine Mt.

Small to medium tree to about 15 m.; younger branchlets puberulent to tomentose. Leaves trifoliolate (occasional leaves unifoliolate, or, in a few collections, leaves entirely unifoliolate); petiole tomentose to glabrate, 0.8–8.5 cm. long; leaflets chartaceous to subcoriaceous, usually pubescent

14

15

FIGURE 14. *Acronychia cartilaginea* Hartley, photograph of type (LAE). FIGURE 15. *Acronychia wabagensis* Hartley, photograph of type (A).

below, at least on the midrib and veins, glabrous to sparsely pubescent above, elliptic-oblong to narrowly or broadly oblanceolate or occasionally elliptic, 5.5–22 cm. long, 1.8–7.7 cm. wide, base cuneate or occasionally attenuate or obtuse, main veins 9–13 on each side of the midrib, apex acuminate (the acumen to 2.3 cm. long) or occasionally obtuse. Inflorescences few- to many-flowered, 3–5.5 cm. long, axes and branches densely pubescent to tomentose. Flowers 6.5–10 mm. long; pedicels tomentose, 1–4.5 mm. long; sepals tomentose, obtusely triangular to suborbicular, 1–2.5 mm. long, 1.5–2.5 mm. wide; petals densely appressed-pubescent to tomentose abaxially, glabrous adaxially, semipersistent in fruit; disc glabrous, 0.3–0.7 mm. high, 1.6–2.5 mm. wide; ovary pubescent throughout or pubescent only in the apical one third to one fourth, with septicidal fissures extending for about one half the length; style densely spreading-pubescent toward the base, otherwise glabrous. Fruits yellow, drying dark reddish brown, pubescent throughout or only toward the apex, with septicidal fissures extending for at least one third the length, occasionally with two longitudinal wings to about 8 mm. wide on each carpel, ellipsoid to subglobose, 12–20 cm. wide, base rounded to truncate, apex rounded to acute; epicarp drying less than 0.7 mm. thick, semifleshy, without evident mesocarp; endocarp cartilaginous. Seeds reddish brown, 4–4.5 mm. long.

ILLUSTRATION. Bailey, F. M., Comprehensive Cat. Queensl. Pl. *t. 59.* 1912 (as *Melicope pubescens*).

DISTRIBUTION. Southeast Queensland and northeast New South Wales; rain forests to 1080 meters. See MAP 5.

Queensland. DARLING DOWNS DISTRICT: The Head, Killarney, *Jones*, February, 1960 (BRI); Spring Creek Plateau, *Goy & Smith 359* (BRI); E of Bald Mt., about 23 miles E of Warwick, *Smith 11456* (BRI, CANB); Mt. Superbus, *Whaite*, August 22, 1949 (NSW 127066). MORETON DISTRICT: Eumundi, *Bailey & Simmonds*, May, 1892 (BRI, K, MEL, NSW, UC), *Kandler*, August, 1931 (BRI), *Simmonds*, June, 1895 (A); Blackall Range, *Field Naturalists Club Excursion*, March 1, 1891 (BRI, MEL), April, 1918 (BRI, NSW); Yandina, *Field Naturalists Club Excursion*, March 1, 1891 (BRI, lectotype; MEL, isotype), *Shirley* (A); Eudlo, *Bailey*, March, 1891 (A); Mt. Glorious, *Clemens*, January, 1945 (BRI, GH, MICH, NY, UC), *Hoogland 5236* (CANB), *White 12071* (A, BRI, US); Tamborine Mt., *Clemens*, March, 1947 (BRI, GH, MICH, UC), *Domin 5638* (PR, holotype of *Melicope pubescens* F. M. Bailey var. *superba* Domin), *Longman & White*, February, 1917 (BRI), *Scortechini 15* (MEL), *Shirley*, December, 1915 (NSW), *Simmonds*, October, 1909 (BRI, US), *White 3338* (A), August 17, 1927 (A); Mudgeeraba, *Ledward*, August, 1937 (BRI); 4 miles S of Canungra, *Williams*, January 24, 1971 (BRI); Lamington National Park, *Johnson*, May 21, 1951 (NSW 127068), *Schodde 3376* (CANB), *Smith 10934* (BRI), *Smith & Webb 3595* (CANB), *Tryon & White*, February, 1920 (A, NSW), *Webb 2105* (CANB), *White 6026* (A, BRI, NY, UC), January, 1912 (BRI); Springbrook, *Clemens 43057* (A, US), *White 6264* (BRI). **New South Wales.** Acacia Creek, near Killarney, Queensland, *Boorman 25* (NSW), *Constable*, May 15, 1947 (NSW 127071), *Dunn 125* (NSW), *Jones 1373* (CANB), *White 12514* (BRI); Richmond River, *Simmonds*, April, 1897 (BRI); Tweed River area, *Betche*, April, 1896 (NSW 127074); Wardrop Valley Road, *Buchanan*, August 6, 1966 (NSW 127073); upper Crystal Creek 7 miles NW of Murwillumbah, *Clark, Pickard & Coveny 1590* (NSW); 3 miles S of Murwillumbah, *Buchanan*, April 16, 1966 (NSW 127075); Mt. Lindsay, NE of Kyogle, *Constable*, May 25, 1949 (NSW 10541); near Kyogle, *Jones*, June, 1943 (NSW); Whian Whian State Forest, *Cheel*, September 6, 1926 (NSW 127077), *Johnson & Constable*, June 10, 1957 (A, NSW 42343), *Olsen 301* (NSW), *Webb & Tracey*, 1953–1958 (BRI, CANB); Lismore, *Baeuerlen*, April, 1895 (A, K); Wollongbar, *Baeuerlen*, March, 1893 (NSW 127078); Marshall Falls, near Alstonville, *Tanner*, September, 1911 (NSW 127079 & 127080); Tintenbar, *Baeuerlen*, April, 1896 (NSW 127151), *531* (MEL), *781* (U); Clarence River, *Moore* (MEL, holotype of *Acronychia melicopoides* F. Muell. var. *lasiantha* F. Muell.; K, NSW 127083, isotypes), *Wilcox*, November, 1875 (MEL); NE of Glen Innes District, end of new Grafton Road deviation, *Turner*, February, 1955 (NSW 127081); Poverty Point, New England, *Stuart* (MEL, NSW); Dorrigo & vicinity, *Cleland*, January 23, 1918 (AD), *Fraser*, January 23, 1934 (NSW 127090 & 127091), *Heron*, June, 1910 (NSW 127089), *Maiden*, December, 1893 (NSW 127086), *Tindale*, March 3, 1944 (NSW 127088), *Walker*, June, 1917 (NSW 127087), *White 7555* (BRI), *Williams*, August, 1963 (NSW 127085); Coffs Harbour, *Boorman*, May 26, 1909 (NSW 127084).

Melicope pubescens var. *superba* was previously placed in the synonymy of *Acronychia pubescens* by White, Proc. Roy. Soc. Queensl. **50**: 68. 1939.

Acronychia pubescens does not appear to be very closely related to any of the other species of the genus. In characters of the fruit it is similar to a number of other apparently primitive species, such as *A. suberosa*, *A. baeuerlenii*, and *A. wilcoxiana*, but vegetatively it is quite distinct. A New Guinean species, *A. wabagensis*, has similarly fissured, pubescent fruits and may be the nearest relative.

The lectotype of *Melicope pubescens* is one of two collections (the other being *Field Naturalists Club Excursion*, March 1, 1891, Yandina) cited in the original description.

29. **Acronychia wabagensis** Hartley, sp. nov.

Arbor 12 m. alta; ramulis glabris; foliis trifoliolatis (foliis infrequentibus unifoliolatis); petiolo glabro, 2–4.5 cm. longo; foliolis subcoriaceis, glabris, ellipticis vel oblanceolatis, 7.5–15 cm. longis, 3–6.3 cm. latis, basi cuneatis vel attenuatis, venis primariis utrinsecus costa 9–11, apice obtusis vel obtuse acuminatis, acumine usque 1 cm. longo; inflorescentiis paucifloris, 4 cm. longis, axi et ramulis puberulis; floribus 6.5–7 mm. longis, pedicellis puberulis, ca. 5 mm. longis; sepalis puberulis, rotundatis, 1 mm. longis, 2 mm. latis; petalis abaxialiter subtiliter adpresse pubescentibus, adaxialiter sparse adpresse pubescentibus; disco glabro, 0.5 mm. alto, 2 mm. lato; ovario pubescenti, fissuris septicidalibus fere ad basin extensis; stylo basin versus dense pubescenti, aliter glabro; fructibus albis, in sicco rubiginosis, sparse adpresse pubescentibus, fissuris septicidalibus fere ad basin extensis, ambitu subglobosis, valde 4-lobatis, ca. 7 mm. latis, basi subtruncatis, apice apiculatis, apiculo 0.5–1 mm. longo; epicarpio in sicco ca. 0.5 mm. crasso, mesocarpio spongioso-crustaceo; endocarpio cartilagineo; seminibus immaturis. HOLOTYPUS: *Womersley NGF 11247* (A). FIGURE 15.

DISTRIBUTION. Known only from the type collection.

Territory of New Guinea. WESTERN HIGHLANDS DISTRICT: Porget logging area 12 miles N of Wabag, 2100 m., *Womersley NGF 11247* (A, holotype; BISH, L, LAE, MEL, NSW, isotypes).

A rare species, *Acronychia wabagensis* is distinguished by having pubescent ovary and fruit with septicidal fissures extending almost to the base. As is mentioned above, *A. pubescens* may be its nearest relative.

30. **Acronychia intermedia** Hartley, sp. nov.

Arbor magna; ramulis glabris; foliis trifoliolatis; petiolo glabro, 3–5 cm. longo; foliolis subcoriaceis, glabris, elliptico-oblongis vel sublanceolatis, 8–19 cm. longis, 3.5–5.5 cm. latis, basi cuneatis vel attenuatis, venis primariis utrinsecus costa 12–14, apice obtusis; inflorescentiis ca. 15-floris, ca. 5.5 cm. longis, axi et ramulis glabris; floribus 15–17 mm. longis, pedicellis glabris, 2–5 mm. longis; sepalis glabris vel glabratis, late rotundatis, 1.5–2 mm. longis, 2.5–2.7 mm. latis; petalis abaxialiter puberulis, adaxialiter glabris; disco glabro, 0.6 mm. alto, 2.2 mm. lato; ovario apice pubescenti, aliter glabro, fissuris septicidalibus 1/3 vel 1/2 longitudine extensis; stylo basin versus pubescenti, aliter glabro; fructibus (non plane maturi) in sicco rubiginosis, apice pubescentibus, aliter glabris, fissuris septicidalibus ca. 1/3 longitudine extensis, subglobosis, 10 mm. latis, basi truncatis, apice rotundatis; epicarpio in sicco ca. 2 mm. crasso, mesocarpico spongioso-crustaceo; endocarpio cartilagineo; seminibus non visis. HOLOTYPUS: *Brass 22918* (US). FIGURE 16.

DISTRIBUTION. Known only from the type collection.

Papua. MILNE BAY DISTRICT: Mt. Dayman, Maneau Range, tall mossy forest, 2100 m., *Brass 22918* (US, holotype; CANB, isotype).

The epithet *intermedia* refers to the fact that this species is morphologically more or less intermediate between *Acronychia wabagensis* and *A. montana*. It differs from the former in having ovary and fruit pubescent only at the apex. From the latter it differs in having trifoliolate leaves.

31. **Acronychia montana** Hartley, sp. nov.

Arbor parva vel mediocris usque 17 m. alta; ramulis glabris; foliis unifoliolatis; petiolo glabrato, 0.8–3.5 cm. longo; foliolo subcoriaceo, glabro, elliptico vel elliptico-oblongo, 5.5–16 cm. longo, 2.5–8 cm. lato, basi rotundato vel obtuso vel cuneato, venis primariis utrinsecus costa 9–12, apice rotundato vel obtuso vel obtuse acuminato, acumine usque 1 cm. longo; inflorescentiis paucifloris, 2–4 cm. longis, axi et ramulis glabris vel puberulis; floribus 12–16 mm. longis, pedicellis glabris vel puberulis, 3–7 mm. longis; sepalis glabris vel puberulis, late rotundatis, 1.5–2 mm. longis,

16

17

FIGURE 16. *Acronychia intermedia* Hartley, photograph of type (US). FIGURE 17. *Acronychia montana* Hartley, photograph of type (CANB).

2-3.5 mm. latis; petalis abaxialiter glabris vel puberulis, adaxialiter glabris; disco glabro, 0.5-1 mm. alto, 1.6-2 mm. lato; ovario omnino glabro vel tantum apice pubescenti, fissuris septicidalibus ca. 1/2 longitudine extensis; stylo basin versus sparse vel dense pubescenti, aliter glabro; fructibus luteolis, in sicco rubiginosis, omnino glabris vel tantum apice pubescentibus, fissuris septicidalibus ca. 1/2 longitudine extensis, ambitu subglobosis, saepe acute 4-angulatis, 8-9 mm. latis, basi truncatis, apice rotundatis vel breviter apiculatis; epicarpio in sicco 1-1.5 mm. crasso, mesocarpio spongioso-crustaceo; endocarpio cartilagineo; seminibus rubiginosis, ca. 4.5 mm. longis. HOLOTYPUS: *Pullen 440* (CANB). FIGURE 17.

DISTRIBUTION. Territory of New Guinea and Papua; montane rain forests and cloud forests, 2100-2850 meters. See MAP 5.

Territory of New Guinea. WESTERN HIGHLANDS DISTRICT: McNicoll-Andabare Plateau SW of Laiagam, *Robbins 3328* (CANB); headwaters of the Lagaip River, *Hoogland & Schodde 7557* (CANB); Sirunki, E of Laiagam and N of Yamara, *Walker ANU 759* (CANB); 4 miles SW of Kompiam, *Flenley ANU 2804* (CANB); Kubor Range above Kuli, *Robbins 1120* (CANB). EASTERN HIGHLANDS DISTRICT: Mt. Wilhelm & vicinity, *Brass 30377* (CANB), *Gillison & Streimann NGF 30680* (CANB); Marafunga & vicinity, about 20 miles NW of Goroka, *Buderus NGF 23903* (CANB), *Collins W991* (LAE), *Grubb & Edwards 34* (LAE), *Hartley 13228* (CANB), *Millar NGF 40660* (CANB), *Tuckwell 1* (LAE); Asaro-Mairifutica Divide ½ mile S of Daulo Camp, *Pullen 440* (CANB, holotype). MOROBE DISTRICT: Wau, *McAdam 238* (BRI, LAE). **Papua.** SOUTHERN HIGHLANDS DISTRICT: Lei Camp on track to Mt. Ambua, *Frodin NGF 28102* (CANB); Kagaba Camp, Mt. Hagen-Mendi Road, Lat. 6° 5′ S., Long. 143° 50′ E., *Vandenberg et al. NGF 40052* (CANB). CENTRAL DISTRICT: below The Gap, *Carr 15026* (A, K, L, NY), *15027* (A, K, L, NY), *15148* (A, L, NY).

A rather common species in the mountains of eastern New Guinea, *Acronychia montana* may be distinguished from its closest relatives, *A. intermedia*, *A. carrii*, and *A. pullei*, by its unifoliolate leaves.

32. **Acronychia carrii** Hartley, sp. nov.

Arbor mediocris vel magna usque 30 m. alta; ramulis glabris; foliis trifoliolatis; petiolo glabro, 2.7-5 cm. longo; foliolis subcoriaceis, glabris, ellipticis vel elliptico-oblongis, 4-11.5 cm. longis, 1.8-5 cm. latis, basi cuneatis vel attenuatis, venis primariis utrinsecus costa 9-13, apice obtusis vel obtuse acuminatis, acumine usque 0.5 cm. longo; inflorescentiis paucifloris, 4.5-6 cm. longis, axi et ramulis glabris; floribus 10 mm. longis, pedicellis glabris, 2-3 mm. longis; sepalis glabris, late rotundatis, 2 mm. longis, 2.5-3 mm. latis; petalis glabris; disco glabro, 0.8 mm. alto, 2 mm. lato; ovario glabro, sine fissuris septicidalibus; stylo basin versus pubescenti, aliter glabro; fructibus luteis, in sicco rubiginosis, glabris, sine fissuris septicidalibus, subglobosis, ca. 10 mm. latis, basi et apice rotundatis; epicarpio in sicco minus quam 0.5 mm. crasso, semicarnoso, mesocarpio non evidenti; endocarpio subcartilagineo; seminibus atro-brunneis vel nigricantibus, ca. 4 mm. longis. HOLOTYPUS: *C. E. Carr 15249* (CANB). FIGURE 18.

18

19

FIGURE 18. *Acronychia carrii* Hartley, photograph of type (CANB). FIGURE 19. *Acronychia gurakorensis* Hartley, photograph of type (US).

DISTRIBUTION. Central District, Papua; montane rain forests from 1800 to 1950 meters.

Papua. CENTRAL DISTRICT: Uniri River, *Carr 15249* (CANB, holotype); Alola, *Carr 13681* (CANB), *14179* (L, LAE), *14180* (L).

Acronychia carrii is apparently most closely related to *A. pullei*, differing in having shorter pedicels and smaller leaves. There also may be a fairly close relationship to *A. trifoliolata* var. *microcarpa* (q.v.).

33. **Acronychia pullei** Lauterb. Bot. Jahrb. **55**: 250, 251. 1918; Nova Guinea (Bot.) **14**: 144. 1924. TYPE: *Pulle 645*, West Irian, Mt. Hellwig.

Small to medium tree to 27 m.; branchlets glabrous. Leaves trifoliolate (occasional leaves unifoliolate); petiole glabrous, 1.5–6 cm. long; leaflets subcoriaceous to coriaceous, glabrous, elliptic to obovate to broadly oblanceolate, 5.5–20 cm. long, 2.5–7.5 cm. wide, base obtuse to attenuate, main veins 10–14 on each side of the midrib, apex rounded to obtuse or occasionally obtusely acuminate, the acumen to 0.3 cm. long. Inflorescences usually many-flowered, 4.5–8.5 cm. long, axes and branches glabrous. Flowers 9–13 mm. long; pedicels glabrous to finely pubescent, 4–13 mm. long; sepals glabrate to puberulent, broadly rounded, 1–1.5 mm. long, 2–2.2 mm. wide; petals glabrous to sparsely appressed-pubescent abaxially, glabrous to appressed-pubescent adaxially; disc glabrous, 0.6–1 mm. high, 2–2.8 mm. wide; ovary glabrous, without septicidal fissures; style glabrous. Fruits yellow, drying blackish, gabrous, without septicidal fissures, subglobose to subturbinate, 9–10 mm. wide, base rounded to narrowly truncate, apex rounded or obtusely apiculate, the apiculum to 1 mm. long; epicarp drying less than 0.5 mm. thick, semifleshy, without evident mesocarp; endocarp subcartilaginous. Seeds gray-brown, about 4 mm. long.

DISTRIBUTION. West Irian, Territory of New Guinea and Papua; montane rain forests and cloud forests; 1750–3210 meters. See MAP 6.

West Irian. Mt. Hellwig, *Pulle 645* (K, L, U, isotypes). **Territory of New Guinea.** WESTERN HIGHLANDS DISTRICT: 8 miles NW of Wabag, *Saunders 1045* (CANB); lower slopes of Mt. Hagen, *Saunders 630* (CANB, US). EASTERN HIGHLANDS DISTRICT: Mt. Wilhelm, *Brass 30443* (CANB, US), *Stone LAE 53239* (LAE), *Wade ANU 7335* (CANB); Marafunga, about 20 miles NW of Goroka, *Hartley 13262* (CANB), *Millar NGF 40671* (CANB), *NGF 40699* (CANB); Daulo Camp, *Pullen 487* (CANB, US). MOROBE DISTRICT: Mt. Sarawaket, *Clemens 8342* (A); Sambanga, *Clemens 7750* (A, L); Busu River, *Clemens 6274* (A). **Papua.** CENTRAL DISTRICT: Mt. Tafa, *Brass 4883* (A, NY).

The type collection of *Acronychia pullei*, from West Irian, differs from the remaining material of this species, all of which is from eastern New Guinea, in having fewer-flowered inflorescences with slightly longer, more slender flowers. In other respects the specimens from the two areas are reasonably similar.

34. **Acronychia gurakorensis** Hartley, sp. nov.

Arbor parva usque 6 m. alta; ramulis glabris; foliis trifoliolatis (foliis frequentibus unifoliolatis); petiolo glabro, 3.5–7 cm. longo; foliolis chartaceis, glabris, ellipticis, 9–16.5 cm. longis, 4–6.2 cm. latis, basi cuneatis vel attenuatis, venis primariis utrinsecus costa 8–12, apice acuminatis, acumine usque 1.5 cm. longo; inflorescentiis unifloris vel paucifloris, 2.5–4 cm. longis, axi et ramulis glabratis; floribus 7–8 mm. longis, pedicellis glabratis, ca. 3.5 mm. longis; sepalis glabris, obtuse triangularibus, 1 mm. longis, 1.7 mm. latis; petalis glabris; disco glabro, 1 mm. alto, 1.8 mm. lato; ovario pubescenti, sine fissuris septicidalibus; stylo basin versus pubescenti, aliter glabro; fructibus luteis, in sicco atrorubiginosis, mox glabris, sine fissuris septicidalibus, subglobosis, ca. 20 mm. latis, basi rotundatis, apice parum depressis; epicarpio in sicco minus quam 0.5 mm. crasso, semicarnoso, mesocarpio non evidenti; endocarpio subcartilagineo; seminibus nigricantibus, ca. 5 mm. longis. HOLOTYPUS: *Brass 29484* (US). FIGURE 19.

DISTRIBUTION. Known only from the type locality; foothill rain forests from 450 to 640 meters.

Territory of New Guinea. MOROBE DISTRICT: Gurakor, *Brass 29484* (US, holotype); Buko Creek just S of Gurakor, *Hartley 9704* (CANB), *Millar NGF 14443* (CANB).

Acronychia gurakorensis is apparently closely related to *A. macrocalyx* and *A. dimorphocalyx*, the three having in common unusually large fruits with semifleshy epicarp. *Acronychia gurakorensis* is distinguished from the other two species by its smaller sepals.

35. **Acronychia macrocalyx** Hartley, sp. nov.

Arbor 13 m. alta; ramulis glabris; foliis trifoliolatis; petiolo glabro, 4–7 cm. longo; foliolis subcoriaceis, glabris, ellipticis, 9.5–17 cm. longis, 5–8.5 cm. latis, basi cuneatis, venis primariis utrinsecus costa 10–11, apice obtusis; inflorescentiis paucifloris, 6–8 cm. longis, axi et ramulis glabris vel glabratis; floribus 10 mm. longis, pedicellis puberulis, ca. 3.5 mm. longis; sepalis puberulis, in fructu deciduis, late ovatis vel suborbicularibus, 4.5–5 mm. longis, 4–5 mm. latis; petalis basin versus abaxialiter subtiliter pubescentibus, adaxialiter glabris; disco glabro, 0.3 mm. alto, 2.4 mm. lato; ovario apice pubescenti, aliter glabro, sine fissuris septicidalibus; stylo basin versus pubescenti, aliter glabro; fructibus in sicco atro-brunneis, apice subtiliter pubescentibus, aliter glabris, sine fissuris septicidalibus, subglobosis, ca. 18 mm. latis, basi et apice rotundatis; epicarpio in sicco ca. 0.8 mm. crasso, semicarnoso, mesocarpio non evidenti; endocarpio subcartilagineo; seminibus (non plane maturi) rubiginosis, ca. 4 mm. longis. HOLOTYPUS: *Henty NGF 29016* (BRI). FIGURE 20.

DISTRIBUTION. Known only from the type collection.

Territory of New Guinea. MOROBE DISTRICT: Lake Trist, mossy fagaceous forest, 1620 meters, *Henty NGF 29016* (BRI, holotype; CANB, LAE, isotypes).

20

FIGURE 20. *Acronychia macrocalyx* Hartley, photograph of type (BRI).

Acronychia macrocalyx differs from all other species of the genus in having sepals that are deciduous early in fruit. This is an unusual character in this instance since at the stage of dehiscence the sepals are quite thick and not at all withered as might be expected.

36. **Acronychia dimorphocalyx** Hartley, nom. & stat. nov.

Acronychia trifoliolata Zoll. & Mor. var. *pauciflora* Val. Bull. Dept. Agr. Ind. Neerl. **10:** 23. 1907. TYPE: *Atasrip* (*Wichmann Expedition*) *175*, West Irian, Temena River.

Small tree 2 m.; branchlets glabrous. Leaves trifoliolate (occasional leaves unifoliolate); petiole glabrous, 3–12 cm. long; leaflets chartaceous to subcoriaceous, glabrous, elliptic-oblong to narrowly oblanceolate, 12.5–22 cm. long, 3.5–5.5 cm. wide, base cuneate to attenuate, main veins 11–15 on each side of the midrib, apex obtuse to acuminate, the acumen to 1 cm. long. Inflorescences few-flowered, 5.5–6 cm. long, axes and branches glabrate to finely pubescent. Flowers 5.5 mm. long; pedicels finely pubescent, 0.5 mm. long; sepals puberulent, strongly dimorphic, the outer pair suborbicular, 4 mm. long, 4.5 mm. wide, the inner pair obovate, 3.5 mm. long, 2.5 mm. wide; petals glabrate abaxially, glabrous adaxially, semipersistent in fruit; disc glabrous, 0.3 mm. high, 1.5 mm. wide; ovary densely pubescent, without septicidal fissures; style pubescent toward the base, otherwise glabrous. Fruits yellowish green, drying reddish brown, glabrous at maturity, without septicidal fissures, subglobose, about 20 mm. wide, base and apex rounded; epicarp drying less than 0.5 mm. thick, semifleshy, without evident mesocarp; endocarp pergamentaceous. Seeds not seen.

DISTRIBUTION. West Irian, widely disjunct from the Sorong District to the Temena River; lowland rain forests.

West Irian. Sorong District, *van Royen 3329* (CANB); Temena River, *Atasrip* (*Wichmann Expedition*) *175* (L, isotype of *Acronychia trifoliolata* Zoll. & Mor. var. *pauciflora* Val.).

The two collections of this species differ greatly in leaf size: *van Royen 3329* has petioles to 12.5 cm. long and leaflets to 22 cm. long, while the *Atasrip* collection has petioles to 6 cm. long and leaflets to 12.5 cm. long. Flowers and fruit (the latter immature in the *Atasrip* collection) of the two collections are so similar, however, that it seems best to consider them as one species.

A new name is required here since the epithet *pauciflora* is pre-empted at the level of species in *Acronychia*.

37. **Acronychia trifoliolata** Zoll. & Mor. in Zoll. Nat. Geneesk. Arch. Neerl. Ind. **2:** 585. 1845. TYPE: *Zollinger 2530*, Java, Tengger prope Gebok Klakka.

This species is extremely variable, having three nearly allopatric varieties (see MAPS 7 and 8) and a number of lesser entities, especially in the typical variety. Although the fruits of the varieties differ greatly at the extremes, there is, nevertheless, nearly complete intergradation in this character. There are no clear-cut flower differences.

KEY TO THE VARIETIES

1. Fruits 5–18 mm. wide, epicarp drying 0.3–4 mm. thick, with woody, subwoody, or spongy-crustaceous mesocarp.
    2. Sepals 0.7–1 mm. long; fruits 5–15 mm. wide, epicarp drying 0.3–2 mm. thick, with woody or subwoody mesocarp; disc glabrous to pubescent. . . . . 37a. var. *trifoliolata.*
    2. Sepals 1–1.5 mm. long; fruits 10–18 mm. wide, epicarp drying 2.5–4 mm. thick, with woody to spongy-crustaceous mesocarp; disc glabrous. . . . . 37b. var. *ampla.*
1. Fruits 4–6 mm. wide, epicarp drying less than 0.3 mm. thick, semifleshy, without evident mesocarp. . . . . 37c. var. *microcarpa.*

37a. **Acronychia trifoliolata** Zoll. & Mor. var. **trifoliolata.**

Acronychia halmaheirae Miq. Ann. Mus. Lugd.-Bat. 3: 245. 1867. TYPE: *Teysmann HB 5651*, Moluccas, Halmahera.

Jambolifera trifoliata O. Ktze. Rev. Gen. Pl. 1: 102. 1891 (based on *Acronychia trifoliolata* Zoll. & Mor.).

Acronychia andrewsi Baker f. in Andrews, Monog. Christmas Isl. 174. 1900. TYPE: *Andrews*, 1897, Christmas Island.

Small to medium tree to 25 m.; branchlets glabrous. Leaves trifoliolate; petiole glabrous or occasionally glabrate, 1.8–6.5 cm. long; leaflets chartaceous to subcoriaceous, glabrous, elliptic to elliptic-oblong or occasionally obovate to oblanceolate, 5.5–19.5 cm. long, 1.7–7 cm. wide, base cuneate to attenuate, main veins 9–16 on each side of the midrib, apex acuminate (the acumen to 1.5 cm. long) or occasionally obtuse or rounded. Inflorescences few- to many-flowered, 2–9 cm. long, axes and branches glabrous to puberulent. Flowers 4.5–8 mm. long; pedicels glabrous to puberulent or occasionally finely pubescent, 1.5–7 mm. long; sepals glabrous to puberulent or occasionally finely pubescent, obtusely triangular to rounded, 0.7–1 mm. long, 1–1.5 mm. wide; petals glabrous or occasionally sparsely to densely appressed-pubescent abaxially, glabrous adaxially; disc glabrous to pubescent, 0.5–1 mm. high, 1–1.5 mm. wide; ovary pubescent throughout or pubescent only at the apex, with or without apical septicidal fissures; style pubescent toward the base, otherwise glabrous. Fruits yellowish, drying brown, reddish brown or blackish, glabrous throughout, pubescent only at the apex, pubescent at the base and apex, or pubescent throughout, with or without apical septicidal fissures, usually subglobose or ellipsoid but grading to ovoid, turbinate or pyriform, 5–13 mm. wide, base obtuse to rounded or truncate, apex depressed to rounded to apiculate, the apiculum to 2 mm. long; epicarp drying 0.3–2 mm. thick, with woody or subwoody mesocarp; endocarp cartilaginous, glabrous or rarely pubescent. Seeds reddish brown to blackish, 2.5–4.5 mm. long.

DISTRIBUTION. Java and Christmas Island east, discontinuously, to the Solomon Islands; primary and secondary rain forests from sea level to 1750 meters. See MAP 8.

MAP 8. Distributions of *Acronychia trifoliolata* Zoll. & Mor. var. *trifoliolata* (dots) and *A. trifoliolata* var. *ampla* Hartley (triangles).

Java and neighboring islands. WESTERN JAVA: Tjisokan, Tjidadap, *Winckel 10* (L), *660β* (U). CENTRAL JAVA: Mt. Oengarang, Medini, *Junghuhn* (L); Jogjakarta District, Sleman, *NIFS Ja 2573* (A, L); Djapara District Semanding, *NIFS Ja 3816* (A, L); Mt. Moerjo, Tjolo, *Kostermans 6247* (A, K, L); Mt. Moerjo, Argodjembanga, *Kostermans 6304* (A, L). EASTERN JAVA: Pasoeroean District, Malang, Djoenggo, *NIFS Ja 1748* (L); Tengger prope Gebok Klakka, *Zollinger 2530* (G, isotype of *Acronychia trifoliolata* Zoll. & Mor.); Klatak River, *Mousset 1037* (L); Banjoewangi District, Mt. Leboeagoeng, *NIFS Ja 2153* (L); Banjoewangi District, Mt. Deleman, *NIFS Ja 2177* (L); Panaroekan District, Kajoemas, *NIFS Ja 3562* (A); Idjen, *van Steenis 12004* (L). Without definite locality: *Junghuhn 274* (L), *274x* (L), *Koorders 6931β* (L), *13126β* (L). CHRISTMAS ISLAND: *Andrews*, 1897 (BM, holotype of *Acronychia andrewsi* Baker f.; K, isotype), KANGEAN ISLAND: N of Ardjasa, *Backer 26924* (L). BAWEAN ISLAND: N of Soerabaja, *Buwalda 3014* (*NIFS Ja 4199*) (A, L, NY). **Lesser Sunda Islands.** BALI: Mt. Batukau, *Dilmy 906* (K, L), *Kostermans et al. KK&SS 106* (CANB, L, US). SUMBAWA: Batudulang, Batu Lanteh Mt., *Kostermans 18087* (L); Olat Sekedit, *Kuswata 129* (A, K, L). FLORES: Ruteng & vicinity, *Kostermans & Wirawan 754* (L), *860* (K, L), *Schmutz 431* (L), *467* (L), *476* (L), *985* (L), *1077* (L), *1953* (L), *Verheijen 2147* (L), *2350* (L), *2734* (L); Mt. Ndeki, *Kostermans & Wirawan 105* (L), *180* (K, L); without definite locality, *Schmutz 452* (L), *651* (L), *652* (L), *2095* (L), *Verheijen 2046* (L). ALOR: Kabola Peninsula, *Jaag 358* (L). TIMOR: *Forbes 3893* (A, L), *Metzner 262* (L). WETAR: *Elbert 4676* (CANB, US). **Celebes.** Masamba, Omboan, *NIFS bb 26292* (A, L); Singkang, *Noerkas Expedition van Vuuren 279* (L); Kendari and vicinity, *Beccari*, July, 1874 (K), *NIFS bb 24984* (A, L). **Moluccas.** Morotai, *Kostermans 1146* (A, K, L, LAE), *1155* (A, L), *1158* (L); Halmahera, *De Vriese & Teysmann*, 1859–1860 (A, L), *Idjan & Mochtar 291* (L), *Teysmann HB 5651* (K, L, U, isotypes of *Acronychia halmaheirae* Miq.). **West Irian.** VOGELKOP PENINSULA: Tamrau Range, Aifat River Valley, *van Royen & Sleumer 7112* (CANB, K); Arfak Mts., Angi Gita Lake, *Kostermans 2234* (A, K, L), *2429* (A, K, L). **Papua and neighboring islands.** LOUISIADE ARCHIPELAGO: Rossel Island, Abaleti, *Brass 28294* (A, L, LAE, US), *28377* (A, L, LAE). **Solomon Islands.** Guadalcanal, Sorvarhio Basin, *Kajewski 2699* (A, BISH).

There are several recognizable entities in this variety which are, to a large degree, geographically distinct. They are listed below and their morphological differences are shown in TABLE 1.

1. Java entity — includes all of the collections from Java and the islands of Kangean, Bawean, Bali, Sumbawa, and Alor and the following collections from the island of Flores: *Schmutz 467, 651, 652, 1077,* and *2095* and *Kostermans & Wirawan 105* and *180.*

2. Christmas entity — includes all of the collections from Christmas Island, Timor, and Wetar and *Noerkas Expedition van Vuuren 279* from the Celebes. The single collection from Christmas Island is the type of *Acronychia andrewsi* Baker f.

3. Flores entity — includes the following collections from the island of Flores: *Schmutz 431, 452, 985,* and *1953; Verheijen 2046, 2147, 2350,* and *2734*; and *Kostermans & Wirawan 754* and *860.*

4. Moluccas entity — includes the collections from Kendari and vicinity, in the Celebes, and all of the collections from the Moluccas (among the latter the type collection of *Acronychia halmaheirae* Miq.). *Van Royen & Sleumer 7112*, from the Tamrau Range, West Irian, may belong here, but is in immature fruit.

5. Arfak entity — includes the two collections from the Arfak Mountains, West Irian.

6. Rossel entity — includes the two collections from Rossel Island.

7. Solomon entity — includes the single collection from the Solomon Islands.

TABLE 1. **Morphological variation in entities of Acronychia trifoliolata var. trifoliolata.**

	Java	Christmas	Flores	Moluccas	Arfak	Rossel	Solomon
Petals glabrous abaxially	X	X	X			X	
Petals pubescent abaxially				X	X		X
Disc glabrous		X	X	X	X	X	
Disc at least partially pubescent	X						X
Ovary pubescent only at apex		X	X			X	
Ovary pubescent throughout	X			X	X		X
Fruits 4–7 mm. wide	X	X				X	X
Fruits 8–13 mm. wide			X	X	X		
Fruit apex rounded to apiculate	X	X		X	X	X	X
Fruit apex depressed			X				
Endocarp glabrous	X	X	X	X		X	X
Endocarp pubescent					X		

37b. **Acronychia trifoliolata** Zoll. & Mor. var. **ampla** Hartley, var. nov.

Arbor parva vel mediocris usque 20 m. alta; ramulis novellis glabris vel glabratis; foliis trifoliolatis; petiolo glabro vel raro sparse puberulo, 2.5–9 cm. longo; foliolis chartaceis vel subcoriaceis, glabris, ellipticis vel elliptico-oblongis vel oblanceolatis, 7–21 cm. longis, 3–7 cm. latis, basi cuneatis vel attenuatis, venis primariis utrinsecus costa 7–13, apice acuminatis, acumine 0.5–1.5 cm. longo; inflorescentiis paucifloris vel multifloris, 2.5–6.5 cm. longis, axi et ramulis glabratis vel puberulis; floribus 7.5–9 mm. longis, pedicellis puberulis vel subtiliter pubescentibus, 0.5–4.5 mm. longis; sepalis glabris vel puberulis, triangularibus vel late rotundatis, 1–1.5 mm. longis, 1–3.5 mm. latis; petalis abaxialiter glabris vel dense adpresse pubescentibus, adaxialiter glabris vel sparse pubescentibus; disco glabro, 0.7–1 mm. alto, 1.5–2 mm. lato; ovario omnino pubescenti vel tantum apice pubescenti vel interdum tantum basi et apice pubescenti, fissuris septicidalibus apicalibus vel nullis; stylo basin versus pubescenti, aliter glabro; fructibus luteis, in sicco rubiginosis vel nigricantibus, glabris vel sparse adpresse pubescentibus, fissuris septicidalibus apicalibus vel nullis, globosis vel subglobosis vel interdum subturbinatis, 10-18 mm. latis, basi rotundatis, apice rotundatis vel apiculatis, apiculo usque 2 mm. longo; epicarpio in sicco 2.5-4 mm. crasso, mesocarpio ligneo vel spongioso-crustaceo; endocarpio cartilagineo; seminibus rubiginosis vel nigricantibus, 4.5-5 mm. longis. HOLOTYPUS: *Hartley 12083* (CANB).

DISTRIBUTION. West Irian, Territory of New Guinea (including New Britain) and Papua; primary and secondary rain forests and monsoon forests; sea level to 1650 meters. See MAP 8.

West Irian. Hollandia (Djajapura) and vicinity, *Brass 8955* (A, BRI, L), *Gjellerup 952* (K, L), *Koster BW 4296* (CANB), *van Royen & Sleumer 6465* (CANB, K), *van der Sijde BW 4085* (CANB), *BW 5514* (CANB). **Territory of New Guinea.** SEPIK DISTRICT: Vanimo Subdistrict, Krisa, *Gillison NGF 25250* (CANB); Aitape Subdistrict, near Goiniri, *Darbyshire & Hoogland 8026* (CANB); Ambunti Subdistrict, near Wagu, *Hoogland & Craven 10366* (CANB). WESTERN HIGHLANDS DISTRICT: Jimmi Valley, Tagan River, *Womersley & Millar NGF 8556* (CANB, LAE); Baiyer River, *Millar NGF 40818* (BRI, L, LAE). EASTERN HIGHLANDS DISTRICT: 5 miles S of Sassaura, *Hartley 12083* (CANB, holotype); Kassam Pass, *Henty & Vandenberg NGF 29336* (CANB). MOROBE DISTRICT: Boana, *Clemens 8269* (A, L), *41670a* (A); Ogeramuang, *Clemens 5079* (A); near Aregenang, *Foreman NGF 48131* (CANB); Yunziang, *Clemens 2340a* (A), *4102* (A), *6428a* (A); Wagau, *Womersley NGF 19325* (CANB); Aseki, *Streimann LAE 51972* (LAE), *Streimann & Kairo NGF 39063* (BRI, CANB, L, LAE); upper Watut River, Minnoa Creek, *Kairo NGF 47683* (CANB, LAE); without definite locality, *Clemens 6642* (A). NEW BRITAIN: upper Pulei River near Benum, *Henty & Frodin NGF 27297* (CANB, LAE); near Asuk, *Buderus NGF 25511* (CANB, L). **Papua.** CENTRAL DISTRICT: Laloki River about 3 miles E of Sogeri, *Hartley 10731* (CANB); Sirinumu area about 3 miles S of Sogeri, *Schodde 2985* (CANB).

The epithet *ampla* refers to the relatively large fruit of this variety.

As in *Acronychia trifoliolata* var. *trifoliolata*, there is considerable variation here in the indumentum of the petals, which range from glabrous to densely pubescent abaxially and glabrous to sparsely pubescent adaxially. The ovary is also variable in this characteristic, ranging from pubescent only at the apex to pubescent throughout.

Acronychia acronychioides, an endemic of north Queensland, appears to be closely related to variety *ampla* of *A. trifoliolata*, being especially similar to the collections from Hollandia (Djajapura) and vicinity.

37c. **Acronychia trifoliolata** Zoll. & Mor. var. **microcarpa** Hartley, var. nov.

Arbor parva vel mediocris usque 27 m. alta vel frutex; ramulis glabris; foliis trifoliolatis (foliis infrequenter unifoliolatis); petiolo glabro, 1-7 cm. longo; foliolis chartaceis vel subcoriaceis, glabris, anguste vel late ellipticis vel interdum oblanceolatis, 5-15 cm. longis, 2.3-6 cm. latis, basi cuneatis vel attenuatis, venis primariis utrinsecus costa 8–15, apice acuminatis (acumine usque 2 cm. longo) vel interdum obtusis; inflorescentiis pauci-floris vel multifloris, 2–8 cm. longis, axi et ramulis glabris vel puberulis; floribus 5–9 mm. longis, pedicellis glabris vel puberulis, 3–6 mm. longis; sepalis glabris vel puberulis, obtuse triangularibus vel rotundatis, 0.3–0.8 mm. longis, 0.5–1 mm. latis; petalis abaxialiter sparse adpresse pubescentibus vel glabris, adaxialiter glabris; disco glabro, 0.5–1 mm. alto, 1–1.7 mm. lato; ovario omnino pubescenti vel tantum apice pubescenti, fissuris septicidalibus apicalibus vel nullis; stylo basin versus pubescenti, aliter glabro; fructibus luteis vel albis, in sicco rubiginosis vel nigricantibus, sparse adpresse pubescentibus vel glabris, fissuris septicidalibus apicalibus vel nullis, subglobosis, 4–6 mm. latis, basi et apice rotundatis; epicarpio in sicco minus quam 0.5 mm. crasso, semi-carnoso, mesocarpio non evidenti; endocarpio pergamentaceo; seminibus nigricantibus, 2.5–3.5 mm. longis. HOLOTYPUS: *Schodde & Craven 4805* (CANB).

DISTRIBUTION. Territory of New Guinea and Papua; primary and secondary foothill and montane rain forests; 1050–2400 meters. See MAP 7.

Territory of New Guinea. EASTERN HIGHLANDS DISTRICT: Goroka Subdistrict, near Dunantina, *Hoogland & Pullen 5256* (CANB). MOROBE DISTRICT: Wagau, *Womersley NGF 17911* (CANB), *19190* (CANB); Aseki and vicinity, *Craven & Schodde 1138* (CANB), *Schodde & Craven 4805* (CANB, holotype), *Streimann LAE 51969* (LAE); Yamap and vicinity, *Kairo NGF 27549* (CANB), *Streimann & Kairo NGF 47592* (CANB, L, LAE); Wau-Salamaua Road near Skindewai, *Womersley & Millar NGF 8337* (CANB); Lake Trist, *Henty NGF 29014* (CANB), *Womersley NGF 24903* (CANB, LAE). **Papua.** CENTRAL DISTRICT: Mt. Tafa, *Brass 5043* (A, NY, UC, US); Woitape, *Corner & Gray NGF 12920* (BRI), *Lelean LAE 54522* (CANB, LAE), *Ridsdale & Woods NGF 33782* (CANB); Woitape-Kosipi Road near Uriko, *van Royen NGF 20243* (CANB); Mt. Kumme, E of Woitape, *van Royen NGF 20417* (CANB); Piati, *Carr 16119* (CANB); Isuarava, *Carr 15377* (CANB), *15553* (CANB); Alola, *Carr 13879* (CANB); Lala River, *Carr 15659* (CANB), *15706* (CANB); Boridi, *Carr 14382* (CANB). MILNE BAY DISTRICT: N slopes of Mt. Dayman, Maneau Range, *Brass 23184* (A, L, LAE), *23303* (CANB); NE outlying ridge of Mt. Simpson, *Pullen 7823* (CANB).

The petals and ovaries have the same variations in indumentum in var. *microcarpa* as in the preceding variety of *Acronychia trifoliolata*, variety *ampla*.

The small fruits, lacking evident mesocarp, distinguish this variety from the two above. It is most closely related to the small-fruited entities of var. *trifoliolata*, some collections of which have very thin, subwoody mesocarp. There also may be a close relationship with *Acronychia carrii*, which, ex-except for having larger flowers and fruits, matches very closely some of the higher-elevation collections of this variety (see especially *Brass 5043* and *van Royen NGF 20243* and *NGF 20417*).

38. **Acronychia reticulata** Lauterb. Bot. Jahrb. **55**: 251. 1917. LECTOTYPE: *Ledermann 10294*, Territory of New Guinea.

Acronychia reticulata Lauterb. var. *glabra* Lauterb. *ibid. 252.* TYPE: *Branderhorst 336*, West Irian.

Small tree to 15 m.; younger branchlets densely pubescent to tomentose. Leaves trifoliolate (occasional leaves unifoliolate); petiole densely pubescent to tomentose, becoming glabrate with age, 3–7 cm. long; leaflets subcoriaceous, pubescent below, becoming glabrate with age, usually glabrous above, elliptic to obovate to oblanceolate, 6–21 cm. long, 3.5–8 cm. wide, base cuneeate, main veins 10–15 on each side of the midrib, apex rounded to obtuse to acuminate, the acumen to 1 cm. long. Inflorescences few- to many-flowered, 4–7.5 cm. long, axes and branches densely pubescent to tomentose, becoming glabrate with age. Flowers about 9 mm. long; pedicels densely pubescent, 1–2 mm. long; sepals densely to rather sparsely pubescent, obtusely deltoid to triangular, 1.5–2 mm. long, 1.2–2.5 mm. wide; petals densely appressed-pubescent abaxially, glabrous adaxially; disc glabrous, 1 mm. high, 2–2.5 mm. wide; ovary pubescent, with or without apical septicidal fissures; style pubescent toward the base, otherwise glabrous. Fruits drying reddish brown, finely appressed-pubescent, with or without apical septicidal fissures, subglobose, 12–16 mm. wide, base and apex rounded; epicarp drying 2–3 mm. thick, with spongy-crustaceous mesocarp; endocarp cartilaginous. Seeds dark reddish brown, 4.5 mm. long.

DISTRIBUTION. West Irian and Territory of New Guinea; foothill rain forests to 1100 meters.

West Irian. Noord River, *Branderhorst 336* (K, L, U, isotypes of *Acronychia reticulata* Lauterb. var. *glabra* Lauterb.). **Territory of New Guinea.** SEPIK DISTRICT: Prospect Creek near Frieda River, *Henty & Foreman NGF 42543* (CANB, LAE); Mt. Turu, Prince Alexander Range, *Pullen 1436* (CANB); Lordberg, Sepik River, *Ledermann 10294* (K, lectotype of *Acronychia reticulata* Lauterb.).

The type collection of *Acronychia reticulata* var. *glabra* has only very mature leaves which have lost most of their pubescence with age.

Lauterbach cited three collections, all from the Sepik River, in the original description of *Acronychia reticulata: Ledermann 9781, 10294,* and *12869.*

This species, *Acronychia reticulata*, appears to be closely related to *A. trifoliolata* var. *ampla*, differing mainly in being more pubescent. There also may be a fairly close relationship with *A. cartilaginea* (q.v.).

39. **Acronychia ledermannii** Lauterb. Bot. Jahrb. **55**: 252. 1917. NEOTYPE: *Brass 30585*, Territory of New Guinea.

Small to medium tree to 20 m.; branchlets glabrous. Leaves trifoliolate (occasional leaves unifoliolate); petiole glabrous, 1.8–6 cm. long; leaflets chartaceous to coriaceous, drying reddish brown when young, pale green or yellowish green when older, glabrous, elliptic to elliptic-oblong or obovate to oblanceolate, 5–17 cm. long, 2–6.2 cm. wide, base cuneate to attenuate, main veins 9–12 on each side of the midrib, apex acuminate, the acumen to 2 cm. long. Inflorescences few-flowered, 4–10 cm. long, axes and branches glabrous to glabrate. Flowers 9–14 mm. long; pedicels glabrate, 1–3 mm. long; sepals puberulent, rounded, 0.7–1.5 mm. long, 1.2–2 mm. wide; petals glabrous to finely appressed-pubescent abaxially, sparsely to rather densely pubescent adaxially; disc glabrous, 0.7–1 mm. high, 1.5–2.3 mm. wide; ovary sparsely pubescent at the apex, otherwise glabrous, with or without apical septicidal fissures; style pubescent at the base, otherwise glabrous. Fruits pale yellow, drying yellowish brown to dark brown, glabrous, with or without apical septicidal fissures, globose to subpyriform, 12–23 mm. wide, base rounded to truncate, apex rounded; epicarp drying about 4 mm. thick, with spongy-crustaceous mesocarp; endocarp subcartilaginous. Seeds reddish black, 3.5–5 mm. long.

DISTRIBUTION. Territory of New Guinea and Papua; montane rain forests from 1500 to 2700 meters.

Territory of New Guinea. WESTERN HIGHLANDS DISTRICT: Minj Subdistrict, upper Nona River, *Saunders 757* (CANB). EASTERN HIGHLANDS DISTRICT: Mt. Wilhelm, *Brass 30585* (A, neotype; CANB, US, isotypes); Marafunga, *Millar NGF 40761* (CANB, LAE), *Stevens LAE 51016* (CANB, LAE); Goroka, *Womersley NGF 4466* (L, LAE); Korofunota, via Goroka, *Womersley & Floyd NGF 6942* (CANB); Omahaiga River, Mt. Otto area, *Robbins 833* (CANB); Mt. Otto, *Brass 30843* (CANB, US); near Waisa, about 15 miles SW of Okapa, *Hartley 13110* (CANB); Purosa, Okapa area, *Brass 31608* (CANB, US). MOROBE DISTRICT: Spreader Divide about 6 miles NW of Aseki, *Schodde & Craven 4987* (CANB). **Papua.** SOUTHERN HIGHLANDS DISTRICT: Ialibu, *Pullen 2750* (CANB), *Womersley & Woolliams NGF 12384* (BRI, L, LAE).

The color of the leaves in dried condition distinguishes *Acronychia ledermannii* from the other species of the genus.

Chalcid wasps, noted in the fruits of several other species of *Acronychia* as well, were found in the majority of the fruits of this species. The wasps have no apparent effect on the size or external structure of the seed in which they are contained or on that of the fruit. There is also a lack of any noticeable galling effect on the flowers.

The collections cited by Lauterbach in the original description, *Ledermann 12054, 12134,* and *12162,* all from montane forest at 2070 meters in the Schrader Range, Territory of New Guinea, were apparently destroyed during World War II.

The nearest relative of *Acronychia ledermannii* is probably *A. trifoliolata* var. *ampla.*

40. **Acronychia acronychioides** (F. Muell.) Hartley, comb. nov.

Euodia acronychioides F. Muell. Frag. Phytogr. Austral. 4: 117. 1864. TYPE: *Dallachy*, Queensland, Rockingham Bay.

Acronychia melicopoides F. Muell. Frag. Phytogr. Austral. **5:** 3. 1865 (*nomen illegit.*, based on *Euodia acronychioides* F. Muell.).

Jambolifera melicopodes O. Ktze. Rev. Gen. Pl. **1:** 102. 1891 (*nomen illegit.*, based on *Acronychia melicopoides* F. Muell.).

Small to rather large tree to 25 m.; younger branchlets puberulent to glabrate. Leaves trifoliolate (rarely occasional leaves unifoliolate); petiole puberulent, at least adaxially or at the base, becoming glabrous with age, 3–8 cm. long; leaflets chartaceous to subcoriaceous, glabrous, elliptic-oblong to oblanceolate, 7–21 cm. long, 2.3–6.5 cm. wide, base cuneate to attenuate, main veins 10–13 on each side of the midrib, apex obtusely acuminate, the acumen to 0.8 cm. long. Inflorescences many-flowered, 3–9 cm. long, axes and branches puberulent to finely pubescent. Flowers 9–11 mm. long; pedicels puberulent to finely pubescent, 3–7.5 mm. long; sepals puberulent, obtusely triangular to broadly elliptic to orbicular, 1.5–3 mm. long, 2–3 mm. wide; petals glabrous, occasionally semipersistent in fruit; disc glabrous, 0.8–1 mm. high, 1.6–1.8 mm. wide; ovary pubescent, with or without apical septicidal fissures; style densely pubescent toward the base, otherwise glabrous. Fruits yellow, drying reddish brown to blackish, glabrate at maturity, with or without apical septicidal fissures, subpyriform or occasionally subglobose, 8–11 mm. wide, base broadly stipitate or occasionally rounded, apex rounded; epicarp drying about 1 mm. thick, with woody mesocarp; endocarp cartilaginous. Seeds blackish, about 4 mm. long.

Distribution. North Queensland, Cape York Peninsula south to the Eungella Range west of Mackay; rain forests to 1200 meters. See Map 7.

Queensland. Cook District: Tozer Range, ½ mile E of Mt. Tozer, *Brass 19467* (BRI, CANB); Leo Creek, Upper Nesbit River, *Brass 19932* (BRI, CANB); McIvor River N of Cooktown, *Webb & Tracey 7820* (BRI); Upper Parrot Creek, Annan River, *Brass 20214* (BRI, CANB), *20220* (BRI, CANB); Copper Lode Falls on Freshwater Creek 6 miles S of Cairns, *Gittins 2219* (BRI, NSW); Barron River, *Johnson*, 1891 (MEL); Danbulla, *Webb & Tracey 7195* (BRI); Gillies Highway, Atherton Tableland, *Olsen 373* (BRI, NSW); Lake Barrine, *Kajewski 1244* (A, BRI, NY); Gadgarra, *Jones 1494* (CANB), *Kajewski 1078* (A, BRI, K, NY, UC), *1151* (A, BM, BRI, NY); Mulgrave River, *Johnson*, 1891 (MEL); Bellenden Ker Ranges, *Johnson*, 1891 (MEL); Johnstone River, *Ladbrook*, August, 1917 (BRI), *Michael 141* (BRI); Innisfail, *Michael 274* (GH); Tully Falls, *Webb 729* (CANB); El Arish, *Jones 1273* (CANB). North Kennedy District: Herberton Range, *Webb & Tracey 7944* (BRI); head of Wild River, *Bailey*, July 3, 1899 (BRI, NSW); Clump Point Farm, 30 miles SE of Innisfail, *Wyer*, May 11, 1945 (NSW 127105); Mt. Macalister, *Dallachy*, April 9, 1869 (MEL); Sea View Range, *Dallachy*, November, 1864 (MEL); Dalrymple's Gap, *Dallachy*, May 11, 1864 (BRI, MEL); Coast Range, *Dallachy*, February 8, 1866 (MEL); Rockingham Bay, *Dallachy*, March, 1864 (MEL, holotype of *Euodia acronychioides* F. Muell.; BM, BRI, K, L, W, isotypes); Mt. Spec forestry camp near Bambaroo, *Francis*, November, 1933 (BRI). South Kennedy District: Cawley State Forest W of Cathu, between Mackay and Proserpine, *Webb & Tracey 7682* (BRI); Dalrymple Heights & vicinity, *Clemens*, July-November, 1947 (BRI), September-October, 1947 (BRI, MICH, NY, UC), September-November, 1947 (AD, BISH, GH, K, MICH, NY, UC); Eungella, Netherdale area, *Forest Foreman Cole 17* (BRI); Eungella Range, *White 12872* (BRI).

As is mentioned above, in the discussion of the phylogeny of *Acronychia*, this species, *A. acronychioides*, and *A. imperforata* appear to be of extra-Australian ancestry. The idea is supported in this instance since the closest relative of *A. acronychioides*, *A. trifoliolata* var. *ampla*, has the most advanced type of fruit in the entirely-Malesian *A. trifoliata* complex.

41. **Acronychia imperforata** F. Muell. Frag. Phytogr. Austral. 1: 26. 1858. LECTOTYPE: *Hill*, Queensland, Moreton District, Moreton Bay.

Jambolifera imperforata (F. Muell.) O. Ktze. Rev. Gen. Pl. 1: 102. 1891.
Acronychia scortechinii F. M. Bailey, Queensl. Agr. Jour. 3: 281. 1898. SYNTYPES: *Lovell*, Queensland, Wide Bay District, Fraser Island; *Scortechini*, Queensland, Moreton District, Logan River.

Shrub or small tree to 9 m.; branchlets glabrous or rarely glabrate. Leaves unifoliolate; petiole glabrous or rarely glabrate, 0.3–2.5 cm. long; leaflet chartaceous to subcoriaceous, glabrous, often drying somewhat blue-gray above, especially when young, elliptic to elliptic-oblong or obovate to oblanceolate, 3.3–12.5 cm. long, 1.6–5.5 cm. wide, base obtuse to cuneate to attenuate, main veins 6–10 on each side of the midrib, apex rounded to obtusely acuminate, the acumen to 0.5 cm. long. Inflorescences usually few-flowered, 2.5–5 cm. long, axes and branches glabrous to puberulent. Flowers 6–9.5 mm. long; pedicels glabrous to puberulent, 1.5–4.5 mm. long; sepals glabrous or glabrate, obtusely triangular to suborbicular, 1–1.5 mm. long, 1.5–2.5 mm. wide; petals glabrous abaxially, glabrous to sparsely pubescent adaxially; disc glabrous, 0.2–0.5 mm. high, 1.4–2 mm. wide; ovary glabrous throughout or sparsely pubescent only at the apex, without septicidal fissures; style spreading-pubescent toward the base, otherwise glabrous. Fruits orange-yellow, drying dark reddish brown to blackish, glabrous throughout or with a few hairs at the apex, without septicidal fissures, pyriform to subglobose, 10–12 mm. long, base obtuse to broadly stipitate, apex rounded, short-apiculate or somewhat depressed; epicarp drying 0.7–1 mm. thick, with woody mesocarp; endocarp cartilaginous. Seeds reddish black, 4–6 mm. long.

DISTRIBUTION. Cape York Peninsula, Queensland, south to Port Macquarie, New South Wales; coastal scrub except for a few inland localities. See MAP 6.

Queensland. COOK DISTRICT: Newcastle Bay, 2.5 miles S of Somerset, *Brass 18668* (BRI, CANB); Bamaga Mission, 11.2 km. SW of Cape York, *Smith 12350* (BRI); Endeavour River, *Peraich (?) 753* (MEL); Shipton's Flat, on Tin Mine Road, *Smith 14346* (BRI); Granite Creek Road W of Bloomfield, *Webb & Tracey 6210* (BRI); upper Mowbray River, *Brass 2522* (A, BISH, BRI, US). NORTH KENNEDY DISTRICT: Rockingham Bay, *Dallachy* (MEL). PORT CURTIS DISTRICT: Curtis Island, *Dietrich 1013* (MEL); Gladstone, *Hedley* (BRI);

Baffle Creek area, *White*, April, 1920 (BRI). WIDE BAY DISTRICT: Bundaberg, *Boorman*, August, 1912 (NSW 127015); Saw Mill Scrub, Dundowran via Nikenbah, *Tryon*, July, 1928 (BRI); Nikenbah, *Tryon* (BRI); Fraser Island, *Blake 22698* (BRI), *Epps*, October 18, 1919 (BRI), *Hubbard 4420* (BRI, K), *Lovell*, August, 1894 (BRI, syntype of *Acronychia scortechinii* F. M. Bailey), *Petrie*, June, 1917 (BRI), *Webb & Tracey 6334* (BRI); Noosa River 23 miles NE of Gympie, *Smith 12116* (BRI); Hibbett's Mt., Gundiah, *Kajewski 1518* (A, BRI, NY); Lake Cootharaba, *Keys* (BRI); Sunshine Beach via Tewantin, *Harrold*, April 1, 1964 (BRI). MORETON DISTRICT: Coolum Beach, *Clemens*, March 22, 1945 (BRI, GH, MICH, UC); Eumundi, *Bailey & Gunn*, June, 1895 (BRI); Maroochy River, *Kenny*, August, 1912 (BRI); Lake Curramundi, N of Caloundra, *Anderson*, July 14, 1964 (BRI, CANB), *Williams*, March 8, 1969 (BRI); Caloundra, *Blake 4002* (BRI), August, 1933 (BRI); Somerset, *Bailey*, June, 1897 (BRI); Bribie Island, *Clemens 44072* (GH), *Kenny*, August, 1906 (BRI), *Wilson 710* (A); Moreton Bay, *Cunningham 7* (BM, K), *Hill* (MEL, lectotype; K, isotype), *Mueller* (MEL), *Parker*, July, 1918 (A); Brisbane River, *Dietrich 2669* (MEL); Mosquito Creek, *White*, April, 1917 (BRI, NSW); mouth of the Pine River, *Smith 11407* (CANB); Sandgate, *Statter*, April, 1882 (BM), *White*, June, 1918 (A, BRI); Kedron Brook, *Bailey*, June, 1875 (BRI); Toowong, Brisbane, *Everist*, October, 1934 (A, BRI); Stradbroke Island, *Cribb BRIU 1333* (BRI), *White 3367* (A); Logan River, *Scortechini* (BRI, syntype of *Acronychia scortechinii* F. M. Bailey; K, isosyntype); Tugun, *Clemens 42625* (A), *Hubbard 3946* (A); Currumbin, *Longman*, March, 1916 (BRI), *Webb 1534* (CANB), *White Field Naturalists Club Excursion*, September, 1913 (BRI). Without definite locality: *Brown 5332* (BM). **New South Wales.** Cudgen, *Jones 1229* (CANB), *McKee 9518* (CANB, P); Mt. Warning, *Fraser*, January 15, 1936 (NSW 127018); Byron Bay, *White 10449* (A, BRI, NY); Lennox Head, *Baeuerlen*, November, 1891 (NSW 127019); Pebbley Beach, North Ballina, *Johnson & Constable*, June 12, 1957 (NSW 42338); Ballina, *Baeuerlen 429* (NSW); 2.5 miles N of Evans Head, *McGillivray 1938* (NSW); Woody Head, N of Iluka, *Hayes, Turner & McGillivray 2671* (NSW); Iluka, *O'Hara & Coveny 3508* (BRI, NSW), *Williams*, April 12, 1964 (NSW 127021); Clarence River, *Hartley*, July–August, 1915 (NSW 127021), *Wilcox 1875* (MEL); Woolgoolga, *de Beuzeville 700* (NSW); Coffs Harbour, *Boorman*, May 26, 1909 (NSW 127024), June, 1910 (NSW 127025), *Meebold 3474* (NY), *White 7420* (BRI); Bundagen, near Repton, Bellinger River, *Blaxell 153* (NSW); Hat Head, E of Kempsey, *Constable*, January 18, 1953 (NSW 22361); Crescent Head, *Davis*, October 4, 1941 (NSW); 15 miles N of Port Macquarie, *Rodway* (NSW 127026).

Mueller's syntypes of this species, a collection by Hill and another by Mueller, both from Moreton Bay, are mixed: the Kew and Melbourne sheets of the Hill collection are *Acronychia imperforata* and the British Museum duplicate is *A. pauciflora*; and one of several Melbourne sheets of the Mueller collection is *A. imperforata* whereas the others, and the Kew duplicate, are *A. pauciflora*. They were apparently mixed at the time Mueller studied them, since his description applies to both species. The choice of the lectotype and the description of the species presented here is in accordance with the prevailing interpretation of *A. imperforata* by Australian botanists.

Acronychia scortechinii was considered distinct by Bailey on the basis of its having fruit with unusually fleshy exocarp. It is now evident that this is a minor variation since there are a number of collections, from scattered localities, with similarly fleshy fruits.

Although the geographical distribution of this species is remarkable in Queensland, with a disjunction of about 500 miles between Rockingham Bay and Curtis Island, I have not found sufficient differences among the collections to recognize more than a single taxon. The northern collections, most of which are from rain forest habitats away from the coast, do tend to have larger, thinner-textured leaflets and larger sepals, but the southern collections grade into them so completely that I have not been able to separate them in a key.

The closest relative of *Acronychia imperforata* appears to be the widespread *A. pedunculata*, the collections of the latter from Papua being very similar to the northern Queensland collections of the former. Of the two species, *A pedunculata* appears to be the more primitive since the ovary and fruit often have septicidal fissures. This would suggest that *A. imperforata*, which lacks septicidal fissures, was derived from Malesian stock.

42. **Acronychia pedunculata** (L.) Miq. Fl. Ind. Bat. Suppl. 532. 1861.

Jambolifera pedunculata L. Sp. Pl. **1**: 349. 1753. Type: *Jambolifera* L. *Fl. Zeyl. 139.*

Cyminosma ankenda Gaertn. Fruct. **1**: 280. *t. 58, fig. 6.* 1788 (*nomen illegit.*, based on *Jambolifera* L.).

Gela lanceolata Lour. Fl. Cochinch. 232. 1790. Type: *Loureiro*, Cochinchina (not seen; at BM, according to Merrill, 1935: 220).

Jambolifera rezinosa Lour. Fl. Cochinch. 231. 1790. Type: *Loureiro*, Cochinchina (not seen).

Laxmannia ankenda (Gaertn.) Raeuschel, Nomencl. Bot. ed. 3. 99. 1797.

Cyminosma pedunculata (L.) Roxb. Hort. Beng. 88. 1814; Fl. Ind. **2**: 239. 1832.

Doerrienia malabarica Dennst. Schluess. Hort. Ind. Malab. 31. 1818. Type: *Hort. Malab. 5: t. 15.* 1685 (*nomen nudum* according to Manitz, Taxon **17**: 501. 1968).

Acronychia laurifolia Bl. Cat. Gew. Buitenz. 63. 1823; Bijdr. 245. 1825. Type: *Blume*, Java.

Ximenia? lanceolata (Lour.) DC. Prodr. **1**: 533. 1824.

Cyminosma resinosa DC. Prodr. **1**: 722. 1824 (based on *Jambolifera rezinosa* Lour.).

Acronychia arborea Bl. Bijdr. 244. 1825. Type: *Blume*, Java, Mt. Salak.

Selas lanceolatum (Lour.) Spreng. Syst. Veg. **2**: 216. 1825.

Melicope conferta Blanco, Fl. Filip. ed. 2. 205. 1845. Typified by *Reillo BS 19255* (*Merrill Species Blancoanae 55*), Philippines, Luzon, Rizal Province.

Clausena simplicifolia Dalzell, Hook. Jour. Bot. Kew Gard. Misc. **3**: 180. 1851. Type: *Dalzell*, India, Mysore.

Jambolifera arborea (Bl.) Zoll. & Mor. Syst. Verz. Zoll. 14. 1854.

Acronychia apiculata Miq. Fl. Ind. Bat. Suppl. 532. 1861. Type: *Teysmann HB 4514*, southern Sumatra.

Acronychia barberi Gamble, Kew Bull. **1915**: 345. 1915. SYNTYPES: *Wight 364*, southern India, Pulney Hills; *Barber 6027*, southern India, Anamalai Hills.

Acronychia lanceolata (Lour.) Forst. ex Crevost & Lemarié, Cat. Prod. Indochina **1**: 173. 1917.

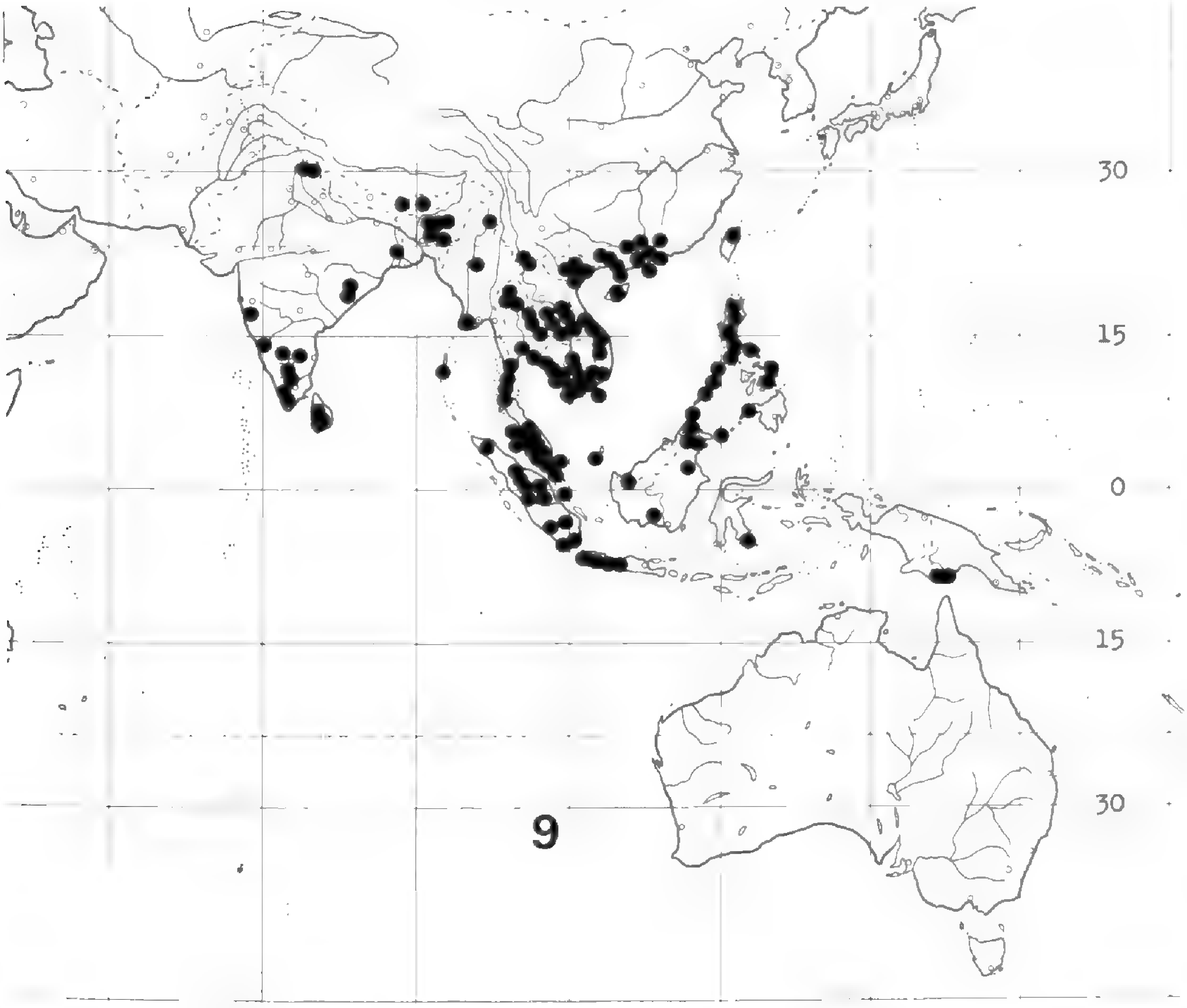
Acronychia resinosa Forst. ex Crevost & Lemarié, Cat. Prod. Indochina **1**: 173. 1917 (based on *Jambolifera rezinosa* Lour.).

Acronychia elliptica Merr. & Perry, Jour. Arnold Arb. **22**: 56. 1941. TYPE: *Brass 6309*, Papua, Western District.

Shrub to small to large tree to 28 m.; younger branchlets glabrous to finely pubescent. Leaves unifoliolate; petiole glabrous to finely pubescent, 0.5–5 cm. long; leaflet chartaceous to coriaceous, glabrous, usually elliptic or elliptic-oblong but grading to obovate, oblanceolate or nearly oblong, 3.5–24.5 cm. long, 2–8.5 cm. wide, base cuneate or occasionally rounded or attenuate, main veins 7–14 on each side of the midrib, apex obtusely acuminate (the acumen to 2 cm. long) or occasionally obtuse or rounded. Inflorescences few- to many-flowered, 2–25 cm. long, axes and branches glabrous to finely pubescent. Flowers 4–12 mm. long; pedicels glabrous to finely pubescent, 2–12 mm. long; sepals glabrous to finely pubescent, triangular to broadly rounded, 0.6–1.5 mm. long, 0.8–2 mm. wide; petals glabrous to sparsely pubescent abaxially, densely to sparsely pubescent or occasionally glabrous adaxially; disc glabrous to pubescent, 0.5–1 mm. high, 1–2 mm. wide; ovary pubescent throughout or rarely pubescent only at the apex, with or without apical septicidal fissures; style pubescent toward the base, otherwise glabrous. Fruits yellowish or white, drying brown to blackish, usually rather sparsely pubescent with a ring of dense, appressed hairs at the base, but grading to tomentose or glabrous, with or without apical septicidal fissures, usually subglobose but grading to ellipsoid, pyriform or broadly conical, occasionally more or less 4-lobed or with several low, longitudinal ribs, 5–15 mm. wide, base obtuse to truncate, apex rounded to acute to apiculate, the apiculum to 4 mm. long; epicarp drying 0.5–3 mm. thick, with woody or subwoody mesocarp; endocarp cartilaginous. Seeds reddish-black to black, 3–7 mm. long.

ILLUSTRATIONS. Engler, A., Nat. Pflanzenfam. III. **4**: 180. *t. 104.* 1896 (as *Acronychia laurifolia*). *Ibid.* ed. 2. **19a**: 308. *t. 140.* 1931 (as *Acronychia laurifolia*). Gaertner, J., *loc. cit.* Koorders, S. H., Exkursionsflora von Java **2**: 423. *t. 77.* 1912 (as *Acronychia laurifolia*). Koorders, S. H. & Th. Valeton, Atlas der Baumarten von Java **2**: *t. 353* 1914 (as *Acronychia laurifolia*). Li, H. L., Woody flora of Taiwan 364. *t. 130.* 1963. Loddiges, C., The Botanical Cabinet **10**: *t. 938.* 1824 (as *Gela lanceolata*). Ochse, J. J. & R. C. Bakhuizen, Indische Groenten 640. *t. 391.* 1931. Vahl, M., Symbolae Botanicae **3**: *t. 61.* 1794 (as *Jambolifera pedunculata*).

DISTRIBUTION. India and Ceylon east to Taiwan and southeast in Malesia to Papua; primary and secondary rain forests and coastal scrubs; sea level to 2200 meters. See MAP 9.



MAP 9. Distribution of *Acronychia pedunculata* (L.) Miq.

India. UTTAR PRADESH: Dehra Dun District, *Datta 19* (A), *Kanjilal 759* (A), *760* (K), *Mukharjee 24* (US), *Osmaston 1207* (NSW), January 30, 1916 (W), *Punj 22* (NY), *Rawat 20* (A), *Singh 26* (MEL, NSW), *33* (NY). MAHARASHTRA: Concan (Konkan), *Law & Stocks* (K), *Stocks, Law, etc.* (BM, GH, MEL, NY, W). MYSORE: Mt. Syhadree, near Tulkut-ghat, *Dalzell* (K, holotype of *Clausena simplicifolia* Dalzell); Hassan District, Harihalli, *Saldanha 9046* (US). MADRAS: Anamalai Hills, *Barber 6027* (K, syntype of *Acronychia barberi* Gamble); Nilgiri Hills, *Clarke 10823B* (BM), *Gamble 16811* (K), *17850* (BM), *20558* (K), *Thomson* (BM, GH, MEL, NY, U, W); Pulney Hills, *Anglade* (A), *Herb. Beddome 1017* (BM), *Bourne 212* (K), *1452* (K), *Janaki 51* (MICH), *Wight 364* (K, syntype of *Acronychia barberi* Gamble); without definite locality, *Cole 54* (K), *67* (K). KERALA (TRAVANCORE): Malabar, *Wight 362* (GH, K, MEL); Courtallum, *Wight 181* (NSW, NY); without definite locality, *Meebold 17107* (W). ORISSA: Ranpur, near Habadih, *Mooney 1353* (K); Puri District, Aran Forest, *Haines 5503* (K). WEST BENGAL: vicinity of Calcutta, *Helfer*, 1836–1838 (A, BM, NY, US), *Wallich 4325* (W). ASSAM: Khasi Hills, *Chand 1923* (MICH), *1967* (MICH), *2065* (MICH), *5927* (MICH), *5974* (MICH), *6112* (MICH), *6354* (MICH), *8291* (MICH, UC), *Clarke 6209* (BM), *45716D* (BM), *Hooker f. & Thomson* (BM, K, MEL, NY, US, W), *King's Collector*, November, 1890 (BM, W), August, 1892 (BM), *Koelz 23582* (MICH), *30245* (MICH, UC), *30302A* (MICH, W), *30389* (MICH), *30633* (MICH), *31075* (MICH, UC, W), *Kurz 242* (US), *Ward* (W); Bamanigaon, *Chand 2499* (MICH); Lushai Hills, Aijal, *Chand 4283* (MICH, UC);

without definite locality, *Jenkins 614* (K), *615* (K). Andaman Islands: South Andaman, *King*, August 22, 1891 (US), *King's Collector*, June 4, 1892 (MEL), June 1, 1893 (A), September 16, 1893 (A), August 11, 1894 (US), January 19, 1895 (A); without definite locality, *Herb. Helfer 1190* (GH, W), *Prain's Collector 58* (A, MEL), *95* (NSW). Without definite locality: *Roxburgh* (BM), *van Royen*, 1779 (BM), *Wallich Cat. No. 1205* (BM, W), *Wight 309* (K, W). **Ceylon.** Iriyagolla, *de Silva 40* (A), *256* (NY); Madulkele, *Worthington 141* (BM); Mt. Allagalla, *Worthington 49* (BM, NSW); Kandy Forest Reserve, *Lam 7346* (A); Nilambe, *Worthington 2864* (BM); Henaratgoda, *Petch*, March 4, 1923 (A); Moon Plains, Parawella, *St. John 24114* (BISH); Patana, Madugoda-Urugala Road, *Simpson 8796* (BM); above Madugoda, *Simpson 9479* (BM); Hurasgiriya, *de Silva 55* (MEL, NY); without definite locality, *Gardner 162* (K, NY), *Koenig* (BM), *Rechinger 2479* (W), *Rudolf*, February, 1896 (MICH), *Thomson* (BM, GH, W), *Thwaites CP 1249* (BM, MEL, W), *Walker 438* (K), *Worthington 1579* (BM), *1754* (BM). **Sikkim.** *Cave* (A, BM), *Hooker f.* (K), *King*, August 29, 1876 (MEL), *Native Collector 605* (GH). **Bhutan.** *Bulley leg. Cooper 1112* (BM). **East Pakistan.** Sylhet, *Wallich Cat. No. 1205B* (K, L, MICH, W); Chittagong, *Hooker f. & Thomson* (GH); Chittagong Hill Tracts, *King's Collector 506* (A); without definite locality, *Herb. Griffith 1190* (GH, W). **Burma.** Myitkyina District, *Parkinson 378* (K); Maymyo Plateau, *Lace 5952* (K); Bassein District, Kyathaung River, Mezali Reserve, *Kermode 7317* (K). **Thailand.** Northern: Doi Pa Ta, *Kerr 4916* (BM); Doi Suthep, *Kerr 1983* (BM), *2299* (BM), *2681* (BM); Doi Angka, *Kerr 6345* (BM, K); Nam Heng (Nam Haeng), *Winit 1740* (K). Northeastern: Loei, *Bunchuai 147* (K), *1670* (K, P); Phu Kha Ding, *Smitinand 1962* (K); Sakol Nakorn (Sakon Nakhon), *Lakshnakara 1004* (BM, K); Nakorn Panom (Nakhon Phanom), *Lakshnakara 977* (BM). Eastern: Korat (Nakhon Ratchasima), *Noe 200* (BM), *270* (BM, K), *Put 2241* (BM), *3065* (BM, K); Ubon Ratchathani, *Kerr 8332* (BM), *Lakshnakara 892* (BM), *Phusomsaeng 35* (K, P). Central: Sriracha (Si Racha), *Collins 408* (BM, K), *472* (K), *577* (US), *736* (US), *830* (US), *905* (A. BISH, US), *905A* (K), *954* (BM, US), *985* (US), *1308* (US), *1371* (US), *1744* (BM, US), *2035* (K, US), *Kerr 2063* (BM, K), *4527* (BM, K). Southeastern: Rayaung (Rayong), *Put 2676* (BM); Watana (Watthana Nakhon), *Put 1938* (BM); Chantabun (Chanthaburi), *Kerr 9536* (BM, K), *Lakshnakara 484* (BM); Krat (Ban Bang Phra), *Kerr 9436* (BM), *17837* (BM), *21764* (BM). Southwestern: Hua Hin, *Collins 1590* (US), *Kerr 13485* (BM), *16137* (BM); Prachuap (Prachuap Khiri Khan), *Put 3156* (BM, K). Peninsular: Bangtapan (Ban Bang Saphan), *Put 1386* (BM), *1395* (BM); Surat Thani, *Put 4115* (K), *Kerr*, August 2, 1927 (BM); Pattani, *Kerr 7244* (BM); Yala, *Put 3681* (BM). Without definite locality: *Collins 426* (BM), *Kerr 11413* (BM), *20139* (BM). **Laos.** Savannakhet, *Poilane 11911* (P), *16349* (P); Phon Than, *Spire 93* (P); Saravane Province, *Poilane 16144* (P); without definite locality, *Poilane 13525* (P). **Cambodia.** Compong Phom (Kompong Thom), *Gourgand* (P); Pursat, *Godefroy 550* (P); Pobang, *Poilane 14322* (P); Kompong Cham, *Béjaud*, July 18, 1930 (A, P); Prey Khmuonh, *Viginein-Roche 1* (P), *2* (P), *3* (P); Kampot, *Geoffray 133* (P), *407* (P), *Hahn 41* (P), *Poilane 385* (P); Elephant Mt., *Poilane 22983* (P). **North Viet Nam.** Phu Tho, *Pételot 1048* (NY, P, US), *1048 bis* (P), *1059* (P); Chan Mong Forest Reserve, *Fleury 32155* (P); Mt. Tam Dao, *Pételot 3883* (NY, P, US); Vinh Yen to Tam Dao, *Pételot 4303* (NY, P, US); Thai Nguyen, *Pételot 5840* (P); Phuc Yen, *Pételot 5841* (NY, P); Quonbi, *Balansa 1180* (P); Tu Phap, *Balansa 3104* (P), *3106* (P); Son Tay, *Balansa 3105* (P), *Pételot 7856* (A); Cho Bo, *Poilane 13160* (P); Hanoi, *Demange*

7782 (P); Hao Nho, *Bon 683* (P); De Tham (Tinh Dao), *Bois 267* (P); Yen Ninh, *Bon 1439* (P); Vinh-yen, *Eberhardt 3752* (P), *3788* (P), *4903* (P); Nam Dinh, *Mouret 99* (P); Haphong, *Balansa 1178* (K, P); Quang Yen, *Balansa 1179* (P); between Hongay and Quang Yen, *Service Forestier du Tonkin* (P); Pho Ba Che, *Service Forestier d'Indo-Chine*, 1924 (P); Phong Du, *Fleury 37905* (P); between Bui Bong and Tien Yen, *Service Forestier du Tonkin* (P); Tien Yen, *Tsang 27469* (A); Ha-coi (Hacai), *Tsang 27161* (A, P), *29180* (A, K, P), *29577* (K); Dam Ha, *Tsang 29911* (A), *30295* (A, P); Mon Cay (Mong Cai), *Tsang 26946* (A); without definite locality, *d'Alleizette 130* (P), *Bon 19* (P), *519* (P), *719* (P), *789* (P), *1508 bis* (P). **South Viet Nam.** Quang Tri, *de Pirey 41237* (P), *Poilane 1057* (P); Hue, *Bauche 77* (P); Can Hai, *Pételot leg. Colani 3545* (P), *4545* (NY, P); Huong Thuy, *Eberhardt 2421* (P); Mt. Bani, *Clemens 3476* (A, BM, K, MICH, NY, P, U, US, W); Ba Na, *Poilane 7332* (P); Tourane (Da Nang) and vicinity, *Clemens 4450* (A, MICH, NY, P, U, US); Da Bac, *Godefroy 854* (P); Kontum Province, *Poilane 32276* (P); Nhatrang, *Poilane 3085* (P), *3371* (P), *5499* (P); Lang Bian Mts., Djiring (Djirinh), *Chevalier 31259* (P); Cam Ranh Peninsula, *Kiêt 202* (P); Blao, *Poilane 20981* (P), *21794* (P), *21968* (P), *23399* (P); Braian Mt., *Poilane 23843* (P); Ba Rau, *Poilane 10117* (P); Tayninh, *Muller 1610* (P); Ca Na, *Evrard 2490* (P), *Poilane 9261* (P), *9601* (P), *12408* (P); Trang Bom, *Dien 93* (P); Bien Hoa and vicinity, *Lefèvre 104* (P), *Dien 139* (P); Saigon vicinity, *Lefèvre 241* (P); Baria Province, *Poilane 637* (P), *651* (P); Phu Quoc (Fukwok) Island, *Contest-Lacour 311* (P); Mekong Delta, *Harmand 517* (P); Con Son Islands (Poulo Condor), *Germain 27* (P), *Harmand*, 1875–1877 (P); without definite locality, *Godefroy 782* (P), *795* (P), *Dien 1635* (P), *Harmand 795* (P), *Talmy*, 1868 (P), *Thorel 1188* (BM, NY, P), *Poilane 12231* (P). **China.** YUNNAN PROVINCE: Szemoa (Ssu-mao) *Henry 12263* (A, K, NY, US, W), *12263A* (A, W), *12263B* (A, NY), *12263C* (A), *12263D* (A, K, NY, US), *12263E* (A, NY); Luh-shun (Kuan-fang) Hsien, *Wang 81135* (A); Chei-li Hsien (Ching-huang), *Wang 75711* (A), *75866* (A), *75935* (A), *77427* (A), *77650* (A), *78110* (A), *78616* (A), *78653* (A), *79114* (A), *79133* (A), *79494* (A), *79662* (A); Fo-hai (Meng-hai), *Wang 74212* (A), *74387* (A), *74438* (A), *77201* (A); Meng-la, *Wang 80660* (A). KWANGSI PROVINCE: South Nanning, Seh-feng, Dar Shan, *Ching 7806* (NY, W), *7951* (A, NY, US), *7993* (A, NY, US), *8209* (A, NY, US); Shap Man Taai Shan, SE of Shang-sze (Shang-ssu), *Tsang 22468* (A), *23815* (A, NY), *24099* (A, NY), *24522* (A, NY). KWANGTUNG PROVINCE: Fang-ch'eng District, Kung P'ing Shan, *Tsang 26754* (A); Lei-chou Pan-tao (Luichow Peninsula), near Pon-tan, *Tsiang 2562* (NY); Kochow (Kaochou), *Tsiang 938* (W), *939* (A); Ting-hu Shan, *Liou 855* (NY); Kao-yao District, Teng Wo Shan, *Lau 20130* (NY, US, W), *Levine 3115* (A), *Levine & Groff CCC 35* (A, US), *Tsiang 758* (A, MEL), *811* (A, W); Lo-fou Shan, *Merrill 10881* (NY), *Tsiang 1625* (A), *1634* (A), *1641* (A); Canton (Kuang-chou) and vicinity, *Fung A382* (NY), *A461* (NY), *Henry Herb. Hance 430* (BM), *Levine CCC 350* (A, GH, US), *CCC 773* (A, BM, US), *CCC 1150* (GH, US), *CCC 1225* (A, GH, US), *CCC 1620* (A, GH, US), *CCC 1700* (A, BM, GH, US), *Levine leg. Ah To CCC 1712* (A), *Levine CCC 2171* (A), *CCC 3048* (A), *Levine leg. Ah To CCC 3156* (A, GH, US), *Sampson*, June 17, 1884 (K), January 11, 1885 (K); Nanhoi (Fo-shan) District, *Chun 7809* (A); Lantao Island, *Taam 1644* (NY, US), *Tsang LU 16540* (A, W), *Tsiang 627* (A, NY, US); Wa Shan Tau, *Levine & McClure CCC 6978* (BM); Hweichang District, Lin Fa Shan, *Tsang 25660* (A); without definite locality, *Wang 521* (A, MEL). HAINAN ISLAND: Lamko (Lin-kao) District, *Tsang 380* (A, K, NY, US); Ch'eng-mai District, *Lei 50* (NY, US, W); Nodoa (Tan-hsien), *Chun Nanking Univ. 5867* (US), *Gressitt 882* (A, BM), *Lau 1008* (A, BM, NY), *McClure CCC 7958* (BM, P), *Tsang 106* (A, NY, US), *359* (A, US); Dung Ka to Wen Fa Shi, *Chun & Tso 43678* (A, NY, W), *43757* (A, NY, US); Tai Pin, *Gressitt 1091* (A, BM); Wen-ch'ang District, *Fung 20337* (BM, K, NY, US, W); Kachek (Ch'iung-hai), Wong Chuk (Huang-chu), *McClure CCC 9780* (US, W); Kan-en (Kan-ch'eng) District, Chim Fung Mt., *Lau 5282* (A); Five Finger Mt. (Wu-chih Shan), *McClure CCC 8483* (BISH); Yaichow (Yai-ch'eng), *How 70960* (A, BISH, NY), *How & Chun 70074* (A, NY), *70156* (A, NY, US), *Liang 62021* (NY), *62233* (NY, US); without definite locality, *Chun & Tso 44182* (BISH, NY, W), *Ford* (US), *Henry 13* (K), *8091* (K, NY), *8119x* (GH), *8220x* (K), *8552* (K), *Lau 426* (A, BM, K, MICH, NY, US, W), *Liang 63301* (NY, US), *63594* (NY), *63685* (NY), *63727* (NY), *64631* (NY), *65057* (NY, US), *McClure CCC 7732* (A, K), *CCC 9711* (US, W), *Tsang & Fung 635* (A, K, NY), *Wang 33193* (NY), *33624* (A, NY), *33944* (NY), *35794* (NY), *36019* (NY), *36504* (NY), *36557* (NY, US). HONG KONG ISLAND: *Chun 5012* (A, US), *6054* (A, W), *6087* (A), *6553* (MEL), *6561* (A, MICH), *Gibbs Herb. Hong Kong 7411* (NSW), *Jelinek Exped. "Novara,"* 1857–1859 (W), *Lamont 119* (BM), December, 1873 (BM), March, 1874 (BM), *Liou 800* (NY), *Murray* (MEL), *Sargent*, November 5, 1903 (A), *Taam 1479* (NY, US), *Tang 354* (A), *Tenison-Woods* (MEL), *Vachell 119* (K), *Wilford 367* (K), *Wright U.S. North Pacific Exploring Exped.*, 1853–1856 (GH, L, NY, US). Without definite locality: *Seemann 2475* (BM, K). **Taiwan.** Kelung (Kiirun), *Faurie 36* (A, W), *Ford*, June, 1884 (GH, K); without definite locality, *Nakahara 702* (US). **Sumatra and neighboring islands.** RES. ATJEH: Gajo Lands, between the confluence of the Kapi and Aoenan Rivers and Paja, *van Steenis 9920* (L). RES. TAPANOELI: NW side of Toba Lake, *W. & C. Bangham 1168* (A, NY); between Anggoli and Sipirok, *NIFS bb 5232* (L). WEST COAST: Mt. Sago, *Ichlas 2* (L), *Maradjo 63* (L), *Meijer 1504* (L), *7373* (K, L); without definite locality, *Meijer 7318* (L). EAST COAST: Asahan District, Banderpoelo, *Yates 2170* (MICH, L, NY, W); Kota Pinang District, *Rahmat si Toroes 3385* (A, L, NY, US), *3496* (A, L, NY, US), *3526* (A, NY, US), *3600* (A, L ,NY, US), *3744* (A, NY, US), *3812* (A, NY, US), *3832* (L, NY, US), *3984* (A, L, NY, US); Pakanbaru, *Soepadmo 187* (A, AD, K, L, UC). RES. BENKOELEN: Mt. Kemala, *NIFS bb 8764* (L). RES. PALEMBANG: *Anonymous* (L). LAMPONG DISTRICTS: Mt. Tanggamus, *Jacobs 8156* (L, BISH), *8216* (L); Kebang, *Teysmann HB 4514* (L, U, isotypes of *Acronychia apiculata* Miq.). LINGGA ISLAND: *Anonymous 14621* (L). **Malay Peninsula and neighboring islands.** LANGKAWI ISLAND: near Kuah, *Turnau 742* (L); without definite locality, *Curtis* (BM, US, W). KEDAH: Tampei Forest Reserve, *Whitmore FRI 437* (A, K, L); Besut District, Mt. Kluang, *Sinclair & Salleh SF 40801* (L). PENANG ISLAND: Penang Hill, *Corner SF 31599* (A), *Nauen SF 37658* (A); Telok Bahang, *Sinclair SF 39302* (L); Muka Head, *Hardial 665* (LAE); Highland Hill, *Haniff & Nur SF 3023* (K); Highlands Forest Reserve, *Sweklie 1454* (K); without definite locality, *Curtis 315* (BM), *694* (BM, US, W), *Porter 1205* (K). PERAK: Larut, *King's Collector 4928* (MEL), *Ridley 3090* (BM, K, L); Gunong Bubu, *Chew 1202* (A, K, L, UC); Dindings, Telok Kopia Forest Reserve, *Whitmore FRI 3108* (L); Dindings, *Ridley 7940* (BM); Pangkor, *Corner SF 31657* (K). PAHANG: Kuantan, *Bidin*, September 20, 1921 (A), *Dolman 6622* (K), *Wood Kepong Field No. 76118* (K, L); Tioman Island, *Henderson 18447* (A); Mt. Peta, *Whitmore FRI 3859* (L). SELANGOR: Klang, Jupra Forest Reserve, *Hamid & Yeob CF 3273* (K). JOHORE: Mt. Panti, *Everett FRI 13815* (L); Mt. Kendok, *Ogata KEP 105017* (L). Without definite locality: *Maingay 281* (BM, GH, K, L). **Java.** WESTERN JAVA: Mt. Pajung, Udjung Kulon

Reserve, *Kostermans UNESCO 148* (CANB, NSW, P), *Wirawan 102* (A, BISH, L), *211* (L, LAE); Tjiteras, *Backer 26499* (L); Mt. Njoentjoeng, *Saimoendt 24* (L, UC); Djasinga, *Backer 23437* (L), *Bakhuizen v. d. Brink 1134* (L), *Esche & Wasyat NIFS Ja 6165* (L); Tjidadap, *Winckel 1815β* (L, U), *1851β* (K, L, U); Djakarta vicinity, *Backer*, February, 1905 (L), *Kollmann*, 1838 (BM, NY); Depok and vicinity, *Bakhuizen v. d. Brink f. 2047* (L, U, W), *Beumée*, March, 1927 (UC, W), *Kern 7518* (L), *van Ooststroom 12615* (CANB); Sawangan, *Bakhuizen v. d. Brink f. 1871* (L); Bogor, *NIFS Ja 2377* (A); Tjisiing, *Bakhuizen v. d. Brink 7937* (L); Mt. Salak, *Blume* (BM, GH, L, NY, U, isotypes of *Acronychia arborea* Bl.), *Zollinger 1699* (A, BM, MEL, P); Mt. Gadjah, Salak, *Bakhuizen v. d. Brink 4152* (L, UC), *Bakhuizen v. d. Brink f. 598* (U); "Houtsoorten van den Gedeh" (probably Mt. Gede), *Anonymous* (*probably Junghuhn*) *643* (A, L, US); Mt. Gede, *Ridley*, February 13, 1915 (K); Radjamandala, *Docters van Leeuwen 7690* (L, U); Bandoeng, *NIFS Ja 3984* (L), *NIFS Ja 4011* (L); Mt. Tangkoebanprahoe, *Junghuhn 357* (A, CANB, K, L); Mt. Malabar, *Monterie 4* (L), *50* (A, L, U); Mt. Wajang, *Smith & Rant 593* (L, U); Telaga Patengan, *Backer 12516* (L); Mt. Semboeng, *Backer 12438* (L); Tjiawi, *NIFS Ja 1936* (L); Pangrango-Gedeh Reserve, Tjibeureum, *Kostermans UNESCO 278* (A, BM, L, LAE, NSW, NY, P); Mt. Sawal above Tjikoneng, *Backer 8449* (L); Mt. Tjareme, *van Steenis 12797* (L); Pangandaran Peninsula, *Kostermans 23070* (L); without definite locality, *Ploem* (L). CENTRAL JAVA: N slope of Mt. Slamet, *Kostermans*, August, 1968 (L); Mt. Oengarang, near Medini, *Junghuhn* (L). Without definite locality: *Blume* (BM, GH, L, NY, U, isotypes of *Acronychia laurifolia* Bl.), *Junghuhn 351* (L), *352* (A, L, US), *353* (L), *355* (L), *Koorders 7058β* (L), *7060β* (K), *7067β* (L), *13918β* (P), *15356β* (L), *Lobb* (K), *Reinwardt* (L), *Teysmann*, 1867 (L), 1868 (K, NY), *Zollinger 402* (A, L, P), *402A* (BM, L), *643* (K). **Borneo and neighboring islands.** SARAWAK. Lundu District: Mt. Pueh, *Smythies 15651* (K, L). British North Borneo (Sabah). Kudat District: Banggi Island, *Ampuria SAN 40780* (L); Kedayan, *Balajadia North Borneo Forestry Dept. 4068* (K, L); Nangka, *Apostol North Borneo Forestry Dept. 7679* (A, K, L). Ranau District: Mt. Ampuan, *Meijer SAN 20715* (L), *Singh SAN 24185* (L), *SAN 28328* (L); Mt. Kulong, *Singh SAN 28315* (K, L). Tawau District: Quoin Hill Road, *Gibot SAN 32547* (K, L), *SAN 32992* (L), *SAN 47409* (L), *SAN 47439* (L); Mt. Pyramid Forestry Reserve, *Saikeh SAN 68115* (L); Tawau, *Elmer 21044* (A, BISH, BM, GH, L, NY, U), *21056* (BISH, BM, GH, L, NY, U); Apas Road, *Gibot SAN 29617* (L), *Sinanggul SAN 40518* (L), *SAN 56223* (K, L), *Wood SAN 17199* (L). Lahad Datu District: Segama River, *Chai SAN 31667* (L); Mt. Silam, *Sinanggul SAN 57283* (L); Silam and vicinity, *Pereira SAN 43436* (L), *Talip SAN 47695* (K, L), *SAN 52924* (L), *SAN 54976* (K). Without definite locality: *Keith North Borneo Forestry Dept. 9456* (L), *Wood 2474* (A, W). KALIMANTAN. Samarinda District: Kelindjau River near Bentuk, *Kostermans 9684* (A, L). Kapoeas-Barito District: Bangkal, *Sauveur 1160* (L). ANAMBAS ISLANDS. Djemadja Island, *Henderson SF 20458* (K). **Philippines.** PALAWAN ISLAND. Quezon, Mono, *Reynoso PNH 87756* (CANB); without definite locality, *Cenabre FB 29991* (L). CALAMIAN GROUP. Busuanga Island: Concepcion, *Lopez BS 41365* (A, MEL). MINDORO ISLAND. Mt. Yagaw, *Conklin PNH 18637* (A, L). LUZON ISLAND. Ilocos Norte Province: Burgos, *Ramos BS 27357* (A, GH, US); without definite locality, *Paraiso FB 23857* (GH). Cagayan Province: Gonzaga, *Edaño BS 78279* (MICH); Camalaniugan, *Lizardo FB 29527* (A); Sitio Babayuan SW of Camalaniugan, *Bartlett 14941* (BISH, MICH, NY); between Lal-lo and Magapit, *Lagrimas & Lomibao PNH 40639* (BM, L); Pinagteponan River, *Edaño BS 78347*

(MICH); Mt. Bawa, *Edaño BS 78489* (MICH); Calamanugan, *Bacani FB 16990* (BM, NSW); Penablanca, *Ramos BS 76745* (MICH, NY); without definite locality, *Bernardo FB 13126* (P), *FB 27080* (A, BM), *Ramos BS 7394* (L). Benguet Subprovince: *Merrill 9693* (US). Pangasinan Province: Mt. San Isidro, *Fenix BS 29976* (A, L). Nueva Ecija Province: Mt. Umingan, *Ramos & Edaño BS 26379* (A, US). Bulacan Province: *Leuterio FB 24727* (GH). Rizal Province: *Loher 15053* (P), *Ramos BS 1060* (U, US), *Reillo BS 19255* (*Merrill Species Blancoanae 55*) (A, BM, K, L, NSW, NY, P, US, W). Bataan Province: Mt. Mariveles, *Borden FB 1333* (BM, NSW), *Elmer 6724* (NY), *Foxworthy BS 1581* (NY, US), *Loher 5025* (K), *Merrill 298* (A, MICH, NY, UC, US), *3185* (K, NY), *3870* (K, NY, P, US), *Williams 606* (GH, NY, US). Quezon Province: Tagcawayan, *Foxworthy & Ramos BS 13089* (BM, US), *Mendoza PNH 97817* (BM, K); without definite locality, *Cailipan FB 26024* (L). Without definite locality: *Vidal 1194* (A, L). SAMAR ISLAND. *Oro FB 20826* (US). LEYTE ISLAND. Palo, *Elmer 7086* (A, NY). SULU ARCHIPELAGO. Tawitawi Island: *Yates BS 36320* (L). MINDANAO ISLAND. Zamboanga Province: Port Santa Maria, *Simbajon FB 31428* (NY). **Celebes and neighboring islands.** KABAENA ISLAND: *Elbert 3465* (CANB, P, US). **Papua.** WESTERN DISTRICT: Bensbach Subdistrict, Weam, *Ridsdale NGF 33503* (CANB); upper Wassi Kussa River, *Brass 8643* (A, K, L, LAE); Mai Kussa River, Sebidiro, *Henty & Katik NGF 38761* (CANB); Daru Island, *Brass 6309* (A, holotype of *Acronychia elliptica* Merr. & Perry; BRI, L, LAE, isotypes). **Cultivated.** MAURITIUS: *Telfair* (NY). INDIA: Botanic Gardens, Calcutta, *Voigt 270* (US). JAVA: Botanic Gardens, Bogor, *Anonymous* (K, U).

The nomenclature of this species has a long history of confusion, stemming, according to Dryander (1794: 232) and Trimen, in his study of Hermann's Ceylon herbarium and Linnaeus's *Flora Zeylanica* (1888: 140), from the fact that Linnaeus, in his *Flora Zeylanica*, mixed up the native names of species 139, *Jambolifera*, and species 185, *Myrtus* [*M. cumini* L. Sp. Pl. **1**: 471. 1853 = *Syzygium cumini* (L.) Skeels], giving *Jambolones*, *Jambolons*, and *Madan* for the former and *Ankenda* for the latter when it should have been the reverse. Trimen referred the specimen in the Hermann herbarium representing species 139 to *Acronychia laurifolia* Bl. Alston [in Trimen, Handb. Fl. Ceylon **6** (suppl.): 37. 1931] correctly assigned the plant to *A. pedunculata* (L.) Miq. and listed *A. laurifolia* as a taxonomic synonym.

A note (apparently written by Dryander) on one of the British Museum sheets cited above, *Koenig*, from Ceylon, further confirms Trimen's identification of the Hermann specimen of *Jambolifera*. It reads (in part): "Mr. Schumacher says that Prof. Rottboell has compared this plant (of which Koenig has sent him specimens) with *Jambolifera pedunculata* in Hermann's herbarium, now in possession of Count Moltke, and found it to be the same."

Apparently because of the confusion surrounding the identity of *Jambolifera pedunculata*, a number of authors besides Trimen, for example, Engler (1896: 180; 1931: 310) and Hooker f. (Fl. Brit. Ind. **1**: 498. 1875), have chosen to use the name *Acronychia laurifolia* for this plant. Other authors, including Merrill (Enum. Philip. Fl. Pl. **2**: 333. 1923, Alston (*loc. cit.*)) and Li (Woody Fl. Taiwan 364. 1963), have used the name *A. pedunculata* even though doing so was an acknowledgment that *Jambolifera*, rather than *Acronychia*, is the correct name for the genus.

As is mentioned above in the discussion of generic nomenclature, a proposal has been submitted for the conservation of *Acronychia* against *Jambolifera.*

Several of the taxonomic synonyms given above were previously reduced to that status: *Gela lanceolata* and *Jambolifera rezinosa* were placed in synonymy under *Acronychia pedunculata* by Merrill (1935: 200); *A. laurifolia* has been treated as a synonym of *A. pedunculata* by a number of authors including Alston (*loc. cit.*), Merrill (1935: 200), and Li (*loc. cit.*); *A. arborea* was placed in the synonymy of *A. laurifolia* by Ridley (Fl. Malay Pen. 1: 347. 1922); *Melicope conferta* was recognized as a synonym of *A. pedunculata* by Merrill (Sp. Blancoanae 199. 1918); and *Clausena simplicifolia* was placed in the synonymy of *A. laurifolia* by Hooker f. (*loc. cit.*).

The type of *Acronychia apiculata* falls well within the range of variation of *A. pedunculata* as delimited here. Miquel inadvertently credited Junghuhn with the type collection, actually made by Teysmann in the Lampong Districts of southern Sumatra.

Acronychia barberi was based on what appear to be abnormal specimens. Both of the syntypes have a fair proportion of leaves that are unusually small and thin-textured for *A. pedunculata.* These reduced leaves tend to predominate on some branchlets and not on others, indicating, perhaps, that somatic mutations may be responsible for their presence.

In the original description of *Acronychia elliptica*, Merrill and Perry noted its similarity to *A. pedunculata* but pointed out that the former differed in having glabrous petals and disc and a shorter inflorescence. These features have now proven to be variable in *A. pedunculata* and it is not possible to maintain the Papuan plant as a separate species.

The closest relative of *Acronychia pedunculata* appears to be *A. trifoliolata* var. *trifoliolata*, some specimens of the two seeming to be identical except for the difference in leaf complexity.

As is indicated in the description, *Acronychia pedunculata* is extremely variable. I have not found it possible to recognize more than a single taxon, however, since the variants either occur in mosaic patterns of geographic distribution or are rendered unkeyable by intergradation. The disc, for instance, is consistently pubescent in specimens from northeast India, Ceylon, and Java; consistently glabrous in specimens from the Philippines, Celebes, and Papua; and either pubescent or glabrous in specimens from southern India, Indochina, China, Sumatra, Malaya, and Borneo. The fruits, further illustrating the problem, are generally of the large size range (10–15 mm. wide) in Sumatra, yet grade into the small size range on that island. Similar gradations in fruit size also occur in India, Ceylon, Indochina, Malaya, and Borneo.

UNMATCHED OR OTHERWISE EXCLUDED NAMES

Acronychia albiflora Rechinger, Denkschr. Akad. Wiss. Wien **85:** 294. 1910 = **Melicope.**[11]

?*Acronychia anomala* Lauterb. Bot. Jahrb. **55:** 253. 1918; Nova Guinea (Bot.) **14:** 145. 1924 = **Evodia anomala** (Lauterb.) Linden, Nova Guinea (New Ser.) **10:** 148. 1959.

Acronychia baueri Schott, Rutaceae. Frag. Bot. 5, *t. 3.* 1834 [*Jambolifera baueri* (Schott) O. Ktze. Rev. Gen. Pl. **1:** 102. 1891] = **Bauerella.**[12]

Acronychia baueri Schott forma *majoriflora* Domin, Bibliot. Bot. **22**(89): 294. 1927 = **Bauerella.**

Acronychia boweriana Christophersen, Bishop Mus. Bull. **128:** 106, *fig. 13.* 1935 = **Melicope.**

Acronychia cauliflora Lauterb. Bot. Jahrb. **55:** 253, *fig. 5.* 1918 = **Evodiella cauliflora** (Lauterb.) Linden, Nova Guinea (New Ser.) **10:** 147. 1959.

Acronychia cunninghamii Hook. Bot. Mag. *t. 3994.* 1843 = **Medicosma cunninghamii** (Hook.) Hook. f. in Benth. & Hook. Gen. Pl. **1:** 297. 1862.

Acronychia cuspidata Lauterb. Bot. Jahrb. **55:** 254. 1917. The holotype of this species was apparently destroyed at Berlin and I have not seen any isotypes. Described from the Sepik River of New Guinea on a flowering collection, it seems rather close to *Acronychia brassii* Hartley but differs, judging from Lauterbach's description, in having cuspidate leaflets, each with tip 1.5 cm. long; inflorescences 2.5 cm. long; the acutely lanceolate sepals 1.7 mm. long; and in having glabrous staminal filaments. The ovary is described merely as "glabrum truncatum," so there is no certainty that this is an *Acronychia.*

Acronychia diversifolia A. Gray, Bot. U.S. Expl. Exped. **1:** 334. 1854, *sphalm.* = **Melicope.**

Acronychia endlicheri Schott, Rutaceae. Frag. Bot. 3, *t. 2.* 1834 [*Jambolifera endlicheri* (Schott) O. Ktze. Rev. Gen. Pl. **1:** 102. 1891], *nomen illegit.*, cf. Green, Jour. Arnold Arb. **51:** 209. 1970 = **Bauerella.**

Acronychia eriocarpa Panch. ex Guillaumin, Not. Syst. Paris **2:** 98. 1911, *nomen illegit.*, cf. Green, Jour. Arnold Arb. **51:** 211. 1970 = **Bauerella.**

Acronychia esquirolii Léveillé, Fl. Kouy-Tchéou 374. 1915. I have not seen any authentic material of this species. It is doubtful that it belongs in *Acronychia,* however, since the leaves are described as verticillate and the flower color as rose-violet.

---

[11] As is indicated in the key given in the introduction, *Melicope* and *Euodia* differ only in stamen number. This is a highly impractical distinguishing characteristic since it is often impossible to determine in fruiting specimens, especially as is often the case in both genera, in species with functionally unisexual flowers. Also, there is evidence that the two genera, thus delimited, are unnatural. At the present, therefore, I am not sure that both genera should be maintained, and new combinations are not made for the species that were originally described in *Acronychia.*

[12] The genus *Bauerella* will be the subject of a future study and the necessary new combinations will be made at that time.

Acronychia heterophylla A. Gray, Bot. U.S. Expl. Exped. **1:** 333. 1854 & *t. 32.* 1857 [*Jambolifera heterophylla* (A. Gray) O. Ktze. Rev. Gen. Pl. **1:** 102, 1891] = **Melicope.**

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

Acronychia leiocarpa P. S. Green, Jour. Arnold Arb. **51:** 213, *fig. 1(d).* 1970 = **Bauerella.**

Acronychia ligustroides Panch. ex Guillaumin, Not. Syst. Paris **2:** 98. 1911, *nomen illegit.*, cf. Green, Jour. Arnold Arb. **51:** 213. 1970 = **Bauerella.**

Acronychia lobocarpa F. Muell. Jour. Bot. **30:** 17. 1892 = **Melicope.**

Acronychia niueana St. John, Bishop Mus. Bull. **178:** 67, *fig. 3.* 1943 = **Melicope.**

Acronychia obovata Merr. Philip. Jour. Sci. Bot. **12:** 274. 1917.[13]

Acronychia oligophlebia Merr. Philip. Jour. Sci. Bot. **23:** 246. 1923.[13]

Acronychia ovalifolia Panch. ex Guillaumin. Not. Syst. Paris **2:** 98. 1911, *nomen illegit.*, cf. Green, Jour. Arnold Arb. **51:** 213. 1970 = **Bauerella.**

Acronychia ovata Endl. ex Heynh. Nomencl. Bot. Hort. **2:** 8. 1846, *nomen illegit.*, cf. Green, Jour. Arnold Arb. **51:** 210. 1970 = **Bauerella.**

Acronychia petiolaris A. Gray, Bot. U. S. Expl. Exped. **1:** 335. 1854 & *t. 33(A).* 1857 [*Jambolifera petiolaris* (A. Gray) O. Ktze. Rev. Gen. Pl. **1:** 102. 1891; *Acronychia simplicifolia* (Endl.) McGillivray & Green subsp. *petiolaris* (A. Gray) P. S. Green, Jour. Arnold Arb. **51:** 212, *fig. 1(c).* 1970] = **Bauerella.**

Acronychia porteri Hook. f. Fl. Brit. Ind. **1:** 498. 1875 [*Jambolifera porteri* (Hook. f.) O. Ktze. Rev. Gen. Pl. **1:** 102. 1891].[13]

Acronychia retusa A. Gray, Bot. U. S. Expl. Exped. **1:** 338. 1854 & *t. 34(A).* 1857 [*Jambolifera retusa* (A. Gray) O. Ktze. Rev. Gen. Pl. **1:** 102. 1891] = **Melicope.**

Acronychia rhytidocarpa Merr. & Perry. Jour. Arnold Arb. **22:** 55. 1941 = **Euodia.**

Acronychia richii A. Gray, Bot. U. S. Expl. Exped. **1:** 336. 1854 & *t. 33(B).* 1857 [*Jambolifera richii* (A. Gray) O. Ktze. Rev. Gen. Pl. **1:** 102. 1891] = **Melicope.**

Acronychia rubescens Lauterb. Bot. Jahrb. **55:** 252. 1917. I have not seen any authentic material of this species, described from the Sepik District of New Guinea, and have not been able to match its description, based on a single collection in flower bud only, with any of the known species of *Acronychia.*

Acronychia serrata Hochr. Pl. Bogor. Exsicc. 49. 1904 = **Schizomeria serrata** (Hochr.) Hochr. Ann. Conserv. Jard. Bot. Genève **10:** 118. 1907.

Acronychia simplicifolia (Endl.) McGillivray & Green subsp. *neoscotica* P. S. Green, Jour. Arnold Arb. **51:** 211, *fig. 1(b).* 1970 = **Bauerella.**

---

[13] As is noted in the introduction, *Acronychia obovata, A. oligophlebia,* and *A. porteri* are considered to be distinct from *Acronychia,* but further study is needed to determine their correct generic placement.

Acronychia tetrandra F. Muell. Frag. Phytogr. Austral. **9**: 104. 1875, *nomen illegit.*, based on *Euodia haplophylla* F. Muell. = **Euodia.**

Euodia haplophylla F. Muell. Frag. Phytogr. Austral. **5**: 179. 1866 [*Acronychia haplophylla* (F. Muell.) Engl. Nat. Pflanzenfam. III. **4**: 180. 1896] = **Euodia.**

Evodia minahassae Teysm. & Binnend. Natuur. Tijdschr. Nederl. Ind. **29**: 255. 1867 [*Acronychia minahassae* (Teysm. & Binnend.) Miq. Ann. Mus. Lugd.-Bat. **3**: 245. 1867] = **Melicope.**

Evodia muelleri Engl. Nat. Pflanzenfam. III. **4**: *121, fig. 67(G–D)*. 1896 [*Acronychia muelleri* (Engl.) W. D. Francis, Kew Bull. **1931**: 190. 1931] = **Evodiella muelleri** (Engl.) Linden, Nova Guinea (New Ser.) **10**: 147. 1959.

Jambolifera chinensis Spreng. Syst. Veg. **2**: 216. 1825 [*Cyminosma chinensis* (Spreng.) G. Don, Gen. Syst. **1**: 781. 1831], *nomen illegit.*, based on *Jambolifera pedunculata* sensu Lour. Fl. Cochinch. 231. 1790 = **Syzygium.**

Jambolifera coromandelica Houtt. Natuur. Hist. Ser. 2. **2**: *273, pl. VII, fig. 2.* 1774. I do not recognize the genus but this is not an *Acronychia.*

Jambolifera odorata Lour. Fl. Cochinch. *231*. 1790 [*Cyminosma odorata* (Lour.) DC. Prodr. **1**: *722*. 1824; *Acronychia odorata* (Lour.) H. Baill. ex Crevost & Lemarié, Cat. Prod. Indochina **1**: *172*. 1917]. I have not seen authentic material of this species. Merrill, A commentary on Loureiro's "Flora Cochinchinensis," 220, 1935, refers it to *Acronychia* sp., but this determination seems unlikely since the inflorescence is described as racemose and the fruit as one-seeded.

Vepris simplicifolia Endl. Prodr. Fl. Norfolk 89. 1833 [*Acronychia simplicifolia* (Endl.) McGillivray & Green, Jour. Arnold Arb. **51**: 209. 1970] = **Bauerella.**

LITERATURE CITED

DARLINGTON, P. J. Biogeography of the southern end of the world. vii + 236 pp. Harvard University Press, Cambridge, Massachusetts. 1965.

DRYANDER, J. On genera and species of plants which occur twice or three times, under different names, in Professor Gmelin's edition of Linnaeus's *Systema Naturae*. Trans. Linn. Soc. London **2**: 212–235. 1794.

ENGLER, A. Rutaceae. In ENGLER & PRANTL, Nat. Pflanzenfam. III. **4**: 95–201. 1896.

———. Rutaceae. Nat. Pflanzenfam. ed. 2. **19a**: 187–358. 1931.

MERRILL, E. D. A commentary on Loureiro's "Flora Cochinchinensis." Trans. Am. Phil. Soc. (N.S.) **24**: 1–403. 1935.

RAVEN, P. H., & D. I. AXELROD. Plate tectonics and Australasian paleobiogeography. Science **176**: 1379–1386. 1972.

SMITH-WHITE, S. Chromosome numbers in the Boronieae (Rutaceae) and their bearing on the evolutionary development of the tribe in the Australian flora. Austral. Jour. Bot. **2**: 287–303. 1954.

ST. JOHN, H. The date of publication of Forsters' *Characteres Generum Plantarum* and its relation to contemporary works. Naturaliste Canad. **98**: 561–581. 1971.

TRIMEN, H. Hermann's Ceylon herbarium and Linnaeus's *Flora Zeylanica*. Jour. Linn. Soc. London **24**: 129–155. 1888.

INDEX TO EXSICCATAE

The numbers in parentheses refer to the corresponding species and varieties in the text.

Kiêt *202* (42).
King's Collector *506*, *4928* (42).
Koelz *23582*, *30245*, *30302A*, *30389*, *30633*, *31075* (42).
Koorders *6931β* (37a); *7058β*, *7060β*, *7067β* (42); *13126β* (37a); *13918β*, *15356β* (42).
Koster *BW 4296* (37b).
Kostermans *UNESCO 148*, *UNESCO 278* (42); *1146*, *1155*, *1158*, *2234*, *2429*, *6247*, *6304* (37a); *9684* (42); *18087* (37a); *23070* (42).
Kostermans & Wirawan *105*, *180*, *754*, *860* (37a).
Kostermans *et al. KK&SS 106* (37a).
Kurz *242* (42).
Kuswata *129* (37a).

Lace *5952* (42).
Lagrimas & Lomibao *PNH 40639* (42).
Lakshnakara *484*, *892*, *977*, *1004* (42).
Lam *1728* (12); *1933* (9); *7346* (42).
Lamont *119* (42).
Lau, S. K., *426*, *1008*, *5282* (42).
Lau, S. Y., *20130* (42).
Ledermann *10294* (38).
Leenhardt *212*, *455* (11).
Lefèvre *104*, *241* (42).
Lei *50*, *481* (42).
Lelean *LAE 54522* (37c).
LeRat *35*, *110*, *662*, *1471*, *1642*, *2391*, *2601* (11).
Leuterio *FB 24727* (42).
Levine *CCC 350*, *CCC 773*, *CCC 1150*, *CCC 1225*, *CCC 1620*, *CCC 1700*, *leg. Ah To CCC 1712*, *CCC 2171*, *CCC 3048*, *3115*, *leg. Ah To CCC 3156* (42).
Levine & Groff *CCC 35* (42).
Levine & McClure *CCC 6978* (42).
Liang *62021*, *62233*, *63301*, *63594*, *63685*, *63727*, *64631*, *65057* (42).
Liou *800*, *855* (42).
Lizardo *FB 29527* (42).
Loher *5025*, *15053* (42).
Lopez *BS 41365* (42).

Maingay *281* (42).
Maradjo *63* (42).
Martensz *203* (6).
Martin & Hyland *1877* (2).
McAdam *238* (31).
McBarron *11841* (6).
McClure *CCC 7732*, *CCC 7958*, *CCC 8483*, *CCC 9711*, *CCC 9780* (42).
McGillivray *499* (21); *714*, *757* (6); *1938* (41).
McKean *MB 1* (24).
McKee *1022* (11); *1286* (20); *2002*, *2156*, *3460*, *9138* (11); *9518* (41).
McKee & Floyd *NGF 6340* (20).
McMillan *5171* (11).
Meebold *3474* (41); *17107* (42).
Meijer *5104*, *7318*, *7373*, *SAN 20715* (42).
Mendoza *PNH 97817* (42).
Merava & Kairo *NGF 17163* (12).
Merrill *298*, *3185*, *3870*, *9693*, *10881* (42).
Metzner *262* (37a).
Michael *131* (24); *141* (40); *150* (24); *274* (40); *1071* (11); *2227* (5).
Millar *NGF 14443* (34); *NGF 23654* (18); *NGF 23657* (12); *NGF 23669* (18); *NGF 40660* (31); *NGF 40671*, *NGF 40699* (33); *NGF 40761* (39); *NGF 40818* (37b).
Millar & van Royen *NGF 18749* (12).
Millar & Womersley *NGF 12248* (12).
Monterie *4*, *50* (42).
Mooney *1353* (42).
Moriarty *819* (22).
Mouret *99* (42).
Mousset *1037* (37a).
Mukharjee *24* (42).
Muller *1610* (42).

Nakahara *702* (42).
Nauen *SF 37658* (42).
Netherlands Indies Forest Service (*NIFS*), the following by anonymous collectors: *Ja 1748* (37a); *Ja 1936* (42); *Ja 2153*, *Ja 2177* (37a); *Ja 2377* (42); *Ja 2573*, *Ja 3562*, *Ja 3816* (37a); *Ja 3984*, *Ja 4011*, *bb 5232*, *bb 8764* (42); *bb 24984*, *bb 26292* (37a).
Noe *200*, *270* (42).
Noerkas *Exped. van Vuuren 279* (37a).

Ogata *KEP 105017* (42).

Williams *606* (42).
Wilson *710* (41).
Winckel *10, 660β* (37a); *1815β, 1851β* (42).
Winit *1740* (42).
Wirawan *102, 211* (42).
Womersley *NGF 4364* (20); *NGF 4466* (39); *NGF 4490, NGF 4873, NGF 6026* (20); *NGF 6049* (25); *NGF 9427* (20); *NGF 11247* (29); *NGF 11383* (20); *NGF 11720* (25); *NGF 14125* (20); *NGF 14127* (25); *NGF 15230* (12); *NGF 17911, NGF 19190* (37c); *NGF 19325* (37b); *NGF 24501* (18); *NGF 24642* (20); *NGF 24903* (37c); *NGF 37188* (20).
Womersley & Floyd *NGF 6942* (39).
Womersley & Millar *NGF 8337* (37c); *NGF 8556* (37b).
Womersley, van Royen & Versteegh *NGF 5998* (20).
Womersley & Sleumer *NGF 13906, NGF 13918* (12); *NGF 13938* (18).
Womersley & Woolliams *NGF 12384* (39); *NGF 37080, NGF 37090* (26).
Wood, D. D., *2474* (42).
Wood, G. H. S., *SAN 17199, Kepong Field No. 76118* (42).
Worthington *49, 141, 1579, 1754, 2864* (42).

Yates *2170, BS 36320* (42).

Zollinger *402, 402A, 643, 1699* (42); *2530* (37a).

HERBARIUM AUSTRALIENSE
DIVISION OF PLANT INDUSTRY
C.S.I.R.O.
CANBERRA, AUSTRALIA 2601

A NUMERICAL-TAXONOMIC STUDY OF THE SUBTRIBE NASSAUVIINAE (COMPOSITAE, MUTISIEAE)

JORGE VICTOR CRISCI

PLANTS BELONGING TO GENERA of the subtribe Nassauviinae (Compositae, Tribe Mutisieae) are an important component of the Andean flora of South America. Several species of Nassauviinae are dominant elements of extended areas, such as *Nassauvia axillaris* in Patagonia; *Proustia cuneifolia* in the phytogeographical region of Prepuna (Cabrera, 1971c), and *Proustia ilicifolia* in the Mediterranean region of Chile.

Several genera of the subtribe have been monographed recently, among them *Panphalea* [as *Pamphalea*] (Cabrera, 1953a), *Proustia* (Fabris, 1968), and *Perezia* (B. S. Vuilleumier, 1969). The arrangement of the genera in the subtribe, however, is very unclear. This has prompted me to undertake the present study, because I thought that numerical techniques could profitably be applied to quantify the taxonomic distances between the genera.

The limits of the genera of the Nassauviinae have been determined on the basis of my personal knowledge and published works on the subtribe by others. Two unresolved problems remain after following this procedure; first, a number of species continue to be hard to place in the classically accepted genera, and second, the relationship between the genera is still uncertain.

This paper reports the results of a numerical study undertaken in an attempt to solve these problems.

CONCEPT OF GENUS

Generic concepts have recently been discussed from various points of view by several biologists, notably Anderson (1940), Greenman (1940), Bartlett (1940), Camp (1940), Sherff (1940), Lawrence (1953), Bailey (1953), Eames (1953), Cave (1953), Mason (1953), Rollins (1953), Tutin (1956), Stebbins (1956), Cain (1956), Anderson (1957), Michener (1957), Inger (1958), Solbrig (1960), Simpson (1961), Löve (1963), Rosen and Bailey (1963), Davis and Heywood (1963), Kirpicznikov (1968), Mayr (1969), and Legendre and Vaillancourt (1969). Nevertheless, a few points might be pertinent to the problem under consideration. They also will illustrate my ideas about these matters and the underlying principles of this work.

Definition of any taxonomic category is very difficult, but probably no taxonomic category causes as much difficulty as the genus. Since there is no operational definition available, one is forced to adopt a pragmatic definition: the genus is the lowest higher category and the lowest of all categories established strictly by comparative data; it may contain a single species, or a monophyletic group of species; it is separated from other taxa of the same rank (other genera) by a decided gap (Cain, 1956; Mayr, 1969).

There are no taxonomic characters which prove generic distinctness. Characters useful in one family for delimitation of genera may be useful in other families only for delimiting sections or species, or they may have no taxonomic value.

Recognition of a genus is generally based on the occurrence of correlated character complexes.

Delimitation of genera is largely determined by an author's concepts and is therefore somewhat subjective. It also is likely to be influenced by traditional usage in a particular family.

In the Compositae the tendency has been to distinguish many genera. In a family as large and homogeneous as this one, it is difficult to obtain a good understanding of large genera, e.g., *Senecio*, *Haplopappus*, *Baccharis*, *Solidago*, etc., while smaller groups (which are not necessarily *too* small) can be better understood. Furthermore, "small" genera are more likely to represent natural groups, that is to say, phylogenetic units.

The criteria used in this paper to determine generic limits in the Nassauviinae are the following: each genus should be (1) internally homogeneous; (2) separated from the other genera by a discontinuity (gap); (3) consistent with the evolutionary concept (phylogenetic units); and (4) consistent with the traditional usage of the concept of genus in the family Compositae. If after use of these criteria there were several alternate ways of delimiting the genera, the same principles were used as in the recognition of any scientific theory: "Where alternatives are available, we stand by the theory or concept that is most useful, the one that generalizes the most observations, and permits the most reliable predictions" (Inger, 1958: 383).

Finally the subtribe Nassauviinae serves as another example of Stebbins's (1956: 242) observations: "They make it impossible for us to erect a system of genera in which all intergeneric gaps have the same degree of validity from the standpoint of interspecific relationships."

In the manner presented above, the limits of the genera of Nassauviinae have been determined on the basis of the criteria described. Twenty-two genera were accepted. Four species of uncertain parentage were difficult to place in these genera, and for the purposes of this paper these critical taxa were treated as monotypic genera.

Each of the 26 "genera" was considered to be a basic unit possessing a "pool" of characters. In reality each genus includes one or more species and each species is composed of a number of populations, but in this case all taxa below the rank of genus contributed independently to that "pool." The boundaries of our units are the generic boundaries, and we considered each of these units potentially able to produce any of the characters that its components (species) have.

Macrachaenium, *Proustia*, *Lophopappus*, and *Calopappus* were included

TABLE 1. **List of Revisionary Studies of Genera Currently included in the subtribe Nassauviinae.**

GENUS	REVISIONARY STUDIES
PEREZIA Lagasca	B. S. Vuilleumier (1969)
ACOURTIA D. Don	Bacigalupi (as *Perezia* section *Acourtia*, 1931)
NASSAUVIA Commerson ex Jussieu	Cabrera (partial, 1971)
TRIPTILION Ruiz & Pavon	Crisci (in preparation)
LEUCHERIA Lagasca	Crisci (in preparation)
MOSCHARIA Ruiz & Pavon	Crisci (1974b)
OXYPHYLLUM Philippi	monotypic
POLYACHYRUS Lagasca	Ricardi (in preparation)
MARTICORENIA Crisci	monotypic
LEUNISIA Philippi	monotypic
MACRACHAENIUM Hooker f.	monotypic
PLEOCARPHUS D. Don	monotypic
JUNGIA Linnaeus f.	Cerrate (partial, 1951)
TRIXIS Browne	Cabrera (partial, 1936), Loja (partial, 1969), Anderson (partial, 1972).
AMEGHINOA Spegazzini	monotypic
DOLICHLASIUM Lagasca	monotypic
PANPHALEA Lagasca	Cabrera (1953a)
HOLOCHEILUS Cassini	Cabrera (1968)
LOPHOPAPPUS Rusby	Cabrera (1953b)
PROUSTIA Lagasca	Fabris (1968)
CEPHALOPAPPUS Nees & Martius	monotypic
CALOPAPPUS Meyen	Crisci (in preparation)

among the 22 genera accepted, but some authors have placed these four genera in other subtribes of the Mutisieae.

Both *Proustia* and *Macrachaenium* have sometimes been placed in the Mutisiinae (Hoffmann, 1893; Cabrera, 1961) because of their rounded styles. But for each genus the presence of flowers with bilabiate corollas, tailed anthers, and the type of exine stratification show that its position in Nassauviinae is not unnatural. Species of *Lophopappus* also have rounded styles and in some there are 5-partite corollas, characters which have led Cabrera (1961) to place this genus in an uncertain position (Mutisiinae or Gochnatiinae), but the presence of predominantly bilabiate corollas, tailed anthers, and the exine stratification again indicate *Lophopappus* is best placed in Nassauviinae.

De Candolle (1838) was the only author who excluded the genus *Calopappus* from the Nassauviinae, but its truncate style, bilabiate corollas, tailed anthers, and the exine stratification indicate *Calopappus* is also best placed in Nassauviinae.

METHODS

A thorough search of the literature on the morphology, phytogeography, and taxonomic history of the subtribe and of each group was undertaken.

TABLE 2. **Chromosome numbers of members of the subtribe Nassauviinae.**

TAXON	*n*	2*n*	REFERENCES
ACOURTIA (sub *Perezia* sect. *Acourtia*)			
A. microcephala		54	Raven, P. (ex Vuilleumier, B. S. 1969).
A. thurberii		54	Vuilleumier, B. S. 1969.
A. nudicaulis	28		Powell, M., *et al.* [in press].
HOLOCHEILUS			
H. pinnatifidus (sub *Trixis pinnatifida*)	11		Coleman, J. R. 1968.
JUNGIA			
J. paniculata		36	Diers, L. 1961.
MOSCHARIA			
M. pinnatifida	20		Crisci, J. V. unpublished.
LEUCHERIA			
L. suaveolens	20		Moore, D. 1967.
L. hahnii	19 & 20		Moore, D. unpublished.
L. thermarum	20		Crisci, J. V. unpublished.
L. glacialis	20		Crisci, J. V. unpublished.
L. millefolium	20		Crisci, J. V. unpublished.
L. rosea	20		Crisci, J. V. unpublished.
L. runcinata	20		Crisci, J. V. unpublished.
L. achillaeifolia	19 or 20		Crisci, J. V. unpublished.
MARTICORENIA			
M. foliosa	22		Crisci, J. V. 1974.
NASSAUVIA			
N. darwinii	11		Moore, D. unpublished.
N. gaudichaudi	22		Moore, D. 1967.
N. magellanica	11		Moore, D. unpublished.
N. serpens	11		Moore, D. 1967.
PEREZIA			
P. multiflora		16	Diers, L. 1961; Vuilleumier, B. S. 1969. Sneider (ex B. S. Vuilleumier, 1969).
P. squarrosa subsp. *cubaetensis*	4		Coleman, J. R. 1968.
P. pungens		24	Heiser, C. 1963.
P. ciliaris		24	Vuilleumier, B. S. 1969.
P. carduncelloides	12		Sneider (ex B. S. Vuilleumier, 1969).
P. ciliosa		24	Vuilleumier, B. S. 1969.
P. calophylla		24	Vuilleumier, B. S. 1969.
P. coerulescens		24	Vuilleumier, B. S. 1969; Diers, L. 1961.
P. recurvata		24 or 26	Vuilleumier, B. S. 1969.
P. recurvata	12		Moore, D. unpublished.
P. magellanica		24	Moore, D. unpublished.
P. pilifera		16	Moore, D. unpublished.

TABLE 2. **Chromosome numbers of members of the subtribe Nassauviinae.** (*continued*)

TAXON	*n*	*2n*	REFERENCES
PROUSTIA			
P. ilicifolia		54	Covas, G., & B. Schnack, 1946.
TRIXIS			
T. californica	27		Turner, B. L., *et al.* 1962. Powell, M., *et al.* [in press]. Powell, M., & B. L. Turner, 1963.
T. radialis	27		Turner, B. L., *et al.* 1962. Powell, M., *et al.* [in press].
T. paradoxa		54	Diers, L. 1961.
T. nelsonii	27		Powell, M., *et al.* [in press].
T. inula	27		Raven, P. (ex C. Anderson, 1972).
T. inula		47 ± 3	Turner, B. L., *et al.* (ex C. Anderson, 1972).
T. antimenorrhoea var. *discolor*	27		Powell, M., *et al.* [in press].

These data were augmented by morphological studies of the genera based on herbarium material. All the organs were boiled in water before observation. Some pollen grains were acetolized (Erdtman, 1960), other pollen grains were placed in 95 per cent ethanol with basic fuchsin and mounted in glycerine jelly. The styles were treated with cloral-hydrate for 24 to 48 hours. Other styles were examined with a Scanning Electron Microscope (SEM). Taken directly from the herbarium material, the styles were placed on specimen holders, then coated with 50 Å to 100 Å carbon and about 200 Å to 300 Å gold-palladium alloy for conductivity. Finally the specimens were photographed using high resolution SEM, AMR model 900.

The abbreviations for herbaria are taken from the fifth edition of the Index Herbariorum (Lanjouw & Stafleu, 1964).

The computational work was done in an IBM system 360–70, at the Computing Center of the Office of Information Technology of Harvard University.

NUMERICAL TECHNIQUES

Twenty-six OTU's (Operational Taxonomic Units, *fide* Sneath & Sokal, 1973), including 22 genera and 4 critical taxa, were accepted.

Data accumulation. All characters used were qualitative or transformed to it and divided into their possible states (e.g., character: flower color; states: blue, red, yellow, etc.). Each one of these states was scored for presence (1) or absence (0). The decision to score the states of the characters in this way was governed in part by the requirements of the logic of the work, which deals with units (genera) able (*or not*) to produce more than one state in one OTU.

In some cases such as: "receptacle pubescent (1) or not (0)" it is found that some genera include both species with pubescent receptacle and species with glabrous receptacle. It is clear that one state will not be enough to cover the possibilities and for this reason it was scored in the following way:

receptacle pubescent (1) or not (0)
receptacle glabrous (1) or not (0)
receptacle glabrous *and* pubescent (1) or not (0)

This seems to be logically acceptable and a better presentation of the real situation.

The characters' states were scored for each OTU as follows:

(1) Pappus paleaceous (1) or not (0).
(2) Pappus setose (1) or not (0).
(3) Pappus plumose (1) or not (0).
(4) Pappus in one series (1) or not (0).
(5) Pappus white (1) or not (0).
(6) Pappus white *and* colored (1) or not (0).
(7) Pappus colored (1) or not (0).
(8) Involucre campanulate (1) or not (0).
(9) Involucre hemispherical (1) or not (0).
(10) Involucre cylindrical (1) or not (0).
(11) Involucre turbinate (1) or not (0).
(12) Involucre with 1 to 2 rows of bracts (1) or not (0).
(13) Involucre with 1 to 2 *and* 3 to 7 rows of bracts (1) or not (0).
(14) Involucre with 3 to 7 rows of bracts (1) or not (0).
(15) Involucre with more than 5 bracts (1) or not (0).
(16) Involucre with foliaceous bracts (1) or not (0).
(17) Involucre with foliaceous *and* nonfoliaceous bracts (1) or not (0).
(18) Involucre with nonfoliaceous bracts (1) or not (0).
(19) Involucral bracts with wings (1) or not (0).
(20) Involucral bracts with spines (1) or not (0).
(21) Involucral bracts dimorphic (1) or not (0).
(22) Involucre more than 3 mm. high (1) or not (0).
(23) Involucral bracts with mucro (1) or not (0).
(24) Involucral bracts with *and* without mucro (1) or not (0).
(25) Involucral bracts without mucro (1) or not (0).
(26) Inflorescence solitary (1) or not (0).
(27) Inflorescence a cyme or panicle (1) or not (0).
(28) Inflorescence a glomerulum or pseudocephalium (1) or not (0).
(29) Capitula sessile (1) or not (0).
(30) Capitula subsessile (1) or not (0).
(31) Capitula with pedicel (1) or not (0).
(32) Pollen grains prolate (1) or not (0).
(33) Pollen grains subprolate (1) or not (0).
(34) Pollen grains spheroidal-prolate (1) or not (0).

(35) Pollen grains oblate (1) or not (0).
(36) Colpi membrane with sexine process (1) or not (0).
(37) Pollen grains with polar elevations (1) or not (0).
(38) Exine Oxyphyllum-a type (1) or not (0) [see text].
(39) Exine Oxyphyllum-b type (1) or not (0).
(40) Exine Trixis type (1) or not (0).
(41) Exine Proustia type (1) or not (0).
(42) Exine Cephalopappus type (1) or not (0).
(43) Exine Nassauvia remyana type (1) or not (0).
(44) Present in West Indies (1) or not (0).
(45) Present in Andes of South America, Patagonia (1) or not (0).
(46) Present in South Brazil, Uruguay, Paraguay, NE of Argentina (1) or not (0).
(47) Present in tropical South America (1) or not (0).
(48) Present in Central and North America (1) or not (0).
(49) Leaves entire (1) or not (0).
(50) Leaves entire *and* partite (1) or not (0).
(51) Leaves partite (1) or not (0).
(52) Leaves with spines (1) or not (0).
(53) Leaves with *and* without spines (1) or not (0).
(54) Leaves without spines (1) or not (0).
(55) Lower leaves sessile (1) or not (0).
(56) Leaves six times or more longer than wide (1) or not (0).
(57) Achenes six times or more longer than wide (1) or not (0).
(58) Leaf bases cordiform (1) or not (0).
(59) Achenes with "rostrum" (1) or not (0).
(60) Achenes pubescent (1) or not (0).
(61) Achenes pubescent *and* glabrous (1) or not (0).
(62) Achenes glabrous (1) or not (0).
(63) Style Proustia type (1) or not (0) [see text].
(64) Style Acourtia type (1) or not (0).
(65) Style Leucheria type (1) or not (0).
(66) Style Onoseris stricta type (1) or not (0).
(67) Woolly pubescence present (1) or not (0).
(68) Receptacle with paleae in all flowers (1) or not (0).
(69) Receptacle with paleae only in marginal flowers (1) or not (0).
(70) Receptacle without paleae (1) or not (0).
(71) Receptacle pubescent (1) or not (0).
(72) Receptacle glabrous *and* pubescent (1) or not (0).
(73) Receptacle glabrous (1) or not (0).
(74) Habit of herbs (1) or not (0).
(75) Habit of shrubs (1) or not (0).
(76) Habit of vines (1) or not (0).
(77) Capitula with 2 to 5 flowers (1) or not (0).
(78) Capitula with 6 to 14 flowers (1) or not (0).
(79) Capitula with 15 to 178 flowers (1) or not (0).
(80) Corollas pubescent (1) or not (0).
(81) Corollas 5-partite (1) or not (0).
(82) Corollas bilabiate (1) or not (0).
(83) Corollas bilabiate *and* 5-partite (1) or not (0).
(84) Corollas blue (1) or not (0).

(85) Corollas yellow (1) or not (0).
(86) Corollas orange (1) or not (0).
(87) Corollas red (1) or not (0).
(88) Corollas white (1) or not (0).
(89) Corollas violet (1) or not (0).
(90) Anthers pubescent (1) or not (0).

Doubtless there will be slight distortion in the product resulting from the comparison of genera with different numbers of species, since the genera with the greater numbers of species may (but not always) have greater possibilities of producing more character states than those with fewer species. The project might have been more objective if the genera had the same number of species, but it is not likely that the result would have been seriously affected.

Data Processing. Given a basic data matrix (BDM) of 90 character states by 26 OTU's, the data were analyzed by three methods of numerical taxonomy. The aim of the use of more than one method is to minimize the defects of the technique. The various schemes produced can be compared in the search for common features. If such common features are found their validity is enhanced since they seem independent of the method used.

An eclectic approach was already used by Solbrig (1969) in the genus *Gutierrezia* (Compositae). As in every study based on methods of numerical taxonomy, each method included the following steps:

1) The obtaining of a similarity coefficient ("distance" between each pair of the 26 OTU's), this from a BDM.
2) The linking together (clustering) of the OTU's in a two-dimensional graph on the basis of the similarity coefficients obtained in (1).

METHOD 1. The similarity coefficient D (A, B) used here is the sum, over all character states, of the absolute values of the differences between the character states in OTU A and OTU B. In the case where X (A, i) denotes the character state "i" for OTU A,

$$D\ (A, B) = \Sigma \mid X\ (A, i) - X\ (B, i) \mid .$$

The resulting OTU × OTU "distance table" (an n × n taxa matrix), TABLE 3, which gives the distance between all taxa, served as input in the calculation of a "Prim network." The Prim network technique was developed by R. C. Prim (1957) in order to determine the shortest possible network of direct links between a given set of telephone terminals. His technique can be applied as well to problems in systematic biology (Edwards & Cavalli-Sforza, 1964; Solbrig, 1969). Basically the procedure consists of choosing the shortest links connecting any two OTU's, and then by a process of elimination adding more links until all OTU's are connected in a network. This allows the construction of a two-dimensional graph representing the possible taxonomic structure.

METHOD 2. The similarity coefficient used in this method is the "distance measure" defined by Rogers and Tanimoto (1960). This quantity D (A, B) is the negative logarithm to the base 2, of the ratio of the number of character states possessed in common by OTU's A and B to the number of distinct character states possessed by A and B.

$$D(A, B) = -\log_2 \frac{\text{Character states in common in A and B}}{\text{Distinct character states possessed by A and B}}$$

The resulting OTU × OTU "distance table" (TABLE 4) served as input to the clustering algorithm developed by Van Rijsbergen. This algorithm operates on a similarity coefficient to generate the clusters of the numerically stratified hierarchy (phenogram) specified by the single-link method. The clusters are generated level by level, starting at the lowest, so that the algorithm is of the agglomerative type. The detailed instructions for doing this are given by Van Rijsbergen (1970).

METHOD 3. The "distance table" (TABLE 3) obtained in method 1 was used as input to the clustering algorithm of Van Rijsbergen used in method 2.

TAXONOMIC HISTORY

In 1756 Patrick Browne described the genus *Trixis* in his *The Civil and Natural History of Jamaica* . . . . However, Browne did not use binomials in the first edition of his work, and in 1766 Crantz named Browne's plant *Trixis inula*. This was the first genus and the first species described in the subtribe Nassauviinae.

Several other genera were described during the next fifty years; *Jungia* Linn. f. (1781), *Nassauvia* Comm. ex Juss. (1789), *Trinacte* Gaertn. (1791), *Moscharia* Ruiz & Pavon (1794), *Triptilion* Ruiz & Pavon (1794), and *Rhinactina* Willd. (1807).

In 1811, Lagasca grouped several genera into his order "Chaenanthophorae." This order included three "sections"; the first section included those genera which are the nucleus of the subtribe Nassauviinae. The presence of only bilabiate corollas and tailed anther appendages were the diagnostic characters for his first section, which contained fourteen genera, including ten new ones, divided into two groups, those with the receptacle glabrous and those with the receptacle pubescent. Of these genera, ten are recognized today; the other four are treated as synonyms of some of these.

In 1812, Alphonse de Candolle published a paper which dealt with a new assemblage of ligulate Compositae, the Labiatiflorae. This paper was the result of research parallel with Lagasca's work on the Chaenanthophorae. The interesting history of these two parallel works has been described by Bacigalupi (1931) and by B. S. Vuilleumier (1969).

In 1817 Henri Cassini divided the "Chaenanthophorae" (or "Labiatiflorae") into two tribes on the basis of the shape of the style. His first tribe is the Mutisiées, with the stylar branch tips rounded (corresponding to sections 2 and 3 of Lagasca's Chaenanthophorae). The second tribe with

TABLE 3. Matrix of "distances" between OTU's obtained by summing, over all character states, the absolute values of the differences between the character states in each pair of OTU's (used in METHODS 1 and 3).

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
1. Perezia	x	31	29	21	35	31	33	31	32	34	33	30	33	26	32	23	19	27	28	33	29	25	30	30	29	29
2. Nassauvia		x	8	24	16	30	16	28	37	31	38	33	38	33	37	26	28	32	33	34	34	32	13	31	38	28
3. Triptilion			x	28	14	30	16	32	37	31	38	37	38	31	35	26	28	32	33	32	34	34	13	31	38	26
4. Leucheria				x	28	24	22	22	31	19	26	25	34	25	29	26	18	28	31	30	34	28	29	31	28	30
5. Moscharia					x	30	10	26	35	27	32	35	36	25	31	18	22	34	35	32	32	34	19	29	36	30
6. Oxyphyllum						x	28	24	35	25	30	35	32	23	29	30	30	28	27	40	32	30	29	29	32	28
7. Polyachyrus							x	28	37	25	32	31	36	29	33	26	24	30	29	36	30	32	23	27	36	32
8. Marticorenia								x	27	25	14	19	28	19	29	22	18	26	29	28	24	24	31	23	28	26
9. Leunisia									x	22	19	28	15	18	8	33	25	27	30	27	27	27	32	28	21	27
10. Macrachaenium										x	23	28	29	24	20	29	23	27	32	21	31	27	28	28	25	31
11. Pleocarphus											x	17	14	15	23	28	22	26	27	26	22	26	35	25	24	26
12. Jungia												x	19	28	32	31	25	27	30	31	25	21	36	26	33	29
13. Trixis													x	17	19	30	26	26	27	30	22	24	35	25	24	26
14. Ameghinoa														x	12	19	13	27	26	31	23	27	30	26	19	25
15. Dolichlasium															x	29	21	31	34	33	33	33	32	34	25	29
16. Panphalea																x	10	28	31	22	26	28	27	23	26	28
17. Holocheilus																	x	24	27	22	22	22	27	19	18	24
18. Lophopappus																		x	9	26	16	14	27	19	24	14
19. Proustia																			x	31	17	19	30	18	27	21
20. Cephalopappus																				x	26	26	25	23	20	26
21. Proustia vanillosma																					x	12	27	9	22	18
22. Acourtia																						x	27	9	24	16
23. Calopappus																							x	26	33	23
24. Gochnatia glomeriflora																								x	21	21
25. Onoseris stricta																									x	24
26. Perezia lanigera																										x

stylar branch tips truncate is the Nassauviées. This was the first use of the name, but it was not until 1819 that Cassini formally circumscribed the group as a tribe. Cassini, as did Lagasca, considered the bilabiate corollas and the tailed anthers to be important tribal characters, but he thought the truncate stylar branches were the single most unifying character. Cassini's circumscription is essentially that which is recognized today, although at the level of subtribe.

In 1825 Cassini divided the "Nassauvieae" into three sections. The first section, containing the genera *Trixis*, *Leucheria*, *Perezia*, *Jungia*, and *Panphalea*, was the most "ancient" because it showed similarities with the Senecioneae, presumably for Cassini an "ancient" group. The remaining genera, *Nassauvia*, *Triptilion*, *Polyachyrus*, *Triachne*, *Mastigophorus*, *Caloptilium*, and *Panargyrus*, were placed into a second section which Cassini considered more "specialized" than the first. The third section contained those genera which Cassini regarded as doubtful. He excluded *Proustia*, placed in this group by Lagasca, from the Nassauviées because of its rounded stylar branches.

Lessing (1830) divided the tribe "Nassauvieae" of Cassini into two subtribes, Nassauvieae and Trixideae, and here for the first time the name Nassauviinae was used at the level of subtribe (Solbrig, 1963). Bentham and Hooker (1873) retained Cassini's circumscription at the subtribal level, placing the Nassauviinae in the tribe Mutisieae. This work established the generic composition of the subtribe Nassauviinae (as well as that of the entire family) which is still used today with but minor variations. Their most important conclusions were that *Nassauvia* is closely allied to *Triptilion; Proustia*, which they reassigned to the Nassauviinae, is closest to *Perezia*; the genus *Cleanthes* (= *Holocheilus*) is a synonym of *Trixis*.

Hoffmann (1893) followed the classification of Bentham and Hooker, but like Cassini excluded *Proustia* and *Macrachaenium* from the Nassauviinae solely on the basis of their stylar branch tips. He did recognize *Cleanthes* as a genus distinct from *Trixis*.

Modern attempts to assess the systematics of the subtribe Nassauviinae have been made by Wodehouse (1929) on the basis of pollen morphology, by Jeffrey (1967), and by B. S. Vuilleumier (1969), each of these a preliminary survey of the group.

NOMENCLATURE

The list which follows is comprised of names that have been included in the Nassauviinae, with an indication of their present status. Those names printed in large and small CAPITALS are accepted in this paper. Names printed in *italics* are considered synonyms of accepted genera as indicated.

Acanthophyllum H. & A. = NASSAUVIA
ACOURTIA D. Don
AMEGHINOA Spegazzini

Bowmania Gardner = TRIXIS
Bridgesia Hooker = POLYACHYRUS

Caloptilium Lagasca = NASSAUVIA
CALOPAPPUS Meyen
Castra Vellozo = HOLOCHEILUS; TRIXIS (pro parte)
CEPHALOPAPPUS Nees & Martius
Clarionea Lagasca ex DC. = PEREZIA

Clarionea Cassini = PEREZIA
Clarionema Philippi = PEREZIA
Cleanthes D. Don = HOLOCHEILUS
Clybatis Philippi = LEUCHERIA
Chabraea DC. = LEUCHERIA

Diaphoranthus Meyen = POLYACHYRUS
DOLICHLASIUM Lagasca
Drozia Cassini = PEREZIA
Dumerilia Lagasca ex DC. = JUNGIA
Dumerilia Lessing = PEREZIA

Elizaguirrea Romy = LEUCHERIA

Gastrocarpha D. Don = MOSCHARIA

Heteranthus Cassini = PEREZIA
HOLOCHEILUS Cassini
Homanthis HBK. = PEREZIA
Homoianthus DC. = PEREZIA

JUNGIA Linnaeus f.

LEUCHERIA Lagasca
Lasiorrhiza Lagasca = LEUCHERIA
LEUNISIA Philippi
LOPHOPAPPUS Rusby

MACRACHAENIUM Hooker f.
MARTICORENIA Crisci
Martrasia Lagasca = JUNGIA
Martrasia Cassini = JUNGIA
Mastigophorus Cassini = NASSAUVIA
Mimela Philippi = LEUCHERIA

MOSCHARIA Ruiz & Pavon
Moschifera Molina = MOSCHARIA
Mosigia Sprengel = MOSCHARIA

NASSAUVIA Commerson ex Jussieu

OXYPHYLLUM Philippi

Panargyrum D. Don = NASSAUVIA
Panargyrus Lagasca = NASSAUVIA
PANPHALEA Lagasca
Pentanthus Lessing [non H. & A.; non Raf.] = NASSAUVIA
PEREZIA Lagasca
Perezia DC. = PEREZIA Lagasca
Platycheilus Cassini = HOLOCHEILUS
PLEOCARPHUS D. Don
POLYACHYRUS Lagasca
Portalesia Meyen = NASSAUVIA
Prionanthes Schnark = TRIXIS
PROUSTIA Lagasca
Ptilurus D. Don = LEUCHERIA

Rhinactina Willd. = JUNGIA

Sphaerocephalus Lagasca ex DC. = NASSAUVIA
Strongyloma DC. = NASSAUVIA

Tenorea Colla = TRIXIS
Triachne Cassini = NASSAUVIA
Trianthus Hooker = NASSAUVIA
Trinacte Gaertner = JUNGIA
TRIPTILION Ruiz & Pavon
TRIXIS Browne

OTHER NAMES THAT HAVE BEEN INCLUDED IN THE NASSAUVIINAE

Bertolonia DC. ex Cassini, Opus. Phyt. **2**: 153. 1826. A name attributed to De Candolle by Cassini and considered a synonym of *Lasiorrhiza* Lag. In Ann. Mus. Paris **19**: 65, 71. *Pl. 5* (*Tab. XIV*). 1812, De Candolle described the new genus *Chabraea* and made the combination *Chabraea purpurea* based on *Perdicium purpureum* Vahl. He referred to *Tab. XIV* on the facing page (from 71), an illustration labeled *Bertolonia purpurea*, a name which does not occur anywhere else in that paper.

Cassiopea D. Don, Trans. Linn. Soc. I. **16**: 215. 1830. This name is frequently listed as a synonym of *Leucheria*, but it was actually used only as a sectional name by Don and by De Candolle.

Clariona Sprengel, Linn. Syst. Veg. ed. 16. **3**: 504. 1826. An orthographic variant of *Clarionea* Lag. ex DC.

Clarionia D. Don, Trans. Linn. Soc. I. **16**: 204. 1830. An orthographic variant of *Clarionea* Lag. ex DC.

Frageria Delile ex Steudel, Nomencl. ed. 2. **1**: 645. 1840. A nomen nudum attributed to Delile by Steudel who considered it a synonym of *Lasiorrhiza* Lag.

Homoeanthus Sprengel, Linn. Syst. Veg. ed. 16. **3**: 503. 1826. An orthographic variant of *Homoianthus* Bonpl. ex DC. Ann. Mus. Paris **19**: 65.

Isanthus DC. Prodr. 7: 63. 1838. An invalid name listed in the synonymy of *Homoianthus* by De Candolle.

Maclovia DC. ex Steudel, Nomencl. ed. 2. **1**: 338. 1840. Listed in the synonymy of *Chabraea* DC. by Steudel, but published by De Candolle only as a section of *Chabraea.*

Microspermum Lag. Gen. Sp. Nov. 25. 1816. Although this genus has been included in the Nassauvinae by several authors, it is a member of the Helenieae.

Moscaria Persoon, Synopsis Plantarum **2**: 379. 1807. An orthographic variant of *Moscharia* Ruiz & Pavon.

Pentanthus H. & A., Hooker, Comp. Bot. Mag. **1**: 32. 1835 (non Lessing, nec Raf.). This taxon was cited by De Candolle as a member of the Nassauvieae, but is, rather, a member of the Senecioneae and at present is considered a synonym of *Paracalia* Cuatrecasas.

Perezia LaLlave & Lexarza ex DC. Prodr. 7: 65. 1838. A name listed by De Candolle as a synonym of *Acourtia* D. Don.

Pogonura DC. ex Lindley, Introd. Nat. Syst. ed. 2. 263. 1836. A nomen nudum attributed to De Candolle by Lindley but apparently never published by De Candolle. Frequently listed as a synonym of *Perezia* Lagasca.

Scolymanthus Willd. ex DC. Prodr. 7: 63. 1838. An invalidly published name listed by De Candolle only in the synonymy of *Homoianthus* DC.

Leukeria Endl. Enchiridion 249. 1841. An orthographic variant for *Leucheria* Lagasca.

Leuceria is an orthographic variant of *Leucheria* Lagasca which has been used rather consistently since 1830 when D. Don first took it up. In addition to Lagasca's original description (1811) and Don's paper of 1830, De Candolle in 1812 published a description of the genus using another orthographic variant, *Leucaeria*, and Lessing in 1830 called it *Leuchaeria.* There is no provision in the Code for changing Lagasca's original spelling of the name.

Anargyrum Steudel, Nomencl. ed. 2. **1**: 84. 1840. A nomen nudum attributed to De Candolle by Steudel and considered a synonym of *Nassauvia.* It was published by De Candolle (Prodr. **7**: 54) in a subgeneric category of *Panargyrum.*

Nassovia Batsch, Tab. Affin. Reg. Veg. 251. 1802. An orthographic variant of *Nassauvia* Comm. ex Jussieu.

Piptostemma Spach, Hist. Veg. Phan. **10**: 34. 1841. A nomen nudum attributed to D. Don by Spach and considered a synonym of *Nassauvia*, but apparently never published.

Table 4. **Matrix of "distances" between OTU's obtained using the "distance measure" defined by Rogers and Tanimoto** (used in Method 2).

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
1. Perezia	x	1.58	1.42	1.10	2.17	1.86	1.91	1.78	1.78	1.80	1.83	1.54	1.70	1.37	1.68	1.34	1.00	1.38	1.34	1.89	1.68	1.32	1.58	1.76	1.53	1.68
2. Nassauvia		x	0.42	1.10	0.79	1.50	0.74	1.33	1.74	1.55	1.90	1.40	1.86	1.61	1.74	1.37	1.36	1.51	1.65	1.74	1.74	1.63	0.55	1.61	1.92	1.43
3. Triptilion			x	1.46	0.87	1.64	0.91	1.66	2.02	1.69	2.20	1.80	2.14	1.64	1.78	1.50	1.48	1.63	1.79	1.78	1.90	1.88	0.61	1.75	2.10	1.45
4. Leucheria				x	1.45	1.14	1.02	1.17	1.63	0.94	1.30	1.17	1.75	1.41	1.53	1.48	0.94	1.42	1.56	1.63	1.84	1.53	1.44	1.71	1.38	1.63
5. Moscharia					x	1.76	0.51	1.33	2.05	1.58	1.72	1.71	2.05	1.41	1.79	1.17	1.26	2.00	2.18	1.92	1.92	2.02	1.03	1.76	2.29	1.79
6. Oxyphyllum						x	1.42	1.29	2.10	1.32	1.66	1.76	1.74	1.36	1.61	1.79	1.75	1.37	1.43	2.39	1.72	1.61	1.50	1.58	1.79	1.50
7. Polachyrus							x	1.45	2.02	1.28	1.61	1.42	1.90	1.64	1.78	1.61	1.37	1.53	1.58	2.02	1.66	1.77	1.15	1.53	1.97	1.78
8. Marticorenia								x	1.53	1.35	0.82	0.97	1.55	1.00	1.53	1.26	0.97	1.40	1.66	1.53	1.32	1.33	1.53	1.29	1.58	1.42
9. Leunisia									x	1.15	1.00	1.30	0.83	1.00	0.41	1.94	1.35	1.40	1.66	1.42	1.53	1.53	1.64	1.61	1.16	1.53
10. Macrachaenium										x	1.12	1.33	1.48	1.32	1.06	1.72	1.28	1.33	1.68	1.06	1.66	1.45	1.45	1.53	1.19	1.66
11. Pleocarphus											x	0.71	0.64	0.79	1.28	1.64	1.21	1.36	1.41	1.28	1.18	1.29	1.92	1.35	1.32	1.37
12. Jungia												x	0.80	1.28	1.58	1.63	1.24	1.29	1.43	1.39	1.22	1.00	1.68	1.28	1.63	1.39
13. Trixis													x	0.88	1.08	1.61	1.38	1.25	1.30	1.45	1.08	1.11	1.88	1.24	1.30	1.26
14. Ameghinoa														x	0.63	1.03	0.67	1.37	1.33	1.61	1.19	1.30	1.50	1.36	1.03	1.29
15. Dolichlasium															x	1.58	1.06	1.50	1.77	1.75	1.75	1.74	1.53	1.84	1.26	1.53
16. Panphalea																x	0.55	1.45	1.72	1.16	1.36	1.48	1.47	1.23	1.52	1.47
17. Holocheilus																	x	1.24	1.38	1.15	1.15	1.17	1.35	1.03	1.00	1.25
18. Lophopappus																		x	0.44	1.30	0.76	0.64	1.30	0.91	1.15	0.68
19. Proustia																			x	1.66	0.83	0.78	1.55	0.88	1.40	1.00
20. Cephalopappus																				x	1.32	1.33	1.32	1.19	1.06	1.32
21. Proustia vanillosma																					x	0.55	1.42	0.37	1.16	0.75
22. Acourtia																						x	1.43	0.43	1.28	0.71
23. Calopappus																							x	1.39	1.70	1.22
24. Gochnatia glomeriflora																								x	1.13	0.90
25. Onoseris stricta																									x	1.26
26. Perezia lanigera																										x

RESULTS

The tribe Mutisieae is represented in both hemispheres, but most of the genera occur in the Southern Hemisphere with a great center of concentration in the southern part of the Andes of South America. Centers of lesser importance are in Mexico, in the mountains of China, and in tropical and southern Africa. In Europe there occurs only one genus, *Berardia*, its position in the Mutisieae doubtful since it presents combinations of the usual characters of the Mutisieae and of the Cynareae. The tribe Mutisieae includes about 86 genera and nearly 1000 species; these have been divided by various authors into 3 to 5 subtribes — Bentham & Hooker (1873), Barnadesieae, Onoserideae, Gochnatieae, Gerbereae, and Nassauvieae; Hoffmann (1893), Gochnatinae, Gerberinae or Mutisinae, and Nassauvinae; Cabrera (1961), Barnadesinae, Gochnatinae, Mutisinae, and Nassauvinae.

The subtribe Nassauviinae is an American group, with most genera occurring in the extratropical parts of South America. The greatest concentration of genera and of species is in the southern Andes. With the exception of *Trixis*, *Acourtia*, and *Jungia*, all of the genera of the Nassauviinae are endemic to South America. The subtribe includes about 300 species and 40 per cent of the included genera are monotypic.

Distribution and ecological conditions. Genera of the Nassauviinae occur in extratropical South America (very few in tropical parts of the continent), in Central America, in the West Indies, and in North America south of the 32nd parallel. This general area can be divided into five regions.

REGION 1: Andes of South America, north Chilean deserts, and Patagonia. Seventy per cent of the genera and species are endemic to this region. Here occur *Nassauvia*, *Triptilion*, *Leucheria*, *Moscharia*, *Oxyphyllum*, *Polyachyrus*, *Marticorenia*, *Leunisia*, *Macrachaenium*, *Pleocarphus*, *Ameghinoa*, *Dolichlasium*, *Lophopappus*, *Proustia*, *Calopappus*, and one of the critical taxa, *Perezia lanigera*. Although *Jungia*, *Trixis*, and *Perezia* are not endemic to this region, they do occur here, and most of the species of *Perezia* occur in the Andes.

Several major kinds of vegetation, each occupying numerous microhabitats, occur in the Andes, and in each of these microhabitats there are found some species of Nassauviinae. Most of this region is dry and/or at high altitudes, but it does include some moist environments, such as the páramos of Venezuela, Colombia, and Ecuador, where a few species of *Perezia* occur, and, in the south, the *Nothofagus* forest, where there occur a few species of *Perezia* and of *Leucheria* and *Macrachaenium*, which is endemic to the forest. This region is topographically young, for the final Andean uplift occurred only in the Tertiary.

REGION 2: Southern Brazil, Paraguay, Uruguay, and northeastern Argentina. Here occur *Panphalea*, *Holocheilus*, *Trixis*, *Jungia*, *Perezia*, and one of the critical taxa, *Onoseris stricta*. This is a region of plains and low mountains, with a temperate and moist climate.

Region 3: Tropical South America. There are very few species and genera of Nassauviinae in this region; those that do occur are sparsely distributed. The monotypic genus, *Cephalopappus*, endemic to the state of Bahia in Brazil, occurs in this region as do also a few species of *Trixis* and *Jungia*. The climate is warm and moist.

Region 4: Central America, Mexico, and the United States (south of the 32nd parallel). Here there occur *Acourtia*, *Trixis*, a few species of *Jungia*, and one of the critical taxa, *Gochnatia glomeriflora*. The climate is relatively warm.

Region 5: West Indies. In this region occur only two species of *Trixis*, *T. inula* and *T. divaricata*, and one of the critical taxa, *Proustia vanillosma*. The climate where these plants are found is warm and semiarid.

Since most of the species occur in regions which are dry and/or at high altitudes, with frequent frosts, they show many adaptations to xerophytic conditions. Some of these adaptations are reflected in the time of flowering, in habit, type of growth, and in seed germination. Some correspondences between habit and habitat were pointed out by B. S. Vuilleumier (1969: 20) for the genus *Perezia*, and these observations can be generalized for the majority of species of Nassauviinae.

Morphological Analysis. A. Habit: Comparative studies of the genera and species of Compositae indicate that the ancestral prototype probably was a woody plant, either a large shrub or a small tree (Carlquist, 1966). This assumption can be extended to the Nassauviinae in which occur three kinds of habit, herbaceous, shrubby, and scandent. We can further assume that the herbs and climbers have evolved from shrubby ancestors in two different lines. At the levels of both genus and species the herbaceous habit is predominant and *Perezia*, *Leucheria*, *Moscharia*, *Triptilion*, *Macrachaenium*, *Calopappus*, *Panphalea*, *Holocheilus*, *Cephalopappus*, *Polyachyrus*, and *Onoseris stricta* are all perennial or annual herbs.

Most of the species of *Nassauvia* are perennial herbs, but some are small shrubs. *Jungia* includes both shrubby and scandent species, but one, *J. stuebellii*, is herbaceous. *Acourtia* includes perennial herbs and shrubs. All of the species of *Oxyphyllum*, *Marticorenia*, *Leunisia*, *Pleocarphus*, *Ameghinoa*, *Dolichlasium*, and *Trixis* are shrubby, as is one of the critical taxa, *Gochnatia glomeriflora*. *Proustia* includes both shrubby and scandent species; one of the critical taxa, *P. vanillosma*, is scandent. *Perezia lanigera* is a cespitose shrub.

B. Pappus: In *Cephalopappus* and *Panphalea* the pappus is absent; species of both genera occur in similar habitats, in moist places near water courses, and if water is the agent of achene dispersal, it might be that the pappus has become functionally superfluous. In species of *Moscharia* and *Polyachyrus* the pappus is greatly reduced. In both genera the capitula are reduced and only 2-flowered, but an enlarged involucral bract surrounds the achenes and apparently plays a part in dispersal. An analogous case is that in *Madia*, a genus of Heliantheae, but at the level of the flower and paleae.

The pappus in genera of Nassauviinae is made up of hairs or paleae.

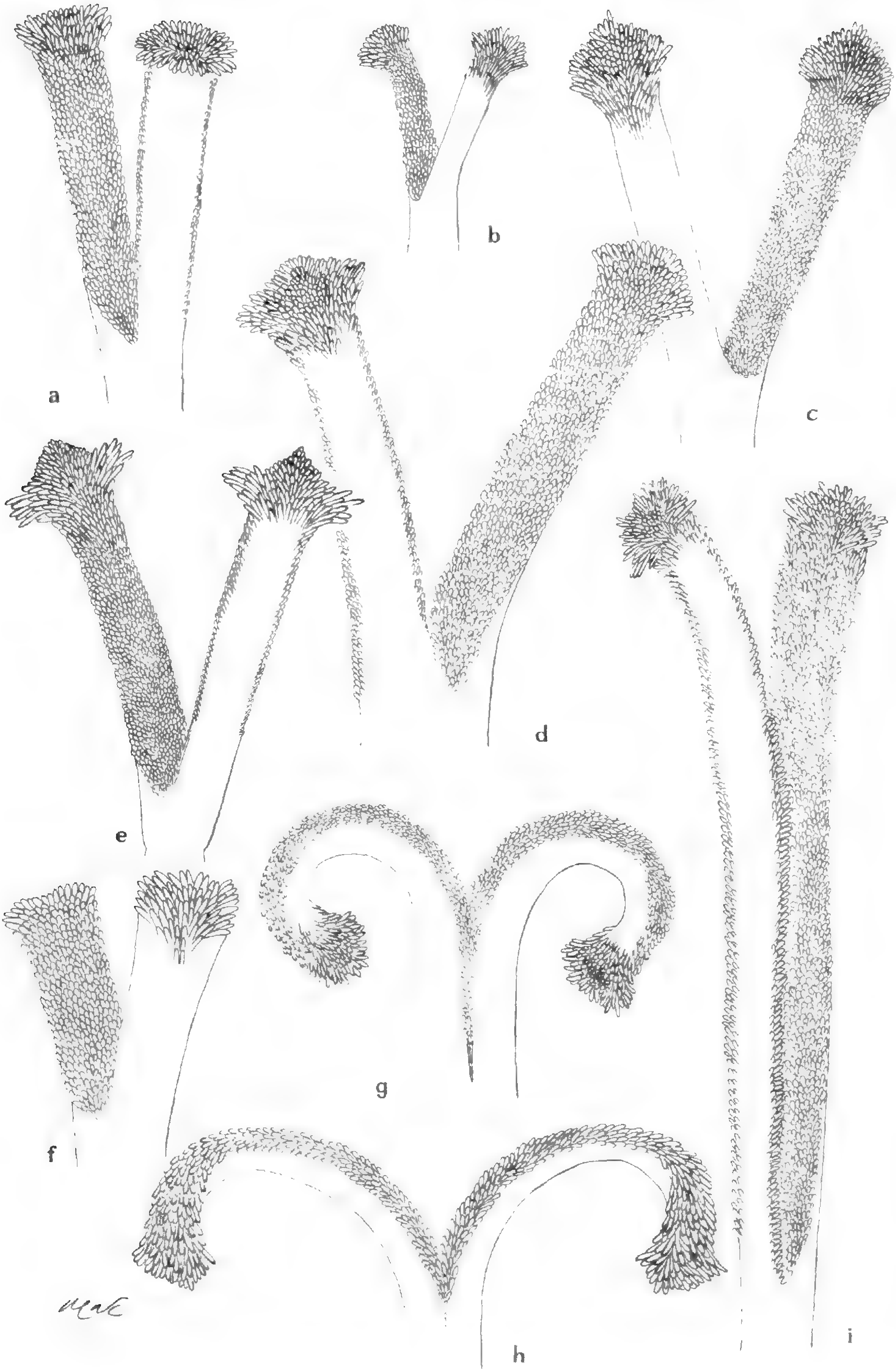


FIGURE 1. Types of styles in Nassauviinae. Truncate type: a, *Perezia magellanica*, × 35 (*Cunningham s.n.*, GH); b, *Panphalea commersonii*, × 35 (*Dusén 930*, GH); c, *Triptilion spinosum*, × 35 (*Walter 230*, GH); d, *Ameghinoa patagonica*, × 35 (*Donat 236*, GH); e, *Nassauvia magellanica*, × 35 (*Hatcher 1897*,

Chaffy pappus occurs in *Moscharia*, *Nassauvia*, *Triptilion*, and *Calopappus*. Hairy pappus can be of two kinds: setose, as in *Perezia*, *Acourtia*, *Leucheria*, *Polyachyrus*, *Leunisia*, *Pleocarphus*, *Jungia*, *Trixis*, *Ameghinoa*, *Dolichlasium*, *Holocheilus*, *Lophopappus*, *Proustia*, *Proustia vanillosma*, *Gochnatia glomeriflora*, *Onoseris stricta*, and *Perezia lanigera*, or plumose, as in *Nassauvia*, *Leucheria*, *Polyachyrus*, *Jungia*, *Oxyphyllum*, *Macrachaenium*, and *Marticorenia*. The pappus can be disposed in a single series (*Nassauvia*, *Triptilion*, *Leucheria*, *Moscharia*, *Oxyphyllum*, *Polyachyrus*, *Jungia*, *Calopappus*, *Marticorenia*) or in more than one (*Perezia*, *Acourtia*, *Leunisia*, *Macrachaenium*, *Pleocarphus*, *Trixis*, *Ameghinoa*, *Dolichlasium*, *Holocheilus*, *Lophopappus*, *Proustia*, *Proustia vanillosma*, *Gochnatia glomeriflora*, *Onoseris stricta*, *Perezia lanigera*). It can be white (*Nassauvia*, *Triptilion*, *Leucheria*, *Moscharia*, *Oxyphyllum*, *Polyachyrus*, *Leunisia*, *Macrachaenium*, *Dolichlasium*, *Holocheilus*, *Calopappus*, *Marticorenia*, *Gochnatia glomeriflora*) or colored (*Pleocarphus*, *Ameghinoa*, *Lophopappus*, *Proustia vanillosma*, *Onoseris stricta*), and there are genera such as *Perezia*, *Acourtia*, *Jungia*, *Trixis*, and *Proustia* which include both species with white and those with colored pappus.

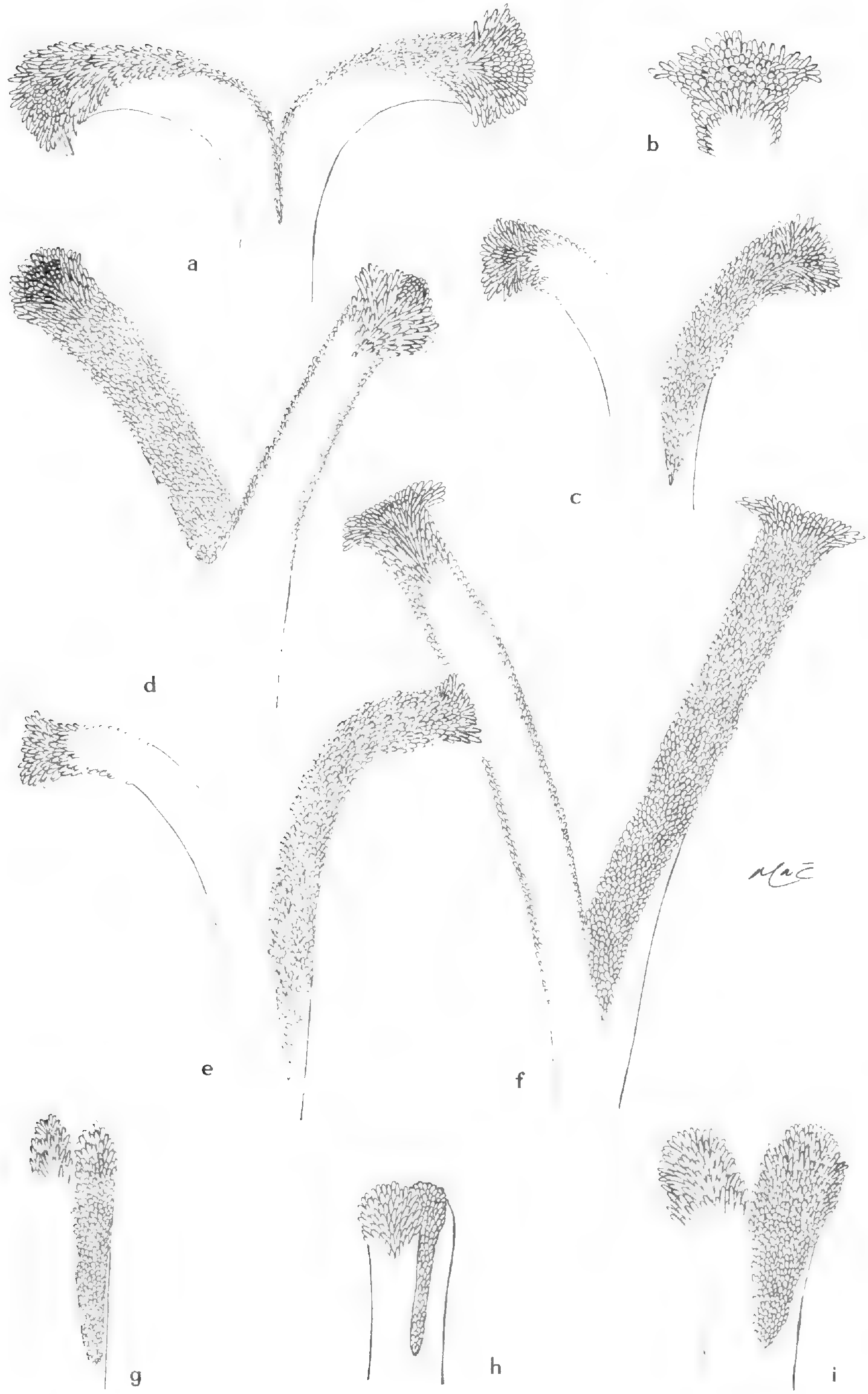
Cronquist (1955) has pointed out that chaffy pappus is the most primitive type, but it is difficult to reconcile this assumption with the situation in the Nassauviinae, for chaffy pappus is always associated, as in the genus *Nassauvia*, with evolutionarily advanced features.

C. INFLORESCENCES: In the Nassauviinae there is a group of genera, *Triptilion*, *Nassauvia*, *Polyachyrus*, and *Moscharia*, which shows a trend toward reduction of the number of flowers in the capitula and aggregation of the capitula themselves into a capitate secondary inflorescence, as a "pseudocephalium." The occurrence of a pseudocephalium, as compared to a regular capitulum, is believed to be an evolutionarily advanced feature. In the genus *Nassauvia* are found all stages between a solitary capitulum and a pseudocephalium. Characters of the inflorescence show the following variations: capitula solitary (*Perezia*, *Acourtia*, *Leucheria*, *Leunisia*, *Macrachaenium*, *Dolichlasium*, *Holocheilus*, *Lophopappus*, *Cephalopappus*, *Calopappus*, *Onoseris stricta*, *Perezia lanigera*); spicate (*Nassauvia*); cymose or paniculate (*Perezia*, *Acourtia*, *Leucheria*, *Oxyphyllum*, *Pleocarphus*, *Jungia*, *Trixis*, *Ameghinoa*, *Panphalea*, *Holocheilus*, *Lophopappus*, *Proustia*, *Marticorenia*, *Proustia vanillosma*, *Gochnatia glomeriflora*); in a glomerulum or in a pseudocephalium (*Nassauvia*, *Triptilion*, *Moscharia*, *Polyachyrus*). Three kinds of capitula can be recognized: sessile (*Nassauvia*, *Triptilion*, *Moscharia*, *Polyachyrus*, *Calopappus*); subsessile (*Acourtia*, *Proustia*, *Proustia vanillosma*, *Gochnatia glomeriflora*, *Perezia lanigera*); and pedicellate (*Perezia*, *Leucheria*, *Oxyphyllum*, *Leunisia*, *Macrachaenium*, *Pleocarphus*, *Jungia*, *Trixis*, *Ameghinoa*, *Dolichlasium*, *Panphalea*, *Holocheilus*, *Lophopappus*, *Cephalopappus*, *Marticorenia*, *Onoseris stricta*).

D. RECEPTACLE: Receptacular bracts are not common in the Mutisieae,

---

GH); f, *Perezia lanigera*, × 35 (*Ruiz Leal 26875*, LP); g, *Oxyphyllum ulicinum*, × 35 (*Johnston 5153*, GH); h, *Jungia ferruginosa*, × 35 (*Skutch 3622*, GH); i, *Marticorenia foliosa*, × 35 (*Zollner 2994*, LP).


a
b
c
d
e
f
g
h
i

occurring on only 10 per cent of the genera. When receptacular bracts do occur, they can either subtend all the flowers or be restricted to the marginal flowers. Among the genera of Nassauviinae receptacular bracts subtending all the flowers occur in species of three genera, *Jungia*, *Pleocarphus*, and *Marticorenia*. In other cases the paleae are restricted to the margin of the receptacle, as in *Oxyphyllum* and some species of *Leucheria*. In the genus *Polyachyrus* occurs a bract which can be interpreted either as an involucral bract or as a receptacular bract. Most authors, such as Cronquist (1955), who have dealt with evolution in the Compositae regard the presence of receptacular bracts as primitive.

The receptacle can be glabrous, as in *Nassauvia*, *Moscharia*, *Holocheilus*, *Calopappus*, *Polyachyrus*, *Macrachaenium*, *Ameghinoa*, *Dolichlasium*, *Panphalea*, *Holocheilus*, *Calopappus*, and *Leucheria*, or pubescent, as in *Acourtia*, *Leunisia*, *Pleocarphus*, *Jungia*, *Trixis*, *Lophopappus*, *Proustia*, *Cephalopappus*, *Marticorenia*, *Gochnatia glomeriflora*, *Onoseris stricta*, and *Perezia lanigera*. There are also genera including both species with a glabrous receptacle and species with the receptacle pubescent (*Perezia* and *Triptilion*). At present it is nearly impossible to describe evolutionary trends for this character, but when it is associated with other characters, it would seem that the pubescent receptacle is the more primitive.

E. FLOWERS: The Nassauviinae have always been described as having the corollas bilabiate with the outer lip three-toothed and the inner bifid. However, some of the taxa here considered have 5-partite corollas. Transition from one type to the other is simple; it requires only that the cleft between two of the corolla segments be deepened. Such a transition occurs also in other subtribes of Mutisieae, as in the genera *Flotovia* and *Chuquiraga*. On the other hand, complete or partial fusion of three segments of the corolla results in a bilabiate corolla. In the genus *Lophopappus* are found all stages between 5-partite and bilabiate corollas. In *L. peruvianus* all the flowers have 5-partite corollas; in *L. berberidifolius* most are 5-partite, but some are bilabiate; in *L. blakei* all the flowers have bilabiate corollas, but the outer lip is irregularly divided; in *L. cuneatus* and *L. foliosus* all flowers have the corolla bilabiate with the outer lip deeply three-toothed. In the genus *Proustia* some individuals of *P. pyrifolia* have some flowers with the corolla 5-partite in a capitulum in which most of the flowers have a bilabiate corolla. In *Acourtia collina* 5-partite corollas occur, as they do in *Gochnatia glomeriflora*, one of the critical taxa. Another critical taxon, *Onoseris stricta*, has capitula with both types of corolla, but in a radiate position.

FIGURE 2. Types of styles in Nassauviinae (continued). Truncate type: a, *Polyachyrus annuus*, × 35 (*Worth & Morrison 15758*, GH); *b*, *Leucheria purpurea*, × 35 (*Goodall 4146*, GH); c, *Holocheilus brasiliensis*, × 35 (*Pedersen 6122*, GH); d, *Trixis inula*, × 35 (*Skutch 2614*, GH); e, *Pleocarphus revolutus*, × 35 (*Zollner 475*, GH); f, *Dolichlasium lagascae*, × 22 (*Cabrera 17942*, LP). Proustia type: g, *Macrachaenium gracile*, × 35 (*Parodi 11739*, GH); h, *Cephalopappus sonchifolius*, × 35 (*Martius 1816*, M); i, *Lophopappus foliosus*, × 35 (*Buchtien 598*, GH).

It is possible that the trend of evolution in this character has been from flowers 5-partite to flowers bilabiate, for the 5-partite condition occurs in genera of the subtribe Gochnatiinae which is thought to be the most primitive of the subtribes of Mutisieae. On the other hand, very advanced genera, such as *Moscharia* in which pseudocephalia occur, have flowers with bilabiate corollas. Among genera of the Nassauviinae, the number of flowers per capitulum varies from 2 to 178. As was pointed out by Stebbins (1967), the number of flowers per capitulum is more nearly constant when there are only few flowers; in many-flowered inflorescences the range of variation is greater. This generalization seems to be valid for the Naussauviinae. On the basis of this assumption the total range of variation, i.e., from 2 to 178, has been divided into three sets: 2–5, 6–14, and 15–178. There occur 2 to 5 flowers per capitulum in *Nassauvia*, *Triptilion*, *Moscharia*, *Polyachyrus*, and *Calopappus*; 6 to 14 in *Acourtia*, *Oxyphyllum*, *Trixis*, *Panphalea*, *Lophopappus*, *Proustia*, *Gochnatia glomeriflora*, and *Perezia lanigera* (in some individuals in species of these genera there very rarely occur more than 14 flowers); 15 to 178 in *Perezia*, *Leucheria*, *Leunisia*, *Jungia*, *Macrachaenium*, *Pleocarphus*, *Ameghinoa*, *Dolichlasium*, *Holocheilus*, *Cephalopappus*, *Marticorenia*, and *Onoseris stricta*. To determine the trend of evolution for this character is difficult; the character may be used for taxonomic purposes, but not to determine the evolutionary pathway.

In the Nassauviinae the corolla can be glabrous (*Perezia*, *Nassauvia*, *Triptilion*, *Leucheria*, *Oxyphyllum*, *Polyachyrus*, *Leunisia*, *Macrachaenium*, *Dolichlasium*, *Lophopappus*, *Proustia*, *Calopappus*, *Onoseris stricta*) or pubescent (*Acourtia*, *Moscharia*, *Pleocarphus*, *Jungia*, *Trixis*, *Ameghinoa*, *Panphalea*, *Holocheilus*, *Cephalopappus*, *Marticorenia*, *Proustia vanillosma*, *Gochnatia glomeriflora*, *Perezia lanigera*).

The color of the flowers can be blue (*Perezia*, *Nassauvia*, *Triptilion*, *Leucheria*), yellow (*Leunisia*, *Pleocarphus*, *Trixis*, *Ameghinoa*, *Dolichlasium*, *Calopappus*, *Proustia vanillosma*, and a few species of *Perezia* and *Jungia*), orange (*Cephalopappus* and *Onoseris stricta*), red (*Perezia*, *Polyachyrus*, *Proustia*), white (*Perezia*, *Nassauvia*, *Triptilion*, *Leucheria*, *Moscharia*, *Polyachyrus*, *Jungia*, *Panphalea*, *Holocheilus*, *Lophopappus*, *Proustia*, *Perezia lanigera*), or violaceous (*Perezia*, *Acourtia*, *Nassauvia*, *Leucheria*, *Oxyphyllum*, *Macrachaenium*, *Jungia*, *Marticorenia*). Cronquist (1955) has pointed out that yellow is the primitive stage of this character in the Compositae.

In *Leunisia*, *Dolichlasium*, and *Proustia* there occur anthers with hairs.

F. ACHENES: The achenes show a wide range of morphological variation. In genera such as *Leunisia*, *Macrachaenium*, *Pleocarphus*, *Jungia*, *Trixis*, *Dolichlasium*, and *Cephalopappus*, the achenes are 5 times longer than wide. Other genera have a rostrum, well developed in *Dolichlasium*, less so in *Leunisia*, *Macrachaenium*, *Pleocarphus*, *Jungia*, *Trixis*, and *Cephalopappus*. The achenes can be glabrous (*Macrachaenium*, *Cephalopappus*, *Calopappus*) or pubescent (*Perezia*, *Acourtia*, *Moscharia*, *Oxyphyllum*, *Leunisia*, *Pleocarphus*, *Jungia*, *Trixis*, *Ameghinoa*, *Dolichlasium*, *Panphalea*, *Holocheilus*, *Lophopappus*, *Proustia*, *Cephalopappus*, *Marticorenia*,

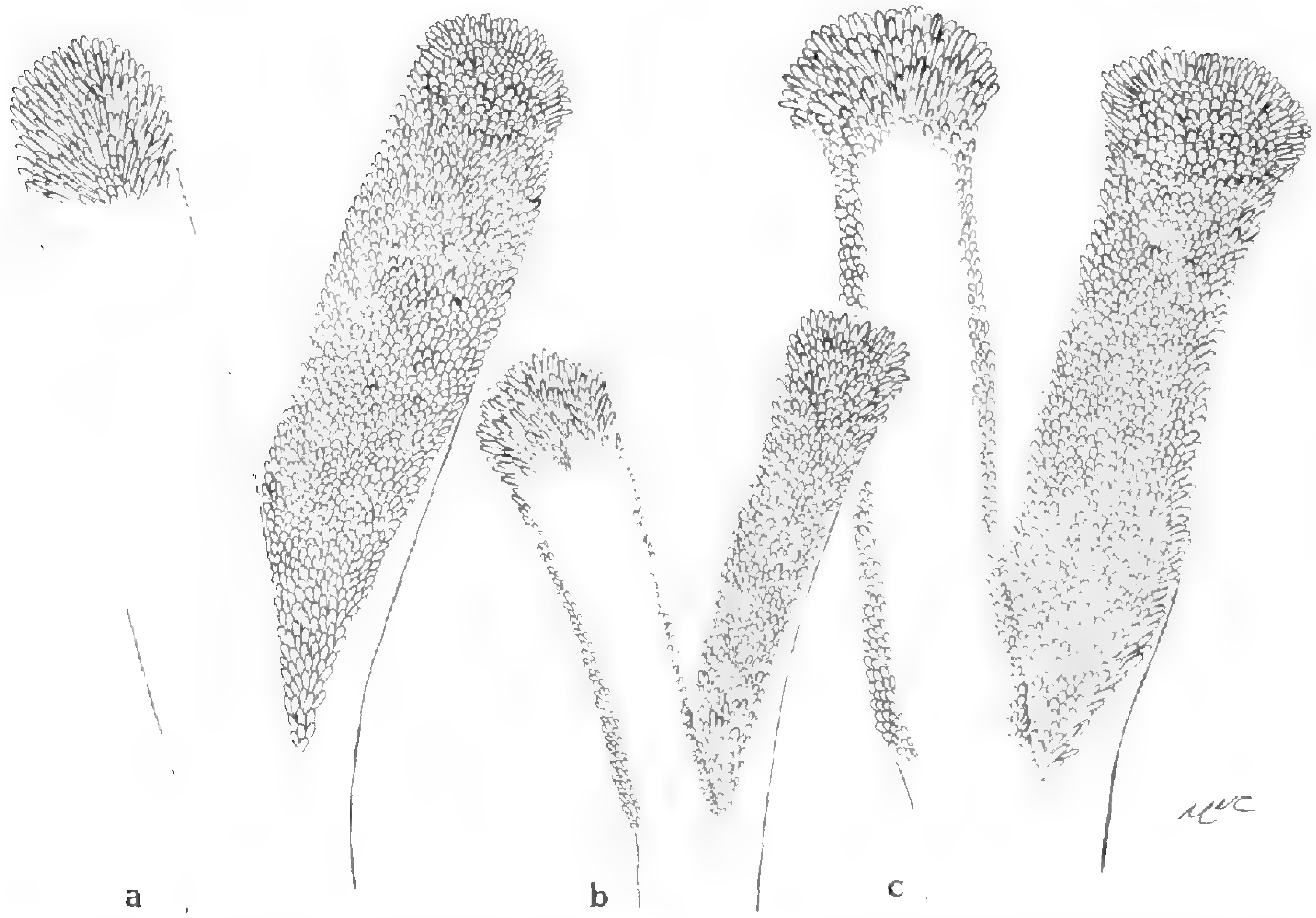


FIGURE 3. Types of styles in Nassauviinae (continued). Acourtia type: a, *Perezia nutans*, × 35 (*Vuilleumier 223*, GH); b, *Acourtia glomeriflora*, × 35 (*Pringle 9946*, GH); c, *Leunisia leata*, × 35 (*Morrison 17024*, GH).

Proustia vanillosma, *Gochnatia glomeriflora*, *Onoseris stricta*, *Perezia lanigera*) and there are also genera including both species with glabrous achenes and species with pubescent achenes (*Nassauvia*, *Triptilion*, *Leucheria*, *Polyachyrus*).

G. TYPE OF PUBESCENCE: The commonest type of pubescence, made up of woolly trichomes, occurs in *Acourtia*, *Leucheria*, *Oxyphyllum*, *Polyachyrus*, *Macrachaenium*, *Pleocarphus*, *Jungia*, *Trixis*, *Lophopappus*, *Proustia*, *Cephalopappus*, *Proustia vanillosma*, *Onoseris stricta*, *Gochnatia glomeriflora*, and *Perezia lanigera*. There do occur other kinds of trichomes, such as glandular uniseriate, nonglandular uniseriate, and double trichomes ("Zwillingshaare"), but until trichome types have been more thoroughly studied, they cannot be used for taxonomic purposes. Stebbins's (1967: 111) observation that "The strong development of multicellular glandular trichomes is a widespread feature of xeric and semixeric species of Compositae" is valid for the Nassauviinae.

H. LEAVES: All the genera of the subtribe have alternate leaves; leaf morphology is very useful for the separation of species, but much less so for the delimitation of genera. It is, however, possible to point out some features. *Jungia* has orbicular cordate leaves (except *J. stuebelii*). In both *Trixis* and *Pleocarphus* the blades are several times (at least five) longer than wide. In *Marticorenia* all leaves are sessile. In some genera all the species have entire leaves (*Acourtia*, *Nassauvia*, *Leunisia*, *Pleocarphus*, *Jungia*, *Trixis*, *Lophopappus*, *Proustia*, *Cephalopappus*, *Calopappus*, *Marti-*

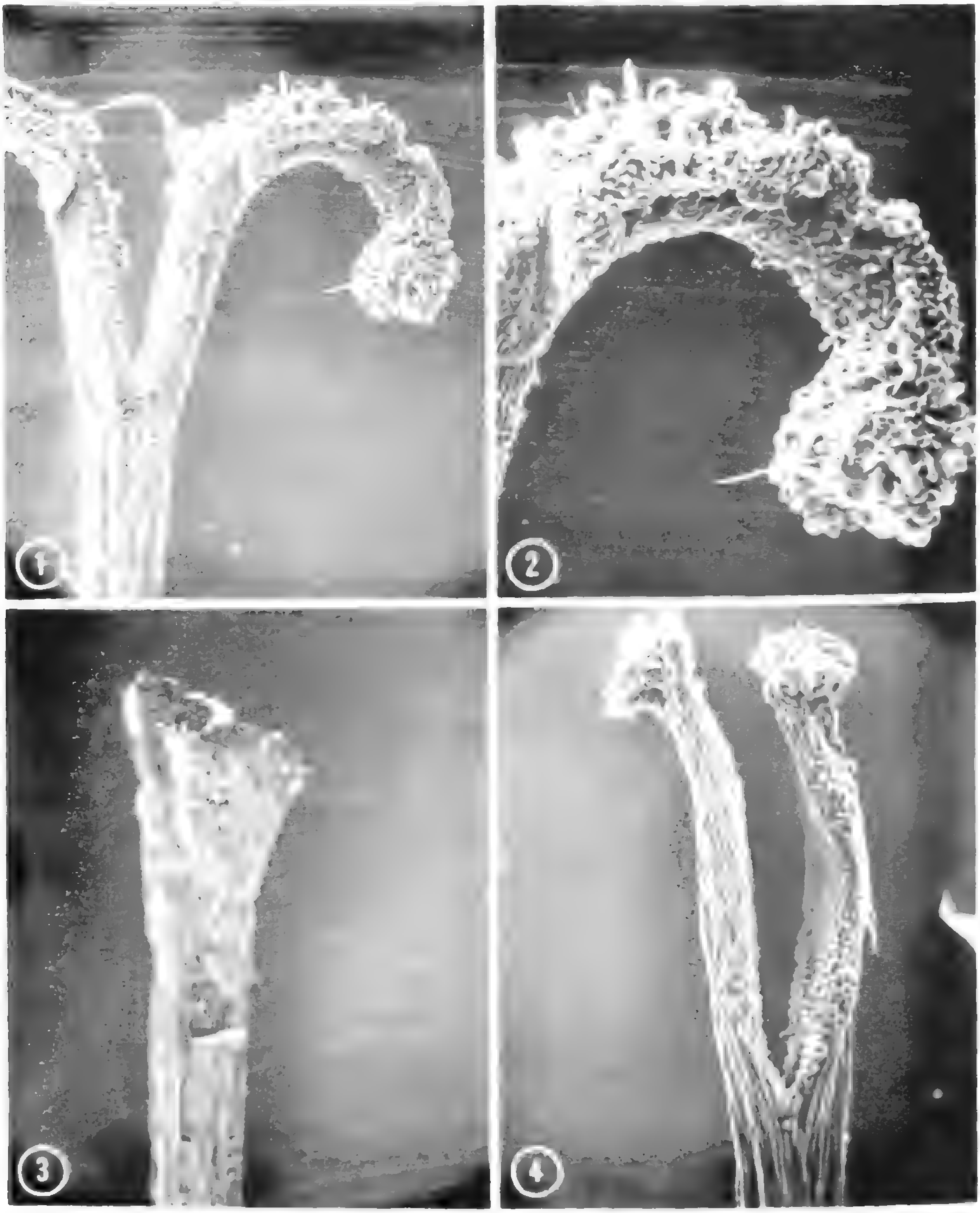


FIGURE 4. Types of styles in Nassauviinae (continued). Scanning electron micrographs (SEMG). Truncate type. 1 and 2. *Jungia ferruginosa*, × 65 and × 130 (*Skutch 3622*, GH); 3. *Calopappus acerosus*, × 33 (*Wederman 638*, GH); 4. *Leucheria purpurea*, × 65 (*Goodall 4149*, GH).

coronia, *Proustia vanillosma*, *Gochnatia glomeriflora*, *Onoseris stricta*, *Perezia lanigera*); in other genera all the species have partite leaves (*Triptilion*, *Moscharia*, *Oxyphyllum*, *Polyachyrus*, *Macrachaenium*, *Ameghinoa*, *Dolichlasium*) and there are genera including species with entire leaves and species with partite leaves (*Perezia*, *Leucheria*, *Panphalea*, *Holocheilus*).

In *Nassauvia*, *Triptilion*, *Oxyphyllum*, *Calopappus*, and *Perezia lanigera* all species have leaves with a spiny margin; this character occurs also in *Perezia*, *Acourtia*, *Lophopappus*, and *Proustia*, but not in all species.

I. STYLE: The Nassauviinae have always been described as having the styles bifid, the branches flattened and truncate, glabrous on the outer surface, crowned with elongate collecting hairs at the apices and papillose with shorter ones on the adaxial surfaces. However, a careful study of styles in the taxa dealt with here shows that there occur four basic types. In every genus except *Perezia* the stylar type is uniform among all the species.

The first type has truncate stylar branches (*Perezia*, *Nassauvia*, *Tripti-*

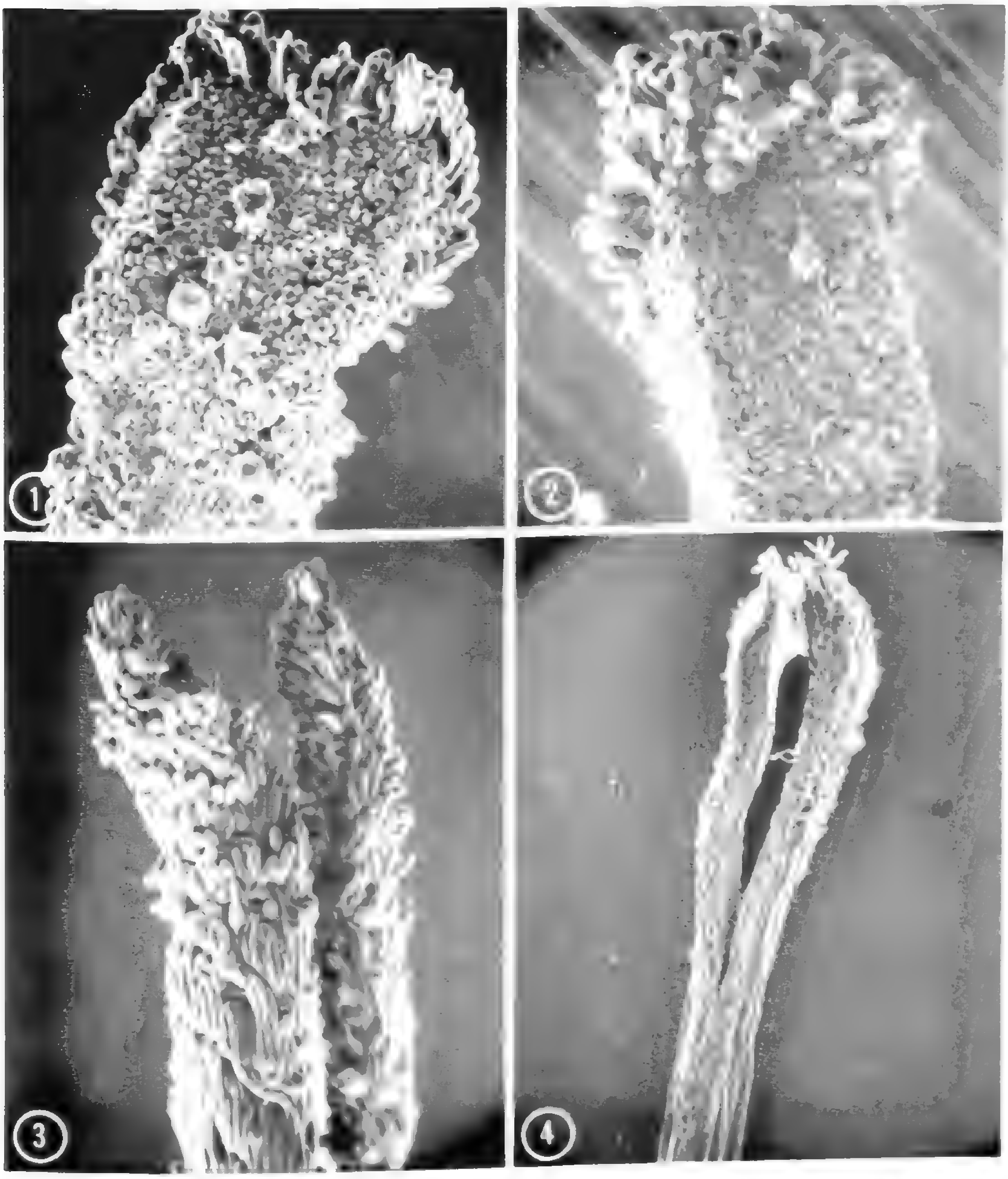


FIGURE 5. Types of styles in Nassauviinae (continued). Scanning electron micrographs (SEMG). Acourtia type: 1, *Acourtia reticulata*, × 130, stigma (*Bourgeau 3096*, GH); 2, *Acourtia vanillosma*, × 130 (*Otero 391*, GH). Proustia type: 3, *Proustia pyrifolia*, × 130 (*Morrison 17163*, GH). Onoseris stricta type: 4, *Onoseris stricta*, × 33 (*Ibarrola 1174*, GH).

lion, *Leucheria*, *Moscharia*, *Oxyphyllum*, *Polyachyrus*, *Pleocarphus*, *Jungia*, *Trixis*, *Ameghinoa*, *Dolichlasium*, *Holocheilus*, *Calopappus*, *Marticorenia*, and *Perezia lanigera*). The second (*Proustia*) type has the branches less than 1 mm. long, rounded at the apex, bearing long papillae on the distal half of the outer surface, but completely papillose on the inner surface (*Macrachaenium*, *Lophopappus*, *Proustia*, *Cephalopappus*). The third (*Acourtia*) type has the branches more than 1 mm. long with the apices rounded and slightly expanded. The outer surfaces bear long papillae on the distal fifth; the inner surfaces are completely papillose. This type occurs in *Acourtia*, *Leunisia*, *Proustia vanillosma*, *Gochnatia glomeriflora*, and in two species of *Perezia*, *P. nutans* and *P. prenanthoides*. The fourth type occurs only in *Onoseris stricta*. The stylar branches are spathulate. The inner surfaces are completely covered with short papillae, and the distal third of the outer surfaces bears very long papillae. FIGURES 1 to 5 show the different types of styles found in Nassauviinae.

J. POLLEN: Pollen characteristics have been very useful in delimiting genera of the Nassauviinae, but much less so for separating species. Wodehouse (1929), Stix (1960), Skvarla and Turner (1966), Crisci (1971a and b), and Parra and Marticorena (1972) have contributed to our knowledge of pollens in the Nassauviinae. In this study the following characters have been used: grain shape, exine morphology, presence or absence of polar elevations, presence or absence of sexine processes.

On the basis of shape, pollen grains of the Nassauviinae can be divided into four types (the fractions refer to the relation between polar axis and equatorial axis): oblate-spheroidal (7/7–8/8) (*Perezia*, *Nassauvia*, *Triptilion*, *Leucheria*, *Cephalopappus*, *Calopappus*, *Perezia lanigera*); prolate-spheroidal (8/8–8/7) (*Perezia*, *Acourtia*, *Nassauvia*, *Triptilion*, *Leuceria*, *Moscharia*, *Oxyphyllum*, *Polyachyrus*, *Jungia*, *Panphalea*, *Holocheilus*, *Lophopappus*, *Proustia*, *Cephalopappus*, *Calopappus*, *Marticorenia*, *Proustia vanillosma*, *Gochnatia glomeriflora*, *Perezia lanigera*); subprolate (8/7–8/6) (*Perezia*, *Acourtia*, *Leucheria*, *Oxyphyllum*, *Polyachyrus*, *Macrachaenium*, *Pleocarphus*, *Jungia*, *Holocheilus*, *Lophopappus*, *Proustia*, *Marticorenia*, *Proustia vanillosma*, *Gochnatia glomeriflora*); prolate (8/6–8/4) (*Leucheria*, *Oxyphyllum*, *Leunisia*, *Macrachaenium*, *Pleocarphus*, *Trixis*, *Ameghinoa*, *Dolichlasium*, *Proustia*, *Onoseris stricta*).

As is shown, some taxa include more than one type. Sexine processes are structures found on the membrane of the colpus in the pollen of some taxa (*Perezia*, *Acourtia*, *Nassauvia*, *Triptilion*, *Leunisia*, *Jungia*, *Trixis*, *Ameghinoa*, *Dolichlasium*, *Panphalea*, *Holocheilus*, *Lophopappus*, *Proustia*, *Cephalopappus*, *Calopappus*, *Proustia vanillosma*, *Gochnatia glomeriflora*, *Onoseris stricta*, *Perezia lanigera*). They are more or less spherical and seem to be connected to the membrane by short thin pedicels.

In some genera (*Perezia*, *Leucheria*, *Holocheilus*, and *Proustia*) the pollen grains have polar elevations; these are extremely well developed in *Oxyphyllum*, *Leunisia*, *Trixis*, *Ameghinoa*, *Dolichlasium*, and in *Onoseris stricta*.

Morphology of the exine is a very useful character in the systematics of the genera of Compositae. Stix has pointed out that in Compositae there occur 42 types of exine stratification. Five types of exine are found in the Nassauviinae; two were pointed out by Stix, two by Parra and Marticorena, and the last (*Cephalopappus*) type is from unpublished data kindly provided by C. Marticorena.

Oxyphyllum type: The tectum and infratectum are of the same thickness and are separated from each other by a thin layer not parallel to the nexine (zigzag). It occurs in two subtypes: (a) the tectum with short ramifications (bacules) near the terminal membrane (*Perezia, Moscharia, Oxyphyllum, Panphalea*) and (b) the tectum lacking ramification (*Nassauvia, Triptilion, Leucheria, Polyachyrus*).

Trixis type: The tectum and infratectum are of different thicknesses and are separated from each other by a thick layer parallel to the nexine. This type is found in *Acourtia, Leunisia, Macrachaenium, Pleocarphus, Jungia, Trixis, Ameghinoa, Dolichlasium, Holocheilus, Marticorenia, Proustia vanillosma, Gochnatia glomeriflora, Onoseris stricta*, and *Perezia lanigera*. Stix recognized in this group two types, the Trixis type and the Ameghinoa type, on the basis of the presence of vestiges of spines, but this is a feature seen in all genera of the group.

Proustia type: The tectum and infratectum are of equal thickness and are separated from each other by a thick layer almost parallel to the nexine. This type occurs in *Proustia* and in *Lophopappus*. There is here a tendency toward the Trixis type.

Calopappus type: (= *Nassauvia remyana* type of Parra & Marticorena, 1972). The infratectum is thicker than the tectum. The tectum and infra-

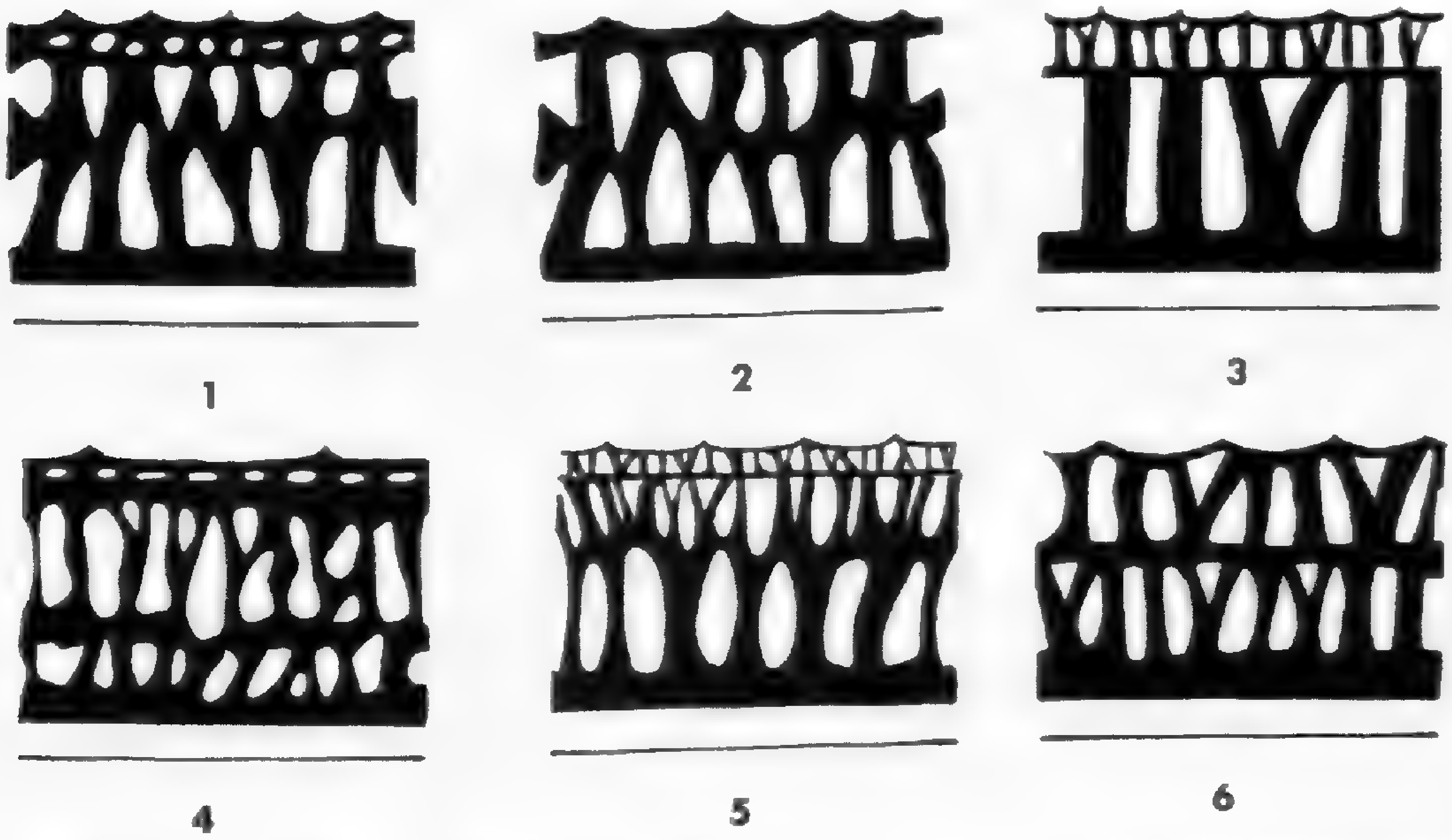


FIGURE 6. Types of exine stratification in Nassauviinae in a simplified form (see text): 1, Oxyphyllum (a) type; 2, Oxyphyllum (b) type; 3. Trixis type; 4, Cephalopappus type; 5, Calopappus type; 6. Proustia type.

tectum are separated from each other by a thick layer not parallel to the nexine (zigzag). This type occurs in *Calopappus*.

Cephalopappus type: The tectum has short ramifications and is thicker than the infratectum. The tectum and infratectum are separated by a thick layer parallel to the nexine. This type occurs in *Cephalopappus*.

In FIGURE 6 are shown in a simplified form the types of exine stratification in Nassauviinae.

Wodehouse (1929) pointed out that the Nassauviinae may represent the culmination of three more or less distinct developmental trends in pollen morphology; i.e., toward reduction of spines, toward lengthening of the furrows, and toward elliptical grains. On the basis of pollen morphology Wodehouse concluded that the various genera of the Nassauviinae seem to be closely related, and to represent the end of a phylogenetic line within the tribe Mutisieae. Wodehouse's conclusion seems to be correct, but some characters, such as elliptical grains, are found associated with other features thought to be primitive. At present characters of the pollen seem to be very useful in the systematics of the group, but are not so helpful in determining phylogenetic relationships within the group.

K. INVOLUCRE: The involucre offers numerous characters useful in the systematics of the subtribe.

Four involucre shapes occur: (1) campanulate (*Acourtia, Leucheria, Leunisia, Macrachaenium, Dolichlasium, Lophopappus, Jungia, Trixis, Perezia lanigera*); (2) hemispherical (*Perezia, Leucheria, Pleocarphus, Ameghinoa, Panphalea, Holocheilus, Cephalopappus, Marticorenia, Onoseris stricta*); (3) cylindrical (*Perezia, Acourtia, Nassauvia, Triptilion, Oxyphyllum, Polyachyrus, Jungia, Trixis, Lophopappus, Proustia, Calopappus, Proustia vanillosma, Gochnatia glomeriflora*); (4) turbinate (*Perezia, Acourtia, Leucheria, Jungia*). There can be one or two rows of involucral bracts (as in *Nassauvia, Triptilion, Moscharia, Polyachyrus, Leunisia, Pleocarphus, Jungia, Trixis, Ameghinoa, Macrachaenium, Dolichlasium, Panphalea, Holocheilus*, and *Marticorenia*) or three or more (as in the genera *Acourtia, Oxyphyllum, Lophopappus, Proustia, Cephaloppus, Calopappus, Proustia vanillosma, Gochnatia glomeriflora, Perezia lanigera*, and *Onoseris stricta*). In both *Perezia* and *Leucheria* there are species with one or two rows of involucral bracts and others with the bracts in three or more rows. In *Moscharia* and *Polyachyrus* the number of bracts is reduced and dimorphic, five in *Polyachyrus* and two in *Moscharia*. In species of *Leunisia* and *Dolichlasium*, the involucral bracts are foliaceous, a phenomenon seen also in some species of *Perezia* and *Trixis*. In *Panphalea* and a few species of *Perezia* the bracts are conspicuously winged. In *Panphalea* and *Cephalopappus* the bracts are small, being less than 3 mm. long. In *Oxyphyllum, Perezia lanigera*, some other species of *Perezia*, and some species of *Triptilion* the involucral bracts are mucronate. As far as the involucres of the Nassauviinae are concerned, the primitive state is a monomorphic involucre with foliaceous multiseriate bracts.

Cytology. The cytology of the Mutisieae has so far been little studied.

Chromosome numbers are known for 10 per cent of the species in the tribe. The following numbers have been found: n = 4, 8, 9, 10, 11, 12, 13, 14, 16, 17, 18, 20, 22, 23, 24, 25, 27, and 28. The numbers most common at the level of genus are n = 27 and then n = 18. Within the subtribe Nassauviinae there are known chromosome counts for 37 of some 300 species. As our knowledge is scanty in this respect, cytological data were not used in the numerical analysis. However, there is appended a list of numbers now known for members of the Nassauviinae (TABLE 2) with some comments about the cytology of the group. In the subtribe the chromosome numbers of interest are: *Acourtia*, with n = 27 and 28, and *Perezia*, with n = 4, 8, and 12, taxa which were formerly considered congeneric. The number (n = 27 or $2n$ = 54) is found in *Acourtia*, *Trixis*, and *Proustia*. The haploid number, n = 11, has been found in species of genera such as *Nassauvia* and *Holocheilus*, which are not very closely related. The same is true of *Marticorenia* and *Nassauvia* where the haploid number is n = 22. *Moscharia* and *Leucheria* present n = 20.

DISCUSSION

The results of the numerical analysis permit me to make the following taxonomic conclusions, starting with the four critical taxa (a complete list of synonyms of these taxa is given in the appendices).

Gochnatia glomeriflora Gray. This is a species of small shrubs occurring on warm rocky hillsides near Guadalajara in Mexico. The flowers have 5-partite corollas and for this reason the species was ascribed to *Gochnatia* (Mutisieae, Gochnatiinae) by Gray. Sereno Watson described the same taxon as *Perezia capitata*, placed in section *Acourtia* of *Perezia*. Blake, in 1926, listed Watson's species as a synonym of Gray's *Gochnatia glomeriflora*. When Bacigalupi (1931) monographed *Acourtia*, as section *Acourtia* of *Perezia*, he neglected to include this species. Cabrera (1971a) in his monograph of *Gochnatia* excluded this species from that genus and suggested that it is an abnormal species of *Perezia*.

From the viewpoint of Aristotelian logic, the presence of 5-partite corollas is enough to exclude this species from *Acourtia*, but if all characters are considered, it is clear that this species must belong to *Acourtia*, as indeed the results of the numerical study show. There is already one species of *Acourtia*, *A. collina*, which has flowers with 5-partite corollas. The transition between 5-partite and bilabiate corollas is seen also in another genus, *Lophopappus*, of the Nassauviinae, accordingly placed very close to *Acourtia*. I conclude that this species must be placed in *Acourtia*.

Proustia vanillosma Wright. This is a species of scandent shrubs endemic to the islands of Cuba, Santo Domingo, and Puerto Rico. The only other genus of Nassauviinae occurring in this area is *Trixis*. The position of this species in *Proustia* is doubtful because of its yellow flowers, type of style, exine stratification, and its geographical distribution disjunct from other species of *Proustia* which occur in southern South America. Hoffmann (1893: 343) pointed out that *P. vanillosma* differs from the other species

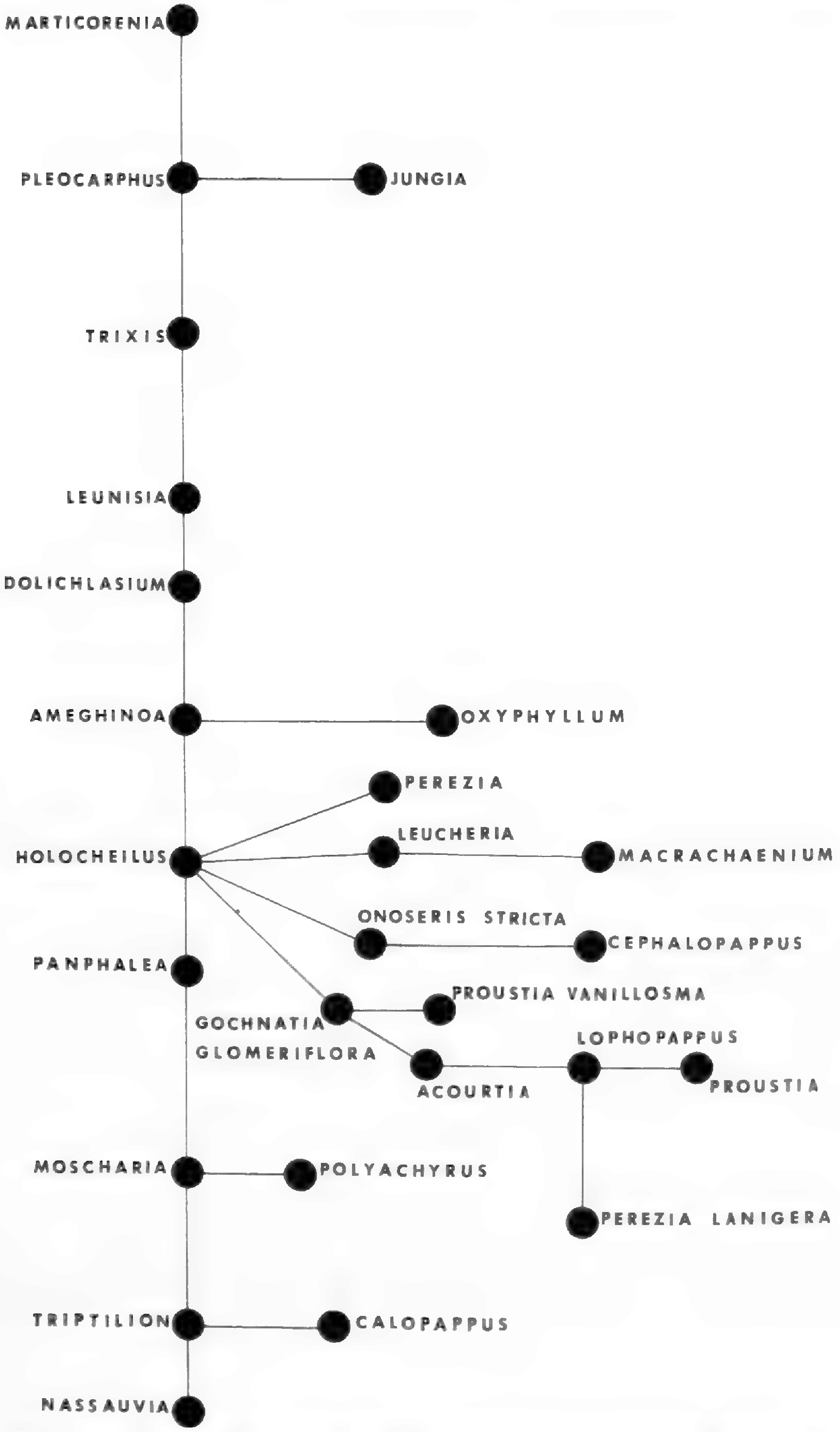


FIGURE 7. PRIM network of 26 OTU's based on TABLE 3 (Method 1).

of *Proustia* in having a different type of style. The results of the numerical study show that this taxon is close to *Acourtia glomeriflora* (= *Gochnatia glomeriflora*) and to the genus *Acourtia* in general. There is a gap between *Acourtia* and *P. vanillosma* in habit and in flower color, but the position of this species in *Acourtia* seems to be a natural one, representing a branch of this genus in the West Indies.

Perezia lanigera Hooker & Arnott. This is a species of prostrate shrubs occurring on the Patagonian steppe. B. S. Vuilleumier (1969) excluded this taxon from the genus *Perezia* because it has densely woolly trichomes in the axils of the leaves, only two rows of involucral bracts, and achenes with a type of pubescence found in no other species of *Perezia*. Cabrera (1972) replaced this species in *Perezia*; however, on the basis of the numerical study it is clear that it does not belong in that genus but seems to be related to *Lophopappus*, although the "distance" between the two taxa is fairly great. This taxon might be best treated as a new monotypic genus.

Onoseris stricta Sprengel. This is a species of perennial herbs abundant in sandy or rocky soils of Rio Grande do Sul (Brazil), Uruguay, and in northeastern Argentina. This species has "fluctuated" among genera and even subtribes, having been placed in *Trixis*, *Trichocline*, and *Perezia*. The numerical results point out that this taxon is far distant from any other in the Nassauviinae, and it might be that *O. stricta* is best placed in a subtribe other than this one. Its exact placement must await further work on the other subtribes of the Mutisieae.

From the time of Bentham and Hooker (1873) until the present, *Acourtia* has been treated as a synonym of *Perezia*. The results show that the "distance" between them is great. The gap is large enough to indicate that *Acourtia* should be treated as a distinct genus, thus confirming my preliminary decision to treat *Acourtia* as a separate OTU.

Ameghinoa and *Dolichlasium* have been treated by several authors as congeneric with *Trixis*. However the results show that the distances between them are rather large.

Pleocarphus has been treated as congeneric with *Jungia* from the time of Bentham and Hooker (1873) until now. The results show that the inclusion of *Pleocarphus* in *Jungia* is unnatural, for it produces a gap in the internal consistency of *Jungia*.

Calopappus was placed by De Candolle into another subtribe, Mutisiinae, of the tribe Mutisieae. Weddell (1855) thought it to be synonymous with *Nassauvia*. My results confirm that it is indeed a distinct genus, and it must be placed in Nassauviinae.

Holocheilus has been treated as congeneric with *Trixis* since Bentham and Hooker so placed it, but Cabrera (1968) considered *Holocheilus* to be a distinct genus and our results agree with his conclusion.

Cephalopappus, a monotypic genus, occurring only in the state of Bahia in Brazil, has been collected very few times and the only material available for this study has been the type material. The results indicate that it is far removed from the other genera of Nassauviinae, but its inclusion in this subtribe does not seem to be unnatural.

GENERIC AFFINITIES AND EVOLUTIONARY HISTORY

In our results we have obtained a measure of phenetic resemblances. The use of these measures as an indicator of relationship or affinities can be criticized from the viewpoint of the existence of convergence or of parallelism. However, in this group we could detect neither convergence nor parallelism. For this reason we concluded that in the Nassauviinae phenetic resemblances are probably consistent with phylogenetic affinities.

On the basis of these results, the genera of the Nassauviinae can be divided into four groups and five "isolated" genera.

The first group includes *Acourtia*, *Proustia*, and *Lophopappus*. This seems to be a primitive group showing affinities with other subtribes of the Mutisieae, for in this group the styles have rounded tips and in some cases 5-partite corollas; these are characters of the Mutisiinae (sensu Cabrera, 1961). *Proustia* and *Lophopappus* are very closely related and occur in much the same area; *Acourtia* seems to represent another line of evolution in Central America and in North America.

The second group includes *Marticorenia*, *Pleocarphus*, *Jungia*, *Trixis*, *Leunisia*, *Dolichlasium*, and *Ameghinoa*. In this group there are several monotypic genera. *Marticorenia* and *Pleocarphus* seem to be closely related and the closest to these two genera is *Trixis*. *Dolichlasium* and *Leunisia* show one of the closest relationships between any genera of the Nassauviinae. *Jungia* seems to occupy a position equidistant from the other genera. This group has some characters which suggest that it is a primitive one, among them the occurrence of paleae in all flowers in *Jungia*, *Pleocarphus*, and *Marticorenia*, the shrubby habit, the many-flowered capitula, and the general occurrence of yellow flowers.

The third group includes only *Holocheilus* and *Panphalea*, and seems to have evolved from genera of the third group. This group shows some advanced characters such as the herbaceous habit, the flowers lacking pappus in *Panphalea*, and the occurrence of non-yellow flowers.

The fourth group includes *Polyachyrus*, *Moscharia*, *Triptilion*, *Nassauvia*, and *Calopappus*. It seems an advanced group, for there is a trend toward reduction of the number of flowers in each capitulum, and toward the aggregation of the capitula themselves in a capitate secondary inflorescence, a pseudocephalium. The occurrence of pseudocephalia, as compared to ordinary capitula, is thought to be an evolutionarily advanced feature. In this group are found all stages intermediate between capitula and pseudocephalia. In the genus *Moscharia* there occur pseudocephalia with a great reduction and a close aggregation of the capitula, which may be the evolutionary culmination of the trend in the Nassauviinae (Crisci, 1974b).

Nassauvia and *Triptilion* are closely related genera, and the "taxonomic distance" between them is one of the shortest between any two genera of

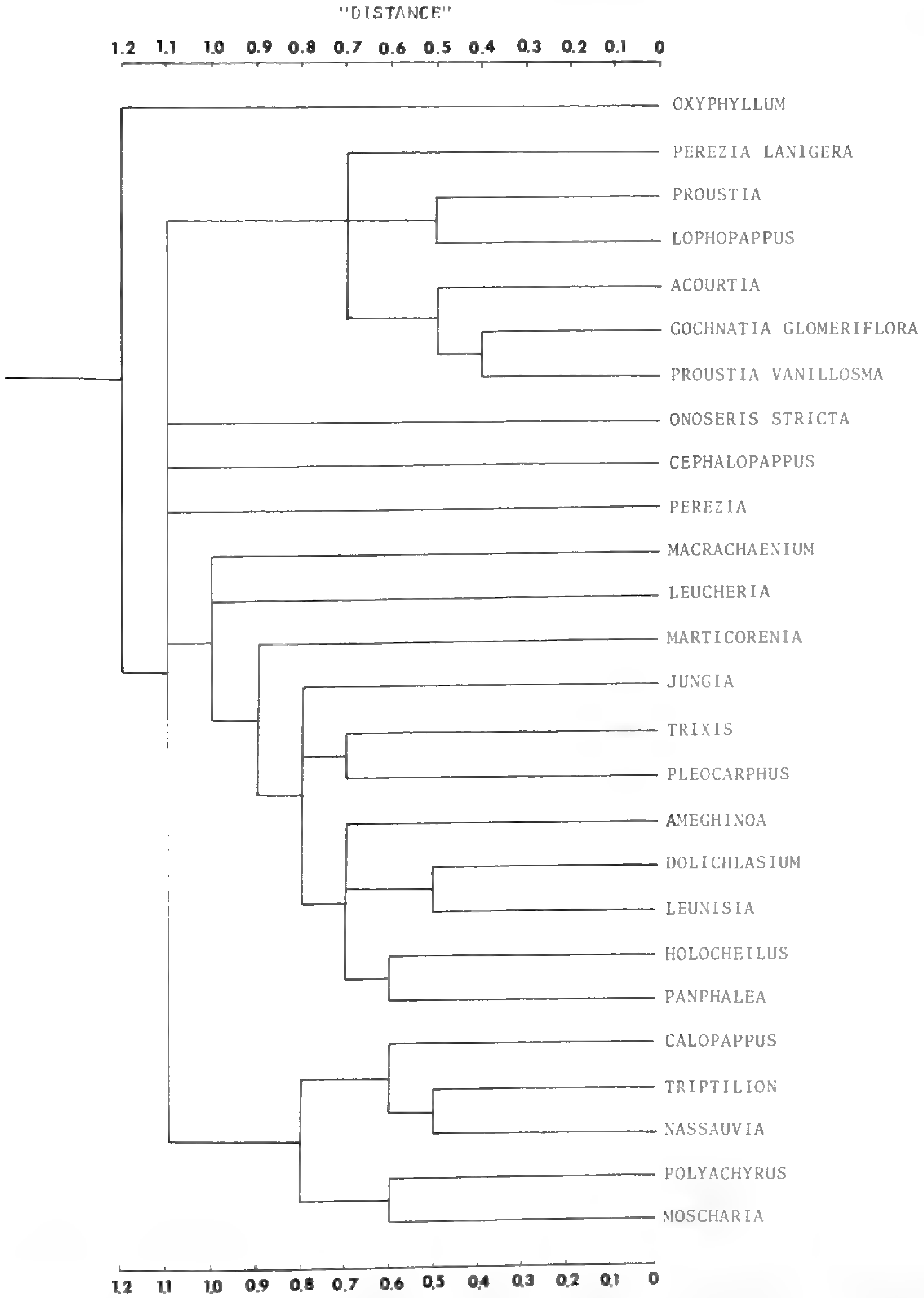


FIGURE 8. Phenogram of 26 OTU's obtained with Van Rijsbergen's clustering algorithm, based on TABLE 4 (Method 2).

the Nassauviinae. *Polyachyrus* and *Moscharia* show a clear line of evolution from *Polyachyrus* to *Moscharia*.

Throughout this study the remaining five genera have seemed isolated one from the other. Three of these, *Macrachaenium*, *Cephalopappus*, and *Oxyphyllum*, occur in areas where very few other Nassauviinae are found.

Oxyphyllum shows some very advanced features, such as few-flowered

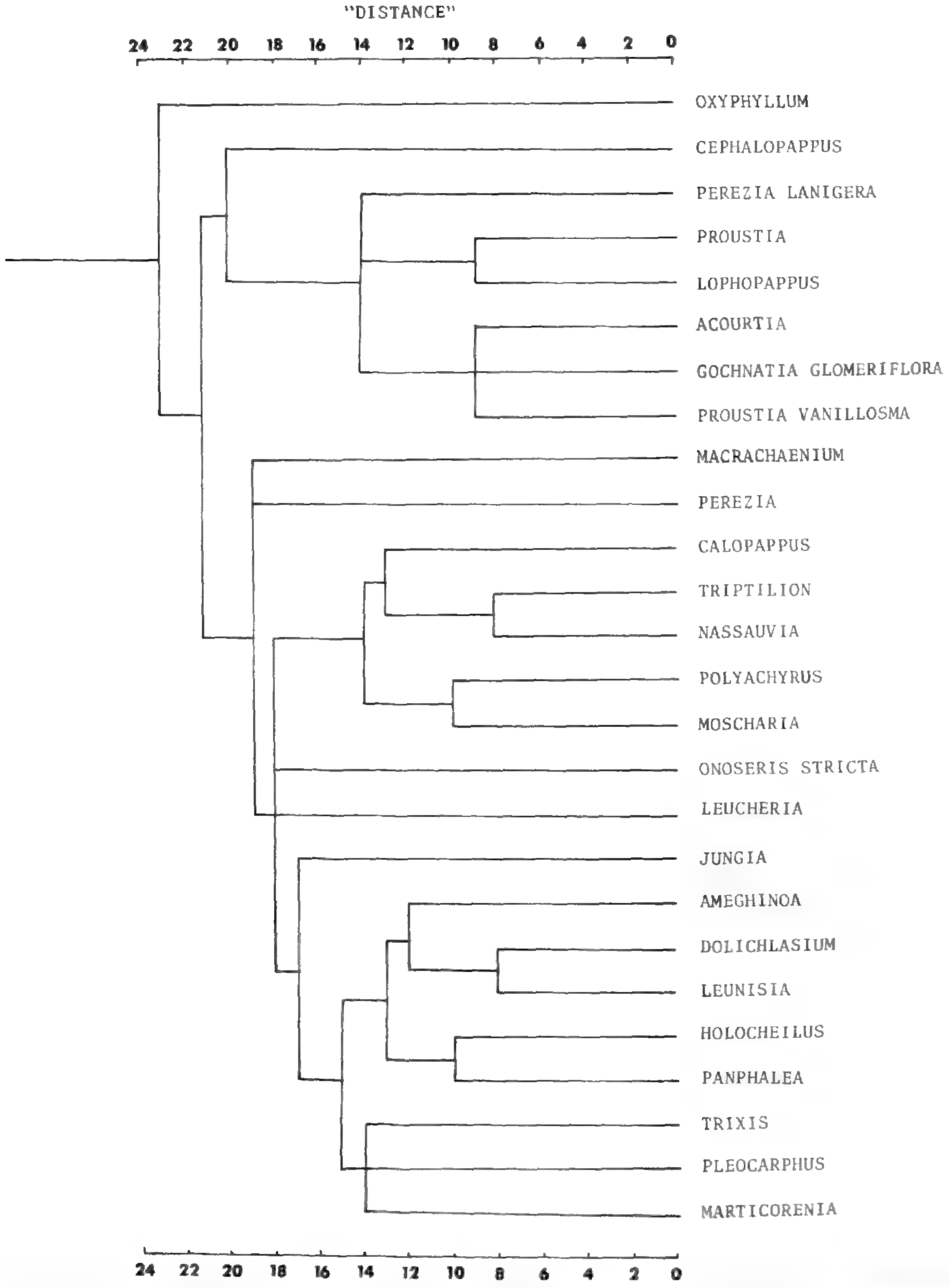


FIGURE 9. Phenogram of 26 OTU's obtained with Van Rijsbergen's clustering algorithm, based on TABLE 3 (Method 3).

capitula and a slight tendency toward aggregation of the capitula themselves, this representing an early stage in evolution of the pseudocephalium. The genus occurs in the Atacama desert of northern Chile. Its pollen resembles that of the *Moscharia* group, and it seems that this genus represents an advanced stage of development in the subtribe, the product of colonization by the Nassauviinae of a very special environment.

Macrachaenium occurs in the *Nothofagus* forest of South America. This genus shows some affinities with other subtribes of Mutisieae, for the stylar branches are rounded; it resembles *Chaptalia*, a genus of Mutisiinae. This genus might represent an evolutionary line diverging early from the other Nassauviinae and having a common ancestry with other subtribes of the Mutisieae.

Cephalopappus occurs in an area (the state of Bahia in Brazil) where there are no other genera of Nassauviinae. It displays a combination of specialized characters such as the herbaceous habit and the pappose flowers, and others less specialized such as terminal capitula. On the other hand, the stylar branches are rounded, a feature which seems to be more common in other subtribes of the Mutisieae. The position of this genus is difficult to determine, but it might be considered to represent an evolutionary line coming from an early stage in the evolution of the subtribe.

Finally, *Perezia* and *Leucheria* have been found to be isolated one from the other. This may be a result of the great spectrum of types presented by the two genera, a spectrum covering specialized and less specialized characters. These genera might have originated as two lines of development early in the evolution of the Nassauviinae.

The subtribe Nassauviinae seems to represent a natural group including several lines of evolution. Most of the genera occur in the Andean area of South America. As was pointed out by B. S. Vuilleumier (1971), the last rise of the Andes occurred in the Tertiary, and the climatic events of the Pleistocene must thus have played a decisive role in the constitution of the flora and fauna of the Andes. It is concluded that the Nassauviinae are as a group young, the product of a relatively recent evolutionary "explosion."

It seems that the Nassauviinae represent an advanced subgroup of Mutisieae. Small (1919) proposed that the Nassauviinae are the basic evolutionary group in the tribe, but our results do not agree with this idea, for it seems that the group is very young and shows advanced characters, such as the occurrence in several genera of pseudocephalia. It is possible that the Nassauviinae have originated from a taxon similar to those in the subtribe Gochnatiinae, whence, in several lines, all of the tribe Mutisieae evolved.

KEY TO THE GENERA OF SUBTRIBE NASSAUVIINAE
(Including *Onoseris stricta*)

1. Paleae in all of the flowers of the head.
    2. Lower leaves with sparse tomentose pubescence, petiolate, stipulate.
        3. Flowers yellow, pappus in more than one series; leaves linear, margin entire, revolute. . . . . PLEOCARPHUS.
        3. Flowers white or pink to violet (rarely yellow), pappus in one series; leaves orbicular, cordate or broadly lanceolate, margin lobulate. . . . . JUNGIA.
    2. Lower leaves sessile, lacking tomentose pubescence, exstipulate. . . . . MARTICORENIA.

1. Paleae present only in the flowers of the margin of the heads or completely absent.
   4. Flowers without pappus.
      5. Style-branch tips rounded; capitulum solitary, receptacle pubescent. .... CEPHALOPAPPUS.
      5. Style-branch tips truncate; capitula disposed in cymes or panicles; receptacle glabrous. .... PANPHALEA.
   4. Flowers with pappus.
      6. Shrubs with leaves reduced to 3-parted spines; paleae in the marginal flowers. .... OXYPHYLLUM
      6. Shrubs with non-spinose leaves and capitula lacking marginal paleae, or herbs.
         7. Inflorescences in glomerula or pseudocephalia.
            8. Capitulum with 2 (rarely 3) flowers.
               9. Pseudocephalium of 7 to 9 capitula. .... MOSCHARIA.
               9. Pseudocephalium of more than 9 capitula. .. POLYACHYRUS.
            8. Capitulum of 3 to 6 flowers.
               10. Pappus formed of 4 to 5 paleae plicate along the median line expanded and laciniate in the upper part. .... TRIPTILION.
               10. Pappus formed of 3 to 6 paleae, narrow and not laciniate, or of setose or plumose hairs. .... NASSAUVIA.
         7. Capitula solitary or in cymes or panicles.
            11. Pappus palaeaceous.
               12. Flowers white or violaceous. .... NASSAUVIA.
               12. Flowers yellow. .... CALOPAPPUS.
            11. Pappus setose or plumose.
               13. Shrubs cespitose, with white flowers; Patagonia. .... *Perezia lanigera.*
               13. Shrubs not cespitose, flowers of various colors.
                  14. Shrubs or vines; flowers yellow.
                     15. Vines; involucre with more than 3 rows of bracts; plants of the West Indies. .... ACOURTIA (*A. vanillosma*).
                     15. Shrubs; involucre with 2 rows of bracts; plants of North and South America and the West Indies.
                        16. Style-branch tips rounded. .... LEUNISIA.
                        16. Style-branch tips truncate.
                           17. Receptacle pubescent. ...... TRIXIS.
                           17. Receptacle glabrous.
                              18. Achenes truncate at the apex. .... AMEGHINOA.
                              18. Achenes with a glandular rostrum at the apex. .... DOLICHLASIUM.
                  14. Shrubs or vines without yellow flowers, or herbs rarely with yellow flowers.
                     19. Plants with a woolly pubescence.
                        20. Capitulum of more than 15 flowers.
                           21. Flowers orange. .... *Onoseris stricta.*
                           21. Flowers white, blue, or violet.

- 22. Style-branch tips rounded, branches less than 1 mm. long. . . . . MACHRACHAENIUM.
- 22. Style-branch tips truncate or rounded, branches more than 1 mm. long.
  - 23. Receptacle and flowers pubescent; North and Central America. . . . . . . ACOURTIA.
  - 23. Receptacle and flowers glabrous; South America. . . . . LEUCHERIA.

20. Capitulum of fewer than 15 flowers.
- 24. Branches of the styles more than 1 mm. long; North America. . . . . ACOURTIA.
- 24. Branches of the styles less than 1 mm. long; South America.
  - 25. Capitula solitary or few in number at the apex of the branches. . . . . LOPHOPAPPUS.
  - 25. Capitula in panicles or racemes of spikes. . . . . PROUSTIA.

19. Plants without a woolly pubescence.
- 26. Involucre with 1 or 2 rows of bracts.
  - 27. Pappus in one series. . . . . LEUCHERIA.
  - 27. Pappus in more than one series. . . . . HOLOCHEILUS.
- 26. Involucre with more than 2 rows of bracts. . . . . PEREZIA.

SYNOPSIS OF THE GENERA OF NASSAUVIINAE

NASSAUVIINAE Lessing, Linnaea **5:** 2. 1830. TYPE GENUS: *Nassauvia* Comm. ex Juss.

PLEOCARPHUS D. Don in Trans. Linn. Soc. I. **16:** 228. 1830. TYPE SPECIES: *P. revolutus* D. Don.

One shrubby species occurring in rocky soils from sea level to 900 m.s.m. in the provinces of Aconcagua, Coquimbo, and Atacama in Chile.

JUNGIA Linnaeus f., Suppl. Pl. 58. 1781. TYPE SPECIES: *J. ferruginosa* Linn. f.

About thirty species of shrubs or vines, rarely herbaceous, occurring in the Andean zone from northern Argentina to Mexico; also in the lowlands of Brazil.

MARTICORENIA Crisci, Jour. Arnold Arb. **55**(1): 38–45. 1974. TYPE SPECIES: *M. foliosa* (Phil.) Crisci = *Leucheria foliosa* Philippi.

One species occurring in the Andean region of central Chile, between 32°S and 35°S and 70°W and 71°W, above timberline from 2700 to 3300 m.s.m.

CEPHALOPAPPUS Nees & Martius, Nov. Acta Nat. Cur. **12:** 5. *t. 1.* 1824. TYPE SPECIES: *C. sonchifolius* Nees & Martius.

One herbaceous species occurring near the river Caxeiras (Ilheos) in the state of Bahia in Brazil; rarely collected.

PANPHALEA Lagasca, Amen. Nat. **1**: 34. 1811. TYPE SPECIES: *P. commersonii* Cass.

Eight species of annual herbs occurring in southern Brazil, eastern Paraguay, Uruguay, and in northeastern Argentina.

MOSCHARIA Ruiz & Pavon, Fl. Peru. Chil. Prodr. 103. 1794. TYPE SPECIES: *M. pinnatifida* Ruiz & Pavon.

Two species of herbs occurring from Coquimbo to Maule in central Chile from sea level to ca. 2000 m.s.m.

POLYACHYRUS Lagasca, Amen. Nat. **1**: 37. 1811. TYPE SPECIES: *P. poeppigii* Kunze ex Less.

About eight species, all herbaceous, occurring in central and northern Chile and in southern Peru.

TRIPTILION Ruiz & Pavon, Fl. Peru. Chil. Prodr. 102. *t. 22.* 1794. TYPE SPECIES: *T. spinosum* Ruiz & Pavon.

About twelve species of herbs, one occurring in Patagonia, the rest in central Chile.

NASSAUVIA Comm. ex Juss. Gen. Pl. 175. 1789. TYPE SPECIES: *N. magellanica* Gmel.

About 40 species of herbs or small shrubs occurring in the Andean zone from Malvinas Island to southern Bolivia, and in Patagonia.

CALOPAPPUS Meyen, Reise **1**: 315. 1834. TYPE SPECIES: *C. acerosus* Meyen.

Two (perhaps only one) species of herbs in the Andean region of central Chile.

OXYPHYLLUM Philippi, Fl. Atacamensis 28. *t 4.* 1860. TYPE SPECIES: *O. ulicinum* Philippi.

One species of spinose shrubs in the Atacama desert of Chile.

ACOURTIA D. Don, Trans. Linn. Soc. I. **16**: 203. 1830. TYPE SPECIES: *A. formosa* D. Don.

About 40 species of herbs or small shrubs occurring from the coastal region of southern California to El Salvador and eastward to central Texas and the West Indies. They are, for the most part, restricted to the forested middle and higher slopes of the Sierra Madre in Mexico and to the high plateaus east of the mountains in central and northern Mexico.

LEUNISIA Philippi, Linnaea **33**: 120. 1864–1865. TYPE SPECIES: *L. laeta* Philippi.

One species occurring in the Andean region of central Chile (Coquimbo and Acacongua).

TRIXIS P. Browne, Civ. Nat. Hist. Jamaica 312. 1756. TYPE SPECIES: *T. inula* Crantz.

About 50 species of shrubs occurring from Mexico to central Argentina and in the West Indies. There are two centers of diversity, one in southwestern Mexico, the other in southern Brazil, northern Argentina, and Uruguay.

AMEGHINOA Spegazzini, Rev. Fac. Agron. Vet. La Plata **3**: 539. 1897. TYPE SPECIES: *A. patagonica* Spegazzini.

One shrubby species endemic to the Patagonian steppe.

DOLICHLASIUM Lagasca, Amen. Nat. **1**: 33. 1811. TYPE SPECIES: *D. lagascae* D. Don.

One species of shrubby plants occurring in the Andean region of west central Argentina (provinces of La Rioja, San Juan, Mendoza, and Neuquén).

LOPHOPAPPUS Rusby emend. Cabrera, Bol. Soc. Arg. Bot. **5**(1–2): 45. 1953. TYPE SPECIES: *L. foliosus* Rusby.

Five or six species of shrubs in the Andean region from Peru to northern Chile.

PROUSTIA Lagasca, Amen. Nat. **1**: 33. 1811. TYPE SPECIES: *P. pyrifolia* DC.

Three species of shrubs and vines in the Andean regions of Chile, Argentina, and Bolivia.

MACRACHAENIUM Hooker f., Fl. Antarct. **2**: 321. 1847. TYPE SPECIES: *M. gracile* Hook. f.

One herbaceous species endemic to the *Nothofagus* forest in southern South America.

PEREZIA Lagasca, Amen. Nat. **1**: 311. 1811. TYPE SPECIES: *Perezia magellanica* (Linn. f.) Lagasca = *Perdicium magellanicum* Linn. f.

Thirty species of herbs, 27 occurring in the Andean region of South America and three in lowland open woods of Paraguay, Uruguay, Brazil, and Argentina.

LEUCHERIA Lagasca, Amen. Nat. **1**: 32. 1811. TYPE SPECIES: *L. hieracioides* Cassini.

Forty-six species of herbs occurring in the Andean region from Malvinas Island to southern Peru, and in Patagonia.

HOLOCHEILUS Cassini, Bull. Sci. Soc. Philomat. **1818**: 73. 1818. TYPE SPECIES: *H. brasiliensis* (Linn.) Cabrera = *H. ochroleucus* Cassini.

Six species of herbs occurring in southern Brazil, Paraguay, Uruguay, and in northern Argentina.

NOMENCLATURAL NOTES

Acourtia vanillosma (Wright) Crisci, comb. nov.
Proustia vanillosma Wright in Sauvage, Anal. Acad. Ci. Habana **6**: 212. 1860.
Perezia vanillosma (Wright) Molt. & Gómez, Anal. Soc. Hist. Nat. Madrid **19**: 268. 1890.
Proustia crassinervis Urban, Symb. Antill. **1**(3): 470. 1900.
Proustia krugiana Urban, *ibid.* 471.
Proustia stenophylla Urban & Ekman, Ark. Bot. **20A**(5): 65. 1926.

Acourtia glomeriflora (Gray) Reveal & King, Phytologia **27**: 229. 1973.
Gochnatia glomeriflora Gray, Proc. Am. Acad. **19**: 57. 1883.
Perezia capitata Watson, Proc. Am. Acad. **25**: 156. 1890.

Acourtia collina (Watson) Crisci, comb. nov.
Perezia collina Watson, Proc. Am. Acad. **26**: 144. 1891.

Perezia lanigera Hooker & Arnott, Hook. Comp. Bot. Mag. **2**: 42. 1836.
Perezia sessiliflora Spegazzini, Rev. Fac. Agron. Vet. **3**: 542. 1897.

Onoseris stricta Sprengel, Linn. Syst. Veg. ed. 16. **3**: 503. 1826.
Trixis stricta (Sprengel) Lessing, Linnaea **5**: 25. 1830.

Trichocline heterophylla sensu Grisebach, Symb. Fl. Argent. 215. 1879, non (Sprengel) Lessing.

Perezia pampeana Spegazzini, Flora de Tandil 33. 1901.

ACKNOWLEDGMENTS

I appreciate the guidance and constant encouragement of Dr. Otto T. Solbrig and the help and advice of Drs. R. C. Rollins, C. E. Wood, C. Marticorena, O. Zöllner, U. Banerjee, A. L. Cabrera, and D. Moore. I am especially grateful for the constant help of my wife Marta who also prepared the illustrations. D. Moore generously provided unpublished chromosome counts.

I am particularly indebted to Dr. Bernice G. Schubert for her advice, suggestions, and expert editorial assistance throughout the work.

Finally, Dr. Elizabeth A. Shaw provided an immeasurable amount of help and advice. Her comments have undoubtedly made this work of much higher quality than it would have been otherwise.

The present study was completed at the Gray Herbarium of Harvard University during my tenure as a Fellow of the John Simon Guggenheim Memorial Foundation. I am grateful to the officers of both these institutions for their support of my work. I appreciate especially the privilege of consulting the rich collections and libraries of the Gray Herbarium and the Arnold Arboretum.

LITERATURE CITED

ANDERSON, E. 1940. The concept of the genus. II. A survey of modern opinion. Bull. Torrey Bot. Club **67**: 363–369.

———. 1957. An experimental investigation of judgements concerning genera and species. Evolution **11**: 260–262.

ANDERSON, C. 1972. A monograph of the Mexican and Central American species of *Trixis* (Compositae). Mem. N. Y. Bot. Gard. **22**(3): 1–68.

BACIGALUPI, R. 1931. A monograph of the genus *Perezia*, section *Acourtia*, with a provisional key to the section *Euperezia*. Contr. Gray Herb. Harvard Univ. **97**: 1–81. *7 pls.*

BAILEY, I. W. 1953. The anatomical approach to the study of genera. Chronica Botanica **14**(3): 121–125.

BARTLETT, H. H. 1940. The concept of the genus. I. History of the generic concept in botany. Bull. Torrey Bot. Club **67**: 349–362.

BENTHAM, G. 1873. Notes on the classification, history, and geographical distribution of Compositae. Jour. Linn. Soc. Bot. **13**: 335–577. *4 pls.*

——— & J. D. HOOKER. 1873. Compositae. *In*: Genera Plantarum **2**: 163–533.

BLAKE, S. F. 1924. New American Asteraceae. [*Gochnatia*.] Contr. U.S. Natl. Herb. **22**(8): 651–653.

———. 1926. *Gochnatia*. *In*: P. C. STANDLEY, Trees and shrubs of Mexico. Contr. U.S. Natl. Herb. **23**(5): 1636, 1637.

CAIN, A. J. 1956. The genus in evolutionary taxonomy. Syst. Zool. **5**: 97–109.

CABRERA, A. L. 1936. Las especies argentinas y uruguayas del género *Trixis*. Revista Mus. La Plata Bot. (N. S.) **1**: 31–86. *2 pls.*

———. 1953a. Las especies del género *Pamphalea* (Compositae). Notas Mus. La Plata Bot. **16:** 225–237.

———. 1953b. Compuestas peruanas nuevas o criticas. Bol. Soc. Argent. Bot. **5:** 37–50.

———. 1961. Compuestas argentinas. Clave para la determinación de los géneros. Rev. Mus. Arg. Cienc. Bernardino Rivadavia **2**(5): 291–362. *12 pls.*

———. 1968. Rehabilitación del género *Holocheilus* Cassini (Compositae). Revista Mus. La Plata Bot. (N. S.) **11:** 1–15.

———. 1971a. Revision del género *Gochnatia* (Compositae). *Ibid.* **12:** 1–160.

———. 1971b. Compositae. *In*: M. N. Correa, Flora Patagónica (República Argentina). Parte VII. I.N.T.A. **8:** 1–432.

———. 1971c. Fitogeografía de la República Argentina. Bol. Soc. Argent. Bot. **14**(1–2): 1–42. *8 pls.*

Camp, W. H. 1940. The concept of the genus. V. Our changing generic concepts. Bull. Torrey Bot. Club **67:** 381–389.

Candolle, A. P. de. 1812. Observations sur les plantes composées, ou syngenèses. Troisième mémoire. Sur les composées a corolles labiées, ou labiatiflores. Ann. Mus. Hist. Nat. Paris **19:** 59–72. *2 pls.*

———. 1838. Nassauviaceae. Prodr. **7**(I): 48–74.

Carlquist, S. 1957a. Wood anatomy of Mutisieae (Compositae). Trop. Woods **106:** 29–45.

———. 1957b. Anatomy of Guayana Mutisieae. I. Pollen. Mem. N. Y. Bot. Gard. **9**(3): 441–476.

———. 1958. Anatomy of Guayana Mutisieae. Part II. Mem. N. Y. Bot. Gard. **10**(1): 157–184.

———. 1966. Wood anatomy of Compositae: A summary, with comments on factors controlling wood evolution. Aliso **6**(2): 25–44.

Cassini, H. 1817. Chénantophores. Dict. Sci. Nat. [Paris] **8:** 393–395.

———. 1825. Nassauviées. *Ibid.* **34:** 204–238.

Cave, M. S. 1953. Cytology and embryology in the delimitation of genera. Chronica Botanica **14**(3): 140–153.

Cerrate, E. 1951. Revision de las especies peruanas del género *Jungia*. Publ. Mus. Hist. Nat. Lima Bot. (Ser. B.) **4:** 1–24. *3 pls.*

Coleman, J. R. 1968. Chromosome numbers in some Brazilian Compositae. Rhodora **70:** 228–240.

Covas, G., & B. Schnack. 1946. Número de cromosomas en Antófitas de la región de Cuyo (República Argentina). Revista Argent. Agron. **13:** 153–166.

Crisci, J. V. 1971a. Sobre una especie de *Jungia* (Compositae) del Perú. Bol. Soc. Argent. Bot. **13:** 341–346.

———. 1971b. Sobre una especie de *Leuceria* (Compositae) de Chile. Darwiniana **16:** 627–633.

———. 1974a. *Marticorenia*: A new genus of Mutisieae (Compositae). Jour. Arnold Arb. **55:** 38–45.

———. 1974b. Revision of the genus *Moscharia* (Compositae: Mutisieae) and a reinterpretation of its inflorescence. Contr. Gray Herb. Harvard Univ. **205:** 163–173.

Cronquist, A. 1955. Phylogeny and taxonomy of the Compositae. Am. Midl. Nat. **53:** 478–511.

Davis, P. H., & V. H. Heywood. 1963. Principles of angiosperm taxonomy. 558 pp. Oliver & Boyd, Edinburgh & London.

DIERS, L. 1961. Der Anteil an Polyploiden in den Vegetationsgürteln der Westkordillere Perus. Zeitschr. Bot. **49:** 437–488.

EAMES, A. J. 1953. Floral anatomy as an aid in generic limitation. Chronica Botanica **14**(3): 126–132.

EDWARDS, A. W. F., & L. L. Cavalli-SFORZA. 1964. Reconstruction of evolutionary trees. *In:* V. H. HEYWOOD & J. MCNEILL, eds., Phenetic and phylogenetic classification. xi + 164 pp. Systematics Assoc. Publ. No. 6. London. Pp. 67–76.

ERDTMAN, G. 1960. The acetolysis method. A revised description. Sv. Bot. Tidskr. **54:** 561–564.

FABRIS, H. 1968. Revision del género *Proustia* (Compositae). Revista Mus. La Plata Bot. (N. S.) **11:** 23–49.

GREENMAN, J. M. 1940. The concept of the genus. III. Genera from the standpoint of morphology. Bull. Torrey Bot. Club **67:** 371–374.

HEISER, C. 1963. Numeración cromosómica de plantas ecuatorianas. Ciencia y Naturaleza **6:** 2–6.

HOFFMANN, O. 1893. Mutisieae. Compositae. *In:* ENGLER, A., & K. PRANTL, Nat. Pflanzenfam. **4**(5): 333–350.

INGER, R. F. 1958. Comments on the definition of genera. Evolution **12:** 370–384.

JEFFREY, C. 1967. Notes on Compositae: II. The Mutisieae in east Tropical Africa. Kew Bull. **21:** 177–224.

KIRPICZNIKOV, M. E. 1968. On the concept of genus in flowering plants. Bot. Zhur. **53:** 190–202. [English summary.]

LAGASCA, M. 1811. Disertación sobre un orden nuevo de plantas de la clase de las Compuestas. Amen. Nat. de las Españas **1:** 26–44.

LANJOUW, J., & F. A. STAFLEU. 1964. The herbaria of the world. Index Herbariorum I, ed. 5. Regnum Veg. **31:** 1–251.

LAWRENCE, G. H. M. 1953. Plant genera, their nature and definition. The need for an expanded outlook. Chronica Botanica **14**(3): 117–120.

LEGENDRE, P., & P. VAILLANCOURT. 1969. A mathematical model for the entities species and genus. Taxon **18:** 245–252.

LESSING, C. F. 1830. Nassauvieae. Linnaea **5:** 1–42.

———. 1832. Synopsis generum Compositarum. 473 pp. Berolini, Paris.

LOJA, B. HERRERA ALARCÓN DE. 1969. Revision de las especies peruanas del género *Trixis*. Publ. Mus. Hist. Nat. Lima Bot. (Ser. B.) **25:** 1–16. *8 pls.*

LÖVE, A. 1963. Cytotaxonomy and generic delimitation. Regnum Veg. **27:** 45–51.

MAGUIRE, B. 1956. Distribution, endemicity, and evolution patterns among Compositae of the Guayana Highland of Venezuela. Proc. Am. Philos. Soc. **100:** 467–475.

MASON, H. L. 1953. Plant geography in the delimitation of genera. The role of plant geography in taxonomy. Chronica Botanica **14**(3): 154–159.

MAYR, E. 1963. Animal species and evolution. 797 pp. Harvard Univ. Press, Cambridge.

———. 1969. Principles of systematic zoology. 428 pp. McGraw-Hill, New York.

MICHENER, C. D. 1957. Some bases for higher categories in classification. Syst. Zool. **6:** 160–173.

MOORE, D. M. 1967. Chromosome numbers of Falkland Islands angiosperms. British Antarct. Surv. Bull. **14:** 69–82.

PARRA, O., & C. MARTICORENA. 1972. Granos de polen de plantas chilenas. II. Compositae Mutisieae. Gayana Botanica **21:** 1–107.

PRIM, R. C. 1957. Shortest connection networks and some generalizations. Bell Syst. Tech. Jour. **36:** 1389–1401.

POWELL, A. M., & B. L. TURNER. 1963. Chromosome numbers in the Compositae. VII. Additional species from the southwestern United States and Mexico. Madroño **17:** 128–140.

POWELL, M., D. KYHOS, & P. RAVEN. Chromosome numbers in Compositae. X. Am. Jour. Bot. [in press].

ROGERS, D. J., & T. T. TANIMOTO. 1960. A computer program for classifying plants. Science **132:** 1115–1118.

ROLLINS, R. C. 1953. Cytogenetical approaches to the study of genera. Chronica Botanica **14**(3): 133–139.

ROSEN, D. E., & R. M. BAILEY. 1963. The poeciliid fishes (Cyprinodontiformes), their structure, zoogeography and systematics. Bull. Am. Mus. Nat. Hist. **126:** 1–176.

SHERFF, E. E. 1940. The concept of the genus. IV. The delimitations of genera from the conservative point of view. Bull. Torrey Bot. Club **67:** 375–380.

SIMPSON, G. G. 1961. Principles of animal taxonomy. 247 pp. Columbia Univ. Press, New York.

SKVARLA, J. J., & B. L. TURNER. 1966. Systematic implications from electron microscopic studies of Compositae pollen — a review. Ann. Missouri Bot. Gard. **53:** 220–256.

SMALL, J. 1919. The origin and development of the Compositae. New Phytol. Reprint, No. 11. William Wesley & Son, London.

SNEATH, P. H. A., & R. R. SOKAL. 1973. Numerical taxonomy; the principles and practice of numerical classification. xv + 573 pp. Freeman & Co., San Francisco.

SOLBRIG, O. T. 1960. The status of the genera *Amphipappus*, *Amphiachyris*, *Greenella*, *Gutierrezia*, *Gymnosperma* and *Xanthocephalum* (Compositae). Rhodora **62:** 43–54.

———. 1963. Subfamilial nomenclature of Compositae. Taxon **12:** 229–235.

———. 1970. The phylogeny of *Gutierrezia*: an eclectic approach. Brittonia **22:** 217–229.

STEBBINS, G. L. 1956. Taxonomy and the evolution of genera, with special reference to the family Gramineae. Evolution **10:** 235–245.

———. 1967. Adaptive radiation and trends of evolution in higher plants. *In*: T. DOBZHANSKY, M. K. HECHT, & W. C. STEERE, *eds.*, Evolutionary Biology. Vol. 1. Appleton-Century-Crofts, New York. Pp. 101–142.

STIX, E. 1960. Pollenmorphologische Untersuchungen an Compositen. Grana Palyn. **2**(2): 41–114.

TURNER, B. L., M. POWELL, & R. M. KING. 1962. Chromosome numbers in the Compositae. IV. Additional Mexican and Guatemalan species. Rhodora **64:** 251–271.

TUTIN, T. G. 1956. Generic criteria in flowering plants. Watsonia **3:** 317–323.

VAN RIJSBERGEN, C. J. 1970. A fast hierarchic clustering algorithm. Comput. Jour. **13:** 324–326.

VUILLEUMIER, B. S. 1969. The systematics and evolution of *Perezia* sect. *Perezia* (Compositae). Contr. Gray Herb. Harvard Univ. **199:** 1–163.

———. 1971. Pleistocene changes in the fauna and flora of South America. Science **173:** 771–780.

WAGNER, W. H., Jr. 1961. Problems in the classification of ferns. *In*: Recent advances in botany. Vol. I. 974 pp. Univ. Toronto Press, Toronto. Pp. 841–844.

WEDDELL, H. A. 1855. Chloris Andina Vol. 1. Chez P. Bertrand, Paris. [*Perezia*, pp. 36–45].

WODEHOUSE, R. P. 1929. Pollen grains in the identification and classification of plants. III. The Nassauvinae. Bull. Torrey Bot. Club **56:** 123–138. *1 pl.*

GRAY HERBARIUM
HARVARD UNIVERSITY
CAMBRIDGE, MASSACHUSETTS 02138

Permanent address:
DIVISIÓN PLANTAS VASCULARES
MUSEO DE LA PLATA
LA PLATA, ARGENTINA

THE GENERA OF ROSACEAE IN THE SOUTHEASTERN UNITED STATES *

KENNETH R. ROBERTSON

Tribe ROSEAE

17. **Rosa** Linnaeus, Sp. Pl. 1: 491. 1753; Gen. Pl. ed. 5. 217. 1754.

Mostly deciduous shrubs with upright, arching, trailing, or climbing stems; armature of stem, petiole, rachis, inflorescence branches, and floral cup of variously sized and shaped prickles and/or bristles (acicles), rarely absent; indumentum of simple hairs and/or sessile to stalked glands, variable in density and distribution. Leaves petiolate, imparipinnate or trifoliolate [very rarely simple]; leaflets toothed, the lateral ones nearly sessile, the terminal one long-petiolulate; stipules paired, conspicuous [rarely absent], entire to pinnatifid, sometimes fringed with glands, commonly adnate to the base of the petiole and forming wings, usually persistent. Inflorescences of few- to many-flowered, bracteate, determinate "corymbs" or "panicles" terminating primary or lateral stems, or the flowers solitary; flowers produced mostly on short shoots from the growth of last year. Flowers perfect, 5 (rarely 4) -merous, large, showy, often fragrant. Calyx without an epicalyx, the lobes quincuncial in aestivation, persistent or not, all entire or the outer two and half of the middle lobe fringed, toothed, or pinnatifid or with lateral appendages,[9] the apices acute to long attenuate or dilated; floral cups urceolate to globose, campanulate, or nearly tubular, the opening usually constricted; disc commonly prominent, forming a ring around the opening of the floral cup. Petals 5 (to numerous in double-flowered forms), white, yellow, or various shades of pink [orange or nearly red], narrowly to broadly obovate, the apices usually emarginate, tapering at the base, inserted at the outer edge of the disc. Androecium of many stamens in several whorls, the outer ones longer than the inner; filaments slender, persistent; anthers small, yellow. Gynoecium of numerous sessile or stipitate carpels included within and inserted at the base of, or on the inner walls of, the floral cup; styles terminal, shortly or long exserted beyond the mouth of the floral cup, free

---

* Continued from volume 55, p. 401.

[9] This type of aestivation has been noted in verse:

> On a summer's day, in sultry weather,
> Five brethren were born together.
> Two had beards and two had none,
> And the other had but half a one.

For other versions of this poem in English, Latin, and German, see Stearn and Bell.

below and free or connate into a column above; stigmas terminal, discoid, often tightly grouped together into a button-shaped structure blocking the opening of the floral cup; each carpel with one anatropous pendulous ovule. Fruit accessory (a hip), of numerous achenes enclosed by the enlarged, fleshy, usually red floral cup; achene wall hard; seed coat thin; embryo filling the seed and achene, the radicle superior. Base chromosome number 7. LECTOTYPE SPECIES: *R. centifolia* L.; see Britton & Brown, Illus. Fl. No. U. S. Canada, ed. 2. 2: 282. 1913.[10] (The ancient Latin name.) — ROSE.

About 120 or more species (several thousand described) in four subgenera of the Northern Hemisphere, extending from the arctic and boreal regions southward in North America to central Florida, Texas, Mexico, and Baja California, and in Eurasia to the Philippine Islands, Burma, southern India, and Persia, as well as in Ethiopia, and Mediterranean Africa. The largest concentration of species is in the region between western Asia and China. Members of the genus usually inhabit borderland or open habitats, such as fence rows, roadsides, scrublands, pastures, and the edges of woods. Because of the variability within species and the weak barriers to interspecific hybridization, the taxonomy of the genus is confusing, and many morphological variants have been described as distinct species. Several subgeneric classification schemes have been proposed (see Herring, 1925); the one outlined by Crépin (1889) and adopted by Rehder is accepted today as best reflecting natural relationships within the genus.

Most species of the genus are in cultivation, and in many ways the genus is remarkably well known. The chromosome numbers for most species have been reported, and some hybridization, breeding, and genetic studies have been made. However, nearly all the taxonomic investigations were done much earlier, were based primarily on cultivated plants, and had a strong horticultural emphasis. A modern review needs to be made with particular attention given to the species as they occur in nature; the Chinese species are particularly in need of study.

Only about 12 species, representing three sections of subg. ROSA are native to eastern North America, although more than a hundred have been described from this region; four species are indigenous to our area. Species belonging to all four subgenera and to all ten sections of subg. ROSA are cultivated in the southeastern United States, and some of these persist, become naturalized, or hybridize with native plants.

---

[10] Two other species, belonging to two other sections, have been proposed as the type species: *R. cinnamomea* L. (Rydberg, N. Am. Fl. **22**: 483. 1918) and *R. canina* L. (Rehder, Bibliogr. Cult. Trees Shrubs, 296. 1949). Objections can be raised against the selection of any of these species: *R. centifolia* is not a wild species but a complex hybrid involving four species, *R. rubra*, *R. phoenicia*, *R. moschata*, and *R. canina* (see Hurst, 1941); *R. cinnamomea* clearly does not agree with the protologue with regard to the calyx lobes; and *R. canina* "is unsuitable as the name has been used in different senses by different authors" (Hitchcock & Green, Int. Bot. Congr. Cambridge Nomencl. Prop. Brit. Bot. 1929). However, all of these are clearly members of this genus.

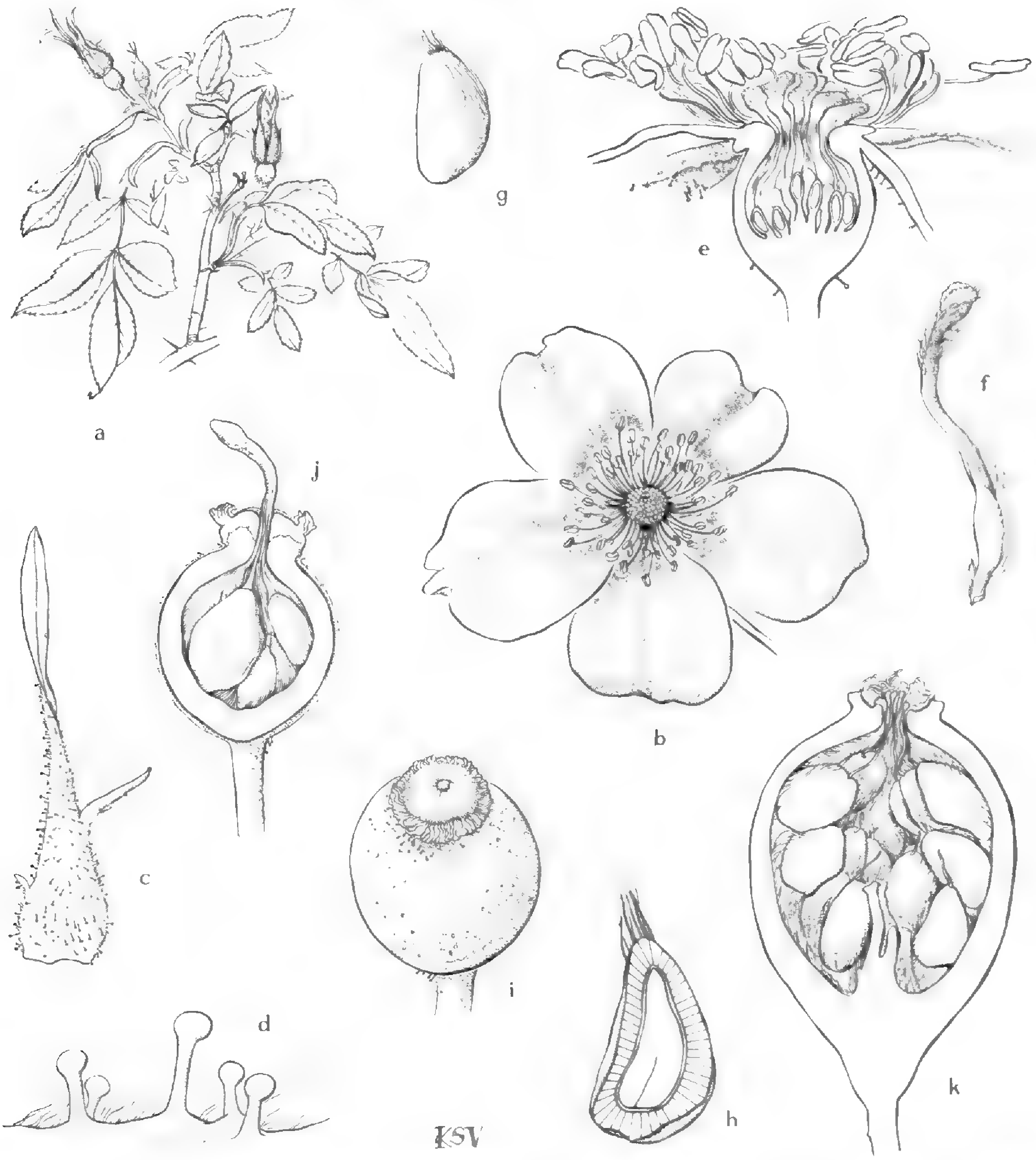


FIGURE 8. **Rosa.** a–h, *R. carolina*: a, branch with flower buds, note stipules adnate to petioles, × 1/2; b, flower, × 1; c, abaxial side of outer calyx lobe with 2 lateral appendages, × 2; d, simple and glandular trichomes on margin of calyx lobe, × 25; e, flower in longitudinal section, calyx lobes, petals, and stamens attached at apex of, and carpels at base of, floral tube, × 3; f, carpel, × 6; g, achene (nutlet), × 3; h, achene in vertical section, wall hatched, embryo and seed coat unshaded, × 5. i, j, *R. setigera*: i, mature fruit (hip), persistent filament bases surrounding disc with stylar scar in center, × 3; j, longitudinal section of fruit, styles connate into column above disc, × 3. k, *R. Eglanteria*: longitudinal section of mature fruit, carpels attached to wall at various levels, × 2.

The great majority of species of *Rosa* belong to subg. ROSA (floral cups glabrous or with glands or bristles, not with prickles), which is subdivided into ten sections. Three of our native roses, *R. carolina*, *R. palustris*, and *R. foliolosa*, belong to sect. CAROLINAE Crépin (carpels inserted at the base of the floral cup; calyx lobes deciduous from the hip, elongate, apically dilated and flattened, the outer with a few linear appendages or entire; floral cups glandular), which is restricted to eastern North America. Because each of the distinguishing characters of this section is found in some species of sect. CINNAMOMEAE DC., sect. CAROLINAE is sometimes merged with that section (see discussion in Lewis, 1957b).

Rosa carolina L., $2n = 28$, a variable and taxonomically complex species, occurs from peninsular Florida, Alabama, Mississippi, Louisiana, and Texas, northward to New England, Nova Scotia, and Ontario to Michigan, Wisconsin, and Nebraska. This species, distinguished from related ones by the fine and mostly straight infrastipular prickles that are round in cross section and not particularly broad based, the usual abundance of internodal prickles and bristles, the narrow stipular auricles (less than 2.5 mm. wide), the mostly solitary flowers, and the ovate or elliptic leaflets that are usually glabrous above and below, is particularly variable in the height of the plants, flower size, abundance of prickles, leaflet size, and indumentum density. Many of these characters can be altered by the environment, and *R. carolina* is one of the most heterogeneous roses of eastern North America. Segregate species ascribed to our area include *R. Lyonii* Pursh; *R. serrulata* auct., not Raf.; *R. subserrulata* Rydb.; *R. Treleasei* Rydb.; and *R. texarkana* Rydb. Toward the northern part of its range, *R. carolina* is sympatric with and hybridizes with *R. virginiana*, as it does toward the western part of its range with *R. arkansana* Porter.

Along the Atlantic seaboard from Newfoundland and New England to New Jersey, Delaware, and eastern Pennsylvania, there are a number of rather homogeneous populations of roses with stout, usually curved, broad based infrastipular prickles on the floral branches (but few or no internodal prickles or bristles), inflorescences of three or more flowers, apically dilated stipular auricles more than 2.5 mm. wide, obovate, shiny leaflets, and a sporophytic chromosome number of 28; these plants are properly called *Rosa virginiana* L. Similar, more variable plants with at least some of these features are found southward and westward to Virginia, North Carolina, Alabama, Tennessee, and Missouri; these are either included in *R. virginiana* (Fernald, Gray's Manual, ed. 8; Steyermark, Fl. Missouri) or considered to be the result of hybridization and introgression between *R. carolina* and *R. virginiana* or *R. arkansana* (Gleason, New Britton & Brown; Lewis, 1958).

Rosa palustris Marshall, swamp rose, $2n = 14$, a tall shrub with finely toothed leaflets, convolute stipules, and large, stout infrastipular prickles (but lacking internodal prickles and bristles), ranges from Florida to Arkansas, north to Nova Scotia, Ontario, Michigan, Wisconsin, and Minnesota; it is especially common along the Atlantic seaboard. As the specific and common names indicate, this species is largely restricted to wet habitats, such as swamps, marshes, wet woods, and the borders of streams, bayous, sink holes, and drainage ditches. Plants with fewer (usually 5) and smaller leaflets and depressed-globose, instead of globose or ellipsoidal, floral cups have been separated as *R. floridana* Rydb.

The other species of sect. CAROLINAE in our area is *R. foliolosa* Nutt. ex Torrey & Gray, $2n = 14$, a distinctive low shrub of dry, open areas, mostly with nine, narrow, elliptic leaflets per leaf and stems that are unarmed or have a few small, straight prickles. This species has one of the narrowest distributions of any native North American rose: extreme western Arkansas, the eastern two-thirds of Oklahoma, and central and north-central Texas. *Rosa nitida* Willd., $2n = 14$, the only other species of this section, occurs in New England, Quebec, and the Maritime Provinces of Canada.

The largest section of the genus is sect. CINNAMOMEAE DC. (sect. *Cassiorhodon* Dumort.) (erect, deciduous shrubs with bristles and usually slender, straight prickles in infrastipular pairs or scattered; flowers numerous, in bracteate corymbs; calyx lobes persistent, all entire; carpels lining the sides of the floral cup), which includes more than fifty species of both hemispheres. Although this section does not occur in our area, four species are indigenous to North America, and *Rosa rugosa* Thunb., $2n = 14$, a native of eastern Asia, has become thoroughly naturalized within the past 70 years along beaches from the Bay of Fundy to Long Island Sound and New Jersey and also around the lower Great Lakes.

Our only other indigenous rose is *Rosa setigera* Michx., prairie rose, $2n = 14$, the only New World species of sect. SYNSTYLAE DC. (styles exserted, united into a column). This plant, a large shrub with long (to 5 m. or more), climbing, leaning, or trailing stems, trifoliolate leaves (the leaflets large, coarsely toothed), uniform-sized infra- and internodal prickles (but no bristles), and glandular stipules, petioles, pedicels, calyx lobes, and floral cups, is indigenous to the region from northeastern Texas, Oklahoma, Kansas, and Nebraska, east to the eastern foothills of the Appalachians. It has become naturalized along the Atlantic seaboard from New England to South Carolina. Two varieties, var. *setigera*, with the leaflets glabrous below or with trichomes only on the veins, and var. *tomentosa* Torrey & Gray, with the leaflets pubescent below, can be distinguished. Unarmed plants of both varieties occur, as do white-flowered individuals of var. *tomentosa*.

Two eastern Asiatic species of sect. SYNSTYLAE are naturalized in eastern North America. *Rosa multiflora* Thunb., $2n = 14$, Japanese or multiflora rose, an arching or trailing shrub with numerous small flowers in pyramidal inflorescences, fimbriate-pectinate stipules, glabrous styles, and only infrastipular prickles, is commonly planted along fence rows and roadsides, particularly as a "living fence." It is reproducing by seed from New England and New York, south and west to the Carolinas, Mississippi, Tennessee, Missouri, Oklahoma, and Texas. The memorial rose, *R. Wichuraiana* Crépin, $2n = 14$, a low, semi-evergreen plant with long, prostrate or trailing branches, pubescent styles, jagged-dentate stipules, and scattered prickles, is often grown as a ground cover along highways and railroads, and it has spread locally in at least Virginia, the Carolinas, and Ohio.

Rosa laevigata Michx., $2n = 14$, Cherokee rose, the only species of sect. LAEVIGATAE Crépin, was for some time thought to be indigenous to the southern United States (Michaux described it from plants collected in Georgia), but it is actually a Chinese plant that was introduced and became naturalized at an early date. This distinctive species is a high-climbing shrub with evergreen, glossy, ternately compound leaves; large, white, solitary flowers; bristly floral cups, pedicels, and hips; and uniform curved internodal and infranodal prickles.

Rosa bracteata Wendl., $2n = 14$, of sect. BRACTEATAE Crépin (stems, inflorescence branches, and floral cups tomentose; flowers few or solitary, short-stalked, subtended by large, foliaceous bracts; stipules pectinate; infrastipular prickles stout, curved; internodal regions mostly with bristles and stipitate glands) is a native of China and Taiwan that is commonly planted in the southern United States as a "living fence"; it readily escapes and is naturalized from Florida to Texas, northward to Virginia and Tennessee. This is a handsome shrub with long, stout branches that clamber, ramble, or recline (sometimes forming mounds 5 m. or more tall), large white flowers, and evergreen leaves with 5 to 9 small, leathery, glossy leaflets. The only other species of this section is *R. clinophylla* Thory, of India.

Section CANINAE DC., dog roses, includes deciduous shrubs with numerous, uniform-sized prickles (bristles mostly absent), usually pinnate outer calyx lobes, and long stipitate carpels. This group is nearly confined to Europe and is taxonomically quite difficult. Three species have escaped from cultivation locally in the eastern United States: *Rosa Eglanteria* L.,[11] $2n = 35$, sweet briar (leaflets pubescent and densely glandular below, styles villous or lanate, calyx lobes persistent); *R. micrantha* Smith (similar to the preceding but the styles glabrous); and *R. canina* L., $2n = 35$, dog rose (leaflets glabrous and eglandular below, calyx lobes caducous).

All species of sect. CANINAE are polyploid (mostly pentaploids), as far as is known, and they have a type of reproduction that is unlike that of any other flowering plant. During meiosis, 7 bivalents and 14, 21, or 28 univalents are formed. The univalents are not incorporated into pollen grains, which have 7 chromosomes. The megaspores, however, contain all of the univalents plus a set of 7 chromosomes from the bivalents. At fertilization the original, parental chromosome number is restored. Thus in pentaploid species, the pollen contains 7 chromosomes, while the egg cells have 28 chromosomes. Inheritance is strongly maternal, and reciprocal hybrids between species result in plants differing in chromosome inheritance. A hybrid of *R. canina* and *R. Eglanteria* can be 4/5 *canina* and 1/5 *Eglanteria* or *vice versa*. This mechanism is genetically controlled and can be broken down when crosses are made with species belonging to other sections.

---

[11] In some European floras *R. Eglanteria* L., Sp. Pl. **1**: 491. 1753, is considered an ambiguous name and is replaced by *R. rubiginosa* L., Mantissa Alt. 564. 1771.

Section ROSA (erect, low, deciduous, rhizomatous shrubs with bristles and hooked prickles; flowers often solitary, without subtending bracts; calyx lobes deciduous, the outer pinnate; carpels sessile) includes one wild species, *Rosa gallica* L., $2n = 28$, French rose, Provins rose, red rose of Lancaster, a native of southern and central Europe that occasionally persists or escapes from cultivation in the eastern United States. This species has given rise by mutation and hybridization to several groups of "old garden roses": damask roses (*R. damascena* Miller), cabbage roses (*R. centifolia* L.), moss roses (*R. centifolia* var. *muscosa* (Miller) Ser.), and alba roses (*R. alba* L.).

The remaining sections of subg. ROSA are PIMPINELLIFOLIAE DC. (about 10 Old World species), CHINENSES DC. (two species of China), and BANKSIAE Crépin (*R. Banksiae* Aiton, China). The other subgenera are HULTHEMIA (Dumort.) Focke (*R. persica* Michx. ex J. F. Gmelin, southwestern and central Asia), PLATYRHODON (Hurst) Rehder (*R. Roxburghii* Tratt., China and Japan), and HESPERHODOS Rehder (*R. stellata* Wooton, New Mexico and Texas; *R. minutifolia* Engelm., northern Baja California).

The genus has been studied cytologically in some detail. The base chromosome number is 7 (aneuploidy is known only in cultivars) and the chromosomes are small and morphologically similar to one another, differing mostly in number and behavior at meiosis. The species of subgenera HULTHEMIA, PLATYRHODON, and HESPERHODOS and sects. SYNSTYLAE, CHINENSES, BANKSIAE, LAEVIGATAE, and BRACTEATAE of subg. ROSA are all diploid. Sections PIMPINELLIFOLIAE and CAROLINAE have diploid and tetraploid species; CINNAMOMEAE, diploid, tetraploid, hexaploid, and octoploid species; GALLICANAE, one tetraploid species; and CANINAE, heterogamous polyploid species. Täckholm (see map in Hurst, 1928) showed that in Europe there is a regular series of ploidy levels from south (diploid) to north (octoploid). A somewhat similar phenomenon seems to occur in North America, with the octoploid *Rosa acicularis* subsp. *acicularis* in Alaska and the hexaploid subsp. *Sayi* in northern North America (extending southward in the Rocky Mountains). Tetraploid and diploid species are widely distributed, but the diploids do occur farther south than the tetraploids (see map in Lewis, 1970).

Roses have long been one of the favorite flowers of peoples of many lands and cultures, and they often figure in song, poetry, literature, and painting. Historical events, such as the War of Roses, are sometimes associated with the genus. The common garden roses are of complex hybrid origin involving *Rosa chinensis* Jacq., *R. odorata* (Andrews) Sweet, *R. gallica*, *R. moschata* Herrm., *R. foetida* Herrm., *R. multiflora*, and *R. Wichuraiana*. Rose hips are flavorful, contain a large concentration of vitamin C, and are sometimes eaten fresh or made into jelly or tea. *Rosa damascena* is grown commercially in Bulgaria, France, and the Middle East for the production of Attar of roses and rose water.

REFERENCES:

The literature on *Rosa* is voluminous; the list below includes mostly botanical titles and a few basic horticultural and historical works. Under family references see BATE-SMITH, BEAN, BOUTINEAU, BUNTING, CROCKER & BARTON, DIPPLE, HARA, HEGI, HULTÉN (1971), LUBBOCK, REHDER, ROBERTSON, ROSS-CRAIG, SCHNEIDER, STEPHENS, L. A. TAYLOR, and VINES.

ANDERSON, E., & W. H. JUDD. *Rosa rugosa* and its hybrids. Arnold Arb. Bull. Pop. Inf. III. **6**: 29–35. 1932.

BECHTEL, E. DeT. Our rose varieties and their Malmaison heritage. 20 pp. New York Bot. Gard. 1949. [See other articles in Herbarist **16**: 6–17. 1950 and *ibid.* **23**: 10–20. 1957.]

BELL, L.. Rose signatures. Morris Arb. Bull. **23**: 59–66. 1972. [Excellent illustrated article on the morphological diversity in the genus.]

BOND, T. E. T. On sepal phyllody in roses and some related phenomena. Experimental data and a quantitative interpretation. New Phytol. **44**: 220–230. 1945.

BOULENGER, G. A. Introduction a l'étude du genre *Rosa*. Les caractères morphologiques passés en revue au point de vue de leur valeur pour la systématique. Bull. Jard. Bot. Bruxelles **14**: 241–273. 1937. [See also revisions of certain sects. in vols. 9, 10, 12, 13, 14.]

BOYNTON, K. R. *Rosa rugosa*. Addisonia **16**: 91, 92 [19, 20]. *pl. 522.* 1931.

CAYEUX, H. *Rosa gigantea* and its hybrids. Jour. Hered. **20**: 305–307. *frontisp.* 1929.

COCKERELL, T. D. A. The evolution and classification of roses. Torreya **29**: 97–103. 1929.

CRÉPIN, F. Primitiae monographiae rosarum. Matériaux pour servir a l'histoire des roses. 856 pp. Gand [Ghent], Belgium. 1869–1882. [Issued in six parts. Reprinted from Bull. Soc. Bot. Belg. **8**: 226–349. 1869; **11**: 15–130. 1872; **13**: 242–290. 1874; **14**: 3–46, 137–168. 1875; **15**: 12–100. 1876; **18**: 221–416. 1879; **21**: 7–196. 1882. See G. TAYLOR, Bull. Jard. Bot. Nat. Belg. **37**: 25–29. 1967; HERRING (1930); and MELVILLE.]

———. Nouvelles remarques sur les roses américaines. Bull. Soc. Bot. Belg. **26**(2): 40–49. 1887. *Ibid.* **28**(2): 18–33. 1889.

———. Sketch of a new classification of roses. Jour. Roy. Hort. Soc. II. **11**: 217–228. 1889. [The subgeneric classification system commonly used today first proposed.]

———. Rosae americanae I. Observation upon the genus *Rosa* in North America. Bot. Gaz. **22**: 1–34. 1896.

DAHLGREN, K. V. O. A peculiar proliferation in the flower of *Rosa centifolia* L. var. *muscosa* (Mill.) Ser. Sv. Bot. Tidskr. **53**: 229, 230. 1959.

ERLANSON, E. W. Cytological conditions and evidences for hybridity in North American wild roses. Bot. Gaz. **87**: 443–506. *pls. 16–19.* 1929.

———. The phenological procession in North American wild roses in relation to the polyploid series. Pap. Mich. Acad. Sci. **11**: 137–150. *table.* 1929 [1930].

———. Sterility in wild roses and in some species hybrids. Genetics **16**: 75–96. 1931.

———. Experimental data for a revision of the North American wild roses. Bot. Gaz. **96**: 197–259. 1934.

———. Phylogeny and polyploidy in *Rosa*. New Phytol. **37**: 72–81. 1938.

Erlanson McFarlane, E. W. Report on hybrids of American wild rose species at the botanical gardens at Ann Arbor, Michigan. Am. Rose Annual **46:** 107–116. 1961.

Fagerlind, F. Influence of the pollen-giver on the production of hips, achenes and seeds in the "Canina roses." Acta Horti Berg. **16:** 121–168. 1951.

———. Hip and seed formation in newly formed *Rosa* polyploids. *Ibid.* **17:** 229–256. *pls. 1–7.* 1958.

Fernald, M. L. *Rosa blanda* and its allies of northern Maine and adjacent Canada. Rhodora **20:** 90–96. 1918.

Flory, W. S., Jr. Pollen condition in some species and hybrids of *Rosa* with a consideration of associated phylogenetic factors. Virginia Jour. Sci. II. **1:** 11–59. 1950.

Gleason, H. A. A botanist looks at a rose. Jour. N.Y. Bot. Gard. **46:** 215–220. 1945.

Gustafsson, Å. The constitution of the *Rosa canina* complex. Hereditas **30:** 405–428. 1944.

——— & J. Schröderheim. Ascorbic acid in *Rosa* hybrids. *Ibid.* **31:** 489–497. 1945.

Hellyer, A. G. L. Rose classification. Chairman of sub-committee's remarks. Rose Annual **1972:** 114–130. 1972. [A new functional, nonbotanical, classification scheme of garden roses proposed for international consideration.]

Herring, P. Classifications of *Rosa.* Dansk Bot. Ark. **4**(9): 1–24. 1925. [Useful enumeration of the various classification schemes that have been proposed.]

———. François Crépin. (In Danish.) 156 pp. *frontisp.* Kjøbenhavn. 1930.

Hurst, C. C. Differential polyploidy in the genus *Rosa* L. Zeitschr. Indukt. Abst. Vererbungslehre Suppl. **2:** 886–906. 1928.

———. The genetics of the rose. Rose Annual **1929:** 37–64. *11 pls.* 1929.

———. Embryo-sac formation in diploid and polyploid species of Roseae. Proc. Roy. Soc. London B. **109:** 126–148. *pls. 10–15.* 1931.

———. Notes on the origin and evolution of our garden roses. I. Ancient garden roses (2000 B.C. to A.D. 1800). Jour. Roy. Hort. Soc. **66:** 73–82. 1941. II. Modern garden roses (1800–1940). *Ibid.* 242–250, 282–289. [Reprinted in Thomas, 1963.]

Jackson, G. A. D., & J. B. Blundell. Germination of *Rosa arvensis.* Nature **205:** 518, 519. 1965. [Chiefly dormancy.]

Jessen, K. On hydrochorous dissemination of *Rosa rugosa* and other species of the genus. (In Danish; English summary.) Bot. Tidsskr. **54:** 353–366. 1958.

Kalkman, C. The genus *Rosa* in Malesia. Blumea **21:** 281–291. 1973.

Klášterská, I. Cytology and some chromosome numbers of Czechoslovak roses. I. Folia Geobot. Phytotax. Praha **4:** 175–189. 1969. [Also see Taxon **18:** 310–315. 1969.]

———. New phenomena during meiosis in the genus *Rosa.* Hereditas **67:** 55–63. 1971.

——— & A. T. Natarajan. Cytological studies of the genus *Rosa* with special reference to the section *Caninae.* Hereditas **76:** 97–108. 1974.

Lewis, W. H. A monograph of the genus *Rosa* in North America east of the Rocky Mountains. 459 pp. Ph.D. Thesis. Univ. Virginia. 1957a. [Diss. Abstr. **17:** 2389. 1957.]

———. An introduction to the genus *Rosa* with special reference to *R. acicularis.* Virginia Jour. Sci. II. **8:** 197–202. 1957b.

———. The roses of Virginia and West Virginia. Castanea **23:** 77–83. 1958. [See additions, p. 135.]

———. Minor forms of North American species of *Rosa.* Rhodora **60:** 237–243. 1958.

———. A monograph of the genus *Rosa* in North America. I. *R. acicularis.* Brittonia **10:** 1–24. 1959. II. *R. foliolosa.* Southwest Nat. **3:** 145–153. 1958 [1959]. III. *R. setigera. Ibid.* 154–174. IV. *R.* × *dulcissima.* Brittonia **14:** 65–71. 1962. V. Subgenus *Hesperhodos.* Ann. Missouri Bot. Gard. **52:** 99–113. 1965.

———. Species roses in the United States and their relation to modern roses. Am. Rose Annual **55:** 78–85. 1970. [Includes distribution maps for the species native to eastern North America.]

——— & R. E. BASYE. Analysis of nine crosses between diploid *Rosa* species. Proc. Am. Soc. Hort. **78:** 572–579. 1961.

MCFARLAND, J. H. Modern roses. 6. xvii + 497 pp. *frontisp. 30 pls.* Harrisburg, Pennsylvania. 1965. ["A check list of rose names prepared in cooperation with the International Registration Authority for Roses." Ed. 7, 1969, not seen.]

MELVILLE, R. The problem of classification in the genus *Rosa.* Bull. Jard. Bot. Nat. Belg. **37:** 39–44. 1967.

MILLER, N. F. A preliminary study of rose fragrance. Am. Rose Annual **47:** 79–89. 1962.

MITRA, G. C. The origin, development and morphology of adnate stipules in *Rosa centifolia* Linn. Indian Bot. Soc. Jour. **28:** 68–83. 1949.

NILSSON, Ö. Drawings of Scandinavian plants. 1–2. *Rosa* L. Bot. Not. **120:** 1–8. 1967; 3–4 *Ibid.* 137–143; 5–6. *Ibid.* 249–254; 7–8. *Ibid.* 393–408.

PROSSER, M. V., & G. A. D. JACKSON. Induction of parthenocarpy in *Rosa arvensis* Huds. with gibberellic acid. Nature **184:** 108. 1959. [See also Naturwissenschaften **46:** 407, 408. 1959.]

REDOUTÉ, P. J. Les roses. Avec le texte par cl. Ant. Thory. Vol. **1.** 158 pp. *60 pls.* 1817–1819. Vol. **2.** 124 pp. *59 pls.* 1819–1821. Vol. **3.** 128 pp. *54 pls.* 1821–1824. Paris. [One of the most famous and treasured of all botanical books; the splendid plates were made by the stipple engraving method.]

ROWLEY, G. Ancestral China roses. Jour. Roy. Hort. Soc. **84:** 270–273. 1959.

———. Aneuploidy in the genus *Rosa.* Jour. Genet. **57:** 253–268. 1961.

———. Chromosome studies and evolution in *Rosa.* Bull. Jard. Bot. Nat. Belg. **37:** 45–52. *figs. 4, 5.* 1967.

SHAHARE, M. L., & S. V. S. SHASTRY. Meiosis in garden roses. Chromosoma **13:** 702–724. 1963.

SHEPHERD, R. E. History of the rose. viii + 264 pp. *12 pls.* New York. 1954.

STEARN, W. T. The five brethern of the rose: an old botanical riddle. Huntia **2:** 180–184. 1965. [See footnote 9.]

STEYERMARK, J. S. Notes on some roses in the Gray's Manual range. Rhodora **56:** 70–79. 1954.

TÄCKHOLM, G. Zytologische Studien über die Gattung *Rosa.* Acta Horti Berg. **7:** 97–381. 1922.

THOMAS, G. S. Shrub roses of today. 240 pp. *frontisp., 8 colored pls., 24 figs. on 16 pls.* London. 1962. [Includes key to the major groups of cultivated roses by G. D. ROWLEY.]

———. The old shrub roses. ed. 4. 232 pp. *frontisp., 8 colored pls., 21 figs. on 16 pls.* London. 1963. [Includes a reprint of articles by Hurst on origin and evolution of garden roses.]

VALADON, L. R. G., & R. S. MUMMERY. Changes in carotenoid composition of certain roses with age. Ann. Bot. II. **33:** 671–677. 1969.

WATSON, S. Contributions to American botany. 1. A history and revision of the roses of North America. Proc. Am. Acad. Arts **20:** 324–352. 1885.

WILLMOTT, E. The genus *Rosa.* Drawings by A. PARSONS. 25 pts. in 2 vols. viii + xxv + xxvii + 552 pp. London. 1910–1914. [Many colored and monochrome illustrations; 180 spp. recognized; illustrated glossary in pt. 3.]

WILSON, E. H. The story of the modern rose. Gard. Mag. N.Y. **21:** 253–256. 1915. [See chart in *Ibid.* **24:** 96, 97. 1916.]

WYLIE, A. P. Masters Memorial Lecture, 1954. The history of the garden roses. I. Jour. Roy. Hort. Soc. **79:** 555–571. *figs. 161–163.* 1954. II. *Ibid.* **80:** 8–24. 1955. III. *Ibid.* 77–87. [A basic history of the development of the various classes of cultivated roses.]

Subfam. MALOIDEAE C. Weber

(Subfam. Pomoideae, nom. invalid.)

A very natural group of perhaps 19 genera of the Northern Hemisphere. Only four genera, *Chamaemeles* Lindley (monotypic, Madeira), *Hesperomeles* Lindley (15 spp., Central and South America, often included in *Osteomeles* Lindley), *Heteromeles* Roemer (monotypic, California and Baja California; sometimes included in *Photinia* Lindley), and *Peraphyllum* Nutt. ex Torrey & Gray (monotypic, western United States), do not have species in Asia. Three genera, *Amelanchier* Medicus, *Pyrus* L. (including *Malus, Sorbus,* and *Aronia*), and *Crataegus* L., have species indigenous to eastern North America, and *Pyracantha* Roemer is naturalized in that region.

Two tribes are sometimes recognized, Crataegeae Koehne with the inner walls of the carpels becoming hard and each carpel developing into a separate nutlet (the fruit called by Kalkman a polypyrenous drupe) and Sorbeae Koehne with the inner walls of the carpels becoming chartaceous or cartilaginous, rarely bony, and the carpels laterally connate (the fruit with one multilocular "core"). Tribe Crataegeae includes *Chamaemeles, Cotoneaster* Ehrh., *Crataegus* L., *Hesperomeles, Mespilus* L., *Osteomeles,* and *Pyracantha*; tribe Sorbeae includes *Amelanchier, Chaenomeles* Lindley, *Cydonia* Miller, *Dichotomanthes* Kurz, *Docynia* Decaisne, *Eriobotrya* Lindley, *Heteromeles, Peraphyllum, Photinia, Pyrus, Rhaphiolepis* Lindley corr. Poiret, and *Stranvaesia* Lindley. The characters of the consistency (induration) of the endocarp and the degree of lateral connation of the carpels seem to be more variable than originally thought, and the division of the subfamily into two tribes as outlined above may not best reflect generic relationships.

Generic limits are notoriously difficult to define in subfam. Maloideae. On morphological grounds alone, it would not be difficult to distinguish

30 genera. The flowers and fruits of all species of the subfamily are quite similar, but there are numerous variations (often difficult to see on herbarium specimens). Some floral differences are the type and position of inflorescences, the number of flowers, the arrangement of the calyx lobes at anthesis, the color of the petals, the number of stamens and staminal whorls, the number of carpels, the degree of adnation of the carpels to the floral cup, the degree of connation of the styles, the shape of the stigmas, and the number of ovules. Fruits differ in color, shape, and size, the presence or absence of grit cells, the consistency and degree of lateral connation of the inner carpel walls, and the persistence of the calyx lobes. *Pyrus* subg. SORBUS is particularly critical, since within it are found many of the characters used to delineate the other genera. Barriers to hybridization between both species and genera are usually weak. Hybrids between *Pyrus* subg. SORBUS and *Amelanchier*, *Cotoneaster*, *Crataegus*, *Mespilus* (see Kovanda), and *Pyrus* subg. ARONIA, subg. MALUS, and subg. PYRUS are known. Also reported are hybrids between *Crataegus* and *Mespilus*; *Crataegus* and *Pyrus* subg. PYRUS; *Pyracantha* and *Osteomeles*; *Pyracantha* and *Cotoneaster*; *Cydonia* and *Pyrus* subg. PYRUS; *Cydonia* and *Pyrus* subg. MALUS (see Rehder); and *Pyrus* subg. PYRUS and *P.* subg. MALUS. Sax (1931, subfam. ref.) went so far as to say that on genetic and cytological grounds "all of the present genera of the Pomoideae might be classed as genetic species under one genus. In at least one case two genera [*Sorbus* and *Aronia*] should be combined in one species." It does not seem likely that a universally acceptable system of generic delimitation can be devised in the forseeable future.

Most Maloideae have partly to completely inferior ovaries that develop into characteristic fruits, pomes, in which the carpels are practically surrounded by the enlarged, usually fleshy floral cup. The nature of the inferior ovary, floral cup, and fruit is debatable. According to the "axial" or "receptacular" theory, the carpels are sunken in the pith of the invaginated stem, so the flesh of the pome is largely receptacular in origin (see Black and Tukey & Young under *Pyrus*). The "appendicular" theory holds that the floral cup consists of the adnate bases of the sepals, petals, and stamens, and the fleshy part of the fruit is thus appendicular (see MacDaniels and Blaser & Einset, *Pyrus* ref.). In a recent Hungarian investigation of the pear (Gracza, *Pyrus* ref.), both axial and appendicular regions were identified in the mature fruit. Virtually all studies on the nature of the pome have been made on the cultivated apple or pear; other genera of Maloideae need to be investigated; perhaps then a definitive explanation of the maloidean floral cup can be given.

The base chromosome number in the Maloideae is 17, a number unknown in other Rosaceae, except *Quillaja brasiliensis* (St. Hil.) Martius (Spiraeoideae-Quillajeae). Fifteen genera have been examined cytologically. The species of small genera are predominantly diploid, while tetraploid or triploid species (or hybrids) are common in large genera; higher polyploid levels and aneuploidy are quite rare. Several hypotheses have been proposed to explain the base number of 17: *Malus* is an aneuploid derived from a halved pentaploid ancestor that had a base number of seven ($x = 1/2\ (35 - 1)$; Nebel, *Pyrus* ref.); or the Maloideae are triple tetrasomics developed from a seven-chromosome type with four chromosomes represented twice and three chromosomes represented three times ($x = 8 + 8 + 1$; Sax, 1931, subfam. ref.); or the Maloideae are allotetraploids that arose from a cross between plants with base numbers of eight and nine and involving either two members of the Spiraeoideae or representatives of the Spiraeoideae and Rosoideae ($x = 8 + 9$; Sax, 1932, subfam. ref.); or the Maloideae are amphidiploids derived from hybridization of ancestral Spiraeoideae and Amygdaloideae ($x = 9 + 8$; Stebbins, subfam. ref.).

REFERENCES FOR MALOIDEAE:

ASHE, W. W. Notes on Pomaceae of upper South Carolina. Bull. Charleston Mus. **12:** 37–43. 1916.

BAKER, K. F. Fire blight of pome fruits: the genesis of the concept that bacteria can be pathogenic to plants. Hilgardia **40:** 603–633. 1971. [Extensive bibliography.]

BROWICZ, K. Distribution of woody Rosaceae in W. Asia. II. On the distribution of *Mespilus germanica* L. Arb. Kórnicke **13:** 27–36. 1968.

CHALLICE, J. S. Phenolic compounds of the subfamily Pomoideae: a chemotaxonomic survey. Phytochemistry **12:** 1095–1101. 1973.

CHURCH, A. H. Types of floral mechanisms. Part 1. vii + 211 pp. *52 pls.* Oxford. 1908. [Type *Cydonia japonica,* 168–187, *6 pls.*]

DECAISNE, M. J. Mémoire sur la famille des Pomacées. Nouv. Arch. Mus. Hist. Nat. Paris **10:** 113–192. *pls. 8–15.* 1874. [Considers the concept of genera in subfamily; good illustrations of floral and fruit morphology.]

DERMEN, H. Are the pomes amphidiploids? A note on the possible origin of Pomoideae. Jour. Hered. **40:** 221, 222. 1949.

DIAPULIS, C. Beiträge zur Kenntnis der orientalischen Pomaceen (*Pirus, Sorbus, Crataegus*). Repert. Sp. Nov. **34:** 29–72. *pls. 141–161.* 1933.

FLINCK, K. E., & B. HYLMÖ. A list of series and species in the genus *Cotoneaster.* Bot. Not. **119:** 445–463. 1966.

FOLGNER, V. Beiträge zur Systematik und pflanzengeographischen Verbreitung der Pomaceen. Österr. Bot. Zeitschr. **47:** 117–125, 153–178, 199–206, 296–300. 1897. [Also issued separately with continuous pagination.]

GLADKOVA, V. N. On the systematic position of the genus *Dichotomanthes* Kurz. (In Russian; English summary.) Bot. Zhur. **54:** 431–436. 1969. ["The genus . . . occupies an intermediate position between different subfamilies of Rosaceae . . . a new subfamily, Dichotomanthoideae, is distinguished." Includes a detailed plate.]

KALKMAN, C. The Malesian species of the subfamily Maloideae (Rosaceae). Blumea **21:** 413–442. 1973. [Comments on generic limits.]

KLOTZ, G. Die Hybridisation, ein wichtiger Evolutions-Faktor in der Gattung *Cotoneaster* Medicus. Wiss. Zeitschr. Friedrich-Schiller Univ. Jena Math. Natur. **19:** 329–344. 1970. [Also see other articles in vols. 12, 15, and 17.]

KOEHNE, E. Die Gattungen der Pomaceen. 33 pp. *pls. 1, 2.* Berlin. 1890.

KOVANDA, M. On the generic concepts in the Maloideae. Preslia **37:** 27–34. 1965.

LINDLEY, J. Observations on the natural group of plants called Pomaceae. Trans. Linn. Soc. London **13:** 88–106. *pls. 8–11.* 1822. [The first monograph of the subfamily; still pertinent.]

MOFFETT, A. A. The chromosome constitution of the Pomoideae. Proc. Roy. Soc. London B. **108:** 423–446. 1931.

SAX, H. J. Polyploidy and apomixis in *Cotoneaster.* Jour. Arnold Arb. **35:** 334–365. 1954. [Includes brief summary of polyploidy and apomixis in Rosaceae.]

SAX, K. The origin and relationships of the Pomoideae. Jour. Arnold Arb. **12:** 3–22. *pl. 28.* 1931.

———. Chromosome relationships in the Pomoideae. *Ibid.* **13:** 363–367. *pl. 50.* 1932.

———. The origin of the Pomoideae. Proc. Am. Hort. Soc. **30:** 147–150. 1933.

STEBBINS, G. L., JR. Variation and evolution in plants. xx + 643 pp. New York and London. 1950. [Origin of Maloideae, 359–361.]

———. On the hybrid origins of the angiosperms. Evolution **12:** 267–271. 1958. [Expands discussion from book on origin and evolution of Maloideae.]

VIDAL, J. E. Notes sur quelques Rosacées asiatiques. II. *Photinia, Stranvaesia.* Adansonia II. **5:** 221–237. 1965. III. Révision du genre *Eriobotrya* (Pomoideae). *Ibid.* 537–580. IV. *Malus* sect. *Docyniopsis*; *Docynia. Ibid.* **6:** 563–571. 1967.

WEBER, C. The genus *Chaenomeles* (Rosaceae). Jour. Arnold Arb. **45:** 161–205. 302–345. 1964. [Contains information on relationships and hybrids of the genera of Maloideae.]

ZWET, T., VAN DER. Recent spread and present distribution of fire blight in the world. Pl. Disease Rep. **52:** 698–702. 1968.*

18. **Pyracantha** M. J. Roemer, Fam. Nat. Reg. Veg. Syn. Monograph. 3: 104, 219. 1847.

Evergreen, compactly branched shrubs with slender but rigid stems, thorns (bearing leaves or leaf scars), and spine-tipped lateral branches; buds small, sessile, solitary or collaterally branched in spine formations, the scales dry. Leaves alternate, shortly petiolate; blades elliptic to obovate with crenate [serrate, or entire margins], the teeth often glandular tipped; leaf scars somewhat raised, narrowly crescent shaped or 3 lobed with 3 bundle traces; stipules minute, caducous. Inflorescences several-flowered compound cymes or corymbs terminating short lateral shoots. Flowers perfect. Calyx without an epicalyx, the 5 small lobes broadly triangular, sometimes glandular toothed, persistent, imbricate in aestivation; floral cup turbinate at anthesis. Petals 5, whitish, spreading, deciduous, equal, subcircular with uneven margins, the lower adaxial surfaces slightly pubescent, inserted at the edge of the floral cup, imbricate. Androecium of 20 stamens; filaments free except at the base, unequal in length, inserted in 2 series at the edge of the floral cup between the perianth and a fleshy nectar ring surrounding the mouth of the floral cup. Gynoecium of 5 antesepalous carpels, adaxially and laterally free but abaxially half-adnate to the floral cup (the ovaries half-inferior), the exposed upper surfaces densely pubescent; styles 5, terminal on the adaxial margins, deciduous; stigmas discoid; each carpel with 2 ascending, anatropous ovules on an adaxial and basal placenta, the micropyle inferior. Fruit a small, ± globose, orange to red pome [yellow or white in cultivars], open at the apex; carpels remaining distinct from each other, becoming stony and forming 2- or 1-seeded nutlets surrounded by the enlarged, fleshy floral cup crowned by the persistent calyx lobes; mature seed or seeds filling the nutlet cavity, the testa membranaceous, endosperm absent; embryo erect, the cotyledons plano-convex. Base chromosome number 17. LECTOTYPE SPECIES: *Mespilus Pyracantha* L. = *P. coccinea* Roemer; see A. Rehder, Bibliogr. Cult. Trees Shrubs, 239. 1949. (Name from Greek *pyr*, fire, and *acantha*, thorn, in reference to the red fruits and thorny branches.) — FIRETHORN.

A genus of about eight species, with *Pyracantha coccinea* in southern Europe and western Asia, *P. Koidzumii* Rehder in eastern Formosa, and five or more species in China (the greatest concentration of species in Yunnan) and Indochina. *Pyracantha crenulata* (Roxb.) Roemer var. *crenulata* occurs in the Himalayas as far east as Bhutan; other varieties of this species are disjunct in southwestern and northwestern China and North Vietnam. The genus is taxonomically straightforward (excluding cultivars) but needs a modern review to update nomenclature, clarify the status of a few taxa, and work out geographical distributions.

Pyracantha coccinea has escaped from cultivation and become locally naturalized in the eastern United States from Pennsylvania to Florida and Louisiana; it also persists near old house sites. This species is distinguished from others by the pubescent, but not tomentose, lower leaf surfaces, calyx lobes, floral cups, and pedicels and the elliptic to obovate leaf blades usually with crenulate-serrulate margins. Today *P. coccinea* occurs in the Old World from the Pyrénées to Italy, southeastern Europe, Turkey, Crimea, Caucasia, and Iran. Some authors believe that this species does not occur naturally west of Italy; others place the westernmost natural limit in Dalmatia. *Pyracantha Koidzumii* has recently been reported as escaped in Spartanburg Co., S. C. (Clark *et al.*, Castanea 38: 300. 1973).

Pyracantha is closely related to *Cotoneaster* Medicus (in which it was included by Focke, Small, and Fernald), as well as to *Crataegus* L. It differs from the former in having thorns and usually serrate (rather than always entire) leaves and from the latter in its unlobed and evergreen (rather than lobed and deciduous) leaves, its caducous instead of partly persistent stipules, and its often two- rather than one-seeded nutlets. An intergeneric hybrid, × *Pyracomeles Vilmorinii* Rehder ex Guillaumin, arose spontaneously in a French nursery between *Pyracantha crenato-serrata* (Hance) Rehder and *Osteomeles subrotunda* K. Koch. A hybrid between *Pyracantha* and *Cotoneaster* has been obtained by W. E. Silva (cf. Egolf & Drechsler). The six species and many cultivars that have been examined cytologically have a chromosome number of $2n = 34$, the same as the majority of Maloideae.

Plants of *Pyracantha* are extensively grown as shrubs, hedges, or espaliers. They are particularly attractive in autumn when the colorful fruits mature. The species are reasonably distinct in nature, but in cultivation they hybridize readily, and true species are rarely found in gardens, since many nurseries raise the plants from seed of open-pollinated flowers.

REFERENCES:

Under subfamily references see CHALLICE, DECAISNE, FOLGNER, KOEHNE, and LINDLEY. Under family references see BEAN, DIPPEL, REHDER, SCHNEIDER, STERLING (IV), and VINES.

BROWICZ, K. Distribution of woody Rosaceae in W. Asia. VI. *Pyracantha coccinea* Roem. (Polish and Russian summaries.) Arb. Kórnickie **15:** 17–27. 1970. [Includes list of species recognized in genus and their geographical distributions.]

DE VOS, F. Cultivated firethorns. Proc. Pl. Propag. Soc. **8:** 32–38. 1958. [Rates 48 cvs. for hardiness, resistance to fire blight, and lasting qualities of fruit.]

———. The cultivated Pyracanthas. Gard. Jour. N.Y. Bot. Gard. **10:** 215–217. 1960. [Review of species and their horticultural aspects.]

EGOLF, D. R., & R. F. DRECHSLER. Chromosome numbers of *Pyracantha* [Rosaceae]. Baileya **15:** 82–88. 1967. [Six species and many cultivars are all diploid with $2n = 34$.]

MONTANI, R. G. Species of the genus *Pyracantha* (Rosaceae) grown in Argentina. (In Spanish.) Revista Inst. Munic. Bot. **2:** 31–50. 1962.*

SEALEY, J. R. *Pyracantha Rogersiana.* Bot. Mag. **166:** *pl. 74.* 1949.

———. *Pyracantha Koidzumii. Ibid.* **169:** *pl. 205.* 1953.

STAPF, O. *Pyracantha angustifolia.* Bot. Mag. **136:** *pl. 8345.* 1910.

———. *Pyracantha atalantioides* et *Pyracantha yunnanensis. Ibid.* **151:** *pl. 9099.* 1926.

19. **Crataegus** Linnaeus, Sp. Pl. 1: 475. 1753; Gen. Pl. ed. 5. 213. 1754.

Deciduous or semi-evergreen shrubs or small trees, often much branched, with terete, slender but rigid and ± zigzag branches; usually armed with simple or branched axillary spines; bark scaly and/or deeply fissured and crosschecked, ashy gray to dark brown; buds small, subglobose, sessile, solitary or collaterally branched in spine formations, the outer scales brownish, the inner fleshy and green to red. Leaves alternate, petiolate; blades usually toothed (the teeth glandular tipped) and lobed or deeply divided, ovate to elliptic or obovate, leaves at ends of vegetative shoots usually larger, more deeply lobed and differently shaped than those of flowering branches; leaf scars slightly elevated, narrowly crescent shaped with 3 bundle-scars; stipules commonly glandular toothed, large and persistent on vegetative branches, or small and deciduous on flowering branches. Inflorescences few- to many-flowered, simple or compound, ± convex cymes terminating short lateral, leafy branches; bracts and bractlets linear, often brightly colored and glandiferous, caducous, leaving a prominent glandlike scar. Flowers perfect, 5-merous. Calyx without an epicalyx, the 5 lobes reflexed at anthesis, acute or acuminate, rarely foliaceous, often glandular-serrate and gland tipped, deciduous or persistent, imbricate in aestivation; floral tube cup shaped to urceolate at anthesis, adnate to the carpels. Petals white to light or dark pink, spreading, equal, subcircular with entire to erose margins, deciduous, inserted at the edge of the floral tube, imbricate. Androecium of 5–25 stamens, when 10, in one whorl of 5 pairs, when more than 10, the outer whorl consisting of 5 pairs; filaments free except at base, usually unequal in length, inserted on the rim of a small to prominent, fleshy nectar ring surrounding the mouth of the floral tube; anthers pale to intense yellow, pink, or purple. Gynoecium of 1–5 carpels, abaxially half to completely adnate to the floral cup (the ovaries half to completely inferior) and adaxially and laterally free to ± connate; styles as many as the carpels, distinct or weakly connate, terminal on the adaxial margins, persistent; stigmas discoid; each carpel with 2 erect, anatropous ovules on an adaxial and basal placenta, the micropyle inferior. Fruit red, orange, yellow, blue, or black, a small subglobose, ovoid, obovoid, or pyriform pome, slightly open at the apex with the persistent styles protruding; carpels remaining or becoming distinct from each other, forming stony, usually one-seeded nutlets surrounded by the enlarged, fleshy to mealy floral tube; mature seed filling nutlet cavity. Testa membranaceous; endosperm absent; embryo erect, the cotyledons planoconvex, the radicle short, inferior. LECTOTYPE SPECIES: *C. Oxyacantha* L.; see W. W. Eggleston in N. L. Britton, N. Am. Trees, 444. 1908.[12] (Name from Greek *krataigos*, a kind of flowering thorn, evidently applied by Theophrastus to a species of *Crataegus*, perhaps in turn derived from *kratos*, strength, alluding to the strong wood or the numerous thorns that protect the plants from browsing animals.) — HAWTHORN, THORN, HAW.

One of the taxonomically most difficult genera in the eastern United States with well over a thousand described "species." The actual number of biological entities worthy of taxonomic recognition is impossible to determine at present due to the large number of local variants that may be hybrids, apomicts, or both. The genus is most abundant, both as to individuals and diverse forms, in the region from Newfoundland westward through the St. Lawrence River basin to northwestern Minnesota and south to Florida and the mouth of the Colorado River in Texas. Relatively few species occur in the Rocky Mountains, the Pacific Coast region, through the highlands of Mexico to the Andes, and in Europe, the Middle East, central and southwestern Asia, Siberia, China, and Japan. The majority of *Crataegus* species are calciphilous and occur in somewhat disturbed habitats along the borders of streams, rocky ledges or woods, and in prairies, glades, copses, fence rows, and pastures. In our area nu-

---

[12] Medicus (Philosoph. Bot. 1: 150, 154, 155. 1789) referred this species to his genus *Oxyacantha*. It is debatable whether *Crataegus Oxyacantha* L. can then be designated as the lectotype species of *Crataegus*, although it appears that all subsequent authors have followed Eggleston's selection; the current Code of Botanical Nomenclature provides few guidelines for the lectotypification of generic names.

merous species are restricted to dry, sandy, upland woods with acidic soils; others inhabit swamps or rich, low, wet grounds.

The genus may be subdivided into about thirty series, but the exact number currently recognized is difficult to determine since there is no recent treatment of the genus on a worldwide basis (Rehder's *Bibliography* lists all series in cultivation). Additionally, there are varying concepts as to the criteria to be used in delimiting series and the species to be included, and the nomenclature is badly tangled. The author citations of the series need reviewing, since neither Beadle nor Sargent designated the rank of their subgeneric categories, although many of their names have been adopted. The morphological distinctiveness of the series varies considerably, some being clearly delimited (e.g., AESTIVALES (Sargent ex Palmer) Rehder; BREVISPINAE Beadle ex Rehder; MICROCARPAE (Loudon) Rehder; CORDATAE Beadle ex Rehder), while others have indefinite discontinuities between them (MOLLES (Sargent ex Palmer) Rehder; COCCINEAE (Loudon) Rehder; TENUIFOLIAE (Sargent ex Palmer) Rehder; DILATATAE (Sargent ex Palmer) Rehder; PUNCTATAE (Loudon) Rehder; VIRIDES (Beadle ex Palmer) Rehder; and PULCHERRIMAE (Beadle ex Palmer) Robertson).[13]

In his synopsis of North American hawthorns, Palmer listed about 300 species in 18 sections (and one group of unassignable species) as occurring in our area. In the second edition of Small's *Flora of the Southeastern United States* (1913), Beadle assigned 185 species to 33 infrageneric groups of undesignated rank, but Tidestrom distinguished only 33 species in 16 groups in Small's *Manual* (1933). Radford, Ahles, & Bell recognized 13 species in the Carolinas. These very diverse treatments are indicative of the problems encountered in *Crataegus*. While it is clearly beyond the scope of this paper to enumerate all taxonomic entities in our area, a few generalizations are possible.

Representatives of 21 series occur in the southeastern United States, to which several series are entirely or predominantly restricted (AESTIVALES; APIIFOLIAE (Loudon) Rehder; BRACTEATAE (Sargent ex Palmer) Rehder; BREVISPINAE; FLAVAE (Loudon) Rehder; MICROCARPAE; PULCHERRIMAE; TRIFOLIAE (Beadle ex Palmer) Rehder; and VIRIDES). Other series have a more northern or western primary distribution with only one or a few species occurring toward the periphery of our area (PRUINOSAE (Sargent ex Palmer) Rehder; TENUIFOLIAE). Not many series have species ranging throughout the eastern United States (CRUS-GALLINAE Rehder; MOLLES; PUNCTATAE), and no series or species has a transcontinental distribution.

The taxonomic and nomenclatural confusion in *Crataegus* today is a relatively recent phenomenon. Before the year 1896, fewer than 17 species and varieties were commonly recognized as occurring naturally or spon-

---

[13] *Crataegus* series **Pulcherrimae** (Beadle ex Palmer) Robertson, stat. nov. *Crataegus* sect. *Pulcherrimae* Beadle ex Palmer, Jour. Arnold Arb. **6**: 78, 79. 1925 (based on group "Pulcherrimae" of Beadle in Small, Fl. Southeast. U.S. 532. 1903).

taneously in the eastern United States. Then, during the first decade of the Twentieth Century, descriptions of new species appeared at a prodigious rate, largely as the result of the efforts of W. W. Ashe, of the U.S. Forest Service (who named at least 177 species), C. D. Beadle, of the Biltmore Herbarium (whose contribution amounted to 143), and C. S. Sargent, of the Arnold Arboretum (who added over 700). (See Sutton for an excellent account of Sargent's work with *Crataegus*). This plethora of new *Crataegus* species inevitably drew criticism (see Bessey and Camp). Because of the sheer numbers of taxa described, most subsequent authors and collectors have largely ignored the genus, considering the situation hopeless.

That numerous species described during what Palmer called "the period of expansion for the genus" are synonyms of previously described species is now clear, although the morphological variations that caused the deluge of descriptions are very real. The explanation usually advanced is that relatively few species are sexually reproducing diploids, the majority being triploids or other polyploids (sometimes derived by hybridization) that frequently set seed apogamously. This conclusion is based on the following evidence: there is a high incidence of pollen sterility among members of the genus; of the more than 130 representatives that are known cytologically, more than half are triploids and less than 25% are diploids; triploid and pollen-sterile plants often set seed that produce offspring very similar to the parent plants; and flowers with the stigmas and anthers removed before anthesis often set fruit. All of these phenomena suggest analogies to other rosaceous genera, such as *Rubus* and *Potentilla*, in which apomixis and hybridization are well documented. However, since irrevocable proof that these last phenomena occur in *Crataegus* has not yet been presented, the generalization given above is only a plausible hypothesis based on largely circumstantial evidence.

With the widespread clearing of the great forest that once extended from the Atlantic Coastal Plain to the prairies of midwestern North America, the habitats favorable for hawthorns were greatly expanded. It can be postulated that as the land was cleared, many discrete populations were able to expand their ranges (the nutlets are transported in the digestive tracts of birds and other animals) until their distributions were contiguous or overlapping. In such areas hybrids could have arisen, and if the hybrids were sexually sterile but able to set seed apogamously, local clones that superficially appear to be species (since they breed true from seed) could become established. Although the destruction of the eastern forests was largely by European settlers, Rousseau suggested that the *Crataegus* problem was created by the agricultural practices of the Iroquois Indians.

Probably no one has been more familiar with the myriad forms of *Crataegus* than was E. J. Palmer, whose knowledge was based on extensive field work, the examination of thousands of herbarium specimens, and the long-term observation of the more than 1400 plants (largely removed in the 1940's) representing nearly 700 forms of *Crataegus* that covered the Peters' Hill tract of the Arnold Arboretum. After his initial publication on *Crataegus* (in 1925, before the death of Sargent), Palmer adopted a more conservative approach, and his later papers and treatments reflect this philosophy. Palmer (1932) thought that ". . . a revision is urgently needed and that enough progress has now been made in understanding the genus to carry it out along conservative lines, that will neither seek to reduce arbitrarily species by throwing together as synonyms forms that are clearly recognizable, nor to maintain as species such as have been proven to have been based on inconstant distinctions or morphological characters too slight or obscure to be worthy of specific rank." Although Palmer never finished the revision, he did solve many nomenclatural and taxonomic problems. E. P. Kruschke, who has studied extensively the morphology of the *Crataegus* species found in the northern United States (especially Wisconsin), has made further contributions toward clarifying the complexities of the genus.

It seems likely that the genus will never be understood taxonomically until detailed studies that include cytology, genetics, and observations on reproductive biology, as well as morphology, have been made on a broad geographical basis. The situation was well summarized by Palmer (1943): "Much more experimental work is needed in many groups of plants before species problems can be resolved, and *Crataegus* offers one of the promising fields. It is also one of the most difficult. Some bright young man should start in it early in life, and it is hoped that he will have the background of a large endowment. In the meantime some adequate but conservative treatment of the genus is urgently needed, even though it may not be possible to dispose of all questions."

Because of the difficulty of identifying specimens of *Crataegus*, collectors should take special care to include both flowering or fruiting and vegetative shoots (making certain that both come from the same rootstock, since the branches of different species may intermingle) and to note the number of stamens and the color of the anthers, or the color of the fruit and the number of nutlets and the ease with which they may be separated from one another. If at all possible, flowering and fruiting collections should be made from the same plant.

The known intergeneric hybrids involving *Crataegus* and *Mespilus* bear the name × *Crataemespilus* Camus, with × *C. grandiflora* (Smith) Camus (*Crataegus monogyna* or *C. Oxyacantha* × *M. germanica*) and × *C. Gillotii* Beck (*Crataegus monogyna* × *M. germanica*). Graft-chimaeras between *Crataegus* and *Mespilus* are known as + *Crataegomespilus* Simon-Louis ex Bellair. A presumed graft-chimaera is also known between *Crataegus* and *Pyrus* (+ *Pyrocrataegus* Daniel; Weber was evidently referring to this chimaera when she mentioned an intergeneric hybrid between *Crataegus* and *Pyrus*).

Several species of *Crataegus* are commonly grown as ornamentals in the North Temperate Zone and are particularly attractive in spring, when in full bloom, and in autumn, when the leaves and plentiful fruits often take on brilliant colors. Although the fruits of a few species are eaten fresh or used in preserves and jellies, most are unpalatable and commonly are infested with weevils. However, few genera of plants are more important in the eastern United States than *Crataegus* in providing food during autumn and winter for birds and game animals.

REFERENCES:

Under subfamily references see ASHE, CHALLICE, DECAISNE, DIAPULIS, FOLGNER, KOEHNE, and LINDLEY. Under family references see BEAN, BOUTINEAU, DIPPEL, HEGI, HESS *et al.*, REHDER, ROBERTSON, ROSS-CRAIG, SARGENT, SCHNEIDER, STEPHENS, STERLING (III), and VINES.

ALEXANDER, E. J. *Crataegus Harbisoni.* Addisonia **21:** 41, 42, *pl. 693.* 1941.

ALLARD, H. A. Some common species of *Crataegus* at Thompson's Mills, Georgia. Bull. Torrey Bot. Club **38:** 25–32. 1911.

ANGELL, V. C. The *Crataegi* of Grand Rapids, Michigan, and vicinity. Pap. Mich. Acad. Sci. Arts Lett. I. **17:** 1–50. *pls. 1–9.* 1933. [Interesting observations and illustrations; many informal "specific" names used.]

ASHE, W. W. New East American species of *Crataegus.* Jour. Elisha Mitchell Sci. Soc. **16:** 70–79. 1899 [1900]. [First of numerous papers on *Crataegus* in this Journal.]

BEADLE, C. D. Studies in *Crataegus* — I. Bot. Gaz. **28:** 405–417. 1900. [The first of Beadle's numerous papers on *Crataegus.*]

———. *Crataegus. In*: J. K. SMALL, Fl. Southeast. U.S. ed. 2. 532–569. 1913. [185 spp. in 33 subgeneric categories of undesignated rank.]

BERGANN, F. Untersuchungen an den Blüten und Früchten der *Crataegomespili* und ihrer Eltern. Flora **143:** 219–268. 1956.

BESSEY, C. E. Multiplication of species in botany. Science **15:** 795. 1902. [Criticism of the large numbers of species described in *Crataegus.*]

BRADSHAW, A. D. Man's influence on hybridisation in *Crataegus.* VIII^e Congr. Int. Bot. Rapp. Commun. **9/10:** 217. 1954. [In Great Britain, *C. monogyna* and *C. oxyacanthoides* hybridize where the disturbance of the original vegetation has allowed them to come in contact with one another.]

BROWN, H. B. The genus *Crataegus*, with some theories concerning the origin of its species. Bull. Torrey Bot. Club **37:** 251–260. 1910. [Report of questionnaires sent to C. S. SARGENT, W. W. EGGLESTON, W. W. ASHE, C. D. BEADLE, E. BRAINERD, and J. DUNBAR.]

BUSH, B. F. The geographic origin of *Crataegus viridis* L. Rhodora **14:** 81–86. 1912. [The Virides group may have migrated southward through the Mississippi River valley instead of northward, as is generally presumed.]

CAMP, W. H. The *Crataegus* problem. Castanea **7:** 51–55. 1942. [Hypothesis presented on the role of apomixis in the genus; also see Ecology **23:** 368, 369. 1942.]

DAVIS, W. E., & R. C. ROSE. The effect of external conditions upon the after-ripening of the seeds of *Crataegus mollis.* Bot. Gaz. **54:** 49–62. 1912. [Seeds have a latent period of one or more years.]

EGGLESTON, W. W. VI. The thorn trees, genus *Crataegus* Linnaeus. *In*: N. L. BRITTON, N. Am. Trees, 443–482. 1908.

———. Sketch of the *Crataegus* problem, with special reference to work in the South. Jour. N. Y. Bot. Gard. **11:** 78–83. 1910.

FLEMION, F. Breaking the dormancy of seeds of *Crataegus* species. Contr. Boyce Thompson Inst. **9:** 409–423. 1938.

GLADKOVA, V. N. Karyological studies on the genera *Crataegus* L. and *Cotoneaster* Medik. (Maloideae) as related to their taxonomy. (In Russian; English summary.) Bot. Zhur. **53:** 1263–1273. 1968. [Includes 40 spp. and 2 vars. of *Crataegus*.]

KRUSCHKE, E. P. The hawthorns of Wisconsin. I. Status, objectives, and methods of collecting and preparing specimens. Milwaukee Public Mus. Publ. Bot. **2.** 124 pp. Milwaukee. 1955.

———. Contributions to the taxonomy of *Crataegus*. *Ibid.* **3.** 273 pp. Milwaukee. 1965. [New taxa; list of series and subseries and their included species.]

LAUGHLIN, K. Manual of the hawthorns of Cook and Du Page counties of Illinois. 76 pp. Chicago. 1956. [Also see Third revised key to the species of hawthorns of Cook and Du Page counties of Illinois. 9 pp. 1960.]

LEAVITT, R. G. The defences of the cock-spur thorn. Pl. World **8:** 239–244. 1905. [The spines of *C. crus-galli* are inserted at angles that discourage the browsing of certain animals.]

LONGLEY, A. E. Cytological studies in the genus *Crataegus*. Am. Jour. Bot. **11:** 295–317. *pls. 16–18*. 1924. [The hypothesis of $x = 16$ is incorrect.]

MURRILL, W. A. Ecologic notes on Florida hawthorns. Ecology **23:** 121–123. 1942.

NASH, G. V. *Crataegus macrosperma*. Addisonia **4:** 35. *pl. 138*. 1919.

———. *Crataegus Calpodendron*. *Ibid.* 67, 68. *pl. 154*.

———. *Crataegus Phaenopyrum*. *Ibid.* **5:** 33. *pl. 177*. 1920.

PALMER, E. J. Synopsis of North American *Crataegi*. Jour. Arnold Arb. **6:** 5–128. 1925. [Discussion and an important list of sections and their included species.]

———. The *Crataegus* problem. *Ibid.* **13:** 342–362. 1932. [Discussion only.]

———. The hawthorns (*Crataegus*; over 50 species in Arkansas). Native plant material (famous in garden lore). Arkansas state program for garden clubs, landscape gardening & landscape art, 1935–36, May. 14 pp. Mimeographed and distributed by the General Extension Service, University of Arkansas. 1936. [Includes discussion on *Crataegus* in folklore, poetry, and other topics.]

———. The species concept in *Crataegus*. Chron. Bot. **7:** 373–375. 1943 [1944].

———. *Crataegus* in the northeastern and central United States and adjacent Canada. Brittonia **5:** 471–490. 1946. [Discussion and list of recognized taxa and synonyms.]

———. *Crataegus*. *In:* M. L. FERNALD, Gray's Man. Bot. ed. 8. 767–801. 1950.

———. *Crataegus*. *In:* H. A. GLEASON, New Britton & Brown. Illus. Fl. Northeast U. S. **2:** 338–375. 1952.

POJARKOVA, A. I. De systemate generis *Crataegi* L. orientis. Novit. Syst. Pl. Vasc. Leningrad **1964:** 151–174. 1964.

RICKETT, H. W. Forms of *Crataegus pruinosa*. Bot. Gaz. **97:** 780–793. 1936. [Includes discussion of infraspecific variation.]

———. Forms of *Crataegus crus-galli*. *Ibid.* **98:** 609–616. 1937.

———. The inflorescence of *Crataegus*. Bull. Torrey Bot. Club **70:** 489–495. 1943.

ROUSSEAU, J. Movement of plants under the influence of man. Pp. 81–99. *In:* R. L. TAYLOR & R. A. LUDWIG, The evolution of Canada's flora. viii + 137 pp. *3 pls*. 1966. [*Crataegus*, 89; references to other papers.]

SARGENT, C. S. Notes on *Crataegus* in the Champlain Valley. Rhodora 3: 19–31. 1901. [The first of many papers with descriptions of new spp.]

———. The genus *Crataegus* in North America. Jour. Bot. **45**: 289–292. 1907. [Discussion of Sargent's philosophy regarding *Crataegus*.]

———. Manual of the trees of North America (exclusive of Mexico). ed. 2. xxvi + 910 pp. *frontisp.* Boston & New York. 1922. [*Crataegus*, 397–549.]

SHCHERBANIVSKYI, L. R., & V. M. KOSYKH. Investigation of some biologically active substances of the Crimean species of *Crataegus* L. Ukrain. Bot. Zhur. **27**: 763–767. 1970.

SHILOVA, N. V. The formation of vegetative buds in certain species of the genus *Crataegus* L. (Rosaceae). (In Russian; English summary.) Bot. Zhur. **54**: 1169–1185. 1969. [15 spp. belonging to 5 sects. studied.]

STANDISH, L. M. What is happening to the hawthorns? Jour. Hered. **7**: 266–279. 1916. [Pollen fertility examined in 171 forms.]

SUTTON, S. B. Charles Sprague Sargent and the Arnold Arboretum. xvii + 382 pp. Cambridge, Massachusetts. 1970. [Chapter 11, *Crataegus*: A thorny problem, pp. 279–298.]

TIDESTROM, I. *Crataegus*. *In*: J. K. SMALL, Man. Southeast. Fl. 637–644. 1933.

20. **Amelanchier** Medicus, Philosophische Botanik 1: 135, 155. 1789.

Deciduous, unarmed shrubs (sometimes stoloniferous or surculose) or trees with slender, terete branches; bark smooth, pale, on old trunks with shallow, scaly, longitudinal fissures; buds solitary, the lateral ones adpressed, fairly large, acute, sometimes with brightly colored and twisted scales; leaf scars elevated, narrowly crescent shaped or U-shaped with 3 bundle scars. Leaves alternate, petiolate; blades conduplicate [or imbricate] in bud, simple with serrate or rarely entire margins; stipules reddish, linear, caducous, leaving no scar. Inflorescences erect or drooping racemes [the flowers rarely solitary or paired] terminating growth of the season (the infructescences sometimes appearing axillary due to sympodial branching of the shoots), the flowers appearing shortly before or with the foliage; bracts pinkish, linear, deciduous. Flowers perfect, 5-merous. Calyx lobes erect, reflexed, or spreading at anthesis, persistent, imbricate in aestivation; floral tube campanulate to urceolate at anthesis, adnate to at least the bases of the carpels. Petals white [to pinkish], flaccidly spreading or narrowly ascending, obovate to lanceolate, tapering toward the base but usually not clawed, the margins entire or slightly erose at the apices, undulating, imbricate, inserted at the apex of the floral tube. Androecium usually of 20 stamens in 3 whorls; filaments free, persistent, unequal in length, shorter than the petals, inserted at the apex of the floral tube between the petals and a large, fleshy, 5-lobed nectar ring (the lobes opposite the petals); anthers dorsifixed. Gynoecium of 5 [or 2–4] carpels, abaxially partly to nearly completely adnate to the floral tube (the ovaries partly to completely inferior) and adaxially free with the margins unsealed but laterally connate; styles as many as the carpels, connate below to form a hollow column [or distinct], the lower part persistent; stigmas terminal, discoid; each carpel with 2 erect, hemianatropous ovules on an adaxial and basal or lateral placenta, the micropyle inferior, the 2 ovules soon ± separated by a partition that grows inward from the outer carpel wall. Fruit a dark blue to purple or nearly black (sometimes reddish when immature), globose or pyriform berry-like pome, often covered with a bloom, open at the apex, in section appearing 10 [or 4–8] locular due to the incomplete false septa; carpels ± adhering together, the locules with cartilaginous or membranaceous walls and surrounded by the enlarged, mealy to fleshy floral tubes. Seeds 2 per carpel and 1 per locule, or sometimes not all ovules maturing; seed coat membranaceous, smooth, dark brown; endosperm mostly absent; embryo erect, the cotyledons plano-convex, the radicle short, bent, inferior. TYPE SPECIES: *Mespilus Amelanchier* L. = *A. ovalis* Medicus. (Name perhaps derived from *amelanche*, the Provençal name of the European serviceberry, *A. ovalis*, evidently in reference to the honey-like taste of the fruit.) — SHADBUSH, SERVICEBERRY, SARVIS, JUNEBERRY.

About 20 to 30 species of the North Temperate region, with three species in Europe, northern Africa, and southwestern Asia; *Amelanchier asiatica* (Sieb. & Zucc.) Endl. (closely related to *A. arborea* of eastern North America) in Japan, southern Korea, and central China; no more than eight closely related species in western North America; perhaps nine species largely confined to the triangular area between Labrador, the western shores of Lake Superior, and New England; and seven species rather widely distributed in eastern North America and occurring in our area. *Amelanchier denticulata* (HBK.) K. Koch (western Texas to Guatemala) and *A. nervosa* (Decaisne) Standley (Mexico and Guatemala) have been placed in *Amelanchier* sect. MALACOMELES (Decaisne) Rehder or the genus *Malacomeles* (Decaisne) G. N. Jones. *Peraphyllum ramosissimum* Nutt., of the western United States, is closely allied to *Amelanchier.*

The taxonomic and nomenclatural complexities of *Amelanchier* perhaps are exceeded in the Rosaceae only by *Crataegus* and *Rubus*, and treatments of the genus differ greatly in the number of taxa recognized and the names applied to them. The bases for modern treatments of the American species are the extensive studies of Wiegand, Nielsen, Fernald, and Jones (whose revision has been critized for recognizing too few Eastern and too many Western species). Through their collective works, the entities occurring in our area can be ascertained fairly well, but their taxonomic status and names are still subject to debate. Wiegand (1912) summarized the problems in the genus: "*Amelanchier*, like *Rubus*, is a group in which it will never be possible to have the clearly cut condition found in so many genera where specimens will fall easily into one or another specific category. . . . It is no less difficult to determine what names should be applied to the species recognized. Synonymy here is very extensive and very much involved. It is complicated by the fact that many of the species of the earlier authors were undoubtedly aggregates, and also by the fact that several specific names were based upon material

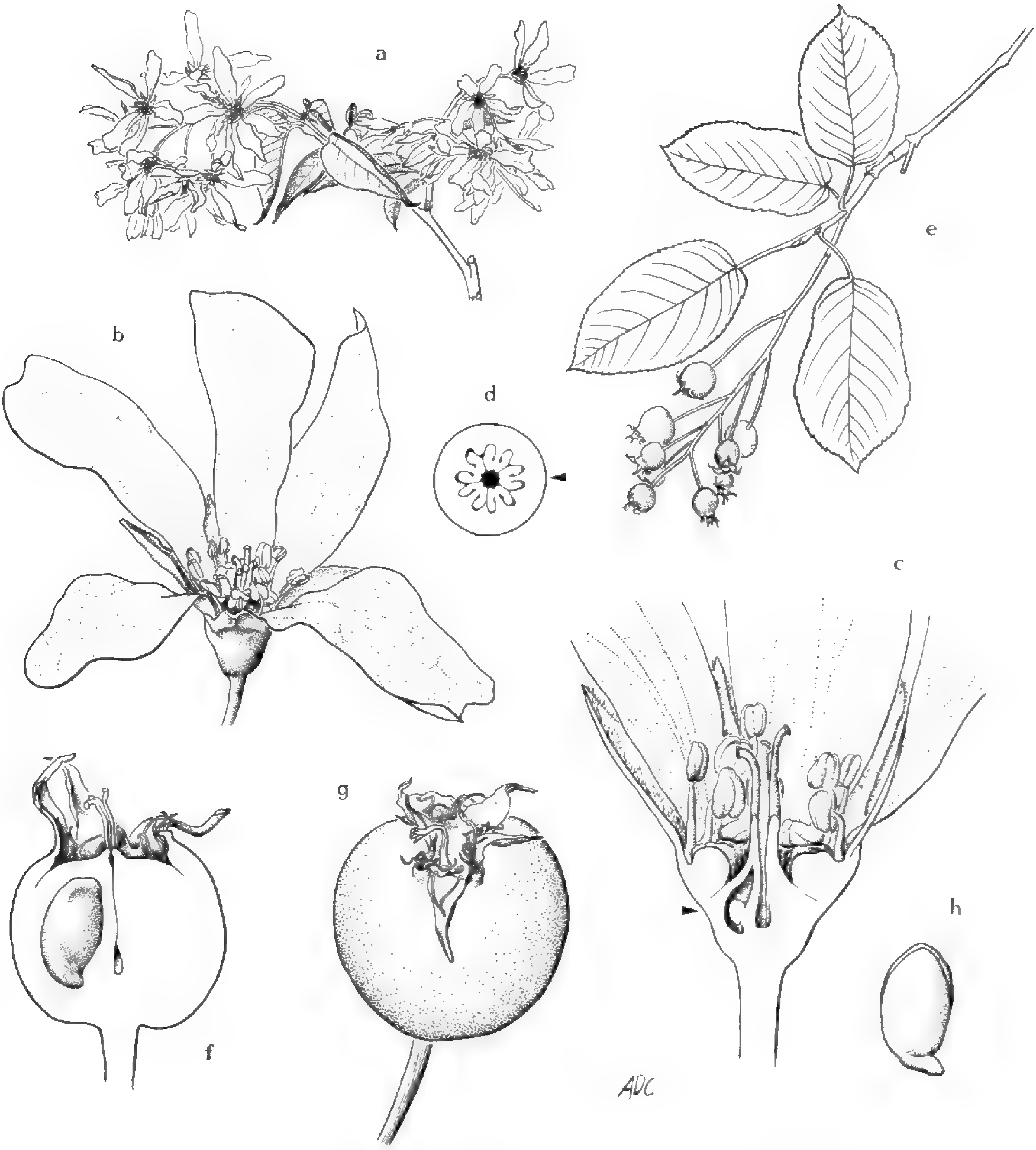


FIGURE 9. **Amelanchier.** a–h, *A. laevis*: a, flowering branchlet, × 1/2; b, flower, × 3; c, flower in vertical section to show placentation, carpels adaxially free, abaxially partly adnate to floral cup, note annular disc above carpels, cut at level of arrow in "d," × 6; d, cross section of ovary at level of arrow in "c," × 6; e, fruiting branchlet, × 1/2; f, nearly mature fruit in vertical section to show orientation of seed, calyx lobes, filaments, and persistent styles, × 3; g, mature fruit, × 3; h, embryo, oriented as in seed in "f," × 6.

from European gardens unlike any species now known to grow in the wild state. There is also some reason to believe that a few names were based on hybrid specimens."

All species in our area have leaves that are conduplicate in bud, racemose inflorescences, and five carpels with the styles at least basally connate. They can be divided into two broad groups (of no assigned taxonomic rank), the first of which is composed of species with the summits of the ovaries glabrous (or rarely slightly pubescent) and includes our two arborescent or fastigiately shrubby species that also have finely toothed, acuminate leaves and large flowers in nodding inflorescences. *Amelanchier arborea* (Michx. f.) Fernald, $2n = 68$,[14] with ascending branches, the leaves small and folded at anthesis and densely tomentose beneath when expanding, compact racemes, and maroon-purple, dry, insipid fruits, is represented in our area by three varieties. The typical variety (*A. canadensis* of Wiegand and others) has a wide habitat tolerance, occurring in rich to dry or rocky woods, thickets, or on slopes and bluffs from southwestern New Brunswick to southern Ontario, northern Michigan, and Minnesota south to northern Florida, Louisiana, and eastern Oklahoma and adjacent Kansas. Varietas *austromontana* (Ashe) Ahles, a short tree or tall shrub with smaller leaves, is evidently confined to southeastern Virginia and the mountains of western North Carolina, and Georgia. The identity and validity of this taxon need review. Jones clearly misinterpreted *A. austromontana* Ashe by selecting an "isotype" that does not match Ashe's description and locality and then considering that species a taxonomic synonym of *A. spicata* (Lam.) K. Koch. Also in need of further study is *A. arborea* var. *alabamensis* G. N. Jones, which differs from var. *arborea* by the somewhat pubescent apices of the ovaries. This character is usually associated with the "*sanguinea*" group of species and its occurrence in an obvious relative of *A. arborea* is unexplained; perhaps it is the result of hybridization. This peculiar variation occurs sporadically in southeastern Virginia, the Carolinas, Alabama, and Arkansas.

Amelanchier laevis Wiegand (*A. canadensis* of some authors, *A. arborea* var. *laevis* (Wiegand) Ahles), $2n = 68$, is characterized by spreading branches; leaves half-grown, reddish, and mostly glabrous at anthesis; rather loose inflorescences; and purple or nearly black, juicy, sweet pomes. Perhaps the most handsome of our eastern shadbushes, *A. laevis* is found in or at the borders of dry to moist woods or thickets, balds, rocky openings, and swamps from Newfoundland to southern Quebec, northern Wisconsin, Minnesota, and Iowa south to Ohio, Pennsylvania, and Maryland, extending in the Appalachians to Georgia and Alabama. The wood of this species is heavy and extremely hard, but the trees are too small for commercial lumbering.

The remaining species in our area with the ovary summit glabrous are shrubs with finely toothed and rounded or slightly mucronate mature leaves, erect inflorescences, and smaller flowers. *Amelanchier canadensis* (L.) Medicus (*A. oblongifolia* (Torrey & Gray) Roemer, see footnote 14; *A. Botryapium* (L. f.) Borkh.), $2n = 68$, tall, erect, clump-forming shrubs with the leaves heavily tomentose and only slightly developed at anthesis

---

[14] *Amelanchier canadensis* (L.) Medicus was applied by many early botanists to the species now called *A. arborea* and *A. laevis*; Wiegand (1912) restricted the name *A. canadensis* to the first of these two species, and this usage is still found in some manuals (such as Rehder). However, Fernald (1941) pointed out that *A. canadensis* (L.) Medicus should be applied to a tall, shrubby species that had previously been called *A. oblongifolia* (Torrey & Gray) Roemer.

and the racemes compact, is largely restricted to noncalcareous habitats on the Atlantic Coastal Plain from Georgia and Alabama to New England and southern Quebec, occurring inland to western New York. Plants with nearly entire leaves from the low pine barrens of southeastern Virginia have been segregated as var. *subintegra* Fernald. In a study of *A. arborea* (the identity of the plant studied should be checked since it is listed as having pubescent ovary summits), *A. laevis,* and *A. canadensis* in the Delaware River valley of New Jersey and Pennsylvania, Cruise found intermediates between *A. laevis* and *A. arborea* and between *A. laevis* and *A. canadensis,* but not between *A. arborea* and *A. canadensis*; it was postulated that *A. laevis* might have evolved as a result of introgression between the other two species, and Cruise felt it appropriate to treat the entire complex as a single variable species (*A. canadensis*).

Very similar to *A. canadensis,* and differing from it by the lower growth habit, the often purplish coloring of the well developed and nearly glabrous leaves at flowering time, the shorter and broader mature leaves, and the more open inflorescences, *A. intermedia* Spach is a somewhat doubtful taxon of often moist, calcareous habitats from Newfoundland to Michigan and Minnesota south to New England, Virginia, and the uplands of North Carolina. *Amelanchier obovalis* (Michx.) Ashe is a low stoloniferous shrub with compact racemes of flowers that precede the initially densely tomentose leaves. This species occurs in acid soils in dry, open pinelands, pocosins, and low woods, chiefly on the Coastal Plain but also in the mountains from Georgia and Alabama to South Carolina, North Carolina, inland Virginia, and southern New Jersey and Pennsylvania.

Members of the second group of species in our area have the top of the ovaries densely pubescent at anthesis, with some of the indumentum persisting on the fruit. *Amelanchier sanguinea* (Pursh) DC., $2n = 34$, a moderately tall shrub (sometimes weakly surculose) with few stems, reddish branches, coarsely toothed leaves, and lax, nodding inflorescences, is found on various noncalcareous substrata along river banks or in rocky, open woods or on slopes from southern Quebec to Thunder Bay District, Ontario, south to New England, New York, northern Ohio, Michigan, Wisconsin, Minnesota, and Iowa and disjunctly in the mountains of Virginia and North Carolina. *Amelanchier stolonifera* Wiegand, $2n = 34, 68$, a low stoloniferous shrub, with finely toothed leaves and dense, erect racemes, occurs in dry, sterile, rocky or sandy, often acidic open areas from Newfoundland to Thunder Bay District, Ontario, south to Nova Scotia, New England, Long Island, Virginia, the Carolinas, Michigan, and Minnesota. This species is often included, along with *A. humilis* Wiegand, in *A. spicata* (Lam.) K. Koch, a name disallowed by Fernald (1946a) for any North American shadbush (but Fernald's conclusion often has been ignored or disputed). The name *A.* × *spicata* is now frequently used for a commonly cultivated form that is probably a hybrid between *A. canadensis* and *A. ovalis* Medicus.

Numerous interspecific hybrids have been reported in *Amelanchier*; of the species in our area only *A. alabamensis*, *A. intermedia*, and *A. obovalis* are not yet known to hybridize with others. Each of our five other species ostensibly crosses with at least three species. *Amelanchier* × *grandiflora* Rehder[15] (*A. arborea* × *A. laevis*), $2n = 68$, perhaps the most beautiful shadbush with the largest flowers, is commonly cultivated in Europe and North America; in forma *rubescens* Rehder the flowers are pale purplish-pink in bud and tinged with pink when fully open. *Amelanchier alnifolia* (Nutt.) Nutt. and *Pyrus scopulina* (Greene) Longyear (*Pyrus* subg. *Sorbus*), both of the Pacific Northwest, have hybridized to produce × *Amelasorbus Jackii* Rehder, which has predominantly the floral characteristics of *Amelanchier.*

In 1931, Sax wrote that all the species that had been studied up to that time were diploids, while two hybrids were tetraploids. This generalization is occasionally quoted even today, but it is now quite incorrect, since the majority of species are tetraploids. Higher levels of polyploidy and aneuploidy are thus far unknown in *Amelanchier.*

Some of the variability in *Amelanchier* may be due partly to the same phenomena that occur in *Crataegus.* As the land in eastern North America was cleared, formerly isolated species expanded their ranges and were able to interbreed, with the hybrid progeny competing more successfully than the species in disturbed habitats. Certainly shadbushes found today in recently cleared or burned areas often have perplexing combinations of characters. However, unlike *Crataegus*, apomictic clones are not known in *Amelanchier.* Jones vehemently dismisses the commonly accepted hypothesis that hybridization regularly occurs between *Amelanchier* species and has been a major force in the evolution of infrageneric taxa. Instead, he speculates that "polyploidy may have played a more important part in the differentiation of genera and species in this subfamily . . . ."

Amelanchier species and hybrids are frequently cultivated in temperate regions for their graceful habit, the magnificent display of pure white flowers in early spring, the often abundant and colorful fruits that mature in mid-summer, and the fine shades of red or yellow the leaves assume in autumn. One common name of the eastern North American species, shadbush, comes from the fact that the plants are often in full bloom as the shad (*Alosa spidissima*) begin to ascend the streams to spawn. The fruits of all species, except *A. arborea*, are edible, but, because of their small size, are used mostly as fresh supplements on hiking and camping trips and in making jellies; many species of birds relish the mature fruits. Pemmican, the preserved, pressed-cake food of American Indians, contained dried buffalo or deer meat, fat, and saskatoon berries (the fruits of *A. alnifolia*). It has been suggested that serviceberries could become a major fruit crop in the basic soils of the Great Plains if a breeding program similar to Coville's work with blueberries (*Vaccinium* spp.) were undertaken.

---

[15] Schroeder (1968) considers *A.* × *grandiflora* to be a nomen ambiguum and places this under *A. Lamarckii* Schroeder.

REFERENCES:

Under subfamily references see BAKER, CHALLICE, DECAISNE, FOLGNER, KOEHNE, and LINDLEY. Under family references see BEAN, CROCKER & BARTON, DIPPEL, HEGI, HESS *et al.*, HILTON *et al.*, LÖVE & LÖVE, REHDER, ROBERTSON, SARGENT, SCHNEIDER, STEPHENS, STERLING (V), L. A. TAYLOR, and VINES.

BEAN, W. J. *Amelanchier florida.* Bot. Mag. **141:** *pl. 8611.* 1915.

BROWICZ, K. Distribution of woody Rosaceae in W. Asia. VII. Genus *Amelanchier* Med. (Polish and Russian summaries.) Arb. Kórnickie **16:** 5–26. 1971. [4 spp. recognized in Old World.]

CINQ-MARS, L. Le genre *Amelanchier* au Québec. Nat. Canad. **98:** 329–345. 1971. [Reprinted in Ludoviciana **9.**]

CRUISE, J. E. Studies of natural hybrids in *Amelanchier.* Canad. Jour. Bot. **42:** 651–663. 1964. [*A. canadensis, A. arborea,* and *A. laevis* in New Jersey and Pennsylvania.]

FAVARGER, C., & P. CORREVON. Mise en évidence de "races chromosomiques" chez l'Amélanchier. Bull. Soc. Neuchâteloise Sci. Nat. III. **90:** 215–218. *pl. 6.* 1967. [*A. ovalis*; plants in southern France are diploid, those at the foot of the Jura Mountains near Neuchâtel are tetraploid.]

FERNALD, M. L. Another century of additions to the flora of Virginia (continued). Rhodora **43:** 559–630. *pls. 672–692.* 1941. [*Amelanchier* in southeastern Virginia, 559–567, *pl. 672*; discussion on nomenclature of *A. canadensis* and *A. arborea.*]

———. *Amelanchier spicata* not an American species. *Ibid.* **48:** 125–129. *pls. 1027–1030.* 1946. [This taxon probably arose in the Jardin du Roi as a cross between *A. canadensis* and *A. ovalis.*]

HARGRAVE, P. D. Seed germination of the saskatoon and pincherry. Sci. Agr. Ottawa **17:** 736–739. 1937. [*Amelanchier alnifolia, Prunus pensylvanica.*]

HARRIS, R. E. The genus *Amelanchier.* Jour. Roy. Hort. Soc. **95:** 116–118. *figs. 83–85.* 1970.

HOOKER, J. D. *Amelanchier canadensis,* Medic. var. *oblongifolia,* Torr. & Gr. Bot. Mag. **124:** *pl. 7619.* 1898. [= *A. canadensis.*]

JONES, G. N. *Malacomeles,* a genus of Mexican and Guatemalan shrubs. *Madroño* **8:** 33–39. 1945. [*M. nervosa* and *M. denticulata,* species often included in *Amelanchier.*]

———. American species of *Amelanchier.* Illinois Biol. Monogr. **20:** 1–126. 1946. [Reviewed by M. L. FERNALD, Rhodora **48:** 129–134. 1946, and by R. MCVAUGH, Madroño **8:** 237–240. 1946.]

LINDLEY, J. *Amelanchier sanguinea.* Bot. Regist. **14:** *pl. 1171.* 1828.

———. *Amelanchier florida. Ibid.* **19:** *pl. 1589.* 1833.

MILLER, W. S., & C. STUSHNOFF. A description of *Amelanchier* species in regard to cultivar development. Fruit Var. Hort. Dig. **25**(1): 3–10. 1971.

NIELSEN, E. L. A taxonomic study of the genus *Amelanchier* in Minnesota. Am. Midl. Nat. **22:** 160–206. 1939.

SARGENT, C. S. *Amelanchier.* Silva N. Am. **4:** 125–132. *pls. 194–196.* 1892. [*A. canadensis = A. arborea*; *A. canadensis* var. *obovalis = A. obovalis*; *A. alnifolia.*]

SCHROEDER, F. G. Zur Nomenklatur in der Gattung *Amelanchier* (Rosaceae). (English summary.) Taxon **17:** 633, 634. 1968. [*A. Lamarckii* Schroeder, nom. nov.]

———. *Amelanchier*-Arten als Neophyten in Europa. Mit einem Beitrag zur

Soziologie der Gebüschgesellschaften saurer Böden. Abh. Naturw. Ver. Bremen **37:** 287–419. 1972.

SPRAGUE, R., & F. D. HEALD. A witches' broom of the service berry. Trans. Am. Microscop. Soc. **46:** 219–247. 1927. [A mold, *Dimerosporium collinsii*, is associated with the witches' broom of *A. alnifolia*.]

STAPF, O. *Amelanchier oligocarpa*. Bot. Mag. **139:** *pl. 8499*. 1913. [= *A. Bartramiana*.]

WEATHERBY, C. A. Staminody of the petals in *Amelanchier*. Rhodora **18:** 48. 49. 1916. [*A. nantucketensis*; in all specimens the petals were inrolled, yellowish, and contained pollen.]

WEAVER, R. E., JR. The shadbushes. Arnoldia **34:** 22–31. 1974. [Includes key to spp. most commonly cultivated in the northeastern U.S.]

WIEGAND, K. M. The genus *Amelanchier* in eastern North America. Rhodora **14:** 117–161. *pls. 95, 96.* 1912. [The first modern revision based on extensive field observations, the nomenclature now out of date; for corrections and additions see *ibid.* 239–241 and *ibid.* **22:** 146–151. 1920.]

———. A taxonomist's experience with hybrids in the wild. Science **81:** 161–166. 1935. [Includes discussion of Wiegand's work on *Amelanchier*.]

WRIGHT, P. H. Amelanchiers. Horticulture **51:** 62, 63, 70. 1973.

21. **Pyrus** Linnaeus, Sp. Pl. 1: 479. 1753; Gen. Pl. ed. 5. 214. 1754.

Deciduous or rarely semi-evergreen shrubs (sometimes rhizomatous) or small to medium-sized trees with slender to stout terete twigs; lateral spurs sometimes produced; unarmed or with axillary spines; bark smooth, longitudinally fissured, scaly, or forming plates; buds solitary, sessile, ovoid, oblong, or subconical, acute or obtuse, terminal buds often much larger than lateral ones; bud scales leaving prominent, narrow, semicircular scars; leaf scars low, elevated, or the nodes swollen below them, and linear, crescent shaped, or U-shaped with 3 or 5 (rarely 7) bundle scars. Leaves alternate, petiolate; blades conduplicate, convolute, or involute in bud, simple, with serrate to dentate [or rarely entire] margins, often lobed (the leaves of vegetative shoots more deeply lobed than those of flowering branches), or imparipinnate with serrate-margined leaflets; stipules small, deciduous, leaving no discernible scar. Inflorescences umbel-like racemes terminating lateral spurs or few to many-flowered corymbs terminating elongated shoots (the fruit seemingly axillary in subg. ARONIA), the flowers opening as the leaves expand or afterward; bracts linear, caducous. Flowers small to large, perfect, 5-merous. Calyx without an epicalyx, the lobes triangular, recurved or erect at anthesis, persistent [or deciduous], imbricate in aestivation; floral tube funnelform, campanulate, cup shaped, or urceolate at anthesis, adnate to the carpels. Petals white to pink [reddish or yellowish], spreading [or erect], ± equal, subcircular, broadly elliptic, or obovate with entire to crenate or erose margins, slightly to distinctly clawed at the base, sometimes pubescent on the adaxial surface, inserted at the edge of the floral tube, imbricate. Androecium of 15 to many stamens in one or several whorls; filaments free, persistent, unequal or equal in length, inserted at the apex of the floral tube, a nectar ring either not obvious or prominent and surrounding or covering the mouth of the floral tube; anthers red, purple, or yellow, dehiscing centrifugally or centripetally. Gynoecium of 2–5 carpels, abaxially half to completely adnate to the floral tube (the ovaries half to completely inferior) and adaxially and laterally half to completely connate; styles as many as the carpels, distinct to connate for more than half their length, often pubescent below, terminal on the adaxial margins of the carpels, persistent; stigmas discoid or in bands on the styles; each carpel with 2 (rarely more) erect, anatropous ovules on an adaxial and basal or lateral, sometimes elevated, placenta, the micropyle inferior. Fruit a red, yellow, green, purple, black, brown [or white] small to large, subglobose, ovoid, obovoid, or pyriform pome, the bases and apices sometimes depressed; carpels ± adhering together, the loculi with cartilaginous, membranaceous, or leathery [rarely almost stony] walls and surrounded by the enlarged, fleshy or mealy floral tubes, grit cells absent or abundant. Seeds one or two per carpel; testa membranaceous, smooth or with fine, longitudnal striations; endosperm essentially absent; embryo erect, the cotyledons plano-convex, the radicle short, straight, inferior. (Including *Malus* Miller, *Sorbus* L., and *Aronia* Medicus.) LECTOTYPE SPECIES: *P. communis* L.; see N. L. Britton, N. Am. Trees, 429. 1908. (Classical name of the pear tree; the spelling is often altered to *Pirus*, which is linguistically preferable but nomenclaturally unacceptable.)

A complex genus of perhaps 125 species in four subgenera of the North Temperate Zone. Although often treated as four distinct genera, it becomes exceedingly difficult to draw mutually exclusive generic limits when the group is examined on a world-wide basis. Additionally, all the subgenera, except subg. MALUS, freely hybridize. About sixteen species are indigenous and six exotic species are adventive or naturalized in North America; ten (including three introduced) occur in our area.

Subgenus PYRUS (*Pyrus* L. of many authors; sect. *Pyrophorum* DC.), pears, is composed of species with simple leaves involute in bud; large whitish flowers in few-flowered cymes that terminate short, lateral spurs; free styles; reddish anthers; and (in ours) pyriform fruits containing numerous grit cells. *Pyrus communis* L.,[16] the only representative of this subgenus in our area, has occasionally escaped from cultivation and become naturalized in thickets, fence rows, and clearings and along roadsides and the edges of woods in many regions of the United States. This "species" is now thought to be of hybrid origin with numerous European species in its genealogy, and it is known only in or as an escape from cultivation. According to Fernald, *P. pyrifolia* (Burm. f.) Nakai has spread from cultivation in southeastern Virginia; thus far this native of eastern Asia is not known to be adventive in our area.

---

[16] Several Europeans (see references in Staritsky) have recently applied the name *P. communis* L. to a wild Central European species and have used *P. domestica* Medicus for the cultivated pear.

The subgenus, often divided into four sections, contains more than thirty species distributed throughout most of temperate Eurasia. There are two morphologically, geographically, and perhaps ecologically distinct groups. The occidental pears (calyx persistent, pedicels fleshy, fruits pyriform) occur in western Eurasia from Turkestan to northern Africa and southern and western Europe, with the greatest diversity in Caucasia and the lands adjoining the western Mediterranean. The oriental pears (calyx deciduous, pedicels not fleshy, fruits subglobose) are plants of eastern Asia, from the Tien Shan and Hindu Kush to China, Korea, Japan, and Taiwan. They are particularly diverse in Yunnan and Hupeh provinces, China. *Pyrus Pashia* D. Don, of the Himalayas, is intermediate in morphology between the eastern and western groups. No species of this subgenus is native to the New World or to the Southern Hemisphere.

Pyrus communis hybridizes with *P. Aria* (L.) Ehrh. of subgenus SORBUS to produce what has been called × *Sorbopyrus auricularis* (Knoop) Schneider. The intergeneric hybrid between *P. communis* and *Cydonia oblonga* Miller is known as × *Pyronia Veitchii* (Trabut) Guillaumin. Graft-chimaeras between these two species are given the "generic" name + *Pirocydonia* H. Winkler ex Daniel. A presumed graft-chimaera between *Crataegus* and *Pyrus* is + *Pyrocrataegus* Daniel (*C. Oxyacantha* + *P. communis*).

All species of subgenus PYRUS that have been examined cytologically are diploid with $2n = 34$; polyploidy and aneuploidy are known only in cultivars. The study of Zielinski & Thompson (1967) supports Sax's theory on the allopolyploidy origin of the base number of $x = 17$ in the Maloideae (see subfamily account).

Several studies have shown that species of this subgenus are largely self-incompatible. Zielinski (1965) found that *Pyrus Fauriei* Schneider (a native of Korea) is quite self-compatible, but two clones of this species were reported by Westwood & Bjornstad to be self-incompatible but cross-compatible. According to Griggs & Iwakiri, the commonly cultivated 'Bartlett' pear (called 'Bon Chrétien William' in other countries) is largely sterile and does not set seed unless pollinated by pollen from other varieties, although seedless, parthenocarpic fruit are produced in the absence of cross-varietal pollination. Again, Westwood & Bjornstad were in contradiction, saying that the tetraploid 'Bartlett' was highly self-fertile. Interspecific sterility barriers are seemingly poorly developed in subg. PYRUS, since numerous hybrids are reported in the literature. Most of fifty-five interspecific crosses made by Westwood & Bjornstad were fertile. Apomixis is thus far unknown in this subgenus.

Subgenus MALUS (Miller) Pers. (*Malus* Miller; lectotype species: *Malus Malus* (L.) Britton = *P. Malus* L., see N. L. Britton, N. Am. Trees, 430. 1908), apples, with the leaves simple and involute, conduplicate, or convolute in bud, the flowers large, pink or reddish (at least in bud) and in few-flowered cymes that terminate short lateral spurs, the styles connate, the anthers yellow or red, and the fruits subglobose and usually lacking grit cells, includes perhaps thirty species in five sections in temperate Eurasia and eastern and western North America. Two sections are represented in the southeastern United States; the other three, which are largely Asiatic, present taxonomic problems critical in generic delimitation (cf. Browicz, Huckins).

Section MALUS S. F. Gray (*Malus* sect. *Calycomeles* Koehne; *Malus* sect. *Eumalus* Zabel) is composed of about ten species of Eurasia (Japan to the British Isles), with the greatest diversity in the region from Caucasia to the Hindu Kush and Tien Shan. The leaves are unlobed and involute in bud, the anthers are yellow, and the ovary is completely inferior and fused throughout its length to the fleshy floral tube. *Pyrus Malus* (*Malus pumila* Miller), the cultivated apple, probably of hybrid origin, persists after cultivation and evidently is reproducing from seed in many areas of the United States. Two Asiatic members of this section, *P. prunifolia* Willd. and *P. baccata* L., have spread from cultivation in eastern North America, but are not yet known to occur in our area.

Section CHLOROMELES (Decaisne) Robertson[17] (leaves conduplicate in bud, those of at least the vigorous shoots lobed; anthers reddish; apex of ovary in fruit pointed and free from the floral cup) is restricted to the eastern United States and adjacent Canada and includes our native crab apples. Although quite distinct from other sections of subg. MALUS, this section is very plastic, its members being particularly variable in leaf shape and degree of lobing, indumentum density, and fruit size. Yet, it is on the basis of these characters that nine species and numerous varieties have been recognized. The situation evidently has also been complicated by hybridization and perhaps introgression among the native crabs and between them and the cultivated apple. Until the taxonomy of the group has been more thoroughly studied, it seems best to recognize only three variable species and two named hybrids.

Pyrus angustifolia Aiton (*Malus angustifolia* (Aiton) Michaux; *M. bracteata* Rehder), the southern or narrow-leaved crab, is a spinescent shrub or small tree with abaxially glabrous or glabrescent calyx lobes and lanceolate to narrowly elliptic leaves with obtuse or short-mucronate apices. In the southern part of its range, it may be evergreen or semi-evergreen. The leaves of the flowering spurs are entire to serrate while those of rapidly growing vegetative branches are broader, much larger, and coarsely toothed or lobulate. Most abundant on the Coastal Plain from New Jersey to Florida, Louisiana, and southeastern Texas, *P. angustifolia* also occurs inland to Tennessee, Kentucky, and southeastern Missouri. *Pyrus coronaria* L. (*Malus coronaria* (L.) Miller, *M. fragrans* Rehder, *M. glabrata* Rehder,

---

[17] The proper combination under *Pyrus* does not appear to have been made previously for this section. *Pyrus* L. sect. **Chloromeles** (Decaisne) Robertson, comb. nov. *Malus* Miller subg. *Chloromeles* Decaisne, Nouv. Arch. Mus. Hist. Nat. Paris **10**: 155. 1874; *Chloromeles* (Decaisne) Decaisne, Fl. des Serres **23**: 156. 1881; *Malus* subsect. *Coronariae* Rehder in Sargent, Trees Shrubs **2**: 142. 1911; *Malus* sect. *Chloromeles* (Decaisne) Rehder, Jour. Arnold Arb. **2**: 48. 1920. TYPE SPECIES: *P. angustifolia* Aiton.

M. glaucescens Rehder, *M. lancifolia* Rehder), wild or sweet crab, distinguished by abaxially glabrous calyx lobes and broadly lanceolate to broadly ovate leaves with acute to acuminate apices, has a more northerly distribution, occurring from central New York to Wisconsin and southern Ontario, south to upland North Carolina, Tennessee, and Missouri. The leaves of the vegetative branches of this and the following species are usually distinctly lobed. In *Pyrus ioënsis* (Wood) Bailey (*Malus ioënsis* (Wood) Britton), Iowa or Bechtel crab, the calyx lobes and floral tubes are densely tomentose and the leaves are persistently pubescent below. This species enters our area only on the west, ranging from Indiana to Minnesota south to Kentucky, Louisiana, and the Edwards Plateau of Texas. The sweetly fragrant flowers of the eastern crab apples are pink in bud, becoming nearly pure white at anthesis, and finally turning dark pink or rose with age. At maturity the fruits are two to three centimeters in diameter, greenish yellow, with a fragrant, waxy coat and a tart, acidic taste.

Hybrids between the cultivated apple and the native eastern crabs have generally unlobed or weakly lobed leaves and fruits suffused to varying degrees with red and larger than 5 cm. in diameter. *Pyrus Malus* crosses with *P. angustifolia* and *P. coronaria* to produce *P.* × *platycarpa* (Rehder) Bailey, pro. sp., while hybrids of *P. Malus* and *P. ioënsis* are called *P.* × *Soulardii* Bailey, pro. sp.

Subgenus MALUS does not have the uniformity of chromosome number found in subgenus PYRUS. Diploid, triploid, and tetraploid species occur in the subgenus; pentaploidy, hexaploidy, and aneuploidy apparently exist only in cultivars and interspecific hybrids. Many of the reports are from cultivated material of doubtful identity, and possible correlations between chromosome number and the classification of the subgenus are uncertain. A thorough cytological study of our native crab apples seems in order, since their reported sporophytic chromosome numbers are: *P. angustifolia*, 34, 51, 68; *P. coronaria*, 51, 68; *P. ioënsis*, 34; *P.* × *platycarpa*, 51, 68; and *P.* × *Soulardii*, 34.

There are numerous reports in the literature on reproductive abnormalities of apples. Unreduced gametes evidently are produced rather frequently, and, although the role of such gametes in nature is a matter of conjecture, they have been of considerable importance in the production of new polyploid cultivars. Apomixis occurs in several species of sects. MALUS and SORBOMALUS. In most cases the plants are ostensibly facultative apomicts, with the embryo sacs developing from unreduced megaspores. The triploid *P. hupehensis* Pamp. is almost an obligate apomictic with the embryo sacs produced aposporously; the aposporous egg cells are occasionally fertilized by pollen from other species, giving rise to hybrids of a higher polyploid level. Pseudogamy also occurs in this subgenus.

Interspecific hybridization is common within subgenus MALUS. Species of sect. CHLOROMELES cross with members of sect. MALUS but not with those of sect. SORBOMALUS; hybrids between sects. MALUS and SORBOMALUS occur.

The cedar-apple rust-fungus (*Gymnosporangium juniperi-virginianae*) is endemic to eastern North America and is remarkable for the correlation between its hosts and their taxonomic relationships. All species of *Pyrus* sect. CHLOROMELES harbor the spermogonial and aecial stages of the fungus (only *P. Malus*, *P. fusca*, and possibly *P. communis* and *P. glauca* are other such hosts), and all hosts of the telial stage belong to *Juniperus* sect. SABINA (with the exception of the doubtful host *J. communis*).

Subgenus SORBUS (L.) Reichenb. (*Sorbus* L.; lectotype species: *Sorbus Aucuparia* L. = *Pyrus Aucuparia* (L.) Gaertner; see A. Rehder, Bibliogr. Cult. Trees Shrubs, 252. 1949, and G. K. Brizicky, Jour. Arnold Arb. **49**: 502–508. 1968 [18]), mountain ashes, encompasses more than eighty species (in five sections) of the temperate regions of the Northern Hemisphere. The species that approach members of the other subgenera of *Pyrus* morphologically make it difficult to define this variable group concisely. In subg. SORBUS the leaves are simple or odd-pinnate and conduplicate, convolute, or involute in bud; the flowers are smallish and in many-flowered compound corymbs terminating short or long shoots (inflorescences rarely on short, woody spurs); the anthers are yellow or red; and the fruits are small to large, globose, ovoid, or pyriform pomes with grit cells either absent or abundant.

Perhaps eight species occur in North America: *Pyrus americana* (Marshall) DC. is restricted to the eastern part of the continent; two species occur in Greenland, as well as on the American mainland; three species and five varieties are native to western North America; *P. sambucifolia* Cham. & Schlecht., an Asiatic species, extends to the westernmost Aleutian Islands; and *P. Aucuparia* is introduced from Europe. All these species belong to sect. SORBUS (L.) S. F. Gray (*Aucuparia Medicus*, nom. illegit.; *Sorbus* sect. *Aucuparia* K. Koch; *Sorbus* subg. *Aucuparia* Kovanda; *Sorbus* sect. *Eusorbus* Boiss.) (leaves imparipinnate, ovary of 2 to 4 or rarely 5 carpels that are only basally connate), a holarctic group with a particularly large number of species in western Asia.

Pyrus americana (*Sorbus americana* Marshall; *P. microcarpa* (Pursh) DC.), $2n = 34$, American mountain ash, rowan-tree, or missey-moosey, occurs primarily in moist woods from Newfoundland and Côte Nord, Quebec, to northeastern Minnesota, southward to northern Illinois, Pennsylvania, and New Jersey, and extending in the mountains to Virginia, Tennessee, the Carolinas, and Georgia. A related species, *P. decora* (Sargent) Hyland, $2n = 34$, with villous, rather than glabrescent, inner bud scales and broader, less acute, firm leaflets, has a more northern distribution ranging from southern Greenland and Labrador to northern Ontario and southeastern Manitoba, south to Nova Scotia, northern New England, New York, Ohio, Indiana, Iowa, Wisconsin, and Minnesota. Restricted to alpine or subalpine regions in southern Greenland, coastal Labrador, Newfoundland, the Gaspé Peninsula, and the mountains of northern New

---

[18] Brizicky's argument that, since *Sorbus domestica* L. does not agree with the essential features of the generic protologue, *S. Aucuparia* L. must be taken as the type species of *Sorbus* L. seems to be correct.

England, *P. groenlandica* (Schneider) Robertson,[19] $2n = 68$, is distinguished from *P. decora* by the membranaceous leaflets that taper from near the middle to a prolonged acumination. Löve & Löve hypothesized that this species is an allopolyploid between *P. americana* and *P. decora*. *Pyrus Aucuparia*, $2n = 34$, a small tree with permanently pubescent branchlets, leaflets, and peduncles, and with bright orange fruit, has spread from cultivation and become naturalized in many parts of Canada and the northern United States (see Hultén, 1971, under family references). Thus far this species, the widespread European parallel of *P. americana*, is not known to be adventive in our area.

The other sections of subgenus SORBUS are sect. CORMUS (Spach) Robertson,[20] with *Pyrus Sorbus* Gaertner (*Sorbus domestica* L.; *Pyrus domestica* (L.) Smith, non Medicus), of southern Europe and northern Africa; sect. ARIA (Pers.) DC. (*Sorbus* subg. *Aria* Pers.; *S.* sect. *Aria* (Pers.) Dumort.; *Hahnia* Medicus), a taxonomically difficult group of about 35 species that is particularly diverse in Caucasia; sect. TORMINARIA DC. (*Sorbus* sect. *Torminaria* (DC.) Dumort.; *Sorbus* subg. *Torminaria* (DC.) K. Koch), with *P. torminalis* (L.) Ehrh., of southern, western, and central Europe, and northern Africa; and sect. CHAMAEMESPILUS (Medicus) Lindley (*Chamaemespilus* Medicus; *Sorbus* subg. *Chamaemespilus* (Medicus) Koch; *Sorbus* sect. *Chamaemespilus* (Medicus) Schauer), with *P. Chamaemespilus* (L.) Ehrh. in the mountains of central and southern Europe.

Interspecific barriers to hybridization are weakly developed in some species of subg. SORBUS. *Pyrus americana* crosses with *P. Aucuparia* and *P. Aria* (L.) Ehrh., of this subgenus, and with *P. floribunda* and *P. melanocarpa*, of subg. ARONIA (see discussion under subg. ARONIA for other hybrids between these two subgenera). *Pyrus Aria* also hybridizes with *P. communis* of subg. PYRUS. Hybrids occur between members of sect. ARIA and sects. SORBUS, TORMINARIA, and CHAMAEMESPILUS, but members of the last three sections do not interbreed. *Pyrus Sorbus* (sect. CORMUS) rarely crosses with other species. An intergeneric hybrid is × *Amelasorbus Jackii* Rehder (*Amelanchier florida* Lindley × *Pyrus scopulina* (Greene) Longyear). Kovanda (1961) mentions hybrids between members of subg. SORBUS and *Crataegus, Cotoneaster*, and *Mespilus*. It is interesting that most of the known intergeneric and intersubgeneric hybrids have arisen spontaneously in nature, botanical gardens, or nurseries; attempts to make such hybrids artificially often fail.

Subgenus SORBUS is taxonomically difficult in Europe and has been studied in some detail in Scandinavia and the British Isles. There are four

---

✓ [19] **Pyrus groenlandica** (Schneider) Robertson, comb. nov. *Sorbus americana* Marshall var. *groenlandica* Schneider, Bull. Herb. Boiss. II. **6**: 314. 1906. *Sorbus decora* var. *groenlandica* (Schneider) Jones; *Pyrus decora* var. *groenlandica* (Schneider) Fernald; *Sorbus groenlandica* (Schneider) Löve & Löve.

[20] *Pyrus* L. sect. **Cormus** (Spach) Robertson, comb. nov. *Cormus* Spach, Hist. Nat. Vég. **2**: 96. 1834. *Sorbus* sect. *Cormus* (Spach) Boiss.; *S.* subg. *Cormus* (Spach) Ducharte; *S.* subg. *Sorbus* Kovanda; *Pyrus* b. *Cormus* Ascherson & Graebner.

wide-ranging, diploid, sexually reproducing primary species: *Pyrus Aria, P. Aucuparia, P. torminalis,* and *P. Chamaemespilus* (*P. Sorbus* is also diploid but is evidently not involved in the evolution of the numerous biotypes). It has been hypothesized that diploid and partly sterile hybrids were produced between *P. Aria* and the other three species, and allotetraploids were formed from these F_1 hybrids. In some instances, autotetraploids were derived from the diploid species, and triploid plants resulted from crosses between diploids and tetraploids. Individual polyploid plants can be apomictic, and, since some are only facultatively so, backcrossing with either parental species (or with another species not in the hybrid's genealogy) is possible. This evolutionary pattern is remarkably similar to that postulated by Babcock & Stebbins for the western North American species of *Crepis* (see discussion in Liljefors, 1955, p. 105).

Subgenus ARONIA Reichenb. (*Aronia* Medicus, nom. cons. prop., non Mitchell; type species: *Mespilus arbutifolia* L. = *Pyrus arbutifolia* (L.) L. f.; *Pyrus* sect. *Adenorachis* DC.; *Adenorachis* (DC.) Nieuwland), chokeberries, comprises three closely related species of eastern North America that are shrubs with finely serrate leaves with numerous glands along the upper midrib, smallish flowers in simple to more or less compound inflorescences that generally terminate long shoots (these shoots may branch sympodially and the inflorescences then appear to be axillary), and small, berrylike fruits. The three taxa of subg. ARONIA have been treated variously as three species, one species with three varieties, or two species with one of them having two varieties. The group is often considered a distinct genus or placed under *Sorbus* L.

Pyrus arbutifolia (*Aronia arbutifolia* (L.) Ell.; *Sorbus arbutifolia* (L.) Heynhold), $2n = 34, 68$, a shrub with reddish, long-persistent fruits, glandular calyx lobes, dull green leaves that turn red in autumn, and tomentose branchlets, pedicels, and lower leaf surfaces, ranges from Florida, Georgia, Alabama, Mississippi, Louisiana, and eastern Texas northward to New York, New England, and Newfoundland. In our area this species is most frequently encountered on the Coastal Plain in low woods, swamps, bogs, thickets, savannahs and damp pine barrens. Usually a rhizomatous shrub one to three meters high, some individuals may be small trees to six meters in height, and dwarf forms of bogs, pine barrens and subalpine regions are few stemmed and less than a half meter tall. Several varieties and forms based on habit, leaf size, and indumentum density have been described; these need to be studied.

Pyrus melanocarpa (Michaux) Willd. (*Aronia melanocarpa* (Michaux) Ell.; *A. nigra* Koehne; *Sorbus melanocarpa* (Michaux) Heynhold), $2n = 34$, is usually shorter than the above species and can be recognized by the black, short-persistent fruits, somewhat glandular calyx lobes, lustrous leaves that mostly turn brown in autumn, and mostly glabrous branches and leaves. This species occurs in similar or drier habitats from Newfoundland to northwestern Ontario and Minnesota southward to New England, Virginia, the Carolinas, Georgia, Tennessee, northwestern Alabama and Kentucky; in our area it is most common in the Piedmont.

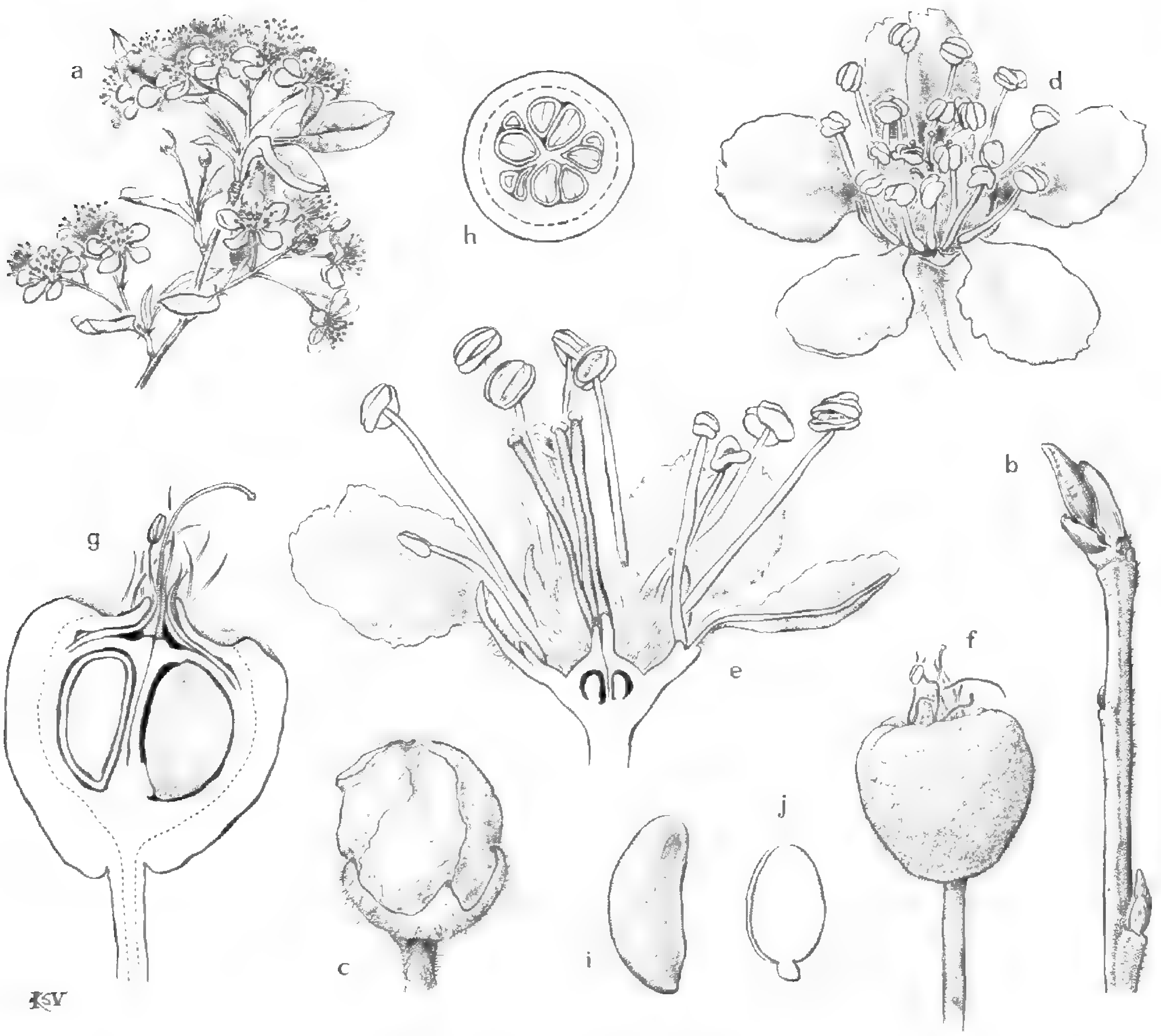


FIGURE 10. **Pyrus** subg. **Aronia.** a–j, *P. arbutifolia*: a, tip of branchlet with inflorescences, × 1/2; b, twig with terminal and lateral winter buds, × 2; c, flower bud, petals imbricate, × 5; d, flower, × 3; e, flower in vertical section to show placentation and insertion of petals and stamens, × 5; f, fruit, note persistent calyx lobes, filaments, and styles, × 3; g, fruit in vertical section, seed on left in section, dotted line shows division between tissues of floral cup and carpels, × 5; h, cross section of fruit, some seeds aborted, × 3; i, seed, oriented as in fruit, × 6; j, embryo, oriented as in seed, × 6.

Pyrus floribunda Lindley (*Aronia prunifolia* (Marshall) Rehder; *A. atropurpurea* Britton; the proper combination under *Sorbus* does not appear to have been made) is similar to *P. arbutifolia*, differing by its purple, long-persistent fruits, mostly eglandular calyx lobes, and moderately pubescent vegetative parts. It is found in similar habitats from Newfoundland, southward to New England, Virginia, North Carolina, Georgia, and Florida, west to Ontario (Algome District), Michigan, Indiana, Kentucky, Tennessee, Alabama, and Missouri. This plant, clearly intermediate between *P. arbutifolia* and *P. floribunda*, has been considered to be either a distinct species or a variety of each of the others. Hardin, in an excellent review of the chokeberries (which he recognized as the genus *Aronia*), concluded that *A. prunifolia* is of hybrid origin "by means of ancient as well as current hybridization and introgression . . ." Evidence was presented by Hardin that agamospermy probably occurs in *P. floribunda*, and this "could effectively stabilize the hybrid forms, and aid the distribution beyond the zone of sympatry of the parental species." Hardin preferred to recognize only *A. arbutifolia* and *A. melanocarpa* including *A. prunifolia* (*P. floribunda*) in the latter species.

Because the species of this subgenus are so variable and closely related, interspecific hybrids are difficult to detect; Fernald lists a hybrid between *Pyrus floribunda* and *P. melanocarpa*. There are numerous intersubgeneric hybrids between subgenera ARONIA and SORBUS (when these are maintained as genera, such hybrids have the name × *Sorbaronia* Schneider); *Pyrus arbutifolia* crosses with *P. Aucuparia* and with *P. Aria*; *P. floribunda* with *P. americana*, *P. Aucuparia*, and *P. decora*; and *P. melanocarpa* with *P. americana*, *P. Aucuparia*, and *P. Aria*. In these hybrids, the stamens are pinkish, the leaves have glands on the upper midrib, and, if either *P. americana*, *P. Aucuparia*, or *P. decora* is one of the parents, the leaves are partly pinnate; in addition, the plants are somewhat sterile and meiosis is irregular.

Pyrus is of considerable economic importance. Pears and apples are major fruit crops in temperate regions and are consumed fresh, dried, or canned or converted into juice (unfermented or fermented), jelly, or purée. Numerous species of pears, apples, mountain ashes, and chokeberries are widely grown as ornamentals for both their abundant flowers and colorful fruits. Although not a major timber crop, the wood of the arborescent species is used in musical instruments and tool handles. Apple wood is prized for golf-club heads. A homeopathic treatment has been made from the astringent inner bark of *P. Aucuparia*. During the winter months, the fruit of the native and introduced species is a primary food for many kinds of animals, especially birds.

REFERENCES:

Under subfamily references see ASHE, BAKER, CHALLICE, CHURCH, DECAISNE, DIAPULIS, FOLGNER, KOEHNE, and LINDLEY. Under family references see BEAN, BOUTINEAU, BUNTING, CROCKER & BARTON, DIPPEL, FREE, GUSTAFSSON, HEGI, HILTON *et al.*, HULTÉN (1971), JESSEN, LÖVE & LÖVE, REHDER, ROBERTSON, ROEMER & RUDORF, ROSS-CRAIG, SARGENT, SCHNEIDER, STEPHENS, STERLING (V), L. A. TAYLOR, and VINES. Many references dealing mostly with horticultural aspects of pears and apples have been omitted.

AHLGREN, C. E. Phenological observations of nineteen native tree species in northeastern Minnesota. Ecology **38**: 622–628. 1957. [*P. americana*.]

BADIZADEGAN, M. Physiological studies of dormancy and germination of apple (*Malus sylvestris* Mill.) seed. Ph.D. Thesis, Michigan State University. 104 pp. 1967.* [Diss. Abstr. **28**(3): 755B. 1967.]

BAILEY, L. H. Notes from a garden herbarium VI. The Soulard crab and its kin. Am. Garden **12**: 469–474. 1891. [4 spp. discussed.]

———. The *Pyrus-Malus* puzzle. Gent. Herb. **8**: 40–43. 1949. [Explanation of why Bailey in post-1941 publications treated *Pyrus* and *Malus* as distinct genera.]

BEACH, S. A. The apples of New York. Vol. 1. xx + 409 pp. *129 pls. frontisp.* Albany. 1905; vol. 2. iv + 360 pp. *85 pls.* Albany. 1905

BEAN, W. J. *Pyrus ioensis*. Bot. Mag. **139**: *pl. 8488*. 1913.

BLACK, C. A. The nature of the inflorescence and fruit of *Pyrus Malus*. Mem. N. Y. Bot. Gard. **6:** 519–547. *pls. 33–40.* 1916.

BLASSER, H. W., & J. EINSET. Flower structure in periclinal chimeras of apple. Am. Jour. Bot. **37:** 297–304. 1950. [Patterns of diploid and tetraploid tissues used in a reinterpretation of the pome.]

BOER, A. F. DEN. Ornamental crab apples. 226 pp. *3 unnumbered col. pls. frontisp.* Chicago. 1959. [Includes cultivars of native species.]

BOYNTON, K. R. *Malus glaucescens.* Addisonia **10:** 55. *pl. 348.* 1925 [1926].

BRADFORD, F. C., & R. H. BRADFORD. Pollination of native crab apples of the northeastern United States. Proc. Am. Soc. Hort. Sci. **54:** 133–136. 1949.

BRITTON, N. L. *Aronia atropurpurea.* Addisonia **3:** 1, 2. *pl. 81.* 1918.

———. *Aronia arbutifolia. Ibid.* **33:** *pl. 97.*

BROWICZ, K. '*Malus florentina*' — its history, systematic position and geographical distribution. Fragm. Fl. Geobot. **16:** 61–83. 1970. [Hybrid generic name × *Malosorbus* proposed.]

CHALLICE, J. S. [Phenolic compounds of the genus *Pyrus.* V.] Phenolics of *Pyrus* interspecific hybrids. Phytochemistry **11:** 3015–3018. 1972. [9 interspecific crosses.]

——— & M. N. WESTWOOD. Phenolic compounds of the genus *Pyrus* [IV]. *Ibid.* **11:** 37–44. 1972.

——— & ———. Numerical taxonomic studies of the genus *Pyrus* using both chemical and botanical characters. Bot. Jour. Linn. Soc. **67:** 121–148. 1973.

——— & A. H. WILLIAMS. Phenolic compounds of the genus *Pyrus.* I. The occurrence of flavones and phenolic acid derivatives of 3, 4-dihydroxybenzyl alcohol 4-glucoside in *Pyrus Calleryana.* Phytochemistry **7:** 119–130. 1968; II. A chemotaxonomic survey. *Ibid.* 1781–1801; III. A chemotaxonomic study of further Oregon specimens. *Ibid.* **9:** 1271–1276. 1970.

CHEVALIER, A. Histoire et amélioration des pommiers et spécialement des pommiers a cidre. Revue Bot. Appl. Agr. Colon. **1:** 149–215. 1921. [32 spp. recognized in *Malus.*]

CRANDALL, C. S. Native crabs: their behavior in breeding. Bull. Agr. Exper. Sta. Univ. Illinois **311:** 535–560. 1928. [Mostly crosses between 6 native spp. and cultivars of *P. Malus.*]

CRANE, M. B., & E. MARKS. Pear-apple hybrids. Nature **170:** 1017. 1952. [Evidently sexual artificial hybrids obtained.]

CROWELL, I. H. The hosts, life history, and control of the cedar-apple rust fungus *Gymnosporangium Juniperi-virginianae* Schw. Jour. Arnold Arb. **15:** 163–232. *pls. 91–98.* 1934. [Includes list of the known maloid hosts.]

DARLINGTON, C. D., & A. A. MOFFETT. Primary and secondary chromosome balance in *Pyrus.* Jour. Genet. **22:** 129–151. *pl. 5.* 1930. [The species discussed belong to subg. *Malus.*]

DERMEN, H. Aposporic parthenogenesis in a triploid apple, *Malus hupehensis.* Jour. Arnold Arb. **17:** 90–105. *pls. 179–181.* 1936.

EINSET, J. The occurrence of a tetraploid and two triploid apple seedlings in progenies of diploid parents. Science **99:** 345. 1944.

———. Spontaneous polyploidy in cultivated apples. Proc. Am. Soc. Hort. Sci. **59:** 291–302. 1952.

ESAU, K. Vascular differentiation in the pear root. Hilgardia **15:** 299–324. 1943.

ESELTINE, G. P. VAN. Notes on the species of apples. 1. The American crabapples. N. Y. State Agr. Exper. Sta. Tech. Bull. **208.** 1933; * 2. The Japanese flowering crabapples of the *Sieboldii* group and their hybrids. *Ibid.* **214.** 1933.*

EVERT, R. F. Phloem structure in *Pyrus communis* L. and its seasonal changes. Univ. Calif. Publ. Bot. **32:** 127–193. 1960.

———. Ontogeny and structure of the secondary phloem in *Pyrus Malus*. Am. Jour. Bot. **50:** 8–37. 1963.

———. The cambium and seasonal development of the phloem in *Pyrus Malus*. *Ibid.* 149–159.

FERNALD, M. L. Minor transfers in *Pyrus*. Rhodora **49:** 229–233. 1947. [Includes discussion of *Pyrus*, *Malus*, *Sorbus*, and *Aronia* and why they should be treated as congeneric.]

FLEMION, F. After-ripening, germination, and vitality of seeds of *Sorbus aucuparia* L. Contr. Boyce Thompson Inst. **3:** 413–439. 1931.

FRANCO, J. DO AMARAL, & M. L. DE ROCHA AFONSO. Das Pereiras Bravas Portuguesas. Revista Fac. Ci. Univ. Lisboa II. C. **13:** 175–213. 1965. [English summary; includes discussion on nomenclature of *Pyrus communis*.]

FULFORD, R. M. The morphogenesis of apple buds. I. The activity of the apical meristem. Ann. Bot. II. **29:** 167–180. *2 pls.* 1965; II. The development of the bud. *Ibid.* **30:** 25–38. 1966; III. The inception of flowers. *Ibid.* 207–219; IV. The effect of fruit. *Ibid.* 596–606.

FULLING, E. H. *Malus platycarpa Hoopesii*. Addisonia **16:** 21, 22. *pl. 523.* 1931.

GABRIELIAN, E. The genus *Sorbus* L. in Turkey. Notes Bot. Gard. Edinburgh **23:** 483–496. 1961. [Includes references to Russian and eastern European literature; also cf. Izv. Akad. Nauk. Armian. SSR Biol. **15**(3): 61–71. 1962.]

GLADKOVA, V. N. A cytological investigation of *Sorbocotoneaster* Pojark. (Maloideae), a hybridogenous genus of spontaneous origin. (In Russian.) Bot. Zhur. **52:** 981–983. 1967.

GOLLMICK, F. Beobachtungen an *Malus*-Artbastarden. I. (English summary.) Arch. Gartenb. **6**(5): 359–382. 1958.*

GRACZA, P. Some observations on pistil organization of *Pyrus communis* L. (In Hungarian; English summary.) Bot. Közlem. **57:** 175–182. 1970.

GRIGGS, W. H., & B. T. IWAKIRI. Pollination and parthenocarpy in the production of Bartlett pears in California. Hilgardia **22:** 643–678. 1954.

HARDIN, J. W. The enigmatic chokeberries (*Aronia*, Rosaceae). Bull. Torrey Bot. Club **100:** 178–184. 1973. [Two spp. recognized; *A. prunifolia* probably facultatively apogamous and of hybrid origin.]

HARTMAN, H. Hybrids between *Pyrus Malus* and *Pyrus fusca*. Jour. Hered. **20:** 378–380. 1929. [Both artificial and natural hybrids reported.]

HASKELL, G. The stamen constancy of diploid and polyploid pears. New Phytol. **53:** 349–353. 1954.

HEDLUND, T. Monographie der Gattung *Sorbus*. Bihang Sv. Vet.-akad. Handl. Afd. 3. **35**(1): 1–147. 1901. [The basic taxonomic treatment in subg. *Sorbus*.]

———. Concerning the rise of new biotypes within the genus *Sorbus*. (In Swedish; English summary.) Bot. Not. **101:** 381–392. 1948.

HEDRICK, V. P. The pears of New York. Rep. N. Y. Agr. Exper. Sta. 1921. II. xi + 636 pp. *80 unnumbered col. pls., chart., frontisp.* 1921.

HENKE, O. Phytochemisch-systematische Untersuchung über die Flavonoide der Gattung *Malus*. Flora **153:** 358–372. 1963. [65 spp., cultivars, and hybrids examined.]

HENNING, W. Morphologisch-systematische und genetische Untersuchungen an Arten und Artbastarden der Gattung *Malus*. Züchter **17/18:** 289–349. 1947. [The author's doctoral dissertation, published posthumously by M. Schmidt.]

Hensen, K. J. W. Het *Pyrus*-Sortiment. Meded. Bot. Tuinen Belmonte Arb. **6:** 17–24. 1962. [Reprinted in Belmontia IV. **1962**(6): No. 14. 1962.]

Hjelmqvist, H. On the embryology of two *Malus* hybrids. Bot. Not. **112:** 453-464. 1959. [*M.* × *Sieboldii* hybrids; see also *ibid.* **110:** 455–467. 1957.]

Hooker, W. J. *Pyrus arbutifolia.* Arbutus-leaved *Aronia.* Bot. Mag. **65:** *pl. 3668.* 1838.

Hortleder, A. Some anatomical features *of Sorbopyrus auricularis.* Trans. Kansas Acad. Sci. **33:** 29, 30. 1930.

Huckins, C. A. Flower and fruit keys to the ornamental crabapples cultivated in the United States (Malus–Rosaceae). Baileya **15:** 129–164. 1968.

———. A revision of the sections of the genus *Malus* Miller. Ph.D. Thesis. Cornell Univ. 410 pp. 1972.* [Cf. Diss. Abstr. **33:** 1031B, 1032B. 1972.]

Jefferson, R. M. History, progeny, and locations of crabapples of documented authentic origin. Natl. Arb. Contr. **2.** iv + 107 pp. 1970.

Jones, G. N. A synopsis of the North American species of *Sorbus.* Jour. Arnold Arb. **20:** 1–43. *pls. 226, 227.* 1939.

———. Nomenclature of American mountain-ash. Rhodora **55:** 358–360. 1953. [The correct citation under *Sorbus* is *S. americana* Marshall.]

Kárpáti, Z. Die *Sorbus*-Arten Ungarns und der angrenzenden Gebiete. Repert. Sp. Nov. **62:** 71–331. 1960.

———. Die pflanzengeographischen Beziehungen der Entstehung der *Sorbus*-Arten. (In Russian; German summary.) Kert. Szölész. Föisk. Közlem. **28**(2): 31–46. 1964.*

———. Geobotanische Betrachtung zur Taxonomie der europäischen *Sorbus*-Arten. Drudea **5**(1): 67–74. 1966?*

Koidzumi, G. A synopsis of the genus *Malus.* Acta Phytotax. Geobot. **3:** 179–196. 1934. [36 spp. recognized.]

Kovanda, M. Flower and fruit morphology of *Sorbus* in correlation to the taxonomy of the genus. Preslia **33:** 1–16. 1961. [Includes synopsis of the 5 recognized subgenera of *Sorbus.*]

———. Spontaneous hybrids of *Sorbus* in Czechoslovakia. Acta Univ. Carol. Biol. **1961:** 41–83. 1961.

———. Taxonomical studies in *Sorbus* subg. *Aria.* Acta Dendrol. Čechoslov. **3:** 23–70. *2 maps.* 1961 [1962]. [About 35 spp. in 5 series.]

Laughlin, K. *Malus lancifolia* Rehder. Phytologia **9:** 108–112. 1963.

Lee, S. H. A taxonomic survey of the oriental pears. Proc. Am. Soc. Hort. Sci. **51:** 152–156. 1948. [8 spp. recognized.]

Likhonos, F. D. Some data on systematics of the genus *Malus* Mill. (In Russian; English summary.) Bull. Appl. Bot. Genet. Pl. Breed. **36**(3): 5–16. 1964.*

Liljefors, A. Studies on propagation, embryology, and pollination in *Sorbus.* Acta Horti Berg. **16:** 277–329. 1953.

———. Cytological studies in *Sorbus. Ibid.* **17:** 47–113. 1955. [Discusses the role of apogamy in Scandinavian spp.; extensive references.]

Lincoln, F. B., & L. P. McCann. Polyploidy in native species of *Malus.* Proc. Am. Soc. Hort. Sci. **34:** 26. 1937.

MacDaniels, L. H. The morphology of the apple and other pome fruits. Mem. Cornell Agr. Exper. Sta. **230.** 1940.* [Appendicular theory of pome.]

McVaugh, R. The status of certain anomalous native crabapples in eastern United States. Bull. Torrey Bot. Club **70:** 418–429. 1943. [*P. platycarpa* is a hybrid of the cultivated apple and native crabs.]

NASH, G. V. *Malus ioensis plena.* Addisonia **6:** 31. *pl. 208.* 1921.

OLDÉN, E. J. Sexual and apomictic seed formation in *Malus Sieboldii* Rehd. Bot. Not. **106:** 105–128. 1953.

POJARKOVA, A. × *Sorbocotoneaster* Pojark. — Hybrida intergenerica nova naturalis. (In Russian). Not. Syst. Leningrad **14:** 90–108. 1953.

REHDER, A. *Malus glaucescens*, Rehd. *In*: C. S. SARGENT, Trees and shrubs **2:** 139, 140. *pl. 157.* 1911; *Malus lancifolia* Rehd. *Ibid.* 141–143. *pl. 158* [includes discussion and new varieties of *M. coronaria* and *M. ioensis*]; *Malus glabrata*, Rehd. *Ibid. 225, 226. pl. 188.* 1913; *Malus platycarpa*, Rehd. *Ibid. 227–232. pl. 189.* [Includes key to spp. of subsect. *Coronariae.*]

RIEDHART, J. M., & A. T. GUARD. On the anatomy of the roots of apple seedlings. Bot. Gaz. **118:** 191–194. 1957.

ROSPER, A. Recherches sur le développement du fruit chez quelques variétés du poirier (*Pirus communis* L.) et du pommier (*Pirus Malus* L.). Thèses Fac. Sci. Univ. Paris. 96 pp. + *54 figs.* 1957.

RUBTSOV, G. A. Geographical distribution of the genus *Pyrus* and trends and factors in its evolution. Am. Nat. **78:** 358–366. 1944.

RYBIN, V. A. Cytological investigations of the genus *Malus* (preliminary account). (Russian with English summary.) Bull. Appl. Bot. Genet. Pl. Breed. **16**(3): 187–200. 1926.

SARGENT, C. S. *Pyrus arbutifolia.* Garden Forest **3:** 416, 417. 1890.

SAX, H. J., & K. SAX. The cytogenetics of generic hybrids of *Sorbus.* Jour. Arnold Arb. **28:** 137–140. *pl. 1.* 1947.

SAX, K. Chromosome behavior in *Sorbopyrus* and *Sorbaronia.* Proc. Natl. Acad. Sci. U.S.A. **15:** 844, 845. 1929.

———. The cytogenetics of facultative apomixis in *Malus* species. Jour. Arnold Arb. **40:** 289–297. 1959.

SIMS, J. *Pyrus coronaria.* Sweet-scented crab-tree. Bot. Mag. **45:** *pl. 2009.* 1818.

SKIBINSKAIA, A. M. Historical geography of the genus *Malus.* (In Russian.) Biull. Glavn. Bot. Sada Moskva **61:** 52–59. 1966.

SMITH, W. W. The course of stone cell formation in pear fruits. Pl. Physiol. **10:** 587–611. 1935. [Chemical changes that occur in maturing and stored fruits.]

STAPF, O. *Aronia melanocarpa.* Bot. Mag. **150:** *pl. 9052.* 1925.

STARITSKY, G. The morphogenesis of the inflorescence, flower and fruit of *Pyrus nivalis* Jacquin var. *orientalis* Terpó. (Dutch summary.) Meded. Landb. Wageningen **70**(5): [iv] + 91 pp. 1970.

TERPÓ, A. Magya rország vadkörtéi (*Pyri* Hungariae). (In Hungarian; Russian and German summaries.) Kert Szöléz. Föisk. Évk. **22**(2): 1–258. 1960. [Contains much information; many varieties and forms recognized; brief summary in Excerpta Bot. A. **3:** 510, 511. 1961; see also Ann. Hort. Viticult. **27:** 245–271. 1963.]

TRABUT, L. *Pyronia.* Jour. Hered. **7:** 416–419. 1916. [*Pyrus* × *Cydonia.*]

TUKEY, H. B., & J. O. YOUNG. Gross morphology and histology of developing fruit of the apple. Bot. Gaz. **104:** 3–25. 1942.

VISSER, T. After-ripening and germination of apple seeds in relation to the seed coats. Proc. Nederl. Akad. Wet. C. **57:** 175–185. 1954.

———. The role of seed coats and temperature in after-ripening, germination and respiration of apple seeds. *Ibid.* **59:** 211–222. 1956.

———. Some observations on respiration and secondary dormancy in apple seeds. *Ibid.* 314–324.

———. The growth of apple seedlings as affected by after-ripening, seed maturity and light. *Ibid.* 325–334. *2 pls.*

WELKERLING DE TACCHINI, E. M. L. Descripción de los cultivares de peral (*P. communis*) de la colección pomológica de la Estación Experimental Agropecuaria Mendoza. Colec. Agropecu. I. N. T. A. **15.** v + 641 pp. 1967.

WESTWOOD, M. N., & H. I. BJORNSTAD. Some fruit characteristics of interspecific hybrids and extent of self-sterility in *Pyrus*. Bull. Torrey Bot. Club **98:** 22–24. 1971.

WIŚNIEWSKA, J., B. MACHNIK, & O. KUCEWICZ. The structure of the *Sorbopirus* fruit — natural *Sorbus* and *Pirus* hybrid. (In Polish; English summary.) Prace Inst. Sadow. **14:** 183–190. *pls. 1–4.* 1970. [Parents of hybrid possibly *P. communis* and *S. Aria.*]

WOODCOCK, E. F., & E. C. TULLIS. Extra-floral nectar glands of *Malus Malus* and *Pyrus communis*. Pap. Mich. Acad. Sci. Arts Lett. I. **8:** 239–243. *pl. 19.* 1928.

YÜ, T. T., & C. L. YEN. Study on the Chinese species of genus *Malus* Miller. (In Chinese; English summary.) Acta Phytotax. Sinica **5:** 77–110. *pls. 8–21.* 1956. [20 spp. in 3 sects. and 5 subsects.]

ZIELINSKI, Q. B. Self-incompatibility of *Pyrus* species. Bull. Torrey Bot. Club **92:** 219, 220. 1965.

——— & M. M. THOMPSON. Pollen germination in *Pyrus* species and species hybrids. Euphytica **15:** 195–198. 1966. [39 spp. and cultivars.]

——— & ———. Speciation in *Pyrus*: chromosome number and meiotic behavior. Bot. Gaz. **128:** 109–112. 1967. [28 spp. and 10 cultivars.]

Subfam. AMYGDALOIDEAE Torrey & Gray, "Subordo" (Subfam. Prunoideae Focke)

Four genera, *Prunus* L., sensu lato, *Maddenia* Hooker f. & Thomson (five spp. in China and the Himalaya), *Osmaronia* Greene (*O. cerasiformis* (Torrey & Gray) Greene, western North America), and *Prinsepia* Royle (four spp., eastern Asia). Members of this subfamily are trees or shrubs with simple leaves, carpels inserted at the base of, but free from the floral cup, drupaceous, 1-seeded fruits, and a base chromosome number of eight. *Osmaronia*, because of its flowers with usually five carpels and seeds with folded cotyledons, is sometimes separated as tribe Osmaronieae Rydb. The taxonomic position of *Prinsepia* (style lateral or subbasal; ovules erect, the micropyle inferior) is debatable; Sterling proposed tribe Prinsepieae ("Prinsepioideae") to include it.

SUBFAMILY REFERENCES:

BARANOV, A. Taxonomic studies in the genus *Prinsepia* (Rosaceae). Taiwania **11:** 99–112. 1965. [Revision.]

STERLING, C. The affinities of *Prinsepia* (Rosaceae). Am. Jour. Bot. **50:** 693–699. 1963.

22. **Prunus** Linnaeus, Sp. Pl. 1: 473. 1753; Gen. Pl. ed. 5. 213. 1754.

Deciduous or evergreen trees or shrubs, sometimes producing root sprouts; bark, twigs, and leaves with smell and taste of bitter almond due to presence of cyanogenic glycosides; bark initially reddish-brown, thin, smooth, easily peeled off in layers, remaining that way or breaking into scaly plates, the lenticels pale, usually elongating transversely; branches sometimes spinescent; buds solitary or 3, terminal one present or absent, the bud scales several, imbricate, the inner ones colored, accrescent. Leaves simple, often glossy above, convolute or conduplicate in bud, petiolate, the margins usually serrate, sometimes entire or spine-toothed; prominent, variously sized and shaped glands usually occurring on petioles or at base of leaf blades; stipules paired, free from the petiole, small, early deciduous; leaf scars elevated, with 3 vascular traces. Flowers 5-merous, mostly perfect, in racemes terminating shoots of the season, in racemes from axils of leaves of the previous season, in corymbs or umbels from branchlets of the previous season (appearing before or with the leaves), or solitary and sessile or stalked. Calyx ebracteolate, the lobes triangular, imbricate in bud; floral tube campanulate, tubular, urceolate, or cup shaped, usually circumscissile deciduous; disc lining the floral tube, thin, often colored. Petals white to pink, spreading, quickly falling, orbicular to elliptic, the margins entire or erose, the bases short clawed, inserted at the outer edge of the floral tube [petals indistinguishable from calyx lobes in some species of subg. LAUROCERASUS]. Stamens usually 15–20 (10–80) in two or more whorls and in multiples of 5, perigynous at the outer edge of the floral tube; filaments filiform, exserted, the inner shorter than the outer; anthers small, dorsifixed. Gynoecium of one carpel inserted at the base of, but free from, the floral tube; ovary glabrous to densely pubescent; style terminal, elongated; stigma capitate, discoid, or emarginate; ovules 2, pendulous, the micropyle superior. Fruit a 1-seeded drupe, sometimes sulcate and/or glaucous, the mesocarp fleshy and indehiscent to dryish and dehiscent, usually edible, the endocarp hard, indehiscent, nearly globose or compressed, smooth or textured; seed filling stone, the coat membranaceous, the radicle superior. Base chromosome number 8. (Including *Amygdalus* L., *Armeniaca* Duh., *Cerasus* Mill., *Laurocerasus* Duh., *Padus* Mill., *Persica* Duh., and *Pygeum* Gaertn.) LECTOTYPE SPECIES: *P. domestica* L., see Britton, N. Am. Trees, 480. 1908. (The ancient Latin name of the Plum.) — PLUM, CHERRY, PEACH.

Maybe 200 species mostly of the North Temperate region, particularly abundant in North America, eastern Asia, western Asia, and southern Europe. Unlike most Rosaceae, *Prunus* is well represented in the subtropics and tropics, and the distribution of the genus extends southward in the Old World through Malesia to northern Queensland and in the New World through Central America to Chile and Brazil. The species fall into several reasonably distinct groups that are often treated as genera. However, when studied on a world-wide basis, the morphological discontinuities between the groups decrease, and it becomes more logical to recognize only one inclusive genus with several subgenera (see discussions in McVaugh and Kalkman).

Several systems of subgeneric classifications have been proposed (see enumeration in McVaugh), and there is no general agreement as to how many subgenera or sections should be recognized, how these should be delimited, or what species to include in each. The genus was studied extensively by Koehne, but his classification schemes do not seem to reflect natural relationships well. The basic system proposed by Rehder, in which five subgenera and twelve sections are recognized, is perhaps the one most widely used today. About thirteen species representing four subgenera are indigenous to the southeastern United States; a number of exotic species are cultivated, and some of these persist or escape.

Subgenus PADUS (Miller) Focke (leaves deciduous, conduplicate in bud; inflorescences many-flowered racemes terminating leafy shoots of the current year) includes about 20 species mostly of Eurasia, especially China and Japan, with two species in the Americas. *Prunus serotina* Ehrh., $2n = 32$, black cherry, is a variable species that occurs from Florida to Arizona, Mexico, and Guatemala northward to Nova Scotia, New Brunswick, southern Quebec, southern Ontario, Minnesota, and North Dakota; it has escaped from cultivation in Central and South America and in Europe. This species has been reviewed by McVaugh, who recognizes five subspecies, two of which occur in our area: subsp. *serotina* (eastern North America west to Lake Superior, the Dakotas, and eastern Texas; disjunct in Mexico and Guatemala) and subsp. *hirsuta* (Ell.) McVaugh (Alabama and Georgia; including *P. alabamensis* Mohr, *P. Cuthbertii* Small, and perhaps *P. australis* Beadle). Subspecies *eximia* (Small) McVaugh occurs on the Edwards Plateau and the Belcones Escarpment of Texas; subsp. *virens* (Wooton & Standley) McVaugh ranges from Trans-Pecos Texas to Arizona, south to Baja California and Mexico; and subsp. *Capuli* (Cav.) McVaugh, capulín, is from the highlands of southern Mexico and Guatemala (introduced farther south). The wood of *Prunus serotina* is pale reddish-brown (sapwood yellow), close-grained, light, fairly hard and strong, and has working qualities that make it one of the finest cabinet woods of temperate North America, second only to black walnut (*Juglans nigra*).

Prunus virginiana L., $2n = 32$, choke cherry, occurs from Newfoundland to Saskatchewan south to North Carolina, Tennessee, Missouri, Kansas, Oklahoma, and Texas; also in the West from the Dakotas to New Mexico and west to California and British Columbia. Three varieties can be recognized (see Hitchcock *et al.*, family references); plants in eastern North America belong to var. *virginiana*. *Prunus serotina* and *P. virginiana* are quite similar in many ways; closer examination shows numerous differences, and they have been placed in different sections. Plants of *P. serotina* can be large trees 30 m. tall with trunks 2 m. in diameter (most large ones now logged), the bark is aromatic, the leaves are narrow, tapering ovate, shiny above, and crenate-serrate with callous teeth, the calyx lobes are acute, and the floral cups persist below the nearly black drupes. *Prunus virginiana* is a shrub or small tree with nonaromatic bark, leaves that are obovate or broadly elliptic, dull above, and sharply serrate, obtuse calyx lobes, circumscissile dehiscent floral cups, and deep red or purple fruits. *Prunus Padus* L., European bird cherry, with larger flowers, adaxially pubescent floral cups, and strongly sculptured stones, is cultivated in our area, but it is not known to be naturalized.

Subgenus LAUROCERASUS (Duhamel) Rehder (plant evergreen, leaves often entire; racemes usually solitary in axils of leaves of the previous year, the peduncles leafless) is composed of about 75 species mostly of tropical Asia and tropical America with a few species in southern Europe and southern North America; two species occur in our area. Kalkman recently reviewed the Asiatic members, noting that all American species could be placed in one distinct, unnamed section. *Prunus caroliniana* (Miller) Aiton, $2n = 32$, Carolina cherry laurel, is found on the outer Coastal Plain from southern North Carolina to midpeninsular Florida westward to eastern Texas (reported from Bermuda by Sargent). Plants are evidently rare in nature, but the species is commonly cultivated in the southern United States as a specimen tree or trimmed to a hedge. *Prunus myrtifolia* (L.) Urban (*P. sphaerocarpa* Sw.), West Indian cherry, is found in pinelands and hammocks in southern Florida; it is widely distributed in tropical America, ranging from Florida and the Bahama Islands to the Greater Antilles, Montserrat, Trinidad and Tobago, and Mexico to Brazil. Both *P. caroliniana* and *P. myrtifolia* can have functionally staminate flowers at the base of the racemes. Two species of this subgenus are cultivated in our area, *P. Laurocerasus* L., $2n = 144$, 170–180, cherry laurel, and *P. lusitanica* L., $2n = 64$, Portugal laurel. Native to California and Baja California are *P. ilicifolia* (Nutt. ex Hooker & Arn.) Walp. and *P. Lyonii* (Eastw.) Sargent.

Subgenus CERASUS (Miller) Focke (flowers solitary or in few-flowered corymbs often on short, lateral shoots; fruits not sulcate, glaucous, or pubescent, the stone globose or ovoid, mostly smoothish), cherries, includes numerous species of temperate Eurasia and North America; Rehder recognized seven sections. Two species occur indigenously in the southeastern United States, and several others are cultivated, sometimes becoming naturalized. *Prunus pumila* L., (including *P. cuneata* Raf., *P. susquehanae* Willd., and *P. Besseyi* Bailey) $2n = 16$, sand cherry, is a variable species that occurs mostly in sandy or rocky situations from New Brunswick to Manitoba and North Dakota southward to Delaware, North Carolina, Indiana, Wisconsin, Kansas, Colorado, and Wyoming; it has recently been reported from Arkansas (Gary Tucker, Arkansas Polytechnic College, personal communication). *Prunus pensylvanica* L. f., $2n = 16$, bird-, pin-, or fire-cherry, occurs from Labrador to British Columbia south to Virginia, the mountains of North Carolina and Tennessee, Illinois, Iowa, South Dakota, Colorado, and Montana; this is a pioneer species in recently burned or cleared areas. Reportedly escaped from cultivation in our area are *P. Avium* L., $2n = 16$, sweet cherry (the commonly sold 'Bing' cherry is a cultivar of this species), *P. Cerasus* L., $2n = 32$, sour cherry, and *P. Mahaleb* L., $2n = 16$, Mahaleb or perfumed cherry, all of southern Europe and western Asia.

Subgenus PRUNUS [*Prunophora* Focke] (flowers solitary or in few-

FIGURE 11. **Prunus** subg. **Padus** (a–i), subg. **Cerasus** (j–l), and subg. **Laurocerasus** (m). a, *P. virginiana*: flowering branch with racemes terminating leafy branchlets of current year, × 1/4. b–i, *P. serotina*: b, fruiting branch, × 1/2; c, tip of raceme, × 3; d, vertical section of flower (petals removed) to show perigynous insertion of calyx lobes and stamens, carpel solitary, 2-ovulate, × 10; e, vertical section of ovary at right angles to that in "d" to show pendulous ovule, micropyle superior, × 20; f, stone from drupe, × 3; g, cross section of stone, wall hatched, cotyledons unshaded (seed coat too thin to show), × 3; h, seed removed from stone, × 3; i, embryo, oriented as in seed in "h," × 3. j–l, *P. pensylvanica*: j, tip of branch with corymbose inflorescences, × 1/2; k, tip of short shoot showing leaf bases with glands and stipules, × 3; l, flower, × 3. m, *P. caroliniana*: spinulose-serrate leaf form, × 1/2.

flowered umbels from axillary buds on growth of previous years; fruit sulcate, glaucous or pubescent, the stone compressed) includes about 30 species of Eurasia and North America. The wild plums of North America constitute a distinct section, sect. PRUNOCERASUS Koehne (flowers usually three or more, fruit not pubescent, stones smoothish); seven of the fourteen species occur in the southeastern United States. *Prunus americana* Marsh., $2n = 16$, wild plum, occurs from northern Florida west at least to Arkansas, northward to New England, southern Ontario, Wisconsin, and Manitoba. Plants from the southern part of the range westward to Texas and northern Mexico have the leaves pubescent below to varying degrees, the plants evidently do not often produce root suckers, and the fruit is bluish to purple-red; these plants perhaps are best placed in *P. mexicana* S. Watson (including *P. lanata* auct., not Sudw., *P. americana* var. *lanata* auct., *P. arkansana* Sarg., *P. Palmeri* Sarg., *P. reticulata* Sarg., and *P. tenuifolia* Sarg.), big-tree plum, Mexican plum. These two species need to be studied in detail to ascertain their distinctiveness and distribution (see Correll & Johnston, Man. Vasc. Pl. Texas; Steyermark, Fl. Missouri; Shinners). *Prunus angustifolia* Marsh., $2n = 16$, chickasaw plum, ranges from central Florida to Texas, northward to Maryland, Delaware, and Arkansas; *P. geniculata* Harper, from central Florida, is probably a depauperate form of this species.

The other species of sect. PRUNOCERASUS in our area are *Prunus gracilis* Engelm. & Gray, Oklahoma plum (Arkansas, Oklahoma, and Texas); *P. hortulana* Bailey, $2n = 16$, wild goose plum (southern Indiana to Iowa southward to western Tennessee, northern Alabama, Missouri, Arkansas, and Oklahoma); *P. Munsoniana* Wight & Hedrick, $2n = 16$, wild goose plum (Ohio, Kentucky, and Tennessee to Louisiana, Kansas, Oklahoma, and Texas); and *P. umbellata* Ell. (including *P. injuncta* Small, *P. mitis* Beadle, and *P. tarda* Sarg.), hog or flatwood plum, black sloe (southern North Carolina, South Carolina, Georgia, Florida, Alabama, Mississippi, and southern Arkansas). Numerous varieties of plums have been derived in recent years from the native American species, although it is difficult to judge how important these are commercially.

Old World species cultivated in the southeastern United States include *Prunus domestica* L., $2n = 48$, plum, *P. insititia* L., $2n = 48$, bullace, damson plum, *P. cerasifera* Ehrh, $2n = 16$, cherry plum, *P. spinosa* L., $2n = 32$, sloe, all of subg. PRUNUS sect. PRUNUS; *P. Armeniaca* L., apricot, $2n = 16$, of subg. PRUNUS sect. ARMENIACA (Lam.) W. D. J. Koch; and *P. Amygdalus* Batsch, $2n = 16$, almond and *P. Persica* (L.) Batsch, $2n = 16$, peach, nectarine. Only the last species is known to be naturalized in our area.

REFERENCES:

Under family references see BATE-SMITH, BEAN, BOUTINEAU, BUNTING, CROCKER & BARTON, DEVADAS & BECK, DIPPEL, FREE, HEGI, HESS *et al.*, HILTON *et al.*, REHDER, ROBERTSON, ROEMER & RUDORF, ROSS-CRAIG, SARGENT, SCHNEIDER, STEPHENS, STERLING (I), L. A. TAYLOR, and VINES.

ANDERSON, E., & O. AMES. Botanizing from an airplane. Bull. Pop. Inf. Arnold Arb. III. **6**: 37–44. 1932. [Charting distribution of *P. maritima* along New England coast.]

AUCLAIR, A. N., & G. COTTAM. Dynamics of black cherry (*Prunus serotina* Erhr. [sic.]) in southern Wisconsin oak forests. Ecol. Monogr. **41**: 153–177. 1971.

BAKKER, J. The historical development of *Prunus serotina* Ehrh. in the Netherlands. Nederl. Boschbouw-Tijdschr. **35**: 201–206. 1963.*

BEAN, W. J. *Prunus pennsylvanica*. Bot. Mag. **139**: *pl. 8486*. 1913.

BROOKS, R. M. Comparative histogenesis of vegetative and floral apices in *Amygdalus communis*, with special reference to the carpel. Hilgardia **13**: 249–299. *pls. 1–4*. 1940.

BROWICZ, K. Distribution of woody Rosaceae in W. Asia. I. *Cerasus microcarpa* (C. A. Mey.) Boiss. — Intraspecific division and geographical distribution. Arb. Kórnickie **13**: 5–25. 1968. IV. Almonds from the section *Spartioides* Spach. *Ibid.* **14**: 24–37. 1969. V. *Laurocerasus officinalis* Roem. *Ibid.* **15**: 5–15. 1970.

BUCHANAN, R. E. A contribution to our knowledge of the development of *Prunus americana*. Proc. Iowa Acad. Sci. **11**: 77–93. *pls. 6–8*. 1904.

BYKOVA, N. B. Anatomical structure of the leaf in certain species of *Amygdalus* L. (In Russian; English summary.) Bot. Zhur. **54**: 1717–1726. 1969.

DARLINGTON, C. D. Studies in *Prunus*, I and II. Jour. Genet. **19**: 213–256. *pls. 11–18*. 1928. III. *Ibid.* **22**: 65–93. 1930. IV. *Ibid.* **28**: 327, 328. 1933.

DEFLER, S. E. Black cherry; characteristics, germination, growth and yield. M.S. Thesis. New York State College Forestry. Syracuse. 129 pp. 1937.*

DERMEN, H. Periclinal cytochimeras and origin of tissues in stem and leaf of peach. Am. Jour. Bot. **40**: 154–168. 1953.

DORSEY, M. J., & F. WEISS. Petiolar glands in the plum. Bot. Gaz. **69**: 391–406. *pls. 20, 21*. 1920.

DUNCAN, W. H. Preliminary reports on the flora of Georgia. 2. Distribution of 87 trees. Am. Midl. Nat. **43**: 742–761. 1950. [*P. caroliniana, P. serotina*; distribution maps.]

FERNALD, M. L. *Prunus virginiana* the correct name of the choke cherry. Rhodora **18**: 140, 141. 1916.

———. The identities of the sand cherries of eastern America. *Ibid.* **25**: 69–74. 1923.

FLORY, W. S., JR. Crossing relationships among hybrid and specific plum varieties, and among the several *Prunus* species which are involved. Am. Jour. Bot. **34**: 330–335. 1947.

FOX, W. S., & J. H. SOPER. The distribution of some trees and shrubs of the Carolinian Zone of southern Ontario. II. Trans. Roy. Canad. Inst. **30**: 3–32. 1953. [*P. serotina*, 19–22.]

GUINIER, E. Le cerisier de Virginie (*Prunus virginiana* L., *Cerasus virginiana* DC.) et le cerisier tardif (*Prunus serotina* Ehrh., *Cerasus serotina* DC.). Bull. Soc. Bot. France **49**: 20–23. 1902.

HARPER, R. M. A new plum from the lake region of Florida. Torreya **11**: 64–67. 1911. [*P. geniculata* = *P. angustifolia*.]

———. An overlooked environmental factor for species of *Prunus*. Rhodora **18**: 201–203. 1916. [Species of *Prunus* not often found in habitats subject to frequent fires.]

HASEGAWA, M. Flavonoids of various *Prunus* species. VI. The flavonoids in the wood of *Prunus aequinoctalis*, *P. nipponica*, *P. Maximowiczii*, and *P. Avium*. Jour. Am. Chem. Soc. **79**: 1738–1740. 1957.

——— & T. SHIRATO. Flavonoids of various *Prunus* species. I. The flavonoids in the wood of *Prunus yedoensis*. *Ibid.* **74**: 6114, 6115. 1952. II. The flavonoids of *Prunus speciosa*. *Ibid.* **76**: 5559, 5560. 1954. III. The flavonoids in the wood of *Prunus campanulata*. *Ibid.* 5560, 5561. IV. The flavonoids in the wood of *Prunus donarium* var. *spontanea*. *Ibid.* **77**: 3557, 3558. 1955. V. The flavonoids in the wood of *Prunus verecunda*. *Ibid.* **79**: 450–452. 1957.

HASKELL, G. Stamen number and variation in diploid and tetraploid cherries. Ann. Bot. II. **18**: 95–111. 1954.

——— & P. DOW. The stamen patterns of cultivated plums. *Ibid.* **19**: 467–484. 1955.

HILTON, R. J., A. S. JASWAL, B. J. E. TESKEY, & B. BARABAS. Rest period studies on seeds of *Amelanchier*, *Prunus*, and *Sorbus*. Canad. Jour. Pl. Sci. **45**: 79–85. 1965.

HRUBÝ, K. Chromosome behavior and phylogeny of cultivated *Cerasus*. Preslia **34**: 85–97. 1962.

HRYNKIEWICZ-SUDNIK, J. *Cerasus Avium* (L.) Moench. Its geographical distribution, geological characteristics and studies on variability. (In Polish; English summary, 115–123.) Prace Bot. **13**: 1–172. 1972.

KALKMAN, C. The Old World species of *Prunus* subg. *Laurocerasus* including those formerly referred to *Pygeum*. Blumea **13**: 1–115. 1965. [Detailed morphological description of group; American species of subgenus referred to new, unnamed section.]

KÁRPÁTI, Z. E. Taxonomische Betrachtungen am genus *Prunus*. Feddes Repert. **75**: 47–53. 1967.

KOEHNE, E. Die Gliederung von *Prunus* subg. *Padus*. Verh. Bot. Ver. Brandenb. **52**: 101–108. 1911.

———. *Prunus*. Pp. 59–75, 196–282. *In*: C. S. SARGENT, Pl. Wilson. Vol. 1. Publ. Arnold Arb. 4. 1911. [Key to Chinese species and general summary and list of all known species.]

———. Zur Kenntnis von *Prunus* Grex *Calycopadus* und Grex *Gymnopadus* Sect. *Laurocerasus*. Bot. Jahrb. **52** 279–333. 1915.

LEDBETTER, M. C. Anatomical and morphological comparisons of normal and physiologically dwarfed seedlings of *Rhodotypos tetrapetala* and *Prunus persica*. Contr. Boyce Thompson Inst. **20**: 437–458. 1960.

LITTLE, E. L., JR. Five varietal transfers of United States trees. Phytologia **4**: 305–310. 1953. [Varieties of *Prunus serotina*, 309, 310; nomenclature differs from that of McVaugh.]

LONG, B. Naturalized occurrence of *Prunus Padus* in America. Rhodora **25**: 169–177. 1923.

MCVAUGH, R. A revision of the North American black cherries (*Prunus serotina* Ehrh., and relatives). Brittonia **7**: 279–315. 1951. [Includes history of classification of genus.]

———. Suggested phylogeny of *Prunus serotina* and other wide-ranging phylads in North America. *Ibid.* **7**: 317–346. 1952.

MEROLA, A. Ricerche sull'andromonoicisma di *Prunus caroliniana* Ait. (English summary.) Delpinoa **8**: 109–154. *pls. 1–4*. 1955.

MIRANDA, F., & A. J. SHARP. Characteristics of the vegetation in certain temperate regions of eastern Mexico. Ecology **31**: 313–333. 1950.

OLDÉN, E. J., & N. NYBOM. On the origin of *Prunus Cerasus* L. Hereditas **59**: 327–345. 1968. [Derived from hybrid between *P. Avium* and *P. fruticosa*.]

PELLEGRINI, O. Affinità sistematiche fra Pruneae e Leguminosae dimostrate dai tessuti omologhi dei pericarpi. (English summary.) Delpinoa **5**: 7–48. 1952.

PENNYPACKER, J. Y. Observations on the beach plum, a study in plant variation. Contr. Bot. Lab. Univ. Penn. **4**: 231–269. *pls. 66–70.* 1919.

POPENOE, W., & A. PACHANO. The capulín cherry, a superior form of the northern black cherry developed in the highlands of tropical America. Jour. Hered. **13**: 51–62. *frontisp.* 1922.

SCHNELL, R., & G. CUSSET. Glandularisation et foliarisation. Bull. Jard. Brux. **33**: 525–530. 1963.

———, ———, & M. QUENUM. Contribution a l'étude des glandes extra-florales chez quelques groupes de plantes tropicales. Revue Gén. Bot. **70**: 269–341. 1963. [Rosacées, 302, 303.]

SHINNERS, L. H. *Prunus americana* var. *lanata*, a synonym of *P. nigra*. Rhodora **58**: 330, 331. 1956.

STERLING, C. Vascularization of normal and foliate carpels of *Prunus Laurocerasus*. Bot. Gaz. **115**: 196–199. 1954.

TOMLINSON, P. B. Breeding mechanisms in trees native to tropical Florida — a morphological assessment. Jour. Arnold Arb. **55**: 269–290. 1974. [*P. myrtifolia*, 283, *fig. 6.*]

VAUGHAN, J. G. The structure and utilization of oil seeds. xv + 279 pp. London. 1970. [Rosaceae, 212–218.]

WIGHT, W. F. The varieties of plums derived from native American species. U. S. Dep. Agr. Bull. **172**: 1–44. 1915.

———. Native American species of *Prunus*. *Ibid.* **179**: 1–75. *pls. 1–13.* 1915.

WILBUR, R. L. A reconsideration of Bartram's binomials. Jour. Elisha Mitchell Sci. Soc. **87**: 56–73. 1971. [*P. caroliniana*, *P. nemoralis*.]

ADDENDA

These important family references were received after the first part of this paper went to press:

HEGNAUER, R. Chemotaxonomie der Pflanzen. Band. 6. Dicotyledonae: Rafflesiaceae-Zygophyllaceae. 882 pp. *chart.* Basel & Stuttgart. 1973 [Rosaceae, 84–130; Nachträge, 727–730.

ZARDINI, E. M. Los géneros de Rosáceas espontáneos en la República Argentina. Bol. Soc. Argent. Bot. **15**: 209–228. 1973. [Illustrations, key to subfamilies, tribes, and genera.]

ARNOLD ARBORETUM
HARVARD UNIVERSITY
CAMBRIDGE, MASSACHUSETTS 02138

CYTOLOGICAL STUDIES IN ULMACEAE, MORACEAE, AND URTICACEAE

P. N. Mehra and B. S. Gill

The family Urticaceae, which embraces 42 genera and 600 species of herbs, shrubs, and trees (Lawrence, 1951), is not of any great importance to forestry, but Moraceae and Ulmaceae, which include respectively 15 genera with 150 species and 73 genera with over 1000 species (Lawrence, l.c.), produce valuable timbers like *Piratinera guianensis* Aublet, *Distemonanthus benthamianus* Baillon, species of *Morus* L. and *Artocarpus* Forster (Moraceae), and species of *Celtis* L. and *Ulmus* L. (Ulmaceae). In addition, rubber (*Castilloa elastica* Cerv. and *Ficus elastica* Roxb.), paper (*Broussonetia papyrifera* (L.)Vent. and species of *Streblus* Lour.), dye (*Chlorophora tinctoria* D. Don), etc. are commercially valuable products obtained from Moraceae. In India, nine species of Moraceae, four of Ulmaceae, and one of Urticaceae are recognized as commercial timbers (Pearson & Brown, 1932).

For any rational tree breeding program, comprehensive data pertaining to chromosome number, polyploidy, and aneuploidy in the desired genera, in addition to knowledge of meiotic behavior and variability, are essential. Cytological studies were, therefore, undertaken on the members of Ulmaceae, Moraceae, and Urticaceae from the Western Himalayas as a part of the project on the cytological investigations of the Himalayan hardwoods which we have been carrying on for some years.

MATERIAL AND METHODS

Meiotic studies were made from floral buds fixed in Carnoy's fluid and squashed in 1 per cent acetocarmine. Use of glacial acetic acid saturated with iron acetate in the fixative greatly improved the stainability of the chromosomes. For mitotic studies, young leaf tips and root tips were pretreated with 0.003 M solution of 8-hydroxyquinoline for 3 hours at about 20°C, hydrolyzed in acetolacmoid and N:HCl (9:1), and finally squashed in acetolacmoid. Slides were made permanent in Euparal.

Figures were made at a uniform magnification of 1350 ×. The voucher specimens have been deposited in the Herbarium, Department of Botany, Panjab University, Chandigarh, India.

OBSERVATIONS

Cytological studies were carried out on the material collected mostly from wild populations from the Mussoorie, Nainital, and Simla hills in the

TABLE 1. **Chromosome numbers of woody species in the Ulmaceae, Moraceae, and Urticaceae.**

TAXA	LOCALITY (with altitude in meters)	FLOWERING AND FRUITING PERIODS		CHROMOSOME NUMBER	FIGURE NUMBER	PREVIOUS REPORTS
ULMACEAE						
Holoptelea integrifolia Planchon	Nainital: Ranibag, 800;	2–4	4–6	$2n = 28$	4	$2n = 28$: Capoor, 1937.
	Ambala: Kalesar, 300			$n = 14$	5	
**Ulmus wallichiana* Planchon	Nainital, 1950	2–4	5–6	$2n = 28$	6	
Celtis australis L. var. *australis*	Nainital, 1300	2–4	8–10	$2n = 40$	19	$2n = 40$: Bowden, 1945.
**C. australis* L. var. *eriocarpa* Dcne.	Nainital: Garampani, 1300	2–4	8–10	$n = 10$	20	
**C. tetrandra* Roxb.	Nainital: Kherna, 1250	2–3	8–10	$n = 10$	21	
	Kasauli, 1500	2–3	8–10	$n = 10$		
**C. cinnamomea* Lindley	Khasia & Jaintia hills: Shillong, 1500	4–5	7–8	$n = 10$	7	
**Trema politoria* Planchon	Nainital: Jeolikote, 1300	4–8	1–4	$n = 10 + 1_B$		
	Mussoorie: Jhariapani, 1400;			$n = 10 + 1_B$		
	Simla: Guma, 1230			$n = 10 + 1_B$		
MORACEAE						
Artocarpus lakoocha Roxb.	Nainital: Haldwani, 400	4–5	7–8	$n = 28$	8	$2n = 56$: Banerji & Hakim, 1954; Hans, 1972.
A. heterophyllus Lam. (= *A. integrifolia* non L. f.) (= *A integra* (Thunb.) Merr.)	Nainital: Haldwani, 400	1–3		$n = 28$		$n = 28$: Rao, 1940; Nanda, 1962; Hans, 1972. $2n = 56$: Janaki-Ammal (in Darlington & Wylie, 1955); LeCoq, 1963.
Morus alba L.	Chandigarh, 280	2–4	3–5	$n = 14$	22	$2n = 28$: Tahara, 1910; Osawa, 1920; Valtattorni, 1940, 1947; Janaki-Ammal, 1948; Radhzably, 1962. $2n = 42$: Osawa, 1920.
	Dehra Dun, 400	9		$n = 14$	9	
†*M. serrata* Roxb.	Nainital, 1950	3–5	5–6	$n = 42$	23, 24	$2n = 28$: Janaki-Ammal, 1948.
	Simla, 2200			$n = 42$		
M. laevigata Wall.	Nainital: Dogaon, 1000;	3–5		$n = 14$	10	$2n = 28$: Janaki-Ammal, 1948; Das, 1961.
	Khasia & Jaintia: Nongpoh, 500			$n = 28$	25	$2n = 56$: Datta, 1954; Das, 1961; Hans, 1972.
Ficus religiosa L. (large-leaved)	Nainital: Haldwani, 400	3–7		$2n = 26$	11	$2n = 26$: Condit, 1933.
(small-leaved)	Nainital: Haldwani, 400	3–7		$n = 13$	26	
F. glomerata Roxb.	Nainital: Kaladungi, 400		4–6	$2n = 26$	12	$2n = 26$: Condit, 1928.
F. palmata Forsk.	Nainital: Garampani, 400	3–7		$n = 13$		$2n = 26$: Condit, 1928.
F. hispida L. f.	Nainital: Dogaon, 1000	3–7		$2n = 26$		$2n = 26$: Condit, 1964.

TABLE 1. **Chromosome numbers of woody species in the Ulmaceae, Moraceae, and Urticaceae** (*continued*).

TAXA	LOCALITY (with altitude in meters)	FLOWERING AND FRUITING PERIODS	CHROMOSOME NUMBER	FIGURE NUMBER	PREVIOUS REPORTS
**Ficus cunia* Buch.-Ham.	Nainital: Dogaon, 1000	4–9	$2n = 26$	13	
†*Streblus asper* Lour.	Nainital: Tanakpur, 450	4–5	$n = 13$		$n = 12$: Mitra & Datta, 1967. $n = 13$: Gajapathy, 1961.
Broussonetia papyrifera (L.) Vent.	Dehra Dun, 400	7–9	$n = 13$	14	$2n = 26$: Bowden, 1940; Hsu, 1967.
	Nainital: Bhimtal, 1300		$n = 13$	15	
URTICACEAE					
**Boehmeria rugulosa* Weddell	Nainital: Ratighat, 1350	7–9	$n = 28$	16	
**B. platyphylla* D. Don	Mussoorie: Jhariapani, 1400	6–9	$n = 14$	17	
	Darjeeling: Tista, 300		$n = 28$	18	
Debregeasia longifolia Weddell (= *D. velutina* Gaud.)	Nainital, 1950	9–11	$n = 14$		$2n = 28$: LeCoq, 1963.
**D. hypoleuca* Weddell	Kasauli: Dharampur, 1200	9–11	$n = 14$	27	

* Species investigated for the first time.

† New cytotypes.

Western Himalayas and adjacent plains, except in the case of *Celtis cinnamomea* and *Boehmeria platyphylla*, which were collected from the Eastern Himalayas. The chromosome numbers of 22 woody species belonging to 11 genera of these three families are given in TABLE 1, along with specific localities of collections, previous reports, and flowering and fruiting seasons. The numerals indicate months of the year. Thus 1 stands for January, 2 for February, and so on.

ULMACEAE

Holoptelea Planchon.

H. integrifolia Planchon.

A large deciduous tree, the only representative of the genus, producing valuable timber. Common in the tropical moist deciduous forests along the foot of the Himalayas and in outer ranges. Abundant in the moist Sal-Bearing forests of the Nainital area. Bark: gray to dark gray, slightly rough, cracked on the old trees.

Twenty-eight chromosomes were counted at mitotic metaphase (FIGURE 4). Meiosis was perfectly normal and 14 bivalents regularly constituted at metaphase-I (FIGURE 5).

Ulmus L.

U. wallichiana Planchon.

A medium- to large-sized deciduous tree and a source of commercial timber. Found in the subtropical and temperate forests of the Western Himalayas between 1000 and 3000 m.; not common in the Nainital hills. Bark: brown, rough, vertically fissured.

The somatic chromosome number was determined as $2n = 28$ (FIGURE 6). The karyotype was asymmetrical. Of the 14 pairs of chromosomes, 11 were acrocentric, two metacentric, and in one pair the primary constriction was not clear.

Celtis L.

C. australis L. var. *australis*.

Trees to 25 m. in height, often with straight cylindrical boles, and providing timber of commercial importance. Growing throughout the Western Himalayas up to 2700 m., often in open forests. Bark: ash-gray to gray, smooth on young but rough on old trunks, often with horizontal streaks. Drupe glabrous to pilose.

The chromosome number, as determined from the leaf-tip mitosis, was $2n = 40$ (FIGURE 19). Fifteen pairs were metacentric and three acrocentric, while a centromere could not be located in the remaining two pairs.

C. australis var. *eriocarpa* Dcne.

A tree up to 15 m. in height. Common in the Nainital hills between 1000 and 1800 m. Bark: light gray, slightly rough, often with horizontal streaks. Drupes pubescent to woolly.

The chromosome number as determined from PMC's was $n = 10$ (FIGURE 20). Meiosis was normal.

C. tetrandra Roxb.

A small to large deciduous tree. Found in the subtropical Himalayas from the Sutlej eastwards to Sikkim, between 1000 and 1500 m. Bark: gray to ash-gray, smooth.

Ten bivalents were invariably counted at diakinesis (FIGURE 21) and metaphase-I.

MORACEAE

Artocarpus Forster.

A. lakoocha Roxb.

A large tree attaining a height of 18 m. in the Himalayas, with short bole and spreading branches. Found in the tropical Himalayas from Kumaon eastwards, chiefly in evergreen forests. Not common in the Kumaon hills. Often planted. Wood of commercial value. Bark: reddish brown, rough (FIGURE 1).

FIGURE 1. *Artocarpus lakoocha*, bark pattern. FIGURE 2. *Morus laevigata*, bark pattern, × 4.

The haploid chromosome number was $n = 28$ (FIGURE 8). The species is tetraploid on the base number $x = 14$. Meiosis was found to be normal and pollen fertility 100 per cent.

Morus L.

M. alba L.

A small to medium-sized deciduous tree producing valuable timber for the sports industry. Occurring wild up to 2000 m. in the outer Himalayan ranges, but often planted for its fruit. Bark: pale brown to grayish brown.

The normal flowering season of the species is February to April, but some individuals at Dehra Dun were observed to be in full bloom in the month of September. Meiosis was perfectly normal with 100 per cent pollen fertility.

Fourteen bivalents were regularly constituted at metaphase-I of which one was conspicuously larger than the rest (FIGURES 9, 22).

M. serrata Roxb.

A medium-sized deciduous tree with spreading branches and short bole. Growing in temperate forests of the Western Himalayas, often along moist and shady ravines, but not very common in the Nainital and Simla hills. Timber of some commercial importance. Bark: reddish brown, rough.

The chromosome number $n = 42$ (FIGURE 23) was observed at metaphase-I in populations worked out from various localities in the Nainital and Simla hills. Meiosis was normal and 42 chromosomes were regularly distributed at A-I (FIGURE 24). Pollen fertility was 100 per cent.

M. laevigata Wallich.

A middle-sized deciduous tree and source of timber. Occurring wild (and also cultivated) in the tropical and subtropical Himalayas, but not common in the Nainital area. Bark: reddish brown, rough or somewhat smooth with conspicuous transversely oriented lenticels (FIGURE 2).

Two cytotypes have been discovered. FIGURE 10 shows a pollen mother cell at metaphase-I with 14 bivalents from populations in the Nainital hills. It is diploid. A tetraploid cytotype was discovered in the Khasia and Jaintia hills which showed $n = 28$ at metaphase-I (FIGURE 25).

FIGURE 3. *Ficus religiosa*: a, branches of normal form; b, branches of small-leaved form.

The two are distinct morphologically, the tetraploid being larger in all its parts.

Ficus L.

F. religiosa L.

A large deciduous tree with irregular trunk. Occurring wild in the outer and sub-Himalayan ranges up to 1500 m.; also planted. A source of timber of minor commercial importance. Bark: almost smooth, grayish brown, exfoliating in woody scales.

The chromosome number $2n = 26$ was determined from leaf-tip mitosis (FIGURE 11).

Small-leaved form:

This differs from the normal type in having smaller leaves, shorter petiole, fewer lateral veins but relatively longer acumen (FIGURE 3). However, bark character, stomatal size, and number of stomata per unit area are the same in both types. A comparative account of the normal and small-leaved forms is presented in TABLE 2.

TABLE 2. **A comparison of the normal and small-leaved forms of Ficus religiosa.**

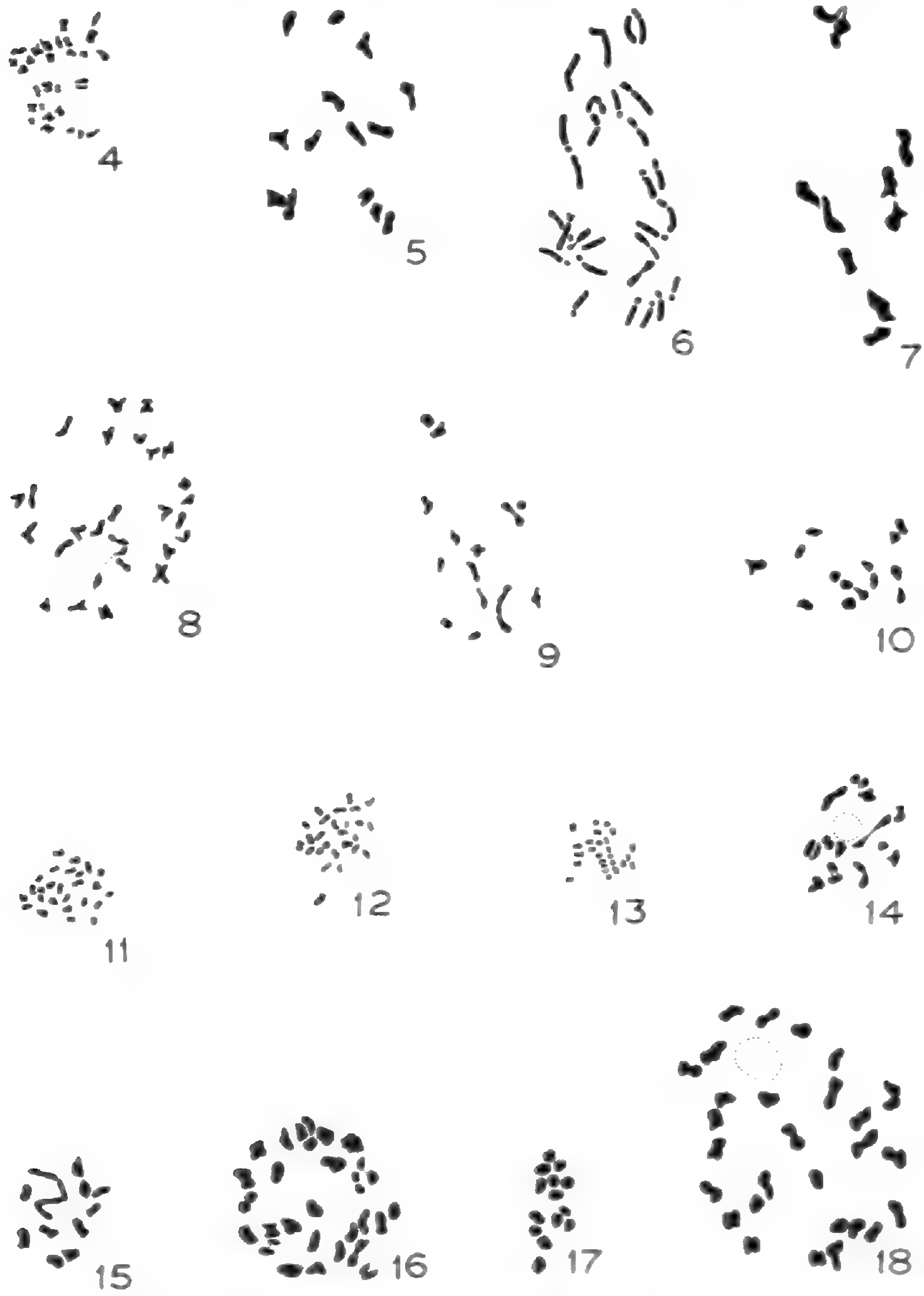
	NORMAL TYPE	SMALL-LEAVED TYPE
HABIT	Large tree.	Large tree.
BARK	Smooth, grayish brown.	Smooth, grayish brown.
LEAVES:		
length	16.0–31.0 cm.	12.5–21.0 cm.
blade size	10.0–21.0 cm. × 8.0–12.0 cm.	8.0–14.0 cm. × 6.0– 8.0 cm.
acumen	3.0– 4.5 cm.	5.0– 6.0 cm.
petiole length	6.0–10.0 cm.	4.5– 7.0 cm.
STOMATA:		
size	35.0–41.0 μm. × 21.0–26.0 μm.	35.0–40.0 μm. × 20.5–26.0 μm.
number per unit area	18.0–20.0	19.0–20.0
DIAMETER OF FIG	0.9– 1.0 cm.	0.6– 0.9 cm.

These forms have sympatric distribution and grow in similar ecological conditions.

At diakinesis, 13 bivalents were invariably counted in the small-leaved form as well (FIGURE 26).

F. glomerata Roxb.

A medium-sized deciduous tree yielding timber of some commercial



FIGURES 4–18. Drawings of chromosome complements. 4 and 5, *Holoptelea integrifolia*: 4, mitotic metaphase, $2n = 28$; 5, M–I, $n = 14$; 6, *Ulmus wallichiana*, somatic metaphase, $2n = 28$; 7, *Celtis cinnamomea*, M–I, $n = 10$; 8, *Artocarpus lakoocha*, M–II, $n = 28$; 9, *Morus alba*, M–I, $n = 14$; 10, *M. laevigata*, M–I, $n = 14$; 11, *Ficus religiosa*, mitotic metaphase, $2n = 26$; 12, *F. glomerata*, mitotic metaphase, $2n = 26$; 13, *F. cunia*, mitotic metaphase, $2n = 26$; 14 and 15, *Broussonetia papyrifera*: 14, diakinesis, $n = 13$; 15, M–I, 10 bivalents and a chain of 6 chromosomes; 16, *Boehmeria rugulosa*, M–I, $n = 28$; 17 and 18, *B. platyphylla*: 17, M–I, $n = 14$; 18, M–I, $n = 28$.

importance. Common in forests at the foot of the Himalayas and its outer ranges up to 1000 m., in moist places, generally along streams. **Bark**: pale brown, smooth.

FIGURE 12 shows the somatic complement of 26 chromosomes.

Broussonetia Vent.

B. papyrifera (L.) Vent.

A fast growing tree of medium size. Adapted to different ecological conditions, but naturalized in many parts of India. Indigenous to China and Burma.

The chromosome number in individuals from several different localities was found to be $n = 13$ (FIGURE 14). Meiosis was normal in the trees from Dehra Dun, whereas those from the Nainital hills showed chain formation at diakinesis and metaphase-I due to heterozygosity for translocations. A chain of six chromosomes and 10 bivalents was observed in many PMC's (FIGURE 15). Pollen fertility in such individuals was 90–95 per cent. The taxa with and without translocations were morphologically identical.

URTICACEAE

Boehmeria Jacquin.

B. rugulosa Weddell.

A small to medium-sized, evergreen tree, often with short bole. Found in the Himalayan subtropical forests ascending to 1800 m., and common in the Nainital and Mussoorie hills. Wood of some commercial value. Bark: dark brown, rough, furrowed.

Twenty-eight bivalents were counted at metaphase-I (FIGURE 16) in the population studied from different localities in the Nainital and Mussoorie hills. Meiosis was perfectly normal.

B. platyphylla D. Don.

A variable common shrub growing in the subtropical and temperate Himalayas.

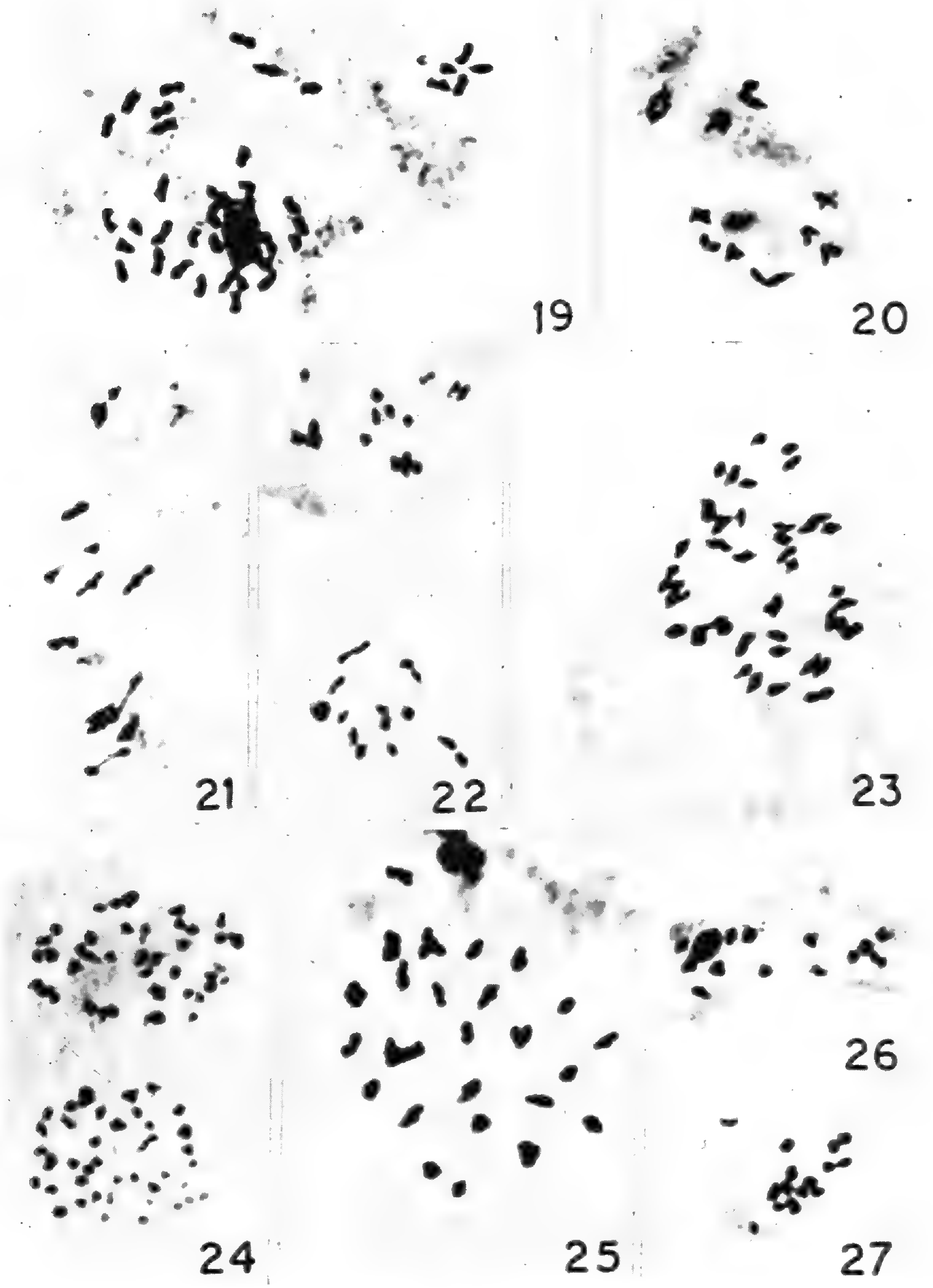
Fourteen bivalents were invariably present in the population from the Mussoorie hills (FIGURE 17), whereas those from the Darjeeling hills were found to have 28 bivalents (FIGURE 18).

DISCUSSION

Of the 22 species presently investigated nine were studied for the first time and new cytotypes for two of these were discovered.

ULMACEAE

Löve and Löve (1961) suggest $x = 7$ as the base number of the genus *Ulmus*, whereas the species of this genus cytologically known up to now, and even those of *Holoptelea* and *Zelkova*, have $n = 14$ or $2n = 28$, except for the intraspecific tetraploid races of *U. americana* and *U. glabra* with $2n = 56$ (Sax, 1933; Santamour, 1969; Ehrenberg, 1949). As such, $x = 14$ seems to be the base number for *Ulmus*, *Holoptelea*, and *Zelkova*, as was proposed by Darlington and Wylie (1955). Like most of the woody taxa, the speciation in these three genera appears to have taken place mostly at the diploid level, rarely involving change in the chromosome number.



FIGURES 19–27. Photomicrographs of chromosome complements. 19, *Celtis australis* var. *australis*, mitotic metaphase, $2n = 40$; 20, *C. australis* var. *eriocarpa*, diakinesis, $n = 10$; 21, *C. tetrandra*, M–I, $n = 10$; 22, *Morus alba*, M–I, $n = 14$; 23, *M. serrata*, M–I, $n = 42$; 24, A–I, $n = 42$; 25, *M. laevigata*, diakinesis, $n = 28$; 26, *Ficus religiosa*, small-leaved, diakinesis, $n = 13$; 27, *Debregeasia hypoleuca*, M–I, $n = 14$.

In *Celtis* and *Trema*, on the other hand, numerical changes in the basic set have been among the factors involved in the evolution of the species. Besides $n = 10$ or $2n = 20$ in several members of the genus *Celtis*, including the presently studied ones, $2n = 22$ was counted in *C. spinosa* (Covas & Schnack, 1947), $n = 13$ in *C. nervosum* (Chuang *et al.*, 1963), $2n = 28$ in *C. occidentalis* (Sax, 1933), and $2n = 40$ in *C. australis* (Bowden, 1945; the present investigations). The prevalence of $n = 10$, which is also the lowest existing haploid number in *Celtis*, suggests the original base number of the genus is $x = 10$, which is also shared by the closely allied genus *Trema* (Hans, 1971).

The present counts of $n = 10$ and $2n = 40$ in the Himalayan populations of *Celtis australis* confirm the report of $2n = 40$ by Bowden (1945) and also establish the existence of intraspecific polyploidy. The tetraploid ($2n = 40$) differs from the diploid ($n = 10$) in having glabrous to pilose drupes, in contrast to the pubescent to woolly ones in the latter.

MORACEAE

The chromosome numbers of the presently studied taxa of Moraceae are based either on $x = 13$ or $x = 14$, which are the prevalent base numbers in the family. Polyploidy seems to have played some evolutionary role in the genera *Ficus*, *Morus*, and *Artocarpus*. Six cases of interspecific polyploidy are recorded in *Ficus* and there are four species which show intraspecific polyploidy (Condit, 1964; Pancho, 1966). In the genus *Morus*, *M. cathayana* with $2n = 56, 84, 112$ (Janaki-Ammal, 1948), and *M. nigra* with $2n = 89$–106 (Voltattorni, 1947) and 308 (Thomas, in Darlington & Wylie, 1955) are the outstanding instances of high intraspecific polyploids. In *M. serrata*, Janaki-Ammal (1948) observed a diploid somatic count, $2n = 28$, while the Nainital and Simla populations of the species with $n = 42$ are hexaploid. *M. laevigata* is another Indian species possessing intraspecific polyploids, a diploid with $2n = 28$ (Janaki-Ammal, 1948; Das, 1961) and a tetraploid with $n = 28$ or $2n = 56$ (Datta, 1954; Das, 1961; Hans, 1972; and the present investigations).

The tetraploid *A. lakoocha* and *A. heterophyllus*, with $n = 28$, and the hexaploid cytotype of *Morus serrata* have perfectly normal meiosis.

Meiotic abnormalities in some populations of *Broussonetia papyrifera*, which is diploid, are obviously a consequence of chromosomal interchanges. In spite of the small size of chromosomes, up to six chromosomes are involved in chain formation. Mehra and Hans (unpublished) observed a ring or chain involving as many as 16 chromosomes and an even smaller second ring in the East Himalayan taxon. The species grows well under varied ecological conditions. Whether these translocations have imparted any selective value for a particular environment is hard to suggest.

URTICACEAE

Darlington and Wylie (1955), and Löve and Löve (1961) proposed $x = 7$ as one of the base numbers for the genus *Boehmeria*. On this basis *B. rugulosa* and the cytotype of *B. platyphylla* from the Eastern Himalayas with $n = 28$ are octoploid, while the West Himalayan taxon of *B. platyphylla* with $n = 14$ is tetraploid. These polyploids, however, are perfectly balanced.

Out of the 25 taxa of the families investigated presently, seven are polyploids. Thus the percentage of polyploidy is 28 per cent in these woody elements.

SUMMARY

Cytological studies on 22 West Himalayan woody species belonging to Ulmaceae, Moraceae, and Urticaceae have been carried out. Of these, the commercial timbers are *Holoptelea integrifolia* ($n = 14$, $2n = 28$), *Ulmus wallichiana* ($2n = 28$), *Celtis australis* ($n = 10$, $2n = 40$) (Ulmaceae); *Artocarpus lakoocha* ($n = 28$), *Morus alba* ($n = 14$), *M. serrata* ($n = 42$), *M. laevigata* ($n = 14$, 28), *Ficus religiosa* ($n = 13$, $2n = 26$), *F. glomerata* ($2n = 26$) (Moraceae), and *Boehmeria rugulosa* ($n = 28$) (Urticaceae). The taxa of *Broussonetia papyrifera* ($n = 13$) with and without chromosomal interchanges are morphologically identical. Morphological forms of *Ficus religiosa* which differ in leaf and fig size have sympatric distribution and the same chromosome number $n = 13$. Intraspecific polyploidy in *Celtis australis* ($2x$, $4x$) and *Boehmeria platyphylla* ($4x$, $8x$) have been recorded here for the first time. Polyploidy seems to have played some role in *Artocarpus*, *Morus*, and *Ficus*, whereas in *Ulmus* and *Holoptelea* speciation has occurred at the diploid level.

ACKNOWLEDGMENTS

We are sincerely thankful to the sponsoring authorities of the U.S. Government for financial help to the senior author under PL 480, grant A7–FS–12.

LITERATURE CITED

Banerji, I., & A. Hakim. 1954. A contribution to the life-history of *Artocarpus lakoocha* Roxb. Proc. Indian Acad. Sci. B. **39:** 128–132.

Bowden, W. M. 1940. Diploidy, polyploidy and winter hardiness relationships in the flowering plants. Am. Jour. Bot. **27:** 357–371.

———. 1945. A list of chromosome numbers in higher plants I. Acanthaceae to Myrtaceae. *Ibid.* **32:** 81–92.

Burnham, C. R. 1956. Chromosomal interchanges in plants. Bot. Rev. **22:** 419–552.

Capoor, S. P. 1937. The life history of *Holoptelea integrifolia* Planch. (Ulmaceae). Beih. Bot. Centralbl. **57:** 233–249.

Chuang, T. I., C. Y. Chao, W. W. L. Hu, & S. C. Kwan. 1963. Chromosome numbers of the vascular plants of Taiwan I. Taiwania **1:** 51–56.

Condit, I. J. 1928. Cytological and morphological studies in the genus *Ficus* I. Chromosome numbers and morphology in seven species. Univ. Calif. Publ. Bot. **11:** 233–244.

———. 1933. Cytological and morphological studies in the genus *Ficus* II. Chromosome numbers and morphology in 31 species. *Ibid.* **17**: 61–74.

———. 1964. Cytological studies in the genus *Ficus* III. Chromosome numbers in sixty-two species. Madroño **17**: 153–155.

Covas, G., & B. Schnack. 1947. Estudios cariologicos en Antofitas. II. Revista Argent. Agron. **14**: 224–231.

Darlington, C. D., & A. P. Wylie. 1955. Chromosome atlas of flowering plants. George Allen & Unwin Ltd., London.

Das, B. C. 1961. Cytological studies on *Morus indica* L. and *Morus laevigata* Wall. Caryologia **14**: 159–162.

Datta, M. 1954. Cytogenetical studies on two species of *Morus*. Cytologia **19**: 86–95.

Delay, C. 1947. Recherches sur la structure des noyaux quiescent chez les phanerogames. Revue Cytol. Cytophys. Vég. **9**: 169–223; **10**: 103–229.

Gajapathy, C. 1961. Cytological studies in some Indian medicinal plants. Bull. Bot. Surv. India **3**: 49–51.

Hans, A. S. 1971. Polyploidy in *Trema* (Ulmaceae). Cytologia **36**: 341–345.

——— 1972. Cytomorphology of arborescent Moraceae. Jour. Arnold Arb. **53**: 216–225.

Hsu, C. C. 1967. Preliminary chromosome studies on the vascular plants of Taiwan (I). Taiwania No. **13**: 117–130.

Janaki-Ammal, E. K. 1948. The origin of the black mulberry. Jour. Roy. Hort. Soc. **53**: 117–120.

Lawrence, G. H. M. 1951. Taxonomy of Vascular Plants. xiii + 823 pp. MacMillan Co., New York.

LeCoq, C. 1963. Contribution à l'étude cyto-taxinomique des Moracées et des Urticacées. Rev. Gen. Bot. **70**: 385–426.

Löve, A., & D. Löve. 1961. Chromosome numbers of central and northwest European plant species. Opera Botanica **5**: 1–581.

Mehra, P. N., & A. S. Hans. 1969. *In* IOPB Chromosome number reports XXI. Taxon **18**: 312–315.

——— & B. S. Gill. 1968. *In* IOPB Chromosome number reports. XIX. Taxon **17**(5): 574–576.

Mitra, K., & N. Datta. 1967. *In* IOPB chromosome number reports XIII. Taxon **16**: 445–461.

Nanda, P. C. 1962. Chromosome numbers of some trees and shrubs. Jour. Indian Bot. Soc. **41**: 271–277.

Osawa, J. 1920. Cytological and experimental studies in *Morus* with special reference to triploid mutants. Bull. Imp. Agric. Exp. Sta. Tokyo **1**: 318.

Pancho, J. V. 1966. *In* IOPB chromosome number reports VII. Taxon **15**: 155–163.

Pearson, R. S., & H. P. Brown. 1932. Commercial Timbers of India. Vol. II. Govt. of India, Central Publ. Branch, Calcutta.

Radzhably, E. P. 1962. Experimental polyploidy in the genus *Morus*. In "Plant Polyploidy." Trud. Mosk. Obsnchest. Ispyt. Prirod. **5**: 360–373.

Rao, S. A. M. 1940. Cytology and embryology in *Artocarpus integrifolia*. Jour. Mysore Univ. **1**: 63–73.

Santamour, F. S., Jr. 1969. New chromosome counts in *Ulmus* and *Platanus*. Rhodora **71**: 544–547.

Sax, K. 1933. Chromosome number in *Ulmus* and related genera. Jour. Arnold Arb. **14**: 82–84.

TAHARA, M. 1910. Über die kernteilung bei *Morus*. Bot. Mag. Tokyo **24**: 281–289.

VOLTATTORNI, S. 1940. Contributo alla conoscenza della embriologia del *Morus alba* L. Boll. R. Staz. Sperim. Gelicolt. e Bachicolt. Ascoli Piceno **19**: 56–63.

———. 1947. Cariologia comparata di alcune varietata di *Morus alba* L. Ann. Sperim. Agrar. N.S. **1**: 163–168.

DEPARTMENT OF BOTANY
PANJAB UNIVERSITY
CHANDIGARH (INDIA)

Present address of the junior author:
DEPARTMENT OF BOTANY
PUNJABI UNIVERSITY
PATIALA-4 (INDIA)

INDEX