JOURNAL
OF THE
ARNOLD ARBORETUM

HARVARD UNIVERSITY

C. E. WOOD, JR.
EDITOR

L. I. NEVLING, JR.
ASST. EDITOR

LAZELLA SCHWARTEN
CIRCULATION

VOLUME XLI

CAMBRIDGE, MASS.
1960

Reprinted with the permission of the
Arnold Arboretum of Harvard University
KRAUS REPRINT CORPORATION
New York
1968

54699

DATES OF ISSUE

No. 1 (pp. 1–110) issued January 15, 1960.
No. 2 (pp. 111–230) issued March 28, 1960.
No. 3 (pp. 231–340) issued July 5, 1960.
No. 4 (pp. 341–457) issued October 15, 1960.

Greenhouse
Am
PRE
1968

Printed in U.S.A.

TABLE OF CONTENTS

JOURNAL

OF THE

ARNOLD ARBORETUM

VOL. XLI JANUARY 1960 NUMBER 1

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

C. E. WOOD, JR. AND R. B. CHANNELL

OF THOSE COMPRISING THE EBENALES in the Englerian sequence of angiosperm families, four — Sapotaceae, Ebenaceae, Styracaceae, and Symplocaceae — occur in the southeastern United States, and it is these which are considered here as constituting the order. These four families, together with the Hoplestigmataceae, Diclidantheraceae, and Lissocarpaceae, also included by Engler and Gilg, are characterized by sympetalous corollas with stamens generally two or three times as many as the corolla lobes (or, by abortion, equal in number to and opposite them) and by superior to inferior, incompletely to completely loculed ovaries with axile placentation.

Wettstein, Engler and Gilg, Rendle, Cronquist, and Benson, among others, have retained the four larger families in a single order (although sometimes with additions), but others, as Hallier and Hutchinson, have split the group in various ways. Copeland (see Styracaceae) suggests that the order is a natural group with a collateral relationship to the Ericales and with an ancestry most nearly represented among living plants by the Theaceae. Altogether, the evidence from floral morphology and anatomy, pollen, wood structure, nodal anatomy, and embryology, insofar as this information is available, is in harmony with this view, and no very convincing data have yet been presented to the contrary. Various items in the

---

[1] Prepared for a biologically oriented generic flora of the southeastern United States, a joint project of the Gray Herbarium and the Arnold Arboretum made possible through the support of George R. Cooley and the National Science Foundation. The scheme follows that outlined at the beginning of the series (Jour. Arnold Arb. **39**: 296–346. 1958). Other published portions of these studies will be found in Jour. Arnold Arb. **40**: 94–112, 161–171, 268–288, 369–384, 391–397, 413–419. 1959, and in the present issue. We are much indebted to the many people who have given freely of advice, information, or materials in connection with the four families treated here. In addition to our immediate colleagues, these include L. J. Brass, G. R. Cooley, W. H. Duncan, R. J. Eaton, R. K. Godfrey, Mrs. J. N. Henry, J. Kucyniak, J. D. Ray, Jr., H. W. Rickett, H. F. L. Rock, H. St. John, W. T. Stearn, F. A. Stafleu, and Mrs. C. E. Wood. The data on nodal anatomy are from the unpublished petiolar studies of R. A. Howard and are used with his kind permission. As in previous papers in this series, the illustrations are the work of Dorothy H. Marsh.

descriptions and discussions which follow will be found to bear on this problem.

At least some of the characteristics which often are cited in connection with the interrelationships of the families of the Ebenales need qualification and a great deal more investigation. For example, although the Sapotaceae are said to have completely septate ovaries, those of at least some (e.g., species of *Bumelia* and *Manilkara*) are at anthesis septate below but are no more completely so above than those of *Styrax*, and in inferior ovaries in both Styraceae and Symplocaceae a similarly incomplete condition occurs. Moreover, that inferior ovaries characterize five of the thirteen genera of the Styracaceae usually is glossed over in comparisons with the Symplocaceae. It should be remarked, too, that in the Ebenaceae, a single ovule in each locule seems to occur much more frequently than two, and there are indications that this condition may have come about through the development of additional septa which have separated the paired ovules. Indeed, all four families may well provide examples of increase in numbers of flower parts, rather than reduction. (Cf. the perianth and gynoecium of Sapotaceae and Ebenaceae and the androecium of Styracaceae and Symplocaceae, for example.) It is also noteworthy in connection with phylogeny that the ovules of Sapotaceae seem to have a single integument, those of Ebenaceae two, of Styracaceae either two or one (by fusion of the two), and of Symplocaceae one, although as yet very few representatives of these families have been examined.

SAPOTACEAE (SAPOTE FAMILY)

Armed or unarmed trees or shrubs with milky sap and alternate [rarely opposite], simple, exstipulate, usually entire and coriaceous leaves, the nodes with 3 traces from 3 leaf-gaps (except some species of *Bumelia*, 1 from 1). Inflorescences axillary, basically dichasial, ours simple, cymose or umbellate, or the flowers sometimes singly disposed, the pedicels bracteolate at the base. Flowers complete, regular. Calyx of 4–9[–12] imbricate, biseriate, or spirally arranged sepals, connate at the base. Corolla sympetalous, the lobes imbricate in the bud, usually as many as the sepals, sometimes with paired lateral or dorsal appendages. Stamens [twice as many as or] as many as and opposite the lobes of the corolla, epipetalous, distinct, the anthers 2-locular, longitudinally dehiscent; staminodia (when present) alternate with the fertile stamens and the lobes of the corolla. Gynoecium syncarpous, the style 1, the stigma unlobed or with as many lobes as locules, the ovary superior, the locules 1–14, typically 4 or 5, the placentation axile, a single, anatropous, 1-integumented ovule in each locule [except in *Diploön* with unilocular ovary and 2 ovules]. Fruit an indehiscent berry, often with a thin, leathery to bony outer layer; seeds large, with fleshy endosperm or none. TYPE GENUS: *Sapota* Mill. = *Manilkara* Adans.

A family of about 40 genera and more than 600 species, all woody, and primarily of the tropics of both hemispheres. Six of the approximately 15 genera of the Western Hemisphere are represented in the southeastern United States, but only *Bumelia* occurs outside of peninsular Florida in this area.

The Sapotaceae are distinguished from the other families of the Ebenales by the superior ovary which is usually completely septate (note illustration of *Bumelia*, however) and by the presence of a solitary ascending, 1-integumented ovule in each locule. The combination of laticiferous elements in leaves and stems and of two-armed hairs (one arm of which is sometimes suppressed) characterizes the family anatomically.

The delimitation of species and of genera, in particular, is difficult in the family, leading to both "splitting" and "lumping" at all taxonomic levels. After a period of neglect, a number of relatively recent studies have clarified the taxonomy and nomenclature of many groups, but it is likely that still further changes of both kinds will be made as the various groups become better understood. Taxonomic characters of generic significance have included especially the presence or absence of staminodia and endosperm, the presence or absence and location of appendages on the corolla lobes, and the general type of seed-scar (hilum).

Unfortunately, very few observations seem to have been made on the biology of the group, and little is known concerning the functioning of staminodia and petal appendages in connection with pollination.

The family is the source of a number of economically important timbers; the seeds of several genera provide edible oils; and a number of groups are valued for the refractive rubbery compounds from the coagulated latex (gutta-percha from species of *Palaquium*, *Payena*, and *Mimusops*; chicle from *Manilkara Zapota* and related plants; balata from *Manilkara bidentata* and related species). The family is also well known for a number of excellent tropical dessert fruits (most of which become quite rubbery and inedible when cooked), including the sapodilla (*Manilkara Zapota*), the sapote or marmalade plum (*Pouteria mammosa* (L.) Cronq., *Calocarpum Sapota* (Jacq.) Merr.), the eggfruit or canistel (*Pouteria campechiana*), and the star apple (*Chrysophyllum Cainito*).

REFERENCES:

ASSEM, J. VAN DEN, A. C. VAN BRUGGEN, MRS. M. P. M. HERRMANN-ERLEE, M. JEUKEN, A. J. G. H. KOSTERMANS, H. J. LAM, P. VAN ROYEN, W. VINK. Revision of the Sapotaceae of the Malaysian area in a wider sense. I–III. Blumea **6**: 547–595. 1952 (*Isonandra, Burckella, Mimusops*); IV, V. *Ibid.* **7**: 364–412. 1953 (*Ganua, Manilkara*); IVa. *Ibid.* 481–483. 1954 (*Ganua*); IIa, Va, VI–IX, IVb. *Ibid.* **8**: 201–513. 1957 (*Burckella, Manilkara, Xantolis, Planchonella, Krausella, Pouteria, Ganua*); X–XII. Nova Guinea II. **8**: 87–128. 1957 (*Leptostylis, Pycnandra, Magodendron*); XIII–XVI. Blumea **9**: 21–142. 1958 (*Chrysophyllum, Diploknema, Payena, Aesandra*); XVII. Blumea Suppl. **4**: 263–267. 1958 (*Aulandra*); IIb, IXa, XVIII, XIX. Nova Guinea II. **10**: 131–142. 1959 (*Burckella, Pouteria, Cassidispermum, Chelonespermum*).

BAEHNI, C. Mémoires sur les Sapotacées. I. Système de classification. Candollea **7**: 394–508. 1938.

BAILLON, H. Sapotacées. Hist. Pl. **11**: 255–304. 1891.

BENTHAM, G., and J. D. HOOKER. Sapotaceae. Gen. Pl. **2:** 650–662. 1876.

CHARLIER, A. Contribution à l'étude anatomique des plantes à guttapercha et d'autres Sapotacées. Jour. Bot. Morot **19:** 127–181, 198–233. 1905; **20:** 22–77. 1906. [Includes "*Palaquium*, *Payena*, *Achras*, *Sideroxylon*, *Bumelia*, *Hormogyne*, *Bassia*, *Argania*, *Lucuma*, *Chrysophyllum*, *Mimusops*."]

CHESNAIS, F. Sur la formation de la cicatrice de la graine chez les Sapotacées. Bull. Soc. Bot. France **90:** 177–181. 1943. [Includes "*Dumoria*, *Autranella*, *Omphalocarpum*, *Achras*."]

CHIMANI, O. Untersuchungen über Bau und Anordnung der Milchröhren mit besonderer Berücksichtigung der Guttapercha und Kautschuk liefernden Pflanzen. Bot. Centralbl. **61:** 353–360, 385–395, 417–426, 449–461. *pls. 1, 2.* 1895.

CRONQUIST, A. Studies in the Sapotaceae — I. The North American species of *Chrysophyllum*. Bull. Torrey Bot. Club **72:** 191–204. 1945. II. Survey of the North American genera. Lloydia **9:** 241–292. 1946. [Key; revision of *Mastichodendron*, *Micropholis*, *Pouteria*.] III. *Dipholis* and *Bumelia*. Jour. Arnold Arb. **26:** 435–471. 1945. IV. The North American species of *Manilkara*. Bull. Torrey Bot. Club **72:** 550–562. 1945. V. The South American species of *Chrysophyllum*. *Ibid.* **73:** 286–311. 1946. VI. Miscellaneous notes. *Ibid.* 465–471. 1946. [Includes key to American genera.]

DECANDOLLE, A. Sapotaceae. Prodr. **8:** 154–208. 1844.

DUBARD, M. Les Sapotacées du groupe Sideroxylinées. Ann. Mus. Col. Marseille **20:** 1–90. 1912. [Includes "*Calocarpum*, *Lucuma*, *Pouteria*, *Bumelia*, *Dipholis*, *Sideroxylon*," and others.]

———. Classification comparée des Sideroxylées et Mimusopées. Compt. Rend. Assoc. Franç. Adv. Sci. **43:** 428–438. 1915.*

ENGLER, A. Beiträge zur Kenntnis der Sapotaceae. Bot. Jahrb. **12:** 496–525. 1890.

———. Sapotaceae. Nat. Pflanzenfam. IV. **1:** 126–144, 145–153. 1890, 1891.

EYMA, P. J. Notes on Guiana Sapotaceae. Rec. Trav. Bot. Néerl. **33:** 156–210. 1936. (Reprinted as Meded. Bot. Mus. Utrecht **27:** 1936.)

HOLLE, G. Ueber den anatomischen Bau des Blattes in der Familie der Sapotaceen und dessen Bedeutung für die Systematik. 59 pp. 1 pl. Inaug. diss., Erlangen, 1892.*

HARTOG, H. M. On the floral structure and affinities of the Sapotaceae. Jour. Bot. **16:** 65–72. 1878. [Includes *Chrysophyllum oliviforme*, *C. Cainito*, *Manilkara Zapota*.]

———. Notes on Sapotaceae. — II. *Ibid.* **17:** 356–359. 1879. [Includes comments on *Bumelia*, *Dipholis*, *Mimusops*.]

LAM, H. J. On the system of the Sapotaceae with some remarks on taxonomical methods. Rec. Trav. Bot. Néerl. **36:** 509–525. 1939. (Reprinted as Meded. Bot. Mus. Utrecht. 65. 1939.)

LECOMTE, H. Á propos du fruit et de la graine des Sapotacées. Bull. Mus. Hist. Nat. Paris **33:** 186, 187. 1927. [Fruit never drupaceous but a berry throughout family.]

PIERRE, L., and I. URBAN. Sapotaceae. Urban, Symb. Antill. **5:** 95–176. 1904.

PLANCHON, L. Étude sur les produits de la famille des Sapotées. ix + 121 pp. Montpellier. 1888.

RECORD, S. J. American woods of the family Sapotaceae. Trop. Woods **59:** 21–51. 1939.

SARGENT, C. S. Sapotaceae. Silva N. Am. **5:** 159–184. *pls. 243–251.* 1893. [*Chrysophyllum*, *Mastichodendron*, *Bumelia*, *Dipholis*, *Manilkara*.]

SMITH, W. The anatomy of some sapotaceous seedlings. Trans. Linn. Soc. II. **7**: 189–200. *pls. 25, 26.* 1909. [Includes *Chrysophyllum oliviforme, C. Cainito, Bumelia tenax, Manilkara Zapota.*]

STURROCK, D. Tropical fruits for southern Florida and Cuba and their uses. Publ. Atkins Inst. Harvard Univ. **1**: 1–131. 1940. (Sapotaceae, 114–119; includes "*Achras Zapota,*" "*Calocarpum Sapota,*" *Chrysophyllum Cainito,* "*Lucuma nervosa,*" *Mimusops.*)

KEY TO THE GENERA OF SAPOTACEAE

A. Sepals imbricate or spiraled, not distinctly biseriate, 4–9, commonly 5, or sometimes in *Pouteria* decussate (2+2) when 4; flowers solitary in the axils or several to many in axillary clusters.
  B. Staminodia present, scale-like or petaloid, secondary lateral leaf-veins reticulate, not parallel to the primary ones; leaves glabrous or variously pubescent beneath (only in *Bumelia* sometimes rufous-sericeous).
    C. Flowers numerous in axillary clusters, small, the sepals 1–3.5 mm. long, the corolla 3–5 mm. long; hilum small, basilateral.
      D. Corolla-lobes without lateral lobes; ovary essentially glabrous; mature fruits 1.5–3 cm. long; endosperm present. .... 1. *Mastichodendron.*
      D. Corolla-lobes with lateral lobes; ovary hairy or glabrous; mature fruits 6–12 mm. long.
        E. Plants unarmed; sepals pubescent; ovary glabrous (rarely slightly hairy); young and mature fruits commonly abruptly tapering into the style; endosperm present; cotyledons thin. .... 2. *Dipholis.*
        E. Plants usually more or less spiny; sepals glabrous or pubescent; ovary usually hairy; young and mature fruits commonly broadly rounded to subtruncate or retuse at the apex; endosperm wanting; cotyledons fleshy. .... 3. *Bumelia.*
    C. Flowers solitary or generally clustered in the axils, relatively large, the sepals 4–9 mm. long, the corolla 8–16 mm. long; hilum long, lateral; endosperm wanting; ovary hairy. .... 5. *Pouteria.*
  B. Staminodia absent; secondary lateral leaf-veins (seen from lower surface after removal of trichomes) parallel to the primary ones; leaves densely rufous-sericeous beneath; flowers 4–7 mm. long; ovary hairy; endosperm present. .... 4. *Chrysophyllum.*
A. Sepals in 2 distinct series, 6 (3+3), or occasionally 8 (4+4); flowers solitary or 2 or 3 together in the axils, relatively large, the sepals 4–10 mm. long, the corolla 4.5–13 mm. long; staminodia present, petaloid to fleshy, or sometimes nearly obsolete; hilum lateral; endosperm present. .... 6. *Manilkara.*

Subfam. SIDEROXYLOIDEAE Lam

1. **Mastichodendron** Cronquist, Lloydia **9**: 245. 1946.

Evergreen shrubs or trees with alternate or subopposite leaves, the midrib elevated on the lower leaf-surface, canaliculate above and often ending in a conical pouch at the summit of the long petiole, the blade pinnately open-reticulate veined, not closely areolate. Flowers numerous in axillary clusters. Sepals 5, suborbicular, spirally arranged. Corolla 5-lobed, firmtextured, subrotate, the tube short, the lobes imbricate. Stamens 5, adnate to the corolla-lobes at or near the level of the sinuses; staminodia 5, not petaloid, shorter than the corolla-lobes. Ovary essentially glabrous, the locules usually 5, the ovules attached basilaterally. Fruit more or less fleshy, 1.5–3[–4.5] cm. long. Seed usually solitary, 1–2.5 cm. long, the hilum lanceolate to circular, to 9 mm. long, but not extending to the middle of the seed; embryo erect; endosperm abundant. (*Sideroxylon* sensu Dubard, Small, not L.) TYPE SPECIES: *Sideroxylon foetidissimum* Jacq. = *Mastichodendron foetidissimum* (Jacq.) Cronq. (The name from Greek, *mastico*, to chew, and *dendron*, tree, presumably alluding to chicle, the coagulated latex used as a base in the manufacture of chewing gum, obtained commercially from *Manilkara Zapota*.) — MASTIC, WILD-OLIVE.

As presently defined, a genus of about seven species of Florida, the West Indies, Mexico, and Central America; represented in our area by a single species in southern Florida.

Mastichodendron foetidissimum is an evergreen tree to 25 m. tall with long-petioled, yellow-green leaves with ovate to elliptic blades, glossy on both surfaces, the margins characteristically minutely puckered. The small, yellowish flowers appear throughout the year and are followed by one-seeded, juicy, yellow fruits 1.5–3 cm. long. The strong, dense, orange-colored heart-wood is sometimes used locally in cabinet-work and boat-building. Varietas *foetidissimum*, with broadly elliptic to suborbicular seed-scars mostly less than 4 mm. long, has a wide distribution from southern Florida through the West Indies from the Bahamas to Guadeloupe and Martinique. It occurs in the coastal hammocks of Florida as far north as Brevard County. Varietas *Gaumeri* (Pittier) Cronq., with larger, lanceolate or narrowly elliptic seed-scars, is known from British Honduras and Campeche and Yucatán, Mexico.

Dubard segregated the American species comprising *Mastichodendron* from the African *Sideroxylon* L. (type species, *S. inerme* L.) on the basis of the vertical (rather than horizontal) embryo and the open-reticulate (rather than closely areolate) venation of the leaf. However, he mistakenly applied *Sideroxylon* to the American species, treating the African as *Calvaria* Commers.; *Mastichodendron* is a renaming of the American group. *Mastichodendron* is considered by Cronquist to be the least specialized of the American genera.

REFERENCES:

See family references, CRONQUIST (1946, Studies in the Sapotaceae — II, pp. 241–292), DUBARD (1912, p. 81), LAM (1939, p. 521), SARGENT (1893, pp. 161, 162, *pls. 241, 245*).

2. Dipholis A. de Candolle, Prodr. 8: 188. 1844, nom. cons.

Unarmed shrubs or trees with pinnately veined leaves, the primary lateral veins not very numerous, sometimes obscure. Flowers of ours numerous in axillary clusters. Sepals (4–)5[–9], pubescent, obtuse. Corolla-lobes 5, rarely 6, obtuse, about as long as the tube, each lobe always with a pair of acute lateral lobes or appendages at the base. Stamens as many as the corolla-lobes, the filaments adnate at or near the level of the sinuses. Staminodia petaloid, erose-fimbriate-laciniate, alternate with the lobes of the corolla and attached at or near the level of the sinuses. Ovary nearly always glabrous, rarely with short, appressed pubescence, 5-locular, the ovules attached basi-laterally. Fruit tapering abruptly into the short, persistent style, fleshy and to 1[–3] cm. long at maturity, black in ours, mostly 1-seeded. Seed with a very nearly basal [or rarely basilateral] hilum, the endosperm well developed, the cotyledons thin. (*Spondogona* Raf., 1836, nom. rejic.) TYPE SPECIES: *Dipholis salicifolia* (L.) A. DC. (The name from Greek, *di*, two, and *pholis*, scale, alluding to the paired corolla-lobe appendages.)

About 14 species, confined to tropical North America, with the principal concentration of species in the Greater Antilles (10 species), only one reaching southern Florida.

Dipholis salicifolia, bustic or cassada, of wide distribution, occurs in the hammocks of the Everglade Keys and the Florida Keys, in the Bahamas, southward through the West Indies to Guadeloupe and Barbados, and in southern Mexico, British Honduras, and Guatemala. It is a large shrub or tree (to 25 m.), evergreen, with elliptic to elliptic-lanceolate or -oblanceolate leaves, acute or acuminate at both ends. The numerous, small, white, fragrant flowers, borne more or less continuously throughout the year in simple, globose clusters at defoliated nodes or in leaf axils are followed by broadly ellipsoid or subglobose black fruits, 6–10 mm. long, containing one (or sometimes two or three) seeds. The very dense, red or dark-brown wood is sometimes used locally in cabinet work.

Similar to and perhaps derived from *Mastichodendron*, *Dipholis* differs from that genus primarily in the presence of lateral lobes on the corolla-segments. It is also closely related to *Bumelia* (see below).

REFERENCES:

See family references, DUBARD (1912), HARTOG (1879), SARGENT (1893, pp. 177–180, *pl. 250*).

CRONQUIST, A. Studies in the Sapotaceae, III. *Dipholis* and *Bumelia*. Jour. Arnold Arb. **26**: 435–471. 1945.

3. **Bumelia** Swartz, Prodr. Veg. Ind. Occ. 49. 1788, nom. cons.

Trees or shrubs, commonly but not always armed with spines or thorns, and with very tough wood. Leaves alternate or subopposite, generally small, the primary lateral veins not numerous, sometimes obscure, our species mostly with conspicuously reticulate-veiny leaves. Flowers 5(rarely 4 or 6)-merous throughout, 3-numerous in axillary clusters, proterogynous. Sepals glabrous or pubescent, oval or orbicular, obtuse. Corolla-lobes each with a pair of lateral lobes or appendages at the base [or these sometimes wanting]. Stamens epipetalous, opposite the corolla-lobes, the anthers extrorse, the filaments slender. Staminodia petaloid, entire, erose or laciniate, attached to the corolla alternate with the stamens at or near the level of the sinuses. Ovary usually hairy, sometimes glabrous, the ovules usually 5, attached basilaterally. Fruit generally broadly rounded, subtruncate or retuse at the apex, 1-seeded, fleshy at maturity, purplish black, and not over about 1.5[–2.5] cm. in length. Seed with a small, nearly basal hilum, without endosperm, the cotyledons fleshy. (? *Robertia* Scop. 1777, nom. rejic.) TYPE SPECIES: *Bumelia retusa* Sw. (The name ancient Greek for a kind of ash-tree.) — BUCKTHORN, IRONWOOD.

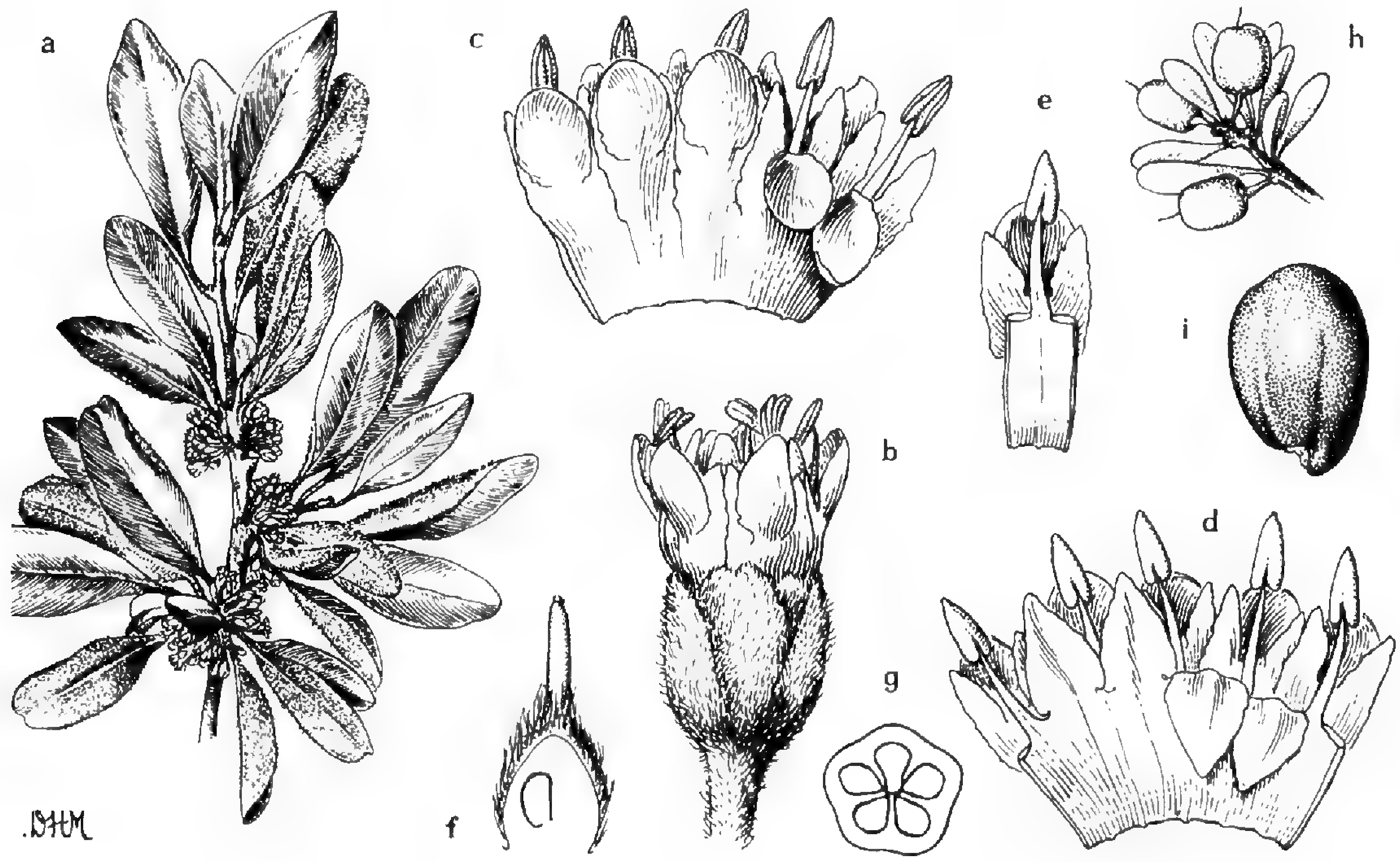


FIG. 1. **Bumelia.** a–g, *B. lanuginosa* subsp. *lanuginosa*: a, flowering branchlet, × ½; b, flower, × 6; c, opened corolla, from without, two petals turned down to show lateral appendages and stamens, × 6; d, opened corolla from within, two staminodia turned down to show lateral appendages of petals, one staminodium removed, anthers drawn as though erect (cf. b), × 6; e, single petal with appendages and stamen from within, × 6; f, gynoecium, with ovary in vertical section to show ovule, × 10; g, cross section of ovary above point of attachment of ovules to show five ovules and incomplete septation of ovary (semidiagrammatic), × 15. h, i, *B. celastrina*: h, tip of fruiting branchlet, × ½; i, seed, lateral view, × 2.

About 25 species, chiefly of the warm regions of North America, a few species in South America, reaching northern Argentina. The genus is well developed in both continental and Caribbean North America. About six species occur in our area.

A number of the species of *Bumelia* are widespread and variable. Specific lines are difficult to determine, and constant morphological characters are few in number. Pedicel-length, used in the past as a basis for specific distinctions, is extremely variable and unreliable. Form and color of pubescence are helpful in delimiting the entities, but considerable changes may accompany age, the young leaves and twigs being quite different in appearance from the mature ones. Clark recognized 12 species in the southeastern United States; Cronquist admitted only 6 from the same area, but included essentially the same number of entities under a different hierarchical arrangement.

Five of the species of the southeastern United States have conspicuously reticulate leaves and short styles 0.8–2 mm. long. *Bumelia lanuginosa* (Michx.) Pers., of wide distribution (Florida to Missouri, Kansas, Texas, southern Arizona and northern Mexico), is a more or less thorny shrub or tree to 15 m. tall, with leaves loosely woolly-villous beneath and fruits 7–15 mm. long. Two of its three subspecies occur in our area: subsp. *lanuginosa* (*B. rufa* Raf.) with tawny pubescence, ranges almost entirely east of the Mississippi River, and subsp. *oblongifolia* (Nutt.) Cronq., with gray to almost white pubescence, almost entirely to the west. Subspecies *rigida* (Gray) Cronquist, with small leaves and a different altitudinal range occurs entirely to the west of our region. *Bumelia lycioides* (L.) Pers. (including var. *virginiana* Fern., *B. Smallii* Clark, *B. cassinifolia* Small, *B. lucida* Small), a shrub or small tree with leaves silvery strigose or sericeous beneath, but glabrate in age, and with fruits 7–13 mm. long, ranges from Florida north to southern Virginia, southern Indiana, southern Missouri and to Arkansas and eastern Texas. *Bumelia reclinata* (Michx.) Vent., with small leaves, hairy when young but soon glabrate, and with small fruits (4–7 mm. long), is restricted to Florida and southern Georgia. It consists of var. *reclinata* (including *B. microcarpa* Small), with whitish or grayish leaf-pubescence and sparsely hairy young twigs, and of var. *rufotomentosa* (Small) Cronq., with coarser, rufous leaf-pubescence and densely rufous-tomentose twigs, which is of local distribution from Alachua to Orange and Hillsborough counties, Florida. *Bumelia Thornei* Cronq., of Early, Baker, and Calhoun counties, Georgia, appears to combine the characters of *B. reclinata* and *B. lanuginosa*. *Bumelia tenax* (L.) Willd. (including *B. lacuum* Small, *B. megacocca* Small), a shrub or small tree with leaves densely sericeous or sericeous-tomentose beneath with tawny, rufous or white [f. *anomala* (Sarg.) Cronq.] hairs, is restricted to the Coastal Plain from South Carolina to Florida.

The sixth species, *Bumelia celastrina* HBK. (*B. angustifolia* Nutt.), is characterized by small, fascicled, inconspicuously reticulate leaves, by twigs, leaves, pedicels and sepals glabrous from the outset, by styles about 2.5–4 mm. long, and by fruits 7–13 mm. long. It occurs in the Bahamas, central Cuba, and southern Florida, northward along the coasts to Brevard and Levy counties, and from southern Texas southward through Central America to Venezuela.

Cronquist suggests that *Bumelia persimilis* Hemsl. (Mexico to Venezuela) is the most primitive species of the genus and that evolutionary trends are toward reduction in size of plant, in size of leaves and prominence of reticulation, in size of fruits, and sometimes in number of flowers in a cluster.

Bumelia differs from *Dipholis* primarily by the possession of endosperm. The presence or absence of endosperm (admittedly difficult to determine in herbarium specimens) apparently parallels natural groupings on other bases, so that the genera usually may be distinguished without resort to this character. In *Bumelia* the plants are commonly spiny or thorny, the lateral appendages of the corolla-lobes wanting (although present in our species), the ovary usually hairy (or only occasionally glabrous), the young as well as the mature fruits broadly rounded to subtruncate or even retuse at the apex, and the cotyledons fleshy. In *Dipholis*, by contrast, the plants are unarmed, the lateral appendages of the corolla-lobes always present, the ovary nearly always glabrous, the fruits tapering abruptly into the style, the cotyledons thin. Preliminary studies of woods also appear to justify separation of the two genera (Record, 1939).

REFERENCES:

See family references, CHARLIER (1905), DUBARD (1912), HARTOG (1879), SARGENT (1893, pp. 167–176, *pls. 246–249*), SMITH (1909).

BROWN, W. L., and R. B. CLARK. The chromosome complement of *Bumelia lanuginosa* and its phylogenetic significance. Am. Jour. Bot. **27**: 237, 238. 1940. [$2n = 24$.]

CLARK, R. B. A revision of the genus *Bumelia* in the United States. Ann. Missouri Bot. Gard. **29**: 155–182. 1942.

———. Woolly buckthorn (*Bumelia lanuginosa oblongifolia*) for hedges. Missouri Bot. Gard. Bull. **35**: 127–130. 1957.

CRONQUIST, A. Studies in the Sapotaceae, III. *Dipholis* and *Bumelia*. Jour. Arnold Arb. **26**: 435–471. 1945.

———. Noteworthy plants of Georgia. Castanea **14**: 101–108. 1949. [Includes *B. Thornei* Cronq.]

SMALL, J. K. The genus *Bumelia* in North America. Bull. N. Y. Bot. Gard. **1**: 437–447. 1900.

4. **Chrysophyllum** Linnaeus, Sp. Pl. 1: 192. 1753; Gen. Pl. ed. 5. 88. 1754.

Evergreen shrubs or trees with alternate, short-petioled leaves, ours smooth, shining above, satiny beneath with lustrous golden to brown hairs, the secondary lateral veins parallel to the primary, and the long axes of the areolae more or less parallel to the lateral veins. Flowers few to many in axillary clusters, or occasionally solitary. Sepals 5, in ours not over 3 mm. long, broader than long, obtuse. Corolla not over 6 mm. long, campanulate-cylindric, the lobes 5[4–11], the tube about as long as the lobes. Stamens 5[–10], adnate to the corolla at or near the level of the sinuses, the anthers extrorse; staminodia none (or occasionally in individual flowers 1 or more irregularly developed in the corolla-sinuses). Ovary surmounted by a short, columnar style and a 5[–7–12]-lobed stigma; ovules attached laterally or basilaterally. Seeds 1, or sometimes several, the seed-scar 5 mm. or more in length, broadly elliptic to subcordate [or narrow or covering nearly the whole surface of the seed]; endosperm abundant. TYPE SPECIES: *Chrysophyllum Cainito* L. (The name from Greek, *chrysos*, gold, and *phyllon*, leaf, in reference to the hairs on the lower leaf-surfaces.) — GOLDEN-LEAF, SATIN-LEAF.

About 11 species in tropical North America, 30 in South America, 15 in tropical West Africa, and 25 in Australasia (16 in New Caledonia); a single species indigenous in subtropical Florida.

Chrysophyllum oliviforme L., satin-leaf, is an evergreen shrub or small tree with an upright plume-like crown of dark green, smooth and shining, ovate leaves, the under surfaces densely covered with lustrous, copper-colored hairs. The small, white flowers, produced irregularly throughout the year, are followed by olive-like dark purple one-seeded fruits. The hard, close-grained, light brown wood is sometimes used locally in cabinet-work. Varietas *oliviforme* ($2n = 52$), with leaves more than 5 cm. long and several to many flowers in a cluster, is occasional in thickets and coastal hammocks of southern peninsular Florida and the Keys, northward to Brevard and Lee counties, and is common in the Bahamas and the Greater Antilles. Varietas *picardae* (Urb.) Cronq., characterized by smaller leaves and fewer flowers per cluster, is known from a few collections from Hispaniola.

Chrysophyllum Cainito, the star apple ($2n = 26$), a handsome tree grown for its excellent fruit, is frequent in cultivation in southern Florida.

REFERENCES:

See family references, SARGENT (1893, pp. 159–162, *pl. 243*), SMITH (1909), STURROCK (1940).

CRONQUIST, A. Studies in the Sapotaceae — I. The North American species of *Chrysophyllum*. Bull. Torrey Bot. Club **72**: 121–204. 1945. V. The South American species of *Chrysophyllum*. *Ibid.* **73**: 286–311. 1946.

LOWE, B. K. The star-apple in Dade County. Proc. Fla. State Hort. Soc. **50**: 60, 61. 1937.* [*C. Cainito*.]

VINK, W. Revision of the Sapotaceae of the Malaysian area in a wider sense. XIII. *Chrysophyllum* L. Blumea **9**: 21–74. 1958.

5. **Pouteria** Aublet, Hist. Pl. Guiane Franç. 1: 85. *pl. 33.* 1775.

Trees or shrubs with alternate, occasionally subopposite leaves, the primary lateral veins strongly arcuate near the margin, scarcely crowded. Flowers solitary or generally several in axillary clusters. Sepals 4–6[–12], distinct, decussate when 4, otherwise imbricate, in ours 4–9 mm. long. Corolla white to yellow or green, subrotate to cylindric, 4–7 (commonly 5 or 6)-lobed, the inner lobes sometimes larger than the outer, shorter than the tube, papillate or sericeous outside. Stamens epipetalous, attached at or near the level of the sinuses [or at the base of the corolla], sometimes abortive. Staminodia alternate with the corolla-lobes and sometimes apparently in the same series [sometimes petaloid, rarely absent]. Ovary hairy, [1–]5–8[–10]-loculed, the ovules laterally attached. Fruit commonly fleshy, [sometimes sclerotic,] 1–several-seeded. Seeds with a long and often broad lateral hilum (or sometimes nearly the whole surface more or less grown to the pericarp); embryo with thick cotyledons; endosperm a thin layer or lacking. (*Lucuma* Mol., sensu many authors.) TYPE SPECIES: *Pouteria guianensis* Aubl. (The name derived from *pourouma-pouteri*, the Carib vernacular name of the type species.)

A genus of about 150 species, the largest number in tropical America, with a number of species in Africa and in Australasia (about 28 species); representatives of two species in subtropical Florida.

Pouteria dominigensis (Gaertn. f.) Baehni is a small tree to 10 m. tall, with oblanceolate to obovate or elliptic leaves, and with evidently pedicellate yellow or white flowers (6–16 mm. long) either solitary or borne few together in the leaf-axils. The yellow, fleshy, edible fruits are 3–6 cm. in thickness and bear one to several seeds. Varietas *dominigensis*, with leaves essentially glabrous (except when very young) is distributed in Hispaniola, Cuba, the Bahamas, and subtropical Florida (where it apparently is rare). Varietas *cuprea* (Urb. & Ekm.) Cronq., differing in strongly rufous-strigose and only tardily glabrate leaf surfaces, is confined to Hispaniola.

The eggfruit or canistel, *Pouteria campechiana* (HBK.) Baehni, long known as *Lucuma nervosa* A. DC., is native from southern Mexico to Panama. It occurs in the hammocks of the Florida Keys and also in Cuba, either in cultivation or perhaps as a recent escape. A tree which sometimes attains a height of 25 m., this species has elliptic to narrowly obovate, glabrous leaves, rounded to acuminate at the apex, up to 35 mm. long and 10 cm. wide, and borne on petioles up to 4 cm. long. The flowers are clustered in the axils on pedicels about 1 cm. long and the subglobose or pyriform fruits, up to 7 cm. in diameter, are yellow, green or brownish with yellow or orange pulp with the consistency of hard-boiled egg-yolk. The species shows variation in size and shape of leaves, size and number of flower parts, and size and texture of fruits. Some of the numerous segregates which have been proposed may represent geographical varieties, but the final evaluation of these should be preceded by extensive field study.

Pouteria belongs to a complex about which there is little agreement as to generic lines. As currently treated, the group includes such generic segregates as *Calocarpum* Pierre and *Oxythece* Miq., but excludes as separate genera the New World *Micropholis* Pierre and the predominantly Australasian *Planchonella* Pierre.

Aublet's *Pouteria* was based upon a mixture of two discordant elements, for the fruit described and figured with the other parts of the plant is that of a species of *Sloanea* (Elaeocarpaceae). (See Radlkofer.) Although the name might be regarded as a *nomen confusum*, Radlkofer, after reviewing the situation, re-established *Pouteria* for that part of the type belonging to the Sapotaceae. In the past *Lucuma* Mol. (1782) has been applied to the species here considered as *Pouteria*. However, three of the five species originally described by Molina generally are agreed not to be sapotaceous, and, although the identity of the others is uncertain, the description is such that these, too, may be excluded from the Sapotaceae.

REFERENCES:

See family references, CRONQUIST (1946, Studies in the Sapotaceae II, pp. 259–291, revision of N. American species), EYMA (1936, pp. 159–192, including review of nomenclatural and taxonomic history of *Pouteria*), DUBARD (1912), LAM (1939), STURROCK (1940).

BAEHNI, C. Les sections du genre *Pouteria*. Compt. Rend. Soc. Phys. Hist. Nat. Genève **58**: 144, 145. 1941.

———. Mémoires sur les Sapotacées. II. Le genre *Pouteria*. Candollea **9**: 147–476. 1942. [*Sensu lato*, including *Planchonella*, *Micropholis*, *et al.*]

FAIRCHILD, D. The canistel, a winter fruit in South Florida. Fairchild Trop. Gard. Occas. Pap. **13**: 7–9. 1943.* [*P. campechiana*.]

HERRMANN-ERLEE, MRS. M. P. M., and P. VAN ROYEN. Revision of the Sapotaceae of the Malaysian area in a wider sense. IX. *Pouteria* Aublet. Blumea **8**: 452–509. 1957.

RADLKOFER, L. Ueber die Zurückführung von *Omphalocarpum* zu den Sapotaceen und dessen Stellung in dieser Familie. Sitz-ber. Akad. München **12**: 265–344. 1882. [Application of name *Pouteria*, 326–335.]

———. Ueber einige Sapotaceen. *Ibid.* **14**: 397–486. 1884. [Includes further notes on *Pouteria*.]

Subfam. MIMUSOPOIDEAE Lam

6. **Manilkara** Adanson, Fam. Pl. 2: 166. 1763, nom. cons.[2]

Evergreen trees or shrubs with alternate, leathery leaves often approximate or clustered at the ends of the stout branchlets, the primary lateral veins generally parallel, nearly straight, not crowded. Flowers of our species on pendent pedicels, solitary or 2 or 3 together in the leaf-axils. Sepals biseriate, 3 + 3 [rarely 2 + 2 or 4 + 4], persistent, reflexed in age. Corolla white or yellow, glabrous, the lobes as many as the sepals, each with a pair of petaloid dorsal appendages or these obsolete by fusion with the lobes. Stamens as many as corolla lobes and opposite them, epipetalous, the anthers sagittate; staminodia of the same number as stamens and alternating with them, petaloid to fleshy (or almost obsolete). Style linear, exserted; stigma entire; ovary ovoid to depressed globose, pubescent, 6–14-locular (in ours 9–12- or 6-locular), the ovules lateral in attachment. Fruit ellipsoid, ovoid to depressed globose, fleshy, 1- or several-seeded, capped by the persistent style. Seed with a long, lateral hilum; embryo with thin cotyledons; endosperm abundant. (*Mimusops* sensu Sargent, Small and others, in respect to American species; including *Achras* L., *Sapota* Mill., nom. rejic.) TYPE SPECIES: *Manilkara Kauki* (L.) Dubard (*Mimusops Kauki* L.). (The name from Malabar, *manyl-kara*, as given by Rheede in *Hortus Malabaricus*, applied to a species of this genus.)

A genus of about 85 species in four subgenera, in the tropics of both hemispheres (about 30 in Africa, 25 in Australasia, and 30 in the Caribbean, Central America and South America); two species, one native, the other introduced, in subtropical Florida.

Manilkara bahamensis (Baker) Lam & Meeuse (*Achras emarginata* (L.) Little, *Minusops emarginata* (L.) Britton), wild dilly or wild sapodilla, of the Florida Keys and the Bahamas, is an evergreen shrub or small tree with bluish-green, coriaceous, elliptic, blunt or emarginate, petiolate leaves

---

[2] Both *Achras* L. and *Manilkara* Adans. have been proposed for conservation. (See Little, Brittonia 7: 48, 49. 1949, and Lam and Van Royen, Taxon 2: 112. 1953, respectively.) The former has been rejected (Taxon 3: 119. 1954), while the latter has been approved by the Committee for Spermatophyta.

clustered at the ends of the stout branchlets. The small, yellowish flowers on recurved pedicels are borne singly or in two's or three's in the leaf-axils in April or May. The subglobose, fleshy, one-seeded, rusty-brown, mealy-roughened fruits reach 3 cm. or more in diameter. This taxon has been treated either as a species or, in the rather broad specific concept of Cronquist, as one of four subspecies of *Manilkara jaimiqui* (Wright) Dubard.

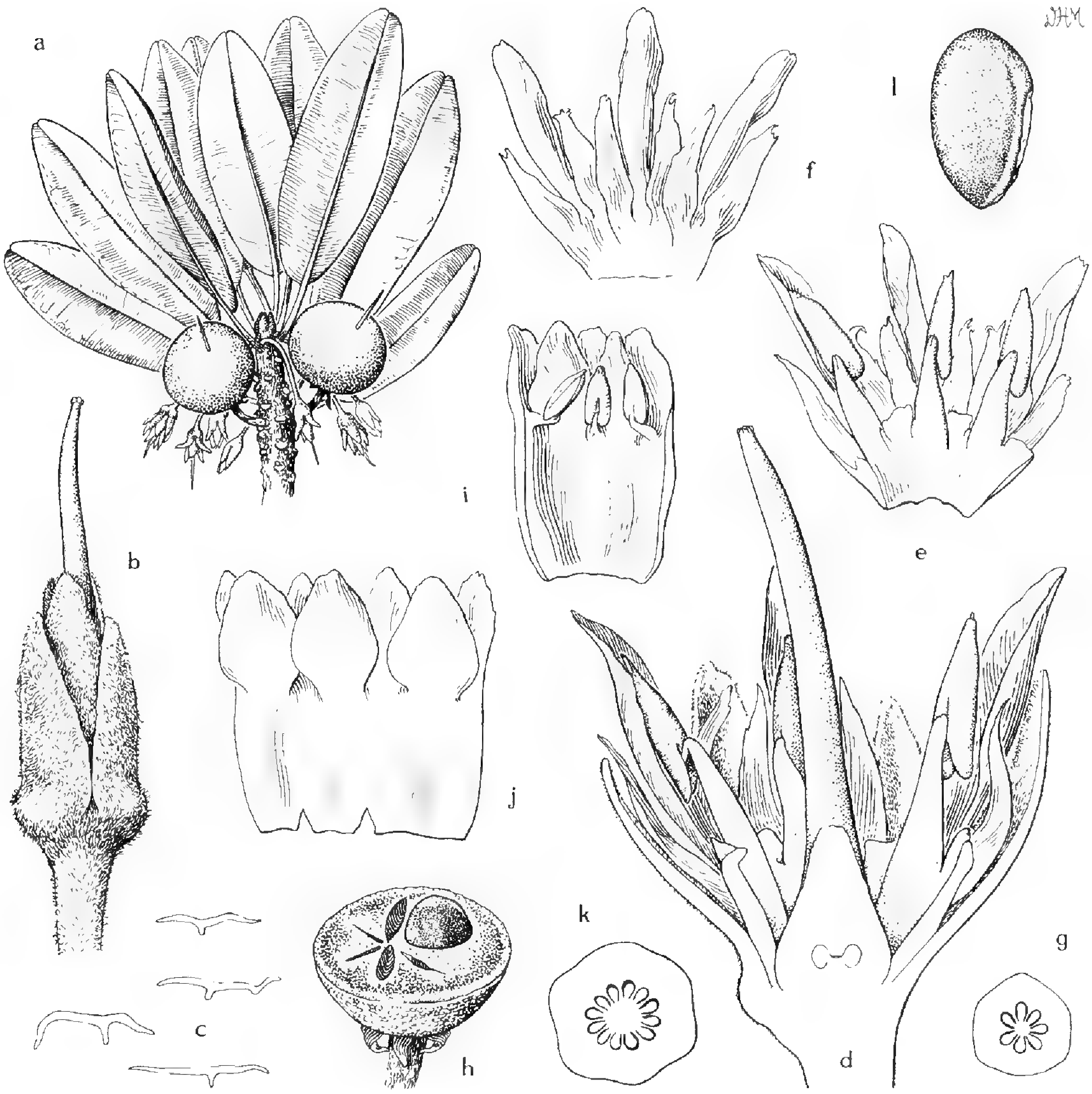


FIG. 2. **Manilkara.** a–h, *M. bahamensis*: a, tip of flowering and fruiting branch, × ½; b, flower, lateral view, after fall of corolla, × 3; c, detached two-armed hairs from calyx, point of attachment below, × 50; d, flower in vertical section, outer sepal to the left — note staminodia alternating with stamens, × 5; e, three corolla-lobes, from within, with appendages, stamens, alternating staminodia, × 3; f, three corolla-lobes, from without, to show dorsal appendages (cf. Fig. 1c, × 3; g, cross section of 7-locular ovary at level of attachment of ovules (semidiagrammatic), × 5; h, nearly mature fruit, the upper half removed, to show single seed, locules with aborted ovules, × 1. i–l, *M. Zapota*: i, portion of corolla, from within, to show three corolla-lobes, two petaloid staminodia alternate with stamens, × 3; j, portion of corolla, from without, to show three corolla-lobes, tips of four staminodia, × 3; k, cross section of 12-locular ovary at level of attachment of ovules (semidiagrammatic), × 5; l, seed, lateral view — note elongate seed-scar, × 1.

Our plant is subsp. *emarginata* (L.) Cronq.; the others are subspp. *jaimiqui* and *Wrightiana* (Pierre) Cronq., of Cuba, and subsp. *haitiensis* (Cronq.) Cronq., of Hispaniola.

Manilkara Zapota (L.) v. Royen (*M. Zapotilla* (Jacq.) Gilly, *Achras Zapota* L.), sapodilla, dilly, or naseberry, $2n = 26$, is cultivated in most of the warmer regions of the world for its excellent fruits. In its native area (Mexico to Costa Rica), especially in Yucatán, northern British Honduras, and Petén, Guatemala, it is also the principal source of chicle for chewing gum. The plant is a handsome evergreen tree with small, white flowers borne singly in the leaf-axils and followed by globose to ellipsoid fruits 3–9 cm. in diameter with translucent, pale brown flesh and several shining, black, compressed seeds. It is quite hardy in southern Florida, and outside of cultivation occurs in hammocks and old fields on the Everglade Keys and Florida Keys.

These two species would be placed respectively with *Manilkara* Adans. and *Achras* L., which, although similar in most respects, have been maintained as separate genera on the basis of the lack of paired dorsal appendages on the petals of the latter. However, the two genera were combined by Gilly who found transitional forms in his study of the *M. Zapota* complex. This union has been accepted generally, but the correct name for the genus so constituted has been a matter of controversy which is only settled by the conservation of *Manilkara* and the rejection of *Achras*.

A segregate of *Mimusops* L. (a group of about 60 species, mostly African), *Manilkara* is usually distinguished from that genus by sepal-number (6 *vs.* 8) and corresponding differences in the number of corolla-lobes, stamens and staminodia, by the seed-scars (relatively long and lateral *vs.* small and basilateral), by the nervation of the leaves (generally straight, parallel, and rather close *vs.* curved, wider apart), by the presence or absence of sclereids in the leaves (according to Lecomte — on the basis of only eight species), by the locules of the ovary (15–6 *vs.* 8), by the embryo (with thin, foliaceous *vs.* thick, plano-convex cotyledons), and by the presence or absence of endosperm. Although most workers at present recognize the two as distinct, a few species appear to be intermediate. On the basis of a preliminary study of Sapotaceous woods, Record thought that both might be included in a single genus.

REFERENCES:

See family references, CHARLIER (1905), CHIMANI (1895), EYMA (1936, pp. 204–210, including distinctions from *Mimusops*), HARTOG (1878), SARGENT (1893, pp. 181–184, *pl. 251*), SMITH (1909), STURROCK (1940).

BRITTON, N. L. The botanical name of the wild sapodilla. Torreya **11**: 128, 129. 1911. [*Mimusops emarginata* (L.) Britton.]

COOK, O. F. Nomenclature of the sapote and the sapodilla. Contr. U. S. Natl. Herb. **16**: 277–285. 1913. [Maintains *Achras Zapota*; includes Plumier's plate of *Sapota*.]

CHEN, C. L. Morphological basis of systematics of *Manilkara* (Sapotaceae). Proc. IX Int. Bot. Congr. **2**: 68. 1959. [*Achras, Northiopsis, Fancherea, Shaferodendron*, and, probably *Muriea* congeneric with *Manilkara*.]

CRONQUIST, A. Studies in the Sapotaceae — IV. The North American species of *Manilkara*. Bull. Torrey Bot. Club **72**: 550–562. 1945. [Including *Achras*; 13 spp.]

DUBARD, M. Les Sapotacées du groupe des Sideroxylinées-Mimusopées. Ann. Mus. Col. Marseille **23**: 1–62. 1915. [Separates *Manilkara* from *Mimusops*; 33 spp. of *Manilkara* (13 in New World).]

DUCKE, A. The genus *Manilkara* Adans. in Brazil, seen by a field botanist. Jour. Linn. Soc. Bot. **55**: 644–656. 1957.

EGLER, F. E. Some statistics of *Achras Zapota* leaves, British Honduras. Bull. Torrey Bot. Club **71**: 235–245. 1944.

GILLY, C. L. Studies in the Sapotaceae, II, The sapodilla-níspero complex. Trop. Woods **73**: 1–22. 1943. [Unites *Achras* and *Manilkara*; 12 spp. recognized in the *Manilkara Zapotilla* (= *M. Zapota*) complex.]

———. Another later homonym. Rhodora **48**: 163, 164. 1946. [*Manilkara emarginata* (L.) Britton & Wilson, a later homonym of *M. emarginata* Lam.]

GONZALES, L. G. A study of the respiration of the chicho, *Achras Zapota* Linn. Philipp. Agr. **20**: 341–348. 1931.*

HOOKER, J. D. *Achras bahamensis*, Baker. Hook. Ic. **18**: *pl. 1795*. 1888.

HOOKER, W. J. *Achras Sapota*. Bot. Mag. **58**: *pls. 3111*, *3112*. 1831.

KARLING, J. S. The laticiferous system of *Achras Zapota* L. I. A preliminary account of the origin, structure, and distribution of the latex vessels in the apical meristem. Am. Jour. Bot. **16**: 803–824. *pls. 73–77*. 1929.

———. Dendograph studies on *Achras Zapota* in relation to the optimum conditions for tapping. Am. Jour. Bot. **21**: 161–193. 1934.

———. The response of *Achras Zapota* in latex yield to wounding by the ibidem method of tapping. Bull. Torrey Bot. Club **69**: 553–560. 1942.

LAM, H. J. Note on the Sapotaceae-Mimusopoideae in general and on the Far-eastern *Manilkara*-allies in particular. Blumea **4**: 323–358. 1941. [15 spp. of *Manilkara*; comparison with *Mimusops*.]

LECOMTE, H. Observations sur les Sapotacées du groupe Mimusopées. Bull. Mus. Hist. Nat. Paris **23**: 35–39. 1917.

LITTLE, E. L., JR. The name of the wild dilly of Florida. Rhodora **49**: 289–293. 1947. [*Achras emarginata*; retains *Achras* over *Manilkara*.]

LUNDELL, C. L. Chicle exploitation in the sapodilla forest of the Yucatan Peninsula. Field Lab. **2**: 15–21. 1933.

MONACHINO, J. V. The South American species of *Manilkara*. Phytologia **4**: 94–118. 1952. (Including *Achras*; 22 spp.; includes notes on *Achras* vs. *Manilkara*.)

PITTIER, H. On the origin of chicle with descriptions of two new species of *Achras*. Jour. Wash. Acad. Sci. **9**: 431–438. 1919. [*Achras Chicle*, *A. calcicola*.]

PONCE DE LEÓN, A. La denominación científica de los zapotes. Revista Soc. Cub. Bot. **2**: 116–122. 1945. [*Achras Zapota* L. and *Calocarpum Sapota* (Jacq.) Merrill.]

RICHARDS, A. Studies in propagation of sapodilla. Trop. Agr. Ceylon **99**: 78–85. 1943.*

ROYEN, P. VAN. Revision of the Sapotaceae of the Malaysian area in a wider sense. V. *Manilkara* Adanson em. Gilly in the Far East. Blumea **7**: 401–412. 1953. [*Achras* the correct name, but *Manilkara* used pending conservation (see Taxon **2**: 112. 1953); includes figures of *M. Zapota* showing development of "fusion triads" (petal + appendages).]

TRAVERSE, A. Pollen analysis of the Brandon lignite of Vermont. U. S. Dep. Interior Bur. Mines Rep. Invest. **5151**: 1–107. 1955. [Most abundant fruit and a frequent pollen in this late Oligocene deposit very similar to fruit and pollen of *M. bahamensis.*]

VENKATARAMAN, R., and F. J. REITHEL. Carbohydrates of the Sapotaceae. I. The origin of lactose in *A. Sapota.* Arch. Biochem. Biophys. **75**: 443–452. 1958.* [*Achras Zapota.*]

EBENACEAE (EBONY FAMILY)

Monoecious, dioecious, or polygamous trees or shrubs with alternate [rarely opposite], simple, entire, exstipulate leaves and watery sap; nodes with 1 trace from 1 gap. Flowers regular, 3–7-merous, sympetalous. Stamens epipetalous or hypogynous, 2–4 times as many as and opposite the lobes of the corolla. Gynoecium syncarpous, the styles wholly or partly distinct, the 2–16(–20)-locular ovary superior, with 1 (or 2) bitegumented ovules suspended from the summit of each locule. Fruit a berry. (Ebenaceae Vent. Tab. Regne Vég. 2: 443. 1799, nom. cons. prop. [Type genus: *Diospyros* L. (*Ebenus* Burm. ex Ktze., not L.; *Maba* J. R. & G. Forster)]; Guaiacanae Juss. Gen. Pl. 155. 1789, nom. illegit. [Type genus: *Diospyros* L. (*Guaiacana* Tourn., not *Guaiacum* L.)].)[3]

A small, geologically old family, well represented in the fossil record, including four or five weakly defined genera (all except *Diospyros* confined to Africa or Madagascar) and about 450 living species, almost all restricted to tropical regions of both Eastern and Western hemispheres, with the greatest concentration of species in India and Malaysia, several in subtropical regions, a few species in the temperate regions of Asia and America, and none in the colder parts of either hemisphere.

The watery sap, usually unisexual flowers, and 2-integumented, pendulous ovules distinguish the Ebenaceae from the Sapotaceae which have milky sap, usually bisexual flowers, and 1-integumented, ascending ovules. The Styracaceae, with which the Ebenaceae are also thought to be allied, have bisexual flowers and an incompletely septate ovary (usually), which may be superior, half-inferior or inferior. Metcalfe and Chalk note a close general similarity between the woods of Sapotaceae and Ebenaceae, and Erdtman indicates that pollen grains more or less similar to those of Ebenaceae are found in the Sapotaceae and Styracaceae. The hairs of

---

[3] The well-known and long-used name Ebenaceae must be conserved, for it is derived not from that of a genus but from ebony, the wood of *Diospyros Ebenum.* (In establishing the family Ventenat wrote, "Les rapports que les plantes de cette famille ont avec l'arbre qui produit la véritable ébène, nous ont déterminés à leur donner le nom d'Ébénacées.") Linnaeus used *Ebenus* for a genus of Leguminosae, and the only post-Linnaean publication of the name in the sense of *Diospyros* (*Maba*) is that of Otto Kuntze, Rev. Gen. 2: 408, 1891. Bullock (See Taxon 7: 14, 17, 160. 1958; **8**: 170. 1959) has proposed conservation of Ebenaceae Vent. and rejection of Guaiacanae Juss. The former certainly must be conserved, but the latter is already illegitimate under the International Code of Botanical Nomenclature, being derived from *Guaiacana* Tourn. (not *Guaiacum* L., of the Zygophyllaceae), which does not seem to have been published as a generic name after 1754.

Ebenaceae are mostly unicellular, but are occasionally in tufts and sometimes are 2-armed.

The family is of economic importance for a number of woods, especially ebony, the hard and heavy, black heartwood of several Asiatic species of *Diospyros*, *D. Ebenum* Koenig being the classical source. Several species, mostly of *Diospyros* (see below), have edible fruits.

REFERENCES:

BAILLON, H. Ébénacées. Hist. Pl. **11**: 221–229. 1891.

BAKHUIZEN VAN DEN BRINK, R. C. Revisio Ebenacearum Malayensium. Bull. Jard. Bot. Buitenzorg III. **15**: 1–515. 1936–1941. [175 spp. of *Diospyros*, in 4 subgenera, 35 sect. See also, Enumeration of Malayan Ebenaceae. Gard Bull. Str. Settlements **7**: 161–189. *pls. 49, 50.* 1933.]

BENTHAM, G., and J. D. HOOKER. Ebenaceae. Gen. Pl. **2**: 662–666. 1876.

DECANDOLLE, A. Ebenaceae. Prodr. **8**: 209–243. 1844.

GÜRKE, M. Ebenaceae. Nat. Pflanzenfam. IV. **1**: 153–165. 1890.

HIERN, W. P. A monograph of the Ebenaceae. Trans. Cambridge Phil. Soc. **12**: 27–300. *pls. 1–11.* 1873. [The basic monograph.]

PARMENTIER, P. Histologie comparée des Ébénacées dans ses rapports avec la morphologie et l'histoire généalogique de ces plantes. Ann. Univ. Lyon **6**: 1–150. *pls. 1–4.* 1892.

1. **Diospyros** Linnaeus, Sp. Pl. 2: 1057. 1753; Gen. Pl. ed. 5. 478. 1754.

Dioecious (or rarely polygamous) trees (or shrubs) with dense, hard wood. Flowers greenish, axillary, cymose, or the pistillate (larger than the staminate) solitary. Calyx [3]4–6[7]-lobed, accrescent in fruit, coriaceous or foliaceous. Corolla urceolate-campanulate with [3]4–6 lobes sinistrorsely contorted in the bud, spreading or recurved at anthesis, the tube usually contracted at the top. Stamens 3–many, usually in two or more rows, unequal, often in pairs, in ours mostly 16 in the staminate flowers (8 imperfect rudimentary ones in the pistillate or these sometimes absent), the filaments short, hairy [or glabrous], the anthers linear-lanceolate, arched inward, apiculate by the excurrent connective, 2-loculed, dehiscing laterally by longitudinal slits. Pollen 3-colporate. Styles usually 4, united below; stigmas emarginate or punctiform; ovary (rudimentary or absent in the staminate flowers) usually 8-locular [3 or 6, or 4 or 8–16-locular in other species], the ovules solitary [or 2] in each locule. Berry depressed-globose, globose, oblong or conical, sessile or subsessile, pruinose, bitter-astringent when green, orange, sweet, and soft-pulpy when ripe. Seed oblong, the testa brown, more or less shining, the endosperm cartilaginous, equable [or in some species ruminated by sinuous intrusions of the testa.] Embryo straight, the contiguous cotyledons foliaceous. Embryo sac development of the "Polygonum" type, seedless fruits sometimes developing. (Including *Maba* J. R. & G. Forster, *Brayodendron* Small.) TYPE SPECIES: *D. Lotus* L. (The name from Greek, *Dios*, of Zeus (genitive), and *pyros*, grain; used by Theophrastus for a fruit, adopted by Linnaeus in preference to *Guaiacana* Tourn., which was not of Greek or Latin derivation.) — PERSIMMON, DATE-PLUM.

A large genus of about 400 species of tropical and warm regions (including about 175 in Malaysia, 70 in Africa, 100 in Madagascar); only a few reaching into the temperate climates of North America and Asia; two species indigenous to the United States: *D. texana* Scheele, of southwestern Texas and northern Mexico (segregated on totally inadequate grounds as *Brayodendron* Small), and *D. virginiana* L., in the eastern United States.

Diospyros virginiana, persimmon, simmon, possumwood, a deciduous tree, usually 10–15 m. tall, with heavy, hard wood, ranges from Texas to Florida and northward to Connecticut and southeastern Iowa, but is uncommon in the area of the Wisconsin glaciation. Although the genus is known from the fossil record to have been distributed at one time far to the north, the present range of this species appears to be limited by temperature and rainfall, few specimens being found north of the 25° F. February isotherm or west of the 30-inch isohyet.

Phenotypically variable, *Diospyros virginiana* has received various taxonomic treatments and is in need of further study. Varietas *pubescens* (Pursh) Dippel (Florida to Arkansas, north to Virginia, southern Illinois, and southern Iowa) is characterized by villous or densely tomentose branchlets and leaves pubescent beneath. The form known as var. *platycarpa* Sarg. (Missouri, Arkansas, Kansas and Oklahoma) has broad, depressed fruits which ripen early, and var. *Mosieri* (Small) Sarg. (peninsular Florida) is said to be a shrub or small tree distinguished by thick-skinned, globose fruits and plump, slightly rugose seeds. Fruit-size and -shape are quite variable in this species and merit careful taxonomic attention. (See also references to *D. Kaki* below.)

The basic chromosome number of the genus appears to be 15, 2*n* having been reported as 30 for *Diospyros texana* and four exotic species (including *D. Lotus*), 60 (tetraploid) and 90 (hexaploid) for *D. virginiana*, and 90 for *D. Kaki* L. f. In *D. virginiana* the tetraploids occupy the central and southeastern parts of the range of the species, with the hexaploids on the periphery throughout. Morphological variation, as well as variation with respect to hardiness in this species, may be related to polyploidy. Sometimes used as a stock upon which *D. Kaki* is grafted, it provides ideal material for the study of stock–scion relationships with respect to ploidy.

Diospyros virginiana is self-pruning (as in species of *Salix*, *Populus*, *Ulmus* and *Quercus*), some of the twigs abscissing after the first year, most after the second, and some during successive years, while only relatively few are retained and become the stark, secondary branches of the tree. Root suckers are readily produced and clonal stands are frequent, especially in old fields.

Although the flowers are visited by bees in large numbers, the occasional development of seedless fruits (cf. *Diospyros Kaki*) has led to speculation concerning the necessity of fertilization for the production of the normal, seed-bearing fruits. There are, however, indications that pollination is necessary for ordinary fruit production and that fertilization does occur, although this latter process has not been observed.

Dormancy of the seeds is due, in part, to the mechanical resistance of the seed coat, particularly the layer overlying the radicle. The physiological effects upon germination of the passage of the seeds through the alimentary tract of animals — such as foxes, deer, raccoons, and opossums — which feed upon the fruits, and the role of such animals in the spread of the species are not known.

A number of selections of *Diospyros virginiana* have been named, and the species is cultivated to a limited degree, although seldom on a commercial scale. Chinese and Japanese cultivars of *D. Kaki*, with large and delicious fruits, are cultivated commercially in northern Florida and California and are grown for ornament and fruit over much of our area. The numerous studies of *D. Kaki* suggest profitable lines of investigation on *D. virginiana.*

The closest relative of *Diospyros virginiana* appears to be *D. Lotus*, which, with *D. Kaki*, *D. Morrisoniana* Walp., *D. glaucifolia* Metc., *D. brideliifolia* Elmer, and, probably, *D. blepharophylla* Standl. (*D. ciliata* A. DC.), *D. ehretioides* G. Don, and *D. mollis* Steud. (according to Bakhuizen van den Brink), constitutes section DIOSPYROS (sect. *Lotus* Bakh.; sect. *Danzleria* (Bert.) Hiern, in part). The studies of the Malaysian species by Bakhuizen van den Brink and of the African by White have clarified many of the specific problems for those areas, but White has pointed out that the entire subgeneric classification needs a complete overhaul which must await careful study of all of the species. Among the African members White has noted well-marked, isolated species and a number of "superspecies" consisting of two to five closely related geographically or ecologically vicarious species. Standley, Bakhuizen van den Brink, and White have all found it impossible to maintain *Maba* as distinct from *Diospyros.*

REFERENCES:

ASAMI, Y., and C. T. CHOW. Is the pollen of Japanese persimmons carried by wind? Jour. Hort. Assoc. Japan **7:** 247–251. 1936.* [No.]

BALDWIN, J. T., JR., and R. CULP. Polyploidy in *Diospyros virginiana* L. Am. Jour. Bot. **28:** 942–944. 1941.

BERRY, E. W. Some ancestors of the persimmon. Pl. World **15:** 15–21. 1912.

BLOMQUIST, H. L. Dormancy in the seeds of the persimmon. Jour. Elisha Mitchell Sci. Soc. **39:** 83–85. 1923.

BUSCH, P. Anatomisch-systematische Untersuchung der Gattung *Diospyros.* Inaug. Diss., Erlangen. 94 pp. 1913.*

CAMP, A. F., and H. MOWRY. The cultivated persimmon in Florida. Fla. Agr. Exp. Sta. Bull. **124:** 1–36. 1945.*

CUNO, J. B. Utilization of dogwood and persimmon. U. S. Dep. Agr. Bull. **1436:** 1–43. 1926.* [*Cornus florida* and *D. virginiana.*]

DAVIS, W. B., and C. G. CHURCH. The effect of ethylene on the chemical composition and the respiration of the ripening Japanese persimmon. Jour. Agr. Res. **42:** 165–182. 1931.

EDDY, C. O. The place of the native persimmon in nature, in relation to other plant communities, and to certain economic insects. Ohio Jour. Sci. **27:** 187–199. 1927.

FLETCHER, W. F. The native persimmon. U. S. Dep. Agr. Farm. Bull. **685**: 1–21. 1915. [Revised, 1928. 24 pp.*]

GERARDI, L. American persimmon varieties and their desirability. Ann. Rep. North. Nut Growers Assoc. **47**: 132–136. 1956.* (See also *ibid.* 136–138; **48**: 45–51. 1957.*)

GRIFFIOEN, K. A study of the dark coloured duramen of ebony. Rec. Trav. Bot. Néerl. **31**: 780–809. 1934. [A chemical study.]

HAGUE, S. M. A morphological study of *Diospyros virginiana.* Bot. Gaz. **52**: 34–44. *pls. 1–3.* 1911. [Mostly embryology.]

HEMSLEY, W. B. *Diospyros Kaki.* Bot. Mag. **133**: *pl. 8127.* 1907. (See also: Persimmons. (*Diospyros Kaki,* Linn. f. and *D. Roxburghii,* Carrière.) Kew Bull. **1911**: 235–245. 1911. [Supplements Bot. Mag.; includes extensive bibliography.])

HODGE, W. H. Freezing persimmons. Natl. Hort. Mag. **37**: 258–260. 1958.

HODGSON, R. W. Floral situation, sex condition, and parthenocarpy in the oriental persimmon. Proc. Am. Soc. Hort. Sci. **37**: 250–252. 1939.

——— and C. A. SCHROEDER. Effect of climate on fruit form in the Kaki persimmon. Proc. Am. Soc. Hort. Sci. **48**: 71–73. 1946.

HOLM, T. Medicinal plants of North America, No. 31: *Diospyros virginiana* L. Merck's Rep. **18**: 229–231. 1909.*

HOOKER, W. J. *Diospyros Sapota.* Bot. Mag. **69**: *pl. 3988.* 1843. [*D. Ebenum.*]

HOWARD, B. J. Tannin cells of persimmons. Bull. Torrey Bot. Club **33**: 567–576. 1906.

HUME, H. H. Non-fruiting of Japan persimmons due to lack of pollen. Science **30**: 308, 309. 1909.

———. The flowers of *Diospyros Kaki* L. f. Trans. St. Louis Acad. Sci. **22**: 125–135. *pls. 25–31.* 1913.*

———. A Kaki classification. Jour. Heredity **5**: 400–406. 1914.

KOMATSU, S., H. UEDA, and M. ISHIMASA. On the biochemical study of the ripening of the Kaki fruit. I–V. Jour. Biochem. **1**: 181–194. 1922; **2**: 291–300, 301–308, 309–313. 1923; **3**: 261–272. 1924.*

LLOYD, F. E. The behavior of tannin in persimmons with some notes on ripening. Pl. World **14**: 1–14. 1911.

———. I. The red colour of the mesocarp of seeded fruits in the persimmon (*Diospyros Kaki*). II. A visual method of estimating astringency. *Ibid.* **19**: 106–113. 1916.

MORETTINI, A. La biologia fiorale e di fruttificazione delle varietà del Diospiro o Kaki. Rivista Soc. Tosc. Ort. **72**: 109–122. 1947. [*D. Kaki, D. Lotus, D. virginana.*]

MOTTIER, D. M. Further notes on the seedless fruits of the common persimmon — *Diospyros virginiana* L. Proc. Indiana Acad. Sci. **1912**: 67, 68. 1913.

NAMIKAWA, I., M. SISA, and K. ASAI. On the flower types of *Diospyros Kaki* L. f. Jap. Jour. Bot. **6**: 139–172. 1932.

NOGUCHI, Y. Metaxenia in the Japanese persimmon. Shape and sweetness. Jap. Jour. Bot. **7**: 61–71. 1934. (See also KADIURA, M., Studies on metaxenia in Japanese persimmons. I. Direct effects of pollen upon fruit size. Jour. Hort. Assoc. Japan **5**: 259–271. 1934.*)

PLUMB, C. S. The American persimmon. Gard. & For. **9**: 442, 443. 1896. (See also **8**: 262. 1895.)

QUISUMBING, E. Continuity of protoplasm in endosperm cells of *Diospyros.* Bot. Gaz. **80**: 439–449. *pls. 23, 24.* 1925. [Plasmodesmata.]

RAO, T. A. Studies on foliar sclereids in dicotyledons. I. Structure and ontogeny of sclereids in the leaf of *Diospyros discolor* Willd. Proc. Indian Acad. Sci. B **34**: 92–98. 1951.*

RYERSON, K. A. Culture of the oriental persimmon in California. Revised by R. W. Hodgson. Univ. Calif. Agr. Exp. Sta. Berkeley Bull. **416**: 1–70. 1927.

SARGENT, C. S. *Diospyros*. Silva N. Am. **6**: 1–12. *pls. 252–254.* 1894.

SCHÖN, K. Studies on carotenoids. I. The carotenoids of *Diospyros* fruits. Biochem. Jour. **29**: 1779–1782. 1935.*

SERGEEVA, K. A. Development of generative buds in different species of persimmon. (In Russian.) Bull. Glav. Bot. Sada **1956**(24): 42–46. 1956.*

SKALLERUP, H. R. The distribution of *Diospyros virginiana* L. Ann. Missouri Bot. Gard. **40**: 211–226. 1953. [Map, ecological relationships, and extensive bibliography.]

———. Our self-pruning persimmon (*Diospyros virginiana*). Missouri Bot. Gard. Bull. **41**: 39, 40. 1953.

SMALL, J. K. *Diospyros virginiana*. Addisonia **3**: 9, 10. *pl. 85.* 1918.

TERAMI, H. A method of identifying the species with the root in *Diospyros Kaki* L. fil., *D. Lotus* L. and *D. virginiana* L. (In Japanese; English summary.) Jour. Hort. Assoc. Japan **9**: 129–133. *col. pl.* 1938.*

TOKUGAWA, Y., and A. YUASA. Notes on the tannin cells of persimmon. (In Japanese; English summary.) Bot. Mag. Tokyo **50**: 277–283. 1936.

TRABUT, L. Les *Diospyros* comestibles. Revue Bot. Appl. Agr. Col. **4**: 725–730, 829–834. 1924; **5**: 663–676. 1925; **6**: 541–547, 675–678. 1926. [*D. virginiana*, 541–546.]

UPHOF, J. C. T. Der persimmon in den Südstaaten von Nordamerika. Tropenpfl. **40**: 479–483. 1937.

———. *Diospyros virginiana* as stock for the Japanese persimmon in the United States. (In Japanese.) Jour. Hort. Assoc. Japan **12**: 11–14. 1941.*

WATTS, R. L. Persimmons. Univ. Tenn. Agr. Exp. Sta. Bull. **11**: 193–223. 1899.

WETTSTEIN, R. VON. Über Parthenokarpie bei *Diospyros Kaki*. Österr. Bot. Zeitschr. **58**: 457–462. 1908.

WHITE, F. Distribution of the African species of "Diospyros." Webbia **11**: 525–540. 1956. (See also, Notes on the Ebenaceae. I, II. Bull. Jard. Bot. Bruxelles **26**: 237–246, 277–307. 1956.)

WOODBURN, W. L. Development of the embryo sac and endosperm in some seedless persimmons. Bull. Torrey Bot. Club **38**: 379–384. *pl. 16.* 1911. [*D. virginiana.*]

YASUI, K. Studies on *Diospyros Kaki*. I. Bot. Gaz. **60**: 362–373. *pls. 12, 13.* 1915. [Monoecious; development of flowers and embryo sac.]

YOUNG, V. H. Persimmon seed for class use. Science **66**: 219, 220. 1927.

STYRACACEAE (STYRAX FAMILY)[4]

Shrubs or trees, usually more or less pubescent with stellate hairs [or peltate scales]. Leaves alternate, exstipulate, simple, entire, serrate or dentate, pinnately veined, the nodes with 1 trace from 1 gap. Flowers bisexual, in variously modified, basically cymose, terminal and axillary inflorescences (sometimes reduced to single axillary flowers). Calyx synsepalous, with 4 or 5 small teeth or lobes (or these obsolete), free from the ovary to completely adnate to it. Corolla sympetalous, usually 4- or 5-lobed [some-

---

[4] By C. E. Wood, Jr.

times more], valvate or imbricate in aestivation. Stamens usually twice (to 4 times) as many as the corolla lobes, inserted in a single series on the base of the corolla, the filaments usually more or less connate at the base, free above, usually continuous with the connective, the anthers oblong, 4-locular; pollen 3-colporate, usually suboblate. Gynoecium syncarpous, the ovary superior to inferior, (2)3–5-locular or 1-locular above by failure of union of the septa; style usually filiform; stigma terminal, usually minutely 3–5-lobed. Ovules 1–many in each locule, axile, anatropous, pendulous, or erect, 2-integumented, or 1-integumented (presumably by fusion of the two). Fruit typically dry, indehiscent or dehiscent; seeds 1 to several, the seed coat thin to indurate; embryo usually straight, with broad cotyledons, surrounded by fleshy endosperm.

A family of about 13 genera, all except *Styrax* small, including about 150 species, centering in eastern Asia, but with numerous species in the New World, none in Australia, one in the eastern Mediterranean region, and about three in Africa. The family exhibits the marked disjunctions indicative of an ancient group.

The Styracaceae are characterized by a series of characters which contrast markedly with those of the Symplocaceae (*q.v.*). They are distinguished from other sympetalous groups by the combination of watery sap; bisexual flowers with stamens at least twice as many as the petals and apparently in a single series; oblong to linear, basifixed anthers with longitudinal dehiscence; single, linear style; superior to inferior, 2–5-locular ovary; and usually dry, capsular to indehiscent fruit. Stellate pubescence is characteristic of the entire family, in contrast with the simple hairs of Symplocaceae, the two-armed hairs of Sapotaceae, and the several types found in the Ebenaceae. Erdtman notes that pollen more or less similar to that of Styracaceae is found in the Ebenaceae, and that at least slightly similar pollen occurs in the Cornaceae and Nyssaceae, while that of Symplocaceae is different.

The Styracaceae include a number of ornamental trees and shrubs (especially *Styrax* and *Halesia*). *Styrax officinale* formerly was the source of storax, a gummy resin used in incense, and from *S. Benzoin* is obtained benzoin, a resin which is secreted when the bark and wood of the tree are injured.

REFERENCES:

BAILLON, H. Loranthacées. III. Styraceae. Hist. Pl. **11**: 458–462. 1892. [Includes *Symplocos*.]

BENTHAM, G., and J. D. HOOKER. Styracaceae. Gen. Pl. **2**: 666–671. 1876.

COPELAND, H. F. The *Styrax* of northern California and the relationships of the Styracaceae. Am. Jour. Bot. **25**: 771–780. 1938.

DECANDOLLE, A. Styracaceae. Prodr. **7**: 244–272. 1844.

GÜRKE, M. Styracaceae. Nat. Pflanzenfam. IV. **1**: 172–180. 1891.

PERKINS, J. Styracaceae. Pflanzenr. IV. **241**(Heft 30): 1–111. 1907.

———. Übersicht über die Gattungen der Styracaceae sowie Zusammenstellung der Abbildungen und der Literatur über die Arten Dieser Familie bis zum Jahre 1928. 36 pp. Leipzig, 1928.

TIEGHEM, P. VAN. Structure de quelques ovules et parti qu'on en peut tirer pour améliorer la classification. Jour. Bot. Morot **12**: 197–220. 1898. [Styracaceae, 201, 202.]

1. **Styrax** Linnaeus, Sp. Pl. **1**: 444. 1753; Gen. Pl. ed. 5. 203. 1754.

Deciduous [or evergreen] shrubs or trees with entire or slightly serrate or dentate leaves; nearly all parts more or less pubescent with stellate hairs (or rarely glabrous). Inflorescences terminal or axillary, basically cymose but appearing racemose, the axillary sometimes reduced to single flowers, as in *S. americanum*, thus giving the appearance of partly foliose racemes. Calyx synsepalous, cup-like, 5-toothed (or rarely 2- or 3-toothed) [or undulate or subentire]. Corolla 5 (rarely 6 or 7)-parted, always white, valvate, valvate-induplicate, or imbricate in aestivation, the tube (usually) much shorter than the lobes. Stamens 10 [8–18], adnate to the tube of the corolla in a ring [and monadelphous in a short tube], the filaments continuous with the connective, glabrous or pilose or densely pilose at the base. Gynoecium syncarpous; stigma small, minutely 3-lobed, terminal; style linear, with a canal; ovary partially adnate to the calyx [or rarely free], 3-locular at the base, 1-locular above (the 3 parietal septa united below but incompletely united above with the central placental mass); ovules axile, usually 4–6 in each locule, 2-integumented and with an obturator (a massive outgrowth of the placenta), one of the uppermost developing into a seed. Fruit globose or oblong, dry, loculicidally 3-valvate [or irregularly dehiscent or indehiscent]; seeds 1 or rarely 2, subglobose or ellipsoid, with a basilateral hilum, the testa hard, smooth [or crustaceous, wrinkled, papillate, or with stellate hairs]. TYPE SPECIES: *S. officinale* L. (The name Greek, *styrax*, the ancient name for storax, a fragrant resin formerly used in incense, and for the plant (*S. officinale*) from which it was obtained.[5] — STORAX.

A genus of about 120 species, mostly tropical and subtropical, of eastern Asia southward to New Guinea (but absent from the Philippines and Ceylon), the eastern Mediterranean region (a single species), South America, the West Indies, and Central America; about six species in the United States, two in our area. Two sections were recognized by Perkins: STYRAX (*Eustyrax* Perk.), with ovary 16–24-ovulate, and FOVEOLARIA (Ruiz & Pavon) Perk., with ovary 3–5 ovulate (2 species, Cuba and Peru).

Styrax americanum Lam., with flowers solitary or in pairs in the axils of leaves and paired at the tips of short branches, partially imbricate to valvate-induplicate aestivation of the corolla-lobes, and leaves 2–10 cm. long,

---

[5] Different authors have treated the genus as neuter, feminine, or masculine. *Styrax* is masculine in Latin. In Greek it is masculine, feminine, or neuter, depending upon its meaning: the spike at the lower end of a spear-shaft (m.), the shrub or tree from which storax was obtained (f.), or the resin storax (n.). Linnaeus took *Styrax* from the Greek (see "Critica Botanica") and treated it as neuter throughout his work. Although one would expect the word to be feminine, following the Greek gender for the plant, in this instance it should be argued that there was a choice. Under Recommendation 75A(1) of the International Code of Botanical Nomenclature, Linnaeus' consistent practice in this matter should be followed, whether or not he followed his own precepts.

is a frequent shrub of low, acid, mostly nonalluvial soils from southwestern Florida, northward on the Atlantic coastal plain to southeastern Virginia, into the mountains of northeastern Alabama, and in the Mississippi embayment to western Tennessee, western Kentucky, southern Illinois, Indiana and Ohio, southeastern Missouri, the southeastern half of Arkansas, and eastern Texas. Pubescence and seed- and fruit-size are variable within the species and should be studied in connection with the status of forma *pulverulentum* (Michx.) Perk. (var. *pulverulentum* (Michx.) Rehd.).

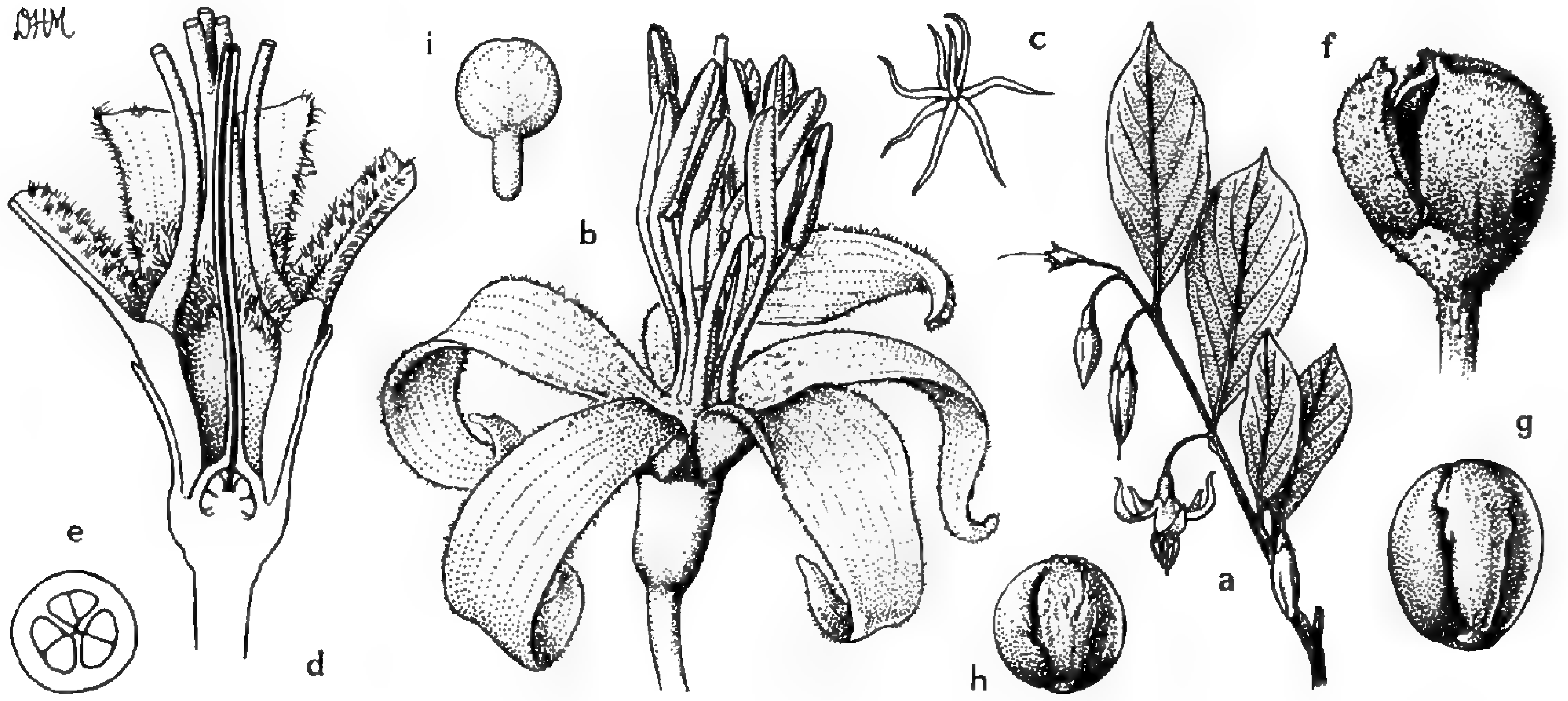


FIG. 3. **Styrax.** a–i, *S. americanum*: a, flowering twig, × ½; b, flower, × 3; c, stellate hair from petal, × 50; d, flower in vertical section, the distal portions of petals, stamens, and style removed — note partially inferior ovary, stylar canal, large placenta, incomplete septation, × 5; e, cross section of ovary through uppermost ovules to show incomplete septation (semidiagrammatic), × 8; f, capsular fruit with single large seed, × 2; g, h, seeds from two Florida collections — compare size, note prominent raphe and basal hilum, × 2; i, embryo, × 3.

Styrax grandifolium Ait., with larger, apparently terminal, mostly bracteate "racemes" (with as many as 20 flowers), imbricate aestivation, obovate leaves 5–20 cm. long, larger, somewhat more elongate fruits, and larger seeds, is a handsome shrub or small tree of woodlands, bluffs, and stream banks, ranging from northern Florida to Louisiana, northward to central Arkansas, northeastern Mississippi, western Tennessee (along the western edge of the Highland Rim), northern Alabama, northeastern Georgia, and through the piedmont and coastal plain of North Carolina to southern Virginia. Although the ranges overlap in large part, the two species seem to be completely isolated ecologically.

Section STYRAX was divided by Gürke and by Perkins into two series, *Valvatae* and *Imbricatae*, on the basis of aestivation of the corolla lobes. As Van Steenis has shown, however, imbrication may vary widely with respect to both the individual and species. (Cf. *S. americanum*.) Although both of our species were placed with the *Imbricatae* by Perkins, neither appears to be closely related to the other, and, with the exception of *S. glabrescens* Benth. (Hidalgo and Veracruz, Mexico, to Costa Rica), which is close to *S. grandifolium*, the relatives of both are all species of eastern Asia. The chromosomes of *S. Obassia* Sieb. & Zucc. (related to *S. grandifolium*) have been reported as $2n = 16$, and those of *S. japonicum* Sieb. & Zucc. (close to *S. americanum*?) as $2n = 40$.

The embryology, morphology, and anatomy of *Styrax officinale* var. *californicum* (Torr.) Rehd. have been studied in some detail, and Van Steenis has pointed out numerous biological features of the species of the East Indies. Curious tubular galls of several characteristic shapes are produced on the Asiatic species by Aphidae of the genus *Astegopteryx*.

Six or more of the hardier species of *Styrax* are in cultivation in the United States for their showy white flowers.

REFERENCES:

COPELAND, H. F. The *Styrax* of northern California and the relationships of the Styracaceae. Am. Jour. Bot. **25:** 771–780. 1938. [*S. officinale* var. *californicum*; morphology, anatomy, embryology.]

CORY, V. L. The genus *Styrax* in central and western Texas. Madroño **7:** 110–115. 1943. [*S. texanum*, *S. Youngiae*, *S. platanifolium* and *S. platanifolium* var. *stellatum*.]

SIMS, J. *Styrax laevigatum* [*S. americanum*]. Bot. Mag. **23:** *pl. 921.* 1806. (See also *S. serrulatum* [*S. japonicum*], **98:** *pl. 5950.* 1872; *S. Obassia*, **115:** *pl. 7039.* 1889; *S. Hemsleyanus*, **136:** *pl. 8339.* 1919; *S. Wilsonii*, **138:** *pl. 8444.* 1912; *S. japonica*, Addisonia **7:** 13. *pl. 231.* 1922.)

STEENIS, C. G. G. J. VAN. The Styracaceae of Netherlands India. Bull. Jard. Bot. Buitenzorg III. **12:** 212–272. 1932. [*Bruinsmia*, *Styrax*; many important notes, extensive bibliography.]

2. **Halesia** Ellis ex Linnaeus, Syst. Nat. ed. 10. 1044, 1369. 1759, nom. cons.

Deciduous shrubs or trees with membranaceous, serrulate leaves. Inflorescences reduced to clusters or irregular short racemes of 2–4(–5) long-pedicelled, pendent flowers in the axils of scars of leaves of the preceding year. Flowers 4-merous, showy, produced in early spring. Calyx almost completely adnate to the ovary, 4-ribbed, with 4 small teeth at the summit, or these obsolete. Corolla white to pale pink, campanulate, 4-cleft or -lobed, imbricate in aestivation but open long before anthesis. Stamens 8–16, united for about ⅓ their length and adnate to the lower part of the corolla; filaments straight, continuous with the connective; anthers oblong, slightly curved outward, introrse, dehiscing lengthwise. Style slender, linear, stigma minutely 4-lobed; ovary almost completely inferior, the sterile tip tapering into the style, 2- or 4-locular, each locule with four 1-integumented ovules attached near the middle of the axis, the 2 upper erect, the 2 lower pendulous. Ovary elongating greatly after anthesis; fruit dry, indehiscent, beaked and winged, with a hard, clavate-fusiform endocarp, a thin, corky mesocarp and 2 or 4 corky, longitudinal wings. Seeds 1–3, nearly cylindrical, against the wall of the endocarp, completely surrounded by a stony covering, the remaining cavity of the endocarp filled with corky tissue. (*Mohria* Britton, not Swartz; *Mohrodendron* Britton, *Carlomohria* Greene;

not *Halesia* P. Br., 1756, nom. rejic.) TYPE SPECIES: *H. carolina* L. (Named in honor of Stephen Hales, 1677–1761, author of "Vegetable Staticks" in 1722.) — SILVERBELL-TREE, SNOWDROP-TREE.

Two to four species of the southeastern United States and one species of Chekiang and Kwantung, China.

The genus is in need of a careful revision with particular emphasis on populations and studies of fully developed flowers and mature fruits. Herbarium materials are not very satisfactory in this group, for corollas and green fruits shrink and become distorted in drying, and the wings of ripe fruits are corky and brittle. In addition, the corolla attains its general shape early and is quite open while still green and half-grown, continuing to enlarge until (? or after) anthesis, thus leading to erroneous comparisons of size. Pubescence may be ephemeral, and plants may begin to flower at an early age.

Halesia diptera Ellis is a well-defined species distributed across the southern Coastal Plain in a band roughly delimited by Chatham County, Georgia; Leon County, Florida; Elmore and Chilton counties, Alabama; Ouachita and Natchitoches parishes, Louisiana; and Sabine and Harris counties, Texas. The type material came from near Augusta, Richmond County, Georgia, and the species has been reported in the Georgia piedmont in Meriwether and Upson counties. The plant is a shrub or tree up to 10 m. tall, with elliptic to obovate, abruptly long-acuminate, remotely sinuate-serrulate leaves, tomentose calyx and pedicels, a deeply cleft corolla 1.5–3 cm. long, with a very short tube and oval to obovate lobes, 8 equal stamens, 2-locular ovary (rarely 4-locular), and a fruit with 2 broad wings. Fruit shape is variable, with the wings either rounded or tapered at the base. Two varieties have been distinguished: var. *magniflora* Godfrey, described as limited to mixed woodlands of upland slopes, river bluffs, and ravine slopes in the limited area from Leon to Jackson County, Florida, with corollas 2–3 cm. long and lobes 1–1.5 cm. broad; and var. *diptera*, inhabiting flood-plain forests of the Escambia and Choctawahatchee rivers of western Florida, and ranging westward and northeastward, with corollas 1–1.5 cm. long and lobes 0.8–1 cm. broad. Further study is needed, for, although plants to the west of Florida appear to be small flowered, the larger-flowered plant apparently occurs in southwestern Georgia and adjacent Alabama, and, in Chatham County, Georgia, the easternmost locality for the species, the flowers are as large as those from Leon County, Florida.

A second group is the *Halesia carolina* complex which is distributed primarily from western North Carolina and eastern Tennessee to the coastal plain of Georgia, northern Florida, Alabama, and Mississippi. The group extends northward across western Virginia into southern West Virginia along the New River drainage, and scattered stations occur along the Cumberland River drainage (Harlan County, Kentucky; Davidson County, Tennessee), along the Tennessee River (Lauderdale County, Alabama; Hardin and Decatur counties, Tennessee), and on the Ohio River near the

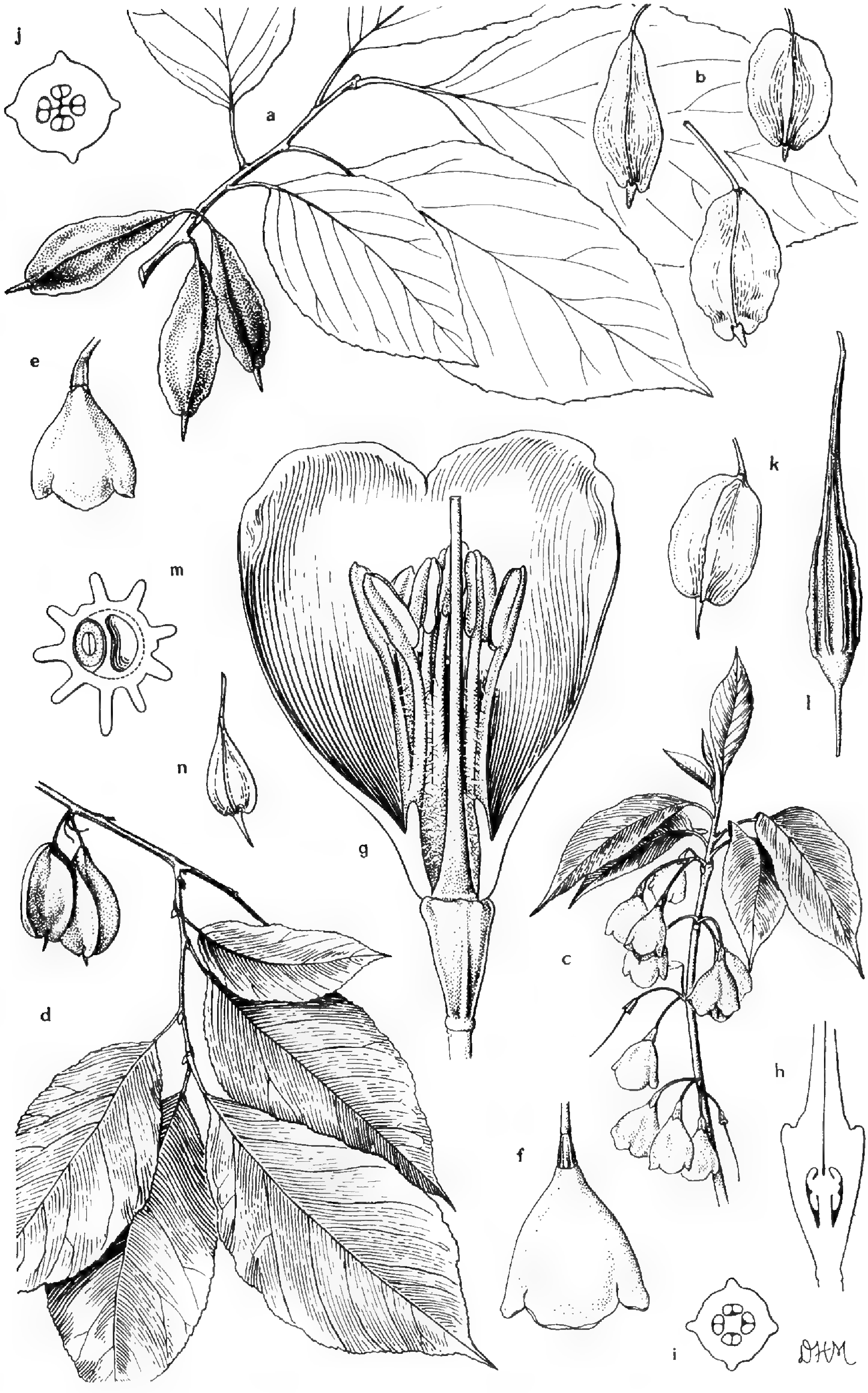


FIG. 4. **Halesia.** a, b, *H. diptera*: a, fruiting branchlet, × ½; b, fruit variants, × ½. c–e, *H. carolina* var. *carolina*: c, d, flowering and fruiting branchlets, × ½; e, flower, lateral view, × 1. f–m, *H. carolina* var. *monticola*: f,

mouth of the Tennessee (Massac County, Illinois), suggesting migration along these routes by means of the floating, corky-winged fruit. An isolated series of stations occurs across central Arkansas into southeasternmost Oklahoma. Members of this complex have ovate to elliptic or oblong-obovate, acuminate, closely serrulate leaves; glabrous to tomentose pedicels and calyx; campanulate, shallowly lobed corollas 1–2.5 cm. long; 10–16 stamens; a 4-locular ovary; and 4-winged fruits 2–6 cm. long, with wings broad to narrow and rounded to long-tapering at the base. The extremes of the complex are distinctive, but the variation is puzzling and the taxa have not been carefully studied or clearly defined. One extreme, *H. monticola* (Rehd.) Sarg. (*H. carolina* var. *monticola* Rehd.), is a tree to 30 m. tall, of the higher mountains of North Carolina, Tennessee, and northern Georgia, with large corollas and large fruit with wings up to 15 mm. wide, truncate or rounded (and often widest) at the base. It appears to pass into *H. carolina* (*H. tetraptera* Ellis[6]), a shrub or tree to 10 m. tall, with

---

[6] Although *Halesia tetraptera* Ellis long has been identified with *H. carolina* L., the name recently has been adopted for *H. parviflora* Michx. on the basis of the illustration in Ellis' paper (Trans. Roy. Soc. London **51**: 931. *pl. 22.* 1761). From this illustration alone one may well conclude that the small flowers and tapering fruits illustrated are those of *H. parviflora* (described from St. Johns Co., Florida), but other evidence from the letters of Alexander Garden to John Ellis and from Ellis to Linnaeus (see J. E. Smith, A Selection of the Correspondence of Linnaeus, and Other Naturalists, from the Original Manuscripts **1**: 82, 83, 88, 92, 93, 373–382. 1821) suggests that the usual disposition of the name is the more correct one. From this correspondence it is clear that the plant was collected "on the hills, 200 miles to the northwest of that city [Charleston, S. C.] at a place called Saluda [Saluda Co., S. C.]," where Alexander Garden went in the course of June and July, 1755. In the spring of 1756, Garden's brother-in-law, a Mr. Perroneau, took to Ellis "the branch with the fruit, and a sprig with the flowers," which were the basis of the illustration by Ehret in Ellis' paper, along with mature fruits which, although planted in June, 1756, did not germinate until May of the following year.

Thus, although Ellis' published account of *Halesia tetraptera* (quoting from Garden) noted only that the plant "grows commonly along the banks of Santee river," the more precise information places the type locality off the Coastal Plain and apparently within the range of *H. carolina*, rather than that of *H. parviflora*. The seedlings raised in England by Ellis were almost certainly *H. carolina*, for as recently as 1951, both Bean (Trees and Shrubs Hardy in the British Isles. ed. 7. **2**: 80) and the Royal Horticultural Society Dictionary of Gardening fail to note *H. parviflora* in cultivation there, and the plant illustrated by Sims in 1806 (Bot. Mag. **23**: *pl. 910*), with the comment that this was first raised in England by Ellis from seeds sent over by Dr. Alexander Garden in 1756, can be only *H. carolina*.

Finally, Ehret's illustration in Ellis' paper, having been prepared from dried specimens sent by Garden, must be considered in terms of the shrinkage of flowers and fruits in drying and of the habit of the corollas of opening when only half grown. Both of these phenomena may apply here. The fruiting branch illustrated (see also reproduction of Ehret's illustration in Rhodora **60**: 86. *pl. 1231.* 1958) appears to represent *H. carolina* with the wings of the fruit somewhat shrunken in drying. The small flowering branch, on the other hand, bears flowers which appear to be not yet

---

flower, lateral view, × 1; g, flower with two petals, eight stamens removed, × 3; h, ovary, vertical section, × 4; i, j, ovary, cross sections through lower and upper ovules, respectively, × 6; k, fruit, × ½; l, endocarp from a very large fruit, × 1; m, endocarp, cross section with seed, endosperm (stippled), embryo, and cavity, × 3; h–j, m, semidiagrammatic. n, *H. parviflora*: fruit, × ½.

smaller corollas and smaller fruit with narrower wings often tapering into the pedicel. The other extreme, *H. parviflora* Michx., a shrub or tree to 10 m. tall, perhaps restricted to sandy woods and bluffs of the Coastal Plain from Georgia and Florida to Mississippi, but possibly entering the Piedmont, has, in its best development, small, rather flaring corollas about 1.2 cm. long, pubescent calyces, and fruits 2.5–3.5 cm. long with narrow wings 3–5 mm. wide tapering into the pedicels (thus giving the effect of a clavate fruit). Most distinctive in northeastern Florida, this plant appears to intergrade with *H. carolina*; plants from the central areas of South Carolina, Georgia, and Alabama need special study in this respect. Throughout this complex the shape and size of the stony endocarp seem to be roughly the same; the varying shape and width of the four wings produces the wide range of fruit-shapes. The length of the style seems also to be more or less constant: thus it is equalled or exceeded by the corollas of *H. carolina* (including *H. monticola*), but protrudes from the short, rather flaring corollas of *H. parviflora*.

The Chinese species, *H. Macgregorii* Chun, combines a deeply parted corolla (as in *H. diptera*), four-winged fruits (as in *H. carolina*), and eight stamens of two lengths (eight equal stamens in *H. diptera*). The ovary is said to be 3-locular. *Halesia* (with *Nyssa, Carya,* and a few others) is of interest in being a genus of the eastern American–eastern Asiatic distribution in which more representatives occur in America than in Asia. In most genera following this pattern the Asiatic contingent appears both to be more numerous and to include more primitive species than the American. *Halesia* is most closely related to *Pterostyrax* Sieb. & Zucc., (5 species, Japan, China, Burma), *Rehderodendron* H. H. Hu (9 species, China, Indochina), *Sinojackia* H. H. Hu (3 species, China), and *Melliodendron* Hand.-Mazz. (2 species, China).

REFERENCES:

GIBSON, H. H. American forest trees — 15. Silverbell tree, *Mohrodendron carolinum* (Linn.) Britton; *Halesia tetraptera* Ellis. Hardwood Rec. **20:** 10, 11. 1905.* [See also pp. 600–604, of his American Forest Trees, Chicago, 1913.]

GIERSBACH, J., and L. V. Barton. Germination of seeds of the silverbell, *Halesia carolina*. Contr. Boyce Thompson Inst. **4:** 27–37. 1932. [Warm stratification followed by cold; see also, Woody plant seed manual. U. S. Dep. Agr. For. Serv. Misc. Publ. **654:** 193, 194. 1948.]

GODFREY, R. K. Some identities in *Halesia* (Styracaceae). Rhodora **60:** 86–88. *pl. 1231.* 1958. [*H. diptera* var. *magniflora*; adopts *H. tetraptera* Ellis for *H. parviflora* Michx.]

---

at full size and which are perhaps somewhat shrunken in drying. The details of the corolla illustrated are hardly compatible with fully developed corollas of either *H. carolina* or *H. parviflora*. Fruiting material shrunken in such a way may be matched by *Fox 5265*, Rutherford Co., N. C. (GH); *Duncan 3349*, Clarke Co., Ga. (A); and *Faxon*, Oct. 1896, cultivated, Jamaica Plain, Mass. (GH). An instructive series is formed by *E. J. Palmer 20739, 20763, 26760* [*20760?*], April 11, 12, 1922, from near Page, LeFlore Co., Oklahoma (A): in these collections corollas of plants in various stages of development are approximately 2, 1.2–1.5, and 0.7 cm. long, respectively.

LITTLE, E. L. Nomina conservanda proposals for ten genera of trees and shrubs. Madroño 7: 240–251. 1944. [*Halesia*, including history, 250, 251.]

OERSTED, A. S. Zur Beleuchtung der Blumen des brasilianischen Theestrauches (*Neea theïfera* Örd. 1863 = *Pisonia Caparrosa* Netto 1866) und des Schneeglockchenstrauches (*Halesia tetraptera* L.). Bot. Zeit. **27**: 216–223. 1869. [*Halesia*, *222, 223*; reports bisexual flowers with 12 stamens, and in the same inflorescence staminate flowers 1/10–1/15 as large with 10–15 sessile stamens and a rudimentary pistil. Merely immature flowers?]

OSBORN, B. *Halesia diptera* Ellis, a new tree record from Oklahoma. Proc. Okla. Acad. Sci. **18**: 21. 1938. [Misidentification; *H. carolina* with wings of young fruit obscured in pressing.]

SARGENT, C. S. *Mohrodendron.* Silva N. Am. **6**: 19–24. *pls. 257–259.* 1894. [*H. carolina*, *H. diptera.*]

SIMS, J. *Halesia tetraptera.* Bot. Mag. **23**: *pl. 910.* 1806. (See also J. Lindley, *Halesia parviflora.* Bot. Reg. **11**: *pl. 952.* 1826. [*H. carolina.*])

SYMPLOCACEAE (SWEETLEAF FAMILY)

Trees or shrubs with alternate, simple, more or less coriaceous, exstipulate leaves, the nodes with one trace from one gap; complete, regular, sympetalous flowers; numerous[–4] stamens with ovate anthers; 2–5-locular inferior or half-inferior ovaries, typically with 2 pendulous, axile, 1-integumented ovules in each locule, and drupaceous or baccate fruits.

A small unigeneric family of approximately 300 species (placed in eight sections in four subgenera by Brand), of the warmer parts of America, Asia, and Australia (absent from Africa and Europe), the species very numerous in South America, about eight species ranging northward into Mexico, about 18 in the West Indies, and one in the United States, this primarily of our area, but extending into adjacent regions. Many of the species apparently are of local distribution, endemic to islands or mountains.

The Symplocaceae presumably are closely related to the Styracaceae, but differ in a number of characteristics: stamens usually in several series, often fasciculate (vs. stamens apparently in a single series in Styracaceae); ovate anthers (vs. oblong or linear anthers); inferior or half-inferior, completely loculed ovary (vs. superior to inferior, incompletely loculed ovary); baccate or drupaceous fruit (vs. dry, capsular to indehiscent fruit); simple hairs (vs. stellate or peltate hairs); usually rubiaceous stomata (vs. ranunculaceous stomata); solitary vessels with elongated pits between vessels and rays in the secondary wood (vs. solitary or clustered vessels with small, round pits between vessels and rays); and the occurrence of spiral thickenings in the vessels, commonly, and in the fibers, occasionally (vs. the lack of such thickenings).

The family is of limited economic importance. A few species are sometimes used for their wood, the leaves and bark of several (including *S. tinctoria*) yield a yellow dye, the roots of some are used in the preparation of tonics, and the leaves of several species are used as a substitute for *maté* (primarily from *Ilex* species). *Symplocos paniculata* (Thunb.) Miq.

(subg. HOPEA, sect. BOBUA), with terminal clusters of white flowers and methyl-blue fruits, and a few other Asiatic species are sometimes grown as ornamental shrubs.

The biological features of the group seem to have been studied hardly at all.

1. **Symplocos** Jacquin, Enum. Syst. Pl. Carib. 5. 1760; Select. Stirp. Am. Hist. 166. *pl. 175, fig. 68.* 1763.

Deciduous or tardily deciduous shrubs or trees with more or less coriaceous, sweet-tasting leaves. Flowers in congested or open, racemose or paniculate inflorescences, in ours about 6–14 in short, sessile, close clusters or racemes axillary to leaves or their scars, yellow, fragrant. Calyx adherent to the lower portion of the ovary, persistent, the 5 lobes valvate or imbricate. Corolla sympetalous, 3–11-lobed, deeply 5-lobed in ours, the tube short. Stamens [4–]many, conspicuous, exserted, in several unequal series, epipetalous at the base of the corolla, [free or monadelphous, the filaments connate in a tube, or] in ours pentadelphous, in 5 groups alternate with the corolla-lobes, the innate anthers short, orange, the filaments slender, white, distinct except at the base. Pollen usually 3-colpate. Gynoecium syncarpous; stigma terminal, slightly dilated or capitate, minutely lobed; style linear, the ovary inferior or half-inferior, in ours surrounded at the top by an orange-colored disc of nectariferous spongy tissue, 3[2–5]-locular; placentation axile, the anatropous (?)1-integumented ovules pendulous, typically 2 in each locule. Fruit drupaceous [or baccate], in ours cylindric-ellipsoid, about 1 cm. long; usually only a single seed developing; embryo straight [or curved], with short cotyledons, and with copious endosperm. (*Hopea* L. f., 1767, not Roxb., 1814.) TYPE SPECIES: *S. martinicensis* Jacq. (The name from Greek, *symplokos*, connected, twisted, entwined, apparently referring to the union of the stamens with each other and with the petals in *S. martinicensis.*)

Symplocos tinctoria (L.) L'Her., sweetleaf, horse-sugar, wild laurel, or yellow-wood, the only species indigenous to the United States, occurs from Sussex County, Delaware, southward to northern Florida and westward to eastern Texas and southeastern Oklahoma. Varietas *tinctoria*, with glabrous fruits, glabrous or glabrate current stems and tardily deciduous leaves, is widespread on the Coastal Plain, where it is largely restricted to hammocks, the margins of swamps and to sandy soils in association with *Pinus*, *Nyssa*, *Persea*, *Magnolia*, etc. Varietas *Ashei* Harbison, with pubescent fruits, persistently hairy stems, and promptly deciduous leaves, is distributed over a limited region of the southern Appalachians in western North and South Carolina, northern Georgia, and southeasternmost Tennessee (a single station in Polk County), between 1800 and 4500 feet in altitude, on dry ridges of chiefly acid, red-clay soils, where it is associated with *Pinus rigida* Mill., *Quercus coccinea* Muenchh., *Q. Prinus* L., and (formerly) *Castanea dentata* (Marsh.) Borkh. It appears largely to be lacking between mountains and Coastal Plain, although scattered stations may be expected in the Piedmont and are known from at least Aiken County, South Carolina, and Wake County, North Carolina. The geographical isolation of these varieties can be determined only after additional stations are sought, particularly in the Piedmont and in northern Alabama (where the species has been reported as far north as Marion, Cullman, and Morgan counties). Varietas *pygmaea* Fern., based upon dwarf, sterile specimens with small leaves, from white sands of dry pine barrens in Isle of Wight County, southeastern Virginia, is doubtfully distinct. The typical variety occurs in abundance in this general area of the state.

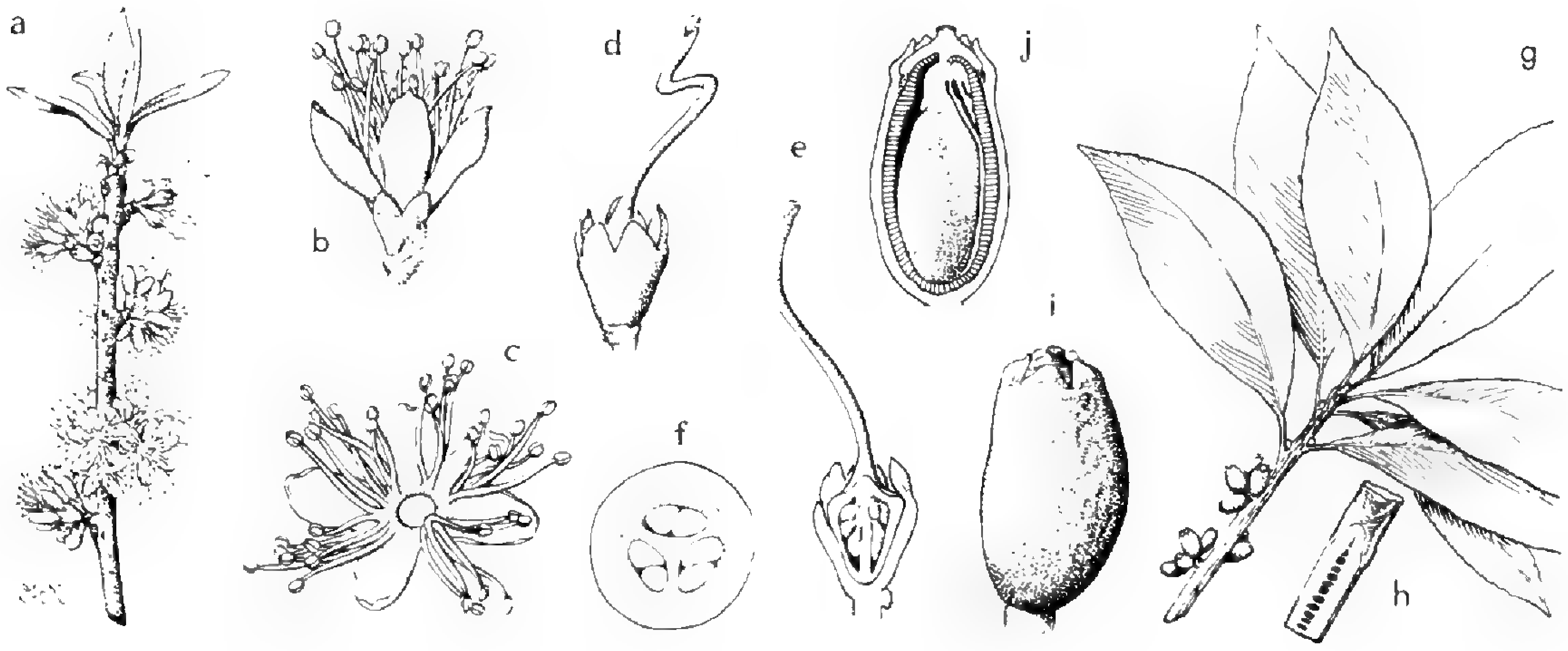


FIG. 5. **Symplocos.** a–j, *S. tinctoria* var. *tinctoria*: a, flowering twig, × ½; b, flower, × 2; c, detached corolla with stamens, × 2; d, flower with corolla removed, × 3; e, same, the ovary in vertical section (semidiagrammatic), × 3; f, cross section of ovary at anthesis — stippled area becomes sclerified in fruit (semidiagrammatic), × 6; g, fruiting twig, × ¼; h, portion of twig in oblique section to show diaphragmed pith, × ½; i, mature fruit, × 2; j, mature fruit, vertical section, the fertile locule with seed to left and center, abortive locules to right, × 2.

Characteristically a shrub, *Symplocos tinctoria* occasionally attains arborescent proportions (nearly 30 cm. in diameter and 12 m. tall) in the fertile river bottoms of Mississippi which usually are inundated for several weeks of the year.

Brand placed *Symplocos tinctoria* near *S. japonica* A. DC. and *S. setchuensis* Brand as the only American species of subg. HOPEA (L. f.) C. B. Clarke, sect. PALAEOSYMPLOCOS Brand, a group distinguished on the basis of the 3-locular ovary and clearly pentadelphous stamens with filiform filaments. However, because the summit of the ovary is glabrous and the united portion of the stamen-filaments is flattened (instead of round in section), Handel-Mazzetti and Peter-Stilbal excluded *S. tinctoria* from the subgenus (which was then renamed as subg. EOSYMPLOCOS), suggesting that its relationships should be sought among the New World species. Inconsistently, sections LODHRA and BOBUA (also of subg. HOPEA) were defined by the latter authors to include species with the apex of the ovary either glabrous or pubescent! It may be significant that at least some specimens of *S. tinctoria* var. *Ashei* have a few hairs on the summit of the ovary at anthesis.

The subdivisions of *Symplocos* have been treated by some authors as separate genera, although most have maintained the group as a single genus with well-marked subgenera or sections. Erdtman, noting a variety of pollen types in *Symplocos*, suggests that pollen morphology "may be instrumental in subdividing the genus (or — if considered appropriate — in referring the different species to a number of genera now usually regarded as sections etc. under *Symplocos*)."

REFERENCES:

ANONYMOUS. *Symplocos tinctoria.* Natl. Hort. Mag. **15:** 268, 271. 1936; **19:** 132, 133. 1940. [Fruiting and flowering plants, respectively.]

BENTHAM, G., and J. D. HOOKER. Styracaceae. Gen. Pl. **2:** 666–671. 1876. [*Symplocos*, 668.]

BRAND, A. Symplocaceae. Pflanzenr. IV. **242**(Heft 6): 1–100. 1901. [281 species; 114 described as new.]

CADOR, L. Anatomische Untersuchung der Mateblätter unter Berücksichtigung ihres Gehaltes an Thein. Bot. Centralbl. **84:** 241–251, 275–283, 309–315, 340–345, 369–374. 1900. [*Symplocos*, 248, 249, 345, 369–371.]

CHIRTOIU, M. Remarques sur le *Symplocos Klotzschii* et les affinités des Symplocacées. Bull. Soc. Bot. Genève II. **10:** 350–361. 1918.

DECANDOLLE, A. Styracaceae. Prodr. **8:** 244–272. 1844. [*Symplocos*, 246–258.]

GAYTONDE, N. S., K. C. CHATTERJEE, and M. L. KHORANA. Pharmacognostic studies of *Symplocos racemosa*, Roxb., and *S. baddomei*, C. B. Clarke. Indian Jour. Pharm. **12:** 290–300. 1950.* [Detailed information on morphology.]

GÜRKE, M. Symplocaceae. Pflanzenfam. IV. **1:** 165–172. 1890.

HANDEL-MAZZETTI, H., and E. PETER-STILBAL. Eine Revision der chinesischen Arten der Gattung *Symplocos* Jacq. Beih. Bot. Centralbl. **62:** 1–42. 1943. [68 spp.; comments on relationships of *S. tinctoria.*]

HARBISON, T. G. *Symplocos tinctoria Ashei*, a new dyebush from the southern mountains. Jour. Elisha Mitchell Sci. Soc. **46:** 218–220. 1931.

KEARNEY, T. H. Report on a botanical survey of the Dismal Swamp region. Contr. U. S. Natl. Herb. **5:** 321–550. 1901. [Leaf anatomy of *S. tinctoria*, 503, 504.]

MIERS, J. On the Symplocaceae. Jour. Linn. Soc. Bot. **17:** 283–306. 1880. [Splits *Symplocos* into several genera.]

MOLISCH, H. Vergleichende Anatomie des Holzes der Ebenaceen und ihrer Verwandten. Sitz-ber. Akad. Wien **80**(1): 54–83. 1879.

MOLLIARD, M. Notes de pathologie végétale. Revue Gén. Bot. **10:** 87–101. 1898. [IV. Modifications anatomiques déterminées chez un *Symplocos* par l'*Exobasidium Symploci* Ellis, 96–101. *pl. 15.*]

SARGENT, C. S. *Symplocos.* Silva N. Am. **6:** 13–16. *pls. 255, 256.* 1894.

TRAVERSE, A. Pollen analysis of the Brandon lignite of Vermont. U. S. Dep. Interior Bur. Mines Rep. Invest. **5151:** 1–107. 1955. [*Symplocos* pollen present; *Symplocos* also noted abundant in German brown coal.]

TURRILL, W. B. *Symplocos paniculata.* Bot. Mag. **168:** *pl. 149.* 1951.

URBAN, I. Addimenta ad cognitionem florae Indiae occidentalis. Bot. Jahrb. **15:** 286–361. *pl. 9.* 1892. [*Symplocos*, 328–337.]

WEHNERT, A. Anatomisch-systematische Untersuchung der Blätter der Gattung "Symplocos." Inaug. Diss. Univ. München. 58 pp. 1906. [69 spp.; *S. tinctoria*, p. 33.]

WILSON, E. H. *Symplocos paniculata.* Gard. Chron. III. **74**: 262, 263. 1923.

THE ARNOLD ARBORETUM
AND
VANDERBILT UNIVERSITY

A TAXONOMIC REVISION OF PODOCARPUS, XII. SECTION MICROCARPUS

NETTA E. GRAY

PODOCARPUS USTUS (Vieillard) Brongniart and Gris, the only species in section *Microcarpus*, is a very curious, small, twiggy shrub found in several places in the mountain forests of New Caledonia. Vieillard and Deplanche, the first collectors, said that the local residents regarded this plant as sacred and attributed marvelous properties to it. The scale-like leaves, similar to some found in section *Dacrycarpus*, are arranged spirally, covering the surface of the twig and adnate to the stem, often with only a millimeter of free leaf blade. A figure showing a vegetative branch and seeds is shown by Pilger (4, 5) in both of his treatments of the genus.

The species has been collected several times since it was described by Vieillard in 1862, but only the most recent collection, that of De Laubenfels (2) in 1957, has shown it growing parasitically on *Dacrydium taxoides* Brongn. & Gris. The color of the plant is variously described as reddish, copperish, bronze, or purple. As Luc Chevalier (1) describes it most recently, "ses rameaux dressés ressemblent à une branch de corail rouge et les cônes femelles au bout des rameaux sont d'un bleu roi légèrement argenté." Indeed, when I soaked some twigs in water in preparation for examination of the leaves, the water turned very reddish purple, the effect of known anthocyanins. In view of the possible absence of chlorophyll, a test was made by analyzing an alcoholic solution from the leaves in a Beckman photospectrometer. The absorption curve showed the drop at 650 millimicrons indicative of the presence of chlorophyll *a*.* These results indicate that the specimen examined most probably was not completely parasitic. It is interesting to note in this connection that the history of the collections shows, in almost every case, that *Dacrydium taxoides*, the host of this specimen, was collected at the same time as *Podocarpus ustus*. Since the knowledge of its semi-parasitic nature became available no further collections have been obtained, but one may reasonably suspect that the plant may prove to be a root-parasite on *Dacrydium* or other gymnosperms.

Podocarpus ustus (Vieillard) Brongniart & Gris, Bull. Soc. Bot. France 13: 426. 1866; Parlatore in DC. Prodr. 16: 521. 1868; Gordon, Pinetum ed. 2. 358. 1875; Warburg, Monsunia 1: 193. 1900; Pilger, Pflanzenr. IV. 5(Heft 18): 58. 1903, Nat. Pflanzenfam. ed. 2. 13:

---

* The author wishes to express her great appreciation to Dr. Herbert Irvin, of the Crime Laboratory, Department of Public Safety of the State of Georgia, for his chlorophyll determination on *De Laubenfels P165*.

245. 1926; Guillaumin, Ann. Mus. Col. Marseille II. **9**: 269. 1911, Bull. Mus. Hist. Nat. Paris **18**: 100. 1912, Fl. N. Caledonia 11. 1948; Compton, Jour. Linn. Soc. Bot. **45**: 425. 1922; White, Wilson & Guillaumin, Jour. Arnold Arb. **7**: 77. 1926; Florin, Svenska Vet.-Akad. Handl. III. **10**: 270. 1931; Dallimore & Jackson, Handb. Conif. 58. 1923, 1931, 84. 1948.

Dacrydium ustum Vieillard, Ann. Sci. Nat. Bot. IV. **16**: 56. 1862; Carrière, Conif. 697. 1867.

A shrub, usually less than 1 meter tall, with dense, short, erect spreading branches, with the twigs entirely clothed by the copperish to purple or red, spirally placed, persistent adpressed scale leaves (Fig. 1), and with the terminal meristems protected by the youngest leaves. Leaves triangular, carinate, with broadly decurrent bases, 1–2 mm. long, 1–1.5 mm. broad; midribs not evident. Leaves differentially amphistomatic, having few stomata on the adaxial surface. Leaves without hypodermis or palisade parenchyma. Male strobili terminal and solitary on axillary leaf-covered peduncles up to 6 mm. long, the strobili short-cylindrical, 5 mm. long. Microsporophylls imbricate, sessile, 1.5–2 mm. long, 2-locular, longitudinally dehiscing; apiculi flat, thin, and broadly triangular. Female strobili terminal; peduncles 2–5 mm. long, clothed in decussate scale leaves, the uppermost not decurrent, succeeded on the strobilus by about 5 spirally placed longer bracts increasing to 2.5 mm. with longer internodes and blades free from the axis; fertile bracts usually only one, sometimes two, terminal, mostly free from the ovules; no fleshy receptacle. Seed globose, purplish, to 2.5 mm., not crested but often drying so there is an apparent acute apex.

Distribution: In forests on mountain slopes, up to 1000 m. altitude, in New Caledonia.

New Caledonia: Ignambi, *Compton 1545* (K *); Pic de Pouébo, *Vieillard 1269* (P), *Deplanche 170* (P); Mt. Penari, *Balansa 3484, 3485* (P); Koe, *Balansa 184* (†P); Mt. Koghi, *Brousmiche 456, 601* (P); Dumbea, *Vieillard 1262* (P); slopes above Rivière Bleue, *De Laubenfels P165* (†GA); Forets bas du Pic, des Sources, *LeRat 903* (†P); Montagnes de Poila, *Vieillard 1267* (†P-Type; †A, K); Baie de Prony, *Jeanneney* (P). No specific locality: *Balansa* (BM, K, †NY); *Pancher*, 1879 (†BR, K); *Hennecart* (BR, †P, †UCLA).

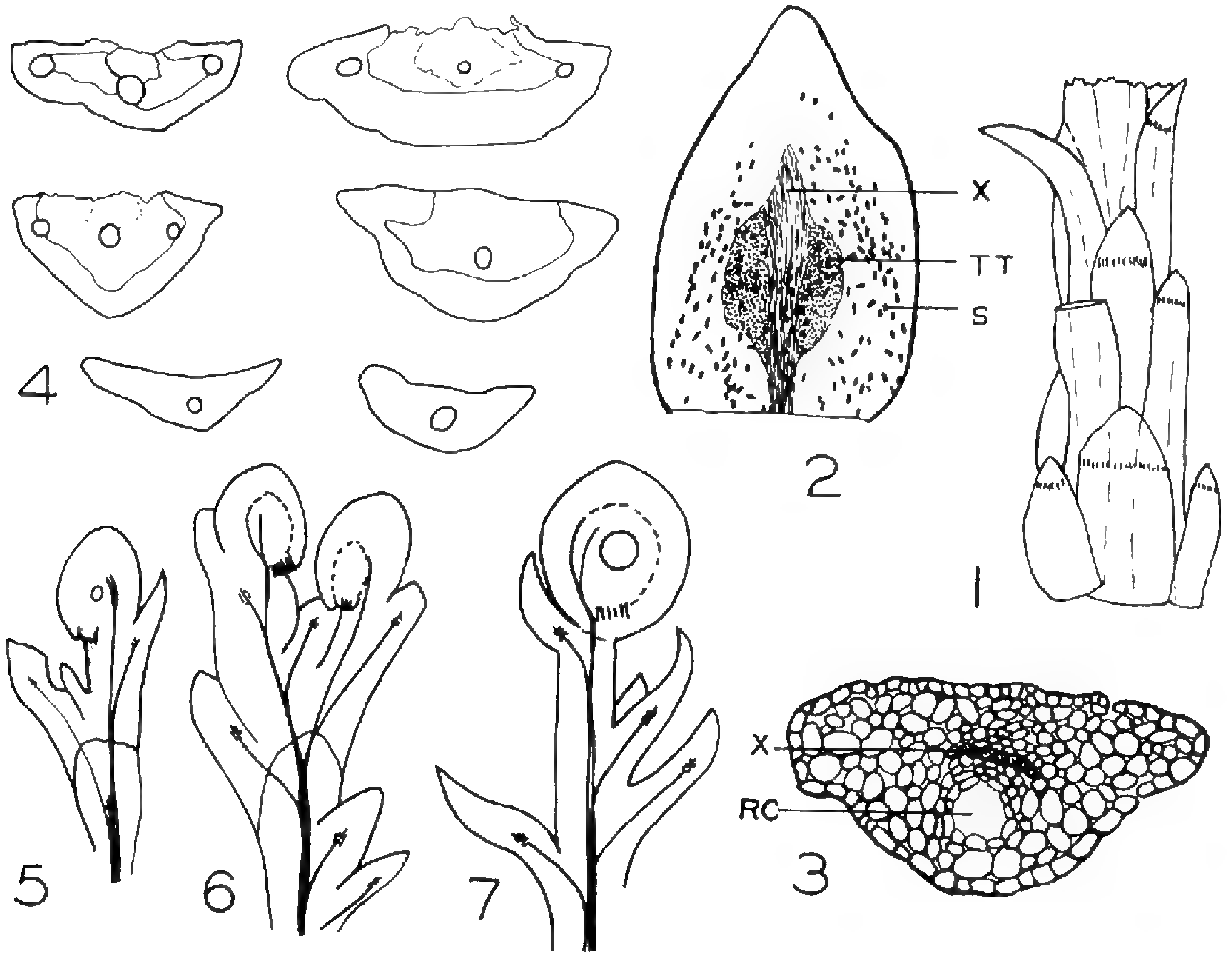
In contrast to the leaves of most other podocarps, which are noted for the variety of cell types in their tissues, there is little differentiation in the mesophyll of the leaves of *Podocarpus ustus*. The walls of the epidermal cells are mostly simple, and the often abundant stomata are mostly on the

---

* The following symbols indicate the location of the specimens cited: Arnold Arboretum (A); British Museum (Natural History) (BM); Brussels Botanical Garden (BR); University of California at Los Angeles (UCLA); Herbarium of the University of Georgia (GA); Royal Botanic Gardens, Kew (K); New York Botanical Garden (NY); Muséum National d'Histoire Naturelle, Paris (P).

† This symbol preceding the abbreviation of an herbarium signifies that the details of the leaves of this specimen have been examined in transverse section.

abaxial surface. The stomata are not arranged in rows, nor are they always oriented longitudinally (FIG. 2), merely being scattered over the surface. Only the smallest amount of vascular tissue connects with that of the stem and there is little vascular tissue in the free part of the blade of the leaf. Just before the bundle disappears the xylem tracheids shorten exceedingly and the vein broadens, with definite short wings of transfusion tissue on each side (FIG. 2), altogether giving a fan-like appearance to the termination of the bundle. The resin canal may continue beyond the end of the bundle but it rarely reaches the tip of the leaf; three resin canals may be present (FIG. 4). The blade of the leaf is swollen or fleshy and packed with roundish cells without conspicuous air spaces between them (FIG. 3). There is no palisade parenchyma and only rarely are a few isolated sclereids of the transfusion type seen.



FIGURES 1–7. **Podocarpus ustus.** 1, Part of stem, showing scale-leaves (*Vieillard 1267*), × 5. 2, Cleared leaf, showing vascular tissue and stomata in abaxial epidermis (*De Laubenfels P165*), × 16; S = stoma, X = xylem, TT = transfusion tissue. 3, Camera lucida outline of transverse section of leaf (from *De Laubenfels P165*), showing homogeneous mesophyll and resin canal (RC), × 35. 4, Outlines of transverse sections of leaves to show shape and one to three resin canals (*Balansa 184*, *3485*), × 15. 5–7, Cleared ovulate strobili, all from *De Laubenfels P165*, × 7: 5, strobilus with very young ovule; 6, strobilus with two young ovules; 7, strobilus with older ovule.

The solitary ovules are terminal on the twigs (FIGS. 5–7). As in other podocarps, a single vascular bundle enters the ovuliferous scale but almost immediately divides, both branches arching over the back to the top of the ovule. One of the specimens of *De Laubenfels P165* has pairs of ovules (FIG. 6) and close examination shows them to be separate on the uppermost bracts.

The lack of hypoderm in the leaves and the lack of a fleshy receptacle below the ovule definitely separate this species (and thus section *Microcarpus*) from section *Dacrycarpus*. If the scale leaves of *Podocarpus ustus* be considered merely evidence of modification toward the parasitic habit, then the species seems to be more closely related to section *Stachycarpus* where the other characters are typical. This position in the genus would be in better accord with the recent genetic studies in *Podocarpus* by Hair and Beuzenberg (3) who found that *P. ustus* has a diploid chromosome number of 36. They found chromosome numbers of 36 and 38 in section *Stachycarpus* and a diploid number in section *Dacrycarpus* of only 20.

LITERATURE CITED

1. CHEVALIER, L. Les conifères actuellement connus en Nouvelle Caledonie. Etudes Mélanésiennes. II. **1**: 105–118. 1957.
2. DE LAUBENFELS, D. J. Parasitic conifer found in New Caledonia. Science **130**: 97. July 1959.
3. HAIR, J. B., and E. J. BEUZENBERG. Chromosomal evolution in the Podocarpaceae. Nature **181**: 1584–1586. 1958.
4. PILGER, R. Taxaceae. Pflanzenreich IV. **5**(Heft 18): 1–124. 1903.
5. ———. Podocarpaceae. Nat. Pflanzenfamilien. ed. 2. **13**: 211–249. 1926.

AGNES SCOTT COLLEGE
DECATUR, GEORGIA

STUDIES IN THE GENUS COCCOLOBA, VIII. NOMENCLATURAL CHANGES

RICHARD A. HOWARD

SINCE THE PUBLICATION of the preceding papers in this series several matters involving nomenclatural changes have come to my attention. These changes concern *Coccoloba novogranatensis*, a species of the Lesser Antilles, Trinidad and northern South America, and *C. nitida* and *C. guianensis*, species of South America. In making the necessary corrections, two Vellozo names must be considered and the species concepts of the previous monographers Meisner and Lindau altered for additional taxa.

Coccoloba novogranatensis

Dr. Armando Dugand has called my attention to a paper of his which was published in *Caldasia* in 1947. I was not aware of this paper in which *Coccoloba coronata* Jacquin is properly identified and in which *Coccoloba novogranatensis* Lindau is placed in the synonymy of the Jacquin species. I do not agree completely with Dugand's treatment, since the proper citation for this species, with additional synonymy, appears to be the following:

Coccoloba coronata Jacquin, Enum. Pl. Carib. 19. 1760, Select. Stirp. Amer. Hist. 114. *t. 77.* 1763; Dugand, Caldasia **4**: 427. 1947, not Lindau, Symb. Ant. 1: *228, 229.* 1899.

Coccoloba virens Lindl. Bot. Reg. **21**: *t. 1816.* 1835.
Coccoloba novogranatensis Lindau, Bot. Jahrb. **13**: 192. 1890; Howard, Jour. Arnold Arb. **40**: 85–87, 208–9. 1959.
Coccoloba dioica Karsten ex Lindau, Bot. Jahrb. **13**: 170. 1890.
Coccoloba caribaea Urban, Symb. Ant. **5**: 337. 1907.
Coccoloba waittii Johnston, Sargentia **8**: 122. 1949.

The type location for Jacquin's species was cited as Cartagena. Dugand, who is familiar with this area and its vegetation, could not find constant or significant characters to separate *Coccoloba coronata* Jacq. from *C. novogranatensis* Lindau and concluded that they were identical. I can agree with him on this. However, Dugand accepts the synonymy given by Lindau (i.e., that *C. punctata* L. and *C. coronata* Jacq. are the same), but I can not agree with this. Lindau's treatments of *C. excoriata, C. punctata*, and *C. venosa* in his monograph of the genus (Bot. Jahrb. 13: 106–229. 1890) and in his later treatment of the West Indian species for Symbollae Antillanae (1: 229. 1890) are confused. This has been discussed previously by Fawcett and Rendle (Jour. Bot. **51**: 123. 1913) and by me (Jour. Arnold Arb. **30**: 398. 1949). *Coccoloba punctata* L. (Sp. Pl. ed. 2.

523. 1762) is not the same as *C. coronata* Jacq., but is a synonym of *C. venosa* L. The name *Coccoloba punctata* L. does not belong among the synonyms given by Dugand.

Coccoloba virens Lindl. was illustrated in the *Botanical Register* on the basis of a specimen which flowered in a British greenhouse in 1833. The place of origin for this plant is uncertain. Lindau first referred this species to the synonymy of his "Coccoloba punctata" (Bot. Jahrb. **13**: 160. 1890) and later to his "Coccoloba coronata" (Symb. Ant. **1**: 228. 1899). *Coccoloba virens* Lindl. can not be the true *Coccoloba venosa* L. to which Lindau's "C. coronata" and "C. punctata" belong, but it is the present species *Coccoloba coronata* Jacq.

Lindau described *Coccoloba dioica*, using a manuscript name appearing on an embossed label of a Karsten collection in the Leningrad herbarium. In spite of the specific epithet and the notes on the collection, Lindau failed to note the unisexual nature of the flowers in the published description. The Karsten specimen represents a pistillate plant, as the flowers have rudimentary stamens with abortive anthers and no pollen. In a key to the species in his monograph, Lindau distinguished between his *C. novogranatensis* and *C. dioica* by the fact that the former has a pubescent, and the latter a glabrous, lower leaf surface. The Karsten type, which I have been privileged to study, has leaves with pubescence along the midrib and on the primary veins. There is no doubt that the type specimens are comparable and that *C. dioica* can be assigned to the synonymy of *C. coronata*.

Coccoloba caribaea Urban and *C. waittii* Johnston have been placed in synonymy and discussed in earlier papers (Jour. Arnold Arb. **40**: 86, 209. 1959).

Coccoloba nitida

A second correction involves the use of the names *Coccoloba nitida*, *C. marginata*, and *C. guianensis* by Meisner, Lindau and Howard, the three monographers of the genus. In an earlier study (Jour. Arnold Arb. **40**: 83–85. 1959) I accepted the interpretation of *C. nitida* as published by Lindau and as indicated by his annotations on specimens. I had not seen the Humboldt type specimen of *C. nitida*, and, in fact, made an additional error in considering still another worker's photograph and annotation of a Martius specimen as the type of the species. Although Lindau cited a Humboldt collection from Colombia in his treatment of the species, he did not state specifically in which herbarium this specimen was located. The collections of *Coccoloba* of the Berlin herbarium, including the Willdenow herbarium, which I have now seen, do not contain such material. Recently, through the kindness of the Director of the Muséum National d'Histoire Naturelle, Paris, I have examined a sheet labelled primarily "Coccoloba laurifolia Knth.," with a smaller annotation of "C. nitida." This specimen was collected at S. Bartholome on the Río Magdalena in May, 1805, and is numbered *1627*. This must be the type of *Coccoloba nitida* H. B. K., for it agrees with the original description of the species.

However, it does not agree with Lindau's description of *Coccoloba nitida*, nor with the specimen he has so annotated. Lindau apparently did not see the type of *C. nitida*. Even though he cited the collection, the only available specimen of it does not bear his annotation. The Paris specimen mentioned is a poor one, consisting of a single short stem with a terminal inflorescence and one and one-half detached leaves. The leaves are insect infested and are abnormal at the tips. The specimen, however, has distinctive characteristics in the spathe-like basal ocrea of the inflorescence, the distinctive ridging of the pubescent rachis, and the closely packed fascicles of pedicels and buds.

It is clear now that *Coccoloba nitida* is properly typified by the Humboldt collection. As such, it is a distinctive species of Colombia, and the synonymy and citation of specimens given in my earlier papers, as well as those of Meisner in the Flora Brasiliensis and of Lindau in his monograph, are incorrect.

To the synonymy of *Coccoloba nitida* H. B. K. must be added *C. microneura* Meisner. Through the courtesy of the Director of the Royal Botanic Gardens, Kew, I have been able to study the Purdie specimen which is the type of *C. microneura*. In the original description, Meisner attributes the specimen he saw to the Arnott herbarium, but no material of this species could be found in the Prodromus or Delessert herbaria in Geneva. Lindau, however, saw the specimen at Kew. The Purdie specimen, without number, was collected in Santa Marta, Colombia, and is a full and ample specimen in flower. The species is not known in fruit. While the leaves are somewhat smaller than the type of *Coccoloba nitida* in all reliable characters, it is evident that *C. microneura* and *C. nitida* are conspecific. The correct nomenclature and the specimens examined follow.

Coccoloba nitida H. B. K. Nov. Gen. Sp. **2**: 176. 1818.

Coccoloba microneura Meisner, DC. Prodr. **14**: 163. 1856.

Colombia. San Bartholome on Río Magdalena, *Humboldt 1627* (P-lectotype); Santa Marta, *Purdie s.n.* (K-type of *C. microneura*); Dept. El Magdalena, Chimichaguá, *Haught 2228* (F, M, NY).

Recently I described *Coccoloba darienensis* (Jour. Arnold Arb. **40**: 159. 1959) based on *Allen 934*, a fruiting specimen from Darien, Panamá. There are minor differences in the number of veins and the general aspect of the leaf, but the close relationship of *C. darienensis* to *C. nitida* is obvious. It is possible that additional collections of either species may prove them to be the same and that the range of *C. nitida* should be extended to Panamá.

There is still the question of what is the remainder of the *Coccoloba nitida* concept of Meisner, Lindau and Howard when the Humboldt type is removed and the name applied to an endemic species of Colombia. Of the suggested synonyms of these authors, a Vellozo name is the oldest and most troublesome.

Polygonum arborescens

Polygonum arborescens Vellozo was described in Florae Fluminensis 162. 1825, and illustrated in the Icones (**4**: *t. 43.* 1827). The location given as "Habitat silvis maritimis ad ripas fluvii vulgo dicti Taguahy, atque etiam fruticetis Parochiae Campo-grande" can not be located exactly on modern maps, but is presumed to be near the town of Santa Cruz, in the Federal District, or in the western half of the State of Rio, Brazil.

Meisner (Fl. Bras. **5**(1): 38. 1855) refers the species with a question to the synonymy of *Coccoloba nitida* H. B. K. Meisner's concept of *C. nitida* was the first broad one which ignored the Humboldt type and was one which I now consider to be incorrect. Lindau also maintained this erroneous concept and also considered *Polygonum arborescens* Vellozo as a possible synonym of *C. nitida.*

Vellozo's description is brief, but the illustration shows several significant characteristics of aid in identifying this plant. It is obviously a liana, with well-developed short-shoots and persisting, nearly foliaceous ocreae which split into lanceolate "stipules." The flowers are on short pedicels in the inflorescence but the pedicels elongate in fruiting condition. On these characteristics the plant is surely the same as *Coccoloba crescentiifolia* Chamisso, and a new combination, *Coccoloba arborescens*, must be made. There is a second Vellozo species and illustration which has been referred to *C. crescentiifolia* which must be considered.

Polygonum frutescens

Polygonum frutescens Vellozo (Flor. Flum. 162. 1825, Icones **4**: *t. 44.* 1827) has had an unstable history. Vellozo's description of this is short ("P. spica simplici, terminali"), but he reports that it occurs in locations similar to his *Polygonum arborescens.* I can not refer the illustration of *P. frutescens* with real conviction to any currently recognized species. I believe that it may represent a terminal scrambling shoot of Vellozo's *Polygonum arborescens.* However, without knowledge of the ocreae (which can be interpreted in the drawing as deciduous or very short), the point of attachment of the petioles, and the curvature and pubescence of the blade, this can be only an attempt at an intelligent guess.

Casaretto was the first to consider *Polygonum frutescens* Vellozo. He cited this name in synonymy when he described *Coccoloba vellosiana* (Novarum Stirpium Brasiliensium Decades 70. 1844.) Casaretto's species, while honoring Vellozo, must be considered to be based on an unnumbered Riedel collection from the vicinity of Rio de Janeiro. Throughout the description Casaretto credits Riedel for the data supplied. The unnumbered collection to which Casaretto refers must be *Riedel 674*, for the descriptive data on the label "In sylvaticis maritimis inque collib. ciccis R. Janeiro Jul. 1832" compare favorably, although not verbatim, with those given by Casaretto, "Habitat in arenosis maritimis et collibus siccis circa Rio de Janeiro (Riedel)."

In 1855, Meisner (Fl. Bras. **5**(1): 36.) reduced *Polygonum frutescens* Vellozo to the synonymy of his new species *Coccoloba gardneri.* He also cited in synonymy *C. vellosiana* Casaretto, although with a question mark. Meisner cited only *Gardner 600* from the Serra dos Orgãos, Prov. Rio de Janeiro. I have examined this collection, but fail to find any similarity with the illustration of *Polygonum frutescens* Vellozo, and therefore believe that *Coccoloba gardneri* should be reëstablished as a valid species for the consideration of future collectors in the Rio area. The type of this species is *Gardner 600* and the synonymy given by Meisner should be excluded.

In 1833, Chamisso described *Coccoloba crescentiifolia* (Linnaea **8**: 134–136.), basing the species on an unnumbered Sellow collection from "Brasilia." Four specimens bearing labels inscribed "Coccoloba crescentiaefolia N" are in the herbaria at Berlin, Leningrad and Munich. The specimens in the Munich herbarium bear a further note which indicates that the collection was made near "Praya grande, prov. Rio de Janeiro."

In his monograph (Bot. Jahrb. **13**: 173. 1890) Lindau accepted *C. crescentiifolia* Cham., but placed in its synonymy *C. vellosiana* Casar. and *C. gardneri* Meisner, as well as *C. fasciculata* Weddell. He also listed in the synonymy, with a question mark, *Polygonum frutescens* Vellozo, as Meisner had done earlier. Lindau also included in his citation of specimens the collection *Gardner 600.* Thus, none of the monographers has been certain of the interpretation of *Polygonum frutescens* Vellozo, but all agree on the possibility of its being the same as *Coccoloba crescentiifolia.* If further collections or study prove this to be true, the acceptable name will be *Coccoloba arborescens* (Vellozo) Howard, since no combination of the Vellozo names has been made previously. If further study should show *Polygonum frutescens* to be distinct from *Coccoloba arborescens* (*C. crescentiifolia* Cham.), then the Vellozo name, being the oldest in use in the Rio area, must be adopted over some other currently accepted name. The correct nomenclature for the concept involving *Coccoloba crescentiifolia* Chamisso is the following:

Coccoloba arborescens (Vellozo) Howard, comb. nov.

Polygonum arborescens Vellozo, Flor. Flum. 162. 1825, Icones **4**: *t. 43.* 1827.
Coccoloba crescentiifolia Chamisso, Linnaea **8**: 134. 1833, "*crescentiaefolia.*"
Coccoloba vellosiana Casaretto, Nov. Stirp. Bras. Decad. 70. 1844.
Coccoloba fasciculata Weddell, Ann. Sci. Nat. III. **13**: 258. 1849.
Coccoloba crescentiifolia var. *obtusata* Meisner, Fl. Bras. **5**(1): 26. 1855.

Coccoloba fasciculata Weddell, based on *Blanchet 769,* was distinguished from *C. crescentiifolia* on the basis of flat leaves which were less rigid and had shorter petioles. The specimens which I have seen of this collection are of short lateral branches, and there is no doubt that the collection should be identified as *C. arborescens.*

Meisner's taxon *Coccoloba crescentiifolia* var. *obtusata* was based on *Claussen 2013.* The characteristics Meisner indicated as distinguishing this variety are not consistent in the several examples of the collection which I have seen. As Lindau has already indicated, the variety is not worthy of recognition.

Returning now to Lindau's concept of *Coccoloba nitida*, two synonyms are easily removed from further consideration. *Coccoloba pendula* Salzmann first was published in synonymy by Meisner (Fl. Bras. **5**(1): 38. 1855), and *C. recurva* Newman was placed in synonymy by Lindau (Bot. Jahrb. 13: 180. 1890). The specimens labelled "C. pendula Salzm." at Leningrad and Paris are to be referred to *C. marginata* Benth., a name to be considered shortly. I have been unable to find material labeled "C. recurva Newman" at Geneva and am unable to associate this name. The reference "Coccoloba foliis cordato-oblongis Plum. Pl. am. 137 tab. 146 f. 1" referred with a question to *Coccoloba nitida* by Lindau. Urban (Repert. Spec. Nov. Beih. **5**: 69–70. 1920) has referred the Plumier illustration and reference to the species now known as *C. venosa* L. I am not convinced that either author is correct. The origin of the material which Burmann illustrated is not certain. As Urban suggested that it may have come from Trinidad, I believe its correct identity is *C. marginata*.

The specimens Lindau cited in his monograph as *Coccoloba nitida* are to be distributed among *C. arborescens*, *C. marginata* and *C. nitida*. Although I have not seen the collections Lindau cited from Dutch and British Guiana, I suspect that these will prove to be *C. marginata*. *Friedrichsthal 398*, reported from Guatemala, was cited by Meisner in the original description of *C. martii*. The specimen was attributed to the Vienna herbarium and was reported to have come from "S. Thomas, Guatemala." Lindau placed *C. martii* in the synonymy of his *C. nitida* and cited the Friedrichsthal collection. All of the material of *Coccoloba* in the Vienna herbarium was lost during World War II, so the identity of this collection may never be established. I have not seen specimens of *C. arborescens*, *C. marginata*, or *C. nitida* in the collections from Guatemala which I have already studied.

Coccoloba guianensis

In a review of *Coccoloba* in the Lesser Antilles, Trinidad and Tobago, I accepted the name *C. nitida* with six taxa as synonyms. The correct name for this species should be *C. marginata* Bentham, with the following synonymy:

Coccoloba marginata Bentham, London Jour. Bot. Hooker **4**: 626. 1845.

Coccoloba guianensis Meisner, Linnaea **21**: 264. 1848.
Coccoloba martii Meisner, Fl. Bras. **5**(1): 37. 1855.
Coccoloba martii var. *major* Meisner, Fl. Bras. **5**(1): 38. 1855.
Coccoloba martii var. *minor* Meisner, loc. cit.
Coccoloba nitida var. *rotundata* Meisner, loc. cit.
Coccoloba nitida var. *cordata* Meisner, loc. cit.
Coccoloba trinitatis Lindau, Bot. Jahrb. **13**: 182. 1890.
Coccoloba douradensis Glaziou, Bull. Soc. Bot. France. IV. **11**(Mem. 3f): 571. 1911 (provisional name with mixed type).

Lindau recognized *Coccoloba guianensis*, *C. marginata*, and *C. trinitatis* as distinct species. He considered *C. martii* a synonym of his *C. nitida*. I have indicated in an earlier paper (Jour. Arnold Arb. **40**: 84. 1959) the variations in habit and leaf shape found on one plant of *C. marginata* in Trinidad, and I remain convinced that *C. marginata*, *C. guianensis*, and *C. trinitatis* are one and the same species. *Coccoloba guianensis* is the well known and widely used name for this species. *Coccoloba marginata*, the oldest name for the complex, was considered distinct only on the basis of the slightly recurved leaf margin. The type of *C. marginata* is Schomburgk's second collection numbered *118* (*216*) from British Guiana. The holotype is in the herbarium at Kew and an isotype is in Paris. All of the specimens which I cited as *C. nitida* in an earlier paper must be renamed *C. marginata* Benth.

Coccoloba martii Meisner is typified by a Martius collection from the vicinity of Salgao, on the river San Francisco, in Minas Geraës, Brazil. The specimen illustrates the nonscrambling aspect of the species.

Coccoloba douradensis Glaziou was used in a list of Glaziou collections with a question as to its status as a new species. Because only four words were used to describe the plant, the name should be considered a nomen nudum. The collection cited, *Glaziou 21978*, may prove to be a mixture. As has happened with other numbers of the Glaziou collection, the specimens and associated labels or numbers were mixed in the field or in distribution to herbaria. Sheets labeled *Coccoloba douradensis*, *Glaziou 21978*, may be referred to *Coccoloba densifrons* or to *C. marginata*.

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

Kenneth A. Wilson

The Arales (Spathiflorae), in the view of most authors, include only the families Araceae and Lemnaceae, the latter representing highly reduced plants of aroid ancestry. A much broader interpretation of the order is the one of Wettstein, who included in his "Spadiciflorae" not only the Araceae and Lemnaceae, but also the Palmae and Cyclanthaceae. Other authors (e.g., K. Fritsch, Ber. Deutsch. Bot. Ges. **50a**: 162–184. 1932) have interpreted this group as including also the families Pandanaceae, Sparganiaceae, and Typhaceae. Such an interpretation of the order is subject to considerable disagreement, and these families may indeed not be very closely related to each other. The Arales are here interpreted in the Englerian sense to include only the families Araceae and Lemnaceae, which are generally agreed to be closely allied.

ARACEAE (Arum Family)

Tuberous or rhizomatous, terrestrial or aquatic (rarely floating) herbs with watery, milky or acrid sap. Leaves simple or compound, basal and solitary or clustered, or cauline and alternate. Inflorescence a spadix (an axis with small, sessile, tightly grouped flowers), subtended by an herbaceous spathe (or spathe absent). Flowers bisexual, with a perianth (in ours), or unisexual, without a perianth (the plants then monoecious or dioecious); perianth, when present, of 2–6 parts; stamens 1–6, free or united into a synandrium; gynoecium completely syncarpous, the ovary 1(–many)-locular, superior or inferior (i.e., embedded in the spadix); ovules 1–many in each locule. Fruit usually a berry. Seeds with or without endosperm, the embryo large. (Including Pistiaceae.)

A large family, primarily tropical or subtropical in its distribution, of over 100 genera grouped into eight subfamilies by Engler (18 tribes by

---

[1] Prepared for a biologically oriented generic flora of the southeastern United States, a joint project of the Arnold Arboretum and the Gray Herbarium made possible through the support of George R. Cooley and the National Science Foundation, and under the direction of Reed C. Rollins and Carroll E. Wood, Jr. The scheme follows that outlined at the beginning of the series (Jour. Arnold Arb. **39**: 296–346. 1958). Other published portions of these studies will be found in Jour. Arnold Arb. **40**: 94–112, 161–171, 268–288, 369–384, 391–397, 413–419. 1959, and in the present issue. In connection with the treatments of the Araceae and the Lemnaceae, I am particularly indebted to Carroll E. Wood, Jr., for his valuable suggestions, advice, and information. The illustrations are the skillful work of Dorothy H. Marsh, and are based on material collected by Carroll E. Wood, Jr., and Richard J. Eaton. I wish also to express my indebtedness to R. B. Channell, George R. Cooley, Joseph Ewan, R. K. Godfrey, H. F. L. Rock, and Edward G. Voss, who kindly assisted in supplying information, aided in the obtaining of specimens, and helped in various other ways.

Hutchinson) with about 1500 species. Eight genera, representing five subfamilies, are native to the United States, while at least two exotic genera, *Colocasia* and *Pinellia*, are becoming established. All but three of these (*Calla* L., *Lysichitum* Schott, and *Pinellia* Tenore) are represented in our area.

The family may be recognized by the inflorescence, a spadix, which usually is subtended or enveloped by a spathe. Great diversity exists with respect to the nature, position and distribution of the flowers on the spadix. the habitat, habit, leaf morphology, flower structure and other morphological characters. The subdivision of the family is based not only on floral but also on anatomical characters, such as the presence or absence of raphides and the occurrence of latex.

Although there appears to be no doubt that the family represents a natural group, much speculation exists with respect to its origin and phylogenetic relationships. Engler considered the Araceae to be derived from the Palmae through the Cyclanthaceae. Hutchinson, on the other hand, thought the group to be monophyletic and derived from the stock of the tribe Aspidistreae of the Liliaceae. Other authors have considered it as having evolved from the ancestors of the Liliaceae through various phylogenetic lines.

The Araceae as a group are notable for the occurrence of the needle-like crystals of calcium oxalate (raphides) in "packets" which occur in small capsules in almost all tissues. These account for the immunity of most Araceae to herbivorous mammals and for the intense irritation or "burning" sensation which is experienced when raw or improperly cooked corms of *Colocasia, Xanthosoma*, or *Arisaema* are eaten. In *Dieffenbachia*, the dumb-cane, widely grown as an ornamental foliage plant, the irritation is so severe as to produce temporary inability to speak. When the cells of the plant are broken in chewing, the capsules absorb water and the needles are discharged with sufficient force to penetrate the tissues of the mouth. The prolonged cooking which is necessary with the "edible" Araceae renders the capsules inactive. (Cf. *Colocasia*.)

Many genera are popular in cultivation as ornamentals, some, such as *Philodendron*, *Syngonium*, *Pothos*, *Scindapsus*, and *Caladium*, for their decorative foliage, others, such as *Zantedeschia* and *Anthurium*, for their showy spathes. Some of these may possibly escape sparingly in subtropical areas.

REFERENCES:

BARRAU, J. Les aracées à tubercules alimentaires des îles du Pacifique Sud. Jour. Agr. Trop. Bot. Appl. **4**: 34–52. 1957. [Includes *Colocasia, Xanthosoma, Cyrtosperma, Alocasia, Amorphophallus*.]

BIRDSEY, M. R. The cultivated aroids. 140 pp. Gillick Press, Berkeley. 1951.

CAMPBELL, D. H. Studies in the Araceae. Ann. Bot. **14**: 1–25. 1900. [Ovule and embryo sac of *Dieffenbachia, Aglaonema, Lysichitum*, and *Anthurium*.] (See also, *ibid*. **17**: 665–687. 1903.)

CHRYSLER, M. A. The development of the central cylinder of Araceae and Liliaceae. Bot. Gaz. **38**: 161–184. 1904.

DALITZSCH, M. Beiträge zur Kenntniss der Blattanatomie der Aroideen. Bot. Centralbl. **25:** 153–156, 184–186, 217–219, 249–253, 280–285, 312–318, 343–349. 1886. [Includes *Anthurium, Spathiphyllum, Rhaphidophora, Monstera, Philodendron, Scindapsus, Colocasia*, and *Acorus*.]

DAUMANN, E. Nektarabscheidung in der Blütenregion einiger Araceen zugleich ein Hinweis auf die bargersche Methode. Planta **12:** 38–48. 1930 [1931]. [Includes *Anthurium, Arisaema consanguineum, A. amurense, Aglaonema, Arum*.]

DELAY, C. Diagramme nucléaire des Aracées. Compt. Rend. Acad. Sci. Paris **222:** 1512–1514. 1946.

ENGLER, A., and K. KRAUSE. Araceae. Pflanzenr. IV. **23A**(Heft 74): 1–71. 1920. [Pars generalis et Index familiae generalis]; **23B**(Heft 21): 1–330. 1905 [Pothoideae]; **23B**(Heft 37): 1–160. 1908 [Pothoideae, Monsteroideae, Calloideae]; **23C**(Heft 48): 1–130. 1911 [Lasioideae]; **23Da** (Heft 55): 1–134. 1912 [Philodendroideae–Philodendreae: Homalomeninae, Schismatoglottidinae]; **23Db**(Heft 60): 1–143. 1913 [Philodendroideae: Philodendrinae]; **23Dc**(Heft 64): 1–78. 1915. [Philodendroideae: Anubiadeae, Aglaonemateae, Dieffenbachieae, Zantedeschieae, Typhonodoreae, Peltandreae]; **23E**(Heft 71): 1–139. 1920 [Philodendroideae, Colocasioideae]; **23F**(Heft 73): 1–274. 1920 [Aroideae, Pistioideae.]

FERNALD, M. L., and A. C. KINSEY. Edible wild plants of eastern North America. 452 pp. Idlewild Press. Cornwall, N.Y. 1943. [Araceae, 111–122. Includes recipes for *Arisaema, Peltandra, Calla, Symplocarpus, Orontium*, and *Acorus*.]

GATIN, C. L. Première contribution a l'étude de l'embryon et de la germination des Aracées. Ann. Sci. Nat. Bot. X. **3:** 145–180. 1921. [*Pothos, Anthurium, Spathiphyllum, Aglaonema, Acorus, Nephthytis, Dieffenbachia, Zantedeschia, Caladium, Arum*.]

GOW, J. E. Phylogeny of the Araceae. Proc. Iowa Acad. Sci. **20:** 161–168. 1913. [Derived from sepaloid and entomophilous ancestral plants. Arales and Helobiales represent a common line of descent which has diverged in recent times.]

———. Studies in Araceae. Bot. Gaz. **46:** 35–42. 1908. [Development of the embryo in *Nephthytis, Dieffenbachia*, and *Aglaonema*.]

———. Observations on the morphology of the aroids. *Ibid.* **56:** 127–142. 1913. [Embryo of *Aglaonema, Anthurium, Philodendron, Arum, Xanthosoma* and others.]

HARTER, L. L. Storage-rots of economic aroids. Jour. Agr. Res. **6:** 549–572. 1916.*

JONES, G. E. Chromosome numbers and phylogenetic relationships in the Araceae. Diss. Abs. **17:** 2394. 1957.*

MOOKERJEA, A. Cytology of different species of aroids with a view to trace the basis of their evolution. Caryologia **7:** 221–291. 1955. [Cytology supports Hutchinson's classification in most cases.]

PFITZER, P. Chromosomenzahlen von Araceen. Chromosoma **8:** 436–446. 1957.

SHARMA, A. K., and N. K. DAS. Study of karyotypes and their alterations in aroids. Agron. Lusit. **16:** 23–48. 1954. [*Colocasia, Alocasia*, and *Caladium*.]

WICHMAN, MRS. H. J. *Dracunculus vulgaris* in Tennessee. Castanea **22:** 139. 1957. [Persisting in an abandoned yard in Rugby.]

KEY TO THE GENERA OF ARACEAE

- A. Perianth present; flowers (at least the basal) bisexual, frequently proterogynous.
  - B. Spadix lateral on a leaf-like axis; leaves sword-shaped; perianth segments 6; fruit a berry. . . . . 1. *Acorus*.
  - B. Spadix terminal on peduncle; leaves cordate, ovate, or oblong-elliptic.
    - C. Spathe fleshy, enveloping the subglobose spadix; perianth segments 4; fruit embedded in swollen spadix (multiple fruit.) . . . . 2. *Symplocarpus*.
    - C. Spathe bract-like, ensheathing base of peduncle of oblong spadix; perianth segments (in lower flowers) 6; fruit a berry, not embedded in spadix. . . . . 3. *Orontium*.
- A. Perianth wanting; flowers unisexual.
  - D. Plants rooted in soil; spadix free from spathe.
    - E. Leaves simple; stamens united into a peltate synangium.
      - F. Leaves sagittate or hastate; spadix almost completely covered by flowers. . . . . 4. *Peltandra*.
      - F. Leaves ovate-cordate and peltate; apex of spadix naked or covered with sterile flowers; plants spreading by runners. . . . . 5. *Colocasia*.
    - E. Leaves palmately or pedately divided; stamens 2–4-locular, subsessile. . . . . 6. *Arisaema*.
  - D. Plants floating; spadix adnate to spathe. . . . . 7. *Pistia*.

Subfam. POTHOIDEAE Engl.

1. **Acorus** Linnaeus, Sp. Pl. 1: 324. 1753; Gen. Pl. ed. 5. 151. 1754.

Plant herbaceous, with a thick, creeping rhizome. Leaves equitant, sword-shaped. Spadix borne laterally on an axis resembling a foliage leaf, spathe absent (the prolongation of the fertile axis often interpreted as an open spathe). Flowers bisexual, 3-merous, greenish; perianth of 2 whorls of 3 concave tepals; stamens 6, filaments linear; gynoecium with a 2- or 3-loculed superior ovary, each locule with several orthotropous ovules apically attached. Fruit a gelatinous, few-seeded berry. TYPE SPECIES: *Acorus Calamus* L. (*Acorus*, an ancient Latin name for an aromatic plant.) — SWEET-FLAG.

A genus of two or three species, as currently interpreted, from the northern temperate regions of the world. It is represented in our area by the widespread *Acorus americanus* Raf. which grows in low, wet areas, marshes and along the banks of quiet streams. Although generally known as *A. Calamus* and considered to have been introduced into the United States from Europe, recent cytological evidence indicates that the American plant is most likely a native one. The American plants are diploid ($2n = 24$) and fertile, while the European plants, which were introduced from southern Asia, are triploid ($2n = 36$) and sterile. Whether or not the European sterile triploid has been introduced into North America still remains to be shown. The plants of "*A. Calamus*" from Siberia and Asia are tetraploid ($2n = 48$) and fertile. Various characters have been found to be correlated with the degree of polyploidy in *A. Calamus*. These include the blade width/length ratio, the angle of the spadix insertion, the oil content of the rhizome (greater with polyploidy), water content, and also the amount of calcium oxalate (decreases in polyploids). It has been suggested that each polyploid group be considered a variety of *A. Calamus*, but perhaps each might better be regarded as separate species. The American diploid (*A. americanus* Raf., *A. Calamus* var. *americanus* (Raf.) Wulff) needs further study to establish the possible validity of separation of northern and southern plants as was done by Rafinesque.

REFERENCES:

BUELL, M. F. *Acorus Calamus* in America. Rhodora **37**: 367–369. 1935.

———. Seed and seedling of *Acorus Calamus*. Bot. Gaz. **96**: 758–765. 1935.

———. Embryogeny of *Acorus Calamus*. Bot. Gaz. **99**: 556–568. 1938.

GUENTHER, E. S. Oil of calamus. Chemurgic Digest **2**: 138–140. 1943.*

HARPER, R. M. Is *Acorus Calamus* native in the United States? Torreya **36**: 143–147. 1936. [Apparently not, but was introduced for medicinal purposes and other reasons.]

LÖVE, A., and D. LÖVE. Drug content and polyploidy in *Acorus*. Proc. Genetics Soc. Canada **2**: 14–17. 1957. [A general review of Wulff's papers and other evidence.]

———. Biosystématique du genre *Acorus*. (Abs.) Ann. ACFAS **23**: 100. 1955/56 [1957].

MÜCKE, M. Über den Bau und die Entwicklung der Früchte und über die Herkunft von *Acorus Calamus* L. Bot. Zeit. **66**: 1–23. 1908. [Introduced into Europe in the middle of the 16th century.]

PARMELEE, J. A., and D. B. O. SAVILE. *Uromyces* rusts of *Sparganium* and *Acorus* and their alternate hosts. (Abs.) Proc. Canad. Phytopath. Soc. **21**: 15. 1953.*

SCHANTZ, M. VON. Über das ätherische Öl beim Kalmus, *Acorus Calamus* L. Acta Bot. Fenn. **59**: 1–138, *pls. 1–16*. 1958. [Includes notes on anatomy.]

SMALL, J. Calamus. A pocket-lens study. Food **11**: 195. 1942.*

WULFF, H. D. Über die Ursache der Sterilität des Kalmus (*Acorus Calamus* L.). Planta **31**: 478–491. 1941.

———. Der Ölgehalt verschiedenchromosomiger Rassen vom Kalmus (*Acorus Calamus* L.). Zeitschr. Naturf. **1**: 600–603. 1946.

———. Ölgehalt und Chromosomenzahl des nordamerikanischen Kalmus (*Acorus Calamus* L.). Arch. Pharm. **283**: 155–161. 1950.

———. Zur Zytologie, geographischen Verbreitung und Morphologie des Kalmus. *Ibid.* **287**: 529–541. 1954.

——— and B. Hoffmann. Kalziumoxalat-Gehalt und Polyploidie bei *Rosa* und *Acorus*. Ber. Deutsch. Bot. Ges. **70**: 383–388. 1957.

Subfam. CALLOIDEAE Engl.

2. **Symplocarpus** Salisbury ex Nuttall, Gen. N. Am. Pl. 1: 105, 106. 1818, nom. cons.[2]

Herbs with a stout, erect rhizome bearing numerous large, clustered leaves; entire plant with a strong odor, often compared with that of a

---

[2] Conservation unnecessary; see Taxon **8**: 230. 1959.

skunk. Leaves entire, ovate or cordate, conspicuously veined. Spathe thick, fleshy, purple spotted, ovoid, with a tapering, arched tip, the margin inrolled. Spadix ellipsoid or globose, completely covered by the crowded flowers. Flowers bisexual, proterogynous, maturing basipetally; perianth segments 4, fleshy; stamens 4, opposite the perianth segments, the filaments slender, flattened, the anthers 2-loculed, extrorse; gynoecium with a 1(-seldom 2)-loculed ovary imbedded in the spadix, the solitary ovule pendent, orthotropous; style 4-angled, subulate. Fruits embedded in the spongy tissue of the globose spadix which is roughened by the persistent perianth parts and styles. Seeds naked, without endosperm or seedcoat, subspherical, depressed on the funicular side. (*Spathyema* Raf., nom. rejic.) TYPE SPECIES: *S. foetidus* (L.) Nutt. (Name from Greek, *symploce*, connection, and *carpos*, fruit, in allusion to the multiple fruit.) — SKUNK-CABBAGE.

Symplocarpus foetidus, is known from two widely disjunct areas: eastern Asia (the Japanese plant has been named *S. nipponicus* Makino), and eastern North America, where it ranges from Quebec and Nova Scotia, south to

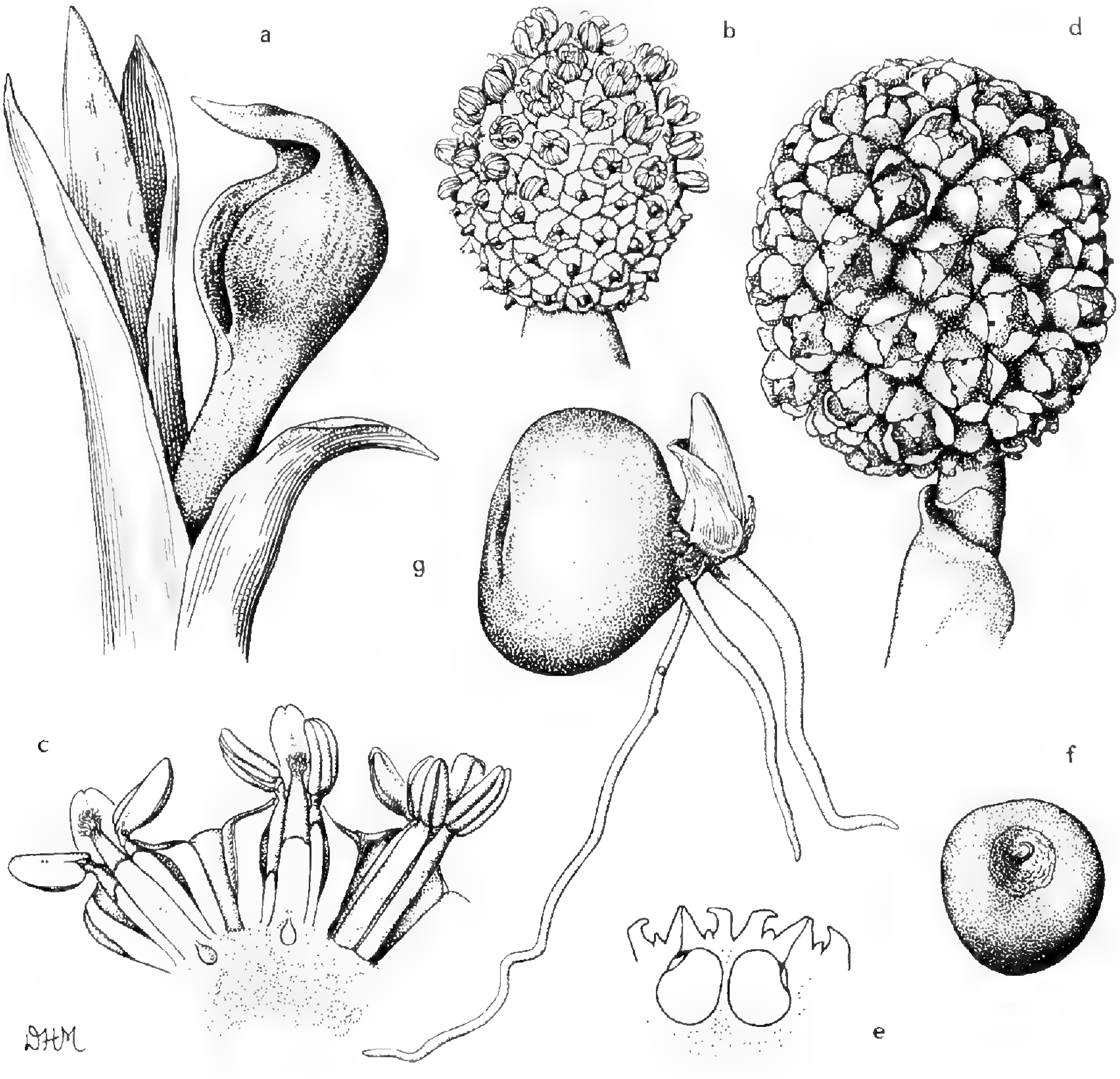


FIG. 1. **Symplocarpus.** a–g, *S. foetidus*: a, habit, showing inflorescence, × ⅜; b, spadix, × 1½; c, section through spadix, showing flowers in vertical section, × 4; d, fruiting spadix, × 1; e, section through fruiting spadix, showing seeds in vertical section, × 1; f, seed, × 1½; g, seedling, × 2.

New England, North Carolina, Georgia, and Tennessee and west to Ontario, northern Michigan, Minnesota, and Iowa. (It has also been recorded from Florida and Missouri.) It occurs in swamps, wet meadows, and woods, where it often forms dense stands. *Symplocarpus* is one of the earliest plants to flower in the spring. The inflorescence appears barely above the surface of the ground, long before the leaves appear. The flowers are all perfect and proterogynous and mature basipetally on the inflorescence. As the embryo develops it absorbs both endosperm and integuments, so that when mature it possesses no seed coat. Except in the younger stages, during which it has a monopodial branching system, the plant is sympodial, each branch producing two leaves and a terminal inflorescence, although many of the inflorescences do not mature (Shull). The roots are contractile and function in pulling the plant into the soil.

The closest relative of *Symplocarpus* apparently is *Lysichitum*, a western American and Asiatic genus of two species, although Hutchinson, primarily on the basis of the more differentiated spathe of *Symplocarpus*, placed these two genera in different tribes. This view, however, does not seem to be supported by the morphology of the flowers, of the inflorescence, and of the vegetative body (including odor!), which are similar enough to indicate a close relationship between the two.

REFERENCES:

BONNER, W. D., and C. S. YOCUM. Spectroscopic and enzymatic observations on the spadix of skunk cabbage. (Abs.) Pl. Physiol. **31** (Suppl.): xli. 1956.*

BREWSTER, W. Occurrence of the skunk cabbage in an unusual place. Rhodora **11**: 63, 64. 1909. [Elevated, dry locality in Massachusetts.]

BROWN, W. L., JR. Drosophilid and chloropid flies bred from skunk cabbage. Psyche Boston **63**: 13. 1956.

DUGGAR, B. M. Studies in the development of the pollen grain in *Symplocarpus foetidus* and *Peltandra undulata*. Bot. Gaz. **29**: 81–98. 1900.

GOW, J. E. Morphology of *Spathyeme foetida*. Bot. Gaz. **43**: 131–136. 1907.

GROUT, A. J. Leaves of the skunk cabbage. Torreya **3**: 6. 1903. [Largest leaf measured 26.5 × 19.5 inches.]

HACKETT, D. P. Respiratory mechanism in the aroid spadix. Jour. Exp. Bot. **8**: 157–171. 1957.* (See also, YOCUM and HACKETT. Pl. Physiol. **32**: 186–191. 1957; HACKETT and HAAS. *Ibid.* **33**: 27–32. 1958.)

ROSENDAHL, C. O. Preliminary note on the embryogeny of *Symplocarpus foetidus* Salisb. Science **23**: 590. 1906.*

———. Embryo-sac development and embryology of *Symplocarpus foetidus*. Minn. Bot. Stud. **4**: 1–9. 1909.

SEKIMOTO, H. Account of the discovery of *Symplocarpus nipponicus*. (In Japanese.) Jour. Jap. Bot. **6**: 319–328. 1929. [*S. nipponicus* Makino.]

SHULL, J. M. A Methuselah of the plant world. The skunk cabbage. Jour. Hered. **15**: 443–450. 1924. [Vegetative morphology.]

———. *Spathyema foetida*. Bot. Gaz. **79**: 45–59. 1925. [Vegetative morphology.]

STRAUSBAUGH, P. D. An abnormal inflorescence of *Symplocarpus foetidus*. Bot. Gaz. **84**: 328, 329. 1927. [A spadix enveloped by two spathes.]

VAN NORMAN, R. W. Cyanide-resistant respiration in skunk cabbage. (Abs.) Pl. Physiol. **30**(Suppl.): xxix. 1955.*

WILLIAMS, K. A. A botanical study of skunk cabbage, *Symplocarpus foetidus*. Torreya **19**: 21–29. 1919.

3. **Orontium** Linnaeus, Sp. Pl. 1: 324. 1753; Gen. Pl. ed. 5. 151. 1754.

Perennial aquatic herbs with stout, deeply sunken rhizomes. Leaves simple, oblong-elliptic, prominently nerved and long petioled, usually floating. Spadix on an elongated scape, oblong, golden yellow, the scape green, with a band of white below the flowers.. Spathe obscure, forming a sheath at the base of the scape, the blade bract-like. Flowers variable: perfect at the base of spadix, with 6 tepals, 6 stamens and a 3-carpellate gynoecium, gradually becoming staminate towards the tip; tepals yellow, 6 in two whorls to 2 in a single whorl; stamens 6–1, 1 or 2 staminodia sometimes present; gynoecium 3- or 2-carpellate; ovary 1-locular with a single basal, anatropous ovule. Fruit a 1-seeded berry with thin pericarp. TYPE AND SOLE SPECIES: *Orontium aquaticum* L. (*Orontium*, an ancient name for a plant which is said to have grown in the Syrian river Orontes.) — GOLDEN CLUB.

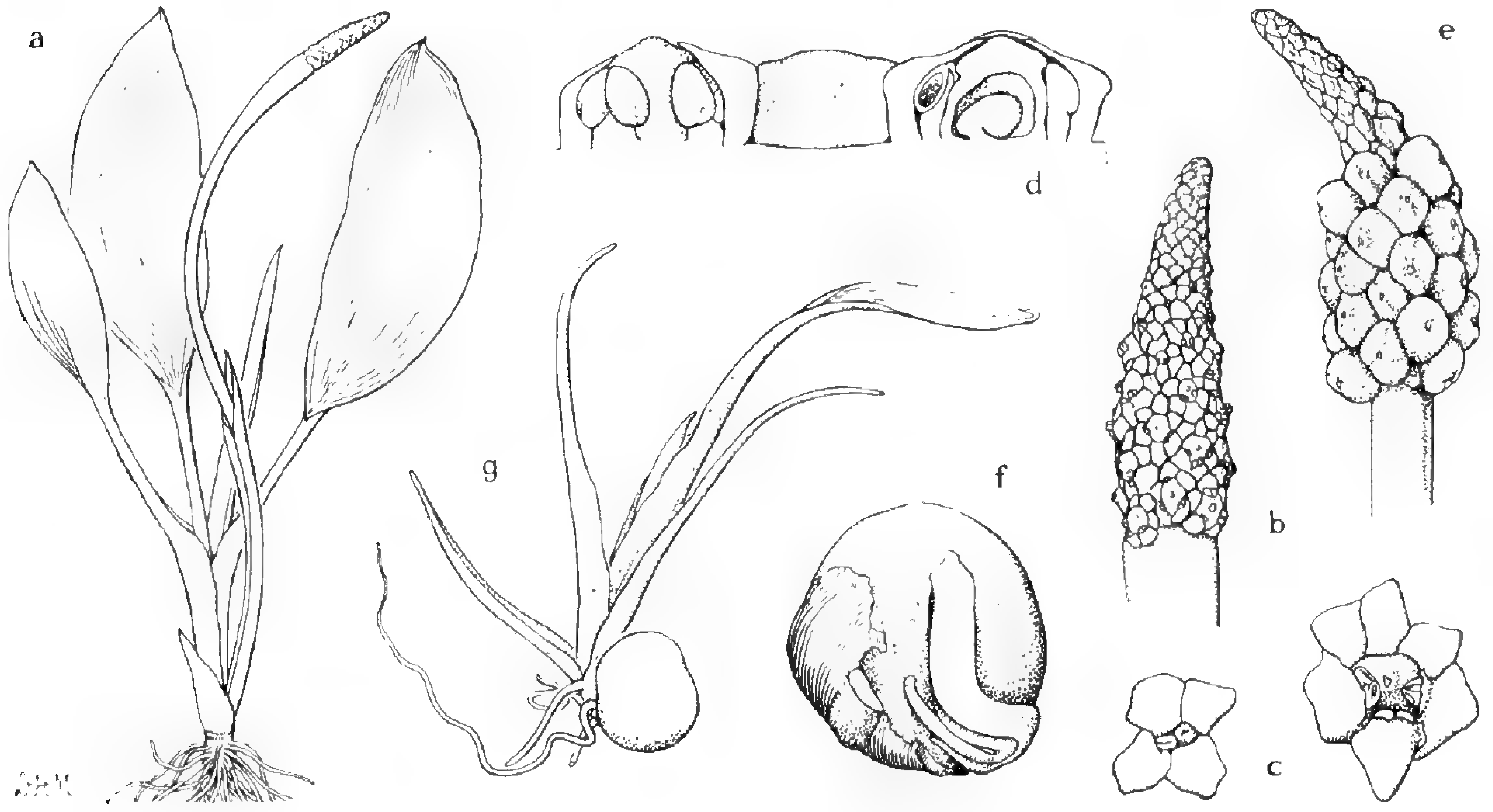


FIG. 2. **Orontium.** a–g, *O. aquaticum*: a, habit, × 1/8; b, spadix, × 1; c, flowers, × 4; d, spadix, longitudinal section, showing flowers in lateral view and in vertical section, × 4; e, fruiting spadix, × 1/2; f, seed with seed coat partially removed to show embryo, × 2; g, seedling, × 1.

Orontium aquaticum L. is known only from the eastern United States, primarily on the Coastal Plain, where it occurs growing in the shallow water of pools or streams and on their moist banks or shores, from Florida, north to Massachusetts, and west to Louisiana and Kentucky. The flowers, which are crowded on the spadix, show a remarkable amount of variation, ranging from those with six perianth segments, six stamens and a 3-carpellate gynoecium, to those with only two perianth segments, one stamen, and one staminodium and no pistil. Numerous intermediate or transitional conditions may also be found on the spadix. The morphological and biological details of this plant merit further investigation.

REFERENCES:

COCKERELL, T. D. A. A miocene *Orontium* (Araceae). Torreya **26**: 69. 1926. [*Orontium fossile*, spadix from Colorado.]

RAFFILL, C. P. *Orontium aquaticum*. Gard. Chron. **119**: 159. 1946. [Notes on cultivation.]

SCHAFFNER, J. H. The flowers of the golden-club. Am. Bot. **43**: 99–103. 1937. [Variation in flower structure.]

Subfam. PHILODENDROIDEAE Engl.

4. **Peltandra** Rafinesque, Jour. Phys. Chem. **89**: 103. 1819, nom. cons.

Herbs with long, stout-petioled, clustered leaves. Leaf blades sagittate or hastate with 3 prominent palmate nerves. Scape about as long as the petioles. Spathe convolute throughout or dilated and spreading above. Spadix completely covered with flowers, or with the apex naked. Flowers unisexual, a perianth wanting; staminate flowers covering apical portion of spadix, sessile, consisting of 4–8 two-loculed anthers embedded in the margin of a peltate shield-like scale; anthers dehiscing by terminal pores. Car-

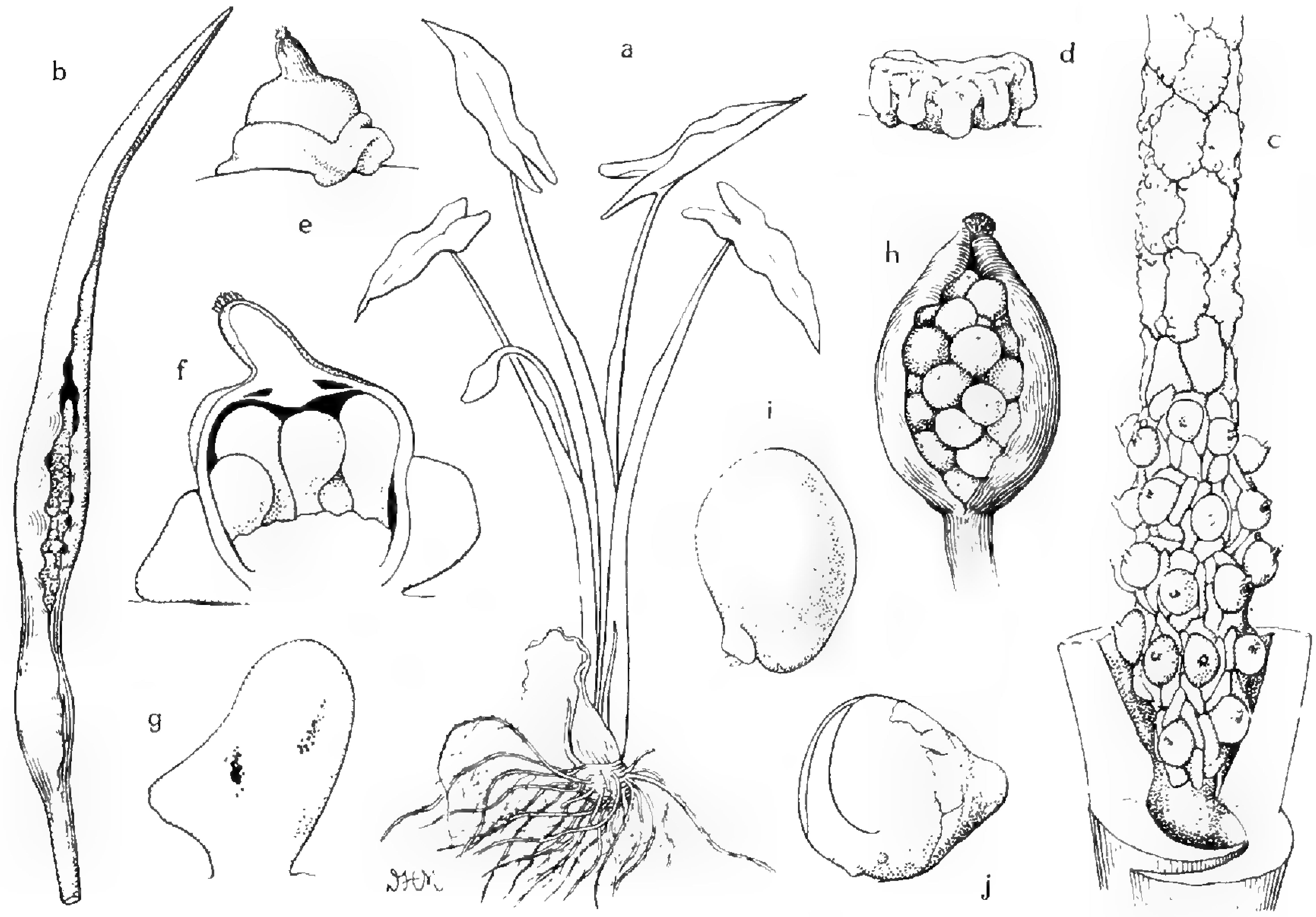


FIG. 3. **Peltandra.** a–j, *P. virginica*: a, habit, × 1/8; b, inflorescence, × 1/2; c, spadix, basal portion, showing staminate and carpellate flowers, spathe removed, × 2; d, staminate flower, lateral view, × 5; e, carpellate flower, lateral view, × 5; f, carpellate flower, vertical section, showing ovules, × 10; g, ovule, × 20; h, fruiting spadix enveloped by base of spathe, × 1/2; i, seed, × 2; j, seed, apical view, seed coat partially removed to show embryo, × 2.

pellate flowers covering basal portion of spadix, consisting of the 1-loculed gynoecium surrounded by 4 or 5 white, fleshy staminodia; ovules 1-few, basal, amphitropous. Fruits 1–3-seeded berries aggregated in a fleshy head inclosed by the leathery base of the spathe; scape recurved at maturity. (*Houttinia* Necker, nom. rejic.) TYPE SPECIES: *P. undulata* Raf. = *P. virginica* (L.) Schott & Endl. (The name from Greek, *pelta*, a small shield, and *andros*, of a man, in reference to the peltiform stamens.) — ARROW-ARUM.

Three species, all of which occur in our area, of wet soils or shallow water along stream and pond borders, marshes, swamps, and wet woods in the eastern areas of North America. The best known and most widespread species is *Peltandra virginica* ($2n$ = c. 44, 88), which is exceedingly variable in the shape of the blades, having seven named forms. The northern and southern extremes of this species also differ in the shape of the spathe and in the undulation of the margin of the spathe. *Peltandra sagittifolia* (Michx.) Morong (*P. glauca* (Ell.) Feay ex Wood), with an entirely white spathe and red fruits, is found from southeastern North Carolina to Florida, entirely on the Coastal Plain. The third species, *P. luteospadix* Fern., has a white-bordered spathe and yellow spadix and occurs from southeastern Virginia, southward to Florida. It has been suggested that *P. luteospadix* may have arisen as a hybrid of *P. virginica* and *P. sagittifolia* but no investigations have been made either to confirm or refute this hypothesis.

REFERENCES:

BARKLEY, F. A. Noteworthy plants of Texas. II. A new species of *Peltandra*. Madroño **7**: 131–133. 1944. [*P. Tharpii*.]

BLAKE, S. F. The forms of *Peltandra virginica*. Rhodora **14**: 102–106. 1912.

DUGGAR, B. M. Studies in the development of the pollen grain in *Symplocarpus foetidus* and *Peltandra undulata*. Bot. Gaz. **29**: 81–98. 1900. [*P. virginica*.]

EDWARDS, T. I. The germination and growth of *Peltandra virginica* in the absence of oxygen. Bull. Torrey Bot. Club **60**: 573–581. 1933.

———. Seed frequencies in *Cytisus* and *Peltandra*. Am. Nat. **68**: 283–285. 1934.

FERNALD, M. L. Are two species passing as *Peltandra virginica*? Rhodora **42**: 430–432. 1940. [Does not answer the question; presents the problem.]

———. A Virginian *Peltandra*. Rhodora **50**: 56–59. 1948. [*P. luteospadix*.]

GOLDBERG, B. Life history of *Peltandra virginica*. Bot. Gaz. **102**: 641–662. 1941. [A morphological study.]

HART, H. T. Delayed germination in seeds of *Peltandra virginica* and *Celastrus scandens*. Publ. Puget Sound Biol. Sta. **6**: 255–261. 1928. [Seed dormancy.]

TIDESTROM, I. Notes on *Peltandra*. Rafinesque. Rhodora **12**: 47–50. 1910. [*P. virginica* vars. *heterophylla* and *angustifolia*.]

Subfam. COLOCASIOIDEAE Engl.

5. **Colocasia** Schott, Meletemata Bot. 18. 1832.

Perennial herbs with starch-filled corms and tubers. Leaves ovate-cordate and peltate, dark velvety green above. Plants monoecious; inflorescence stoutly peduncled, shorter than the petioles; spathe ovate-lanceolate, constricted below the middle; the spadix inclosed by the spathe, with pistillate flowers on the basal portion and staminate flowers above, the two groups separated by a group of sterile flowers, the terminal portion of the spadix naked (or covered by sterile flowers). Perianth wanting. Staminate flowers of several stamens united into a peltate body, the anthers elongate, laterally adnate or partially free and pendent, dehiscing by an apical slit. Carpellate flowers consisting of the short-styled gynoecium, the ovary 1-locular, with numerous orthotropous ovules on the ovary wall. Fruit a berry. TYPE SPECIES: *Colocasia antiquorum* (L.) Schott, *C. esculenta* (L.) Schott, or *C. acris* (R. Br.) Schott, a lectotype apparently not yet chosen. (An old Greek name derived from the Arabic *colcas* or *culcas.*) — DASHEEN, TARO.

A genus of tropical Asiatic herbs, variously interpreted as consisting of seven or more species. *Colocasia esculenta* (L.) Schott is widely cultivated throughout the tropics for its starchy, edible tuber. Numerous cultivars occur, and several have been introduced into the United States, where the species has been grown in the lowlands of the Coastal Plain from South Carolina to eastern Texas. *Colocasia esculenta* var. *aquatilis* Hasskarl has escaped cultivation and is an aggressive weed which forms large clones spreading vegetatively by slender, rapidly growing stolons. This plant has been poorly collected in the southeastern United States, and herbarium material is rare. It has been reported to be spreading in southern Louisiana, and it is known also from several localities from central to southern Florida growing along streams, marshes, and roadsides. The leaves of naturalized plants observed in southern Florida have a purple centrum and a purple band at the summit of the petiole. No flowering material of this form has been collected in our area. Other clones may well occur, however, and a form lacking purple markings, locally naturalized at Tallahassee, Florida, flowers in September and October (Godfrey).[3]

Care must be taken to cook the starchy corm thoroughly before it is eaten. Small capsules containing calcium oxalate raphides are found in abundance in all tissues of the plant. If improperly cooked, the capsules discharge the raphides with such force that they penetrate the tissues of the mouth causing great irritation. Prolonged cooking renders the capsules inactive.

[3] A plant grown from a corm collected in Dade County, Florida, in May, 1958, flowered in the greenhouse at the Arnold Arboretum on October 28, 1959. The firm, fleshy spathe was 28 cm. long and light orange in color, except for the green basal portion inclosing the carpellate region of the spadix. The erect, cream-colored staminate region and the sterile appendix of the spadix were exserted from the spathe which was inclined backward above the carpellate region at an angle of about 45 degrees and which was open for about 10 cm. between this and the strongly convoluted terminal 18 cm. Flowering lasted two days: the carpellate flowers were receptive the first day and the pollen was shed on the second. The leaves of these plants bore purple markings when collected, but those produced in the greenhouse lacked this coloring.

REFERENCES:

ARCENEAUX, G. A new weed on the spread in Louisiana. Sugar Bull. **24**: 35, 36. 1945. [*Colocasia esculenta* var. *aquatilis*.]

HILL, A. F. The nomenclature of the taro and its varieties. Bot. Mus. Leafl. **7**: 113–118. 1939. [*Colocasia esculenta* (L.) Schott, not *C. antiquorum* Schott.]

KUMAZAWA, S., K. NIUCHI, and F. HONDA. Classification of the taro varieties in Japan. (In Japanese.) Jour. Hort. Assoc. Japan **25**: 1–10. 1956.*

MOURSI, M. A. A comparative physiological study of dasheen (*Colocasia antiquorum* (Schott). Indian Jour. Hort. **13**: 15–19. 1956.*

RAO, N. S. A note on the chromosome number in *Colocasia antiquorum* Schott. Curr. Sci. Bangalore **16**: 229. 1947.* [$2n = 36$.]

RATTENBURY, J. A. Chromosome numbers in New Zealand angiosperms. Trans. Roy. Soc. N. Zealand **84**: 936–938. 1957. [Includes several varieties of *Colocasia antiquorum* from the Pacific area, $2n = 28, 42$.]

SAFFORD, W. E. The useful plants of Guam. Contr. U. S. Natl. Herb. **9**: 1–416. 1905. [29–71, raphides of *Colocasia* and their method of discharge.]

SEDGWICK, T. F. The root rot of taro. Hawaii Agr. Exp. Sta. Bull. **2**: 1–21. 1902.*

YARBROUGH, J. A. Stomatal count of a single leaf of *Colocasia*. Proc. Iowa Acad. Sci. **41**: 71–73. 1934.

YOUNG, R. A. The dasheen; a Southern root crop for home use and market. U. S. Dep. Agr. Farmers' Bull. **1396.** 36 pp. 1924. (Revised 1946.)

Subfam. AROIDEAE Engl.

6. **Arisaema** Martius, Flora **14**: 459. 1831.

Perennial herbs with globose or subglobose corms each bearing a simple scape sheathed by the leaf petioles. Leaves palmately or pedately divided. Spathe convolute below, spreading and arched above. Spadix obovoid and fertile at the base, above sterile (appendix) and cylindric, clavate or long attenuate. Plants dioecious or at times monoecious with both staminate and carpellate flowers in an inflorescence. Flowers without a perianth. Staminate flowers of numerous 2–4-locular, subsessile anthers opening by a slit or a pore. Carpellate flowers consisting of a gynoecium with a unilocular ovary containing 5 or 6 erect, orthotropous ovules. Fruits 1-few-seeded red berries, few to many borne on the enlarged, ovoid base of the spadix. (Including *Muricauda* Small). TYPE SPECIES: *A. nepenthoides* Mart. (Name from Greek, *aris*, an ancient plant name, and *haima*, blood, in reference to the red-spotted leaves of some species.) — JACK-IN-THE-PULPIT, INDIAN TURNIP.

A genus of over 100 species in 15 sections, of eastern Asia, Africa (Ethiopia), North and Central America; represented in our area by three to five species in two sections.

Section TORTUOSA Engl., with seven eastern Asiatic and one eastern American and Mexican species, is represented in our flora by *A. Dracontium* (L.) Schott ($2n = 28, 56$), green dragon or dragon root, widespread from Florida to Texas, north to southern Quebec and Ontario, and also with disjunct stations in eastern Mexico. The pedately divided leaves and the long-exserted, slender, tapering appendix are characteristic.

Our other species belong to sect. PISTILLATA Engl., which includes about eight species of eastern Asia and three or four of eastern North America. The species of this section have a distinctly stipitate appendix which is more or less cylindrical and shorter than the spathe. *Arisaema quinatum* (Nutt.) Schott ($2n = 28$), of rich woods from Florida north to North Carolina and west to Louisiana, is a well-marked plant with a curved spadix and leaves generally with five leaflets. *Arisaema Stewardsonii* Britton ($2n = 28$), with the back of the spathe fluted, occurs primarily to the north of our area (Nova Scotia and southern Quebec, southward along the Appalachians at higher elevations in cold, wet woods) reaching its

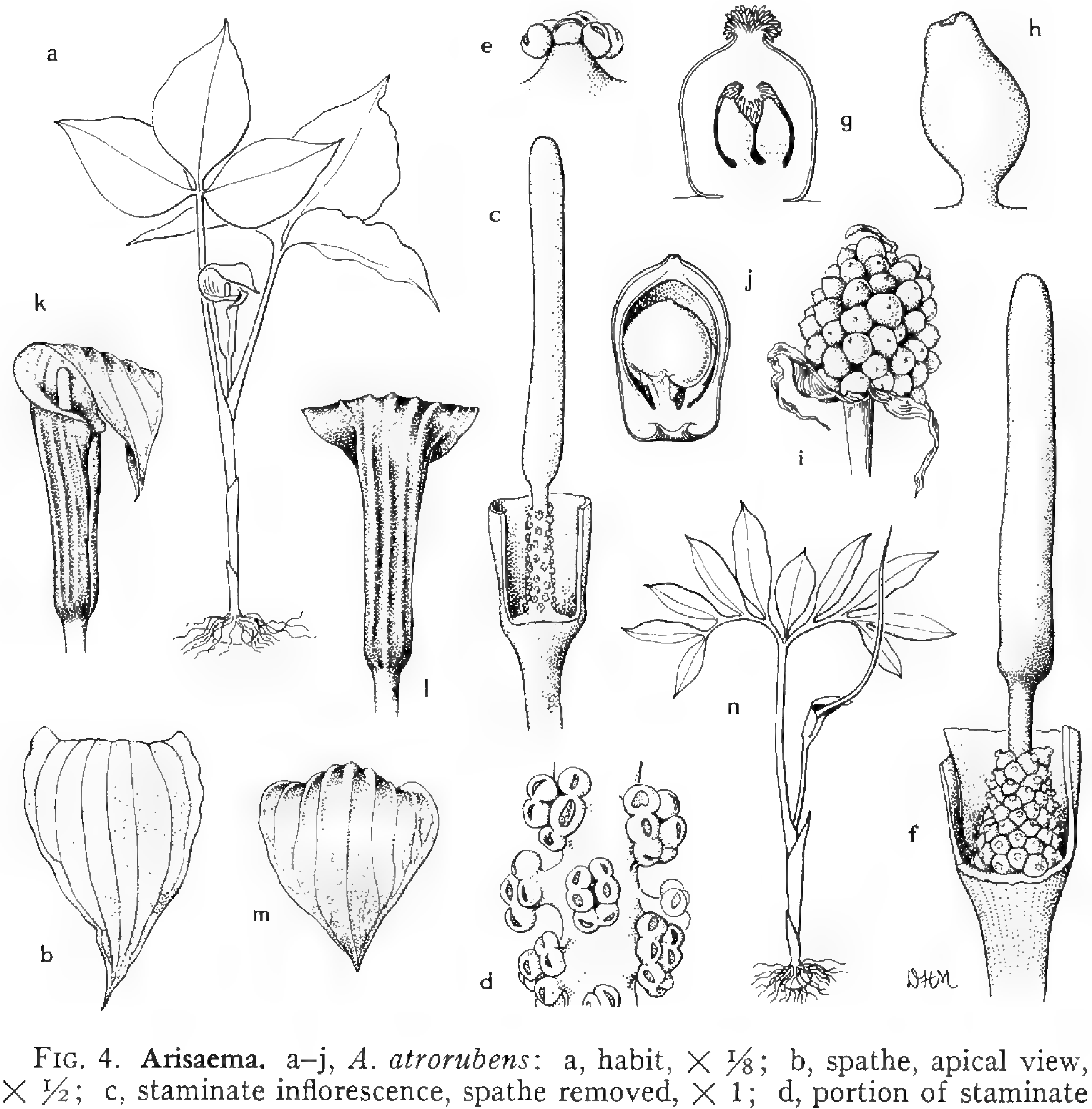


FIG. 4. **Arisaema.** a–j, *A. atrorubens*: a, habit, × 1/8; b, spathe, apical view, × 1/2; c, staminate inflorescence, spathe removed, × 1; d, portion of staminate spadix, × 6; e, staminate flower, lateral view, × 8; f, carpellate inflorescence, spathe removed, × 1; g, carpellate flower, vertical section, showing ovules, × 8; h, ovule, × 20; i, fruiting spadix, unusually large, × 1/2; j, fruit, vertical section, showing seed, × 2. k-m, *A. Stewardsonii*: k, inflorescence, lateral view, × 1/2; l, inflorescence, back view, × 1/2; m, spathe, apical view, × 1/2. n, *A. Dracontium*: habit, × 1/8.

southern limit in western North Carolina. Most of the taxonomic difficulties in the genus in our area center around the widespread *A. atrorubens* (Ait.) Blume (*A. triphyllum* sensu Huttleston) ($2n = 28, 56$), a plant primarily of woodlands in the northeastern United States, southward to South Carolina and Tennessee, and its close relatives. The status of this familiar and abundant plant and that of the smaller, later-flowering *A. triphyllum* (L.) Schott (*A. triphyllum* subsp. *pusillum* (Peck) Huttleston) ($2n = 28$) are still unsettled. Although the two are quite distinctive in some areas, in others forms of intermediate morphology occur; *A. acuminatum* Small, of the southeastern Coastal Plain, is perhaps one of these latter.

All of these species have been distinguished on morphological grounds and, for the most part, appear to be distinct ecologically. In instances in which *Arisaema atrorubens* and *A. Stewardsonii* come in contact (to the north of our range), hybrid colonies may occur. Such local hybridization and intergradation has led to the interpretation of the latter as a subspecies of the former. However, with local exceptions, these plants appear to represent distinct groups which maintain themselves as natural units.

Further careful population studies are essential. Collectors should note conformation (especially fluting of *A. Stewardsonii*), coloration and markings of the spathe, width of flange at the upper margin of the spathe, and diameter of fruits. Careful notes on habitat, flowering time, and variability of colonies should be taken.

Apart from the differing taxonomic interpretation, the nomenclatural application of the name *A. triphyllum* L. has been a matter of controversy. It is used here in the sense of Fernald (1940) for the plant formerly known as *A. pusillum* Peck; almost all literature references to *A. triphyllum* prior to 1940 apply to the plant here called *A. atrorubens.*

Numerous morphological studies have been made of *A. atrorubens* (mostly as *A. triphyllum*) and *A. Dracontium.* The factors influencing the sex of the flowers in the inflorescence of *A. atrorubens* apparently are environmental or nutritional. By manipulating the growth conditions it is possible to control the sex of the flowers that will be produced. Thus, in rich soil with an abundant water supply, carpellate flowers are produced, while staminate flowers are produced with the reduction of the root system and leaf surface of the plant.

REFERENCES:

ALEXANDER, E. J. Southern plant notes. Castanea **5**: 91–93. 1940. [*A. Stewardsonii* in Buncombe Co., N. C.]

ATKINSON, G. F. Studies on reduction in plants. Bot. Gaz. **28**: 1–26. 1899. [Meiosis in "*A. triphyllum*"; $n = 16$.]

BOWDEN, W. M. Diploidy, polyploidy, and winter hardiness relationships in the flowering plants. Am. Jour. Bot. **27**: 357–371. 1940. [Includes *A. Dracontium, A. quinatum, A. atrorubens, A. concinnum.*]

BRUCKMAN, L. Fasciations in *Arisaema, Rudbeckia* and *Viola.* Torreya **6**: 193–195. 1906.

FERNALD, M. L. What is *Arisaema triphyllum*? *In* Some spermatophytes of eastern North America. Rhodora **42**: 247–254. 1940.

GOW, J. E. Embryogeny of *Arisaema triphyllum*. Bot. Gaz. **45**: 38–44. 1908.

HOLM, T. Seasonal dimorphism in *Arisaema triphyllum*. Am. Midl. Nat. **8**: 41–48. 1922.

HUTTLESTON, D. G. The three subspecies of *Arisaema triphyllum*. Bull. Torrey Bot. Club **76**: 407–413. 1949.

MACDOUGAL, D. T. Seedlings of *Arisaema*. Torreya **1**: 2–5. 1901. [*A. triphyllum* and *A. Dracontium*.]

MAHESHWARI, S. C., and P. P. KHANNA. The embryology of *Arisaema wallichianum* Hook. f. and the systematic position of the Araceae. Phytomorphology **6**: 379–388. 1956.

MEEHAN, T. Notes on *Arisaema triphyllum*. Bot. Gaz. **11**: 217. 1886.

MOTTIER, D. M. On the development of the embryo-sac of *Arisaema triphyllum*. Bot. Gaz. **17**: 258–260. 1892.

PICKETT, F. L. Length of life of *Arisaema triphyllum* corms. Proc. Indiana Acad. Sci. **1912**: 77, 78. 1913. [About 4 years.]

———. The development of the embryo-sac of *Arisaema triphyllum*. Bull. Torrey Bot. Club. **40**: 229–235. 1913.

———. The germination of seeds of *Arisaema*. Proc. Indiana Acad. Sci. **1913**: 125–128. 1914. [*A. triphyllum* and *A. Dracontium*.]

———. A contribution to our knowledge of *Arisaema triphyllum*. Mem. Torrey Bot. Club **16**: 1–55. 1915. [A morphological study.]

PIJIL, L. VAN DER. On the flower biology of some plants from Java with general remarks on fly-traps. [Includes species of *Arisaema*.] Ann. Bogor. **1**: 77–99. 1953.

PUTNAM, B. L. Determination of sex in *Arisaema triphyllum*. Asa Gray Bull. **6**: 50–52. 1898.

RENNERT, R. J. Teratology of *Arisaema*. Bull. Torrey Bot. Club **28**: 247–250. 1901. [*A. triphyllum*, *A. Dracontium*.]

———. Seeds and seedlings of *Arisaema triphyllum* and *Arisaema Dracontium*. *Ibid.* **29**: 37–54. 1902.

ROBINSON, B. L. A notable monstrosity of *Arisaema triphyllum*. Rhodora **18**: 222, 223. 1916.

SCHAFFNER, J. H. Control of the sexual state in *Arisaema triphyllum* and *Arisaema Dracontium*. Am. Jour. Bot. **9**: 72–78. 1922.

———. The sexual nature of vegetative or dichotomous twins in *Arisaema*. Ohio Jour. Sci. **22**: 149–154. 1922.

———. Siamese twins of *Arisaema triphyllum* of opposite sex experimentally induced. *Ibid.* **26**: 276–280. 1926.

STONE, W. *Arisaema pusillum* in Pennsylvania and New Jersey. Torreya **3**: 171, 172. 1903.

WHERRY, E. T., and J. E. BENEDICT. Plant finds in June, 1939. *Arisaema Stewardsonii*. Castanea **4**: 137. 1939. [Watauga Co., N. C.]

Subfam. PISTIOIDEAE Engl.

7. **Pistia** Linnaeus, Sp. Pl. 2: 963. 1753; Gen. Pl. ed. 5. 411. 1754.

Floating, aquatic, stoloniferous herb with a short stem bearing a rosette of leaves and numerous branching, adventitious roots. Leaves sessile, with simple, ovate to obovate-cuneate, densely pubescent blades, 3–15 cm. long, each surrounded at its base by a membranous sheath. Spathe 2–4 cm. long, tubular at its base, but free and spreading above, slightly constricted above the middle. Plants monoecious, the spadix both staminate and carpellate; spadix fused to the median line of the spathe, free at its distal end. Flowers without a perianth, the carpellate solitary on the lower part of the spadix, the staminate whorled above; stamens 2–8, appearing to terminate the spadix. Staminate flowers subtended by a membranous collar surrounding the free portion of the spadix, this in turn subtended by a short-stalked, cordate, membranous flap. Gynoecium 1-carpellate with a 1-locular ovary containing numerous orthotropous ovules. Fruit green, ovoid to ellipsoid, many-seeded, crowned by the persistent style. Seed with a rugose, thick testa, a minute embryo, and abundant endosperm. TYPE AND SOLE SPECIES: *P. Stratiotes* L. (Generic name from Greek, *pistos*, liquid, in reference to the aquatic habitat.) — WATER-LETTUCE.

FIG. 5. **Pistia.** a–g, *P. Stratiotes*: a, habit, × ½; b, inflorescence, × 3; c, inflorescence, lateral view, portion of spathe removed, × 3; d, gynoecium, vertical section, showing ovules, × 4; e, ovule, × 12; f, mature fruit, × 3; g, seed, × 6.

A genus of a single species, *Pistia Stratiotes* L. ($2n = 28$), found floating in ponds and streams of tropical and subtropical Africa, Asia, and America. In our area it occurs in Florida and the Gulf States where it frequently forms dense mats on the water. *Pistia* is of considerable biological importance not only because of its weedy nature, which frequently results in the clogging of waterways, but also because it may represent the evolutionary line through which the Lemnaceae developed. The embryo-sac development is of the Polygonum (normal) type.

At least in Florida, *Pistia* does not seem to produce seeds, although the ovary tends to enlarge and to become somewhat inflated. When the plant is pollinated artificially, seeds and fruit develop normally. Whether the failure of seed development is a result of the absence of suitable pollinating agents must still be established, but the evidence at present seems to favor such an interpretation.

REFERENCES:

ARBER, A. On the vegetative morphology of *Pistia* and the Lemnaceae. Proc. Roy. Soc. London B. **91**: 96–103. 1919.

BROOKS, J. S. The cytology and morphology of the Lemnaceae. Thesis (Ph.D.), Cornell University. 1940. [Includes a morphological study of *Pistia*.]

FU, C. S. Effects of light, temperature, oxygen and storage upon the seed germination of *Pistia Stratiotes* L. (In Chinese.) K'ê Hsüeh T'ung Pao (Scientia) **1958**: 377, 378. 1958. [Light required; best results with water-stored seeds in continuous light of high intensity.]

GOPINATH, K. On the weed-destroying habit of *Etroplus suratensis* (Bloch.). Jour. Bombay Nat. Hist. Soc. **43**: 664, 665. 1943. [A fish; destroys other plants but shows a marked aversion to *Pistia*.]

ITO, T. Floating-apparatus of the leaves of *Pistia Stratiotes* L. Ann. Bot. **13**: 466. 1899.

JAEGER, P. Observations sur la fleur du *Pistia Stratiotes* L. Compt. Rend. Acad. Sci. Paris **220**: 467–469. 1945.

KLOTZSCH, J. F. Über *Pistia*. Abh. Akad. Wiss. Berlin **1852**: 329–359. *pls. 1–3.* 1853.

KOCH, K. Ueber *Pistia* in Allgemeinen und *Pistia Turpini* Blume insbesondere. Bot. Zeit. **10**: 577–585. 1852.

SCHLEIDEN, M. J. Bemerkungen über die Species von *Pistia*. Allgem. Gartenzeit. **6**: 17–20. 1838. [A systematic account of the genus listing nine species.]

UNGER, F. Beitrage zur Physiologie der Pflanzen. I. Bestimmung der in den Intercellulargangen der Pflanzen enthaltenen Luftmenge. Akad. Wien. Sitzber. **12**: 367–378. 1854.*

LEMNACEAE (DUCKWEED FAMILY)

Small aquatic plants, floating on or below the surface of the water, consisting of a highly reduced, fleshy or membranaceous plant body (frond), lacking distinct stems and leaves, and either rootless or with one or many roots. Plants monoecious, the flowers borne in marginal pouches or in pouches on the upper surface of the frond. Staminate flower consisting of a single stamen, borne singly or in pairs; anther 2-locular. Carpellate flowers solitary, consisting of a single carpel; ovary 1-locular with 1 or 2 basal ovules. Fruit a 1- or 2-seeded utricle.

This family, generally considered to be composed of four genera and 26 species, is distributed in streams and other bodies of fresh water in most parts of the world. All four genera occur in our area and are represented by a total of 11 species which are of considerable economic and biological importance. Species of the Lemnaceae have been reported to serve as an important food for wild fowl, marsh birds, and aquatic animals, such as fish and snails.

The small plant body of the Lemnaceae is oval or elongate, and bears at its basal margin one or two reproductive pouches where the buds (and in two genera the flowers) develop. Reproduction is primarily vegetative; a single plant may multiply to several million in one season. It has been estimated that compact floating mats of *Spirodela* contain from 100,000 to 200,000 plants per square yard of water, and mats of *Lemna* 300,000 to 800,000 plants, while those of *Wolffia* may have 1,000,000 to 2,000,000 plants per square yard.

It is generally accepted that the Lemnaceae represent a group derived from the Araceae and that the genera exhibit a reduction and simplification series from *Spirodela* to *Lemna* to *Wolffiella* and *Wolffia*. Lawalrée, however, considered the Lemnaceae to be related to the Helobiales with a close affinity to the Najadaceae.

The frond of the Lemnaceae has been interpreted as a stem functioning as a leaf, as a modified leaf, and as a structure partly foliar and partly axial. Arber compared the structure of *Pistia* with that of *Spirodela* and considered the lemaceous frond to be axial at the base and foliar at the distal region. She interpreted the distal part of the frond as a "petiolar phyllode," and considered the pockets of *Spirodela* on the lower side as being formed by "wings of the leaf-sheath, terminating in two minute ligular flaps" and on the upper side by the axis. A somewhat different point of view was expressed by Brooks who interpreted the plant body of *Spirodela* as a single sympodial branch bearing a prophyllum, a leaf, and a bract and terminating in an inflorescence, all somewhat reduced and fused to each other.

In the fall, modified fronds or "bulblets" (turions) are produced which sink to the bottom of the water where they overwinter, rise again in the spring, and begin to grow. These bulblets may also be produced during other unfavorable growth periods.

The flowers of *Spirodela* and *Lemna* are enclosed in a membranaceous spathe within the reproductive pouch. This spathe is absent in *Wolffia* and *Wolffiella*. The flowers of a single plant mature at different times. When two staminate flowers and a carpellate flower are produced by the plant the sequence of their maturation is basipetal: the distal stamen matures first, then the carpel, and finally the second stamen. This difference in the time of the maturation of the flowers doubtless promotes cross pollination. Apparently pollination may result from direct contact of the flowers as the plants float and also by the agency of insects and other small aquatic animals which are associated with these plants. The pollen grains are spherical, monocolpate and generally have spiny projections on the exine. These grains show some characters in common with certain types of the Araceae, while they are less similar to those of the Najadaceae.

The ovule is bitegmic and the inner integument forms the operculum, which persists, resembling a stopper at the micropylar end of the seed. The endosperm is cellular and forms a chalazal haustorial process, the "caecum." The monocotyledonous embryo has a short suspensor and, in some genera, lacks a radicle.

These genera have been the subject of numerous laboratory experiments dealing with the physiology of flowering and the effects of minerals, light, temperature and other factors on growth and development. Very few physiological races have been found to be present within the Lemnaceae. The small number of races has been interpreted to be a result of the morphological specialization and antiquity of the Lemnaceae, their extreme reduction, and their ability to reproduce vegetatively.

REFERENCES:

ARBER, A. The vegetative morphology of *Pistia* and the Lemnaceae. Proc. Roy. Soc. London B. 91: 96–103. 1919.

ANEANA, L. H. Las Lemnaceae y las larvas de los mosquitos. Anal. Inst. Biol. México **1**: 33–37. 1930.*

BLACKBURN, K. B. Notes on the chromosomes of the duckweeds (Lemnaceae) introducing the question of chromosome size. Proc. Univ. Durham Phil. Soc. 9: 84–90. 1933.

BROOKS, J. S. The cytology and morphology of the Lemnaceae. Thesis (Ph.D.), Cornell University, 1940.

FROMM, F., I. M. VIDAL, and J. COLEMAN. The action of herbicides on Lemnaceae. Proc. Penn. Acad. Sci. **23**: 85–90. 1949.*

GOEBEL, K. Zur Organographie der Lemnaceen. Flora **114**: 278–305. 1921.

HEGELMAIER, F. Die Lemnaceen. Eine Monographische Untersuchung. Leipzig, 1868.

———. Systematische Übersicht der Lemnaceen. Bot. Jahrb. **21**: 268–305. 1895.

HICKS, L. E. Flower production in the Lemnaceae. Ohio Jour. Sci. **32**: 115–128. 1932. [A report on a series of experiments to induce flowering.]

———. Ranges of pH tolerance of the Lemnaceae. *Ibid.* **32**: 237–244. 1932.

———. The Lemnaceae of Indiana. Am. Midl. Nat. **18**: 774–789. 1937.

HOREN, F. VAN. On the hibernation of Lemnaceae. Jour. Bot. **8**: 36–40. 1870.

LANDOLT, E. Physiologische und ökologische Untersuchungen an Lemnaceen. Ber. Schweiz. Bot. Ges. **67**: 271–410. 1957.

LAWALRÉE, A. La position systématique des Lemnaceae et leur classification. Bull. Soc. Bot. Belg. **77**: 27–38. 1945.

MCATEE, W. L. Eleven important wild-duck foods. U. S. Dep. Agr. Bull. **205**: 1–25. 1915. [Lemnaceae, 3–5.]

MCCANN, C. Observation on Indian duckweeds, Lemnaceae. Jour. Bombay Nat. Hist. Soc. **43**: 148–162. 1942.

MAHESHWARI, S. C. Systematic position of the family Lemnaceae. Proc. IX Internatl. Bot. Congr. **2**: 246, 247. 1959. [Most closely related to Araceae.]

MASON, H. L. A flora of the marshes of California. Univ. California. Berkeley. 1957. [Lemnaceae, 327–343. Includes detailed illustrations of the vegetative body, flowers, fruits, and seeds of *Lemna trisulca*, *L. gibba*, *L. minor*, *L. perpusilla*, *L. minima*, *Spirodela oligorrhiza*, *S. polyrhiza*, *Wolffia columbiana*, *W. arrhiza*, *W. cylindrica*, and *Wolffiella lingulata*.]

SAEGER, A. Manganese and the growth of Lemnaceae. Am. Jour. Bot. **20**: 234–245. 1933.

SCHLEIDEN, M. J. Prodromus monographiae Lemnacearum oder conspectus generum atque specierum. Linnaea **13**: 385–392. 1839. [A systematic account.]

THOMPSON, C. H. A revision of the American Lemnaceae occuring north of Mexico. Ann. Rep. Missouri Bot. Gard. **9**: 21–42. 1898.

KEY TO THE GENERA OF LEMNACEAE

A. Plant with 2 marginal reproductive pouches; segments with 1–many roots; inflorescence of 2 staminate and 1 carpellate flower surrounded by a membranaceous spathe.

B. Fronds with 2 or more roots; conspicuously 5–18 nerved. . 1. *Spirodela.*
B. Fronds bearing a single root; obscurely 1–3 nerved. . . . . 2. *Lemna.*
A. Plant with a single marginal reproductive pouch; segments rootless; inflorescence of 1 staminate and 1 carpellate flower without a spathe.
C. Frond elongate, thin; stipe-attachment on one side of the reproductive pouch. . . . . 3. *Wolffiella.*
C. Frond ellipsoid or ovoid, thick; stipe-attachment within reproductive pouch (not evident). . . . . 4. *Wolffia.*

1. **Spirodela** Schleiden, Linnaea 13: 391. 1839.

Plants solitary or in groups of 2–5. Frond round or obovate, thick, purple beneath and green above with 5–18 palmately arranged nerves radiating from the node (centrum). Roots 2–16 to each frond. Each frond with 2 marginal reproductive pouches at the basal region. Inflorescence of 1 carpellate and 2 (rarely 3) staminate flowers, inclosed within a membranaceous spathe. Stamens 2-locular, dehiscing longitudinally. Gynoecium with a 1-locular ovary and 1 campylotropous or 2 anatropous ovules. Utricle with winged margins. TYPE SPECIES: *S. polyrhiza* (L.) Schleid. (Name from Greek, *speira*, a cord, and *delos*, evident, alluding to the conspicuous roots.)

A genus of three species, represented throughout our area by *S. polyrhiza* ($2n = 40$) in aquatic habitats. While *Spirodela* is one of the most abundant and widely distributed of the Lemnaceae it seldom occurs in pure stands but is usually found growing in association with species of *Lemna* and *Wolffia*. *Spirodela oligorrhiza* (Kurtz) Hegelm. has been reported from two collections in Missouri and may possibly be found to occur in our area. It has oblong or narrowly obovate fronds with only four to six nerves and two or three (rarely more) roots.

Spirodela, the least reduced of the Lemnaceae, frequently has been compared to *Pistia*, of the Araceae.

Jacobs, in a morphological study of *Spirodela polyrhiza*, interpreted the lower flap of the reproductive pouch as "bracts which were derived by phylogenetic reduction from leaves." The plant was considered to be a "greatly reduced type of rosette in which the vertical axis has been reduced to three highly compacted nodes." Brooks has shown that the flowers of the plant are always produced in the larger, usually left-hand reproductive pouch, while the smaller, right-hand reproductive pouch produces only vegetative buds. This led him to interpret the right-hand pouch as being formed by the prophyllum and the basal part of the foliage leaf, and the left-hand, flowering pouch by the bract and foliage leaf. Occasional plants may be found, however, in which this arrangement is reversed.

The embryo sac was described by Brooks as being of the "Polygonum" (normal) type. This is the same type found in *Pistia* but differs from the other known types in the Lemnaceae, all of which are bisporic and of the "Allium" type. However, in contrast to *Pistia*, which forms four megaspores, three of which disintegrate, *Spirodela* forms two megaspores and one dyad cell; the dyad and one megaspore degenerate. The mature ovule is campylotropous when only one is present in the ovary; when two are present they are almost completely anatropous.

In addition to its possession of numerous roots, *Spirodela* differs from the other genera of the Lemnaceae by the presence of vascular tissue in the roots, the formation of two ovules in the ovary (*L. gibba* L. is described as having as many as 7 ovules), and by the "Polygonum" type of development of the embryo sac. Brooks reports the presence of a root in the embryo of *Spirodela*, but this needs confirmation, since *Lemna* has recently been shown not to form one during its development within the seed.

REFERENCES:

BITCOVER, E. H., and D. H. SIELING. Effect of various factors on the utilization of nitrogen and iron by *Spirodela polyrhiza* (L.) Schleid. Pl. Physiol. **26**: 290–303. 1951.*

CLARK, N. A., and E. E. FRAHM. Influence of auxins on reproduction of *Lemna major*. *Ibid.* **15**: 735–741. 1940.* [*S. polyrhiza.*]

——— and E. M. ROLLER. The stimulation of *Lemna major* by organic matter under sterile and nonsterile conditions. Soil Sci. **31**: 299–308. 1931.* [*S. polyrhiza.*]

GEISSMAN, T. A., and L. JURD. The anthocyanin of *Spirodela oligorrhiza*. Arch. Biochem. Biophys. **56**: 259–263. 1955.*

GORHAM, P. R. Growth factor studies with *Spirodela polyrrhiza* (L.) Schleid. Am. Jour. Bot. **32**: 496–505. 1945.

HEGELMAIER, F. Über die Fructifikationstheile von *Spirodela*. Bot. Zeit. **29**: 621–629, 645–666. 1871.

JACOBS, D. L. An ecological life-history of *Spirodela polyrhiza* (Greater Duckweed) with emphasis on the turion phase. Ecol. Monogr. **17**: 437–469. 1947.

KANESEKI, S. The influence of "ukikusa" (*Spirodela polyrrhiza* Schleid.) on the micrometeorology in the bare water field. (In Japanese.) Soc. Agr. Met. Japan J. Agr. Met. **11**: 37–38. 1955.*

MAHESHWARI, S. C. *Spirodela polyrrhiza*: the link between the aroids and the duckweeds. Nature **181**: 1745, 1746. 1958.*

SAEGER, A. *Spirodela oligorrhiza* collected in Missouri. Bull. Torrey Bot. Club **61**: 233–236. 1934.

SOUÈGES, R. Embryogénie des Lemnacées. Développement de l'embryon chez le *Lemna minor* L. Compt. Rend. Acad. Sci. Paris **248**: 1896–1900. 1959.

STERKI, V. Winter-buds of *Spirodela polyrhiza* (L.). Ohio Nat. **10**: 181, 182. 1910.

2. Lemna Linnaeus, Sp. Pl. 2: 970. 1753; Gen. Pl. ed. 5. 417. 1754.

Fronds solitary or in groups of 2–5, each frond with 1–3 nerves and a single root without vascular tissue. Marginal reproductive pouches 2, of unequal size, at the basal region of each frond, the flowers, when produced, always appearing in the smaller pouch, the vegetative buds in both. Inflorescence of 1 carpellate and 2 staminate flowers surrounded by a membranaceous spathe. Anther 2-loculed, dehiscing transversely. Gynoecium with a 1-loculed ovary and 1 campylotropous ovule. Utricle ovoid and smooth. TYPE SPECIES: *L. minor* L. (Name from Greek, *lemna*, an aquatic plant, possibly *Callitriche*, mentioned by Theophrastus.) — DUCKWEED.

A genus of about ten species, five of which occur within our area. By far the most common is *Lemna minor* L. ($2n = 40, 42$), which frequently forms dense covers over quiet waters. *Lemna trisulca* L. ($2n = 44$), although less conspicuous because it floats beneath the surface of the water, occurs almost as frequently as *L. minor*. Three other species known from our area are *L. valdiviana* Phil., *L. minima* Phil., and *L. perpusilla* Torr.

Several of the species of *Lemna* have been used extensively in physiological studies, although *L. minor* and *L. gibba* L. have been the subject of the greater number of the papers on the subject. (Reports of experiments on *L. major* Griff. refer to *Spirodela polyrhiza*.) Recently Kandeler has been able to induce flowering in *Lemna gibba* ($2n = 64$); under controlled conditions it has a day-length requirement of 12–14 hours. (See also Hillman, 1959).

Lemna usually is described as having one to seven ovules in the ovary; Hegelmaier described *L. gibba* as possessing one to six. It appears that our species have only a single ovule per carpel, but a careful investigation of the various species should be made to determine this accurately.

During the development of the embryo sac most of the nucellus disappears, but a few cells persist as the nucellar or micropylar cap. The endosperm is cellular and has a chalazal haustorial outgrowth or "caecum." According to Maheshwari, no radicle is formed in the embryo. However, both Lawalrée and Brooks describe the development of a root in the embryo. Brooks has also shown that the embryo of *Lemna* has only one pouch, the vegetative pouch. These embryological characters of *Lemna* seem to agree much more closely with those of Araceae than with those of the Helobiales, which differ in the nature of their endosperm, the absence of a caecum, and in the absence of a nucellar or micropylar cap.

REFERENCES:

ASHBY, E. The interaction of factors in the growth of Lemna. III. The interrelationship of duration and intensity of light. Ann. Bot. **43:** 333–354. 1929. (See also, I. **42:** 771–782. 1928; II. **43:** 329–332; IV. 805–831. 1929.)

——— and E. WANGERMANN. The effects of meristem ageing on the morphology and behavior of fronds in *Lemna minor*. Ann. N. Y. Acad. Sci. **57:** 476–483. 1954.

——— and others. Studies in the morphogenesis of leaves. III. New Phytol. **48:** 374–381. 1949; VII, Parts I & II. **50:** 186–199, 200–209. 1951; VIII. **51:** 355–358. 1952; IX. **52:** 298–311. 1953; X. **54:** 182–198. 1955. [Experimental studies on *L. minor*.]

BEATSON, M. E. Sub-fossil pollen of *Lemna* in Quaternary deposits. Data for the study of post-glacial history. XV. New Phytol. **54:** 208. 1955.

BIERHUIZEN, J. F. Observations on potassium deficiency in *Lemna minor* L. Meded. Landb. Wageningen **54:** 311–319. 1954.

BLACKMAN, G. E., and R. C. ROBERTSON-CUNINGHAME. The influence of pH on the phytotoxicity of 2:4-dichlorophenoxyacetic acid to *Lemna minor*. New Phytol. **52:** 71–75. 1953.

BLODGETT, F. H. Homologies of the frond in *Lemna*. Science **39:** 291, 292. 1914.

———. Development of the embryo and the germination in *Lemna perpusilla*. *Ibid.* 292.

———. Morphology of the *Lemna* frond. Bot. Gaz. **60:** 383–390. 1915.

———. The embryo of *Lemna*. Am. Jour. Bot. **10:** 336–342. 1923.

BOTTOMLEY, W. B. Some effects of organic growth-promoting substances (auximones) on the growth of *Lemna minor* in mineral culture solutions. Proc. Roy. Soc. London B. **89:** 481–507. 1917.

BRONGNIART, A. Note sur la structure du fruit des *Lemna*. Arch. Bot. **2:** 97–104. 1833. [An account of the structure of the seed and fruit in *Lemna minor* and *L. gibba*.]

CALDWELL, O. W. On the life-history of *Lemna minor*. Bot. Gaz. **27:** 37–66. 1899. [Special attention is paid to the gametophytes and fertilization.]

DUTAILLY, G. Sur la nature réelle de la "fronde" et du "cotylédon" des *Lemna*. Bull. Mens. Soc. Linn. Paris **1:** 147–149. 1879. [Frond of *Lemna* regarded as "un sympode d'embryons disposés à la suite les uns des autres."]

ERICKSON, L. C., and R. T. WEDDING. Effects of ozonated hexene on photosynthesis and respiration of *Lemna minor*. Am. Jour. Bot. **43:** 32–36. 1956.

FERNALD, M. L. *Lemna cyclostasa* an invalid name. Rhodora **37:** 75, 76. 1935.

GORHAM, P. R. Heterotrophic nutrition of seed plants with particular reference to *Lemna minor* L. Canad. Jour. Res. C. **28:** 356–381. 1950.

———. Measurement of the response of *Lemna* to growth promoting substances. Am. Jour. Bot. **28:** 98–101. 1941.

GUPPY, H. B. On the habits of *Lemna minor*, *L. gibba*, and *L. polyrrhiza*. Jour. Linn. Soc. Bot. **30:** 323–330. 1894.

HILLMAN, W. S. Experimental control of flowering in *Lemna*. I. General methods. Photoperiodism in *L. perpusilla* 6746. Am. Jour. Bot. **46:** 466–473. 1959. II. Some effects of medium composition, chelating agents and high temperatures on flowering in *L. perpusilla* 6746. *Ibid.* 489–495.

HOPKINS, E. F. Manganese and the growth of *Lemna minor*. Science **74:** 551, 552. 1931.

JOHNSON, E. L. Effect of X-radiation upon the growth of *Lemna minor*. Univ. Colo. Stud. D. **1:** 165–175. 1941.

KANDELER, R. Über die Blütenbildung bei *Lemna gibba* L. I. Kulturbedingungen und Tageslängenabhängigkeit. Zeitschr. Bot. **43:** 61–71. 1955.

LAWALRÉE, A. L'embryologie des Lemnaceae: observations sur *Lemna minor* L. Cellule **54:** 305–326. 1952.

LEELADRISHNAN, G. Occurrence of diatoms in the leaf of *Spirodela polyrrhiza* Schleid. Curr. Sci. **28:** 116. 1959.*

LINDEMAN, W. The influence of phosphate on the photosynthesis of *Lemna minor* L. Proc. Nederland. Akad. Vetensch. C. **54:** 287–295. 1951.*

LUDWIG, F. Über die Bestaubungsverhaltnisse einiger Susswasserpflanzen und ihre Anpassungen an das Wasser und gewisse wasserbewohnende Insekten. Kosmos Stuttgart **10:** 7–12. 1881.*

MAHESHWARI, S. C. The endosperm and embryo of *Lemna* and systematic position of the Lemnaceae. Phytomorphology **6:** 51–55. 1956.

PIRSON, A., and E. GÖLLNER. Beobachtungen zur entwicklungsphysiologie der *Lemna minor* L. Flora **140:** 485–498. 1953.

SCOTLAND, M. B. The animals of the *Lemna* association. Ecology **15:** 290–294. 1934.

SAEGER, A. The growth of duckweeds in mineral nutrient solutions with and without organic extracts. Jour. Gen. Physiol. **7:** 517–526. 1925.

STEINBERG, R. A. Mineral requirements of *Lemna minor*. Pl. Physiol. **21**: 42–48. 1946.

VINTEJOUX, C. Recherches sur la racine de *Lemna minor* L. (Lemnacées). Ann. Sci. Nat. Bot. XI. **19**: 211–261. 1958.

WILSON, W. *Lemna gibba*. Remarks on the structure and germination. Hook. Bot. Misc. **1**: 145–149. 1830. [Description of seedlings.]

ZOLLINGER, J. *Lemna minor* — die kleine Wasserlinse. Leben Umwelt **12**: 193–197. 1956.* [A morphological study.]

ZURZYCKA, A. The influence of the wave length of light on the movements of chloroplasts in *Lemna trisulca* L. Acta Soc. Bot. Polon. **21**: 17–37. 1951.

ZURZYCKI, J. Formative effects of various spectral regions of light on *Lemna trisulca* L. Meded. Landb. Wageningen **57**(11): 1–14. 1957.

3. **Wolffiella** Hegelmaier, Bot. Jahrb. 21: 303. 1895.

Fronds thin, linear-attenuate or curved, solitary or in groups of several cohering generations, forming a star-shaped colony, rootless, each with a single, triangular vegetative pouch at the base from which arise the daughter fronds; each frond held to its parents by means of a "stipe." Flowering reproductive pouch developing on the upper surface of the frond to one side of the stipe, thus resulting in a tendency toward asymmetry of the frond. Vegetative fronds floating just beneath the surface of the water, but in flowering the inflorescence-bearing portion of the frond breaking the surface. Inflorescence proterogynous and consisting of a single stamen with a 2-loculed anther and a single carpel with one orthotropous ovule, without a spathe. Utricle spherical. TYPE SPECIES: *W. oblonga* (Phil.) Hegelm. (Name a diminutive of *Wolffia*.)

A genus of about five species, primarily of the New World. It is represented in our area by *Wolffiella floridana* (J. D. Sm.) Thompson, which is known in the area from Michigan and Ontario south to Louisiana, Texas, Florida, and Mexico, and by *W. lingulata* (Hegelm.) Hegelm., which has been reported from Louisiana.

The flowers of *Wolffiella* were first found and described in *W. oblonga* (Phil.) Hegelm., from Argentina, in 1935. In 1938, flowering plants of *W. lingulata* were discovered in California, and, in 1948, a report of the discovery of the flowers of *W. floridana* was published. The flowers of the three species are remarkably similar, and their resemblance to the flowers of *Wolffia* is also striking. The flowering plants of *Wolffiella floridana* are slightly shorter, but wider and thicker at the base, than the vegetative plants. Furthermore, individuals are separated from the colonies during flowering time. Stomata are found only on the emergent portion of the frond during flowering.

The carpellate flower of both *Wolffia* and *Wolffiella* matures before the staminate flower. The position of the inflorescence and the structure of the flowers of the two genera are alike in all essential features. Thus, the primary basis for maintaining *Wolffiella* as distinct from *Wolffia* is the position of the vegetative shoot axis with respect to the vegetative pouch. In *Wolffiella* the vegetative pouch is formed on one side of the stipe which attaches it to the parent plant, while in *Wolffia* the stipe and the bud develop on the lower side of the pouch near the apex of the cavity. *Wolffia* tends to be bilaterally symmetrical, while *Wolffiella* tends to be asymmetrical. This vegetative difference is presumably a very fundamental one in the morphology of the two genera.

REFERENCES:

BLAKE, S. F. *Wolffiella lingulata* in Louisiana. Rhodora **35**: 226. 1933.

GIARDELLI, M. L. Las flores de *Wolffiella oblonga*. Revista Argent. Agron. **2**: 17–20. 1935.

HARTMAN, R. T., and S. M. ENGLISH. *Wolffiella floridana* in western Pennsylvania. Castanea **24**: 45–47. 1959. [Includes drawing showing origin of new fronds.]

KURZ, H., and D. CROWSON. The flowers of *Wolffiella floridana* (J. D. Sm.) Thompson. Quart. Jour. Fla. Acad. Sci. **11**: 87–98. 1948.

MASON, H. L. The flowering of *Wolffiella lingulata* (Hegelm.) Hegelm. Madroño **4**: 241–251. 1938.

THOMPSON, C. H. The ligulate Wolffias of the United States. Ann. Rep. Mo. Bot. Gard. **7**: 101–111. *pls. 64–66.* 1896.

4. **Wolffia** Horkel ex Schleiden, Linnaea 13: 389. 1839.

Fronds solitary or in pairs, globose or ellipsoid, without roots or veins. Frond with a single funnel-shaped, basal vegetative pouch from within which arise the young fronds, which soon become detached. Inflorescence of a single stamen with a 2-loculed anther and a single carpel containing 1 orthotropous ovule. Spathe absent. Utricle spherical and smooth. (*Horkelia* Reichb., 1830, not Cham. & Schlect., 1827; *Bruniera* Franch.; *Bruneria*, Small.) TYPE SPECIES: *W. Delilii* Schleid., not Kurtz. = *W. hyalina* (Delile) Hegel. (Name in honor of J. F. Wolff, 1788–1806, who wrote on *Lemna* in 1801.) — WATER-MEAL.

A genus of about 15 species, primarily of the tropics and subtropics, represented in our area by *W. columbiana* Karst., *W. punctata* Griseb. ($2n$ = ca. 40), and *W. papulifera* C. H. Thompson. These are the smallest and simplest (by reduction) of the flowering plants, resembling small dots or grains floating in the water. Because of their minute size and the rarity of flowers these plants have been a subject of considerable botanical controversy. Dried, pressed plants are usually so shriveled and distorted that their natural shape is impossible to determine, with consequent taxonomic difficulties. The dots which are described for *W. punctata*, for instance, are apparent in dried material, but not in living plants. It has been recommended that plants of *Wolffia* be preserved in formalin-acetic alcohol and placed in flattened glass ampules which can be mounted on herbarium sheets.

Recent studies of the flowers and embryo development indicate that the anther is two- rather than one-loculed as has been previously reported. In *Wolffia* the carpel matures before the stamen, and pollination probably is effected through the agency of wind or rain.

REFERENCES:

CAMP, W. H. Distribution and flowering in *Wolffia papulifera*. Ohio Jour. Sci. **33:** 163. 1933.

DORE, W. G. *Wolffia* in Canada. Canad. Field-Nat. **71:** 10–16. 1957. [Includes chromosome number of *W. punctata*, comparison of *W. columbiana*, *W. punctata*, and notes on preparation of specimens.]

GUPTA, B. L. Studies in the development of the pollen grain and embryo sac of *Wolffia arrhiza*. Curr. Sci. Bangalore **4:** 104, 105. 1935.*

JACOBS, D. L. *Wolffia papulifera* in Florida. Am. Midl. Nat. **42:** 110, 111. 1949.

LAWALRÉE, A. La multiplication végétative des Lemnacées, en particulier chez *Wolffia arrhiza*. Cellule **49:** 337–382. 1943.

MAHESHWARI, S. C. The embryology of *Wolffia*. Phytomorphology **4:** 355–365. 1954.

———. Endosperm and seed of *Wolffia*. Nature **178:** 925, 926. 1956.

THOMAS, R. F. Vascular plants previously unreported from Georgia. Castanea **16:** 29–47. 1951. [*Wolffia papulifera*.]

STUDIES IN ARTOCARPUS AND ALLIED GENERA, IV. A REVISION OF ARTOCARPUS SUBGENUS PSEUDOJACA [1]

FRANCES M. JARRETT

Subgenus **Pseudojaca** Trécul, Ann. Sci. Nat. Bot. III. **8**: 117. 1847.

Artocarpus section *Pseudojaca* Renner, Bot. Jahrb. **39**: 368. 1907.

Leaves alternate and distichous, simple, entire or nearly so; gland-hairs superficial or slightly immersed, heads 1(–6)-celled; spongy mesophyll compact, lacking resin-cells. *Stipules* small, nonamplexicaul, scars lateral or intrapetiolar. *Inflorescences* without sterile, solid, elongate perianths. *Male head*, perianths 2–4-lobed or -partite, intermediates between perianths and interfloral bracts frequently present. *Syncarp* globose or ± lobed, fleshy, the surface smooth, or papillate from perianth apices or from the clavate heads of interfloral bracts (series *Clavati*; the heads enlarged in *A. styracifolius* to form flexuous processes).

LECTOTYPE SPECIES: *Artocarpus lakoocha* Roxb.

In discussing the classification of *Artocarpus* in the previous paper in this series (Jour. Arnold Arb. **40**: 125–127. 1959) it was pointed out that a marked contrast, which is reflected in the differing taxonomic treatments adopted, exists between the two rather distinct subgenera in the range of variation exhibited by their species. Subgenus *Artocarpus*, which was revised in that paper, was divided into two sections and a number of series based on a variety of morphological characters (e.g., orientation of the embryo, structure of the pericarp and position of the style, thin-walled *vs.* hypertrophied fruiting perianths, well-developed *vs.* vestigial interfloral bracts, and, in the leaves, presence or absence of a hypodermis and the shape of its cells, and the details of the gland-hairs).

In subgenus *Pseudojaca*, a very different taxonomic pattern is found, due partly to a more reduced inflorescence structure, but also to the more restricted variation in vegetative characters and the occurrence of parallel evolution. Quantitative rather than qualitative characters have had to be used with much greater frequency than in subg. *Artocarpus*, both in distinguishing and in arranging the species. Nineteen of the twenty species

---

[1] The preceding papers in this series will be found in Jour. Arnold Arb. **40**: 1–29; 30–37; 113–155, 298–368. 1959.

The loan of material for study from two additional institutions is acknowledged with gratitude, namely, the Blatter Herbarium, St. Xavier's College, Bombay, India (BLAT), and the Forest Research Institute, Kepong, Federation of Malaya (KEP). Especial thanks are due to the Director of the Herbarium of the Department of Systematics and Plant Geography of the Botanical Institute of the Academy of Sciences of the U.S.S.R., Leningrad, for the gift to the Arnold Arboretum of two isotypes and one other duplicate from the collections made by the Sino-Russian Expedition to Yunnan, 1956.

recognized here are assigned to section *Pseudojaca*, in which the species have been divided into two series on the basis of the shape of the interfloral bracts. They have been arranged within the larger of these according to the length of the peduncles relative to the inflorescence heads and the shape of the male head, in conjunction with various other characters. There is a single anomalous species, *Artocarpus altissimus*, which appears to be referable to subg. *Pseudojaca*, but which is distinguished by the trinerved base and glandular-crenate margin of the leaves and by the deeply bifid styles. This is placed in a separate section, *Glandulifolium*, at the end of the paper and is further discussed there.

Before proceeding to a discussion of section *Pseudojaca*, some general comments will be made on characters that have been of use in distinguishing the species in this subgenus. In contrast to subg. *Artocarpus,* the internal structure of the syncarp has been found to provide characters of taxonomic significance only at the specific level. The fusion of the proximal regions of the perianths, the clear differentiation of an endocarp (as opposed to the induration of the entire pericarp wall), and the development of fleshy fruiting perianths (slight as compared with subg. *Artocarpus*) may distinguish apparently allied species. However, with one exception, only the first of these characters is taken into account in this discussion since evidence is still inadequate concerning the others. It is probable that a larger number of species have somewhat fleshy fruiting perianths than is recorded here, since these can only be recognized in very well preserved syncarps. External characters of the female inflorescence are of considerable value in providing specific distinctions (as in subg. *Artocarpus*). These include whether the surface is smooth or papillate at anthesis and maturity, the degree of exsertion of the styles, and whether or not the syncarp is lobed.

The leaves also differ markedly from those of subg. *Artocarpus* in being rather uniform in their internal structure and in the details of the gland-hairs. However, the characters of the indumentum are of considerable taxonomic value, though once more primarily at the specific level. The hairs on the leaves and twigs may be straight, undulate or crisped, with either smooth or rough walls. In some species a varying proportion are rather stout, smooth-walled and hooked at the tip, and the presence of such hairs can be of assistance in identifying sterile material. In general, the hairs on the leaves are restricted almost entirely to the venation, and the prominence of the latter on the lower surface of the leaf is correlated with the density of the indumentum. However, in two of the species with prominent, pubescent venation, and in three others having the venation not or slightly prominent beneath and subglabrous, nearly all the cells on the areolae on the lower surface may bear crisped hairs. The minute tomentum which is thus produced causes the leaves to appear glaucous beneath and seems to have been developed independently at least twice within the subgenus. There are six taxa in which the leaves are consistently glabrous or nearly so, and in five of these (*A. gomezianus* ssp. *gomezianus*, *A. rubrovenius*, *A. nitidus*, *A. vrieseanus* var. *subsessilis* and *A. xantho-*

carpus) a prominent reticulum is also lacking. With the exception of the last two, however, the similarity of the leaves in this respect is not, apparently, an indication of close taxonomic affinity. In *A. reticulatus* the subglabrous venation is acutely prominent beneath.

The male inflorescences have been found to be of value in indicating wider affinities with the subgenus, but, unlike the female inflorescences, they quite often fail to provide satisfactory distinctions between the species. There is usually a characteristic shape for each species, but the variation in size may be considerable, so that the dimensions in allied species overlap. Specimens bearing male inflorescences, especially if immature, must often, therefore, be identified primarily by the use of vegetative characters, whereas specimens bearing female heads at any stage from anthesis to maturity usually can be identified chiefly on their characteristics.

The species have been delimited primarily on the basis of inflorescence characters, and, in nearly all, one or more collections have been seen bearing both male and female inflorescences, enabling the characters to be correlated with certainty. However, since so many of the collections bear inflorescences of one sex only, or are sterile, vegetative characters have been of considerable practical importance in assigning material to the species recognized. (It may be remarked that the matching of collections on vegetative characters was equally necessary in subg. *Artocarpus*, although the more clear-cut specific distinctions made the proceeding less critical.)

In spite of the rather minor differences between some of the taxa in the characters of the leaves and twigs, it is possible to identify nearly all of the collections with male inflorescences and the majority of sterile collections. While this is partly a question of becoming familiar with the group, there are usually definable distinctions, and these are pointed out in notes to the species. For the purpose of identifying specimens on vegetative characters, subg. *Pseudojaca* may be divided artificially into three groups of species characteristically having "pubescent," "glabrous" and "glaucous" leaves respectively. (Two species have subspecific taxa in both "pubescent" and "glabrous" groups, and in at least two of the "pubescent" species the leaves may also be glaucous beneath). The majority of the specimens can be assigned readily to one of these groups, and the notes give the distinguishing characters for all the species in the appropriate group that have overlapping ranges.[2]

The two series recognized in section *Pseudojaca* are distinguished on the basis of a difference in the shape of the heads of the stalked interfloral bracts. Most of the species have bracts with peltate, discoid, ciliate heads, and are placed in series *Peltati*. There are, however, three species occurring in northern Indochina and southern China, in which the bracts have clavate or spathulate heads. These are assigned to series *Clavati*, which is further

---

[2] Notes on "pubescent" species will be found for India under *Artocarpus gomezianus* ssp. *zeylanicus* (31), for southeast Asia under *A. tonkinensis* (30), for western Malaysia under *A. dadah* (32), *A. fulvicortex* (40) and *A. tomentosulus* (41), and for the Philippines and eastern Malaysia under *A. vrieseanus* (33) and *A. fretessii* (35); notes on "glabrous" species are given under *A. nitidus* (43) and on "glaucous" species under *A. hypargyreus* (45).

distinguished by a small but significant difference in the length of the anthers, these measuring 0.3–0.5 mm., as compared with 0.15–0.2 mm. in series *Peltati.* The dense pubescence on the bracts gives the surface of the male head a characteristic appearance; in series *Peltati* the surface is not conspicuously pubescent and the discoid heads of the bracts can be distinguished under the binocular microscope. In two of the species in series *Clavati, Artocarpus hypargyreus* and *A. petelotii,* the heads of the bracts form papillae on the surface of the syncarp (not to be confused with the papillate apices of the perianths found in some members of series *Peltati*), but in the third, *A. styracifolius,* they are enlarged to form numerous flexuous, cylindric processes. The proximal region of the perianths is free in *A. hypargyreus,* partially fused in *A. petelotii* and completely fused in *A. styracifolius.* However, in spite of the very distinctive syncarp, this last species shows a relationship to *A. hypargyreus* in having leaves that are tomentulose on the areolae and hence glaucous beneath, with subglabrous main veins. In *A. petelotii,* on the other hand, the leaves are similar to those of most pubescent-leaved members of series *Peltati* in having the venation pubescent beneath, but the areolae glabrous.

In series *Peltati,* as already indicated, it has been found that the most "natural" arrangement of the species apparently can be achieved by subdividing them according to the relative length of the head and the peduncle in the inflorescences at anthesis. The sixteen species then fall into two groups, in the first of which the peduncle is nearly always as long as, or longer than the head, and in the second of which it is less than half the length of the head, at least in the male inflorescence. The length of the peduncle in the female inflorescence seems to be inherently more variable than in the male inflorescence. Its relationship to the size of the head does not, in any case, hold beyond anthesis, owing to the enlargement of the latter as the syncarp matures, although the absolute length of the peduncle is usually greater in the first group. In this group, four pairs of species can be recognized (defined by a combination of characters), but their interrelationships are not clear, and there are also two species showing reticulate alliances. The order adopted for the species is, in consequence, partly one of convenience. In the second group, the six species can again be assigned to three pairs showing a more or less close affinity to each other. An informal review of series *Peltati,* which is intended to indicate the type of variation that is found, and the reasons for the arrangement adopted, follows.

In the first group of species, *Artocarpus longifolius* (Borneo) and *A. ovatus* (Philippine Islands) are distinguished by the long-pedunculate, rather small syncarps, the usually narrowly obovoid male head and the relatively narrow, pubescent leaves with short petioles. The syncarp has the perianths completely fused in *A. longifolius,* but free proximally in *A. ovatus,* and in the latter there are abundant persistent bracts on the surface. Except for *A. tonkinensis* the remaining species have globose or pulvinate to short-obovoid male heads often overlapping in size and shape in the different species.

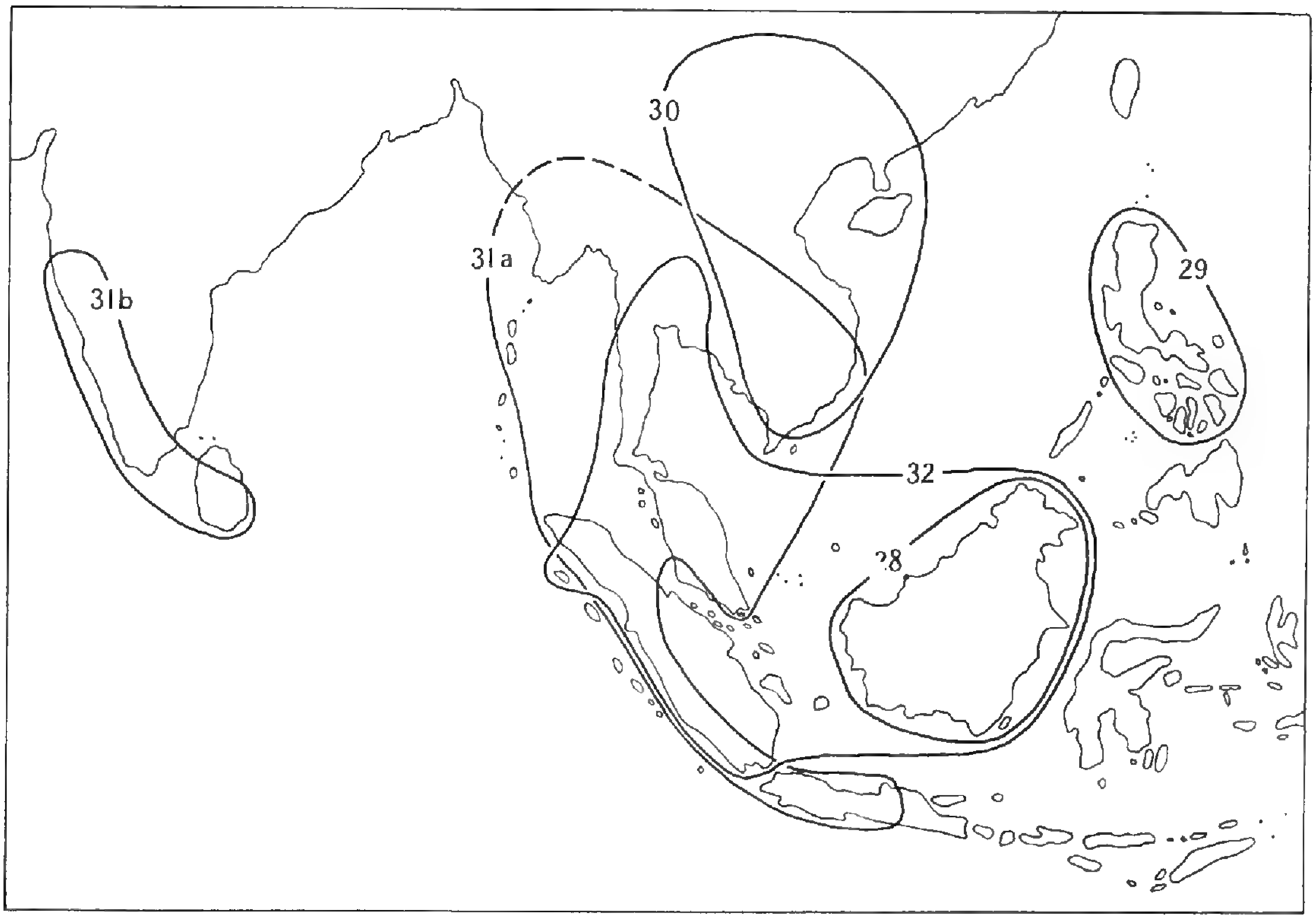


FIG. 17. Distribution of some species of subg. PSEUDOJACA. 28, *Artocarpus longifolius*; 29, *A. ovatus*; 30, *A. tonkinensis*; 31, *A. gomezianus*, a, ssp. *gomezianus* (omitting records from Assam and Cagayan Sulu), b, ssp. *zeylanicus*; 32, *A. dadah*.

The next pair of species consists of *A. gomezianus* (ssp. *gomezianus* from Burma and Indochina to western Malaysia, and ssp. *zeylanicus* in southern India and Ceylon) and *A. dadah* (Siam, Tenasserim and western Malaysia), both of which have smooth, globose syncarps with few or no interfloral bracts and free, fleshy fruiting perianths. The former is a species of monsoon regions and the latter chiefly of everwet forests, so that they are distributed differently in western Malaysia. *Artocarpus dadah* is also distinguished from ssp. *gomezianus* by having pubescent, not glabrous leaves, and from ssp. *zeylanicus* by the colour of the hairs, which are red-brown, not greyish.

Artocarpus vrieseanus (Mindanao to New Guinea and Melanesia) and *A. xanthocarpus* (northern and central Philippines) have syncarps that are very similar externally to those of the two preceding species, but are distinguished from these and the syncarps of the following species-pair by the complete fusion of the perianths. *Artocarpus vrieseanus* is a very variable species in which the proportions of the head and peduncle characteristic of this group do not always hold; of the four varieties recognized, three have more or less pubescent leaves, but one has glabrous leaves and consistently short-pedunculate inflorescences. Superficially, this species often bears a strong resemblance to *A. dadah* or to *A. fretessii*, which is placed after *A. xanthocarpus*, although it is distinguished from the former by the frequently crisped indumentum on the twigs. This similarity has determined the arrangement adopted for these species, and the syncarp character, although a convenient distinction, may not have any great taxonomic significance. *Artocarpus xanthocarpus* is superficially similar to *A. nitidus*, a species belonging to the second group, in its small, glabrous leaves and short-pedunculate male inflorescences. However, the male head is often little or no longer than the peduncle and this, with the fused perianths in the syncarp, suggests that *A. xanthocarpus* is best placed here.

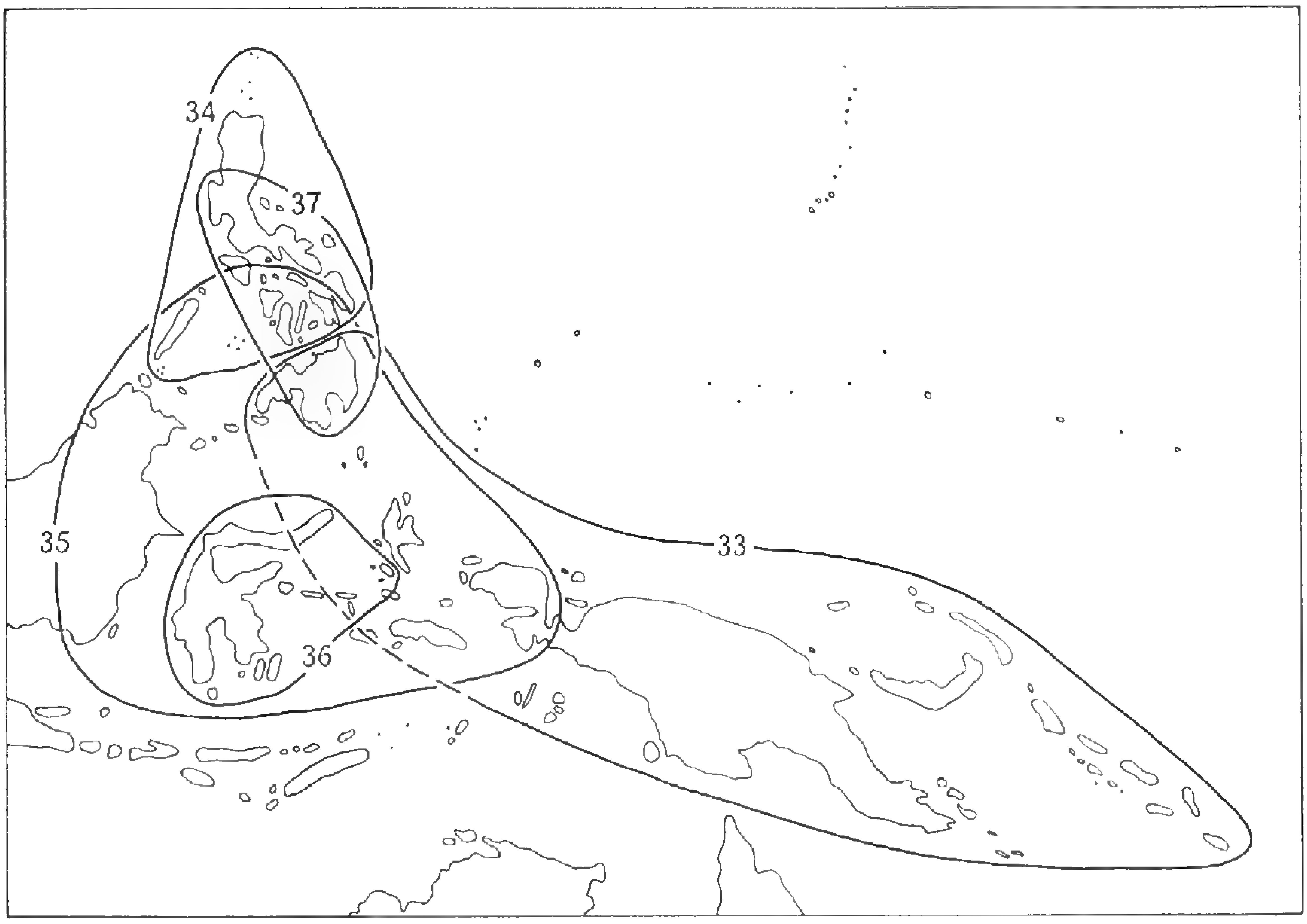


FIG. 18. Distribution of some species of subg. PSEUDOJACA. 33, *Artocarpus vrieseanus*; 34, *A. xanthocarpus*; 35, *A. fretessii*; 36, *A. reticulatus*; 37, *A. subrotundifolius*.

Artocarpus fretessii (Borneo and the Philippines to western New Guinea) and *A. reticulatus* (Celebes and Moluccas) have female inflorescences that are distinguished by being distinctly papillate at anthesis and usually strongly lobed at maturity with rather few bracts. The former has a distribution overlapping that of *A. vrieseanus* and is often difficult to distinguish when sterile, the hairs likewise being crisped on the twigs. *Artocarpus reticulatus* differs from *A. fretessii* in being larger in all its parts and in having nearly glabrous leaves which, as noted above, have an acutely prominent reticulum, unlike those of the other glabrous-leaved species.

There remain two species assigned to this group which show reticulate interrelationships. *Artocarpus tonkinensis* (Indochina and southern China) is placed after *A. longifolius* and *A. ovatus*, since it resembles both in having a relatively narrow, obovoid or ellipsoid male head and the latter in having numerous persistent bracts on the syncarp. It differs from these species, however, in having crisped hairs, as in *A. vrieseanus* and *A. fretessii*. The perianths are fused in the syncarp, and the leaves have fewer lateral veins than in any other species of this group. *Artocarpus subrotundifolius* (Philippine Islands), which is placed last in this group, does not show any very clear alliances with the other members. The length of the peduncles, although exceedingly variable, as is the size of the very large male head, suggests that the species should be placed in this group; it also resembles *A. fretessii* and *A. reticulatus* in having a distinctly papillate female head at anthesis, with the perianths free proximally, although the syncarp is only shallowly lobed and the indumentum of the twig is patent. However, in all these characters, and in the long-exserted styles (also found, however, in *A. reticulatus*) and the broad, long-petiolate, pubescent leaves, often with an oblique base, it also resembles *A. lakoocha*, placed first in the following group of species.

The species of the second group may be characterized by the consistently short male peduncle and show no obvious alliances with members of the first group, with the exception of *A. subrotundifolius*. There is a considerable range of variation and, unlike the members of the first group, the species are most readily defined on characters of the male inflorescences and the vegetative parts, although syncarp characters can also be used.

The first four species have rather large, broad leaves, with long petioles and an often oblique base, but fall into two quite distinct pairs. *Artocarpus lakoocha* (India to Indochina and Yunnan) and *A. rubrovenius* (Philippine Islands) both have rather large, obovoid to clavate (rarely ellipsoid) male heads, but differ considerably in their leaves, those of the former being pubescent on the prominent reticulum, and those of the latter being glabrous, without a prominent reticulum. The second pair of species, *A. fulvicortex* (Malaya and Sumatra) and *A. tomentosulus* (Borneo), both of which are newly described, are distinguished from the other pubescent-leaved members of subgenus *Pseudojaca* by having the areolae on the lower surface, between the markedly prominent, pubescent reticulum, frequently tomentulose, and by the twigs being merely puberulent when young. They also differ from the other species of this second group in having globose male heads, but, whereas the syncarps in *A. fulvicortex* are subsessile, like the male heads, in *A. tomentosulus* the single syncarp seen has a peduncle 25 mm. long. In the former the syncarp has completely fused perianths; in the latter the structure is unknown, but in the remaining species of this group the perianths are free proximally.

Finally, *Artocarpus glaucus* (western Malaysia) and *A. nitidus* (Assam to southern China, western Malaysia and the Philippines), have obovoid, clavate or cylindric male heads rather smaller than in the first pair of species, and leaves that are also smaller with shorter petioles. *Artocarpus glaucus* is distinguished by the very long, narrow male head, and, as the name suggests, by the leaves, which are tomentulose on the areolae beneath, while the main veins are subglabrous. Although this indumentum resembles that found in two species of series *Clavati,* there is no other indication of an alliance between these species and *A. glaucus,* nor is there any evidence of a close relationship with the preceding pair of species. The last species in this group is *A. nitidus*, which has a smaller male head than *A. glaucus*. It is widely distributed, and five subspecies are recognized on the basis of differences in the size and indumentum of the syncarp, associated with slight, but characteristic, variations in the glabrous leaves.

The species of section *Pseudojaca* are thus separated by a variety of relatively minor characters, so that, although they are readily distinguishable (given adequate material), they require somewhat complex definition. There has also been some parallel evolution, especially, it would seem, in the loss of the indumentum, or the development of a tomentum, and in the complete fusion of the perianths in the syncarp. The distribution of some types of hairs among the species, especially between *A. fretessii* and *A. vrieseanus*, suggests the occurrence of some introgression. In view of all this it does not seem desirable to discuss in further detail interrelationships or evolutionary trends among the species, nor is it possible to define satisfactorily any supra-specific taxa beyond the two series here recognized.

The key which follows is based, as far as possible, on "natural" characters, but practical considerations have, where necessary, taken first place in its construction. It is hoped that it will make possible the identification of most collections with male or female inflorescences at any stage from anthesis to maturity. (Where a dichotomy has had to be based on the inflorescences of one sex only, the specimens bearing inflorescences of the other sex are eliminated, if possible, further on in the key under the first alternative.) For sterile specimens, or those with very young inflorescences, the use of the footnote given above as a guide to the notes on vegetative distinctions is suggested. It should perhaps be pointed out that, while the species may be classified as characteristically "pubescent," "glabrous" or "glaucous," there are sufficient inconsistencies in the first two of these groups to limit the value of this distinction in preparing the key. The numbering of the species follows on from the previous paper in this series.

KEY TO THE SPECIES OF ARTOCARPUS SUBGENUS PSEUDOJACA

1. Styles bifid; leaves glandular-crenate, base trinerved. . . . . 47. *A. altissimus*.
1. Styles simple; leaves not as above.
    2. Leaves densely greyish tomentulose beneath, except for the subglabrous main veins.
        3. Syncarp peduncle to 5 mm.; male peduncle to 3 mm.; leaves with 8–15 pairs lateral veins. . . . . 42. *A. glaucus*.
        3. Syncarp peduncle 10–50 mm.; male peduncle 5–25 mm.; leaves with 4–9 pairs lateral veins.
            4. Syncarp covered with flexuous processes; male head 4–7 mm. across; leaves with lamina decurrent on petiole, reticulum not prominent beneath. . . . . 46. *A. styracifolius*.
            4. Syncarp papillate; male head 10–15 mm. across; leaves cuneate at the base, not decurrent, reticulum prominent beneath. . . . . 45. *A. hypargyreus*.

2. Leaves not tomentulose beneath, *or* main veins and reticulum also patent-pubescent.

5. Peduncles in inflorescences at anthesis at least as long as the head, *or*, if shorter in the male inflorescence, at least 7 mm.; in mature syncarp at least 13 mm.[3]

6. Male peduncle to 3 mm., head to 7 mm. across; leaves glabrous, reticulum not prominent beneath.

7. Styles exserted to 0.4 mm.; male head with bracts stoutly stalked; leaves rounded or auriculate at the base, not decurrent; (syncarp peduncle to 7 mm.). . . . . 33. *A. vrieseanus* var. *subsessilis.*

7. Styles exserted to c. 1 mm.; male head with bracts slenderly stalked; leaves usually cuneate and slightly decurrent at the base; (syncarp peduncle to 11 mm.). . . . 34. *A. xanthocarpus.*

6. Male peduncle at least 7 mm. *and/or* leaves with the reticulum prominent and usually pubescent beneath.

8. Petiole 3–8 × 3.5–5 mm., base of leaf cuneate or auriculate; syncarp peduncle 30–60 mm.; male head obovoid, 8–20 × 5–12 mm., peduncle 12–30 mm. . . . . 28. *A. longifolius.*

8. Petiole not so short and stout, *or* base of leaf cordate.

9. Female head at anthesis with styles exserted to at least 1 mm. (a few usually persisting on syncarp).

10. Styles exserted to 1–2.5 mm.; syncarp peduncle 40(?)–75 mm.; male head 25–50 × 20–35 mm.; petiole (15–)25–65 mm. . . . . 37. *A. subrotundifolius.*

10. Styles exserted to 1–1.5 mm.; syncarp peduncle to 45 mm.; male head smaller.

11. Leaves glabrous or scabrid-puberulent on the prominent reticulum from hooked hairs, petiole 13–25 mm.; female head verrucose from conical papillae, or lobed at maturity and smooth over the lobes, peduncle 25–45 mm.; male head c. 15 mm. across. . . . . 36. *A. reticulatus.*

11. Leaves pubescent, without hooked hairs; female head papillate to nearly smooth.

12. Syncarp peduncle 35–40 mm.; leaves with 7–11 pairs lateral veins; petiole to 18 mm.; surface of the male head densely pubescent from the spathulate (not peltate and discoid) heads of the bracts. . . . . 44. *A. petelotii.*

12. Syncarp peduncle 8–25 mm.; leaves with 9–18 pairs lateral veins, petiole 15–45 mm.; (male head 12–23 × 10–18 mm., surface covered by peltate, discoid, ciliate heads of bracts, peduncle 2–5 mm.). . . . . . . 38. *A. lakoocha.*

9. Female head at anthesis with styles exserted to 0.7 mm. (a few usually persisting on syncarp).

13. Syncarp subglobose or shallowly lobed, numerous dis-

---

[3] There are a few species in which the length of the peduncle in relation to that of the head is variable, or in which the proportions differ in the male and female inflorescences; these are brought down on both sides of this dichotomy, the characters of the discordant inflorescences being given in parentheses.

coid heads of bracts persisting on surface, often completely covering head at anthesis; male head obovoid to ellipsoid, at least 8 mm. across, peduncle at least 7 mm.

14. Leaves glabrous, reticulum not prominent beneath. ...... 31. *A gomezianus* ssp. *gomezianus*.
14. Leaves pubescent, reticulum distinctly prominent beneath.
    15. Petiole 15–45 mm.; (male head to 7 mm. across, peduncle to 2 mm.). .... 41. *A. tomentosulus*.
    15. Petiole to 15 mm.
        16. Syncarp peduncle (40–)70–80 mm., perianths free proximally; male peduncle 20–40 mm.; twigs with patent hairs; leaves with 11–20 pairs lateral veins. .... 29. *A. ovatus*.
        16. Syncarp peduncle 30–40(–65) mm., perianths completely fused; male peduncle 7–12 mm.; twigs with appressed and crisped hairs; leaves with 6–9 pairs lateral veins. ...... 30. *A. tonkinensis*.

13. Syncarp subglobose or lobed, bracts lacking at least on lobes, often nearly all deciduous before anthesis; male head pulvinate, globose or obovoid, if obovoid less than 8 mm. across.
    17. Young twigs greyish pubescent, *or*, if glabrous, leaves without prominent intercostal veins beneath. .... 31. *A. gomezianus*.
    17. Young twigs red-brown to yellow pubescent, *or*, if glabrous, leaves with prominent intercostal veins beneath.
        18. Syncarp with well-defined, subglobose lobes (unless many seeds are formed), the surface between papillate and often with bracts persisting, perianths free proximally; male heads to 7 mm. across, often borne on short-shoots on older wood, bracts slenderly stalked; twigs usually with subappressed and crisped hairs. .... 35. *A. fretessii*.
        18. Syncarp globose or shallowly lobed, bracts usually nearly all deciduous; male heads to 15 mm. across, usually in leaf-axils, bracts stoutly stalked.
            19. Syncarp yellow, subglobose and smooth, or (in var. *papillosus*) papillate at anthesis and often shallowly lobed at maturity, perianths completely fused; twigs usually with some or all of the hairs subappressed and crisped, varying subglabrous; larger leaves with up to 13 pairs lateral veins. .... 33. *A. vrieseanus*.

19. Syncarp green with pink flesh, subglobose and smooth, perianths free proximally; twigs with patent hairs; larger leaves with up to 20 pairs lateral veins. .... 32. *A. dadah.*

5. Peduncles in inflorescences at anthesis less than half the length of the heads, in male inflorescence to 5 mm., in mature syncarp to 12 mm.
  20. Leaves glabrous, reticulum not or scarcely prominent beneath.
    21. Male head 15–45 × 10–25 mm.; leaves often broadly elliptic to ovate, with a broad, oblique base, petiole 15–30 mm. .... 39. *A. rubrovenius.*
    21. Male head to 12 × 7 mm.; petiole 5–25 mm.
      22. Female head with perianths free proximally, styles exserted to 0.5 mm.; male head obovoid, cylindric or clavate. .... 43. *A. nitidus.*
      22. Female head with perianths completely fused; male head short-obovoid to globose.
        23. Styles exserted to 0.4 mm.; male head with bracts stoutly stalked; leaves rounded or auriculate at the base, not decurrent. .... 33. *A. vrieseanus* var. *subsessilis.*
        23. Styles exserted to c. 1 mm.; male head with bracts slenderly stalked; leaves usually cuneate and slightly decurrent at the base. ....34. *A. xanthocarpus.*
  20. Leaves pubescent, reticulum distinctly prominent beneath.
    24. Petiole to 15 mm. .... 33. *A. vrieseanus.*
    24. Petiole 15–45 mm.
      25. Male head 12–25 × 10–18 mm.; styles exserted to 1–1.5 mm.; twigs pubescent; leaves never with the intervenium tomentulose beneath. ...... 38. *A. lakoocha.*
      25. Male head to 7 × 6 mm.; styles exserted to 0.5 mm.; twigs subglabrous; leaves often with the intervenium tomentulose beneath.
        26. Leaves with 6–10 pairs lateral veins and few intercostals; syncarp peduncle to 5 mm. .... 40. *A. fulvicortex.*
        26. Leaves with 10–14 pairs lateral veins and numerous intercostals; (syncarp peduncle c. 25 mm.). ....41. *A. tomentosulus.*

Section **Pseudojaca**

Folia margine non glandulifera. *Capitula feminea* stylis simplicibus.

Series **Peltati** Jarrett, ser. nov.

Inflorescentiae bracteis interfloralibus peltatis. *Capitula mascula* cellis antherum 0.15–0.2 mm. longis.

28. **Artocarpus longifolius** Becc. For. Borneo, 629. 1902, "*longifolia.*" Holotype, Borneo, *Teysmann HB 11312* (FI).

Trees, height to 21 m. *Twigs* 4–6 mm. thick, subglabrous to densely pubescent, hairs red-brown to yellowish, patent, straight or some longer and hooked at the tip. *Leaves* 9–33 × 4.5–11 cm., obovate-elliptic or elliptic, with an acumen to 2 cm. long, base cuneate, often auriculate, margin entire; main veins and reticulum very prominent beneath; glabrous above except for the pubescent main veins, venation beneath pubescent, hairs colourless, straight, varying to subglabrous; lateral veins 9–14 pairs, curved; intercostals parallel; green, drying pale or reddish brown, lighter beneath, venation concolorous; petiole 3–8 mm. long, stout.

Inflorescences solitary in leaf-axils. *At anthesis*: *male head* 8–20 × 5–12 mm., obovoid; perianths of c. 3 free segments 0.4 mm. long; stamen 0.5 mm. long, filament broad, contracted above, anther-cells globose, 0.15 mm. long; bracts slenderly stalked, heads peltate, to 0.3 mm. across, these and perianths minutely pubescent; peduncle 12–30 × 1 mm., pubescent, hairs rufous or whitish; *female head* with styles exserted to 0.2 mm. through low papillae emerging between peltate bracts. *Syncarp* (submature) 2 cm. across, ellipsoid, drying fulvous, the surface nearly smooth, very shortly pubescent, with scattered persistent bracts; proximal region of perianths fused; peduncle 30–60 × 2–4 mm., pubescent, hairs rufous or whitish.

DISTRIBUTION: endemic to Borneo.

Borneo. SARAWAK. Kuching, *Haviland 2189* (BM, K, SING, ♂, ♀), *Haviland & Hose 3205* (BM, ♂ ♀), *3206* (K, ♂, ♀). WEST BORNEO. Landak, *Teysmann HB 11312*, 1875 (FI, ♂, ♀). SOUTH AND SOUTHEAST BORNEO. Puruktjahu, *bb 11109* (BO). EAST AND NORTHEAST BORNEO. W. Kutei: near Lahum, *Endert 1840* (L, ♂). E. Kutei: Samarinda, Blajan River, Loa Lampong, *Nedi 769* (CGE, L, ♂, ♀).

The material of *Artocarpus longifolius* is limited and the variation in the indumentum is considerable, but the collections agree in the characters of the inflorescences and in the distinctive shape of the leaves and petioles. The large stipules (5–15 mm. long), which are frequently persistent, and the short, stout petioles are unique in subg. *Pseudojaca*. The subglabrous collections may be from saplings or sucker shoots, since the leaves and internodes are somewhat longer than in the pubescent collections. The cuneate base of the leaf and the shorter petiole, in addition to the smaller inflorescences and the completely fused perianths in the syncarp, distinguish this species from *Artocarpus ovatus*.

29. **Artocarpus ovatus** Blanco, Fl. Filip. 666. 1837, "*Arctocarpus ovata*," non Noronha, 1790 (nomen nudum), ed. 3. 3: 73. *plate*. 1879; Vidal, Revis. Pl. Vasc. Filip. 254. 1886; Ahern, Timber Tree Sp. Philip. 21. *plate*. 1901. Neotype, Luzon, *Merrill SB 254* (BM).

Artocarpus cumingiana Tréc. Ann. Sci. Nat. Bot. III. **8**: 119. *t. 4, figs. 117, 118.* 1847, "*Cummingiana*"; Fern.-Villar, Noviss. App. 203. 1880; Merr. Publ. Gov. Lab. Philip. **27**: 80. 1905, Sp. Blancoanae, 125. 1918, Enum. Philip. Pl. **2**: 40. 1923; Renner, Bot. Jahrb. **39**: 370. 1907; Elmer, Leafl. Philip. Bot. **2**: 620. 1909; Whitford, Bull. Bur. For. Philip. **10**(2): 28. *t. 6*. 1911; Brown, ibid. **22**(2): 70. *fig. 23*. 1921. Holotype, Cebu, *Cuming 1784* (P); isotypes (BM, CGE, K).

Artocarpus acuminatissima Merr. Philip. Jour. Sci. **18:** 49. 1921, Enum. Philip. Pl. **2:** 40. 1923. Holotype, Luzon, *De Mesa & Rosario FB 22777* (PNH, destroyed); isotypes (K, US); lectotype (K).

Trees, height to 25 m., bark brown. *Twigs* 2.5–4.5 thick, smooth or finely rugose, short-pubescent, hairs red-brown to pale yellow, patent, straight, or some longer and undulate. *Leaves* 15–33 × 6–16 cm., oblong to obovate-oblong, varying elliptic, with an acumen to 2(–4) cm. long, base cordate, varying rounded, rarely cuneate, margin entire; main veins and reticulum prominent beneath; glabrous or nearly so above except for the pubescent main veins, venation beneath thinly to densely pubescent, hairs colourless, straight or undulate, some on main veins stout and with hooked tips; lateral veins 11–20 pairs, curved, basal 2–3 pairs crowded; intercostals parallel or reticulate; deep green above, paler beneath, drying red-brown to blue-grey above, pale or reddish brown beneath, venation usually concolorous; petiole 8–15 mm. long.

Inflorescences solitary or paired in leaf-axils, the male heads also on short shoots on older wood. *At anthesis*: *male head* 12–32 × 10–15 mm., obovoid (rarely subglobose); perianths 2- or 3-lobed, divided nearly to the base, 0.5 mm. long; stamen 0.8 mm. long, filament flattened, tapering above, anther-cells ellipsoid, 0.15 mm. long; bracts stoutly stalked, heads peltate, to 0.4 mm. across, these and perianths sparsely ciliate; peduncle (15–)20–40 × 2 mm., indumentum as twigs; *female head* with styles exserted to 0.5 mm. through a dense covering of peltate bracts. *Syncarp* to 3 cm. across, subglobose, shallowly lobed, yellowish white, drying brown, the surface smooth, very shortly pubescent, with numerous persistent bracts; wall c. 2 mm. thick; proximal region of perianths free, fruiting perianths c. 4–6, thin-walled, "seeds" (endocarps) subellipsoid, 12 × 9 mm.; core c. 8 mm. across; peduncle (40–)70–80 × 2.5 mm., indumentum as twigs.

VERNACULAR NAMES: *cubi, anubing.* USES: provides a hard timber; the wood of other species of subg. *Pseudojaca* in the Philippines is sold under the same vernacular names.

DISTRIBUTION: in forests to 2500 ft.; northern and central Philippine Islands.

Philippine Islands. MINDORO. *Medina FB 24178* (A, ♀). Mansalay: Barrio Manaul, *Sulit PNH 17175* (K, L, PNH, ♂); Mt. Yagaw, *Conklin PNH 17464* (K, PNH, ♀). LUZON. *Ahern 119* (BO, ♂ ♀), *786* (BO, ♀). Abra: Manabo, *Paraiso FB 31103* (SING, ♂). Mountain Province: Kalinga Subprov., Lubuagan, *Celestino PNH 7846* (A, ♂ ♀). Benguet: *Leano FB 24712* (US, ♀). Isabela: San Mariano, *Clemens 17032* (C), *Ramos & Edano BS 46810* (C, SING, ♂ ♀). Nueva Viscaya: near Dupax, *McGregor 11495* (C, SING, ♂). Zambales: Mt. Pinatubo, *Fox PNH 4677* (PNH). Bataan: *Alambra FB 25303* (SING, ♂). Nueva Ecija: *Alvarez FB 22143* (L). Bulucan: Angat, *Vidal 3841* (K, ♀). Rizal: *Ahern FB 2905* (BO, K, P, SING, ♂, ♀), *Maneja FB 23978* (A, BO, L, ♂), *Reillo BS 15173* (BO, L, P, ♂, ♀); Antipolo, *Merrill 1680* (K, ♂), *SB 254* (A, BM, BO, GH, K, L, P, ♂); Bosoboso, *Merrill 2822* (A, BM, K, ♀); Montalban, *Loher 6948* (K, ♂); Mt. Angilog, *Lopez FB 42035* (A, BM, K, SING, ♂, ♀). Laguna: Los Banos, *Elmer 8175* (BO, K, ♂), *Holman 93* (A, ♂); Los Banos, Mt. Makiling, *Banaga*

PNH 33385 (L, ♂), *Elmer 18467* (A, BM, K, L, ♂), *Rivera PNH 9481* (BM, L, PNH, ♂), *Sulit & Paa 38* (A, ♀); Santa Maria, Maritac, *Curran FB 10040* (BO). Tayabas: *Cailipan FB 26019* (BO, L, ♂, ♀), *Manuel FB 27456* (P); Ainoboan, *De Mesa & Rosario FB 22777*, Sept. 1913 (K, US, ♀); Langumanoc, *Ware FB 7* (BO, ♂, ♀); Lucban, *Elmer 9163* (A, BO, K, L, ♂). Camarines: *Alambra 28085* (A, ♀), *Curran FB 10426* (BO, ♂); Mt. Bagacay, *Ramos & Edano BS 33922* (A, K, ♂, ♀); Mt. Isarog, *Curran FB 10444* (BO, ♂). Sorsogon: *Curran FB 10523* (BO, ♂); Irosin, Mt. Bulusan, *Elmer 14424* (A, BM, K, L, ♂, ♀), *14458* (A, BM, K, L, ♀). MARINDUQUE. *Rosenbluth BS 12152* (BO, ♂). CATANDUANES. *Ramos & Edano BS 75302* (SING, ♂, ♀). SIBUYAN. Magellanes, Mt. Giting-Giting, *Elmer 12332* (A, BM, BO, K, L, ♂). MASBATE. *Merrill 3078* (A, BM, K, P, ♀). TICAO. *Vidal 3840* (A, K, ♂). CEBU. *Cuming 1784*, 1841 (BM, CGE, K, P, ♂). NEGROS. *Cardona FB 24219* (A, US, ♀), *Everett 7301* (BO). Occidental: *Danao FB 15036*, *Everett 4305* (BO, ♂); Cadiz, *Oliveros FB 29891* (NY, ♂). Oriental: Dumaguete, Cuernos Mts., *Elmer 9890* (A, BM, BO, K, L, ♂). PANAY. Ilo-ilo, *Vidal 596* (K, L, ♂).

Blanco's description of *Artocarpus ovatus* is clearly identifiable, but his name was reduced by Fernandez-Villar (1880) to *A. cumingiana* Tréc. (the misspelling of which as "*cummingiana*" arose from a misprint on the labels in the Paris herbarium). Merrill (1905) also used Trécul's name since he found (presumably from "Index Kewensis") that Noronha had published an *Artocarpus ovatus* in 1790 and was unaware that the latter was a *nomen nudum*.

Artocarpus ovatus is quite distinct from the other Philippine species of subg. *Pseudojaca* in its long-pedunculate, relatively small inflorescences. Nevertheless, it has frequently been confused with *A. fretessii*. Under the latter are given characters distinguishing these two species and *A. subrotundifolius*, another pubescent-leaved species which occurs in the Philippines.

30. **Artocarpus tonkinensis** A. Chev. ex Gagnep. Bull. Soc. Bot. Fr. **73**: 90. 1926; Gagnep. in Lecomte, Fl. Gén. Indoch. **5**: 737. 1928; Merr. Lingnan Sci. Jour. **6**: 275. 1930, **7**: 303. 1931; Metcalf, Jour. Arnold Arb. **26**: 198. 1945. Syntypes, Indochina, *Balansa 2486*, *Castellini 111*, *Poilane 1859*, *Service Forestier s.n.* (P); lectotype, *Poilane 1859* P).

Artocarpus tonkinensis A. Chev. Bull. Écon. Indo-Chine **20**(no. 132): 861. 1918, nomen nudum.
Artocarpus sp., Merr. Lingnan Sci. Jour. **5**: 63. 1928.

Trees, height to 15 m. *Twigs* 1.5–2.5 mm. thick, reddish brown, short-pubescent or puberulent, hairs usually appressed and crisped. *Leaves* 9–23 × 4–10 cm., elliptic, obovate- or oblong-elliptic, or obovate-oblong, acuminate, base cuneate or rounded, margin entire; juvenile leaves with margin shallowly dentate towards apex; main veins and reticulum prominent beneath; glabrous above or the main veins puberulent, venation beneath thinly pubescent, hairs colourless and undulate; lateral veins 6–9 pairs, curved; intercostals parallel; deep green above, paler beneath, usually drying greyish green with reddish main veins and reddish or straw-coloured reticulum; petiole 4–12(–20) mm. long.

Inflorescences solitary in leaf-axils. *At anthesis*: *male head* 10–25 × 8–15 mm., obovoid to ellipsoid; perianths of 2 or 3 free segments 0.5 mm. long; stamen 0.7 mm. long, filament tapering above, anther-cells ellipsoid, 0.2 mm. long; bracts slenderly stalked, heads peltate, to 0.4 mm. across, these and perianths short-ciliate; peduncle (5–)7–12 × 1.5 mm., velutinous; *female* head with styles exserted to 0.7 mm. through a dense covering of peltate bracts. *Syncarp* to 6.5 cm. across, subglobose, shallowly lobed, yellow, drying rufous, the surface smooth, pubescent, with scattered persistent bracts; wall 5–8 mm. thick; proximal region of perianths fused, fruiting perianths 6–12, thin-walled, "seeds" (endocarps) subellipsoid, 12–15 × 9–12 mm.; core c. 10 mm. across; peduncle 30–40(–65) × 2.5 mm., velutinous.

Uses: cultivated for the edible fruit.

Distribution: in forests to 4000 ft.; Indochina and southern China.

Indochina. Cambodia. *d'Alleizette*, 1909 (P, ♂). Annam. Bu Khang, near Vinh, *Poilane 16644*, *16647* (P, ♀). Thank Hoa Prov.: Na bam, *Poilane 1859* (K, P, ♂). Tonkin. Bac-giang Prov.: Bac le, *Serv. For.* (P, ♀). Ha-coi: Sai Wong Mo Shan, *Tsang 30266* (A, ♂); Taai Wong Mo Shan, *Tsang 29321* (A, ♂). Song Hoa, *Castellini 111*, Oct. 1905 (P). **China.** Yunnan. Szemao, *Henry 13015* (A, K, ♂). Kweichow. Bua-li, Chenfeng, *Teng 91028* (A, ♀). Kwangsi. Ping Nam Hsien, *Wang 40423* (A, ♀). Kwantung. Fan Ch'eng district, Kung P'ing Shan, *Tsang 26749* (A, ♂); Sunyi district, Sie River, *Tsiang Ying 2677* (K, SING, ♂). Hainan. *Wang 33671* (A, P, ♂, ♀); Ching Mai district, Pak Shik Ling, *Lei 830* (A, K, L, SING, ♀); Lai area, Hung Mo Shan, *Tsang & Fung 295* (A, BM, K, NY, P, ♂, ♀), *661* (K, NY, US, ♂); Lam Ko district, Siu Shui Hang, Lin Fa Shan, *Tsang 250* (A, BM, K, ♂); Ling Shui district, Chim Shan, Fan Maan Ts'uen, *Fung 20192* (A, BM, K, NY, P, US, ♂); Lokwui, *How 72358* (A, P, ♂); Ngai district, Chiu Sam Tsuen, *Lau 395* (A, BM, K, P, ♂); Po-ting, *How 72008* (A, BM, P, ♂), *72552* (A, BM), *73076* (A, P, ♂), *73252* (A, SING, ♂), *73471* (A, BM, P, ♀); Taam-chau district, Shan Tong To, *Tsang 706* (A, BM, K, ♀); Wik Tsok Man, *McClure 9752* (K); Yaichow, *Liang 62632* (A, NY, US, ♀). **Cultivated.** Indochina. Tonkin, Ké Só, *Balansa 2486*, May 1886 (P, ♀). China. Kwangtung, Loh Kong Tung, Taai Shaan, *McClure 13564* (K, P).

Chevalier, in 1918, gave details of the wood only under the name *Artocarpus tonkinensis*, and this was not validly published until 1926, when Gagnepain supplied a botanical description. In the same area there are two other pubescent-leaved species with which *A. tonkinensis* might be confused. In *Artocarpus lakoocha*, the styles are exserted to 1–1.5 mm., the peduncles are shorter (the male to 5 mm., the female to 15(–25) mm.), the leaf has more numerous lateral veins (9–18 pairs), and the petiole is longer ((10–)15–45 mm.). In *A. petelotii* the interfloral bracts are clavate, and the surface of the syncarp hence more or less papillate, while the indumentum of the twigs and leaves is longer and not crisped.

31. **Artocarpus gomezianus** Wall. ex. Tréc. Ann. Sci. Nat. Bot. III. **8**: 118. 1847, "*Gomeziana*"; Kurz, For. Fl. Burma **2**: 433. 1877; King in Hook. f. Fl. Brit. Ind. **5**: 544. 1888; King, Ann. Bot. Gard. Calcutta 2: 15. 1889, pro parte, excl. *t. 14A* et spec. *King 4189, 5078, 7535, 8838, Maingay 1486* (*A. nitidus* ssp. *griffithii*) et *Wallich 4658A* (*Ficus callophylla* Bl.); Parkinson, For. Fl. Andaman Is. 253. 1923; Kanjilal et al. Fl. Assam **4**: 269. 1940. Holotype, Burma, *Wallich 4660* (G, not seen, photograph in A); isotypes (CAL, CGE, K).

Artocarpus gomeziana Wall. Cat. no. 4660. 1831, nomen nudum.

Artocarpus petiolaris Miq. Fl. Ind. Bat. Suppl. 422. 1861. Holotype, Sumatra, *Teysmann HB 752* (U); isotype (BO).

Artocarpus pomiformis Teysm. & Binnend. Natuurk. Tijdschr. Ned. Ind. **25**: 400. 1863; Koord. & Val. Bijdr. Boomsoort. Java **11**: 23. 1906; J. J. Smith, Ic. Bogor. **3**: 87. *t. 235.* 1907; Backer, Beknopte Fl. Java **6**: 15. 1948.

Artocarpus lakoocha Roxb. var. *β gomeziana* (Wall.) Trimen, Handb. Fl. Ceylon **4**: 99. 1898, quoad nomen, non quoad plantam.

Artocarpus masticata Gagnep. Bull. Soc. Bot. Fr. **73**: 88. 1926; Gagnep. in Lecomte, Fl. Gén. Indoch. **5**: 739. 1928. Holotype, Annam, *Poilane 5492* (P); isotypes (K, P).

ssp. **gomezianus**

Evergreen trees, height to 40 m., bark dark grey-brown. *Twigs* 2–4 mm. thick, smooth or finely rugose, appressed-puberulent, soon glabrescent. *Leaves* 11–25 × 7–16 cm., oblong, varying to elliptic, short-acuminate, base broadly rounded, varying to cuneate or subcordate, glabrous, margin entire or shallowly crenate; main veins prominent beneath; lateral veins 10–15(–20) pairs, straight or slightly curved; intercostals parallel; deep green above, paler beneath, main veins greenish white, usually drying pale greenish or greyish brown with straw-coloured main veins; petiole 15–30 mm. long.

Inflorescences solitary in leaf-axils. *At anthesis*: *male head* 10–25 mm. across, obovoid to subglobose; perianths 2- or 3-lobed, divided nearly to the base, 0.5 mm. long; stamen 0.6 mm. long, filament stout, abruptly contracted above, anther-cells globose, 0.2 mm. long; bracts stoutly stalked, heads narrowly peltate, to 0.4 mm. across, these and perianths with sparse, short hairs; peduncle 7–17 × 1 mm., puberulent; *female head* with peltate bracts being shed or already fallen and styles exserted to 0.3 mm. through perforations in the surface. *Syncarp* to 8 cm. across, subglobose, yellow with pink flesh, drying brown or black, the surface smooth, velutinous; wall c. 8 mm. thick; proximal region of perianths free, fruiting perianths several, fleshy, "seeds" (indurated endocarps) ellipsoid, 12 × 10 mm.; core c. 20 mm. across; peduncle 15–45 × 8 mm., velutinous.

USES: there is one record of the fruit being edible (Poulo Condore, *Harmand 700*); the roots are chewed with betel (Annam, *Poilane 5492*).

DISTRIBUTION: in evergreen and semi-evergreen forest to 2000 ft. in regions with a distinct dry season; Assam ?, Burma, Andaman Islands, Siam, southern Indochina, Malaya, Sumatra, Java (western and central provinces), Philippine Islands (Cagayan Sulu, ? introduced).

Burma. Pinmona [? Pyinmana], *Huk*, Aug. 1890 (P, SING). Tenasserim. Tavoy: *Wallich 4660* (leg. *Gomez*), Nov. 1827 (CAL, CGE, K, ♂). Mergui: Victoria Point, *Po Khant 11343* (DD, ♀). **Andaman Islands.** *King 416* (K, ♀). **Siam.** Ko Kahdat, *Schmidt 556* (C, ♂); Muak Tek, Sanaburi, *Kerr 9064* (BM, ♂); Chantaburi, *Jeppeson*, May 1947 (C); Sraburi, Phu Khae, *Smitinand 1549* (CGE). Peninsular Siam. Bangtapan, *Kerr 1436* (BM, ♀); Krabi, Ao Luk, *Kerr 18608* (BM, ♂); Surat, Kaw Tao, *Kerr 12700* (BM, K, L, P, ♂); Trang, Chum Het, *Kerr 15214* (BM, K, P, ♀); Trang, Thap Tiang, *Fox 3845* (SING, ♂, ♀). **Indochina.** Cambodia. *Béjeaud 640* (NY, P, ♀). Annam. Nhatrang Prov., Phu-hu, between Nhatrang and Ninhoa, *Poilane 5492*, Jan. 1923 (K, P, ♂). Poulo Condore. *Harmand 700* (P, ♀).

Malaya. Novadens Hill, *Maingay 1486* (GH, K, L, ♂). Kedah. Baling, *Abdullah KEP 27356* (KEP); Kokmoi For. Res., *Hassan KEP 42427* (KEP, ♀); P. Songsong, *Curtis*, June 1890 (P); Sik, *Mohamed KEP 11327* (KEP, ♀). Kelantan. Tumpat, *Corner SFN 33529* (SING, ♂), *Ngadiman SFN 33698* (SING, ♀). Pahang. Bentong, Clough For. Res., *KEP 78746* (KEP); Bentong, Ulu Benus, *Symington KEP 51821* (KEP, ♀). Johore. Sungei Rhu Riba, Jason Bay, *Corner* (SING, ♂). Lankawi Islands. P. Butong, *Curtis 906* (K, SING, ♂). Penang. Road to Balik Pulau, *Curtis 2462* (K, SING, ♂). Singapore. *Didrichsen 4412* (C, ♂). P. Tioman. Telok Paya, *Nur SFN 21742* (BO, KEP, SING, ♂).

Sumatra. Atjeh. Seulimeum, Lam Temot, *bb 5876* (BO, L). Tapanuli. Padang Lawas, Purbasinamba, *bb 6186* (BO). West Coast. *Teysmann HB 798* (BO, U, ♀); Baros, *Teysmann HB 721* (L), *752* (BO, U, ♂). East Coast. Huta Padang Estate, near Kisarin, *Krukoff 225* (BO, ♂). Benkulen. Redjang, Sukamarindu, *bb 8861* (BO); Redjang, Tabah Penandjung, *bb 2822* (BO, L). P. Weh. Baloken, *Koorders 10578, 10579, 10580* (BO, ♀).

Java. West Java. Buitenzorg: Djampang Kulon, Tjikankung, Tjidjaringao, *NIFS Ja 1250* (BO, ♀). Preanger: Palabuanratu, Sukabumi, *Koorders 8687* (BO, ♂). Central Java. Pekalongan: Mayasari, *Burger 3340* (BO, ♂); Prupuk, *Wind 26* (BO, L, ♀). Semarang: *Koorders 9419* (BO, L); Kedungdjati, *Koorders 8674* (BO, L), *8676* (BO, L, ♂), *8677* (BO, ♂, ♀), *8690* (BO, L, ♂), *25251* (BO, L, P, ♀), *25322, 26139* (A, BO, L), *33701* (BO, K, L, ♂, ♀); Kedungdjati, Deras, *Koorders 8675* (BO, L, ♂, ♀), *8691, 9271, 25319* (BO, L); Kedungdjati, near Gunong Kenting, *Koorders 24957* (BO, L, ♂); Kedungdjati, Prizi, *Koorders 25475* (BO, L); Kedungdjati, Pungge, *Koorders 8678* (BO, P), *8679* (BO, L); Kedungdjati, Trimze, *Koorders 8689, 8692* (BO, L, P), *8693* (BO); Telawa, *Jansen 4637* (BO, ♂). Jogjakarta: Zuidergebergte, *Teysmann* (BO).

Philippine Islands. Cagayan Sulu. *Antonio FB 30634* (NY), *Merrill 5304* (BO, L, NY, P, US, ♂, ♀); Buluan Ranch, *Santos 4772* (L, ♂, ♀). **Cultivated.** Java. Bogor, Hort. Bot., *HB 7289* (BO, P), *VIII B 41* (L).

The synonyms listed above all refer to *Artocarpus gomezianus* ssp. *gomezianus*, but the name *A. lakoocha* Roxb. var. *gomeziana* (Wall.) Trimen was used by Trimen and later authors in the sense of *A. gomezianus* ssp. *zeylanicus*.

The variety *griffithii*, based on Malayan material, which was described under *Artocarpus gomezianus* by King in 1888 and 1889, is here transferred to *A. nitidus* as a subspecies; the distinguishing characters and the confusion that has occurred between the entities in Malaya are discussed there. All other references in the literature to *A. gomezianus* as occurring in Malaya are based on *A. nitidus* ssp. *griffithii*. *Artocarpus gomezianus* ssp. *gomezianus* is mainly restricted to the north of Malaya and the east coast, where there is a distinct dry season, although a single specimen has been seen from Singapore.

The distribution of ssp. *gomezianus* in western Malaysia is apparently somewhat discontinuous, corresponding to its climatic requirements. However, no significant variation is shown within this subspecies and the maintenance of *A. pomiformis* Teysm. & Binnend. as a distinct species in Java presumably arose from its comparison with King's description and plate, which were largely (the latter solely) based on material which should have been referred to his var. *griffithii*. The subspecies is apparently absent from Borneo and it is possible that the specimens from Cagayan Sulu were taken from a tree, or trees, that had been introduced, although there is no evidence for this. Kanjilal *et al.* (1940) also record *A. gomezianus* for the Lakhimpur district of Assam.

ssp. **zeylanicus** Jarrett, ssp. nov.

Artocarpus lakoocha auct. non Roxb., Thwaites, Enum. Pl. Zeylan. 262. 1861; Beddome, For. Man. 219. 1873, pro parte; Trimen, Handb. Fl. Ceylon **4**: 99. 1898; Cooke, Fl. Bombay **2**: 657. 1907, p.p.; Bourdillon, For. Trees Travancore, 371. 1908, p.p.; Talbot, For. Fl. Bombay **2**: 529. 1911, p.p., incl. *fig. 533*; Fischer in Gamble, Fl. Madras **3**: 1369. 1928, p.p.; Macmillan, Trop. Pl. & Gard. ed. 4. 250. 1935; Abeyes. & Rosayro, Checklist Ceylon, 48. 1939; Watanabe, Ic. Econ. Pl. S. Asia **2**: 527. 1945.

Artocarpus lakoocha Roxb. var. *β gomeziana* (Wall.) Trimen, Handb. Fl. Ceylon **4**: 99. 1898, quoad descr. et spec. cit.

Artocarpus gomezianus Tréc., Worthington, Ceylon Trees. 420. 1959.

Differt ab typo *ramulis junioribus* saepe appresse pubescentibus, pilis undulatis, cinereis, raro flavis, *foliis* ovatis, ovati-lanceolatis, ovati-ellipticis vel elliptici-oblongis, acumine ad 2 cm. longo, basi subcordata, late rotunda vel late cuneata, costa nervis lateralibusque subtus prominentibus, venulis prominulis, pubescentibus, pilis canescens undulatis, vel glabris, nervis lateralibus utrinque 10–13, petiolo (7–)13–25(–30) mm. longo, *capitulis masculis* 8–11 mm. diametro, globosis, pedunculis 5–18 mm. longis, *syncarpiis* 3 cm. diametro, flavis, carne flava, pedunculis 13–15(–20) mm. longis.

HOLOTYPE: Madras, *Wight 2717* (K); isotypes (C, GH, L).

VERNACULAR NAMES: *otamb*, *watamba*, *lowi*, southern India; *kanagona*, Ceylon. USES: the fruit is eaten and the tree appears to be planted in both Ceylon and southern India.

DISTRIBUTION: in evergreen forests to 3000 ft.; in the wetter parts of the Western Ghats and Ceylon.

India. Cutahey, *Buchanan*, Mar. 1801 (BM, ♀); Malabar, Concan, *Stocks & Law* (GH, P); Kanara, Yacombi, *Cooke*, Feb. 1893 (K, ♂, ♀). BOMBAY. North Kanara, Karwar, *Fernandes 119* (A, ♂); Sanklu [? Sangli], *Stocks* (K, ♂); Supa, *Fernandes 1143* (A, BLAT, ♀), *Ritchie 1381* (K, ♂). MYSORE. Marnhalli, *Meebold 8435* (K, ♂). COORG, Near Mercara, *Hohenacker 557* (BM, C, K, L, ♂). MADRAS. Mangalore, *Wight 2717*, Mar. 1852 (C, GH, K, L, ♀).

Ceylon. *Macrae 692* (BM, CGE, ♂), *Thwaites CP 2232* (BM, CGE, GH, P, ♂), *2463* (K, ♂); Galle, *Champion* (CGE, ♀); Galle, Batapola, *Worthington 2462* (BM); w. of Ginganga, Hiniduma, *Worthington 2312* (BM, ♂); Kadugannawa, Kolugala, *Hancock 1379* (BM); Kadugannawa, Udawela Fort Jungle, *Worthington 1426* (BM, ♀); Narawella [= Nuwara Eliya], *Champion* (CGE, ♂); Ratnapoora, *Thwaites CP 2831* (BM, CGE, GH, K, P, ♀). **Cultivated.** CEYLON. Mellue, *Gardner* (K, ♀); Peradeniya, Hort. Bot., *Worthington 6744* (CGE, ♀), *Worthington*, Feb. 1955 (CGE, ♂).

Artocarpus gomezianus ssp. *zeylanicus*, which is described here from the Western Ghats and Ceylon, has not previously been distinguished from *A. lakoocha*. However, within the Indian subcontinent, the latter appears to be restricted, as an indigenous tree, to the north and east. The new entity is differentiated by the smaller, globose head (8–11 mm. diameter *vs.* 12–25 × 10–18 mm.) and the longer peduncle (5–18 × 1 *vs.* 2–5 × 2 mm.) of the male inflorescence, by the smooth surface of the female head at anthesis and the shorter exsertion of the styles (to 0.3 mm. *vs.* 1–1.5 mm.) and, apparently, by the smaller size and smoother surface of the mature syncarp. In addition, the collections seen from India have rather distinctive ovate-lanceolate leaves, which are densely greyish pubescent beneath. In those seen from Ceylon, on the other hand, the leaves vary to elliptic-oblong in outline and these and the twigs are often subglabrous, so that specimens are not clearly distinguishable from *A. gomezianus, sensu stricto.* Since the dimensions of the male inflorescences, although usually smaller in the western entity, also overlap, it seems best to treat the latter as a subspecies of *A. gomezianus.* The nature of the variation found in Ceylon is not entirely clear, but it appears to occur between different trees and not merely to represent sapling and adult stages. Subglabrous collections from Ceylon were identified with *A. gomezianus* by both Thwaites and Trimen, and were described by the latter under the name *A. lakoocha* var. *β gomeziana.*

32. **Artocarpus dadah** Miq. Fl. Ind. Bat. Suppl. 420. 1861, Ann. Mus. Lugd.-Bat. 3: 213. 1867; S. Moore, Jour. Bot. **63,** Suppl. 112. 1925; Corner, Gard. Bull. Singapore **10**: 282. 1939, Wayside Trees, 653. 1940. Holotype, Sumatra, *Teysmann HB 4391* (U); isotypes (BO, K, L).

Artocarpus mollis Miq. Fl. Ind. Bat. Suppl. 420. 1861, non Wallich, 1831 (nomen nudum), Ann. Mus. Lugd.-Bat. 3: 211. 1867. Holotype, Sumatra, *Teysmann HB 4211* (L); isotype (BO).

Artocarpus rufescens Miq. Fl. Ind. Bat. Suppl. 420. 1861; Renner, Bot. Jahrb. **39**: 370. 1907. Holotype, Sumatra, *Teysmann HB 3793* (U); isotypes (BO, K, L).

Artocarpus tampang Miq. Fl. Ind. Bat. Suppl. 421. 1861, Ann. Mus. Lugd.-Bat. 3: 211. 1867. Holotype, Sumatra, *Teysmann HB 3997* (U); isotypes (BO, K, L).

Ficus tampang Miq. Fl. Ind. Bat. Suppl. 425. 1861. Holotype, Sumatra, *Teysmann HB 710* (U); isotype (BO).

Ficus inconstantissima Miq. Fl. Ind. Bat. Suppl. 431. 1861. Holotype, Sumatra, *Teysmann HB 3529* (U); isotypes (BO, CAL, L).

Artocarpus inconstantissima Miq. Ann. Mus. Lugd.-Bat. 3: 211. 1867.

Artocarpus dadah Miq. var. *pubescens* Miq. Ann. Mus. Lug.-Bat. 3: 213. 1867. Holotype, Sumatra, *Korthals s.n.* (L).

Artocarpus erythrocarpa Korthals ex Miq. Ann. Mus. Lugd.-Bat. 3: 213. 1867, pro syn.

Artocarpus lakoocha Roxb. var. *malayana* King in Hook. f. Fl. Brit. Ind. 5: 544. 1888; King, Ann. Bot. Gard. Calcutta 2: 15, excl. spec. *De Fretes*, Amboina. Syntypes, Malaya, King *1640, 4187, 5653* (CAL, not seen; duplicates examined, K, etc.).

Artocarpus reniformis Becc. For. Borneo, 631. 1902. Syntypes, Sarawak, *Beccari PB 3107, 3551* (FI); lectotype, *Beccari PB 3107* (FI).

Artocarpus peltata Merr. Jour. Str. Br. Asiat. Soc. 85: 166. 1922. Holotype, British North Borneo, *Villamil 168* (PNH, not seen, photograph in A); isotype (BO).

Artocarpus lakoocha auct. non Roxb., King in Hook. f. Fl. Brit. Ind. 5: 543. 1888, pro parte; King, Ann. Bot. Gard. Calcutta 2: 14. 1889, p.p., quoad spec. *Griffith 4666, Maingay 1479*; Ridley, Fl. Malay Penin. 3: 355. 1924.

Artocarpus dasyphylla auct. non Miq., Merr. Pl. Elmer. Born. 46. 1929.

Deciduous trees, height to 35 m. *Twigs* 2.5–5 mm. thick, rugose, densely short-pubescent, hairs red-brown or fulvous, straight, varying undulate, a few sometimes longer and hooked at tip. *Leaves* 10–30 × 5–17 cm., obovate- or elliptic-oblong, varying to ovate-elliptic, acute or acuminate, base rounded, varying to broadly cuneate or shallowly cordate, margin entire; juvenile leaves with the lamina pinnatifid or reduced to a narrow sinuate wing along the midrib; main veins prominent beneath, reticulum less so; glabrous above, or nearly so, except for the short-pubescent main veins, venation beneath densely to thinly pubescent, hairs rufous to colourless, patent, straight or slightly undulate (in Borneo, except British North Borneo, hairs often inserted along edges of reticulum and appressed over areolae), subdeciduous, the lower surface scabrescent, varying persistent; lateral veins 10–20 pairs, curved; intercostals parallel; dark green, drying dark or reddish brown to blue-grey above, pale or reddish brown beneath, the areolae sometimes greyish and, with the colourless hairs, appearing glaucous, venation concolorous or often nigrescent; petiole 5–20 mm. long.

Inflorescences solitary in leaf-axils. *At anthesis*: *male head* 8–15 mm. across, globose or pulvinate; perianths of 2 or 3 free segments 0.3 mm. long; stamen 0.5 mm. long, filament cylindric, abruptly contracted above, anther-cells globose, 0.2 mm. long; bracts stoutly stalked, heads narrowly peltate, to 0.4 mm. across, these and perianths short-ciliate; peduncle 8–15 (Borneo, 8–20) × 1 mm., indumentum as twigs; *female head* with peltate bracts already fallen (densely covering young head) and styles exserted to c. 0.5 mm. through low papillae. *Syncarp* to c. 5 cm. across, subglobose, green with deep pink flesh, the surface smooth, velutinous; wall c. 7 mm. thick; proximal region of perianths free, fruiting perianths several, fleshy, "seeds" (indurated endocarps) ellipsoid, 12 × 8 mm.; core c. 15 mm. across; peduncle 12–25(–40) (Borneo, 23–45(–80)) × 4 mm., indumentum as twigs.

VERNACULAR NAMES: *tampang* (Malay), Malaya, Sumatra, Borneo; *dadah*, Sumatra (recorded only twice).

DISTRIBUTION: in evergreen forest to 3000 ft.; Tenasserim, Siam, Malaya, Sumatra, Simalur, Banka, Borneo.

Lower Burma. TENASSERIM. Mergui: Mergui range, *sine nom. 421* (DD, ♀); Thamihla Chaungbya, *Po Khant 13252* (K). **Siam.** Phetchbun, Lom Kao, Ban Phuhee, *Smitinand 2587* (CGE). PENINSULAR SIAM. Kaw Pa-ngan, *Kerr 1187* (BM, ♀); Ranawng, Nok Nang, *Kerr 16835* (BM, ♀); Satul, Klawng Ton, *Kerr 14594* (BM, ♀); Trang, Chawng, *Kerr 15170* (BM, ♂), *Put 2371* (CGE); Trang, Kuantan, *Kerr 17488* (BM, ♀); P. Terutao, *Kerr 14229* (BM, ♂).

Malaya. KEDAH. *Meh CF 21885* (SING); Gunong Raya, *Dolman CF 21496* (SING, ♀). PROV. WELLESLEY. Krian, *Ridley 9385* (CAL, SING, ♀); Kubang Ulu, *Curtis*, June 1890 (SING, ♀); Tasek Gelugur, *Ridley 6978* (BM, ♂), *6980* (SING, ♂, ♀). PERAK. *Scortechini 37b* (L), *s.n.* (BM, K, P, SING, ♂, ♀); Larut, *King 2678* (K, L, ♀), *4187*, Apr. 1883 (K, ♀); Larut, Chanderaing, *King 5653*, Mar. 1884 (BM, K, L, P, ♀); Larut, Goping, *King 6098* (BM, BO, K, P, ♀); Sungei Larut, *Wray 2479* (SING, ♂); Trong, *Wray 3176* (SING, ♂, ♀); Waterfall Hill, *Wray 2560* (SING, ♀). KELANTAN. *Walton KEP 32681* (KEP). TRENGGANU. Bukit Kajang, Ulu Bendol, Kemaman, *Corner*, Nov. 1935 (SING). PAHANG. Cameron Highlands, *Batten Pooll*, Nov. 1939–Jan. 1940 (SING); Gali near Raub, *Burkill & Haniff SFN 16918* (SING, ♂); Kuantan, *Lamban CF 2707* (K, SING, ♀); Sungei Rompui, *Bidin CF 15658* (SING, ♀). SELANGOR. Klang Gates, *Murdoch 57* (BM, ♂); Kuala Lumpur, *Mohamor*, June 1890 (SING, ♀); Kuala Lumpur, Weld Hills For. Res., *Ahmad CF 2949*, *5025* (SING, ♀), *Guard CF 863* (SING, ♂). NEGRI SEMBILAN. Triang Res., *Tahir CF 607* (SING, ♀). MALACCA. *Maingay 1479* (BO, GH, K, L, ♂, ♀); Ayer Punnas, *Griffith 4666* (K, P, ♀). JOHORE. Kluang For. Res., *Holttum SFN 9204* (K, SING, ♂); Sungei Berassau, Mawai-Jemalaung road, *Corner*, Jan. 1936 (SING); Sungei Kayu, Mawai-Jemalaung road, *Kiah SFN 32185* (BO). LANKAWI ISLANDS. *Wyatt-Smith KEP 71197* (K, KEP, ♂, ♀); near Kuah, *Curtis* (SING); P. Butong, *Curtis 906* (K, SING, ♀). PENANG. *King 1532* (K, ♂), *1640*, Aug. 1881 (BO, CGE, K, ♀), *Wallich 4658B* (CGE); Government Hill, *Curtis 1222* (SING, ♂); West Hill, *Curtis 1251* (SING, ♀), *1743* (CAL, SING, ♂). SINGAPORE. *Cantley 3086* (SING, ♂); Bukit Kalang, *Ridley*, 1892 (SING); Bukit Timah, *Ngadiman SFN 34682* (A, BO, K, P, SING, ♂), *Ridley 4722* (BM, K, L, P, SING, ♀); Chan Chu Kang, *Ridley* (SING, ♀); Changi, *Ridley 3358* (CAL, K, SING, ♂, ♀), *4724* (K, ♂); Government House Domain, *Best SFN 25995* (SING, ♀); MacRitchie Reservoir, Thompson Road end, *Corner*, June 1937 (SING); Mandai road, *Corner SFN 32545* (K, SING), *Ridley 4130* (BM, SING, ♀); 11½ miles Mandai road, by shore of Seletar Reservoir, *Sinclair*, Mar. 1953 (K); Pulau Ubin, *Ridley 4721* (SING, ♀); Reservoir Jungle, *Corner*, Feb. 1937 (SING, ♂).

Sumatra. *Grashoff 1032b* (BO, L, ♀), *Korthals* (L, ♀). TAPANULI. Sibide, Parduaan, *Rahmat si Boeea 6096* (L, ♂); Padang Lawas, Purbasinamba, *bb 6202* (BO). WEST COAST. Fort de Kock, *Teysmann 710* (BO, U); Mt. Sago near Pajahkumbuh, *Meijer 7197* (L); Priaman, *Diepenhorst 2186* (P). EAST COAST. Amplas, *Jochems 3168* (BO); Asahan, Aek Salabat, *Rahmat si Boeea 9622* (A, L, ♂); Asahan, Huta Padang, *Krukoff 4368* (A, BO, L, NY, SING, ♂); Asahan, Simpang Toba, *bb 6344*, *7184* (BO, L); Beneden Langkat, Alur Gusta, *bb 16375* (A, BO, L); Langkat, Sungei Sedapan, *bb 9364* (BO); Lubuk Mambang, *Koorders 10453* (BO, ♀); Sibolangit, *Lörzing 5151* (BO, L, ♀). DJAMBI. Danau Lama, *bb 13640* (BO, ♀). PALEMBANG. Banjuasin and Kubustreken, *NIFS T 65* (BO, L, U, ♀), *777* (BO, K, L, SING, ♀); Banjuasin, Bajunglintjir, *NIFS T 902* (BO, L, ♂); Batu Radja, *Teysmann HB 3529* (BO, CAL, L, U); Dermo Enim, *Teysmann HB 3793* (BO, K, L, U, ♂, ♀); Komering Ulu, *Grashoff 579* (BO); Lematang Ilir, Darmo, *bb 8720* (BO); Lematang Ilir, Gunong Megang, *NIFS T 889* (BO, L, ♂), *1207* (BO); Lematang Ulu, *Grashoff 179* (BO, L), *Lambach 1200* (BO, L, ♀); Muara Dua, *Grashoff 436* (BO, L, ♀), *Teysmann HB 3856* (BO, P); Muara Dua, Kisau, *bb 9234* (BO); Mulak Ulu, *Grashoff 330* (BO, L, ♂); Pandananan, Oganulu, *Teysmann HB 3742* (P), *3997* (BO, K, L, U); River Ruput, W. Suka Radja, *Forbes 2948a* (CAL, L); Tandjong Ning, River Bliti, *Forbes 2789* (BM, L, SING, ♀). LAMPONGS. Kebang, *Teysmann HB 4211* (BO, L); Mangala, *Teysmann HB 4391* (BO, K, L, U, ♀). SIMALUR. *Achmad 1259* (BO, K, L, P, SING, U, ♀); Landschap Tapah, Defajan, *Achmad 1805* (BO, K, L, SING, ♀). BANKA. Blinju, *Teysmann HB 7249* (BO, K, L, ♀), *Vordermans 41* (BO, ♀); Djebus, *Teysmann HB 7255* (C, K, L, P); Pangkalpinang, *Teysmann HB 6842* (BO, K, L, ♀), *6856* (BO, C, K, L, P, ♂); Sungei Liat, *Teysmann HB 7256* (L, P); Zapadong, *Teysmann HB 3290* (P). BILLITON. Tandjungpandan, *Teysmann* (BO). RIOUW ARCHIP. P. Bintang, *Teysmann HB 7285* (BO, K, L, P, ♀).

Borneo. SARAWAK. Kuching, *Beccari PB 3107*, Nov. 1867 (FI, K, ♀), *3551*, June 1867 (A, FI, ♂); Nanga Temulan, *Daud & Tachun 35690* (SING, ♀). WEST BORNEO. Sambas, Perigi Limus, *bb 7064* (BO, ♀); Sungei Sambas, *Hallier 1153* (BO, L, SING, ♂). SOUTH AND SOUTHEAST BORNEO. Martapura, Djungur, *bb 10377* (BO, ♂, ♀); Tanah Bumbu, Kampong Baru, *bb 13308* (BO, L), *13366* (BO, K, L, ♀). EAST AND NORTHEAST BORNEO. Balikpapan: *Lam 3871* (L); Mentawir, *Sauveur 97* (K, ♂, ♀). Berouw: Domaring, *bb 18865* (A, BO, L, SING, ♂); Inaran, *bb 12175* (BO). W. Kutei: Longbleh, *bb 16133* (BO, L), *16145* (A, BO); Tandjong Isui, *Endert 1945* (A, K, L, ♂, ♀); Upper Mahakam, Udjoh Bilang, *bb 20612* (A, BO, L). E. Kutei: Loa Djanan, w. of Samarinda, *Kostermans 6644* (L), *9970* (L, ♂, ♀); Tandjong Bangko region, near mouth of Mahakam River, *Kostermans 7018* (L). BRITISH NORTH BORNEO. *Agama 484* (A, K, ♀); Elphinstone prov., Tawao, *Elmer 21110* (A, BM, K, L, ♀); Mt. Kinabalu, Dallas, *Clemens 26322* (A, BM, K, L, ♂, ♀), *27444* (A, BO, BM, K, L, ♀); Sandakan, *Melegrito 9044* (SING), *Ramos 1904* (A, BM, K, L, ♂), *Villamil 168*, Mar. 1916 (BO, PNH, ♀); Sandakan, Ebpura, Beatrice Road, *Alendre A 3252* (L, SING, ♀); Sandakan, Leila For. Res., Bukit Makara, *Wood SAN A 3476* (A, K, L, SING, ♂).

This common and variable species was described under six different specific names by Miquel in 1861. Of these, the one chosen here is *Artocarpus dadah*. This has been the name most widely used on herbarium specimens and Corner, in 1939, correctly identified as *A. dadah* the Malayan entity which had hitherto been regarded as representing *A. lakoocha*. The latter is a species of the monsoon forest which has not been found south of the Siamese border, and the error arose from its treatment by King in his monograph. He described under *A. lakoocha* a variety *malayana*, citing three collections here referred to *A. dadah*, and giving *A. tampang* and *A. rufescens* of Miquel correctly as synonyms. However, under the type itself two further collections of *A. dadah* were listed and the description was partly based on these. As a result, the variety was not recognized by later workers and all Malayan material was identified as *A. lakoocha.* The fourth collection cited by King under var. *malayana, De Fretes s.n.* from Ambon, is a sterile specimen which may be referable to *A. vrieseanus.*

The variation shown by *Artocarpus dadah* occurs chiefly in the length of the peduncles and in the indumentum. It has some geographical basis, but separation into geographical units is not possible, since the variation is continuous and is not parallel in the different characters. Collections seen from Borneo tend to have inflorescences with longer peduncles, as is indicated above in the description. In this area the indumentum of the leaves is also usually persistent, whereas elsewhere the leaves generally become subglabrous and slightly rough beneath. Some specimens from Sumatra and Malaya are, however, densely and persistently pubescent, and this character is often associated with a rather more prominent reticulum. A peculiarity found in material from Borneo (but apparently not in that from British North Borneo) is that hairs are inserted along the edges of the veins of the reticulum on the lower surface and appressed over the areolae. This is not to be confused with the minute tomentum developed from the epidermis of the areolae in some other species of subgenus *Pseudojaca.*

The characters distinguishing *Artocarpus dadah* from *A. fulvicortex* and *A. tomentosulus* are noted below under those species. The only other species occurring within its area with which *A. dadah* might be confused is *A. fretessii,* which extends into the eastern part of Borneo. This differs in the more prominent, straw-coloured reticulum of the leaves, in the paler indumentum, crisped on the twigs, and also in the smaller male inflorescences and the lobed syncarp. Characters distinguishing *A. dadah* from *A. vrieseanus* are given below.

33. **Artocarpus vrieseanus** Miq. Ann. Mus. Lugd.-Bat. 3: 212. 1867.

Artocarpus cumingiana auct. non Tréc., Diels, Bot. Jahrb. 67: 176. 1935.

Trees, height to 28 m. *Twigs* 2–4 mm. thick, pubescent to subglabrous, hairs red-brown to yellowish, ± appressed and crisped or undulate, varying patent and straight or hooked at the tip. *Leaves* 7–30 × 3–15 cm., obovate-oblong to elliptic or ovate-elliptic, varying narrowly oblong, oblong-lanceolate or elliptic, acute or with an acumen to 2.5 cm. long, base narrowly to broadly rounded or shallowly cordate, margin entire; main veins prominent beneath, reticulum not at all to markedly prominent; glabrous above except for the usually pubescent main veins, venation beneath moderately to sparsely pubescent, varying subglabrous, hairs colourless, weak and undulate or crisped, or some, rarely almost all, stouter and hooked at the tip; lateral veins 8–14 pairs, curved; intercostals parallel, varying reticulate; dark green, drying brown, grey-green or greenish, venation concolorous, varying straw-coloured; petiole 5–18 mm. long.

Inflorescences solitary in leaf-axils or the male heads sometimes borne on short-shoots on older wood. *At anthesis*: *male head* (3–)5–15 mm. across, globose to short-obovoid; perianths of 3 or 4 segments, free or fused for half their length, 0.4–0.5 mm. long; stamen 0.75 mm. long, filament tapering above, anther-cells globose, 0.2 mm. long; bracts stoutly stalked, heads peltate, to 0.6 mm. across, these and perianths puberulent; peduncle 2–15 × 1 mm., velutinous, hairs usually crisped, varying subglabrous; *female head* with peltate bracts nearly all shed and styles exserted to 0.4 mm. through perforations in the surface (in var. *papillosus* through papillae). *Syncarp* to 6 cm. across, subglobose, yellow, drying orange to brown or black, the surface smooth, velutinous, often glabrescent, varying subglabrous and then clearly areolate; wall c. 2 mm. thick; proximal region of perianths fused, fruiting perianths numerous, thin-walled, "seeds" (indurated pericarps) ellipsoid, variously compressed, 11 × 8–10 mm.; core 10–15 mm. across; peduncle 3–35 × 3 mm., velutinous, hairs usually crisped, varying subglabrous.

DISTRIBUTION: in rain forest to 6000 ft.; Philippines (Mindanao), Celebes (Manado) ?, Moluccas, New Guinea, Bismarck Archipelago, Japen, Salawati, Aru Islands, Louisiade Archipelago, Solomon Islands.

This widely distributed species exhibits a range of variation in the type and abundance of the indumentum, the length of the peduncles, the shape of the leaves and the prominence of their venation which is greater than in any other member of subgenus *Pseudojaca*. Four variants can be distinguished, each with a consistent geographical distribution, and, although three of these are based primarily on vegetative characters, it seems desirable to describe them all at the varietal level, and so to bring some order into the rather chaotic variation presented by this species at first sight.

The most widely distributed of the varieties is var. *refractus*, which extends from Mindanao through New Guinea to the Louisiade Archipelago, and has fairly broad, obovate-oblong (varying to elliptic) leaves with moderately prominent venation and a variable indumentum, a relatively large male head (5–15 mm. across), and variable peduncles (3–15 mm. in the male inflorescence and (?2–)15–30 mm. in the syncarp). Specimens from a limited area in the mountains of eastern New Guinea, which have rather small, narrow leaves with a more strongly developed reticulum, are assigned here, but are discussed further under the variety. In the Solomon Islands, var. *papillosus* is distinguished primarily by the papillate surface of the female head at anthesis, but also by the often ovate-elliptic leaves. The indumentum is variable, as is the length of the peduncles (3–5 mm. in the male inflorescence and 5–35 mm. in the syncarp), and the male head is rather smaller than in var. *refractus* (3–8 mm. across).

The two other varieties recognized in *Artocarpus vrieseanus* have ranges overlapping that of var. *refractus* in New Guinea, but are distinguished by the thinly pubescent to subglabrous leaves, which are often rather thinly coriaceous and narrow in outline, and by the small male heads (4–7 mm. across). The type variety extends from northeastern New Guinea westward to the Moluccas and perhaps Celebes (with one doubtfully identified collection from Bougainville). The leaves have a slender, slightly prominent reticulum, and these and the twigs are thinly pubescent or subglabrous; except in a few almost entirely glabrous specimens some of the hairs are consistently hooked at the tip (such hairs being found otherwise only in a few collections of var. *refractus*). The peduncles are rather long, measuring (4–)6–17 mm. in the male inflorescence and 15–35(–65) mm. in the syncarp. Finally, var. *subsessilis*, which is found in New Guinea, the Bismarck Archipelago and Bougainville, has glabrous leaves lacking a prominent reticulum. Only the young twigs are puberulent, with straight or crisped, but not hooked, hairs, and the inflorescences have short peduncles (2–3 mm. long in the male inflorescence and 3–7(–13) mm. in the syncarp).

The biological significance of these varieties, apart from var. *papillosus* which has presumably arisen through geographical isolation, is not clear. The three others appear to be genuinely distinct, and not merely adult or sapling forms. Whereas var. *refractus* occurs widely in New Guinea, var. *vrieseanus* and var. *subsessilis* have not yet been recorded from the southern regions, and these entities may be separated in northern New Guinea by slightly different ecological requirements, although no evidence in support of this can be gained from field notes.

The species that appears to be most closely related to *Artocarpus vrieseanus* is *A. xanthocarpus*, from the northern and central Philippine Islands, and the characters distinguishing the latter are discussed below, under that species. Some of the varieties of *A. vrieseanus* may, however, bear a strong superficial resemblance to two apparently less closely allied species, *A. dadah* and *A. fretessii*, and the variability of *A. vrieseanus* is such that only the complete fusion of the perianths in the syncarp provides an entirely satisfactory taxonomic distinction. The west Malaysian *A. dadah*, in addition to having the proximal region of the perianths free, differs in the colour of the syncarp, which is green with deep pink flesh (instead of yellow), in the straight hairs on the twigs (sometimes hooked at the tip), and in the more numerous lateral veins on the larger leaves (to 20 instead of 13(–14) pairs).

The range of *Artocarpus fretessii*, which extends from Borneo and the Philippines to the Vogelkop of New Guinea, overlaps that of *A. vrieseanus* to a considerable extent, but the syncarps of these two species, also, can usually be distinguished externally. In *A. vrieseanus* the syncarp is subglobose, with numerous seeds, but in *A. fretessii* it is distinctly lobed, each lobe usually containing one of the relatively few (up to 12) seeds. There is a further difference between the species in the interfloral bracts of the male heads: in the former rather few of these have well-developed, peltate heads, with stout stalks expanding gradually into the head, and there are numerous intermediates to the perianth segments, whereas in the latter there are many peltate bracts with slender stalks and well-defined heads, and few intermediates. These distinctions, and also the complete fusion of the perianths in the syncarp, have been confirmed for all the varieties recognized in *A. vrieseanus.* No satisfactory vegetative characters can be found serving to distinguish this species and *A. fretessii* over the whole of their ranges, but notes are given below, under the three varieties with a range overlapping that of *A. fretessii,* that will, it is hoped, aid in the identification of sterile material.

KEY TO THE VARIETIES OF ARTOCARPUS VRIESEANUS

1. Leaves without a prominent reticulum, glabrous; young twigs puberulent, the hairs straight or crisped; male peduncle to 3 mm., syncarp peduncle to 7(–13) mm. long. .... var. *subsessilis.*
1. Leaves with the reticulum slightly to markedly prominent beneath; reticulum and twigs usually pubescent, or if subglabrous, some of the hairs hooked at the tip.
    2. Leaves rather thinly coriaceous, often narrow, the reticulum slightly prominent beneath; reticulum and twigs subglabrous to thinly pubescent, except when nearly glabrous some of the hairs hooked at the tip; male peduncle (4–)6–17 mm., syncarp peduncle 15–35(–65) mm. long. .... var. *vrieseanus.*
    2. Leaves moderately to thickly coriaceous, the reticulum distinctly prominent beneath; reticulum and twigs pubescent, rarely subglabrous, the hairs undulate or crisped, rarely a few hooked at the tip.
        3. Female head papillate at anthesis (Solomon Islands). .... var. *papillosus.*
        3. Female head smooth at anthesis. .... var. *refractus.*

var. **refractus** (Becc.) Jarrett, stat. nov.

Artocarpus refracta Becc. For. Borneo, 630. 1902. Holotype, Aru Islands, *Beccari s.n.* (FI); isotypes (FI).

Twigs pubescent or rarely subglabrous, the hairs appressed and crisped, varying patent and straight or undulate, rarely a few stouter and hooked at the tip. *Leaves* obovate-oblong, varying obovate-elliptic, elliptic or oblong, sometimes narrow; main veins prominent beneath, the reticulum moderately, sometimes markedly, prominent, pubescent or rarely subglabrous, the hairs undulate or crisped, rarely a few stouter and hooked at the tip. *Inflorescences at anthesis*: *male head* 5–15 mm. across, peduncle 3–15 mm. long; *female head* with the surface smooth. *Syncarp,* peduncle (?2–)15–30 mm. long.

DISTRIBUTION: in primary and secondary forest from sea level to 6000 ft.; Mindanao, Moluccas, New Guinea, Salawati, Aru Islands, Louisiade Archipelago.

Philippines. MINDANAO. *Ahern 676* (BO, ♀). Bukidnon: Mt. Katanglad, *Sulit PNH 9951* (A, L, ♂). Davao: *De Mesa FB 27486* (K, ♀); Todaya, *Copeland 1244* (P, ♂); Todaya, Mt. Apo, *Elmer 10932* (A, BM, BO, K, L, ♀). Zamboanga: San Ramon, *Hallier 4671a* (L). **Moluccas.** OBI. *Atasrip 45* (L).

New Guinea. VOGELKOP. Manokwari: Bostuin Tafelberg, *Versteegh BW 3830* (L, ♀). Sorong: Sausapor, *Versteegh BW 4619* (L, ♂). DUTCH NORTH NEW GUINEA. Idenburg River, Bernhard Camp, *Brass & Versteegh 14004* (A), *14021* (A, ♀); Mamberamogebiet, Pionier Bivac, *Lam 730* (BO, K, L, U, ♂, ♀). DUTCH SOUTH NEW GUINEA. Bian River, *Branderhorst 275* (BO, K, ♀); Sungei Aëndua, Mimika, *bb 32900* (K, L). PAPUA. Central Division: Iawarere, *Brass 674* (A, K, ♂); Mafulu, *Brass 5184* (A, BO, US, ♀), *5394* (A, BO, K, US, ♀); Sogeri, *Forbes 86* (BM, L, ♂). Northern Division: Isuarava, *Carr 15351* (A, BM, K, L, SING, ♂), *15552* (BM, K, L, SING, ♂), *15762* (BM, K, L, SING); c. 8 km. n. of Saiho along road to Divinikoari, *Hoogland & Macdonald 3492* (A, K, L, ♀); Tufi Subdistrict, halfway between Wanigela and Itoto, *Hoogland 4822* (A, BM, K, L, ♂, ♀). Western Division: lower Fly River, e. bank, opposite Sturt Island, *Brass 8117* (A, L, ♂, ♀). MANDATED TERRITORY OF NEW GUINEA. Madang District: Kani-gebirge, *Schlechter 17065* (A, K, L, ♂, ♀). Morobe District: Matap, *Clemens 11174* (A, ♀); Ogeramnang, *Clemens 4550, 5138* (A, ♂, ♀); Quembung mission trail to Sattelberg, *Clemens 1244* (A, ♀); Sattelberg, *Clemens 7584* (A). SALAWATI. Kaloal, *Koster BW 4253* (L). ARU ISLANDS. Giabulengan, *Beccari*, May 1873 (FI, ♂, ♀). LOUISIADE ARCHIP. Rossel Island, Jinju, *Brass 28569* (A, L, ♂).

With the type of *Artocarpus refractus*, which came from the Aru Islands, Beccari cited an additional specimen, *PB 74*, from Kapaor, Papua Onin, but this is apparently not in the Herbarium Universitatis Florentinae and has not been found elsewhere.

Quite a wide range of variation is found within this variety, particularly, as noted above, in some collections from the mountains of eastern New Guinea. Elsewhere in New Guinea, var. *refractus* has not been seen from above 3000 feet (although one of the collections from Mindanao was made at 5500 feet), but from the Central and Northern Divisions of Papua, and the Madang and Morobe Districts of northeast New Guinea several collections from an altitude of 3000 to 6000 feet have been seen. Some of these (*Brass 5184*, *5394*, *Forbes 86*, *Carr 15351*, *15552*, *15762* and *Clemens 11174*) have rather small, narrow leaves characterized by a very strongly developed, netted reticulum and could, perhaps, be regarded as representing a distinct entity. However, the remaining four (*Schlechter 17065* and *Clemens 4550*, *5138* and *7584*) are intermediate to the typical form, having rather broadly elliptic leaves with a netted, but less prominent, reticulum.

It is not possible to give satisfactory characters for distinguishing male or sterile collections of *Artocarpus vrieseanus* var. *refractus* from *A. fretessii*, apart from the difference in the bracts mentioned above. However, in the former the male heads are usually somewhat larger, with shorter peduncles relative to the size of the head; they are also only rarely borne on short-shoots, whereas this is very common in the latter. On the whole, *A. fretessii* tends to have a smaller leaf, with a more distinct, often straw-coloured reticulum, and somewhat more ascending lateral veins, but rather similar leaves are found in the mountain form of var. *refractus*. In the eastern Moluccas and New Guinea, *A. fretessii* is also distinguished by the rather markedly cordate base of the leaf.

var. **papillosus** Jarrett, var. nov.

Ramuli juniores pubescentes, pilis appressis crispatisque, vel patentibus et rectis undulatisve. *Folia* ovati-elliptica, elliptica vel obovati-elliptica;

costa nervi lateralesque subtus prominentes, venulae prominulae, pubescentes, pilis plus minusve undulatis, ad subglabri. *Inflorescentiae ad anthesin*: *capitula mascula* 3–8 mm. diametro, pedunculis 3–5 mm. longis; *capitula feminea* superficie plana. *Syncarpia* pedunculis 5–35 mm. longis.

HOLOTYPE: Solomon Islands, *Kajewski 2360* (A); isotypes (BM, K, L, P).

DISTRIBUTION: in rain forest from sea level to 4000 ft.; Solomon Islands.

Solomon Islands. BOUGAINVILLE. Kugumaru, Buin, *Kajewski 1920* (A, K, ♂). GUADALCANAL. Berande, *Kajewski 2436* (A, BM, K, P, ♀); Vulolo, Tutuve Mt., *Kajewski 2501* (A, BM, P, ♀). MALAITA. Quoimonapu, *Kajewski 2360*, Dec. 1930 (A, BM, K, L, P, ♂, ♀). SAN CRISTOBAL. Balego-nagonago, *Brass 2826* (A, K, L, ♂, ♀).

Seed formation in this variety is often somewhat irregular, so that the syncarp is slightly lobed, while the surface between the lobes remains papillate as in *A. fretessii*; the lobes, however, differ from those found in the latter species in being shallow and ill defined.

var. vrieseanus

Artocarpus vrieseana Miq. Ann. Mus. Lugd.-Bat. **3**: 212. 1867; Renner, Bot. Jahrb. **39**: 369. 1907. Syntypes, Batjan, *De Vriese s.n.*, Celebes, Manado, *De Vriese s.n.* (L); lectotype, Batjan, *De Vriese s.n.* (L).

Artocarpus antiarifolia Becc. For. Borneo, 630. 1902. Holotype, Jobi [Japen], *Beccari s.n.* (FI); isotype (FI).

Artocarpus cumingiana Tréc. var. *stenophylla* Diels, Bot. Jahrb. **67**: 177. 1935. Holotype, northeast New Guinea, *Ledermann 12863* (B); isotype (K).

Twigs thinly pubescent to subglabrous, except when nearly glabrous some hairs patent or recurved and hooked at tip, the rest patent to crisped. *Leaves* oblong-elliptic to elliptic or obovate-elliptic, often narrowly so; main veins prominent beneath, reticulum slightly so, indumentum as on twigs. *Inflorescences at anthesis*: *male head* 4–7 mm. across, peduncle (4–)6–17 mm. long; *female head* with the surface smooth. *Syncarp*, peduncle 15–35(–65) mm. long.

DISTRIBUTION: in primary and secondary forest from sea level to 3000 ft.; Celebes (Manado) ?, Moluccas (Batjan), New Guinea.

Celebes. (?) NORTH PENINSULA. Manado, *De Vriese* (L, ♀). **Moluccas.** BATJAN. *De Vriese* (L, ♂, ♀).

New Guinea. DUTCH NORTH NEW GUINEA. Geelvink Bay, Nabire, *Kanehira & Hatusima 11538* (A, BO, ♂), *11584* (A, BO, ♀); Sarmi, Tor River, Dirdjan, *Leden BW 5364* (L, ♂, ♀). MANDATED TERRITORY OF NEW GUINEA. Madang District: near the Gogol River, near Mawan village, *Hoogland 4928* (A, K, L, ♂, ♀); Kani-gebirge, *Schlechter 17854* (A, K, L, ♂); Wobbe, *Schlechter 16439* (A, K, L, ♂). Sepik District: Kaiserin Augusta [Sepik] River, Felsspitze, *Ledermann 12863*, Aug. 1913 (BM, K, ♂). JAPEN. Ansus, *Beccari s.n.*, Apr. 1875 (FI, ♂); near Serui, Kaunda, *Aet & Idjan 568* (L, ♂); Serui, Watibu, *bb 30249* (BO, L, SING, ♀).

The type material of *Artocarpus vrieseanus* in the Rijksherbarium, Leiden, consists of six sheets purporting to come from both Celebes and Batjan, but comparison of these indicates that only three gatherings are involved and that there has been some confusion in the labelling. The two sheets labelled as coming from Celebes, one of which has an attached submature syncarp (peduncle 55 mm.), match exactly the leaves and detached syncarp (peduncle also 55 mm.) of one of the sheets stated to be from Batjan. Since the other two gatherings are both labelled as from Batjan the record from Celebes appears somewhat doubtful at present. The second gathering consists of two sheets with immature male inflorescences attached and in an envelope (the head to 7 mm. across and the peduncle to 17 mm. long). A twig on one of these sheets, which bears a leaf and a syncarp comparing closely with the first gathering, was probably mounted here by mistake, and the other sheet is therefore chosen as the lectotype. The third gathering, which is very similar to the first, is represented by a sterile sheet from Batjan (matched by another sheet from Hasskarl's herbarium not annotated by Miquel). All the material is undoubtedly referable to the entity under consideration, since the perianths in the syncarp are completely fused, the bracts in the male head are stoutly stalked, and the leaves are thinly coriaceous with a slightly prominent reticulum. No hooked hairs were found on the leaves or twigs, but this is true of a few other almost completely glabrous collections of var. *vrieseanus*, such as *Kanehira & Hatusima 11584*, which is a good match for the first gathering mentioned above.

A collection from Kugumaru, Buin, Bougainville, *Kajewski 1940* (A, BM, K, L, P, SING, ♂, ♀), may be referable to this variety; the leaves are rather broadly elliptic, and these and the twigs are definitely pubescent, but many of the hairs are hooked at the tip and the young syncarps are smooth, not papillate as in var. *papillosus*. A sterile collection from Ambon, *De Fretes s.n.* (CAL, GH, L, U), which likewise has pubescent leaves but abundant hooked hairs, may also be referable here since the leaves are, in addition, scarcely cordate (see below); it is, however, discussed further under *A. fretessii*. The latter may be distinguished vegetatively by the definitely pubescent leaves with a more prominent reticulum, the absence of hooked hairs (occasionally a few present in specimens from the Vogelkop), and, in the eastern Moluccas and New Guinea, by the rather markedly cordate leaf base.

var. **subsessilis** Jarrett, var. nov.

Ramuli juniores, puberulentes, pilis appressis et rectis crispatisve, mox glabrescentes. *Folia* elliptica vel obovati-elliptica, saepe angusta; costa nervi lateralesque tantum subtus prominentes et puberulentes vel glabri. *Inflorescentiae ad anthesin*: *capitula mascula* 5–7 mm. diametro, pedunculis 2–3 mm. longis; *capitula feminea* superficie plana. *Syncarpia* pedunculis 3–7 mm. (*Floyd 3453* ad 13 mm.) longis.

HOLOTYPE: northeast New Guinea, *Hoogland 4999* (A); isotypes (K, L).

DISTRIBUTION: in primary and secondary forest from sea level to 5500 ft.; New Guinea, Bismarck Archipelago, Solomon Islands (Bougainville).

New Guinea. VOGELKOP. Steenkool, road to Tembuni, *van Royen 3591* (L). DUTCH NORTH NEW GUINEA. Hollandia, Holtekang, *Brouwer BW 1539* (L, ♀); Wissel Lake region, Lake Tigi, *Eyma 4883* (L, ♀); Wissel Lake region, foot of Mt. Bubiro and Enarotali, *Eyma 5124* (L, ♀). PAPUA. Milne Bay District: Cape Vogel Peninsula, Menapi, *Brass 21660* (A, ♀). Northern Division: Kokoda, *Carr 16420* (L); Tufi Subdistrict, near Koreaf village, *Hoogland 4813* (A, BM, K, L, ♀). MANDATED TERRITORY OF NEW GUINEA. Madang District: Gogol River valley, near Jal village, *Hoogland 4999*, July 1955 (A, K, L, ♂, ♀). Morobe District: Lae, Botanic Gardens ("indigenous"), *Womersley NGF 9079* (A, L, ♀). NEW BRITAIN. Keravat, *Floyd 3453* (A, BM, K, L, ♀). **Solomon Islands.** BOUGAINVILLE. Teop Island *Waterhouse 46* (K, ♂).

This variety can readily be distinguished from *Artocarpus fretessii* by the almost entirely glabrous leaves lacking a prominent reticulum.

34. **Artocarpus xanthocarpus** Merr. Publ. Gov. Lab. Manila 17: 10. 1904, "*xanthocarpa*," Philip. Jour. Sci. 1, Suppl. 43. 1906; Elmer, Leafl. Philip. Bot. 2: 626. 1909. Holotype, Luzon, *Whitford 367* (PNH, destroyed); isotypes (K, P, US); lectotype (P).

Artocarpus lamellosa Blanco, nomen dubium, Elm. Leafl. Philip. Bot. 2: 625. 1909.
Artocarpus lanceolata auct. non Tréc., Merr. Enum. Philip. Pl. 2: 42. 1923.
Artocarpus rubrovenius auct. non Warb., Merr. Philip. Jour. Sci. Bot. 3: 401. 1908.

Small trees, height to 8 m. *Twigs* 1.5–3 mm. thick, smooth or finely rugose, appressed-puberulent, soon glabrescent. *Leaves* 5.5–20 × 2.5–9 cm., obovate-elliptic, varying obovate- or elliptic-oblong, with an acumen to 3 cm. long, base cuneate, varying narrowly rounded, glabrous, margin entire; main veins prominent beneath, intercostals slightly so; lateral veins 6–11 pairs, curved; intercostals few, not parallel; green, drying brownish or greenish, venation straw-coloured, reddish or nigrescent in young leaves; petiole 5–23 mm. long.

Inflorescences solitary or paired in leaf-axils. *At anthesis*: *male head* 3–6 × 3–4 mm., globose to obovoid; perianths tubular, bilobed above, 0.5 mm. long; stamen 1 mm. long, filament cylindric, tapering above, anther-cells ellipsoid, 0.2 mm. long; bracts slenderly stalked, heads peltate, to 0.3 mm. across, these and perianths ciliate; peduncle 2–3 × 0.5 mm., velutinous; *female head* with peltate bracts mostly shed and styles exserted to 0.8–1 mm. through low papillae. *Syncarp* to 5 cm. across, subglobose, shallowly lobed, yellow, drying pale or reddish brown, the surface smooth or nearly so, velutinous, with a few persistent bracts; wall c. 3 mm. thick; proximal region of perianths fused, fruiting perianths several, thin-walled. "seeds" (pericarps with an indurated endocarp) ellipsoid, 8 × 6 mm.; core c. 4 mm. across; peduncle 6–11 × 3 mm., velutinous.

DISTRIBUTION: in forest to 1300 ft.; Mangsi Islands, northern and central Philippine Islands.

Borneo. MANGSI ISLANDS. *Wilkes* (GH, ♂, ♀). **Philippine Islands.** MINDORO.

Merritt FB 9894 (BO, US, ♂); Mansalay, Mt. Yagaw, *Conklin PNH 17465* (A, L, PNH, ♂). BATANES ISLANDS. *Fenix BS 3581* (BO, ♂), *3814* (NY, US, ♀); Mt. Iraya, *Ramos BS 80012* (K, NY, ♂, ♀), *80305* (K, NY, ♀). LUZON. Benguet: *Leano FB 24715* (NY, US, ♀). Cagayan: *Klemme FB 6670* (K, NY, US, ♂). Bataan: Lamao River, *Borden 183* (A, NY, ♂); Lamao River, Mt. Mariveles, *Whitford 367*, June 1904 (K, P, US, ♀). Laguna: Majayjay, *Curran & Merritt FB 8055* (NY, P, US, ♂). Tayabas: *Labitag FB 25414* (A, K, P, US, ♂, ♀). Camarines: *Aguilar FB 14345* (US, ♂); Camarines Sur, Iriga, *Vidal 1539* (A, K, ♂); Mt. Bagacay, *Ramos & Edano BS 33925* (SING, ♀). Sorsogon: Irosin, Mt. Bulusan, *Elmer 16247* (BM, GH, K, L, ♂). BOHOL. *Ramos 42581* (BM, BO, P, SING, ♀). SIQUIJOR ISLAND. *Piper 398* (K, P, ♀).

Artocarpus xanthocarpus is, as noted above, apparently most closely allied to *A. vrieseanus*, from which it differs in the longer styles, exserted to c. 1 mm. at anthesis instead of only 0.4 mm., and the slenderly stalked bracts in the male head. Otherwise it is rather similar to *A. vrieseanus* var. *subsessilis*, but it may be distinguished by the base of the leaf, which is usually cuneate and slightly decurrent, instead of rounded or auriculate. The small, entirely glabrous leaves, lacking a prominent reticulum, give *A. xanthocarpus* a strong superficial resemblance to *A. nitidus* ssp. *nitidus*, which also occurs in the Philippines, and distinguishing characters are given below, under the latter entity.

The type material of *A. xanthocarpus* bears mature syncarps only, but styles 1 mm. long have been found persisting on the specimen at the Muséum National d'Histoire Naturelle, Paris. The Wilkes expedition collection from the Mangsi Islands off the northeastern tip of Borneo represents, at present, a rather outlying locality for the species. However, although the specimen is in rather poor condition, it, too, has the long styles on the syncarp and the characteristic, very small male inflorescences. The collections from the Batanes Islands are all distinguished by having a very long, slender acumen to the leaf.

35. **Artocarpus fretessii** Teysm. & Binnend. in Hassk. Abh. Naturf. Ges. Halle **9**: 189. 1866, "*Fretissi*"; Merr. Interpr. Rumph. Herb. Amb. 191. 1917.

Metrosideros spuria Rumph. Herb. Amb. 3: 26. *t. 13.* 1743.

Antiaris fretessii Teysm. & Binnend. Cat. Hort. Bog. 84. 1866, nomen nudum.

Artocarpus dasyphylla Miq. Ann. Mus. Lugd.-Bat. **3**: 212. 1867; Renner, Bot. Jahrb. **39**: 369. 1907; J. J. Smith, Ic. Bogor. **3**: 83. 1907. Syntypes, Celebes, *Riedel HB 5841*, *Teysmann HB 5787* (U); lectotype, *Teysmann HB 5787* (U).

Artocarpus erythrocarpa Teysm. ex Miq. Ann. Mus. Lugd.-Bat. **3**: 212. 1867, pro. syn.

Prainea rumphiana Becc. For. Borneo, 636. 1902.

Artocarpus dasyphylla Miq. var. *flava* J. J. Smith, Ic. Bogor. **3**: 85. *t. 234.* 1907.

Artocarpus leytensis Elm. Leafl. Philip. Bot. **1**: 279. 1908, **2**: 622. 1909; Merr. Enum. Philip. Pl. **2**: 42. 1923. Holotype, Leyte, *Elmer 7243* (PNH, destroyed); isotypes (A, BO, K); lectotype (K).

Artocarpus paloensis Elm. Leafl. Philip. Bot. **1**: 280. 1908, **2**: 621. 1909. Holotype, Leyte, *Elmer 7244* (PNH, destroyed); isotypes (A, BO, K); lectotype (K).

Artocarpus rotundifolia Elm. ex Merr. Enum. Philip. Pl. **2**: 42. 1923, pro syn.

Trees, height to 40 m., buttresses small or none, bark pale brown, peeling off in flakes. *Twigs* 1.5–4 mm. thick, pubescent, hairs pale yellow to rufous, usually subappressed and crisped. *Leaves* 6–29 × 3–12 (–32 × 16) cm., obovate-oblong to elliptic, acute, attenuate or acuminate, base broadly cuneate to shallowly cordate (varying to deeply so in the Moluccas and New Guinea), margin entire; juvenile leaves pinnatifid; main veins and reticulum distinctly prominent beneath; glabrous above or nearly so except for the pubescent main veins, venation beneath moderately to sparsely pubescent, hairs colourless, straight or slightly undulate; lateral veins 9–13 pairs, curved, basal 2–4 pairs crowded; intercostals parallel; dark green above, pale green or greyish beneath, usually drying greyish or brownish, paler beneath, venation concolorous, varying straw-coloured; petiole 5–15 mm. long.

Inflorescences solitary or paired in leaf-axils, or more frequently on short-shoots on older wood. *At anthesis*: *male head* 3–7 mm. across, subglobose or obovoid; perianths of 2 or 3 free segments 0.4–0.5 mm. long; stamen 0.8 mm. long, filament slightly flattened, tapering above, anther-cells subglobose, 0.15 mm. long; bracts slenderly stalked, heads peltate, to 0.3 mm. across, these and perianths sparsely ciliate; peduncle 3–7 mm. long, short-pubescent; *female head* with peltate bracts mostly shed and styles exserted to 0.5 mm. through papillae. *Syncarp* to 4 cm. across, with one to several subglobose lobes, yellow, or dark red to purple, drying olive-brown to rufous, the surface smooth over the lobes, papillate between them, short-pubescent, with a few persistent bracts; wall c. 2 mm. thick over lobes; proximal region of perianths free, fruiting perianths 1–c. 12 (New Guinea, 1 or 2), thin-walled, "seeds" (thin, horny pericarps) subglobose, 8 × 7 mm.; core c. 4 mm. across; peduncle 20–25(–30) mm., short-pubescent.

VERNACULAR NAMES: *maumbi*, *kelembi*, Celebes; *taewan*, Ambon.

DISTRIBUTION: in forest up to 2000 ft.; eastern Borneo, Philippines, Celebes, Moluccas, New Guinea (Vogelkop).

Borneo. SOUTH AND SOUTHEAST BORNEO. Martapura, Tewingan, *Boschbouwprufstation 2108* (BO, ♂); Martapura, Twang Bangkal, *bb 2475* (BO, L, ♀). EAST AND NORTHEAST BORNEO. Loa Haur, w. of Samarinda, *Kostermans 6902* (L, ♂, ♀). BRITISH NORTH BORNEO. Kamang-sian, *Goklin 1302* (K, ♂).

Philippine Islands. PALAWAN. Brooks Point, Addison Peak, *Elmer 12609* (A, BM, K, L, ♂, ♀); Puerto Princesa, Mt. Pulgar, *Elmer 12944* (A, BM, K, L, ♀). LEYTE. *Franco FB 26409* (P), *Wenzel 811* (BM, GH, ♀); Abuyog, Lake Danao, *Krukeberg*, Sept. 1945 (A, ♂); Palo, *Elmer 7243*, Jan. 1906 (A, BO, K, ♀), *7244*, Jan. 1906 (A, BO, K, ♂, ♀). BILIRAN. *McGregor BS 18663* (A, BO, P, SING, ♀). PANAY. Ilo-ilo: Miagao, *Vidal 3833* (A, K, ♂, ♀). MINDANAO. Surigao: *Ramos & Pascasio BS 34350* (BM, L, NY, SING, ♀). CAMIGUIN DE MINDANAO. *Ramos 1196* (BM, P, U, US, ♀).

Celebes. NORTH PENINSULA. Gorontalo: Molinggapoto, *bb 18022* (A, BO, L). Minahassa: Manado, *Koorders 19061* (BO, L), *Riedel HB 5841* (BO, L, U, ♀), *7264* (BO, P), *Teysmann HB 5723* (BO), *5863* (BO, L, U); Sondaho, *bb 5573* (BO, L); Tana Wangko, *Teysmann HB 5787* (BO, U, ♀); Kajuwatu, *Koorders 19039, 19048, 19055* (BO, L), *19058* (BO, L, ♀), *19431* (BO); Lubu, Amurang, *Koorders 19052* (BO, L, ♂); Masuka, *Koorders 19185* (BO, L); Pakuere, *Koorders 19045* (BO, L); Pinamorangan Mts., *Koorders 19054* (BO, K, L, ♀); Ratahan, *Koorders 19043* (BO), *19060* (BO, L, ♀), *19306* (BO); Sembolei, *Koorders 19062* (BO, ♀); Tondano, *Koorders 19312* (BO, ♀). CENTRAL CELEBES. Malili, *NIFS Cel./V–216 no. 226* (BO, L); Malili, Toli Toli, *NIFS Cel./V–216 no. 109* (BO, ♂); Malili, Usu, *NIFS Cel./III–55 no. 81* (BO, ♀), *no. 238* (BO, L, ♂); Palu, Tomado, *bb 28212* (BO, L); Poso, Tokosondo, *bb 17977* (A, BO). SOUTHWEST PENINSULA. Baleh-Angien, *Teysmann HB 12359* (BO, L, ♀), *12481* (BO); Bonthain, Saluang, *NIFS Cel./I–19* (BO, L, ♀); Maleku, *bb 23909* (BO, L). SOUTHEAST PENINSULA. Kolaka, Parso, *bb 32510* (A, BO, L, ♀). P. MUNA. Labunti, *bb 6041* (BO, L, U, ♀).

Moluccas. TALAUD ISLANDS. Karakelang, e. of Beo, *Lam 2626* (L, ♀). HALMAHEIRA. Djailolo, Tuguair, *bb 23734* (A, BO, L); Galela, *Beguin 1867* (BO, L, ♂, ♀); W. Tobelo, *Beguin 2303* (BO, K, L, SING, ♀). BATJAN. Nanggapil, *sine nom. IX* (BO, ♂). SULA ISLANDS. Mangoli, *bb 29771* (A, BO, L); Sanana, Kali Waj Gaj, *bb 28811* (A, BO, L, SING, ♂); Taliabu, n. of Samuja, *bb 29937* (A, BO, L, SING, ♂). BURU. Wae Ula, *bb 22801* (BO, ♂).

New Guinea. VOGELKOP. Manokwari: Momi, *bb 33417* (A, BO, K, L, ♂); Oransbari, *Brouwer BW 2512, 2576, 2594, Mangold BW 2133* (L); Prafi, *Schram 554* (L); Ransiki, Mioswaas, *Koster BW 1270* (L); Ransiki, Warsuwi, *Kostermans 87* (BO, K, L, SING, ♀); Sidai, 65 km. w. of Manokwari, *Koster BW 4450* (L, ♂); Warnapi, *bb 33627, 33629* (BO, K, L). Sorong: Warsamson, 25 km. e. of Sorong, *Schram BW 5904* (L).

Cultivated. MALAYA. Singapore, Hort. Bot., *Cantley 136* (K, ♂, ♀), *Ridley 3359* (BM, CAL, K, SING, ♂, ♀). JAVA. Bogor: Hort. Bot., *VII G 105* (BO, L, ♀), *VIII B 5* (L, ♂), *Sutrisno 82* (cult. sub. VII G 105; origin Celebes), Oct. 1957 (L, ♂); Tjiliwung river, *Kostermans*, Aug. 1953 (K, L).

The nomenclatural type of *Artocarpus fretessii* is *Metrosideros spuria* [i] *Taewan mas* of Rumphius, for which Hasskarl provided an identification in 1866 in his key to the "Herbarium Amboinense" with the phrase "*Artocarpus Fretissi* T. & B. Teysm. in litt." The identity of Rumphius' *Taewan mas* with the species under consideration can be established with certainty from the plate (*t. 13A*), which shows the characteristic mature syncarps with rounded lobes and between these the papillate unexpanded surface. The artist has added a "calyx" to one of the fruits, but the likeness is unmistakable and extends to the vegetative characters, while the description is also in agreement. Hasskarl offered no identification for the second plant, *Taewan femina*, treated by Rumphius under *Metrosideros spuria*, but, from the plate (*t. 13B*), it appears to represent the same species at anthesis, when the female heads are globose with the entire surface papillate. In 1754, Linnaeus, in his key to Rumphius (Herb. Amb. 11 [resp. O. Stickman]), had incorrectly identified *Metrosideros spuria* as *Ochna jabotapita* L. (see Sprague, Proc. Linn. Soc. **165**: 151–156. 1955, for a discussion of Linnaeus' later treatment of this species). Merrill, in his consideration of the "Herbarium Amboinense" (1917), mentioned Teysmann and Binnendijk's name, but was unable to refer Rumphius' plant to any known species of *Artocarpus*. However, on the Bogor sheet of *Beguin 1876*, which was collected in 1921 in Halmaheira, there is a note to the effect that Beguin thought he had found *Metrosideros spuria*.

Artocarpus fretessii antedates by one year and must replace the name *A. dasyphylla* Miq. (1867) under which the species has been known in Indonesia. Teysmann and Binnendijk's epithet was based on the name of De Fretes, a resident of Ambon who presumably sent them the living material that appeared in their catalogue (1866) of the Hortus Bogoriensis under a *nomen nudum*, *Antiaris fretessii*, with the source given as Ambon and the vernacular name as *taewan*. The assumption that this plant was identified with *Taewan mas* and the generic name corrected to *Artocarpus* in Teysmann's communication to Hasskarl is supported by a specimen at Leiden from the Hortus Bogoriensis, collected from a plant numbered *VII G 105*, which is referable to this species and bears the determination "*Artocarpus fretessii*," with another note referring to *Antiaris fretessii* of the catalogue.[4] (A recent collection from this tree, however, gives the source as Celebes.) There is also in existence a sterile collection by De Fretes from Amboina, *HB 5562*, which bears on the sheet in the herbarium at Utrecht a reference to *Metrosideros spuria*. However, as already noted under *Artocarpus vrieseanus*, the identity of the collection is doubtful and it is perhaps better referred to that species. It was determined only as *Artocarpus* but was cited as *A. lakoocha* by Miquel (Ann. Mus. Lugd.-Bat. 3: 313. 1867) and under *A. lakoocha* var. *malayana* (= *A. dadah*) by King (Ann. Bot. Gard. Calcutta 2: 15. 1889).

Artocarpus fretessii again shows considerable variability in both inflorescences and vegetative characters, particularly in the colour of the syncarp. Red or purple fruits are reported from Celebes and the Sula Islands, while yellow ones are recorded from Borneo, Celebes and the Moluccas. Although it would seem, from the frequent absence of syncarps from collections for which their colour is reported, that the yellow male inflorescences may be mistaken for them in the field, the variation is undoubtedly genuine. *Artocarpus dasyphylla* was described by Miquel as having red fruits, and J. J. Smith (1907) described the yellow-fruited form as var. *flava* from a plant of unknown provenance in the Hortus Bogoriensis. There appears to be no other difference correlated with that of the fruit colour, nor is there any geographical separation of the two forms. If the two were to be maintained as distinct, a new name would be required for the red form, since in Rumphius' description the fruit was stated to be yellow. There does not, however, seem to be any real justification for erecting a new variety for such a colour variant.

Variation in leaf shape, on the other hand, shows a definite pattern of distribution in which the leaf tends to become markedly cordate (and often

---

[4] It seems best to take *fretessii* as the form in which Teysmann and Binnendijk intended to Latinize the name and to treat the spelling found in Hasskarl as an orthographic error.

somewhat elongate) in the Moluccas and New Guinea, and this is accompanied by a reduction in the number of lobes on the syncarp (each of which usually contains a single seed).

The distinctions between *Artocarpus fretessii* and *A. vrieseanus* are discussed fully above, under the latter species. In the Philippines *A. fretessii* overlaps the ranges of two further species with pubescent leaves. The first of these, *A. ovatus*, may be distinguished by the relatively longer and narrower leaves with more numerous lateral veins (11–20 *vs.* 9–13 pairs), and by the patent hairs on the twigs. The second, *A. subrotundifolius*, may be differentiated from all these species by the broad leaves with long petioles (25–35 mm. *vs.* 5–18 mm.).

36. **Artocarpus reticulatus** Miq. Ann. Mus. Lugd.-Bat. **3**: 213. 1867, "*reticulata,*" non Heyne ex Wallich, 1831 (nomen nudum), nec Hunter ex Ridley, 1909; Renner, Bot. Jahrb. **39**: 369. 1907; Koord. Suppl. Fl. N. O. Celebes **2**: *t. 3*, **3**: 1. 1922. Syntypes, Celebes, *Teysmann HB 5272* (U), Ternate, *De Vriese & Teysmann s.n.* (L); lectotype, *Teysmann HB 5272* (U).

Trees, height to 30 m., with small buttresses, bark rough, grey. *Twigs* 3–6 mm. thick, rugose, puberulent with hooked hairs, or glabrous. *Leaves* 15–35 × 8–16 cm., oblong-elliptic, acute or acuminate, base rounded or broadly cuneate, margin entire; main veins and reticulum prominent beneath, the reticulum rather acutely so; glabrous, or the main veins above and the venation beneath scabrid-puberulent, the hairs hooked at the tip; lateral veins 12–15 pairs, curved, basal pairs slightly crowded; intercostals parallel; green, paler beneath, drying brown to yellow-green, usually paler beneath, venation concolorous; petiole 13–25 mm. long.

Inflorescences solitary or paired in leaf-axils. *At anthesis*: *male head* (immature) c. 15 mm. across, obovoid; perianths of 3 or 4 free segments 0.2 mm. long; stamen . . . ; bracts slenderly stalked, heads peltate, to 0.3 mm. across, short-ciliate; peduncle 13 × 1 mm., short-pubescent; *female head* with peltate bracts mostly shed and styles exserted to 1.5 mm. through prominent papillae. *Syncarp* to 6 cm. across, subglobose or lobed, orange, drying brown, the surface verrucose throughout from conical papillae, or becoming nearly smooth over the lobes, pubescent, with scattered persistent bracts; wall c. 5 mm. thick over lobes; proximal region of perianths free, fruiting perianths several, somewhat fleshy, "seeds" (indurated endocarps) ellipsoid, 12 × 8 mm.; core c. 15 mm. across; peduncle 25–45 × 4 mm., velutinous.

VERNACULAR NAMES: *maumbi, maumbi sela,* Celebes.

DISTRIBUTION: in forest to 2000 ft.; Celebes, Moluccas (Ternate).

Celebes. NORTH PENINSULA. Minahassa: Karoa, near Papo, *Koorders 19051* (BO, L, ♂); Lolombulan, near Pakuere, *Koorders 19049* (BO, L); Amurang, *sine nom. et num.* (BO, ♀); Amurang, Lobah Kolai, *bb 17125* (A, BO); Lemo, *bb 7536* (BO); Ratahan, *Koorders 19053* (BO, L), *Teysmann HB 5272* (BO, CAL, L, U, ♀); Pingsan, near Kajuwatu, *Koorders 19046, 19047* (BO, L). CENTRAL CELEBES. Malili, Kawata, *NIFS Cel./V-88* (BO, K, L, ♂, ♀). P. MUNA. Lamiko, *bb 21754* (A, BO, L, ♀). **Moluccas.** TERNATE. *De Vriese & Teysmann* (L).

The inflorescence characters of *Artocarpus reticulatus* are intermediate between those of *A. fretessii* and *A. subrotundifolius*, but provide clear distinctions from each of these species. The syncarp is usually strongly lobed as in *A. fretessii*, but the surface is more prominently papillate, and the styles are long-exserted as in *A. subrotundifolius* (to 1.5 mm. instead of to 0.5 mm.), though fewer seeds are formed than in the latter species. The male inflorescence, although it has been seen only when immature, apparently lies between the two other species in both the size of the head and the length of the peduncle. Vegetatively, *A. reticulatus* may be distinguished from *A. fretessii* by the glabrous or nearly glabrous leaves and twigs, and by the rather acutely prominent reticulum. From *A. vrieseanus* var. *vrieseanus* it is less readily distinguished, but the leaves are usually larger with more numerous, parallel intercostals, and a longer petiole (13–25 *vs.* 5–15 mm.).

37. **Artocarpus subrotundifolius** Elmer, Leafl. Philip. Bot. 1: 281. 1908, "*subrotundifolia*," 2: 619. 1909; Merr. Enum. Philip. Pl. 2: 43. 1923. Holotype, Leyte, *Elmer 7265* (PNH, destroyed); isotypes (A, BO, K); lectotype (K).

Artocarpus nitidus auct. non Tréc., Ahern, Timber Tree Sp. Philip. 35. 1901, tabula sola.

Trees, height to 25 m. *Twigs* 4–6 mm. thick, smooth or rugose, red-brown to fulvous pubescent, hairs straight or undulate, subappressed or patent, slowly glabrescent. *Leaves* 18–36 × 11–22 cm., broadly elliptic to obovate-oblong, short-acuminate, base cordate, varying broadly rounded and slightly oblique, margin entire; main veins and reticulum prominent beneath; glabrous or nearly so above except for the pubescent main veins, venation beneath pubescent, hairs colourless, straight, or some on the main veins stout and hooked at the tip, old leaves glabrescent, slightly scabrid; lateral veins 10–14 pairs, basal 2–3 pairs crowded; intercostals parallel; bright green above, duller beneath, drying red-brown to blue-grey above, paler beneath, venation usually concolorous; petiole (15–)25–35(–65) mm. long.

Inflorescences solitary or paired in leaf-axils. *At anthesis*: *male head* (20–)25–50 × 20–35 mm., obovoid, ellipsoid or subglobose; perianths of 3 or 4 free segments 0.6 mm. long; stamen 1 mm. long, filament tapering slightly above, anther-cells subglobose, 0.2 mm. long; bracts rather slenderly stalked, heads peltate, to 0.5 mm. across, these and perianths ciliate; peduncle (7–)15–22 × 3 mm., indumentum as twigs; *female head* with peltate bracts mostly shed and styles exserted to 1–2.5 mm. through conical papillae. *Syncarp* to c. 6 cm. across, globose, shallowly lobed, drying brown, the surface papillate or becoming nearly smooth, pubescent, with scattered persistent bracts; wall c. 2 mm. thick; proximal region of perianths free, fruiting perianths numerous, thin-walled, "seeds" (indurated endocarps) subglobose, 14 mm. across; core c. 30 mm. across; peduncle 40(?)–75 × 5–7 mm., indumentum as twigs.

DISTRIBUTION: in forest to 1000 ft.; Philippine Islands.

Philippine Islands. LUZON. Zambales: Mt. Pinatubo, *Fox PNH 4677* (A, ♀). Camarines: *Alvarez FB 21235* (K, US, ♀). Sorsogon: *Curran FB 10541* (BO, K), *10542* (NY, US, ♀), *Vidal 3838* (K, ♀); Irosin, Mt. Bulusan, *Elmer 16990* (A, BM, K, L, ♂, ♀). SAMAR. *Lasquety FB 27032* (BO), *Ramos 1604* (BM, BO, GH, L, P, SING, ♂), *Phasis 25774* (P, ♀). LEYTE. *Rosenbluth FB 12789* (K, NY, US, ♂, ♀), *Wenzel 860* (BM, GH, ♂, ♀), *1576* (A, BM, GH, ♂); near Gacao, *Glassman 794* (A, ♂, ♀); Palo, *Elmer 7265*, Jan. 1906 (A, BO, K, ♂). MINDANAO. Surigao: *Wenzel 3297* (A, BO, GH, K, ♂), *Ramos & Pascasio BS 34757* (NY, ♂).

The maximum size attained by the male inflorescence in this species is considerably larger than in any other species of subgenus *Pseudojaca*, but the dimensions of both the head and the peduncle are rather variable. However, the characteristic, broad, long-petiolate leaves enable male and sterile collections to be assigned to this species with certainty. The well-exserted styles at anthesis and the large syncarps, usually with long peduncles (but measuring only 7 mm. at anthesis in *Glassman 794, cf.* the male inflorescence), are equally distinctive. Older leaves and twigs are often almost completely glabrescent, and, since growth usually occurs in flushes, there may be a considerable difference in appearance between young and old shoots.

[*To be concluded*]

JOURNAL

OF THE

ARNOLD ARBORETUM

VOL. XLI APRIL 1960 NUMBER 2

STUDIES IN ARTOCARPUS AND ALLIED GENERA, IV. A REVISION OF ARTOCARPUS SUBGENUS PSEUDOJACA *

FRANCES M. JARRETT

38. **Artocarpus lakoocha** Roxb. Fl. Ind. 3: 524. 1832, *"Lakoocha"*; Graham, Cat. Bombay Pl. 193. 1839; Wight, Ic. Ind. Or. 2: *t. 681.* 1843; Tréc. Ann. Sci. Nat. Bot. III. 8: 117. 1847; Dalz. & Gibson, Bombay Fl. 244. 1861; Brandis, For. Fl. N.-W. & C. Ind. 426. 1874, pro max. parte; Kurz, For. Fl. Burma 2: 433. 1877; King in Hook f. Fl. Brit. Ind. 5: 543. 1888, pro parte; King, Ann. Bot. Gard. Calcutta 2: 14. 1889, p.p., quoad *t. 13,* excl. spec. *Griffith 4666, Maingay 1479*; Renner, Bot. Jahrb. 39: 370. 1907; Kanjilal, For. Fl. Siwalik & Jaunsar, 379. 1911; Duthie, Fl. Upper Gang. Plain 3: 141. 1915; Troup, Silvicult. Ind. Trees 3: 883. *fig. 326.* 1921; Parkinson, For. Fl. Andaman Is. 253. 1923; Haines, Bot. Bihar & Orissa 5: 824. 1924; Parker, For. Fl. Punjab ed. 2. 487. 1924; Osmaston, For. Fl. Kumaon, 504. 1927; Fischer in Gamble, Fl. Madras 3: 1369. 1928, p.p., quoad spec. *Gamble* et *Lushington*; Parker & Singh, Common Indian Trees, 26. *t. 20.* 1933; Kanjilal et al. Fl. Assam 4: 268. 1940; Benthall, Trees Calcutta, 401. 1946. Holotype(?), Bengal, *Roxburgh s.n.,* Sept. 1812 (BM).

Artocarpus lacucha Roxb. Hort. Beng. 66. 1814, nomen nudum.
Artocarpus bengalensis Roxb. ex Wall. Cat. no. 4655C. 1831, nomen nudum.
Artocarpus reticulata Heyne ex Wall. Cat. no. 4655D. 1831, nomen nudum.
Artocarpus mollis Wall. Cat. no. 4661. 1831, nomen nudum.
Artocarpus yunnanensis H. H. Hu, Bull. Fan Inst. Biol. Peking Bot. 8: 32. 1937. Holotype, Yunnan, *Wang 77078* (PE, not seen); isotype (A).
Artocarpus ficifolia W. T. Wang, Acta Phytotax. Sin. 6: 274. *t. 15, fig. 23.* 1957. Holotype, Yunnan, *Exped. Biol. Sino-ross. ad prov. Yunnan 676* (PE ?, not seen); isotype (A).

Deciduous trees, height to 20 m., bark rough, grey or brown. *Twigs* 3–6 mm. thick, shallowly rugose, densely pubescent, hairs yellow to rufous, patent or subappressed, straight. *Leaves* 13–37 × 6–21 cm., elliptic, oblong or ovate, short-acuminate, base broadly cuneate, rounded or

---

* Continued from volume XLI, p. 109.

subcordate, often oblique, margin entire or denticulate towards the apex; juvenile leaves shallowly pinnatifid; main veins and reticulum prominent beneath, the areolae often slightly bullate; glabrous or nearly so above, venation beneath pubescent, hairs colourless to pale rufous, undulate; lateral veins 9–18 pairs, straight or curved; intercostals parallel; green, drying greyish, greenish or pale brown, venation straw-coloured, smallest meshes of reticulum nigrescent; petiole (10–)15–45 mm. long.

Inflorescences solitary in leaf-axils. *At anthesis: male head* 12–25 × (7–)10–18 mm., ellipsoid, obovoid or clavate; perianths of 2(or 3) free segments, 0.5 mm. long; stamen 0.9 mm. long, filament tapering above, anther-cells ellipsoid, 0.15 mm. long; bracts rather stoutly stalked, heads peltate, to 0.5 mm. across, these and perianths ciliate; peduncle 2–5 × 2 mm., short-pubescent; *female head* with styles exserted to 1–1.5 mm. through low papillae emerging between peltate bracts. *Syncarp* to 6 cm. across (to 12 cm. fide *Winit 301*), subglobose, shallowly lobed, yellow, drying brown, the surface irregularly papillate, pubescent, with numerous persistent bracts; walls c. 3 mm. thick; proximal region of perianths free, fruiting perianths several, fleshy, "seeds" (pericarps with a thin, horny endocarp) ellipsoid, 10 × 6 mm.; core c. 10 mm. across; peduncle 8–15(–25) × 4 mm., short-pubescent.

Vernacular names: *lakuch* (Sanskrit), *barhal* (Hindi), *dahu* or *dheu* (Bengali), India; *myauklok*, Burma; *hat lom*, *hat non* (Lao), Siam. Uses: the tree is often planted, especially in northern India, for its edible fruit.

Distribution: in evergreen, semi-evergreen and moist deciduous forest to 6000 ft., in areas with a distinct dry season; eastern and northern India (Madras, Orissa and Bihar to Assam and Chittagong, and westward along the sub-Himalayan tract to East Punjab), Burma, Andaman Islands, Siam, Indochina, Yunnan; cultivated through much of its range and south to Bombay in India, sparingly introduced elsewhere in the tropics.

India. Not localized: "East India," *Roxburgh* (K, ♀); Himalaya, Tikoli Valley, *Edgeworth 216* (K, ♂); Nouholly, *Hooker f. & Thomson*, Dec. 1850 (K, L, U, P); Punkabarry, *Gamble 1179A* (K, ♂); Tenga Ghats, *sine nom. 1204* (K). East Punjab. Kangra, Bhadwar, *Koelz 4367* (A, ♂). Himachal Pradesh. Lower Kanaor [= Kunawara], *Royle* (GH, P, ♀). Uttar Pradesh. Kumaon: above Kota, *Strachey & Winterbottom* (GH, K); Outer Hills, *Strachey & Winterbottom 18* (GH, K, ♂). Madras. Ganjam District, Khalingia Ghat, *Gamble 13699* (K); Vizagapatam, Rangalu Shola, *Lushington*, June 1914 (K, ♀). Bihar. Hazaribagh, *Meebold 3873* (K, ♂, ♀); Singbhum, Karampoda forest, *Haines 636* (K, ♀). Orissa. Nilghiris, *Pierre 6* (P). Sikkim: *Hooker f.* (K, ♀); below Kasseong, *Hooker f.*, Apr. 1850 (K, ♂); Rangit River, *Clarke 27255* (K), *King*, July 1876 (K, ♀). Bengal. *Roxburgh*, Sept. 1812 (BM, ♀), *Voigt* (C, ♂), *sine nom. et num.*, Dec. 1837 (L); Siligoree, *Clarke 11615B* (BM, ♀). Assam. Cachar, Luckhipoor, *Clarke 7018* (A); Haflong Hill, *Blatter 29156* (K, ♀); Khasia Hills, *Hooker f. & Thomson* (C); Naga Hills, *Prain*, 1886 (CGE); Naga Hills, Lang, *Meebold 7156* (K, ♂). MANIPUR. On the way to Chamoo [? = Tamu], *Watt 5167* (CAL). CHITTAGONG. Hill Tracts, *King 340* (SING, ♀), *417* (L, SING, ♂), *s.n.*, 1882 (L); Khana, *Hooker f. & Thomson* (K).

Burma. Diamond Island, *Prain*, 30 Nov. 1889 (CAL); Myaungmya, Labwuta, *Lace 2977* (K, ♀); Phanac, fl. Saluan [? = Salween River], *Wallich 4661* (CGE, K, P, ♂, ♀); Rangoon *Buchanan Hamilton* (BM), *Dickason 6947* (A, ♂); Rangoon, Kamayut, *Dickason 8256* (A, ♂, ♀); Sandoway, near Taungup, *Lace 2930* (K, ♂). TENASSERIM. Amherst: Moulmein, *Falconer 991* (L). Mergui: *Griffith 1053* (K, ♀). **Andaman Islands.** Ali Masfid Reserve, *Parkinson 385* (K, ♀); Baradang, *Parkinson 205* (DD, ♂); Boru-Lung-Da, *Parkinson 928* (DD, ♀). **Siam.** Dan Sai, Kao Keo Kang, *Kerr 5804* (BM, ♂); Me Kok, Muang Fang, *Kerr 5158* (BM, ♂); Me Lee, Lampoon, *Winit 301, 302* (BM, ♂). PENINSULAR SIAM. Trang, Chawng, *Buncoed 20* (CGE).

Indochina. LAOS. Pac Bac, near Luang Prabang, *Poilane 20478* (P, ♀); between Phinh Ha and Lao Phu Tai, *Poilane 25926* (P, ♂); Vientiane, *Poilane 20782* (P, ♀). TONKIN. Lao Kay prov., between Nam Long and Phouy Tho, *Poilane 25496* (P, ♂). **China.** YUNNAN. *Anderson*, 1875 (CAL), *Forrest 12252* (K, ♂); Chen-Kang Hsien, *Wang 72645* (A, ♂); Chin-ping, Meng-la, *Exped. Biol. Sino-ross. 676*, Apr. 1956 (A, ♂); Fo-Hai, *Wang 74902* (A, ♀), *77078*, June 1936 (A, ♀); Lan-Tsang Hsien, *Wang 76647*(A, ♀); Mienning, Nanya, *Yu 18102* (A, ♂); Shunning, Hila, *Yu 16805* (A, ♀); Szemao, *Henry 11746* (A, K, ♂, ♀).

The distribution of *Artocarpus lakoocha* has generally been given as India, Ceylon, Burma and Malaya, but three corrections to this must be made. Firstly, it was shown by Corner in 1939 (Gard. Bull. Singapore 10: 282) that the entity hitherto identified in Malaya as *A. lakoocha* in fact represented *A. dadah*, a species of western Malaysia. As already noted, the misidentification originated in King's description of this taxon as *A. lakoocha* var. *malayana*, which he did not distinguish satisfactorily from the type. His account of the latter is a mixture of the two species, but the plate was based on Roxburgh's original drawing of *A. lakoocha* (as was the plate in Wight's "Icones"). No collections of this species have been seen from farther south than peninsular Burma and Siam.

Secondly, it has been found that in India, also, two different taxa have been confused under the name *Artocarpus lakoocha*. This species appears to occur as an indigenous tree only in northern India and along the Eastern Ghats, although it is planted more widely. Several collections have been seen from the Bombay area, but none, apparently, is from a wild tree. This is supported by a statement by Graham in 1839 (the sole information traced in the literature) to the effect that *A. lakoocha* was only found in a cultivated state in Salsette and the North Concan. On the Western Ghats and in Ceylon there occurs another entity which has usually been identified as *A. lakoocha*. However, it has been found that it is quite distinct and it is described above as *A. gomezianus* ssp. *zeylanicus*, the differentiating characters being given there. *Artocarpus lakoocha* was described from Bengal and the type and drawing leave no doubt as to the application of Roxburgh's name. The references in which the two entities have been confused are indicated above as far as possible;

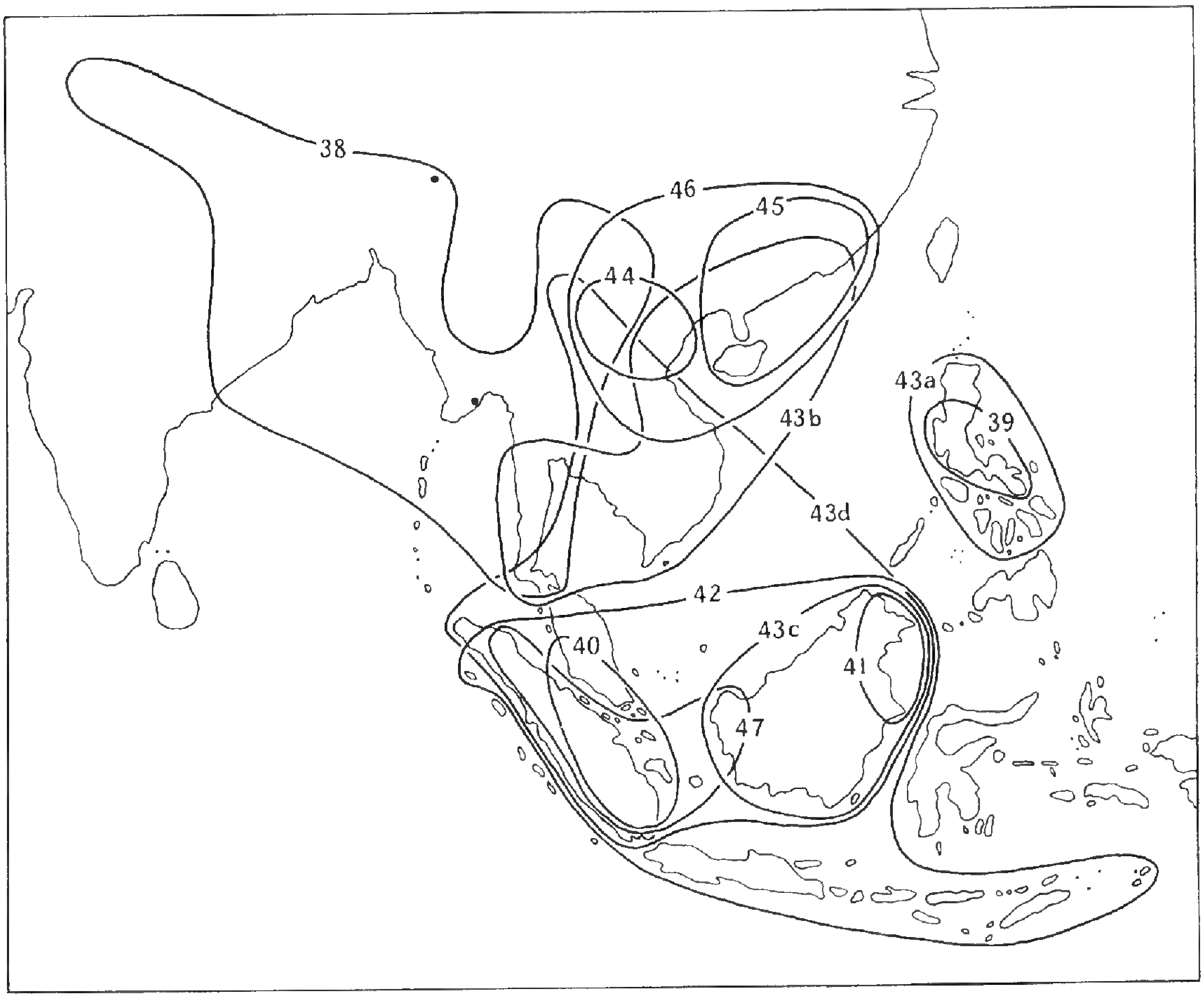


FIG. 19. Distribution of some species of subg. PSEUDOJACA. 38, *Artocarpus lakoocha*; 39, *A. rubrovenius*; 40, *A. fulvicortex*; 41, *A. tomentosulus*; 42, *A. glaucus*; 43, *A. nitidus*, a, ssp. *nitidus*, b, ssp. *lingnanensis*, c, ssp. *humilis* and ssp. *borneensis*, d, ssp. *griffithii*, dots, records not identified to subspecies; 44, *A. petelotii*; 45, *A. hypargyreus*; 46, *A. styracifolius*; 47, *A. altissimus*.

only those which were based primarily on *A. gomezianus* ssp. *zeylanicus* are cited under the latter.

Finally, the area of *Artocarpus lakoocha* must be extended eastward through Siam to Indochina, and to Yunnan from which it has been described twice without reference to Roxburgh. Most of the Indochinese collections were made after Gagnepain wrote up the Moraceae for the "Flore Générale de L'Indochine" (1928), and he did not mention *A. lakoocha*. The distinctions between this species and *A. tonkinensis* are given above, under the latter entity.

39. **Artocarpus rubrovenius** Warb. in Perkins, Frag. Fl. Philip. 166. 1905, *"rubrovenia"*; Merr. Philip. Jour. Sci. 1, Suppl. 43, 1906, Enum. Philip. Pl. 2: 43. 1923; Elmer, Leafl. Philip. Bot. 2: 622. 1909; Brown, Useful Pl. Philip. 1: 470. 1941. Holotype, Luzon, *Warburg 12949* (B).

Trees, height to 15 m., bark mottled grey and brown. *Twigs* 2.5–5 mm. thick, appressed-puberulent, soon glabrescent. *Leaves* 11–26 × 5–14 cm., ovate to elliptic, with an acumen to 2.5 cm. long, base broadly rounded to broadly cuneate, often oblique, glabrous, margin entire; main veins prominent beneath, intercostals slightly so; lateral veins 8–13 pairs, curved; intercostals parallel; green with yellowish-white main veins, drying brown or blue-grey above, paler brown beneath, venation reddish or nigrescent in young leaf, straw-coloured when mature; petiole 15–30 mm. long.

Inflorescences solitary or paired in leaf-axils. *At anthesis: male head* 15–45 × 10–20 mm., obovoid to clavate; perianths of 2–4 segments, free or fused at the base, 0.5 mm. long; stamen 0.7 mm. long, filament cylindric, abruptly contracted above, anther-cells ellipsoid, 0.2 mm. long; bracts stoutly stalked, heads peltate, to 0.3 mm. across, these and perianths pubescent; peduncle 1.5–3 × 1.5 mm., velutinous; *female head* with styles exserted to 0.5–0.8 mm. through papillae emerging between peltate bracts. *Syncarp* (submature) to 3 cm. across, subglobose or shallowly lobed, drying brown or cinereous, the surface nearly smooth, short-pubescent, with numerous persistent bracts; proximal region of perianths free; peduncle 5–10 × 3 mm., velutinous.

Distribution: in forest to 1200 ft., Luzon (? also in Mindoro).

Philippine Islands. Luzon. *Haencke 433* (NY, ♀). Quezon (Tayabas): Baler, *Merrill 1034* (K, US, ♀), *Quisumbing PNH 2511* (A, PNH, SING, ♀); Casiguran, *Ramos & Edano BS 45226* (BO, NY, ♂); Lagumanoc, *Merrill 2590* (K, US, ♂); Lucban, *Elmer 9128* (A, BO, K, L, ♂), *McGregor BS 47395* (NY, ♀); Sampolor, *Warburg 12949*, Mar. 1888 (B, ♂, ♀). Bataan: *Curran 5439* (US); Lamao River, Mt. Mariveles, *Borden FB 2562* (BO, K, SING, ♀), *2915* (NY, US, ♂), *2498* (BO, K, P, SING, ♂). Pampanga: Camp Stotsenburg, Mt. Pinatubo, *Elmer 22030* (BM, GH, L, ♂, ♀). Rizal: *Ahern FB 3197* (BO, K, SING, US, ♀); Morong district, *Vidal 3832* (K, US, ♀); San Mateo, *Vidal 1548* (A, K, L, ♂). Batangas: *Ramos & Deroy BS 22656* (A, BM, GH, K, L, P, SING, ♂). Camarines: *Alvarez FB 21440* (BM, BO, K, P, ♂, ♀), *Ramos 1517* (BM, BO, GH, L, P, SING, ♂, ♀). Albay: Banao, Guinabatan, *Mendoza PNH 18505* (L, PNH, ♀). Sorsogon: *Curran FB 10524* (K, SING, ♀), *Vidal 3839* (K, ♂); Irosin, *Vidal 3836* (K, ♀); Irosin, Mt. Bulusan, *Elmer 15598* (A, BM, K, L, ♂, ♀), *Sulit PNH 2753* (A, BO, PNH, SING, ♀).

Although, as was pointed out in the discussion of section *Pseudojaca*, *Artocarpus rubrovenius* shows a relationship with *A. lakoocha*, it is readily distinguished by the glabrous leaves lacking a prominent reticulum, and, at anthesis, by the shorter styles. The differences from the other glabrous-leaved members of subgenus *Pseudojaca* that occur in the Philippines, *A. xanthocarpus* and *A. nitidus* ssp. *nitidus*, are given under the latter entity.

Merrill stated in 1923 that *Artocarpus rubrovenius* occurred on Mindoro and Cagayan Sulu, in addition to Luzon. The former record may be based on the two collections cited by Merrill that have not been seen, *Darling FB 14704* and *Merrill 1517*. It is presumed, from the identification on the herbarium sheet, that the latter is based on *Merrill 5304*, although the number was not cited. This collection is here referred to *A. gomezianus* ssp. *gomezianus*.

40. **Artocarpus fulvicortex** Jarrett, sp. nov.

Artocarpus sp., Corner, Wayside Trees, 658, *t. 197*. 1940.

Ramuli juniores puberulentes; folia late elliptica vel subrotunda, nervis lateralibus utrinque 6–10, nervis transversalibus paucis, costa nervis lateralibus venulisque subtus valde prominentibus, pubescentibus, intervenio saepe minute pubescenti; inflorescentiae subsessiles; capitula mascula subglobosa, 4–6 mm. diametro; syncarpia globosa, superficie plana, pubescentia, bracteis persistentibus.

Arbores [ad 35 m. altae], deciduae, cortice nova fulva vel rufi-brunnea. *Ramuli juniores* 4–8 mm. crassi, subrugosi, puberulentes, cortice in sicco mox squamis decidua; [ramuli juveniles pubescentes]. *Folia* c. 15 × 10 [10–20 × 7–14] cm., late elliptica vel subrotunda, obtusa vel breviter acuminata, basi cuneata [vel rotunda], integra, supra subglabra, costa nervis lateralibusque pubescentibus exceptis, subtus costa nervis lateralibus venulisque valde prominentibus, pubescentibus, pilis rufis, interdum sparsis, intervenio minute pubescenti vel puberulenti, [foliis juvenilibus subglabro], supra saturata viridia, subtus subglauca, in sicco utrinque rufi-brunnea vel caesia; nervi laterales utrinque 7 [6–10], curvati; nervi transversales pauci, paralleli vel reticulati; petiolus 20 [15–25] mm. longus.

Inflorescentiae axillis foliorum solitariae vel geminae. *Ad anthesin: capitula mascula* 4–7 × 4–6 mm., globosa vel obovoidea; perianthia profunde bifida, 0.7 mm. longa, breviter ciliata; stamina 0.8 mm. longa, filamentis supra attenuatis, cellis antherum ellipsoideis, 0.15 mm. longis; bracteae crasse stipitatae, capitibus peltatis, ad 0.5 mm. latis, breviter ciliatis; pedunculus 0.5–1.5 × 1 mm., breviter pubescens; *capitula feminea* stylis inter bracteas peltatas crebras 0.5 mm. exsertis. [*Syncarpia* ad 5 cm. diametro, globosa, fulva, carne lutea, in sicco rufi-brunnea, superficie plana, pubescenti, bracteis numerosis persistentibus, inconspicuis, in indumento immersis; stratum externum syncarpii c. 5 mm. crassum; "semina" (endocarpia cornea) plura, obovoidea, 10 × 5 mm., perianthiis omnino conjunctis inclusa; axis syncarpii c. 15 mm. diametro; pedunculus 4 × 4 mm., breviter pubescens.] (Inflorescentiae typi anthesin atque syncarpium maturum (*Corner SFN 34663*) ab eadem arbore collectum omnes spiritu vini conservae descriptae.)

Holotype: Malaya, *Corner SFN 33686* (SING).

Distribution: in lowland evergreen forest to 250 ft.; Malaya, Sumatra, Banka.

Malaya. Perak. Batu Gajah, *Corner*, Aug. 1936 (SING); Slim River, *Corner*, Aug. 1937 (SING). Pahang. Kemansul For. Res., *Symington KEP 49822* (KEP). Negri Sembilan. Seremban, *Walton KEP 63363* (KEP, ♀). Malacca. *Maingay 1485* (K). Singapore. *Cantley* (SING); Cluny Road, *Ridley 4829* (BM, CAL, SING, ♀); Chanchu Kang, *Ridley 4129* (K, SING, ♂, ♀); Krangi, *Goodenough 3379* (CAL, SING); ne. end of MacRitchie Reservoir, *Sinclair SFN 38916* (SING, L, ♂); Reservoir Jungle, *Corner*, Jan. 1937 (SING). **Sumatra.** Palembang. Banjuasin, Bentajan, *NIFS T 1030* (BO); Lematang Ilir, Gunong Megang, *NIFS T 364* (BO, L, ♂), *592* (BO, L, U, ♂, ♀). LAMPONGS. Kotabumi, *bb 35005* (BO); Tulang Bawang Ilir, Bandjar Agung, *bb 8951* (BO). BANKA. Blinju, *Grashoff 20* (BO, L); Koba, *Teysmann HB 7242* (BO, C, CAL, K, L); Muntok, Batu Balai, *Teysmann HB 6843* (BO, CAL, K, L, P). **Cultivated.** MALAYA. Singapore, Hort. Bot. (all from tree in potting yard), *Corner SFN 33686*, Sept. 1937 (SING, ♂, ♀), *34501*, *34663* (SING, ♀), *Merah SFN 33549* (SING).

This species was described as *Artocarpus* sp., "Orange-barked *Tampang*," in 1940 by Corner, who stated (p. 650) that the bark colour was distinctive, since it was grey or brown in other Malayan species of the genus. The broadly elliptic or subrotund leaves, with few lateral veins and a markedly prominent reticulum on the lower surface, have a characteristic appearance which enables this species to be identified readily when sterile. However, no previous description under a scientific name has been found, and specimens have been identified as either *A. lakoocha* or *A. dadah*. *Artocarpus fulvicortex* differs from the latter in the leaf characters given above, and also in the very short peduncles of the inflorescences, the numerous bracts persisting on the syncarp and the nearly glabrous young twigs.

41. **Artocarpus tomentosulus** Jarrett, sp. nov.

Differt ab *A. fulvicortice* foliis ellipticis, elliptici- vel ovati-oblongis, nervis lateralibus utrinque 10–14, nervis transversalibus plurimis, syncarpio pedunculo 25 mm. longo.

Arbores ad 20 m. altae. *Ramuli juniores* 2.5–4.5 mm. crassi, rugosi, puberulentes. *Folia* c. 18 × 10 [11–23 × 6–12] cm. elliptica ad elliptici- vel ovati-oblonga, acuminata [acumine ad 2 cm. longo], basi rotunda [vel late cuneata], integra, supra glabra, costa nervis lateralibusque pubescentibus exceptis, subtus costa nervis lateralibus venulisque prominentibus, pubescentibus, intervenio minute tomentoso [vel glabro], in sicco supra pallidi- vel rufi-brunnea, subtus pallidi-brunnea; nervi laterales utrinque c. 12 [10–14], curvati; nervi transversales plurimi, paralleli; petiolus 15[–45] mm. longus.

Inflorescentiae axillis foliorum solitariae. [*Capitula mascula* (immatura) ad 7 mm. diametro, globosa; perianthia tubulosa, 0.6 mm. longa, supra bilobata, minute pubescentia; stamina (nondum exserta) cellis antherum ellipsoideis, 0.15 mm. longis; bracteae tenuiter stipitatae, capitibus peltatis, ad 0.4 mm. latis, minute pubescentibus; pedunculus c. 2 × 2 mm., brevissime pubescens.] *Syncarpium* (submaturum) 3 cm. diametro, subglobosum, fulvum, in sicco brunneum, superficie parum papillosa, pubescenti, bracteis peltatis plurimis persistentibus; pedunculus 25 × 3.5 mm., breviter pubescens.

HOLOTYPE: British North Borneo, *Keith 7671* (SING).

DISTRIBUTION: in forest to 2000 ft.; endemic to northeastern Borneo.

Borneo. EAST AND NORTHEAST BORNEO. Berouw: *bb 18909* (A); Bekmuari, *bb 19133* (A, BO, L). Bulungan: Mara, *bb 10806* (BO). BRITISH NORTH BORNEO. Kabili-Sepilok For. Res., *Keith 7671*, Sept. 1937 (SING, ♀); Kalabakan, 30 miles wnw. of Tawau, *Wood SAN A 3684* (A, KEP, L, SING, ♂).

The material of *Artocarpus tomentosulus* is very limited, but the collections are well characterized by the leaves, which have fairly closely set, spreading lateral veins with numerous parallel, rather slender intercostals. The type, *Keith 7671*, bears a submature syncarp, and this specimen and *bb 10806*, which is sterile, have the intervenium minutely tomentose. The remaining collections, *Wood SAN A 3684* (with male inflorescences), *bb 18909* and *bb 19133* (sterile), have a glabrous intervenium. It is possible that the latter are taken from juvenile shoots, since the leaves are somewhat larger than in the previous collections. If these three collections are matched with the other two on the basis of the venation, as seems justifiable, the characters of this species correspond with those of *A. fulvicortex* in the small, subsessile, more or less globose male heads, and in the combination of prominent, patent-pubescent venation on the lower surface of the leaf with a frequently minutely tomentose intervenium, although the syncarp peduncle is considerably longer (25 mm. instead of 4 mm.). These leaf characters are unique in the subgenus; in other species with a tomentose intervenium (*A. glaucus*, *A. hypargyreus* and *A. styracifolius*) the venation is less prominent, and the main veins, at least, are subglabrous. Collections of *A. dadah* from Borneo (which can be distinguished by the narrower leaves and the pubescent twigs) may also appear to have hairs on the intervenium of the leaf, but these are nearly all inserted along the edge of the veins of the reticulum and appressed over the areolae.

42. **Artocarpus glaucus** Blume, Bijdr. 483. 1825, *"glauca"*; Tréc. Ann. Sci. Nat. Bot. III. **8**: 121. 1847; Miq. in Zoll. Syst. Verz. Ind. Archip. **2**: 90, 96. 1854; Miq. Pl. Jungh. 293. 1854, Fl. Ind. Bat. 1(2): 288. 1859, Ann. Mus. Lugd.-Bat. 3: 212. 1867; Koord. & Val. Bijdr. Boomsoort. Java **11**: 26. 1906; Backer, Beknopte Fl. Java **6**: 16. 1948. Neotype, Java, *Zollinger 704* (P).

Artocarpus glaucescens Tréc. Ann. Sci. Nat. Bot. III. **8**: 120. 1847; Miq. in Zoll. Syst. Verz. Ind. Archip. **2**: 90. 1854; Miq. Fl. Ind. Bat. **1**(2): 288. 1859, Ann. Mus. Lugd.-Bat. 3: 212. 1867; Renner, Bot. Jahrb. **39**: 369. 1907. Holotype, Java, *Zollinger 704* (P); isotypes (BM, GH, K, L, P).

Artocarpus zollingeriana Miq. in Zoll. Syst. Verz. Ind. Archip. **2**: 90, 95, 1854; Miq. Fl. Ind. Bat. **1**(2): 289. 1859. Syntypes, Java, *Zollinger 512* (P), Bogor, Hort. Bot., *Zollinger s.n.* (U); lectotype, *Zollinger 512* (P).

Artocarpus biformis Miq. Fl. Ind. Bat. Suppl. 419. 1861. Holotype, Sumatra, *Teysmann HB 4444* (U); isotypes (BO, L).

Artocarpus tephrophylla Miq. Fl. Ind. Bat. Suppl. 422. 1861. Holotype, Sumatra, *Teysmann 4504* (U); isotypes (BO, L).

Artocarpus inaequalis Teysm. & Binnend. Cat. Hort. Bog. 382. 1866, nomen nudum.

Artocarpus glaucescens Tréc. var. *tephrophylla* Miq. Ann. Mus. Lugd.-Bat. **3**: 212. 1867.

Artocarpus denisoniana King in Hook. f. Fl. Brit. Ind. **5**: 544. 1888; King, Ann. Bot. Gard. Calcutta **2**: 14. *t. 8B.* 1889; Ridley, Fl. Malay Penin. **3**: 355. 1924. Syntypes, Malaya, *King 10318, 10843, 10987* (CAL, not seen; duplicates examined, K, etc.).

Artocarpus glaucus Blume var. *villosiusculus* Warb. ex Renner, Bot. Jahrb. **39**: 369. 1907, nomen nudum.

Evergreen trees, height to 40 m., buttressed or not, bark dark grey, peeling. *Twigs* 1.5–4 mm. thick, finely rugose, appressed-puberulent, soon glabrescent. *Leaves* 4–33 × 2–16 cm., elliptic to elliptic-oblong, varying to oblong, obovate, ovate, or ovate-lanceolate, small leaves often rather narrow, acuminate or attenuate, base cuneate, varying to rounded, often slightly unequal and decurrent, margin entire; juvenile leaves lobed; main veins prominent beneath, intercostals slightly so; glabrous above, venation appressed-puberulent beneath, glabrescent, intervenium minutely tomentose (juvenile leaves subglabrous to short-pubescent beneath); lateral veins 8–15 pairs, curved; intercostals parallel; old leaves becoming bullate above between venation; glossy dark green above, light green to dull grey beneath, drying yellowish to bluish grey above, greyish glaucous beneath from the tomentum, young leaves brown with nigrescent main veins; petiole 7–25(–45) mm. long.

Inflorescences solitary or paired in leaf-axils. *At anthesis: male head* 11–24 × 5–6 mm., narrowly oblong or clavate; perianths 2- or 3-lobed, divided nearly to the base, 0.6 mm. long; stamen 0.8 mm. long, filament cylindric, contracted above, anther-cells ellipsoid, 0.2 mm. long; bracts slenderly stalked, heads peltate, to 0.4 mm. across, these and perianths short-ciliate; peduncle 1–3 × 1 mm., velutinous; *female head* with styles exserted to 0.3 mm. through a dense covering of peltate bracts, later through papillae emerging between bracts. *Syncarp* to 3 cm. (fide Koorders & Valeton, 1906, to 7 cm.) across, subglobose, often shallowly lobed, yellow to orange-brown with light-orange flesh, drying dark brown to black, the surface papillate or becoming nearly smooth, short-pubescent, with numerous persistent bracts; wall c. 3 mm. thick; proximal region of perianths free, fruiting perianths several, "seeds" (horny pericarps) ellipsoid, 10 × 7 mm.; core c. 10 mm. across; peduncle 2–5 × 2 mm., velutinous.

VERNACULAR NAME: *tiwu landu* (Sundanese), Java.

DISTRIBUTION: in evergreen forest to 2500 ft., Malaya, Sumatra, Simalur, Banka, Borneo, Java, Lesser Sunda Islands (Sumba, Roma, Tanimbar Islands).

Malaya. KEDAH. Katumbah, *Meh 17874* (K, SING, ♂). PERAK. Ulu Bubong, *King 10161* (A, SING, ♀), *10318*, June 1886 (BM, K, L, ♂, ♀), *10843*, Aug. 1886 (BM, K, ♀), *10987*, 1886 (K, P, SING, ♂, ♀). PAHANG. Bentong, *Ahmad CF 5052* (K, ♂); 3 miles s. of Kuala Lipis, *Burkill & Haniff SFN 17168* (BO, K, SING, ♂, ♀). SELANGOR. Ulu Gombak, *Murdoch 304* (SING, ♂, ♀). JOHORE.

10½ miles Kota Tinggi-Jemalaung road, *Sinclair SFN 40348* (K, L, SING, ♂, ♀).

Sumatra. Tapanuli. Padang Lawas, Hatiran, *Rahmat si Boeea 4883* (A, K, L, ♀), *4920* (A, K, L, ♂). West Coast. Priaman, *Diepenhorst HB 1325* (BO, L, P, U). East Coast. Aer Kandis, near Rantau Parapat, Bila, *Rahmat si Boeea 2467* (A, L, SING, ♂, ♀); Sibolangit, *Docters van Leeuwen-Reijnvaan 12711* (BO, K, L, ♂), *Lörzing 5170* (BO, ♂). Djambi. Danau Lama, *bb 13643* (BO); Simpang, *bb 13115* (BO). Benkulen. Kroi, Gunong Nemala, *bb 8758* (BO); Ranaumeer, Talangtotong, between Simpang and Sepatuhu, *Van Steenis 3378* (BO, ♀). Palembang. Lematang Ilir, Gunong Megang, *NIFS T 886, 891* (BO, L, ♀); Musi Ilir, Muara Punojung, *bb 9202* (BO); Musi Ulu, *Endert 159* (BO). Lampongs. Kalianda, Gunong Kadjabasu, *De Wit 14* (BO); Kalianda, Ketjapi, *bb 8954* (BO, L); Siring Kebou, *Teysmann HB 4504* (BO, L, U); Tarabangi Ilir, *Teysmann HB 4444* (BO, L, U). Simalur. *Achmad 966* (BO, K, L, SING, U, ♂, ♀); Landschap Tapah, Defajan, *Achmad 1405* (BO, L, U, ♂, ♀), *1675* (BO, L, P, ♂), *1721* (BO, L, SING, ♂, ♀). Banka. S. Banka, Rindik, *bb 11585* (BO).

Borneo. Sarawak. Sungei Sama, *Daud & Tachun SFN 35729* (SING, ♀). West Borneo. Ketapang, Riamdadap, *bb 8306* (BO); Sambas, Sai, *bb 7086* (BO, L, ♂). South and southeast Borneo. Bandjarmasin, *Motley 1279* (CGE, K, ♂, ♀); Muara Tewe, Dusun Ulu, Sungei Pararawen, *Dachlan 2411* (L). British North Borneo. *Wood 2159* (BO, ♂, ♀); Beaufort south mile 18, *Wood 2608* (SING, ♂); Tenom, Pangie, *Angian Herb. For. Dept. B.N.B. 10482* (KEP, ♂).

Java. *Hasskarl HB 1869* (L), *De Vriese* (K, L, U), *Zippelius 1332* (*HB 7267*) (BO), *Zollinger 512* (P, ♂), *701* (K), *s.n.* (K, L, P, U). West Java. Bantam: Gunong Kantjana, *Koorders 41644* (BO); Gunong Mung, Gunong Karang, Pulasari, *Koorders 40118* (BO, L); Tapos, *Teysmann HB 7268* (BO); Tjibadui, Kosala, *Forbes 450* (BM, BO, CAL, SING, ♂, ♀); Tjikoja, *Zollinger 704* (BM, GH, K, L, P, ♂), *706* (U); Tjimara-Udjong Kulon, Gunong Marang, *Koorders 8672* (BO, L, P); Tjimara-Udjong Kulon, Gunong Rompang, *Koorders 8671* (A, BO, L, P) *9932* (BO). Buitenzorg: Leeuwiliang, Pasir Honje, *Bakh. van den Brink 6953* (BO, K, L, P, SING, U, ♂); Nangala, *Bakh. van den Brink 7629* (BO, L, ♀); Nangala, Gunong Menteng, *Bakh. van den Brink 7717* (BO, K, L); Nangala, Gunong Tjiputih, *Bakh. van den Brink 7726* (BO, K, L, P, U, ♂, ♀); Nangala, Tjilankop near Tjiputih, *Bakh. van den Brink 7719* (BO); Tjibinong, *NIFS Ja 2702* (BO, ♀). Preanger: Sukabumi, Tjisahong, Tjisalak, *Koorders 39445* (BO, K, L, P, ♀); Njalidung, *Uhl 6555* (BO, ♀). Central Java. Banjumas: Bandjarnegara, Pagedongan, *NIFS Ja 2549* (A, BO); Bandjarnegara, Pringombo, *Koorders 8673* (BO, L), *33881* (BO), *39184* (BO, K, L), *39194* (BO, L, P). Pekalongan: Subah, Pesan, *Koorders 27594* (BO, L, P, ♀). Semarang: Ungaran, Telomojo, *Koorders 39234* (A, BO, K). East Java. Pasuran: Tangkil Zuidergebergte, *Koorders 23784* (BO).

Lesser Sunda Islands. Sumba. E. Sumba, Djuli, *bb 15133* (BO). Roma. Hila, *bb 7219* (BO). Tanimbar Islands. P. Jamdena, between Kampong Ilgnei and Otimmer, *Buwalda 4131* (K, L, ♂, ♀) = *bb 24224* (A, BO, L, SING, ♀). **Cultivated.** Java. Bogor, Hort. Bot., *Teysmann HB 7274* (BO, P, ♀), *s.n.*, 1867 (BM, L, ♀), *Zollinger* (U).

No collections determined as *Artocarpus glaucus* by Blume himself have been found, but the description is clearly identifiable. The glaucous lower surface of the leaf distinguishes this species from any other member of the genus growing in Java, and, with the elongate, subsessile male head, from the rest of subgenus *Pseudojaca*. The leaves vary considerably, but continuously, in shape from tree to tree, and they also become markedly coriaceous with age. Several specimens bear what appear to be galled shoots. These are short and highly branched, and bear many inflorescences, which are usually male, but are abnormally shaped. The heads are obovoid with peduncles to 5 mm. in length, and the flowers are often malformed.

43. **Artocarpus nitidus** Tréc. Ann. Sci. Nat. Bot. III. **8**: 119. 1847.

Evergreen trees, height to 35 m., buttressed or not, bark red-brown. *Twigs* 1–4 mm. thick, smooth or finely rugose, appressed-puberulent, soon glabrescent. *Leaves* 3.5–23 × 1.5–9 cm., elliptic, obovate- or oblong-elliptic, to obovate- or ovate-oblong, obtuse to attenuate or with an acumen to 2.5 cm. long, base cuneate or rounded, margin entire; main veins prominent beneath, intercostals slightly so; glabrous, or puberulent beneath on the main veins (rarely throughout in ssp. *lingnanensis*); lateral veins 5–15 pairs, straight or curved; intercostals few, usually parallel; dark green above, paler or yellowish green beneath; petiole 5–15(–25) mm. long.

Inflorescences solitary or paired in leaf-axils. *At anthesis: male head* 3.5–12 × 2.5–7 mm., oblong, obovoid or clavate; perianths of 2–4 segments free or fused at the base, 0.5–0.7 mm. long; stamen 0.8–1 mm. long, filament broad, tapering or contracted above, anther-cells short-ellipsoid, 0.2 mm. long; bracts slenderly stalked, heads peltate, to 0.4 mm. across, these and perianths ciliate; peduncle 1–3 × 1 mm.; *female head* with the styles exserted to 0.5 mm. through a covering of peltate bracts, or through perforations or low papillae, the bracts scattered. *Syncarp* 1.5–6 cm. across, subglobose, the surface smooth, with scattered persistent bracts, the indumentum various; wall 1–5 mm. thick; proximal region of perianths free, fruiting perianths 1–12, thin-walled, "seeds" (pericarps with a horny endocarp), subglobose to ovoid, 8–10 × 7–8 mm.; core 5–8 mm. across; peduncle 1.5–4(–20) × 1.5–3 mm.

DISTRIBUTION: in forest or savannah to 5000 ft.; Assam, Burma, Siam, Indochina, southern China, Malaya, Sumatra, Borneo, northern and central Philippines.

Four taxa which have previously been recognized as species (with several additional synonyms) are here reduced to subspecific rank under *Artocarpus nitidus*, since they are only separable from this species and from each other on the size and indumentum of the syncarp, and on slight differences in the shape and venation of the leaves. The type subspecies, which occurs in the Philippines, is readily distinguished by the very small, few-seeded, velutinous syncarp. The two subspecies placed following this, ssp. *lingnanensis*, which extends from southern China to peninsular Siam, and ssp. *humilis*, which is restricted to Borneo, appear to be very closely allied to each other. They have larger, also velutinous syncarps, and are distinguished only by minor, but characteristic, differences in the leaves. However, in view of the variation found in the length of the female peduncle in ssp. *humilis* (discussed under the subspecies), it seems best to retain them as distinct taxa of equal rank for the present. The remaining subspecies, which usually have more numerous lateral veins in the leaves than the three preceding entities, are ssp. *borneensis*, from Borneo, and ssp. *griffithii*, extending from Yunnan and Indochina to Sumatra and Borneo. They are likewise very closely related, differing only in the indumentum of the syncarp. In ssp. *borneensis* the surface is densely covered by minute hairs with readily deciduous, multicellular, clavate heads which, when fallen, often form a reddish powder around the dried syncarp. These hairs are presumably equivalent to the gland-hairs occurring generally within *Artocarpus*, although in subg. *Pseudojaca* the heads of the latter are usually unicellular. In ssp. *griffithii*, on the other hand, the syncarp is almost entirely glabrous.

The occurrence of three subspecies in Borneo has led to difficulties in identification which are increased by the finding of specimens, all bearing very small, elliptic, long-acuminate leaves, which are referable on the characters of the syncarp to all three entities. Larger-leaved collections of ssp. *humilis*, lacking or bearing only male inflorescences, can be distinguished on vegetative characters, but no such characters have been found that would separate ssp. *borneensis* and ssp. *griffithii*. Collections from Borneo which lack syncarps and which are referable to one or other of these subspecies, are listed separately under ssp. *borneensis*. There are, in addition, a few male or sterile collections from Borneo and elsewhere that could not be identified to subspecies and have not been cited. On the evidence of specimens bearing syncarps (none seen from western Borneo), ssp. *borneensis* is relatively common in British North Borneo, whereas ssp. *griffithii* is absent there, though widely distributed outside Borneo. The provenance of the small-leaved collections appears to be variable, since Corner noted for ssp. *griffithii* (Wayside Trees, 654. 1940, as *A. gomezianus*) that such specimens came from the crowns of large trees, whereas Beccari derived the specific epithet for *A. humilis*, of which the type has small leaves, from its being a small tree.

Three collections referable to *Artocarpus nitidus* have been seen from Burma and Assam, but they bear only male inflorescences and, from the shape of the leaves, might represent either ssp. *lingnanensis* or ssp. *griffithii*. They are: *Dickason 6938, 6981*, Rangoon (A, ♂); *Kanjilal 4145*, Makum Range, Barjan, Lakhimpur (K, ♂). A collection from the Lushai Hills, *Sen Gupta 7643*, is cited by Kanjilal *et al.*, Fl. Assam **4**: 269. 1940, as *A. gomeziana* Wall. var. *griffithii* King (= ssp. *griffithii*).

KEY TO THE SUBSPECIES OF ARTOCARPUS NITIDUS

1. Syncarp to 1.5(–3) cm. across, velutinous, seeds 1–3(–6). . . . . . ssp. *nitidus*.
1. Syncarp larger, seeds more numerous.
    2. Syncarp velutinous; larger leaves with 5–11 pairs lateral veins.

3. Leaves obtuse to shortly and bluntly acuminate. . . ssp. *lingnanensis.*
3. Leaves with an acumen to 2.5 cm. long, lateral veins often markedly ascending . . . . ssp. *humilis.*
2. Syncarp not velutinous; larger leaves with 8–15 pairs lateral veins.
4. Syncarp covered by readily deciduous, clavate hairs. . . ssp. *borneensis.*
4. Syncarp subglabrous. . . . . ssp. *griffithii.*

ssp. **nitidus**

Artocarpus nitidus Tréc. Ann. Sci. Nat. Bot. III. **8:** 119. 1847, "*nitida*"; Miq. Fl. Ind. Bat. **1**(2): 288. 1859; Fern.-Villar, Noviss. App. 203. 1880; Vidal, Revis. Pl. Vasc. Filip. 254. 1886; Renner, Bot. Jahrb. **39:** 368. 1907; Elmer, Leafl. Philip. Bot. **2:** 624. 1909. Syntypes, Luzon, *Cuming 1078, 1081* (P); lectotype, *Cuming 1078* (P).

Artocarpus lanceolata Tréc. Ann. Sci. Nat. Bot. III. **8:** 121. 1847; Miq. Fl. Ind. Bat. 1(2): 288. 1859; Fern-Villar, Noviss. App. 203. 1880; Vidal, Revis. Vasc. Pl. Filip. 255. 1886; Elmer, Leafl. Philip. Bot. **2:** 624. 1909. Holotype, Luzon, *Callery 60* (P); isotype (P).

Artocarpus lamellosa auct. non Blanco, Merr. Publ. Gov. Lab. Manila **27:** 80. 1905, Sp. Blancoanae, 124. 1918, Enum. Philip. Pl. **2:** 41. 1923.

Leaves 4–13 × 2–5.5 cm., obovate-oblong, with an acumen to 1.5 cm. long, base rounded, varying broadly cuneate, margin entire; juvenile leaves to 16 × 7.5 cm., denticulate towards the apex; lateral veins 6–9 pairs, curved; drying brown to blue-grey above, brownish or greenish below, the venation often straw-coloured, reddish in some young leaves. *Male head* 6–10 × 3 mm., oblong or clavate; peduncle 1–2 × 1 mm., velutinous. *Syncarp* to 1.5(–3) cm. across, drying light brown or cinereous, short-pubescent; seeds 1–3(–6); peduncle 2(–6) × 1.5 mm., velutinous.

DISTRIBUTION: in forest to 500 ft.; northern and central Philippine Islands.

Philippine Islands. LUZON. Ilocos Norte: Burgos, *Ramos BS 27283* (A, BO, P, ♂). Abra: *Valera PNH 13846* (A, PNH, ♀). Pangasinan: *Lopez FB 24217* (A, ♂, ♀), *Medina FB 13503* (US, ♂). Rizal: Calawan, *Callery 60*, 1840 (P, ♂). Cavite: Maragondong, *Merrill 4167* (BM, L, P, US, ♂). Batangas: *Merrill SB 100* (A, BM, BO, GH, K, L, P, ♂, ♀); Lobo, *Vidal 1540* (A, K, L, ♂, ♀). Laguna: Mt. Makiling, *Canicosa PNH 9802* (A, PNH, ♂), *Elmer 18279* (A, BM, K, L, ♂, ♀), *Sulit PNH 16923* (PNH). Albay: *Cuming 1078* (BM, CGE, K, L, P, SING, ♂), *1081* (BM, CGE, K, L, P, SING, ♂, ♀). TABLAS. *Cortes & Rendal FB 17845* (K, US, ♂, ♀). CEBU. *Lopez & Reyes FB 27333* (SING), *Ramos BS 11022* (BM, K, ♂). PANAY. Miagao, Ilo-ilo, *Vidal 3834* (A, K, ♂, ♀). GUIMARAS. *Sulit PNH 11697* (A, L, PNH, ♂, ♀); Buenavista, Bo. Salvacion, So. Lande, *Sulit PNH 11832* (A, L, ♂, ♀).

Artocarpus nitidus was reduced by Merrill in 1905 to the earlier *A. lamellosa* Blanco which has, since then, been accepted as the correct name for the species (in the restricted sense of *ssp. nitidus*). In making this identification Merrill was following Fernandez-Villar, who in 1880 had also regarded the two species as synonymous, although he retained Trécul's name. However, while Blanco's description undoubtedly refers to one of the three glabrous-leaved members of subg. *Pseudojaca* that occur in the Philippines, it does not agree with the entity under consideration. *Artocarpus lamellosa* was described as having a fruit the size of a hen's egg, which was full of seeds, whereas in *A. nitidus* ssp. *nitidus* the syncarp does not usually exceed 1.5 cm. in diameter or have more than three seeds. The account could apply to either of the two other species, *A. xanthocarpus* Merr. (1904) or *A. rubrovenius* Warb. (1905), but no characters are given that would differentiate between them. In view of the long-standing misidentification it seems best, therefore, to reject *A. lamellosa* as a *nomen dubium*.

Artocarpus nitidus ssp. *nitidus* has frequently been confused with *A. xanthocarpus*, but the latter is distinguished by the globose to obovoid, rather than oblong or clavate male head (3–6 × 3–4 mm. *vs.* 6–10 × 3 mm.), by the longer styles (exserted to 0.8–1 mm. *vs.* 0.5 mm.), and by the larger syncarp (to 5 cm. *vs.* 1.5(–3) cm. across) with a longer peduncle (6–11 mm. *vs.* 2(–6) mm.) and several (instead of 1–3(–6)) seeds. In *Artocarpus nitidus* ssp. *nitidus* the leaves are usually obovate-oblong with a rounded base, and dry (when mature) blue-grey above and light brown beneath; in *A. xanthocarpus* the leaves are longer and narrower in outline, with a cuneate or sometimes narrowly rounded base, and they dry brown or greenish on both surfaces. Merrill, in 1923, reduced *A. xanthocarpus* to *A. lanceolata* Tréc. but examination of Trécul's type has shown that it is merely a collection of *A. nitidus* ssp. *nitidus* with rather narrow leaves, the male inflorescences being characteristic of the latter entity. *Artocarpus rubrovenius* can be distinguished from both these taxa by the larger male inflorescences and leaves, the latter often having a broadly rounded and oblique base.

The specimen *Borden FB 2946* (BO, SING), which Merrill cited in his enumeration of the flora of the Lamao Forest Reserve (Philip. Jour. Sci. 1, Suppl. 43. 1906) under *A. lanceolata* (as a species distinct from *A. nitidus* and *A. xanthocarpus*) must be referred to *Antiaris toxicaria* Lesch. Elmer (1909) cited under *A. lanceolata*, with some doubt, *Borden 1145* from the same locality, but, unless this is the field number of the same collection, no specimens have been seen in the course of this study.

ssp. **lingnanensis** (Merr.) Jarrett, stat. nov.

Artocarpus parva Gagnep. Bull. Soc. Bot. Fr. **73**: 89. 1926; Gagnep. in Lecomte, Fl. Gén. Indoch. **5**: 735. *fig. 90.* 1928. Syntypes, Tonkin (cultivated), *Balansa 740, 4112, 4544, Bon 412, 466, Fleury 37765* (P); lectotype, *Balansa 4112* (P).

Artocarpus sampor Gagnep. Bull. Soc. Bot. Fr. **73**: 90. 1926, excl. syncarp.; Gagnep. in Lecomte, Fl. Gén. Indoch. **5**: 738. 1928. Syntypes, Cambodia, *Chevalier 31915, 36953, Fleury 30049*, Cochinchina, *Pierre 1637* (excl. syncarp), Annam, *Poilane 6879*, Siam (cultivated), *Thorel 2784* (P); lectotype, *Poilane 6879* (P).

Artocarpus lingnanensis Merr. Lingnan Sci. Jour. **7**: 302. 1931, **13**: 56. 1934. Syntypes, Kwangtung (cultivated), *McClure 13471* (UC, not seen; duplicates examined, K, P), Honam Island, *McClure s.n.*, Sept. 1924 (UC, not seen).

Leaves 6–14 × 3.5–8 cm., elliptic to oblong- or obovate-elliptic, the outline often somewhat irregular, obtuse or shortly and obtusely acuminate, base rounded or cuneate, usually slightly decurrent, margin entire or shallowly and irregularly crenate; lateral veins 6–10 pairs, straight or curved; drying brown or grey, venation concolorous or, in young leaves, nigrescent. *Male head* 4–12 × 3–4 mm., obovoid, varying oblong; peduncle 1–1.5 × 1 mm., velutinous. *Syncarp* to 5 cm. across, red with pink flesh, drying brown, velutinous; seeds c. 5–12; peduncle 1.5–3 × 2 mm., velutinous.

VERNACULAR NAMES: *ma hat*, Siam; *sampor*, Cambodia; *cay chay*, Annam; *hung kwai muk*, *kwai muk*, southern China. USES: planted for the edible fruit; the bark and roots are also added to betel.

DISTRIBUTION: in evergreen and mixed forest, and in savannah, to 3000 ft.; Siam, Indochina, southern China (Kwangtung, Hainan); cultivated, especially in Tonkin.

Siam. Chantaburi, Klung, *Kerr 17956* (BM, ♀); Chantaburi, Ma Kaun Kaim, *Kerr 493* (BM, ♂); Kao Ngon, Loi, *Kerr 8795* (BM, ♂); Ko Chang, *Schmidt 129* (C); Sriracha, *Collins 892* (US, ♀). PENINSULAR SIAM. Krabi, Tambon Kao Panom, *Kerr 18647* (BM, ♀); Satul, Kuan Po, *Kerr 13809* (BM, ♂); Surat, Tha Chang, *Ratn 2373* (CGE, ♂). **Indochina.** CAMBODIA. *Béjeaud* (P, ♀). Kompong Chnang Prov.: near Kompong Chnang, *Chevalier 31915*, Mar. 1914 (P, ♀); Kralanh For. Res., *Fleury 30049*, Mar. 1914 (P, ♀); Prey Chang Ka Tamau, *Chevalier 36953*, Jan. 1918 (P, ♂, ♀); Prey Phum Laung, *Chevalier 36903* (P, ♂). Stung Treng Prov.: between Pra Pranap and Chéom Khsan, *Poilane 14881* (P, ♂). COCHINCHINA. Bien Hoa Prov.: Song Lu, *Pierre 1637*, Mar. 1877 (K, P, US, all with fruit of *A. gomezianus* ssp. *gomezianus* [A, sterile twig of *A. gomezianus*]). ANNAM. Kontum Prov.: between Zakha and Dakto, *Poilane 32307* (P, ♂). Nhatrang Prov.: peninsula of Nui Han Heo, *Poilane 6879*, June 1923 (A, P, ♀); near Pham Rang, *d'Alleizette*, June 1919 (P, ♀). TONKIN. Phu Tho Prov.: Trung-Giap For. Res., *Fleury 37615* (P, ♀).

China. KWANGTUNG. Near Canton, *Levine 2807* (A, ♂), *2124* (A, GH, K, ♀); Chung Shan Ooi T'ung, *Fung Hom 68* (NY, ♀); Heungshan, *Chun 1* (NY); Honam Island, *Levine 1009* (A, GH, US, abnormal infl.). HAINAN. *Wang 32813* (A, NY, P, ♀); Ch'ang-kiang district, Ue Lung Ling, *Lau 1349* (A, BM, P, ♂); Kan-en district, Chim Fung Ling, *Lau 3385* (A, P, ♂), *5644* (A, ♀); Kaingchow, *Henry 8255* (K, P, ♀); Lokwui, *How 72283* (A, ♀); Man Ch'eung district, *McClure 20016* (K, ♂); near Manning, *How 71529* (A, SING, ♂); Ngai district, Ko Leng, *Lau 566* (A, BM, K, P, US, ♀); Yiachow, *Liang 62103* (A, NY, P, US, ♀).

Cultivated. SIAM. Ubon, Kemmarat, *Thorel 2784*, 1866–1868 (A, P, ♂). INDOCHINA. Cochinchina: Saigon, Hort. Bot., *Pierre 18* (P), *Ciep 553* (P, ♀). Annam: Haut Douai Prov., Laonan, *Poilane 23405* (P, ♂), near Tourane, *Clemens 3369*, *3988* (A, ♀). Tonkin: Hanoi and vicinity, *d'Alleizette*, May 1908 (L), *Balansa 740*, July 1885 (P, abnormal infl.), *4112*, May 1889 (P, ♂), *4544* (P, ♀), *Fleury 37765*, Apr. 1918 (P, ♂); Ninh-binh Prov., Ton Dac, *Bon 412* (P, ♂), Ninh-binh Prov., Yen Moi, *Bon 466*, May 1881 (P, ♂); Quang Yen Prov., region of Yen Lap, *Chevalier 37584* (P, ♂). CHINA. Kwangtung: Canton Christian College Campus, *Kwok Yan 9973* (NY, ♀), *McClure 13471*, May 1925 (K, P, ♀), *To Kang Ping 11178* (NY, US, ♀), *13898* (A, BM, K, L, P, US, ♀).

Of the three synonyms available to provide an epithet for this subspecies of *Artocarpus nitidus* it seems desirable to choose *A. lingnanensis*, which was described by Merrill in 1931. The two species, *A. parva* and *A. sampor*, that were published simultaneously by Gagnepain in 1926, had somewhat confused descriptions and the second of the species was, furthermore, based on mixed material.

One of the syntypes of *Artocarpus parva, Balansa 740*, bears an abnormal inflorescence with free, tubular perianths, which measures 10 × 8 mm. This corresponds to the maximum size given by Gagnepain for the male head and is apparently the source of the difference from the measurements given above (4–12 × 3–4 mm.). He was also in error in describing and drawing the male perianths as tubular and shortly 4-lobed; in the collection he examined (shown by the sketch attached to the sheet), and in others, the perianths have been found to consist of free segments.

The description of the syncarp of *Artocarpus sampor* was based on *Pierre 1637*, which consists at Paris, Kew, and Washington of a sterile shoot of *A. nitidus* ssp. *lingnanensis* and a detached syncarp, about 7.5 cm. in diameter with a peduncle 3.5 cm. long, which agrees in its characters with *A. gomezianus* ssp. *gomezianus*. It was presumably the large size of the latter that misled Gagnepain into describing a female head of ssp. *lingnanensis* at anthesis as the male inflorescence (shown by a drawing attached to *Fleury 30049*), and thus into stating that the male head was globose and 10 mm. in diameter.

ssp. **humilis** (Becc.) Jarrett, stat. nov.

Artocarpus humilis Becc. For. Borneo, 629. 1902; Renner, Bot. Jahrb. **39**: 369. 1907. Holotype, Sarawak, *Beccari PB 3128* (FI); isotypes (FI, K, P).

Leaves 6–18 × 1.5–8 cm., elliptic, varying obovate-elliptic, with an acumen to 2.5 cm. long, base cuneate, margin entire; lateral veins 5–9 pairs, curved, ascending; drying red-brown to pale brown, lighter beneath, venation concolorous or straw-coloured. *Male head* 5–6 × 3–4 mm., obovoid; peduncle 1 × 1 mm., velutinous. *Syncarp* (submature) to 2 cm. across, drying pale brown, short-pubescent; peduncle 2–20 × 3 mm., velutinous.

VERNACULAR NAMES: *selangking*, west Borneo; *betoh, tampang*, south and east Borneo.

DISTRIBUTION: in evergreen forest to 3000 ft.; Borneo.

Borneo. SARAWAK. Batan Lupar, Marop, *Beccari PB 3128*, Mar. 1867 [1866 on label] (FI, K, P, ♂, ♀). WEST BORNEO. Melawi, *bb 27034* (BO, L); Pamangkat, Paloh, *bb 11345* (BO); Pontianak, Batu Ampar, *bb 17421* (A, BO, L, ♀); Simpang, Lubuk Batu, *bb 7333* (BO). SOUTH AND SOUTHEAST BORNEO. Sungei Malohapan, Buntok, *Lot Obi 2140* (BO, L, ♀). EAST AND NORTHEAST BORNEO. E. Kutei: Loa Djanan, near Samarinda, *Kostermans 6363* (K, L, SING), *9953* (L); Tandjong Banko, near mouth of Mahakam River, *Kostermans 7129* (L, SING, ♀). W. Kutei: near Muara Kamaw, bank of Mahakam River, *Endert*

1704 (A, K, L, ♀). BRITISH NORTH BORNEO. Mt. Kinabalu, Dallas, *Clemens 27571* (BM, K, L, SING, ♀).

As noted in the general discussion of *Artocarpus nitidus*, the length of the peduncle of the female inflorescence in ssp. *humilis* shows considerable variation. In four collections, namely, *Beccari PB 3128* and *Clemens 27571* (at anthesis) and *bb 17421* and *Kostermans 7129* (submature), the peduncles are about 2 mm. long. In two others, *Endert 1704* (at anthesis) and *Lot Obi 2140* (submature), the peduncles are 16–20 mm. long. This variability is not correlated with any other character and, therefore, in view of the rather distinctive appearance of the larger leaves which have markedly curved, ascending veins, all the specimens are at present assigned to a single taxon.

In his description of *Artocarpus humilis,* Beccari stated that the female inflorescence had some unopened male flowers. No such inflorescence has been found on the type collection, the male and female heads being quite normal in appearance, but Beccari was presumably describing one of the abnormal inflorescences quite frequently found in *A. nitidus.*

ssp. **borneensis** (Merr.) Jarrett, stat. nov.

Artocarpus borneensis Merr. Jour. Str. Br. Asiat. Soc. **85:** 165. 1922. Holotype, British North Borneo, *Ramos 1592* (PNH, not seen, photograph in A); isotypes (A, BM, BO, K, L, P, SING).

Leaves 3.5–23 × 1.5–9 cm., elliptic-oblong, varying obovate- or ovate-oblong, attenuate or acuminate, base cuneate or rounded, margin entire; lateral veins 8–15 pairs, curved; drying dark brown to blue-grey above, pale red-brown to greenish beneath, venation concolorous or straw-coloured. *Male head* 3.5–10(–12) × 2.5–7 mm., obovoid or clavate; peduncle 1.5–3 × 2 mm., subappressed-pubescent. *Syncarp* to 6 cm. across, brownish green to purple, drying chestnut- to purple-brown, with a dense indumentum of readily deciduous, clavate, multicellular hairs; peduncle 2–4 × 3 mm., subappressed-pubescent to puberulent.

DISTRIBUTION: in evergreen forest to 5000 ft.; Borneo.

Borneo. SARAWAK. 12 mile Penurision road, *Egon A 0921* (KEP, ♀). EAST AND NORTHEAST BORNEO. Balikpapan: Gunong Beratus, *Kostermans 7365* (K, L, PNH, ♀). W. Kutei: near L. Petah, *Endert 3191* (A, L, SING, ♂, ♀). BRITISH NORTH BORNEO: Mt. Kinabalu, Dallas, *Clemens 26350* (A, BM, BO, K, L, NY, ♀); Mt. Kinabalu, Gurulau Spur, *Clemens 50472* (A, BM, K, L, ♀); Penibukan, *Clemens 31233* (A, BM, K, L, NY), *40504* (BM, K, ♀); near Sandakan, *Ramos 1592* (A, BM, BO, K, L, P, SING, ♀); Sandakan, Batu Lima, *Ramos 1749* (A, BO, K, P, SING, ♂, ♀).

The following collections are referable either to ssp. *borneensis* or to ssp. *griffithii.*

Borneo. SARAWAK. Kuching, Semengoh For. Res., *Herb. Sar. Mus. 7728* (K, L, ♂); Saribas, Pakeo, *Haviland & Hose 3315* (A, BM, K, L, ♂). WEST BORNEO. Ketapang, Muara Kajan, Sungei Kelilo, *bb 7460* (BO); Palo, *Becking 44* (BO).

SOUTH AND SOUTHEAST BORNEO. Martapura, Kalaan, *bb 12054* (BO); Pleihari, Kintap, *bb 7759*, *7761* (BO); Sampit, Sansang, *bb 10538* (BO). EAST AND NORTH-EAST BORNEO. Berouw: Tandjong Redeb, Labanan, *bb 11508* (BO). E. Kutei: Sg. Tiram, *bb 35021* (K, L, abnormal infl.). W. Kutei: Tandjong Isui, *Endert 1954* (K, L).

ssp. **griffithii** (King) Jarrett, comb. et stat. nov.

Artocarpus gomeziana Wall. var. *griffithii* King in Hook. f. Fl. Brit. Ind. **5**: 544. 1888; King, Ann. Bot. Gard. Calcutta **2**: 16. *t. 14B*. 1889. Syntypes, Malaya, *Griffith 4665*, *King 6651*, *7533*, *Scortechini 683* (CAL, not seen; duplicates examined, K, SING, etc.).

Artocarpus eberhardtii Gagnep. Bull. Soc. Bot. Fr. **73**: 87. 1926; Gagnep. in Lecomte, Fl. Gén. Indoch. **5**: 737. 1928. Holotype, Annam, *Eberhardt 3288* (P).

Artocarpus eberhardtii Gagnep. var. *poilanei* Gagnep. Bull. Soc. Bot. Fr. **73**: 87. 1926; Gagnep. in Lecomte, Fl. Gén. Indoch. **5**: 737. 1928. Syntypes, Laos, *Poilane 11777*, *11955* (P); lectotype, *Poilane 11955* (P).

Artocarpus griffithii (King) Merr. Pap. Mich. Acad. I. **24**: 64. 1939.

Artocarpus gomezianus auct. non Tréc., King, Ann. Bot. Gard. Calcutta **2**: 15. 1889, pro parte, quoad *t. 14A* et spec. *King 4189*, *5078*, *7535*, *8838*; Renner, Bot. Jahrb. **39**: 368. 1907; Ridley, Fl. Malay Penin. **3**: 355. 1924; Corner, Wayside Trees, 654, *t. 195*. 1940; Watanabe, Ic. Econ. Pl. S. Asia, 528. 1945.

Artocarpus lanceolata auct. non Tréc., Gagnep. in Lecomte, Fl. Gén. Indoch. **5**: 738. 1928.

Differs from ssp. *borneensis* as follows: *syncarp* orange-pink with bright pink flesh, or yellow, nigrescent on drying, glabrous or with sparse rufous hairs; peduncle 3–5(–15) mm.

VERNACULAR NAME: *tampang* (Malay), Malaya and Sumatra. USES: the syncarp is edible.

DISTRIBUTION: in evergreen forest to 5000 ft.; peninsular Siam, Indochina, Yunnan.

Siam. PENINSULAR SIAM. Kantang, *Haniff & Nur 3298* (SING, ♀); Pattani, Toh Moh, *Kerr 584* (BM, ♂). **Indochina.** CAMBODIA. Kampot Prov.: Cam Chay Mts., near Kampot, *Pierre 4696* (A, BM, K, P, ♀). Pursat Prov.: near Trassay, *Poilane 15094* (P, ♀). ANNAM. Thu Thien Prov.: near Huê, *Eberhardt 3288* (P, ♂). LAOS. Savannaket, *Poilane 11777*, Jan. 1925 (K, P, ♂), *11955*, Feb. 1925 (P, ♂); Tatom, Chieng Kwang, *Kerr 20844* (BM, K, ♂); upper Tchépone and Quangtri River, *Poilane 13524* (A, P, ♀). **China.** YUNNAN. Che-li Hsien, *Wang 78652* (A, ♀); Fo-hai, *Wang 77124* (A, ♂).

Malaya. KEDAH. Katumbah, *Boswell KEP 12581* (KEP, ♀); Kuala Muda, *Ali KEP 73794* (KEP, ♀); Semling, Kedah Peak, *Bell & Haniff*, Mar. 1911 (K, ♂, ♀). PROV. WELLESLEY. *Ridley 12624* (BM, ♀). PERAK. *King 6651*, Sept. 1884 (SING, ♀), *Scortechini 683* (K, SING, ♀), *1837* (K, ♂); 14 miles Bruas, *Hashim KEP 207* (KEP, ♀); Larut, *King 4189* (K, ♀), *5078* (K, P, SING, ♀), *7533*, Apr. 1885 (BM, CGE, K, P, SING, ♀), *7535* (BM, K, SING, ♀); Matang, Jamba, *Wray 2520* (SING, ♀); Taiping Hill, *Haniff SFN 13201*, *Ridley 11393* (K, SING, ♀); Ulu Selangor, *King 8838* (K, L, ♀); Waterfall Hill, *Wray 2073* (SING, ♀). DINDINGS. Bruas, *Murdoch 207* (SING, ♀). KELANTAN. *Walton*

KEP 32682 (KEP). Trengganu. Kemaman, *Corner SFN 30568* (SING, ♀). Pahang. Kuantan: Bukit Belai, Betinbang Chini, *Lambak CF 2716* (K, SING, ♀); Bukit Sembambu, *Soh KEP 15742* (KEP, ♂, ♀). Selangor. Ampang For. Res., *Strugnell KEP 12720* (KEP, ♀); Bukit Kulu, *Goodenough 10535* (CAL, SING, ♀); Kanching, *Symington CF 20192* (SING); Kepong, *Murdoch 314* (BM, ♀); Kepong, Bukit Lagong For. Res., Sungei Kroh, *Sinclair SFN 40120* (KEP, L, ♂); Klang Gate, *Murdoch 94* (BM, ♀); Kuala Lumpur, *Curtis 2386* (BM, SING, ♀); Kuala Lumpur, Carcosa Domain, *Foxworthy 10944* (SING, ♂); Kuala Lumpur, Public Gardens [? planted], *Ahmad CF 3034, 4986* (K, SING. ♂, ♀), *Omar CF 8872* (K, SING, ♀), Kuala Lumpur, Weld Hills For. Res., *Hashim CF 3002* (K, SING, ♀); 20th mile Pahang road, *Ridley 8466* (SING, ♂). Negri Sembilan. Bukit Kaju Arang, *Alvins* (SING); Bukit Payong, *Alvins 772* (SING); Nilai Jindaram Estate, *Shah 65* (K, L, ♂); Tampin, Kuala Pila road, *Nur SFN 2814* (K, ♂); Tampin, Seremban road, *Nur SFN 1414* (K, SING, ♀). Malacca. *Griffith 4662* (K, P, ♀), *4665*, 1845 (GH, K, P, ♂, ♀), *s.n.* (CGE, K, ♂, ♀), *Maingay 1482* (K, ♂, ♀); Brisu, *Derry 551* (P, SING, ♀); Bukit Bruang, *Derry 435* (SING, ♀); Bukit Senggeh, *Goodenough 1835* (BM, SING, ♀); Panchor, *Goodenough 1667* (SING, ♀); Selandar, *Alvins 246* (SING, ♀); Sungei Udang, *Alvins 1* (SING, ♀); 14th mile Sungei Udang For. Res., *Sinclair SFN 40565* (K, SING, ♀); N. Sunklar, *Alvins 58* (SING, ♀). Johore. 7th mile Kota Tinggi-Mawai road, *Corner SFN 21349* (A, BM. BO, K, SING, ♂, ♀). Penang. Government Hill, *Curtis 657*(K, SING, ♂, ♀); Penara Bukit, *Curtis 1201* (K, SING, ♀). Singapore. *Hullett 16* (SING), *Marton 90* (K, ♂); Changi, *Ridley 4832* (SING, ♀).

Sumatra. Atjeh. Gajo Lueus, Penosan, Gunong Gerupal, *bb 22364* (A, BO, L). Tapanuli. Angkola and Sipirok, Panobasan, *bb 25248* (A, BO, L, ♀). West Coast. Mt. Sago near Pajakumbuh, *Meijer 4056a* (L, ♀ and abnormal infls.), *4746* (L, abnormal infls.); Painan, Barung Balantai, *NIFS SWK/I-15* (BO). East Coast. Asahan: Aek Munte, *Rahmat si Boeea 9293* (A, L, ♀); Huta Padang, *Krukoff 4372* (A, BO, NY, SING, ♀); near Lumban Ria, *Rahmat si Boeea 7514, 8042* (A, L, SING, ♀). Palembang. *Praetorius* (L); Banjuasan and Kubustreken, Bajunglintjir, *NIFS T 704* (BO, L, U, ♂, ♀); Lematang Ilir, Gunong Megang, *NIFS T 808* (BO, L, ♀); Muara Dua, Kisau, *bb 9231* (BO).

Borneo. Sarawak. Kuching, 6th mile For. Res., *Herb. Sar. Mus. 9436* (K, L, ♀). East and northeast Borneo. E. Kutei: Samarinda, Loa Djanan region along road to Balikpapan, *Kostermans 10202* (K, ♀).

In describing *Artocarpus gomezianus* var. *griffithii*, on which ssp. *griffithii* is based, King failed to distinguish accurately between the type and his variety, although the latter differs clearly in the shorter petioles and peduncles, the smaller, narrower male head, and the glabrous syncarp. King's description of *A. gomezianus* [ssp. *gomezianus*] was partly based on specimens which should have been referred to the variety and the illustration (*t. 14A*) was drawn from one of these. In consequence the two entities were not distinguished by later authors and Malayan collections of both were identified as *A. gomezianus*. Merrill, in 1939, realized that they should be assigned to two distinct species, and raised var. *griffithii* to specific rank, without, however, noting any affinity between it and *A. borneensis*, described by him in 1922.

Artocarpus nitidus ssp. *griffithii* is considerably more common and widely distributed in Malaya than *Artocarpus gomezianus* ssp. *gomezianus*, and the descriptions under *A. gomezianus* given by Ridley (1924) and Corner (1940) are based solely on ssp. *griffithii*.

Several specimens of ssp. *griffithii* from peninsular Siam, the northern part of Malaya, and Penang have syncarps with rather long peduncles (to 15 mm.), but they otherwise agree well with the rest of the collections assigned to this subspecies. The edible ripe syncarp is described in Malaya as orange-pink with bright pink flesh (fide Corner, 1940, and various field notes), but in Indochina the notes on several collections state that it is yellow. In spite of evidence in this species, as in *A. fretessii*, of some confusion with the male inflorescences, there appears to be a genuine difference in colour. No further information is available concerning the precise distribution of the two variants, but, according to present evidence, the pink form occurs south and the yellow form north of a discontinuity in the distribution of the subspecies between peninsular Siam and Indochina.

Series **Clavati** Jarrett, ser. nov.

Inflorescentiae bracteis interfloralibus clavatis vel spathulatis. *Capitula mascula* cellis antherum 0.3–0.5 mm. longis.

TYPE SPECIES: *Artocarpus hypargyreus* Hance.

44. **Artocarpus petelotii** Gagnep. Bull. Soc. Bot. Fr. **73**: 89. 1926; Gagnep. in Lecomte, Fl. Gén. Indoch. **5**: 739. 1928. Holotype, Tonkin, *Petelot s.n.* (P).

Artocarpus brevisericea C. Y. Wu & W. T. Wang, Acta Phytotax. Sin. **6**: *273. t. 55, fig. 22.* 1957. Holotype, Yunnan, *Exped. Biol. Sino-ross. ad prov. Yunnan 1196* (PE ?, not seen); isotype (A).

Trees, height to 10 m. *Twigs* 3–4 mm. thick, pubescent, hairs white or rufous, patent, straight. *Leaves* 9–23 × 4–9 cm., elliptic to narrowly elliptic, with an acumen to 1.5 cm. long, base cuneate, margin entire or denticulate towards the apex; main veins and reticulum prominent beneath; glabrous above except for the pubescent main veins, venation beneath moderately to thinly pubescent, hairs rufous or colourless, straight; lateral veins 7–11 pairs, curved, ascending; intercostals few, parallel; drying grey-green or dingy brown, paler beneath, venation concolorous or straw-coloured; petiole 13–18 mm. long.

Inflorescences solitary in leaf-axils. *At anthesis: male head* 18–23 × 5–7 mm. (fide Wu & Wang, 1957), narrowly obovoid; perianths of 2 or 3 spathulate, free segments 0.8 mm. long; stamen (not exserted), anther-cells oblong, 0.35 mm. long; bracts stoutly to slenderly stalked, heads spathulate, secund, to 0.7 mm. across, these and perianths densely pubescent; peduncle 5–10 mm. long (fide Wu & Wang, 1957), greyish pubescent; *female head* irregularly rugose and papillate, with the styles exserted to 1.5 mm. through low papillae (2–)3(–4)-fid at the apex, and longer, cylindric papillae projecting to c. 1.5 mm. scattered on the surface between these. *Syncarp* to 3 cm. across, subglobose, shallowly lobed, drying rufous, pubescent, smooth over the lobes, the surface between papillate, the longer papillae mostly broken off; wall c. 2 mm. thick; proximal region of perianths fused above, walls double and separable below, fruiting perianths 1–8(?), slightly fleshy, "seeds" (pericarps with a horny endocarpic layer) ellipsoid, 13 × 10 mm.; core c. 5 mm. across; peduncle 35–40 × 3 mm., pubescent.

DISTRIBUTION: in forest to 6000 ft.; Tonkin and Yunnan.

Indochina. TONKIN. Chapa, *Petelot 6028* (A, P, ♀); [probably Cho-ganh, fide Gagnepain, 1926] *Petelot* (P, ♀). **China.** YUNNAN. Chin-ping, Ho-tou-chai, *Exped. Biol. Sino-ross. 1196*, May 1956 (A, ♂).

The two collections of *Artocarpus petelotii* from Tonkin bear female inflorescences; these are at anthesis on the holotype and mature or nearly so on *Petelot 6028* (collected in 1930). The styles are exserted through low papillae with lobed apices, but between these the surface bears, in addition, numerous larger, irregular papillae. The presence of the latter, and the complete absence of discoid peltate bracts indicates an affinity with the two other species assigned to series *Clavati*, rather than with any member of series *Peltati*, although the leaves are patent-pubescent beneath instead of tomentulose, as in these two species.

The recent collection cited from Yunnan bears male inflorescences and shows a strong vegetative resemblance to the Indochinese specimens, apart from a difference in the colouration when dried, which will be discussed below. This collection was described in 1957 as *Artocarpus brevisericea* by Wu and Wang, who compared it with *A. hypargyreus*, but made no mention of *A. petelotii.* They noted that the interfloral bracts in the male inflorescence differed in shape from the clavate bracts found in *A. hypargyreus*, but described them incorrectly as peltate, and thus presumably regarded them as similar to the bracts of *A. ficifolia* (= *A. lakoocha*), published by Wang in the same paper (A preliminary report on the study of the tropical and subtropical flora of Yunnan I. Acta Phytotax. Sinica **6**: 267–300. *t. 55.* 1957). The heads of the bracts are not, however, discoid and centrally attached, with a ciliate margin, as in *A. lakoocha* and other members of series *Peltati,* but spathulate and secund, with a densely pubescent upper surface. In the smaller, slenderly stalked bracts the shape is easily observable, but it is somewhat obscured by the pubescence in the scattered, larger, stoutly stalked bracts. Thus, in the shape of the interfloral bracts this collection, also, shows an affinity with the other species of series *Clavati,* an affinity which is confirmed by the large size of the anthers (fully developed in the inflorescences on the isotype at the Arnold Arboretum, although not yet exserted).

The three collections resemble each other closely in the shape and venation of the leaves, and in the type and distribution of the indumentum, which consists of patent hairs having a rather broad lumen, especially on the twigs. However, whereas in the isotype of *A. brevisericea* the hairs are colourless or whitish, giving a greyish tinge to the specimen, and the leaves dry grey-green, in the Petelot collections most of the hairs are rufous, though some are colourless, and the leaves dry a dingy brown. The latter colouration is abnormal for this series, since both *A. hypargyreus* and *A. styracifolius* dry grey or grey-green, with a greyish pubescence, and it is perhaps an artifact due to the method of drying.

In view of the vegetative similarity of the three collections except in their colour when dried, and the general agreement of the characters of both the male and the female inflorescences with those of the other members of series *Clavati*, it is assumed that only a single species is represented, and *A. brevisericea* is therefore reduced to *A. petelotii*.

45. **Artocarpus hypargyreus** Hance in Benth. Fl. Hongkong. 325. 1861, "*hypargyrea*"; Chung, Mem. Sci. Soc. China **1**: 33. 1924; Walker, Lingnan Sci. Jour. **6**: 51. 1930; Merr. ibid. **13**: 56. 1934; Lee, For. Bot. China, 444. *t. 125.* 1935; Herklots, Hongkong Countryside, 153. 1951. Holotype, Hongkong, *Hance 4484*, June 1859 (K); isotype (BM).

Evergreen trees, height to 10 m., bark dark purple, peeling off in flakes. *Twigs* 1.5–2 mm. thick, finely rugose, greyish or rufous subappressed-pubescent. *Leaves* 8–17 × 4–8 cm., elliptic to obovate- or oblong-elliptic, acuminate, base cuneate, margin entire; juvenile leaves pinnatifid; main veins and intercostals prominent beneath, reticulum slightly so; glabrous above except for the puberulent midrib, venation beneath appressed-puberulent, glabrescent, intervenium minutely tomentose; lateral veins 7–9 pairs, curved; intercostals parallel or reticulate; dark green above, grey-green or whitish beneath, drying greyish above, greyish glaucous beneath from the tomentum, the main veins nigrescent; petiole 10–20 mm. long.

Inflorescences solitary in leaf-axils. *At anthesis: male head* 15–20 × 10–15 mm., obovoid to clavate; perianths of c. 4 linear or spathulate free segments 1 mm. long; stamen 1.2 mm. long, filament cylindric, anther-cells ellipsoid, 0.3 mm. long; bracts slenderly stalked, heads clavate, to 0.3 mm. across, these and perianths densely and minutely pubescent; peduncle 10–23 × 1 mm., shortly greyish pubescent; *female head* with the surface papillate and the styles exserted to 0.5 mm. through perforations between the papillae. *Syncarp* (submature) to 2 cm. across (the size of an apricot, fide Herklots, 1951), subglobose, yellow or apricot with reddish orange flesh, drying brown, pubescent, nearly smooth, papillae persistent but inconspicuous; proximal region of perianths free, fruiting perianths c. 12 (fide Herklots, 1951); peduncle 35–50 × 2.5 mm., short-pubescent.

VERNACULAR NAMES: *hung kwai muk, kwai muk.*

DISTRIBUTION: in forests and open woods, southern China (Kwangtung, Hainan, Hongkong).

China. KWANGTUNG. Lochang district, Yao Shan, Tau Kung, *Tso 20851* (A, K, P, SING, ♂, ♀); Sin-fung district, Hau T'ong Shan, Fuk Lung Monastery, *Taam 885* (A, ♀); Sin-fung district, Sha Lo Shan, Lo Lo Ha, *Taam 929* (A, ♀); Tapu district, Tai Mo Shan, *Tsang 21182* (A, K, P, ♀). HAINAN. *Ford* (A, ♀); Ching Mai district, Pak Shik Ling, Ku Tung village, *Lei 448* (A, K, L, NY, P, SING, ♂); Taam Chau district, Hung Shek Shan, *Tsang 16850* (A, K, ♂). HONGKONG. *Chun 40037* (NY, ♂), *Hance 4484*, June 1859, and 1878 (BM, K, ♂, ♀), *s.n.* (GH, K, ♂, ♀); Aberdeen New Road, near Little Hongkong, *Chun 7460* (NY, ♀), *Gibbs 7473* (A, ♂); Mt. Gough, *Bodinier 1208* (P, ♀); Pokfoolung stream, *Esquirol 1167* (P, ♂, ♀); Shuitong Road near Peak, *Taam 2259* (A, US, ♂, ♀); Ty-tam-took, *Lamont 696* (BM). **Cultivated.** CHINA. Hongkong, Hort. Bot., *Fond*, July 1880 (K, ♀).

The surface of the syncarp in *Artocarpus hypargyreus* is papillate between the perforations through which the styles are exserted at anthesis. By analogy with the structure of the male inflorescence, it is assumed that in this species, and also in *A. petelotii*, the papillae are formed by the heads of interfloral bracts.

Artocarpus hypargyreus is readily distinguished from *A. styracifolius* when sterile by the broader leaves having a slightly prominent reticulum, and by the stouter, pubescent twigs. It may be noted that the western Malaysian *A. glaucus*, which resembles these two species in having a minute tomentum on the under surface of the leaf, although it is not closely related, can be distinguished by the more numerous lateral veins (8–15 *vs.* 4–9 pairs), in addition to the inflorescence characters. Fernandez-Villar recorded *A. hypargyreus* incorrectly from the Philippines (Noviss. App. 203. 1880).

46. **Artocarpus styracifolius** Pierre, Bull. Soc. Bot. Fr. **52**: 492. 1905, "*styracifolia*"; Gagnep. in Lecomte, Fl. Gén. Indoch. **5**: 733. 1928; Wu & Wang, Acta Phytotax. Sin. **6**: 272. 1957. Holotype, Laos, *Spire 344* (P); isotypes (P).

Artocarpus bicolor Merr. & Chun, Sunyatsenia **1**: 52. 1930; Chun in Hu & Chun, Ic. Pl. Sin. **4**: 6. *t. 156.* 1935, descr. addend.; Merr. Lingnan Sci. Jour. **11**: 41. 1932; McClure, ibid. **13**: 586. 1934. Holotype, Kwangtung, *Wang & Ling 7409* (UC, not seen); isotypes (BM, K, P; K and P both as *Wong 7409*).

Trees, height to 20 m., bark dark grey, rough. *Twigs* 1–1.5 mm. thick, finely rugose, appressed-puberulent, soon glabrescent. *Leaves* 4–11 × 1.5–4 cm., elliptic to obovate-elliptic, with an acumen to 1.5 cm. long, base cuneate and decurrent, margin entire; juvenile leaves pinnatifid; main veins only prominent beneath; glabrous above, main veins appressed-puberulent beneath, glabrescent, intervenium minutely tomentose; lateral veins 4–8 pairs, curved; intercostals few, reticulate; deep green above, pale green or glaucous beneath, drying greyish green above, greyish glaucous beneath from the tomentum, the midrib reddish or nigrescent; petiole 6–12 mm. long.

Inflorescences solitary in leaf-axils. *At anthesis: male head* 6–12 × 4–7 mm., ellipsoid, obovoid or cylindric; perianths 2–3-lobed above, 1.3 mm. long; stamen 2.5 mm. long, filament slender, slightly tapered above, anther-cells oblong, 0.5 mm. long; bracts slenderly stalked, heads clavate, to 0.2 mm. across, these and perianths minutely pubescent; peduncle 5–13 × 1 mm., velutinous; *female head* with numerous flexuous cylindric processes and the styles exserted to 0.5 mm. through perforations in the surface between these. *Syncarp* to 4 cm. across, globose, yellow, drying red-brown, pubescent, bearing numerous flexuous, cylindric processes to c. 5 × 0.5 mm.; wall c. 2 mm. thick; proximal region of perianths fused, fruiting perianths to c. 6, thin-walled, "seeds" (pericarps with a horny endocarpic layer) globose, c. 10 mm. across; core c. 5 mm. across; peduncle (10–)18–25 × 2 mm., velutinous.

DISTRIBUTION: in thickets and forests to 4000 ft., often in dry localities, northern Indochina, southern China.

Indochina. LAOS. Phoutane, *Spire 334* (P, ♀); upper Tchépone, *Poilane 12219* (P, ♂). TONKIN. Pac-si, ne. of Mon-cay, *Tsang 26970* (A, ♀); Tien Yien, *Fleury 37946* (P). **China.** YUNNAN. Si-chour-hsien, Ting-mann, *Feng 12296* (A, ♂, ♀). KWEICHOW. Sanhoa, *Tsiang 6350* (A, K, ♂). KWANGSI. N. Lin Yen, Tsin Lung Shan, *Ching 6950* (A, NY, ♂, ♀); W. Poseh, Bako Shan, *Ching 7654* (A, NY, US, ♂); Sup-man-ta Shan, *Liang 69783* (A, ♂, ♀); Tou Ngok Shan, *Tsang 23151, 23259* (A, P, ♀). KWANGTUNG. Fang Ch'eng district, Kung P'ing Shan, T'aan Faan, *Tsang 26803* (A, ♂); North River, *Wang & Ling* (or *Wong*) *7409*, Nov. 1928 (BM, K, P, ♀); Poon Yue district, *Levine 3158* (A, ♀); Wang Yuen district, Fan Shiu Shan, near Fan Shiu Au, *Lau 2754* (A, ♀); Wang Yuen district, Tsing Wan Shan, near Wong Chuk Island, *Lau 2196* (A, ♂); Ying Tak, *Wang 30010* (BM, ♀). HAINAN. *Liang 62258* (A, ♂, ♀), *65506* (NY); Ah Ping, *Chung & Tso 43998* (A, NY, US, ♂); Dai Land, Dung Ka, *Chun & Tso 43895* (A, K, P, ♀); Hung Mo Tung, *Shing 816* (NY); Po-ting, *How 73288* (A, BM, P, ♂), *73505* (A, BM, P, ♀); Yiachow, *Liang 62258* (K, ♂).

Artocarpus styracifolius is unique among the species of subgenus *Pseudojaca* in that the syncarp is covered by flexuous processes. These have been mistaken by all previous authors for the elongate apices of perianths, but the styles can be seen to be exserted through perforations in the surface between the processes, and the latter apparently represent hypertrophied interfloral bracts (see the introductory paper for a discussion of their morphology, Jour. Arnold Arb. **40**: 15. *fig. 4b.* 1959). In the male inflorescence the bracts are clavate, as in *A. hypargyreus.* The small, elliptic, acuminate, glaucous leaves are also very distinctive in their appearance.

In 1957, Wu and Wang reduced *Artocarpus bicolor* Merr. & Chun, under which name this species had been known previously in China, to *A. styracifolius.* These authors also cited the following collections from Yunnan, which have not been seen in the course of this study: *P. I. Mao 538, 551, 2356, 3066, 5416, 12296; Wang 85909, 86018, 86028.*

Section **Glandulifolium** Jarrett, sect. nov.

Folia margine glandulifera. *Capitula feminea* stylis bifidis.

TYPE SPECIES: *Artocarpus altissimus* (Miq.) J. J. Smith.

47. **Artocarpus altissimus** (Miq.) J. J. Smith, Ic. Bogor. 3: 79. *t. 233.* 1907, *"altissima"*; Douglas & Baas Becking, Bull. Jard. Bot. Buitenzorg III. 17: 291, *297. t. 10.* 1947.

Morus ? altissima Miq. Fl. Ind. Bat. Suppl. 415. 1861. Syntypes, Sumatra, *Teysmann HB 3903, 3972* (L); lectotype, *Teysmann HB 3972* (L).

Grewia ? subcordata Miq. Fl. Ind. Bat. Suppl. 404. 1861; Burret, Notizbl. Bot. Gart. Berlin 9: 736. 1926. Syntypes, Sumatra, *Teysmann HB 3734, 4042* (L); lectotype, *Teysmann HB 4042* (L).

Artocarpus altissima Teysm. & Binnend. Cat. Hort. Bog. 85. 1866, nomen nudum.

Deciduous trees, height to 30 m., stoutly buttressed, bark brown, peeling off in long flakes. *Twigs* 1.5–3 mm. thick, shallowly rugose, short-pubescent, soon glabrescent. *Leaves* 6–15 × 5–10 cm., ovate to ovate- or obovate-oblong, acuminate, base usually shallowly cordate, margin glandular-crenate; juvenile leaves with 1–2 pairs lateral lobes; main veins and intercostals prominent beneath, reticulum slightly so; puberulent above with the main veins short-pubescent, rather thinly pubescent on the venation beneath, glabrescent; lateral veins 5–9 pairs, straight, basal pair usually rather strongly developed and leaf base hence trinerved; intercostals parallel, basal tertiaries strongly developed; green (turning orange-yellow on the tree), drying blue-grey to brown above, paler brown beneath; petiole 10–25 mm. long, often geniculate at the junction with the lamina.

Inflorescences axillary on short-shoots borne on older wood before the new leaves appear. *At anthesis: male head* 5–8 × 2–3 mm., ellipsoid or cylindric; perianths of 4 free segments 0.7 mm. long, puberulent; (stamen not exserted), anthers oblong, 0.4 mm. long; bracts slenderly stalked, heads peltate, to 0.6 mm. across, ciliate; peduncle 5–7 × 0.5 mm., velutinous; *female head* 5 mm. across, globose, the surface velutinous, with deeply bifid styles exserted to 1 mm. through papillae, and numerous peltate bracts; proximal region of perianths fused; peduncle to 12 × 2 mm., velutinous. *Syncarp* . . . .

VERNACULAR NAME: ***klutum***, Sumatra.

DISTRIBUTION: in evergreen forest to 1800 ft.; Sumatra, west Borneo.

Sumatra. ATJEH. Langsa, A. Tjanang, *bb 14504* (BO). TAPANULI. Angkola and Sipirok, *bb 5626* (BO, L). EAST COAST. Simelungun, G. Maligas, *bb 20436* (BO, L). PALEMBANG. *Heyne* (BO, L, ♂, ♀), *Praetorius* (L); Batu Radja, *Teysmann HB 3734* (BO, L); Muara Dua, *Teysmann HB 3903* (BO, L); Muara Enim, *Teysmann HB 4042* (BO, L); Sekaju Munie, *Teysmann HB 3972* (BO, L). LAMPONGS. Kebang, *Teysmann HB 4214* (BO, L). **Borneo.** WEST BORNEO. Sanggau, *bb 18789* (BO, L). **Cultivated.** JAVA. Bogor, Hort. Bot., *HB 7241* (BO), *VIII B 46* (L).

The material available of *Artocarpus altissimus* is inadequate for the preparation of a full description of the species. The type is sterile, as are all the other collections cited, except for one made by Heyne in

Palembang which has inflorescences at anthesis. These agree with the description, based on material from two trees in the Hortus Bogoriensis, that was published by J. J. Smith in transferring Miquel's *Morus altissimus* to *Artocarpus*. Smith stated that the syncarps did not mature on these trees, but I am informed by Mr. E. J. H. Corner that he found fruit on them containing seeds measuring c. 7 × 5 mm. The germination of these was characteristic of *Artocarpus*, since the cotyledons remained enclosed in the seed-coat, while the epicotyl lengthened and the first pair of foliage leaves were opposite, the subsequent ones being arranged spirally.

The specimens match closely in their vegetative characters, which are aberrant for the genus in several respects. The leaves are palmately trinerved at the base, usually with a strong development of the basal tertiary veins, and the petiole is frequently geniculate at the junction with the lamina. The margin is crenate-dentate, with evenly spaced patches of glandular tissue lying at the end of short nerves running out to the edge of the leaf. These patches are present in addition to the glandular hairs with unicellular heads that are characteristic of subg. *Pseudojaca*. The leaves have a superficial resemblance to some members of the Tiliaceae, and Miquel described another collection as *Grewia subcordata*, which was reduced to *Artocarpus altissimus* by Burret in 1926.

The inflorescence characters are, nevertheless, those of *Artocarpus*, although the long-exserted, deeply bifid styles are again unusual, at least for subg. *Pseudojaca*. The tree is deciduous and the inflorescences are borne on short-shoots before the new flush of leaves appears. Smith, however, shows a young leaf with a crenate margin attached to the shoot-bearing inflorescences. These shoots are entirely leafless on the Heyne collection, but very young leaves dissected from the buds appear to show the glandular margin, while the twigs and buds agree with those of leafy shoots.

This species thus appears to be correctly described and referred to *Artocarpus*. In the more or less distichous arrangement of the leaves on the ultimate twigs, and the nonamplexicaul stipules, as well as in the size and shape of the inflorescences and the completely divided male perianth, *A. altissimus* agrees with subg. *Pseudojaca*. However, there is no obvious affinity with any other members of the subgenus and, in view of the very aberrant vegetative characters, the species is assigned to a separate section *Glandulifolium*.

SPECIES EXCLUDENDAE [5]

ARTOCARPUS (?) AFRICANA Sim, For. Fl. Port. E. Africa, 102. *t. 32.* 1919 (holotype, Mozambique, *Sim 5999* (PRE, not seen)) = **Treculia** cf. **africana** Dcne ex Tréc. Ann. Sci. Nat. Bot. III. 8: 109. 1847.

---

[5] The concluding portion of this paper refers to the genus *Artocarpus* as a whole, i.e., to this and the preceding paper, Studies in *Artocarpus* and allied genera, III. A revision of *Artocarpus* subgenus *Artocarpus*. Jour. Arnold Arb. **40**: 113–155, 298–368. 1959.

Artocarpus bracteata King in Hook. f. Fl. Brit. Ind. 5: 540. 1888; King, Ann. Bot. Gard. Calcutta, 2: 7. *t. 1B.* 1889 = **Parartocarpus bracteatus** (King) Becc.

Artocarpus canarana Miq. Verh. Ned. Inst. III. 5: 20. 1852 (holotype, Kanara, near Mangalore, *Hohenacker 796a* [leg. *Metz*] (u); isotypes (c, k, l, p)) = **Hopea wightiana** Wall. ex Wight & Arn. Prodr. 85. 1834. Metz' collection bears echinate insect galls that were mistaken by Miquel for the male inflorescences of *Artocarpus.* In describing this specimen as *A. canarana* he erroneously suggested that it might be the same as *A. lanceifolius* Roxb. (a species of western Malaysia described from Penang). The latter determination appeared on the herbarium labels and Thiselton Dyer, who cited the collection correctly under *Hopea wightiana* in the "Flora of British India" (1: 309. 1874), quoted only this identification, on Miquel's authority, without mention of *A. canarana.* This is the origin of the statement by Watt (Dict. Econ. Prod. India 4: 273. 1890), followed by Cooke (Fl. Bombay 1: 86. 1903), that Roxburgh had described the galls of *Hopea wightiana* under the name *Artocarpus lanceifolius.* The same galls were the basis of the name *A. ponga* Dennst., and they are commented on further below.

Artocarpus cannoni W. Bull in T. Moore, Florist & Pomol. 1875: 210. 1875; Van Houtte, Fl. Serres 21: 131. *tab.* 1875 = **Ficus cannonii** (W. Bull) N. E. Brown, Gard. Chron. III. 3: 9. 1888, "*canoni*"; Solereder, Bull. Herb. Boiss. II. 3: 515. *t. 3.* 1903. See below under *Artocarpus laciniata* Veitch.

Artocarpus cerifera Miq. Ann. Mus. Lugd.-Bat. 3: 212. 1867 = **Parartocarpus venenosus** (Zoll. & Mor.) Becc.

Artocarpus elongata Miq. Fl. Ind. Bat. Suppl. 419. 1861, Ann. Mus. Lugd.-Bat. 3: 213. 1867 (holotype, Sumatra, Sibolga, *Teysmann HB 767*) = **Sloetia elongata** (Miq.) Koord. Exkursionsfl. Java 2: 90. 1912.

Artocarpus exsculpta W. Bull, Gard. Chron. II. 10: 84. *t. 11.* 1878 (*Ficus exsculpta* in ind.) = **Ficus exsculpta** W. Bull, Cat. no. 154, 5. *t. 1.* 1879. This species was mentioned briefly in the Gardeners' Chronicle of 1878 as having been exhibited recently by W. Bull at Preston under the provisional name of *Artocarpus exsculpta.* The figure given of a sterile shoot closely resembles the plate of a fertile shoot of *Ficus exsculpta*, which appeared as new introduction from the South Sea Islands in Bull's Catalogue for 1879. The latter was also stated to have been exhibited at Preston, and the names may be assumed to refer to the same plant. This is supported by the apparent correction in the index of the Gardeners' Chronicle.

Artocarpus forbesii King in Hook. f. Fl. Brit. Ind. 5: 539. 1888; King, Ann. Bot. Gard. Calcutta 2: 7. *t. 1A.* 1889 = **Parartocarpus venenosus** (Zoll. & Mor.) Becc. ssp. **forbesii** (King) Jarrett.[6]

Artocarpus frutescens Renner, Bot. Jahrb. 39: 367. 1907 = **Prainea frutescens** Becc.

Artocarpus involucrata K. Schum. in Schum. & Hollr. Fl. Kais. Wilhelmsland, 39. 1889 = **Parartocarpus venenosus** (Zoll. & Mor.) Becc.

Artocarpus laciniata Veitch, Gard. Chron. II. 4: 159. 1875; Solereder, Bull. Herb. Boiss. II. 3: 515. *t. 3.* 1903 = **Ficus cannonii** (W. Bull) N. E. Brown,

---

[6] This footnote is to draw attention to the new combination which it is necessary to make here: **Parartocarpus venenosus** (Zoll. & Mor.) Becc. ssp. **forbesii** (King) Jarrett, comb. et stat. nov.; basionym *Artocarpus forbesii* King, Ann. Bot. Gard. Calcutta 2: 7. *t. 1A.* 1889.

Gard. Chron. III. 3: 9. 1888. Both *Artocarpus laciniata* and *A. cannoni* were introduced as seedlings from the Society Islands. They were valued for their dissected, brightly coloured leaves and the two species were based on differences in these. On flowering both proved to be figs and Solereder, who studied them in some detail, showed that they were conspecific, agreeing in characters of the fig and of leaf anatomy. The dissected leaves were juvenile forms, whereas the adult leaves were entire. Solereder considered that the differences in leaf colour between the two species and a variety of *A. laciniata*, described by Veitch as *A. laciniata metallica*, might be due to cultural conditions.

ARTOCARPUS LIMPATO Miq. Fl. Ind. Bat. Suppl. 421. 1861 = **Prainea limpato** (Miq.) Beumée ex Heyne.

ARTOCARPUS PAPUANUS Renner, Bot. Jahrb. **39**: 367. 1907 = **Prainea papuana** Becc.

ARTOCARPUS PONGA Dennst. Schlüssel Hort. Ind. Mal. 30. 1818, nomen illegitimum; Hassk. Hort. Mal. Rheed. Clav. 34. 1867 = **Hopea wightiana** Wall. ex Wight & Arn. Prodr. 85. 1834. This species is based on Rheede's *Ponga* (Hort. Ind. Malab. **4**: 73. *t. 35*, 1683, as *Pongu* on the plate); I am indebted to the late A. H. G. Alston for its identification. Echinate galls bearing a superficial resemblance to the inflorescences of some species of *Artocarpus* frequently occur in *Hopea wightiana* and were shown in the illustrations of Wight (Ill. Ind. Bot. *t. 37*. 1840) and Beddome (Fl. Sylvat. *t. 96*. 1871). The appearance of these galls, and also of the leaves, agrees well with Rheede's picture, and the galls, which are formed from terminal or axillary buds, sometimes occur in clusters, as shown there. Rheede described these structures as calices containing several seeds, which were presumably the pupae of the insects. Brandis (Ind. Trees, 68. 1906) records *ila pongu* as a Tamil name for *Hopea wightiana*. No precise determination for *Ponga* appears to have been published previously, although the suggestion that it might be a species of *Broussonetia* was made by Hamilton in a key to the "Hortus Malabaricus" (Jour. Linn. Soc. **17**: 195. 1835). *Artocarpus ponga* antedates *Hopea wightiana*, but this will not necessitate any nomenclatural change, since Dennstedt's name was based on a monstrosity (Int. Code, Art. 67. 1956).

ARTOCARPUS RIEDELII Miq. Ann. Mus. Lugd.-Bat. **3**: 213. 1867 = **Parartocarpus venenosus** (Zoll. & Mor.) Becc.

ARTOCARPUS SCANDENS Renner, Bot. Jahrb. **39**: 367. 1907 = **Prainea scandens** King.

ARTOCARPUS TYLOPHYLLA Miq. Fl. Ind. Bat. **1**(2): 289. 1859 = **Parartocarpus venenosus** (Zoll. & Mor.) Becc.

ARTOCARPUS VENENOSA Zoll. & Mor. Natur- en Geneesk. Arch. Ned.-Ind. **2**: 213. 1845 = **Parartocarpus venenosus** (Zoll. & Mor.) Becc.

ARTOCARPUS VENENOSA Zoll. & Mor. var. TYLOPHYLLA Miq. in Zoll. Syst. Verz. Ind. Archip. **2**: 89, 95. 1854 = **Parartocarpus venenosus** (Zoll. & Mor.) Becc.

ARTOCARPUS WOODII Merr. Philip. Jour. Sci. Bot. **3**: 221. 1908 = **Parartocarpus venenosus** (Zoll. & Mor.) Becc.

ARTOCARPUS sp., Merr. Pl. Elmer. Born. 46. 1929 (*Elmer 20978*) = **Aporosa nitida** Merr. l.c. 143.

Two nomina nuda are also to be excluded from the genus.

Artocarpus bifaria Wall. ex Miq. Ann. Mus. Lugd.-Bat. **3:** 213. 1867, pro syn. *Sloetia sideroxylon* Teysm. & Binnend. ex Kurz, Jour. Linn. Soc. Bot. **8:** 167. 1864, nomen superfluum = **Sloetia elongata** (Miq.) Koord. Exkursionsfl. Java **2:** 90. 1912.

Artocarpus ? ? finlaysoniana Wall. Cat. no. 4662. 1831, nomen nudum = **Sloetia elongata** (Miq.) Koord. The two collections that were cited by Wallich under this number consist, in his herbarium at Kew, of specimens of *Sloetia elongata. Wallich 4662A* was collected by Finlayson and has abnormal, much branched inflorescences. Under the number *4662B* there are two sheets collected from a plant in the Calcutta Botanic Garden which had been introduced from Penang. One bears a shoot with normal inflorescences. The other bears a single leaf and a label with the determination in Wallich's hand "*Morus ? ? bifaria* Wall." This suggests that the source of the name *Artocarpus bifaria* Wall. mentioned above is another sheet of this collection which had been assigned to the latter genus.

NOMINA DUBIA

Artocarpus dimorphophylla Miq. var. macrophylla Miq. Fl. Ind. Bat. Suppl. 417. 1861. No specimens bearing this determination have been seen and the description is not identifiable.

Artocarpus lamellosa Blanco, Fl. Filip. 667. 1837, ed. 2. 465. 1847, ed. 3. **3:** 74. 1880; Ahern, Timber Tree Sp. Philip. 35. 1901, excl. tab. The reasons for treating *A. lamellosa* as a *nomen dubium* are discussed above, under *A. nitidus* ssp. *nitidus*, which Merrill erroneously reduced to Blanco's species in 1905 (Publ. Gov. Lab. Manila **27:** 80).

Artocarpus parvifolia Voigt, Syll. Ratisb. **2:** 53. 1828. The brief description of trilobed leaves, drawn up from a cultivated specimen from the garden of Belvedere, Thuringia, is not identifiable.

Artocarpus reticulata Hunter ex Ridley, Jour. Str. Br. Asiat. Soc. **53:** 114. 1909. Ridley thought that *A. reticulata* was probably referable to *A. lanceifolius*, and this seems likely, but the description is inadequate for identification.

Artocarpus rotunda (Houtt.) Panzer in Panzer & Christmann, Pflanzensyst. **10:** 380. 1783; Merr. Jour. Arnold Arb. **19:** 331. 1938. Merrill identified this plant with *Artocarpus rigidus* and it has been discussed under that species (Jour. Arnold Arb. **40:** 153. 1959).

Rademachia rotunda Houtt. Nat. Hist. II. Pl. **11:** 455. 1779. This is the basionym of *Artocarpus rotunda* (Houtt.) Panzer.

NOMINA NUDA[7]

Artocarpus angustifolia Roxb. Hort. Beng. 66. 1814.

Artocarpus blumei Tréc. var. sarawakensis Boerl. Handl. Fl. Ned. Ind. **3:** 370. 1900; Merr. Bibl. Enum. Born. Pl. 218. 1921.

Artocarpus (?) foeniformis Eeden, Houtsoort. Ned. Oost.-Ind. 122. 1886, ed. 2. 242. 1905.

Artocarpus madagascariensis Bojer, Hort. Maurit. 290. 1837.

---

[7] The following list of names, published without description and of undetermined application, is appended for the sake of completeness.

ARTOCARPUS NEO-CALEDONICA Linden, Cat. 52. 1871; Guillaumin, Bull. Soc. Bot. Fr. **90**: 35. 1943.

ARTOCARPUS OVATUS Noronha, Verh. Batavia. Genoot 5(5): 7. 1790. Noronha gives the Javanese name for this species as *riandelica* and this may be an error for *mandelica*, a name which is recorded for *Artocarpus rigidus*.

THE ARNOLD ARBORETUM,
HARVARD UNIVERSITY

Present Address: ROYAL BOTANIC GARDENS,
KEW, ENGLAND

SOME USEFUL TECHNIQUES IN THE STUDY AND INTERPRETATION OF POLLEN MORPHOLOGY

I. W. BAILEY

EACH OF THE VARIOUS TECHNIQUES that has been utilized in the study of pollen morphology has limitations as well as advantages. It is essential, therefore, that the conclusions attained by the use of any single technique be in harmony with those obtained by other techniques. This is particularly true where pollen is subjected to more or less drastic treatments during preparation for visual examination. In all such cases evidence should be obtained regarding the effects of each treatment upon the normal form and structure of living pollen.

A large amount of research in recent years has been focused upon the visible structure of the exine of acetylated pollen. Comparatively scant attention has been devoted to the study of the intine and the protoplast. If the various layers of the pollen wall are to be accurately defined and classified, it is necessary that more be learned concerning their chemical composition and physical properties. Summations of accumulated circumstantial evidence obtained by the use of diversified techniques can provide significant clues in this connection. In so doing, generalizations should be based, not solely upon the pollen of one or two randomly selected species, but upon investigations of a wide range of representative gymnosperms and angiosperms.

Mangin attempted to do this in a brief paper published in 1889. The significance of this paper cannot be adequately appreciated without reading Mangin's other papers dealing with the differential staining, differential solubilities, and other properties of the polysaccharides that occur in plant tissues in general. He recognized, not only that the intine differs markedly from the exine, but also that it is chemically heterogeneous. He concluded that it is composed of a mixture of polysaccharides, in most cases largely of cellulose and "pectose," the cellulose being concentrated adjacent to the protoplast and disappearing in the external zone or zones and particularly in the so-called "Zwischenkörper" of Fritzsche (1837) which commonly occurs in the apertural regions of the pollen wall. It should be noted in this connection that the results of Mangin's researches on pollen were published before he obtained a sample of ruthenium red (ammoniated oxychloride of ruthenium) from Joly (1892). He (1893) considered this dye superior, in the differential staining of pectic compounds, to such basic dyes as phenosafranin, methyl blue, etc., that he utilized so extensively in his earlier investigations. However, he does not appear to have used ruthenium red at a later date in an extensive investigation of pollen.

UTILITY AND RELIABILITY OF RUTHENIUM RED

In microscopy, ruthenium red has the advantage of being soluble in water but insoluble in alcohols, anhydrous glycerin, chloroform, benzene, xylol, clove oil, and other reagents utilized in preparing sections for microscopic examination. However, in aqueous solution it has the disadvantage of deteriorating rapidly in the light at ordinary room temperatures. This difficulty can be overcome by keeping solutions in the dark in a refrigerator. I have solutions of the dye (Edward Gurr, Ltd.) that are in good condition after more than a year. A more serious difficulty occurs in attempting to make permanent mounts of stained pollen, as also of sections of plant tissues. In all cases thus far the red color disappears in time from stained parts of the preparations.

There have been two extreme views regarding the utility of ruthenium red. At one extreme are those who assume that it is specific for pectic compounds, whereas at the other extreme are individuals who have shown that it stains a variety of chemical substances and therefore conclude that it is utterly unreliable and useless in microchemical investigations. In this connection, I have made in the past extensive observations upon the staining reactions in aqueous ruthenium red of a wide range of inorganic and organic substances of known chemical composition. Tests have been made not only with naturally occurring gums and mucilages and pectic compounds and "polyuronide hemicelluloses" extracted from plant tissues, but also, through the cooperation of Professors Ernest Anderson and Karl P. Link, with fractions of these substances of known chemical composition. It seems that galacturonic and glucuronic acids when methylated, as salts, or in intimate chemical association with hexose and pentose sugars stain characteristically in aqueous ruthenium red. Where the substances themselves are soluble in water, their staining reactions may be studied by using a concentrated solution of the dye in admixture with a proportion of alcohol which inhibits or retards their rapid solution. In contrast to the general uniformity in the behavior of these naturally occurring substances, their free acids when isolated and purified are very variable in their reactions in aqueous solutions of ruthenium red. When they stain, they may give a yellow, rather than a red, coloration, and likewise may turn the color of the ruthenium solution from red to yellow. The rapidity and the intensity of staining varies in buffers of widely different pH. This raises complex questions regarding the effects of reagents in buffers upon the dye and upon the chemical composition of the substances being tested. Preliminary treatments of cells and tissues with acids, alkalies and other reagents should be avoided if possible. The most significant results are obtained when living cells or freshly cut sections of living tissues are quickly immersed in a solution of ruthenium red in distilled water or in relatively pure spring water.

Although the dye stains oxycellulose, hydrocellulose, the nucleus, protoplast, and other organic substances, as well as pectic compounds, gums, mucilages, and "polyuronide hemicelluloses," there are significant differences in its behavior in these cases. In my investigations of cell walls of the higher plants, I have found that those naturally occurring polysaccharides which contain sugar acids (e.g., galacturonic, glucuronic) or their methylated or salt (e.g., calcium pectate) derivatives tend to stain very intensely and with extraordinary rapidity in dilute (1/5000) solutions of ruthenium red, whereas other naturally occurring organic substances, if they stain at all, do so more gradually and commonly less intensely. Of course, it should be realized in this connection that the staining may be inhibited or masked by lignification, cutinization, or suberization of cell walls. Thus, although the dye is not specific for pectic compounds and must be used with adequate precautions, its use does provide a simple and rapid method of obtaining useful clues or leads in studying the occurrence and distribution of polyuronides in plant cells and tissues. Although not conclusive by itself, it becomes increasingly so when in harmony with evidence obtained by other techniques, e.g., differential solubilities, polarized light, electron microscopy, etc.

The so-called intine of pollen commonly stains with remarkable clarity and rapidity when freshly collected pollen, viable dry pollen, dead pollen from herbarium specimens, and pollen preserved in alcohol are immersed in dilute aqueous solutions of ruthenium red. Frequently the differential staining is so rapid that it is clearly visible by the time that a mount can be made and examined under a microscope. In fact, it may sometimes be advantageous to retard the staining by using the aqueous solution in admixture with a high proportion of glycerin. Such admixtures are relatively stable when kept in the dark at ordinary refrigerator temperatures. Intense staining of the intine occurs first in the apertural region or regions of the pollen wall and subsequently in parts that subtend the exine. The exine does not stain, retaining its original greenish yellow or other colors. On the contrary the protoplast may in time develop a red coloration. The accelerated staining of thicker parts of the intine in apertural regions may be due to a higher concentration of stainable substances in such areas or to retarded penetration and diffusion of the dye through the exine of nonapertural parts. That the proportion of stainable substances varies is indicated by differences in the ultimate intensity of staining, not only as between the intines of different types of pollen, but also in different zones or layers of a single thick intine. That penetration of the dye is retarded or actually inhibited at times by the exine (or by external coatings of oily or resinous substances) is indicated by the fact that the intine of inaperturate pollen may not stain at times unless the exine is mechanically ruptured or abraded.

Ruthenium-red staining of the intine of pollen from herbarium specimens, as well as of freshly collected living pollen, provides a simple, rapid, and reliable means of studying variations in the normal form of the intine in the various taxa of the angiosperms. It is particularly useful in demonstrating variations in the form and thickness of the intine in apertural regions of pollen. Although the spectacular differences in color between the intine and exine require illustration in color, the intense red staining of the thicker parts of the intine can be reproduced in intense black by the use of a green filter as illustrated in PLATE I.

The pollen of *Calycanthus* varies from monocolpate (*Fig. 1*) to zonaperturate or belted (*Fig. 3*) to bicolpate (*Fig. 2*) and infrequently to tricolpate. In each case the aperture or apertures are subtended by conspicuously thickened parts of the intine which stain intensely and with remarkable rapidity in dilute aqueous solutions of ruthenium red. In these pollen grains, as in those of *Illicium* (*Fig. 4*) which have three narrow grooves that extend from pole to pole,[1] the thicker parts of the intine are considerably broader than the transverse diameter of the furrows. This is in contrast to those forms of pollen (*Fig. 5*) in which the excessively thickened parts of the intine, "Zwischenkörper" of Fritzsche (1837), "oncus" of Hyde (1955), are but slightly broader than the diameter of the apertures. In the case of the Winteraceae, where the pollen occurs characteristically in tetrads, the New World representatives differ conspicuously from the Old World representatives of the family (Bailey and Nast, 1943). In the monoporate grains of the latter genera and species, the intine is somewhat thicker in the apertural part but does not protrude (*Fig. 7*), whereas in the New World representatives the protoplast protrudes and is jacketed by a thick coating of intensely staining intine (*Fig. 8*). In a majority of the angiosperms the thickenings of the intine subtend the apertures of varying form, size, and number, but this is not invariably the case, as has been shown by Dressler (1957) in the Euphorbiaceae. For example, in the tricolporate pollen of *Pedilanthus* (*Fig. 6*) there are six riblike thickenings which extend nearly from pole to pole. These thickenings of the intine are lateral to the elongated colpae, rather than directly beneath them.

OCCURRENCE AND DISTRIBUTION OF CELLULOSE IN POLLEN

Although the intense ruthenium-red staining of the outer part of the intine, particularly in apertural regions of pollen, is not necessarily indicative of pectic composition, it suggests, in correlation with the isotropy of this part in polarized light, plasticity during pollen tube emergence, expansion and contraction during wetting and drying, and solubility in cold 4% sodium hydroxide and other reagents which do not dissolve cellulose, that the outer part of the intine commonly contains a large proportion of uronide polysaccharides in its chemical composition.

As regards the inner part of the intine, the differing conclusions attained by Mühlethaler (1953) and Sitte (1953) by the use of electron microscopy raise an important question regarding the occurrence of cellulose in the inner part of the intine adjacent to the protoplast as hypothesized by Mangin (1893). In diversified representatives of both gymnosperms and angiosperms this part of the intine, although staining more or less

---

[1] For illustrations compare Wodehouse (1935), page 336, *Fig. 92*, or Erdtman (1952), page 256, *Fig. C*.

intensely in ruthenium red, exhibits anisotropy in polarized light. Furthermore, it stains a characteristic blue when pollen grains are immersed directly in chloro-iodide of zinc or in 65% sulphuric acid following staining in iodine. Where the intine is very tenuous and obscured by the exine, the cellulosic part may be retained and rendered clearly visible by removing the protoplast and the noncellulosic constituents of the intine in 3% sodium hydroxide at 56° C. (*Figs. 9–11*).

Not only is the inner part of the intine insoluble in reagents which do not dissolve cellulose, but also it is removed by standard solvents of cellulose, e.g., 72% sulphuric acid, cuprammonium reagents, as well as during prolonged acetylation of pollen. Furthermore, its microfibrillar composition can be revealed by electron microscopy as demonstrated by Sitte (1953). In addition, it should be noted that when the noncellulosic constituents of the intine are completely removed the cellulose-containing inner layer no longer stains rapidly and intensely in ruthenium red.

In general (with the exception of certain unusual forms of pollen, e.g., *Eupomatia*), the cellulose-containing inner layer of the intine of both gymnosperms and angiosperms is tenuous and of relatively uniform thickness. This is in contrast to the striking variations in the thickness of the outer part of the intine that occur so frequently in various taxa of the higher plants. During the disruption of pollen walls due to differences in the contraction or expansion of the protoplast and wall layers, the cellulosic layer of the intine commonly tends to remain adjacent to the protoplast.

SOLUBILITY OF THE EXINE IN MONOETHANOLAMINE

The exine of pollen, like the cuticle of plants, is generally considered to be relatively inactive chemically since it persists for such prolonged periods in geological strata and dissolves only after prolonged drastic treatments. Much to my surprise, therefore, I have found that exines of freshly collected living pollen at anthesis (e.g., of such gymnosperms as *Taxus*, *Tsuga*, *Pseudotsuga*, *Pseudolarix*, and *Pinus* and of such angiosperms as *Liriodendron*, *Magnolia*, *Asimina*, *Taraxacum*, *Coreopsis*, *Ostrya*, *Populus*, and *Calycanthus*) dissolve in three hours or less when immersed in monoethanolamine at a temperature of 97° C. The only exceptions that I have encountered thus far in a preliminary investigation are pollen of *Ephedra* and *Pinus strobus* from old herbarium specimens and of *Eupomatia* preserved for a long period in F.A.A. fixative (formalin-acetic acid-alcohol). The fact that the exine of freshly collected pollen of *Pinus* dissolves suggests that changes occur under certain conditions of prolonged drying which inhibit solubility. Unfortunately no freshly collected pollen of *Ephedra* and *Eupomatia* is available, as yet, for such comparative purposes. In the case of *Liriodendron*, it is possible, by adequately controlling temperature and time of treatment, to remove the thick exine (*Fig. 12*) leaving the protoplast, the layers of the intine and oil globules but slightly modified visually (*Fig. 13*). Of course, this raises an important question, viz., whether dissolving the exine of a large amount of pollen in monoethanolamine might yield a solute capable of separation and analysis. Such analyses might afford significant clues regarding the chemical composition of the exine and deserve to be more intensively investigated.

DISCUSSION

Summations of evidence obtainable by the application of diversified techniques indicate that the cellulosic part of the intine of both gymnosperms and angiosperms occurs in a comparatively narrow zone adjacent to the protoplast. The anisotropic cellulose occurs, however, in association with an isotropic polyuronide (or mixture of polyuronides and polysaccharides) which stains rapidly and intensely in dilute aqueous solutions of ruthenium red and which is readily removable by reagents which do not dissolve cellulose. The outer part of the intine, particularly in thickenings related to apertures, contains little, if any, cellulose and is composed of a polyuronide (or a mixture of polyuronides and polysaccharides) which stains and dissolves as does the material associated with the cellulose in the innermost part of the intine. The noncellulosic constituent in thicker parts of the intine (related to apertures in the exine) is plastic (i.e., easily penetrated or pushed aside during emergence of the pollen tube) and contracts and swells, with corresponding invagination and evagination, during drying and rewetting of living pollen. The consistency in the occurrence and behavior of this part of the intine in a wide range of taxa suggests that it serves two important functions, (1) to protect the protoplast in apertural parts of the wall and (2) to facilitate emergence of the pollen tube. Professor A. Orville Dahl and I plan to discuss this aspect of the intine in greater detail in a subsequent joint paper. We are also correlating evidence obtained by phase and electron microscopy and other diversified techniques in detailed studies of specific forms of pollen. The question of a revised terminology for wall layers, e.g., whether the use of intine should be restricted to the cellulosic layer and exintine or mesine used in referring to material that intervenes between the cellulosic layer and the exine, had best be deferred until comprehensive investigations of a wide range of representative pollen forms have been completed.

ACKNOWLEDGMENTS

This investigation was supported by a grant from the American Philosophical Society. I am much indebted to the curators of the Gray and Arnold herbaria for permission to collect pollen from a wide range of herbarium specimens, to Dr. A. C. Smith for assistance in obtaining pollen of the Winteraceae and other families, to Dr. C. E. Wood for pollen obtainable in his collection of flowers preserved in 70% alcohol, to Mr. L. J. Brass for collecting and preserving flowers of critical genera in F.A.A. fixative, and to Dr. R. L. Dressler for living pollen of *Pedilanthus*. I am also indebted to Professors A. Orville Dahl and Kenneth V. Thimann for kindly reading the manuscript of this paper and for making a number of helpful suggestions.

LITERATURE CITED

BAILEY, I. W., and CHARLOTTE G. NAST. 1943. The comparative morphology of the Winteraceae I. Pollen and stamens. Jour. Arnold Arb. **24**: 340–346.

DRESSLER, R. L. 1957. The genus *Pedilanthus* (Euphorbiaceae). Contr. Gray Herb. **182**: 1–188.

ERDTMAN, G. 1952. Pollen morphology and plant taxonomy. Chronica Botanica Co.

FRITZSCHE, J. 1837. Ueber den Pollen. Mém. Sav. Étrang. Acad. St. Petersburg **3**: 649–770.

HYDE, H. A. 1955. Oncus, a new term in pollen morphology. New Phytol. **54**: 255–256.

JOLY, A. 1892. Composés ammoniacaux dérivés du sesquichlorure de ruthénium. Compt. Rend. Acad. Sci. Paris **115**: 1299–1301.

MANGIN, L. 1889. Observations sur la membrane du grain de pollen Mûr. Bull. Soc. Bot. France **36**:274–283.

———. 1893. Sur l'emploi du rouge de ruthénium en anatomie végétale. Compt. Rend. Acad. Sci. Paris **116**: 653–656.

WODEHOUSE, R. P. 1935. Pollen grains. McGraw-Hill Book Co.

EXPLANATION OF PLATES

PLATE I

Pollen differentially stained in aqueous ruthenium red and photographed with a green filter at a magnification of 770. FIGS. 1–3, 6, freshly collected living pollen; 5, 8, pollen from herbarium specimens; 4, pollen preserved in 70% alcohol; 7, pollen preserved in FAA fixative. FIGS. 1–3, *Calycanthus* sp. (cultivated, Cambridge, Mass.): 1, monocolpate grain viewed in optical section parallel to long axis of colpus; 2, dicolpate grain viewed in optical section parallel to the long axis of the colpus; 3, zonaperturate grain viewed in diagonal optical section. FIG. 4, *Illicium floridanum* Ellis (cultivated, Henry Foundation, Gladwyne, Pa.), tricolpate grain, polar view. FIG. 5, *Nouhuysia arfakensis* (Gibbs) Steenis (*Kostermans 2198* [A]), triporate grain. FIG. 6, *Pedilanthus* sp. (*Dressler*), tricolporate grain, polar view. FIG. 7, *Zygogynum Baillonii* Tiegh. (*Buchholz*, New Caledonia, 1947), each grain of the tetrad with a single more or less circular aperture. FIG. 8, *Drimys granadensis* L. f. var. *mexicana* (DC.) A. C. Smith (*Hinton 14441* [GH]), characteristic tetrad of New World section *Wintera*, each grain of the tetrad with a single aperture and protruding protoplast jacketed by a thick coating of stainable intine.

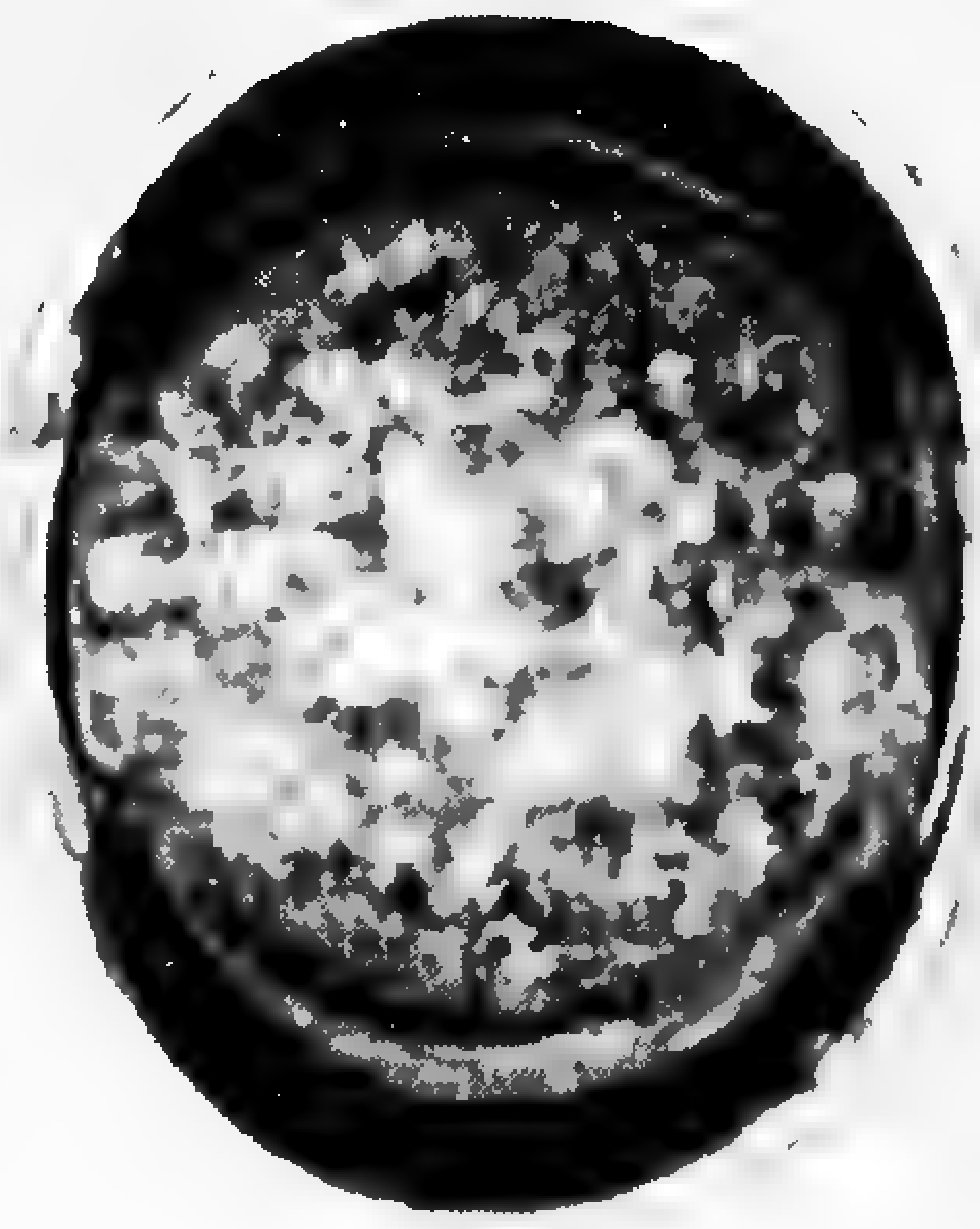
PLATE II

FIGS. 9, 10, *Liriodendron tulipifera* L. (cultivated, Arnold Arboretum): 9, pollen after treatment in 3% NaOH at a temperature of 56° C. which removes the protoplast and the noncellulosic constituents of the intine — when immersed in chloro-iodide of zinc the contracted cellulosic residue of the intine stains a deep blue, in striking contrast to the greenish-yellow color of the exine, × 1130; 10, characteristic anisotropy of two cellulosic residues in polarized light, × 400. FIG. 11, *Pinus strobus* L. (Norwell, Massachusetts), freshly collected living pollen following the same treatment as in FIG. 9, × 1130.

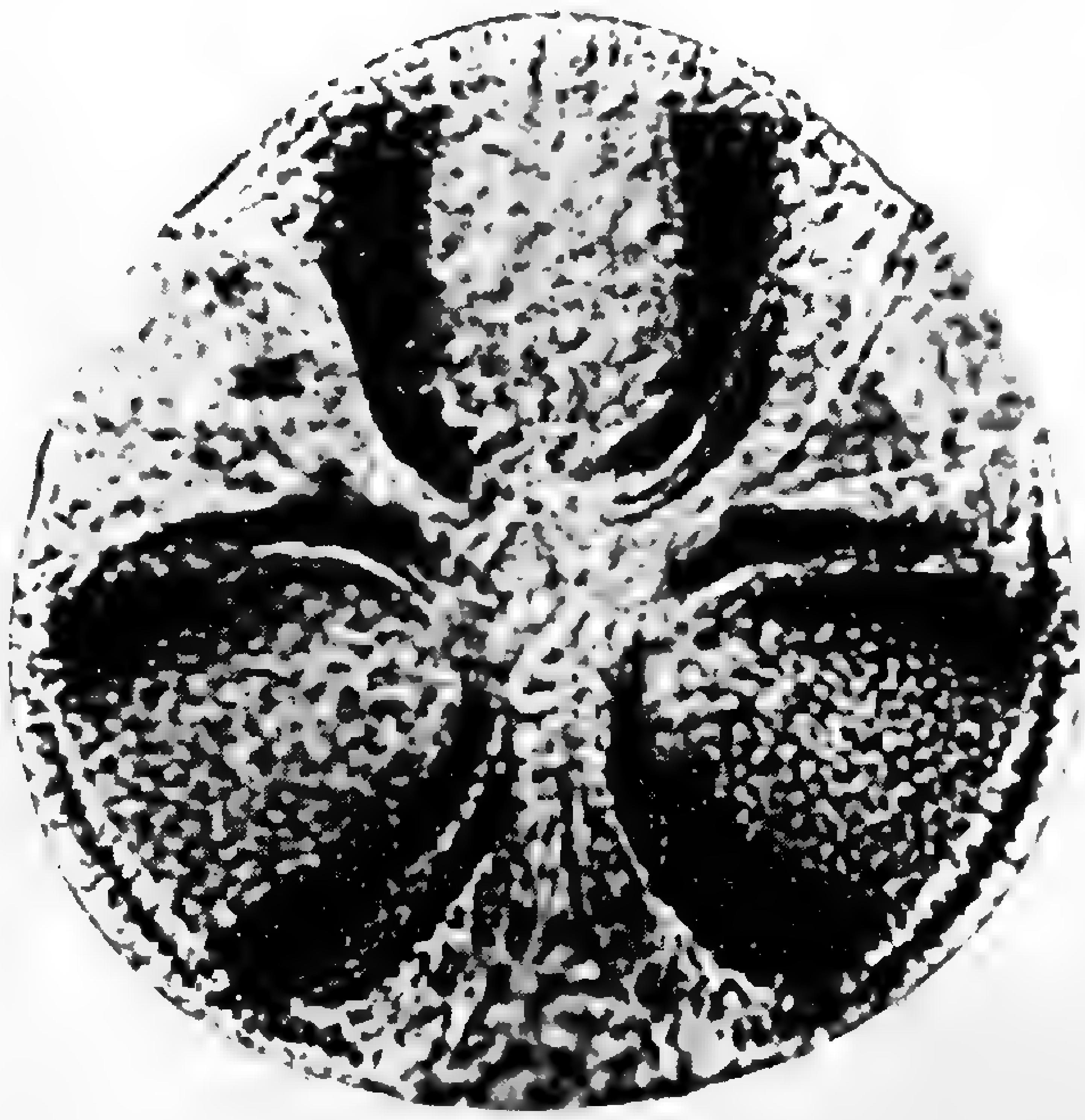
PLATE III

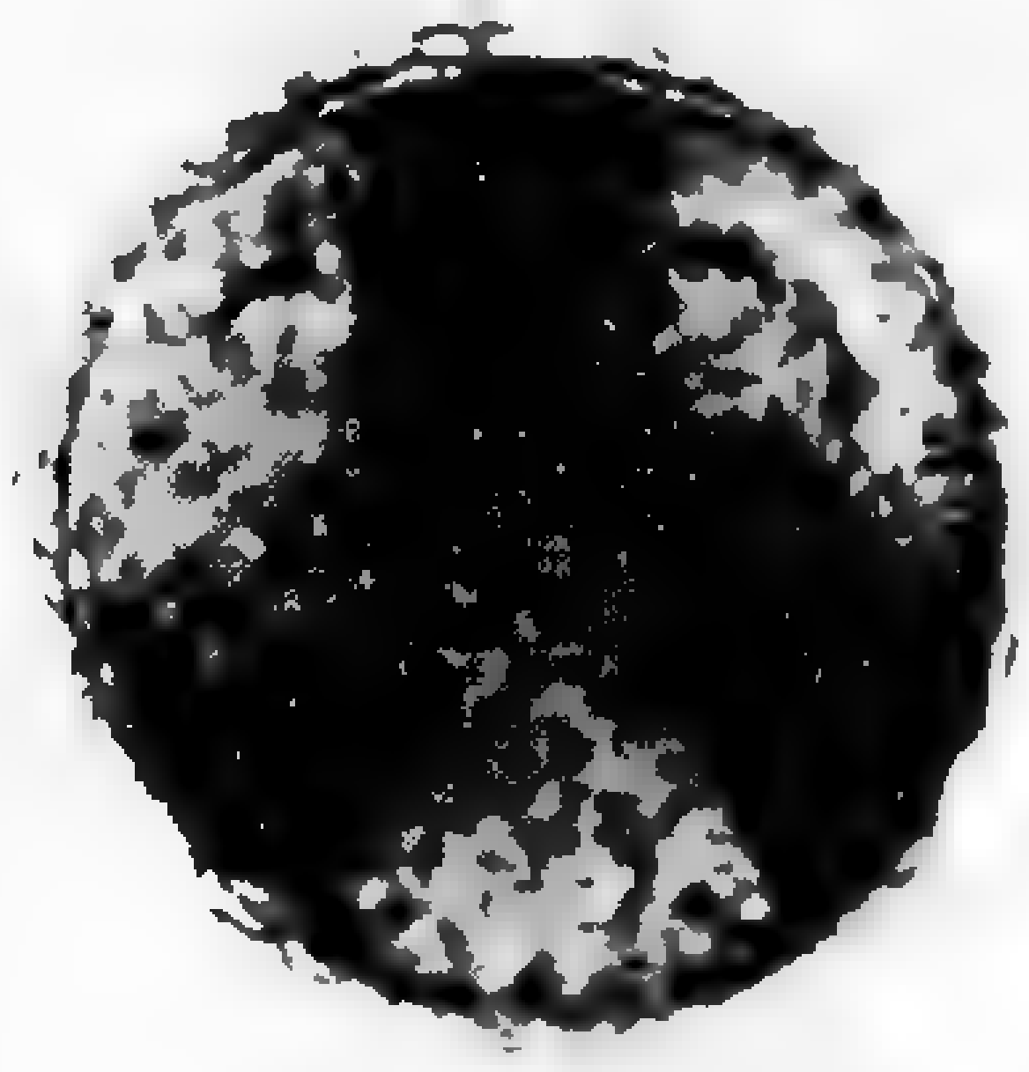
FIGS. 12, 13, *Liriodendron tulipifera* (cultivated, Arnold Arboretum): 12, freshly collected living pollen in a mixture of water and glycerine, viewed in optical section parallel to the long axis of the colpus, showing coarsely warty exine and conspicuous thickening of the intine in the apertural region, × 1130; 13, pollen grain after a brief treatment in monoethanolamine at a temperature of 97° C. — exine has been removed leaving the intine, protoplast, and oil globules in place, × 1130.


1


2

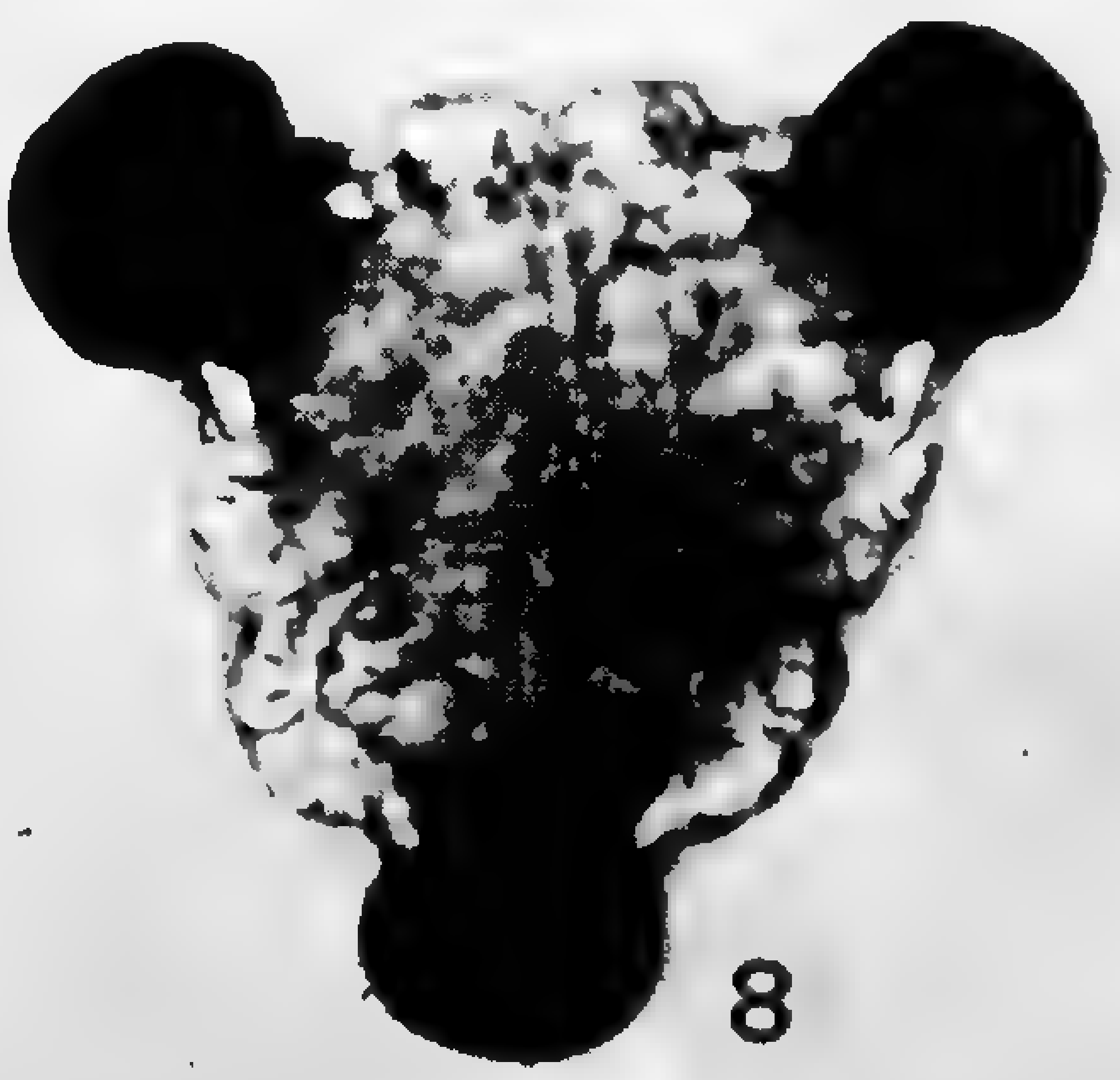

3


6

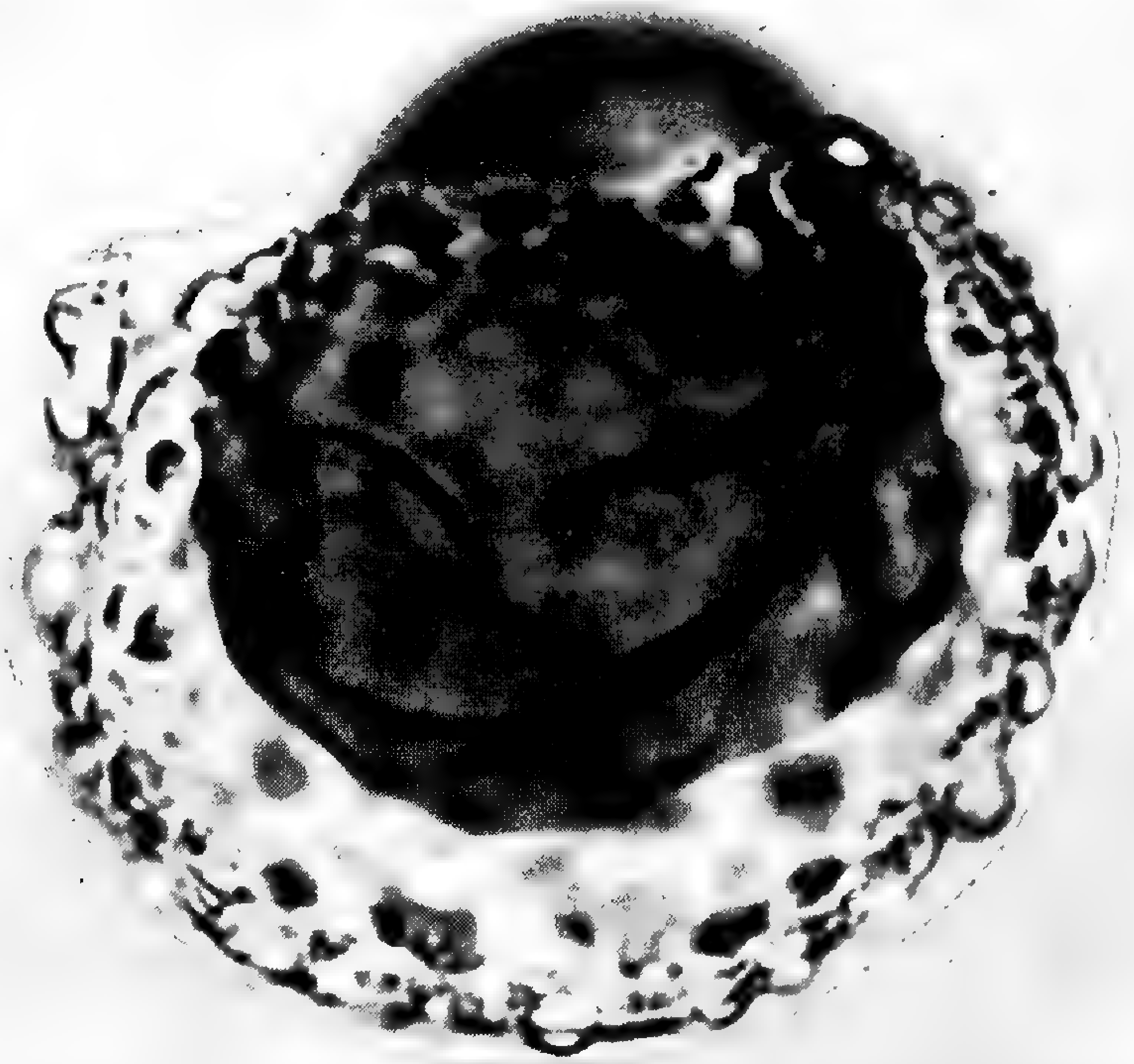

4


5


7

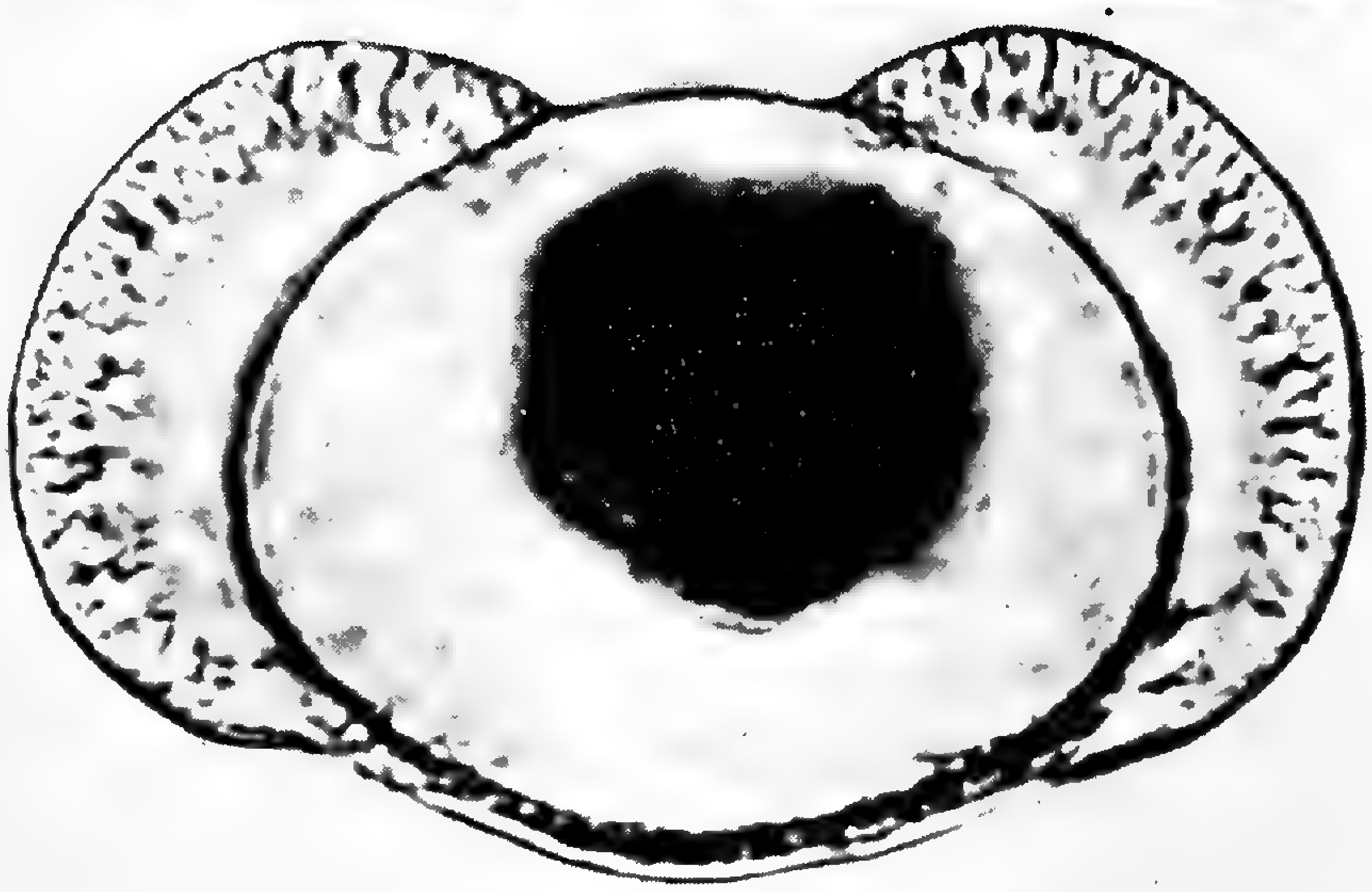

8

Bailey, Pollen Morphology



9

10



11

BAILEY, POLLEN MORPHOLOGY

12

13

BAILEY, POLLEN MORPHOLOGY

THE GENERA OF SARRACENIACEAE AND DROSERACEAE IN THE SOUTHEASTERN UNITED STATES[1]

CARROLL E. WOOD, JR.

SARRACENIACEAE Dumortier (PITCHER-PLANT FAMILY)

Perennial, rhizomatous insectivorous herbs with tubiform or pitcher-like leaves. Flowers bisexual, solitary [or few and racemose], nodding, the scape naked [or few-bracteolate]. Flowers regular, 5[4,6]-merous, the insertion hypogynous. Sepals 5[4,6], free, imbricate at the base, persistent, sometimes colored [and petaloid]. Petals 5 [or none], free, deciduous. Stamens numerous, free, the filaments filiform, the anthers versatile, extrorse, 2-locular; pollen grains single, polycolporoidate to 5–6-colporoidate. Gynoecium syncarpous, the style simple below, the apex [entire or lobed or] peltate-dilate, the ovary 5[3]-locular, the placentation axile; ovules numerous, anatropous, 2-integumented. Fruit a 5[3]-valved, loculicidal capsule. Seeds numerous, small, winged [or not], with abundant endosperm, the embryo minute, near the hilum. TYPE GENUS: *Sarracenia* L.

A small, distinctive family of disjunct distribution, with three well-marked genera: *Sarracenia* (eight species of eastern North America), *Darlingtonia* Torr. (*D. californica* Torr. [*Chrysamphora californica* (Torr.) Greene], $2n = 30$, of northern California and southern Oregon), and *Heliamphora* Benth. (six species described from the isolated table-top mountains of northern South America).

The highly modified pitcher-leaves and the large, bisexual, pentamerous flowers with axile placentation are characteristic. The group has been allied with various families or combinations of families: Papaveraceae

---

[1] Prepared for a biologically oriented generic flora of the southeastern United States, a joint project of the Gray Herbarium and the Arnold Arboretum made possible through the support of George R. Cooley and the National Science Foundation. The scheme follows that outlined at the beginning of the series (Jour. Arnold Arb. **39**: 296–346. 1958). It may be remarked here, however, that the area covered is bounded by and includes North Carolina, Tennessee, Arkansas, and Louisiana, that descriptive material inapplicable to our species is included in brackets, and that references marked by an asterisk have not been checked. Other published portions of these studies will be found in Jour. Arnold Arb. **40, 41.** 1959, 1960.

In connection with these families I am especially indebted for various comments and helpful suggestions to Dr. Patricia R. Roberts and to Dr. C. R. Bell, upon whose respective work on *Dionaea* and *Sarracenia* I have drawn heavily. I am also grateful to my immediate colleagues for their continuing interest and advice and to W. L. Brown, Jr., R. B. Channell, G. R. Cooley, D. Demaree, C. W. James, C. E. Jenner, J. Kucyniak, Jeanette Renshaw, H. F. L. Rock, and A. J. Sharp for their help in various ways. As in previous papers in this series, the illustration is by Dorothy H. Marsh.

and Nymphaeaceae or these plus Ranunculaceae; Droseraceae or Nepenthaceae, or both; Cephalotaceae; Francoaceae; Cistaceae. Although now placed with the insectivorous Nepenthaceae and Droseraceae by many authors, the true relationships are still in need of careful study in terms of the entire plant.

REFERENCES:

BAILLON, H. Nymphaeacées. Hist. Pl. 3: 77–104. 1872. [Includes Sarraceniaceae.]

BENTHAM, G., and J. D. HOOKER. Sarraceniaceae. Gen. Pl. 1: 48. 1862; 965. 1867.

GRAY, A. Sarraceniaceae. Gen. Pl. U. S. 1: 105–108. *pls. 45, 46.* 1848.

LLOYD, F. E. The Carnivorous Plants. xv + 352 pp. Chronica Botanica, Waltham, Mass., 1942. [Chap. I. *Heliamphora*; II. *Sarracenia*; III. *Darlingtonia*. Comprehensive review of structure and biology; extensive bibliography.]

MACFARLANE, J. M. Sarraceniaceae. Pflanzenr. IV. **110**(Heft 34): 1–38. 1908.

MARKGRAF, F. Les homologies des feuilles et les relations taxinomiques chez les Sarraceniales. VIII^{e} Congr. Int. Bot. Rapp. Comm. I. **Sect. 2, 4, 5, 6:** 50–52. 1954. [Interprets leaves of *Sarracenia, Drosera, Dionaea, Nepenthes, Dioncophyllum* as showing basically the same morphology.]

UPHOF, J. C. T. Sarraceniaceae. Nat. Pflanzenfam. ed. 2. **17b**: 704–727. 1936.

WUNSCHMANN, E. Sarraceniaceae. Nat. Pflanzenfam. III. 2: 244–252. 1891.

1. **Sarracenia** Linnaeus, Sp. Pl. 1: 510. 1753; Gen. Pl. ed. 5. 226. 1754.

Perennial insectivorous herbs of bogs, seeping terraces and wet savannas. Plants rhizomatous, the 3–8 leaves clustered, erect and trumpet-shaped to decumbent and pitcher-shaped, liquid-filled to varying degrees, with a ridge or wing on the adaxial side and a terminally expanded hood; leaves green, yellow, maroon, or variegated; ensiform leaves sometimes present. Flowers solitary, nodding on erect scapes. Sepals 5, with 3 appressed, persistent bracts. Petals 5, yellow or maroon (or deep red), deciduous. Stamens 70–80 (arising in ontogeny in 10 groups). Gynoecium 5-carpellate; style simple below, the upper portion expanded into a large, persistent, 5-lobed umbrella-like structure, with a small stigma under each of the notched lobes; ovary 5-locular. Fruit 5-valved; seeds winged on one side. Chromosomes 2–4 microns long, similar, $2n = 26$. TYPE SPECIES: *S. purpurea* L. (Named for Michel Sarrazin de l'Étang, 1659–1734, physician at the Court of Quebec, who sent *S. purpurea* to Tournefort.) — PITCHER PLANTS, TRUMPETS, BUGLE-GRASS, BOG-BUGLES, DUMB-WATCHES, WATCHES, BUTTERCUPS, EVE'S CUPS, FROG-BONNETS.

Eight species, all confined to the southeastern United States, with the exception of *S. purpurea*, the most widespread species, which ranges from western North Carolina northward along the mountains and from southern Mississippi eastward and northward along the Coastal Plain to Newfoundland, Labrador, Mackenzie, and Saskatchewan.

Form and habit (and in some instances, color and marking) of pitchers are the most useful taxonomic characteristics, in conjunction with color and shape of petals, odor, curvature of sepals, and presence of ensiform leaves. Leaf size is not a constant characteristic. (See Bell for key, ranges, and comments.)

The six species of sect. ERECTAE Uphof have upright, tubular or trumpet-shaped leaves with variously shaped hoods which largely prevent the entrance of rain. The group includes *Sarracenia leucophylla* Raf. (*S. Drummondii* Croom) and *S. rubra* Walt. with maroon petals, and *S. minor* Walt., *S. flava* L., *S. oreophila* Wherry, and *S. alata* (Wood) Wood (*S. Sledgei* Macfarl.) with yellow petals. The last three are closely related vicariads with yellow-green trumpet-shaped leaves bearing large hoods with more or less reflexed margins. They differ in ensiform leaves, hoods, petal shape and texture, and odor. Insofar as is known, the three are geographically separated: *S. flava* distributed on the Atlantic coastal plain (southeastern Virginia to western Florida and southern Alabama and a few disjunct stations inland in North Carolina); *S. oreophila* at the southern end of the Appalachians (northeastern Alabama to Elmore County, Alabama, westernmost central Georgia, and perhaps formerly Fentress County, Tennessee); and *S. alata* on the Gulf coastal plain (Mobile County, Alabama, to eastern Texas). *Sarracenia rubra* f. *Jonesii* (Wherry) Bell (*S. Jonesii* Wherry) has the fragrant maroon flowers, recurving sepals, and characteristically maroon-reticulate hoods of f. *rubra* and differs only in its larger leaves being more sharply expanded toward the leaf opening which is less closely covered than in f. *rubra*.

Sarracenia purpurea and *S. psittacina* Michx., both with maroon petals and decumbent pitchers and the latter with the most highly modified leaves in the genus, constitute sect. SARRACENIA (sect. *Decumbentes* Uphof). *Sarracenia purpurea* supposedly is represented southward by var. *venosa* (Raf.) Fern. (ssp. *venosa* (Raf.) Wherry), a doubtfully distinct taxon based upon proportions of "pitcher" and hood.

Sarracenia is confined to wet, mediacid soils and hence occurs largely in bogs, wet savannas, at the edges of pocosins, and on springy, sandy slopes on the Coastal Plain. The greatest concentration of species and individuals is in the southern half of Georgia and Alabama and in northern Florida. Only *S. minor* is known from peninsular Florida (as far south as Highlands County). The ranges of *S. purpurea*, *S. psittacina*, *S. leucophylla*, and *S. rubra* overlap at least in part those of all species except *S. oreophila*, which is completely isolated geographically.

The genus is a homoploid complex ($2n = 26$) of interfertile but morphologically distinct species. Sixteen of nineteen "geographically possible" natural hybrids have been reported from the wild, and two others have been produced artificially. Artificial hybrids involving three or four species have been made. No hybrids of *S. oreophila* are known. Most hybrids are sporadic where two or more species occur, but around Mobile Bay, where *S. leucophylla* and *S. alata* commingle, much hybridization and backcrossing are evident. The extent to which introgression occurs is not known. Over most of their ranges the various species seem to retain their biological identities primarily through geographical and seasonal isolation.

The remarkable leaves are provided with nectar glands and are sometimes conspicuously colored (e.g., bright yellow-green to red in *S. flava*, the upper part of leaf and hood white, reticulate with red and green in *S. leucophylla*) or translucent spotted (*S. psittacina*, *S. minor*). Insects attracted by nectar or coloration may fall or crawl into the pitchers, and, if unable to escape, die and are digested. Only the pitchers of *S. purpurea* are water-filled; those of others which are provided with protective hoods secrete varying quantities of fluid, however. The morphological homologies of the leaves are still under discussion.

Sarracenias are fed upon by a number of moths known from no other plants: *Olethreutes* feeds upon the flowers and seeds; *Papaipema* is a rhizome-borer; and three species of *Exyra* eat the leaves. Other insects, including a sarcophagan fly, a gnat, a sciarid fly, and two harmless mosquitoes dwell in the pitchers. The larvae of the last, members of the tropical genus *Wyeomyia*, inhabit the water-filled leaves of *S. purpurea*. The larvae are purely aquatic and overwinter in the pitchers, surviving freezing and thawing. Pupation with subsequent emergence as the adult does not occur (at least in the North) until the proper photoperiod and suitable temperatures for growth are reached in the spring. Although pitcher-plants in some areas are accused of harboring mosquitoes, larvae of other genera do not occur in the pitchers, and the adult *Wyeomyia smithii* does not bite man.

Sarracenias are highly ornamental and were popular horticultural plants in Great Britain from about 1880 to 1890. With care, all of the species succeed in cultivation in pots filled with fine, sandy, acid muck and standing in about an inch of water. Full sunlight with a bright southeastern exposure is desirable. A cool, winter dormant period is usual.

REFERENCES:

Many references prior to 1942 omitted; see review and bibliography in LLOYD, Carnivorous Plants.

ARBER, A. On the morphology of the pitcher leaves of *Heliamphora*, *Sarracenia*, *Darlingtonia*, *Cephalotus* and *Nepenthes*. Ann. Bot. II. **5**: 563–578. 1941.

BELL, C. R. A cytotaxonomic study of the Sarraceniaceae of North America. Jour. Elisha Mitchell Sci. Soc. **65**: 137–166. *pls. 8–14*. 1949. [*Sarracenia*, *Darlingtonia*.]

———. Natural hybrids in the genus *Sarracenia*. I. History, distribution, and taxonomy. *Ibid.* **68**: 55–80. *pls. 1–7*. 1952.

———. *Sarracenia leucophylla* Rafinesque. *Ibid.*, **70**: 57–60. 1954. [*S. leucophylla* for *S. Drummondii* Croom, and *S. alata* (Wood) Wood replaces *S. Sledgei* Macfarlane.]

——— and F. W. Case. Natural hybrids in the genus *Sarracenia*. II. Current notes on distribution. *Ibid.* **72**: 142–152. 1956.

CASE, F. W., Jr. Some Michigan records for *Sarracenia purpurea* forma *heterophylla*. Rhodora **58**: 203–207. 1956. [A yellow-flowered form.]

HARPER, R. M. The American pitcher-plants. Jour. Elisha Mitchell Sci. Soc. **34:** 110–125. *pls. 2–6.* 1918.

HEGNER, R. W. The protozoa of the pitcher plant, *Sarracenia purpurea.* Biol. Bull. Woods Hole **50:** 271–276. 1926.

HEPBURN, J. S., and F. M. JONES. Occurrence of antiproteases in the larvae of the *Sarcophaga* associates of *Sarracenia flava.* Contr. Bot. Lab. Univ. Penn. **4:** 460–463. 1919.

———, ——— and E. Q. ST. JOHN. The biochemistry of the American pitcher plants. Trans. Wagner Free Inst. Sci. **11:** 1–95. 1927.* [Full bibliography.]

HOLM, T. Contributions to the knowledge of the germination of some North American plants. Mem. Torrey Bot. Club **2:** 57–108. *pls. 5–19.* 1890–1891. [*S. purpurea*, 63, 64, *pl. 7, figs. 23–27.*]

LIVINGSTON, M. J. Microsporogenesis in *Sarracenia minor* Walt. Quart. Jour. Fla. Acad. Sci. **13:** 61–71. 1950.

MACFARLANE, J. M. Observations on *Sarracenia.* Jour. Bot. **45:** 1–7. 1907. [Includes history of name, notes on various spp.]

MARKGRAF, F. Les homologies des feuilles et les relations taxinomiques chez les Sarraceniales. VIII^e Congr. Int. Bot. Rapp. Comm. **Sect. 2, 4, 5, 6:** 50–52. 1954.

NICHOLS, M. L. The development of the pollen of *Sarracenia.* Bot. Gaz. **45:** 31–37. *pl. 5.* 1908. [Five species, two hybrids.]

RUSSELL, A. M. The macroscopic and microscopic structure of some hybrid Sarracenias compared with that of their parents. Contr. Bot. Lab. Univ. Penn. **5:** 3–41. *pls. 1–5.* 1919.

SHREVE, F. The development and anatomy of *Sarracenia purpurea.* Bot. Gaz. **42:** 107–126. *pls. 3–5.* 1906.

SIMS, J. *Sarracenia flava.* Bot. Mag. **20:** *pl. 780.* 1804. (See also *S. minor.* **21:** *pl. 849.* 1805; *S. purpurea.* **41:** *pl. 1710.* 1825; *S. rubra.* [*S. leucophylla?*] **63:** *pl. 3515.* 1836.)

SMITH, J. B. Report of the New Jersey State Agricultural Experiment Station upon the mosquitoes occurring within the state, their habits, life history, etc. v + 482 pp. Trenton, N. J. 1904. [342–353, description and life history of *Wyeomyia smithii* Coquillet.]

WALCOTT, M. V. Illustrations of North American pitcher-plants. (Including E. T. WHERRY, Distribution of North American pitcher plants, pp. 1–23, and F. M. JONES, Pitcher plants and their insect associates, pp. 25–34.) 34 pp. *15 col. pls.* Smithsonian Inst., Washington, D. C., 1935.

WALTI, A. Determination of the nature of the volatile base from the rhizome of the pitcher plant *Sarracenia purpurea.* Jour. Am. Chem. Soc. **67:** 2271. 1945.* [For use in medicine.]

WHERRY, E. T. Acidity relations of the Sarracenias. Jour. Wash. Acad. Sci. **19:** 379–390. 1929. [Includes description of *S. Jonesii.*]

———. The geographic relations of *Sarracenia purpurea.* Bartonia **15:** 1–6. *pl. 1.* 1933.

———. The Appalachian relative of *Sarracenia flava.* Bartonia **15:** 7, 8. 1933. [*S. oreophila* Wherry.]

DROSERACEAE Salisbury (SUNDEW FAMILY)

Annual or perennial, rosulate or short-stemmed [or caulescent], insectivorous herbs of damp or wet soils [a few completely aquatic or of dry soils], the leaves alternate, infolded or circinate in vernation, the blades modified as active traps (*Dionaea, Aldrovanda*) or equipped with mucilage-tipped irritable tentacles (*Drosera, Drosophyllum*). Roots mostly adventitious. Flowers bisexual, regular, the insertion hypogynous. Sepals and petals 5, free. Stamens 5–15(–20), extrorse; pollen in tetrads (except *Drosophyllum*). Gynoecium syncarpous; styles 3[5] and deeply bifid [or otherwise divided] or single and with fimbriate stigma; ovary 1-locular with 3[5] parietal placentae or the ovules at the base of the locule; ovules anatropous, 2-integumented. Seeds small, numerous, the embryo minute, straight, embedded in abundant endosperm. (Including Dionaeaceae Small.) TYPE GENUS: *Drosera* L.

Four genera, *Drosophyllum* Link, *Dionaea* Ellis, *Aldrovanda* L., and *Drosera* L., the first three monotypic, *Dionaea* and *Drosera* in our area. The sensitive leaves, bisexual, usually pentamerous flowers, unilocular ovary, and parietal or basal placentation mark the family. Numerous reticulate interrelationships link all four genera and make separation into two families an arbitrary matter.

In addition to its present position, the family has been placed near the Violaceae and Ochnaceae in the Parietales (Violales) near the Saxifragaceae, and near the Lentibulariaceae. The validity of the present association with Sarraceniaceae and Nepenthaceae (the three constituting the Sarraceniales) is in need of careful examination, and the relationships of the family are still unsettled.

REFERENCES:

BAILLON, H. Droséracées. Hist. Pl. **9:** 225–235. 1888.

BENTHAM, G., and J. D. HOOKER. Droseraceae. Gen. Pl. **1:** 661–664. 1865.

DARWIN, C. Insectivorous plants. ed. 2. London, 1875.

DIELS, L. Droseraceae. Pflanzenr. IV. **112**(Heft 26): 1–136. 1906.

———. Droseraceae. Nat. Pflanzenfam. ed. 2. **17b:** 766–784. 1936.

DRUDE, O. Droseraceae. Nat. Pflanzenfam. III. 2: 261–272. 1891.

GRAY, A. Droseraceae. Gen. Pl. U. S. **1:** 191–200. *pls. 83–86.* 1849. [*Drosera, Dionaea, Parnassia.*]

LLOYD, F. E. The Carnivorous Plants. xv + 352 pp. Chronica Botanica, Waltham, Mass., 1942. [Chap. X. *Drosera*; XII. *Dionaea* and *Aldrovanda.* Comprehensive review of the structure and biology of these plants; extensive bibliography.]

KEY TO THE GENERA OF DROSERACEAE

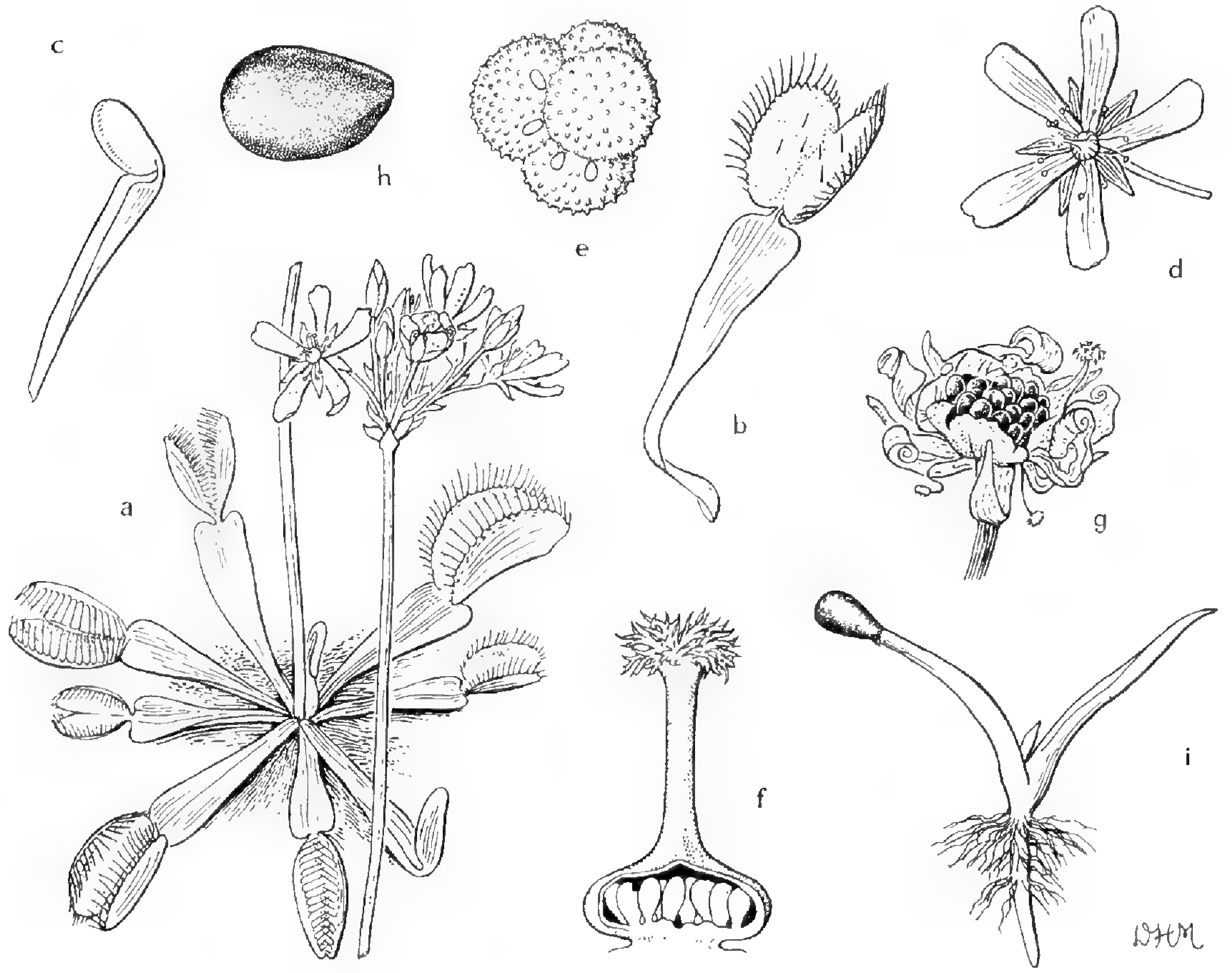
Leaf blades 2-lobed, hinged lengthwise in the middle, sensitive and closing, the marginal bristles interlocking; stamens mostly 15 (10–20); styles united; placentation basal. .... 1. *Dionaea.*

Leaf blades linear to suborbicular, equipped on margins and upper surfaces with numerous gland-tipped irritable tentacles; stamens 5; styles 3, so deeply bifid as to appear to be 6; placentation parietal. .... 2. *Drosera.*

1. **Dionaea** Ellis, Directions for bringing over seeds and plants from the East Indies and other distant countries, etc., 38. 1770; Nov. Act. Upsal. 1: 98. *pl. 8.* 1770.

Rosulate, scapose, insectivorous herbs, the leaf blades hinged medially and forming a sensitive trap, the petioles winged (scarcely so in full sun in summer), their bases forming a subterranean bulb-like structure around the short, horizontal, sympodial rhizome, the roots adventitious. Inflorescence from the terminal bud, cymose-umbelliform. Sepals 5. Petals 5, white, marcescent. Stamens usually about 15. Gynoecium of 5 united carpels, style 1, the stigma with numerous papillae, the ovary 1-locular, the placentation basal. Capsule opening irregularly; seeds obovoid, numerous, black and shining. Embryo sac development normal (Polygonum type). Type and sole species: *D. Muscipula* Ellis. (Name from Greek, *Dione*, originally the mother of Aphrodite [Venus] but later used as "daughter of Dione," hence Aphrodite or Venus.) — Venus' fly-trap, fly-trap.

Dionaea Muscipula ($2n = 30$ or 32?) is known to occur only on the Atlantic coastal plain from Beaufort County, inland to Moore County,



Dionaea. *D. Muscipula:* a, habit, × 1/2; b, mature leaf, × 1/2; c, young leaf, the marginal bristles folded within the blade, × 1/2; d, flower, × 1; e, pollen tetrad, × ca. 200; f, gynoecium, a portion of ovary wall removed to show basal placentation of ovules, semidiagrammatic, × 5; g, open fruit, showing irregular dehiscence, seeds, and marcescent stamens and petals, × 2; h, seed, × 10; i, seedling (after Smith, 1931), × 8.

North Carolina, and southward to the south bank of the Santee River, Charleston County, South Carolina. Roberts and Oosting suggest that the total range is determined by gross soil characteristics (those of the St. Johns soil series), while local populations are restricted by the depth to which the surface soil desiccates in dry periods and by light intensity. Fire influences the latter and helps to maintain the limited habitat which is ecotonal between wet, evergreen-shrub bogs (pocosins) and the dry sands of *Pinus australis-Aristida* savannas. The slow seed dispersal (probably by rain), the short period of seed viability, and the summer germination under rather particular requirements of high humidity and loose organic matter on a sand surface are additional factors.

Dionaea is famous for its bear-trap-like hinged leaf blades, each half of which is equipped with three sensitive bristles, which, when stimulated, cause the trap to close. Entrapped insects are prevented from leaving by overlapping marginal bristles and are digested by enzymes secreted by minute glands on the blade surface. Many problems remain in connection with the operation of the traps (which have been compared with those of *Aldrovanda*) and with the nutrition (both mineral and organic) of *Dionaea*. The occurrence of *Dionaea*, *Sarracenia*, *Drosera*, *Utricularia*, and *Pinguicula* together in soils low in mineral nutrients is suggestive.

Although often occurring in widely scattered colonies, the species is locally abundant. Vast numbers formerly were sold as novelties, only to perish in cultivation, but the plant is now protected by law in North Carolina (General Statutes of North Carolina, Section 14–129.1). *Dionaea* can be cultivated for scientific purposes in constantly moist peat or peaty sand in full sunlight with a cool, dormant period in winter. If grown in shade the petioles become more broadly winged, successive traps diminish in size and the plant eventually dies. (Bright light is also important in flower production.) Propagation may be by seeds or by cuttings from the vegetative parts or the inflorescence before the flowers open.

Flowering occurs from late May to mid-June (or July). Each proterandrous flower is open about three days. Seeds are shed by mid-July and germinate immediately. (Prompt storage under cold, moist conditions will maintain seed viability for up to a year, however.) Embryology and seed germination are similar to those of *Drosera rotundifolia*. In drying, leaves and flowers tend to blacken, as with various hemiparasites.

REFERENCES:

Many references prior to 1942 omitted; see review and bibliography in LLOYD, Carnivorous Plants.

CLARK, A. H. A new locality for Venus' fly-trap (*Dionaea Muscipula*). Science **88**: 188. 1938. [Se. corner of Moore Co., N. C.]

COKER, W. C. The distribution of Venus' fly trap (*Dionaea Muscipula*). Jour. Elisha Mitchell Sci. Soc. **43**: 221–228. *pl. 33.* 1928. [Includes map, reprint of Ellis' description.]

DUBOIS, C. G. *Dionaea Muscipula.* Bot. Gaz. **16**: 200, 201. 1889. [Reports proterandry, duration of flowering, pollination.]

FRAÜSTADT, A. Anatomie der vegetativen Organe von *Dionaea Muscipula* Ell. Beitr. Biol. Pflanzen **2:** 27–64. *pls. 1–3.* 1877.

HARSHBERGER, J. W. An unusual method of vegetative reproduction in *Dionaea Muscipula.* Bot. Gaz. **44:** 382, 383. 1907. [Leafy branchlets in the inflorescence; see also Contr. Bot. Lab. Univ. Penn. **1:** 46–49. *pls. 5, 6.* 1892.]

MACFARLANE, J. M. Contributions to the history of *Dionaea Muscipula,* Ellis. Contr. Bot. Lab. Univ. Penn. **1:** 7–44. *pl. 4.* 1892. [Concerned mostly with leaf function.]

ROBERTS, P. R., and H. J. OOSTING. Responses of Venus fly trap (*Dionaea Muscipula*) to factors involved in its endemism. Ecol. Monogr. **28:** 193–218. 1958. [The most comprehensive study.]

SMALL, J. K. *Dionaea Muscipula.* Addisonia **10:** 1, 2. *pl. 321.* 1925. [See also J. SIMS, Bot. Mag. **20:** *pl. 785.* 1804.]

SMITH, C. M. Development of *Dionaea Muscipula.* I. Flower and seed. Bot. Gaz. **87:** 507–530, *pls. 20–24.* 1929. II. Germination and development of seedling to maturity. *Ibid.* **91:** 377–394. 1931. [Includes comments on relationships. See also HOLM, T., Mem. Torrey Bot. Club **2:** 71, 72. 1891, for seed germination.]

STUHLMAN, O. A physical analysis of the opening and closing movements of the lobes of Venus' fly-trap. Bull. Torrey Bot. Club **75:** 22–44. 1948. [See also BROWN and SHARP, Bot. Gaz. **49:** 290–302. 1910.]

———. The fundamental action potentials developed in the lobes of Venus' fly-trap (*Dionaea Muscipula*) due to a stimulus. (Abs.) Jour. Elisha Mitchell Sci. Soc. **66:** 112–114. 1950. [A compound action potential of two components, "one attributed to a transient comparable to the neural C-action-potential of unmyelinated mammalian nerve fibers and the other to the movement of an electrolyte associated with the hydrodynamic reactions of the lobes in closure."]

——— and E. B. DARDEN. The action potentials obtained from Venus's-flytrap (*Dionaea Muscipula*). Science **111:** 491, 492. 1950.

2. **Drosera** Linnaeus, Sp. Pl. 1: 281. 1753; Gen. Pl. ed. 5. 136. 1754.

Perennial or annual, insectivorous herbs, mostly of acid sands and bogs; plants rosulate, scapose [or sometimes caulescent and up to 1 m. high]. Leaves usually petiolate, the blades suborbicular to filiform, the margins and upper surfaces in ours with irritable, gland-tipped tentacles; stipules present or absent. Flowers 5-merous, the petals white, pink, rose-purple [or yellow], marcescent. Stamens 5. Gynoecium of 3[5] united carpels, the 3 styles deeply bifid in ours, the ovary 1-locular with 3 parietal placentae. Capsule splitting between the placentae, 3-valved, with numerous minute seeds. Embryo sac development normal (Polygonum type). TYPE SPECIES: *D. rotundifolia* L. (Name from Greek, *droseros,* dewy, from the glittering, glutinous droplets secreted by the glandular tip of each tentacle.) — SUNDEW, CATCH-FLY.

More than 100 species in three subgenera, twelve sections, distributed primarily in the Southern Hemisphere (more than 50 species in Australia and New Zealand alone). Only sect. DROSERA (sect. *Rossolis* Planch.) is represented in North America. Seven well-marked species occur in the United States, two, *D. linearis* Goldie and *D. longifolia* L. (*D. anglica Huds.*), entirely to the north of our area.

Characters of seeds, stipules and leaves are especially diagnostic in *Drosera*. The genus is vegetatively plastic in response to environment, and, as a result, seeds are among the most dependable taxonomic criteria. Petal color, seldom noted, varies in some species: the petals of *D. intermedia* Hayne, white or pinkish in the North, are purple in South America, and those of *D. brevifolia* Pursh, usually white or pink, are pink to purple in Texas (and perhaps in South America).

Drosera rotundifolia, of circumboreal distribution, extends southward on the Coastal Plain to southeastern Virginia (and Charleston, South Carolina?) and along the mountains to northern Georgia. Leaf shape, stipules, and pale sigmoid-fusiform seeds are characteristic. *Drosera capillaris* Poir. (*D. tenella* Willd.), vegetatively similar, but smaller, with ellipsoid seeds coarsely papillose-corrugated in 14–16 ridges, and with a very different range (Virginia to Florida and Texas; Cuba, Jamaica; northern South America; southern Mexico, British Honduras), is sometimes confused with this species. *Drosera brevifolia* (Virginia to Florida, Tennessee, Arkansas, Texas, Cuba, northern South America (?), Paraguay, Uruguay, and northern Argentina) lacks stipules and has glandular scapes and sepals and obovoid seeds with crateriform markings. *Drosera intermedia*, with conspicuous stipules, oblong-spatulate leaf blades, scapes which curve outward at the base, and oblong, densely papillate seeds, is of wide distribution from Europe to Newfoundland and westward to Minnesota, southward along the Coastal Plain to Florida and Texas, and to Cuba, Hispaniola, and northern South America. *Drosera filiformis* Raf. var. *filiformis*, with erect, filiform leaves to 25 cm. long, and purple tentacles and petals, is confined to the Coastal Plain from Cape Cod, Massachusetts, southward to southeastern North Carolina (? South Carolina and Georgia). Varietas *Tracyi* Diels (*D. Tracyi* Macfarl.), of western Florida and southern Georgia to Mississippi, seems to be separated geographically from var. *filiformis*, although it has been reported from South Carolina. It is a distinct taxon, differing in the larger leaves (to 40 cm. long), the greater size of the floral parts, and the green tentacles.

Section DROSERA is a polyploid group of about 40 species among which chromosome numbers of $2n = 20$, 40, and 80 are known. The North American taxa are diploid, with the exception of *D. longifolia* ($2n = 40$) which appears to be of amphiploid origin. (Species of other sections have been reported with $2n = 28$, 32, 34, and 60.) Three naturally occurring diploid hybrids and two triploids, all sterile, are known from this section. Chromosomal sterility is indicated in one of the diploid hybrids. In some areas, *D. brevifolia, D. capillaris, D. filiformis*, and *D. intermedia* occur in close proximity, but hybrids are unreported in our area, although that of the latter two has been found once in New Jersey. An artificial hybrid might show whether a genetic barrier exists between *D. filiformis* var. *filiformis* and var. *Tracyi*.

The leaves of *Drosera* catch and digest various small animals (mostly insects) which become entangled in the mucilaginous secretion of the tentacular glands. The tentacles bend inward, pressing the capture against the leaf blade which, in some species (e.g., *D. rotundifolia*, *D. intermedia*, but not *D. filiformis*), may also bend enfolding the prey. Both movements involve cell elongation; a single tentacle is capable of bending approximately three times before the limit of growth is reached.

The genus exhibits remarkable regenerative powers, and, in some species (e.g., *D. rotundifolia*), asexual reproduction by adventitious plantlets from inflorescences or detached leaves is common. Individual flowers of the scorpioid (rarely forked) cyme are open for only a single morning in sunlight and are self-pollinated upon closing if cross-pollination has not already occurred. Some of our species produce overwintering buds of tightly compacted leaves, but *D. brevifolia* apparently behaves as an annual in many areas and has been so described (*D. annua* Reed).

REFERENCES:

See family references. LLOYD (1942) summarizes especially structure and function of leaves. Most references included by him have been omitted.

ARISZ, W. H. Absorption and transport by the tentacles of *Drosera capensis*. V. Influence on the transport of substances inhibiting enzymatic processes. Acta Bot. Neerl. **2**: 74–106. 1953. [See his bibliography for I–IV.]

BARCLAY, H. G. A preliminary report of the ecology of a *Drosera* meadow. Proc. Okla. Acad. Sci. **18**: 22–25. 1938. [*D. brevifolia* (as *D. annua*) in se. Okla.]

BRAT, L., G. KENDA, and F. WEBER. Rhabdoide fehlen den Schleisszellen von *Drosera*. Protoplasma **40**: 633–635. 1951.*

BRUMMER-DINGER, C. H. Notes on Guiana Droseraceae. Acta Bot. Neerl. **4**: 136–138. 1955. [Taxonomic notes; includes 2 or 3 of our spp.]

CHURCHILL, J. R. An unusual form of *Drosera intermedia*, var. *americana*. Rhodora **2**: 70, 71. *pl. 15, fig. 8*. 1900. [Caulescent form in deep water (= f. *natans* Heuser).]

FAVARD, A. Étude histologique de la formation du point végétatif dans le bourgeonnement de[s] pétioles de *Drosera rotundifolia* L. Compt. Rend. Acad. Sci. Paris **237**: 1753–1755. 1953.

———. Formation et premières différenciations du système conducteur chez *Drosera rotundifolia* L. au state jeune. *Ibid.* **240**: 338–340. 1955.

———. Influence d'une différenciation précoce sur l'évolution du système conducteur de *Drosera rotundifolia* L. lors de la germination. Avortement de la racine. *Ibid.* **242**: 405–407. 1956.

———. Évolution du point végétatif de *Drosera rotundifolia* L. Deuxième étape. *Ibid.* 2386–2389.

———. Transformation du point végétatif en méristème d'inflorescence chez *Drosera rotundifolia* L. *Ibid.* **243**: 2124–2127. 1956.

———. Étude des inflorescences de *Drosera intermedia* Hayne: la cyme unipare scorpoïde et ses modifications. *Ibid.* **246**: 2508–2511. 1958.

———. Étude cytologique du développement de l'embryon de *Drosera rotundifolia* L.: ontogenèse des méristèmes primaires. *Ibid.* **248**: 1570–1573. 1959.

FERNALD, M. L. A peculiar variety of *Drosera rotundifolia*. Rhodora **7**: 8, 9. 1905. [Var. *comosa* Fern. See also M. LEVINE, Further observations on chloranthy in *Drosera intermedia.* Bot. Gaz. **62:** 389–399. *pl. 13.* 1916. Both instances a response to unfavorable ecological conditions?]

Hall, B. A. The floral anatomy of *Drosera* and *Begonia* and its bearing on the theory of carpel polymorphism. Am. Jour. Bot. **36:** 416–421. 1949.

Hamet, M. R. Observations sur le genre *Drosera.* Bull. Soc. Bot. Fr. IV. **7:** 26–38, 52–76. *pl. 2.* 1907. [Taxonomy; key to all spp.; includes drawings of seeds of some.]

Hooker, H. D., Jr. Mechanics of movement in *Drosera rotundifolia.* Bull. Torrey Bot. Club **44:** 389–403. 1917.

Hultén, E. The amphi-Atlantic plants and their phytogeographical connections. Sv. Vet-akad. Handl. IV. **7**(1): 1–340. 1958. [*D. intermedia,* p. 56, *map 38*; dots in western Canada probably *D. longifolia.*]

Leavitt, R. G. Seedlings and adventitious plants of *Drosera.* Torreya **9:** 200–203. 1909.

Levine, M. Somatic and reduction divisions in certain species of *Drosera.* Mem. N. Y. Bot. Gard. **6:** 125–147. *pls. 16–19.* 1916.

Macfarlane, J. M. Observations on some hybrids between *Drosera filiformis* and *D. intermedia.* Contr. Bot. Lab. Univ. Penn. **2:** 87–99. *pl. 12.* 1899.

Narasimhachar, S. G. A contribution to the embryology of *Drosera burmanni* Vahl. Proc. Indian Acad. Sci. B. **29:** 98–104. 1949.*

———. A contribution to the embryology of *Drosera indica,* L. *Ibid.* **33:** 290–295. 1951.*

Paris, R., and J. C. Denis. Les droséras: leur charactérisation dans divers médicaments. Ann. Pharm. Fr. **15:** 145–159. 1957.*

Pace, L. *Parnassia* and some allied genera. Bot. Gaz. **54:** 306–324. 1912. [Includes development of embryo sac of *D. rotundifolia.*]

Patankar, T. B. V. Further contribution to the embryology of *Drosera burmanni* Vahl. Proc. Indian Acad. Sci. B. **43:** 161–171. 1956.

Raju, M. V. S., and T. B. V. Patankar. Pollen morphology in three species of *Drosera* L. Grana Palynologica II. **1:** 153–155. 1956. [*D. Burmannii, D. indica, D. peltata.* See also G. Erdtman, Sv. Bot. Tidskr. **39:** 290. 1945.]

Reed, E. L. Ecologic notes on *Drosera annua.* Torreya **16:** 125–130. 1916. [See also *ibid.* **15:** 246, 247. 1915.]

Rosenberg, O. Cytologische und morphologische studien an *Drosera longifolia* × *rotundifolia.* Sv. Vet-akad. Handl. **43**(11): 1–65. *4 pls.* 1909. [Classic study of chromosomal behavior in a triploid hybrid; embryo sac and pollen development.]

Souèges, E. C. R. Embryogénie des Droséracées. Développement de l'embryon chez le *Drosera rotundifolia* L. Compt. Rend. Acad. Sci. Paris **202:** 1457–1459. 1936.

Trankowsky, D. A. La spermatogènese et la fécondation chez la Drosère (*Drosera*). (In Russian; French résumé.) Bull. Mosk. Obsch. Isp. Pri. Biol. **47:** 104–112. 1938.

Wood, C. E., Jr. Evidence for the hybrid origin of *Drosera anglica.* Rhodora **57:** 105–130. 1955. [= *D. longifolia* L.; includes miscellaneous notes on U. S. spp.; summary of chromosome numbers.]

Wynne, F. E. *Drosera* in eastern North America. Bull. Torrey Bot. Club **71:** 166–174. 1944. [Key, descriptions, maps, illustrations of seeds of the North American spp.]

———. *Drosera filiformis.* Addisonia **22:** 39, 40. *pl. 724.* 1945. [See also W. J. Hooker, Bot. Mag. **63:** *pl. 3540.* 1836.]

A REVISION OF THE GENUS CLETHRA IN CHINA

SHIU-YING HU

TWENTY SPECIES OF CLETHRA have been recorded from China. Ninety per cent of these were described as new entities. These descriptions were prepared by British, French, American, Austrian, Dutch, and Chinese botanists, and their research was conducted in nine different European and American botanical institutions. In reviewing their work, it becomes apparent that some of them had no proper understanding of the variability of a species of *Clethra*. Consequently, repetition and confusion were created for the taxonomy of the Chinese species. Under these conditions the naming of a new collection of *Clethra* becomes a seemingly hopeless task. Even in the herbarium of the Arnold Arboretum where outstanding collections of Chinese specimens, including many types and photographs of types accompanied by fragments of the type-material, are deposited, one found it difficult to name an unidentified specimen of *Clethra*. A generalized treatment of the genus which contains a well-balanced key to the species and concise descriptions of them to aid in the identification of specimens is lacking. To supply such a treatise is the immediate aim of this revision.

The genus *Clethra* has an Asiatic-American distribution. An analysis of the countries of origin of the species as listed in the *Index Kewensis* shows that China and Mexico have the largest numbers of species. Careful examination of the species described from these two countries and their adjacent land-masses indicates that morphological variations among the Chinese species are far more diverse than among their tropical American allies. Actually, all the outstanding morphological features of the American species can be found among some of the Chinese species; yet the variations of certain Chinese forms are not to be found among the New World species. For this reason, a systematic revision of the Chinese *Clethra* has a more far-reaching significance than the merely utilitarian aim mentioned above. It seems that the problems involved in the classification of Chinese *Clethra* constitute the core of investigations which may lead to an understanding of the morphology, taxonomy, and geographical distribution of the genus as a whole. A proper knowledge of the Chinese species may throw some light on future studies of the American species.

Dr. Robert C. Foster of the Gray Herbarium, Harvard University, has kindly read this manuscript and given many helpful suggestions. To him I wish to express my grateful appreciation.

Unless accompanied by a note of explanation, all the specimens cited in this article are deposited in the herbaria of the Arnold Arboretum and the Gray Herbarium.

HISTORY

The genus *Clethra* was established on a North American species, *C. alnifolia*, originally known to European naturalists from Carolina and Virginia. The name *Clethra* (derived from the ancient Greek name for the alder, *klethra*, in allusion to the resemblance of the leaves of the type species to those of *Alnus*) first appeared in Gronovius' *Flora Virginica*, published in 1739. When Gronovius created this name he cited two earlier references, one from Plukenet's *Phytographia*, published in 1691, and the other from Catesby's *The Natural History of Carolina*, published from 1731 to 1743. He even quoted Catesby's diagnostic comment on the taxon intact, "Alni folia Americana serrata, floribus pentapetalis albis, in spicam dispositis." Linnaeus used Gronovius' name, giving the same quotation. A specimen of *C. alnifolia* is preserved in the Linnaeum herbarium, number 567.1. The species was introduced into European gardens in the early eighteenth century.

For a century and a quarter after the establishment of the genus, the classification of *Clethra* was based principally on American species. In 1839, De Candolle, in his *Prodromus*, placed *Clethra* in the tribe Andromedeae of the family Ericaceae. His description of the anthers represented an erroneous observation. Apparently he mistook the developmental stage in the flower bud to be the mature anther and, though he did mention the inversion, he interpreted the cordate portion as the base and the mucronate and muticous end as the apex. In regard to the classification of the species, he arranged those known at that time in two sections, *Euclethra* and *Cuellaria*. He characterized his section *Euclethra* as having exserted stamens and pistils and deciduous leaves, and placed five North American species in this section. He characterized the section *Cuellaria* as having the stamens and pistils included and assigned 17 species from Central and South America and a single species from the Madeira Islands to this section. Although Blume had published *C. canescens* Reinw. from Celebes and Borneo, De Candolle did not include this species in his system.

In 1851 in an article, *Studien über die natürliche Klasse Bicornes*, Klotzsch separated *Clethra* from the family Ericaceae and raised it to a family, Clethraceae, on the strength of its choripetalous corolla, corolla and stamens deciduous after anthesis, its obcordate anthers which are retroflexed at first and then introrse and dehiscent by apical rimiform pores, and its bifid or trifid stigmas.

The portion of the Bentham and Hooker's *Genera Plantarum* that covers *Clethra* was prepared by Hooker. In this work Hooker placed *Clethra* at the end of the family Ericaceae as "Genus Anomalum." By this time several species had been introduced into cultivation in England, e.g., *C. arborea* from the Madeira Islands, *C. quercifolia* from Jalapa in Mexico, *C. tomentosa* and *C. alnifolia* from eastern North America. With live plants as well as herbarium specimens at his disposal, he gave the most accurate description of the important characters of the genus. Regarding the anthers, he pointed out that they are affixed at the middle of the back, are often obovate in shape and acute at the base, are extrorse at first then turning introrse, and dehisce above the middle by elongate pores.

The Chinese *Clethra* were not known to botanists until 1883. In that year Hance published *C. faberi* from Loh-fau Mountain of Kwangtung Province. Two years before this, Franchet, in his *Plantae Davidianae*, had published *Clethra scandens.* However, this species is not a true *Clethra*, and since then has been made the type species of the genus *Clematoclethra* Maxim.

When Hemsley prepared the enumeration of the plants from China, he saw Henry's collections of *Clethra* from Hupei. He was indeed not critical in his observation. In publishing Forbes and Hemsley's *Index florae sinensis* in 1889, he treated Henry's collections as *C. canescens* Reinw., a species known only from Western Malaysia. In the same work he reduced *C. faberi* Hance (from Kwangtung), *C. lancifolia* Turcz. (from the Philippines), and *C. barbinervis* Sieb. & Zucc. (from Japan) to *C. canescens.*

In the same year O. Drude published his contributions on Clethraceae, Ericaceae, and other related families in Engler and Prantl's *Die natürlichen Pflanzenfamilien.* In this work Drude accepted Klotzsch's proposal of raising the genus to a family and in the description of the genus, followed Hooker. In the classification of the species, he adopted De Candolle's two sections and placed the Asiatic species *C. barbinervis* in section *Euclethra.* He separated *C. arborea* Ait., a species from the Madeira Islands, from section *Cuellaria* and assigned it to an unnamed section which he placed between *Euclethra* and *Cuellaria.*

Meanwhile, material collected by French missionaries who were stationed in central and western China reached Paris. Franchet in 1895 published *C. fargesii* from eastern Szechuan and *C. delavayi* from western Yunnan. Incidentally, these species define the northern and western limits of the range of the genus in China.

Bodinier, Cavalerie and Esquirol were French missionaries who were sent to Kweichow in later years. Their collections reached Léveillé who in 1912–3 published six more species of *Clethra: C. bodinieri, C. cavaleriei, C. esquirolii, C. kaipoensis, C. lineata* and *C. pinfaensis.* As indicated by a key to these species which he prepared in the *Flore du Kouy-Tchéou*, Léveillé observed several characters which are important for distinguishing the Chinese species of *Clethra.* He observed that some species possess entire stigmas, while others have lobate or cleft ones. He also noticed that some species have elongate pedicels, while others have short ones. The arrangement of the racemes was also mentioned in his key, as some were umbellate while others were solitary.

After E. H. Wilson returned from his third trip to West China, Rehder and Wilson worked cooperatively on Wilson's numerous collections. In 1913, they described *C. monostachya*, a species characterized by its pilose styles. When Rehder worked over the ligneous plants described by Léveillé, he was able to examine the types of Léveillé's six species of *Clethra* which were described from Kweichow. In 1934 Rehder recognized three of them and merged *C. esquirolii* and *C. lineata* with *C. cavaleriei* and *C. pinfaensis* with *C. kaipoensis.*

Aside from the species described by these workers, seven additional binomials were added to the genus by Handel-Mazzetti, Sleumer, Hao, Fang, and Li. None of these authors seems to have attempted to place his species in the existing taxonomic system, and some of these names are synonymous with earlier described species.

TAXONOMIC CHARACTERS

Habit of growth. The species of *Clethra* generally have the habit of growth common in the family Ericaceae. The branches have subverticillate branchlets with leaves crowded at the apex. The majority of the Chinese species are deciduous and two of them are evidently evergreen.

In the deciduous species, each vegetative branchlet has a large, subsessile terminal bud and 1–3 subterminal axillary buds (Fig. 24, right). In the following year, the large terminal bud of a mature plant develops into a flowering shoot provided with a few smaller leaves, a bracteate raceme or panicle, and 1–3 axillary buds immediately below the inflorescence (Fig. 24, left). The subterminal buds of a vegetative branchlet and the axillary buds of a flowering branchlet are of the same nature and function. They are all active during the growing season and consequently attain various stages of development before the leaves fall in the autumn. The more vigorously growing ones develop into stems 4–6 cm. long, each bearing 3 or 4 leaves crowded at the shoot apex around the terminal winter bud. The weaker ones generally develop into short stems 1–2 cm. long, each bearing 1 or 2 very small, bract-like leaves surrounding the terminal winter bud. Often the stem-portion becomes so short that the bud appears as though it were a stalked winter bud. In this case, it bears no leaf. In the next growing season these winter buds either unfold and develop into short vegetative shoots with large leaves and strong, fat terminal buds ready to produce flowers the third year, or they may develop into flowering shoots, depending upon the vigor of the plant, the environmental condition, and the heredity of the species.

In an evergreen species, an average branchlet of a mature plant is usually a flowering branchlet (Fig. 25). From one to four axillary buds immediately below the inflorescence develop into leafy shoots, each bearing a terminal bud and several normal leaves crowded at the apex. Normally, this terminal bud produces a flowering shoot during the next growing season. The inflorescences of the Chinese evergreen species are all simple racemes.

Schneider in 1910 observed the evergreen habit of *C. arborea* Ait. and used it as a key character in the classification of the then-known cultivated species of *Clethra*. With the Chinese species the evergreen habit is correlated with an entire stigma. It is an obvious key character for distinguishing species.

Leaves. The leaves on the branchlets of a deciduous species are of two kinds. Those developed from a winter bud are the normal leaves and are usually the larger ones. Those developed from axillary buds which become active during the same season in which they are produced are always smaller and narrower. They often become bract-like and are more pubescent than the normal leaves on the same plant. In the study of *Clethra,* whenever the comparison of leaf-characters is employed, care must be exercised so that the comparison is made between leaves of the same origin. With the Chinese species, the normal leaves of a species seem to be quite stable in shape, indumentum, dentation and venation. Any variation occurring in these respects is usually correlated with some flower character, and, for this reason, the leaf-characters are used as auxiliary criteria for distinguishing species.

Inflorescences. The Chinese species of *Clethra* are summer bloomers. The earliest flowering species, *C. bodinieri,* begins to flower in June and its fruits mature in early August. The latest flowering species, *C. kaipoensis,* is in full bloom in middle September. The majority flower in July and August, however.

The inflorescences of most Chinese species of *Clethra* are either simple terminal racemes (FIGS. 25, 26), or paniculate racemes. The panicles are sessile and subumbelliform (FIG. 27). The inflorescences of weak or old branchlets of a species normally bearing panicules may appear simply racemose. However, a good specimen of the species usually has paniculate inflorescences. The form of inflorescences, when correlated with leaf and flower characters, is a convenient and rather reliable character for distinguishing species. For this reason, it has been used as a key character in most manuals.

Rachis. The rachises of all the species of *Clethra* are densely pubescent. Those of the majority of the Chinese species have stellate hairs, but the rachises of *C. bodinieri* have simple, straight, appressed hairs. The type and density of the indumentum on the rachises is a useful aid in the recognition of species.

Bracts. The bracts subtending individual flowers have been used by American botanists for distinguishing *C. alnifolia* and *C. acuminata.* Some botanists put special emphasis upon the relative length of the bracts and the flowers. Actually, the bract is a rather poor character to employ for distinguishing species, for the bracts of *Clethra* are caducous. In general, the first opened flower of a raceme is situated a little below the middle of the inflorescence and the other buds open progressively towards both ends. The bracts and the mature flowers are not present at the same time (FIGS. 26, 27). It is only when the inflorescences are in the bud stage that the flower buds are subtended by bracts. The degree of maturity of the inflorescence makes a great difference in the relative length of the bracts and the flowers. This character should be used with great caution. It can never be used as the only criterion for distinguishing species.

Pedicels. The pedicels of *Clethra* exhibit a definite pattern of elongation during anthesis. As illustrated by FIGS. 1–6, which show stages from a fully grown flower bud to the dropping of the petals, the pedicels normally increase three times in length. The lengths of the pedicels of individual flowers of a species at comparable stages of development are rather uniform, however, and, for this reason, the Chinese species may be divided into two distinct groups, the long-pedicellate and the short-pedicellate.

Species in the long-pedicellate group have pedicels 5 mm. or more long immediately before anthesis (FIG. 1). When the petals begin to open, the length of the pedicels has doubled (FIG. 2), and by the time the petals drop off, the pedicel is three times as long as that of a mature flower bud (FIG. 3). After anthesis the pedicel elongates slightly; therefore the fruiting pedicel of a species is longer than that of the flower.

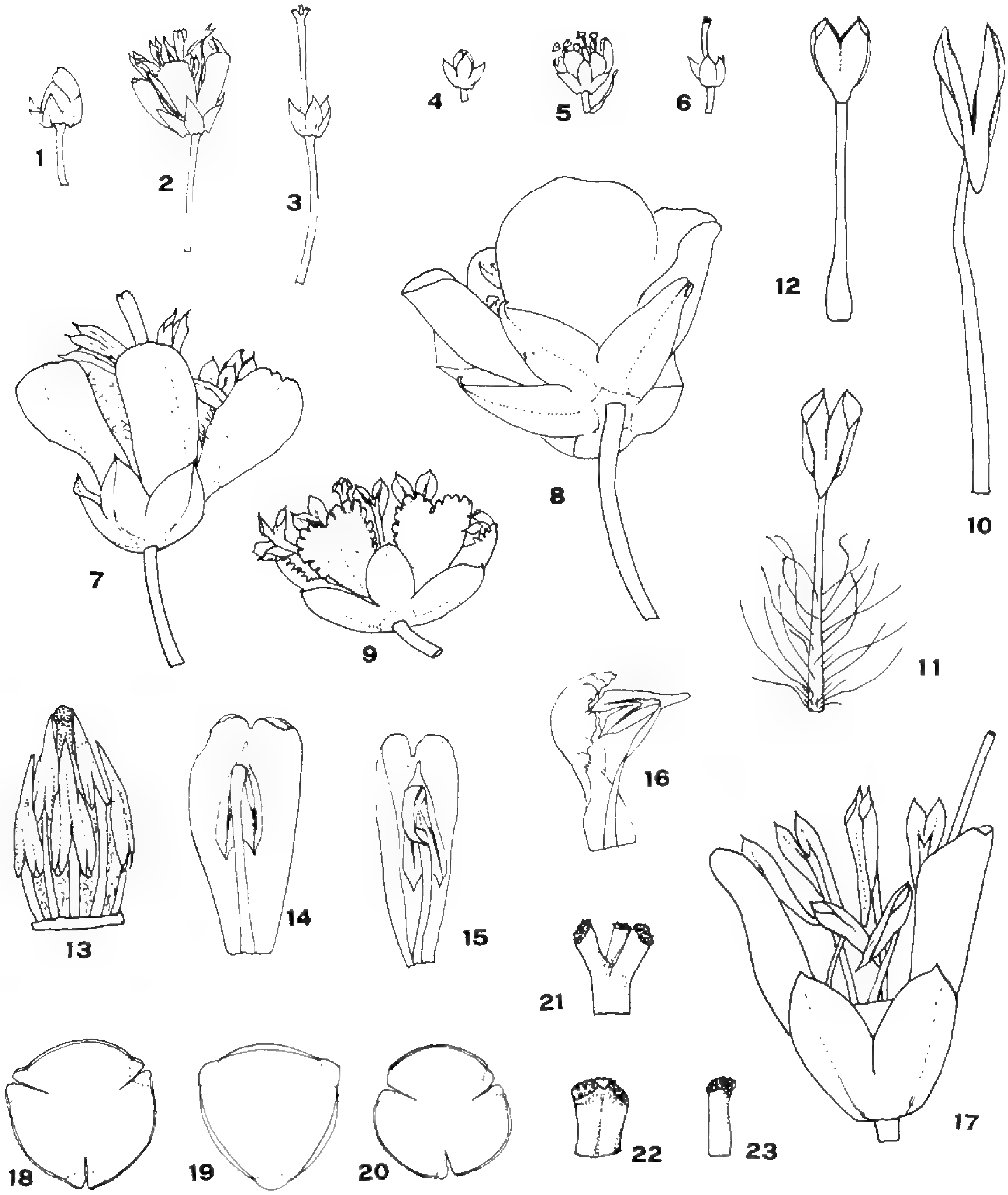
The pedicels of the short-pedicellate species are 1–2 mm. long immediately before anthesis (FIG. 4) and are normally shorter than the sepals. During anthesis, these pedicels elongate three-fold. As the sepals do not increase in size during this period, the length of the pedicels and that of the sepals are almost equal (FIGS. 5, 6).

The relative length of the pedicels and sepals is a reliable taxonomic character in *Clethra*. In employing this character one may use it only when the pedicels of the specimens are in comparable stages of development.

Calyx. The Chinese species of *Clethra* are distinctly gamosepalous. The calyx is essentially patelliform, deeply divided into 5 lobes. The short united portion is truncate and ridged at the basal end. The imbricate lobes vary in shape and size. The calyx attains mature size early in the development of the flower and maintains its shape and size during anthesis. Thus the calyx of a young flower bud and that of the young fruit of a species are about the same shape and size.

The calyces of the Chinese species of *Clethra* differ in the degree of division and in the shape and size of the lobes. The calyx of *C. bodinieri* is cut half way to the middle and its lobes are ovate, only 3 mm. long (FIG. 7). The calyx of *C. delavayi* is deeply cut with lanceolate lobes (FIG. 9) while the calyx of *C. kaipoensis* is deeply cut with oblong lobes (FIG. 8). The characters drawn from the calyx and sepals are reliable and are usually correlated with the length of the pedicel, the shape of the petals, and the relative length of the filaments. They can serve as good criteria for distinguishing sections and series.

Corolla. All the species of *Clethra* are choripetalous. Like the sepals, the petals of different Chinese species of *Clethra* can be grouped into three types. In *C. bodinieri* the petals are oblong, ciliate along the margin, ven-



FIGS. 1–23. MORPHOLOGICAL DETAILS OF CHINESE SPECIES OF CLETHRA.

FIGS. 1–6. Elongation of pedicels during anthesis, showing stages before, at, and after anthesis, × 1: 1–3, a long-pedicellate species, *C. esquirolii* (*Tsoong 83440*); 4–6, a short-pedicellate species, *C. brammeriana* (*Wang 247*).

FIGS. 7–9. Calyces, × 3: 7, shallowly divided calyx of *C. bodinieri* var. *parvifolia* (*Tsang 22450*) with ovate lobes; 8, deeply divided calyx of *C. delavayi* (*Delavay 3319*); 9, deeply divided calyx of *C. kaipoensis* (*Tsang 27916*) with oblong lobes.

FIGS. 10–12. Stamens, × 7: 10, *C. cavaleriei* (*Tsang 21413*), stamen from rather large flower with exserted stamens — note glabrous filaments, V-shaped elongate anther, slim thecae, elongate rimiform apical pores, and long basal process; 11, *C. delavayi* (*Forrest 11590*), stamen from large flower with included stamens — note villous filament, oblong-obovate anther, rather plump thecae, broad apical pores, short basal process; 12, *C. brammeriana* (*Wang 247*), stamen from small flower with exserted stamens — note glabrous filament trally barbate, and emarginate at the apex (FIG. 7). In *C. delavayi* the petals are large, almost entire, neither ciliate nor barbate, and are longer than the stamens (FIG. 8). In *C. faberi* and *C. kaipoensis* the petals are obovate, fringed, glabrous or slightly villose on the inside, and shorter than the stamens (FIG. 9). Petal characters, when correlated with characters of the pedicel, sepal, and stamen, can be used for distinguishing series.

Stamens. A flower of *Clethra* has ten stamens disposed in two whorls, the outer opposite the petals, and with shorter filaments (FIG. 13). In *C. bodinieri* the sepalad anthers are slightly longer. In *C. barbinervis* the difference in the size of the anthers is not appreciable.

The filaments of *Clethra* may be glabrous, hirsute, or villose. The indumentum of the filament has been used as a specific character. Before experimental evidence of the importance of hairs in the speciation of *Clethra* is available, this easily detected character is used for distinguishing species.

In the historical review we have noted that Hooker in 1876 gave a very accurate description of the stamens of *Clethra.* He pointed out that the anthers of this genus are obovate and the thecae dehisce above the middle by elongate pores. It appears now that in some widely accepted manuals and text books on the taxonomy of vascular plants published in recent years, different descriptions of the anthers and their dehiscence are given. Some of these statements give a rather incomplete picture, while others involve inaccurate observations. For example, Fernald in 1950 stated, "anthers extrorse in bud and opening by pores at base and inverted in flower" and Lawrence in 1951 noted, "anthers 2-celled, extrorse, sagittate, inverted and inflexed in bud, dehiscing by apical pores." The determination of the apex and base of an anther and the introrse or extrorse dehiscence of its thecae depends upon the attachment of the anther to the filament. The anther in *Clethra* is dorsifixed, often appearing versatile at

---

abruptly enlarged at base, very short obcordate anther, rather plump thecae, small apical pores.

FIGS. 13–16. Stages in maturation of stamens to show straightening of filaments in *C. cavaleriei* (*H. H. Chung 2932*), × 5: 13, position of young anthers in half-grown bud, sepals and petals removed, anthers in an upside-down position, outer whorl of stamens with short filaments; 14, adaxial view of young stamen and petal, showing bend of filament below point of attachment; 15, same, at a later stage of development, showing knee-shaped bend produced by elongation of filament; 16, lateral view of stamen and petal at a more advanced stage, the filament almost straightened.

FIG. 17. Fully opened flower of *C. bodinieri* (*Tsang 22450*), showing short stamens of outer whorl and long stamens of inner whorl, some petals and stamens removed, × 5.

FIGS. 18–20. Pollen grains of *C. delavayi*, *C. bodinieri*, and *C. faberi* respectively.

FIGS. 21–23. Style and stigma types, × 10: 21, trifid style with three stigmas (*C. cavaleriei*); 22, undivided style with 3 apical lobes, 3 stigmas (*C. brammeriana*); 23, undivided style with single punctiform stigma (*C. bodinieri*).

FIGS. 24–27. Habit and inflorescence types of Chinese species of Clethra, × ½. 24, Flowering branchlets of *C. esquirolii* (*Steward & Cheo 394*), showing formation of vegetative shoots from active axillary buds; 25, Fruiting branchlet of *C. bodinieri* var. *parvifolia* (*Tsang 23822*), showing leaves on growth of two years; 26, *C. delavayi* (leaf, *Delavay 3319*; flowering branchlet, *Forrest*

anthesis. A mature anther is V-shaped (Fig. 10), obovate-oblong (Fig. 11), or obcordate (Fig. 12). The thecae dehisce by rimiform apical pores situated slightly on the ventral side of the anther.

In a flower bud, the inverted position of the anther is caused by the outward folding of the filament which occurs at a point about one-fifth below the attachment of the anther (Figs. 13, 14). As the flower opens, the apical half of the filament increases in length several times faster than the basal half becoming geniculate in character (Fig. 15). The tension created by the elongating filament pushes the anther up (Fig. 16) and as the filament becomes straightened, the anther is set at its normal position with the apical pores pointing upward and inward (Figs. 1–12, 17). In 1952 Kavaljian published on the floral morphology of *Clethra*, and regarding the inversion of the anther he stated, "the morphological base becomes the apparent apex." This statement is unnecessary because the rolling and folding of filaments in flower buds and the straightening of the filaments at anthesis are as common as the vernation and the unfolding of leaves. They are normal processes of growth. In *Clethra* the change of position of the anthers from bud to fully grown flower occurs in the filaments, not at the points of attachment of the anthers to the filaments. Therefore, what Kavaljian termed the "apparent apices" of the anthers are the "morphological apices."

Because of the change of the length of the filament during the short period of anthesis, specimens collected at different stages in the development of the flower may have different appearances. For this reason the nature of the flower in regard to its included or exserted anthers is not a very satisfactory criterion for distinguishing species. It can be used only as an auxiliary character. Variations in the size and shape of the anthers of different species are obvious. The longest anthers, such as those found in *C. bodinieri* and *C. cavaleriei,* are 2.5–3 mm. long, V-shaped in outline, deeply parted above, with relatively slim thecae and elongated rimiform apical pores (Fig. 10). The medium-sized anthers, such as those found in *C. delavayi* and *C. monostachya*, are 1.75–2 mm. long, obovate-oblong in outline, moderately parted above, with rather plump thecae and short and wide apical pores (Fig. 11). The short anthers, such as those found in *C. kaipoensis* and *C. brammeriana*, are only 1 mm. long, obcordate in outline, shallowly parted above, the thecae short, plump and with small apical pores (Fig. 12). Anther characters correlate with the size of flowers and the shape and sizes of sepals and petals. They can be used as auxiliary characters for distinguishing sections or series.

Pollen grains of *C. delavayi*, *C. bodinieri* and *C. faberi* taken from herbarium specimens were examined. They differ in shape and structure in their apertures (Figs. 18–20). The grains of *C. delavayi* and *C. faberi* are tricolporate. The grains of *C. faberi* lack the protruding roof of the ora which Erdtman considered to be a characteristic feature of the pol-

---

15889); 27, *C. fargesii* (*Henry 7270*), showing subumbelliform racemes, small vegetative shoots developed from active axillary buds.

len of the genus. The pollen of *C. bodinieri* seems to be porate and not colporate. The significance of pollen morphology in the taxonomy of infrageneric groups of *Clethra* awaits further research and judgment by competent palynologists.

Pistil. The pistil is tricarpellate. The ovary is always pubescent, while the style may be pubescent or glabrous, trifid or undivided at the apex. The presence or absence of hairs on the style has been used as a specific character, and this practice is adopted here. The trifid style has three terminal stigmas (FIG. 21). Most of the Chinese species of *Clethra* have trifid styles. The undivided style may have 3-lobed stigmas such as are found in *C. brammeriana* (FIG. 22), or it may have a single punctiform stigma such as is found in *C. bodinieri* (FIG. 23). The type of style and stigma may be used as an auxiliary character for distinguishing species in *Clethra*.

Fruits. The fruit is a loculicidal capsule with persistent sepals and style. The relative length of the fruiting pedicels is a helpful character for distinguishing species. There seems to be a positive correlation between the size of the flower and fruit of a species. The fruits of the large-flowered species *C. delavayi* are 4–6 mm. in diameter, while those of the small-flowered species *C. kaipoensis* are 2.5–3 mm. in diameter. Most of the herbarium specimens which I have examined lack fruits, and their significance in the classification of the species is not emphasized.

Seeds. Material with fully grown seeds is scarce in our herbaria. The seeds of *C. bodinieri, C. barbinervis, C. cavaleriei, C. delavayi* and *C. monostachya* were examined. Those of the first three species are irregularly angular, extremely reticulate and not winged. The seeds of *C. delavayi* and *C. monostachya* are slightly compressed, 1 mm. long, 0.5 mm. wide, reticulate and the cells along the margin are enlarged, but no wings are evident. The seeds of the Chinese *Clethra* are very different from the highly compressed and winged seeds of the North American species.

ECOLOGICAL NOTES AND GEOGRAPHICAL DISTRIBUTION

The Chinese species of *Clethra* are essentially mountainous forms. They occur in thickets or at the margin of woods in acid soil. The available material in our herbaria indicates that there are two distinct groups of species, the western and the eastern, which are separated by six hundred miles. No collection of *Clethra* has been recorded in the area in between.

The western species constitute a small series, *Delavayanae*, of high mountain forms. They usually occur at altitudes of 2400–3800 meters. *Clethra delavayi, C. yuiana,* and *C. monostachya* belong to this group. In *C. delavayi* a glabrous variety has been recorded from a higher altitude than the pubescent variety. In this western range, *C. monostachya* occurs in the North and *C. delavayi* and *C. yuiana* in the South (MAP 1).

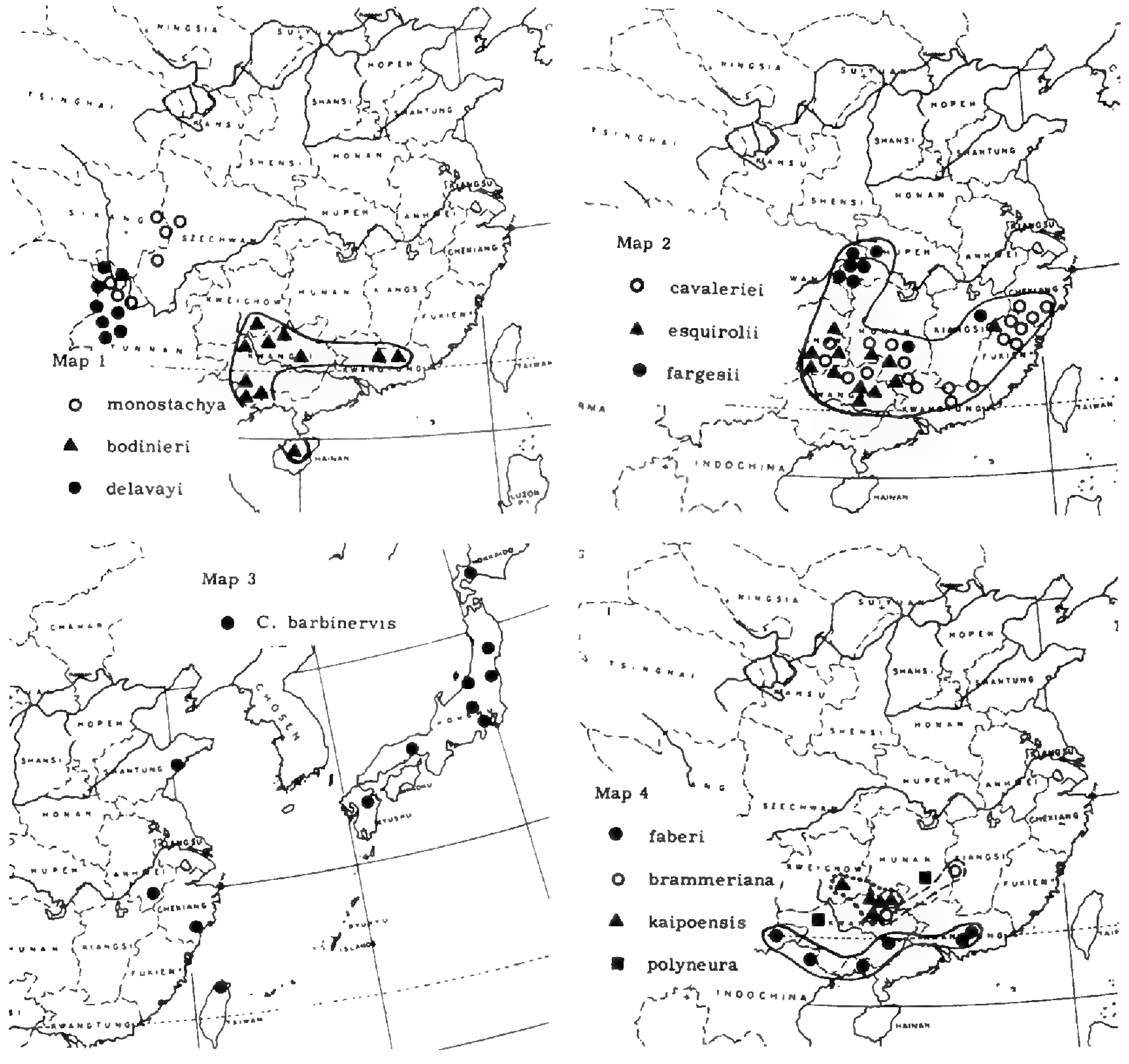
The eastern group involves a more heterogeneous assemblage of species.

The area covered by these species is at lower altitudes, the majority of the species occurring between 600 and 1000 meters above sea level. A couple of species may reach an altitude of 1250–1600 meters. *Clethra kaipoensis* has been collected at altitudes of 1000–2100 meters.

The distribution maps of different species involved in the eastern region indicate that the Nan-ling Range constitutes the center of the aggregation of species. This range represents a chain of much-dissected ancient hills and mountains extending along the Tropic of Cancer from the Yunnan-Kwangsi border, eastward to the Kweichow-Hunan-Kwangsi-Kwangtung borders, and then northeastward to the Kiangsi-Fukien-Chekiang borders.

Clethra bodinieri, the only species of section *Monostigma*, occurs principally on the southern flank of the Nan-ling Range, and from the western end, its range extends southward to Hainan (MAP 1).

The distributions of three closely related species, *C. cavaleriei*, *C. esquirolii* and *C. fargesii*, form a U-shaped pattern with the base falling over the Nan-ling Range, the left arm extending along the Kweichow-Hunan border northward to the Szechuan-Hupei border, and the right arm ex-



MAPS 1–4. Distribution of some Chinese species of *Clethra*.

tending along the Kiangsi-Fukien border northward to southern Chekiang (MAP 2). It is worthy of note that *C. fargesii* has its best development in the north on the western arm while *C. cavaleriei* is better developed in the north of the eastern arm.

MAP 3 shows the distribution of *C. barbinervis* in China and Japan. This species and *C. fargesii* are the eastern Asiatic representatives of series *Alnifoliae*. The other species of this series, *C. alnifolia* and *C. acuminata,* occur in eastern North America. The distribution of the species of *Clethra* in series *Alnifoliae* gives specific evidence to support the floristic relationship between the Lower Yangtze Region in China and eastern United States of America.

Clethra faberi is a unique species. In geographical distribution its range does not overlap that of any other Chinese species (MAP 4). In morphological characters it has the subcoriaceous leaves of the evergreen species in section *Monostigma*, the umbelliform-paniculate racemes and fringed petals of species in section *Cuellaria*, and the V-shaped anther of species in section *Clethra*. Evidently the distribution of *C. faberi* is on the northern periphery of the range of the series *Faberianae*. *Clethra petelotii* from Indochina, *C. lancifolia* from the Philippines, *C. canescens* from the Philippines, Borneo, and Celebes, and *C. ledermannii* from the western highlands of New Guinea are all related species.

The Chinese species of section *Cuellaria* are concentrated in a more limited area of the middle Nan-ling Range (MAP 4). It is noteworthy that all other species of this section are found in tropical America from Mexico to Brazil. In interpreting the distribution of the fresh-water fishes from tropical eastern Asia to the New World, Darlington in 1957 suggested that during different geological times, many kinds of fresh-water fishes evolved in the eastern Tethys region have radiated by way of the north temperate region to North and Central America. The distribution of *Clethra* in geological time probably followed the same direction.

Clethra is an Asiatic-American genus. It is evident that *C. arborea* Ait., the single species described from the Madeira Islands, is out of the natural range of the genus. A comparative study of all the material in the Gray Herbarium and the Arnold Arboretum reveals that *C. arborea* from the Madeira Islands is closely allied to *C. pulcherrima* of the east coast of Sumatra. The two species are alike in their arborescent habit, large, oblong-elliptic, pubescent leaves, paniculate racemes, large flowers, elongate petals, included stamens, hirsute filaments and V-shaped anthers. It is very clear that *C. arborea* is an introduction from the East Indies to the Madeira Islands in historical time. The small hairy capsules and the very minute seeds are adapted for attachment. It was probably accidentally introduced in connection with the spice trade, and was firmly established in the late eighteenth century when it first caught the attention of British naturalists. Both *C. pulcherrima* and *C. arborea* are closely related to *C. delavayi* of western China.

TAXONOMY

Clethra Linn. Sp. Pl. 396. 1753, Gen. Pl. ed. 5. 188. 1754; Benth. & Hook. f. Gen. Pl. 2: 603. 1876; Rehder, Bibl. Cult. Trees Shrubs 502. 1949.

TYPE SPECIES: *C. alnifolia* Linn.

Evergreen or deciduous trees or shrubs 1–18 m. high. Leaves alternate, simple, exstipulate, chartaceous, rarely coriaceous or subcoriaceous, obovate, oblong, rarely lanceolate, base cuneate, rarely acute or rounded, apex acuminate, margin serrate, rarely subentire. Flowers in simple, paniculate, or subumbelliform racemes, rachis and pedicels stellate-pubescent, rarely covered by simple, straight hairs; calyx patelliform, with broad-ovate to lanceolate lobes; corolla choripetalous, emarginate, erose or fringed; stamens 10, in two whorls, the outer whorl opposite the petals, filaments glabrous or hirsute, reflexed in bud, straightened at anthesis, anthers 4-celled in bud, at anthesis V-shaped, oblong-obovate or obcordate, connective extending into a basal sterile process, thecae opening by terminal rimiform pores; pollen grains simple, tricolporate or triporate; ovary superior, pubescent, 3-locular, style trifid or undivided, 3-lobed or not lobed; stigmas 3, rarely 1; ovules 20–40 in each locule, on axile placentas. Fruit a subglobose capsule with persistent calyx and style, loculicidal. Seeds small, ovoid and irregularly angular or dorso-ventrally compressed, the seed coat of one layer of cells, extremely reticulate, in some species winglike; endosperm fleshy and oily. About 120 species with Asian-American distribution.

KEY TO THE SECTIONS, SERIES AND SPECIES

A. Petals densely barbate on the inside; style undivided; stigma 1, punctiform; fruits globose, villose-hirsute; leaves evergreen; pollen triporate; hairs on the rachis and pedicels simple, gray, appressed. Sect. 1. MONOSTIGMA. .... 1. *C. bodinieri.*

A. Petals glabrous or sparsely villose at the base on the inside; style trifid or undivided, 3-lobed with 3 stigmas; leaves deciduous (except *C. smithiana*); pollen tricolporate; hairs on the rachis and pedicels stellate or tufted, hirsute, usually ferrugineous.

  B. Anthers V-shaped or oblong-obovate; pedicels longer than the sepals at anthesis; petals emarginate, rarely fringed; racemes various. .... Sect. 2. CLETHRA.

    C. Flowers large, the petals 8–10 mm. long; stamens included; filaments hirsute, the hairs white; anthers oblong-ovate; racemes solitary. .... Series A. DELAVAYANAE.

      D. Style pubescent; petals papillose on the outside; leaves elliptic, attenuate at both ends, 6–14 cm. long, 2.5–5.5 cm. wide. .... 2. *C. monostachya.*

      D. Style glabrous; petals smooth outside; leaves various in shape and size.

        E. Leaves uniformly hispid above, pubescent beneath (except the glabrous variety), obovate or oblong, 7–23 cm. long, 3.5–9 cm. wide. . . . . 3. *C. delavayi.*

E. Leaves glabrous above, inconspicuously appressed-pilose on the midrib and lateral nerves beneath, lanceolate, 10–15.5 cm. long, 3–4 cm. wide. . . . . 4. *C. yuiana.*

C. Flowers small, the petals 4–6 mm. long; stamens exserted, the filaments glabrous or villose with ferrugineous or nigrescent hairs; racemes various.

F. Racemes solitary; sepals ovate-lanceolate, 4–5 mm. long; petals emarginate; anthers V-shaped, 3 mm. long. . . . . Series B. ESQUIROLIANAE.

G. Filaments glabrous; petals not glaucous; leaves oblong-elliptic, the base acute or obtuse. . . . . 5. *C. cavaleriei.*

G. Filaments pubescent; basal half of the petals glaucous; leaves ovate-elliptic, the base obtuse or rounded. . . 6. *C. esquirolii.*

F. Racemes paniculate or subumbelliform; sepals ovate-orbicular, 2–4 mm. long; petals more or less fringed. . Series C. ALNIFOLIAE.

H. Fruiting pedicels 2–3 times as long as the diameter of the capsules; leaves chartaceous.

I. Filaments glabrous; leaves obovate or broad-elliptic, the base cuneate; racemes paniculate; sepals broad-ovate, 2–2.5 mm. long, obtuse. . . . . 7. *C. barbinervis.*

I. Filaments pubescent; leaves ovate-oblong, the base obtuse; racemes subumbelliform; sepals lanceolate, 4–5 mm. long. . . . . 8. *C. fargesii.*

H. Fruiting pedicels about as long as the diameter of the capsules; leaves subcoriaceous. . . . . Series D. FABERIANAE. . . . . 9. *C. faberi.*

B. Anthers cordate; pedicels shorter than the sepals at anthesis; petals fringed; racemes subumbelliform. . . . . Sect. 3. CUELLARIA.

J. Style pubescent near the base. . . . . 10. *C. pinfaensis.*

J. Style glabrous.

K. Leaves deciduous, distinctly serrate, elliptic or oblong, chartaceous, 11–20 cm. long; 5–7 cm. wide; petals glabrous.

L. Primary lateral nerves parallel-arcuate, 6–10 mm. apart; hairs on the lower leaf-surface or nerves stellate.

M. Filaments glabrous.

N. Leaves stellate-hirsute on the nerves beneath, otherwise glabrous; margin sharply serrate. . . . . 11. *C. kaipoensis.*

N. Leaves uniformly velvety beneath; margin subentire, minutely mucronulate-ciliate or serrate. . . . . 12. *C. brammeriana.*

M. Filaments villose at the base. . . . . . 13. *C. kwangsiensis.*

L. Primary lateral nerves parallel, 4–6 mm. apart; hairs on the nerves beneath simple, appressed. . . . . 14. *C. polyneura.*

K. Leaves evergreen, subentire or remotely serrate near the apex, linear-lanceolate, 7–13 cm. long, 2–3 cm. wide. . . . . 15. *C. smithiana.*

Section 1. MONOSTIGMA S. Y. Hu

Clethra, sect. **Monostigma,** sect. nov.

TYPE SPECIES: *C. bodinieri* Lévl.

Frutices sempervirentes ramulosis hornotinis pilosis; foliis coriaceis; racemis solitariis, rachibus pedicellisque pilosis; sepalis ovatis; petalis intus barbatis, filamentis hirsutis; stylis glabris, apice punctiformibus. One species, Kwangtung, Kwangsi, Hainan and Kweichow.

1. **Clethra bodinieri** Lévl. Repert. Sp. Nov. Fedde **10**: 475. 1912; Hand.-Mazz. Sinensia **5**: 3. 1934; Merr. & Chun, Sunyatsenia **5**: 156. 1940.

var. **bodinieri**

An evergreen shrub, 2–5 m. high, the branchlets ascending, the current year's growth 2–3 mm. thick, inconspicuously pilose, the hairs simple. Leaves coriaceous, lanceolate, 5–9 cm. long, 1–2.5 cm. wide, base cuneate to acute, apex caudate-acuminate, the acumen 1.5–2 cm. long, glabrous above, inconspicuously pilose on the midrib beneath, angles of principal nerves slightly barbate; margin mucronate-denticulate, the basal half or one-third entire, lateral nerves 8, arcuate, obscure above, conspicuous beneath; petioles 5–12 mm. long, pilose. Racemes solitary, 3–13 cm. long, peduncles distinct, rachis pilose, the hairs simple, gray; pedicels 7–8 mm. long at anthesis; sepals ovate, 2.5–3 mm. long; petals oblong, 5 mm. long, 2.5 mm. wide, densely barbate inside; filaments hirsute; style glabrous, the stigma entire. Capsules globose, densely villose-hirsute; persistent style 7–9 mm. long; pedicels 10–12 mm. long. Seeds brown, 0.5–1 mm. long, angular-ovoid.

KWANGTUNG: *W. T. Tsang 25451, 25620, 25828.* KWANGSI: *R. C. Ching 5695, 5734, 5804, 7181*; *W. T. Tsang 22450, 24023*; *C. Wang 39602.*

Occurring in open thickets or woods at altitudes of 600–1600 meters; the white flowers with pinkish sepals and pedicels appear in June; a very distinct species with no close relationship to any other Chinese species of *Clethra.*

var. **latifolia,** var. nov.

Frutex sempervirens 4 m. altus, ramulis hornotinis incanis; foliis obovato-oblongis vel obovato-ellipticis, 7–9.5 cm. longis, 2.5–3 cm. latis, basi obtusis, apice acuminatis, acumine 5–10 mm. longo, margine serratis, supra glabris, subtus barbatis; racemis 6 cm. longis; filamentis dense villosis; stylo glabro.

HAINAN: Loktung, in dense woods, *S. K. Lau 27312* (type, A), June 27, 1936 (shrub 4 m. high, leaves green above).

Occurring in dense woods; flowering in late June; distinguished from the typical *C. bodinieri* by its obovate-oblong leaves with obtuse bases.

var. **parvifolia,** var. nov.

Frutex 1.5–2.5 m. altus ramulis hornotinis sparse pilosis; foliis ellipticis, raro obovato-ellipticis, 3–5 cm. longis, 8–17 mm. latis, basi cuneatis et acutis, apice acuminatis, acumine 5–9 mm. longo, supra glabris, subtus barbatis aliter glabris; racemis 6–9 cm. longis; filamentis hirsutis; stylo glabro.

KWANGSI: Shang-sze District, fairly common, in thickets, dry steep slope, *W. T. Tsang 22450* (type, A), June 2–7, 1933 (woody, 5 ft. high, flowers white, fragrant); *W. T. Tsang 23822, 22456.*

Occurring in thickets and woods; flowering in early June; distinguished from the typical *C. bodinieri* by its small leaves which seldom reach 5 cm. in length.

Section 2. CLETHRA

Clethra, sect. **Clethra**

Clethra sect. *Euclethra* DC. Prodr. 7: 588. 1839; Drude in Engler & Prantl, Pflanzenfam. IV. 1: 1. 1897.

TYPE SPECIES: *C. alnifolia* Linn.

Deciduous trees or shrubs, branchlets stellate-pilose. Leaves chartaceous, rarely subcoriaceous. Rachis and pedicels stellate-pilose; racemes solitary or paniculate or subumbelliform, pedicels elongate; sepals ovate to lanceolate; petals glabrous inside or rarely slightly pilose near the base; style trifid or undivided and 3-lobed at the apex, stigmas 3. About 15 species, eastern Asia and eastern North America. Subdivided into four series.

Series A. DELAVAYANAE S. Y. Hu

Clethra, sect. **Clethra,** series **Delavayanae,** ser. nov.

TYPE SPECIES: *C. delavayi* Franch.

Arbores vel frutices, foliis chartaceis, serrato-dentatis; racemis solitariis, pedicellis elongatis; staminibus inclusis, filamentis hirsutis; stylis trifidis; capsulis hispidis; seminibus dorso-ventralibus compressis. Three species in West China, the related species in Sumatra.

2. **Clethra monostachya** Rehder & Wilson in Sargent, Pl. Wils. 1: 501. 1913; Rehder, Man. 675. 1927, ed. 2. 690. 1940, Bibl. 502. 1949; Chen, Ill. Man. Chin. Trees Shrubs 942. 1937.

Clethra delavayi sensu Stapf in Bot. Mag. **148:** *t. 8970.* 1923; sensu Rehder, Man. 675. 1927, ed. 2. 690. 1940, non Franchet.

A tall shrub or small tree, 2–8 m. high. Leaves elliptic, or ovate-elliptic, rarely lanceolate, 7–13 cm. long, 2.5–5.5 cm. wide, base cuneate, apex acuminate, acumen 1–1.5 cm. long, apiculate, margin sharply serrate, primary lateral nerves 16–21 pairs, both surfaces glabrous, the large nerves slightly pilose and their angles barbate beneath; petioles 1–2.5 cm. long, inconspicuously stellate-pilose in the grooves above; leaves produced by active lateral buds lanceolate, 4–6.5 cm. long, 1.3–2 cm. wide, both surfaces subglabrous, the nerves and their angles pilose beneath. Racemes solitary, 7–18 cm. long, the rachis densely ferrugineous-hirsute, the hairs tufted; pedicels 6–10 mm. long at anthesis; sepals 4–5 mm. long, acute; petals 5–6 mm. long, papillose outside; filaments hirsute; style pubescent, apex 3-cleft. Capsules subglobose, 4 mm. in diameter; pedicels 15–18 mm. long; persistent style 7–8 mm. long.

YUNNAN: *R. C. Ching 21452*; *M. K. Li 2079*; *T. T. Yu 17303*. SIKANG (Szechuan on labels): Tien-chuan, *Y. S. Liu 1329*; Han-Yuen, Ta Hsiang Ling, *C. Y. Chiao 1616*; Moupin, *E. H. Wilson 1192* (paratype). West China, without precise locality, *E. H. Wilson*, Veitch Exp. *3927* (type).

Occurring on the margins of woods and thickets at altitudes of 1700–2800 meters in the mountains of the Yunnan-Szechuan-Sikang borders; a very distinct species closely related to *C. delavayi*; distinguished by its elliptic leaves attenuate at both ends, smaller flowers, papillose petals, pubescent filaments and styles.

The specimens from Yunnan are not typical. The stamens are enclosed, as in *C. delavayi*. The material illustrated by Stapf has pilose styles, and it apparently belongs here. Rehder's account in his *Manual* is based on Stapf's illustration. The isotype of *C. delavayi* has glabrous styles.

3. **Clethra delavayi** Franchet, Jour. de Bot. 9: 370. 1895; P. Dop, Bull. Soc. Bot. France **75**: 731. 1928; Rehder, Man. 675. 1927, ed. 2. 690. 1940. Bibl. 502. 1949; Chen, Ill. Man. Chin. Trees Shrubs 942. 1937; Merr. in Brittonia **4**: 137. 1941.

var. **delavayi**

A tall shrub or small tree 4–5 m. tall, the current year's growth densely stellate-hispid, 3–6 mm. thick. Leaves obovate or elliptic-oblong, 7–15 cm. long, 3.5–6 cm. wide, base cuneate, apex acuminate or acute, the acumen 5–10 mm. long, uniformly hispid above, tomentose beneath, margin serrate, lateral nerves 20 or 21 pairs; petioles 10–17, densely villose; axillary buds more or less stalked, usually bearing no leaves, the stalk 3–40 mm. long. Racemes solitary, 18–25 cm. long, the rachis densely ferrugineous-hispid, the hairs tufted; pedicels 6–7 mm. long at anthesis; sepals ovate-lanceolate, 5–6 mm. long; petals oblong-obovate, 10 mm. long, 5 mm. wide, apex emarginate, ciliate; filament hirsute at the base, the hairs white; style glabrous, the apex trifid. Capsules subglobose, 4 mm. in diameter; persistent style 6–7 mm. long; pedicels 14–20 mm. long.

YUNNAN: *Delavay 3319* (isotype); *G. Forrest 11590, 15528, 15839, 17545*; *McLaren (C Collector 237)*; *H. T. Tsai 58408*; *T. T. Yu 20979.*

Occurring in mixed forest at altitudes of 2400–3200 meters; a very distinct species, closely related to *C. monostachya*, distinguished by its obovate leaves which are uniformly tomentose beneath, large flowers with enclosed anthers, hispid filaments, and glabrous styles.

var. **lanata,** var. nov.

Arbor parva 4 m. alta; foliis obovatis vel oblongo-ellipticis, 11–12 cm. longis, 3.5–5.5 cm. latis, supra hispidis, subtus dense lanatis; pedicellis fructorum 1.5–2 cm. longis.

YUNNAN: Che-tse-lo, Pi-lo-shan, alt. 4000 m., *H. T. Tsai 58263* (type, A), August 27, 1934 (tree, flower white); *H. T. Tsai 58459.*

This variety occurs in the forest of Che-tse-lo of western Yunnan. The dense-lanate lower leaf-surface is very distinctive.

var. **glabra,** var. nov.

Arbor parva 3–5 m. alta; foliis oblongo-ellipticis vel obovato-oblongis, 13–23 cm. longis, 5.5–9 cm. latis, supra glabris, subtus glabrescentibus, ad costam et nervos lateralibus sparse pilosis; pedicellis florum 8–15 mm longis.

YUNNAN: *R. C. Ching 20478, 22107*; *K. M. Feng 3301*; *G. Forrest 8875*; *McLaren (D Collector 130)*; *J. F. Rock 17111, 18461*; *H. T. Tsai 59905, 59951*; *C. W. Wang 63886, 68702*; Wei-Hsi, Mount Shang-Ma-Kou, alt. 3400 m., *J. F. Rock 17174* (type, A), August 1928 (tree, 3–5 m. high, flowers white).

Occurring in mixed forests by streams at altitudes of 2800–3800 meters; the white flowers open in August; distinguished by its leaves which are glabrous above and pilose beneath on the principal nerves only.

4. **Clethra yuiana,** sp. nov.

Arbor 7–10 m. alta, ramulis hornotinis 4 mm. diametro, glabrescentibus; foliis lanceolatis, 10–15.5 cm. longis, 3–4 cm. latis, utrinque acuminatis, acumine 1 cm. longo, margine mucronato-serratis, supra glabris; subtus ad nervos primarios et costam pilosis, aliter glabris, nervis lateralibus utrinque 22–24, foliis ramulorum axillarium ellipticis vel lanceolatis, 1.5–2.5 cm. longis, 6–8 mm. latis, utrinque praesertim ad nervos pilosis; racemis solitariis, 22 cm. longis, densifloribus; rachibus stellato-pilosis, pilis brevibus; pedicellis florum 8–10 mm. longis; sepalis ovato-lanceolatis 5–6 mm. longis; petalis obovatis, 8 mm. longis, 5–6 mm. latis, apice emarginatis, utrinque glabris; filamentis hirsutis; stylis glabris, apice trifidis; capsulis ignotis.

YUNNAN: Shunning, Hila, Wumulung, alt. 2750 m., among forest, common, *T. T. Yu 1720* (type, A), July 13, 1938 (tree, 20–30 ft. high, flowers white).

Occurring frequently in mixed forest at an altitude of 2750 meters; flowering in mid-July; closely related to *C. monostachya*, but distinguished by its larger flowers and glabrous styles.

Series B. ESQUIROLIANAE S. Y. Hu

Clethra, sect. **Clethra,** series **Esquirolianae,** ser. nov.

TYPE SPECIES: *C. esquirolii* Lévl.

Frutices foliis ellipticis vel ovato-ellipticis, chartaceis, arguto-serratis; racemis solitariis, pedicellis elongatis; sepalis lanceolatis, staminibus exsertis, antheris V-formibus, elongatis; seminibus ovoideo-polygonis. Two species, southeastern China.

5. **Clethra cavaleriei** Lévl. Repert. Sp. Nov. Fedde **10**: 476. 1912; Rehder, Jour. Arnold Arb. **15**: 267. 1934; Hand.-Mazz. Beih. Bot. Centralbl. **56B**: 449. 1937.

Clethra lineata Lévl. Repert. Sp. Nov. Fedde **12**: 534. 1913.
Clethra longebracteata Sleumer, *ibid.* **38**: 205. 1935.
Clethra sinica Hao, *ibid.* **42**: 85. 1937.

A shrub or small tree 1–5 m. high, the current year's growth densely pilose, the hairs short-stellate. Leaves elliptic, 6–10 cm. long, 1.5–4 cm. wide, base acute, apex acute or shortly acuminate, glabrous above, very sparsely pilose on the principal nerves beneath, margin serrate, lateral nerves 12 or 13 pairs, reticulations of veinlets distinct beneath; petioles 1–1.5 cm. long, appressed pilose and glabrescent; leaves produced by active axillary buds lanceolate, 2–7 cm. long, 1–1.5 cm. wide, both surfaces sparsely stellate-pilose. Racemes solitary, 9–15 cm. long, bracts longer than the pedicels; pedicels 7–10 mm. long at anthesis; sepals lanceolate, 5 mm. long; petals 6 mm. long; filaments glabrous; style glabrous, the apex trifid. Capsules subglobose, 4–5 mm. in diameter; persistent style 9 mm. long; pedicels 14–15 mm. long.

FUKIEN: *R. C. Ching 2250, 2300*; *H. M. Fan 9474, 9493, 9515*; *H. H. Chung 2923.* KWANGTUNG: *R. Mell 883*; *W. T. Tsang 21413, 21661.* KWANGSI: *S. K. Lau 28753, 28755.* CHEKIANG: *R. C. Ching 2101*; *Y. L. Keng 164* (isosyntype of *C. sinica*), *175* (isotype of *C. longebracteata*). KWEICHOW: *J. Cavalerie 5* (fragment and photo of type); *J. Esquirol 3238* (photo and fragment of type of *C. lineata*); *Handel-Mazzetti 172* = 10557. HUNAN: *Fan & Li 253.*

Occurring in woods and thickets at altitudes of 780–1250 m.; flowering in August; closely related to *C. esquirolii*, distinguished by its glabrous filaments.

6. **Clethra esquirolii** Lévl. Repert. Sp. Nov. Fedde **10**: 475. 1912.

Clethra cavaleriei sensu Rehder, Jour. Arnold Arb. **15**: 267. 1934, p.p.; sensu Hand.-Mazz. Symb. Sin. **7**: 760. 1936, p.p., non Lévl.

A shrub 1–3 m. high, current year's growth sparsely stellate-pilose, 3–4 mm. in diameter, subterete or angular. Leaves ovate-elliptic or elliptic, 6.5–10 cm. long, 2.5–4.5 cm. wide, base obtuse or rounded, apex short-acuminate, the acumen 1 cm. long, glabrous above, the nerves sparsely pilose and their angles slightly barbate beneath, margin serrate, lateral nerves 10–12 pairs; petioles 1–2 cm. long, hirsute, straight and stellate hairs intermixed; leaves produced on active axillary buds elliptic, 3–4.5 cm. long, 12–15 mm. wide, both surfaces stellate-pilose, the midrib and lateral nerves lanate beneath. Racemes solitary, 10–16 cm. long, the rachis ferrugineously stellate-hirsute; pedicels 9–11 mm. long at anthesis; sepals ovate-lanceolate, 4–5 mm. long; petals oblong, 6–7 mm. long, 3–4 mm. wide, sparsely villose inside, basal half glaucous outside; filaments villose, the hairs ferrugineous or nigrescent; style glabrous, trifid at the apex. Capsules subglobose, 4 mm. in diameter; pedicels 1.5–2 cm. long; persistent style 9–12 mm. long.

FUKIEN: *R. C. Ching 2300.* KWANGTUNG: Lokchong, *Y. Tsiang 1422.* KWANGSI: Ling-Chuan, *W. T. Tsang 27871*; Tzu-yuen, *T. S. Tsoong* (= *Z. S. Chung*) *83440*; *C. Wang 39565, 40068.* HUNAN: Sinning, *Fan & Li 453*; Wu-kang, *Handel-Mazzetti 842 = 12397.* HUPEI: *A. Henry 2838.* KWEICHOW: *J. Cavalerie*, July 19, 1898; *J. Cavalerie 69* (E. Bodinier); *J. Esquirol 651* (type, fragment and photo); *Steward, Chiao & Cheo 394*; *Y. Tsiang 5460.*

Occurring in open ridges or ravines of the Nan-ling Range, its range extending from northern Kwangsi and Kweichow, eastward through Hunan to northern Kwangtung and northern Fukien, and northward to western Hupei; closely related to *C. cavaleriei*, distinguished by its ovate or ovate-elliptic leaves with obtuse or rounded base, its glaucous petals and pubescent filaments.

Rehder and Handel-Mazzetti both interpreted this species as synonymous with *C. cavaleriei.* The fragment of the type of *C. esquirolii* and *Handel-Mazzetti 12397* both have pubescent filaments. In this respect, they are different from the type of *C. cavaleriei. Clethra esquirolii* is distinguished from *C. fargesii* by its larger flowers and solitary racemes.

Series C. ALNIFOLIAE S. Y. Hu

Clethra sect. **Clethra,** series **Alnifoliae,** ser. nov.

TYPE SPECIES: *C. alnifolia* L.

Frutices foliis chartaceis, obovatis vel lato-ellipticis, crasso-serratis; racemis paniculatis; staminibus exsertis, antheris V-formibus; seminibus polygonis vel compressis. Five species, eastern United States of America and the Lower Yangtze Region of China.

7. **Clethra barbinervis** Sieb. & Zucc. Abh. Phys.-Math. Cl. Akad. Wiss. München IV. 3: 128. 1846; Gilg, Bot. Jahrb. Engler 34(Beibl. 75): 56. 1904; Loes. in Beih. Bot. Centralbl. 37(2): 164. 1919; Rehder, Man. 1927, ed. 2. 690. 1940, Bibl. 502. 1949; Kai, Pl. Sin. Ill. 306. *fig. 538.* 1937.

A shrub up to 10 m. high, the current year's growth 3–4 mm. thick, subglabrescent or minutely stellate-pilose. Leaves obovate-elliptic, 7–14 cm. long, 3–6.5 cm. wide, base cuneate and acute, apex abruptly short-acuminate, the acumen deltoid, 5–10 mm. long, glabrous above, midrib and principal nerves hirsute and their angles barbate beneath, the hairs simple; margin sharp-serrate; lateral nerves 12–14 pairs, arcuate; petioles 1–2.5 cm. long, pilose, the hair appressed; leaves produced by active axillary buds obovate, 3.5–6.5 cm. long, 1.5–2.5 cm. wide, sparsely stellate-pilose above, sparsely villose beneath, straight and stellate hairs intermixed. Racemes 3–6, paniculate, the rachis densely ferrugineous-hispid, the hairs tufted; pedicels 4–6 mm. long at anthesis; sepals suborbicular-ovate, 2–2.5 mm. long; petals obovate, 5–6 mm. long, 3–4 mm. wide; apex emarginate, and fringed; filaments glabrous; style glabrous, the apex trifid. Capsules subglobose, 4 mm. in diameter; persistent style 6–8 mm. long; pedicel 6–8 mm. long.

TAIWAN: *R. Kanehira*, Sept. 5, 1920. CHEKIANG: *R. C. Ching 1642.* ANHWEI: *R. C. Ching 3237, 3277.* SHANTUNG: Tsingtao, *Zimmermann 432.*

Occurring in thickets on open hills at an altitude of 1000 meters; related to *C. faberi* and *C. fargesii* through its paniculate inflorescences, short sepals, and fringed petals; distinguished from *C. faberi* by its obovate leaves and elongate pedicels and from *C. fargesii* by its glabrous filaments and obovate leaves cuneate at the base. Kanehira and Zimmermann's collections are out of the normal range of the species. Probably these collections were made from cultivated plants. This species is common in Japan, and it is most likely that this species was introduced into Tsingtao and Taiwan from Japan.

8. **Clethra fargesii** Franch. Jour. de Bot. **9**: 369. 1895; Rehder & Wilson in Sargent, Pl. Wils. **1**: 502. 1913; Rehder, Man. 674. 1927, ed. 2, 690. 1940, Bibl. 502. 1949; Chen, Ill. Man. Chin. Trees Shrubs 942. *fig. 835.* 1937.

Clethra canescens sensu Forbes & Hemsl. Jour. Linn. Soc. Bot. **26**: 33. (Ind. Fl. Sin. II). 1889, non Reinw. ex Blume.
Clethra sleumeriana Hao, Repert. Sp. Nov. Fedde **42**: 84. 1937.

A tall shrub up to 4 m. high, the current year's growth densely stellate-pilose, 3–5 mm. thick. Leaves ovate-elliptic, 7–14 cm. long, 3–5 cm. wide, base obtuse or rotundate, apex acuminate, the acumen 1–2 cm. long, glabrous above, along the midrib and the principal nerves stellate-villose and their angles barbate beneath, lateral nerves 16–17 pairs, arcuate; margin mucronate serrate; petioles 14–17 mm. long, sparsely stellate pilose; leaves produced by the active axillary buds lanceolate, 4–10 cm. long, 1.5–3.3 cm. wide, both sides stellate pubescent. Racemes 3–7, subumbelliform-paniculate, the rachis densely brown-hirsute, the hairs tufted; pedicels 6–10 mm. long at anthesis; sepals lanceolate, 4–5 mm. long; petals obovate, 5–6 mm. long; filaments hirsute near the base; style glabrous, the apex trifid. Capsules subglobose, 3 mm. in diameter; persistent style 5 mm. long; pedicels 12–13 mm. long.

KIANGSI: *H. H. Hu 1320.* HUPEI: *Cheng & Hwa 821, 1068, 1110*; *H. C.*

Chow 885, 1178; *W. Y. Chun 3714, 3734*; *A. Henry 5818, 6407, 7220*; *E. H. Wilson* (Veitch Exp.) *1326, 2222*. HUNAN: *S. S. Sin 615* (type of *C. sleumeriana*. Hao, not seen). SZECHUAN: *Farges 108* (type, not seen).

Common in open woodlands and thickets in the middle Yangtze Region; closely related to *C. esquirolii*, but distinguished by its umbelliform-paniculate racemes, smaller flowers and densely stellate-pubescent branchlets.

Series D. FABERIANAE S. Y. Hu

Clethra, sect. **Clethra,** series **Faberianae,** ser. nov.

TYPE SPECIES: *C. faberi* Hance.

Frutices foliis subcoriaceis, subglabris vel subtus stellato-pilosis, canescentibus, serratis; racemis subumbelliformibus, pedicellis brevibus; petalis fimbriatis. About 10 species, China, Indo-China, the Philippines, Borneo, Celebes and New Guinea.

9. **Clethra faberi** Hance, Jour. Bot. Brit. For. **21**: 130. 1838, *"fabri"*; Merr. Philipp. Jour. Sci. Bot. **13**: 154. 1918; P. Dop, Bull. Soc. Bot. France **75**: 732. 1928.

Clethra canescens sensu Forbes & Hemsl. Jour. Linn. Soc. Bot. **26**: 33. (Ind. Fl. Sin. II). 1889, p.p.; sensu Dunn & Tutcher, Kew Bull. Add. Ser. **10**: 155. (Fl. Kwangt. Hongk.) 1912, non Reinw.
Clethra liangii Li, Jour. Arnold Arb. **24**: 449. 1943.

A deciduous shrub 2–2.5 m. high, the current year's growth sparsely pilose or glabrescent, 3 mm. in diameter. Leaves subcoriaceous, elliptic, or obovate-elliptic, rarely oblanceolate, 6–11 cm. long, 2–3.2 cm. wide, base acute, apex acuminate, the acumen 1 cm. long, margin sharply serrate, primary lateral nerves 10 or 11 pairs, parallel-arcuate, 6–8 mm. apart, impressed above, reticulations of the veinlets distinct beneath, lamina glabrous on both surfaces, on the principal nerves very sparsely pilose beneath; petioles 6–8 mm. long, sparsely stellate pilose; leaves produced by active axillary buds elliptic, 2.5–8 cm. long, 1–2.5 cm. wide, glossy, glabrous above, hispid on the nerves beneath. Racemes 2–7, paniculate, rarely on weak branchlets solitary, densely and ferrugineously caespitose-hirsute; many bracts persistent; pedicels 3–4 mm. long; sepals suborbicular-ovate, 2.5–3 mm. long, apex obtuse, mucronate; petals 4 mm. long, 2 mm. wide, inside sparsely villose below the middle; filaments glabrous, anthers acute at the base, divergent at the apex; style glabrous, 4 mm. long after anthesis, the apex subcapitate, lobed or shallowly cleft. Capsules 2.5 mm. in diameter.

KWANGTUNG: *C. Ford 56*; *W. T. Tsang 26761*. KWANGSI: *H. Y. Liang 69645* (type of *C. liangii*); *S. P. Ko 55527*. YUNNAN: *H. T. Tsai 60876*.

Occurring in densely shaded forest or on open, grassy slopes at altitudes of 970–1100 meters; the white flowers appearing in late July and early

August; a very distinct species. Its short, obtuse sepals suggest a relationship with *C. barbinervis*, but its short pedicels, subcoriaceous leaves and small anthers are very different. The isosyntypes of *C. annamensis* P. Dop (*M. Poilane 7519, 7616*) apparently belong here.

Section 3. CUELLARIA (Ruiz & Pav.) DC.

Clethra, sect. **Cuellaria** (Ruiz & Pav.) DC. Prodr. 7: 589. 1839.

Cuellaria Ruiz & Pav. Fl. Per. Chil. Prodr. 59. *t. 10.* 1794, Syst. Veg. 103. 1798.

TYPE SPECIES: *C. ferruginea* Ruiz & Pav.

Trees or shrubs, branchlets densely stellate-pubescent. Leaves coriaceous or chartaceous. Rachis and pedicels densely ferrugineous-stellate-pubescent; racemes paniculate or subumbelliform, pedicels very short; sepals oblong or ovate; petals erose or fimbriate; stamens exserted or included. Seeds winged, or polygonous. About 85 species, chiefly in tropical America, 4 in China.

10. **Clethra pinfaensis** Lévl. Repert. Sp. Nov. Fedde **10**: 476. 1912.

Clethra kaipoensis sensu Rehder, Jour. Arnold Arb. **15**: 268. 1934; sensu Hand.-Mazz. Symb. Sin. **7**: 760. 1926, non Lévl.

A tree up to 13 m. high, the trunk 30 cm. in diameter, the bark smooth, brownish. Leaves oblong-elliptic, 8–15 cm. long, 3–5 cm. wide, base obtuse, apex acuminate, the acumen 1.5–2 cm. long, margin sharp-serrate; primary lateral nerves 14 or 15 pairs, parallel-arcuate, glabrous above, glabrescent beneath, the hairs on the nerves beneath simple, appressed; petioles 8–20 mm. long; leaves produced by active axillary buds 3–7.5 cm. long, 1.5–2.5 cm. wide, sparsely stellate-pubescent above. Racemes 4–6, subumbellate, 14–18 cm. long, rarely shorter, densely ferrugineous-hirsute, the hairs tufted; pedicels 2–3 mm. long at anthesis; sepals ovate, 2–3 mm. long; petals 4 mm. long, 2 mm. wide; filaments glabrous; style pubescent at the basal end. Capsules 3 mm. in diameter; fruiting pedicels 4 mm. long; persistent style 5–6 mm. long, the stigma trifid. Seeds varying in size and shape, compressed ovoid, triangular, or subcylindric, 1–1.5 mm. long, 0.5–1 mm. wide, reticulate, brownish.

KWANGSI: *R. C. Ching 6026, 7000, 7116.* KWEICHOW: *J. Cavalerie 346* (photo and fragment of type); *Handel-Mazzetti 254 = 10766, 325 = 10997.*

Occurring in woods at altitudes of 1300–1500 meters; flowering in late July and early August; closely related to *C. kaipoensis*, but distinguished by its styles being pubescent near the base. The style-character is clear in the fragment of the type. When Rehder and Handel-Mazzetti interpreted *C. pinfaensis* and *C. kaipoensis* as conspecific, they ignored this distinct character.

11. **Clethra kaipoensis** Lévl. Repert. Sp. Nov. Fedde **10**: 475. 1912; Rehder, Jour. Arnold Arb. **15**: 268. 1934, p.p.

A deciduous shrub 1–3 m. high. Leaves oblong-elliptic, 13–19 cm. long, 4–9 cm. wide, base obtuse or rotund, apex acuminate, the acumen 2 cm. long, margin coarse- and sharp-serrate, primary lateral nerves 16–18, 7–13 mm. apart, glabrescent above, sparsely stellate-pubescent along the nerves and barbate in their angles beneath; petioles 1.5–2.5 cm. long, densely ferrugineous-hirsute; leaves produced by the active axillary buds broad elliptic, 3–4 cm. long, 1.5–2 cm. wide, densely velvety on both surfaces, the hairs stellate. Racemes 4–8, subumbellate, occasionally solitary on weak branchlets, densely golden villose-hirsute; pedicels 3 mm. long; sepals deltoid-ovate, 3–4 mm. long; petals 4–5 mm. long; filaments glabrous, anthers 1.5 mm. long, base obtuse; style glabrous, the apex slightly enlarged, 3-lobed, after anthesis 5–6 mm. long. Capsule 4 mm. in diameter.

KWANGSI: *Steward & Cheo 958; Y. W. Taam 24; W. T. Tsang 27900, 27916, 28425.* KWEICHOW: *J. Cavalerie 1221* (holotype, photo and fragment).

Occurring in forest at altitudes of 1000–2100 meters in Kweichow and northern Kwangsi; closely related to *C. kwangsiensis*; distinguished by its unusually large leaves and its glabrous filaments.

12. **Clethra brammeriana** Hand.-Mazz. Anzeig. Akad. Wiss. Wien Math.-Nat. Kl. **58**: 151. 1921, Symb. Sin. 761. 1936.

A deciduous tree, the branchlets densely ferrugineous-hirsute, the hairs tufted, current year's growth 5 mm. in diameter. Leaves oblong-elliptic or obovate-oblong, 11–15 cm. long, 4.5–8 cm. wide, base obtuse or rotundate, apex acute or shortly acuminate, margin subentire and minutely mucronulate-ciliate or aristate-serrate, glabrous above, evenly velvety beneath, primary lateral nerves 15 or 16, parallel-arcuate, 8–12 mm. apart; petioles 14–18 mm. long, ferrugineously or castaneously hirsute. Racemes 5–13, subumbelliform-paniculate, 10–18 cm. long, densely and ferrugineously lanate-hirsute, some bracts persistent; pedicels 2 mm. long, sepals ovate-deltoid, 3–5 mm. long; petals 4 mm. long, 2.5 mm. wide; filaments glabrous, anthers obcordate, exserted; style 5 mm. long after anthesis, the apex undivided, 3-lobed. Fruit and seed not known.

KIANGSI: *T. H. Wang 247* (isotype). KWANGSI: *T. S. Tsoong* (= *Z. S. Chung*) *83414*.

Occurring in woods along ravines at an altitude of 600 meters; closely related to *C. kaipoensis*, but distinguished by its uniformly velvety lower leaf-surfaces. The flowers of *Tsoong 83414*, collected on July 15, are in very young bud.

13. **Clethra kwangsiensis,** sp. nov.

Arbor, ramulis hornotinis teretibus, 5 mm. diametro, dense ferrugineopubescentibus pilis stellatis; foliis chartaceis, ovato-ellipticis, 16–17 cm. longis, 6–7.5 cm. latis, basi rotundatis vel obtusis, apice acuminatis, acumine 2 cm. longis, margine serratis, nervis lateralibus utrinque 20, arcuatis, supra glabris, subtus sparse stellato-pilosis, ad nervis villosis; petiolo 1.5 cm. longo, dense hirsuto; foliis ramulorum axillarium breviter ellipticis, 5–5.9 cm. longis, 3 cm. latis, utrinque stellato-tomentosis, pilis supra rigidis; racemis 6, subumbelliformi-paniculatis, 15–17 cm. longis, dense ferrugineis, pilis stellatis; pedicellis 2–4 mm. longis; sepalis deltoideo-ovatis, 3.5–4 mm. longis, acutis; petalis 5 mm. longis, 2 mm. latis, fimbriatis; filamentis villosis; stylo glabro, apice trifido; capsulis ignotis.

KWANGSI: Tzu Yuen District, in woods near a stream, *T. S. Tsoong* (= *Z. S. Chung*) *83570* (type, A), August 6, 1937 (tree, flowers white).

Occurring in woods along a stream; the white flowers appearing in early August; closely related to *C. kaipoensis,* but distinguished by its filaments being villose on the basal half.

14. **Clethra polyneura** Li, Jour. Arnold Arb. **24**: 449. 1943.

Trees up to 18 meters high. Leaves oblong-lanceolate or oblong-elliptic, 9–15 cm. long, 3–6 cm. wide, base obtuse or rotund, apex acuminate, the acumen 1–2 cm. long, margin densely serrate, principal lateral nerves 18–25 pairs, parallel, 4–6 mm. apart, glabrous above, glabrescent beneath, the midrib and primary nerves sparsely pilose, the hairs simple and appressed; petioles 1–2.5 cm. long, sparsely stellate-hirsute; leaves produced by active axillary buds lanceolate, 4–7 cm. long, 1.3–2 cm. wide, sparsely stellate above, only the nerves ferrugineously stellate-pubescent beneath. Racemes 6–8, subumbellate-paniculate, 10–14 cm. long, densely ferrugineous-hirsute, the hairs tufted; pedicels 1.5–2 mm. long at anthesis; sepals ovate, acute, 2–3 mm. long; petals 3 mm. long, 1.75 mm. wide; filaments glabrous; style glabrous. Capsules 3 mm. in diameter, pericarp velvety; persistent style 6 mm. long, glabrous; fruiting pedicels 3–4 mm. long. Seed ovoid, reticulate, 1 mm. long, 0.5 mm. wide.

KWANGSI: *S. K. Lau 28767* (type). HUNAN: *Fan & Li 519.*

Occurring on hilly slopes at altitudes of 650 m.; closely related to *C. kaipoensis*, but distinguished by its glabrous style and numerous parallel lateral nerves.

15. **Clethra smithiana** Fang, Contr. Biol. Lab. Sci. Soc. China. Bot. Ser. **12**: 121. 1939.

An evergreen shrub or small tree 6–8 m. high, branchlets glabrous, the current year's growth 3–4 mm. in diameter. Leaves coriaceous, lanceolate, 7–13 cm. long, 2–3.5 cm. wide, base cuneate, apex acuminate, the acumen 1–2 cm. long, lateral nerves 15–17 pairs, arcuate, 8–13 mm. apart, obscure above, reticulations of veinlets conspicuous beneath; margin subentire, the apical half remotely sharp-serrate, both surfaces glabrous, the principal nerves very sparsely pilose beneath; petioles 10–15 mm. long, sparsely pilose. Racemes 2–8, subumbelliform, 8–12 cm. long, densely castaneous-hirsute, the hairs tufted; pedicels 1.5–2 mm. long; sepals ovate, 2 mm. long, obtuse or acute; petals 2.5–3 mm. long, 1.5 mm. wide; filaments glabrous, apex of the anthers divergent; style undivided, 3 mm. long after anthesis, the apex slightly enlarged, lobate. Fruit 3 mm. in diameter.

KWANGSI: *R. C. Ching 6854, 7209.* YUNNAN: *H. T. Tsai 51447* (type, not seen).

Occurring in woods at altitudes of 1130–1600 m.; a very distinct species, closely related to *C. faberi,* but distinguished by its subentire leaves, very small flowers, short pedicels and its short, persistent style.

POLYPLOIDY IN ENKIANTHUS (ERICACEAE)

HALLY J. SAX

ENKIANTHUS is a comparatively small genus belonging to the Ericaceae. According to Rehder (1940, 1949) there are about ten species, although more than double that number have been reported. Many of the so-called species which were described in isolated instances were considered by Rehder (1940) and Wilson (1907, 1929) to be geographical forms of species already described.

Most species of *Enkianthus* are attractive shrubs or small trees growing wild in southeastern Asia, Japan, southern, central and western China, and the Himalayas. Fang (1935), in a preliminary study of the Chinese species, said that there is not a single species in the northern provinces of China. He commented that only six of the twenty-one species described are valid.

The confusion in the classification of the genus is not surprising. J. D. Hooker (1879) wrote, "The Eastern genus *Enkianthus* presents four types of structure which almost indicate as many genera and would do so if the species had not been united by habit and if the characters were associated instead of applying to one species only."

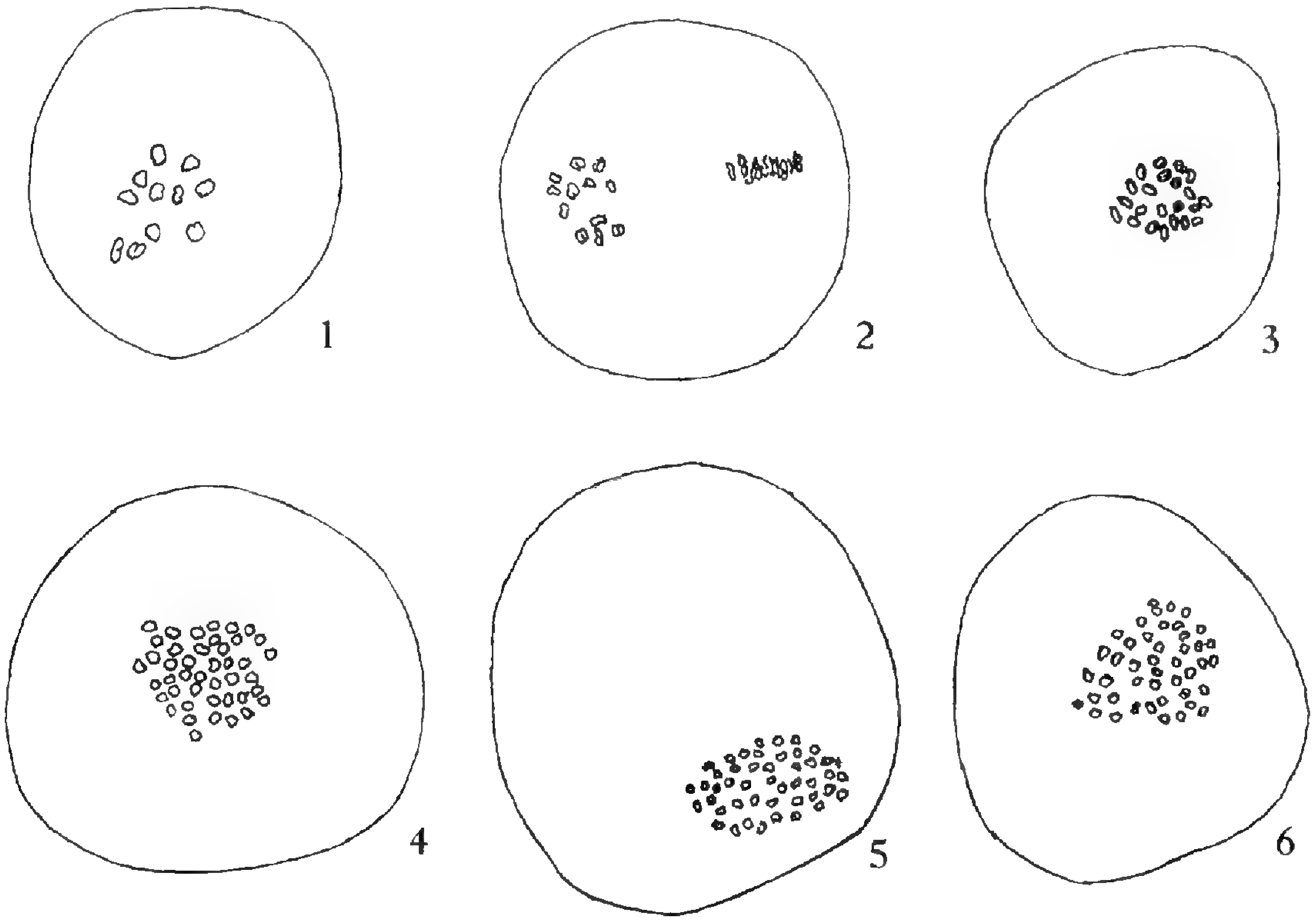
The number of chromosomes in *Enkianthus* was studied to determine if there was polyploidy in the genus. The variety in the structure of the flowers in the small number of species of *Enkianthus*, as well as their limited distribution, would offer possibilities of interesting combinations. Stomatal size and shape were also determined to learn if there was any correlation between stomatal size and chromosome number in the genus.

Three species of *Enkianthus* with some varieties are growing in the Arnold Arboretum: *E. campanulatus* (Miq.) Nichols, with vars. *albiflorus* Mak. and *palibinii* Bean; *E. perulatus* (Miq.) Schneider; and *E. subsessilis* (Miq.) Mak. Some of these on Bussey Hill were planted as early as 1890. A more recent and successful planting of the same species was made on low ground along the meadow road to the administration building. *Enkianthus cernuus* (Sieb. & Zucc.) Mak. var. *rubens* (Maxim.) Mak. is now being propagated in the Arboretum greenhouse. The chromosome numbers of the species of *Enkianthus* in the Arnold Arboretum were studied from meiotic divisions in the pollen mother cells, from the divisions of somatic cells in the ovary and from regenerating parenchyma of the stem. Very good preparations of divisions in both metaphase and anaphase in the dividing egg cell were also obtained.

The regenerating parenchyma is obtained according to the bark-peel method developed by Sax (1959). A longitudinal section of the bark is removed from the growing stem. The wound is covered with a strip of polyethelene film and left for several days. The newly developed tissue is then sliced off and fixed. The anthers, ovules and bark tissue were fixed in alcohol-acetic solution for twenty-four hours. The material was then changed to 95 per cent alcohol. Pieces of these tissues were macerated and smeared on a slide and stained with acetocarmine. Camera lucida drawings were made from some of the slides. I wish to thank Dr. Karl Sax for making the bark peels and for checking most of the counts.

The chromosomes were counted in the divisions of the pollen mother cells in *Enkianthus subsessilis* and several plants of *E. campanulatus* including the varieties *albiflorus* and *palibinii.* The chromosomes were also counted in the somatic tissue of the ovules. In the case of *E. perulatus,* counts were made in the somatic tissue in the ovule where it was possible to obtain several very good division figures where the chromosomes could be counted. Counts were also made from the regenerating bark in *E. perulatus* and *E. campanulatus,* where very good preparations of the divisions in the large parenchyma cells were obtained. In all cases several very good preparations were obtained.

Enkianthus subsessilis was found to be a diploid with 11 chromosomes in the meiotic divisions in the pollen mother cells. They were very clear in the preparations and could easily be counted in both the metaphase and anaphase stages. The camera lucida drawings show clearly 11 bivalent chromosomes in the first metaphase of the dividing nucleus of the pollen mother cell (Fig. 1). The 11 anaphase chromosomes are very clear in



Figs. 1–6. Chromosomes of *Enkianthus.* 1, *E. subsessilis,* first meiotic metaphase; 2, *E. subsessilis,* second meiotic metaphase; 3, *E. perulatus,* somatic metaphase; 4, *E. campanulatus,* first meiotic metaphase; 5, *E. campanulatus,* second meiotic metaphase; 6, *E. campanulatus* var. *albiflorus,* second meiotic metaphase. All figures approximately × 1000.

FIG. 2 just as they are oriented at the poles. There were 22 chromosomes in the somatic tissue of the developing ovule (TABLE I).

Enkianthus perulatus is also a diploid. The count in this case was made in the somatic tissue of the ovule and in the parenchyma of the regenerating bark. Very clear counts in both metaphase and anaphase were obtained. There were 22 chromosomes in the somatic tissue, as is shown in FIG. 3 which was drawn from parenchyma tissue obtained by the bark-peel technique.

Enkianthus campanulatus is a high polyploid — presumably an octoploid — with approximately 88 chromosomes. There were about 44 chromosomes in the divisions of the pollen mother cells of several plants labeled as this species. Multivalent chromosomes were present and an occasional univalent was seen. The divisions were regular, suggesting some degree of allopolyploidy. Only in a few cases were there any lagging chromosomes. Camera lucida drawings were made of the dividing nuclei from several of these plants; all show approximately 44 chromosomes (FIGS. 4, 5).

Enkianthus campanulatus var. *albiflorus* is also an octoploid with $n = 44$ at meiosis. Multivalent associations of three and four chromosomes were seen in some cases, but bivalents predominated. The divisions were regular except in rare instances (FIG. 6). The number of chromosomes in the regenerating bark and in the ovule was over 80, the counts varying from 82 to 89. The chromosomes were small and it was difficult to be exact with such large numbers. TABLE I shows the number in each case.

The two diploid species belong in different sections of the genus, while the octoploid is in a third section. Polyploidy is not necessarily associated

TABLE I. **Chromosome Numbers in Enkianthus**

SPECIES	ARBORETUM NO.	MEIOTIC	SOMATIC	ZONE *
E. campanulatus	14528–1–D	44±	80–87	IV
	14528–1–G	44±		
	14528–1–C		88±	
	23001–1–C		88±	
	7692	44		
	507–58–D		88±	
	507–58–E		78–87	
var. *albiflorus*	14783–E	44±		IV
	7039–3–A	44±		
	14783–G		88±	
E. perulatus	20153–B		22	V
	10128–B		22	
	3591		22	
E. subsessilis	2449–B	11	22	V
	2449	11		

* A map of the climatic zones is found in Rehder (21). The zones are numbered from the North Pole southward. They are irregular according to the prevailing climate.

with taxonomic diversity. The fact that the octoploid species shows predominantly bivalent chromosomes at meiosis indicates that it is an amphiploid with different genomes.

Chromosome numbers have been reported for many genera of the Ericaceae (Darlington and Janaki-Ammal, 1945). Longley published the chromosome numbers of *Vaccinium*, a polyploid series with the basic number 12. Hagerup (1928) studied several genera: *Calluna vulgaris*, with 16; *Kalmia*, 24 and 48; *Cassiope hypnoides*, 48; *Erica*, 24; *Chimaphila umbellata*, 26; *Ledum*, 26 and 52; *Ramischia*, 38; and *Pyrola*, 46 and 92.

Wanscher (1933) reported 24 chromosomes in *Phyllodoce*; Wulff (1939), 22 chromosomes in *Moneses uniflora*; Maude (1940), 24 in *Daboecia cantabrica*; Newcomer (1941), 24 in *Gaultheria procumbens*; Callan (1941), 36 chromosomes in *Bruckenthalia*, 22, 44, 66 in *Pernettya*, 22, 44, 88 and 26 in *Gaultheria*, 24 in *Pieris*, 48 in *Andromeda*, 24 in *Leucothoë*, 24 in *Erica*, and 26 in *Arbutus*, *Arctostaphylos*, and *Ledum*. Hagerup (1941) counted 60 chromosomes in *Enkianthus campanulatus*, 26 in *Chimaphila*, and 52 in *Ledum*. Baldwin (1942) found 24 chromosomes in *Oxydendrum arboreum*.

Sax (1930) reported the number of chromosomes in *Rhododendron* as 26 for many species and 52 for two higher polyploids, the latter being native to North America. Nakamura (1931) found 26 to be the chromosome number for nine more species of *Rhododendron*. Janaki-Ammal (1950) reported *Rhododendrons* with 4*x*, 6*x*, 8*x*, and 12*x* chromosomes in the high Himalayas in Eastern Asia, polyploidy increasing with altitude. Li (1957) also found 26 chromosomes in all the species of the "luteum" section of the azaleas, excepting the tetraploid *R. calendulaceum* and its hybrids and one triploid.

Thus, with few exceptions (*Calluna vulgaris*), the basic numbers of chromosomes are 11, 12, and 13. Polyploidy is prevalent in many genera, e.g., *Vaccinium*, *Pernettya*, *Gaultheria*, *Pieris*, and *Ledum*. As noted above, Hagerup (1941) reported 60 chromosomes for *Enkianthus campanulatus*, considering it a high polyploid, and suggesting 12 as the basic number both for *Enkianthus* and for the family.

Enkianthus has a very narrow distribution: southeastern Asia, central and western China, and Japan. The polyploid *E. campanulatus* is more widely distributed than the diploids, which have a narrow range and are limited to the warmer parts of China and Japan. Yet, compared with the *Rhododendrons*, which are native to a large part of both hemispheres, the polyploid *E. campanulatus* which extends from northern Japan to southern and central China and to the Himalayas in West China is a naturally limited species. However, when in cultivation it grows very well in the North Temperate Zone in Europe and the United States. The diploid species *E. perulatus* and *E. subsessilis*, as well as *E. cernuus* var. *rubens*, are also able to grow fairly well when introduced as far north as Boston, Massachusetts.

Stomatal size was also studied in three species of *Enkianthus*. The epidermis was peeled from the leaf and mounted on a slide in a drop of acetocarmine. Camera lucida drawings were made from the mounted epidermis. The diploids *E. perulatus* and *E. subsessilis* showed very little difference in size, but there was some difference in shape. Although no appreciable difference in size was found between the stomata in *E. perulatus* and *E. subsessilis*, there is a striking difference in size between these diploids and the high octoploid *E. campanulatus*. The stomata of *E. campanulatus* are very much larger than those of the diploids, as was noted by comparing the figures in camera lucida drawings of the stomata of these species. There is a very definite correlation between stomatal size and number of chromosomes in the species of *Enkianthus* studied.

Counts were made of the fertile and sterile pollen grains in the different species. Usually the fertility was high, around 85 per cent, but as low as 35 per cent was found. These latter cases were not consistent for any of the species studied and may not be typical, the aberrance having been caused, perhaps, by factors not studied.

SUMMARY

There are 11 meiotic chromosomes in *Enkianthus subsessilis*, 22 somatic chromosomes in *E. perulatus* and *E. subsessilis*. Both are diploid species.

The meiotic chromosomes in *Enkianthus campanulatus* and var. *albiflorus* are 44, and there are about 88 ± chromosomes in the dividing somatic cells. *Enkianthus campanulatus* and its varieties are octoploids.

The stomatal size in *Enkianthus perulatus* and *E. subsessilis*, both diploid species, is about the same. The stomata of the two differ somewhat in shape. The stomata are much larger in *E. campanulatus*, the octoploid, and its varieties than in the diploids, showing a definite correlation between stomatal size and chromosome number.

Although there is some pairing in threes and fours in *Enkianthus campanulatus*, most of the chromosomes are bivalents in the polyploids.

LITERATURE CITED

BALDWIN, J. T. Cytogeography of *Oxydendrum arboreum*. Bull. Torrey Bot. Club **69:** 134. 1942.

CALLAN, H. G. The cytology of *Gaulthettya wisleyensis* (Marchant) Rehder. Ann. Bot. **5:** 579. 1941.

DARLINGTON, D. C., and E. K. JANAKI-AMMAL. Chromosome atlas of cultivated plants. 379 pp. G. Allen, London. 1945.

FANG, W. P. A preliminary study of the Chinese species of *Enkianthus* Loureiro. Contr. Biol. Lab. Sci. Soc. China **10:** 1935.

HAGERUP, O. Morphological and cytological studies of Bicornes. Dansk. Bot. Ark. **6:** 1. 1928.

———. Zytoökologische Bicornes Studien. Planta **32:** 6. 1941.

HOOKER, J. D. *Enkianthus himalaicus*. Bot. Mag. III. **35:** *pl. 6460*. 1879.

JANAKI-AMMAL, E. K. Polyploidy in the genus *Rhododendron*. Rhododendron Year Book, London **5:** 92–98. 1950.

LI, H. L. Chromosome studies in the azaleas of eastern North America. Am. Jour. Bot. **440:** 8–14. 1957.

LONGLEY, A. E. Chromosomes in *Vaccinium*. Science **66:** 566. 1927.

LOUREIRO, J. *Enkianthus quinqueflorus*. Flora Cochinchinensis **1:** 277. 1790.

MAUDE, P. F. Chromosome numbers in some British plants. New Phytol. **39:** 17. 1940.

NAKAMURA, M. Cytology of *Rhododendron*. Trop. Agric. Tohoku Imp. Univ. **3:** 103. 1931.

NEWCOMER, E. H. Chromosome numbers of some species and varieties of *Vaccinium* and related genera. Proc. Am. Soc. Hort. Sci. **38:** 4–68. 1951.

REHDER, A. *Enkianthus*. *In* Manual of Cultivated Trees and Shrubs. Ed. 2. 729–730. 1940.

———. *Enkianthus*. *In* Bibliography of cultivated trees and shrubs hardy in the cooler temperate regions of the Northern Hemisphere. Arnold Arboretum, Harvard University. Jamaica Plain, Mass. 1949.

SAX, K. Chromosome stability in the genus *Rhododendron*. Am. Jour. Bot. **17:** 247. 1930.

———. The cytogenetics of facultative apomixis in *Malus* species. Jour. Arnold Arb. **40:** 289–297. 1959. [Bark-peel technique, p. 290.]

WANSCHER, J. H. Secondary (chromosome) associations in Umbelliferae and Bicornes. New Phytol. **33:** 58. 1933.

WILSON, E. H. The genus *Enkianthus*. Garden Chron. III. **41:** 311, 344, 363. 1907.

———. *Enkianthus*, page 248 *in* China, Mother of gardens. 4 + 408 pp., map, 6 illustrations. Stratford Co., Boston, Mass. 1929.

———. *Enkianthus*. *In* If I were to make a garden. pp. 205–210. 1931.

WULFF, H. D. Chromosomenstudien an der schleswigholsteinischen Angiospermen Flora, IV. Ber. Deutsch. Bot. Ges. **57:** 424. 1939.

THE GENERA OF HYDROPHYLLACEAE AND POLEMONIACEAE IN THE SOUTHEASTERN UNITED STATES[1]

KENNETH A. WILSON

HYDROPHYLLACEAE R. Brown ex Edwards (WATERLEAF FAMILY)

Annual, biennial or perennial herbs [or rarely shrubs] with alternate or opposite, entire, pinnately or palmately divided leaves. Inflorescences terminal, axillary, or opposite the leaves, the flowers in cymes, panicles, or solitary. Flowers bisexual, regular, 5-merous. Calyx 5-parted, the sinuses sometimes bearing appendages. Corolla rotate, campanulate or funnelform, 5-parted. Stamens 5, epipetalous. Gynoecium syncarpous; styles 2 (rarely more) or 1, terminal; ovary superior, 1-locular with 2 parietal placentae or 2-locular and the placentation axile. Ovules 4–many, anatropous or amphitropous. Fruit a capsule.

A family of about 18 genera and 250 species in three tribes, primarily of North America, but extending into South America, Asia, and Africa. The family is represented in the United States by 15 genera centered in the Southwest; six genera occur in our area.

The family is regarded as being closely allied to the Polemoniaceae and the Boraginaceae. It may be distinguished from them by the combination of bicarpellary 1- or 2-locular ovary (usually with numerous ovules) and the usually imbricate aestivation of the flowers which are generally borne on scorpioid cymes. Considerable variation is evident in the structure and nature of the ovary. The gynoecium is 2-carpellate; the placentae may be parietal and fleshy or they may be narrow, extending into the ovary to meet without fusing and partition the ovary into two locules. In *Hydrolea* further elaboration of the placentae, accompanied by a fusion of the dividing wall, has produced a 2-locular ovary with axile placentation.

The Hydrophyllaceae are cytologically perhaps the best known family of any size. Information on the chromosome numbers of the species in

---

[1] Prepared for a biologically oriented generic flora of the southeastern United States, a joint project of the Gray Herbarium and the Arnold Arboretum made possible through the support of George R. Cooley and the National Science Foundation, and under the direction of Reed C. Rollins and Carroll E. Wood, Jr. The scheme follows that outlined at the beginning of the series (Jour. Arnold Arb. **39**: 296–346. 1958). Other published portions of these studies will be found in Jour. Arnold Arb. **40, 41.** 1959, 1960. I am grateful to Lincoln Constance who has offered many helpful suggestions and comments in connection with the Hydrophyllaceae. I wish also to express my indebtedness to R. B. Channell, G. R. Cooley, and H. F. L. Rock for their assistance in supplying information, aiding in the obtaining of specimens, and helping in various ways.

the family has been accumulating, and, along with morphological studies, has already contributed to the understanding of the group. Cytological information, for instance, supports the recognition of subg. *Cosmanthus* of *Phacelia,* and also points to the relationship of *Lemmonia* to *Nama.* A comprehensive knowledge of the cytology of the members of this family will give a clearer indication of the value of chromosomal data in systematic studies. Presently the chromosomes of about 67 per cent of the species (about 200) have been counted, and counts are available for at least one species in each of the described genera.

REFERENCES:

BRAND, A. Hydrophyllaceae. Pflanzenr. IV. **251**(Heft 59): 1–210. 1913.

———. Die Hydrophyllaceen der Sierra Nevada. Univ. Calif. Publ. Bot. **4**: 209–227. 1912.

CAVE, M. S., and L. CONSTANCE. Chromosome numbers in the Hydrophyllaceae. Univ. Calif. Publ. Bot. **18**: 205–216. 1942; II. **18**: 293–298. 1944; III. **18**: 449–465. 1947; IV. **23**: 363–382. 1950; V. **30**: 233–258. 1959.

CONSTANCE, L. The genera of the tribe Hydrophylleae of the Hydrophyllaceae. Madroño **5**: 28–33. 1939. [Includes key to genera.]

———. Hydrophyllaceae. *In* L. Abrams, Ill. Fl. Pacific States **3**: 476–532. 1951.

———. Hydrophyllaceae. Inst. Paran. Catal. Gen. **4**: 1, 2. 1956.

GRAY, A. A conspectus of the North American Hydrophyllaceae. Proc. Am. Acad. Arts Sci. **10**: 312–332. 1875.

PETER, A. Hydrophyllaceae. Nat. Pflanzenfam. IV. **3a**: 54–71. 1897.

SVENSSON, H. G. Zur Embryologie der Hydrophyllaceen, Borraginaceen und Heliotropiaceen mit besonderer Rücksicht auf die Endospermbildung. Uppsala Univ. Årsskr. 1925. **2**(Math. Nat. 2): 1–176. 1925.

KEY TO THE GENERA OF HYDROPHYLLACEAE

A. Leaves dissected, lobed or toothed; style 1, entire or 2-cleft.
  B. Placentae parietal, dilated, ovary 1-locular.
    C. Flowers in scorpioid cymes; stamens exserted; leaves mostly basal and alternate; seeds not cucullate; plants biennial or perennial. . . . . 1. *Hydrophyllum.*
    C. Flowers solitary opposite the leaves or terminal in a loose cyme; stamens included; leaves mostly cauline, all alternate or the lower opposite and the upper alternate; plants annual.
      D. Calyx sinuses auriculate; seeds cucullate; leaves all alternate. . . . . 2. *Nemophila.*
      D. Calyx sinuses without auricles; seeds not cucullate; leaves opposite below, alternate above. . . . . 3. *Ellisia.*
  B. Placentae parietal, narrow, projecting into ovary and partitioning it into 2 locules but not fusing; flowers in scorpioid cymes; calyx sinuses without auricles; seeds not cucullate; leaves alternate. . . . . 4. *Phacelia.*
A. Leaves entire, simple; styles 2 (rarely 3–5).
  E. Flowers axillary, solitary or paired; placentae parietal, narrow, projecting into ovary and partitioning it into 2 locules but not fusing. . . . 5. *Nama.*
  E. Flowers in cymose inflorescences; ovary 2-locular; placentae axile. . . . . 6. *Hydrolea.*

Tribe HYDROPHYLLEAE A. Gray

1. **Hydrophyllum** Linnaeus, Sp. Pl. 1: 146. 1753; Gen. Pl. ed. 5. 72. 1754.

Erect, perennial or biennial herbs with membranaceous, pinnate or pinnatifid basal leaves and alternate cauline leaves similar to the basal ones or orbicular to reniform, palmately lobed or divided. Inflorescences simple or branched cymes, terminal. Calyx campanulate, 5-lobed, at times the sinuses with a small appendage. Corolla campanulate, 5-parted, greenish-white or white to purple or violet, with a pair of elongated scales adnate to the corolla tube at the base of each filament. Stamens 5, exserted, the filaments more or less villous; pollen smooth, tricolpate. Style solitary, once branched at the apex, the stigmas capitate; ovary 1-locular with 2 parietal placentae. Fruit a globose, 1–3-seeded capsule. Seeds reticulate, without cucullus. (Including *Decemium* Raf.) TYPE SPECIES: *H. virginianum* L. (Name from Greek, *hydor*, water, and *phyllon*, leaf, in reference to the succulent stems and petioles of *H. virginianum.*) — WATERLEAF.

A genus of eight species in two sections with four species in eastern and four in western North America. All four of the eastern American species occur in our area, all in rich, moist woods. The species of *Hydrophyllum* are very similar in floral and fruit characters, but are distinguishable in the characters of the leaf and of pubescence.

Section HYDROPHYLLUM (perennial and rhizomatous, calyx rarely appendaged) includes seven species, four restricted to western North America, and three in our area. *Hydrophyllum virginianum* ($2n = 18$) ranges from Quebec west to eastern North and South Dakota and south to Maryland, Virginia, Tennessee, Arkansas, and Kansas. Deep-violet-flowered plants from the mountains of West Virginia, Virginia, and North Carolina have been described as *H. virginianum* var. *atranthum* (E. J. Alex.) Constance. Additional field study is needed to determine whether this is merely a color-form occurring among other forms (white to purple) or whether it is in fact the only representative of the species in its area and restricted in its distribution. *Hydrophyllum macrophyllum* Nutt. ranges from western Virginia and West Virginia, west to Illinois, and south to Georgia, Alabama, and Arkansas; and *H. canadense* L. ($2n = 18$) occurs from Massachusetts and Vermont to Ontario and Illinois south to northern Alabama and eastern Missouri.

Section DECEMIUM (Raf.) Gray (biennial with taproot, calyx always appendaged) includes only *Hydrophyllum appendiculatum* Michx. ($2n = 18$) which is distributed from Ontario to Minnesota, south to Pennsylvania, Tennessee, Missouri, and eastern Kansas. The presence of appendages in the sinuses of the calyx lobes and the biennial habit have served as characters in the recognition of the monotypic genus *Decemium* Raf. However, since appendages may occasionally be found in *H. canadense* and other distinguishing features are only minor floral variations, *Decemium* is to be retained in *Hydrophyllum* which it closely resembles in all other respects.

REFERENCES:

CONSTANCE, L. The genus *Hydrophyllum* L. Am. Midl. Nat. 27: 710–731. 1942. [Monograph.]

GARCIN, M. Étude anatomique de l'*Hydrophyllum canadense*. Bull. Soc. Bot. Lyon II. 5: 77–85. 1887.

SELBY, A. D. A peculiar *Hydrophyllum*. Jour. Columbus Hort. Soc. 8: 128–130. 1893–1894.*

2. **Nemophila** Nuttall in Barton, Fl. N. Am. 2: 71. 1822; Nuttall, Jour. Acad. Nat. Sci. Phila. 2: 179. 1822, nom. cons.

Weak, annual herbs with alternate [or opposite, or the lower opposite and the upper alternate] oblong to orbicular, pinnate, pinnatifid or lobed leaves. Flowers solitary on peduncles opposite the leaves or in terminal cymes. Calyx campanulate, deeply 5-parted, the sinuses auriculate [or exauriculate.] Corolla campanulate to rotate, 5-lobed, white or blue, with a pair of scales adnate to corolla lobes at the base of each filament. Stamens 5, included; pollen smooth, tricolpate. Style solitary, shallowly or deeply cleft; ovary 1-locular with 2 parietal placentae. Fruit an ovoid or globose, 1–4[–20]-seeded loculicidal capsule. Seeds cucullate, regularly [or irregularly] pitted [or without evident pits]. (*Viticella* Mitch., nom. rejic.; *Galax* L. 1753 [partim], 1754, nom. rejic.) TYPE SPECIES: *N. phacelioides* Nutt. in Barton. (Name from Greek, *nemos*, a grove, and *philein*, to love, in reference to the habitat of *N. phacelioides*.)

A genus of eleven species with nine in western North America and two in the southeastern United States. The species are distinguished on the basis of leaf shape and arrangement, nature of the seeds, color and shape of the corolla, nature of the auricles, and pubescence of the stems and leaves. A number of growth forms of various species have been described and named, mostly as a result of misinterpretation of the behavior of the species during the growing season. As the season progresses, most species pass from a small, erect, and unbranched stage to an elongated, decumbent, and branched one. The flowers also often become smaller and altered in their shape.

Our two species occur in moist and shaded woods. *Nemophila phacelioides* Nutt. ($2n = 14$) (corollas blue or purplish, 1–3 cm. broad, auricles prominent) ranges from southern Texas and Louisiana north to Arkansas and Oklahoma. It is cytologically unique in its seven pairs of chromosomes which are nearly twice as large as the nine pairs of the ten other species. *Nemophila microcalyx* (Nutt.) Fisch. & Mey. (corollas white, 0.5 cm. or less broad, auricles minute) ($2n = 18$) ranges from southeastern Texas north to Arkansas, and southeastern Missouri, east and north to Florida, Tennessee and Virginia.

REFERENCES:

BERG, R. Y. Seed dispersal, morphology, and phylogeny of *Trillium*. Skr. Vid.-Akad. Oslo 1: 1–36. 1958. [Includes note on the dispersal of seeds of *Nemophila* by ants.]

BIOLETTI, F. T. Notes on the genus *Nemophila*. Erythea 3: 139–142. 1895.

CHANDLER, H. P. A revision of the genus *Nemophila*. Bot. Gaz. **34**: 194–215. 1902.

CONSTANCE, L. The genus *Nemophila* Nutt. Univ. Calif. Publ. Bot. **19**: 341–398. 1941. [Monograph.]

CRÉTÉ, P. Embryogénie des hydrophyllacées. Développement de l'embryon chez le *Nemophila insignis* Benth. Compt. Rend. Acad. Sci. Paris **224**: 749–751. 1947.

EASTWOOD, A. Observations on the habits of *Nemophila*. Erythea 3: 151–153. 1895. [Flowers of *N. insignis* (= *N. Menziesii*).]

WULFF, H. D., and T. S. RAGHAVAN. Beobachtungen an Pollenschlauchkulturen von der Hydrophyllacee *Nemophila insignis*. Planta **27**: 466–473. 1937.

3. **Ellisia** Linnaeus, Sp. Pl. ed. 2. 2: 1662. 1763, nom. cons.

Simple or diffusely branched, weak annual herbs with oblong to ovate or deltoid-ovate, pinnately divided leaves, the lower opposite and the upper alternate. Flowers solitary on peduncles opposite the leaves or in terminal cymes. Calyx campanulate, deeply 5-parted, auricles none. Corolla narrowly campanulate, 5-lobed, white or bluish, with a pair of minute scales adnate to each corolla lobe at the base of each stamen. Stamens 5, included; pollen smooth, tricolpate. Style solitary, 2-cleft; ovary 1-locular with 2 parietal placentae. Fruit a globose, usually 4-seeded capsule. Seeds without a cucullus, regularly reticulate. $2n = 20$. (*Macrocalyx* Ehret ex Trew, Nova Acta Acad. Leop.-Carol., nom rejic.; *Nyctelea* Scopoli.) TYPE AND SOLE SPECIES: *E. Nyctelea* (L.) L. (Named in honor of the English naturalist John Ellis, 1710–1776.)

A monotypic genus with disrupted distribution, occurring in rich woods and on stream banks from New Jersey and Pennsylvania to North Carolina (?) and on the prairies and plains of Manitoba to Alberta, southeast and south to Indiana, Illinois, Arkansas, Oklahoma, and New Mexico. It is also known as an adventive in disturbed areas in the northeastern United States.

Ellisia resembles *Pholistoma* and *Nemophila*, but is distinguished by its seeds which lack a cucullus, its unarmed capsules, and its hispid or glabrate stems. Although closely related to these groups, *Ellisia* is believed to be a distinct and natural genus.

REFERENCES:

CONSTANCE, L. The genus *Ellisia*. Rhodora **42**: 33–39. 1940.

ROBERTSON, C. Flowers and insects. X. Bot. Gaz. **18**: 47–54. 1893. [Pollination of *Ellisia* by bees.]

Tribe PHACELIEAE A. Gray

4. **Phacelia** Jussieu, Gen. Pl. 129. 1789.

Annual, biennial [or perennial] herbs with alternate, lobed or pinnately divided leaves. Inflorescences scorpioid cymes. Calyx deeply 5-parted. Corollas rotate to campanulate, 5-lobed, white to lavender or bluish violet, without scales, a gland bearing two parallel flaps adnate to the corolla tube between each pair of stamens. Stamens 5, exserted or included. Style 2-cleft; ovary with two 2–14-ovuled parietal placentae which meet and partition the ovary into 2 locules. Fruit an ovoid 4–many-seeded capsule. Seeds finely reticulate to alveolate or rugose. TYPE SPECIES: *P. secunda* J. F. Gmelin (*P. magellanica* (Lam.) Coville). (Name from Greek, *phacelos*, a fascicle, in reference to the cymose inflorescences.) — SCORPION WEED.

A genus of perhaps 100 species of temperate North and South America, placed by Brand in six sections. All of our species belong to subg. COSMANTHUS (Nolte ex A. DC.) Constance (sect. *Cosmanthus* Nolte ex A. DC.). The genus itself is characterized by the scorpioid cymes and by the narrow placentae which project into the ovary and meet, thereby producing two locules.

Subgenus COSMANTHUS, with 14 species, occurs from the highlands of Guatemala and Mexico, north into Texas, east to Georgia and North Carolina, and north to Oklahoma, Missouri, Illinois, Ohio, Pennsylvania and New York, primarily in rich woods, clearings, and fields. Ten species and varieties occur in our area. All of our species are annuals, except *Phacelia bipinnatifida* Michx. (including *P. brevistyla* Buckl.) ($2n = 18$), a biennial distributed from West Virginia to Georgia and Alabama, west to Illinois, Missouri, and northeastern Arkansas. This species, formerly placed in sect. PHACELIA because of its prominent glands and their associated scales, belongs properly in subg. COSMANTHUS on the basis of its other morphological features and its distribution.

Phacelia Purshii Buckl. (including *P. Boykinii* (A. Gray) Small and *P. Bicknellii* Small) ($2n = 18$) is widely distributed in eastern North America. Both large-flowered plants of *P. Purshii* and similar small-flowered plants (*P. Bicknellii* ?) grow together in the vicinity of Nashville, Tennessee, suggesting the need for additional investigation. *Phacelia dubia* (L.) Trel. var. *dubia* ($2n = 10$) is also of wide distribution in eastern North America, while *P. dubia* var. *georgiana* McVaugh is an endemic of the granite flat rocks of Georgia and Alabama.

Phacelia strictiflora (Engelm. & Gray) Gray var. *Robinsii* Constance ($2n = 18$), of Alabama, Missouri, Oklahoma, and Texas, has characters intermediate between *P. strictiflora* var. *Lundelliana* Constance ($2n = 18$) (Texas and Oklahoma) and *P. hirsuta* Nutt. ($2n = 18$) (Missouri, Kansas, Arkansas, Louisiana, Oklahoma, Texas) and is suspected of having arisen through the hybridization of those two taxa. Similarly, hybridization of *Phacelia hirsuta* and *P. Purshii* appears to have given rise to *P. gilioides* Brand ($2n = 18$) (Missouri, Kansas, Oklahoma).

Our other species are *Phacelia ranunculacea* (Nutt.) Constance (*P. Covillei* S. Wats.) ($2n = 28$), peculiar in its tubular-campanulate corolla, vestigial glands, semiglobose seeds, chromosome number, and disrupted distribution (Maryland, District of Columbia, Virginia and Indiana, Missouri, Tennessee, North Carolina, Arkansas); *P. maculata* Wood ($2n = 10$), from the southern Appalachians; *P. glabra* Nutt. ($2n = 16$), unique in its chromosome number; and *P. fimbriata* Michx. ($2n = 18$). In spite of the different chromosome numbers among the species in subg. COSMANTHUS, the absence of the number 11, which is common among the other members of the genus, supports the distinctness of the group. It is also the only group of *Phacelia* in which there is a 9-paired perennial species (*P. platycarpa* (Cav.) Spreng.).

REFERENCES:

ALLARD, H. A. *Phacelia ranunculacea* (Nutt.) Constance, its length of day, temperature reactions and seasonal adaptations. Castanea **5**: 94–97. 1940.

CONSTANCE, L. A revision of *Phacelia* subgenus *Cosmanthus* (Hydrophyllaceae). Contr. Gray Herb. **168**: 1–48. 1949.

———. Some interspecific relationships in *Phacelia* subgenus *Cosmanthus*. Proc. Am. Acad. Arts Sci. **78**: 135–147. 1950.

———. *Howellanthus*, a new subgenus of *Phacelia*. Madroño **11**: 198–203. 1952.

CRÉTÉ, P. Embryogénie des hydrophyllacées. Développement de l'embryon chez le *Phacelia tanacetifolia* Benth. Compt. Rend. Acad. Sci. Paris **223**: 459, 460. 1946.

FERNALD, M. L. Overlooked species, transfers and novelties in the flora of eastern North America. Rhodora **46**: 32–57. 1944. [51–56, The plants passing as *Phacelia hirsuta*.]

GILLETT, G. W. Variation and genetic relationships in the Whitlavia and Gymnobythus Phacelias. Univ. Calif. Publ. Bot. **28**: 19–78. 1955. [$2n = 22$ in all 7 species.]

GREENE, E. L. Some *Phacelia* segregates. Pittonia **5**: 17–23. 1902.

HECKARD, L. R. Cytotaxonomy of a polyploid complex. VIII^e Congr. Int. Bot. Rapp. & Comm. **Sect. 9, 10**: 72, 73. 1954. [*Phacelia magellanica* complex.]

HOWELL, J. T. A revision of *Phacelia* sect. *Euglypta*. Am. Midl. Nat. **36**: 381–411. 1946.

———. A revision of *Phacelia* section *Miltitzia*. Proc. Calif. Acad. Sci. IV. **25**: 357–376. 1944.

———. Studies in *Phacelia* — I–IV. Leafl. West. Bot. **3**: 95, 96, 1941; 117–120, 190–192. 1942; **4**: 150–152. 1945.

———. Studies in *Phacelia* — revision of species related to *P. Douglasii*, *P. linearis* and *P. Pringlei*. Am. Midl. Nat. **33**: 460–494. 1945.

———. Studies in *Phacelia* — a revision of species related to *P. pulchella* and *P. rotundifolia*. Am. Midl. Nat. **29**: 1–26. 1943.

———. Sertulum Greeneanum. Am. Midl. Nat. **30**: 6–39. 1943. [I. A systematic study of *Phacelia humilis* and its relatives. II. Types of *Phacelia* in the Greene herbarium.]

JANOTA, D. Erste Erfahrungem mit dem Nektarbetrag der *Robinia pseudoacacia* und *Phacelia tanacetifolia.* (In Czech.) Brno. Vysoká Zeměděl. a Lesn. Fakul. Sborn. Rada A. **1956**(4): 225–234. 1956.*

KARTASHOVA, N. Minor elements and nectar-yielding *Phacelia.* (In Russian.) Sel'sk. Khoz. Sibiri **1958**(8): 82–84. 1958.*

KRUCKEBERG, A. R. Notes on the *Phacelia magellanica* complex in the Pacific Northwest. Madroño **13**: 209–221. 1956. [I. A new *Phacelia* from southwestern Oregon. II. The hexaploid *Phacelia leptosepala* Rydberg.]

LIVENTSEVA, E. On determining the seed germination of *Phacelia.* (In Russian.) Pchelovodstvo **29**(3): 42–44. 1952.*

QUICK, C. R. Germination of *Phacelia* seeds. Madroño **9**: 17–20. 1947. [Seeds of many annual species will grow without special treatments; seeds of many perennial species must be stratified.]

ROLLIN, P. Action qualitative de la lumière sur la germination des graines de *Phacelia tanacetifolia.* Compt. Rend. Acad. Sci. Paris **247**: 1484–1487. 1958.

VOSS, F. W. A revision of the *Phacelia crenulata* group for North America. Bull. Torrey Bot. Club **64**: 81–96. 1937.

5. **Nama** Linnaeus, Syst. Nat. ed. 10. 2: 950. 1759, partim, emend. Choisy in DC. Prodr. **10**: 182. 1846, nom. cons.

Prostrate or ascending, annual [or perennial] herbs with alternate [rarely opposite] entire leaves. Flowers solitary or paired in the axils of leaves [or in reduced lateral or terminal cymes]. Calyx deeply 5-parted, accrescent. Corolla tubular, 5-lobed, purple or white. Stamens 5, included, unequally inserted on the corolla tube, the filament bases usually dilated, the adnate portion with [or without] free margins. Styles 2, free, or at times united about half their length [or completely united]; ovary multiovulate, appearing 2-locular as a result of the intrusion of the 2 parietal placentae. Fruit a loculicidal [or either loculicidal or septicidal] many-seeded capsule. Seeds variously pitted, alveolate [or reticulate to smooth]. (*Nama* L., 1753, *Conanthus* S. Wats., *Marilaunidium* O. Ktze., nomina rejicienda; not *Nama* sensu Small = *Hydrolea* L.) TYPE SPECIES: *N. jamaicensis* L. (Name from Greek, *nama*, a river or stream, in reference to the habitat of *Nama zeylanica* L. [= *Hydrolea zeylanica* (L.) Vahl.] the only species mentioned by Linnaeus in 1753.)

A genus of about 35 species in five sections, primarily of Mexico and the southwestern United States, but also in South and Central America, the West Indies, and (one species) the Hawaiian Islands. In our area the genus is represented only by *Nama jamaicensis* L. ($2n = 28$), of sect. NAMA (leaves entire, styles free or only partially united, capsules membranous), which occurs in hammocks, roadsides, and disturbed areas, and ranges from El Salvador and the West Indies, north to Texas, Florida, and Louisiana.

REFERENCES:

HITCHCOCK, C. L. A taxonomic study of the genus *Nama.* I. Am. Jour. Bot. **20**: 415–430; II. 518–534. 1933. [Monograph.]

———. The perennial Mexican namas. Am. Jour. Bot. **26**: 341–347. 1939.

Tribe HYDROLEAE Choisy

6. **Hydrolea** Linnaeus, Sp. Pl. ed. 2. 1: 328. 1762, nom. cons.

Annual or perennial herbs with alternate, simple leaves. Inflorescences axillary or terminal cymes. Calyx deeply 5-parted. Corolla rotate to campanulate, 5-parted, blue, rarely white, without scales. Stamens 5, exserted or included, the filament bases dilated, inserted on corolla tube. Styles 2, rarely 3–5; ovary 2-locular, multiovulate, placentation axile, the placentae 2-branched [or entire]. Fruit a 2–4-valved, or irregularly dehiscent capsule. Seeds longitudinally ribbed. (*Nama* L., 1753, not 1759, nom. rejic.) TYPE SPECIES: *H. spinosa* L. (Name from Greek, *hydor,* water, apparently in reference to the aquatic habitat.)

A genus of about 19 species (in two sections) in aquatic habitats in the tropics of the world. Section ATTALERIA Brand (placentae entire) with about five species, is entirely Old World (occurring primarily in Africa and Asia). Section HYDROLEA (sect. *Sagnonea* (Aubl.) Brand) (placentae divided into two parts) is limited to the Americas and contains about 14 species ranging from Paraguay and Uruguay, to Brazil, north to Mexico, the West Indies, and the eastern United States.

Hydrolea uniflora Raf. (*H. affinis* Gray) (Texas to Mississippi and northern Florida, north to Oklahoma, southern Missouri, southern Indiana, and southern Illinois) has glabrous stems and lance-ovate calyx lobes which equal the corolla in length. *Hydrolea quadrivalvis* Walt. ($2n = 20$) (northern Florida to Louisiana, north to southeastern Virginia) has stems which are villous-hispid, and linear or linear-lanceolate calyx lobes which equal the corolla. These two species seem to be very closely related and differ mainly in the pubescence of the stem. Field observations and collections of the two, particularly in the area where they overlap, should be valuable in clarifying their relationship. Our other two species are *H. ovata* Nutt. (Texas to Georgia, north to Missouri) with ovate leaves, pubescent stems and calyx segments shorter than the corolla, and *H. corymbosa* Macbride ex Elliott (southern Florida to Georgia and South Carolina) with elliptic to elliptic-lanceolate leaves, glabrate stems, and calyx segments shorter than the corolla.

Hydrolea spinosa L., of the American tropics, has also been reported to have 20 pairs of chromosomes.

POLEMONIACEAE Jussieu (PHLOX FAMILY)

Annual, biennial, or perennial herbs [shrubs, vines, or small trees], with opposite or alternate, simple or pinnately [or palmately] dissected leaves. Inflorescences cymose or flowers rarely solitary. Flowers bisexual. Calyx 5-parted. Corolla 5-parted, salverform to rotate, the aestivation contorted. Stamens 5, alternate with the corolla lobes, equally or unequally inserted on the corolla, the anthers introrse. Gynoecium syncarpous, stigmas 3[rarely 2]-lobed, style 1, ovary superior, 3[rarely 2]-locular, each locule with 1–many anatropous ovules, the placentation axile. Fruit a loculicidal capsule [rarely indehiscent]. Seeds with a straight embryo and abundant endosperm. TYPE GENUS: *Polemonium* L.

A family of about 300 species variously interpreted to represent about 12 to 23 genera placed in four tribes and two subfamilies by Brand, and in five tribes by Grant. The tribes COBAEEAE Baill., CANTUEAE Peter and BONPLANDIEAE Baill. contain tropical genera of shrubs, vines or small trees (*Cobaea* Cav., *Cantua* Juss., *Huthia* Brand, *Bonplandia* Cav. and *Loeselia* L.) and range from Mexico south to Chile. The temperate, primarily herbaceous, genera fall in tribe POLEMONIEAE Baill., which includes the well-marked genera *Phlox* and *Polemonium*, and in the tribe GILIEAE Reichb., which includes *Gilia*, a genus which has been considered by some authors to include almost all of the remaining species in the subfamily, a complex of polymorphic species which is poorly understood. The Polemoniaceae are centered primarily in western North America, but extend south into Mexico, Peru, and southern Chile, east to eastern North America, and also into Asia and Europe. In our area the family is represented by *Phlox*, *Polemonium*, and *Ipomopsis*. The weedy *Collomia linearis* Nutt. ($2n = 16$) is known in Missouri and may perhaps also become established within our region.

The family has been a perplexing problem with respect to its phylogenetic relationships. It has been considered to be derived from a sympetalous relative of the Rosales, from the Geraniales, and from the Primulales. The Polemoniaceae seem to be allied to the Convolvulaceae, which they resemble in their inflorescences, corolla, stamens, and anatropous ovules. However, on the basis of a morphological study of the flowers, Dawson concluded that they are closely related to the Caryophyllaceae and Geraniaceae, and interpreted the family as representing an evolutionary line from a 3-carpellate caryophyllaceous stock which arose prior to the establishment of the free-central placentation of the Caryophyllaceae. *Cantua* and *Cobaea* were interpreted as primitive genera; they differ from other Polemoniaceae in their woody habit and in having two whorls of stamen traces. Cytologically, the subfamily COBAEOIDEAE differs in having a larger number of chromosomes which have a much smaller size than those of the genera of the POLEMONIOIDEAE.

The family is particularly popular in horticulture, and almost all of the genera are known in cultivation.

REFERENCES:

See also SOUÈGES under *Polemonium*.

BRAND, A. Polemoniaceae. Pflanzenr. IV. **250**(Heft 27): 1–203. 1907.

DAWSON, M. L. The floral morphology of the Polemoniaceae. Am. Jour. Bot. **23**: 501–511. 1936.

FLORY, W. S. Chromosome numbers in the Polemoniaceae. Cytologia Fujii Jubil. Vol. **1**: 171–180. 1937.

GRANT, V. Natural history of the *Phlox* family. I. Systematic Botany. 280 pp. The Hague. 1959. [Morphology, chromosome numbers, phylogeny, phytogeography, taxonomy; not a taxonomic revision.]

GRAY, A. Revision of the North American Polemoniaceae. Proc. Am. Acad. Arts Sci. **8**: 247–282. 1870.

HÜLLER, G. Beiträge zur vergleichenden Anatomie der Polemoniaceen. Beih. Bot. Centr. **21**: 173–244. 1907.

INGRAM, J. Notes on the cultivated Polemoniaceae. 1. A key to the genera. Baileya **7**: 80–86. 1959.

MASON, H. L. The genus *Eriastrum* and the influence of Bentham and Gray upon the problem of generic confusion in Polemoniaceae. Madroño **8**: 65–91. 1945.

———. Polemoniaceae. *In* L. ABRAMS, Ill. Flora Pacif. States **3**: 396–474. 1951.

———. Polemoniaceae. Inst. Paran. Catal. Gên. **5**: 1, 2. 1956.

——— and A. D. GRANT. Some problems in the genus *Gilia*. Madroño **9**: 201–220. 1948.

PETER, A. Polemoniaceae. Nat. Pflanzenfam. IV. **3a, b**: 40–54. 1897.

WHERRY, E. T. Picking out the Polemoniaceae. Bartonia **11**: 1–4. 1929.

———. The Polemoniaceae of Pennsylvania. Proc. Penn. Acad. Sci. **9**: 150–155. 1935.

———. The Polemoniaceae of Virginia. Claytonia **2**: 3, 4, 11–14. 1935.

———. Polemoniaceae of the middle Appalachian region. Castanea **1**: 13–15. 1936; 32–35. 1936.

———. Miscellaneous eastern Polemoniaceae. Bartonia **18**: 52–59. 1936. [Includes key to native and adventive genera.]

———. A provisional key to the Polemoniaceae. Bartonia **20**: 14–17. 1940.

KEY TO THE GENERA OF POLEMONIACEAE

A. Leaves simple, opposite; perennials or annuals; stamens unequally inserted on the corolla tube. . . . . 1. *Phlox*.

A. Leaves pinnately divided, alternate; stamens equally inserted on the corolla tube.

  B. Leaves once pinnately divided, the leaflets oval to lanceolate; flowers blue or white; perennial. . . . . 2. *Polemonium*.

  B. Leaves deeply pinnately dissected into narrow, linear lobes; flowers red, pink, or white; biennial. . . . . 3. *Ipomopsis*.

Tribe POLEMONIEAE Baill.

1. **Phlox** Linnaeus, Sp. Pl. 1: 151. 1753; Gen. Pl. ed. 5. 75. 1754.

Perennial or annual, herbaceous or more or less woody, erect, decumbent or trailing plants with opposite, alternate or subopposite sessile or petioled leaves. Inflorescences cymose, terminal or in the axils of the uppermost leaves. Calyx tubular, angled, 5-parted, not accrescent, rupturing as the capsule expands. Corolla salverform, 5-parted, purple, to lavender, to pink to white. Stamens 5, unequally inserted on the corolla tube, exserted or included. Style 1; stigmas 3; ovary 3-locular, each locule with 1–3 anatropous ovules. Fruit a loculicidal capsule. TYPE SPECIES: *P. glaberrima* L. (Name from Greek, *phlox*, flame, the ancient name for *Lychnis*, transferred to this genus.)

A genus of about 67 species primarily of North America, ranging from northern Mexico to the United States and southern Canada, and in Alaska to adjacent Yukon and Northwest Territories; a single species in northeastern Asia (Siberia). In our area the genus is represented by about seventeen species, most of which are known also in cultivation.

The genus has been variously subdivided into six sections by Peter; two subgenera, five sections and two subsections by Brand; and into three sections and eighteen subsections by Wherry. The major subgeneric divisions are based on such characters as the habit of the plant, the length of the style, the size of the seed and embryo, and the length of the stamens. Additional divisions are based on the shape of the corolla, minor leaf variations, as well as leaf arrangement, and pubescence. It seems questionable that the numerous subdivisions of the genus are natural and that all are worthy of taxonomic recognition. It is probable that a genetic study of the genus would help to clarify problems of interrelationships of the species which are not apparent on the basis of morphological studies alone.

The variation within the species of *Phlox* has often led to widely different taxonomic treatments. The variation in a population of *Phlox bifida* Beck from Tennessee has been interpreted as the result of introgressive hybridization with *P. amoena* Sims. Further studies of this kind are needed to help explain the nature of the variation in different species. *Phlox Drummondii* Hook., an annual native to Texas, is widely grown as an ornamental and has become naturalized as far east as Georgia and Florida. Hundreds of forms of *P. Drummondii*, differing in flower color, shape of the corolla, and pubescence have arisen in cultivation, and the remarkable variation in the species has been the subject of numerous studies. At least some of the corolla variations seem to be related to single genes.

Most of the species which have been examined cytologically are diploids ($2n = 14$). Both diploid and tetraploid ($2n = 14, 28$) plants have been reported in *Phlox Drummondii*, as well as in *P. subulata* L. A triploid known in cultivation may possibly represent a hybrid of *P. maculata* L. and *P. carolina* L., although tetraploids are not known in either of the supposed parental species. Short- and long-styled species of *Phlox* occur, but whether style-length serves as a barrier to fertilization, as has been suggested in *Polemonium*, is not known.

REFERENCES:

AINSWORTH, W. Notes on color, lobing and freaks in *Phlox subulata*. Bartonia **28**: 34, 35. 1957.

ANDERSON, E., and A. GAGE. Introgressive hybridization in *Phlox bifida*. Am. Jour. Bot. **39**: 399–404. 1952.

BANCHER, E. Studien an der Blüte von *Phlox panniculata* hybr. Österr. Bot. Zeitschr. **100**: 308–318. 1953.

EIGSTI, O. J., and H. TAYLOR. The induction of polyploidy in *Phlox* by colchicine. Proc. Okla. Acad. Sci. **22**: 120–122. 1942. [*P. Drummondii.*]

FERNALD, M. L. Studies of eastern American plants. Rhodora **51**: 61–83. 1949. [Notes on *Phlox*, 78–82.]

FLORY, W. S., JR. Chromosome numbers in *Phlox*. Am. Nat. **65**: 473–476. 1931. [Counts for 25 varieties distributed among 13 species.]

———. A cytological study of the genus *Phlox*. Cytologia **6**: 1–18. 1934.

GABRIELSON, I. N. Some North American dwarf *Phlox*. New Fl. Silva **3**: 157–164. 1931.

GILBERT, A. W. Heredity of color in *Phlox Drummondii*. Jour. Agr. Res. **4**: 293–302. 1915.

KELLY, J. P. Cultivated varieties of *Phlox Drummondii*. Jour. N. Y. Bot. Gard. **16**: 179–191. 1915. [Origin and history of the varieties.]

———. Further observations on *Phlox Drummondii*. *Ibid*. **18**: 83–86. 1917.

———. A genetical study of flower form and flower color in *Phlox Drummondii*. Genetics **5**: 189–248. 1920.

———. Astylis *Phlox*. The relation of this variation of *Phlox Drummondii* to the large-eyed flower. Jour. Hered. **13**: 339–342. 1923.

———. Fasciation in *Phlox Drummondii*. The origin and nature of fasciation in *Phlox*. *Ibid*. **18**: 323–327. 1927.

———. Single and semi-double flowers in *Phlox*. *Ibid*. **20**: 549–554. 1929. [*P. Drummondii*.]

———. The "eye" of *Phlox*. *Ibid*. **25**: 182–186. 1934. [*P. Drummondii*.]

———. Irregular flowers in *Phlox*. *Ibid*. **31**: 169–171. 1940.

———. Hoodedness in *Phlox*. *Ibid*. **36**: 25–28. 1945. [*P. Drummondii*.]

KRAEMER, H. The histology of the rhizome and roots of *Phlox ovata* L. (*Phlox carolina* L.). Am. Jour. Pharm. **82**: 470–475. 1910.*

MAINS, E. B. *Phlox* resistant to powdery mildew. Phytopathology **32**: 414–418. 1942. [*P. paniculata*, *P. maculata*, and *P. Drummondii*.]

MEYER, J. R. Chromosome studies of *Phlox*. Genetics **29**: 199–216. 1944.

MILLER, H. A., and R. H. WETMORE. Studies in the developmental anatomy of *Phlox Drummondii* Hook. I. The embryo. Am. Jour. Bot. **32**: 588–599; II. The seedling. 628–634. 1945; III. The apices of the mature plant. **33**: 1–10. 1946.

RAU, M. A. Studies in growth in vitro of excised ovaries. I. Influence of colchicine on the embryo and endosperm in *Phlox Drummondii* Hook. Phytomorphology **6**: 90–96. 1956.*

SEVERIN, H. H. P. Breaking in color of flowers of annual *Phlox* caused by the aster-yellow virus. Phytopathology **33**: 741–743. 1943.

STOUT, A. B. Variation in the moss pink, *Phlox subulata*. Jour. N. Y. Bot. Gard. **18**: 75–83. 1917.

WHERRY, E. T. The eastern subulate-leaved phloxes. Bartonia **11**: 5–35. 1929.

———. The eastern short-styled phloxes. *Ibid*. **12**: 36–53. 1930.

———. The eastern long-styled phloxes. I. *Ibid*. **13**: 18–37. 1932. II. **14**: 14–26. 1932.

———. The eastern veiny-leaved phloxes. *Ibid*. **15**: 14–26. 1933.

———. A variety of *Phlox ovata* from the Alabama mountains. *Ibid*. **16**: 37, 38. 1934. [*P. ovata* var. *pulchra*.]

———. Supplementary notes on the eastern phloxes. *Ibid*. 38–45. 1934.

———. Our native phloxes and their horticultural derivatives. Natl. Hort. Mag. **14**: 209–231. 1935.

———. Variation in *Phlox floridana*. Bartonia **22**: 1, 2, 1943.

———. The *Phlox carolina* complex. *Ibid*. **23**: 1–9. 1945.

———. Rock garden phloxes. Bull. Amer. Rock Gard. Soc. **4**: 17–31. 1946.
———. Subspecies of three eastern phloxes. Castanea **16**: 97–100. 1951. [*P. subulata, P. bifida, P. maculata.*]
———. The genus *Phlox*. 174 pp. Morris Arb. Univ. Pa., Philadelphia. 1955. [Monograph.]
———. Validation of new combinations in *Phlox*. Baileya **4**: 97, 98. 1956. [Validation of subspecific epithets published in "The genus *Phlox*."]
WHITEHOUSE, E. Annual *Phlox* species. Am. Midl. Nat. **34**: 388–401. 1945.

2. **Polemonium** Linnaeus, Sp. Pl. 1: 162. 1753; Gen. Pl. ed. 5. 76. 1754.

Perennial [or annual], erect or decumbent herbs with alternate, pinnately divided leaves. Inflorescences cymose, terminal or axillary. Calyx campanulate, herbaceous, accrescent. Corolla campanulate to funnelform, 5-parted, blue or white, [yellow, pink, or purple]. Stamens 5, equally inserted on the corolla tube, included [or exserted]. Style 1; stigmas 3; ovary 3-locular, each locule with 1–10 ovules. Fruit a loculicidal capsule. TYPE SPECIES: *P. caeruleum* L. (Derivation of name uncertain; perhaps from Greek, *polemos*, war, or perhaps named for *Polemon*, an early Greek philosopher.) — JACOB'S LADDER, GREEK VALERIAN.

About 20 species, primarily of western North America, ranging from the mountains of Mexico north to Alaska and northern Canada, extending into eastern North America, and also into Asia and Europe; a single species in southern South America. Represented in our area by only one species, *Polemonium reptans* L., of rich woods and damp meadows from Wisconsin to New Hampshire, south to Oklahoma, Arkansas, Mississippi, Alabama, Georgia, and North Carolina.

The variation of most of the species of *Polemonium* has not been studied in great detail and, consequently, considerable confusion exists in the understanding of the species and their interrelationships. *Polemonium reptans* varies in its size, in the shape and number of the leaflets, in the shape of the sepals and in the degree and nature of pubescence. Varietas *villosum* E. L. Br. was described from Ohio and Kentucky and is characterized by its densely glandular-villous inflorescence. The correlation of the restricted distribution of var. *villosum* with the disjunct occurrence of other species which have been considered to have a relic distribution has led to the interpretation that its present range is a remnant of an earlier, more extensive one. The pubescence of some plants of the widespread *P. reptans* var. *reptans* in Ohio, and also in Pennsylvania, is considered to show evidence of introgression with var. *villosum*. Further studies of the variation of *P. reptans* in other areas should contribute more information on the validity of this hypothesis.

The species which have been examined cytologically have a chromosome number of $2n = 18$; polyploidy has been reported in *Polemonium californicum* Eastwood ($2n = 36$) and in *P. caeruleum* L. subsp. *Van-Bruntiae* (Britt.) Davidson (*P. Van-Bruntiae* Britt.) ($2n = 36$), of Maryland and West Virginia and north to Vermont.

REFERENCES:

BRAUN, E. L. Variation in *Polemonium reptans*. Rhodora **58**: 103–116. 1956.

CLAUSEN, J. Genetic studies in *Polemonium*. III. Preliminary account on the cytology of species and specific hybrids. Hereditas **15**: 62–66. 1931. [Notes on chromosome morphology, cytology and various crosses.]

DAVIDSON, J. F. The genus *Polemonium* (Tournefort) L. Univ. Calif. Publ. Bot. **23**: 209–282. 1950. [Monograph.]

MARKOVA, L. G. On certain anomalies in the embryology of *Polemonium coeruleum* L. Compt. Rend. Acad. URSS **49**: 144, 145. 1945.*

OSTENFELD, C. H. Genetic studies in *Polemonium*. II. Experiments with crosses of *P. mexicanum* Cerv. and *P. pauciflorum* Wats. Hereditas **12**: 33–40. 1929. [*P. pauciflorum* ♀ × *P. mexicanum* ♂ impossible, reciprocal cross fertile.]

SOUÈGES, R. Les lois du développement chez le *Polemonium caeruleum* L. Affinités des polémoniacées. Bull. Soc. Bot. France **86**: 289–297. 1939. [Allied with the Solanaceae and the Boraginaceae.]

———. Embryogénie des polémoniacées. Développement de l'embryon chez le *Polemonium caeruleum* L. Compt. Rend. Acad. Sci. Paris **208**: 1338–1340. 1939.

———. Embryogénie des polemoniacées. Développement de l'embryon chez le *Polemonium pauciflorum* Wats. Compt. Rend. Acad. Sci. Paris **220**: 897–900. 1945.

WHERRY, E. T. *Polemonium* and *Polemoniella* in the eastern states. Bartonia **17**: 5–12. 1936. [Includes *Polemonium* (*Polemoniella*) *micrantha* adventive in Massachusetts.]

———. The genus *Polemonium* in America. Am. Midl. Nat. **27**: 741–760. 1942.

3. **Ipomopsis** Michaux, Fl. Bor.-Am. 1: 141. 1803.

Biennial [perennial, or annual] herbs with alternate pinnatifid leaves, the tips of the leaf segments bearing a horny mucro. Inflorescences cymose, each flower subtended by a bract. Calyx herbaceous, 5-parted, not accrescent, rupturing as the capsule expands. Corolla salverform or funnelform, 5-parted, red, pink, white [violet or yellow]. Stamens 5, equally inserted on the corolla tube or in the sinuses of the corolla, included or exserted. Style 1; stigmas 3; ovary 3-locular, each locule with 1–many ovules. Fruit a loculicidal capsule. TYPE SPECIES: *I. elegans* Michx. (= *I. rubra* (L.) Wherry). (Name from *Ipomoea* and Greek, *opsis*, aspect, in reference to the similarity of the corolla to that of species of *Ipomoea* of sect. *Quamoclit* Meissn.)

A genus of about 20 or more species in three sections, centered primarily in the Rocky Mountains and the adjacent plains, but extending west to the Pacific coast and east to the Carolinas and Florida, south to Texas and Mexico; one species in Argentina and Chile. A single species in our area, the biennial *Ipomopsis rubra* (L.) Wherry ($2n = 14$), occurring in sandy soil in fields and roadsides from Texas to Oklahoma, east to North Carolina and Florida, also escaped from cultivation and naturalized as far north as Illinois, Michigan, and Massachusetts.

A segregate of the heterogeneous genus *Gilia* R. & P., *Ipomopsis* appears, on the basis of the presently available information, to form a natural group. It is distinguished by the primarily perennial or biennial habit of the species, the leafy stems, pinnately dissected leaves, bracteate flowers, salverform or funnelform corollas (without an evident throat), waxy, curved seeds, and seven pairs of large chromosomes (insofar as studied). Further studies on the cytology, genetics, morphology and ecology of the members of this group are needed in order to establish more clearly the validity of the genus as a segregate of *Gilia*. In a discussion of the genus, Grant remarked that "*Ipomopsis* seems to be as distinct from *Gilia* as is *Eriastrum* or *Langloisia* or *Navarretia*. If the system of classification is to be internally consistent, therefore, the only alternative to recognizing *Ipomopsis* as a genus is to treat it and *Eriastrum*, *Linanthus*, etc., as subgenera of *Gilia*. Phylogenetically it does not matter whether we recognize a tribe *Gilieae* composed of the genera *Gilia*, *Ipomopsis*, *Eriastrum*, *Linanthus*, etc., or one inclusive genus with subgenera."

REFERENCES:

ALEXANDER, E. J. *Gilia rubra*. Addisonia **15**: 63, 64. *pl. 512*. 1930 [1931].

GRANT, V. A synopsis of *Ipomopsis*. Aliso 3: 351–362. 1956.

LAZENBY, F. The standing-cypress (*Gilia rubra*). Horticulture **24**: 418. 1946.*

STUDIES IN THE GENUS COCCOLOBA, IX.
A CRITIQUE OF THE SOUTH AMERICAN SPECIES

RICHARD A. HOWARD

THE FIRST SIX PAPERS of this series treated the West Indian species of the polygonaceous genus *Coccoloba*, with the work based largely upon field studies in this area. The seventh paper dealt with the species of Central America and Mexico; the writer has only a slight knowledge of these species in the field, but fortunately had available an unusually large number of collections as well as extensive field notes made by recent collectors. This paper will treat the species of South America. The limitations of this study are greater both from lack of field knowledge and the fewer specimens available. For these reasons, this treatment is probably more conservative than future workers will deem necessary. The goals of this study have been 1) to bring together all records of taxa of *Coccoloba* for South America; 2) to correct existing errors of literature citation; 3) to evaluate and compare published species where possible; 4) to locate the existing type collections; and 5) to select lectotypes of many species. It is hoped that these notes will encourage collectors and botanists in the area to gather complete material of the species and to record adequately the variations so as to allow a better understanding of certain morphological problems. Only then can the monographer prepare complete descriptions and keys for the species in South America.

The earliest comprehensive treatment of the species of *Coccoloba* in South America was prepared by Meisner for the *Flora Brasiliensis* (5(1): 23–44. 1855). Although some species were illustrated, the descriptions in general were inadequate and no keys were given. Specimens cited previously from the Martius herbarium have since been found in Brussels, Munich, and Leningrad, and a few numbers have been widely scattered. Representative specimens of several species attributed to Martius could not be located for this study and in some other species the selection of a lectotype has required very careful comparisons between specimens from several herbaria and published descriptions.

In 1856 Meisner provided a synopsis of the genus for DeCandolle's *Prodromus* (14: 150–171). One might expect that many of the specimens which Meisner cited would be in the Prodromus herbarium or in the Delessert herbarium at Geneva, but, unfortunately, very few are represented in either collection. Meisner's personal herbarium, which has been acquired by the New York Botanical Garden, includes specimens of most species of *Coccoloba*. A few of these are small fragments, yet they represent the only existing type material for certain species.

The only complete monograph of *Coccoloba* was prepared by Lindau and published in 1890 in Engler's *Botanischer Jahrbücher* (13: 106–229). Many adjustments are necessary therefore to bring the specific names into conformity with the present rules of nomenclature. Lindau's descriptions are not models of accuracy, and the key published in the monograph contains so many errors of fact that it is almost unusable. Following the description of a plant, Lindau cited the collector's name and collection number and at the end gave a list of the herbaria in which he had seen the material. In the selection of a lectotype, therefore, it has been necessary to associate the collection with a particular herbarium. The information supplied in this paper should make easier the work of the next monographer who wishes to obtain material for study.

Lindau frequently cited specimens to be found only in the Berlin herbarium. A study of these, annotated by Lindau, has shown them to be fragments of specimens from other herbaria. There is a question whether the holotype is really the Berlin fragment and only specimen the author cited, or the more ample specimen in some distant herbarium which the author may not have seen and did not annotate.

The specimens of *Coccoloba* in the Vienna herbarium were lost or destroyed during World War II. According to Lindau's citations some of the Jacquin material was at Vienna and is no longer available. A very few of the Vienna specimens were photographed before 1940, and prints of these in the herbarium of the Chicago Natural History Museum are the basis for discussion of these names here.

Most existing treatments of the genus have assumed the flowers to be perfect. During field study of the species in the West Indies the author determined that the flowers are functionally unisexual and that the plants are dioecious. Recently Buchinger and Sanchez examined the species found in Argentina and concluded (Bol. Soc. Argent. Bot. 7: 251–255. 1959) that one species of *Coccoloba* in that country is truly dioecious, but that the remainder have perfect flowers or are monoecious. Very few collections are cited in their work and none of those was available to me. I have examined many specimens which I assign to these same species from Argentina and find no evidence in the herbarium specimens to support their conclusions. In the specimens which I examined the flowers with conspicuous pistils have small or rudimentary stamens which do not produce pollen. Flowers with large stamens which produce pollen appear to have undeveloped or rudimentary pistils. There were no specimens with pollen-producing flowers and fruits on the same branches. I do not doubt their decision, since it was based on field study of carefully selected material, but I do point out the difficulty of stating definitely the sexual condition in herbarium specimens and the futility of using in a key such contrasting characteristics as plants monoecious or plants dioecious.

The species in the West Indies were studied in the field to determine leaf variation. I found that vigorous terminal shoots, short branches, branches of average growth, and adventitious shoots might all have different sizes and shapes of leaves. This leads one to question Lindau's descriptions and keys, since he seems to have relied much on the size and shape of leaves and particularly on the shape of the leaf base.

The habit of the plant also was found to be variable in West Indian species. Some are shrubby or tree-like at the base, but with scrambling branches having the appearance of lianas. Thus herbarium specimens consisting of flowering or fruiting branches without adequate habit notes may not be indicative of the true character of the species.

Relatively few of the South American species considered in the following notes are represented by both flowers and fruit. In some cases it has been possible to associate as one taxon certain flowering and fruiting specimens originally described as separate species. When peculiarities of growth can be properly associated with flowering and fruiting specimens additional species will undoubtedly be combined. Throughout the following text I have been conservative in maintaining as distinct species all specimens concerning which there may be some question. When further evidence becomes available, many of these species may be united.

I have been fortunate to have on loan for study the important historical collections of *Coccoloba* from the Botanisches Museum, Berlin, which formed the basis for Lindau's work; the Jardin Botanique de l'État, Brussels, which include many Martius collections; the Botanische Staatssammlung, Munich, also rich in Martius material; the New York Botanical Garden which include recent collections, as well as Meisner's personal herbarium; and the Herbarium of the Department of Systematics and Plant Geography of the Botanical Institute of the Academy of Sciences of the U.S.S.R., Leningrad, which contains so many duplicates of classic collections. I am most grateful to the directors and curators of these institutions for making their collections available for an unusually long period of time. Selected collections have been borrowed from other institutions and I have visited still more herbaria for study. The many courtesies which made this publication possible are much appreciated. The standard abbreviations of Index Herbariorum have been used in this paper.

Species of *Coccoloba* have been reported from every country in South America, with the sole exception of Chile. In the citation of specimens the countries and their subdivisions, as well as the specific localities of collections, are listed in alphabetical order.

Coccoloba acrostichoides Chamisso, Linnaea **8**: 132–133. 1833; Meisner, Fl. Bras. 5(1): 33. *pl. 13, fig. 2.* 1855; Lindau, Bot. Jahrb. **13**: 138. 1890.

Coccoloba rubiginosa Martius ex Meisner, Fl. Bras. 5(1): 33. 1855, in syn.

Chamisso did not cite a specimen in the original description, and previous monographers have not indicated a type. There is a specimen in the Leningrad herbarium collected by Sellow and bearing on the label the name "*Coccoloba acrostichoides* N" and the annotation "Hb. Cham." This specimen is probably authentic. A more ample specimen in the Berlin herbarium has a tag which bears the number "1393" attached but lacks the reference to the Chamisso herbarium. Lindau did not see or cite either of these collections, yet one must be considered the lectotype and I so designate the specimen at Berlin. All other Sellow collections, including those cited by Lindau, are annotated "*Coccoloba acrostichoides* Cham. et Schl."

The illustration in *Flora Brasiliensis* well represents this species. A printer's proof of this drawing is in the Brussels herbarium and the specimen *Claussen 330* is mounted on the same sheet. There is little similarity between the two, and the illustration appears to be a compilation.

Coccoloba acrostichoides is one of the most distinctive species of the genus, with copious dark-brown pubescence on the lower leaf surface. In leaf shape and in the nature of the inflorescence it is similar to *C. brasiliensis.* The species is not known in fruit and I have not seen any collections more recent than those of Glaziou.

Coccoloba rubiginosa Martius ex Meisner was published in synonymy and has no validity. A specimen at Munich from the Martius herbarium bears this name, but no location or collector is indicated.

Brazil. MINAS GERAIS: Ouro Preto, *Glaziou 15356* (BR, LE); without specific location, *Claussen 330* (BR). RIO DE JANEIRO: San Antonio, *Sellow "B 1393. c 429"* (B). LOCATION NOT KNOWN: Herb. *Martius s.n.* (M–type of *C. rubiginosa*), *Sellow 1251* (B), *1393* (B–lectotype; LE).

Coccoloba acuminata HBK. Nov. Gen. 2: 176. 1817.

Coccoloba acuminata var. *pubescens* Lindau, Bot. Jahrb. 13: 193. 1890.
Coccoloba acuminata var. *glabra* Lindau, *ibid.* 194.
Coccoloba strobilulifera Meisner, Fl. Bras. 5(1): 25. 1855.

I discussed this species in an earlier paper (Jour. Arnold Arb. 40: 185. 1959) when I concluded that the amount of pubescence on the plant varied with the age and the vigor of the specimen. I cannot find any value or significance in the two varieties Lindau published.

A specimen from the Brazilian state of Pará, *Huber 4393*, bears an unpublished herbarium name attributed to Huber. The specimen is clearly referable to synonymy here.

A collection in the herbarium of the University of Wisconsin numbered "*45*" but without collector was supposedly made in La Lima, Chile. The authenticity is to be questioned as the specimen compares favorably with material from Colombia and Peru.

In addition to the specimens cited below, I have seen material from Guatemala, Honduras, Nicaragua, Costa Rica and Panama (Howard, *loc. cit.*).

Brazil. ACRE: Rio Macauhan, *Krukoff 5666* (A, LE, M, NY). AMAZONAS: Rio Embira, *Krukoff 4715* (A, LE, M, NY); Yuruá Miry, *Ule 5723* (B). PARÁ: Pará, Alto Purus, Ponto Alegre, *Huber 4393* (F, U). **British Guiana.** Courantyne, *Schomburgk 1600* (B). **Colombia.** ANTIOQUIA: Río Magdalena, Brazuela de Perales, *Pennell 3699* (GH). BOLÍVAR: San Martín de Loba, *Curran 40* (GH), *100* (Y), *211* (Y). MAGDALENA: Río Magdalena near Mompós, *Humboldt 1479*

(Herb. Willd.–type of *C. acuminata*); Río Sevilla, *Record 9* (A, GH, Y). SANTANDER: Río Magdalena, *Kalbreyer 1280* (B). LOCALITY NOT SPECIFIED: *Goudot 3* (B), *Moritz s.n.* (BR, LE, P–type of *C. strobilulifera* and *C. acuminata* var. *glabra*), *Triana s.n.* (B). **Ecuador.** Balao, *Eggers 14239* (A, BR, LE, M). **Peru.** LORETO: lower Río Huallaga, *Llewelyn Williams 4804* (A). **Venezuela.** YARACUY: Los Cañizos, plains of Yaracuy River, *Pittier 8753* (GH). ZULIA: Perija, *Tejera 253* (GH), *Mocquerys 845* (P).

Coccoloba alagoensis Weddell, Ann. Sci. Nat. III. 13: 260. 1850.

Weddell based this species on *Gardner 1389* from the state of Alagoas, Brazil. At present I am unable to determine the relationship of this species to *Coccoloba obtusifolia* Jacq. and *C. peruviana* Lindau. A full discussion will be found under *C. obtusifolia.*

Coccoloba alnifolia Casaretto, Nov. Stirp. Bras. 71. 1844.

Coccoloba populifolia Weddell, Ann. Sci. Nat. III. 13: 257. 1850; Meisner, Fl. Bras. 5(1): 40, *pl. 18.* 1855; Lindau, Bot. Jahrb. 13: 198. 1899.

Lindau accepted the Weddell name for this species, although he cited in synonymy the epithet Casaretto published several years earlier. Casaretto did not cite a specimen in the original publication, but it seems clear to me that the description and data given are based on his collection numbered *1194.* This collection consists of two sheets in the Turino herbarium and I have designated one of them as the lectotype.

There is a possibility that the older epithet *Coccoloba firma* Martius ex Colla (1836) is the correct one for this species. The current difficulty in determining the type of *C. firma* will be discussed under that name.

Brazil. BAHIA: *Blanchet 1486* (C, G–type collection of *C. populifolia*); *Sellow 1137* (B), *793* (B). PERNAMBUCO: *Tapera, Pickel 3681* (GH, NY). RIO DE JANEIRO: Tijuca, *Lützelburg 343* (M); without specific locality, *Casaretto 1270* (TO), *Gaudichaud 420* (B, G, P), *Luschnath 835* (LE), *s.n.* (M), *Martius s.n.* (M), *Riedel 7* (BR, LE), *673* (LE, M), *Widgren 719* (BR). STATE NOT SPECIFIED: Copacabana, *Casaretto 1194* (TO–lectotype of *C. alnifolia*), *Nadeaud s.n.* (P). CULTIVATED: São Paulo Botanical Garden, *Hoehne 28527* (A).

Coccoloba arborescens (Vellozo) Howard, Jour. Arnold Arb. 41: 44. 1960.

Polygonum arborescens Vellozo, Flor. Flum. 162. 1825, Icones 4: *t. 43.* 1827.
Coccoloba crescentiifolia Chamisso, Linnaea 8: 134. 1833, "*crescentiaefolia.*"
Coccoloba vellosiana Casaretto, Nov. Stirp. Bras. 70. 1844.
Coccoloba fasciculata Weddell, Ann. Sci. Nat. III. 13: 258. 1849.
Coccoloba crescentiifolia var. *obtusata* Meisner, Fl. Bras. 5(1): 26. 1855.

The previous paper in this series (Howard, *loc. cit.*) contains a discussion of the nomenclature of this species. For the present, the type is considered to be the Vellozo illustration. After a careful study of this species in the field it may be desirable for some future monographer to select a modern specimen as neotype.

Brazil. BAHIA: *Blanchet 796* (F, NY, P–type of *C. fasciculata*). RIO DE JANEIRO: Praya Grande, *Sellow s.n.* (B, LE, M–type collection of *C. crescentiifolia*); *Glaziou 143* (BR); *Riedel 674* (A, BR, P). STA. CATARINA: Hooker Herb. without collector or number (K). STATE NOT SPECIFIED: Copacabana, *Luschnath s.n.* (BR); between San Juan and Rio dos Oistres, *Prince Maxim. Neuwied. s.n.* (BR, NY). LOCALITY NOT SPECIFIED: *Claussen 2013* (G, NY–type collection of *C. crescentiifolia* var. *obtusata*).

Coccoloba argentinensis Spegazzini, Physis **3**: 176. 1917; Buchinger and Sanchez, Bol. Soc. Argent. Bot. **7**: 251. 1959.

Coccoloba praecox Herter, Rev. Sudam. Bot. Montevideo **10**: 38. 1952.

Spegazzini failed to select a type in the original description. He referred to material collected by M. Rigou in 1902 from the station "Margherita," Prov. Santa Fe, and to material collected the following year in Reconquista. Correspondence with several Argentine botanists indicates that the Spegazzini herbarium has been neglected in the past and that some material has been lost. Dr. Maria Buchinger reported that she saw the "type" several years ago but currently there are no specimens of the species in the herbarium of Spegazzini at La Plata and no other herbarium contains such material. As long as there is a possibility that the original material may be located, a neotype should not be selected. In their recent paper Buchinger and Sanchez cite only one collection, *Schulz 240*, which I have not seen. They further consider the species to be endemic to the Chaco territory and to be found only in the provinces of Salta and Chaco, thereby eliminating the locality of the type collection.

The material cited below appears to me to correspond with the original description. *Coccoloba argentinensis* is easily recognized by the small obovate-elliptic leaves, the long fruiting pedicels, and the flowering of the plant before the leaves are fully developed.

Coccoloba praecox Herter was distinguished on these same characteristics but without comparison with the present species. I have examined an isotype and conclude that the reduction of *C. praecox* to the synonymy of *C. argentinensis* is necessary. *Coccoloba praecox* Herter is also a later homonym of *C. praecox* Wright ex Lindau (Bot. Jahrb. **13**: 142. 1890).

Argentina. CHACO: Fontana, *Meyer 2517* (F); Las Palmas, *Jorgensen 2103* (GH, US), *2106* (GH); Resistencia, Colonia Benítez, *Petersen 3986* (A). JUJUY: Este Hacienda, s. of Jujuy, *Eyerdam & Beetle 22432* (GH). SALTA: Orán, Manuela Pedraza, *Eyerdam & Beetle 22647*, *22790* (G, GH); Pichanal, *Rodriquez 1121* (GH, NY); Rosario de la Frontera, Los Baños, *Venturi 9402* (GH). TUCUMÁN: Capital, Barranca Colorada, *Venturi 955* (GH), *Schreiter 1516* (GH); Trancas, Tapia a Roca, *Schreiter* (*Herb. Lillo 84971* (US), Vipos, *Venturi 9792* (A, GH, LE). **Uruguay.** Salto, Arapey, *Herter* (*Herb. Herter 50852*–type collection of *C. praecox*; F, P); Isla Gaspar, *Berro 3334* (G).

Coccoloba ascendens Duss ex Lindau, Bot. Jahrb. **13**: 156. 1890.

In a previous discussion of this species (Jour. Arnold Arb. **40**: 72, 73. 1959), I selected a specimen from Martinique, *Hahn 1005*, in the Berlin herbarium as the lectotype. The species is well represented in the Lesser Antilles from Guadeloupe south to Trinidad. Lindau (Bot. Jahrb. 13: 156. 1890) cited specimens only from Guadeloupe, Martinique and Brazil. Eyma (Meded. Bot. Mus. Utrecht 4: 110. 1932) mentioned the distribution of the species as "Guyana, Brazil, Guadeloupe, Martinique." I have seen neither the specimens cited from the Guianas (*B.W. 6560, 6600,* and possibly *B.W. 6490* and *6550b*) nor those Lindau cited from the states of Pará and Goyaz in Brazil (*Burchell 8034, 9345* and *Gardner 3966*). On the basis of an unnatural range I question particularly the Brazilian determinations given by Lindau. Future workers with additional material at their disposal doubtless will check the relationship of *Coccoloba ascendens* and *C. sparsifolia.*

Coccoloba barbeyana Lindau, Bot. Jahrb. 13: 185. 1890.

I have examined the single collection cited by Lindau (*Ruiz & Pavon s.n.*, Peru, without definite locality, in the Barbey-Boissier herbarium) and failed to find the holotype or the species distinct in any way from *Coccoloba densifrons* Martius ex Meisner. Although Lindau accepted *C. densifrons* (based on a Martius collection from Ega in the Brazilian Amazon) he did not list the epithet in the key to the species.

Coccoloba billbergii Lindau, Bot. Jahrb. 13: 219. 1890.

Lindau cited "*Coccoloba obtusifolia* Meissn. (non Jacq.)" in synonymy when he described *C. billbergii* based on *Billberg 204* and *204a* from Carthagena, implying that Meisner was in error. However, Meisner noted both the similarity of these Billberg collections to *C. obtusifolia*, as described and illustrated by Jacquin, and the discrepancy in the specimens so labeled in the Willdenow herbarium and the reference in the Willdenow catalogue. Lindau chose to interpret *C. obtusifolia* on the basis of the specimen in the Willdenow herbarium and incorrectly to consider *C. obtusifolia* as a species from the West Indies. I have examined the Billberg collections cited by Lindau from the Berlin and Stockholm herbaria. These are correctly associated with *C. obtusifolia* Jacq. as a South American species. *Coccoloba billbergii* Lindau must be considered a synonym of *C. obtusifolia* Jacq.

"*Coccoloba obtusifolia*" as used by Lindau (*loc. cit.* 146, 147) is correctly assigned to synonymy under *C. microstachya* Willd. (Howard, Jour. Arnold Arb. 38: 217–219. 1957).

Coccoloba blanchetiana Weddell, Ann. Sci. Nat. III. 13: 257. 1850.

Weddell cited *Blanchet 3561*, from near Jacobina, Bahia, Brazil (G, P). This species is to be referred to the synonymy of *C. ochreolata* Weddell and will be discussed there.

Coccoloba bolivarana Llewelyn Williams, Trop. Woods **68**: 39. 1941.

In a list of the forest trees of Venezuela, Williams refers to "Brusquillo Blanco, *Coccoloba bolivarana* (a new species), a tree about 8 m. high, growing in rocky areas, with a trunk ramified from the base, and bearing a juicy, lustrous black fruit." The species has not been published validly with a Latin description, to my knowledge, and the brief description given above is scarcely to be considered diagnostic in this difficult genus. Specimens in the herbaria of the Chicago Natural History Museum and the Royal Botanic Gardens, Kew, bear this name but attribute it to Standley. The specimens (*Williams 13374*) were collected at El Tigre, Los Garzones, on Río Cuchivero, Bolivar, Venezuela. They cannot be assigned to any recognized species and will be described in a later paper.

Coccoloba bracteolosa Meisner, Fl. Bras. 5(1): 30. 1855.

No type was selected in the original description, but a Martius collection without number from Joazeiro, on the Rio San Francisco, in Bahia, Brazil, has been photographed by other workers in the Munich herbarium and distributed as the type. I am referring this species to the synonymy of *Coccoloba ochreolata* Weddell and will discuss the problem under that name.

Coccoloba brasiliensis Nees & Martius, Nov. Act. Acad. Nat. Cur. **11**: 30. 1823; Meisner, Fl. Bras. **5**(1): 32. *t. 13, f. 1.* 1855.

Coccoloba senaei Lindau ex Glaziou, Bull. Soc. Bot. France **58**: 571. 1911.

The original description cites first the locality of "X Valos" and then a general littoral distribution in Bahia, "Maragnanum" and Para, the latter attributed to Martius. I have seen no Martius specimens which fit the original description among the material from the Martius herbarium now at Brussels, Leningrad, or Munich. In his treatment of the genus for *Flora Brasiliensis*, Meisner redescribed the species and cited collections by Prince Maximilian and Martius. The illustration in *Flora Brasiliensis* is based on the specimen collected by Prince Maximilian and I select this as the lectotype.

A previous worker, possibly Meisner, has annotated some sheets to indicate a similarity to or a relationship with *Coccoloba rigida* Meisner. (Lindau, not following the homonym rule, accepted *C. parvifolia* Schott 1827, not Poiret 1804, and included in synonymy *C. rigida* Meisner.) Lindau distinguished between *C. brasiliensis* and "*C. parvifolia*" on the puberulent inflorescence axis in the latter species and the glabrous one in *C. brasiliensis*. An examination of the specimens cited below will show that the stem, ocreae, petioles, and frequently the base of the leaf blade are puberulent to short pilose in *C. brasiliensis*. The bracts and ocreolae of the inflorescence are likewise slightly puberulent to glabrous. On the characteristic of pubescence there is scant reason for separating *C. brasi-*

liensis and "*C. parvifolia*." However, the leaves of *C. brasiliensis* are variable in size and shape. In the type, and in the most recent collections, the leaves are thicker in texture and the bases are rounded-cordate, in contrast to those of "*C. parvifolia*." The inflorescence of the type is as compact as that of "*C. parvifolia*" but recent collections show longer, more lax inflorescences in which the ocreolae do not expand with the developing flower buds, and are, in fact, shorter than the bracts in all stages of development. Until these characteristics can be evaluated by field studies it seems desirable to retain *C. brasiliensis* as a species distinct from *C. rigida*.

The several sheets of the collections by Glaziou cited below suggest that the existing descriptions of *Coccoloba brasiliensis* are unsatisfactory and must be changed to accommodate the narrow, lanceolate-oblong leaves of the vigorous shoots and the large, oblong, but sessile, leaves of adventitious shoots. The Glaziou collection without number in the Paris herbarium has some leaves with blades 18 cm. long and 9 cm. wide. The largest leaf on the lectotype is 4 cm. long and 2.3 cm. wide, yet the collections cited below show all intermediates between these extremes.

The phrase "*Coccoloba senaei* Lindau n. sp." is used by Glaziou in a list of determinations of his collections. The brief description "Arbuste sarmenteux, fl. blanchâtres" can scarcely be considered diagnostic in this genus and I consider *C. senaei* to be a *nomen nudum.*

Brazil. MATO GROSSO: Barao de Capanema, Rio Cravary, *Baldwin 3129* (US). MINAS GERAIS: Conselheiro Mata, *Brade 13815* (B), *13816* (B); "in deserto Minarum," *Martius s.n.* (M); Rio dos Pedras, Valu, *Glaziou 19762* (B, LE), *19763* (B, K, LE); Serra do Cipó, *Schwacke 8005* (B), *Brade 14841* (B). WITHOUT SPECIFIC LOCALITY: Valos, *Prince Maximilian 88* (B, BR–lectotype; LE); *Glaziou s.n.* (P).

Coccoloba brasiliensis Sprengel, Syst. Veg. **2**: 252. 1825.

This epithet is a later homonym of *Coccoloba brasiliensis* Nees & Martius. The species was based on a Sellow collection from Brazil which I have not seen. The description is not that of a species of *Coccoloba*. It was referred to the genus *Hedyosmum* of the Chloranthaceae by Chamisso (Linnaea **4**: 36. 1833). I have not determined whether this is the same as *Hedyosmum brasiliense* Mart., recognized by Occhioni in his recent monograph of the genus (Contribuccão ao estudo de família Chloranthaceae com especial referencia ao gênero *Hedyosmum* Sw. Rio de Janeiro, 1954).

Coccoloba candolleana Meisner, Fl. Bras. 5(1): 41. 1855.

Meisner based this species on the collection *Blanchet 1818* from Bahia, Brazil. He noted its similarity to *Coccoloba cordata* Chamisso. I am unable to distinguish the two and so refer *C. candolleana* to the synonymy of the older name, *C. cordata*.

Lindau (Bot. Jahrb. **13**: 201. 1890) cited *Goudot 4*, from Colombia, in his treatment of *Coccoloba candolleana*. Several recent collections from Colombia have also been identified as this species. The Goudot specimen in the Berlin herbarium cited by Lindau is a fragment of a larger specimen in the Paris herbarium. A study of the latter sheet clearly indicates that this collection is to be referred to *C. padiformis* Meisner, the type of which is from Caracas, Venezuela.

Coccoloba caracasana Meisner, DC. Prodr. **14**: 157. 1856; Howard, Jour. Arnold Arb. **40**: 193. 1959.

Coccoloba caracasana f. *glabra* Lindau, Bot. Jahrb. **13**: 211. 1890.
Coccoloba cyclophylla Blake, Contr. U.S. Natl. Herb. **20**: 238. 1919.

In an earlier paper I discussed the significance of pubescence in this species and cited the collections seen from Mexico and Central America. *Coccoloba cyclophylla* Blake is now added to the synonymy of this species. Blake compared his species, based on *Curran 47*, from Colombia, with one from Hispaniola and concluded that they were distinct. A proper comparison would have been with *C. caracasana* from Venezuela, which is clearly the same.

Colombia. ATLÁNTICO: La Plaza, Juan Mina, *Dugand 643* (Y); Molinero, *Dugand 568* (Y). BOLÍVAR: Castillo Maldonado, *Sessé & Mociño 5430* (F); San Martín de Loba, *Curran 47* (US–type of *C. cyclophylla*; GH, Y). Magdalena, Santa Marta, *Smith 1702* (A, GH); Tucurinca, *Romero 1388* (US). LOCALITY NOT KNOWN: *Moritz 1109* (BR, LE). **Venezuela.** APURE: San Fernando de Apure, *Grisol s.n.* (A, P). ARAGUA: Maracay, *Vögl 1009* (M); San Juan de los Morros, *Alston 6023* (BM). CARABOBO: Between San Joaquín and Mariara, *Pittier 12111*, *12112* (G, LE, M); Valencia, *Pittier 8705* (GH). DISTRITO FEDERAL: Caracas, *Vargas 30* (G); *Humboldt 732* (Herb. Willd.); *Bonpland 732* (B–holotype). GUARICO: El Sombrero, *Pittier 11460* (A, G, GH, M), *12367* (M, NY); La Rubiera, *Pittier 12328* (G, M). LARA: Between Yaritagua and Duaca, *Pittier 343* (A, M). MERIDA: Tovar, *Fendler 2053* (GH). YARACUY: Bruzual, *Curran 642* (NY).

Coccoloba carinata Ruiz ex Meisner, DC. Prodr. **14**: 150. 1856.

Meisner published this epithet in synonymy under *Muehlenbeckia leptobotrys* Meisner and stated that it was a manuscript name found in the herbarium at Berlin. I have not seen authentic material.

Coccoloba caurana Standley, Field Mus. Publ. Bot. **22**: 73. 1940; L. Williams, Explor. Bot. Venez. 189. 1942.

Although the description of this species was published twice as new, the taxon belongs in the synonymy of *Coccoloba fallax* Lindau and is discussed in more detail under that name. The type, in the herbarium of the Chicago Natural History Museum, is *Williams 11366*, from Venezuela.

Coccoloba cerifera Schwacke, Pl. Nov. Mineir. 1: 7. 1898.

I have not seen the original publication to check the validity of this name and so, for the present, must interpret the species from the specimen indicated as the type in the Berlin herbarium. The plant is unlike any other species found in southern Brazil. It resembles *Coccoloba schomburgkii* in the shape and thickness of the leaves, but differs from it in having long pedicels from which the apparently staminate flowers have fallen. The Pires and Black collection cited below compares well with the type specimen.

Brazil. MINAS GERAIS: Serra do Cipó, *Schwacke 11780* (B-holotype), *Pires & Black 2816* (NY).

Coccoloba charitostachya Standley in A. C. Smith, Lloydia 2: 176. 1939.

The type of this species is *A. C. Smith 2356*, collected near the mouth of the Charwair Creek, in the basin of the Rupununi River, British Guiana. The holotype is in the herbarium of the Chicago Natural History Museum.

This species is not well defined in the original description and has not been recollected. Additional material is badly needed for an understanding of the species. At present the species may be characterized by the slightly rugose leaf blades which are elliptic-ovate in shape, rounded at the apex and lighter in color on the lower surface. The fruits are all insect-infested and abnormal and of no diagnostic value. Flowers are not known.

Coccoloba chacoensis Standley, Field Mus. Publ. Bot. 17: 239. 1937.

This species is to be referred to the synonymy of *Coccoloba spinescens. Coccoloba chacoensis* was based on *Cardenas 2529*, from Bolivia; the holotype is in the Chicago Natural History Museum. Buchinger and Sanchez (Bol. Soc. Argent. Bot. 7: 253. 1959) recognized this species and maintained it as distinct from *C. spinescens* Morong because of the absence of lateral branches terminating in spines and the presence of "glands" on the lower leaf surface. Although the Argentine botanists undoubtedly know these species in the field, the characteristics they have chosen to separate the species are not reliable in herbarium specimens. The holotype compares favorably with such collections as *Morong 882* (the type of *C. spinescens*) and *Hassler 11476* and *2486*.

Coccoloba confusa Howard, nom. nov.

Coccoloba declinata Martius, Beibl. Flora **20**: 90. 1837; Meisner, Fl. Bras. **5**(1): 29. 1855, as to plants, not as to name.
Coccoloba declinata var. *major* Meisner, Fl. Bras. **5**(1): 30. 1855.
Coccoloba declinata var. *minor* Meisner, *ibid.*

Polygonum declinatum Vellozo (Flor. Flum. 162. 1825, Icon. **4**: *t. 41.* 1827) was described briefly and in general terms. The illustration given in the Icones is a poor one showing scarcely any characteristic of value in defining the taxa in *Coccoloba*. It was suggested by Dr. I. M. Johnston in his library notes that Pharmacopolis, the locality given, might be near the mouth of the Rio Taquari in the western part of the state of Rio near Paraty.

The transfer of the Vellozo name to *Coccoloba* made by Martius in an obscure paper is seldom correctly cited. Martius refers to two specimens, one from "Montem Talegraphi," in "Prov. Sebastionopolitana," and the other near Pendamonhangaba and Taubaté, in São Paulo. Martius' brief description of *Coccoloba declinata* is obviously based on the specimens cited and could scarcely be drawn from either the description or the plate given by Vellozo.

In 1855 when Meisner prepared the treatment of the genus for the *Flora Brasiliensis*, he described the species and established three new varieties: α *minor*, β *Velloziana* and γ *major*. For *Coccoloba declinata* var. *minor*, Meisner cited in reference "*Coccoloba declinata* Mart. Herb. propr." and a specimen from the Rio Doce collected April 1816 by Prince Maximilian. I have not seen this specimen in material from Brussels, Leningrad, Munich, or New York, the usual places for Martius and Meisner specimens. Meisner's variety, *Velloziana*, is based on the epithet and reference "Polygonum declinatum Vellozo Flor. Flum. IV. t. 41" and in place of a specimen Meisner cites "in prov. Rio de Janeiro."

Neither Meisner nor more recent authors cite the specimen from "Montem Talegraphi" which Martius mentioned in the original transfer of the Vellozo name. The specimen from Pendamonhangaba is referred by Meisner to his var. *major*.

Meisner prepared the treatment for *Coccoloba* in DeCandolle's *Prodromus*, using the same broad concept of varieties comprising the species *C. declinata*. In this treatment, however, the assignment of var. *major* to the species is questioned.

In his monograph of the genus Lindau reduced to synonymy Meisner's varieties *minor* and *Velloziana*. Lindau recognized the var. *major*, but commented on the poor condition of the type specimen and suggested that it might be a new species.

There appear to be no Vellozo collections available; thus the interpretation of the species must be made from the inadequate original description and the rather poor drawing. In comparing the drawing with the specimens cited by Martius, Meisner and Lindau, I am convinced that these authors have misinterpreted Vellozo's species. Vellozo's drawing shows that a scrambling plant is intended, but the material cited by previous authors for *Coccoloba declinata* is shrubby, with geniculate branches. Again, the drawing shows a short, regular inflorescence, while the young inflorescences of the specimens cited by earlier authors are geniculate, with the older inflorescences elongate. The most obvious match for the Vellozo species is the Martius specimen cited as the type of *C. racemulosa*. This is a liana with short lateral branches and comparable inflorescences. The venation of the type of *C. racemulosa* compares favorably with that illustrated by Vellozo, while the venation of specimens cited by Martius, Meisner and Lindau does not. It appears to me that the drawing of *Polygonum declinatum* Vellozo most nearly compares to *Coccoloba racemulosa* Meisner.

The material which Martius, Meisner and Lindau cited and described as *Coccoloba declinata* therefore requires a new name. I propose the name *C. confusa*, to call attention to this problem. Lindau's description (Bot. Jahrb. **13**: 166. 1890) applies to the specimens cited, including those originally mentioned by Martius in transferring Vellozo's specific epithet.

The inclusion of the Krukoff and the Archer collections from Amazonas and Pará creates a sizeable gap in the known range of this species. On the basis of available material, these specimens must be assigned here.

Brazil. AMAZONAS: Humaytá near Livramento, *Krukoff 6669* (NY). PARÁ: Belém, *Archer 7830* (F, K). RIO DE JANEIRO: Caju, *Riedel s.n.* (LE); Copacabana, *Luschnath s.n.* (LE); Rio de Janeiro, *Glaziou 3089* (BR), *Riedel 675* (A, BR, LE, M), *676* (A, BR, LE, M); Telegraphenberg, *Luschnath*, Oct. 1833 (BR). SÃO PAULO: Pedamhongaba, Taubaté, *Martius "66"* (BR, LE, M–type of *C. declinata* var. *major*).

Coccoloba conduplicata Maguire, Bull. Torrey Bot. Club **75**: 304. 1948.

A clear-cut species, but known only from the material cited in the original description. The folded leaf blade noted in the specific name appears to be of less significance than the author indicates, since the majority of the leaves are not conduplicate.

Surinam. Tafelberg, *Maquire 24437* (A, BR; NY–holotype), *27205* (A, NY).

Coccoloba cordata Chamisso, Linnaea **8**: 133. 1833.

Coccoloba candolleana Meisner, Fl. Bras. **5**(1): 41. 1855.
Coccoloba cordata var. *praecox* Hassler, Repert. Nov. Sp. **14**: 162. 1915.

Both Meisner and Lindau have indicated the similarity of *Coccoloba cordata* Chamisso and *C. candolleana* Meisner. Lindau distinguished between these in his key by placing *C. candolleana* in a group of species having leaves glabrous on both surfaces and *C. cordata* in one having leaves pubescent along the midrib and nerves on the lower surface. Lindau has placed the two species adjacent to one another in the text. Among the major characters of these species, Lindau described *C. candolleana* as having tomentose ocreae while those of *C. cordata* are glabrous.

The type collection of *Coccoloba cordata* is *Sellow s.n.* from the Rio Pardo area of Brazil. I have seen three sheets of this collection. One in the herbarium at Berlin bears the full data given by Chamisso and is selected as the lectotype. The other two were annotated only "*C. cordata N.*"

The descriptions given by Chamisso and Lindau are not entirely accurate. Various branches of the specimens comprising the type collection have puberulent or tomentose ocreae, although other portions are glabrous. Most of the leaves are coarsely pubescent along the midrib at the base of the leaf, but some are completely glabrous.

Coccoloba candolleana was based on *Blanchet 1818*. A single specimen is cited as being at Geneva while a smaller specimen from the Meisner herbarium, now at the New York Botanical Garden, bears several of Meisner's annotations: (1) "*C. cordata* Cham. ?" which he declared to be different on the basis of the shorter petiole and more coriaceous blades; (2) a variety of *C. cordata* named for Blanchet, a name which was not published, and finally (3) "Coccoloba candolleana n." The Blanchet collection has broader leaves and shorter petioles, but can be compared favorably with portions of the Sellow collection which is the type of *C. cordata*.

In his monograph Lindau included a collection from Colombia (*Goudot 4*) in the description of *Coccoloba candolleana*. This collection is better referred to *C. padiformis*, a species known from Venezuela and Central America (Howard, Jour. Arnold Arb. **40**: 210. 1959).

Coccoloba cordata var. *praecox* Hassler was based on a specimen, *Hassler 7279*, from Paraguay which is staminate, in contrast to the pistillate type of *C. cordata*. The deciduous characteristic of the plant is not significant, and the variety is not worthy of recognition.

Argentina. CHACO: Barranqueras, Isla de Temores, *Curran 402* (US). FORMOSA: Comán, *Jórgensen 2064* (GH, US); Pirané, *Morel 432* (BR). JUJUY: San Pedro, *Di Lella and Garcia 2820* (A). MISIONES: Apóstoles on Río Chimiray, *Ibarrola 1150* (V). SALTA: Embaracación, *Eyerdam & Beetle 22916, 22928* (GH); Orán, Tabacal, *Schreiter 5472, 8455* (GH); Orán, Vespució a las Hablillas, *Schreiter 11492* (F); Río Blanco, *Venturi 5585* (F, GH, LE, M); Río Piedras, *Rodríguez 73* (F). TUCUMÁN: Capital, Barranca Colorada, *Venturi 955* (F); Raco, *Schreiter 1516, 8443* (GH). **Brazil.** BAHIA: *Blanchet 1818* (G, NY–type collection of *C. candolleana*). RIO GRANDE DO SUL: Rio Pardo, *Sellow s.n.* (B–lectotype; M). SÃO PAULO: *Gaudichaud 140* (P). **Paraguay.** CHACO: Villa Rica, *Balansa 3277* (G). Concepcíon, *Hassler 7279* (GH-type of *C. cordata* var. *praecox*).

Coccoloba cordifolia Meisner, Fl. Bras. **5**(1): 37. 1855.

Meisner cited several specimens but did not indicate a type. A sheet in the Delessert herbarium has been cited as the type by previous workers, although it bears two branches and two labels (*Blanchet 100* and *Blanchet 3528*). Meisner (DC. Prodr. **15**: 155. 1856) suggested that *Coccoloba laevis* might be identical with *C. cordifolia*. Lindau (Bot. Jahrb. **13**: 186. 1890) combined the two, accepting the older *C. laevis* Casaretto, a step which I believe to be correct.

Coccoloba coronata Jacquin, Enum. Pl. Carib. 19. 1760, Select. Stirp. Am. Hist. 114. *t. 77.* 1763; Dugand, Caldasia **4**: 427. 1947; Howard, Jour. Arnold Arb. **41**: 40. 1960, not Lindau, Symb. Ant. **1**: 228. 1899.

Coccoloba virens Lindley, Bot. Reg. **21**: *t. 1816*. 1835.
Coccoloba novogranatensis Lindau, Bot. Jahrb. **13**: 192. 1890; Howard, Jour. Arnold Arb. **40**: 85–87, 208, 209. 1959.
Coccoloba dioica Karsten ex Lindau, Bot. Jahrb. **13**: 170. 1890.
Coccoloba caribaea Urban, Symb. Ant. **5**: 337. 1907.
Coccoloba waittii Johnston, Sargentia **8**: 122. 1949.

The correct name of this species has evolved through the series of my papers cited above with the final correction suggested by one of Dugand's papers which I had overlooked. It is possible that *Coccoloba fagifolia* Jacq. should be assigned to the synonymy of this species as well. The identity of that plant will be discussed under that epithet.

I have not seen any material collected by Jacquin, and the species is regarded as typified by an illustration. Specimens from St. Vincent, south to Trinidad and Tobago, and from Guatemala and Panama are cited in earlier papers (Jour. Arnold Arb. **40**: 85, 209. 1959). I have also examined the following specimens from South America.

Colombia. BOYACÁ: Between Anapoima & Apulo, *Triana 978* (B, P–type of *C. novogranatensis*); El Humbo, *Lawrance 760* (A); Santa Marta, *H. H. Smith 2421* (A, BR). BOLIVAR: Sabanilla, *Karsten s.n.* (B, LE). CAQUETÁ: Hetuchá on Río Orteguaza, *Woronow & Juzepczuk 6100* (F). MAGDALENA: Molino, *Haught 4148* (F, NY). DEPT. NOT KNOWN: Pozo del Higuerón, Usiacuri, *Dugand 788* (Y). **Ecuador.** El Oro, Arenillas, *Little 6721* (F). **Peru.** LORETO: Río Putumayo, *Klug 2240* (A, B, GH). **Venezuela.** ANZOATEGUI: Soledad, *Gines 3913* (US). BOLÍVAR: Between Upata & Altagracia, *Steyermark 57681* (F). DISTRITO FEDERAL: Barrancas, *Tamayo 1315* (US); Caracas, *Karsten s.n.* (LE–holotype of *C. dioica*). SUCRE: Cristóbal Colón, *Broadway 143, 144, 491* (GH, NY, US). ZULIA: Perija, *Tejera 91* (US). DEPT. NOT KNOWN: Sta. Ana, Paraguana, *Tamayo 854* (US).

Coccoloba corrientina Rojas, Bull. Geogr. Bot. **28**: 162. 1918.

The original description of this species is brief and generalized. No specimens are cited and, in fact, a broad general distribution is attributed to the species. Through personal correspondence I have learned from Dr. Maria Buchinger and other Argentine botanists that no Rojas collections can be attributed to this species. The species appears to be impossible to typify.

Buchinger and Sanchez (Bol. Soc. Argent. Bot. **7**: 255. 1959) list *Coccoloba corrientina* as a questionable species, but suggest its similarity to *C. morongii*, the correct name of which is *C. paraguariensis*. I concur with this suggestion.

Coccoloba crescentiifolia Chamisso, Linnaea **8**: 134–136. 1833, *"crescentiaefolia."*

The correct name of this species is *Coccoloba arborescens* (Vellozo) Howard based on *Polygonum arborescens* Vellozo. For a discussion of the nomenclature and additional synonymy see the previous paper in this series (Jour. Arnold Arb. **41**: 43–45. 1960). Specimens previously referred to this species are listed under *C. arborescens* above.

Coccoloba cruegeri Lindau, Bot. Jahrb. **13**: 209. 1890.

Coccoloba ernstii Johnston, Proc. Am. Acad. **40**: 685. 1905.
Coccoloba oblonga Lindau, Bot. Jahrb. **13**: 136. 1890.

This species was based on a Crueger collection from Trinidad. Lindau described the fruits and assigned the species to the section *Campderia*. Currently available collections from Berlin and Göttingen are fragmentary and sterile. The specimen from the Trinidad herbarium appears to have had flowering parts at one time. There is some doubt as to what Lindau actually saw and described, for there is no evidence in the vegetative parts that the species is related to the others which he assigned to section *Campderia*.

Coccoloba oblonga Lindau was described at the same time as *C. cruegeri* and was based on *Riedel 614*, reported to be in "herb. Petrop." I have now seen that specimen and the others cited below, and there is no question that *C. oblonga* is the same as *C. cruegeri*. The Riedel collection from Ilheos, Bahia, represents a sizeable, but not unlikely, extention of range. As Lindau indicated, the material is for all practical purposes sterile, although the specimens do have immature and poorly preserved inflorescences and flowers.

The range of this species is now from the islands of Trinidad and Margarita to British Guiana and Bahia in Brazil. Collections from Trinidad and Margarita were cited in an earlier paper (Jour. Arnold Arb. **40**: 75, 76. 1959).

British Guiana. Ituribisi Lake, Essequebo Coast, *Forest Dept. B.G. 5474* (A, K). **Brazil.** BAHIA: Ilheos, *Riedel 614* (B, LE, P-type of *C. oblonga*); without specific location, *Blanchet 3160A* (P). **Venezuela.** SUCRE: Cristóbal Colón, *Broadway 697* (GH).

Coccoloba cujabensis Weddell, Ann. Sci. Nat. III. **13**: 259. 1850.

Coccoloba longiochreata Hassler, Repert. Spec. Nov. Reg. Veg. **14**: 162. 1915.

One specimen of *Martius 1241* in the Munich herbarium has been designated as the lectotype of this species. *Coccoloba cujabensis* is suggestive of *C. ruiziana* Lindau, but field study or additional collections are necessary to determine their correct relationship.

Hassler compared his new species, *Coccoloba longiochreata*, with *C. alagoensis* Weddell and *C. floribunda* Lindau. He distinguished it on the basis of the larger ocreae. The type selected by Hassler is a vigorous staminate flowering specimen. The type of *C. cujabensis* is a fruiting collection. On the basis of vegetative characteristics they are similar, and any question is resolved by a study of the Werdermann and Kuntze collections cited below. These show the intermediate conditions of ocreae and leaf venation between the type specimens of *C. cujabensis* and *C.*

longiochreata. *Coccoloba cujabensis* is not at all comparable to *C. alagoensis* or "*C. floribunda*."

Bolivia. Beni, Trinidad, Missiones Guarayos, *Werdermann 2366* (MO). **Brazil.** MATO GROSSO: Corumbá, *Kuntze s.n.* (NY); Cuyabá at Patricio da Silva Manso, *Martius 1241* (B, BR, LE; M–lectotype). **Paraguay.** Chaco, *Fiebrig 1284* (M–type collection of *C. longiochreata*).

Coccoloba cyclophylla Blake, Contr. U. S. Natl. Herb. 20: 238. 1919.

The type is *Curran 47*, from San Martín de Loba, Dept. Bolivar, Colombia (US 537207). Blake compared his new species with "*Coccoloba rotundifolia* Meisner," now known as *Coccoloba leoganensis* Jacq., from Hispaniola. There is no question that *C. cyclophylla* is the same as *C. caracasana* Meisner, which was based on material from Caracas, Venezuela.

Coccoloba cylindrostachya Lindau, Bot. Jahrb. 13: 163. 1890.

Lindau described consecutively *Coccoloba cylindrostachya* (based on *Glaziou 13135*) and *C. glaziovii* (based on *Glaziou 8089*) in his monograph of the genus. Both collections were made in the vicinity of Rio de Janeiro. An examination of the specimens fails to support the differences which Lindau felt would separate the two species. Therefore, *C. cylindrostachya* has been referred to the synonymy of *C. glaziovii*.

[*To be continued*]

JOURNAL
OF THE
ARNOLD ARBORETUM

VOL. XLI JULY 1960 NUMBER 3

STUDIES IN THE GENUS COCCOLOBA, IX. A CRITIQUE ON THE SOUTH AMERICAN SPECIES *

RICHARD A. HOWARD

Coccoloba declinata (Vellozo) Martius, Beibl. Flora 20: 90. 1837; Meisner, Fl. Bras. 5(1): 29. 1855, as to name only.

Polygonum declinatum Vellozo, Flor. Flum. 162. 1825; Icon. 4: 41. 1827.
Coccoloba racemulosa Meisner, Fl. Bras. 5(1): 30. 1855.
Coccoloba declinata var. *velloziana* Meisner, *ibid.*

A full discussion of the identity of *Coccoloba declinata* has been given under the name *C. confusa.*

In the original description of *Coccoloba racemulosa* Meisner cited only an unnumbered specimen, now in the herbarium at Munich, which was collected in September, 1818, along the river San Francisco near Carinhanha in Minas Geraes, Brazil. Lindau placed a fragment of this Martius collection in the Berlin herbarium, but in his monograph he also cited *Perrottet 83* from British Guiana. I have seen the latter collection and have referred it to *C. lucidula.* Both *C. declinata* and *C. lucidula* are poorly represented by herbarium material. When additional collections are available for study the relationship of these two species should be re-examined.

Coccoloba declinata, as represented by the Martius collection, is not well defined. The type specimen has partially mature leaves and functionally staminate flowers. The distinguishing characteristic, given by both Meisner and Lindau, is the origin of the ocreolae at the apex of the pedicel. However, careful dissection proves that this is an effect of drying and that while the ocreolae are fused to the pedicels in the type specimen, they may be free in other collections. The species is similar to *C. ilheensis, C. bracteolosa* and *C. glaziovii,* differing in the more scandent habit, the shorter inflorescences and the smaller leaves, though this characteristic may be due to immaturity. Field studies or additional collections may clarify the relationship of these species.

---

* Continued from volume XLI, p. 229.

Coccoloba densifrons Martius ex Meisner, Fl. Bras. **5**(1): 26. *pl. 7.* 1855.

Coccoloba barbeyana Lindau, Bot. Jahrb. **13**: 185. 1890.
Coccoloba pichuana Huber, Bol. Mus. Goeldi **5**: 342. 1909.
Coccoloba douradensis Glaziou, Bull. Soc. Bot. Fr. IV. **11**(Mem. 3f): 571. 1911 (provisional name with mixed type).

Although Lindau recognized *Coccoloba densifrons* in his monograph (Bot. Jahrb. 13: 177. 1890), citing the holotype (*Martius s.n.*, from Ega in Brazil), he did not include the species in his key to the genus.

Coccoloba barbeyana is based on a Ruiz and Pavon collection from Peru, but I fail to find any reliable differences between these species, either in Lindau's descriptions or in the specimens he annotated.

Coccoloba pichuana Huber was based on a Ducke collection from Obidos, Brazil. In the original description it was compared with *C. padiformis*, a very similar species occurring on the north coast of South America and in Central America. At present the two species are distinguished on the basis of leaf size and shape and the nature of the venation, but these differences may prove to be unreliable when both species are represented by more adequate material. For the present, therefore, the authentic material of *C. pichuana* is best referred to the synonymy of *C. densifrons.*

I have indicated previously (Jour. Arnold Arb. **41**: 46. 1960) that *Coccoloba douradensis*, published as a provisional name with a short, four-word description, is best considered as a *nomen nudum.* Furthermore, the collection cited by Glaziou is a mixture, parts of which are *Coccoloba marginata* Benth. while the remainder is more correctly assigned here.

Another specimen which may be referred to *Coccoloba densifrons* is *Haenke s.n.,* collected in Peru on May 24, 1897, and now in the Berlin herbarium. The sheet, bearing Gross' annotation label, has been given an unpublished name referring to the city of Guayaquil.

Coccoloba densifrons is similar to *Coccoloba sphaerococca* (*C. padiformis*), the former being known only in flower and the latter in fruit. Additional collections may prove these to be the same. On the basis of the specimens I have seen, they are presently to be distinguished by the finely reticulate upper leaf surface of *C. sphaerococca,* in which the primary veins are scarcely evident. In *C. densifrons* the primary veins are arcuate and clearly evident, impressed above but sharply ridged when dry.

Brazil. ACRE: *Ule 9348* (G, K). AMAZONAS: Borba, Rio Madeira, *Ducke 466* (A, F, K, NY, US); Ega, on Rio Negro, *Martius s.n.* (M–lectotype, B, NY); Humaytá near Tres Casas, *Krukoff 6120, 6228* (A, BR, LE, NY); Rio Embira, *Krukoff 4667* (G, LE, NY); São Paulo de Olivença near Palmares, *Krukoff 8331* (A, BR, F, LE, NY). GOYAZ: Serra Dourada, *Glaziou 21978* (P–in part, type of *C. douradensis.* PARÁ: Obidos, *Ducke 4866* (BM–type of *C. pichuana*). **Colombia.** ANTIOQUIA: Río Carepa, *Haught 4722* (NY, US). MAGDALENA: Santa Marta, *Espina 87* (Y). META: Sierra de la Macarena, *Philipson, Idrobo & Jaramillo 2104, 2265* (GH). PUTUMAYO: Río Putumayo, *Cuatrecasas 10820* (US). Dept.

unknown: Aguaviva, *Dugand 850* (Y); Arroyo de Piedras and Luruaco, *Dugand 985* (Y); Molinero, *Dugand 573* (Y); Río Toribio, *Espina and Giacometto A95* (F, Y); Río Tucurinca, *Dugand 1012* (Y). **Ecuador.** Guayaquil, *Haenke 2288* (NY), *s.n.* (B). **Peru.** LORETO: Florída, Río Putumayo, *Klug 2260* (A, F, GH, NY); Gamitana Cocha, Río Mazán, *Schunke 76* (A, F, NY); Iquitos, Mishuyacu, *Klug 1077* (F, NY); Iquitos, Rancho Indiana, *Mexia 6426* (F, GH); Puerto Arturo, Yurimaguas, *L. Williams 5138* (F); Ucayali, *Tessmann 3399* (G, NY, US). SAN MARTÍN: Chazuta, Río Huallaga, *Klug 4127* (F, GH, NY). Without definite locality: *Ruiz & Pavon s.n.* (G–type of *C. barbeyana*).

Coccoloba dioica Karsten ex Lindau, Bot. Jahrb. **13**: 170. 1890.

A single fragmentary specimen in the Leningrad herbarium, to which is attached Karsten's embossed label, bears this epithet. I have previously referred this species, the type of which was collected near Caracas, Venezuela, to the synonymy of *Coccoloba coronata* Jacq. (Jour. Arnold Arb. **41**: 40. 1960).

Coccoloba dioica Steudel, Nomen. Bot. 390. 1841.

Lindau (Bot. Jahrb. **13**: 220. 1890) refers this epithet to *Muhlenbeckia sagittifolia* Meisner. The name is used in a list without description by Steudel, and was reported to apply to a species from Chile. I have not seen any specimens bearing this name.

Coccoloba diversifolia Jacquin, Enum. Pl. 19. 1760; Hist. Stirp. Am. 114. *pl. 76.* 1763; Howard, Jour. Arnold Arb. **30**: 421–424. 1949, **40**: 195–196. 1959.

Although this species is listed in several floristic treatments of South America, I have not seen correctly identified specimens from the area. Jacquin attributed the species to Hispaniola in his second treatment and I have previously cited specimens from the Greater Antilles, Antigua, Mexico, British Honduras, Guatemala and Florida.

Coccoloba dugandiana A. Fernandez, Mutisia **5**: 1. 1952.

There is no question that this is a distinct species, but unfortunately Fernandez' description has been based on what must be considered anomalous material. Furthermore, he did not indicate that the species was dioecious, or that the flowers he described were functionally staminate. The abnormally emarginate leaves of the type are not characteristic of the species. Fernandez' statement that the immature achenes are pubescent is in error, for the fruiting perianth, not the achene, is pubescent.

Additional collections by Cardona and Llewelyn Williams from the Bolivar and Amazonas regions of Venezuela represent the pistillate plants to be assigned to this species. Whether these are typical I cannot determine. The leaves of these collections are comparable to the type in the thickness of the blade, the denseness of the vein reticulations and the pubescence. However, all the leaves are smaller and of contrasting shapes, the blades varying in shape from ovate, obovate or oblong to obovate-elliptic, and in size from 12 × 10 or 14 × 7 to 15 × 11 cm. long and broad. The leaf base is rounded or truncate and slightly cordate. The apex is obtuse to acute or slightly apiculate. The petioles of the mature leaves are approximately 1.8 cm. long. The inflorescences of these specimens are at most 10 cm. long and 7 cm. wide. Individual branches of the inflorescence are densely flowered and all parts of the flower, including the rachis, are densely tomentose. The tomentum on the perianth characterizes this species. Only three fruits remain attached to the specimens and all are crushed, indicating that the perianth is fleshy. The hypanthium surrounding the mature achene is only slightly vascular. The mature fruit is distinctly pubescent, a most unusual condition in this genus.

It is not clear how the leaf shape of this species will finally be defined. Certainly the pubescent leaves, the compact pistillate inflorescence, and the pubescent fruit clearly distinguish it at present. Additional collections of this species from the interior of Colombia and Venezuela are needed.

Colombia. BOYACÁ: Caño Guira near mouth of Río Meta, *Haught 2624* (US–isotype). **Venezuela.** AMAZONAS: Río Orinoco between San Fernando de Atabapo and San Antonio, *J. Silverio Level 41* (A); Sanariapo, *Williams 15961* (A, F), *16042* (F). BOLÍVAR: Alto Río Paragua, *Cardona 1183* (NY, US).

Coccoloba erecta Glaziou, Bull. Soc. Bot. Fr. IV. 11(Mem. 3f): 572. 1911.

This specific name must be considered a *nomen nudum,* for Glaziou's description states only, "Arbuste droit, fl. blanc jaunâtre." He cited his own collection number *14220* which, unfortunately, is a mixture. Glaziou apparently mixed his field tags and numbers for the sheet of *Glaziou 14220* in the Paris herbarium bearing the annotation "Coccoloba erecta Glaz. n. sp." is actually *C. schwackeana,* while a comparable specimen in the Berlin herbarium, *Glaziou 14219,* is one of two specimens cited by Lindau in describing *C. schwackeana.*

Coccoloba ernstii Johnston, Proc. Am. Acad. **40**: 685. 1905.

This species has been referred to the synonymy of *Coccoloba cruegeri* Lindau in earlier papers (Jour. Arnold Arb. **40**: 74. 1959, **41**: 228. 1960). *Coccoloba ernstii* was based on *Johnston 250* (GH) from El Valle, South Hill, Margarita Island, Venezuela.

Coccoloba excelsa Bentham in Hooker, London Jour. Bot. **4**: 624. 1845.

C. micropunctata Eyma, Meded. Bot. Mus. Utrecht **4**: 1. 1932.
C. parimensis var. *hostmanni* Meisner, Fl. Bras. **5**(1): 35. 1855.

Although I have examined the material cited by Eyma, as well as additional specimens, I cannot distinguish between *Coccoloba excelsa* and *C.*

micropunctata. Eyma believed that *C. micropunctata* could be distinguished on the basis of its narrow, tubular, membranaceous ocreolae and its non-punctulate leaves and inflorescences. The ocreolar distinction appears to be weak, varying with the age and the sex of the flowering material. In the description of *C. micropunctata* Eyma reported his material as "sub lente dense glanduloso(?)-punctulatae," although an examination of his material indicated broken hairs and clear or black hair bases which are comparable to structures often called punctations in *C. excelsa*. *Coccoloba micropunctata* is based on material collected from vines, but the writer's experience in the West Indies indicates that leaf shape and size, as well as texture and pubescence, varies widely in lianas.

In the original description of *Coccoloba parimensis*, Bentham based the species on Schomburgk material from Rio Parime. He reported further that "*Hostmann 245* from Surinam may possibly be a variety of the same species." Meisner (Fl. Bras. **5**(1): 35. 1855) described this Hostmann collection as *C. parimensis* var. *hostmanni.* Lindau (Bot. Jahrb. **13**: 170. 1891) assigned this same material to the synonymy of *C. excelsa.*

British Guiana. Bartica, *Linder 50, 151* (GH, NY); Berbice, *Schomburgk 178* (B), *400* (K–holotype, NY); Malali, Demerara River, *De la Cruz 2737* (GH, NY). **French Guiana.** Acarouany, *Sagot s.n.* (A, P); Caroni, *Melinon s.n.* (GH, P). **Surinam.** Goddo, *Stahel 77* (U–type of *C. micropunctata*); Gonini, *B.W. 3741* (A, NY); Kwatta hede, Saramacca River headquarters, *Maguire 23927, 23929* (A, NY); without specific location, *Hostmann 245* (B–type of *C. parimensis* var. *hostmanni*), *Wullschlagel 804* (GOET).

Coccoloba excoriata Linnaeus, Syst. Nat. ed. 10. 1007. 1759.

Lindau's treatment of *Coccoloba excoriata* (Bot. Jahrb. **13**: 211–212. 1891) is confusing. Of the many specimens which he cited, the ones I have seen should be referred to *C. venosa.* I have not seen a Widgren specimen from Rio de Janeiro to which he referred, nor the one which Schomburgk referred to as "Fl. & Faun. Br. Guy. 821." This reference is to "*Coccoloba nivea*," a synonym of *C. venosa* which applies to a plant under cultivation. *Coccoloba venosa* is represented in the native flora of South America and will be discussed later. *Coccoloba excoriata* L., as correctly applied, is a synonym of *C. tenuifolia* L. (Howard, Jour. Arnold Arb. **38**: 93. 1957), a native species of the Bahamas, Cuba and Jamaica, and has not been reported as either a cultivated or an indigenous plant of South America.

Coccoloba fagifolia Jacq. Hort. Schonbr. 3: 55. *pl. 352.* 1798.

Although Jacquin published an excellent plate of this species and attributed the plant to the vicinity of Caracas, the species has not been collected or recognized in recent years. I find Jacquin's species difficult to place. In the Meisner herbarium, now at the New York Botanical Garden, there is a packet with three detached leaves bearing the legend, "*Coccoloba fagifolia* Jacq. H.S. (mann tremula, verisim. ipsins Jacquini patris script.) folia speciminis sterilis Herb. Jacquini in Hb. Mus. Vindobon." This appears to represent one of the specimens cited by Meisner in his treatment of the species for DeCandolle's *Prodromus* (**14**: 165. 1856– "v.s.c. ex Schoenbr. in herb. Jacq. patr. et fil."). These three leaves have long, thin petioles and blades of thin texture. They do not represent any species of *Coccoloba* known to me, and there is no evidence that they even belong to the genus. Moreover, these detached leaves do not compare favorably with the original illustration.

Lindau (Bot. Jahrb. **13**: 162. 1890) recognized the species and cited a specimen collected by Boos which was in the Vienna herbarium. However, since the *Coccoloba* material in that herbarium was destroyed during World War II, the material which Lindau cited cannot be identified. Presumably the Boos specimen was a small one, for Lindau accumulated for the Berlin herbarium a large number of fragments from important species, but *C. fagifolia* is not represented in the material which I have on loan from that herbarium. No recent material has been assigned to *Coccoloba fagifolia*, so its interpretation must rest on the original illustration, although a comparison of Jacquin's plate with that of *C. virens* Lindley (Bot. Reg. **21**: *pl. 1816.* 1836), which is *C. coronata*, shows many similarities. If Jacquin's plate may be accepted as representing an accurate description, then it seems clear that *C. fagifolia* should be assigned to the synonymy of *C. coronata* Jacq. The proper identification of the Jacquin material in the Meisner herbarium remains unsolved.

Coccoloba fallax Lindau, Bot. Jahrb. **13**: 172. 1890.

Coccoloba caurana Standley, Publ. Field Mus. Bot. **22**: 73. 1940; Llewelyn Williams, Explorac. Bot. Guayana Venez. 189. 1942.

Coccoloba fallax seems to be distinguished by the fascicled inflorescence of simple racemes, the conspicuously large ocreae, especially those clustered at the apex of the stem and around the racemes, and the strongly keeled midrib. The type collection of *Coccoloba caurana* has immature inflorescences, but comparable mature material has been found in Trinidad. There is no question that *C. caurana* is the same as *C. fallax.*

The Trinidad specimens have been cited in a previous paper, in which the species was also recognized as occurring in Venezuela (Jour. Arnold Arb. **40**: 79. 1959). The type of *C. fallax* is *Crueger 114.* The lectotype selected is the specimen in the Göttingen Herbarium. The holotype of *C. caurana* is *Llewelyn Williams 11366* (F).

Coccoloba fasciculata Meisner in Warming, Symbol. Floram Bras. **6**: 128. 1870.

Lindau cited this epithet and reference in the synonymy of "*C. longipendula*" in his monograph (Bot. Jahrb. **13**: 177. 1890). The original publication is a report on Warming's collections from Brazil. One entry is "Coccoloba fasciculata Wedd., Meissner in DC l.c. 166 and Mart. l.c. 27," with a citation of "Lagoa Santa: . . . Serra da Piedade legit Warming Jan.-Febr. florentem." This is obviously a misidentification and not a new entity, as Lindau implied. Lindau referred the epithet to the synonymy of *C. longependula*, which I cannot distinguish from the older *C. sticticaulis* (*q.v.*). Lindau also cited the Warming collections as follows: "Rio de Janeiro in silvis ad Lagoa Santa: Warming n. 129; ad radices montis Serra da Piedada: Warming n. 126." I have seen specimens of each and have referred them to *C. sticticaulis* Weddell.

Coccoloba fasciculata Weddell, Ann. Sci. Nat. III. 13: 258. 1849.

I have discussed this species in an earlier paper (Jour. Arnold Arb. **41**: 44. 1960) and have referred it to the synonymy of *Coccoloba arborescens* (Vellozo) Howard. *Coccoloba fasciculata* Weddell was based on *Blanchet 796* collected in Bahia Province, Brazil. The type is in Geneva.

Coccoloba fastigiata Meisner, Fl. Bras. 5(1): 34. 1855.

Coccoloba goudotiana Meisner, Fl. Bras. 5(1): 35. *pl. 13, fig. 1.* 1855, not Weddell.

In the original description Meisner described the species and a variety "β glabrata," and cited specimens to illustrate both taxa. This is contrary to his usual practice, in the same volume and treatment, of considering the species to consist of varieties for which specimens are cited. The variety *glabrata* Meisner, represented by "*Schott 5537 (914)*" and part of *Schott 5540* (in Vienna), is better assigned to *Coccoloba mosenii.*

For the type variety of the species, Meisner cited *Schott 5540*, collected in Rio de Janeiro Province, Brazil, and *Schomburgk 1262*, in the Berlin herbarium. The latter collection was supposedly made in British Guiana. Lindau, who worked with the Berlin material around the year 1890, mentioned the Schomburgk collection under the name *Coccoloba fastigiata*, but attributed it to Meisner, "pr. p. ex. Meissn." I cannot determine whether Lindau actually saw this material, but I suspect that he did not, for in his citation of specimens seen (Bot. Jahrb. **13**: 224. 1890) he listed *Schomburgk 1262* as *C. marginata*. I have on loan the *Coccoloba* material from the Berlin herbarium and I fail to find the Schomburgk collection represented. I suspect that Meisner was in error in including the Schomburgk specimen and that *C. fastigiata* should be typified only by *Schott 5540*. Meisner stated that the specimen he saw was in the Vienna herbarium. Unfortunately, the *Coccoloba* material in this herbarium was destroyed during World War II. A photograph and a fragment of the holotype is at the Chicago Natural History Museum, and a more complete specimen is in Brussels. Therefore it seems wise to designate the specimen at Brussels as the lectotype.

Coccoloba goudotiana Weddell was based on a Goudot specimen collected near San Luis, Colombia, and now in the Paris herbarium. Meisner elaborated on the original description and illustrated the species. In addition to the Goudot specimen, Meisner also cited a collection by Pohl in the Zuccarini herbarium at Munich. I have seen both of these specimens and it seems clear that the illustration in *Flora Brasiliensis* was made by combining features present in both specimens. *Coccoloba goudotiana* Weddell is *C. obovata,* while *C. goudotiana* as described and illustrated by Meisner is *C. fastigiata.*

Brazil. RIO DE JANEIRO: Aguacú, *Schott 5540* (BR–lectotype, F–photo and fragment of Vienna material); Maná, *Glaziou 7888* (B, C, P); Realengo near Sapopemba, *Glaziou 11441* (LE, P); without specific locality, *Janz s.n.* (LE). Without locality: *Pohl s.n.*, in Herb. Zuccarini as cited by Meisner (M).

Coccoloba fastigiata var. **glabrata** Meisner, Fl. Bras. 5(1): 34. 1855.

Meisner cited "*Schott 5537 (914)*" and, in part, *Schott 5540* as representatives of his new variety with specimens in the Vienna herbarium. Lindau recognized the variety (Bot. Jahrb. 13: 172. 1890), citing *Schott 5537* and *Pohl 914* with specimens at Vienna and Berlin. The Vienna material has been destroyed and material from these collections is not included in the specimens of *Coccoloba* from the Berlin herbarium. A photograph of *Schott 5540* and a fragment of this specimen from Vienna are preserved in the herbarium of the Chicago Natural History Museum and clearly identify the specimen as *C. fastigiata.* It appears that the fragment of *Schott 5537* (F), all that remains of the collection, should be referred to *C. mosenii* Lindau (*q.v.*).

Coccoloba ferruginea Endlicher, Catalogus Hort. Acad. Vind. 1: 274. 1842; Ettingshausen, Blattskel. d. Apetalen 91. *pl. 26. fig. 2.* 1858.

Lindau referred this epithet to the synonymy of his *Coccoloba excoriata* (*q.v.*). Endlicher cited the name without description as a plant which had been obtained from the Berlin botanic gardens and was cultivated in Vienna gardens. Ettingshausen illustrated a leaf skeleton, using the name *Coccoloba ferruginea.* He acknowledged that his material was from a cultivated specimen, but did not discuss the illustration or the species. The leaf skeleton is inadequate for positive identification, although it is probably *C. venosa* L.; none of the specimens I have seen bears the name *C. ferruginea.*

Coccoloba filipes Standley, Trop. Woods 40: 14–15. 1934.

In the original description Standley wrote, "the distinctive characters of the species are the greatly elongate, many-flowered, lax racemes, with flowers on conspicuously long and slender pedicels." The type, *Dugand 380,* was collected in flower at Santa Rosa, west of Barranquilla, Colombia, on March 13, 1933. The flowers, although borne singly at each nodule on the inflorescence axis, are apparently functionally staminate, producing pollen grains. The specimen, now at the U.S. National Herbarium, bears two terminal, thin-textured, darkened leaves, suggesting that the plant is deciduous. The leaves arise from above the base of the ocreae.

No additional material which can be referred to this species has been seen. It appears to be distinct among the Colombian species of the genus and, on the basis of the material available for study, is not closely related to or even similar to any other South American species thus far described. Although several species from Cuba or Puerto Rico have similar long pedicels, none are so tenuous.

Coccoloba firma Martius ex Colla, Herb. Pedem. **5**: 48. 1836; Eyma, Meded. Bot. Mus. Utrecht **4**: 3. 1932.

The original description, while brief, is explicit and clearly intended to be that of a new species. In a list of species Colla attributed the name to Martius. No more definite location than Brazil was given. Eyma also used the name attributed to Martius in comparing it with his proposed new species, *Coccoloba micropunctata*. Eyma cited specimens at Kew and the Natal Herbarium, Durban, which he said were listed under the name *Coccoloba populifolia* Weddell. The correct name for the latter species is *C. alnifolia* Casaretto. Eyma apparently recognized both *C. firma* and "*C. populifolia*." I have not seen the specimen from the Natal Herbarium, South Africa, nor have I been able to locate a specimen so named at Kew. There is a Martius sheet at the British Museum bearing the name *C. firma*, which I believe is properly *C. alnifolia*. No material of *C. firma* was found in the collections of Martius which I have on loan from Munich, Brussels and Leningrad. I am therefore reluctant to accept this unsupported name until the material which Colla saw, or at least that which Eyma cited, has been located. If this should prove to be the same as *C. alnifolia* Casaretto (1844), as I suspect, the older *C. firma* Martius ex Colla should be accepted as the correct name.

Coccoloba gardneri Meisner, Fl. Bras. 5(1): 36. *pl. 15*. 1855; Howard, Jour. Arnold Arb. **41**: 44. 1960.

This species is based on *Gardner 600* from Serra dos Orgaos, Brazil. In the original description, which is clearly based on the Gardner collection, Meisner cited *Polygonum frutescens* Vellozo in synonymy and also *Coccoloba vellosiana* Casaretto, the latter with some doubt. I have previously considered the identity of species described by Vellozo and Casaretto and have also concluded that *C. gardneri* Meisner represents still a third species. Meisner's species was placed in the synonymy of *C. crescentiifolia* by Lindau, but clearly it is not the same as *C. arborescens* (Vell.) Howard, *loc. cit.* I cannot adequately define the species on the basis of the single collection available and wish to call this problem to the attention of future collectors who may visit the area of Rio de Janeiro.

Coccoloba glaziovii Lindau, Bot. Jahrb. **13**: 163. 1890.

Coccoloba cylindrostachya Lindau, Bot. Jahrb. **13**: 163. 1890.

Coccoloba sublobata Heimerl, Denkschr. Akad. Wien. Math.-Nat. Klasse **79**: 244. 1908.

Glaziou 8089 is the only collection cited by Lindau in the original description. Of the specimens cited from four herbaria, I have designated that at Berlin as the lectotype.

I am unable to distinguish between *Coccoloba glaziovii* and *C. cylindrostachya* which Lindau based on *Glaziou 8089* and *13135* respectively. Lindau distinguished between them by placing *C. glaziovii* in a group of species with the rachis glabrous and *C. cylindrostachya* in a contrasting group having the "rachis vario modo pilis instructa." His species descriptions amplify this supposed difference and suggest others, e.g., the position of the petiole in relation to the base of the ocrea, which, however, is not borne out in a re-examination of the type specimens cited. I have seen all of the specimens which Lindau cited from both collections and can only conclude that one species is represented.

Glaziou 3087 was annotated by Lindau as a possible new species. It is a vigorous shoot, probably adventitious in nature, with longer internodes, larger leaf blades and more pubescent parts. Lindau never published the name written on the sheet. I believe the specimen should be included in *Coccoloba glaziovii*. Another unpublished name honoring Lindau is found on the collection *Schwacke 13673* with the author given as Schwacke. Although the specimens seen have more delicate branches, more tenuous and pendant inflorescences and more oblong leaves, I feel that this material is properly assigned to *C. glaziovii.*

The Chicago Natural History Museum has a photograph of the holotype of *Coccoloba sublobata* which was in the herbarium at Vienna. The type was lost during World War II and the only duplicate of this collection which I have seen is in the Berlin Herbarium. This Berlin specimen bears an unpublished name, attributed to Heimerl and referring to the subundulate leaves, which is more appropriate than the one actually published. Although the type of *C. glaziovii* is a staminate plant, there is no question that Wacket's collection represents the same species in fruit. Heimerl's original description does not refer to the type collection by number. The number 12 cited below is legible in the photograph of the type and on the isotype.

In his monographic treatment of *Coccoloba striata* (Bot. Jahrb. 13: 164–165. 1890), Lindau cited numerous specimens from the Brazilian states of Bahia, São Paulo, Rio and Pernambuco. I have seen only one of these, *Mosén 3664,* which I believe to be more properly associated with *C. glaziovii. Coccoloba striata,* based on a Schomburgk collection from the Roraima area, appears to be a northern species. The remainder of the collections cited by Lindau should be examined for their correct relationship here.

Brazil. MINAS GERAES: Itabira do Matto Ventro, *Schwacke 13673* (B, P). PARANÁ: Volta Grande, *Dusén 11966* (GH, NY). RIO DE JANEIRO: Rio de Janeiro, *Glaziou 3087* (BR), *8089* (B-lectotype, BR, C, G, GH, LE, S), *13135* (type collection of *C. cylindrostachya*, B, BR, G, LE). SÃO PAULO: Serra do Cubatao, near Santos, *Wacket 12* (B–isotype of *C. sublobata*); Sorocaba, *Mosén 3664* (P).

Coccoloba goudotiana Weddell, Ann. Sci. Nat. III. 13: 260. 1849.

This species is based on *Goudot s.n.* from San Luis, Colombia. The type specimen is in the Paris herbarium and the species is clearly synonymous with *Coccoloba obovata* HBK. (1817).

Coccoloba goudotiana Weddell sensu Meisner, Fl. Bras. 5(1): 35. *pl. 13. fig. 1.* 1855.

In the original publication Meisner did not intend to describe a new species, but only to list the Weddell species. However, he cited the Goudot material used by Weddell, as well as a Pohl collection from the Zuccarini herbarium which is not the same species. Meisner's description and illustration combined features of both plants. I have seen the Pohl specimen, now in the Munich herbarium, and refer Meisner's interpretation of *Coccoloba goudotiana* to the synonymy of *C. fastigiata* Meisner.

Campderia gracilis Meisner, Fl. Bras. 5(1): 23. *pl. 6.* 1855; DC. Prodr. 14: 170. 1856.

Meisner described and illustrated this species in 1855. He cited a Spruce collection without giving a collector's number from around Barra in the "Prov. Rio Negro." The following year in the *Prodromus* he cited *Spruce 958*, reporting specimens to be in the DeCandolle Herbarium and the *Herbarium Monacense* (Munich). The illustration in *Flora Brasiliensis* appears to be a compilation of the two specimens. The original pencil sketch of the illustration of flowers and fruits is attached to the sheet at Munich and this sheet should be designated as the lectotype. However, I cannot determine the source of the fruiting material which Meisner illustrated, since comparable achenes do not appear on either sheet at the present time. Lindau referred *Campderia gracilis* to the synonymy of *Coccoloba ovata* Bentham. This appears to be the correct specific placement on the basis of the material I have examined, but there is a question as to whether *C. ovata* belongs in the genus *Coccoloba*. This matter will be discussed further under *C. ovata*. I have seen specimens of *Spruce 958* from Munich (lectotype), Berlin, Geneva, the Gray Herbarium, Leningrad and Paris.

Coccoloba gracilis HBK. Nov. Gen. 2: 176. 1818.

Two specimens, one in the Willdenow Herbarium and one at Paris, can be considered to be authentic for this species. Both are relatively small and are characterized by slender, nearly geniculate inflorescences of functionally staminate flowers. The original description has information applicable to labels on both specimens but does not exactly match either. It appears desirable to consider the Paris specimen as the lectotype since the only label on this sheet bears the number 3498 of Humboldt and the geographic location Rio Cachiyacu given at the time of publication.

These two specimens are inadequate for accurate determination as to genus. The floral structure and that of the ocreolae and the bracts appear to bridge the few weak characteristics used to distinguish *Coccoloba* and *Ruprechtia* in staminate flowering condition. With the material available, the only possible course to follow is that taken by the previous authors and monographer who placed the species in *Coccoloba*. Additional material is needed to determine its correct position.

Macbride (Publ. Field Mus. Bot. 13: 460. 1937) assigned a fruiting collection, *Weberbauer 6982*, to this species in his treatment for the *Flora of Peru*. The Weberbauer collection bears no data regarding the plant or the place of collection beyond "Peru." The old inflorescence axes are 4–8 cm. long and are erect. The fruiting peduncles are 2–2.5 mm. long. Fruits, one of which retains the fruiting calyx, are preserved in a packet. The perianth lobes are free nearly to the base in the fruit. The achene is only slightly triangular in outline, dark brown and shiny. This specimen is clearly a *Coccoloba*, though not necessarily the same as the authentic material of *C. gracilis* HBK.

Peru. Río Cachiyacu, *Humboldt 3498* (P–lectotype; without number or location [Herb. Willd. 7701]).

Coccoloba grandiflora Lindau, Bot. Jahrb. 13: 175. 1890.

Lindau cited two collections in the original description, *Glaziou 14217* and *Miers 4657*. The former should be selected as the type collection and the specimen at Copenhagen designated as the lectotype. This is the only sheet among those cited below on which the label states, "*Coccoloba grandiflora* Lindau n. sp." Lindau's work was based upon the material in the Berlin herbarium — the fragment of a branch together with one inflorescence having one detached and two attached leaves. I have not located the Miers collection.

Superficially, this species resembles *Coccoloba tenuiflora* Lindau which is based on cultivated material of unknown origin. The type of *C. tenuiflora* was from a greenhouse plant, while *C. grandiflora* is from native material. I cannot determine whether cultivation (and, specifically, greenhouse conditions) could create the differences seen in these specimens. *Coccoloba grandiflora* has more conspicuous ocreolae which are membranaceous, split longitudinally and flaring. In all other characteristics the species are similar. Both species are known only from flowering material.

Brazil. MINAS GERAES: *Glaziou 20439* (B, LE, NY). RIO DE JANEIRO: Nuovo Freiburg, *Glaziou 14217* (C–lectotype, B, K, LE, US).

Coccoloba grandis Bentham in Hooker, London Jour. Bot. 4: 624. 1845.

This species is based on *Schomburgk 825* collected on the Rio Branco, British Guiana. Lindau placed the species in the synonymy of *Coccoloba latifolia* Lam. After having examined the type in the British Museum, I agree with this placement.

Coccoloba guaranitica Hassler, Repert. Sp. Nov. **14**: 161. 1915.

Coccoloba guaranitica var. *opaca* Hassler, *ibid.* 162.

Hassler compared his new species with *Coccoloba schomburgkii*, but on the basis of the few specimens I have seen, it seems more nearly comparable to *C. padiformis* from Venezuela, although the leaves of *C. guaranitica* are smaller and more rounded at either end. The fruits of both species are known only from immature specimens, but in both the perianth lobes are conspicuous, imbricate and appear to surround only the upper half of the achene.

Hassler did not select a type in the original description in which he mentioned two collections, *Fiebrig 1429* and *1440*. I have not seen the latter, but the former is a shoot of vigorous and rapid growth.

The variety which Hassler described differs from the species in having smaller leaves, the margins of which are undulate-crenate. It also has a shorter inflorescence. The type of the variety, *Fiebrig 4305,* is a mature shoot system with many lateral flowering branches. It seems quite apparent that the specific name has been applied to younger and more vigorous specimens and that of the variety to the more mature branching specimens and thus the variety is not worthy of recognition.

A specimen of *Fiebrig 4305*, the type of *C. guaranitica* var. *opaca,* was studied by Gross and annotated with both a specific name honoring Fiebrig and a varietal name referring to the crisp leaf margin. Neither name has been published, to my knowledge, although Gross published other epithets in the genus in small notes, often in obscure publications.

Paraguay. Boquerón, Puerto Casado, *Pedersen 4043* (A, C); Chaco, *Fiebrig 1429* (M–isotype); between Río Apa and Río Aquidabán, *Fiebrig 4305* (type collection of *C. guaranitica* var. *opaca*, B, GH, M, P); Bahía Negra, *Rojas 13708* (BR, P, W).

Coccoloba guianensis Meisner, Linnaea **21**: 264. 1848.

Several specimens were cited in the original description, but no type was selected. The specimens are obviously the same as the slightly anomalous material described earlier by Bentham as *Coccoloba marginata.* The variation in material called *C. guianensis* and the nomenclature of the complex has been discussed in other papers (Howard, Jour. Arnold Arb. **40**: 84, 85. 1959; **41**: 45, 46. 1960).

Coccoloba gymnorrhachis Sandwith, Kew Bull. **1932**: 221. 1932; Eyma, Polygonaceae, Guttiferae & Lecythidaceae of Surinam, 111. 1932.

Sandwith based the original description of this species on a flowering specimen, *Sandwith 168,* from British Guiana. The plant was described as a "bush-rope" and the type shows strong characteristics of a liana. The leaves, broadest above the middle and narrowed to the base, are rigidly coriaceous with the arcuate venation impressed above. The flowers are borne in clusters with tightly appressed ocreolae. Eyma supplemented the original description with a fruiting specimen from Surinam. The Richard collection cited below is also in fruit and is the same as the material which Eyma cited, but these two fruiting collections are not good matches for the type collection and may not belong here. The fruits are warty, as though insect-infested, but no evidence of insect larvae could be found.

Additional collections are needed before the morphological characteristics of *Coccoloba gymnorrhachis* are fully understood and the species clearly defined.

British Guiana. Essequebo River, Moraballi Creek near Bartica, *Sandwith 168* (K–holotype, NY). **Surinam.** *Brownsberg, B.W. 6773* (K). Location unspecified: *L.C. Richard s.n.* (P).

Coccoloba ilheensis Weddell, Ann. Sci. Nat. III. 13: 258. 1849.

Coccoloba membranacea Klotsch, Linnaea **14**: 289. 1840, *nomen nudum.*

This is a poorly defined species requiring both field study and many more collections for an accurate interpretation. This species is similar to *Coccoloba glaziovii, C. ochreolata* and *C. confusa.* While collections representing the type of each of these species can be distinguished on sight, I cannot find any reliable morphological characteristics useful in separating them in a key.

Brazil. BAHIA: Ilheos, *Martius 1240* (P–holotype, BR, G, GH, LE, M); *Luschnath s.n.* "1839" (LE). Without location: *Luschnath 42* (LE).

Coccoloba japurana Meisner, Fl. Bras. 5(1): 25. 1855.[1]

This species is based on a Martius specimen from Ega in the Rio Negro of Brazil. Authentic material is in the Munich herbarium and is represented in the collections of the Gray Herbarium by a photograph. The photograph is a montage of two herbarium sheets and two labels. One label has the hand-written annotations, "*Coccoloba acuminata*" and "*Coccoloba japurana*" and on the same sheet is the annotation, "*Alsodeia japurana* Radlk." One of the sheets has specimens with immature inflorescences. This almost completely overlaps the other sheet from which an infructescence protrudes. The fruit on this axis is clearly not that of a *Coccoloba.*

The name *Alsodeia japurana* Radlk. (Sitz-ber. Math.-Phys. Klasse Akad. München **20**: 182. 1891) is recorded in the first supplement of Index Kewensis as an observation. There is no reference to the name *Coccoloba japurana* Meisner in the article cited. However, Lindau at-

---

[1] **Rinorea japurana** (Meisner) Howard, comb. nov. Basionym: *Coccoloba japurana* Meisner in Martius, Fl. Bras. **5**(1): 25. 1855.

tributed the transfer to Radlkofer in a list of excluded species and in a footnote in his monograph i.e., "*C. japurana* MEISSN. = *Alsodeia japurana* RADLK." (Bot. Jahrb. 13: 220. 1890).

Alsodeia is a genus of the Violaceae for which most modern writers use the name *Rinorea.* Blake, who monographed the American species of *Rinorea* (Contr. U. S. Natl. Herb. 20: 317. 1924), listed *Alsodeia japurana* as a "doubtful species" with the comment, "This was described from specimens with very young flowers. It is said by Radlkofer to be allied to *A. racemosa.*" So many aspects of this misplaced epithet have been overlooked that I have made the new combination in *Rinorea* primarily to place the name in indices for the aid of future workers. An adequate interpretation of the photograph is impossible. Meisner's original description could well be a *Coccoloba;* Lindau saw the material now in the Munich herbarium and would surely have recognized a *Coccoloba* as to genus; Radlkofer worked on *Alsodeia* and would certainly have recognized that genus; Blake did not accept the species, but it is not clear what material he saw or to which description he referred. The fruit in a photograph of a properly labelled specimen, supposedly the type, is not a *Coccoloba*, but appears to be a *Rinorea.* The writer cannot solve the puzzle and may not have placed the specific epithet in its proper niche.

Coccoloba laevis Casaretto, Nov. Stirp. Bras. 71. 1844; Lindau, Bot. Jahrb. 13: 186. *fig. 40.* 1890.

Coccoloba cordifolia Meisner, Fl. Bras. 5(1): 37. 1855.

Casaretto did not cite a specimen in the original description, but in the same publication he described other species based on his own collections. One sheet, *Casaretto 2264,* in the Turino herbarium, fits the description of *Coccoloba laevis* in all details and should be considered the holotype. I assume that Casaretto unintentionally omitted the citation of a specimen.

In the original description of *Coccoloba cordifolia,* Meisner cited several specimens without selecting a type. He indicated the affinities of his new species with *C. nivea, C. cordata,* and *C. candolleana* and cited in synonymy "*Coccoloba uvifera* Salzmann Mss. in Herb. (non Linn.)." In his treatment for the Prodromus (14: 155. 1856) he cited the same specimens, but he did not repeat the suggested synonymy or the possible relationship. Instead he placed his species next to *C. laevis,* which he suggested might be identical with *C. cordifolia* or *C. candolleana.* Lindau was the first to place *C. cordifolia* Meisner in the synonymy of *C. laevis* Casaretto, a decision with which I agree.

The Salzmann collection from Bahia which Meisner cited is represented in several herbaria and the collection at Kew shows the full range of variation from the small-leaved type of Casaretto's species to the broader and more cordate leaved types found in *Blanchet 3528.*

Lindau described and illustrated the fruit of *Coccoloba laevis,* but although I have seen most of the material he cited, I have not found a fruiting specimen, or even a single fruit, among them. If the figure published by Lindau can be trusted, the possibility of a hybrid origin of this species should be examined. *Coccoloba marginata* or *C. uvifera* would seem quite likely as parents. At present *C. laevis* is an extremely variable species which is not clearly delineated.

Brazil. BAHIA: Amaralina, San Salvador, *Dahlgren s.n.* (F); Ilha de Cal, *Curran 106* (GH, NY, Y); Itaparica Island, *Casaretto 2264* (TO–holotype); Jacobina, Moritiba, *Blanchet 100* (G, NY), *3528* (G, LE, P). PERNAMBUCO: Pernambuco, *Guillamin s.n.* (F). RIO DE JANEIRO: Rio de Janeiro, *Glaziou 11445* (B, K, P), *Salzmann 476* (G), *s.n.* (K, LE, P). Locality uncertain: Maceio, *Gardner 1391* (K).

Coccoloba lanceolata Lindau ex Glaziou, Bull. Soc. Bot. Fr. IV. 11 (Mem. 3f): 573. 1911, nomen nudum.

The collection *Glaziou 19764* was cited by the author in the original publication with the brief description, "liane, fl. blanchâtres, fruit noir." The specimens seen are obviously from climbing plants. The leaves and infructescence are borne on short lateral shoots. While the epithet has no acceptable standing at the present time, I do not wish either to describe the plant more fully or to place the name in synonymy until further material from southern Brazil is available for study. It is probable that this collection should be assigned to *C. salicifolia*. The leaves of the Glaziou specimen, however, are more lanceolate-oblong in shape, less acuminate at the apex and thicker in texture. The fruits match the illustration given by Lindau for *C. salicifolia*.

Brazil. MINAS GERAES: Riacho das Varas, *Glaziou 19764* (B, C, K).

Coccoloba latifolia Lamarck, Dict. Encycl. **6**: 61. *ill. 316, f. 4.* 1804.

Coccoloba grandis Bentham in Hooker, London Jour. Bot. **4**: 624. 1845.

Lamarck described this species from material cultivated in the Jardin des Plantes, Paris. I have not seen authentic material, but his illustration is of a single detached leaf which does not represent well the species as currently accepted. The description, although somewhat vague, seems applicable, but, since *Coccoloba latifolia* is similar to *C. mollis,* comparable field observations would be helpful. It differs in an almost complete lack of puberulence, in its much stouter and generally hollow stems and in having strongly bullate leaves. I have seen *C. latifolia* in Trinidad where it is a characteristic plant of savanna areas. Its habit is distinctive and this, together with the presence of many biting ants in the large ocreae, makes it long remembered by collectors.

Coccoloba grandis Bentham is based on *Schomburgk 825*. Lindau placed the species in the synonymy of *C. latifolia*, where it clearly belongs.

Lindau referred three collections by Burchell from São Paulo and Pará to this species. I have seen one sterile sheet of *Burchell 3982* in the herbarium at Kew and feel that this sheet, at least, should be considered the adventitious leaf form of *Coccoloba warmingii* Meisner.

In addition to the localities listed below, the species is also known from Trinidad and its adjacent islands (Jour. Arnold Arb. **40**: 81. 1959).

Brazil. CEARÁ: Ceará, *Curran 36* (GH). MARANHAO: Campo de Boa Esperanca, *Froes 1817* (A, NY). **British Guiana.** Mapenna, Courantyne River, *B.G. Forest Dept. 2601* (A); Río Branco, *Schomburgk 825* (BM–type of *C. grandis*). **French Guiana.** Cayenne, savannahs along St. Madeleine Rd., *Broadway 750* (GH, NY); without locality, *Barbier s.n.* (A), *Sagot 486* (A). **Surinam.** Koboerie, *Herb. B.W. 5929* (A); without specific locality, *Hostmann 682* (GH), *s.n.* (BR), *Wullschagel s.n.* (M). **Venezuela.** DELTA AMACURO: Serrania Imataca, N. of Río Guanamo, *Wurdack & Monachino 39724* (A).

Coccoloba laurifolia Jacquin, Hort. Schoenbr. **3**: 9. *pl. 267.* 1798.

This remains a troublesome name which I cannot place satisfactorily. Meisner recognized the species (DC. Prodr. **14**: 165. 1856), noting that the type locality was Caracas, Venezuela, and he cited one specimen (*7699*) in the Willdenow herbarium. This specimen consists of two sterile shoots obtained from a plant cultivated in a botanic garden and certainly is not the Jacquin type. It is properly referred to *Coccoloba diversifolia* Jacq.

In his monograph (Bot. Jahrb. **13**: 158. 1890) Lindau also accepted Jacquin's name and cited two specimens (without known collectors and from Caracas, Venezuela) to be found in the Delessert and Vienna herbaria. Lindau cited many additional collections from Florida, the Bahamas, Cuba, Hispaniola, Puerto Rico and the Virgin Islands. A specimen in the Prodromus herbarium at Geneva which Lindau saw, and the one I believe he cited, was probably collected by Bertero in Hispaniola. The Antillean and Florida material cited by Lindau has been referred to *Coccoloba diversifolia* Jacq.

Although I have suggested that *Coccoloba laurifolia* Jacq. and *C. diversifolia* Jacq. may be the same (Jour. Arnold Arb. **40**: 195–196. 1959), I am not entirely convinced of it. A re-examination of all material available to me from Venezuela has failed to reveal any plants which can be compared satisfactorily with the description and illustration supplied by Jacquin. The closest comparison in Venezuela would be with *C. padiformis* Meisner based on the collection *Moritz 377* from Caracas. Material from Central America which I have cited for *C. padiformis* (*loc. cit.* 210–211) and additional collections to be cited in this study are not exactly comparable to Jacquin's description and illustration. These differences at present are primarily in the venation as related to the texture of the leaf blade and in the shape of the leaf apex. A field study of *Coccoloba* plants in the vicinity of Caracas will be necessary to determine what species Jacquin had as a basis for his description and illustration of *C. laurifolia.*

Coccoloba laxiflora Lindau, Bot. Jahrb. **13**: 191. 1890.

The holotype in the Berlin herbarium is *Glaziou 11444* from Rio de

Janeiro, Brazil. This species is to be referred to the synonymy of *Coccoloba ramosissima* Weddell.

Coccoloba lehmannii Lindau, Bot. Jahrb. 29(Beibl. 49): 7. 1895; Howard, Jour. Arnold Arb. **40**: 200. 1959.

Coccoloba lehmanni Lindau, Repert. Sp. Nov. **1**: 156. 1905.
Coccoloba williamsii Standley, Publ. Field Mus. Bot. **11**: 148. 1936.

This species has been discussed in an earlier paper in which its range was extended to Central America and additional species from that area placed in its synonymy. The selection of a lectotype was also discussed at that time. Another similar species is *Coccoloba lepidota* A. C. Smith (*q.v.*). Additional material may show that this, too, should be placed in synonymy here. Two collections from Peru, *Tessman 3896* and *5258* from Iquitos along the Amazon have been tentatively referred to this species. Several herbarium specimens have been seen of a collection made in 1871 from a cultivated plant in the Calcutta Botanic Garden. No collector or data are given on the sheets, which have carried the name "*Coccoloba excoriata.*" These are clearly to be referred to the present species.

Colombia. ANTIOQUIA: Villa Arteaga, *Lopez & Sanchez 40* (US); Cauca, *Lehmann 7560* (B–lectotype). META: Puerto López, *E.L. & R.R. Little 8294* (NY). **Venezuela.** ANZOATEGUI: NE. of Bergantín, *Steyermark 61217* (F); BARINAS: Barinitas, *Aristeguieta 1702* (US). MÉRIDA: Between Hacienda Agua Blanca, above La Azulita and Río Capaz, *Steyermark 56127* (F).

Coccoloba lepidota A. C. Smith, Brittonia **2**: 150. 1936.

This species was distinguished by Smith by the "characteristic scales of the petioles and young stem parts." Smith compared *Coccoloba lepidota* with *C. ovata*, which is clearly distinct. The separation of *C. lepidota* and *C. lehmannii* is more difficult and additional material may show that *C. lepidota* should be another synonym of that species. The lectotype of *C. lehmannii*, *Lehmann 7560* (B), has shorter, more elliptic leaves and a predominance of simple pubescence. *Coccoloba lepidota*, as represented by the type collection, *Krukoff 5660*, has larger obovate-oblong leaves, broadest above the middle and tapering to an obtuse or truncate base. The young stems, petioles and ocreae are covered with lepidote scales and bear lesser amounts of simple hairs and resinous excretions. A tendency towards this development is found in the type collection of *C. lehmannii* and in the other collections cited below. It is probable that *C. lepidota* is an extreme variation of *C. lehmannii.*

Brazil. ACRE: Near mouth of Rio Macauhan, *Krukoff 5660* (NY–holotype, A, LE, M, W), *5659* (A, LE, M, NY).

Coccoloba leptostachya Bentham, Bot. Sulph. 59. 1856; Meisner, DC. Prodr. **14**: 163. 1856.

As has been pointed out in an earlier paper in this series (Jour. Arnold

Arb. **40**: 188. 1959), Bentham described this species, citing the type locality as "Libertad in Colombia." The type is a Barclay specimen at Kew. I have studied this and have concluded that the specimen was collected in Central America. Recent collections from Libertad in El Salvador proved to match the Barclay collection well. I have seen no comparable material from Colombia. *Coccoloba leptostachya* Bentham is referred to the synonymy of *C. barbadensis* Jacquin (1760), which is known from Mexico, Guatemala and El Salvador. The species need no longer be considered in the South American flora.

Coccoloba longependula Martius ex Meisner, Fl. Bras. **5**(1): 27. *pl. 9.* 1855; Lindau, Bot. Jahrb. **13**: 177. 1890.

After an examination of the type of this species (*Martius 759* from Minas Geraes, Brazil [M]), this has been referred to the synonymy of *Coccoloba sticticaulis* Weddell (*q.v.*).

Coccoloba longiochreata Hassler, Repert. Sp. Nov. **14**: 162. 1915.

This species is clearly the same as *Coccoloba cujabensis* (*q.v.*) and has been referred to synonymy there. Hassler cited two collections, *Fiebrig 1284* and *1443,* in his own herbarium. The collections were made in the Gran Chaco at Puerto Talavera, Paraguay.

Coccoloba longipes S. Moore, Trans. Linn. Soc. II. **4**: 446. 1895.

Coccolobis padifolia Rusby, Mem. N. Y. Bot. Gard. **7**: 235. 1927.

In the original description Moore compared his new species with *Coccoloba laxiflora* Lindau, which I now regard as the same as *C. ramosissima* Weddell. There is a striking similarity between these two species in the delicate inflorescences and the long peduncles. There are differences in the leaf size which should be re-examined when additional materials become available from southern Brazil. At present I distinguish *C. longipes* by the ovate-oblong leaf blades which taper from the middle to a blunt apex. *Coccolobis padifolia* Rusby was described without any comparison of other species. A study of the type collection indicates that it should be placed in the synonymy of *C. longipes.*

Bolivia. Rurrenabaque, *Rusby, Mulford Ex. No. 848* (NY–holotype of *C. padifolia,* GH). **Brazil.** Matto Grosso, *S. Moore 577* (BM–holotype, B, NY).

Coccoloba lucidula Bentham in Hooker, London Jour. Bot. **4**: 627. 1845.

Coccoloba sagotii Lindau, Bot. Jahrb. **13**: 184. 1890.

The two species treated here fall into widely separated portions of Lindau's monographic treatment of *Coccoloba*, yet it seems clear to the writer that they are identical. *Coccoloba lucidula* was based on flowering specimens with delicate, membranaceous, immature leaves which crinkled in drying, turned black and became lustrous on the upper surface. Bentham cited only one specimen collected by Schomburgk, "2nd Coll. 947 (1262)." The species has not been collected again and no modern collections have been assigned to it. The mature foliage and fruiting specimens of *C. sagotii* would appear to belong in synonymy here, but since at present there is no comparable material for *C. lucidula*, there is need for additional mature specimens of the latter.

Coccoloba lucidula is described as a woody vine by collectors of the specimens cited below. *Perrottet 1820* (P) is a delicate vine tapering to a tenuous apex. On this specimen the immature condition of the leaves is clearly shown, from minute to fully expanded, though membranaceous, forms. Many of the mature leaves of other collections are folded, indicating that when fresh the midrib is sharply curved downward. The fruit is distinctive, being nearly spherical and smooth. A small stalk is distinguishable at the base of the fruit and the apex is more or less obtuse, with very small, imbricate perianth lobes. *Perrottet 83* from British Guiana which is referred here was cited by Lindau (*loc. cit.* 168) as *Coccoloba racemulosa* and, thus identified, was an important example of his Guiana–northern Brazil distribution (*loc. cit.* 116).

Coccoloba sagotii was described by Lindau and was based on an unnumbered Sagot collection from "Guyana gallica" near Cayenne. This is a fully matured branch of scrambling habit. The infructescence is old but fruits have been preserved. The leaves are coriaceous and shiny above. Lindau distinguished this species from *C. lucidula* by the glabrous branchlets and infructescence rachis, but close examination shows that in all reliable characteristics the type collections are similar. The pubescence present on material of *C. sagotii* was overlooked by Lindau. Lindau also referred to specimens in the herbaria at Berlin and Stockholm, but both of these are merely fragments. The most complete specimen of this collection is in the Paris herbarium.

British Guiana. Coverden, *Persaud 136* (F, K, NY); Demerara River, *Jenman 6309* (K); Ituni, south of Mackenzie, *Cowan 39255* (K, NY); Roraima, *Schomburgk 947* (*1262*) (K–type collection, BR). Without specific location: *Perrottet 83* (G), *s.n.* (P); *Schomburgk 81* (B). **French Guiana.** CAYENNE: *Martin s.n.* (K), *Poiteau s.n.* (K), *L.C. Richard s.n.* (P), *Sagot s.n.* (type collection of *C. sagotii*, B, P, S), *Talbot s.n.* (K); Montagne de Kaw, *Cowan 38798* (NY). **Venezuela.** Bolívar, Tumeremo, *Steyermark 60942* (F).

Coccoloba marginata Bentham, in Hooker, London Jour. Bot. **4**: 626. 1845.

Coccoloba guianensis Meisner, Linnaea **21**: 264. 1848.
Coccoloba martii Meisner, Fl. Bras. 5(1): 37. 1855.
Coccoloba martii var. *major* Meisner, *ibid.* 38.
Coccoloba martii var. *minor* Meisner, *ibid.*
Coccoloba nitida var. *cordata* Meisner, *ibid.*
Coccoloba nitida var. *rotundata* Meisner, *ibid.*

Coccoloba trinitatis Lindau, Bot. Jahrb. **13**: 182. 1890.
Coccoloba douradensis Glaziou, Bull. Soc. Bot. Fr. IV. **11**(Mem. 3f): 571. 1911 (provisional name with mixed type; see also *C. densifrons*).

A discussion of this species is given in two earlier papers (Jour. Arnold Arb. **40**: 84–85. 1959, and **41**: 45–46. 1960). I have seen additional material (cited below) which extends the range of this species to Venezuela and possibly to the Brazilian states of Minas Geraes, Goyas, Bahia, Acre and Santa Catarina. Additional field study is needed to determine the variations in individual plants as these occur in South America.

While I am following Lindau in considering *Coccoloba martii* a synonym of *C. marginata*, I wish to point out the possibility that *C. martii* more properly may be assigned to *C. peltata* Schott. Certainly the Salzmann collections from Bahia previously identified as "*C. pendula*" or *C. nitida* var. *cordata* are intermediate between material of *C. peltata* from Rio de Janeiro and material of *C. marginata* from the Guianas. At present *Coccoloba peltata* may be represented only by anomalous material and therefore the species may be incorrectly interpreted.

Brazil. ACRE: Rio Macauhan, *Krukoff 5479* (G, K, M, NY, W). AMAZONAS: São Paulo de Olivença, *Krukoff 9048* (F, K, NY); without specific locality, *Ule 9347* (G, K). BAHIA: Chapada do Rio das Femmeas, Carrasco, Ilheos, *Riedel 244* (LE, P), *Blanchet 3049* (LE); *Lützelburg 516* (M); without specific locality, *Salzmann 475* (P). GOYAS: Chapada do Rio Preto, *Lützelburg 1304* (M); Patavidado, *Macedo 3.859* (K); without specific locality, *Burchell 7768* (P). MINAS GERAES: Caraca, *Tavares 316* (M). **British Guiana.** Kaieteur Plateau, *Maguire & Fanshawe 23316* (A, NY); Kaieteur Savannah, Potaro River, *Jenmann 831* (K); basin of Kuyuwini River, *A.C. Smith 3030* (A); Waini River, *De la Cruz 3712* (GH); without locality, *Poiteau 179* (LE). **Dutch Guiana.** Paramaribo, *Kappler 1620* (P), *Wullschlagel 882* (BR); without specific locality, *Hostmann 506* (P), *Wullschlagel 992* (BR). **French Guiana.** Cayenne, *Broadway 307* (GH); without specific locality, *Leprieur 187* (A), *Lequillon s.n.* (P), *Melinon 252* (A). **Venezuela.** AMAZONAS: Tamatama, Upper Orinoco, *Llewelyn Williams 15233* (F); without specific locality, *Gines 5105* (US). BOLIVAR: Raudal Guaiquinima, *Cardona 474* (US), *475* (US), *Maguire 33134* (A, NY).

Coccoloba martii Meisner, Fl. Bras. **5**(1): 37. 1855.

Coccoloba martii var. *major* Meisner, *ibid.* 38. 1855.
Coccoloba martii var. *minor* Meisner, *ibid.*

No type had been selected, but the species was considered to consist of its two varieties. An examination of the material cited led to the conclusion that these taxa may be referred to the synonymy of *Coccoloba marginata* Bentham. There is a possibility, as was pointed out in the discussion of *C. marginata*, that *C. martii* and *C. peltata* are the same.

Coccoloba meissneriana (Britton) K. Schum. in Just, Bot. Jahresber. **28**(1): 451. 1902.

Uvifera meissneriana Britton in Rusby, Bull. Torrey Club **27**: 129. 1900.

This species is known from but two collections from the same area. It is similar to *Coccoloba peruviana* and eventually both may be included in *C. obtusifolia* (*q.v.*). At present it can be distinguished by the tomentum on the young stems and petioles, on the entire lower leaf surface and on the midrib of the upper leaf surface. The inflorescence is copiously pubescent, as well. The fruits are comparable to those of *C. obtusifolia*, having the achene surrounded by the imbricated lobes of the perianth. The Rusby collection is from a staminate plant and was in flower in May. The Bang collection, made in July, is in fruit.

Bolivia. Guanai, *Rusby 1918* (NY–holotype, B, GH), *Bang 1595* (A, GH, K, LE, M, NY).

Coccoloba membranacea Klotzsch, Linnaea **14**: 289. 1840.

This species is apparently based on a Luschnath collection from Bahia, Brazil. The original description is brief, "Arborescens, floribus lutescenti-viridibus." Lindau (Bot. Jahrb. 13: 165. 1890) regarded the original epithet as a *nomen nudum* and referred it to the synonymy of *Coccoloba ilheensis*. At that time he cited "*Luschnath 42*," a specimen of which is in the Leningrad herbarium. I have seen that sheet, but there is no annotation to indicate that it is the type of *C. membranacea*. The specimen is properly referred to *C. ilheensis*.

Coccoloba microneura Meisner, DC. Prodr. **14**: 163. 1856; Howard, Jour. Arnold Arb. **41**: 42. 1960.

This species has been discussed in the earlier paper cited above and referred to the synonymy of *Coccoloba nitida* HBK. The type was *Purdie s.n.*, collected in the vicinity of Santa Marta, Colombia. Meisner reported the type specimen to be in the Arnott herbarium, but such a specimen cannot be found, although there is a specimen in the herbarium of the Royal Botanic Garden at Kew.

Coccoloba microphylla Morong in Morong & Britton, Enum. Pl. Coll. Parag. 212. 1892; Ann. N. Y. Acad. **7**: 213. 1893, not Griseb. 1866.

This species was based on *Morong 899*, made along the Río Pilcomayo in Paraguay. Because the epithet is a later homonym of *Coccoloba microphylla* Grisebach, Hassler renamed it *C. morongii*. An examination of the type collections shows that it should be referred to the synonymy of *C. paraguariensis* Lindau.

Coccoloba micropunctata Eyma, Meded. Bot. Mus. Utrecht **4**: 1. 1932.

I am unable to accept Eyma's criteria for distinguishing the material he cited as a species distinct from *Coccoloba excelsa* (*q.v.*), and so have referred his species to synonymy there. The type selected was *Stahel 77* from Dutch Guiana.

Coccoloba mollis Casaretto, Nov. Stirp. Bras. 72. 1844.

Coccoloba polystachya Weddell, Ann. Sci. Nat. III. **13**: 261. 1850.
Coccoloba paniculata Meisner, Fl. Bras. **5**(1): 43. *pls. 20, 21.* 1855.
Coccoloba polystachya var. *mollis* Meisner, DC. Prodr. **14**: 151. 1856.
Coccoloba polystachya var. *glabra* Lindau, Bot. Jahrb. **13**: 133. 1890.
Coccoloba polystachya var. *pubescens* Lindau, *ibid.*

Casaretto cited no collection by number or name of collector in the original publication, so one must assume that he was referring to his own collection. Such a specimen, now in the Turino herbarium, was made on the island of Itaparica, near Bahia, Brazil, and the data on the label agrees in description and location with that published by Casaretto. The label on the specimen also stated the number of the collection as 2218 and the catalogue number as 80. Lindau cited *"Casaretto 2218"* and *"Meisner 80."* These are one and the same sheet. This single sheet in the Turino herbarium, the holotype of this species, is a sterile specimen in poor condition consisting of two leafless twigs and five detached leaves, probably coming from an adventitious shoot since one twig is extremely pubescent. The conspicuous development of the pubescence can be matched on the collection *Lützelburg 295* in the Munich herbarium. The label states that this collection came from a tree 6 meters tall; however, the very large leaves, long internodes and copious pubescence all suggest abnormal or adventitious growth. Other flowering collections by Lützelburg cited below from the state of Ceará appear to be transitional in pubescence, size and shape of leaves and length of internodes.

Weddell described *Coccoloba polystachya,* being unaware of Casaretto's name. He saw a living specimen which was given a catalogue number, and he also cited the collection *"Martius 1242."* No specimens of the living plant appear to have been preserved, so the Martius collection may be taken as the type of *C. polystachya.* The specimens I have seen of *Martius 1242* bear female flowers and a sheet from Leningrad has the fragment of a sterile shoot, but there is no doubt that the Leningrad collection is the same as the more pubescent type of *C. mollis* Casaretto.

In 1855 in the *Flora Brasiliensis* Meisner published a treatment of the genus *Coccoloba.* He accepted *C. polystachya* Weddell and referred *C. mollis* Casaretto to the synonymy of Weddell's species, with a question. He cited specimens collected by Salzmann, Spruce and Weddell. The illustration given for this species is of a staminate plant and does not represent the type of either *C. mollis* or *C. polystachya.*

At the same time Meisner described a new species, *Coccoloba paniculata,* illustrated in two plates by staminate and pistillate plants. He cited an unnumbered collection by Pohl, the collection *Poeppig 2649,* and also *Martius 1242,* which Weddell had cited in the original description of *C. polystachya.* Meisner distinguished between *C. polystachya* and *C. paniculata* by the more abundant pubescence of the former.

In 1856 Meisner repeated for the *Prodromus* the description of the two species and, in addition, listed *Coccoloba polystachya* var. *mollis,* based only on *C. mollis* Casaretto and the collection *"Casaretto 80."* It is of interest to note that Meisner cited *Martius 1242* under both species, but indicated (with an exclamation point) only the citation of this collection as *C. polystachya.*

In 1890 Lindau recognized *Coccoloba polystachya,* with two varieties. *Coccoloba polystachya* var. *glabra* Lindau is based on *C. paniculata* Meisner, while *C. polystachya* var. *pubescens* Lindau is based on *C. mollis* Casaretto. Lindau noted that the varieties were based on the amount of pubescence and that intermediates were to be found.

Eyma (Meded. Bot. Mus. Utrecht 4: 4. 1932) recognized that the oldest name was *Coccoloba mollis* Casaretto and accepted this, including with it *C. polystachya* Weddell and *C. polystachya* var. *pubescens* Lindau. Eyma did not treat *C. paniculata* Meisner or *C. polystachya* var. *glabra,* thus implying his acceptance of them. Macbride's treatment of the genus for the Flora of Peru (Publ. Field Mus. Bot. 13: 460. 1937) appears to be based on the work of Eyma, although no reference is given. I have seen only a few of the specimens cited by Eyma. In general the specimens from French and Dutch Guiana have a different aspect in the texture of the leaves and the color of the pubescence. Moreover, the petioles and branches of the inflorescence tend to be longer. The plants from this area may represent a geographic race, or perhaps even a distinct species. Additional material is needed for an understanding of the conditions seen in these plants.

One collection of Krukoff from the Basin of the Rio Solimoes, also, is difficult to fit into the general pattern of *Coccoloba mollis.* This collection, *Krukoff 8841,* has leaves of still different texture and in this case the branches of the inflorescence are short, resembling those of *Coccoloba dugandiana.* The collection is in fruit and the samples opened, all sterile and hollow, are strongly triangular in outline and section. The lobes of the perianth are appressed against the apex, rather than coronate, as in the few fruits seen of typical *Coccoloba mollis.* At present the collection does not merit description as a new species.

I have not accepted the glabrous variety created by Lindau, since additional field study of this species is needed to understand the variation in pubescence with the age and habit of the plant. The species seems clearly dioecious, the pistillate plants appearing to be more pubescent than the staminate plants. Collections made from the coastal areas are also more pubescent than those from inland stations in South America. The shape of the leaf, particularly the base, and the length of the petiole are extremely variable in the specimens cited. The species is easily recognized, since so few species of *Coccoloba* have paniculate inflorescences; however, no existing description is adequate. I sincerely hope that some botanist in an area where this plant grows can make the necessary study of variations in *C. mollis.*

Bolivia. SANTA CRUZ: Sara, Bosques de Buenavista, *Steinbach 6563* (A). Without specific locality: Yungas, *Bang 299* (G, GH, K, LE, M, NY).

Brazil. ACRE: Rio Macauhan, *Krukoff 5550* (A, M, NY); Seringoel Auristella, *Ule 9346* (G, K). AMAZONAS: Ega, *Poeppig 2649* (B, LE); São Paulo de Olivença, Palmares, *Krukoff 8314, 8337* (A, BR, LE, NY), *8841* (A, BR, NY); Humayta near Tres Casas, *Krukoff 5550* (A, M, NY). BAHIA: Camapuan, *Riedel 628* (A, LE); Itaparica, *Casaretto s.n.* (TO–holotype); São Bento das Lages *Lützelburg 295* (M). CEARÁ: Barxa d'Anta, *Lützelburg 26278* (M); Grangeiro, *Lützelburg 25800* (M, W), *25838* (M); Soure, *Drouet 2377* (GH); without specific locality, *Gardner 1828* (NY). GOYAZ: Rio dos Alnas, *Glaziou 21980* (A, LE); Tocantinopolis, *Pires & Black 1650a* (US); without specific locality, *Burchell 7351–2* (GH). MARANHÃO: Loreto, *Snethlage 656* (F); Maracassumé River, *Froes 1811* (A, NY). MATTO GROSSO: Cuyabá, *Martius 1242* (M–holotype of *C. polystachya*, BR, LE, NY). MINAS GERAES: Paracatu, *Riedel s.n.* (LE). PARÁ: Barra do Rio Negro, *Spruce s.n.* (Oct. 1850) (B, GH, LE, M, NY); Cassipa, Tapajos River region, *Krukoff 1246* (A, NY). PERNAMBUCO: Tapera, *Pickel 2483* (GH). PIAUHY: Urussuhy, *Snethlage 633* (F). RIO DE JANEIRO: Without specific locality, *Burchell 5912* (GH). Locality not specified: *Pohl s.n.* (BR, M, NY). **Dutch Guiana.** Bradilifi, Matoela, *Stahel 189* (A); Zanderij I., *Herb. Surinam 189* (NY), *4903* (A, NY). **Ecuador,** MANABI: El Recreo, Balao, *Eggers 14497* (A, B, LE, M), *15675* (GH, K, LE, M, NY). **French Guiana.** Godebert, *Wachenheim s.n.* (A); without locality, *Melinon 106* (A). **Peru.** LORETO: Florída, Río Putumayo at mouth of Río Zubineta, *Klug 1991* (A, GH, NY); Río Santiago, *Tessmann 4372* (NY); Middle Ucayale, *Tessmann 3195* (NY).

Coccoloba monoica Ruiz ex Meisner, DC. Prodr. **14**: 149. 1856.

Meisner cited this name in synonymy as "*Coccoloba monoica* fl. peruv. Ruiz" and recorded seeing a specimen in the Berlin herbarium. Lindau (Bot. Jahrb. 13: 220. 1890) apparently saw the authentic material, since he referred the epithet to synonymy under *Muhlenbeckia tamnifolia* var. *laxiflora* Meisner. The type specimen was not located during a brief search in the Berlin herbarium several years ago.

Coccoloba morongii Hassler, Repert. Sp. Nov. **14**: 162. 1915.

This was a new name, provided by Hassler for *Coccoloba microphylla* Morong (1893), not *C. microphylla* Griseb. (1866). The species is to be placed in the synonymy of *C. paraguariensis* Lindau.

Coccoloba moritziana Klotzsch ex Meisner, Fl. Bras. **5**(1): 28. 1955.

Meisner published this epithet in the synonymy of his new *Coccoloba moritzii* var. *opaca* and reported that he found the manuscript name in the Berlin herbarium. I have not been able to locate such a specimen, although Lindau (Bot. Jahrb. **13**: 216. 1890) referred the name to the synonymy of *C. ovata.*

Coccoloba moritzii Meisner, Fl. Bras. **5**(1): 28. 1855.

Coccoloba moritzii var. *opaca* Meisner, *ibid.*
Coccoloba moritzii var. *lucida* Meisner, *ibid.*

Lindau (Bot. Jahrb. **13**: 216. 1890) has referred this species and its varieties to the synonymy of *Coccoloba ovata*. The difficulty in typifying these names will be discussed under *C. ovata*. On the basis of the material I have seen, I believe Lindau's action to be correct. In the original publication Meisner attributed the name *Coccoloba moritzii* to Klotzsch and cited in the synonymy of *C. moritzii* var. *opaca* the manuscript name *Coccoloba moritziana* which he found in the Berlin herbarium. I have not been able to find the name published in any of Klotzsch's writings.

Coccoloba mosenii Lindau, Bot. Jahrb. **13**: 173. 1890, *"Moseni."*

Coccoloba fastigiata var. *glabrata* Meisner, Fl. Bras. **5**(1): 34. 1855.

This species represents a climbing plant with the leaves borne on short lateral branches. The leaf blades have a characteristic shape, oblong-obovate to nearly lanceolate-obovate. The range of variation in habit, as well as in shape of leaf cannot be determined from the few specimens on hand. Additional material is needed for further study. The basis for the proper assignment of *Coccoloba fastigiata* var. *glabrata* to synonymy here has been discussed under that epithet.

Brazil. SÃO PAULO. Santos Lorosocaba, *Mosen 3458* (s–lectotype, B, G, P), *Loefgren 10432* (M). Without definite locality, *Burchell 3844* (P).

Coccoloba nigra Fawcett & Rendle, Jour. Bot. **51**: 123. 1913; Fl. Jamaica **3**: 120. 1914; Howard, Jour. Arnold Arb. **38**: 106. 1957.

As I have discussed in an earlier paper, Fawcett and Rendle based this species on a collection annotated "Jamaica," but without the collector's name or number. The type in the Edinburgh herbarium has been studied, and it is certainly a fragment of *Schomburgk 531*, the type of *Coccoloba ovata*, from British Guiana. A specimen of the Schomburgk collection is also in the Edinburgh herbarium and the two sheets match, even to the lichens on the branches. The name *Coccoloba nigra* must therefore be assigned to the synonymy of *C. ovata* Bentham.

Coccoloba nitida HBK. Nov. Gen. **2**: 176. 1818.

Coccoloba microneura Meisner, DC. Prodr. **14**: 163. 1856.

In the eighth paper of this series (Jour. Arnold Arb. **41**: 41–42. 1960), I corrected an earlier mistake and correctly defined *Coccoloba nitida* as a species currently known only from Colombia. A lectotype (*Humboldt 1627*) was designated in the Paris herbarium. It was collected at San Bartholome on the Río Magdalena.

Coccoloba microneura is clearly the same species and was described from the Purdie collection, without number, from Santa Marta, Colombia.

Coccoloba nivea Jacquin, Hist. Stirp. Am. 115. *pl. 78*. 1763.

Several modern writers on South American vegetation have used this epithet without citing specimens which can be identified. *Coccoloba nivea* Jacq. is a synonym of *C. venosa* L. (1759), and specimens from South America will be cited under that name. Schomburgk referred to *Coccoloba nivea* under cultivation in his *Flora and Fauna of British Guiana.*

Coccoloba novogranatensis Lindau, Bot. Jahrb. **13**: 192. 1890; Howard, Jour. Arnold Arb. **41**: 40. 1960.

I have referred this species to the synonymy of *Coccoloba coronata* Jacq. (*q.v.*). In an earlier paper (Jour. Arnold Arb. **40**: 85–86. 1959) I selected as a lectotype one sheet of the collection *Triana 978* in the herbarium of the Muséum d'Histoire Naturelle, Paris. The Triana collection was made between Anapoima and Apulo, Prov. Bogotá, Colombia.

Coccoloba nutans HBK. Nov. Gen. **2**: 175. 1818.

Authentic material of this species indicates that the specific name was proposed by Kunth. The original description is brief and reflects the inadequate and immature condition of the specimens. Ocreae are not present on the stems and the inflorescence, described as nutant, is immature or abortive. Meisner (DC. Prodr. **14**: 155. 1856.) repeated the original description, with minor changes, and reported, "Species non satis nota, nec in herb. Kunth, nec in Willdenowiano extans." Lindau attributed the collection to Bonpland and cited from the Berlin herbarium a specimen which consists of one detached leaf and the fragment of an inflorescence 2 cm. in length. These fragments were obtained from the Paris herbarium. I have been able to examine the original collection in Paris which is, in turn, from the Bonpland herbarium. It currently consists of a short stem, without ocreae, and is broken at both ends. A single recurved lateral inflorescence having very immature flower buds is present. Poor though it is, this collection must be designated as the holotype.

No recent collections have been assigned to this species. Macbride, who treated the genus for the Flora of Peru, saw no material. However, I believe that two of the collections he cited under *Coccoloba sphaerococca* are more properly placed in the present species. A collection, *Killip and Smith 29027* (NY), made at Yurimaguas on the lower Río Huallaga, Dept. Loreto, Peru, consists of the stem and leaves of a woody vine. One detached leaf is comparable to that of the Bonpland collection. Additional smaller leaves are present, but resemble the leaves of *Coccoloba ascendens.* Although Kunth did not record the height or habit of *Coccoloba nutans* in the original description, Meisner, Lindau and Macbride have referred to the plant as a tree. I believe that they are in error and that *Coccoloba nutans* is a woody vine usually with coriaceous, elliptical leaves rounded at the base, but that occasionally on vigorous shoots the oblong-obovate leaves with subcordate bases are produced. The species is similar to *Coccoloba ascendens,* but additional material is required for a proper understanding of the species.

Killip and Smith 27958 and *29027* and that of *Llewelyn Williams 3805*, assigned in various herbaria to *Coccoloba peltata* Schott and *Coccoloba sphaerocarpa* Lindau, appear to be *C. nutans*.

Coccoloba nymphaeifolia Schenk in Zittel, Handb. Palaeont. **2**: 491. 1887; Lindau, Bot. Jahrb. **13**: 181. 1890.

Schenk used the name *Coccoloba nymphaeifolia* in comparing fossil leaf material to living species. At that time a plant called *Coccoloba nymphaeifolia* was under cultivation in the Leipzig botanical garden. A single leaf is preserved in the Berlin herbarium and bears the annotation, "*Coccoloba nymphaeifolia* de Jonge, H. Lips. Brazil." Lindau correctly referred this specimen and name to the synonymy of *C. peltata* Schott. The epithet *C. nymphaeifolia* is a *nomen nudum*.

[*To be concluded*]

LEAF VENATION AND PUBESCENCE IN THE GENUS RAOULIA (COMPOSITAE)

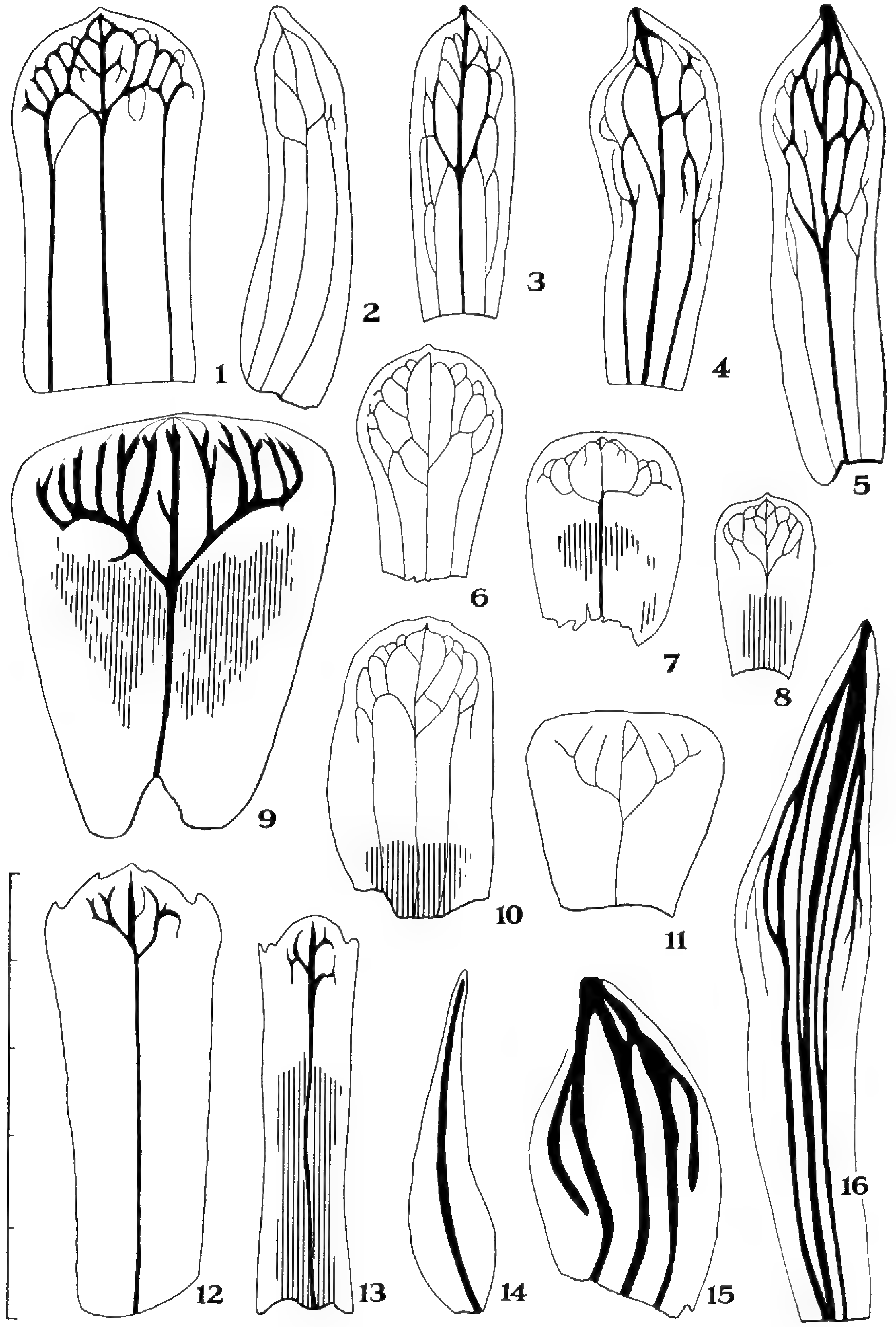
OTTO T. SOLBRIG [1]

MODERN DICOTYLEDONS are characterized by a highly diversified pattern of reticulate foliar venation, and true open venation is a rare occurrence. The persistence of presumably primitive dichotomous open venation in *Kingdonia* (Ranunculaceae?) and *Circaeaster* (Ranunculaceae?, Circaeasteraceae?) as shown recently by Foster (1959a,b) suggests that reticulate venation has probably evolved from dichotomous venation. On the other hand, species of the genus *Raoulia* provide an example of an "open" venation which is derived, rather than primitive. Since the venation of *Raoulia* has not been studied in detail previously, the present investigation is an attempt to provide further data which may contribute both toward a better understanding of the complicated picture of venation in angiosperms and toward a more natural classification of the genus *Raoulia* itself.

Raoulia comprises a group of specialized plants which are typically found in dry, rocky habitats between sea level and 2000 meters in both the North and South Islands of New Zealand (to which the genus is restricted, with one possible exception in New Guinea). The habit varies from small, compact, creeping or tufted herbs to small or large cushion-forming plants of the type commonly known as "vegetable sheep." The genus belongs to the family Compositae, tribe Inuleae, subtribe Gnaphaliinae, a taxonomically difficult subtribe in which limits of genera are not always very clear. Within the group *Raoulia* is, in fact, defined as much by its habit and geographical distribution as by any qualitative character (Cheeseman, 1925). As treated by both Beauverd (1910, 1912) and Cheeseman (1925), the genus is composed of 21 species grouped into two subgenera. These are further divided into two and three sections respectively, according to involucral and foliar characters. Material of seventeen species including representatives of each of the sections has been available for study. In the discussion which follows the nomenclature is that of Beauverd.

---

[1] This investigation was suggested by Dr. Adriance S. Foster, who also encouraged and advised the author during its course. Sincere thanks are expressed for all the invaluable help received. Dr. John Rattenbury of Aukland University College, New Zealand, supplied dried material, and the University of California Botanical Garden grew and supplied living material of some species. Drs. Foster, Sherwin Carlquist, Lincoln Constance, and Carroll E. Wood kindly read the manuscript and made various suggestions. Finally, the help of the directors and curators of the Gray Herbarium (GH), the Arnold Arboretum (A), and the University of California Herbarium (UC) for allowing the use of herbarium material in their custody is acknowledged.



FIGS. 1–16. Leaf venation of species of *Raoulia*. Veins in black, mesophyll sclereids in longitudinal hatching. Differences in width of veins due to sclerenchyma. Each division of scale = 1 mm. 1, *Raoulia Petriensis* Kirk (*Cheeseman s.n.*, GH); 2, *R. glabra* Hook. f. (*Cheeseman s.n.*, GH); 3, *R. subsericea* Hook. f. (*Petrie 193*, GH). 4, *R. tenuicaulis* Hook. f. (*Kirk s.n.*, GH); 5, *R. Monroi*

MATERIAL AND METHODS

Most observations were made from dried herbarium specimens, for only two species, *Raoulia glabra* and *R. australis*, could be studied from living material. The leaves, bracts and flowers of all available species of *Raoulia* were cleared according to the technique of Foster (1955; see also Arnott 1959). In order to extract some dark material which remained after treatment with sodium hydroxide and chloral hydrate, leaves were bleached in a 50% solution of "Clorox" until reasonably clear, usually about five minutes, and then thoroughly washed to assure good subsequent staining. The leaves and stems of certain species of *Raoulia*, especially the cushion-forming ones, are heavily impregnated with tannins and other dark-staining substances. In order to remove these, long treatment with sodium hydroxide and "Clorox" is needed which damages the leaves or makes them so brittle that they disintegrate when the heavy coat of hairs is removed. Therefore, the clearing process often had to be interrupted as soon as a reasonably good view of the venation was obtained.

Both surfaces of the leaves of all species of *Raoulia* are covered with a thick layer of long trichomes which entirely cover the leaf and which it was necessary to remove in order to study the venation. This was done by "shaving" the hairs off with a sharp scalpel after the leaves had been cleared and dehydrated. The smallness of the leaves (less than one centimeter in every case) and their fragility made this operation a tedious, time-consuming, and "nerve-shattering" operation and resulted, in spite of extreme care, in a high degree of tearing of the leaves.

OBSERVATIONS AND RESULTS

Leaf shape. The leaves of all species of *Raoulia* are small. The size of the mature leaves varies from 3 mm. in leaves of *R. lutescens* and *R. Goyenii* to nearly 8 mm. in *R. grandiflora*. Most species have leaves of 4–5 mm. in length.

In general, the leaves are appressed to the shoots. The degree to which they are appressed varies greatly and is correlated with the general habit of the plant. In such creeping species as *R. glabra* or tufted ones as *R. grandiflora*, the leaves are appressed to the shoot only at their bases and are curved outward above. In these cases the leaves are somewhat keeled and divergent. The leaves of these species are generally broadly linear-lanceolate or subulate and are usually longer than the average for the genus.

Hook. f. (*Kirk s.n.*, GH); 6, *R. Parkii* Buchanan (*Anderson 171*, GH); 7, *R. bryoides* Hook. f. (*Cheeseman*, 1911 GH); 8, *R. lutescens* Beauverd (*Anderson 106*, GH); 9, *R. Buchananii* Kirk (*Cockayne 7041*, A); 10, *R. australis* Hook. f. (*Kirk s.n.*, GH); 11, *R. Goyenii* Kirk (*Kirk s.n.*, GH); 12, *R. eximia* Hook. f. (*Cockayne 7048*, GH); 13, *R. mammillaris* Hook. f. (*Kirk s.n.*, GH); 14, *R. subulata* Hook. f. (*Petrie 149*, GH); 15, *R. Hectorii* Hook. f. (*Petrie 203*, GH); 16, *R. grandiflora* Hook. f. (*Petrie*, 1889, GH).

On the other hand, in the cushion-forming species, such as *R. bryoides* or *R. rubra*, the leaves are very much crowded in a tightly appressed spiral, with the lower leaves covering most of the outer surface of those lying above. The leaves are rather flat, not keeled, and usually rectangular or nearly rectangular in shape.

Aside from these two types, there are some intermediate ones, which are correlated with intermediate habit of growth (see TABLE I).

Venation. Three main types of venation can be distinguished in *Raoulia*: the reticulate type (I), with three main veins; the semireticulate (II), with either three or more frequently one main vein; and the striate type (III).

I. RETICULATE TYPE. The basic type is represented by *Raoulia Parkii* (FIG. 6). Three main veins enter the leaf base from the stem. The midvein branches two or three times and these branches in turn form lateral branches which anastomose with the two lateral veins, forming a simple reticulum. The following species can be arranged in a progressively simpler series. In *R. tenuicaulis* (FIG. 4) some of the secondaries do not connect and the leaf presents a "semiopen" pattern. *Raoulia Monroi* (FIG. 5) is very similar in venation to *R. tenuicaulis*. In *R. subsericea* (FIG. 3), the reduction is a little more accentuated: the laterals are less well marked, and the connections between the central and the lateral veins are usually unbranched. Some lateral open veinlets occur in this species. Finally, in *R. glabra* (FIG. 2) there are a main and two lateral veins with three to four connecting veins, and an occasional freely terminating veinlet. The pattern in *R. glabra* is scarcely reticulate.

II. SEMIRETICULATE TYPE. This type is not so clearly delimited as the preceding one, and, although a linear reduction series can be inferred, a subdivision into loosely connected subgroups (indicated by the letters a, b, c, and d) is probably more significant.

a. *Raoulia australis* (FIG. 10) and *R. Petriensis* (FIG. 1) have three main veins, which run unbranched for about three-fourths of the length of the leaves. These veins then branch forming a coarse meshwork with some unconnected veinlets. In *R. australis* the secondaries are relatively fewer than in *R. Petriensis*. These two species are the only ones of this type with three main veins and form a link with the plants of the preceding type, particularly with *R. Parkii*, from which the leaves do not differ greatly.

b. *Raoulia lutescens* (FIG. 8) and *R. bryoides* (FIG. 7) have basically the same or a similar arrangement of the end veinlets as *R. australis*, but, instead of three main veins, they only have a midvein running the length of the leaf. Two open veinlets which point towards the base of the leaf at each side, of the terminal reticulum seem to indicate arrested stages in the development of the two lateral veins, a situation similar to that in *Minuartia aretioides* (Caryophyllaceae) (Troll 1938, pp. 1085, 1086). Whether these veins have disappeared through reduction, or whether this is an indication of a first stage in development, cannot be answered with certainty. However, the increasing specialization in other features of the plant, correlated with the simple leaf venation in this type, indicates that a reduction series is the more likely possibility.

c. *Raoulia Buchananii* (Fig. 9), *R. Goyenii* (Fig. 11), and *R. rubra* (Fig. 24), in this order, show an increasing simplification in the pattern described in the above paragraph. The noteworthy features here are that there is no indication of vestigial lateral traces, and that the ultimate veinlets are dichotomously branched and terminate freely without anastomosing. The maximum degree of simplification is evident in *R. rubra*.

d. *Raoulia mammillaris* (Fig. 13) and *R. eximia* (Fig. 12) also have an extremely simple venation which consists in these species of the midvein and, toward the tip of the leaf, two or three secondaries, which may or may not bifurcate in turn. A very interesting feature is that the midvein and the secondaries are very oddly shaped and enclosed by a sheath of sclereids.

III. Striate type. Three species are of this type which is apparently not connected with the other two types. *Raoulia grandiflora* (Fig. 16) has the most elaborately developed venation of the three species. Three main veins enter the leaf. (Sometimes two of them are anastomosed at the very base of the leaf. Whether this indicates a possible one-trace condition at the node is not known.) The midvein bifurcates once or twice, the branches running parallel and finally anastomosing with the lateral veins towards the tip of the leaf. The lateral veins sometimes bifurcate, the branches of this division running parallel and then uniting again to form an elliptical loop. All three main veins meet at the tip of the leaf. One or more backward-pointing open veinlets are usually present at each side of the lateral veins. Short strands of vascular tissue unconnected with the system of veins are sometimes present. In *R. Hectorii* (Fig. 15) the pattern is essentially the same but much reduced, since usually neither the midvein nor the lateral veins branch. In *R. subulata* (Fig. 14) there is only a single unbranched midvein, the laterals having disappeared. The unique feature, aside from the venation, which unites these three species, is the extreme width of the vascular bundles which are covered by a thick sheath of sclereids.

Sclerenchyma. The leaves of *Raoulia* present always a strong development of sclereids. This is more evident in the older leaves, in which may also be found parenchyma cells (and even epidermal cells) with thickened, lignified walls and forming a sheet that can occupy up to two-thirds of the leaf surface.

The development of sclerenchyma fibers surrounding the vascular bundles varies from species to species. In *R. glabra* there is a relatively small development, but sclerenchyma usually forms an enveloping sheath at least as thick as the bundle proper. In the species with a striate type of venation (*R. grandiflora*, *R. Hectorii* and *R. subulata*) the development of a sheath of sclerenchyma fibers around the bundles is particularly notable (FIGS. 14–16). Still, in other species, such as *R. Buchananii, R. eximia,* and R. *mammillaris* irregularly shaped sclereids are associated with the vascular bundles, particularly towards the end of the veins (FIGS. 9, 12, 13). These sclereids account for the irregular diameter and shape of the bundles. In some species with "open" venation (e.g., *R. Buchananii*) the tip of the bundles may be totally devoid of sclereids.

Sclereids are also present sometimes in the mesophyll. In these cases they are elongated polygonal cells with thickened walls. They are particularly prominent in *R. Petriensis, R. bryoides,* and *R. Buchananii* (FIGS. 1, 7, 9), where they are present in very young leaves. Nevertheless, in most species some mesophyll sclereids are present, particularly in older leaves.

Mesophyll sclereids usually form a broad sheet at each side of the midvein in the lower and middle portion of the leaf. They may also be present in isolated groups or forming small patches. The exact position of these sclereids is unpredictable in any particular leaf, but they are never present in the upper fourth of the lamina.

Trichomes. As already mentioned, the surface of the leaves is covered by a thick cap of trichomes. These are long, uniseriate, multicellular hairs, of a type occurring commonly in Compositae (Metcalfe and Chalk, 1950). The type of hair is the same in all species, but there are differences in the general appearance and distribution of hairs on the leaf surface. The genus can be divided into two groups of species: 1) those which have their leaves covered by a thick layer of tightly interwoven trichomes forming a felt-like cap; 2) those that have their leaves with a cover of more or less straight and somewhat stiff hairs that usually point towards the apex of the leaves. Finally, *Raoulia subulata* has glabrous leaves, whereas *R. glabra* has only a few and widely spaced hairs on the leaf surfaces. Species of the first type usually have the entire leaf surface covered with a thick cap of interwoven hairs which may be as thick as or thicker than the leaf tissues proper. On the other hand, the species which have hairs of the "stiff" type, have these concentrated on the apical end and usually more densely on the adaxial surface in this region. These differences can be correlated with the pattern of apical growth. The species with "interwoven" hairs have more elongated stems and reflexed leaves. On the other hand, the species with "stiff" hairs are true cushion plants. Their cauline leaves are numerous, imbricated, and closely appressed. As a consequence, only the upper third of the leaf is exposed.

DISCUSSION

Raoulia leaves present some of the few instances of open venation in dicotyledonous angiosperms. Although an open dichotomous venation is considered primitive in gymnosperms and vascular cryptogams, this condition is undoubtedly secondary and derived in *Raoulia*, as already pointed out by Troll (1938).

That this is so can be inferred from two sets of facts: 1) the correlation of open venation with specialization in other features of the plant; 2) the entirely different typology of the venation of *Raoulia* and of a typically primitive dichotomous venation as found in some gymnosperms and vascular cryptogams or in the primitive angiosperm *Kingdonia uniflora* (Foster 1959b). Further evidence is to be found in the venation of *Ewartia*, undoubtedly the genus closest to *Raoulia* (Beauverd 1910). The venation of both species of *Ewartia* investigated, *E. catipes* (FIG. 26) and *E. nubigena* (FIG. 25), is reticulate and of a type similar to that of *Raoulia Parkii*, although more elaborate. Since other *Gnaphaliinae*, including *Gnaphalium* itself, have a venation along the same lines as that of *Ewartia*, it may be concluded that the venation of *Raoulia* is atypical and specialized.

At this point it may be of interest to see how the venation of *Raoulia* compares with that of *Kingdonia uniflora*, believed to be truly primitive (Foster 1959b). The nodal anatomy of *Raoulia* is not known, but the vascular supply of the leaf is formed by one to three traces. *Kingdonia* has a unilacunar node, with four bundles (two of which may appear as double strands) forming the vascular supply of the foliage leaf. More significant still is the total venation pattern. The veins in *Kingdonia* are dichotomously branched, the forks of the branches extending usually into the tips of the dentations. Occasional anastomoses, as well as "blind" endings unrelated to the dentations are not uncommon, but in general the pattern is quite regular and symmetric. In contrast with this, the pattern in *Raoulia*, even in those species with a very simple and "open" venation (e.g., *R. eximia* or *R. rubra*), is irregular, and of a type altogether different. While *Kingdonia* has a dichotomous venation, *Raoulia* has a branching pattern with does not follow any regular established system. This is probably due to the connection of the "open" venation of *Raoulia* with the extreme reduction in the lamina and its derivation from a reticulate type. The "open" situation when present is possibly the result of arrested growth of the veinlets. In contrast, the regularity of the "open" venation in *Kingdonia* is the consequence of the full development of the leaf along an established pattern.

It is interesting to note that in *Kingdonia* and in at least one species of *Raoulia* (*R. grandiflora*) short strands of vascular tissue unconnected with the system of veins are found. The reason for this remains unexplained. The position of these strands and their occurrence are rather erratic in both species.

In brief we may say that, notwithstanding the fact that the types of venation present in *Raoulia* and *Kingdonia* have been sometimes classed together (Troll 1938), careful analysis reveals that they are very different. Not only is one clearly derived and the other probably primitive, but there are also differences in number of traces, branching pattern, and regularity of veinlets. This once more demonstrates the necessity for a detailed study of the totality of the venation in angiospermous leaves, as has been repeatedly emphasized by Foster (1950, 1952, 1959b).

From the morphological and anatomical point of view, the unique overall pattern of venation in *Raoulia* is of interest. No other group of species so far investigated shows a similar venation pattern.

The question of what determines the particular pattern of a leaf has occupied the attention of various workers, most of whom have tended to correlate "distribution of growth" with venation pattern. The corresponding bibliography has been reviewed critically by Foster (1952). The main conclusions which Foster draws from the literature are: 1) "that the 'distribution of growth' appears to vary widely in leaves, even between ones which are similar in form at maturity" and 2) "that the course of the main veins of the lamina 'registers' more or less faithfully the distribution of the longitudinal and transverse growth which occurred during ontogeny." Foster's own studies on *Quiina pteridophylla* show that this interpretation is rather "naive" and that intensive ontogenetic and comparative studies are needed before any major conclusion can be drawn. A similar conclusion is reached by Pray (1954) as a result of his studies on *Liriodendron*.

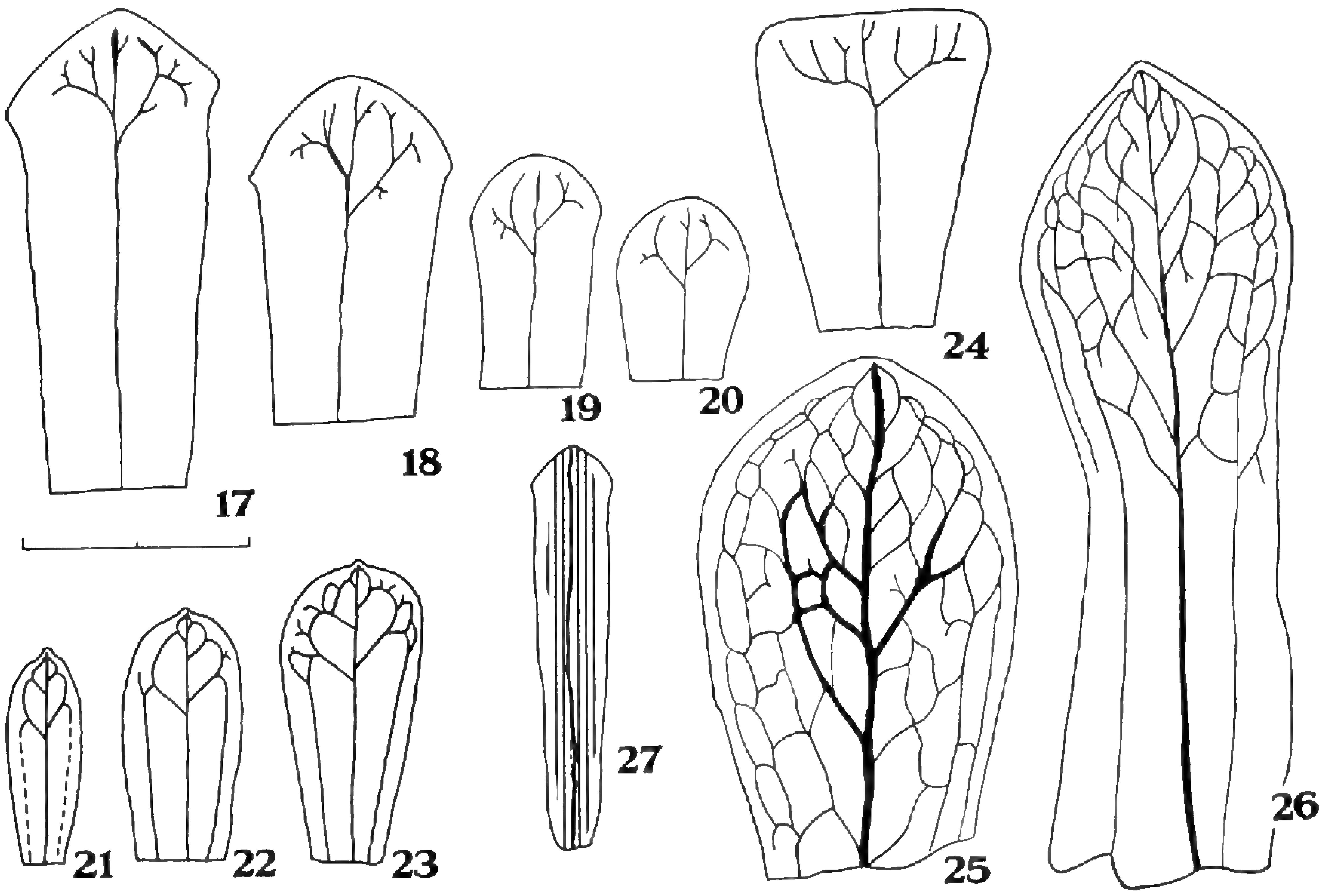
No juvenile material was available for this study, and the extremely small size of the leaves and their heavy coat of hairs militated against the successful examination of leaf primordia. Also, lack of fresh material and of sufficient dried herbarium material of critical species precluded the use of sections. Nevertheless, the few data obtained seem to indicate that the venation pattern is influenced by — among other causes, undoubtedly — the pattern of growth of the leaf, which is, in turn, determined to some degree by the general organography of the shoot.

In FIGURES 17–20 are depicted four successively smaller primordia of *Raoulia eximia* and in FIGURES 23–21 similar stages in leaves of *R. Petriensis*. Growth in width apparently takes place very early, while the primordium is very small (less than 2 mm.). At that time the pattern of the end "reticulum" is laid down and later growth in length has no important effect on it. A full interpretation will have to wait until more physiological and ontogenetical studies have been completed.

In brief, the venation types of *Raoulia* seem to be associated with the habit of the plant and the growth pattern characteristic of it. Simple venation types are correlated with extreme adaptive modification in other structures. A similar conclusion with respect to the node has already been pointed out by Bailey and Nast (1944).

It may be significant that the venation pattern of the leaves of *Raoulia* is similar to that found sometimes in involucral and receptacular bracts of other Compositae. Müller (1938) has made an extensive study of venation patterns in various types of phyllomes. She regards cataphylls, bracts, and perianth members as reduced structures corresponding to the bases of foliage leaves. Her evidence is the overall similarity of venation patterns in the various phyllomes in spite of differences in the nodal anatomy.

Post (1958) finds a similar situation in his investigations on the genera *Frasera* and *Swertia* (Gentianaceae). It might therefore be better from the morphological point of view to classify the foliage leaves of *Raoulia* as bracts, even though they carry the bulk of the photosynthetic activity. This points once more to the difficulty in defining the different types of phyllomes. The venation pattern in the involucral bracts of *Raoulia*, on the other hand, is similar in all species, consisting of a single vein which runs unbranched the entire length of the bracts (FIG. 27).



FIGS. 17–24. Leaf venation of species of *Raoulia*. Veins in black, differences in width due to sclerenchyma. Each division of scale = 1 mm. 17–20, Leaf primordia of *R. eximia* Hook. f. (*Cockayne 7048*, GH); 21–23, Leaf primordia of *R. Petriensis* Kirk (*Cheeseman s.n.*, GH); 24, *R. rubra* Buchanan (*Cranwell*, 1933, UC). FIGS. 25–26. Leaf venation of species of *Ewartia*. Veins in black, differences in width due to sclerenchyma. 25, *E. catipes* Beauverd (*Hooker*, 1839–43, GH); 26, *E. nubigena* Beauverd (*Von Müller s.n.*, GH). FIG. 27. Involucral bract of *Raoulia lutescens* Beauverd (*Anderson 106*, GH), showing midvein and sclerenchyma (hatching).

Finally, one should mention the probable application of the results of these investigations to the taxonomy of the group. TABLE I shows various characteristics of the species here considered.

The genus was divided by Beauverd (1912) into two subgenera, *Raoulia* (*Eu-Raoulia*) and *Psychrophyton*. This division, based mainly on characters of the pappus and number of flowers, is substantiated by the results of this study as far as the species here investigated are concerned. Subgenus *Raoulia* is composed of compact, semicreeping plants which grow between sea level and 1800 m. altitude. The leaves are lanceolate to oblong-lanceolate in shape. All species but one, *R. lutescens*, have three traces forming the vascular supply to the foliage leaf. The venation is either of the reticulate type or of the semireticulate type, but no species with "open" venation belongs to this subgenus. The pubescence is of the "interwoven" type, with exception of *R. glabra* which has very few hairs.

Most members of subg. *Psychrophyton* are true cushion plants from higher altitudes, usually above 1000 m., although *R. Goyenii* can be found at lower altitudes. *R. grandiflora*, *R. Hectorii* and *R. subulata* form small tufts, rather than appressed cushions. The leaf shape of species in subg. *Psychrophyton* is either oblong or subulate. The pubescence type is either straight, in the true cushion plants, or interwoven, in *R. grandiflora*, *R. Hectorii*, and *R. subulata*. These last three species have a striate venation, while the rest of the species of this subgenus investigated have a semireticulate venation with only one trace entering the leaf from the node.

TABLE I. **Characteristics of species of Raoulia.**

SPECIES	HABIT	ALTITUDINAL RANGE (meters)	LEAF SHAPE	PUBESCENCE TYPE	MAIN VEINS	VENATION TYPE
Subg. RAOULIA						
Parkii	semicreeper	750–1800	lanceolate	interwoven	3	I
tenuicaulis	semicreeper	0–1650	lanceolate	interwoven	3	I
Monroi	semicreeper	0–1150	lanceolate	interwoven	3	I
subsericea	semicreeper	300–1600	lanceolate	interwoven	3	I
glabra	semicreeper	0–1500	lanceolate	semiglabrous	3	I
australis	semicreeper	0–1600	lance-oblong	interwoven	3	IIa
Petriensis	semicreeper	1500	lance-oblong	interwoven	3	IIa
lutescens	semicreeper	300–1800	lance-oblong	interwoven	1	IIb
Subg. PSYCHROPHYTON						
bryoides	cushion	1200–2100	oblong	straight	1	IIb
eximia	cushion	1350–2000	oblong	straight	1	IIc
mammillaris	cushion	1300–2000	oblong	straight	1	IIc
Buchananii	cushion	1200–1600	oblong	straight	1	IId
Goyenii	cushion	400–1500	oblong	straight	1	IId
rubra	cushion	1500	oblong	straight	1	IId
grandiflora	tufted	1000–1800	lance-subulate	interwoven	3	III
Hectorii	tufted	1200–1800	subulate	interwoven	3	III
subulata	tufted	1200–2000	subulate	glabrous	1	III

Subgenus *Psychrophyton* was divided by Beauverd (1912) into three sections: *Uninerves*, those species with only one trace entering the leaf and a nontruncate leaf apex; *Truncatae*, species with truncate leaf apices, and *Trinerves*, species with three traces entering the leaf. As can be seen from the data of TABLE I, this is an artificial division. A more natural arrangement is to divide the subgenus into two groups: one including *R. grandiflora*, *R. Hectorii* and *R. subulata*, which share the tufted habit, the subulate or subulate-lanceolate leaves, the interwoven type of pubescence, and the striate venation; the other group comprising the cushion plants with oblong leaves, "straight" pubescence, and the semireticulate type of venation.

LITERATURE CITED

ARNOTT, H. J. 1959. Leaf clearings. Turtox News **37**: 192–194.

BAILEY, I. W., and CHARLOTTE NAST. 1944. The comparative morphology of the Winteraceae. IV. Anatomy of the node and vascularization of the leaf. Jour. Arnold Arb. **25**: 215–220.

BEAUVERD, M. G. 1910. Le genre *Raoulia* et trois genres nouveaux des Composées-Gnaphaliées de la flore océanienne. Bull. Soc. Bot. Genève **2**: 208–252.

———. 1912. Nouvelles recherches sur le genre *Raoulia*. *Ibid.* **4**: 41–55.

CHEESEMAN, T. F. 1925. Manual of the New Zealand Flora. Ed. 2. 1163 pp. Wellington, N. Z.

FOSTER, A. S. 1952. Foliar venation in angiosperms from an ontogenetic standpoint. Am. Jour. Bot. **39**: 752–766.

———. 1955. Comparative morphology of the foliar sclereids in *Boronella* Baill. Jour. Arnold Arb. **36**: 181–198.

———. 1959a. The Phylogenetic significance of dichotomous venation in angiosperms. Proc. IX Int. Bot. Congr. **2**: 119, 120.

———. 1959b. The morphological and taxonomic significance of dichotomous venation in *Kingdonia uniflora* Balfour F. et W. W. Smith. Notes Bot. Gard. Edinb. **23**: 1–12.

METCALFE, C. R., and CHALK, L. 1950. Anatomy of the dicotyledons. 2 vols. Clarendon Press, Oxford.

MÜLLER, EDITH. 1944. Die Nervatur der Nieder- und Hochblätter. Bot. Arch. **45**: 1–92.

POST, D. 1958. Studies in the Gentianaceae I. Nodal Anatomy of *Frasera* and *Swertia perennis*. Bot. Gaz. **120**: 1–14.

PRAY, T. 1954. Foliar venation in angiosperms. I. Mature venation of *Liriodendron*. Am. Jour. Bot. **41**: 663–670.

TROLL, W. 1938. Vergleichende Morphologie der höheren Pflanzen. 1(2): 1044–1094. Berlin.

GRAY HERBARIUM,
HARVARD UNIVERSITY.

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

KENNETH A. WILSON

MYRTACEAE Jussieu (MYRTLE FAMILY)

Shrubs or trees with simple, opposite or alternate, coriaceous, glandular-punctate, exstipulate leaves, often with a continuous intramarginal vein. Inflorescence cymose, racemose, or paniculate or the flowers solitary. Flowers complete, regular, 4- or 5-merous. Calyx 4- or 5-lobed, distinct, or undivided in the bud and splitting irregularly in anthesis, or falling off as a calyptra. Petals 4 or 5 (attached at the apex of the hypanthium) or wanting. Stamens numerous, free or united into 5 bundles, the versatile anthers with gland-tipped connectives. Style and stigma 1, the ovary inferior, (1)2–5-locular, each locule with 2–many ovules. Fruit a 1–many-seeded berry or a many-seeded capsule. Embryo variously shaped.

A family of about 80 genera and 3000 species, primarily of the tropics of both hemispheres. The glandular-punctate leaves, inferior ovary, and numerous stamens usually are distinctive. Two subfamilies based primarily on the nature of the fruit generally are recognized: the Leptospermoideae, centered in Australia, are characterized by dry, dehiscent fruits; the Myrtoideae (with the single tribe, Myrteae) have fleshy, indehiscent fruits and occur in the tropics of both Old and New Worlds. The latter is divided into three subtribes based on the structure of the embryo. Subtribe Myrciinae Berg (cotyledons foliaceous, twisted and folded; the radicle elongate) is represented in our area by *Calyptranthes*. Subtribe Eugeniiae Berg (cotyledons fleshy, distinct, partly or completely fused, or conferruminate (closely adherent); the radicle very short) includes *Eugenia* and *Myrcianthes*, as well as the large Old World genus *Syzygium*. Subtribe Pimentinae Berg (cotyledons very short; embryo spiral or curved; radicle elongate) is represented in our flora by *Myrtus*, *Psidium*, and *Rhodomyrtus*.

---

[1] Prepared for a biologically oriented generic flora of the southeastern United States, a joint project of the Arnold Arboretum and the Gray Herbarium made possible through the support of George R. Cooley and the National Science Foundation, and under the direction of Reed C. Rollins and Carroll E. Wood, Jr. The scheme follows that outlined at the beginning of the series (Jour. Arnold Arb. **39**: 296–346. 1958). Other published portions of these studies will be found in Jour. Arnold Arb. **40, 41.** 1959, 1960. I am grateful to Rogers McVaugh who generously offered many comments and suggestions in connection with this family. I am also indebted to Leonard J. Brass, George R. Cooley, and Richard A. Howard for their aid in obtaining specimens and their help in various other ways.

Generic distinctions are difficult in the family, and, as a result, many different classifications have been proposed. Great emphasis has recently been placed on the structure of the embryo in determining various taxonomic groupings. Evidence from anatomy and pollen morphology has been used in connection with generic problems.

The inflorescence of the Myrtaceae is very variable and has been interpreted as resulting from various modifications of a potentially floriferous branch which develops in the axil of a leaf. The majority of the Myrtaceae which have been studied have a diploid chromosome number of 22.

Representatives of at least *Eucalyptus* L'Her., *Callistemon* R. Br., *Syzygium* Gaertn., *Feijoa* Berg, and *Myrciaria* Berg are cultivated in Florida as ornamentals or for their fruits.

REFERENCES:

ANDREWS, E. C. The development of the natural order Myrtaceae. Proc. Linn. Soc. New S. Wales **38**: 529–568. 1913. [On the origin and distribution of the Myrtaceae.]

ATCHISON, E. Chromosome numbers in the Myrtaceae. Am. Jour. Bot. **34**: 159–164. 1947. [Includes all previously recorded chromosome numbers.]

BARANOV, P. A. Coleorrhiza in Myrtaceae. Phytomorphology **7**: 237–243. 1957 [1958].

BERRY, E. W. The origin and distribution of the family Myrtaceae. Bot. Gaz. **59**: 484–490. 1915.

BROGLI, B. Beiträge zur Anatomie der Myrtaceen Rinden. Thesis, Basel, 84 pp. 1926.*

BUSWELL, W. N. Florida myrtles. Am. Bot. **35**: 138–143. 1929. [General descriptions and notes on the cultivated and native species, with some comments on their economic value.]

INGLE, H. D., and H. E. DADSWELL. The anatomy of the timbers of the southwest Pacific area. III. Myrtaceae. Austral. Jour. Bot. **1**: 353–401. 1953. [Includes some American species.]

KAUSEL, E. Beitrag zur Systematik der Myrtaceen. Ark. Bot. II. **3**: 491–516. 1956. [Proposes a classification of the Myrtaceae on the basis of characters of the seed and embryo, and describes 5 new genera.]

———. Myrtaceae. Inst. Paran. Catal. Gên. **28**: 1–4. 1957. [List of genera and synonyms of the Myrtaceae, excluding the "Leptospermaceae."]

MCVAUGH, R. Nomenclatural notes on Myrtaceae and related families. Taxon **5**: 133–135, 162–167. 1956.

———. Tropical American Myrtaceae. Notes on generic concepts and descriptions of previously unrecognized species. Fieldiana Bot. **29**: 145–228. 1956. [Includes a study of the inflorescence.]

———. Myrtaceae. *In* Flora of Peru. Field Mus. Nat. Hist. Bot. **13**(4^2): 569–818. 1958. [The most recent revisionary study.]

MAURITZON, J. Contributions to the embryology of the orders Rosales and Myrtales. Lunds Univ. Årsskr. II. Sect. 2. **35**(2): 1–120. 1939.*

MENNINGER, E. A. The cultivated eugenias in American gardens. Natl. Hort. Mag. **38**: 92–104, 145–164. 1959. [Species of *Syzygium*, *Acmena*, *Eugenia*, *Myrceugenia*, *Myrciaria*, *Pimenta*, *Myrcianthes*, and *Myrtus*, both native and introduced; includes excellent photographs.]

MOWRY, H., L. R. TOY, and H. S. WOLFE. Miscellaneous tropical and subtropical Florida fruits. Revised by G. D. Ruehle. Fla. Agr. Ext. Serv. Bull. **156A**: 1–116. 1958. [Includes species of *Eugenia*, *Feijoa*, *Myrciaria*, *Psidium*, *Rhodomyrtus*, and *Syzygium*.]

NIEDENZU, F. Myrtaceae. Nat. Pflanzenfam. III. **7**: 57–105. 1893.

PIKE, K. M. Pollen morphology of Myrtaceae from the south-west Pacific area. Austral. Jour. Bot. **4**: 13–53. 1956. [Includes some American species.]

SMITH-WHITE, S. Cytological studies in the Myrtaceae. II. Chromosome numbers in the Leptospermoideae and Myrtoideae. Proc. Linn. Soc. New S. Wales **73**: 16–36. 1948.

SOUBIHE SOBRINHO, J., and J. T. A. GURGEL. Characteristics of the seeds of fruit-producing Myrtaceae. Revista Agr. Piracicaba **27**: 83–90. 1952.* [In Portuguese.]

———. Polyembryony and adventitious embryony in citrus, *Mangifera* and fruit-bearing Myrtaceae. II. Dusenia **4**: 421–428. 1953.* [In Portuguese.]

STURROCK, D. Tropical fruits for southern Florida and Cuba and their uses. Publ. Atkins Inst. Arnold Arb. **1**: 1–131. 1940. [Myrtaceae, 81–92.]

WEBERLING, F. Untersuchungen über rudimentäre Stiplen bei den Myrtales. Flora **143**: 201–218. 1956.

KEY TO THE GENERA OF MYRTACEAE

A. Leaves alternate; inflorescence spicate; stamens united into 5 bundles; fruit capsular; bark white, spongy, peeling off in sheets. .... 1. *Melaleuca*.

A. Leaves opposite, inflorescence paniculate, cymose, racemose or flowers glomerate or solitary; stamens free; fruit a fleshy 1–many-seeded berry.

  B. Inflorescence a panicle; calyx undivided in bud, circumscissile, the lid usually remaining attached at one side; petals absent; embryo with foliaceous, twisted and folded cotyledons and an elongate radicle. .... 2. *Calyptranthes*.

  B. Inflorescence a raceme or dichasium or the flowers solitary or glomerate; calyx-lobes, if developed, 4 or 5; petals white or rarely rose colored.

    C. Inflorescence racemose or the flowers glomerate or fascicled; calyx-lobes 4; fruit 1(rarely 2)-seeded; embryo with fleshy, fused cotyledons. .... 3. *Eugenia*.

    C. Inflorescence a dichasium or the flowers solitary.

      D. Calyx-lobes 4, distinct in the bud, petals 4, white, leaves pinnately veined.

        E. Flowers in dichasia, embryo with 2 distinct, fleshy cotyledons, radicle short; fruit 1(rarely 2)-seeded. ..... 4. *Myrcianthes*.

        E. Flowers solitary, embryo curved, the cotyledons short, radicle elongate; fruit many-seeded. .... 5. *Myrtus*.

      D. Calyx-lobes 5, distinct in the bud, or the calyx closed in the bud and splitting irregularly in anthesis, usually into 5 segments; petals 5.

        F. Petals white; leaves pinnately veined, calyx closed in the bud, splitting irregularly in anthesis. .... 6. *Psidium*.

        F. Petals rose colored; leaves 3-veined; calyx-lobes distinct in the bud. .... 7. *Rhodomyrtus*.

Subfam. LEPTOSPERMOIDEAE Niedenzu

Tribe Leptospermeae DC.

1. **Melaleuca** Linnaeus, Mant. Pl. Gen. 1: 14. 1767, nom. cons.

Tree with alternate, 1–many-veined leaves. Flowers sessile in the axils of bracts, in dense or elongate spikes or occasionally solitary, the axis of the spike growing into a leafy shoot during or after flowering. Calyx-lobes 5, deciduous. Petals 5, white, orbicular, spreading in anthesis. Stamens numerous, united in 5 bundles opposite the petals. Ovary 3-locular, each locule with numerous ovules; hypanthium extending beyond the ovary. Fruit a loculicidal capsule dehiscing at the top, crowned by the hypanthium. (*Cajuputi* Adans., 1763, nom. rejic.) Type species: *M. Leucadendron* (L.) L. (Name from Greek, *melas*, black, and *leukos*, white, alluding to the black trunk and white branches of one of the species.) — Bottle-brush.

The subfamily Leptospermoideae, which is characterized primarily by the capsular fruits, has its center of distribution in Australia, and is represented in our area by a single naturalized species, *Melaleuca Leucadendron* (L.) L. The bottle-brush occurs in southern Florida where it is both cultivated and naturalized. This tree is conspicuous because of its white, spongy bark which peels off in large sections. The chromosome number of three other Old World species has been determined as $2n = 22$.

The closely related genus *Callistemon* R. Br. is frequently cultivated in Florida and may be distinguished by its free stamens which are bright red in color.

Various species of *Eucalyptus* L'Her. in the same subfamily are cultivated in the warmer parts of our area. Although some of the species have become naturalized in California, apparently none has become established in Florida.

References:

Schory, E. A. The cajaput tree in Florida. Carib. Forest. **19**: 50–55. 1958. [*M. Leucadendron*, culture and uses.]

Sharma, V. N., and P. Singh. Preliminary chemical examination of the liquid exudate from abnormal growths in *Melaleuca leucadendron* Linn. Jour. Sci. Indus. Res. **15C**(11): 256. 1956.*

Subfam. MYRTOIDEAE Niedenzu

Tribe Myrteae DC.

Subtribe Myrciinae Berg

2. **Calyptranthes** Swartz, Prodr. Veg. Ind. Occ. 79. 1788, nom. cons.

Trees or shrubs with opposite leaves. Inflorescence a myrcioid panicle (e.g., with the principal branches opposite, elongate, and terminating in single flowers or simple dichasia), the inflorescence axis usually abortive above the first node and the panicles appearing to be paired. Calyx undivided in bud, circumscissile in anthesis but usually remaining attached at one side. Petals wanting. Stamens numerous, inserted on the margin of the hypanthium which is prolonged above the summit of the ovary; anthers versatile, splitting longitudinally. Ovary 2(seldom 3)-locular, each locule with 2 ovules. Fruit a 1- or 2(seldom 3)-seeded berry crowned by the hypanthium. Embryo with twisted and folded foliaceous cotyledons, and an elongate radicle. (*Chytraculia* P. Br., 1756, nom. rejic.; *Chytralia* Adans., 1763, nom. rejic.) TYPE SPECIES: *C. Chytraculia* (L.) Sw. (Name from Greek, *kalyptra*, veil, and *anthos*, flower, alluding to the lidlike dehiscence of the calyx.) — SPICEWOOD, MYRTLE-OF-THE-RIVER.

About 100 species native to tropical America and the West Indies; represented in our area by two species, *Calyptranthes Zuzygium* (L.) Sw. and *C. pallens* (Poir.) Griseb., both of which occur in southern Florida, as well as Cuba and other islands of the West Indies. Because of the hoodlike dehiscence of the calyx, *Calyptranthes* is one of the easiest genera of the American Myrtaceae to recognize. However, many of the species are so variable in size and shape of leaves and in the characters of the flowers that they are by no means well marked. This genus, as well as all others in the family, is in need of a thorough revision which should be accompanied by extensive field study.

Subtribe **Eugeniinae** Berg

3. **Eugenia** Linnaeus, Sp. Pl. 1: 470. 1753; Gen. Pl. ed. 5. 211. 1754.

Trees or shrubs with opposite leaves. Inflorescence racemose, the terminal flower of the axis usually wanting; axis sometimes extremely shortened, the inflorescences then resembling axillary fascicles, umbels, or glomerules [or flowers rarely solitary in the lowermost axils of otherwise leafy branchlets]. Petals 4, orbicular, ovate or obovate, white, spreading in anthesis. Stamens numerous, free, the anthers versatile, splitting longitudinally. Ovary 2-locular, each locule with numerous ovules, the hypanthium extending slightly beyond the ovary or not at all. Fruit a 1(rarely 2)-seeded berry crowned by the persistent lobes of the calyx. Embryo apparently undivided, with thick, fleshy, fused cotyledons. TYPE SPECIES: *E. uniflora* L., $2n = 22$. (Named in honor of Prince Eugene of Savoy, 1663–1736, a patron of botany and horticulture.) — STOPPER.

A tropical genus of about 500 species represented in southern Florida by five indigenous species: *Eugenia anthera* Small, endemic, and *E. myrtoides* Poir. (*E. buxifolia* (Sw.) Willd.), *E. axillaris* (Sw.) Willd., *E. rhombea* (Berg) Krug & Urban, and *E. confusa* DC., which occur also in the West Indies. Although some of the species of *Eugenia* are clear cut and easily recognizable, the great majority are ill defined and difficult to determine, being based on leaf or floral characters which are very variable.

Eugenia has at various times included almost all species of the Eugeniinae, and the inclusive genus has been variously divided into smaller groups on the basis of the structure of the inflorescence and of the embryo. However, authors are by no means in agreement. Evidence from pollen morphology, wood anatomy, and anatomy of the bark supports the conclusion that the New World Eugenias are distinct from those of the Old World which are treated by the majority of recent authors as *Syzygium* Gaertn. *Eugenia* is said to differ from *Syzygium* in the pseudomonocotyledonous, apparently undivided embryo, and in the smooth seed coat which is free from the pericarp; the cotyledons of *Syzygium* are separate and the seed coat roughish, loosely or closely adhering to the pericarp.

Among the Old World species which are cultivated in Florida are *Syzygium Jambos* (L.) Alston, the rose apple ($2n = 28$, c. 42, 46, c. 54); *S. Cumini* (L.) Skeels, the Java plum or jambolan ($2n = 44, 46$); and *S. malaccensis* (L.) Merr. & Perry, the Malay apple ($2n = 22$). *Eugenia Dombeyi* Skeels, *E. Luschnathiana* Klotzsch ex Berg, *E. uniflora* L., Surinam cherry, and other species are know also in cultivation in Florida; the first two, however, are only sparingly grown, while *E. uniflora* is very popular both as an ornamental and for its edible fruits.

REFERENCES:

See family references, McVAUGH (1956, Tropical American Myrtaceae, pp. 166–169).

CHATTAWAY, M. M. The anatomy of bark. VII. Species of *Eugenia* (sens. lat.). Trop. Woods **111**: 1–14. *figs. 1–10* [*2 pls.*]. [Supports the separation of the Old World eugenias from those of the New World.]

DADSWELL, H. E., and H. D. INGLE. The wood anatomy of the Myrtaceae, I. A note on the genera *Eugenia*, *Syzygium*, *Acmena*, and *Cleistocalyx*. Trop. Woods **90**: 1–7. *pls. 1, 2.* 1947.

GAGNEPAIN, F. Classification des *Eugenia*. Bull. Soc. Bot. Fr. **64**: 94–103. 1917.

HENDERSON, M. R. The genus *Eugenia* (Myrtaceae) in Malaya. Gard. Bull. Singapore **12**: 1–293. 1949. [Rejects the removal of *Syzygium* from *Eugenia.*]

JAYAWEERA, D. M. A. Variation in the flower of *Eugenia malaccensis* Linn. Jour. Linn. Soc. Bot. **55**: 721–728. 1957. [A study based on teratologies.]

MERRILL, E. D., and L. M. PERRY. The Myrtaceous genus *Syzygium* Gaertner in Borneo. Mem. Am. Acad. Arts Sci. **18**: 135–202. 1939. [Includes notes on American species of *Eugenia.*]

PIJL, L. VAN DER. Über die Polyembryonie bei *Eugenia*. Rec. Trav. Bot. Néerl. **31**: 113–187. 1934.

TIWARY, N. K. On the occurrence of polyembryony in the genus *Eugenia*. Jour. Indian Bot. Soc. **5**: 124–136. 1926.

4. **Myrcianthes** Berg, Linnaea 27: 315. 1854 [1856].

Trees or shrubs with opposite leaves. Inflorescence an axillary dichasium, the terminal (central) flowers usually sessile in the fork. Calyx 4-lobed [rarely 5-lobed], the lobes distinct, persistent. Petals 4, white, spreading in anthesis. Stamens numerous. Ovary 2-locular, each locule with numerous ovules; hypanthium not extending beyond the summit of the ovary. Fruit a 1(seldom 2)-seeded berry crowned by the persistent lobes of the calyx. Embryo with distinct, fleshy cotyledons, the plumule shorter than the radicle. (Including *Anamomis* Griseb.) TYPE SPECIES: *M. apiculata* Berg (see McVaugh, Taxon **5**: 143. 1956.) (Name from *Myrcia*, and Greek, *anthos*, flower, in reference to the resemblance of the flowers to those of the genus *Myrcia*.) — NAKEDWOOD.

A genus of perhaps 50 or more species ranging from southern peninsular Florida to the West Indies, southward to Bolivia and Argentina, chiefly along the Andes, and southern Brazil. The genus is characterized by having solitary flowers or flowers in simple or compound dichasia, the hypanthium not extending beyond the ovary, the multiovulate ovary, and the embryo, as far as known, with two distinct cotyledons. *Myrcianthes dicrana*[2] occurs in hammocks along both coasts of southern peninsular Florida and on Key West and *M. Simpsonii*[3] in hammocks along the lower east coast of Florida and the Florida Keys. The latter differs in its larger flowers, many-flowered cymes, and the greater number of stamens.

Myrcianthes has been said to differ from *Anamomis* in the 5-parted flowers and in the presence of a plumule in the embryo. In a study of the Peruvian Myrtaceae, McVaugh found no support for separating the two genera, and he reported that 4-merous species occasionally have 5-merous flowers, and that a plumule is present in all mature seeds of species of *Anamomis* which were examined. In other morphological details the two genera are very much alike.

REFERENCES:

See also family references, MCVAUGH (1956, Tropical American Myrtaceae, pp. 169, 170; 1958, pp. 745–757.)

SMALL, J. K. The genus *Anamomis* in Florida. Torreya **17**: 221–224. 1917 [1918].

Subtribe **Pimentinae** Berg

5. **Myrtus** Linnaeus, Sp. Pl. **1**: 471. 1753; Gen. Pl. ed. 5. 212. 1754.

Shrubs or small trees with opposite leaves. Flowers solitary, peduncled, in the axils of leaves or of bracts or reduced leaves at the lowermost nodes of an otherwise leafy branch. Calyx 4[or 5]-lobed, the lobes distinct, persistent. Petals 4, white, spreading in anthesis. Stamens numerous. Ovary 2- or 3-locular, each locule with numerous ovules; hypanthium not extending beyond the summit of the ovary. Fruit a many-seeded berry crowned by the persistent lobes of the calyx. Seed coat bony; embryo

---

[2] **Myrcianthes dicrana** (Berg) K. A. Wilson, comb. nov. *Eugenia dicrana* Berg, Linnaea **27**: 259. 1854 [1856], *Anamomis dicrana* (Berg) Britton, N. Am. Trees 728. 1908.

[3] **Myrcianthes Simpsonii** (Small) K. A. Wilson, comb nov. *Anamomis Simpsonii* Small, Torreya **17**: 222. 1917 [1918].

uncinate-curved, the cotyledons short and inconspicuous. (*Mosiera* Small.) TYPE SPECIES: *M. communis* L. (2*n* = 22). (*Myrtus*, the Latin name, from the Greek name, *myrtos*.) — STOPPER (cf. Small).

A genus of about 16 species, according to the most recent interpretation (Burret), with one species in Europe, one in Africa, and about 14 in Florida and the West Indies; in our area represented by one or perhaps two species. *Myrtus verrucosa* Berg (*Mosiera longipes* (Berg) Small) and *M. bahamensis* (Kiaersk.) Urban (*Mosiera bahamensis* (Kiaersk.) Small) occur in southern peninsular Florida and on the Florida Keys in pinelands and in hammocks. It is questionable that the two, which differ in size of flowers and to some extent in the habit of the plants, are distinct; if united, the correct name is *M. verrucosa.*

The genus has been variously interpreted and has been considered to include as many as 50 species, most of which are now regarded as belonging to other genera. A study of *Myrtus* is badly needed and should take into account the American groups which have been allied with it. Such a study should establish the limits of the genus, and indicate whether our species rightfully belong to it. The nature of the inflorescence, fruit, seed, and embryo, clearly indicate that our species are not allied with *Eugenia*, and, in fact, belong in a different subtribe.

REFERENCES:

See also family references, MCVAUGH (1956, Tropical American Myrtaceae, pp. 173, 174.)

BURRET, M. Myrtaceen-Studien. Notizbl. Bot. Gart. Berlin **15**: 479–550. 1941. [Retains 2 Florida species in *Myrtus*.]

SOUÈGES, R. Embryogénie des myrtacées. Développement de l'embryon chez le *Myrtus communis* L. Compt. Rend. Acad. Sci. Paris **210**: 548–550. 1940.

6. **Psidium** Linnaeus, Sp. Pl. 1: 470. 1753; Gen. Pl. ed. 5. 211. 1754.

Trees or shrubs with opposite, pinnately veined leaves. Flowers axillary and solitary or in 3-flowered dichasia. Calyx undivided in bud, splitting irregularly in anthesis, remaining attached to hypanthium. Petals 4 or 5, white, spreading. Stamens numerous, free, inserted on the hypanthium. Ovary inferior, usually 4- or 5-locular, each locule with numerous ovules. Fruit a many-seeded berry, crowned by the persistent segments of the calyx. Embryo curved, cotyledons short, radicle elongate. TYPE SPECIES: *P. Guajava* L. (Name from Greek, *psidion,* pomegranate [*Punica Granatum*].) — GUAVA.

A genus of about 150 species of tropical and subtropical America. *Psidium Guajava* L., 2*n* = 22, originally introduced and cultivated for its edible fruits, has become naturalized in southern Florida as well as in many other warm parts of the world. The round or pear-shaped, yellow fruit is highly prized and is eaten raw or used to make jellies, preserves, or beverages. Many varieties have arisen in cultivation, but little taxonomic work has been done on them. In view of the industry already built around the production of the guava, and its potentially even greater economic significance, a detailed horticultural and systematic study of this species and its varieties would be highly desirable. Several other species of *Psidium*, among them *P. Cattleianum* Sabine, the strawberry guava, $2n = 88$, are in cultivation in Florida.

REFERENCES:

KUMAR, L. S. S., and S. G. RANADE. Autotriploidy in guava (*Psidium Guajava*, Linn.). Curr. Sci. Bangalore **21**: 75, 76. 1952.*

LYNCH, S. J., and R. O. NELSON. Current methods of vegetative propagation of avocado, mango, lychee and guava in Florida. Ceiba **4**: 315–337. 1956.

MUSTARD, M. J. Mangos and guavas as sources of ascorbic acid. Proc. Fla. State Hort. Soc. **58**: 187–190. 1946.*

RUEHLE, G. D. Promising new guava varieties. Proc. Fla. State Hort. Soc. **59**: 127–131. 1946.*

———. Growing guavas in Florida. Fla. Sub-trop. Exp. Sta. Mimeog. Rep. **12**. Homestead, 1947.*

SCHROEDER, C. A. Priority of the species *Psidium Cattleianum* Sabine. Jour. Arnold Arb. **27**: 314, 315. 1946. [*P. Cattleianum* vs. *P. littorale*.]

WADDINGTON, G., and F. M. CIST. The vitamin C content of *Psidium Guajava*. Proc. Fla. State Hort. Soc. **55**: 110–112. 1943.*

7. **Rhodomyrtus** (DC.) Reichenbach, Nomen. Gen. Pl. 177. 1841.

Shrubs [or trees] with opposite, tomentose, 3-veined leaves. Flowers axillary and solitary or in 3-flowered dichasia. Calyx-lobes 5 [or 4], spreading. Petals 5 [or 4], rose colored, spreading. Stamens numerous, free, inserted on the hypanthium; filaments rose colored. Ovary [1–]3-locular with 2 rows of ovules in each locule separated by a vertical septum, thus appearing 6-locular; hypanthium not at all or only slightly prolonged beyond the ovary. Fruit a blue-black many-seeded berry crowned by the persistent lobes of the calyx. Embryo curved. TYPE SPECIES: *R. tomentosa* (Ait.) Hassk. (Name from Greek, *rhodon*, rose, and *myrtos*, ancient Greek name for myrtle.) — DOWNY-MYRTLE, HILL-GOOSEBERRY.

A small genus of about 25 species native to eastern Asia and Australia. *Rhodomyrtus tomentosa* (Ait.) Hassk. has escaped from cultivation and is becoming naturalized in southern Florida, especially along the Gulf Coast. The three-veined, opposite leaves, pubescent on the lower surface, are characteristic. It is cultivated as an ornamental shrub, and also for its small, globose fruits which are used in making jams and pies.

REFERENCES:

BANDULSKA, H. On the cuticles of some recent and fossil Myrtaceae. Jour. Linn. Soc. Bot. **48**: 657–671. 1931. [Compares species of *Rhodomyrtus* and *Tristania*.]

JAYAWEERA, D. M. A. The morphology of the flower of *Rhodomyrtus tomentosa*, Wight. Ceylon Jour. Sci. A. **13**: 31–42. 1956.

SUPPLEMENT TO A MONOGRAPHIC STUDY OF THE WEST INDIAN SPECIES OF PHYLLANTHUS

Grady L. Webster

With the aid of a grant from the National Science Foundation, the work on the West Indian species of *Phyllanthus* (Euphorbiaceae) earlier published in this journal (1956–1958) is now being expanded by use of various analytical techniques such as chromosome counts. During the summer of 1959, an extended tour through the West Indies made it possible to obtain more information on populations of a number of taxa. Certain species, especially those in sect. *Xylophylla*, will be treated in a future study dealing with intraspecific variation patterns. However, it seems appropriate to present here the observations that have accumulated on other species, as well as to note a few corrections. The numbers in brackets refer to the volume and page numbers of the monographic study in previous issues of this journal. Herbarium collections are those in the Stanley Coulter Herbarium, Purdue University (PUR), unless otherwise noted.

[38: 51.] Sect. 2. **Floribundi.**

4. **Phyllanthus tenellus** Roxb. Add the following locality record: Puerto Rico: Bosque Estatal de Maricao, Hoconuco trail, weedy cleared area, *Webster et al. 8901*. This is the first record of this weedy species from Puerto Rico; it was not found elsewhere on the island. It may be expected to reach Cuba and Hispaniola, but thus far no specimens have been observed from either island.

[38: 56.] Sect. 3. **Kirganelia.**

According to Article 22 of the International Code of Botanical Nomenclature (1956 ed.), *Anisonema* cannot be retained as the epithet of this section, since it contains the type species of subgenus *Kirganelia*. The type species, when the section is given the epithet *Kirganelia*, must be *P. casticum* Willem. instead of *P. reticulatus*. This ruling is unfortunate, in my opinion, since it fallaciously assumes a parallel between typification of a genus or species with that of a subgenus. The subgenus does not appear in the name of a species and is a purely intercalary category, as is the section. That the new rule does not really contribute to stability is shown in the present case. If subgenera are recognized in *Phyllanthus*, the epithet of this section must be *Kirganelia*; but if one chooses not to recognize subgenera then the same section *must* take the epithet *Anisonema*.

[**38**: 297.] Sect. 11. **Phyllanthus.**

The synoptic key to taxa of sect. *Phyllanthus* requires two corrections: (1) the calyx lobes of *P. amarus* (no. 20) could often be described as apiculate, rather than acute; they are, in any event, distinctly more pointed than those in *P. debilis* or *P. fraternus*. (2) A misprint has occurred in lead 5 under the second lead 3. It should read as follows: "5. Style-branches not unusually modified; branchlets mostly with 15–30 leaves. . . ."

[**38**: 299.] Sect. 11. **Phyllanthus,** subsect. a. **Niruri.**

17. **Phyllanthus mimicus** Webster. The following additional collection has been recorded: TRINIDAD: without specific locality, *Fendler 680 ex p.* (BM). This collection resembles *P. niruri* in having only 20–25 leaves per branchlet rather than 35–45 as in the type collection of *P. mimicus*. However, the leaves are mostly only 4.5–5.5 mm. long, the male flowers are solitary and with calyx lobes 0.6–0.7 mm. in length, and the capsule is only c. 2 mm. broad. Since in all these respects Fendler's collection agrees with *P. mimicus*, the breakdown in the leaves-per-branchlet character does not efface the distinctions between *P. mimicus* and *P. niruri*. Further collections of *P. mimicus* are highly desirable, and it was quite disappointing that the plant was not located on the expedition trip to Tobago.

[**38**: 306.] Sect. 11. **Phyllanthus,** subsect. b. **Swartziani.**

18. **Phyllanthus debilis** Klein ex Willd. This species was recollected at Petit Bourg, Guadeloupe, after a 20-year interval (*Webster et al. 8986*), and, in fact, was locally common. It may therefore be considered as established, at least on Guadeloupe. So far, however, it has not been found on any other island.

21. **Phyllanthus stipulatus** (Raf.) Webster. Add the following locality record: ST. LUCIA: along trail, red clay soil, southeast slope of Piton Flor, *Webster et al. 9291*. This collection of *P. stipulatus*, the first recorded from St. Lucia, was interesting because of its small seed size. The mean of 30 seeds measures only 0.95 mm., and the range is from 0.93–1 mm. This is much smaller than measurements of a collection from Puerto Rico and two from Trinidad (*Webster et al. 8954, 9888, 9924*), which yielded mean seed lengths of 1.14, 1.06, and 1.12 mm. respectively. A collection of *P. caribaeus* (*Webster et al. 9677*) gave a mean seed length of only 0.9 mm. and a range of 0.85–0.95 mm. The St. Lucia collection is thus intermediate between the two species in seed size, but is closer to *P. caribaeus* and smaller than any collections of *P. stipulatus* seen elsewhere in Latin America. Nevertheless, in floral characters the St. Lucia collection conforms closely to *P. stipulatus*. It is possible that we are dealing here with an instance of introgressive hybridization. Although *P. caribaeus* has not been collected on St. Lucia, it might be expected to be

there, for it occurs on both Dominica and St. Vincent. Further field studies of this interesting species-pair on all the central Lesser Antilles are most desirable.

[38: 363.] Sect. 13. **Conami.**

As with sect. *Anisonema* (see above), the epithet of this section must be changed from *Nothoclema* to *Conami* in order to conform with the current rules of nomenclature.

[39: 50.] Sect. 15. **Botryanthus.**

For the same reason, sect. *Elutanthos* must be replaced by sect. *Botryanthus.*

45a. **Phyllanthus nutans** Sw. ssp. **nutans.** Additional field studies of this widespread Jamaican plant have only confirmed its previous systematic disposition. Better material obtained of the population in the John Crow Mountains (*Webster et al. 8297*) shows decisively that it cannot be given specific status. This population from the Ecclesdown area is distinguished by persistent stipules, tenuous pendent fruiting thyrses, and particularly by the large seeds. In this it resembles the population in the Cockpit country, as may be seen from the following table.

COLLECTION	LOCALITY	NO. SEEDS MEASURED	MEAN	*s*
Howard et al. 14769 (A)	John Crow Mts.	8	6.29 mm.	0.42
Webster et al. 8297	" " "	15	6.22	0.25
8402	Cockpit Country	15	6.11	0.18
8477	" "	5	6.83	0.26
8575	Seacoast near Lucea	4	4.39	0.16

The number of seeds available is small, so that a statistically satisfactory analysis cannot yet be made, but it would appear that populations of *P. nutans* at higher altitudes and in areas of greater rainfall tend to have larger seeds than those near the seacoast. A collection from Discovery Bay (*Hunnewell 18844* [GH]) had seeds only about 4.1 mm. long, but the number of measurements was unfortunately not recorded. Collections from intermediate situations may have intermediate seed sizes (e.g., 5.29 mm. in *Webster & Proctor 5516* from Big Level).

Such variation as this in the Jamaican populations of *P. nutans* is perhaps correlated with ecotypic differences. It seems possible that in dried, open habitats there is a selection for smaller seed size than in moister, closed ones, as suggested by Salisbury in "The Reproductive Capacity of Plants" (1942).

[39: 153.] Sect. 21. **Epistylium.**

Field studies in Jamaica have clarified to some extent the differences in inflorescence between the three species of this section. Although *Phyllanthus cauliflorus* could not be located, collections of *P. cladanthus* (*Webster et al. 8279*) and *P. axillaris* (*Webster et al. 8464, 8472*) were most helpful toward a better understanding of the morphology of these species. It now appears that the inflorescence difference is more absolute than was previously mentioned. In *P. cladanthus* the flowers are strictly cauliflorous, while in *P. axillaris* they are strictly axillary. Only in *P. cauliflorus* do both types of distribution occur. Each of the three species, therefore, has a distinct pattern of flower production.

[39: 179.] Sect. 24. **Xylophylla.**

Extensive collections of members of this group were made in Jamaica, Puerto Rico, and Guadeloupe. However, the analysis of several of the species (such as *P. arbuscula* and *P. epiphyllanthus*) is still not complete

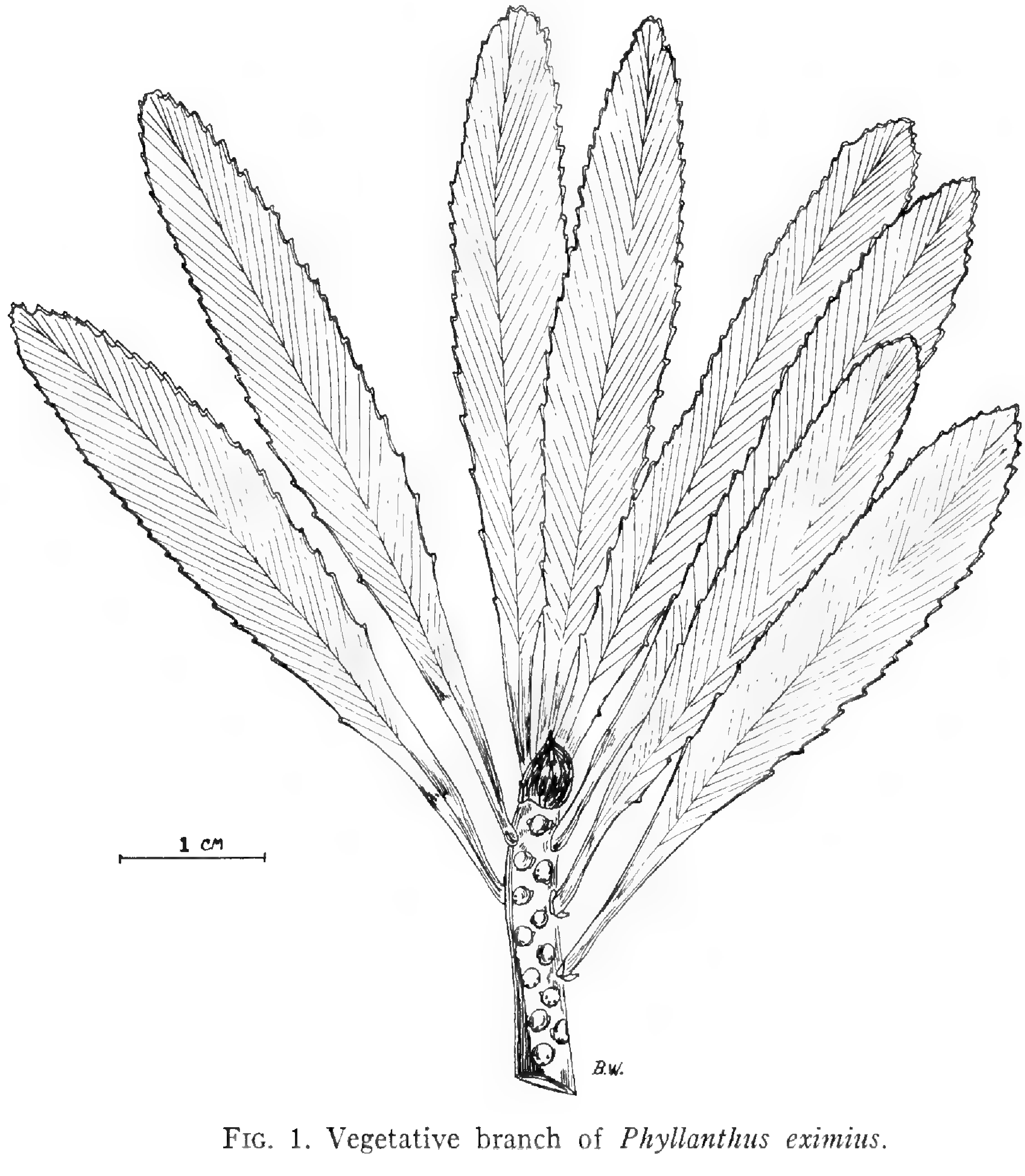


FIG. 1. Vegetative branch of *Phyllanthus eximius*.

and must be deferred to a separate paper. At this time the only addition to record is the following previously undescribed species.

During a botanical trip to Jamaica in the summer of 1954, Mr. George Proctor guided Dr. Kenneth Wilson and the author on a hike into the little-explored John Crow range in the eastern end of the island. About halfway up the rugged slopes of this precipitous limestone massif we discovered in the rain forest what was obviously an undescribed species of *Phyllanthus* sect. *Xylophylla*. Unfortunately the plants were entirely barren, and publication of the species had to be deferred until flowering material could be obtained. During a return trip to the original locality in the summer of 1959, we were fortunate to encounter a considerable number of flowering individuals in the cloud-swept scrubby forest on the upper edge of the plateau at an altitude of somewhat over 2000 feet. Plants previously sent to the Harvard University greenhouses by Mr. Proctor also came into flower in 1959, so that there is no longer a shortage of fertile specimens.

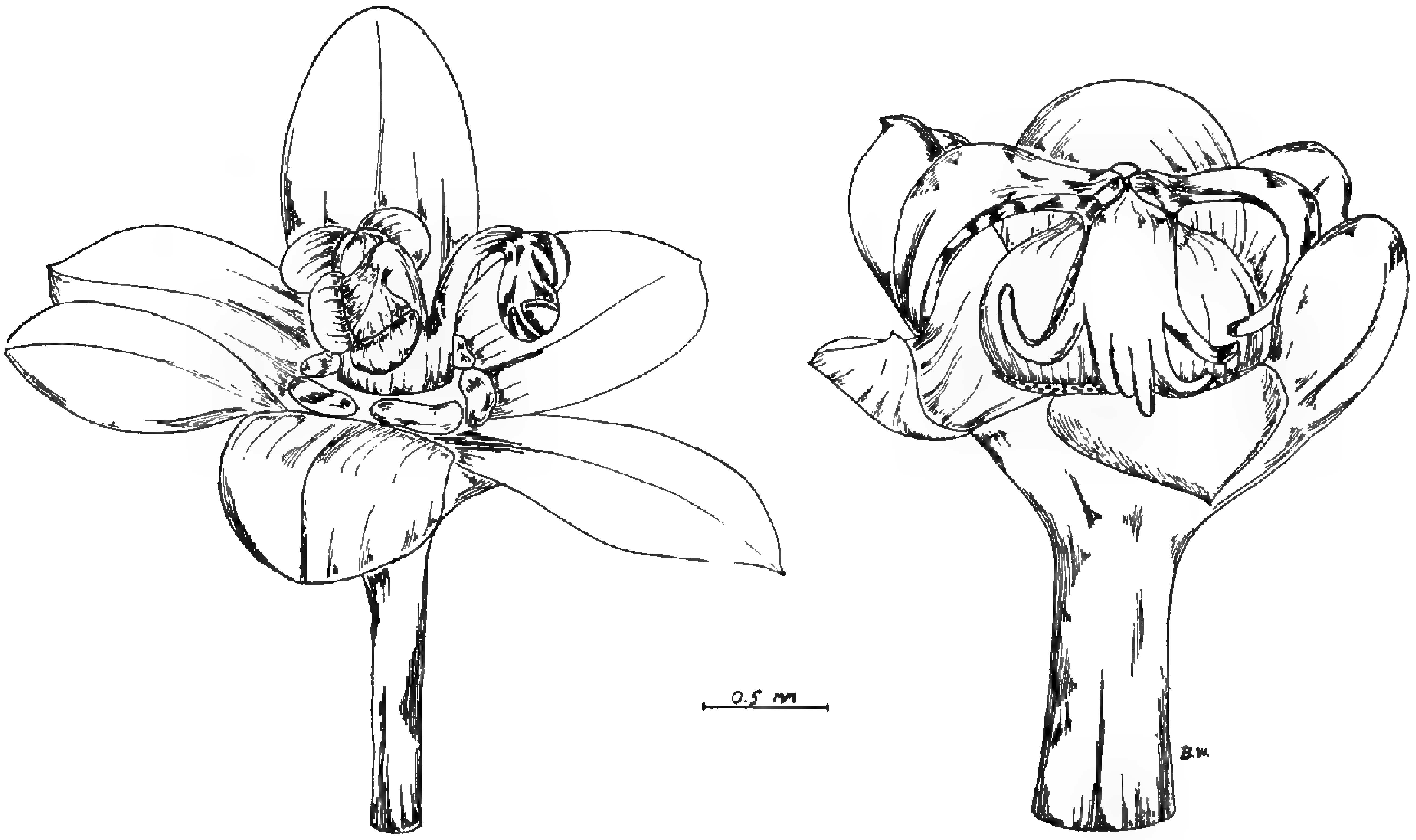


FIG. 2. Male flower and female flower of *Phyllanthus eximius.*

84. **Phyllanthus eximius** Webster & Proctor, sp. nov.

Frutex vel arbuscula monoecia glabra 2–4 m. alta; phyllocladiis simplicibus rigidis spathulatis vel oblanceolatis 8–17.5 cm. longis, 1–4.5 cm. latis, costa venisque conspicuis, marginibus ora cinctis. Floribus ochroleucis vel rufidulis; flore masculo laciniis calycis plerumque 6, c. 1.1–1.6 mm. longis, staminibus 3 filamentis ad basin connatis; flore femineo pedicello crasso c. 1.3–2.2 mm. longo, 0.4–0.6 mm. diametro, laciniis calycis 6, c. 1–1.2 mm. longis; disco inconspicuo; stylis dilatatis subliberis c. 1 mm. longis, c. 4–6-lobis; capsula c. 3.3–3.7 mm. lata.

Glabrous shrub or small tree becoming c. 2–4 m. high; branches of current year's growth 3–7 mm. thick, reddish brown or often greyish or glaucous, smooth. Apical scaly cone irregular in outline, 8–12 mm. long, 5–10 mm. broad. Cataphylls persistent on current year's growth but subsequently deciduous, pale (stramineous or light brown), indurate; stipules and blade free from each other, lanceolate, acuminate (sometimes attenuately so), mostly 3–6 mm. long, tips erect or squarrose. Phylloclades (modified branchlets) unbranched, becoming somewhat rigid, spathulate to oblanceolate, c. (8–) 10–15(–17.5) cm. long, 1–4.5 cm. broad, obtuse or rounded to emarginate at the tip, with (25–)35–55 conspicuously notched nodes, gradually tapering to a petiole-like base c. 1–2 cm. long; midrib prominent on both sides, lateral veins straight, conspicuous, each ending at a marginal notch; margins with distinctly differentiated rim running between the notches. Foliage leaves (euphylls) not seen; cataphylls of phylloclades blackish brown, trifid, the tips soon breaking off, less than 1 mm. long.

Monoecious; cymules mostly bisexual, each with one female and several male flowers; flowers yellowish- or greenish-white, or reddish-tinged.

Male flower: pedicel slender, c. 1–2 mm. long. Calyx-lobes 6 (rarely 5), thin, more or less unequal, spreading, elliptic to obovate, the inner larger ones c. 1.1–1.6 mm. long and 0.9–1.3 mm. broad, the outer smaller ones c. 0.8–1.1 mm. long and 0.6–1 mm. broad; lobes obtuse or rounded (occasional ones apiculate) at the tip, midrib unbranched. Disk-segments 6, not very massive, roundish or ellipsoidal, mostly 0.3–0.5 mm. long. Stamens 3; filaments 0.5–0.8 mm. high, united only at the very base (up to 0.1–0.2 mm.) into a massive pedestal, ascending-spreading, the anthers horizontal or deflexed; anthers emarginate, 0.3–0.4 mm. long, 0.4–0.6 mm. broad.

Female flower: pedicel stout, straight, in fruit becoming 1.3–2.2 mm. long and 0.4–0.6 mm. thick. Calyx-lobes 6, stiff (subcoriaceous), ascending or spreading, unequal, c. 1–1.2 mm. long and nearly as broad, tips acute or obtuse, midrib not conspicuous. Disk inconspicuous, annular, not enclosing any part of the ovary. Ovary smooth; styles c. 1 mm. long, free except at the very base, spreading at anthesis (later more or less ascending), dilated distally, the style-tips cut into 4–6 slender subterete lobes.

Capsule oblate, rounded-trigonous, c. 3.3–3.7 mm. long; cocci c. 2.5 mm. long, reddish brown, not veiny; well-developed seeds not observed.

TYPE COLLECTION: Jamaica, Portland Parish, John Crow Mountains, 2–2.5 miles SW of Ecclesdown, rain forest on top of plateau, alt. c. 2000–2500 ft., 17 June 1959, *Webster, Miller, Ellis, & Proctor 8320* (Holotype, PUR; isotypes to be distributed). An additional collection from the same locality but a lower altitude (c. 1500 ft.) is *Webster & Wilson 5140* (PUR, GH).

This striking and attractive species (whence the epithet *eximius*, extraordinary) appears to be strictly endemic to the rain forest on the middle and upper slopes of the John Crow Mountains. Ecologically, the plant belongs to that sizable class of endemic species of the John Crows adapted to growing on limestone rock almost bare of soil and under nearly continuous rainfall. The two collections cited are similar in most respects and are surely conspecific, but the phylloclades of the type collection are strikingly narrower than those of *Webster & Wilson 5140*, as appears from the following table.

	COLLECTION	NUMBER OF SPECIMENS	RANGE	MEAN	*s*
Phylloclade length	*5140*	25	88–173 mm.	125.8 mm.	40.0
	8320	50	81–165 mm.	130.4 mm.	25.1
Phylloclade width	*5140*	25	20–45 mm.	29.3 mm.	6.3
	8320	50	11–25 mm.	18.7 mm.	4.2
Number of nodes	*5140*	25	25–56	43.4	8.1
	8320	50	35–55	45.2	8.7

In order to accommodate *Phyllanthus eximius* in the treatment of sect. *Xylophylla* (Jour. Arnold Arb. 39. 1958), the key to the species of that section (p. 182) need be modified only at the last lead as follows:

1. Phylloclades each representing an entire branchlet, borne scattered directly on main stems.
   6. Cataphylls on main stem persistent, with stipules and blade fused (at least basally); phylloclades with indistinct lateral veins. . . . . 83. *P. epiphyllanthus*.
   6. Cataphylls on main stem more or less deciduous, stipules and blade free; lateral veins of phylloclades conspicuous. . . . . 84. *P. eximius*.

Although it keys out next to *Phyllanthus epiphyllanthus* because of its unbranched phylloclades, *P. eximius* is much more closely related to *P. arbuscula* and probably represents a highly specialized local population derived from that species. The resemblance to *P. arbuscula* is especially marked in the long, pale cataphylls forming an irregular apical cone and in the prominent lateral veins and distinct marginal rims of the phylloclades. However, in addition to having simple rather than compound phylloclades, *P. eximius* also differs from *P. arbuscula* in having a shorter, thicker fruiting pedicel and in the lesser degree of fusion of filaments in the male flower.

The description of *Phyllanthus eximius* rounds out the preliminary descriptive work in sect. *Xylophylla*; it is almost certain that all the species in the group have now received names. There remains much work of interest to do, however, in analyzing the taxonomic complexities of three species (*P. angustifolius*, *P. arbuscula*, and *P. epiphyllanthus*). From an evolutionary point of view *P. eximius* is most interesting as a demonstration that the reduction of compound to simple phylloclades has occurred twice and independently within the section, the simple phylloclades of *P.*

epiphyllanthus representing a reduction from those of *P. angustifolius*, while the simple phylloclades of *P. eximius* have been derived from compound ones such as those of *P. arbuscula*.

Field work during the summer of 1959 was supported by a grant from the National Science Foundation. Aid in obtaining collections was given by Mr. George Proctor on Jamaica; Mr. Roy Woodbury, of Río Piedras, on Puerto Rico; Dr. Henri Stehlé on Guadeloupe; Mr. Peter Paul on St. Lucia; and the staff of the Imperial College of Tropical Agriculture (including P. T. Richards, W. D. Richardson, and N. W. Simmonds) on Trinidad. The illustrations of *Phyllanthus eximius* (FIGS. 1 and 2) were drawn by Barbara Webster from the author's preliminary sketches.

DEPARTMENT OF BIOLOGICAL SCIENCES
PURDUE UNIVERSITY
WEST LAFAYETTE, INDIANA

THE ANATOMY OF PHENAKOSPERMUM (MUSACEAE)

P. B. TOMLINSON

IN A RECENT ACCOUNT of the anatomy of the Musaceae (Tomlinson, 1959) the anatomy of *Ravenala* is described. Although this dealt with only one species, *R. madagascariensis*, it is there implied that *Phenakospermum* (*Ravenala*) *guianense* (L. C. Rich.) Miq. falls within the range of anatomical variation of *Ravenala*. The anatomy of *Phenakospermum* has, however, never been described in detail.

Recently, thanks to the kindness of Dr. P. Campos-Porto of the Botanic Gardens, Rio de Janeiro, I received pickled material of parts of a mature plant, together with material of a juvenile plant, of *Phenakospermum guianense*. On first examination of this material it was immediately evident that there were significant differences between *Phenakospermum* and *Ravenala*. More recently it has been possible to examine this material in detail, and the present account is based on these anatomical observations. From these results a comparison between *Phenakospermum* and other members of the Musaceae, particularly *Ravenala* and *Strelitzia*, has been made from the standpoint of systematic anatomy.

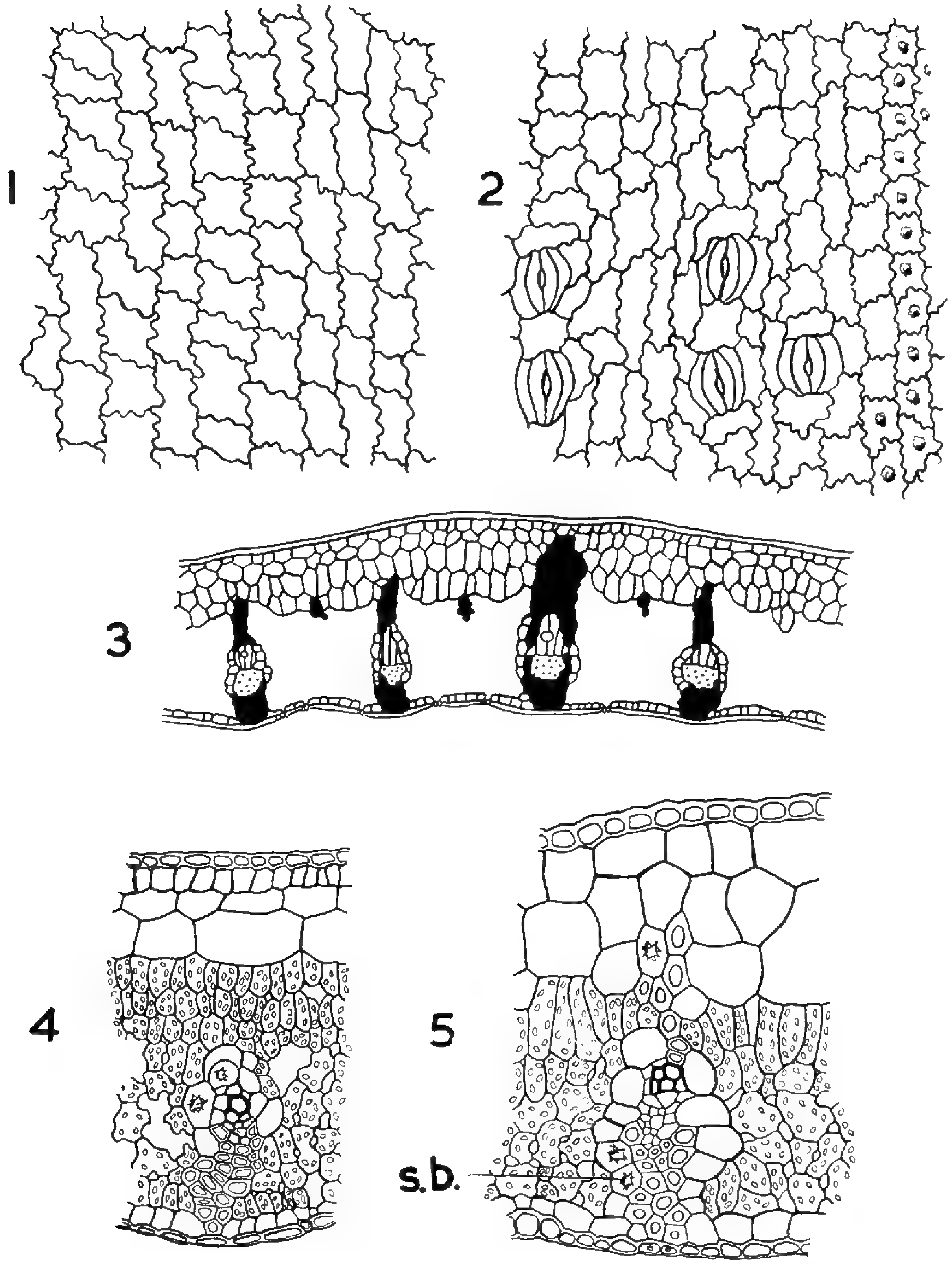
Reasons for accepting *Phenakospermum* Endl. ex Miq. as a valid genus distinct from *Ravenala* Adans., within which it was formerly included, are given by Lane (1955). He also discusses the nomenclatural problems of *Phenakospermum*, and, since they are there satisfactorily resolved, it is not necessary to repeat them in the present paper. The chief diagnostic features which are considered by Lane to be characteristic of *Phenakospermum* are the terminal inflorescence, five stamens in each flower, four or more rows of ovules in each loculus of the ovary, the bright red-orange, filamentous aril and straight embryo with the micropylar opening at the end of the seed. *Ravenala*, on the other hand, has a lateral inflorescence, six stamens in each flower, only two rows of ovules in each loculus of the ovary, while the aril is blue and membranaceous and the embryo is bent so that the micropylar opening is in the side of the seed. In addition, in the material of *Phenakospermum* which I received, there were short stolons covered by overlapping, distichous scales, evidently a means by which the plant could spread vegetatively. *Ravenala* also propagates itself by growth of basal suckers, but these are never at first stoloniferous.

Apparently there are two distinct forms of the plant, the most obvious difference being that one has an erect, ligneous stem, the other having only an underground stem; small differences in the reproductive parts have also been recorded. Nakai (1948) has separated the form with a distinct trunk into a new genus, *Musidendron*. Lane suggests that the differences are not sufficiently constant to warrant this change.

The same methods used in studying the anatomy of other members of the Musaceae were employed (Tomlinson, 1959). In sectioning the stem on the sliding microtome it was found necessary to soften the hard outer sclerotic layer by directing a jet of steam onto the cut surface during the sectioning process.

ANATOMY OF THE VEGETATIVE PARTS

Lamina dorsiventral. HAIRS absent. CUTICLE forming a thick, abaxial, waxy layer, cracking and eroding from mature leaves although persisting as irregular tabular masses, often forming annular ridges above stomata; outer cutinized layer of epidermal cells rather thin. EPIDERMIS with markedly sinuous anticlinal walls. Adaxial epidermis very uniform, outer wall thickened, made up of files of tabular cells; cells in surface view (*Fig. 1*) either square, or rectangular and longitudinally extended although end walls often rather oblique. Abaxial epidermis mostly with inner wall thicker than delicate, wholly cutinized outer wall; made up of narrow costal bands of shallow cells, costal cells more or less square in surface view (*Fig. 2*) and each often including a small silica body; alternating with wider intercostal bands of larger, usually longitudinally extended but rather irregular cells, those in the same file as stomata sometimes wider than cells elsewhere. STOMATA occasional adaxially; abaxially absent below both longitudinal and transverse veins and so restricted to short rectangular areas; not in regular files but 3–5 irregular series situated within each intercostal band. Terminal subsidiary cells usually short, wide but not otherwise different from other epidermal cells. Lateral subsidiary cells narrow, deep, uniformly thin-walled; other epidermal cells sometimes modified adjacent to stomata but not uniformly arranged. Guard cells (*Fig. 11*) not sunken, each with 2 cutinized ledges. HYPODERMIS (*Fig. 3*) 2–3-layered adaxially, often 4-layered above main veins, 1-layered abaxially. Outermost adaxial hypodermal layer rather thick-walled, cells hexagonal and slightly transversely extended in surface view; inner layers composed of larger and more cubical cells with thinner walls. Abaxial hypodermal layers often interrupted by vascular buttresses, cells always smaller than outermost adaxial layer, most irregular in intercostal regions; substomatal chambers each surrounded by an annulus of 2–4 small cells. CHLORENCHYMA including 2 or 3 adaxial layers of palisade cells, uppermost layer most anticlinally extended. Abaxial mesophyll divided into rectangular compartments between longitudinal and transverse veins, including rather loose, isodiametric but shortly lobed cells. VEINS (*Figs. 3, 5*) all attached to each hypodermis by well-developed fibrous buttresses; adaxial buttresses narrow except for massive buttresses above few main veins, composed of unlignified fibers with wide lumina; abaxial buttresses made up of narrow lignified fibers with narrow lumina. Outer parenchymatous bundle sheath 1-layered lateral to all veins, composed of cubical or slightly longitudinally extended cells. Extended protoxylem only present in larger

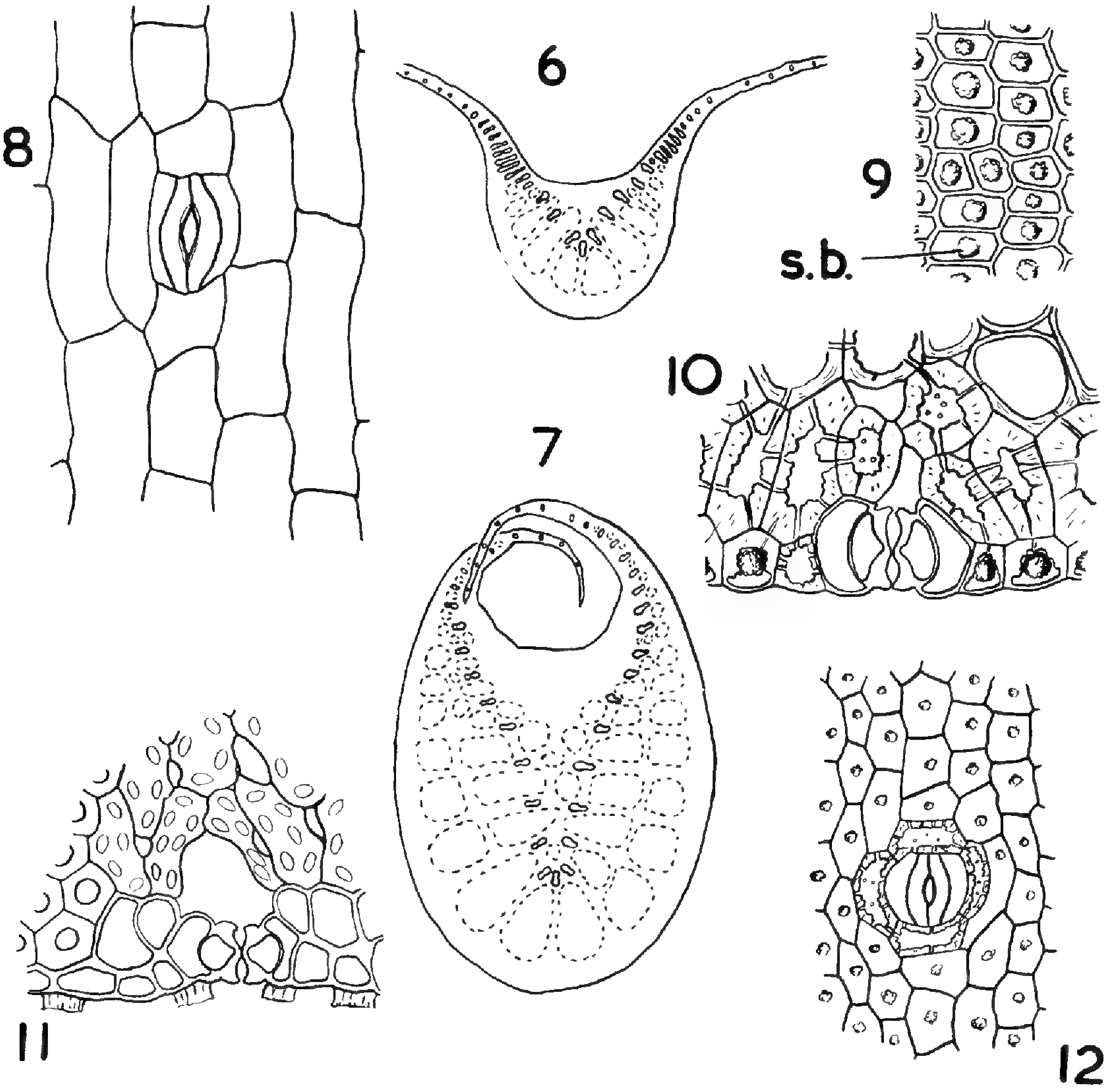


FIGS. 1–5. ANATOMICAL DETAILS OF THE LEAF OF PHENAKOSPERMUM. 1, Adaxial epidermis of lamina, surface view, × 300. 2, Abaxial epidermis of lamina, surface view, including part of a costal band, × 300. 3, Transverse section of lamina, including a main vein, × 54; sclerenchyma solid black, phloem stippled, xylem lined. 4, Longitudinal section of lamina including a transverse vein in transverse section, × 125. 5, Transverse section of lamina, including a small longitudinal vein, × 145; s.b. = silica bodies.

veins, vascular tissues rather inconspicuous in smaller veins. Probable free vein extensions, pectinating with longitudinal veins, visible as occasional fibrous strands below adaxial hypodermis near main veins. TRANSVERSE COMMISSURES (*Fig. 4*) frequent, all buttressed to either abaxial hypodermis or epidermis by short, unlignified, thick-walled prosenchymatous elements or short fibers with wide lumina; adaxial sheath usually consisting of a single layer of colorless parenchyma in contact with the palisade; vascular tissues reduced, xylem often consisting of a single file of tracheal elements, phloem incompletely sheathed by lignified elements. EXPANSION CELLS represented by well-developed hypodermal layers above main veins (*Fig. 3*). Indistinct "pulvinar band" also present at junction of midrib and lamina, veins in this region with very tall and well-developed adaxial buttresses.

Leaf axis (lamina midrib [*Fig. 6*], petiole [*Fig. 7*], leaf sheath). EPIDERMIS varying in structure in different parts: (i) Adaxial epidermis of midrib and upper part of leaf sheath: cells cubical or slightly longitudinally extended, outer walls distinctly thickened, anticlinal walls often slightly sinuous in midrib; rarely containing silica bodies. (ii) Adaxial epidermis of leaf base (*Fig. 8*): cells thin-walled, rectangular and considerably longitudinally extended, anticlinal walls not sinuous. (iii) Abaxial epidermis of midrib and leaf sheath together with whole of epidermis of terete part of petiole (*Fig 12*): cells more or less cubical, inner wall becoming markedly thickened and often enveloping a spherical silica body, especially in leaf sheath (*Fig. 9*). Sometimes slight differentiation between costal and intercostal regions. STOMATA occasional on both surfaces, guard cells and lateral subsidiary cells like those in stomata of lamina, arrangement of other subsidiary cells varying in different parts of leaf axis: (i) Adaxial epidermis of midrib and upper part of leaf sheath: arrangement more or less as in lamina. (ii) Adaxial epidermis of leaf base (*Fig. 8*): terminal subsidiary cells short, thin-walled. (iii) Abaxial epidermis of leaf sheath and whole of epidermis of terete part of petiole: terminal subsidiary cells with uniformly thickened and conspicuously pitted walls, similar cells also usually adjacent to lateral subsidiary cells (*Figs. 10, 12*). HYPODERMIS usually conspicuously different from ground parenchyma cells of leaf axis: (i) Abaxial hypodermis in all parts consisting of 2 to many layers of small, short cells with massively thickened, pitted lignified walls, interrupted by small, loose, lobed cells below stomata but these cells also becoming sclerotic in old leaves (*Fig. 10*). (ii) Adaxial hypodermis in midrib and upper part of leaf sheath including at least 1 regular layer of stone cells either immediately below epidermis (leaf sheath) or separated from epidermis by a thin-walled layer (midrib). (iii) Adaxial hypodermis of leaf base always with thin-walled, markedly tangentially extended cells. CHLORENCHYMA present as an inconspicuous abaxial band. AIR LACUNAE in one to many series extending from leaf insertion to distal part of midrib (*Fig. 6*). Most conspicuous in petiole

(*Fig. 7*) as several arcs of lacunae abaxial to main vascular arc, separated from each other by vertical partitions; represented by a single arc of air canals in leaf sheath; small system of air canals also adaxial to main vascular arc in petiole. Air lacunae segmented at regular intervals by thick TRANSVERSE SEPTA, each septum consisting of 2–3 layers of large, fairly compact, colorless parenchyma cells on either side of a central plate of 2 or 3 layers of small, stellate cells, the arms of which include wide intercellular spaces. Air lacunae in the midrib often containing a loose network of algiform cells. Abaxial FIBROUS STRANDS abundant in all parts of leaf axis, together with the sclerotic abaxial hypodermis forming a peripheral rigid mechanical zone. Fibrous bundles pectinating with abaxial vascular bundles, usually separated from epidermis by a sclerotic hypo-



FIGS. 6–12. ANATOMICAL DETAILS OF THE LEAF OF PHENAKOSPERMUM. 6, Transverse section of midrib, with only main arc of vascular bundles shown, × 2. 7, Transverse section of base of petiole, with only main arc of vascular bundles shown, × 2. 8, Adaxial epidermis of sheathing leaf base in surface view, × 300. 9, Abaxial epidermis of leaf base in surface view, × 300; s.b. = silica bodies. 10, Transverse section of abaxial epidermis of leaf base including a stoma, × 430. 11, Transverse section of stoma from abaxial epidermis of lamina, × 430. 12, Epidermis of petiole in surface view, × 300.

dermis but in petiole often immediately adjacent to epidermis. VEINS arranged in 3 distinct systems: (i) Main V- or U-shaped arc of large vascular bundles mostly adaxial to main system of air lacunae (*Figs. 6, 7*). (ii) A very feeble system either of narrow adaxial bundles with reduced, often obliquely or inversely orientated vascular tissues or of purely fibrous strands, most conspicuous in petiole. (iii) Abaxial system of numerous, mostly medium-sized vascular bundles below main arc, bundles uniformly scattered and not arranged in obvious arcs, frequent in longitudinal partitions between air lacunae, bundles in this position in midrib often inversely orientated. Large vascular bundles with normal Scitaminean construction (cf. Solereder and Meyer, 1930; Tomlinson, 1956); phloem parenchyma often thick-walled and lignified. TRANSVERSE COMMISSURES connecting longitudinal veins at irregular intervals, sometimes extending across transverse partitions of air lacunae. GROUND PARENCHYMA uniform, often including tannin cells.

Stem. Narrow cortex abruptly delimited from central cylinder by a dense sclerotic zone of congested vascular bundles. EPIDERMIS as in abaxial part of leaf sheath with files of cubical cells, each with inner wall thickened and enclosing a spherical silica body. STOMATA occasional, each surrounded by sclerotic subsidiary cells as in the leaf sheath. HYPODERMIS usually including 2 or 3 (locally many more) markedly sclerotic layers. CORTEX including 3 or 4 innermost irregular series of large vascular bundles together with smaller bundles in outer cortex. Each bundle with a well-developed fibrous sheath external to the phloem; xylem sheathed by parenchyma, usually including only one wide metaxylem vessel and without extended protoxylem. CENTRAL CYLINDER with a peripheral zone of congested vascular bundles separated from each other by narrow bands of sclerotic parenchyma. Vascular tissues of peripheral bundles reduced to a single xylem element and a narrow phloem strand and completely sheathed by a wide fibrous cylinder. Inner limit of peripheral sclerotic zone showing a sharp transition to central region of central cylinder with its irregularly scattered bundles. Largest vascular bundles (apparently recently entered leaf traces), each including many wide metaxylem vessels, conspicuously extended protoxylem and a small phloem strand; fibrous sheath narrow and inconspicuous. Other vascular bundles (traces well below their insertion into a leaf), each with a single wide metaxylem vessel, no extended protoxylem and a complete, fibrous sheath. GROUND PARENCHYMA of inner part of central cylinder spongy and enclosing large intercellular spaces, individual cells rounded but not lobed, including abundant starch.

Stolons. Notable features include a wide cortex containing many scattered vascular bundles, the largest of which are either bicollateral or amphivasal, each surrounded by a complete fibrous sheath; a narrow central cylinder delimited from the cortex by a discontinuous endodermis of cells with U-shaped thickenings; peripheral tissues of central cylinder immediately within endodermis consisting of a congested region of irregular vascular bundles. Central vascular bundles less congested, usually collateral.

Root. (Structure described possibly not typical since only underground roots from juvenile plants and aerial roots from base of mature stems available.) (i) Underground roots: piliferous layer sometimes persistent, but usually shrivelled in old roots. EXODERMIS of narrow compact thick-walled cells with truncate ends, often separated from piliferous layer by 2 or 3 thin-walled layers. Cells of inner CORTEX very uniform; air lacunae absent. ENDODERMIS of mature roots with U-shaped wall thickenings; pericycle thin-walled, mostly 1-layered. STELE as in *Ravenala* and *Strelitzia* with wide vessels scattered throughout the central tissues together with scattered phloem strands each containing a wide sieve tube. (ii) Aerial roots: normal polyarch monocotyledonous root structure.

Silica, crystals, tannin, starch. SILICA CELLS. (i) "False stegmata" with thin walls present in discontinuous files, each cell including a stellate, druselike silica body (*Fig. 5, s.b.*); common in leaf and stem adjacent to vascular bundles; in lamina common adjacent to fibrous vascular buttresses and in cells of outer parenchymatous sheath; also common adjacent to transverse commissures. In leaf axis common adjacent to vascular bundles but absent from vicinity of abaxial fibrous strands; also frequent adjacent to transverse veins. (ii) Epidermal cells of stem, abaxial epidermis of leaf axis (*Figs. 9, 10*) and sometimes costal abaxial epidermal cells of lamina (*Fig. 2, s.b.*) developed as "true" stegmata, each with a spherical, spinulose silica body becoming enveloped by thickenings of inner tangential wall of cell; most obvious in leaf base. CRYSTALS. Calcium oxalate abundant as small rhombohedral crystals usually in clusters in ground parenchyma, common in assimilating cells of leaf, especially abundant in cells of transverse diaphragms of air lacunae. Raphide-sacs frequent in all parts but especially abundant in ground parenchyma of stem, common on surface of transverse diaphragms in air lacunae. TANNIN. Abundant in all parts of ground parenchyma in unmodified cells. STARCH. Abundant in ground parenchyma of stem as large, more or less ellipsoidal but not flattened or markedly eccentric grains; small grains often common in cells adjacent to vascular bundles of leaf axis.

Vascular tissues. VESSELS present only in root and stem; elements in underground roots (see root above) of the order of 1500 μ but up to 5000 μ long, 160–200 μ wide with either simple or scalariform perforation plates with few thickening bars on slightly oblique end walls. Elements of aerial roots shorter, narrower, never with simple perforation plates. Elements in stem 2000–2500 μ (or as short as 1250 μ) long, 125–160 μ wide, with oblique or very oblique scalariform perforation plates with many thickening bars. Vessels absent from stolons and leaf. SIEVE TUBES apparently with simple sieve plates in stem and leaf.

DISCUSSION

THE ANATOMY OF PHENAKOSPERMUM IN RELATION TO ITS SYSTEMATIC POSITION

Phenakospermum in relation to the Musaceae as a whole. From the information recorded here and in the previous publication (Tomlinson, 1959) it is evident that *Phenakospermum* shares most of the features by which *Strelitzia* and *Ravenala* can be distinguished from other members of the Musaceae. The following combination of anatomical features is common to these three genera:

Terminal subsidiary cells short and distinct from other epidermal cells; other cells adjacent to stomata sometimes different from remaining epidermal cells; adaxial hypodermis multiseriate (up to six layers deep); abaxial hypodermal cells arranged concentrically around substomatal chambers; longitudinal veins of lamina all buttressed to each hypodermis; all transverse septa of lamina including vascular tissues; petiole including several arcs of air canals; transverse diaphragms of air canals each several cells thick; chlorenchyma of leaf axis situated in an abaxial band; stem often an erect woody trunk without an endodermis; subterranean roots with an anomalous stele including uniformly scattered metaxylem vessels and phloem strands, the latter each including a single, wide sieve tube; internal silica cells thin-walled, each including a stellate, druselike silica body; silica cells often situated adjacent to transverse as well as longitudinal veins.

On the basis of this close anatomical similarity it is evident that these three genera form a very distinct and natural subunit within the Musaceae. This unit corresponds to the Strelitziaceae of Nakai (1948) but not that of Hutchinson (1959) which also includes *Heliconia*.

Phenakospermum, however, is of peculiar interest because it possesses a number of features which are not found in *Ravenala* and *Strelitzia* but which may be present in other members of the Musaceae. These features are indicated below together with the names of other genera of the Musaceae, in parentheses, which also possess them:

Stomata not sunken (*Heliconia, Musa, Orchidantha*); anticlinal epidermal walls of lamina markedly sinuous (*Heliconia*); inner wall of abaxial epidermal cells of lamina thicker than outer; transverse septa of lamina attached to abaxial hypodermis by well-developed, mostly sclerotic buttresses (the corresponding buttresses in *Ravenala* and *Strelitzia* are never markedly sclerotic; in *Musa* the transverse septa only occasionally include sclerotic elements); lateral parenchyma of veins of lamina always one-layered (*Orchidantha*); leaf axis including fibrous and vascular bundles adaxial to main vascular arc (*Heliconia, Musa, Orchidantha*); starch grains neither as flattened as in *Ravenala* nor as spherical as in *Strelitzia*; stegmata, i.e. silica cells with unequally thickened walls, common in abaxial epidermis of leaf (such cells have been recorded and illustrated for *Ravenala* by Solereder and Meyer but they have never been observed by me in either *Strelitzia* or *Ravenala*); vessels in the root sometimes bearing simple perforation plates (*Musa*).

Lane (1955) has emphasized that *Phenakospermum* is sufficiently distinct from *Ravenala* to make its acceptance as a separate genus very desirable. The above information supports this contention, since the anatomical differences between *Strelitzia* and *Ravenala*, both of which are accepted as good genera, are not greater than the structural differences between *Phenakospermum* on the one hand and *Strelitzia* and *Ravenala* on the other. Indeed, it is anatomically easier to recognize *Phenakospermum* than it is to distinguish *Ravenala* from *Strelitzia*. On the whole *Phenakospermum* seems to be something of a connecting link between *Ravenala* and *Strelitzia* and the rest of the Musaceae.

The relation between Phenakospermum, Strelitzia, and Ravenala. Lane has suggested that *Phenakospermum* has more affinity with *Strelitzia* than with *Ravenala* even though it was originally thought to be congeneric with *Ravenala*. Anatomical information which might throw light on the interrelationships between these three genera is presented below.

Phenakospermum and *Ravenala* share the following features which are not found in *Strelitzia*: Wax on abaxial surface of the lamina tabular; abaxial hypodermis of leaf axis markedly sclerotic in most regions; subsidiary cells adjacent to stomata of abaxial surface of the leaf axis sclerotic, especially in *Phenakospermum* (occasionally so in *Strelitzia* according to Solereder and Meyer); periderm apparently never developed. In *Strelitzia* the wax on the abaxial surface of the lamina is rodlike, the abaxial hypodermis of the leaf axis is apparently never sclerotic, and root and stem frequently develop a specialized periderm.

Phenakospermum and *Strelitzia* share the following features which are not developed by *Ravenala*: Abaxial hypodermis mostly one-layered; only two arcs of air canals in the petiole; air lacunae apparently absent from the underground roots; vessels present in the aerial stems.

Ravenala on the other hand has a consistently two-layered abaxial hypodermis, several arcs of air canals in the petiole which may be a result of its great size, air lacunae in the cortex of the root and no vessels in the stem. The last observation, however, is open to doubt and needs confirmation.

Even if these differences are constant, they are not sufficiently large to be of taxonomic significance, although it should be noted that the anatomical resemblances between *Phenakospermum* and *Ravenala* are to be found in features which are likely to be plastic and influenced considerably by environmental conditions and so may not be a reliable indication of phylogenetic affinity. On the basis of this assumption it could be said that

Phenakospermum shows more qualitative anatomical resemblance to *Strelitzia* than to *Ravenala*.

POSSIBLE PHYLOGENETIC IMPLICATIONS FROM THE ANATOMICAL OBSERVATIONS

In some respects *Phenakospermum* forms a connecting link between *Strelitzia* and *Ravenala* on the one hand and the rest of the Musaceae on the other, since, as has been shown above, many of the features in which it differs from *Strelitzia* and *Ravenala* are to be found in the remaining members of the Musaceae. In this respect it is particularly noteworthy that sinuous epidermal walls have previously only been recorded in *Heliconia*. This is of significance as it makes it easy to speculate on the possible evolution of the whole of the Musaceae from some ancestor with a *Phenakospermum*-like habit. *Ravenala* and *Strelitzia* would be least modified descendants, *Heliconia* and particularly *Orchidantha* would be most modified. It may also be significant that the anatomy of the stolons of *Phenakospermum* closely resembles that of the rhizomes of these herbaceous types. Thus by elimination of the erect woody trunk and persistence of the stolons it would be possible to produce rhizomatous plants of the *Heliconia* type. The fleshy corm of *Musa* and *Ensete* could have evolved from a woody trunk by telescoping of its internodes. The derivation of the Musaceae from an ancestor with a caulescent habit is implied by Lane in his paper, and he also suggests how the inflorescences of members of the family may be various modifications of the type shown by *Ravenala*. Thus it is possible to envisage the ancestral type from which the Musaceae have evolved as possessing the growth habit of *Phenakospermum* with the lateral inflorescence of *Ravenala*.

SUMMARY

The anatomy of the vegetative parts of *Phenakospermum guianense* is described for the first time. The systematic implications of these observations are that: (a) *Phenakospermum* is a valid genus; (b) together with *Ravenala* and *Strelitzia* it forms a natural unit within the Musaceae; (c) it may possibly be more closely allied to *Strelitzia* than to *Ravenala*. It is suggested that the Musaceae have evolved from an ancestor with the vegetative habit of *Phenakospermum* and the inflorescence of *Ravenala*.

BIBLIOGRAPHY

HUTCHINSON, J. The families of flowering plants. Vol. II. Monocotyledons. 2nd ed. Oxford. 1959.

LANE, I. E. Genera and generic relationships in Musaceae. Mitt. Bot. Staatssamm. München **13**: 114–141. 1955.

NAKAI, T. A new attempt to the classification of the Strelitziaceae. Bull. Tokyo Sci. Mus. **22**: 19–24. 1948.

SOLEREDER, H., and F. J. MEYER. Musaceae. *In* Systematische Anatomie der Monokotyledonen. Heft **6**: 1–26. 1930.

TOMLINSON, P. B. Studies in the systematic anatomy of the Zingiberaceae. Jour. Linn. Soc. Bot. **55**: 547–592. 1956.

———. An anatomical approach to the classification of the Musaceae. *Ibid.* 779–809. 1959.

DEPARTMENT OF BOTANY
UNIVERSITY OF LEEDS

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

KENNETH A. WILSON

CONVOLVULACEAE Jussieu (MORNING-GLORY FAMILY)

Annual or perennial herbs or woody plants, climbing or prostrate, rarely erect [or shrubby (more rarely trees)] without tendrils, the stem usually twining and with milky sap. Leaves alternate, simple, without stipules, rarely reduced to scales (*Cuscuta*). Flowers solitary or in cymes subtended by two opposite or subopposite bracts. Sepals 5 [rarely 4] free (rarely united at the base), imbricate. Corolla sympetalous, entire, 5-lobed or 5-parted [rarely 4], induplicate-valvate or contorted in bud. Stamens 5 (rarely fewer), inserted on the corolla tube, alternate with the corolla lobes; pollen spherical and spinulose, or spherical and smooth, or ellipsoid with parallel folds. Gynoecium syncarpous, the style solitary and simple or forked, or styles 2 (rarely 3 or 4), the ovary superior, 2- or 1-locular or at times subdivided by false partitions into 4 locules, rarely 3-locular. Ovules erect, anatropous, sessile, 2 in each locule (rarely solitary). Fruit a capsule, 2- or 3-locular with 1 or 2 seeds in each locule, usually dehiscing by valves or circumscissile, irregularly dehiscent, or indehiscent. Embryo straight, cotyledons folded or spirally coiled, rarely small or absent.

A world-wide family, primarily of the tropics and subtropics, but extending also into the temperate regions, and best represented in Asia and the Americas. Characterized by the presence of milky sap, bicollateral vascular bundles, plaited corollas, axile placentation, basal erect ovules, and folded cotyledons, the family consists of about 50 genera and 2000 species and is represented in our area by 10 genera.

On the basis of the structure of the pollen grains Hallier divided the family into two groups, the Psiloconiae with smooth pollen and the Echinoconiae with spinulose pollen (rank not designated) and into nine

---

[1] Prepared for a biologically oriented generic flora of the southeastern United States, a joint project of the Gray Herbarium and the Arnold Arboretum made possible through the support of George R. Cooley and the National Science Foundation, and under the direction of Reed C. Rollins and Carroll E. Wood, Jr. The scheme follows that outlined at the beginning of the series (Jour. Arnold Arb. **39**: 296–346. 1958). Other published portions of these studies will be found in Jour. Arnold Arb. **40, 41.** 1959, 1960. The area covered in this, as in former treatments, is bounded by and includes North Carolina, Tennessee, Arkansas, and Louisiana. Material included in descriptions which is inapplicable to our species is placed in brackets. References which have not been checked are marked by an asterisk.

tribes. Van Ooststroom has recently divided the family into two subfamilies (Cuscutoideae and Convolvuloideae), three tribes, and nine subtribes which are equivalent to Hallier's tribes.

Generic lines are difficult to draw in this family, and treatments vary with different authors depending upon the emphasis placed on the taxonomic characters used (e.g., pollen, bracts, corolla, style, stigmas, and fruit). Hallier's studies on the members of this family form the basis for the system of classification that is most generally followed. This system has found support in the studies of Van Ooststroom and of Meeuse, based on the Malaysian and the South African species respectively. Other studies (e.g., Roberty), discount the value of Hallier's conclusions but add little new information to our knowledge of the family. It is evident that the entire family is in need of intensive study, and that all characters must be thoroughly re-evaluated.

Both flowering and fruiting material is necessary for the correct determination of most of the genera of Convolvulaceae. It is in general not possible to determine species which are sterile. Collectors should therefore make every effort to collect material in both flowering and fruiting condition, to record the shape of the corolla and its color; and to press opened corollas carefully between waxed paper or facial or other similar tissue.

REFERENCES:

ALLARD, H. A. The direction of twist of the corolla in the bud, and twining of the stems in Convolvulaceae and Dioscoreaceae. Castanea **12:** 88–94. 1947.

BAILLON, H. Convolvulacées. Hist. Pl. **10:** 305–331. 1891.

BENTHAM, G., and J. D. HOOKER. Convolvulaceae. Gen. Pl. **2:** 865–881. 1876.

CHOISY, J. Convolvulaceae. DC. Prodr. **9:** 323–462. 1845.

HALLIER, H. Bausteine zu einer Monographie der Convolvulaceae. Bull. Herb. Boiss. **5:** 366–387, 736–754, 996–1013, 1021–1052. 1897; **6:** 714–724. 1898; **7:** 408–418. 1899.

———. Versuch einer natürlichen Gliederung der Convolvulaceen auf morphologischer und anatomischer Grundlage. Bot Jahrb. **16:** 453–591. 1893.

———. Convolvulaceae africanae. *Ibid.* **18:** 81–160. 1893.

———. Zur Convolvulaceenflora Amerika's. Jahrb. Hamburg. Wiss. Anst. **16** (Beih. 3): 19–56. 1899.

HOUSE, H. D. Notes on Convolvulaceae. Muhlenbergia **5:** 65–72. 1909. [Notes and new species in *Convolvulus*, *Jacquemontia*, *Operculina*, *Ipomoea*, and *Rivea*.]

JOHNSTON, M. C. Convolvulaceae in southern coastal Texas. Tex. Jour. Sci. **11:** 191–206. 1959.*

KNIGHT, R. J. An examination of certain evolutionary trends in the Convolvulaceae. Diss. Abs. **19:** 1175, 1176, 1958.*

———. Characters differentiating common morning-glories occurring in Virginia. Va. Jour. Sci. **10:** 63–69. 1959. [Species of *Ipomoea* and *Convolvulus*.]

MACBRIDE, J. F. Flora of Peru. Publ. Field Mus. Bot. **13**(5^1): 1–536. 1959. [Convolvulaceae, 455–536.]

MEEUSE, A. D. J. The South African Convolvulaceae. Bothalia **6:** 641–792. 1957.

O'DONELL, C. A. Convolvuloideas de Uruguay. Lilloa **29:** 349–376. 1959.

———. Convolvuláceas argentinas. *Ibid.* 87–348. *pls. 1–5.*

OOSTSTROOM, S. J. VAN. The Convolvulaceae of Malaysia. I. The genera *Cuscuta*, *Dichondra*, *Evolvulus*, *Bonamia*, *Neuropeltis* and *Porana*. Blumea **3:** 62–94. 1938; II. The genera *Jacquemontia*, *Aniseia*, *Convolvulus*, *Calystegia*, *Shutereia*, *Merremia*, *Operculina* and *Decalobanthus*. *Ibid.* 267–371. 1939; III. The genus *Ipomoea*. *Ibid.* 481–582. 1940; IV. The genera *Mina*, *Lepistemon*, *Stictocardia* and *Argyreia*. *Ibid.* **5:** 339–411. 1943; V. Key to the genera. *Ibid.* 689–691. 1945. VI. The genus *Argyreia* in the Philippine Islands. *Ibid.* **6:** 337–348. 1950.

———. Convolvulaceae. *In* D. G. G. J. VAN STEENIS. Flora Malesiana I. **4:** 388–512. 1953.

PARULEKAR, N. K. Stem anatomy of Convolvulaceae. Proc. Indian Sci. Congr. Assoc. **42**(3, abs.): 229. 1955.*

PETER, A. Convolvulaceae. Nat. Pflanzenfam. IV. **3a:** 1–40, 375–377. 1897.

RAO, K. V. R. Gametogenesis and embryogeny in five species of the Convolvulaceae. Jour. Indian Bot. Soc. **19:** 53–69. 1940. [Species of *Ipomoea*, *Evolvulus*, *Argyreia*.]

ROBERTY, G. Genera Convolvulacearum. Candollea **14:** 11–65. 1952. [An unsatisfactory new system of classification of the family.]

SAYEEDUD-DIN, M. Observations on the anatomy of some of the Convolvulaceae. Proc. Indian Acad. Sci. B. **37:** 106–109. 1953.*

SHARMA, A. K., and A. K. CHATTERJI. A cytological investigation of some Convolvulaceae as an aid in understanding their lines of evolution. Phyton Buenos Aires **9:** 243–257. 1957.

VERDCOURT, B. Notes from the East African Herbarium — VI. Notes on African Convolvulaceae (Part 2). Kew Bull. **1958:** 185–197. 1958. [*Merremia*, *Stictocardia*, *Astripomoea*.]; (Part 3). *Ibid.* 199–217. [*Ipomoea*, *Turbina*.]

———. Some notes on tropical African Convolvulaceae. Webbia **13:** 321–330. 1958.*

WOLCOTT, G. B. Chromosome numbers in the Convolvulaceae. Am. Nat. **71:** 190–192. 1937. [Undocumented.]

KEY TO THE GENERA OF CONVOLVULACEAE

A. Leaves scale-like or absent; plant without chlorophyll (parasitic); corolla bearing scales at base of stamens; embryo coiled, without cotyledons. .... 1. *Cuscuta*.

A. Leaves well developed; plants green (autotrophic); corolla without scales; embryo straight or merely curved; cotyledons large, generally folded.

  B. Styles 2, gynobasic, corolla deeply 5-lobed, ovary and capsule deeply 2-lobed, the carpels distinct or only slightly fused; creeping vines rooting at the nodes with minute flowers. .... 2. *Dichondra*.

  B. Style 1 or 2, terminal; ovary and capsule not 2-lobed, the carpels united.

    C. Styles 2, free or fused near the base.

      D. Styles free, each 2-cleft, stigmas 4, linear-filiform; leaves small, plants never twining. .... 3. *Evolvulus*.

      D. Styles united near the base, stigmas 2, peltate. .... 4. *Bonamia*.

    C. Style solitary.

E. Capsule valvate, irregularly dehiscent or the pericarp basally circumscissile.
  F. Stigmas 2.
    G. Stigmas elliptic or oblong, flattened. 5. *Jacquemontia.*
    G. Stigmas filiform or subulate. .... 6. *Convolvulus.*
  F. Stigmas 1, capitate or 2- or 3-lobed.
    H. Pollen smooth; stigmas 2-lobed, globose; fruit a 4-valved capsule or the pericarp basally circumscissile. .... 7. *Merremia.*
    H. Pollen spinulose; stigma 1, capitate or 2- or 3-lobed, globose; fruit a 4–6-valved capsule. .... 8. *Ipomoea.*
E. Capsule indehiscent, pericarp leathery or woody.
  I. Ovary 2-locular, fruit woody, mostly 1-seeded; leaves glabrate. .... 9. *Turbina.*
  I. Ovary 4-locular, fruit leathery, mostly 4-seeded; leaves densely sericeous on the lower surface. .... 10. *Argyreia.*

1. **Cuscuta** Linnaeus, Sp. Pl. 1: 124. 1753; Gen. Pl. ed. 5. 60. 1754.

Parasitic yellowish, orange or reddish (rarely greenish) twining plants with filiform stems and alternate scale-like leaves; stems attached to the host by small haustoria. Flowers in cymose clusters, white. Calyx of 5 (rarely 4) united (rarely free) sepals. Corolla of 5 (rarely 4) petals, imbricate, with fimbriate scales at the base of the tube, as many as and below and opposite the stamens [or rarely lacking]. Pollen ellipsoid, smooth. Gynoecium of 2 (rarely 3) carpels; ovary 2(rarely 3)-locular, each locule with 2 basal, anatropous ovules; styles distinct or united. Fruit an indehiscent, irregularly dehiscent, or circumscissile capsule. Embryo spirally coiled, without cotyledons. Endosperm fleshy. TYPE SPECIES: *C. europaea* L. (Derivation of name uncertain, perhaps from Arabic.) — DODDER (also LOVE VINE, STRANGLE WEED, DEVIL'S GUT, GOLD THREAD, PULL DOWN, HELLBINE, HAIRWEED, DEVIL'S HAIR, HAILWEED).

A world-wide genus of over 150 species centered primarily in the Americas where they occur from southern Canada south to Chile and Argentina; about 32 native and 18 introduced species in the United States; represented in our area by at least 19 species in two of the three subgenera. None of the species seems to be limited to a single host although certain ones are serious agricultural pests, particularly of clover and alfalfa (*C. Epithymum* Murray, *C. indecora* Choisy, and *C. Gronovii* Willd.).

Subgenus GRAMMICA (Loureiro) Engelm. (flowers with distinct styles and globose, peltate or convoluted stigmas) includes most of the native American species and about sixteen of our species. Subgenus MONOGYNA (Engelm.) Yuncker (flowers with united styles) is primarily Old World in its distribution and is represented in our area by one native (*C. exaltata* Engelm.) and one introduced species (*C. japonica* Choisy). The species of subg. CUSCUTA (flowers with distinct styles and elongate cylindrical stigmas) are all native to the Old World, although several of them, including *C. Epithymum* and *C. Epilinum* Weihe, have been introduced into North America. *Cuscuta Epithymum* may perhaps occur in our area on leguminous crops.

Cuscuta is at times treated as a separate family Cuscutaceae, primarily on the basis of its parasitic habit and imbricate corolla with scales. Embryological details, such as the absence of parietal cells in the nucellus, the persistence of one of the synergids, and the spirally coiled embryo without cotyledons and without tissue differentiation, have been cited in support of this separation. Both floral structure and embryology seem to be very similar to those of the Convolvulaceae, however. Such differences as do exist support the separate tribe Cuscuteae Benth. & Hook. or perhaps even the subfamily Cuscutoideae Peter.

Since the generative cell divides before the pollen is shed, the mature pollen grain is three-celled. All species which have been studied have a monosporic embryo sac of the "Polygonum" type, with the exception of *Cuscuta reflexa* Roxb., which has a bisporic, "Allium" type embryo sac. The ovule has a single integument which is differentiated in the seed into an epidermis, two layers of palisade-like cells, and several layers of small, thin-walled, starch-filled cells. Keys have been prepared for the identification of the seeds of various species, but the seeds require a considerable amount of sectioning in order to show the layers of the seed-coat.

The seed can germinate as soon as it matures, or it may remain viable in the soil for five or more years. The seedling is leafless with a very small root which dries up as soon as the plant becomes established on a suitable host. In order to control and eradicate *Cuscuta* from agricultural fields it is recommended that it be prevented from seeding during its first season's appearance.

Diploid chromosome numbers of 14, 28, 32, 42, 56, and 60 have been found. Both self-fertile and self-sterile species are known. It is possible, however, that the self-sterility of *C. suaveolens* Ser. and *C. subinclusa* Durand & Hilgard is a result of abnormal meiosis, such as has been demonstrated in *C. reflexa* Roxb. ($2n = 28, 32, 42$), rather than of self-incompatibility.

REFERENCES:

(For a more extensive bibliography see DEAN 1936, 1937, and YUNCKER 1921, 1927.)

BENNETT, C. W. Studies of dodder transmission of plant viruses. Phytopathology **34:** 905–932. 1944.

BEZRUCHENKO, N. Z. Biology of dodders. (In Russian) Soviet. Bot. **15:** 213–217. 1947.

BUNNING, E., and R. KAUTT. Über den Chemotropismus der Keimlinge von *Cuscuta europaea.* Biol. Centralb. **75:** 356–359. 1956.*

DEAN, H. L. Dodder overwintering as haustorial tissues within *Cuscuta*-induced galls. Proc. Iowa Acad. Sci. **61:** 99–106. 1954.

———. *Cuscuta* as a parasite on pteridophytes. Ann. Bot. **50:** 823–825. 1936.

———. An addition to bibliographies of the genus *Cuscuta.* Univ. Iowa Stud. Nat. Hist. **17**: 191–197. 1937.

FEDORTSCHUK, W. Embryologische Untersuchung von *Cuscuta monogyna* Vahl und *Cuscuta Epithymum* L. Planta **14**: 94–111. 1931.

FINN, V. V. Vergleichende Embryologie und Karyologie einiger *Cuscuta*-Arten. (In Ukranian; German summary.) Zhur. Inst. Bot. URSR 12(20): 83–99. 1937.

FOGELBERG, S. O. The cytology of *Cuscuta.* Bull. Torrey Bot. Club **65**: 631–645. 1938.

FRITSCHÉ, E., M. BOUILLENNE-WALRAND, and R. BOUILLENNE. Quelques observations sur la biologie de *Cuscuta europaea* L. Bull. Sci. Acad. Roy. Belg. V. **44**: 163–187. 1958.

GAERTNER, E. E. Studies of seed germination, seed identification, and host relationships in dodders, *Cuscuta* spp. Mem. Cornell Univ. Agr. Exp. Sta. **294**: 1–56. 1950.

LACKEY, C. F. Reaction of dodders to stems of other dodders and to their own stems. Phytopathology **36**: 386–388. 1946.

LEE, W. O., and F. L. TIMMONS. Dodder and its control. U. S. Dep. Agr. Farmers' Bull. **2117**: 1–20. 1958.

LOO, S. W. Cultivation of excised stem tips of dodder in vitro. Am. Jour. Bot. **33**: 295–300. 1946.

MACPHERSON, G. E. Comparison of development in dodder and morning glory. Bot. Gaz. **71**: 392–398. 1921. [*C. Gronovii* and *Convolvulus sepium.*]

NARAYANA, H. S. Diffuse type of parasitism in *Cuscuta hyalina* Roth. Sci. Cult. **21**: 447–450. 1956.*

PAZOUREK, J. Anatomical observations of the parasitism of *Cuscuta.* Preslia **30**(2): 121–125. 1958.

RAGHAVAN, R. S. Chromosome numbers in Indian medicinal plants. Proc. Indian Acad. Sci. B. **45**: 294–298. 1957. [*C. reflexa*, $n = 16$.]

SMITH, B. E. A taxonomic and morphological study of the genus *Cuscuta*, dodders, in North Carolina. Jour. Elisha Mitchell Sci. Soc. **50**: 283–302. 1934.

SOUÈGES, R. À propos de l'embryogénie des *Cuscuta.* Bull. Soc. Bot. Fr. **100**: 28–34. 1953. [*C. hyalina* Ruth, *C. planiflora* Tenore, *C. reflexa* Roxb.]

STEVENS, O. A. Dodder (*Cuscuta*) on cultivated plants. N. Dak. Agr. Exp. Sta. Bimonthly Bull. **15**: 80, 81. 1952.*

TIAGI, B. A contribution to the morphology and embryology of *Cuscuta hyalina* Roth and *C. planiflora* Tenore. Phytomorphology **1**: 9–21. 1951.

TRONCHET, J. Action de l'acide 2.4-dichlorophénoxyacétique à 0,2% sur de jeunes plantules de *Cuscuta gronovii* Willd: élongation intense, géotropisme inversé et développement d'entre-noeuds. Compt. Rend. Acad. Sci. Paris **244**: 1811–1813. 1957.

———. Mise en évidence de l'hydrotropisme des plantules de *Cuscuta gronovii* Willd. *Ibid.* **245**: 979–981. 1957.

———. Variations periodique de masse fraiche des plantules de *Cuscuta gronovii* Willd. cultivées en conditions constantes éventualité d'un rythme endogène. Bull. Soc. Fr. Physiol. Veg. **4**(3): 88, 89. 1958.*

TRUSCOTT, F. H. On the regeneration of new shoots from isolated dodder haustoria. Am. Jour. Bot. **45**: 169–177. 1958.

VALENTA, V. A new yellows virus causing flower proliferations in the dodder, *Cuscuta campestris* Yunck. Phytopath. Zeitschr. **33**: 316–318. 1958.

YUNCKER, T. G. Revision of the North American and West Indian species of

Cuscuta. Ill. Biol. Monogr. 6(2/3): 1–141. *pls. 1–13*. 1921. [Includes bibliography.]

———. Additions to a bibliography of the genus *Cuscuta*. Proc. Indiana Acad. Sci. 36: 259–262. 1927.

———. The genus *Cuscuta*. Mem. Torrey Bot. Club 18: 113–331. 1932.

———. *Cuscuta americana* in Florida. Torreya 35: 60. 1935.

———. Convolvulaceae Lindl. 1. *Cuscuta* (Tourn.) L. *In* Fl. Texas 3: 123–150. South. Methodist Univ. 1943.

———. Nomenclatural changes in the genus *Cuscuta*, and notes on some American species. Bull. Torrey Bot. Club 70: 61–67. 1943.

———. *Cuscuta japonica* Choisy, an Asiatic species new to America. Torreya 44: 34, 35. 1944. [Florida and Texas.]

———. Observations on the presence of stomata in some species of *Cuscuta*. Proc. Indiana Acad. Sci. 53: 100–104. 1944.

2. **Dichondra** J. R. & G. Forster, Char. Gen. Pl. 39. *pl. 20*. 1776.

Creeping, perennial, pubescent herbs with reniform to orbicular alternate leaves, the stems rooting at the nodes. Flowers small, inconspicuous, solitary in the axils of the leaves, the peduncle subtended by a minute bract. Calyx of 5 sepals, free or united only at the base. Corolla 5-parted, broadly campanulate to rotate. Styles 2, gynobasic, the stigmas capitate; ovary deeply 2-lobed, each lobe with 2 basal, anatropous ovules. Fruit a 2-lobed, indehiscent or irregularly dehiscent capsule, each lobe 1 (rarely 2)-seeded. TYPE SPECIES: *D. repens* Forst. (Name from Greek, *di*, two, and *chondros*, a grain, in reference to the fruit.)

A genus of perhaps five species, primarily of the Americas, but with one pantropical species (*Dichondra repens* Forst.) which is very variable, especially in the length and shape of the petals, the shape of the leaves, and in the pubescence. In our area the genus is represented by *D. repens* var. *carolinensis* (Michx.) Choisy which occurs on roadsides, in pinelands, hammocks, and as a weed in lawns from Florida to Virginia, west to Texas and Arkansas. *Dichondra repens* is also grown as a ground cover, often as a lawn plant. Although the genus is small and the species are relatively common, the group has not been well collected and is poorly understood. A thorough study is needed to determine the nature and variation of the species and to evaluate the present classification. The differences evident in the size of both plants and leaves of var. *carolinensis* may be in response to the habitat or the difference may be more fundamental.

There seem to be no characters other than the gynobasic style and the two nearly separate carpels of *Dichondra* to support the segregate family Dichondraceae, and the genus otherwise agrees well with the genera of the Convolvulaceae. However, additional studies, both morphological and cytological, should provide evidence with respect to the relationships of this genus. *Dichondra* is most nearly related to *Falkia* L. f., a small genus of about four species of Africa, which is characterized by a 4-lobed ovary and a gamosepalous calyx.

REFERENCES:

DREW, W. B. Dew drop "grass" as a lawn plant in central Missouri. Ecology **25**: 246, 247. 1944. [*Dichondra repens.*]

HOUSE, H. D. A new species of *Dichondra.* Muhlenbergia **1**: 130, 131, 1906. [*D. occidentalis* in California.]

HOWELL, J. T. A ground cover. Leafl. West. Bot. **2**: 174. 1939. [*D. occidentalis.*]

PARODI, D. Nota sobre una nueva especies del género *Dichondra.* Ann. Soc. Cient. Arg. **13**: 5–10. 1882. [*D. villosa.*]

3. **Evolvulus** Linnaeus, Sp. Pl. ed. 2. 1: 391. 1762.

Diffuse herbs or suffrutescent plants with prostrate or ascending branches, never twining, bearing entire leaves. Flowers sessile or pediceled, solitary in the axils of the leaves [or in terminal cymes]. Calyx of 5 free sepals. Corolla white, blue or purple, funnelform to rotate, the limb 5-angled or distinctly 5-lobed. Stamens 5, inserted on the corolla tube, exserted or included. Pollen globular, smooth. Styles 2, free or united at the base, each 2-cleft, the stigmas linear-filiform; ovary 2-locular, each locule with 2 ovules. Fruit a 1–4-seeded capsule. Seeds smooth or minutely verrucose. TYPE SPECIES: *E. nummularius* L. (Name from Latin *evolvere*, to unroll, in reference to the nontwining habit.)

A primarily tropical genus of perhaps 100 species, all of the Americas, from southern United States south to Argentina, but with two (*E. alsinoides* L. and *E. nummularius* L.) extending into tropical areas in the Old World. The genus, characterized by its distinct, 2-cleft styles, has been divided into eight sections, primarily on the basis of the inflorescence, the length of the peduncles, and the habit of the plant. Five species occur in our area, all members of sect. ALSINOIDES Meissn.

Evolvulus alsinoides L. is distributed throughout the tropical regions of the world and occurs in waste places and in hammocks in the Florida Keys. It is a polymorphic species in which 15 varieties have been described, although none seems to be very clear-cut; var. *Grisebachianus* Meissn. is reported from our area. Our other species are *E. glaber* Spreng., *E. sericeus* Sw., *E. Grisebachii* Peter (*E. Wrightii* House), *E. Nuttallianus* Roemer & Schultes (*E. argenteus* Pursh, *E. pilosus* Nutt.). *Evolvulus macilentus* Small, described from the lower Florida Keys, may represent a glabrous form of *E. sericeus.*

REFERENCES:

OOSTSTROOM, S. J. VAN. A monograph of the genus *Evolvulus.* Meded. Bot. Mus. Utrecht **14**: 1–267. 1934.

PERRY, L. M. *Evolvulus pilosus* an invalid name. Rhodora **37**: 63. 1935. [= *E. Nuttallianus* Roemer & Schultes.]

SAYEEDUD-DIN, M. Some common Indian herbs with notes on their anatomical character. VIII. *Evolvulus alsinoides* Linn. Jour. Bombay Nat. Hist. Soc. **42**: 816–818. *pls. 1–3.* 1941.

VARADAN, K. S. S., T. S. VAIDYANATHAN, and M. V. R. RAO. Phytochemistry of *Evolvulus alsinoides* Linn. Indian Jour. Pharm. 20(4): 100–105. 1958.*

4. **Bonamia** DuPetit-Thouars, Hist. Vég. Isl. France Réunion, Madagascar 1: 33. *pl. 8.* 1804, nom. cons.

Perennial, herbaceous [or woody], prostrate or twining vines [rarely erect undershrubs] with alternate, herbaceous or subcoriaceous entire leaves. Flowers axillary, solitary, or in cymes. Sepals 5, equal or subequal. Corolla 5-lobed, blue or white, campanulate or funnelform. Stamens 5, inserted on the corolla tube, included or slightly exserted; pollen smooth. Style deeply 2-cleft (or styles free, 2, rarely 1), stigmas peltate, ovary 2-locular, each locule with 2 ovules. Fruit a 2-, 4- or 8-valved capsule. (Including *Breweria* R. Br., *Stylisma* Raf.; not *Bonamya* Neck., nom. rejic.) TYPE SPECIES: *B. madagascariensis* Poir. (Named in honor of François Bonami, 1710–1786, French physician and botanist.)

A genus of 40 or more species widely distributed in the tropics of the world, represented in our area by seven species. The genus includes species of very different habit but it may be distinguished by the bifid style and the capitate stigmas. Various attempts have been made to split the genus, and, as a result, our species, with the exception of *Bonamia grandiflora* (Gray) Hallier, have been placed in *Stylisma* Raf., primarily on the basis of their more slender stems and more herbaceous habit. This group does not seem to be clearly separable from *Bonamia*, although it may represent a natural group within the genus. The problem of the generic limits of *Bonamia* is further complicated by *Seddera* Hochst. of the Old World, and a detailed study of all these species with a view of clarifying the genera would be highly desirable.

All of our species, except *Bonamia Pickeringii* (Torrey in M. A. Curtis) Gray, occur in Florida in sandy soil or in dry pinelands. Of these *B. humistrata* (Walt.) Gray extends into eastern Texas and north into southeastern Virginia, *B. aquatica* (Walt.) Gray (*Stylisma trichosanthes* of Small) north to Alabama and North Carolina, *B. Michauxii* [2] (*Stylisma aquatica* of Small) west to Texas and north to North Carolina. *Bonamia villosa* [3] and *B. angustifolia* [4] are both limited to Florida. *Bonamia Pickeringii* is represented in the sandhills of Georgia and from Wilmington, North Carolina, by plants which have been interpreted as two different varieties. Additional variants of this species occur in the pine barrens of New Jersey, and from Texas north to Iowa and Illinois.

---

[2] **Bonamia Michauxii** (Fern. & Schubert) K. A. Wilson, comb. nov. *Breweria Michauxii* Fern. & Schub., Rhodora 51: 37. 1949.

[3] **Bonamia villosa** (Nash) K. A. Wilson, comb. nov. *Breweria villosa* Nash, Bull. Torrey Bot. Club 22: 154. 1895.

[4] **Bonamia angustifolia** (Nash) K. A. Wilson, comb. nov. *Breweria angustifolia* Nash, Bull. Torrey Bot. Club 22: 155. 1895.

REFERENCES:

See family references, HALLIER (1893, **16**: 527, 528), VAN OOSTSTROOM (1938, 75–80; and 1953).

FERNALD, M. L., and B. G. SCHUBERT. Some identities in *Breweria*. Rhodora **51**: 35–43. *pls. 1121–1129*. 1949. [Reprinted as Contr. Gray Herb. **169**. 1949.]

HOUSE, H. D. Studies in the North American Convolvulaceae. III. *Calycobolus*, *Bonamia* and *Stylisma*. Bull. Torrey Bot. Club **34**: 143–149. 1907.

5. Jacquemontia Choisy, Mém. Soc. Phys. Genève **6**: 476. 1833.

Herbaceous or woody, prostrate or twining vines [rarely erect undershrubs] with entire or lobed leaves. Flowers axillary in cymes or dense terminal clusters [rarely solitary], with or without an involucre. Sepals 5, equal or unequal. Corolla entire, 5-toothed or 5-lobed, funnelform or campanulate. Stamens 5, inserted on the corolla tube, included; pollen smooth. Style simple, included; stigmas 2, elliptic or oblong, flattened; ovary 2-locular, each locule with 2 ovules. Fruit a 4- or 8-valved capsule. (Including *Thyella* Raf.) TYPE SPECIES: *J. ferruginea* (Steud.) Choisy. (Name in honor of Victor Jacquement, 1801–1832, French botanical explorer.)

About 120 species in 4 sections, primarily of the American tropics and subtropics, but also with a few species in the Old World; represented in our area by five species in two sections. Sections ANOMALAE Meissn. (flowers 1–3, or in loose, many-flowered inflorescences) and CAPITULIFLORAE Ooststr. (flowers in the axils of the upper leaves, aggregated into dense globose or ovoid terminal spikes) are apparently limited to the American tropics in their distribution; neither occurs in our area.

Sect. CAPITATAE Meissn. (inflorescence many-flowered, flowers in dense terminal clusters usually surrounded by bracts) is represented in the southeastern United States by *Jacquemontia tamnifolia* (L.) Griseb. (*Thyella tamnifolia* (L.) Raf.) which occurs in fields and thickets, often as a weed in cultivated areas, from Florida north to southeastern Virginia and west to Louisiana, Arkansas, and Texas. Our other species are in sect. CYMOSAE Meissn. (inflorescence 5–many-flowered loose dichasia), and in our area are found only in southern Florida. *Jacquemontia jamaicensis* (Jacq.) Hallier and *J. pentantha* (Jacq.) G. Don are known also in the West Indies, while *J. Curtissii* Peter ex Hallier and *J. reclinata* House are found only in southern peninsular Florida.

REFERENCES:

See family references, HOUSE (1909), and VAN OOSTSTROOM (1939, p. 266; 1953).

FOX, W. B., R. K. GODFREY, and H. L. BLOMQUIST. Notes on distribution of North Carolina plants — III. Rhodora **54**: 165–182. 1952. [*Jacquemontia tamnifolia* in North Carolina.]

SMALL, J. K. *Jacquemontia reclinata*. Addisonia **18**: 35, 36. *pl. 594*. 1934.

6. **Convolvulus** Linnaeus, Sp. Pl. 1: 153. 1753; Gen. Pl. ed. 5. 76. 1754.

Herbaceous or more or less woody, perennial [or annual], prostrate, twining or erect plants with ovate to oblong leaves, cordate, sagittate or hastate at the base. Flowers axillary, solitary or in peduncled cymes. Calyx of 5 subequal sepals, the bracts minute, linear, and remote from the calyx, or persistent and enveloping the calyx. Corolla campanulate to funnelform, white or pink. Stamens 5, included, unequal in length; pollen smooth, ellipsoid and tricolpate or globular and polyforate. Ovary 1-locular, 2-locular or imperfectly 2-locular; stigmas 2, ovoid to ellipsoid, linear or filiform. Fruit a 4-valved capsule with 4 or fewer seeds. (Including *Strophocaulos* Small, *Calystegia* R. Br.) TYPE SPECIES: *C. arvensis* L. (The name from the Latin *convolvere*, to entwine.) — BINDWEED.

A genus of about 250 species in the temperate and tropical regions of both hemispheres, represented in our area by four or perhaps more species. The genus is interpreted here in the broad sense to include species frequently segregated as *Calystegia* R. Br., here maintained as a section.

Section CONVOLVULUS (*Strophocaulos* Small) is represented in our area by the single weedy species *C. arvensis*, field bindweed ($2n = 50$), native to Eurasia but now widespread in the temperate areas throughout the world and often becoming a serious pest. The species occurs in our area in fields, roadsides, and waste places from northern Florida, north and west throughout our area and beyond it. It is very variable in the shape of its leaves, and at least three of the forms have been named.

Section CALYSTEGIA (R. Br.) Gray, which includes about 25 species of both hemispheres, is represented in our area by three or perhaps more species. Members of this section are distinguished by the two large bracts which subtend the calyx and envelop it, the generally larger flowers, the 1-locular or incompletely 2-locular ovary, the ovoid or ellipsoid stigmas, and the globose, polyforate pollen. *Convolvulus sepium* L. ($2n = 22, 24$), a very variable species distributed throughout most of the temperate areas of the world, is represented in the Southeast by at least three named varieties based primarily on the shape of the leaves. *Convolvulus sepium* var. *sepium* (including *C. americanus* (Sims) Greene), with broadly ovate leaves with angulate, truncate or rounded basal lobes and a U- or V-shaped leaf sinus, is the European form and is now distributed in eastern North America as far west as Missouri and Illinois, and also in New Mexico and Oregon. Varietas *fraterniflorus* Mack. & Bush (leaves with quadrangular sinuses) is reported from Pennsylvania to North Dakota, south to Virginia, Kentucky, and Arkansas, growing on roadsides and in fields and wasteplaces. Varietas *repens* (L.) Gray (leaves lance-ovate to lanceolate, mostly longer than broad) occurs on shores, beaches, and dunes along the coast from Florida north to New Brunswick, west to Texas, and also north to Ohio, Indiana and Wisconsin. *Convolvulus sericatus* House, closely allied to *Convolvulus sepium*, was described from the mountains of Georgia and has also been reported from the mountains of North Carolina.

Convolvulus spithamaeus L. (2*n* = 22) (including *C. Purshianus* Wherry) occurs on sandy or rocky soil, shale barrens, road cuts, rocky woods and dunes from southeastern Canada south to Georgia and Alabama and west to Minnesota and Iowa. The variation of this species is complex and needs careful study on a population basis. Two to four varieties or subspecies have been recognized.

Convolvulus pellitus Ledeb. forma *anestius* Fern. (*Convolvulus japonicus* Thunb. of Small), with double flowers and sterile, has been introduced as a cultivated plant and is now naturalized from Maine to Michigan, south to Virginia, Tennessee, and Missouri.

REFERENCES:

See family references, HOUSE (1909), KNIGHT (1959), VAN OOSTSTROOM (1939, pp. 282–286; 1953).

BROWN, E. O. Notes on some variations in field bindweed (*Convolvulus arvensis* L.). Iowa State Coll. Jour. Sci. **20**: 269–276. 1946.

CALL, L. W., and R. E. GETTY. The eradication of bindweed. Kansas Agr. Exp. Sta. Circ. **101**: 1–18. 1923.*

CRAFTS, A. S., and P. B. KENNEDY. The physiology of *Convolvulus arvensis* (morning-glory or bindweed) in relation to its control by chemical sprays. Pl. Physiol. **5**: 329–344. 1930.

FEHÉR, J. Kleistopetalie bei *Calystegia sepium* und *Pharbitis purpurea*. (Hungarian; German summary.) Bot. Közlem. **27**: 38–42. 1930.

FERNALD, M. L. Studies of eastern American plants. 4. Emendations in the order Tubiflorae. Rhodora **51**: 70–85. 1949. [Notes on *C. spithamaeus*, *C. sepium*, and *C. pellitus*.]

———. Errors in citation in *Agrostis* and *Convolvulus*. Rhodora **51**: 192, 193. 1949. [Correction in citation of *C. sepium* var. *repens*.]

FRAZIER, J. C. Nature and rate of development of root system of *Convolvulus arvensis*. Bot. Gaz. **104**: 417–425. 1943.

———. Amount, distribution and seasonal trend of certain organic reserves in the root system of field bindweed, *Convolvulus arvensis* L. Pl. Physiol. **18**: 167–184. 1943.

———. Food reserve depletion and synthesis in field bindweed, *Convolvulus arvensis* L., as related to 7-day and 14-day intervals of cultivation. *Ibid.* 315–323.

HAMILTON, R. D., C. J. WHITFIELD, and H. E. REA. Soil treatments for field bindweed (*Convolvulus arvensis*) eradication in northwest Texas. Tex. Agr. Exp. Sta. Prog. Rep. **1304**: 1–4. 1950.*

———. Control of extensive infestation of bindweed (*Convolvulus arvensis*) in northwest Texas. Tex. Agr. Exp. Sta. Prog. Rep. **1392**: 1–5. 1951.*

HOUSE, H. D. A new southern *Convolvulus*. Torreya **6**: 149, 150. 1906. [*C. sericatus* from Georgia.]

MACKENZIE, K. K., and B. F. BUSH. New plants from Missouri. Missouri Bot. Gard. Ann. Rep. **16**: 102–108. 1905. [*C. fraterniflorus*.]

MACPHERSON, G. E. Comparison of development in dodder and morning glory. Bot. Gaz. **71**: 392–398. *pls. 25–27.* 1921. [*C. sepium*.]

PALMER, S. C. *Convolvulus Wallichiana* at Swarthmore, Pennsylvania. Rhodora **47**: 332. 1945.

PERSY, J. Nouvelles observations sur le comportement du nucléole dans la caryocinèse somatique de *Calystegia sepium* R. Br. (*Convolvulus sepium* L.) et sur sa nèoformation. Bull. Soc. Bot. Belg. **68**: 222–233. 1936.

PRYOR, M. R. Morning glory: a progress report. Calif. Weed Conf. Proc. **8**: 116–118. 1956.* [*Convolvulus arvensis.*]

PURER, E. A. Growth behavior in *Convolvulus Soldanella* L. Ecology **17**: 541–550. 1936.

SOUÈGES, R. Embryogénie des Convolvulacées. Développement de l'embryon chez le *Convolvulus arvensis* L. Compt. Rend. Acad. Sci. Paris **205**: 813–815. 1937.

TORREY, J. G. Endogenous bud and root formation by isolated roots of *Convolvulus* grown in vitro. Pl. Physiol. **33**: 258–263. 1958.

TRYON, R. M., JR. The varieties of *Convolvulus spithamaeus* and of *C. sepium.* Rhodora **41**: 415–423. *pls. 557, 558.* 1939.

WHERRY, E. T. Four shale-barren plants in Pennsylvania. Proc. Penn. Acad. Sci. **7**: 160–164. 1933. [*C. Purshianus* Wherry, p. 163.]

———. Our dwarf bindweeds. Bartonia **28**: 32, 33. 1957. [*Convolvulus spithamaeus*; recognizes four subspecies.]

7. **Merremia** Dennstaedt ex Hallier, Bot. Jahrb. **16**: 581. 1893.

Herbaceous or woody twining vines [or plants prostrate, rarely erect] with entire, dentate, or palmately lobed or compound leaves. Flowers axillary, solitary or in few- to many-flowered cymose [or variously branched] inflorescences. Calyx of 5 subequal sepals, coriaceous to herbaceous, accrescent in several species. Corolla campanulate or funnelform, white or yellow to orange, slightly 5-lobed. Stamens 5, included, unequal in length, the anthers often contorted; pollen smooth. Ovary 2- or 4-locular, stigma 2-lobed, globose. Fruit a 1–4-seeded, 4-valved capsule or an irregularly dehiscent capsule with the pericarp circumscissile at the base. (*Operculina* of Small.) TYPE SPECIES: *M. hederacea* (Burm. f.) Hallier. (Named in honor of Blasius Merrem, 1761–1824, professor at Marburg.)

About 80 species in five sections widely distributed in the tropics of both hemispheres. Characterized by its bilobed, globose stigmas and its 4-valved or irregularly dehiscent capsule, the genus is represented in our area by four species in two sections. Section XANTHIPS (flower bud obtuse or subacute; midpetaline bands indistinctly defined, never with dark lines) is known in our area by only *Merremia umbellata* (L.) Hallier (*Ipomoea polyanthes* Roem. & Schult.), a very variable species of the tropics of the world represented in the Americas by the yellow-flowered var. *umbellata.* Section STREPTANDRA (flower buds mostly acute; midpetaline bands in the dried state often with 5 dark lines) is represented in our flora by three species. *Merremia tuberosa* (L.) Rendle (*Operculina tuberosa* (L.) Meissn.), $2n = 30$, a glabrous vine with yellow flowers and entire-margined leaf segments, is reported from pinelands, hammocks, and waste places in Florida and Texas (fide Small) and is known also from the West Indies, tropical America, tropical Africa, India, and Ceylon. This species has been placed in the genus *Operculina* S. Manso because the pericarp of the irregularly dehiscent capsule separates from the receptacle, thereby forming an operculum. Van Ooststroom, however, has pointed out that this manner of dehiscence is clearly different from that of *Operculina* in which the pericarp is two layered and only the outer layer, not the entire pericarp, is circumscissile, while the inner layer remains attached. *Merremia dissecta* (Jacq.) Hallier (*Operculina dissecta* (Jacq.) House), $2n = 30$, a pubescent vine with white flowers and coarsely toothed leaf segments which occurs on roadsides and in hammocks and waste grounds from Florida to Georgia and Texas, ranges from the southeastern United States south to Argentina. It is also cultivated in other tropical areas where it occasionally escapes. The capsule of *M. dissecta* is 4-valved and the pericarp does not loosen from the receptacle as it does in *M. tuberosa*. *Merremia tridentata* (L.) Hallier ssp. *angustifolia* (Jacq.) Ooststr. (*Ipomoea angustifolia* Jacq.), a common African species, now occurs in waste places on the Coastal Plain and in other scattered localities.

REFERENCES:

See family references, MACBRIDE (1959), VAN OOSTSTROOM (1939, p. 292; 1953), VERDCOURT (1958).

FALCÃO, J. I. A. Contribuição ao estudo das espécies brasileiras do gênero *Merremia* Dennst. Rodriguesia **16–17**: 105–125. 1954.

HOUSE, H. D. Studies in the North American Convolvulaceae, II. The genus *Operculina*. Bull. Torrey Bot. Club **33**: 495–503. 1906.

O'DONELL, C. A. Las especies argentinas del genero "Merremia." Lilloa **5**: 35–64. *pls. 1–3.* 1940.

———. Revision de las especies americanas de "Merremia." *Ibid.* **6**: 467–554. *pls. 1–9.* 1941.

8. Ipomoea Linnaeus, Sp. Pl. 1: 159. 1753; Gen. Pl. ed. 5. 76. 1754.

Herbaceous or shrubby, annual or perennial, twining, prostrate or erect plants with entire, lobed or divided leaves. Flowers axillary, solitary or in few- to many-flowered cymes. Bracts variable. Calyx of 5 sepals, herbaceous or subcoriaceous. Corolla campanulate or funnelform, rarely salverform, with distinct midpetaline bands. Stamens 5, alternate with the corolla lobes, inserted on the corolla tube, included or rarely exserted; pollen globular, spinulose. Ovary 2- or 4-locular, rarely 3-locular, with 2 anatropous ovules in each locule. Style solitary, the stigma entire, 2(or 3)-lobed, globular, included or exserted. Fruit a 4–6-valved capsule with 4–6 or fewer seeds. (Including *Batatas* Choisy, *Quamoclit* Moench, *Pharbitis* Choisy, *Exogonium* Choisy, *Calonyction* Choisy.) TYPE SPECIES: *I. Pes-tigridis* L. (Name from Greek *ips*, a worm, and *homoios*, resembling, in reference to the twining habit.) — MORNING-GLORY.

A large genus of the tropics and subtropics with about 500 species and perhaps 30 or fewer in our area. The limits of the genus and its subdivision have been matters of considerable disagreement. Following Van Ooststroom, who adopted the system of Hallier with but little modification, the genus is divided into eight sections on the basis of the habit, inflorescence, flower, and seed characters, and includes a number of groups sometimes recognized as separate genera. Several other subdivisions of the genus have been proposed (cf. Choisy, Bentham, Peter, House) but the system most widely accepted is that of Hallier, although often with some minor modifications. A truly satisfactory generic treatment, however, must await a thorough monographic revision.

Section IPOMOEA (§ *Pharbitis* (Choisy) Griseb.) (mostly high-twining plants, hispid or lanate; flowers mostly showy; sepals herbaceous, oblong, lanceolate or linear; seeds glabrous, puberulent or shortly arachnoid) is represented in our area by about five species including *Ipomoea purpurea* (L.) Roth ($2n = 30$), introduced from tropical America as an ornamental, and now a pernicious weed along roadsides, waste places and in cultivated grounds throughout our area and also northward and westward. *Ipomoea hederacea* (L.) Jacq. ($2n = 30$), introduced from tropical America, is equally weedy on roadsides and waste places, and *I. Nil* (L.) Roth ($2n = 30$), a native of Africa has spread from cultivation into hammocks and cultivated grounds in Florida and Louisiana. *Ipomoea barbigera* Sweet and *I. congesta* R. Br. (*Pharbitis cathartica* (Poir.) Choisy) also occur in our area.

Section BATATAS (Choisy) Hallier (flowers mostly small, axillary in umbellate cymes; sepals mostly subcoriaceous, oblong or lanceolate; corolla funnelform; seeds glabrous) includes the widely cultivated *I. Batatas* (L.) Lam. ($2n = 90$), the sweet potato, with a large number of cultivars. The origin of the sweet potato has been the subject of considerable discussion and study. Present cytological evidence seems to indicate that it is an allopolyploid, resulting from the hybridization of a tetraploid and a diploid species. *Ipomoea trichocarpa* Ell. (*I. trifida* (HBK.) G. Don), *I. tiliacea* (Willd.) Choisy, and *I. triloba* L. are members of this section, and *I. pandurata* (L.) G. F. W. Meyer ($2n = 30$) and *I. lacunosa* L. may belong here.

Section LEIOCALYX Hallier (plants mostly glabrous, flowers solitary or in subumbellate dichasia, sepals mostly oblong or lanceolate, seeds mostly glabrous) is represented by *Ipomoea Pes-caprae* (L.) R. Br. in Tuckey ssp. *brasiliensis* (L.) Ooststr. ($2n = 30$) and *I. stolonifera* (Cyr.) J. F. Gmel., both of which occur on sandy beaches and coastal sand dunes from Florida to Texas and in tropical and subtropical countries of both hemispheres. Also to this section belong *I. cairica* (L.) Sweet ($2n = 30$), *I. sagittata* Lam. ($2n = 30$), and *I. heptaphylla* (Rottl. & Willd.) Voigt.

Section CALONYCTION (Choisy) Griseb. (annual or perennial twiners, mostly glabrous; flowers axillary, solitary or in a cincinnus or a dichasial cyme, nocturnal; sepals herbaceous to membranaceous, glabrous, or sometimes hirsute; corolla salverform, the tube long; stamens and style often exserted; ovary 2-locular or rarely 4-locular; capsule 4-valved; seeds glabrous) is represented with us by *Ipomoea alba* L. (*Calonyction aculeatum* (L.) House) in southern Florida where it grows in hammocks, often luxuriously following fire. A native of tropical America, it has been widely cultivated and has now escaped in the tropics of both hemispheres.

Section QUAMOCLIT (Moench.) Griseb. (annual or perennial twiners, mostly glabrous; flowers axillary in a cyme, rarely solitary; sepals herbaceous to membranaceous, glabrous; corolla salverform, often bright red, rarely yellow or white; stamens and style exserted; ovary 4-locular; capsule 4-valved, seeds glabrous rarely puberulent) includes about 15 species of the Americas, three in our area. *Ipomoea Quamoclit* L., with pinnately dissected leaves, a native of tropical America and widely grown as an ornamental, has spread from cultivation as far north as Virginia and Missouri. *Ipomoea coccinea* L., with cordate leaves, ranging from Georgia north to Rhode Island, Pennsylvania and Illinois and west to Kansas, Oklahoma and Arkansas, is limited to the United States in its distribution. This species has often been confused with *I. hederifolia* L., which ranges from Florida, Louisiana, Georgia, and Texas, south to northern Argentina (also in Malaysia and Africa), but may be distinguished by having the inner sepals up to 3 (rarely 4) mm. wide, the cordate leaves with the blade entire, dentate, or 3–5 lobed; fruiting pedicels always erect. (*See* O'Donell, 1959, pp. 45–51, for extensive synonymy.) Species of this section are adapted to pollination by hummingbirds.

Section ERIOSPERMUM Hallier (very variable perennial plants; sepals mostly obtuse; seeds with long-bearded edges, or rarely the whole surface villose) is known in our area by three species. *Ipomoea Tuba* (Schlecht.) G. Don (*Calonyction Tuba* (Schlecht.) Colla = *C. grandiflorum* (Jacq.) Choisy) grows along beaches and in saline situations in coastal hammocks in southern Florida and is distributed throughout tropical America, east tropical Africa, and Asia to Polynesia. *Ipomoea crassicaulis* (Benth.) B. L. Robinson (*I. fistulosa* Mart. ex Choisy) occurs from Florida and the West Indies, Mexico and Central America southward to Brazil and Paraguay, and is cultivated in other tropical countries where it occasionally escapes. *Ipomoea microdactyla* Griseb. (*Exogonium microdactylum* (Griseb.) House) a woody vine with bright red flowers, obtuse sepals, and seeds with long hairs on the edges, occurs in southern Florida and the West Indies.

A number of species of *Ipomoea* are popular in cultivation in the United States. Two of the best known are *I. Nil* Roth 'Scarlett O'Hara' and *I. tricolor* Cav. 'Heavenly Blue.'

REFERENCES:

Most of the extensive technical agricultural literature on *Ipomoea Batatas* has, of necessity, been omitted. See family references, HOUSE (1909), VAN OOSTSTROOM (1940, pp. 481–582; 1953), RAO (1940), and VERDCOURT (1958).

AHLES, H. E. *Ipomoea trichocarpa* Ell. and *Ipomoea trifida* G. Don. Jour. Elisha Mitchell Sci. Soc. **75**: 129. 1959. [The two are conspecific.]

ALLARD, H. A. A new form of the moonvine *Calonyction aculeatum* with divided corolla limb, and length-of-day behavior and flowering of the common form. Jour. Wash. Acad. Sci. **35**: 33–36. 1945. [Forma *apopetalum*.]

ASHBY, E., *et al.* Studies in the morphogenesis of leaves. I. New Phytol. **47**:

153–176. 1948; II. *Ibid.* 177–195. 1948; IV. *Ibid.* **49:** 23–35. 1950; V. *Ibid.* 189–192; VI. *Ibid.* 375–387; XI. *Ibid.* **55:** 91–110. 1956. [Mostly experiments on *I. caerulea.*]

BAEHNI, C. *Ipomoea heptaphylla* in Georgia and Mexico. Rhodora **38:** 164. 1936.

BRITTON, N. L. *Exogonium microdactylum.* Addisonia **1:** 33, 34, *pl. 17.* 1916.

BURKILL, I. H. Aji and Batata as group-names within the species *Ipomoea Batatas.* Ceiba **4:** 227–240. 1954. [History of discovery and diffusion of the sweet potato by the Spaniards and Portuguese.]

DORMER, K. J., and J. A. BENTLEY. Some complex relationships between auxin content and leaf area in *Ipomoea caerulea* Koen. New Phytol. **51:** 116–126. 1952.

FEDORTSCHUK, W. Entwicklung und Bau des mannlichen Gametophyten bei den Arten der Convolvulaceen-Gattung *Quamoclit.* Planta **16:** 554–574. 1932. [*I. coccinea, I. hederifolia, I. Quamoclit.*]

FEHÉR, J. Kleistopetalie bei *Calystegia sepium* und *Pharbitis purpurea.* (In Hungarian; Germany summary.) Bot. Közlem. **27:** 28–42. 1930.

GREULACH, V. A. Photoperiodic after effects in *Ipomoea.* Ohio Jour. Sci. **43:** 65–73. 1943. [*I. hederacea* and *I. purpurea.*]

HAGIWARA, T. Genetic studies of flower-colours in Japanese morning glories. (In Japanese.) Bot. Mag. Tokyo **44:** 573–595. 1930. [*I. Nil.*]

HARTER, L. L. Bud sports in sweet potatoes. Jour. Agr. Res. **33:** 523–525. *pl. 1.* 1926.

——— and J. L. WEIMER. A monographic study of sweet-potato diseases and their control. U.S. Dep. Agr. Tech. Bull. **99:** 1–117. *pls. 1–26.* 1929.

HARTMAN, J. The non-flowering character of sweet potatoes of the Jersey type. Pl. Physiol. **22:** 322–324. 1947.

HAYWARD, H. E. The seedling anatomy of *Ipomoea Batatas.* Bot. Gaz. **93:** 400–420. *pls. 6, 7.* 1932.

HORNELL, J. How did the sweet potato reach Oceania? Jour. Linn. Soc. Bot. **53:** 41–62. 1946.

HOUSE, H. D. Studies in the North American Convolvulaceae — IV. The genus *Exogonium.* Bull. Torrey Bot. Club **24:** 97–107. *pls. 1, 2.* 1908.

———. The North American species of the genus *Ipomoea.* Ann. N. Y. Acad. Sci. **18:** 181–263. 1908.

———. Studies in the North American Convolvulaceae — V. *Quamoclit.* Bull. Torrey Bot. Club **36:** 595–603. 1909.

INAMURA, S. I., and A. TAKIMOTO. Photoperiodic responses in Japanese morning glory, *Pharbitis Nil* Chois., a sensitive short day plant. Bot. Mag. Tokyo **68:** 235–241. 1955. (*See also* **68:** 260–266. 1955; **69:** 23–29. 289–297. 353–358, 1956; **70:** 53–57. 1957; **71:** 254–260. 1958.)

ISBELL, C. L. Regeneration in leaf cuttings of *Ipomoea Batatas.* Bot. Gaz. **91:** 411–425. 1931.

KEHR, A. E., Y. C. TING, and J. C. MILLER. The site of carotenoid and anthocyanin synthesis in sweet potatoes. Proc. Am. Soc. Hort. Sci. **65:** 396–398. 1955.

KENYAN, F. M. G. A morphological and cytological study of *Ipomoea trifida.* Bull. Torrey Bot. Club **55:** 499–512. 1929.

KING, J. R., and R. BAMFORD. The chromosome number in *Ipomoea* and related genera. Jour. Hered. **28:** 279–282. 1937.

KNIGHT, R. J. Morphological variation within a Clarke County population of *Ipomoea hederacea* (L.) Jacquin. (Abs.) Va. Jour. Sci. II. **7**: 288. 1956.

———. Hybridization in *Ipomoea* and its relatives. (Abs.) Va. Jour. Sci. II. **8**: 291, 292. 1957.

KUSE, G. Bud inhibition and correlative growth of petiole in sweet potato stem. Mem. Coll. Sci. Univ. Kyoto B. **21**: 107–114. 1954.

LAM, S. L., and H. B. CORDNER. Flowering hormone in relation to blooming in sweetpotatoes. Science **121**: 140, 141. 1955.

LAURITZEN, J. I. Some effects of chilling temperature on sweetpotatoes. Jour. Agr. Res. **42**: 617–627. *pl. 1.* 1931.

———. Factors affecting infection and decay of sweet potatoes by certain storage rot fungi. Jour. Agr. Res. **50**: 285–329. 1935.

LEE, S. H., and C. H. SHEO. Developmental morphology of the tubers of sweet potatoes. (In Chinese; English summary.) Acta Bot. Sinica **5**: 207–221. *pl. 1, figs. 1–7.* 1956.

McCORMICK, F. A. Notes on the anatomy of the young tuber of *Ipomoea Batatas* Lam. Bot. Gaz. **61**: 388–398. 1916.

MAHESHWARI, P. The seed structure of *Ipomoea*, a criticism. Sci. Cult. **9**: 557. 1944.*

MEDSGER, O. P. The Man-of-the-earth or wild potato vine. Torreya **24**: 39–42. 1924. [*I. pandurata.*]

MIKELL, J. J. The influence of chemical treatments on the growth and flowering of sweet potatoes. Proc. Am. Soc. Hort. Sci. **60**: 295–298. 1952.*

MILLER, J. C. Inducing the sweet potato to bloom and set seed. Jour. Hered. **28**: 347–349. 1937.

———. Further studies and technic used in sweet potato breeding in Louisiana. Jour. Hered. **30**: 484–492. 1939.

NAKAJIMA, G. Cytogenetical studies on the amphidiploid of *Quamoclit*. (In Japanese; English summary.) Jap. Jour. Genetics **26**: 203–209. 1951.*

NAKAYAMA, S. Photoreversible control of flowering at the start of inductive dark period in *Pharbitis Nil*. Ecol. Rev. **14**: 325, 326. 1958.*

NJOKU, E. The effect of defoliation on leaf shape in *Ipomoea caerulea*. New Phytol. **55**: 213–228. 1956.

———. The effect of mineral nutrition and temperature on leaf shape in *Ipomoea caerulea*. *Ibid.* **56**: 154–171. 1957.

NOHARA, S. Genetical studies on *Quamoclit* (*Ipomoea*). Jour. Coll. Agr. Univ. Tokyo **11**: 21–44. *pls. 3–7.* 1930.

O'DONELL, C. A. Nota sobre *Ipomoea fistulosa* Martius ex Choisy. Bol. Soc. Argent. Bot. **4**: 175, 176. 1952.

———. Las especies americanas de "Ipomoea" L. sect. "Quamoclit" (Moench) Griseb. Lilloa **29**: 19–86. 1959.

RAO, N. S. Chromosome studies in the genus *Ipomoea*. Curr. Sci. Bangalore **16**: 156. 1947.*

ROSA, J. T. Mutations in the sweet potato. Jour. Hered. **17**: 167, 168. 1926.

SMALL, J. K. *Ipomoea macrorhiza*. Addisonia **13**: 43, 44. *pl. 438.* 1928.

STOUT, A. B. The flowers and seed of sweet potatoes. Jour. N. Y. Bot. Gard. **25**: 153–168. *pl. 292.* 1924.

———. *Ipomoea Batatas*. Addisonia **9**: 35, 36. *pl. 306.* 1924.

———. Further notes on the flowers and seeds of sweet potatoes. Jour. N. Y. Bot. Gard. **27**: 129–135. 1926.

TAKENAKA, Y. The genes of Japanese morning glory (*Pharbitis Nil*). (Abs.) (In Japanese.) Jap. Jour. Genetics **33**: 326. 1958.

TAKIMOTO, A., K. IKEDA, and S. I. IMAMURA. Über den lichtunempfindlichen Teilprozess in der blühinduzienrenden Dunkelperiode bei *Pharbitis Nil*. Bot. Mag. Tokyo **71**: 317, 318. 1958.

THOMPSON, H. C., and J. H. BEATTIE. Group classification and varietal descriptions of American varieties of sweet potatoes. U. S. Dept. Agr. Bull. **1021**: 1–30. *pls. 1–8*. 1922.

TING, Y. C., and A. E. KEHR. Meiotic studies in the sweet potato (*Ipomoea Batatas* Lam.). Jour. Hered. **44**: 207–211. 1953.

———, ———, and J. E. MILLER. A cytological study of the sweet potato plant *Ipomoea Batatas* (L.) Lam. and its related species. Am. Nat. **91**: 197–203. 1957.

VERDCOURT, B. Typification of the subdivisions of *Ipomoea* L. (Convolvulaceae) with particular regard to the East African species. Taxon **6**: 150–152. 1957.

———. The names of the morning glories cultivated and naturalized in East Africa. *Ibid*. 231–233. [Discussion of the typification of *I. congesta*, *I. hederacea*, *I. purpurea*, and *I. Nil*.]

WARMKE, H. E., and H. J. CRUZADO. The flowering and seed-setting of sweet potatoes in Puerto Rico. Science **109**: 62, 63. 1949.

9. **Turbina** Rafinesque, Fl. Tellur. 4: 81. 1836 [1838].

Herbaceous or more or less woody, trailing or climbing, perennial vines with entire, ovate leaves, cordate at the base. Flowers in axillary peduncled cymes borne on the terminal portion of the branches. Calyx of 5 unequal, ovate or elliptic, obtuse sepals with thin margins. Corolla campanulate, white, with distinct midpetaline bands. Stamens 5, included, unequal in length; pollen spinulose. Ovary 2-locular, the stigma biglobular, the style included. Fruit a 1-locular, usually 1-seeded, indehiscent, ovoid-oblong capsule with a thin, woody pericarp. (*Legendrea* Webb & Berth.) TYPE SPECIES: *T. corymbosa* (L.) Raf. (Name from Latin, *turbinatus*, turbinate, in reference to the shape of the capsule.)

A genus of about ten or perhaps more species of the American tropics and Africa, represented in our area by a single species, *Turbina corymbosa* (*Rivea corymbosa* (L.) Hallier), which occurs throughout tropical South America, Central America, the West Indies, and Mexico, and is reported from southern peninsular Florida, the Florida Keys, and south Texas growing in hammocks and thickets. It has been introduced in various places in the Old World and in some areas has become naturalized. *T. corymbosa* was used by the Aztecs as a narcotic in divination, as a medicine, and as an ingredient in magical and analgesic ointments.

Turbina may be distinguished by the indehiscent, ovoid-oblong, mostly 1-seeded, woody capsules, and by the ovate to oblong, obtuse, spreading sepals which are not accrescent or only slightly so. *Rivea* Choisy has been shown to include species with linear-oblong stigmas and indehiscent, dry or nearly dry fruit and to be restricted to tropical Asia.

REFERENCES:

See family references, HOUSE (1909), MEEUSE (1957, pp. 773–784), VAN OOSTSTROOM (1943, 354), and VERDCOURT (1958).

SCHULTES, R. E. A contribution to our knowledge of *Rivea corymbosa*, the narcotic ololiuqui of the Aztecs. 45 pp. Botanical Museum, Harvard Univ., Cambridge, Mass. 1941.

———. A narcotic morning-glory (Una convolvulácea narcótica). Revista Soc. Cub. Bot. **10**: 61–68, 101–107. 1953; **11**: 14–23. 1954. [*T. corymbosa.*]

TAYLOR, N. Come and expel green pain. Sci. Month. **58**: 176–184. 1944. [Historical account of the narcotic uses of *T. corymbosa* and *Lophophora williamsii.*]

10. **Argyreia** Loureiro, Fl. Cochinchin. 1: 134. 1790.

Perennial, woody, twining vines with ovate to orbicular leaves, cordate at the base and densely sericeous on the lower surface. Flowers in peduncled axillary cymes. Calyx of 5 equal or subequal, coriaceous sepals. Corolla funnelform, campanulate or tubular, rose-purple, with distinct midpetaline bands. Stamens 5, included, unequal in length; pollen spinulose. Ovary [2- or] 4-locular, the stigmas biglobular, the style included. Fruit thick-walled, leathery, 4-seeded or less, indehiscent. TYPE SPECIES: *A. obtusifolia* Lour. or *A. acuta* Lour. (Name from Greek *argyreios*, silvery, in reference to the pubescence on the lower surface of the leaves.) — WOOLLY MORNING-GLORY.

A genus of about 90 species in tropical Asia, Malaysia, and Queensland. A single species of sect. PTYXANTHUS G. Don, *A. nervosa* (Burm. f.) Bojer (*A. speciosa* (L. f.) Sweet), a native of India which is cultivated in tropical areas as an ornamental and occasionally escapes, has been reported in Florida from hammocks along the Everglades (Small).

REFERENCES:

See family references, RAO (1940) and VAN OOSTSTROOM (1950, 1953).

HOOGLAND, R. D. The Convolvulaceae of Malaysia, VIII. The genus *Argyreia* in the Malay Peninsula. Blumea **7**: 179–192. 1952.

SINGH, P. Pharmacognosy of leaf of *Argyreia speciosa* Sweet. Jour. Sci. Indus. **16C**(10): 204–206. 1957.*

BIBLIOGRAPHIC DATA ON THE HILLCREST GARDENS BOOKS, 1911–1941

RICHARD A. HOWARD

THE HILLCREST GARDENS BOOKS constitute a most unusual series of publications, being at once documents on the history of the present Case Estates of the Arnold Arboretum, in Weston, Massachusetts, and a report of the horticultural and agricultural pursuits of Miss Marian Roby Case. In 1909, her mother, Laura Lucretia Williams Case, gave Miss Case a portion of the family estate in Weston. In succeeding years Miss Case bought adjacent pieces of land, including a house which became her home, until a total of 100 acres was acquired. Miss Case operated this land, known from 1910 to 1919 as the Hillcrest Farm and from 1920 to 1944 as the Hillcrest Gardens, as a truck farm, plant introduction station, and school of practical agriculture for boys. The history of the farm and its methods of operation will be described in an issue of *Arnoldia* to be published soon.

Between the years 1911 and 1941, Miss Case published the annual "green books" to record the development of the farm, the gardens and the school. From the beginning, the books consisted primarily of student reports made at the school's Labor Day exercises which concluded the summer's work. In addition, there were included in these books special papers by such horticulturists and botanists as John G. Jack, Elmer D. Merrill, Arthur Williams, E. H. Wilson, and John Wister. The student reports were generally of high quality and lasting value, covering such subjects as agricultural practices, weather data, hurricane damage, monthly flowering lists of herbaceous plants, lists of birds, wild flowers and native trees, trees and shrubs under cultivation in Weston, and records of plant introduction trials. These data have been of value in documenting the age of certain plants at the Case Estates and in determining the date of introduction and the persistence in New England of exotic plant introductions.

During the summer of 1910 Miss Case employed local boys to help with the farm work. The following year the Hillcrest Farm School was organized and the first booklet describing the farm and its activities was published that September under the title "The Second Summer at Hillcrest Farm, Weston, by Marian Roby Case." Similarly, the title of each succeeding "green book" indicated the number of years the school had been functioning, but the complete title and/or the authorship changed from time to time, as follows:

1912–1917: The ——— Summer at Hillcrest Farm, Weston, by the Boys for the Boys.

1918–1919: ......By the Farmers.
1920–1923: Hillcrest Gardens, Weston, Mass., The ——— Summer, by the Gardeners.
1924–1937: ......By Marian Roby Case, F.H.R.S. and the Gardeners.
1938: ......By Marian Roby Case, F.R.H.S. and the Hillcrest Boys.
1939–1941: ......By Marian Roby Case, F.R.H.S., Jack A. Williams and the Hillcrest Boys.

The first booklet consisted of eleven pages with a green cover printed in black. Beginning in 1915, the cover printing was in gold, and from 1916 until 1941 the cover design, with one exception, consisted of a drawing by one of the boys or a visitor to Hillcrest. The sole exception, the issue of 1921, had pasted on the cover a photograph showing the display of produce exhibited by Hillcrest Gardens at the Massachusetts Horticultural Society's fall show. Beginning with the issue of 1924 a group photograph was included in the booklet, and during the succeeding years there appeared photographs of Hillcrest exhibits or produce, student reunions, aerial photographs of the estate, hurricane damage and repair, or pictures of gardens seen by Miss Case in her travels.

The cost of publishing these books was borne by Miss Case and she determined their distribution. She mentioned, or quoted from, letters of acknowledgment received from Herbert Hoover, then in charge of a government program to increase food supplies; David Fairchild, Agricultural Explorer in Charge, Bureau of Plant Industry, U.S. Department of Agriculture; A. Lawrence Lowell, President of Harvard College; and others. Although Miss Case planned to send books regularly to certain libraries — that of the Royal Horticultural Society, England; the City Library, Providence, Rhode Island; the libraries of the Massachusetts Horticultural Society, the Arnold Arboretum, the City of Boston, the Town of Weston, the Boston Athenaeum, the State Library; and the Jones Library, in Amherst — not one of these has a complete file today.

The "green books" remain an informal but highly informative account of horticulture, agriculture, and plant introduction in a period when private gardens flourished in the Boston suburbs.

STUDIES IN ARTOCARPUS AND ALLIED GENERA, V. A REVISION OF PARARTOCARPUS AND HULLETTIA

FRANCES M. JARRETT

Parartocarpus Baillon, Adansonia **11**: 294. 1875; Benth. & Hook. f. Gen. Pl. **3**: 375. 1880; Becc. For. Borneo, 632. 1902, Webbia **5**: 559. 1923; Renner, Bot. Jahrb. **39**: 361. 1907; Backer, Beknopte Fl. Java **6**: 12. 1948; Jarrett, Jour. Arnold Arb. **40**: 9, 11. *fig. 2, a–f, fig. 3, g–i.* 1959. TYPE SPECIES: *Parartocarpus beccarianus* Baillon (= *P. venenosus* (Zoll. & Mor.) Becc.).

Gymnartocarpus Boerl. Ic. Bogor. **1**: 73. *t. 24, 25.* 1897, Handl. Fl. Ned. Ind. **3**: 335, 371. 1900; Koord. & Val. Bijdr. Boomsoort. Java **11**: 28. 1906; Koord. Exkursionsfl. Java **2**: 96. 1912, *"Gymnoartocarpus."* TYPE SPECIES: *Gymnartocarpus venenosa* (Zoll. & Mor.) Boerl. (= *Parartocarpus venenosus* (Zoll. & Mor.) Becc.).

Medium to large trees. *Leaves* spirally arranged, simple, entire, penninerved, thinly to thickly coriaceous, glabrous to pubescent; epidermal gland-hairs superficial, long-stalked, heads cylindric, unicellular; spongy mesophyll compact, without resin-cells; juvenile leaves elongate. *Stipules* simple, axillary, nonamplexicaul, the apex entire or bifid, scar intrapetiolar. *Inflorescences* unisexual, rarely bisexual, capitate, head globose at anthesis, becoming shallowly lobed in syncarp, pedunculate, solitary or paired in leaf-axils; stamens or ovaries sunken in numerous cavities closely set over the entire surface of the receptacle; receptacle armoured from numerous, closely set, indurated, spinous, conical, obtuse or truncate processes (perianth segments or interfloral bracts ?), those surrounding the openings connate basally in groups of 2–4 around each aperture, those covering the intervening surface free; basal involucre of 3–4(–8) deltoid or ovate bracts present, sometimes obsolete. *At anthesis*: anthers or stigmas exserted between the connate processes; *male head* with 1–3 stamens in each cavity, the filaments free or united, anthers 2–3 mm. long, short-exserted; *female head* with the ovaries solitary in each cavity, unilocular, the style apical with a short-exserted, lanceolate or fimbriate stigma, the ovule subapical. *Mature syncarp* formed by the enlargement of the entire female head, with (1–)3 to many flowers forming fruit; mature ovary thick-walled, with a firm exocarp finally decaying and leaving the stony endocarp, the style lateral, the seed large, attached laterally, testa membranous with a thickened apical cap, the embryo curved, the cotyledons incumbent, unequal, the inner one smaller, the appressed faces at an angle of 90° to the median plane of the ovary, the large, straight radicle directed upwards at the hilum with the tip enclosed in a little remaining endosperm; germination epigeal.

Distribution: peninsular Siam, Malaysia (except the Moluccas and the Lesser Sunda Islands), Solomon Islands.

The genus *Parartocarpus*, in which two species are recognized in this revision, has capitate, armoured inflorescences which have frequently been confused with the inflorescences of *Artocarpus*. The characters distinguishing the two genera have been discussed fully in the introductory paper of this series (Jour. Arnold Arb. **40**: 1–29. 1950; keys to the genera on page 26) and they will therefore be recapitulated only briefly here. The inflorescences of *Parartocarpus* differ from those of *Artocarpus* in having a usually well-developed involucre of 3–4(–8) basal bracts and in having the stamens or ovaries enclosed in what are considered to be cavities of the receptacle (formed chiefly by intercalary growth in the walls separating them), rather than enclosed in perianths. The surface of the receptacle is covered by solid, indurated (sessile) processes which vary in shape from cylindric and truncate to spinous and which bear a superficial resemblance to the indurated, tubular, perforate, free perianth apices of *Artocarpus* sect. *Duricarpus*. Many of the processes are connate, either at the base only or for nearly their whole length, in groups of 2–4 around the openings of the receptacular cavities, with the stamens or stigmas exserted between them at anthesis. The processes covering the intervening surface are free but are otherwise identical in appearance to those surrounding the apertures. These processes may represent fertile and sterile perianths respectively, but, taking into account their similarity to the indurated heads of the interfloral bracts in some species of the related, though less reduced, African genus *Treculia*, it is possible that they are secondarily modified interfloral bracts.

The leaves in *Parartocarpus* are spirally arranged as in *Artocarpus* subg. *Artocarpus*, but the stipules are nonamplexicaul and they are not paired as in *Artocarpus*, but are simple and axillary, each being formed from a pair of stipules fused along the intrapetiolar margins.

The generico-specific description of *Parartocarpus beccarianus* was published by Baillon in 1875 and was based on a Beccari collection from Borneo bearing male inflorescences. These were rather poorly preserved and Baillon described them erroneously as being covered by stamens intermixed with [stalked] bracts having obtuse, somewhat thickened heads. He stated that *Parartocarpus* differed from *Artocarpus* in having a basal involucre, in the lack of perianths, and in the nature of the stipules. (But he apparently compared the last only with the amplexicaul stipules of subg. *Artocarpus*, since he described them, in contrast, as lateral and nonamplexicaul which, if correct, would have corresponded with the condition present in subg. *Pseudojaca*.)

The genus was described again as *Gymnartocarpus* by Boerlage in 1897 with a single species, *G. venenosa*, based on *Artocarpus venenosa* Zoll. & Mor. from Java. The latter was published in 1845 and is the earliest account of a species of *Parartocarpus*. Boerlage described the stamens and ovaries in *Gymnartocarpus* as being enclosed in cavities of the receptacle, and he regarded the processes on the surface as representing bracteoles, not observing any fusion between them. He distinguished the genus from *Artocarpus* by the absence of perianths and the different form of the interfloral bracts. On the basis of Baillon's description he also separated it from *Parartocarpus*. He did not comment on the stipules or on the involucre, but the latter appears, from the plates, not to have been well developed in his material.

Several further species that must be referred to *Parartocarpus* had meanwhile been described under *Artocarpus*. *Artocarpus tylophylla* Miq. (1859) and *A. cerifera* Miq. (1867) were both described from Java and were reduced to *Gymnartocarpus venenosa* by Boerlage in 1897. *Artocarpus riedelii* Miq. (1867), from Celebes, and *A. involucrata* Schum. (1889), from New Guinea, were transferred to *Parartocarpus* in 1907 and 1900, respectively. In describing *Artocarpus bracteata* from Malacca and *A. forbesii* from Perak and Sumatra, King (1888, 1889) mistook the spinous processes on the syncarp for the perforate perianth apices of *Artocarpus*, and the discordant stipular characters were the cause of his rejection of Trécul's subgenera in *Artocarpus* when revising the species of "British India" (i.e., India, Pakistan, Ceylon, Burma and Malaya), as explained in an earlier paper (Jour. Arnold Arb. **40**: 123. 1959). King made no mention of *Parartocarpus* and Baillon's description may not have been available to him.

In 1902 Beccari, in an appendix to his *Nelle Foreste di Borneo* (reprinted in Webbia **5**: 550–565. 1923), discussed the inflorescence structure of *Parartocarpus* and listed seven species in the genus: *P. beccarianus* Baill., *P. venenosus* (Zoll. & Mor.) Becc. (*Artocarpus venenosa* Zoll. & Mor., *Gymnartocarpus venenosa* (Zoll. & Mor.) Boerl., *Artocarpus forbesii* King), *P. bracteatus* (King) Becc. (*Artocarpus bracteata* King), *P. borneensis* Becc., *P. excelsa* Becc. (also from Borneo), *P. papuana* Becc. and *P. involucrata* (K. Schum.) Schum. & Lauterb. He reduced *Gymnartocarpus* to *Parartocarpus*, removed King's two wrongly placed species to the correct genus, and described three new species. He minimized the differences between *Artocarpus* and *Parartocarpus*, stating that the only distinguishing character was the presence of an involucre in the latter. He regarded the stamens and ovaries in *Parartocarpus* as being enclosed in perianths which were tubular and laterally fused with each other below, but free and 2–3-fid above. The "sterile" processes he thought were sterile perianths, but he also apparently regarded them as equivalent to the interfloral bracts of *Artocarpus*. In considering this structure as similar to that found in *Artocarpus* he failed to recognize significant differences that exist between the genera, regardless of the morphological interpretation of the inflorescences in *Parartocarpus*. In *Artocarpus* the 2–4-fid or -partite male perianths enclosing the stamens are always completely free from each other. The tubular and perforate female perianths are frequently connate only in a peripheral layer forming an external wall to the syncarp, while they remain free in the proximal region containing the ovaries. Thus each ovary is separated from the next by two perianth walls instead of the single (receptacular) wall found in *Parartocarpus*.

J. J. Smith, in describing *Gymnartocarpus triandra* in 1922 (transferred by him to *Parartocarpus* in 1924) apparently took the same view of the inflorescence structure as Beccari. He was the first author to describe the stipules correctly as connate and intrapetiolar.

The two species recognized in this revision are *Parartocarpus bracteatus*, showing little variation and confined to Western Malaysia, and the variable *P. venenosus*, the distribution of which corresponds to that of the genus, extending beyond Malaysia to peninsular Siam and the Solomon Islands. Four fairly distinct subspecies are here distinguished within the latter and the three that are additional to the type subspecies correspond to the three new species described by Beccari in 1902. For one of these (*P. excelsus*) King's species, *Artocarpus forbesii*, is taken as the basionym for the subspecific epithet.[1] The remaining specific names mentioned above, with the addition of *Artocarpus woodii* described by Merrill in 1908 (transferred to *Gymnartocarpus* in 1921 and to *Parartocarpus* in 1923), are distributed in synonymy among the various subspecies of *Parartocarpus venenosus*.

A few comments on the inflorescences in *Parartocarpus* may be added here. The male and female heads are indistinguishable externally before anthesis, in contrast to *Artocarpus* in which they usually differ in shape. The fusion of some of the processes is only conspicuous in the female head, especially at maturity, although it may be established by cutting transverse sections through the bases of the processes in the male head. While the inflorescences are normally unisexual, heads are found in which male and female flowers occur on different areas of the receptacle, but only very rarely intermingled. The involucre, again, is normally well developed, but in *P. venenosus* the bracts may be indistinct and merged into an annulus at the base of the inflorescence. Both *Parartocarpus* and *Hullettia* are unusual among the Moraceae in that the anthers are extrorse.

Parartocarpus has copious latex which is poisonous (unlike that of *Artocarpus*) and is used as an arrow poison. The ripe fruits are, however, frequently described as being edible, although the young seeds are stated to be poisonous. The bark on the trunk is very distinctive through the presence of abundant, large, pustular lenticels.

KEY TO THE SPECIES OF PARARTOCARPUS

Leaves having 11–15 pairs of lateral veins, rufous pubescent beneath with the intercostals distinctly prominent, 5–10 on each side of midrib; processes on the syncarp spinous, the bases ± bulbous, on inflorescences at anthesis narrowly spinous, c. 3 × 1 mm.; involucral bracts 5–10 mm. long. . . . . 1. *P. bracteatus*.

Leaves having 6–15 pairs of lateral veins, thinly pubescent to glabrous beneath with the intercostals not or shallowly prominent, fewer; processes on the syn-

---

[1] It should be noted that in the introductory paper this was referred to as a distinct species within *Parartocarpus*; it is now considered that the taxon can be recognized only at the subspecific level.

carp truncate to spinous, the bases not bulbous, on inflorescences at anthesis truncate to acute, never narrowly spinous; involucral bracts to 5 mm. long. .... 2. *P. venenosus.*

1. **Parartocarpus bracteatus** (King) Becc. For. Borneo, 632. 1902, *"bracteata"*; Renner, Bot. Jahrb. 39: 362. 1907.

Artocarpus bracteata King in Hook. f. Fl. Brit. Ind. 5: 540. 1888, et in Ann. Bot. Gard. Calcutta 2: 7. 1889, pro parte quoad *t. 1B*, syncarpium solum, et spec. *Griffith 4663*; Ridley Fl. Malay Penin. 3: 352. 1924. Syntypes, Malacca, *Griffith 4663*, *Maingay 2411* (*Kew Distrib. 1476*) (CAL); lectotype, *Griffith 4663* (CAL).

Artocarpus rufescens auct. non Miq., Kurz, For. Fl. Burma 2: 431. 1877.

Trees, height to 45 m., buttressed or not, bark grey, smooth, with very large lenticels. *Twigs* 5–8 mm. thick, rugose, densely rufous pubescent. *Stipules* 5–10 mm. long, broadly lanceolate, rufous pubescent. *Leaves* 10–28 × 6–14 cm., obovate-oblong, obtuse or short-acuminate, base rounded or shallowly cordate, margin entire; venation prominent beneath; glabrous or nearly so above, except the short-pubescent main veins, rufous pubescent beneath; lateral veins 11–15 pairs, curved, basal 2 or 3 pairs slightly crowded; intercostals numerous, usually parallel; dark green, drying yellowish to purplish brown above, red-brown beneath; petiole 20–35 mm. long.

Inflorescences solitary in leaf-axils. *At anthesis: male head* 25–35 mm. across, globose, echinate from closely set, rigid, spinous, often slightly curved processes c. 3 × 1 mm.; stamens 2 in each cavity, to 8 mm. long, filaments free or united at the base, anthers oblong, apiculate, 2.5–3 mm. long; basal involucre of 3 ovate, concave, rufous-pubescent bracts, 5–10 × 5–10 mm.; peduncle 20–35 × 2–3 mm., rufous pubescent; *female head* echinate as in male head, many of the processes basally connate in groups of 2–4 with a lanceolate style exserted to 3 mm. between the free apices. *Syncarp* to 9 cm. across, subglobose, shallowly lobed, drying red-brown, echinate from closely set, rigid, spinous processes, many connate in groups of 2–4, those on the lobes ± bulbous below, 6–8 × 2–5 mm., the rest slender; wall c. 2 mm. thick; "seeds" (pericarps with a thick, stony endocarp) numerous, ellipsoid, 15 × 12 mm.; core c. 40 mm. across; involucre as in male head; peduncle 40–55 × 5 mm., rufous pubescent.

VERNACULAR NAME: *ipoh*, Malaya (cf. *Antiaris toxicaria* Lesch.). USES: the latex is used as an arrow poison.

DISTRIBUTION: in evergreen forest to 2000 ft.; Malaya, Sumatra, Banka, Borneo.

Malaya. SELANGOR. Bukit Cheraka For. Res., *Walton KEP 28387* (KEP, infl.); Kuala Lumpur, Ginting Simpah, *KEP 64942*, *71252* (KEP, ♀); Sungei Lalang Kajang, *Symington CF 22967* (SING). NEGRI SEMBILAN. Senawang Reserve, *Yakim CF 507* (K, KEP, ♂). MALACCA. *Alvins 465* (SING), *Maingay 2411* (*Kew Distrib. 1476*), 1867–8 (GH, K, ♂); Bukit Kemuning, *Derry 1022* (SING);

between Ching and Roombiya, *Griffith 4663*, 1842 and 1845 (CAL, K, L, P, U, ♂, mixed, ♀). PENANG. *Curtis*, March 1893 (SING, ♂, ♀). SINGAPORE. Chanchu Kang, *Ridley 4128* (CAL, SING); MacRitchie reservoir, *Sinclair SFN 39426* (L, SING, ♀); Mandai road, *Nur*, Oct. 1917 (SING, ♀); Serangoon road, *Ridley 8408* (K, ♀); Tanjong Kling, *Corner*, March 1938 (SING). PULAU TIOMAN. Ayer Surin, *Henderson SFN 21692* (BM, BO, K, SING, infl.).

Sumatra. TAPANULI. Barus, Penkalan Tapus, *bb 29549* (A, BO, L). EAST COAST. Huta Padang, near Kisarin, *Krukoff 327* (BO, SING). PALEMBANG. Banjuasin, Bajunglintjir, *NIFS T 761* (BO, L, ♀); Lematang Ilir, Gunong Megang, *NIFS T 816* (BO, L, ♂); Lematang Ilir, Semangus, *bb 32216* (BO, L, SING); Lematang Ilir, Tandjong, *NIFS T 645* (BO, infl.); Rawas, *Grashoff 1001* (BO, L, ♀). BANKA. Blinju, *Berkhout 151, Grashoff 90* (BO).

Borneo. EAST AND NORTHEAST BORNEO. Balikpapan: Pemaluan, *bb 24741, 24753* (A, BO, L); Sungei Warin region, *Kostermans 4303* (K, L, ♀). Berouw: Inaran, *bb 12173* (BO). E. Kutei: Loa Djanan, w. of Samarinda, *Kostermans 6550* (BO, K, L, ♂, mixed). W. Kutei: Mendom, Sungei Alan-Klindjang, *bb 29257* (A, BO, L). BRITISH NORTH BORNEO. Bukit Garam, near Kinabatangan river, *Wood A 4659* (A, KEP, L, SING, infl.).

In publishing the description of *Artocarpus bracteata*, King cited two collections, *Griffith Kew Distrib. 4663* and *Maingay Kew Distrib. 1476*, both from Malacca. While the first of these collections is *Parartocarpus bracteatus* as here understood, the second is a mixture of this species and *Artocarpus rigidus* ssp. *rigidus*, owing to the allocation of the same Kew Distribution number to two different collections. At Kew there are under the number *1476* a sheet of *Parartocarpus bracteatus* bearing Maingay's own number *2411* and a sheet of *Artocarpus rigidus* with his number *2414*. Duplicates distributed under the number *1476* consist at Calcutta and Leiden of *A. rigidus* and at the Gray Herbarium of *Parartocarpus bracteatus*. Although King at some period annotated the Kew specimens correctly, he appears to have drawn up his description from the material at Calcutta, namely the Griffith specimen consisting of detached leaves, a small portion of twig, and a mature syncarp of *Parartocarpus bracteatus*, and the Maingay specimen which was a sterile shoot of *Artocarpus rigidus*. The vegetative characters are a mixture of the two species, and the twigs are described as annulate (as in *Artocarpus* subg. *Artocarpus*). The plate is also a mixture, since comparison with these specimens shows that the artist drew the syncarp of *Griffith 4663* as if attached to the shoot of *Maingay 1476*. The confusion in the type material, the description, and the plate has not been noted previously, and King's specific epithet has always been applied to this species of *Parartocarpus*.

Kurz incorrectly identified this species with *Artocarpus rufescens* Miq. (= *A. dadah* Miq.) and included it under that name in his *Forest Flora of British Burma* (1877), presumably because on *Griffith 4663* at Calcutta the provenance is given as Burma. This is certainly an error, since no other collections have been seen from farther north than Penang and the Kew specimen has notes by Griffith stating that it was collected in Malacca. King corrected Kurz's identification in 1888 and gave the distribution as Malacca only.

The collection made by Curtis in Penang which is cited above resembles *Parartocarpus bracteatus* in the shape and venation of the leaves, but is anomalous in that the shoot is subglabrous except for the youngest parts, and the processes on both male and female inflorescences are much shorter than is usual in this species. In the male head they are shortly conical and in the syncarp they are obtuse with a small, acute umbo. In the absence of other, similar collections this specimen is not treated as distinct, but it would be of interest to have further material from Penang.

2. **Parartocarpus venenosus** (Zoll. & Mor.) Becc. For. Borneo, 632. 1902.

Trees, height to 35 m., not or scarcely buttressed, bark yellow to grey-brown, with numerous large lenticels. *Twigs* 3–7 mm. thick, rugose, appressed pubescent to puberulent, glabrescent or not. *Stipules* to 3 mm. long, deltoid, appressed pubescent. *Leaves* 4.5–23(–30) × 3–10 cm., obovate-oblong to obovate- or oblanceolate-elliptic, obtuse to short-acuminate, base rounded or cuneate, varying auriculate, margin entire; main veins prominent beneath, reticulum not or shallowly so; glabrous or nearly so above, thinly pubescent to glabrous beneath; lateral veins 6–15 pairs, curved; intercostals few, not parallel; dark green above, paler beneath, drying grey-green to purplish brown above, yellow-green to red-brown beneath; petiole 15–45 mm. long.

Inflorescences solitary in leaf-axils. *At anthesis: male head* 15–30 mm. across, globose, covered by closely set, indurated, conical, obtuse, umbonate or truncate processes, 1–1.5 × 1–1.5 mm.; stamens 1–3 in each cavity, to 4.5 mm. long, filaments united for half to nearly all their length, anthers oblong, obtuse or apiculate, 2–2.5 mm. long; basal involucre of 3–4(–8) deltoid, short-pubescent to glabrous bracts, to 5 × 5 mm.; peduncle 12–60 × 2–3 mm., short-pubescent to glabrous, often somewhat thickened below the involucre, sometimes markedly so, the involucre reduced to an annulus; *female head*, surface as male head, many of the processes basally connate (often inconspicuously so) in groups of 2–4 with a lanceolate or fimbriate style exserted to 0.5–1.5 mm. between the free apices. *Syncarp* to 18 cm. across, subglobose, shallowly, sometimes markedly, lobed, brown, covered by closely set, indurated, spinous, umbonate, obtuse or truncate processes, many often clearly connate in groups of 2–4, those on the lobes 1–10 × 2–5 mm., the rest smaller; wall 3–5 mm. thick; "seeds" (pericarps with a thick, stony endocarp) (1–)3 to many, ellipsoid, 15–30 × 13–20 mm.; core c. 30 mm. across; involucre as in male head; peduncle 30–100 × c. 5 mm., short-pubescent to glabrous.

USES: the latex is used as arrow poison; the ripe fruit is said to be edible, but unripe seeds are poisonous.

DISTRIBUTION: peninsular Siam, Malaya, Sumatra, Simalur, Enggano, Riouw-Lingga Archipelago, Borneo, Java, Philippine Islands, Celebes, New Guinea, Bismarck Archipelago, Aru Islands, Solomon Islands.

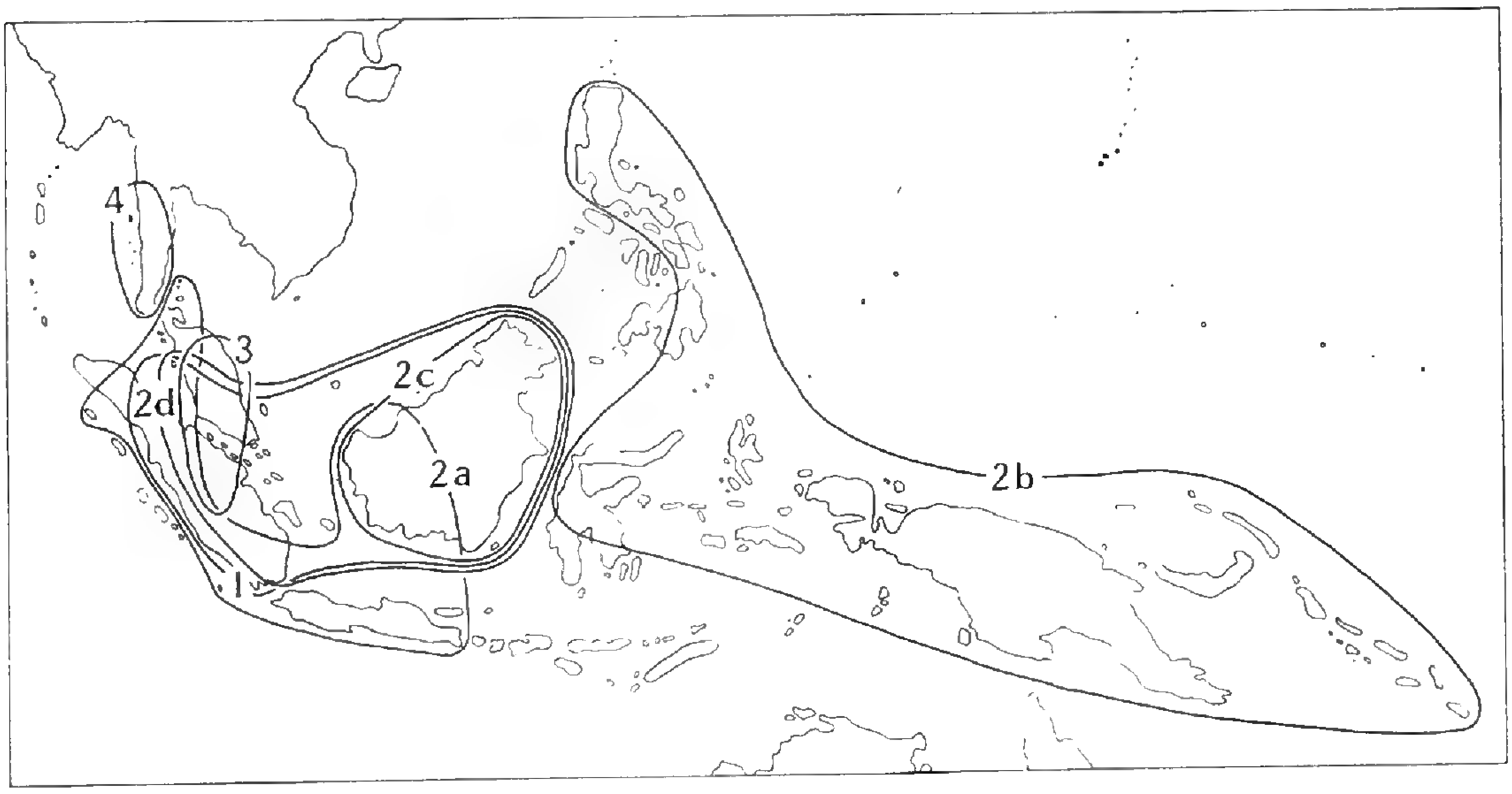


FIG. 20. Distribution of the species of PARARTOCARPUS and HULLETTIA. 1, *Parartocarpus bracteatus*; 2, *P. venenosus*, a, ssp. *venenosus*, b, ssp. *papuanus*, c, ssp. *borneensis*, d, ssp. *forbesii*; 3, *Hullettia dumosa*; 4, *H. griffithiana*.

Parartocarpus venenosus has the widest range of any species within the group of genera under study and extends over the whole of Malaysia and the Solomon Islands, though it is apparently absent from the Moluccas and the Lesser Sunda Islands. Within this area, it shows considerable variation and four subspecies are recognized here with a geographical and ecological basis.

The greatest variation is found in the shape of the processes on the syncarp. They range from broadly truncate, so that the syncarp surface appears tessellated, to spinuous so that the fruit is echinate. The processes enlarge during the maturation of the syncarp by intercalary growth at the base, and it is perhaps due to this that they are particularly subject to variation in shape. In two of the subspecies, ssp. *venenosus* and ssp. *papuanus*, the syncarp is usually tessellated, whereas in the other two, ssp. *borneensis* and ssp. *forbesii*, it is characteristically spinous. However, specimens bearing syncarps having a knobbly surface, with processes of intermediate shape, are found which are referable on their vegetative characters to both ssp. *venenosus* and ssp. *forbesii*. The vegetative distinctions between the four taxa lie in slight differences in indumentum, leaf shape and size, and number and prominence of the lateral veins, as may be seen from the key to the subspecies. The peduncles in ssp. *forbesii* are also rather shorter than in the other subspecies.

These taxa are not absolutely separable, but most of the collections seen can be assigned to one or another without difficulty. In view of their fairly clear geographical and ecological separation, recognition at the subspecific level would seem to be justified. The distribution of ssp. *forbesii* is of particular interest in that it appears to be almost completely confined to peat-swamp forest. Very few other species of this group of genera are found in this habitat, apparently because they require fairly good drainage.

KEY TO THE SUBSPECIES OF PARARTOCARPUS VENENOSUS

1. Peduncles glabrous, the male 12–35 mm., the female 30–40 mm. long; syncarp processes umbonate to spinous; leaves usually to less than 12 cm. long, thickly coriaceous, glabrous, obovate-elliptic, base cuneate, with 6–10 pairs lateral veins. .... ssp. *forbesii.*
1. Peduncles glabrous to pubescent, the male 25–60 mm., the female 35–100 mm. long; syncarp processes truncate to spinous; leaves larger, or obovate-oblong and usually puberulent.
    2. Leaves usually less than 12 cm. long, lateral veins 8–11 pairs, distinctly prominent beneath, reticulum shallowly so; syncarp processes spinous. .... ssp. *borneensis.*
    2. Leaves usually more than 12 cm. long, lateral veins 6–15 pairs, less prominent, reticulum not or scarcely so; syncarp processes truncate or obtuse.
        3. Shoot appressed-pubescent to subglabrous; leaves obovate-oblong to obovate-elliptic, base cuneate or rounded, lateral 8–15 pairs, usually drying red-brown. .... ssp. *venenosus.*
        3. Shoot glabrous or nearly so; leaves obovate-elliptic, apex often rather broadly rounded, lateral veins 6–10 pairs, usually drying greyish to yellowish green. .... ssp. *papuanus.*

ssp. **venenosus**

Artocarpus venenosa Zoll. & Mor. Natuur- en Geneesk. Arch. Neerl.-Ind. **2:** 213. 1845, Flora **30:** 471. 1847; Miq. in Zoll. Syst. Verz. Ind. Archip. **2:** 89, 95. 1854; Miq. Fl. Ind. Bat. **1**(2): 289. 1859. Holotype, Java, *Zollinger 2371* (P); isotypes (BM, BO, P).

Artocarpus venenosa Zoll. var. *tylophylla* Miq. in Zoll. Syst. Verz. Ind. Archip. **2:** 89, 95. 1854. Holotype, Java, *Zolliger 2983* (P); isotypes (BM, L, P, U).

Artocarpus tylophylla Miq. Fl. Ind. Bat. **1**(2): 289. 1859.

Artocarpus callophylla Zoll. & Mor. in Teysm. & Binnend. Cat. Hort. Bog. 85. 1866, nomen nudum.

Artocarpus cerifera Miq. Ann. Mus. Lugd.-Bat. **3:** 212. 1867. Holotype, Java, *Blume 2145* (L).

Parartocarpus beccarianus Baillon, Adansonia **11:** 294. 1875; Becc. For. Borneo, 632. 1902; Renner, Bot. Jahrb. **39:** 363. 1907. Holotype, Sarawak, *Beccari PB 2557* (P); isotypes (A, K).

Gymnartocarpus venenosa Boerl. Ic. Bogor. **1:** 73. *t. 24, 25.* 1897; Koord. & Val. Bijdr. Boomsoort. Java **11:** 28. 1906.

Radermachia cerifera Blume ex Boerl. Ic. Bogor. **1:** 73. 1897, pro syn. *Gymnartocarpus venenosa.*

Parartocarpus venenosus (Zoll. & Mor.) Becc. For. Borneo, 632. 1902, "*venenosa*"; Renner, Bot. Jahrb. **39:** 362. 1907; Backer, Beknopte Fl. Java **6:** 12. 1948.

Twigs, lower surface of leaves, peduncles and involucral bracts appressed pubescent or puberulent, glabrescent or not. *Leaves* to 12–23(–30) × 5–10 cm., obovate-oblong to obovate-elliptic, varying to oblanceolate-oblong or oblanceolate-elliptic, base rounded or cuneate; main veins promi-

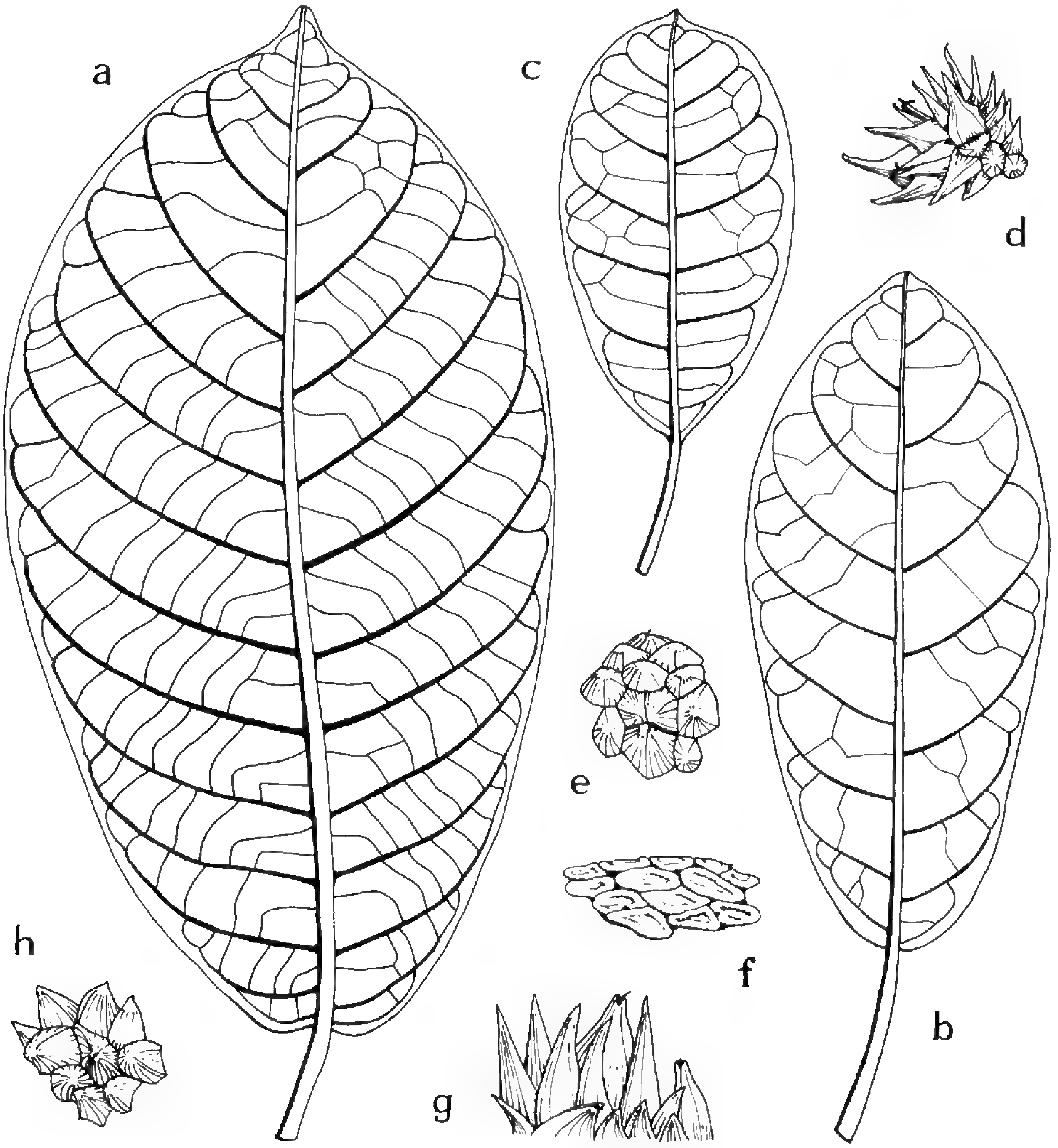


FIG. 21. Leaves and syncarp surface in *Parartocarpus*. a–c, Leaves (× ½): a, *P. bracteatus*; b, c, *P. venenosus*, b, ssp. *venenosus*, c, ssp. *forbesii*. d–h, Surface of the mature syncarp (approx. × 1): d, *P. bracteatus*; e–h, *P. venenosus*, e, ssp. *venenosus*, f, ssp. *papuanus*, g, h, ssp. *forbesii*.

nent beneath, reticulum not or scarcely so; lateral veins 8–15 pairs. *Male head*, peduncle c. 30–60 mm. long. *Syncarp* with obtuse, or truncate and often depressed processes; peduncle c. 40–100 mm. long.

VERNACULAR NAMES: *bulu ongko* (Sundanese), *purut* (Javanese), Java.

DISTRIBUTION: in evergreen and mixed forest to 3000 ft., tolerating a short dry season; peninsular Siam, northern Malaya, Sumatra, Simalur, Enggano, Java.

Peninsular Siam. Islands off e. coast: Kaw Pa-ngan, *Put 1256* (BM, ♂); Kaw Samui, *Put 844* (BM, ♀); Kaw Tao, *Kerr 12771* (BM, ♂, ♀). **Malaya.** PROV. WELLESLEY. Bukit Juru For. Res., *KEP 9831* (KEP), *9843* (KEP, ♀), *Durant*

KEP 9840 (KEP). LANGKAWI ISLANDS. Langkawi, Gunong Raya, *Abdullah KEP 42014* (KEP).

Sumatra. TAPANULI. Sibolga: Aek Labuan Talang, *bb 19303* (BO); Kuala Badung, *bb 19335* (A, BO). INDRAGIRI. Danau Mengkuang, *bb 27558* (A, BO, L). SIMALUR. *Achmad 155* (BO, L, ♂), *920* (BO, K, L, ♀); Landschap Tapah, Defajan, *Achmad 1604* (BO, L). ENGGANO. Bua Bua, *Lütjeharms 4258* (A, BO, K, L, P), *4464* (A, BO, K, L, P, infl.). **Borneo.** SARAWAK. *Beccari PB 2557* (A, K, P, ♂).

Java. *Blume 2145* (L, ♂); between Mt. Smeru and Mt. Kelut, *Blume HB 7314* (BO). WEST JAVA. Bantam: Gunong Karang, Tjimanuk, *Koorders 8686* (BO, K, L), *40107* (BO, L); Menes, *Backer 7063* (BO, ♂, ♀); Tjimara Udjung, Gunong Rompang, *Koorders 8685* (BO, K, L). Batavia: Gunong Salak, *Koorders 24444* (BO), *33285* (BO, L); Tjiampea, *Koorders 30362, 30363* (BO). Buitenzorg: Djasinga, *De Voogd*, April 1941 (BO, K, L); Handjere, *NIFS Ja 6816* (K, L); Natuur Monument, Dungus Iwul, *NIFS Ja 1961* (BO); Pasir Pogor, *Bakhuisen van den Brink 8017* (BO). Preanger: Palabuanratu, *Koorders 5246* (BO, L), *8684* (BO, K, L, P, ♀), *8688* (BO, infl.), *12357* (BO, L, ♀), *42907* (BO, ♀); Tjilumpang, near Tjidadap, *Winckel 1912* (BO). CENTRAL JAVA. Banjumas: Pringombo, Bandjarnegara, *Koorders 8695* (BO, K, L, ♀). Pekalongan: Batu Kumpas, *NIFS s.n.* (BO). EAST JAVA. Besuki: Banjuwangi, *Koorders 8028* (BO), *8680* (BO, L, P), *8681, 8682* (BO, L), *8683* (BO, K, L, P); Tjuramanis, *Koorders 21066, 21406* (BO), *21407* (BO, K, L, infl.), *22238* (L), *38336* (BO, ♂). Madiun: Gunong Wilis, Ngebel, *Koorders 38756* (BO, K, L, P, ♂, ♀). Pasuran: Tangkil-Zuidergebergte, *Koorders 22441* (BO, L), *23891* (BO, K, L, P, SING, U). Probolinggo: Malang, *Zollinger 2371*, Oct. 1844 (BM, BO, L, P, ♀). NUSA KAMBANGAN. *Koorders 8694, 20225* (BO, L), *24126* (A, BO, K, L, ♀), *24627, 24640, 24728, 24729* (BO, L), *27036* (BO, L, ♂). **Cultivated.** JAVA. Bogor: Hort. Bot., *Teysmann*, 1860 (L), *Zollinger 2983* (BM, L, P, U, ♀); Hort. Bot., cult. sub VIII B 1a, *Forman 60, Sutrisno 78* (K, ♀).

The type subspecies of *Parartocarpus venenosus* shows some variation in the outline of the leaves and rather more in the shape of the processes on the syncarp. The leaves are, however, characteristically obovate-oblong with a somewhat acute apex, and persistently puberulent beneath, at least on the main veins. The leaves are usually larger and more thinly coriaceous than in either ssp. *borneensis* or ssp. *forbesii*. The venation is less prominent than in the former and the syncarp processes are never spinous.

The type collection of *Parartocarpus beccarianus*, *Beccari PB 2557*, has small, thinly coriaceous, narrowly obovate-oblong leaves (to 12 × 4 cm.), which are puberulent beneath, but lack a prominent reticulum. The male inflorescences have processes with obtuse apices and the syncarp (presumably at Florence) is described by Beccari in 1902 as having the surface tessellate from the depressed pyramidal apices of the "polygonal scales" or perianth apices. Except in the rather small size of the leaves, the collection agrees with *P. venenosus*, *sensu stricto*, rather than with ssp. *borneensis* or ssp. *forbesii*.

ssp. **papuanus** (Becc.) Jarrett, stat. nov.

Artocarpus riedelii Miq. Ann. Mus. Lugd.-Bat. 3: 213. 1867. Syntypes, Celebes, Manado, *Teysmann HB 5778* (U), *De Vriese s.n.* (L); lectotype, *Teysmann HB 5778* (U).

Artocarpus involucrata K. Schum. in Schum. & Hollrung, Fl. Kais. Wilhelms Land, 39. 1889. Holotype, northeast New Guinea, *Hollrung 522* (B); isotype (BO).

Parartocarpus involucrata (K. Schum.) Warb. ex Schum. & Lauterb. Fl. Deutsch. Schutzgeb. Südsee, 267. 1900; Becc. For. Borneo, 632. 1902; Renner, Bot. Jahrb. **39**: 363. 1907; Lauterb. ibid. **62**: 303. 1928; Diels, ibid. **67**: 174. 1935; White, Jour. Arnold Arb. **31**: 82. 1950.

Parartocarpus papuana Becc. For. Borneo, 633. 1902, non S. Moore, 1923. Holotype, New Guinea, Vogelkop, *Beccari PP 719* (FI); isotype (FI).

Parartocarpus riedelii Warb. ex Renner, Bot. Jahrb. **39**: 362. 1907.

Artocarpus woodii Merr. Philip. Jour. Sci. Bot. **3**: 221. 1908; Elmer, Leafl. Philip. Bot. **2**: 623. 1909. Holotype, Mindanao, *Merrill 5259* (*PNH*, destroyed); isotypes (L, P); lectotype (P).

Gymnartocarpus woodii (Merr.) Merr. Philip. Jour. Sci. **18**: 52. 1921; Brown, Bull. Bur. For. Philip. **22**(2): 270. *fig. 19.* 1921.

Parartocarpus woodii (Merr.) Merr. Enum. Philip. Pl. **2**: 39. 1923.

Artocarpus venenosa Zoll & Mor., Schum. Notizbl. Bot. Gart. Berlin **1**: 48. 1895.

Twigs, lower surface of leaves, peduncles and involucral bracts appressed pubescent or puberulent, soon glabrescent except often the involucre. *Leaves* to 12–23 × 5–10 cm., obovate-elliptic, varying to oblanceolate-elliptic or obovate-oblong, base cuneate, varying to rounded or auriculate; main veins prominent beneath, reticulum not or scarcely so; lateral veins 6–10 pairs. *Male head,* peduncle c. 25–35 mm. long. *Syncarp* with truncate, often depressed processes; peduncle 35–70 mm. long.

DISTRIBUTION: in evergreen forest to 2000 ft.; Philippine Islands, Celebes, New Guinea, Bismarck Archipelago, Aru Islands, Solomon Islands.

Philippines. LUZON. Cagayan: *Klemme FB 6650* (US, ♀). Isabela: San Marino, *Ramos & Edano BS 47015* (BM, SING, ♀), *47176* (SING). Quezon: Baler, mountains e. of Castillo river, *Quisumbing PNH 2518* (A, PNH, ♀). Bataan: *Alvarez FB 12942* (P, US, ♀), *Curran FB 17584* (BM, BO, L, US, ♂). Rizal: *Maneja FB 23961* (P, US, ♀); Orind, *Loher 6946* (K, infl.). Laguna: *Tamesis FB 11993* (L, P, US, ♀); Calauan, *McGregor BS 12392* (BM, P, ♀); Mt. Maquiling, *Forestry School FB 20140* (BM, L, P, US, ♂), *Ramos 1044* (U, US, ♂, ♀), *Villamil FB 20394* (US, ♀), *Whitford FB 19729* (BM, ♀); Mt. Maquiling, Los Banos, *Elmer 18291* (A, BM, K, L, P, ♂); San Antonio, *Ramos BS 15051* (P). Camarines: *Alvarez FB 21453* (BM, P, US, ♀), *23748* (A, BO, ♀), *Hsia FB 21107* (US, infl.); Camarines Sur, *Ahern 41* (BO, US, infl.), *Alambra FB 28088* (A, P, ♀). Albay: Rapu-Rapu Island, *Vidal 3837* (A, K, ♀). Sorsogon: Irosin, Mt. Bulusan, *Elmer 14650* (A, BM, K, L, ♀). SAMAR. *Sherfesee et al. FB 21084* (US, ♀). LEYTE. Dagami, *Ramos BS 15184* (K, US, ♂, ♀). MINDANAO. Surigao: *Ramos & Pascasio BS 34684* (A, P, ♀). Dinagat Island: *Ramos & Pascasio BS 32540* (A, ♀). Bucas Grande Island: *Merrill 5259*, Oct. 1906 (L, P), *Ramos & Pascasio BS 35056* (BO, L, infl.), *35092* (A, K, US, ♀).

Celebes. NORTH PENINSULA. Manado, *DeVriese* (L); Manado, Ratahan, *Teysmann HB 5778* (BO, L, U); Minahassa, *Koorders 19050* (BO, ♂), *19315* (BO, L). CENTRAL CELEBES. Malili: Kawata, *NIFS Cel./II-409 no. 10* (BO, K, L, ♂); Lawoli, *bb 23251* (BO); Usu, *NIFS Cel./II-324* (A, L, SING), *409 no. 409* (BO, L, ♂); Mantano Meer, *Kjellberg 2805* (BO, ♀). Masamba, Mina, *bb 24504* (BO, L, SING).

New Guinea. VOGELKOP. Bomberai: Fakfak, *Lundquist 266* (L); Rauna, *bb 22536* (BO). Inanwatan, *bb 32657* (BO, L). Manokwari: Andai, *Beccari PP 719*, 1872 (FI, ♂, ♀); Momi, *bb 33492* (BO, L); Oransbari, *Brouwer BW 2584* (L); Warnapi, *Kostermans 408* (BO, K, L). Sorong: Warsamson, 25 km. e. of Sorong, *Schram BW 2923, 5949* (L). DUTCH NORTH NEW GUINEA. Hollandia: *Versteeg BW 4825* (L, ♂, ♀); Holtekang, *Schram BW 1508* (L); Idenburg river, Bernhard Camp, *Brass 13547* (A, infl.), *Brass & Versteegh 13547A* (A, ♀); Tami, *Schram BW 2723* (K, L, ♀); mouth of Tami river, *Schram BW 2678* (K, L, infl.), *2811* (K, L, infl.), *2812* (L, infl.), *Versteegh BW 3805* (L). DUTCH SOUTH NEW GUINEA. Merauke, Bot river, halfway between Bupul and Lake Wam, *Van Royen 4737* (K, L). PAPUA. Central Division: Koitaki, *Carr 12623* (A, BM, K, SING, ♂, ♀). Northern Division: Hydrographers Range foothills, *Hoogland 3855* (A, BM, L, ♀). Western Division: Lake Daviumbu, Middle Fly river, *Brass 7476* (A, L, ♂). MANDATED TERRITORY OF NEW GUINEA. Madang District: Constantinhafen, *Hollrung 522*, Feb. 1887 (B, BO, ♂); Gogol valley, hills ne. of Mawan village, *Hoogland 4891* (K, ♀); Ramu valley, c. 5 mi. se. of Faita airstrip, *Saunders 274, 539* (L). Morobe District: near Finschhafen, *Hellwig 286* (SING); Umboi Island, *White NGF 9646* (K, ♀). Sepik District: *Ledermann*, 1912–13 (SING). NEW BRITAIN. West Nanakai, Gorea village, near Cape Hoskins, *Floyd 6448* (K, ♂). SCHOUTEN ISLANDS. Biak, *bb 30684* (BO, K), *30830* (BO, L, SING). JAPEN. *bb 30281* (BO, L, SING); Mentebu, *bb 30228* (A, BO, L, SING, ♀); Rendawaja, *Malinka BW 7014* (L). SALAWATI. Kaloal, *Koster BW 4243* (L). ARU ISLANDS. Kobroor: Dosinamalu, *bb 25319* (A, BO, L, SING, infl.), *Buwalda 5096* (A, K, L, SING, infl.). Trangan: Lutor, *Beccari*, June 1873 (FI, ♂); Ngaibor, *bb 25453* (A, BO, SING, ♀), *Buwalda 5420* (A, K, L, PNH).

Solomon Islands. BOUGAINVILLE. Buin, Marmaromino, *Kajewski 2199* (A, K, infl.). TREASURY ISLAND. *Guppy 55* (K, infl.). SANTA ISABEL. Kalina bay, *Walker BSIP 238A* (A, K, ♀). GUADALCANAL. Beaufort river, Kambou river, *Walker BSIP 238* (A, K, ♀).

Although ssp. *papuanus* is widely distributed, it is rather constant in its characters. It is nearest to ssp. *venenosus* but is distinguished by the consistently subglabrous mature shoot and by the rather few lateral veins and broadly rounded apex of the leaves, which usually dry yellowish or greyish green. The syncarp is apparently always tessellate.

ssp. **borneensis** (Becc.) Jarrett, stat. nov.

Parartocarpus borneensis Becc. For. Borneo, 634. 1902; Renner, Bot. Jahrb. **39**: 362. 1907. Holotype, Sarawak, *Beccari PB 2005* (FI); isotypes (FI, K).

Twigs, lower surface of leaves, peduncles and involucral bracts appressed pubescent when young, usually persistently puberulent. *Leaves* to 8.5–12 × 5–7 cm., obovate-oblong, base rounded or broadly cuneate; main veins distinctly prominent beneath, reticulum shallowly so; lateral veins 8–11 pairs. *Male head*, peduncle 25–35 mm. long. *Syncarp* with spinous processes; peduncle 40–80 mm. long.

DISTRIBUTION: in evergreen forest on sand or loam to 200 (–1200) ft. in low undulating or hilly country; Borneo.

Borneo. SARAWAK. Mt. Mattang, Vallombrosa, *Beccari PB 2005*, June 1866 (K, FI, ♀); Sungei Semenggoh For. Res., *Wyatt-Smith KEP 79306* (K, L, ♀). BRUNEI. Andulau For. Res., *Ashton BRUN 585* (K, KEP, L, ♀), *Smythies et al. SAN 17500* (K, KEP, L, ♂), *Wyatt-Smith KEP 80076* (KEP, ♀). EAST AND NORTHEAST BORNEO. Central Kutei: Belajan river region, *Kostermans 10258* (K, ♀). W. Kutei: Longbleh, *bb 16047, 16054* (A, BO, L); Mujup, *bb 16782* (A, BO, L, infl.); near Tandjong Isui, *Endert 1898* (K, L). Tidung: Birik, *bb 17930* (A, BO, L, SING, ♂). BRITISH NORTH BORNEO. Kabili-Sepilok For. Res., *Enggoh KEP 48779* (KEP, ♂). LABUAN. *Motley 254* (K, infl.).

This subspecies is readily distinguished by the consistently spinous syncarp and the small, obovate-oblong, rather thickly coriaceous, usually thinly pubescent leaves with rather prominent venation.

ssp. **forbesii** (King) Jarrett, Jour. Arnold Arb. **41**: 137. 1960.

Artocarpus forbesii King in Hook. f. Fl. Brit. Ind. **5**: 539. 1888; King, Ann. Bot. Gard. Calcutta **2**: 7. *t. 1A.* 1889; Ridley, Fl. Malay Penin. **3**: 352. 1924; Moore, Jour. Bot. **63**, Suppl. 112. 1925. Syntypes, Malaya, *King 10829* (CAL, not seen; duplicates examined, K, P), Sumatra, *Forbes 3080* (CAL, not seen; duplicates examined, BM, L).

Parartocarpus excelsa Becc. For. Borneo, 634. 1902; Renner, Bot. Jahrb. **39**: 363. 1907. Holotype, Sarawak, *Beccari PB 673* (FI); isotypes (A, BM, FI, K).

Gymnartocarpus triandra J. J. Smith, Bull. Jard. Bot. Buitenzorg III. **4**: 233. *t. 6–8.* 1922. Syntypes, Sumatra, *Beguin 316, 536, 583, Grashoff 798* (BO); lectotype *Beguin 583* (BO).

Parartocarpus triandra J. J. Smith, Bull. Jard. Bot. Buitenzorg III. **6**: 80. 1924; Browne, For. Trees Sarawak, 357. 1955.

Twigs, and involucral bracts appressed pubescent or puberulent, soon glabrescent. *Leaves* to 8–13 × 4–6 cm., obovate-elliptic, base cuneate; main veins prominent beneath, reticulum not or scarcely so; lateral veins 6–10 pairs. *Male head,* peduncle 12–35 mm. long. *Syncarp* with spinous or umbonate processes; peduncle 30–40 mm. long.

VERNACULAR NAME: *tenggajun* (Malay), Sumatra, Borneo.

DISTRIBUTION: in evergreen forest to 2500 ft., usually in low-lying peat-swamp forest; western and southern Malaya, eastern and southern Sumatra, Riouw-Lingga Archipelago, Borneo.

Malaya. PERAK. Ulu Bubong, *King 10829*, Aug. 1886 (K, P, ♀). JOHORE. 8th mile Kota Tinggi-Mawai road, *Corner*, Feb. 1935 (SING); Gunong Pantai, *Corner*, Jan. 1937 (SING); Pengkalan Raja, *Ngadiman SFN 36661, 36682* (SING, ♀); Sungei Kayu, Mawai-Jemalaung road, *Kiah SFN 32185* (K, SING, ♀). PENANG. Ayer Hitam For. Res., *Strugnell KEP 49702* (KEP, ♀). SINGAPORE. Jurong, *Corner SFN 21845* (A, BM, BO, K, SING, ♂, ♀), *28147* (K, SING); 15th mile Jurong, *Corner SFN 26194* (A, K, SING, infl.).

Sumatra. EAST COAST. Asahan, Masihi For. Res., *Krukoff 4124* (A, BO, L, SING, ♀); Benkalis, Sengoro, *Beguin 536* (BO); Benkalis, Sungei Missigit, *Beguin 583* (BO, L, ♂, ♀); Benkalis, Tamansari, *Beguin 316* (BO, L, ♀); Labuan Batu, Sungei Palas, *bb 10642* (BO); P. Mendal, Kelumang, *bb 12472* (BO, SING, infl.); P. Tebing Tinggi, *bb 12926* (BO, infl.). INDRAGIRI. Belimbing, *bb 28537* (A, BO, L); P. Gelang, *bb 29150* (A, BO, L). PALEMBANG. Banjuasin and Kubustreken, *Grashoff 798* (BO, L, ♂); Muara Mengkulem, River Rawas, *Forbes 3080*, 1880 (BM, L, ♀). RIOUW-LINGGA ARCHIP. Karimon: Rutan, Simulur, *bb 6303* (BO). P. Sinkep: Manggu, Ketjil, *bb 5366* (BO, infl.).

Borneo. SARAWAK. Binatang, Surong, Daro For. Res., *Tahir 9715* (K, L, infl.); near Kuching, *Beccari PB 673*, Nov. 1865 (A, BM, FI, K, ♂). BRUNEI. Sebatu-Arur Mangan watershed, *Ashton BRUN 348* (K, KEP, ♀). WEST BORNEO. Kubu, Baru, Telok Meranti, *bb 8041* (BO); Sambas, Paloh, *bb 13891* (BO, ♀); Simpang, Djenu, *bb 12699* (BO). SOUTH AND SOUTHEAST BORNEO. Lower Dajak, Danau Rawah, *bb 13483* (BO); Sampit, Sungei Kereng Bindjai, Sabangau, *bb 7941* (BO). BRITISH NORTH BORNEO. Tambunan, *Wyatt-Smith KEP 80436* (K, KEP, infl.). P. NUNUKAN. *Kostermans 8664* (K, L, ♀); S. Simengkadu, *Meijer B 2372* (K, KEP, ♀).

This subspecies may be distinguished from the type and from ssp. *borneensis* by the obovate leaves, the consistently subglabrous adult shoot, and the shorter peduncles. The syncarp processes are rather variable in shape, overlapping those of both these entities. However, as noted above, the ecological preferences of ssp. *forbesii* seem to be quite distinct from those of the other subspecies. From ssp. *papuanus*, ssp. *forbesii* may be distinguished by the smaller, more thickly coriaceous leaves drying red-brown, and by the syncarp processes. *Artocarpus forbesii* was reduced by Beccari to *Parartocarpus venenosus* in 1902, and King's epithet has not been taken up previously in the latter genus, most specimens having been determined as *P. triandra* J. J. Smith.

SPECIES EXCLUDENDAE

PARARTOCARPUS PAPUANA S. Moore, Jour. Bot. **61**, Suppl. 52. 1923, non Becc., 1902 = **Prainea papuana** Becc. For. Borneo, 635. 1902.

PARARTOCARPUS sp., Benth. & Hook. f. Gen. Pl. 3: 375. 1880 (*Beccari PB 667*) = **Prainea frutescens** Becc. For. Borneo, 635. 1902.

Hullettia King in Hook. f. Fl. Brit. Ind. **5**: 547. 1888; King, Ann. Bot. Gard. Calcutta **5**(2): 163. *t. 197.* 1896; Engler & Prantl, Nat. Pflanzenfam. Nachträge II–IV. 122. 1897; Boerl. Handl. Fl. Ned. Ind. **3**: 338, 372. 1900; Ridley, Fl. Malay Penin. **3**: 358. 1924; Jarrett, Jour. Arnold Arb. **40**: 9, 11. *fig. 2, g–k, fig. 3, j–l.* 1959. LECTOTYPE SPECIES: *Hullettia griffithiana* (Kurz) King.

Kurzia King in Hook. f. Fl. Brit. Ind. **5**: 479. 1888, in clavis.

Shrubs to small trees. *Leaves* spirally arranged, simple, entire, penninerved, thinly to thickly coriaceous, lower epidermis with numerous cells having strongly thickened, pitted walls and bearing hairs or not, the lower surface hence hispid-pubescent, scabrid or smooth, minutely punctate beneath in sicco from the whitish stomata; epidermal gland-hairs superficial, long-stalked, heads globose, unicellular; spongy mesophyll compact, without resin-cells; juvenile leaves elongate. *Stipules* paired, linear, lateral, scars small, round.

Inflorescences unisexual, capitate, head pulvinate or obconical at anthesis, becoming subglobose in syncarp, pedunculate, solitary or paired in leaf-axils; stamens or ovaries sunken in cavities closely set on the upper surface of the receptacle; receptacle naked (perianths and interfloral bracts lacking), fleshy; involucre of 3–6 obtuse to lanceolate, fleshy, flattened bracts present. *At anthesis*: anthers or stigmas exserted through perforations in the upper surface of the receptacle; involucre marginal; *male head* with up to 30 flowers; stamens paired in each cavity with the filaments partially or almost completely united, anthers 0.7–1 mm. long, long-exserted; *female head* with up to 6 flowers, ovaries solitary in each cavity, unilocular, the style apical with a short-exserted, capitate stigma, the ovule apical. *Mature syncarp* formed by the enlargement of the entire female head, with 2–6 flowers forming fruit and completely filling the receptacle; involucre equatorial or becoming sub-basal through the greater expansion of the upper surface of the receptacle; mature ovary pergamentaceous, scar left by the style apical, the seed large, attached apically, testa membranous except the thickened apical cap, endosperm none, embryo straight, orientation longitudinal, cotyledons equal, appressed faces at an angle of 0–90° to median plane of ovary, radicle and plumule small, basal,

DISTRIBUTION: southern Tenasserim and peninsular Siam, Malaya, Sumatra (Indragiri).

The genus *Hullettia* was described by King in 1888 with the two species recognized in the present revision, namely, a species from Tenasserim based on the wrongly assigned *Dorstenia griffithiana* Kurz, and a new species from Malaya, *Hullettia dumosa* King. The new genus appeared in the key to the Urticaceae in the *Flora of British India* as "*Kurzia*," but, finding that this name was preoccupied [by the algal genus *Kurzia* Martius, Flora **53**: 417. 1870], King changed it in the systematic treatment to *Hullettia*, after R. W. Hullett, a schoolmaster in Singapore who served on the Gardens Committee there. In 1896 King published a somewhat more detailed account, with a plate of *H. dumosa*, in "A Century of New and Rare Indian Plants." As with *Prainea*, which he described in the same works, King wrongly stated that the ovule was basal and erect and hence that the position of *Hullettia* was in the tribe Conocephaleae (= subfamily Conocephaloideae). It was rejected from this group by Renner in his study of the leaf anatomy of the Artocarpoideae and Conocephaloideae, but he omitted the genus as being of doubtful affinity (Bot. Jahrb. 39: 419. 1907). *Hullettia* has otherwise been mentioned only in the Nachträge to the Natürlichen Pflanzenfamilien (1897), in the floras of Boerlage (1900) and Ridley (1924), and in Burkill's *Dictionary* (1935).

The morphology of the inflorescences has been discussed in the introductory paper of this series (Jour. Arnold Arb. **40**: 1–29. 1959). The attachment of the ovule has been found to be apical in the two species both at anthesis and at maturity, which indicates (with the erect stamens) that *Hullettia* is related to the genera at present placed in the Artocarpoideae. The capitate inflorescences resemble those of *Parartocarpus* in being clearly involucrate (with fleshy marginal to sub-basal bracts) and in having the stamens and ovaries apparently enclosed in cavities of the receptacle rather than in perianths. Externally, however, the inflorescences of the two genera have a very different aspect, since those of *Parartocarpus* are armoured from indurated processes, whereas those of *Hullettia* have a smooth, fleshy, pubescent surface, with perforations leading to the receptacular cavities. Perianths and interfloral bracts appear to be entirely absent in the latter genus.

The mature syncarp of *Hullettia* differs internally from that of *Parartocarpus* in having pergamentaceous, not indurated, pericarps, and straight, rather folded embryos. However, the testa has a well-developed, thickened cap occupying an apical position in the pericarp, as in *Parartocarpus*. The tips of the cotyledons lie in contact with this cap, which may be compared with the similar thickening of the testa in *Prainea*. The latter, however, is basal (corresponding with the sub-basal attachment of the mature seed) and the orientation of the embryo relative to the pericarp is the reverse of that found in *Hullettia*, the radicle being apical.

It should be noted that this view of the inflorescence structure of *Hullettia* is in complete accord with the account of "*Dorstenia sp.*" given by Griffith (published in 1854), on which *Dorstenia griffithiana* Kurz (= *Hullettia griffithiana* (Kurz) King) was largely based. Griffith apparently dissected fresh inflorescences and the details given by him of the pericarps and seeds support the present description, which is based on an examination of dried syncarps (boiled up in water) of both species. King, on the other hand, regarded the stamens and ovaries as being enclosed in tubular perianths, which were connate with each other and the receptacle. However, as in *Parartocarpus,* no sign of fusion between adjacent perianths has been found in the walls separating the receptacular cavities. In view of the other characters indicating an affinity between the genera, it seems more probable that the inflorescence structure of *Hullettia* is homologous with that of *Parartocarpus*. In the latter the walls have been shown to be largely, if not wholly, of intercalary origin. No material has been available for the study of development in *Hullettia* and it is possible that vestiges of perianths, indistinguishable at later stages, are incorporated in the surface of the receptacle.

The leaves of *Parartocarpus* and *Hullettia* agree in having long-stalked, superficial gland-hairs with unicellular heads. As was noted in the introductory paper, *Hullettia* is distinguished by the numerous enlarged cells with strongly thickened, pitted walls in the lower epidermis. However, it should be observed that the minutely punctate appearance of the under

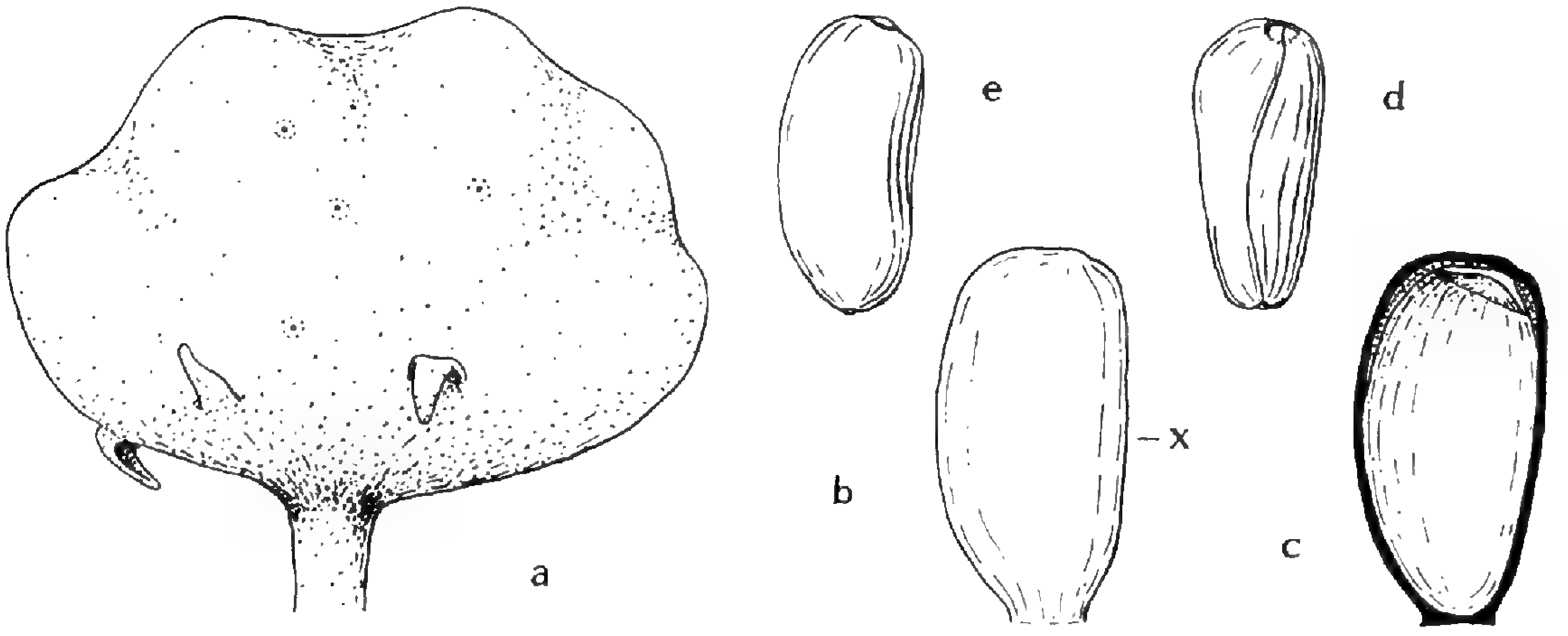


FIG. 22. The syncarp in *Hullettia griffithiana*: a, entire head; b, pericarp, side view; c, pericarp cut in median plane and embryo removed; d, embryo from same view; e, embryo seen from "x" (all approx. × 1).

surface of the leaves when dry is due, not to these cells, as was stated there, but to the whitish guard cells of the stomata.

The distribution of *Hullettia* as a genus is very limited. *Hullettia griffithiana* is known from southern Tenasserim and peninsular Siam, while *H. dumosa* occurs quite widely in Malaya and has recently been collected in central Sumatra. Both species may well be more common than is indicated by the number of collections, since they are small trees or shrubs which are probably relatively inconspicuous except at the time of fruiting. The fleshy, orange syncarps presumably attract arboreal mammals or birds in the same way as the fruits of those species of *Artocarpus* that have fleshy syncarps. The two species in the genus are readily separated on inflorescence characters, especially those of the mature syncarp. The vegetative characters show some overlapping, but there is usually no difficulty in assigning sterile collections to one or other of the species.

KEY TO THE SPECIES OF HULLETTIA

Male head c. 10 mm. across, peduncle to 20 mm.; syncarp with obtuse to obsolete involucral bracts, peduncle to 45(–55) mm.; leaves smooth to scabrid beneath, base cuneate to rounded, petiole to 50 mm. .... 1. *H. dumosa.*

Male head to 7 mm. across, peduncle 25–45 mm.; syncarp with lanceolate involucral bracts, peduncle c. 75 mm.; leaves hispid-pubescent to scabrid beneath, base narrowly and abruptly rounded or auriculate, petiole to 18 mm. .... 2. *H. griffithiana.*

1. **Hullettia dumosa** King in Hook. f. Fl. Brit. Ind. **5**: 547. 1888; King, Ann. Bot. Gard. Calcutta **5**(2): 163. *t. 197.* 1896; Ridley, Fl. Malay Penin. 3: 358. 1924; Burkill, Dict. 1202. 1935. Syntypes, Perak, *King 3959*, *Scortechini s.n.* (CAL, not seen; duplicates examined, K).

Shrubs or small trees, height to 10 m. *Twigs* 3–6 mm. thick, acutely rugose, thinly pubescent to subglabrous, hairs pale yellow, subappressed.

Stipules 3–10(–15) × c. 1 mm., puberulent. *Leaves* 10–40 × 4–12 cm., elliptic to oblong- or obovate-elliptic, rarely oblanceolate-elliptic, with an acumen to 2.5 cm. long, base cuneate to rounded, margin entire; main veins prominent beneath, reticulum less so; smooth on both surfaces or scabrid beneath; lateral veins 8–12(–15) pairs, curved; intercostals few, often one median between and parallel to the lateral veins, mid-green, drying greyish to yellowish green, paler beneath and minutely punctate, venation straw-coloured; petiole 10–35(–50) mm. long.

Inflorescences solitary or paired in leaf-axils. *At anthesis*: *male head* c. 10 mm. across, obconical or pulvinate, short-pubescent, with c. 4 marginal, subacute, fleshy, involucral bracts, c. 3 × 5 mm.; stamens 3 mm. long, paired, filaments united to just below anthers, anther-cells oblong, 1 mm. long; peduncle 10–20 × 1 mm., short-pubescent, often enlarging gradually into receptacle; *female head* with clavate stigmas exserted 0.5 mm. through perforations in the surface. *Syncarp* to 5.5 cm. across, depressed globose, orange with orange-yellow flesh, drying olive-brown, with surface smooth, velutinous, with c. 4 equatorial to sub-basal, obtuse, fleshy, involucral bracts to 3 × 12 mm., often nearly obsolete; wall c. 2 mm. thick; "seeds" (pergamentaceous pericarps) 2–5, ellipsoid, 22 × 11 mm.; peduncle 15–45(–55) × 1.5 mm., short-pubescent.

DISTRIBUTION: in forest to 6700 ft.; Malaya, Sumatra (Indragiri).

Malaya. PERAK. *Scortechini 656* (K), [*Scortechini*] *s.n.* (K, ♀); Batu Kuran, *Curtis*, 1892 (SING); Bujong malacca, *Curtis*, 1892 (SING), *Ridley 9617* (SING, ♀); Gunong Batu Puteh, *Wray*, 1888 (BM, SING, ♂); Gunong Kerbau, *Robinson*, Mar. 1913 (K, ♂, ♀); Kota Lama, Kuala Kangsar, *Haniff SFN 16040* (SING); Larut, *King 2405* (BM, infl.), *3959*, Mar. 1883 (K, ♀); 11th mile from Tapah, *Haniff SFN 14283* (SING); Ulu Bubong, *King 10427* (BM, K, ♀). TRENGGANU. Bukit Kajang, Kemaman, *Corner*, Nov. 1935 (SING). PAHANG. Fraser's Hill, *Corner SFN 33206* (A, K, SING, ♂); Telom, *Ridley 13788* (BM, SING, ♂); Temerloh, Titi Bungor, *Henderson SFN 10543, 10629* (SING, infl.). SELANGOR. Kepong, For. Res. Inst. plantations, *Kochummen KEP 78955* (K, ♀); Klang Gates, *Hume 7231* (SING), *Ridley*, Jan. 1921 (K, SING, ♀); Kuala Lumpur, *Curtis 2404* (SING, ♀); Simpang, *Ridley 15603* (BM, K, ♀); Sunenyih, *Hume 8205* (SING); Sungei Buluk, *Ridley 13343* (BM, K, SING, infl.); Sungei Lalang Kajang, *Symington CF 24185* (SING, infl.). NEGRI SEMBILAN. Gunong Angsi, *Nur SFN 11569* (K, SING, ♀). MALACCA. Mt. Ophir, *Cameron*, Nov. 1941 (SING, ♀), *Lobb* (GH, infl.). **Sumatra.** INDRAGIRI. Taluk region, near bivac Dewan, *Meijer 4281* (CGE, ♂, ♀). **Cultivated.** MALAYA. Singapore, Hort. Bot., *Hassan*, May 1927 (SING, infl.).

2. **Hullettia griffithiana** (Kurz) King in Hook. f. Fl. Brit. Ind. **5**: 547. 1888; King, Ann. Bot. Gard. Calcutta **5**(2): 163. 1896.

Dorstenia sp., Griffith, Not. Pl. Asiat. **4**: 403. 1854.

Dorstenia griffithiana Kurz, Jour. Asiat. Soc. Bengal **42**: 104. 1873, For. Fl. Burma **2**: 462. 1877. Syntypes, Tenasserim, *Griffith 929* (*Kew Distrib. 4676*) (K), *Helfer 4676/1* (CAL, not seen; duplicates examined, GH, K); lectotype, *Griffith 929* (K).

Shrubs or small trees, height to 7 m. *Twigs* 4–5 mm. thick, acutely rugose, thinly to moderately pubescent, hairs pale yellow, subappressed. *Stipules* 6–10 × 1 mm., indumentum as twigs. *Leaves* (12–)16–35 × 4.5–9 cm., oblanceolate- to obovate-elliptic, often narrowly so, acuminate, base narrowly and abruptly rounded, or auriculate, the auricles sometimes joined across the petiole, margin entire; main veins prominent beneath, reticulum less so; glabrous above, moderately to sparsely short hispid-pubescent beneath; lateral veins 11–16 pairs, curved; intercostals few, often one median between and parallel to the lateral veins; drying greyish to yellowish green, paler beneath and minutely punctate, venation straw-coloured; petiole 10–18 mm. long.

Inflorescences solitary or paired in leaf-axils. *At anthesis*: *male head* 4–7 mm. across, pulvinate, short-pubescent, with c. 4 marginal, acute, fleshy, involucral bracts, c. 1.5 × 1 mm.; stamens 3 mm. long, paired, filaments united for half their length, anther-cells oblong, 0.7 mm. long; peduncle (? 20–)28–45 × 1 mm., short-pubescent; *female head*. . . . *Syncarp* to 4.5 cm. across, depressed globose, drying olive-brown, the surface smooth, velutinous, with 4–6 equatorial to sub-basal, lanceolate, fleshy, involucral bracts to 6 × 3 mm.; wall c. 2 mm. thick; "seeds" (pergamentaceous pericarps) c. 4–6, ellipsoid, 22 × 12 mm.; peduncle 75 × 1.5 mm., short-pubescent.

DISTRIBUTION: to 200 ft.; southern Tenasserim and peninsular Siam.

Lower Burma. TENASSERIM. *Helfer 4676/1* (GH, K, ♂). Mergui: Madamacca Island, *Griffith 929* (*Kew Distrib. 4676*), Jan. 1835 (K, ♀); Mergui Island, *Proudlock 52* (BM, K, SING, ♂, ♀), *61* (BM, K, ♀); Tenasserim River, Kanaunggyi, *Parkinson 1978* (K, ♂). **Peninsular Siam.** Klong Bagatac, *Kloss 6564* (K, ♂); Koh Khan, Kopah, *Haniff SFN 2991* (SING, ♂); Tasau, *Kloss 6826* (K, ♂).

It has been noted above that *Hullettia griffithiana* was first described, as *Dorstenia* sp., by Griffith, who stated that he had collected his material in the Mergui Archipelago in January 1835. There is a specimen with mature syncarps at Kew, presumably representing this collection, which bears Griffith's number *929* and the Kew Distribution number *4676*. The latter was not listed in J. D. Hooker's *Catalogue of the plants distributed at the Royal Gardens, Kew, from the Herbaria of Griffith, Falconer, and Helfer* (1865), which indicates, according to the preface, that there were no duplicates. Kurz's description of *Dorstenia griffithiana* was mainly abbreviated from that of Griffith, which he cited, but he made slight changes in the details of the leaves and added their measurements. Although he did not quote any specimens, it may be assumed that the collection available to him in Calcutta was *Helfer Kew Distrib. 4676/1*, since this was listed by Hooker (and hence distributed in 1862–3) and was mentioned by King in his second account of *Hullettia* (1896). This collection, which bears immature male inflorescences, must have been made in the period 1837 to 1839, when Helfer was in Tenasserim, and thus it was not the earliest collection of *Hullettia griffithiana*, as stated by King in 1896. It is concluded that both the Griffith and Helfer collections should be regarded as the syntypes of *Dorstenia griffithiana*; the former is chosen as the lectotype, since Griffith's account provided the chief part of Kurz's description.

ROYAL BOTANIC GARDENS,
KEW, ENGLAND.

JOURNAL
OF THE
ARNOLD ARBORETUM

Vol. XLI October 1960 Number 4

COMPARATIVE ANATOMY OF THE LEAF-BEARING CACTACEAE, I.

FOLIAR VASCULATURE OF PERESKIA, PERESKIOPSIS AND QUIABENTIA

I. W. Bailey

The tribe Pereskieae Britt. & Rose of the subfamily Pereskioideae K. Schum. has long been considered to contain the less specialized representatives of the Cactaceae, i.e., as regards possessing normal leaves and a characteristic dicotyledonous woody habit of growth. Since the publication of Berger's (1926) "Die Entwicklungslien der Kakteen," *Pereskia sacharosa* Griseb. and *P. aculeata* Mill. have been regarded, primarily upon the basis of floral evidence, as the most primitive members of the tribe and therefore of the Cactaceae as a whole (Buxbaum, 1953).

If the normal leaf-bearing cacti are to be utilized as an initial fundamental basis in studying salient trends of phylogenetic specialization within the Cactaceae, and in obtaining evidence of valid taxonomic, physiological and ecological significance, it is essential that both the exomorphic and the endomorphic structures of all organs and parts of *Pereskia* (including *Rhodocactus*), *Pereskiopsis* and *Quiabentia* be thoroughly investigated.

The simple, entire leaves of these genera vary markedly in size and form, not only in different putative species, but also at times in the same clone when grown under different environmental influences (e.g., wild *vs.* cultivated plants), and not infrequently in different parts of a single plant. The thickness of fully matured leaves appears to be somewhat more nearly stabilized at times within species, certain of the pereskias having relatively thin laminas in contrast to the more or less exaggerated succulence of others and particularly of various species of *Pereskiopsis* and *Quiabentia.* It is of interest to determine whether there are endomorphic structures within the leaves which are of reliable taxonomic utility in the differentiation of taxa, particularly genera and tribes. In clearing and sectioning leaves for microscopic examination, I have encountered differences in patterns of venation that appear to be of some significance in this connection.

Especially in the case of foliar succulence, critical details of vasculature are more or less obscure in superficial examination of leaves both from living plants and from herbarium specimens. Adequate clearing of such leaves involves more serious difficulties than I have encountered in dealing with the foliage of other families of the dicotyledons. Simple prolonged treatments with sodium hydroxide, lactic acid, chloral hydrate and other clearing reagents are unsatisfactory, maceration and disintegration of the lamina tending to occur before clearing is adequate. Successive, brief, carefully controlled treatments in 3% sodium hydroxide at 56° C., chloral hydrate, and, where essential, with hydrochloric acid or ferric chloride for the removal of superabundant crystals of calcium oxalate have yielded sufficiently clear preparations for the study of venation in most cases. However, the cleared leaves are so fragile that they must be handled with great care. All of the illustrations in PLATES IV–VI were made from unstained leaves mounted in diaphane.

In the leaves of 33 putative species from which I have succeeded in obtaining evidence, the foliar vasculature varies from dominantly pinnate (FIG. 25) to palmate or radiate (FIG. 26).

SPECIES WITH DOMINANTLY PINNATE VENATION

The leaves of *Pereskia aculeata* Mill., *P. bahiensis* Gürke, *P. bleo* DC., *P. corrugata* Cutak, *P. cubensis* Britt. & Rose, *P. portulacifolia* Haw., *P. grandifolia* Haw., *P. moorei* Britt. & Rose, *P. sacharosa* Griseb. (including *P. amapola* Web. and *P. argentina* Web.), *P. tampicana* Web. and *P. zinniifolia* DC. have a broad, conspicuous midvein which subtends an embossed costa on the abaxial or lower surface of the leaf.[1] In these leaves of typically pinnate vasculature, the comparatively tenuous principal lateral veins extend diagonally outward from contact with the midvein toward the margins of the lamina where they interconnect by curvatures of a "camptodrome" pattern. The details of the vasculature vary somewhat in leaves of different sizes and forms, the narrower and more extensively elongated leaves having more numerous lateral veins than do the proportionally broader and shorter forms. (Compare FIGS. 1 and 2.) The characteristically small leaves of *P. cubensis* (FIG. 4) and *P. portulacifolia* (FIG. 3) have a less conspicuously embossed costa in the upper part of the lamina.

In the case of *Pereskia colombiana* Britt. & Rose, *P. diaz-romeroana* Cárd., *P. guamacho* Web., *P. humboldtii* Britt. & Rose, and *P. weberiana* K. Schum., the 4–6 lateral veins which diverge from the midvein in the basal half of the lamina commonly tend to be conspicuous and extensive in contrast to the tenuous shorter ones in the upper part of the leaf (FIGS. 5–9). These extensive basal lateral veins frequently tend to run more nearly parallel to the contour of the margins of the lamina rather

---

[1] Illustration (Britton & Rose, *fig. 4,* 1919) of the imperfectly known *P. lychnidiflora* DC. suggests that it may likewise belong in this category of putative species.

than abruptly and diagonally toward them. (Compare FIGS. 1 and 9.) The leaves of these putative species are quite variable in size and form. In the case of *P. guamacho*, where the general range of variability in size and form is quite similar to that in *P. colombiana*, some of the leaves, at least at times, have a pseudo-palmate venation as illustrated in FIG. 6.

SPECIES WITH PSEUDO-PALMATE TO PALMATE[2] VENATION

In available material of *Pereskiopsis chapistle* Britt. & Rose, *P. kellermanii* (Rose) Britt. & Rose, *P. rotundifolia* (DC.) Britt. & Rose, *P. scandens* Britt. & Rose and *P. velutina* Rose, there are 3, 5, 7 or 9 conspicuous veins. The extensively arcuate lateral veins usually extend independently of the slender midvein from the base of the leaf toward its apex (FIGS. 17–21). Each of the lateral veins subtends a more or less conspicuously embossed costa on the abaxial or lower surface of the lamina, at least during certain stages of the maturation of the leaf. The lateral veins on each side of the midvein commonly tend to be aggregated slightly above the base of the leaf. In the case of *P. chapistle*, *P. porteri* and *P. velutina*, of which I have several collections both from wild and cultivated plants, the venation remains typically palmate regardless of variations in the size and form of the leaves (FIGS. 17, 18, 20, 21).

In available material of *P. aquosa* (Web.) Britt. & Rose, *P. blakeana* Ortega, *P. gatesii* Baxter, and *P. diguetii* Britt. & Rose, the lateral veins frequently, but not invariably, tend to diverge from contact with the midvein above the base of the leaf (FIGS. 14, 22) and therefore are pseudo-palmate rather than truly palmate. The thick, extremely succulent leaves of *Quiabentia pereziensis* Backbg. (FIG. 33) and *P. zehntneri* (Britt. & Rose) Britt. & Rose (FIG. 24) have a venation that varies from palmate to pseudo-palmate.

The leaves of *Pereskia pititache* Karw., *P. conzattii* Britt. & Rose, *P. autumnalis* (Eichlam) Rose, and *P. nicoyana* Web. are extraordinarily variable in form on shoots of the same plant (FIGS. 10–13, 15–16). The venation varies from pseudo-palmate to palmate. It is significant that the leaves of these putative pereskias differ from those of all other investigated species of *Pereskia* (with the exception of an occasional leaf of *P. guamacho* [FIG. 6]) in having a venation which resembles that of *Pereskiopsis* and *Quiabentia* rather than a dominantly and characteristically pinnate one.

PRELIMINARY OBSERVATIONS UPON THE MICROSCOPIC STRUCTURE OF VEINS, VEINLETS AND LEAF TRACES

Although the patterns formed by the minor veins and veinlets vary considerably, as illustrated in FIGS. 27–32, fundamentally similar ones occur in the three genera *Pereskia, Pereskiopsis* and *Quiabentia*. (Com-

---

[2] As defined by Asa Gray (1880) palmately or radiately veined leaves have "three, five, seven or nine ribs which spread from the top of the leaf-stalk and run through the blade like the toes of a web-footed bird."

pare FIGS. 25, 26.) In these genera the veins, veinlets and the ends of the veinlets are composed of tracheary cells with helical and annular thickenings. The phloem fibers which cap the leaf traces in the stem do not extend outward into the lamina of the leaf (except in rare instances), but are replaced by elongated parenchymatous elements of a pseudo-collenchymatous nature. Nor are there sclereids, either free in the mesophyll or jacketing the veins or veinlets, such as occur at times in xerophytic species of other dicotyledonous families.

Where the veinlets are comparatively slender, as commonly in the large thin leaves of various pinnately veined pereskias (FIG. 27), they may be composed largely of a single linear series of tracheary cells which become shorter in the terminal parts of the veinlets (FIG. 33). Where the terminal parts are coarser (FIGS. 28, 29) as commonly occurs in more succulent leaves, the tracheary cells tend to be more numerous and more nearly isodiametric (FIG. 34). In the case of the coarsest patterns of vasculature (FIGS. 30, 31) the veinlets, as well as their terminal parts may be composed of, or jacketed by, short tracheary cells (FIG. 36).

Although patterns of veinlet vasculature may ultimately prove to be of some taxonomic significance in the differentiation of taxa (e.g., in the case of species of *Quiabentia*; compare FIGS. 31, 32) much more extensive collections of the leaves of different species must be secured and studied than are available at present. This is due to there being considerable variation in the details of vasculature in different leaves of the same clone and at times in those of the same plant. Furthermore, it should be emphasized in this connection that it is essential to compare the vasculature of fully matured leaves, for more or less extensive changes in details of venation occur during the enlargement and expansion of the lamina of immature leaves.

The curious short, wide cells with broad, annular thickenings which have attracted so much attention in literature dealing with highly specialized representatives of the Cactaceae (e.g., Schleiden, 1845; van Tieghem, 1885; Darbishire, 1904) do not occur in any of the pereskias of which I have adequate material. On the contrary, they appear sporadically in the leaves and stems of various putative species of *Pereskiopsis*. Such cells and their possible precursors are of common and abundant occurrence in the basal parts of the leaves of *Quiabentia pereziensis* Backbg. and *Q. zehntneri* (Britt. & Rose) Britt. & Rose. In the leaves of these plants, the veins are composed of broader tracheary cells with coarser thickenings than are those of *Pereskia* and *Pereskiopsis*. (Compare FIGS. 35 and 37.) The cells on the margins of the veins have very broad helical and annular thickenings which project deeply into the lumina of the cells. There are transitions between elongated forms of such tracheary cells and very short ones with a few annular thickenings. Such transitional forms suggest that the short, broad elements which occur in other cacti may have evolved by modification of ordinary tracheary cells with helical or annular thickenings.

The midvein of pereskias which have pinnate venation is not a simple structure, but is composed of discrete vascular strands aggregated in an arc, i.e., as seen in transverse sections of the lamina (FIGS. 45–47). The vascular arc varies considerably in form and size in leaves of different dimensions. In the base of some leaves close to their level of attachment to the stem, the arc is so extensive that it forms a nearly or completely closed cylinder (FIG. 48). The number of constituent vascular strands likewise varies, not only in leaves of different sizes, but also at different levels of the same lamina, i.e., tending to increase in number from the apex of the leaf toward its base (FIGS. 44–48). It is evident from cleared leaves and from serial transverse sections at successive levels of the lamina that such a midvein is constituted of *two* aggregations, the individual vascular strands of which extend diagonally outward into the longitudinal halves of the lamina.

The individual strands of the vascular aggregate in the midvein may fuse or divide in various parts of their longitudinal extension (FIGS. 44, 47). When such changes occur the behavior of the xylem and phloem frequently is not closely synchronized. During fission, the separation of strands of phloem usually precedes division of the xylem. Conversely during fusion concrescence of the xylem is precocious. The collenchymatous parenchyma commonly caps the strands of phloem (FIGS. 45–47) but may at times form a continuous layer over the entire abaxial surface of the arc of vascular strands.

The number of discrete strands at any particular level of the leaf may be an *even* or an *odd* one. It is significant in this connection, however, that in a majority of cases there is no conspicuous larger strand which occupies a median position in the arc of discrete bundles. Instead of this there commonly are two aggregates of strands on either side of a more or less conspicuous median parenchymatous gap (FIGS. 45–47). In the case of *Pereskiopsis*, the slender midvein of palmately veined leaves not infrequently is composed of two discrete strands at least in parts of its extension (FIG. 43). Similarly the terminal part of the midvein in the apex of pinnately veined leaves may be composed at times of two more or less closely approximated strands (FIG. 44).

This evidence suggests from a phylogenetic point of view that, as in the case of Austrobaileyaceae, Trimeniaceae, Monimiaceae, Chloranthaceae and certain other families, the longitudinal halves of the lamina of *Pereskia*, *Pereskiopsis* and *Quiabentia* are vascularized by branches of two independent systems of leaf traces rather than by dichotomies of a single trace (Bailey, 1956). According to this view, the simple midvein which occurs at times in *Pereskiopsis* and *Quiabentia*, and the presence in some cases of a medianly placed strand in the arc of bundles of pinnately veined pereskias, is due phylogenetically to the fusion of branches of two independent systems or to asymmetries and the displacement of a single branch into a median position.

If such an interpretation is valid, additional evidence should be obtainable from nodal and subnodal parts of the stem. The node of the leaf-bearing cacti is a consistently unilacunar one. In stems of *Pereskia aculeata*, and at least in parts of those of such species as *P. autumnalis*, *P. diaz-romeroana*, *P. guamacho* and *P. nicoyana* there commonly are two discrete leaf-traces at the nodal level (FIGS. 38, 39). These traces can be followed downward in serial transverse sections, or in adequately cleared stems, for considerable distances below the node. In the case of *Pereskia sacharosa*, *P. grandifolia*, *P. bleo* and in certain stems of *Pereskiopsis*, there may be four (FIG. 40), six (FIG. 41), or more traces (FIG. 42) at the nodal level, such differences being correlated at least to a certain extent with variations in the size of the leaves, with variations in the diameter of stems to which the leaves are attached, or with combinations of such factors. The alternating phyllotaxy is so complex ($2/5$, $3/8$, $5/13$) that it is difficult to follow these vascular strands downward in the same orthostiche. However, in favorable cleared stems of *Pereskiopsis* it is possible to determine that the vascular strands frequently connect with two traces which may fuse for a varying distance and then diverge to *two* above the subtending leaf of the same orthostiche, where they connect with the traces of two separate adjacent orthostiches.

The totality of available evidence indicates that the vasculature of the leaf-bearing cacti presents varying phylogenetic modifications of a fundamentally two-trace unilacunar structure (Bailey, 1956). It is evident that apparent fission of vascular strands may occur at various levels of the stem, node and leaf. Furthermore, various asymmetries and aberrant fusion or division of vascular strands can lead at any given level to the appearance of an *odd* rather than an *even* number of vascular bundles.

More extensive investigation of nodal anatomy and of the form of the midvein in pinnately veined pereskias might eventually yield some evidence of taxonomic utility. But, as in the case of patterns formed by minor veins and veinlets, the range of structural variation in a single species, clone or plant is frequently so obvious that extensive collections must be studied before valid conclusions can be attained.

DISCUSSION

In the discussion of plant taxa and their relationships, evidence from similarities should be harmonized with that obtained from dissimilarities. In the case of the leaf-bearing cacti the similarities are so numerous in various organs and parts that it raises some question regarding the wisdom of placing putative genera in separate subfamilies or tribes. As regards leaves, the ranges of variability in a single clone (and not infrequently in a single plant) are so extensive that they necessitate a re-examination of putative species based in the past upon assumed differences in the size or external form of the foliar appendages. As I have shown, there are transitions in the leaf-bearing cacti between dominantly pinnate and typically palmate venation. Although the foliage of *Pereskiopsis* and *Quiabentia* appears to be dominantly pseudo-palmate or palmate, it does not differ consistently from that of *Pereskia* (including *Rhodocactus*), since similar venation occurs in *Pereskia autumnalis*, *P. conzattii*, *P. nicoyana* and *P. pititache*. Such species as *P. colombiana*, *P. diaz-romeroana*, *P. guamacho*, *P. humboldtii* and *P. weberiana* have a venation which appears to be transitional between that of the preceding species and those which have a dominantly pinnate venation. Pseudo-palmate and palmate venation is correlated with increasing succulence of the leaves. This suggests, but, by itself without corroborative evidence, does not conclusively prove, that the evolutionary transition is from pinnate to palmate.

It is evident thus far in my preliminary anatomical investigations that there are at least four categories of putative species of leaf-bearing cacti which differ more or less markedly in their foliar vasculature. It will be of interest in subsequent anatomical investigations to determine whether there are other anatomical differences in these categories of species which correlate with those of the foliar vasculature. In so doing, it will be desirable, if possible, to determine whether the similarities within each category are due solely to close genetic relationship or in part to parallel evolutionary changes.

The objection may be raised that it is difficult and uncertain to determine the identity of plants from which material is collected in gardens and in the wild. This is particularly the case at present in dealing with species. However, the possibility of misidentifications does not modify the conclusion that there are four categories of leaf-bearing cacti with differing foliar vasculature.

The two-trace unilacunar vasculature and its various modifications in leaf-bearing cacti is significant in any general discussion of the possible relationships of the Cactaceae to other families of the dicotyledons and particularly to those of the Centrospermae.

ACKNOWLEDGMENTS

This investigation was financed by a grant from the National Science Foundation. I am indebted to the Arnold Arboretum, the Gray Herbarium, the N. Y. Botanical Garden, the Smithsonian Institution and the Chicago Natural History Museum for the loan of herbarium specimens. In addition, I am greatly indebted to the following individuals for their laborious and coöperative efforts in collecting adequately preserved specimens: N. Boke, M. Cárdenas, R. Romero Castañeda, A. Castellanos, I. D. Clement, L. Cutak, R. L. Dressler, Gates Cactus Inc., E. Hernandez, P. C. Hutchison, M. Kimnach, R. M. King, H. E. Moore, Jr., R. Moran, H. F. L. Rock, R. L. Rodríguez, A. J. Sharp, W. L. Stern, J. A. Steyermark, and H. Teuscher.

LITERATURE CITED

Bailey, I. W. 1956. Nodal anatomy in retrospect. Jour. Arnold Arb. **37:** 269–287.

BERGER, A. 1926. Die Entwicklungslinien der Kakteen. Gustav Fischer, Jena.

BRITTON, N. L., and J. N. ROSE. 1919. The Cactaceae. Vol. I. Carnegie Inst. Washington.

BUXBAUM, F. 1953. Morphology of Cacti. Sect. II. The flower. Abbey Garden Press. Pasadena, Calif.

DARBISHIRE, O. V. 1904. Observations on *Mamillaria elongata*. Ann. Bot. **18**: 375–416.

GRAY, A. 1880. Lessons in Botany. Ivison, Blakeman, Taylor & Co. New York.

SCHLEIDEN, M. J. 1845. Beiträge zur Anatomie der Cacteen. Mém. Acad. Imp. Sci. St. Petersbourg **4**: 335–380.

TIEGHEM, P. VAN. 1885. Valeur morphologique des cellules annelées et spiralées des Cactées. Bull. Soc. Bot. France **32**: 103–106.

EXPLANATION OF PLATES

The source of the material figured for each species is given in brackets following the name. A complete listing of materials with all available documentary data will be given at the end of this series of papers.

PLATE I

FIGS. 1–9. LEAVES OF PERESKIA. All leaves drawn natural size. 1, *P. sacharosa* Griseb. [Mo. Bot. Gard.]; 2, *P. aculeata* Mill. [*Moran 7272*]; 3, *P. portulacifolia* (L.) Haw. [*Jiménez 2578*]; 4, *P. cubensis* Britt. & Rose [Atkins Gard.]; 5, *P. weberiana* Schum. [*Cárdenas*]; 6, *P. guamacho* Web. [*Steyermark*]; 7, *P. colombiana* Britt. & Rose [*Record 16495*]; 8, *P. diaz-romeroana* Card. [*Cárdenas*]; 9, *P. guamacho* Web. [*Steyermark*].

PLATE II

FIGS. 10–16. LEAVES OF PERESKIA AND PERESKIOPSIS. All leaves drawn natural size. 10, *Pereskia conzattii* Britt. & Rose [*Kimnach 172*]; 11, *P. pititache* Karw. [Atkins Gard.]; 12, *P. autumnalis* (Eichlam) Rose [*Moore*]; 13, *P. nicoyana* Web. [*Rodríguez 662*]; 14, *Pereskiopsis blakeana* Ort. [*Kimnach 81*]; 15, *Pereskia pititache* Karw. [Atkins Gard.]; 16, *P. autumnalis* (Eichlam) Rose [*Moore*].

PLATE III

FIGS. 17–24. LEAVES OF PERESKIOPSIS AND QUIABENTIA. All leaves drawn natural size. 17, 18, *Pereskiopsis porteri* (T. S. Brandeg.) Britt. & Rose [17, N. Y. Bot. Gard.; 18, *Moran 7349*]; 19, *P. scandens* Britt. & Rose [N. Y. Bot. Gard.]; 20, 21, *P. chapistle* (Web.) Britt. & Rose [20, *Hernandez*; 21, N. Y. Bot. Gard.]; 22, *P. aquosa* (Web.) Britt. & Rose [N. Y. Bot. Gard.]; 23, *Quiabentia pereziensis* Backbg. [*Cárdenas*]; 24, *Q. zehntneri* (Britt. & Rose) Britt. & Rose [*Boke*].

PLATE IV

FIGS. 25, 26. CLEARED LEAVES OF PERESKIA AND PERESKIOPSIS. 25, *Pereskia cubensis* Britt. & Rose [Atkins Gard.], × 5.5. 26, *Pereskiopsis velutina* Rose [Mo. Bot. Gard.], × 5.5; two dark-colored tips of glochids are embedded in the cleared lamina.

PLATE V

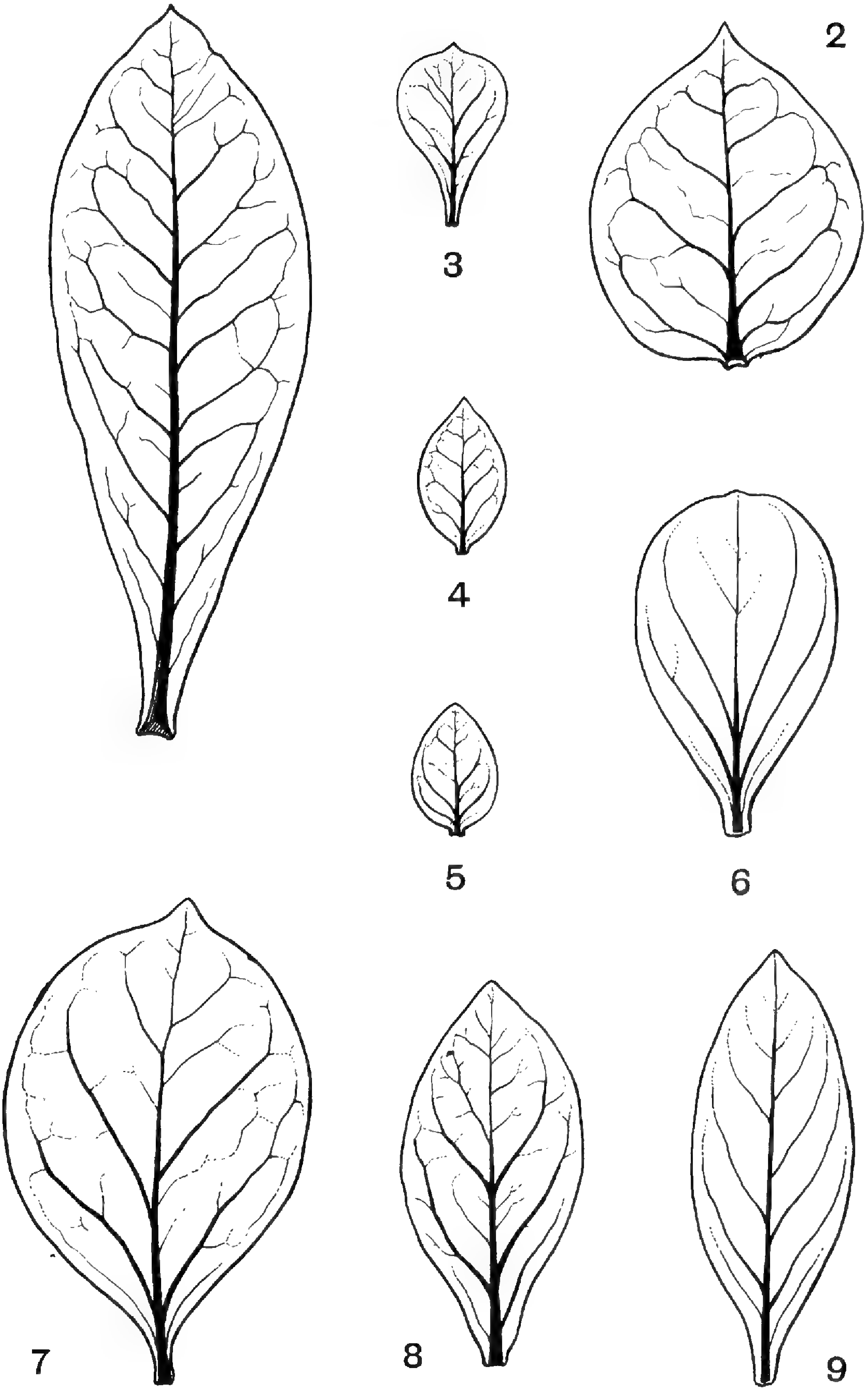
FIGS. 27–32. PORTIONS OF CLEARED LEAVES OF PERESKIA AND QUIABENTIA. All figures × 27. 27, *P. aculeata* Mill. [*Moran 7272*]; 28, *P. weberiana* Schum. [*Cárdenas*]; 29, *P. nicoyana* Web. [*Rodríguez 662*]; 30, *P. pititache* Karw. [Atkins Gard.]; 31, *Q. pereziensis* Backbg. [Cárdenas]; 32, *Q. zehntneri* (Britt. & Rose) Britt. & Rose [*Boke*].

PLATE VI

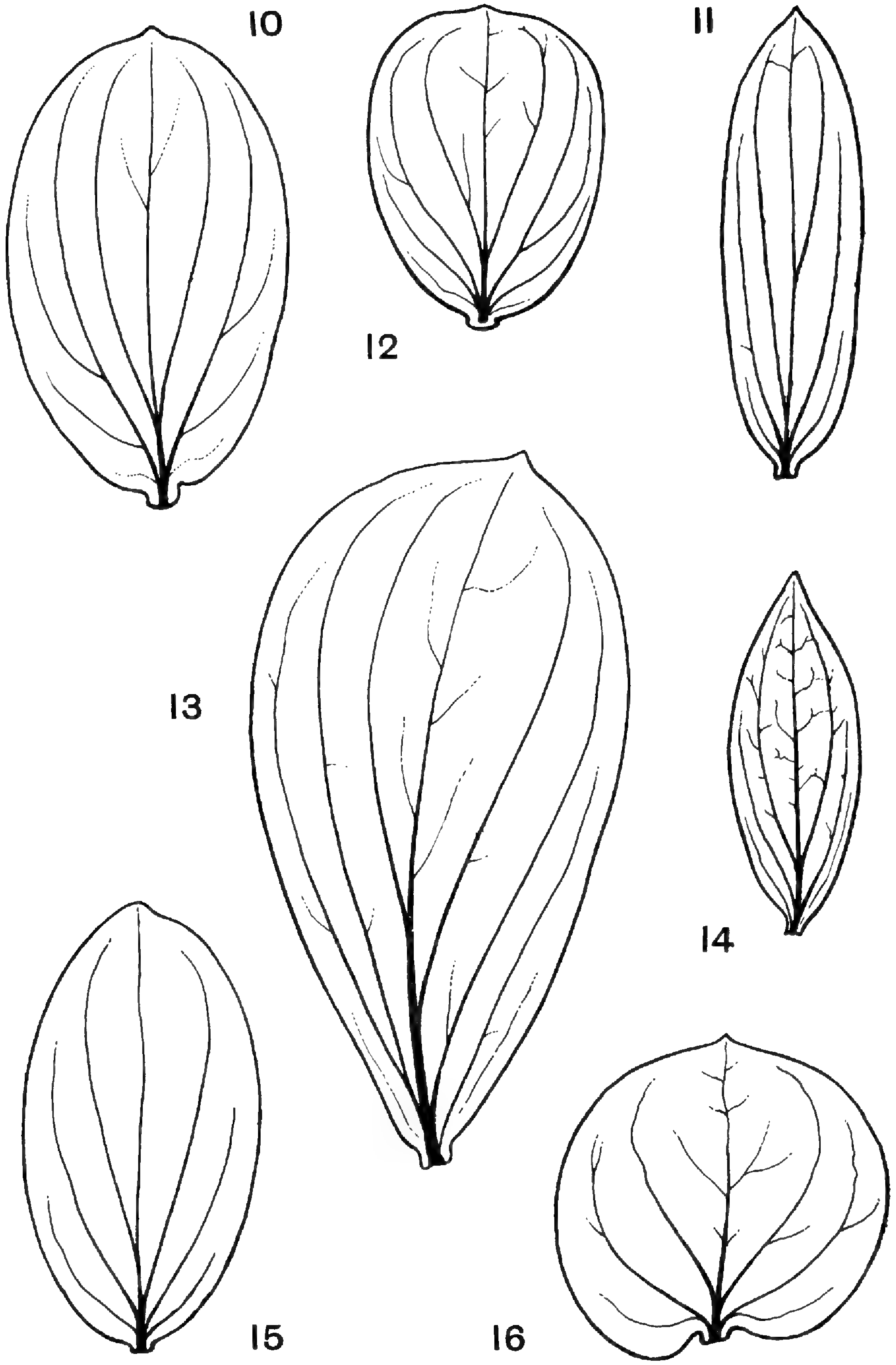
FIGS. 33–37. VASCULAR DETAILS OF VEINS AND VEINLETS IN LEAVES OF PERESKIA AND QUIABENTIA. All figures × 260. 33, *Pereskia aculeata* Mill. [*Moran 7272*]; 34, *P. weberiana* Schum. [*Cárdenas*]; 35, *P. aculeata* Mill. [*Moran 7272*]; 36, *Quiabentia pereziensis* Backbg. [*Cárdenas*]; 37, *Q. zehntneri* (Britt. & Rose) Britt. & Rose [*Boke*].

PLATE VII

FIGS. 38–48. TRANSVERSE SECTIONS OF NODES AND OF MIDVEINS OF PERESKIA AND PERESKIOPSIS. All figures × 25, except FIG. 44, × 72. 38, *Pereskia aculeata* Mill. [*Moran 7272*]; t.s. at 2-trace unilacunar node; 39, *Pereskia diaz-romeroana* Cárd. [Cárdenas], t.s. at 2-trace unilacunar node; 40, *Pereskiopsis porteri* (T. S. Brandeg.) Britt. & Rose [N. Y. Bot. Gard.], t.s. at 4-trace unilacunar node; 41, *Pereskia sacharosa* Griseb. [Mo. Bot. Gard.], t.s. at 6-trace unilacunar node; 42, *Pereskia bleo* DC. [Rodríguez], t.s. at 10-trace unilacunar node; 43, *Pereskiopsis porteri* [N. Y. Bot. Gard.], t.s. of 2-strand midvein of leaf; 44, *Pereskia aculeata* [*Moran 7272*], t.s. of 2-strand midvein in apical part of leaf; 45, *Pereskia sacharosa* [Mo. Bot. Gard.], t.s. of 4-strand midvein some distance below apex of leaf; 46, *the same*, t.s. of 6-strand midvein in central part of leaf; 47, *the same*, t.s. of midvein in basal part of the lamina; 48, *Pereskia grandifolia* Haw. [*Moran 7270*], t.s. at base of petiole.

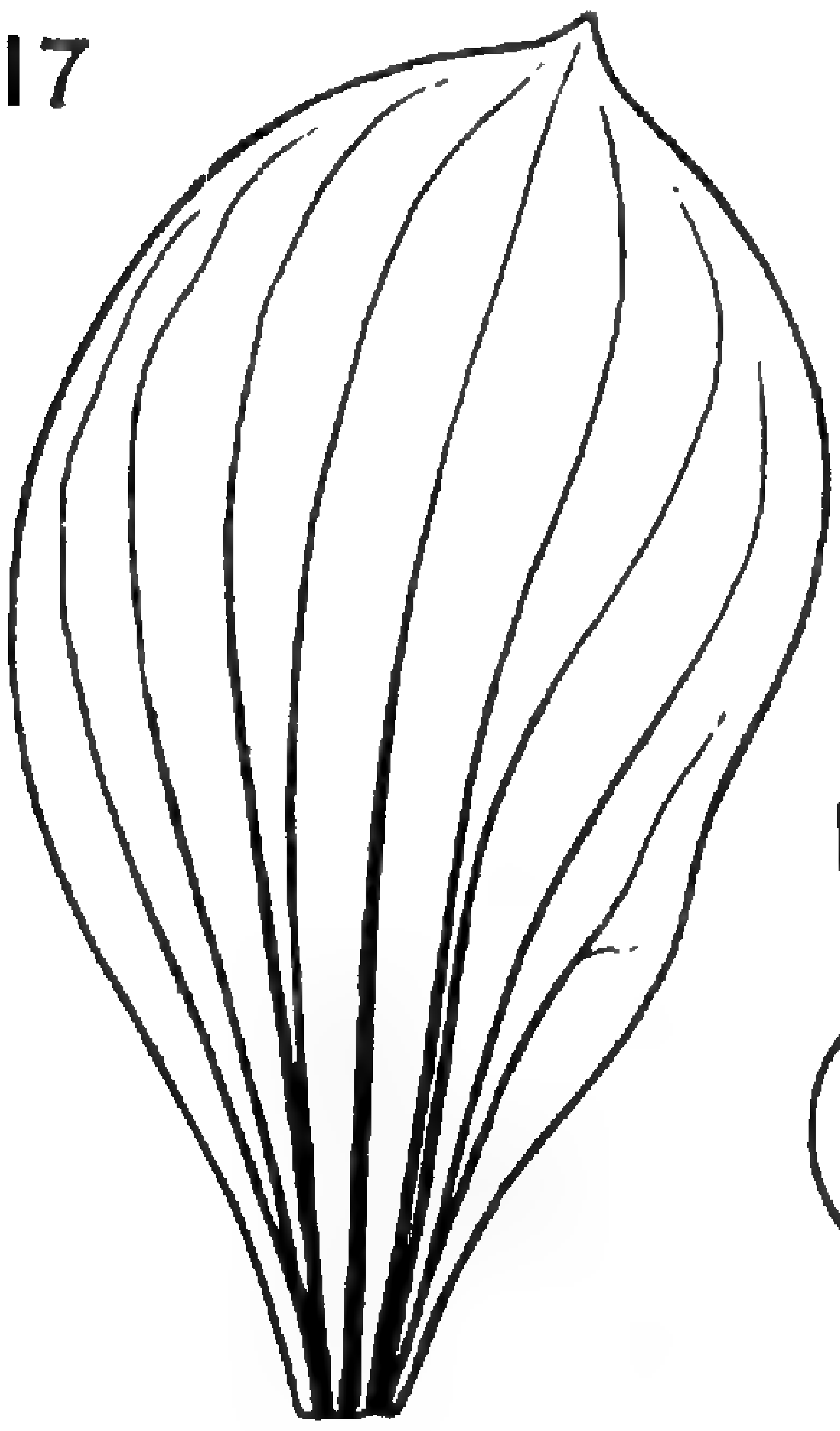


BAILEY, ANATOMY OF LEAF-BEARING CACTACEAE, I

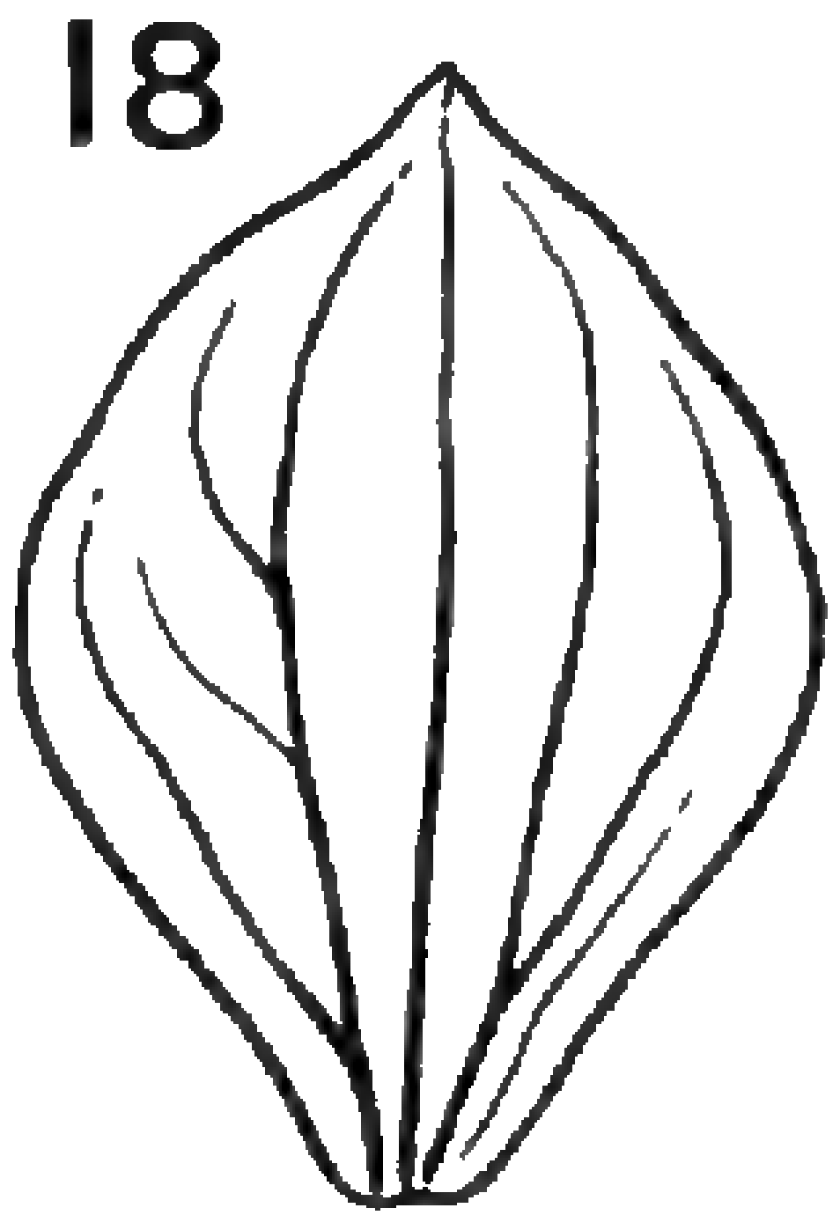


BAILEY, ANATOMY OF LEAF-BEARING CACTACEAE, I

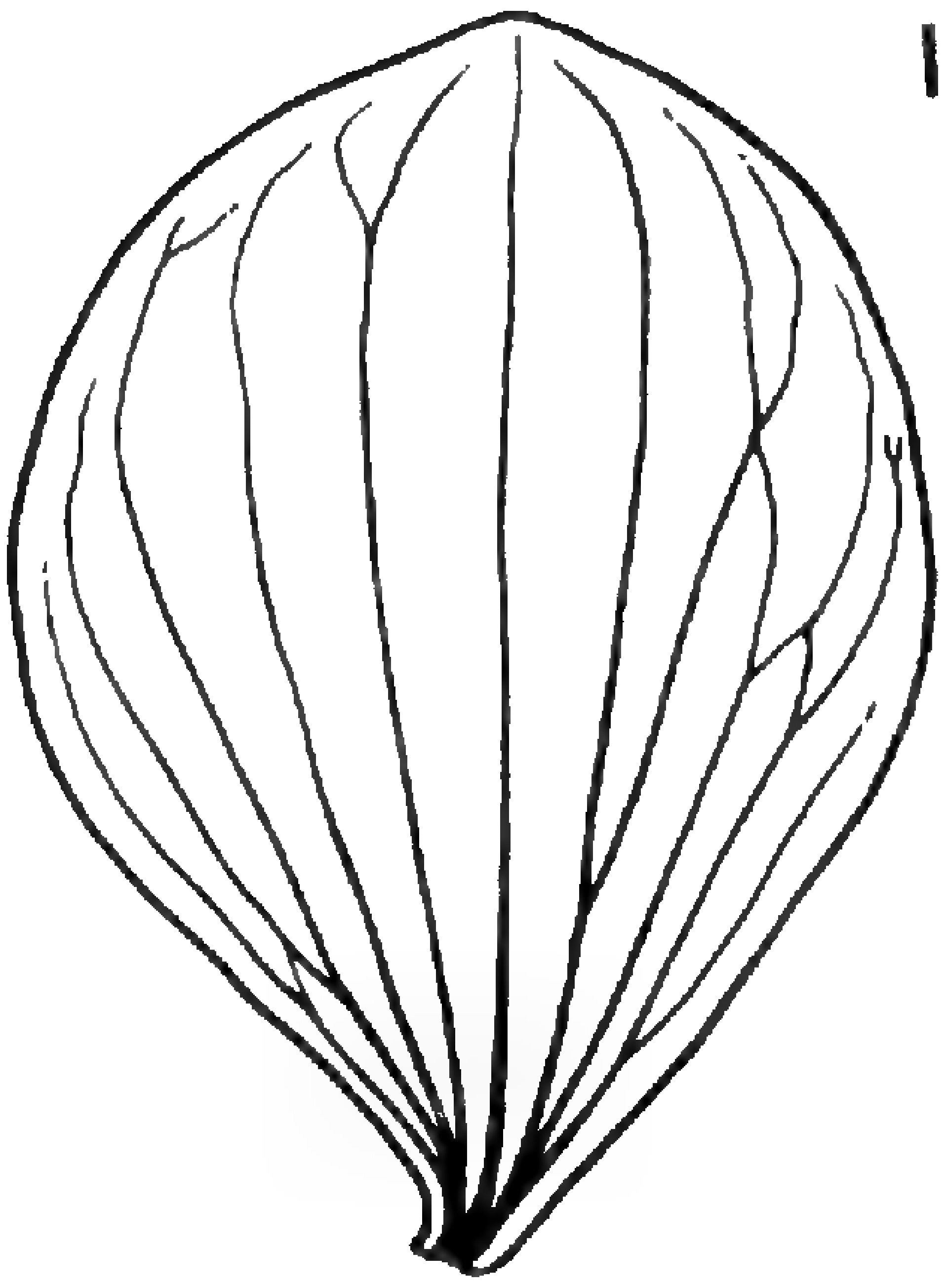
17



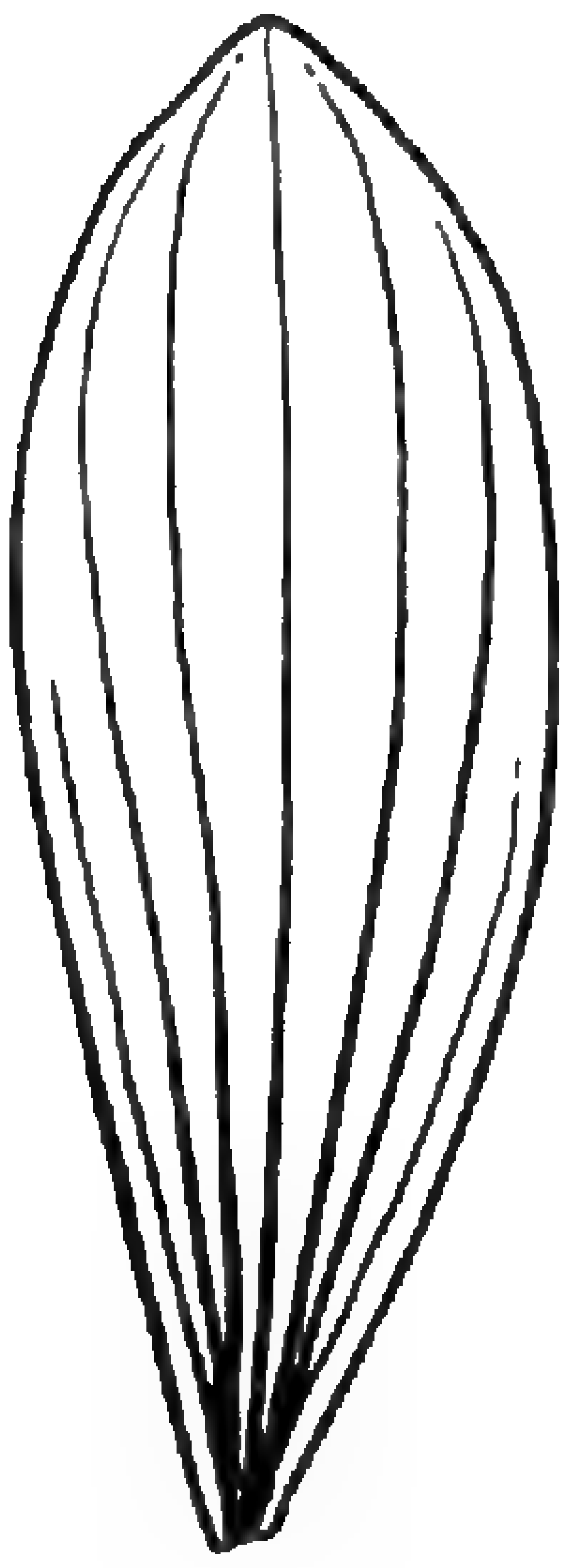
18



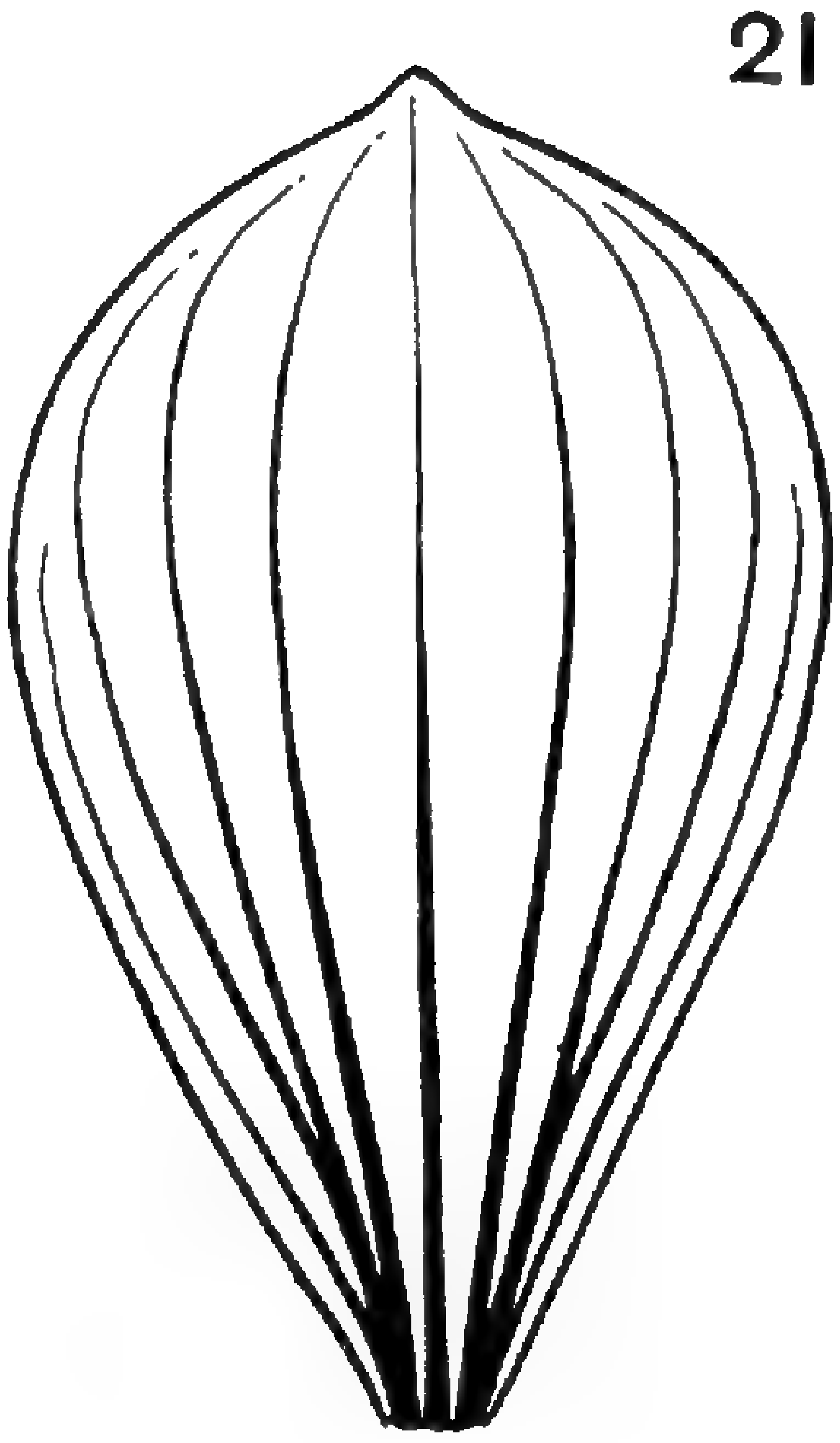
19



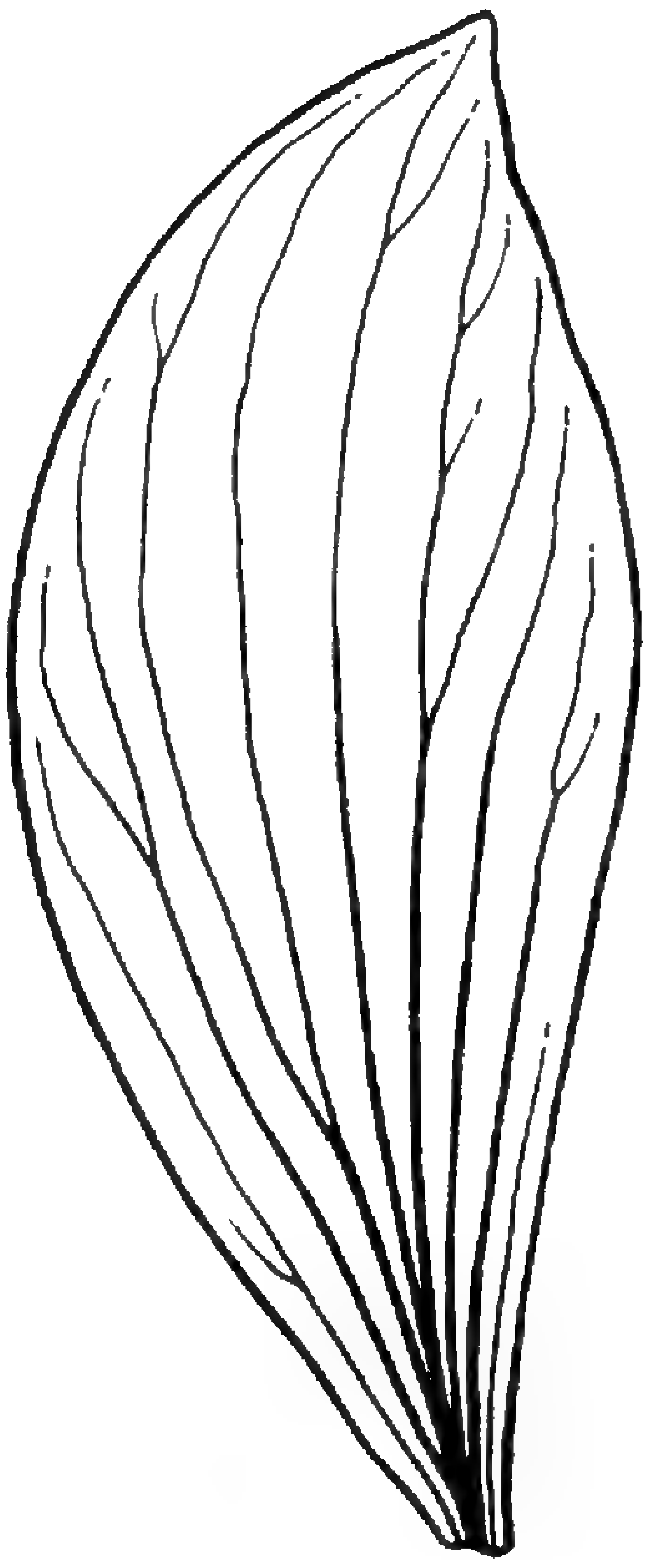
20



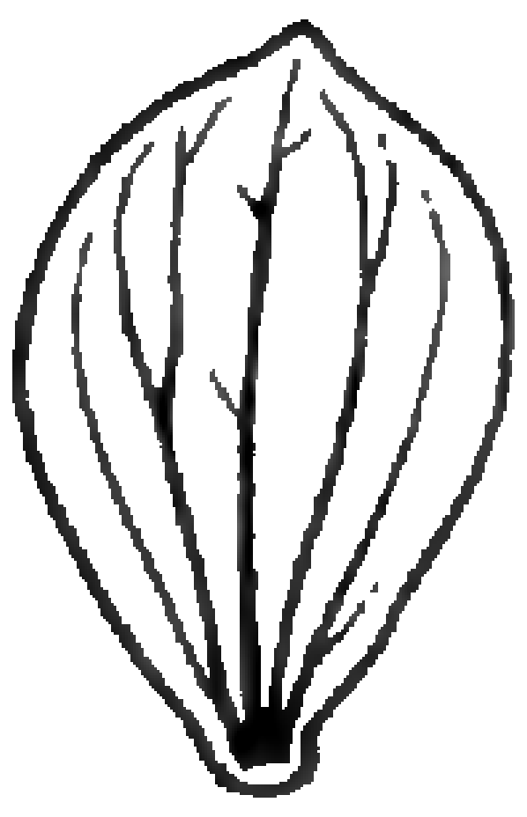
21



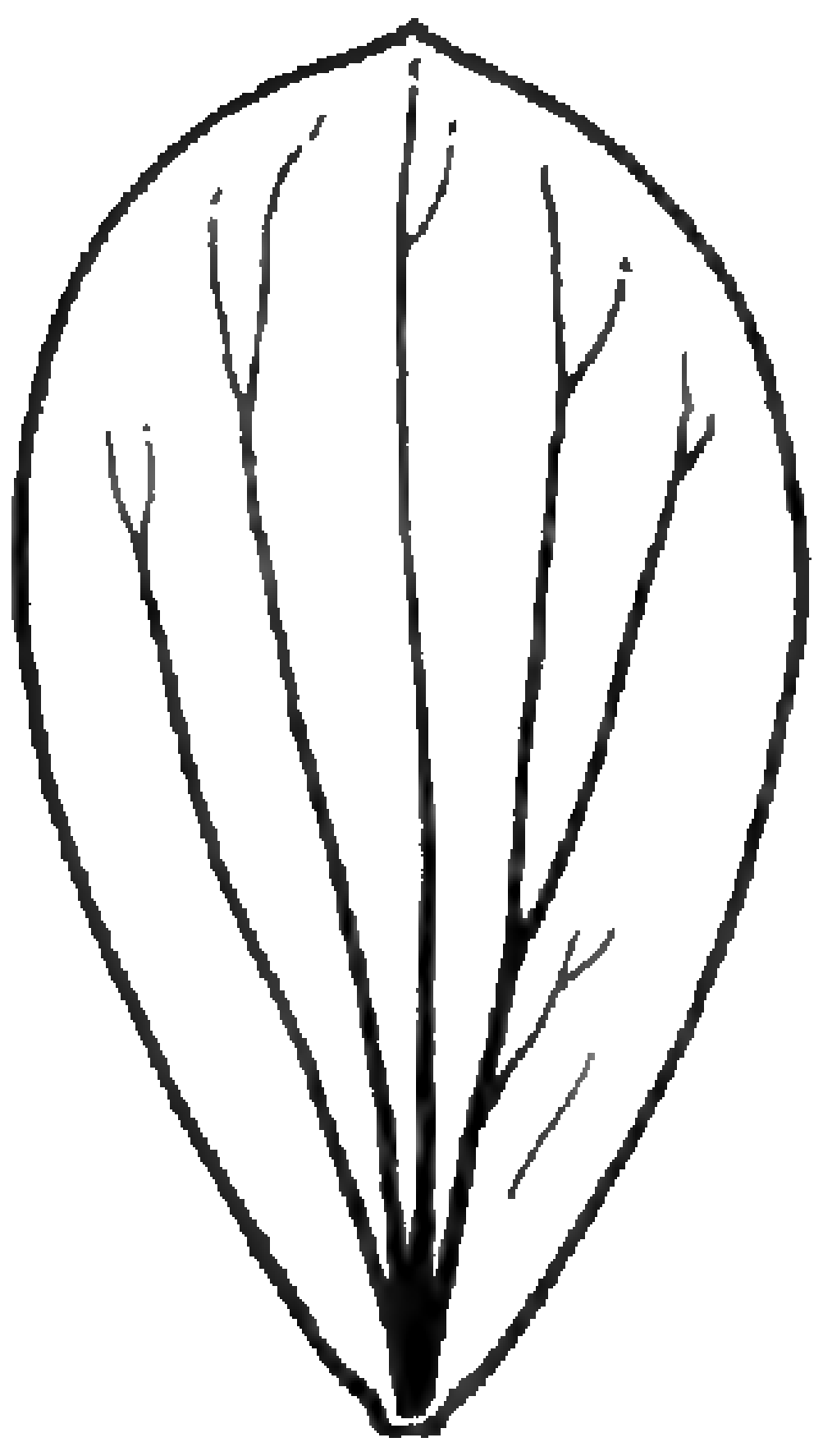
22



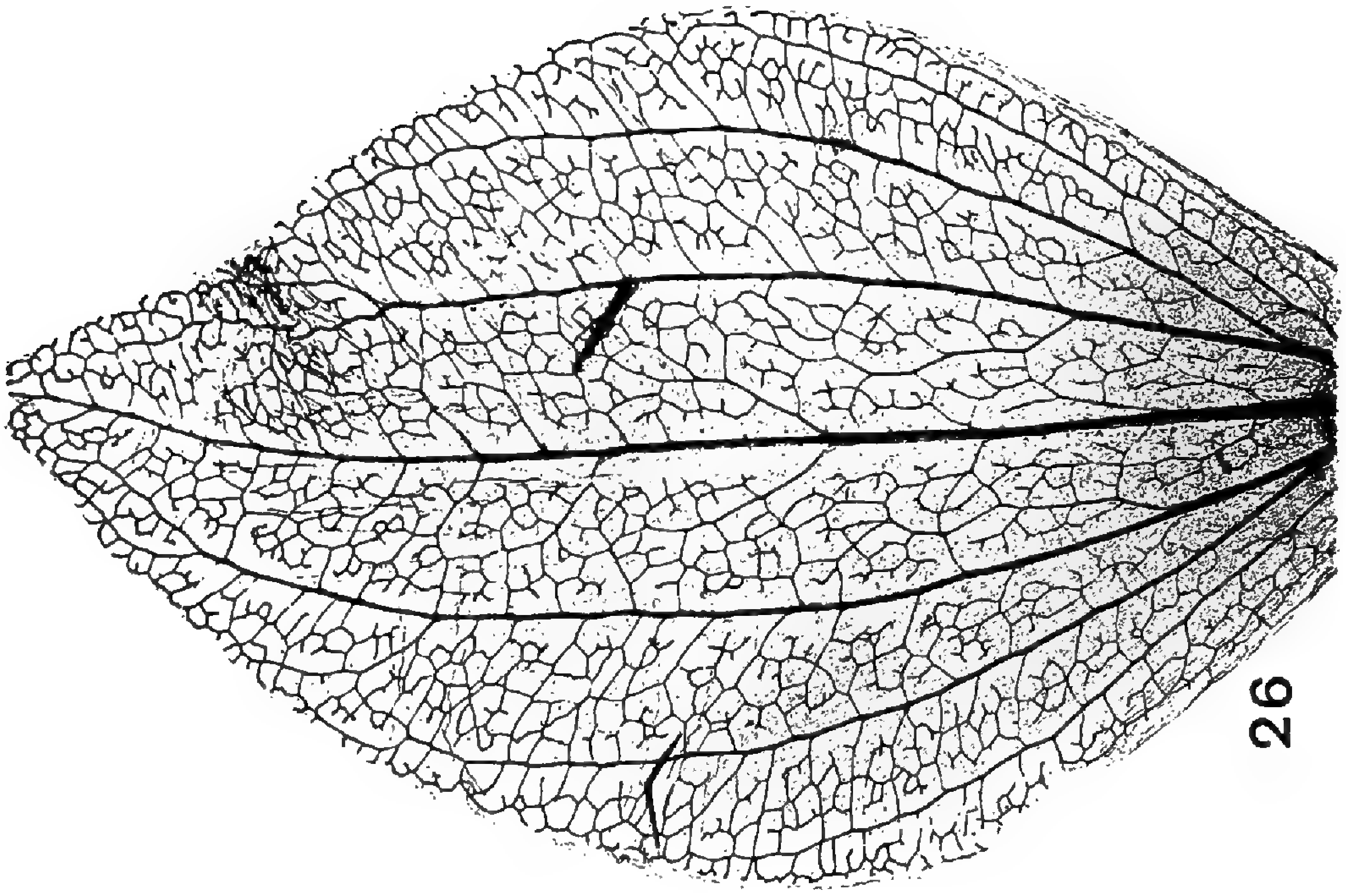
23



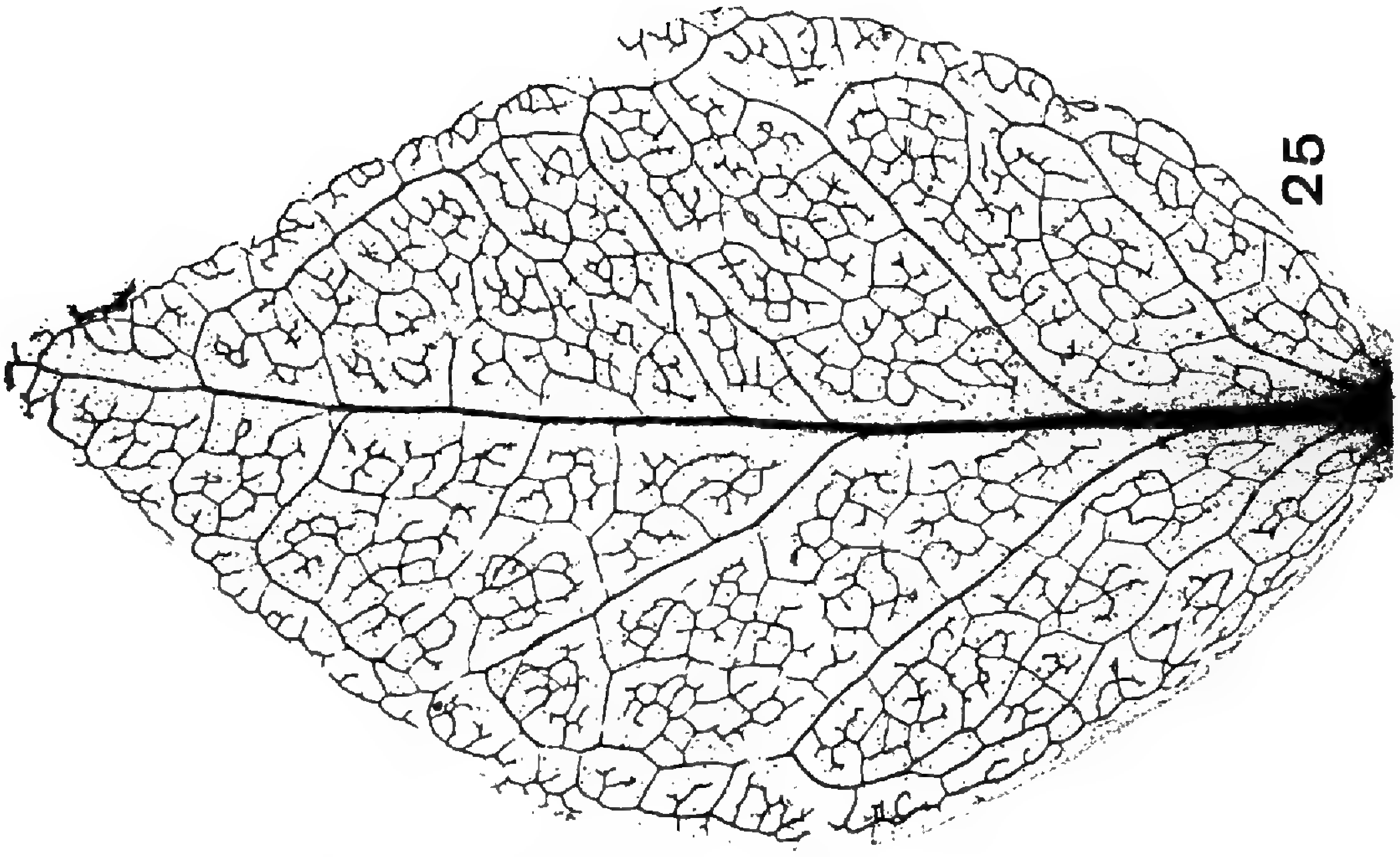
24



Bailey, Anatomy of Leaf-bearing Cactaceae, I



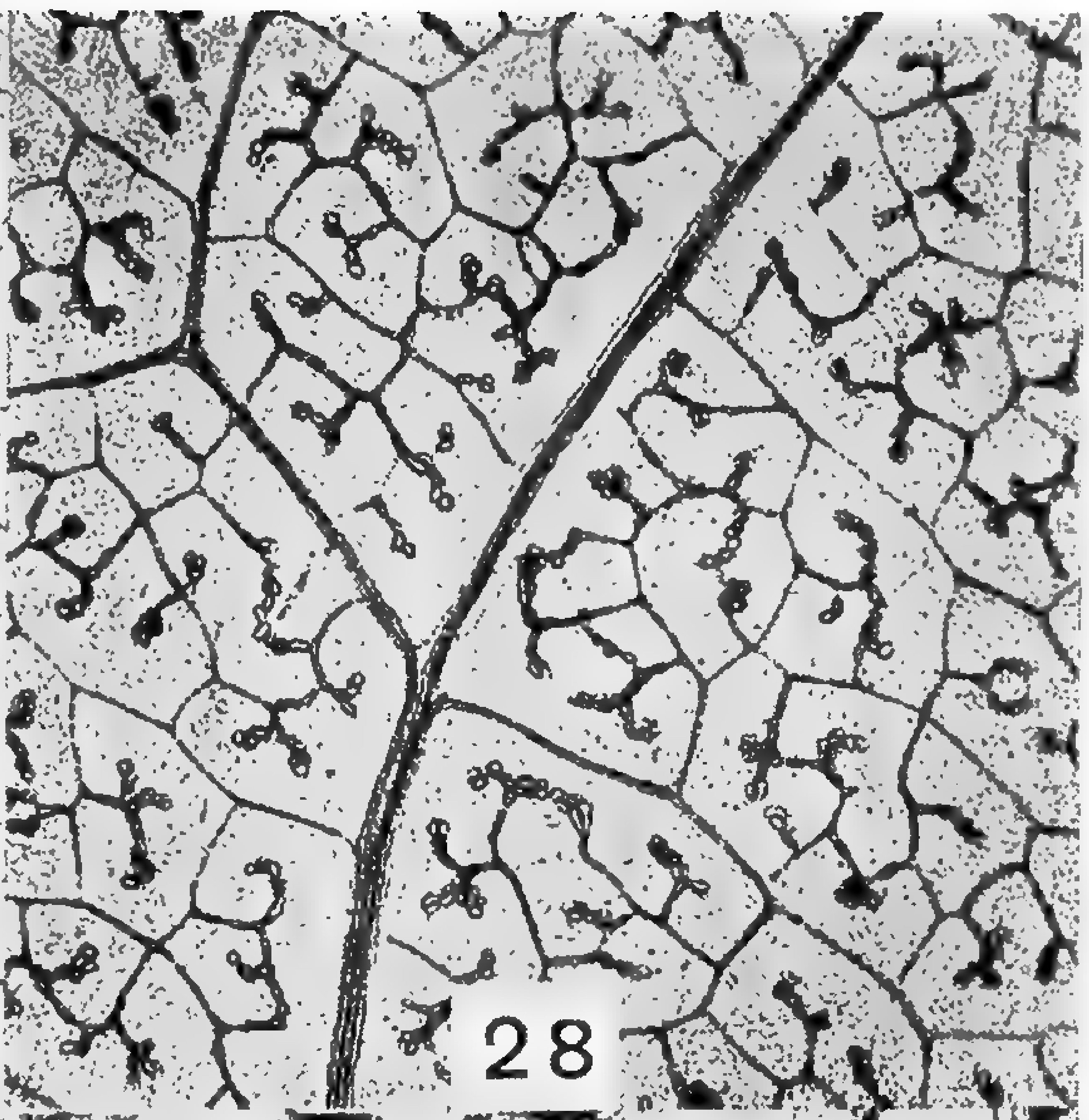
26



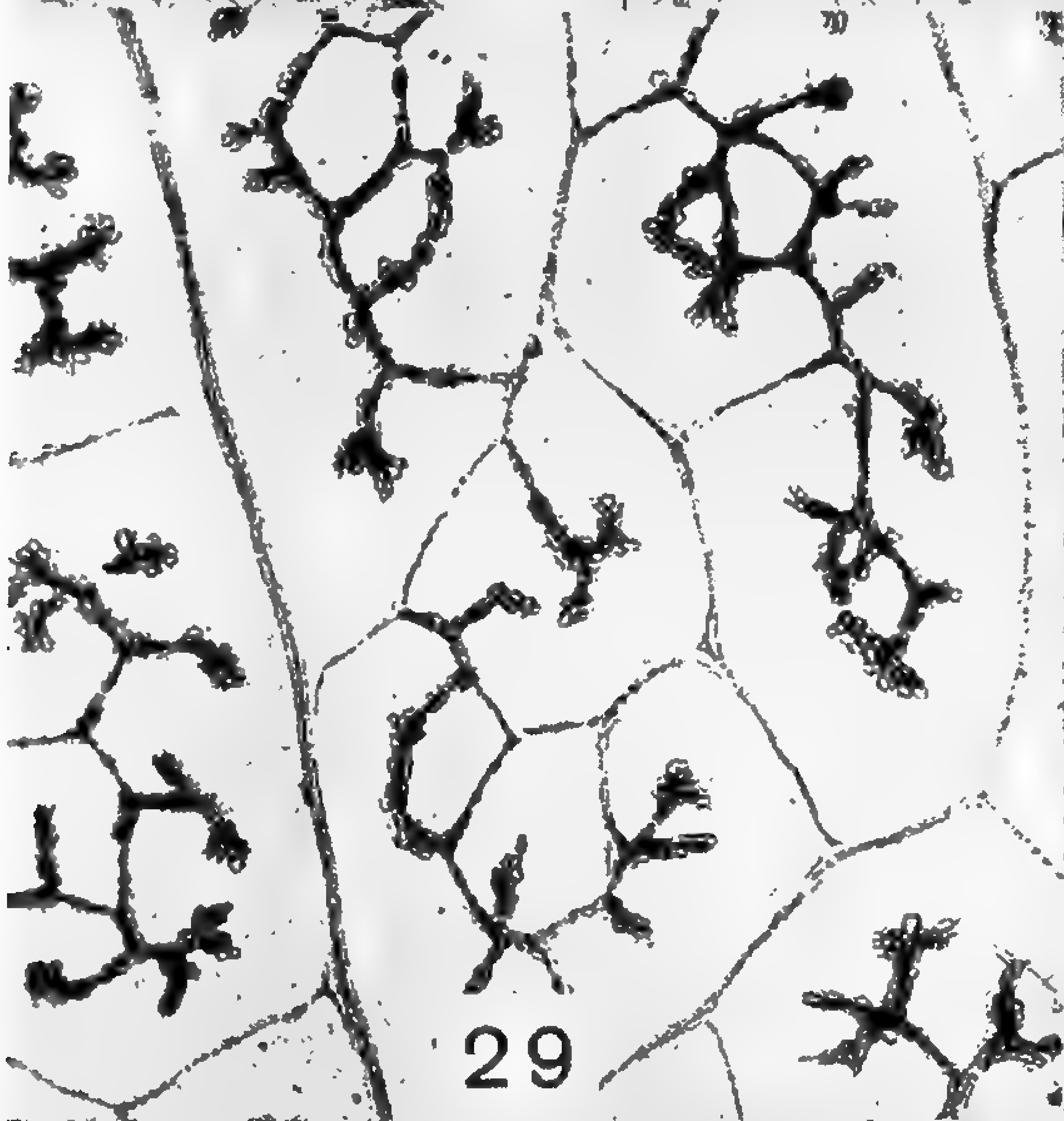
25

Bailey, Anatomy of Leaf-bearing Cactaceae, I

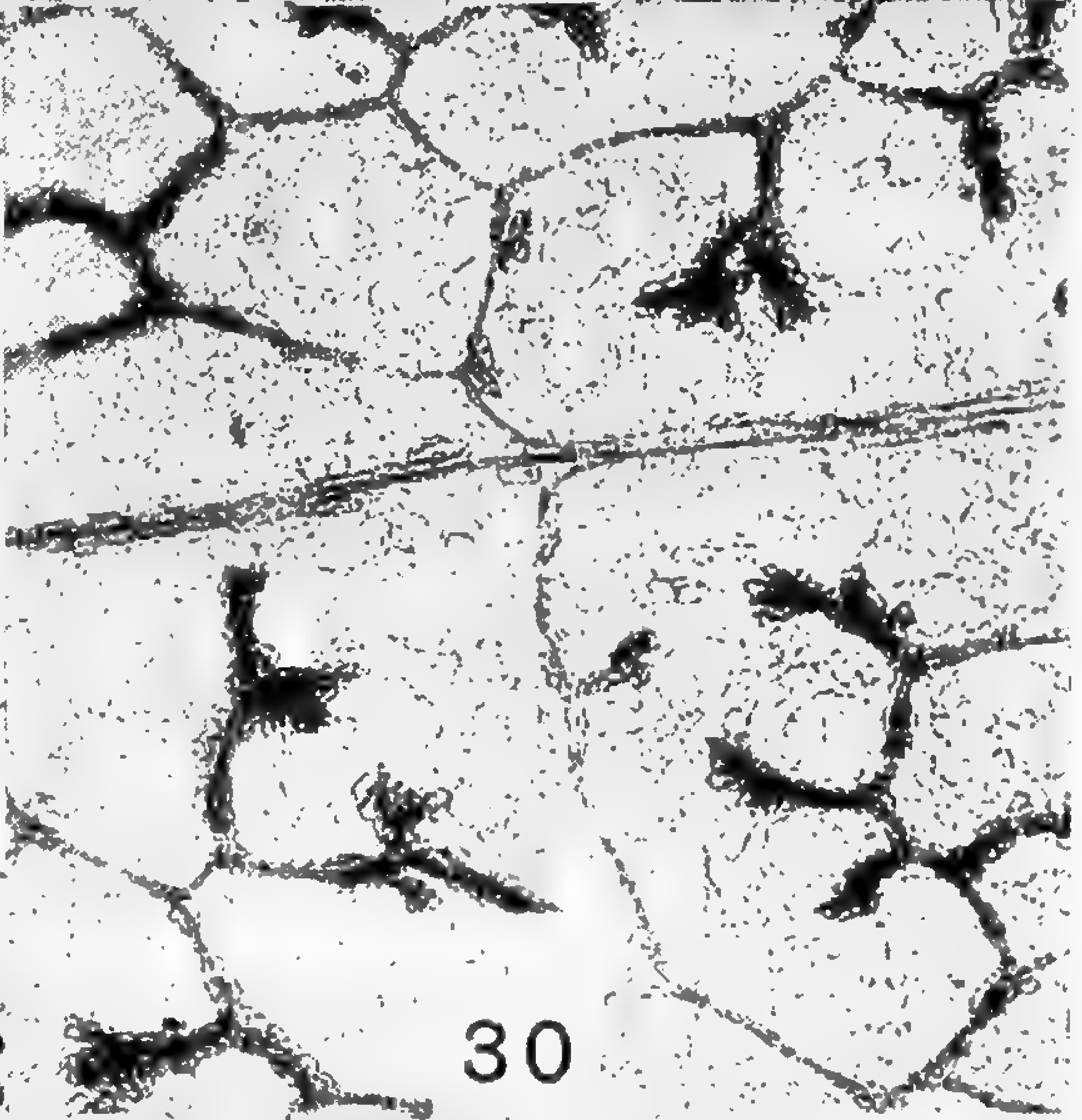
27



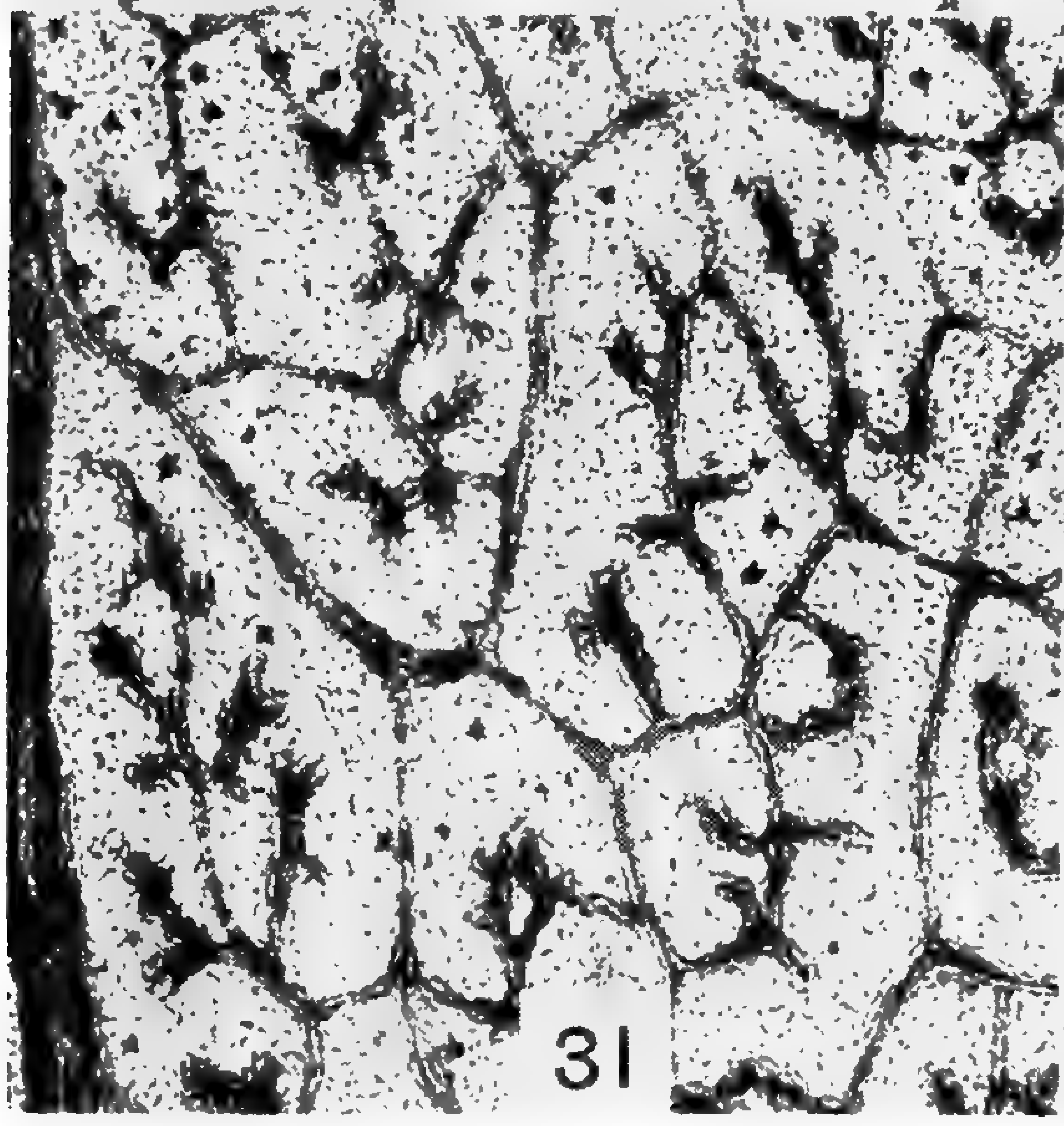
28



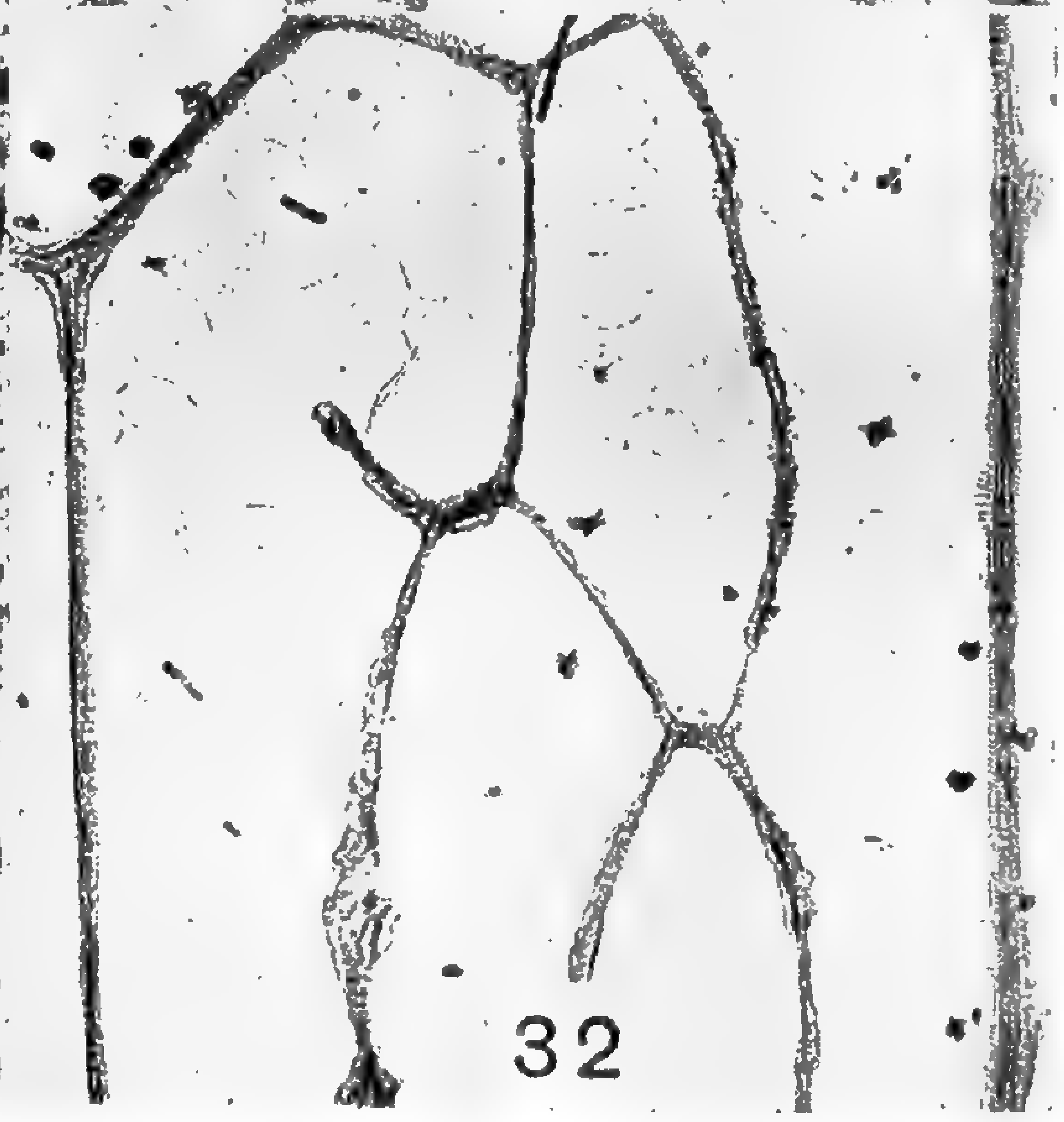
29



30

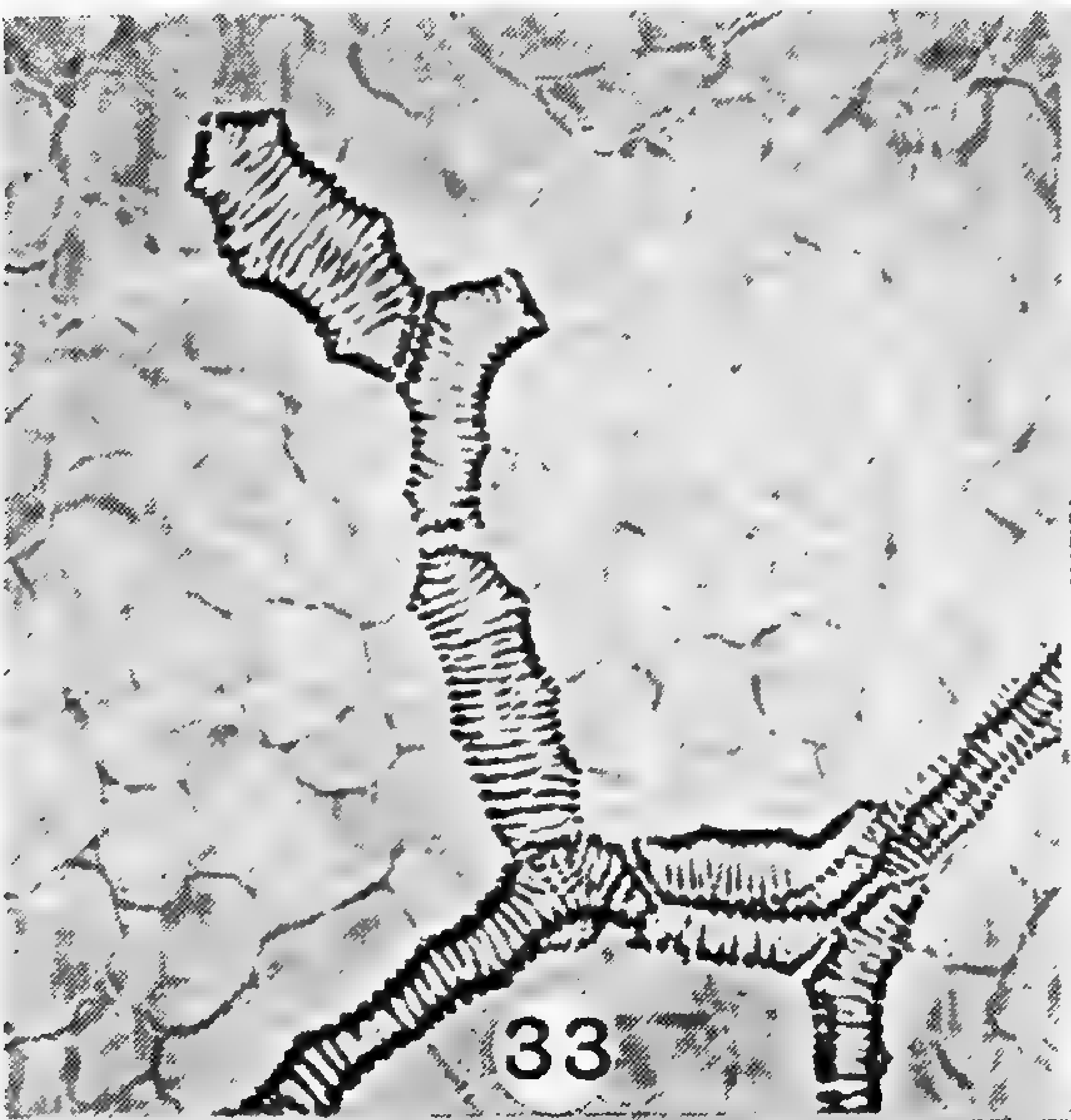


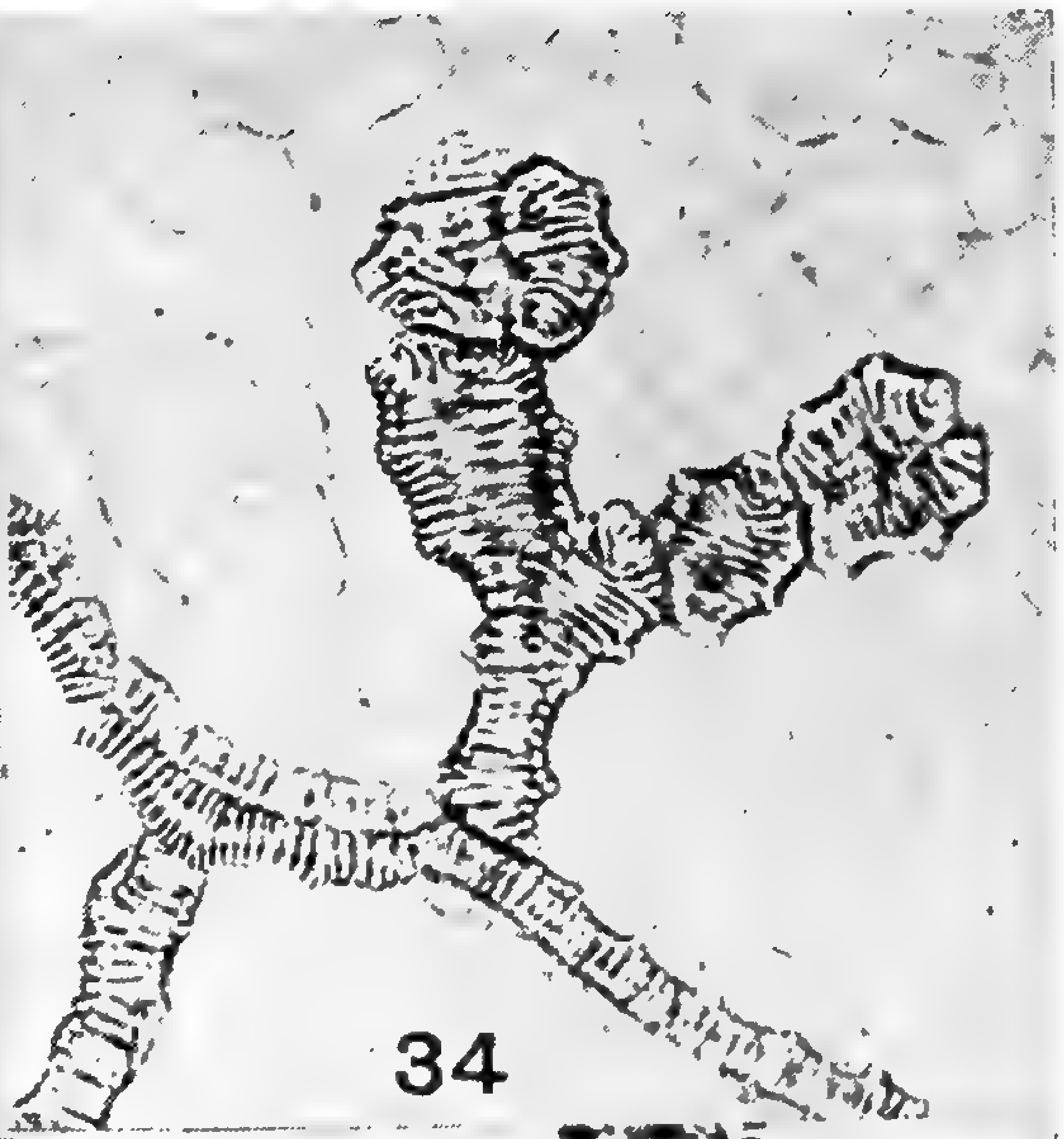
31

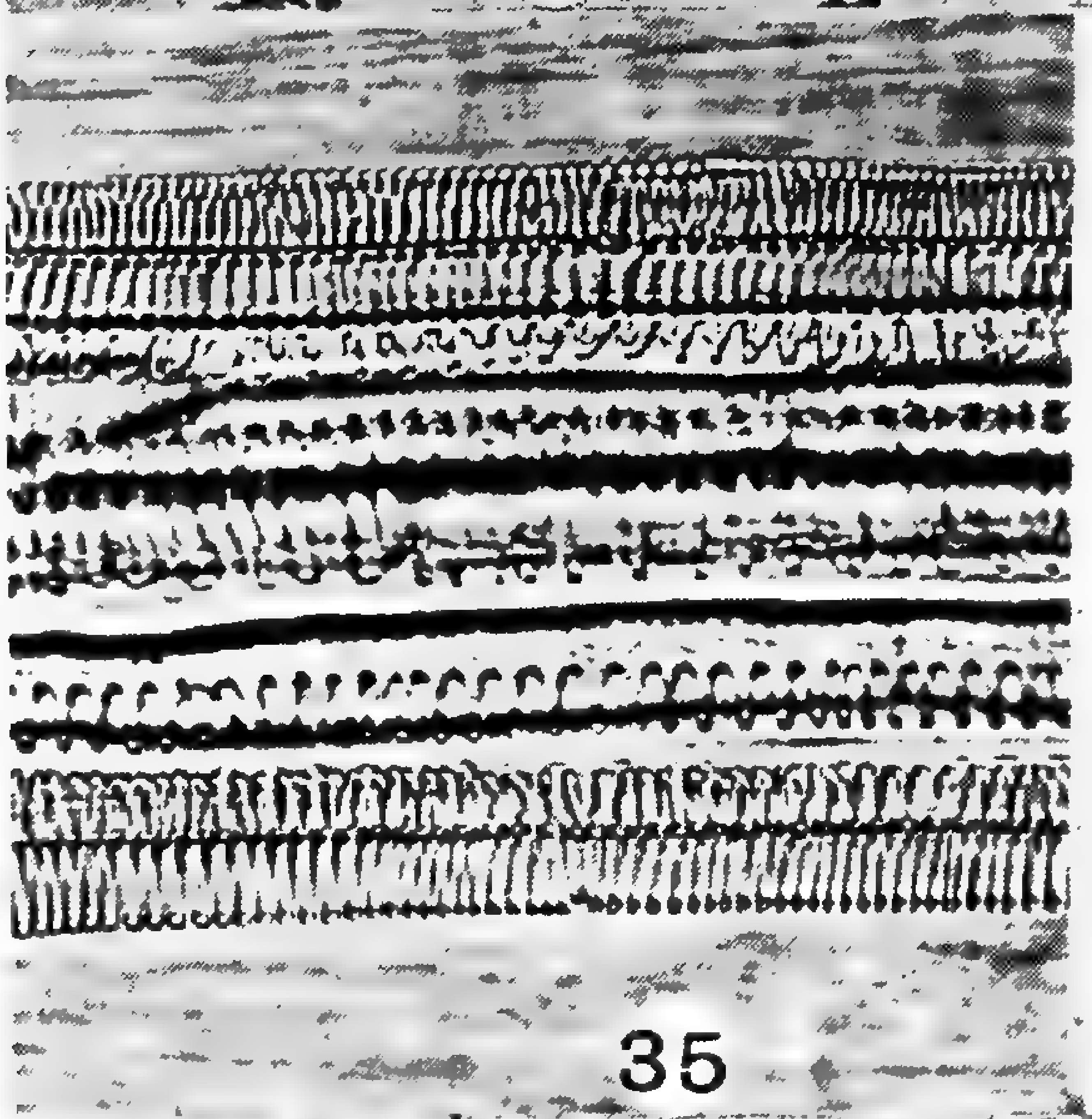


32

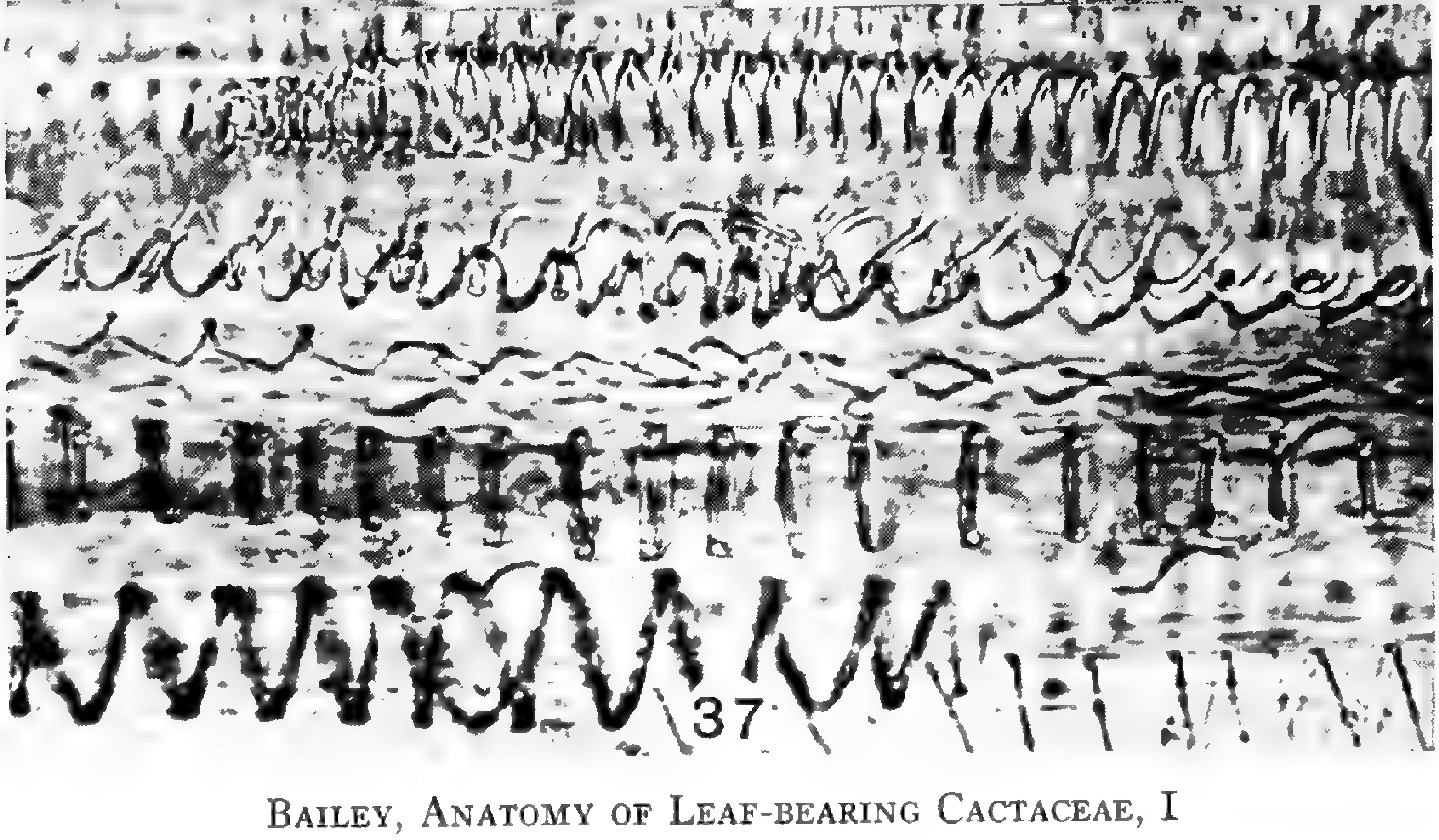
BAILEY, ANATOMY OF LEAF-BEARING CACTACEAE, I


33

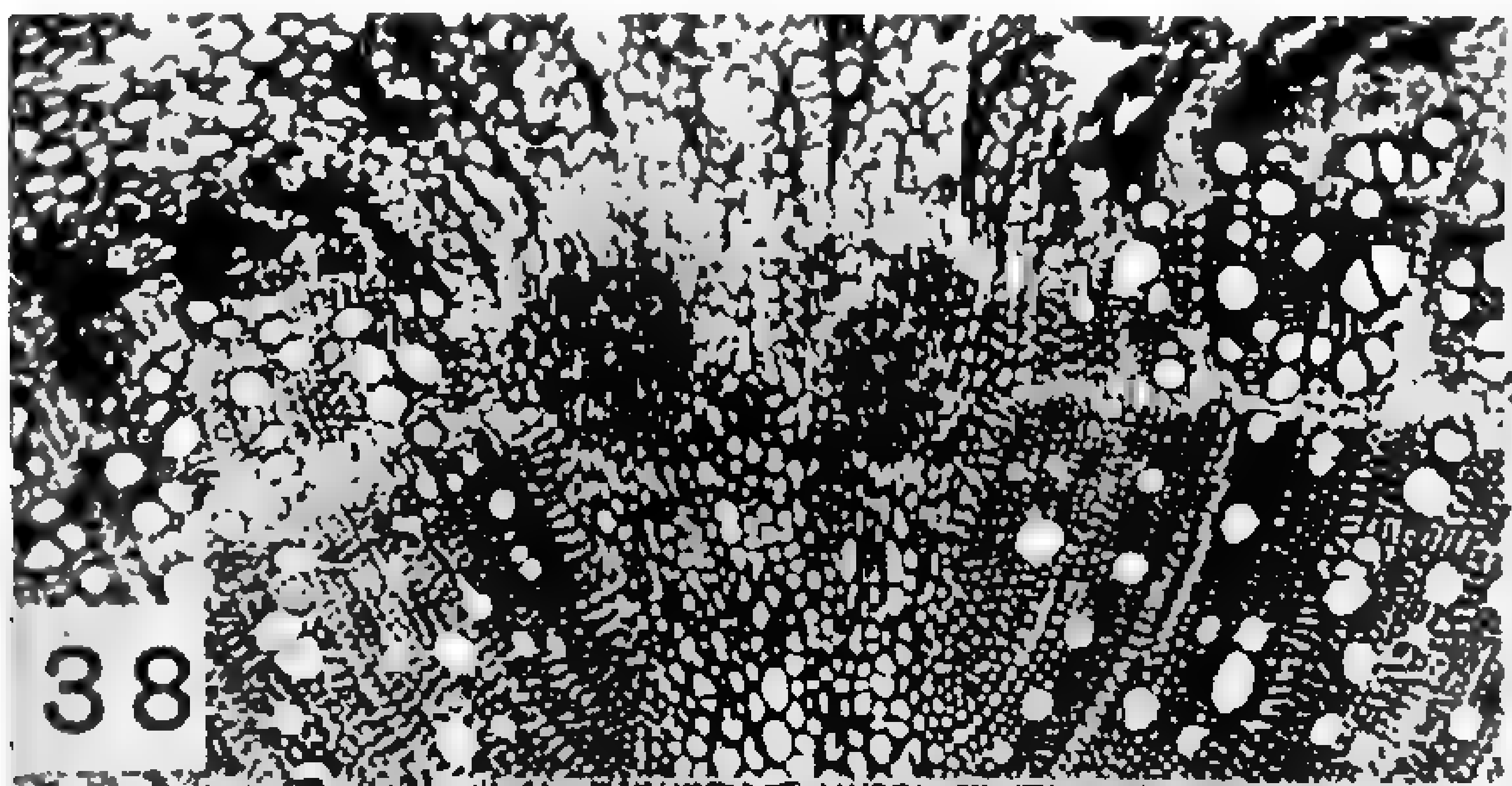

34

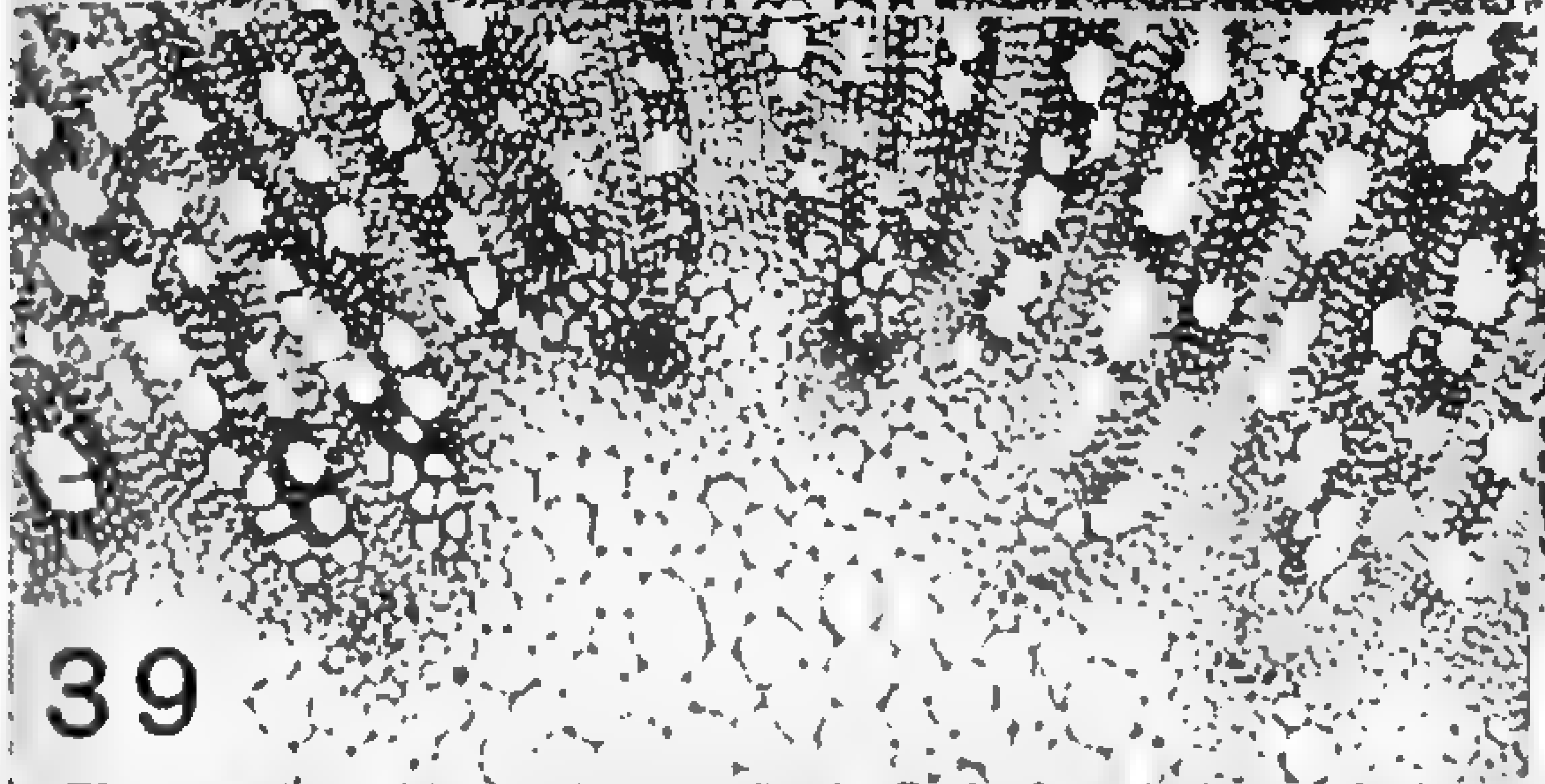

35

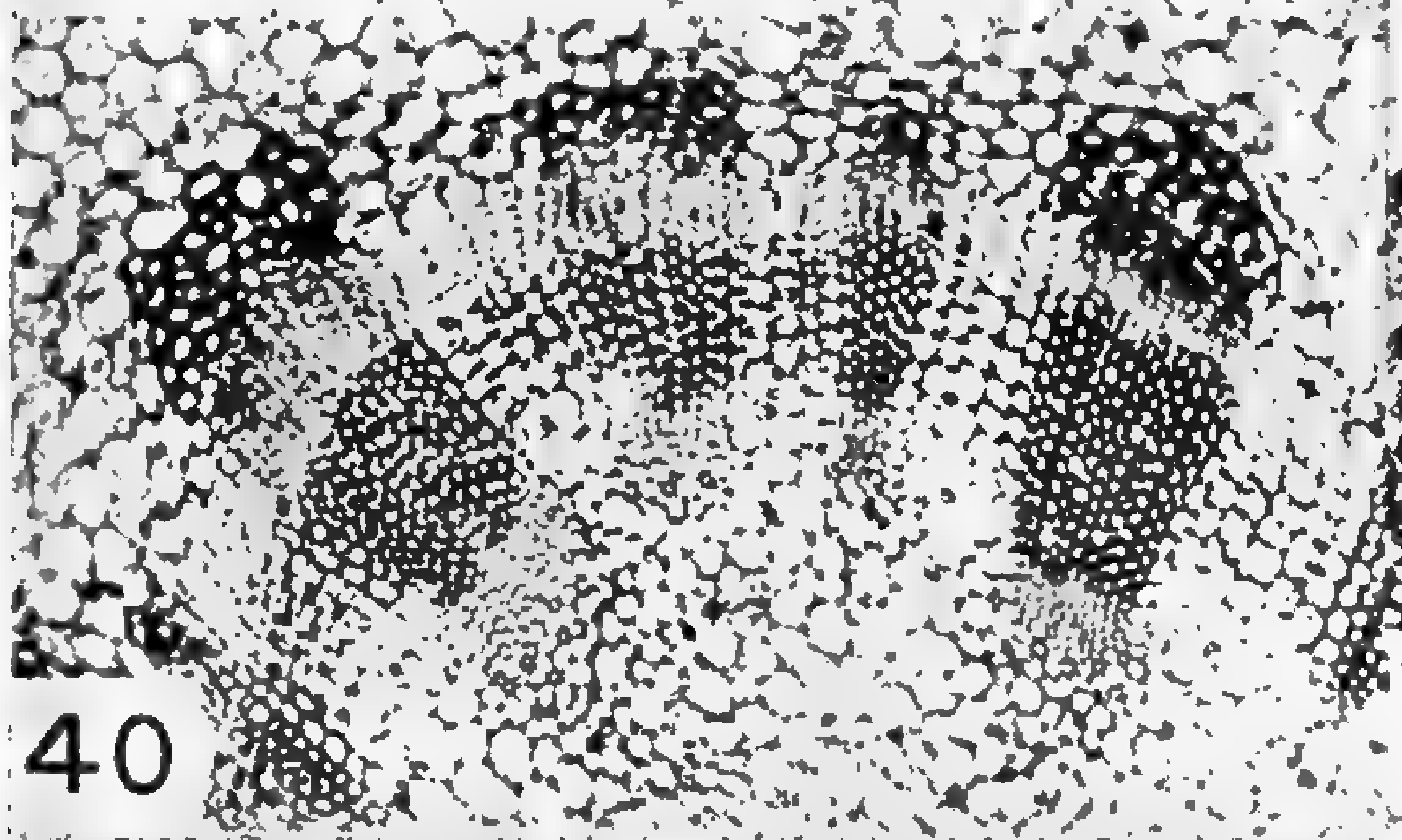

36

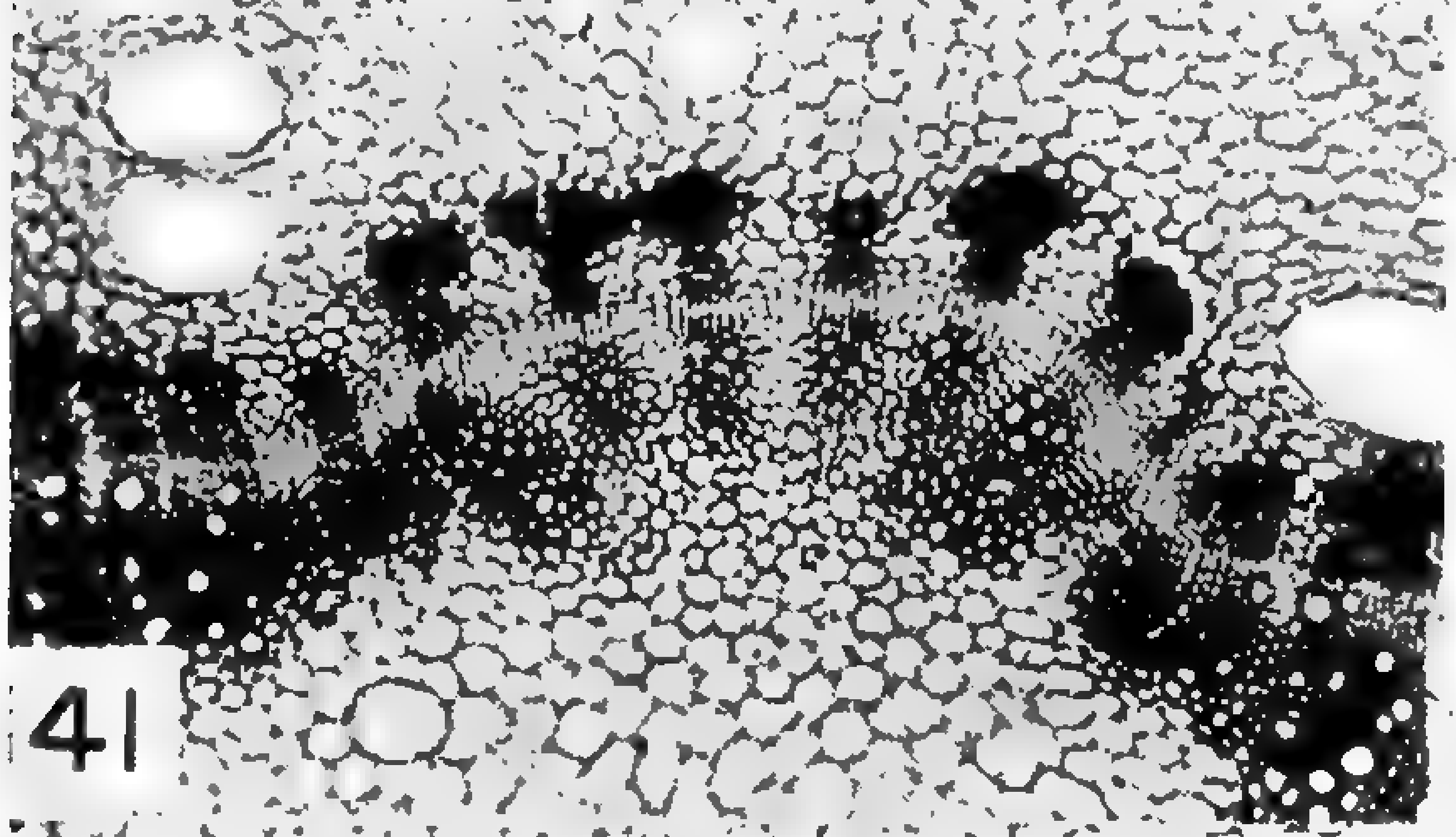

37

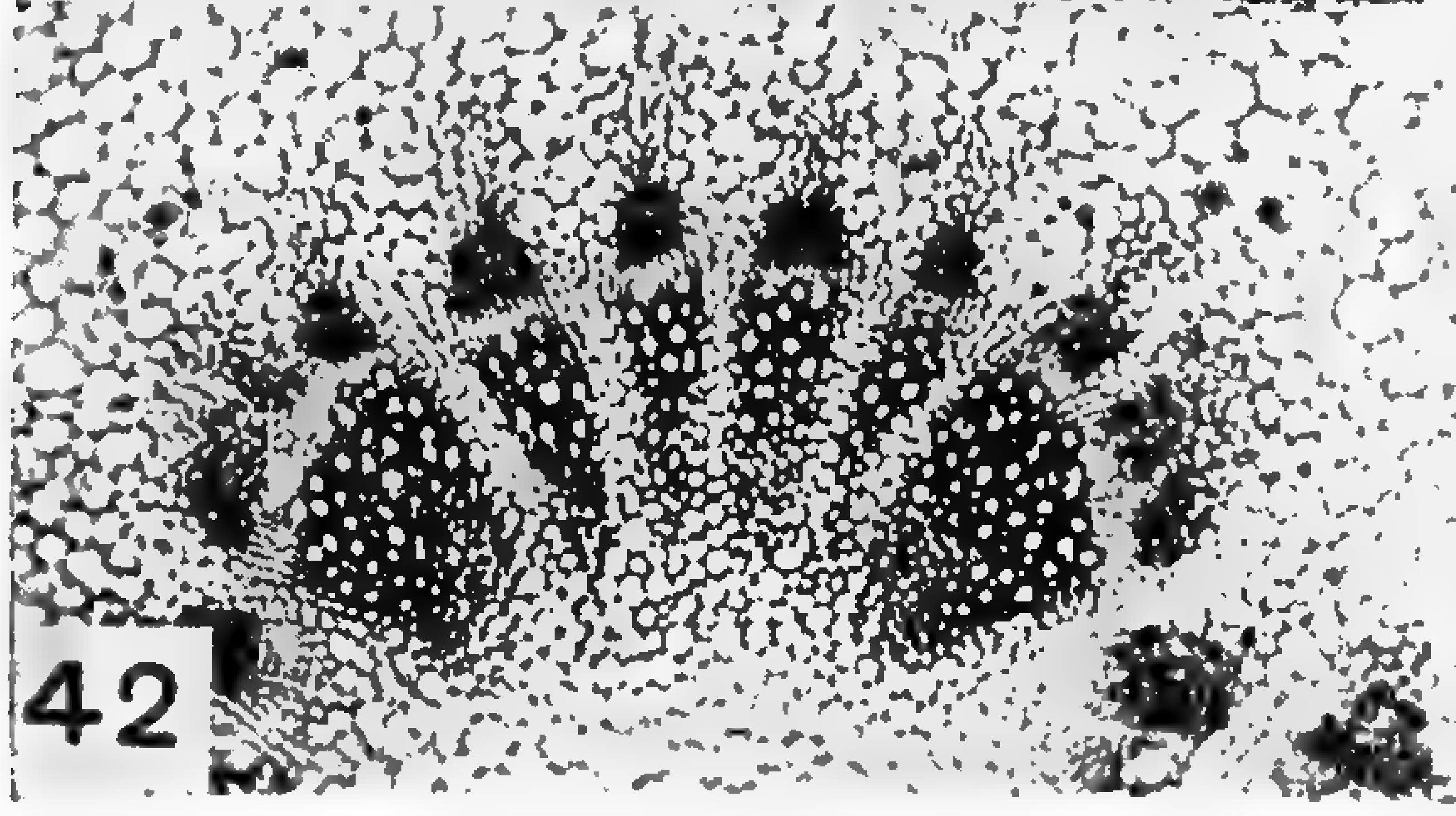
BAILEY, ANATOMY OF LEAF-BEARING CACTACEAE, I

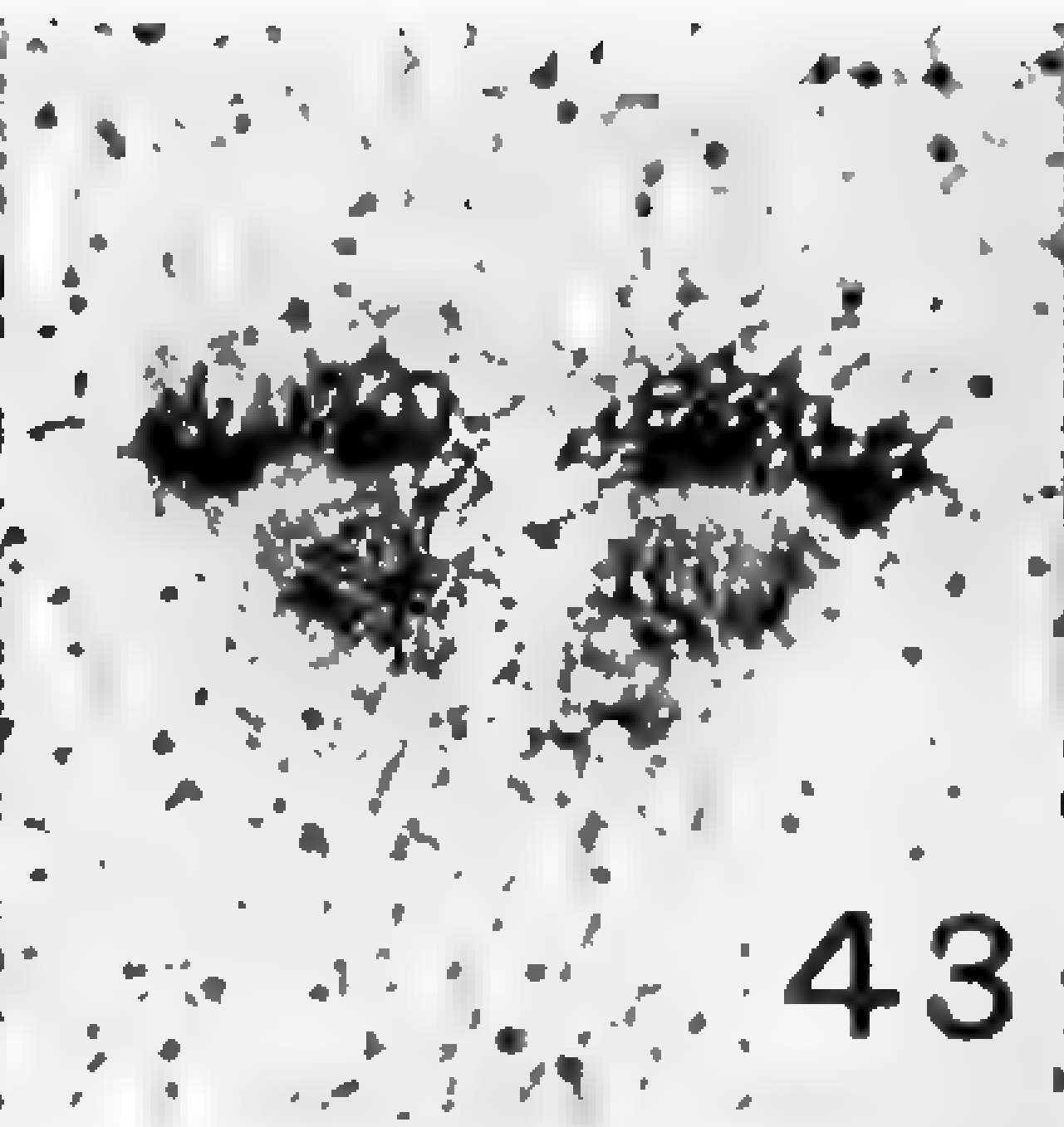

38

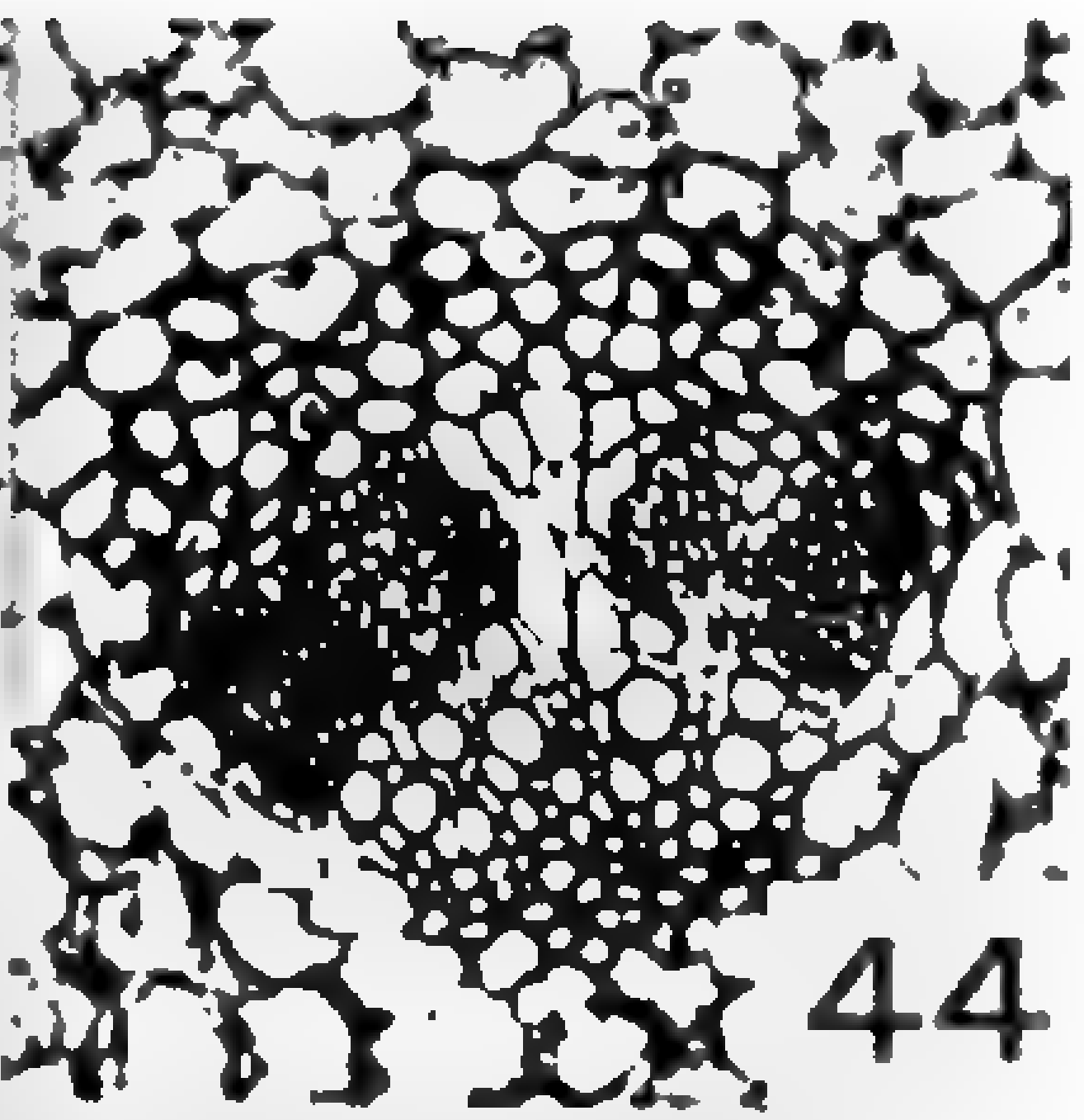

39

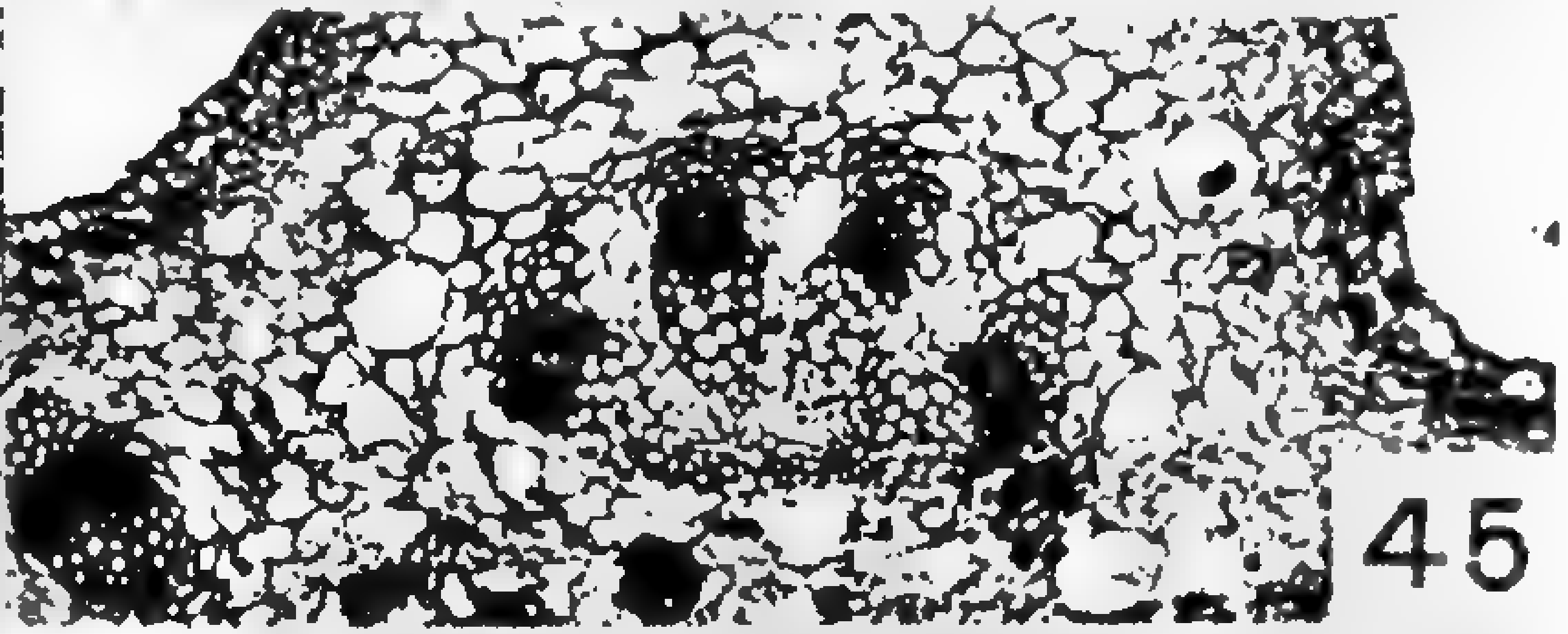

40

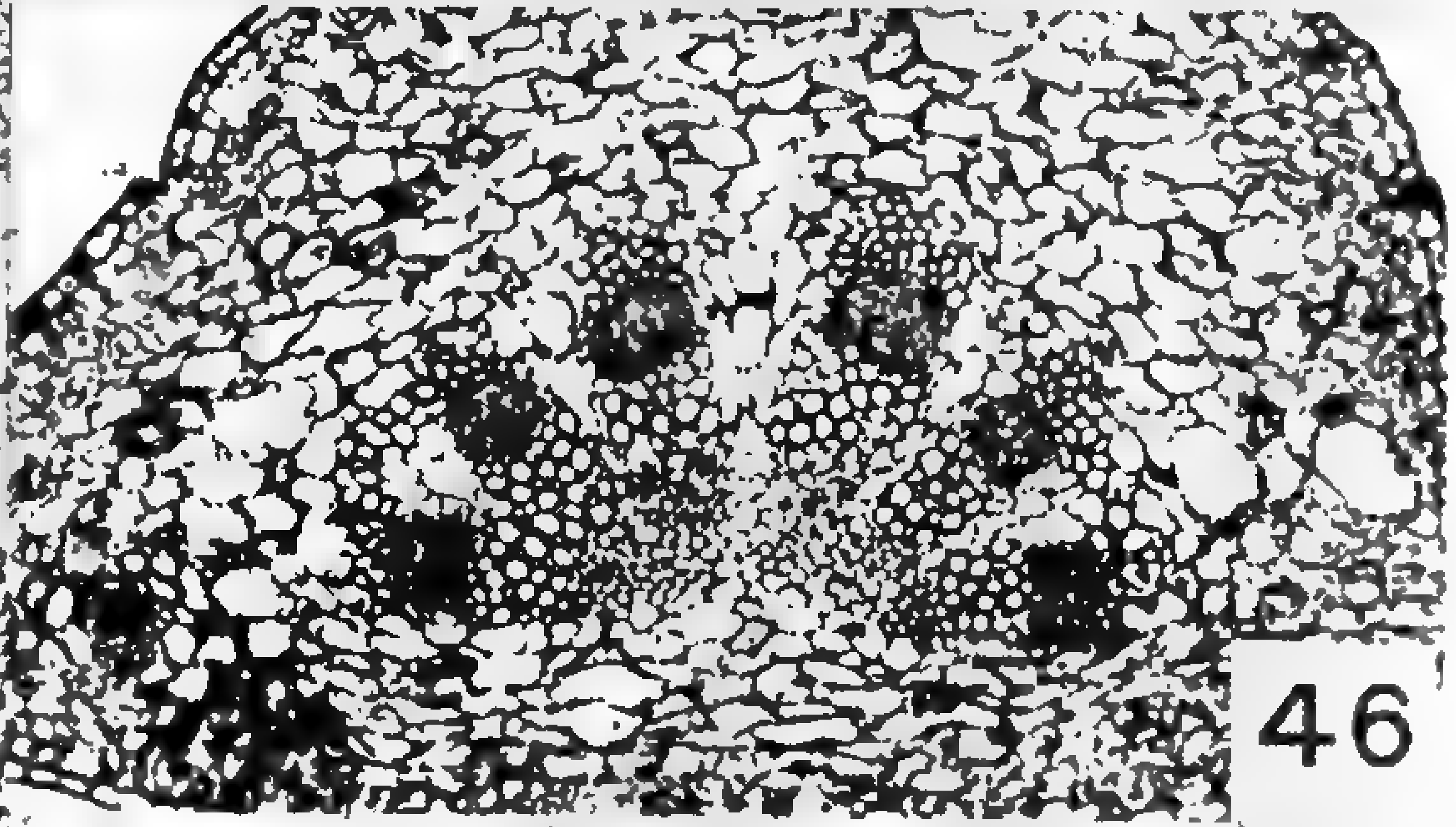

41

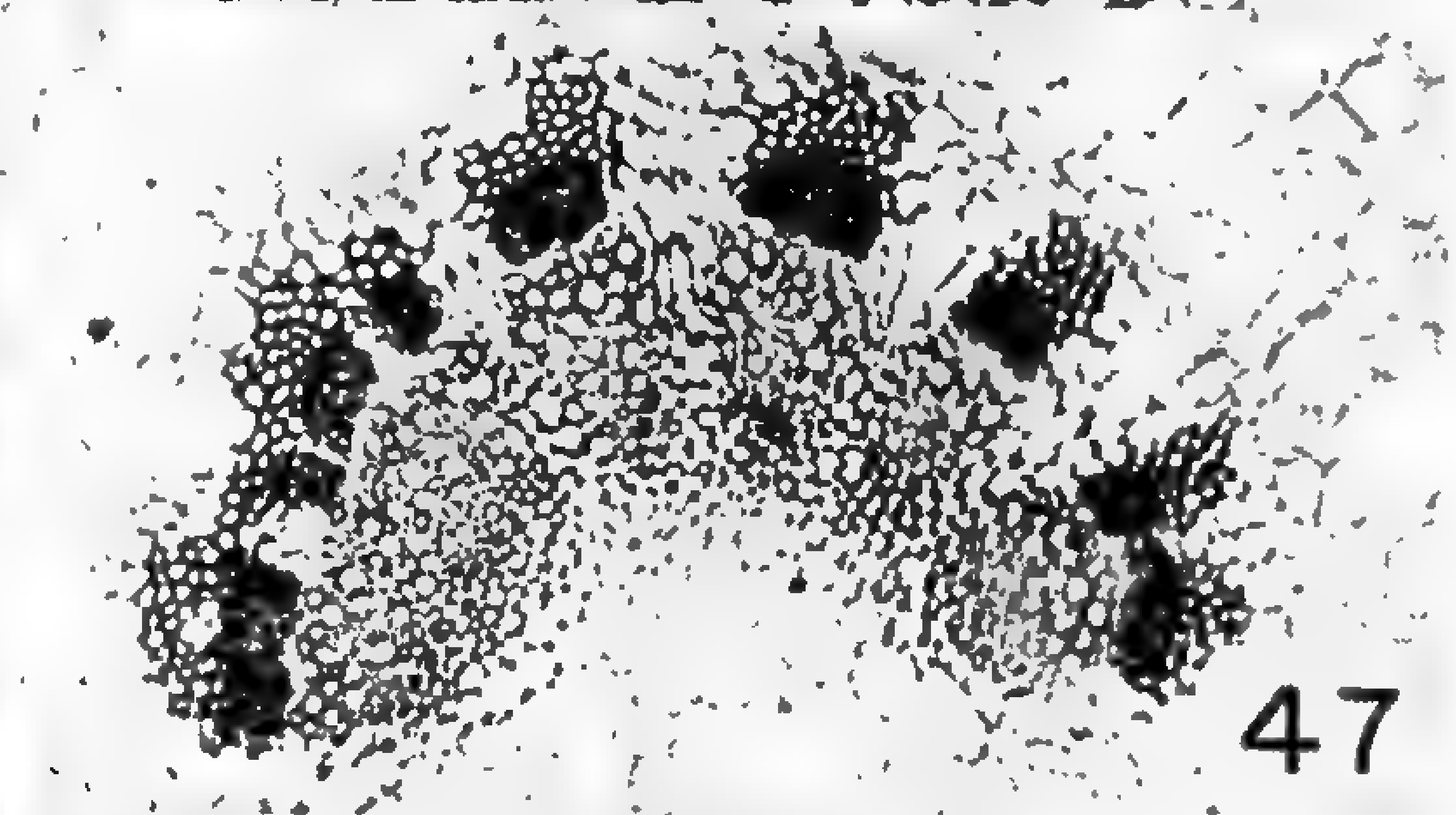

42

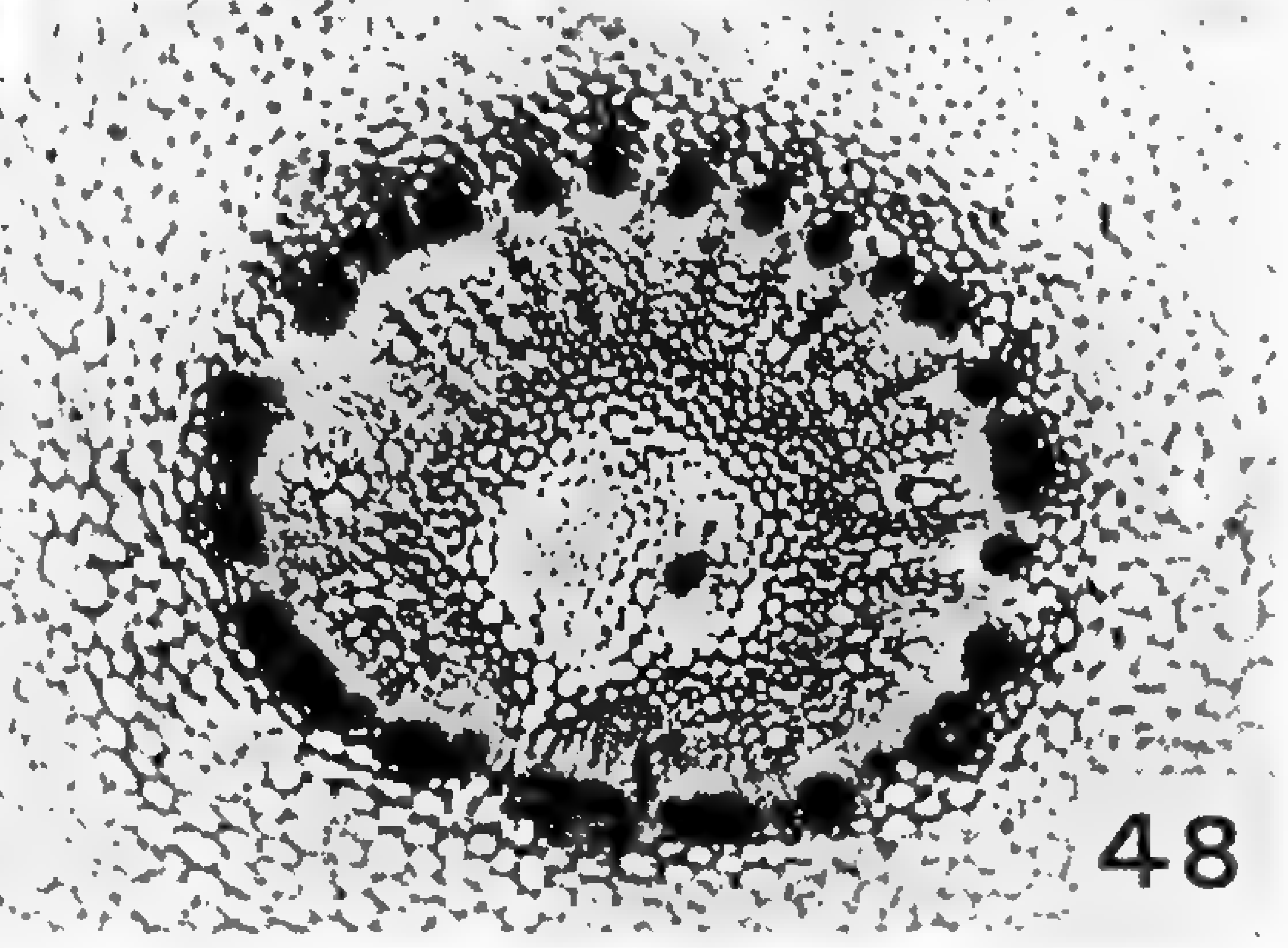

43


44


45


46


47


48

BAILEY, ANATOMY OF LEAF-BEARING CACTACEAE, I

STUDIES IN THE GENUS COCCOLOBA, IX. A CRITIQUE ON THE SOUTH AMERICAN SPECIES *

RICHARD A. HOWARD

Coccoloba oblonga Lindau, Bot. Jahrb. 13: 136. 1890.

This species was based on *Riedel 614* made near Ilheos, Bahia, Brazil. Lindau cited only the Leningrad specimen, although there is a large specimen in the Berlin herbarium. The species has been referred to the synonymy of *Coccoloba cruegeri* Lindau (*q.v.*). Lindau placed *C. cruegeri* in the section *Campderia* and *C. oblonga* in the section *Eucoccoloba.* I have indicated previously (Jour. Arnold Arb. **40**: 74. 1959) that there is no evidence that *C. cruegeri* belongs in *Campderia.*

Coccoloba obovata HBK. Nov. Gen. 2: 141. 1817; Howard, Jour. Arnold Arb. **40**: 209. 1959.

Coccoloba coriacea Willdenow ex Lindau, Bot. Jahrb. **13**: 194. 1890, not Sagra.
Coccoloba goudotiana Weddell, Ann. Sci. Nat. III. 13: 260. 1850.

Coccoloba obovata was based on a Humboldt specimen collected in flower in June, 1805, at Honda, Colombia. A fine specimen in the Paris herbarium bears the most complete label and has been designated as the lectotype. *Coccoloba coriacea,* attributed to Willdenow, was published in synonymy by Lindau. The type of *C. goudotiana* (*Goudot s.n.* from San Luis, Colombia) is deposited in the Paris herbarium. It is clearly the same as *C. obovata.*

Most of the specimens seen have darkened in drying, the upper surface considerably darker than the lower leaf surface. In sterile condition this species is difficult to distinguish from comparable material of *Coccoloba coronata,* especially when it is represented by material from adventitious shoots. In general the ocreae of *C. coronata* are lighter in color and the petioles are shorter and stouter.

The species, with additional synonyms, is also known from Costa Rica and Panama.

Colombia. ANTIOQUIA: Medellín, *Toro 641* (NY); without specific location *Triana 981* (B). MAGDALENA: Cartagena, *Goudot s.n.* (P); San Andrés de la Sierra, *Pittier 1694* (GH). SANTA MARTA: Guamacito, *Record 34* (A, F, NY), *Espina 32* (F); Masinga, *Smith 421* (A, F, G, GH, NY, P), *422* (A, BR, P); Minca, *Espina & Giacometto A10* (F); Valparaíso, *Smith 1702,* in part (A, F, G, GH, NY, P). SANTANDER: Puerto Berrío, *Haught 1729* (NY, W). TOLIMA: Caucho, east

---

* Continued from volume XLI, p. 258.

of Prado, *Little 7171* (US); Hondo, *Humboldt s.n.* (P–lectotype, B), *Pennell 3555* (GH, NY); Mariquita, *Fernández 5637* (A). Without specific location: *Lehmann 1097* (A, F, GH, NY), *Goudot 0* (B), *1* (B). Dept. uncertain: Coyayoua, *Goudot s.n.* (P); San Luis, *Goudot s.n.* (P–type of *C. goudotiana*).

Coccoloba obtusifolia Jacquin, Enum. Pl. 19. 1760; Hist. Stirp. 114. 1763; Dugand, Caldasia **4**: 428. 1947.

Coccoloba billbergii Lindau, Bot. Jahrb. **13**: 219. 1890.

Jacquin's species was misplaced by Lindau and since that time, only Dugand, among the workers in South American floras, has included it. Jacquin stated the location of the species to be "Carthagenae in fruticosis & sylvaticis." Lindau placed the Jacquin name in the synonymy of *Coccoloba microstachya* Willd. under the variety *ovalifolia* Meisner. He did not cite Cartagena as a geographic location of the species or variety, but restricted *C. microstachya* to the northern Antilles. Meisner had previously recognized both *C. obtusifolia* and *C. microstachya*, but Lindau later noted that *C. obtusifolia* was published earlier than *C. microstachya* and so used the former name for the Antillean plant (Symb. Ant. **1**: 222. 1899). In his study of the flora of Colombia Dugand noted that *Coccoloba obtusifolia* was based on a plant from Cartagena and referred several collections to this name. He did not express clearly the geographic distribution of the species, but, from the references given, one infers Dugand's acceptance of the Antillean-Colombian range. However, *Coccoloba obtusifolia* Jacquin and "Coccoloba obtusifolia" of authors of West Indian floras are not the same species, as I have pointed out in a previous paper (Jour. Arnold Arb. **38**: 217. 1957). Lindau described the South American plant as *Coccoloba billbergii* and cited in synonymy "*Coccoloba obtusifolia* Meissn. (non Jacq.)," implying that he was creating a new species and that Meisner was in error.

Coccoloba obtusifolia is similar to and intergrades with several other species which are imperfectly known. The exact relationship to *C. peruviana*, *C. alagoensis*, *C. meissneriana*, *C. trianaei* and even *C. paraguariensis* cannot be determined at the present time. All but *C. meissneriana* were known to Lindau and considered in his monograph as belonging to section *Campderia*. Not one of them was known in fruit, however, and the placement of these species in *Campderia* was based on characteristics of the ocreolae and bracts. In his key to these species Lindau separated them on the basis of pubescence and leaf shape, both extremely variable characteristics. I am still handicapped by the lack of material, especially fruiting material of plants collected from the type locality of each species. I have considered uniting all of these species under *C. obtusifolia*, the oldest name for the complex, but have concluded that a wiser move at this time is to maintain all of the species, since it is impossible at present to distinguish them sufficiently to construct a key.

Coccoloba alagoensis was based on *Gardner 1389* from Alagôas in Brazil. In most of the following specimens assigned to this species the leaves are shorter, thicker and more obtuse at the apex than those of specimens assigned to *C. peruviana*. Lindau assigned *Riedel 821* from Cuyaba, Matto Grosso, to *C. alagoensis*, thus extending the range beyond Alagôas. In his monograph he cited the Gardner collection as well as *Riedel 821* and reported specimens in the Barbey-Boissier, Leningrad and Vienna herbaria without specifying the locations of the individual collections. There is no material of Riedel in the Boissier collection and the Vienna collection has been destroyed, but the Leningrad herbarium has four full sheets of *Riedel 821* comprised of eleven branches. None has been annotated by Lindau. However, in the Berlin herbarium, not cited by Lindau but annotated by him, is one sheet of the Riedel collection which represents only the smallest leaf form of the eleven branches at Leningrad. I believe Lindau received this deceptive fragment and from it cited the material at Leningrad. *Riedel 821* is more similar to material of *C. peruviana* and should be so named. However, if Lindau's identification were followed, *C. peruviana* and *C. alagoensis* could not be distinguished.

The name *Coccoloba alagoensis* can be applied with certainty only to the type. With some hesitation I assign to it also the following Brazilian collections: Bahia, Jacobina, *Blanchet 2668* (B, NY, P), identified and cited by Lindau as *C. ovata*; Rio de Janeiro, *Glaziou 11443* (B), identified and cited by Lindau as *C. floribunda*. Minas Geraes: Serra do Caraca, *Glaziou 19767* (B, P), identified but not cited by Lindau as *C. ramosissima*. *Blanchet 2713*, from Jacobina, Bahia, is apparently a mixture, in part *C. ovata* (*q.v.*), the remainder assigned here.

Coccoloba peruviana is similar and intergrades in leaf size, shape and pubescence. In his key to the species, Lindau distinguished *C. alagoensis* by a glabrous rachis and *C. peruviana* by a rachis more or less puberulent. The problems associated with the accurate identification of *C. peruviana* will be discussed under that name.

Coccoloba meissneriana has leaves larger than those of *C. obtusifolia* but in the same range as *C. peruviana*. The pubescence is uniformly thick on the lower surface and present on the midrib and veins on the upper surface. The few specimens assigned to *C. meissneriana* can be related to typical specimens of *C. obtusifolia* through many intermediate specimens called *C. peruviana*. *Coccoloba trianaei* has leaves with longer acuminate tips and shorter, stouter and more pubescent petioles. *Coccoloba paraguariensis* is similar to *C. alagoensis*, being a smaller-leaved species with thicker, oblong leaf blades, shining when dry and conspicuously veined.

When a large number of these specimens are studied, it becomes obvious that these species are all related, though many questions arise which can be answered only by careful field examination not possible at this time. In his original description of *Coccoloba billbergii* Lindau cited *Billberg 204* and *204a*, with specimens in herbaria at Berlin and Stockholm. I have seen these specimens and find them to be an exact match of Jacquin's illustration. There are apparently no specimens in existence of Jacquin's species, so it must be typified by the illustration. When this is done, Dugand is correct in calling material from Colombia *C. obtusifolia*.

There is also some difficulty in typifying *Coccoloba billbergii* Lindau. Lindau cited two numbered collections, *Billberg 204*, and *204a*, and two herbaria, Berlin and Stockholm. There is only one unnumbered fragment at Berlin, although it bears a label identifying it as a Billberg collection, possibly in Billberg's hand, as well as Lindau's identification label, but the specimen's being small and unnumbered suggests that it may have been taken from one of the Stockholm collections. However, since Lindau saw this fragment in preparing his monograph, it seems proper to designate this specimen in the Berlin herbarium as the lectotype.

Jacquin's illustration is definitive on several points. In fruit, *Coccoloba obtusifolia* has relatively long, reflexed pedicels. The lobes of the fruiting perianth are free below the middle, and the leaf blades, while basically oblong, show some variation in size and shape. Dugand stated that the plants are shrubs, very branched and low, to 2 meters high (or rarely to 4 or 5 meters high) occurring very commonly in the dry thickets of the Colombian Caribbean seacoast. The specimens which Dugand cited are from the states of Atlántico, Bolívar, Guajira and Magdalena. I have seen the majority of them, in addition to the many others cited below, and find in them a great range of variation in size and shape. The final delimitation of this species will require comprehensive field study.

Colombia. ATLÁNTICO: Usiacurí, *Molina & Barkley 19 At 0.54* (US). BOLÍVAR: Cartagena, *Billberg s.n.* (B–lectotype of *C. billbergii*), *Bro. Heriberto 164* (GH, NY), *Schott 857* (NY); Lopopa, *Billberg 204* (S), *204a* (S); Soplaviento, *Killip & Smith 14587* (A, GH, NY). MAGDALENA: Barranquilla, *Bro. Elias 574* (A); Codazzi, *Haught 3711* (A), *3808* (BR, NY); Donjaca, *Record 70* (A, GH, NY, Y); La Paz, *Haught 2326* (A); Palmar de Varela, *Bro. Elias 765* (NY); Puerto Colombia, *Bro. Elias 386* (NY), *Bro. Paul 854* (A); Quemadito, *André 221* (K, NY); Santa Marta, *Goudot "Z"* (B, P), *Smith 412* (A, B, BR, NY, P), *792* (A, BR, NY, P); without definite locality, *André K-1592* (K, NY), *s.n.* (P). Locality uncertain: Isletas (Rio Nari ?Hari?) *André K-1593* (K, NY), Palanda, *André K-1591* (K, NY), Babahoya, *André K-1594* (K, NY). **Venezuela.** DEMOCRACIA: La Crisa, *Christ 41* (NY). ZULIA: San Martín on Río del Palmar, *Pittier 10519* (GH, NY).

Coccoloba ochreolata Weddell, Ann. Sci. Nat. III. 13: 259. 1850.

Coccoloba blanchetiana Weddell, Ann. Sci. Nat. III. 13: 257. 1850.
Coccoloba bracteolosa Meisner, Fl. Bras. 5(1): 30. 1855.

Meisner was the first monographer to suggest that the two species described by Weddell were identical and, although there is some question whether Meisner saw all of the material that Weddell studied, Lindau (Bot. Jahrb. 13: 169. 1890) accepted his decision, citing the complete collections of Blanchet. I have seen the types and duplicates of both Weddell species and agree that they are to be considered identical.

Meisner also described *Coccoloba bracteolosa*, based on Martius collections from the state of Bahia. These flowering specimens have slightly immature leaves. In an earlier paper (Jour. Arnold Arb. **40**: 211. 1959) the species was referred to the synonymy of *C. parimensis* with the qualification that additional material might prove it to be better placed with *C. ochreolata*. I have now seen sufficient material to refer *C. bracteolosa* to the synonymy of *C. ochreolata* without hesitation. Lindau distinguished these species in the key in his monograph on the shape of the leaf base, narrowed in *C. bracteolosa* and rounded or cordate in *C. ochreolata*. He treated the species successively in the text, but I am unable to find any characteristics in the descriptions or in the specimens cited which would sustain a separation.

Mason & Harvey 6700, from Panama, previously cited by Lundell (Contr. Univ. Mich. Herb. 6: 9. 1941) as *Coccoloba bracteolosa* and referred by me to *C. parimensis* is correctly placed there. Likewise a Martius collection from Pará in the Brussels herbarium cited by Lindau as *C. bracteolosa* is also referred to *C. parimensis*.

Coccoloba ochreolata is very similar to *C. ilheensis*, especially at the time of flowering when the leaves are slightly immature. The latter species is not known in fruit. Additional collections are needed to determine the correct relationship of these two species.

Brazil. BAHIA: Jacobina, *Blanchet 3394* (B, LE, P), *3561* (P–holotype of *C. blanchetiana*, BR, LE, NY); Joazeiro, on Rio San Francisco, *Martius s.n.* (M–holotype of *C. bracteolosa*); without specific locality, *Blanchet 3410* (P–holotype), *3410B* (LE, NY, P), *Bondar s.n.* (F), *Clausen 46* (P). ESPÍRITO SANTO: between Campos & Victoria, *Sellow 405* (B). RIO DE JANEIRO: Maná, *Glaziou 18428* (P); Therezopolis, Serra dos Orgãos, *Glaziou 3088* (BR, P).

Coccoloba orbicularis Loddiges Cat. ex Loudon, Hort. Brit. 159. 1830.

In a list of stove plants with accompanying symbols to characterize the horticultural details of the plants Loudon cited this name which he attributed to the catalogue of the Loddiges Nursery at Hackney, near London, where he said the plant was introduced from South America in 1825. The only two Loddiges Catalogues available to me are those of the years 1820 and 1823, in which the name is not used. Later, in a list of excluded species Lindau (Bot. Jahrb. 13: 220. 1890) made the following notation: "*C. orbicularis* Lodd. = *Mühlenbeckia* (?) *orbicularis* Lodd." Jackson (Index Kewensis 1: 573. 1895) listed *Coccoloba orbicularis* Lodd. Cat. ex Loud. Hort. Brit. in italics as an excluded species, but referred it without hesitation to *Muehlenbeckia orbicularis*. However, the name "*Muehlenbeckia orbicularis*" is not listed in Index Kewensis under that genus, nor can I find it in any existing monograph or flora.

Loudon's symbolic description can scarcely be considered valid publication and thus the epithet should be considered a *nomen nudum*. Very probably the plant in question is *Coccoloba caracasana* described by Meisner in 1856.

Coccoloba ovata Bentham in Hooker, London Jour. Bot. 4: 627. 1845.

Coccoloba ovata var. *major* Meisner, Fl. Bras. 5(1): 31. 1855.

Coccoloba ovata var. *minor* Meisner, *ibid.*
Coccoloba ovata var. *lanceolata* Meisner, *ibid.*
Coccoloba moritzii var. *opaca* Meisner, Fl. Bras. **5**(1): 28. 1855.
Coccoloba moritzii var. *lucida* Meisner *ibid.*
Campderia gracilis Meisner, Fl. Bras. **5**(1): 26, *pls. 6.* 1855.
Coccoloba nigra Fawcett & Rendle, Jour. Bot. **51:** 123. 1913; Fl. Jamaica **3:** 120. 1914; Howard, Jour. Arnold Arb. **38:** 106. 1957.

The current delimitation of *Coccoloba ovata* is not a satisfactory one. Only deliberate effort on the part of some collector in the area will obtain the necessary material to allow an understanding of the sexual condition, the habit and leaf variation and the true nature and development of the fruit.

As described by Bentham *Coccoloba ovata* was based on *Schomburgk 531* and *893* from the first Schomburgk expedition. *Schomburgk 531* (K) is designated as the lectotype. In the discussion Bentham stated, "This species appears to have an extensive range, if specimens which I have from various parts of tropical Brazil and from the West Indies are, as they appear to be, referable to it. It agrees in many respects with the characters given of *C. obtusifolia*, Jacq., but the leaves, though variable in form, are never so narrow as those described by Jacquin; nor does the inflorescence agree at all with that attributed to the *C. microstachya*, Willd., which is said to differ chiefly from *C. obtusifolia*, by its broad leaves." Bentham does not cite any specimens from the West Indies and *C. ovata* is not known from there. *Coccoloba obtusifolia* Jacq. and *C. microstachya* Willd. have been misinterpreted and considered synonymous by some authors. In reality *C. obtusifolia*, though a variable species, is from Venezuela while *C. microstachya*, quite distinct from it, has its center of distribution in Puerto Rico and is not known from South America. I can agree with Bentham that *C. ovata* is not at all related to *C. obtusifolia* or to *C. microstachya.*

Bentham indicated the variability in leaf shape and size in the original Latin description and in his discussion. Meisner placed further emphasis on this variability when he described *C. ovata* var. *major,* citing specimens including *Schomburgk 893* and varieties *minor* and *lanceolata* citing *Schomburgk 531*, in part, among the specimens assigned to each variety. I have not seen specimens bearing Meisner's annotation, but the specimens of *Schomburgk 531* and *893* which I have seen I believe are easily accommodated in one species. The specimens appear to come from scrambling branches, although Bentham reported the plant to be a shrub.

Meisner also described *Coccoloba moritzii* in *Flora Brasiliensis*, recognizing two varieties as comprising the species. He cited only a collection from Colombia, *Moritz 550*, as representing *C. moritzii* var. *opaca* and a Schomburgk collection without number from British Guiana for *C. moritzii* var. *lucida*. The name *C. moritzii* was attributed to Klotzsch, who apparently wrote "Coccoloba moritziana Kl." on a specimen in the Berlin herbarium. This specimen cannot be located. A Schomburgk specimen without number bearing the name "Coccoloba moritzii Kl. β lucida Meisn." is in the collections of the Berlin herbarium. I find this specimen comparable in all characters to other material of *Schomburgk 531* and believe the original collector's data were lost from this specimen. Lindau has placed *C. moritzii* and its varieties in the synonymy of *C. ovata*, and I believe this to be the correct handling of Meisner's species.

Bentham did not have the fruit when he described *Coccoloba ovata*, nor did Meisner when he considered the species in *Flora Brasiliensis* and the *Prodromus*. Lindau, however, did describe the fruit in his monograph (Bot. Jahrb. **13**: 216, *fig. 54*. 1890) as follows: "Fructus ovoideus, circa 15 mm. longus, 7 mm. diametro, lobis accrescentibus coronatus, demum pericarpii carne evanida nervis carinalibus nervulisque persistentibus, ruber, facile deciduus." I have not seen all of the collections cited by Lindau, but the fruit which he described for *C. ovata* is present in packets on *Poeppig 2617* and *2634*, as well as on some of the recent collections cited below. The fruit is most unusual and is certainly atypical of even a broad concept of the genus. It is possible that after careful field study of *Coccoloba ovata* a new genus may be created to accommodate this species.

As presently known, *Coccoloba ovata* is a tree (possibly with scrambling branches), a shrub, or a vine. The leaves are mainly ovate but vary from lanceolate-ovate to oblong, narrowed or obtusely cordate at the base and obtuse, acute, or acuminate at the apex. The young branches, ocreae and petioles are crispose-pilose when young, becoming glabrate. The leaves are of firm texture and generally shiny on both sides when dry. The inflorescence ranges in length from 4 to 25 cm. and the flower clusters may be closely arranged or clearly distinct. The principal bract, subtending the flower, is generally black in color, ovate in outline but commonly long-attenuate at the apex. The ocreolae are membranaceous and conspicuous. Functionally staminate flowers tend to be numerous (ca. 10), functionally pistillate flowers (on other inflorescences) fewer (2–6). No specimens are available with both flowers and fruit. The pistillate flowers appear to be typical of *Coccoloba*. In fruiting condition the peduncles elongate, becoming 1–3 mm. long. In an occasional specimen the ocreola is fused to the peduncle. The fruiting perianth is large, becoming 15–17 mm. long. The hypanthium extends to the middle of the elongated achene and the perianth lobes extend well beyond the apex of the achene. The outer two, rarely three, perianth lobes are sharply keeled and appear to have been fleshy. The two inner perianth lobes scarcely exceed the apex of the achene and are flat. The perianth lobes are not tightly imbricate in the fashion found in *C. venosa* or Lindau's section *Campderia*, nor are they coronate, as Lindau stated, in the fashion of *Coccoloba swartzii*. In superficial aspect the fruiting perianth appears to be intermediate between *Symmeria* and *Triplaris*, or a fleshy elaboration of the imbricate-lobed type of the Campderia section. A number of the characteristics given above suggest that a special genus is required for *Coccoloba ovata*, but the lack of adequate field knowledge of this species prevents me from creating one at this time.

Campderia gracilis Meisner was described and illustrated in the *Flora Brasiliensis*. The original description refers to only one collection, *Spruce s.n.*, from Barra on the Rio Negro in Brazil. In the *Prodromus* Meisner reported specimens in Delessert and Munich herbaria. I have seen both of these specimens and six additional ones. No single specimen compares exactly with the illustration given in *Flora Brasiliensis*, and, consequently, I conclude that certain artistic liberties were taken. The original detailed sketch of the flower and fruit which appears on the *Flora Brasiliensis* plate is attached to a sheet in the Munich herbarium. This should be considered the lectotype. No achenes have been found on any specimens of this Spruce collection and I wonder where Meisner obtained the material for the illustration. Lindau assigned *Campderia gracilis* to the synonymy of *Coccoloba ovata*. If Meisner's illustration of the fruit of *Campderia gracilis* is correct and if, in following Lindau I have interpreted the fruit correctly, the species cannot be accommodated in *Coccoloba ovata*. However, if Meisner's illustration of the fruit is in error, as it appears to be on the basis of material I have seen, then *Campderia gracilis* must be considered as known only from flowering specimens and may well be placed correctly in the synonymy of *Coccoloba ovata*.

Passarge and Selwyn 491, made on the German Caura Expedition into the Guiana of Venezuela in 1901–1902, has been annotated with an unpublished name by Gross, who studied this specimen in the preparation of a treatment for *Pflanzenreich*. The majority of the new names he used appear to be unpublished. The present collection in the Berlin herbarium consists of two detached leaves and five detached inflorescences. The leaves are oblong-lanceolate and the inflorescences are from pistillate plants. The material is included in the broad concept of *Coccoloba ovata* which I am using.

Blanchet 2713 apparently is a mixture. A specimen so numbered in the Prodromus herbarium bears the label "villa de Barra" and belongs in this species, but a specimen carrying the same number, originally from Meisner's herbarium but now in the herbarium of the New York Botanical Garden, gives the location as "Serra de Jacobina Prov. Bahia" and is *Coccoloba alagoensis*.

Brazil. AMAZONAS: Barra, *Spruce 958* (M-lectotype of *Campderia gracilis*, B, G, GH, LE, P), *Blanchet 2713* in part (G); Manaos, *Ducke 348* (A, F, K, NY, US); Rio Coary, *Martius s.n.* (M); *Rio Negro*, *Spruce s.n.* (M); Rio Yapurá, *Martius s.n.* (M); without locality, *Poeppig 2617* (LE). BAHIA: Borba, *Riedel 1366* (LE, P). PARÁ: Bôa Vista on the Tapajoz River, *Dahlgren & Sella 61* (B, F); lower Cupari River, *Krukoff 1206* (A, NY, P). State unknown: Ega, *Poeppig 2634* (B, G, LE). **British Guiana.** DEMERARA: Matope Falls of the Cuyuni River, *Forest Dept. F-3380* (NY), *3382* (NY). Without locality: *Jenmann 1074* (P); *Schomburgk 531* (K–lectotype, BM, P), *893* (NY, P), *s.n.* (B). **Colombia.** VAUPÉS: Río Guaviare, *Molina & Barkley 215* (US); Río Inírida, *Fernández 2279* (A, US); Río Papunáua, *Fernández 2038* (A, US). **Venezuela.** AMAZONAS: Río Orinoco near mouth of Río Atabapo, *Wurdack & Adderley 42722* (A, NY). APURE: Río Cinaruco between mouth and Las Galeras de Cinaruco, *Wurdack*

& Monachino 41361 (A, NY). BOLÍVAR: Caño Coroso between Lago Coroso and Río Orinoco, *Wurdack & Monachino 41192* (A, NY); Ciudad Bolívar, *Pittier 13951* (US); Llanos de l'Aprure, *Geay s.n.* (P); Río Orinoco between Río Paragua and Río Horeda, *Wurdack & Monachino 39878* (A, NY); Río Paragua, *Cardona 1088* (F, NY, US); without specific locality, *Passarge & Selwyn 491* (B). Country undetermined: Upper Orinoco, *Gaillard 198* (P).

Coccolobis padifolia Rusby, Mem. N.Y. Bot. Gard. 7: 235. 1927.

The type of this species, *Mulford Biological Expedition 848* (NY) from Rurrenabaque, Bolivia, has been compared with the type of *Coccoloba longipes* S. Moore from the Matto Grosso of Brazil. The species are the same and *C. padifolia* is referred to synonymy.

Coccoloba padiformis Meisner, DC. Prodr. **14**: 166. 1856; Howard, Jour. Arnold Arb. **40**: 210. 1959.

Coccoloba sphaerococca Lindau, Bot. Jahrb. **13**: 185. 1890.

It has been pointed out previously that *Coccoloba padiformis* and *C. densifrons* are very similar. For the present *C. densifrons* is distinguished by its larger and heavier leaves which are generally broadest above the middle, by the conspicuous, arcuate, impressed primary venation and by the stouter and longer inflorescence axis.

Coccoloba padiformis is more similar to *C. sphaerococca.* Lindau described a puberulent inflorescence rachis for *C. padiformis* to distinguish it from *C. sphaerococca* which is supposed to have a glabrous one, but the type specimen of *C. sphaerococca* is an old fruiting specimen with some pubescence present in protected spots on the rachis, while the type specimen of *C. padiformis* is a staminate flowering branch, so Lindau's distinction does not seem reliable. *Coccoloba sphaerococca* was based on material collected at Tarapoto, Peru; *C. padiformis* is typified by a specimen from Caracas, Venezuela. Macbride assigned additional collections (*Killip & Smith 29027, 27958* and *Williams 3805*) to *C. sphaerococca,* but I believe these specimens belong instead to *C. nutans.*

Lindau (Bot. Jahrb. 13: 201. 1890) broadened the original concept of *Coccoloba candolleana* to include material collected by Goudot in Colombia (*Goudot 4*) which is clearly to be referred to *C. padiformis.*

An additional species from Costa Rica has been previously referred to synonymy here (Howard, *loc. cit.*) and material has also been seen from Panama.

Colombia. CAUCA: Vallée du Cauca, *Triana 975* (P). MAGDALENA: Mariquita, Piedras du Magdalena, *Triana 976* (P); Santa Marta, *Smith 1696a* (A, NY), *Goudot 4* (B, P). **Peru.** SAN MARTÍN: Tarapoto, *Spruce s.n.* (K-holotype of *C. sphaerococca*). **Venezuela.** FEDERAL DISTRICT: Caracas, *Moritz 377* (M-holotype, G, LE, NY). MIRANDA: Pice de Naiguatá, *Pittier 6190* (NY). ZULIA: Maracaibo Lake at Río Limón, *Curran & Haman 796* (A, GH).

Coccoloba paniculata Meisner, Fl. Bras. **5**(1): 43. 1855.

The typification of *Coccoloba paniculata* Meisner would be a difficult taxonomic problem, since Meisner included in the original citation the type of *C. polystachya* Weddell. Fortunately a solution is not necessary, since *C. mollis* Casaretto represents the older, legitimate name. A full discussion of the types and relationships is given under *C. mollis.*

Coccoloba paraensis Meisner, Fl. Bras. **5**(1): 38. 1855.

This species was based on *Spruce 957*, from Manáos, Brazil, and a Martius collection from the state of Pará. I indicated in an earlier paper (Jour. Arnold Arb. **40**: 211. 1959) my belief that this species is properly placed in the synonymy of *Coccoloba parimensis* Bentham.

Coccoloba paraguariensis Lindau, Bot. Jahrb. 13: 218. 1890.

Coccoloba microphylla Morong in Morong & Britton, Enum. Pl. 212. 1892; Ann. N.Y. Acad. **7**: 213. 1893, not Griseb. 1866.
Coccoloba morongii Hassler, Repert. Sp. Nov. **14**: 162. 1915.

In the original description Lindau cited the single collection *Balansa 2060* and only the specimen in the herbarium at Göttingen. It is important to note that the description and the specimen agree. Unfortunately this collection has proved to be a mixed one and specimens which I have seen bearing this number are all to be referred to *Coccoloba spinescens*, with the sole exception of the holotype at Göttingen. The misinterpretation of *C. paraguariensis* by recent workers has led to the confusion evident in the synonymy given here and under *C. spinescens.*

Coccoloba microphylla Morong was based on *Morong 899* gathered along the Pilcomayo River in Paraguay. The epithet is a later homonym of *C. microphylla* Grisebach, as was recognized by Hassler, who renamed the species *C. morongii.*

Buchinger and Sanchez (Bol. Soc. Argent. Bot. 7: 251. 1959) have referred *Coccoloba paraguariensis* to the synonymy of *C. alagoensis* Weddell and have accepted *C. morongii* as a distinct species. I cannot agree with this treatment.

Coccoloba correntina Rojas (Bull. Geogr. Bot. **28**: 162. 1918), has been treated by Buchinger and Sanchez, *loc. cit.*, as an "especie dudosa" but with the suggestion of similarities to "C. morongii." Rojas' description is brief and generalized and no specimens are cited. Dr. Buchinger wrote that no material attributable to this species from the Rojas collection could be found. It is my belief that *C. corrientina* Rojas is properly placed in the synonymy of *C. paraguariensis.*

Argentina. CHACO: Fontana, *Meyer 2.276* (A). CORRIENTES: Puenta Pesca, *Ibarrola 251* (W). FORMOSA: *Jórgensen 1985* (GH, US), *Rojas 11557* (A). **Paraguay.** Along the Pilcomayo River, *Morong 899* (NY–type of *C. microphylla*, GH), *Rojas 196* (GH), *196*a (B, GH, K); escarpments along the Río Paraguay, *Balansa 2060* in part (GOET–holotype).

Coccoloba parimensis Bentham in Hooker, London Jour. Bot. **4**: 626. 1845; Howard, Jour. Arnold Arb. **40**: 211. 1959.

Coccoloba parimensis var. *schomburgkii* Meisner, Fl. Bras. 5(1): 35. 1855.
Coccoloba excelsa var. *glabra* Lindau, Bot. Jahrb. 13: 171. 1890.
Coccoloba paraensis Meisner, Fl. Bras. 5(1): 38. 1855.

A full discussion of *Coccoloba parimensis*, its variations and relationships is given in the earlier paper cited above, where additional specimens from Panama are referred to this species.

Brazil. AMAZONAS: Airão, Rio Negro, *Murca Pires 243* (NY, US); Barra, *Spruce s.n.* (B, GH, LE); Ega, *Poeppig 2670* (LE); Humaytá near Livramento, *Krukoff 6606* (A, BR, LE, NY); Manáos, *Ducke 1289* (A, F, NY, US); Panuré, Rio Uapes, *Spruce 2732* (B, G); Paraná, de São José de Arirahá, *Baldwin 3299* (US). PARÁ: Eastern region, *Martius s.n.* (BR); Iquapémirim, *Martius s.n.* (M). **British Guiana.** Barima River, Northwest District, *De La Cruz 3359* (GH, NY, US); east of Atkinson Field, *Irwin 241* (US); Malali, Demerara River, *De La Cruz 2668* (GH, NY, US). **French Guiana.** Cayenne, *Martin s.n.* (K); Savane de Charvin, near St. Laurent, *Cowan 38874* (NY). **Peru.** LORETO: Mishuhuaca near Iquitos, *Klug 1592* (A, F, NY); Yurimaguas, *Llewelyn Williams 4528* (F). **Venezuela.** AMAZONAS: Caño Avatapure, *B. & C. Maguire 35526* (A, NY); Maroa, Río Guainia, *Llewelyn Williams 14259* (F, US); Pimichín, *Llewelyn Williams 14188* (F); Pto. Ayacucho, Río Orinoco, *Curran 1813* (NY). BOLÍVAR: Alto Cuyuni, Río Chicanang, *Cardona 2767* (NY).

Coccoloba parvifolia Schott in Sprengel, Syst. Veg. 4(2): 405. 1827; Lindau, Bot. Jahrb. 13: 175. 1890, not Poiret (1804).

Lindau accepted the epithet *Coccoloba parvifolia* Schott in his monograph of the genus. He referred the older name, *C. parvifolia* Poiret (Lam. Encycl. **6**: 64. 1804), to the synonymy of *C. microstachya* var. *ovalifolia* Meisner. Under the present rules of nomenclature, *C. parvifolia* is preoccupied and *C. parvifolia* Schott is a later homonym. The correct name for this species is therefore *C. rigida* Meisner.

The original description of *Coccoloba parvifolia* Schott is brief and no specimens are cited. A specimen in the Berlin herbarium obtained with the Kurt Sprengel herbarium is presumed to be the holotype. This herbarium was acquired after 1890 and the specimen in question was not annotated (and perhaps not seen) by Lindau. The Berlin herbarium does contain four collections (*Schott 5538*, *Riedel 683*, *Schenck 3939*, and *St. Hilaire 138*) which Lindau saw and annotated. The Sprengel herbarium specimen without number matches *St. Hilaire 138*.

Coccoloba peltata Schott in Sprengel, Syst. Veg. 4(2): 405. 1827; Lindau, Bot. Jahrb. 13: 181. 1890.

Coccoloba peltigera Meisner, Fl. Bras. 5(1): 39, *pl. 17*. 1855.
Coccoloba nymphaeifolia Schenk in Zittel, Handb. Palaeont. 2: 491. 1887, nomen nudum.
Coccoloba erecta Glaziou, Bull. Soc. Bot. Fr. IV. 11(Mem. 3f): 572. 1911, in part.

Coccoloba peltata is listed in Sprengel's *Systema* with a very short description and no specimens are cited. The specimen from the Sprengel herbarium now at Berlin consists of a single detached leaf, but this was collected by Schott. It is not annotated by Lindau and perhaps was not seen by him. Nevertheless, this specimen must be considered the holotype of *C. peltata*.

Meisner recognized *Coccoloba peltata* but did not see any material and only repeated the original description. At the same time Meisner described *C. peltigera*, recognizing it as only slightly different from the inadequately described *C. peltata*. Lindau reduced *C. peltigera* to synonymy under *C. peltata* Schott, and I believe he was correct in doing so.

For *Coccoloba peltigera* Meisner cited *Martius 238* and *Poeppig 2670*, placing in synonymy the manuscript name "Coccoloba scandens Poeppig" for the latter specimen. The illustration given in *Flora Brasiliensis* was compiled from two specimens of *Martius 238*, now in the Munich herbarium. No type was selected, but it seems desirable to designate *Martius 238* as the lectotype of *C. peltigera*. Martius did not give the location of the Poeppig specimen, but Lindau referred to the same manuscript name on a specimen in the Vienna herbarium. This collection at Vienna was lost during World War II, but a specimen of the same number without the manuscript name is in the Leningrad herbarium. This specimen is to be referred to *C. parimensis*.

I have already discussed the epithet *Coccoloba nymphaeifolia* (*q.v.*) which is a *nomen nudum*. I have also previously indicated that *C. erecta* Glaziou must be considered a *nomen nudum*. However, in the place of publication Glaziou cited *Glaziou 14220* for *C. erecta* and *Glaziou 14219* for *C. schwackeana*. Unfortunately both of these collections are mixed and specimens labeled *Glaziou 14219* may be either *C. schwackeana* or the present species.

Coccoloba peltata is not well represented in herbaria but appears to be characterized, as originally described, by having leaves with long petioles and blades which are usually, but not always, peltate. In petiole length it compares with *C. tiliacea* from Argentina, a species which also has peltate or non-peltate leaves. *Coccoloba tiliacea* differs in having pedicellate flowers and fruits on lax or more tenuous rachises. The specimens cited below are mostly from lianas or "ropelike" branches. The species is not known in fruit. Many of the specimens give the impression of representing abnormal growth forms. Leaf blades vary in size and shape, in many cases approaching the thick leaf types of *C. marginata*. The inflorescence has been found divided and is apparently fasciated in *Glaziou 14219* (LE). A study of this species in the field may reveal it to be only a teratological or abnormal form of some other species. For example, it is possible that some of the material I have called *C. marginata*, particularly the Salzmann collections from Bahia labeled "Coccoloba pendula" or "Coccoloba nitida var. cordata" in herbaria, may be the normal expression of *C. peltata*. At present the distinctions between *C. marginata* and *C. peltata* are not clear.

Brazil. RIO DE JANEIRO: Copacabana, *Nadeaud s.n.* (P); Corcovado, *Beyrich s.n.* (P); São Christovão, *Glaziou 14219* in part (LE, P); without specific location, *Glaziou 144* (BR, P), *Martius 238* (M–holotype of *C. peltigera*). Without location: *Schott s.n.* (B–lectotype of *C. peltata*), *Clausen 57* (P). **Cultivated material:** *Herb. Fischer* (LE), *Herb. Lips.* (B).

Coccoloba pendula Salzmann ex Lindau, Bot. Jahrb. 13: 180. 1890.

This epithet was invalidly published by Lindau in the synonymy of his "Coccoloba nitida." I have restricted *Coccoloba nitida* HBK., both in definition and distribution, and cannot include the Salzmann specimens cited by Lindau. These specimens from Bahia, Brazil, are all without numbers but bear different annotations; e.g., "C. pendula," "C. nitida var. cordata" or "C. tenuifolia Lam.," and have been seen in many European herbaria. All should be referred to *C. marginata*, with the possibility that they may represent normal growth forms of *C. peltata*.

Coccoloba persicaria Weddell, Ann. Sci. Nat. III. 13: 256. 1850.

This species is similar to *Coccoloba gracilis*, *C. obtusifolia*, and *C. spinescens*. At present it is distinguished by the broader leaves, shorter petioles and more pubescent branches and foliage. The holotype is in the Paris herbarium and a fragment of the holotype is in Berlin.

A second collection from Bolivia, *Kuntze s.n.*, should be assigned here. In the preparation for a treatment of this genus for Pflanzenreich, Gross assigned new names to many collections. Some of these names were published in short notes, often in obscure publications. This particular collection bears a specific name honoring Otto Kuntze, and, if it has been published, it should be assigned to the synonymy of *C. persicaria*.

Bolivia. Tunari, *Kuntze s.n.* (B, NY); Yungas, *Weddell 4257* (P–holotype, B).

Coccoloba peruviana Lindau, Bot. Jahrb. 13: 213. 1890.

Lindau described this species and cited two collections, *Ruiz & Pavon 229* and *D'Orbigny 571*, in the original publication. Macbride (Field Mus. Pub. Bot. 13: 461. 1937) also considered the species, adding three collections, *Llewelyn Williams 2482*, *6847* and *6852*, and designated as the type *Ruiz & Pavon 229*. No location was given for the lectotype, but a photograph of the Ruiz and Pavon specimen in the Berlin herbarium is deposited at the Chicago National History Museum. The photograph bears the general label, "Types of the Berlin Herbarium," and, since Lindau annotated the sheet, it seems proper to accept the fragments, a small sterile shoot, a detached inflorescence and a single leaf, as the holotype. Additional and better specimens of this collection have been seen in the herbaria at Geneva. Another specimen, presumably of the same collection but without number, was obtained by the Chicago Natural History Museum recently from the Ruiz & Pavon collections at Madrid. I have seen *D'Orbigny 571* from Bolivia in the herbarium at Paris and there is no question that the Ruiz and Pavon and D'Orbigny collections, both of which are in flower, represent the same species. I have also seen the Williams collections cited by Macbride. *Williams 6847* has very few flowers left on one of several inflorescences present on the sheet. *Williams 6852* is comparable in all respects except for a number of immature fruit found in a packet. Both specimens show smaller leaves of thinner texture than do the specimens first cited by Lindau. *Williams 2482* has leaves comparable to the Ruiz & Pavon type, but attached to the sheet is a packet containing fruits which are different from those of *Williams 6852*, although similar to those of *C. ovata* which I find difficult to accommodate in the genus. In mature condition these fruits have a jet-black, triangular achene, one-third to one-half the length of the membranaceous perianth lobes, which are free to the base in fruit and expanded, imbricate, heavily veined and membranaceous. In contrast to these are the fruits of *Ule 9349* made along the Rio Acre. These fruits are typical of *C. obtusifolia*, with tightly appressed perianth lobes free to the base and scarcely exceeding the smaller, tan-colored achenes. The leaves and inflorescences of the Ule collection compare favorably with the Ruiz and Pavon collection. The Riedel collection from Cuyaba has fruits comparable to *Ule 9349*. I am unable to determine from the material at hand which fruit type belongs with *C. peruviana* as typified by *Ruiz & Pavon 229*. Until field studies can be made or more adequate collections are available which will show fruit variation within a population, as well as staminate and pistillate inflorescences, *C. peruviana* will not be clearly defined.

Bolivia. Without specific location, *D'Orbigny 571* (P). **Brazil.** AMAZONAS: Rio Acre, *Ule 9349* (G, K, NY, US). MATTO GROSSO: Cuyabá, *Riedel 821* (B, LE, P). **Peru.** LORETO: Middle Ucayali, *Tesmann 3226* (F, NY), *3231* (NY). SAN MARTÍN: Juan Guerra, *Williams 6847* (F), *6852* (F). Without specific location: *Ruiz & Pavon 229* (B-lectotype, G), *s.n.* (F).

Coccoloba pichuna Huber, Bol. Mus. Goeldi **5**: 342. 1909.

This species is based on *Ducke 4866*, from Obidos, Pará, Brazil. I have seen a duplicate in the British Museum. The species is to be referred to the synonymy of *Coccoloba densifrons* Martius ex Meisner.

Coccoloba pipericarpa Martius ex Meisner, Fl. Bras. **5**(1): 32, *pl. 12*. 1855.

The holotype in the Munich herbarium bears a tag with the number 838. No collector's number has been cited for this specimen and it is possible that the tag was added at a later date. The specimens at Munich bear several geographic locations on each label and the specific location where these collections were made cannot be determined accurately. The specimen selected as the lectotype is in the best condition and has the most definite locality. It is also the specimen on which the illustration in Flora Brasiliensis is based. However, the fruits of this specimen were all insect-infested in the field and considerable artistic liberty was taken in depicting them for the illustration. *Coccoloba pipericarpa* is a small-leaved species not clearly defined at present for want of adequate material.

Brazil. BAHIA: Joazeiro, *Martius s.n.* (M–lectotype). MINAS GERAES: Minas Novas, *Martius s.n.* (B, M). RIO DE JANEIRO: Rio de Janeiro, *Glaziou 15357* (B).

Coccoloba pittieri R. Knuth ex Pittier, Man. Pl. Usuales Venez. 355. 1926.

In an earlier paper (Jour. Arnold Arb. 40: 89. 1959) I have referred this species to the synonymy of *Coccoloba striata*. The species was based on *Pittier 8880* from Carababo, Guaremales, Venezuela.

Coccoloba plantaginea Weddell, Ann. Sci. Nat. III. 13: 257. 1849.

The type and only collection referred to this species is *Blanchet 1491* (G–holotype, B, NY) from the state of Bahia, Brazil. The specimens I have seen are from lianas, for the stems are tenuous with long internodes. The short lateral shoots bear clusters of leaves and immature inflorescences, all parts of which are densely pubescent. I suspect this species of having a close relationship with *C. crescentiifolia*. Further collections from this area of Brazil will doubtless determine whether both species should continue to be recognized.

Coccoloba populifolia Weddell, Ann. Sci. Nat. III 13: 257. 1850.

In the original description Weddell cited two collections, *Blanchet 1486* and *1646*, from Bahia, Brazil, without designating a type.

Meisner (Fl. Bras. 5(1): 40, *pl. 18.* 1855) referred *Coccoloba alnifolia* Casaretto, an older name, to the synonymy of *C. populifolia* with a question. Lindau saw the Casaretto specimen and accepted the two species as identical (Bot. Jahrb. 13: 198. 1890). I have checked authentic material of both species and agree with this conclusion. I have therefore referred *C. populifolia* Weddell to the synonymy of the older name, *C. alnifolia* Casaretto (*q.v.*).

Coccoloba praecox Herter, Revista Sudam. Bot. 10: 38. 1952.

Herter based this species on his own collection (*Herb. Herter 50852*) made near Arapey, Dept. Salto, Uruguay. The species was characterized by having fascicled flowers which appeared before the leaves. I have seen an isotype in the Paris herbarium. The species can be assigned to the synonymy of *Coccoloba argentinensis* Spegazzini (*q.v.*). *Coccoloba praecox* Herter is a later homonym of *C. praecox* Wright ex Lindau (Bot. Jahrb. 13: 142. 1890).

Coccoloba pubescens L. Syst. ed. 10, 1007. 1759.

Coccoloba grandifolia Jacquin, Enum. Pl. Carib. 19. 1760.

This is a well-defined species of the Caribbean Islands and one which is frequently seen and collected in the large-leaved juvenile form. It is not known from South America, although the older literature contains such references.

Meisner (Fl. Bras. **5**(1): 42. 1855; DC. Prodr. **14**: 152. 1856) in his treatments of the genus gave the distribution as the Antilles, Mexico, British Guiana and Dutch Guiana, and suggested that the species might be expected to occur in Brazil. The report of *Coccoloba pubescens* from Mexico was based on *Schiede 60* which I concluded (Jour. Arnold Arb. **40**: 212. 1959) to represent either an adventitious growth form of *C. liebmannii* or cultivated material of doubtful origin.

The reference to this species in Dutch Guiana is based on *Kegel 1339*. Lindau in his monograph (Bot. Jahrb. **13**: 133. 1890) cited this collection under both *Coccoloba polystachya* var. *pubescens* and *C. pubescens,* although he attributed the latter placement to Meisner. I have not seen the Kegel specimen but Eyma, who did, referred the collection to *C. mollis* (Meded. Bot. Mus. Utrecht **4**: 4. 1932).

The occurrence of *Coccoloba pubescens* in British Guiana is based on Bentham's study of the Schomburgk collection from the upper Rupununi River (Hook. London Jour. Bot. **4**: 624. 1845). I have not been able to locate this specimen, but I question its identification as *C. pubescens* and suggest that it be checked against *C. mollis* or *C. savannarum.*

Coccoloba racemulosa Meisner, Fl. Bras. **5**(1): 30. 1855.

This species was described by Meisner on the basis of an unnumbered Martius collection from Minas Geraes. I have previously referred this species to the synonymy of *Coccoloba declinata* (Vellozo) Martius. *Perrottet 83* from British Guiana which Lindau (Bot. Jahrb. **13**: 168. 1890) cited for this species should be identified as *C. lucidula* Bentham.

Coccoloba ramosissima Weddell, Ann. Sci. Nat. III. **13**: 258. 1850.

Coccoloba laxiflora Lindau, Bot. Jahrb. **13**: 191. 1890.

Lindau described *Coccoloba laxiflora* in his monograph of the genus without any comment on its affinities. The type and only specimen cited is *Glaziou 11444* (B), which consists of one detached mature leaf and several attached leaves which are membranaceous and obviously immature. The type of *C. ramosissima* is *Blanchet 2421.* Lindau separated them in his key on the shape of the leaf base. While all the leaves of *Glaziou 11444* are smaller than those of *Blanchet 2421,* there is little doubt that these species are the same. The type of *Coccoloba laxiflora* was collected in Rio de Janeiro, according to the data on the label, but was cited from Espírito Santo by Glaziou (Bull. Soc. Bot. Fr. IV. 11(Mem. 3f): 571. 1911).

Coccoloba longipes S. Moore (*q.v.*) is similar to the present species. The type collection, *Moore 577*, from the Matto Grosso, represents a rampant shrub or a liana. Both growth conditions are apparent in the specimens I have seen. Moore compared his species with *C. ramosissima* and distinguished it on the basis of larger leaves and longer inflorescences. Additional collections from southern Brazil may clarify the relationship of these species.

Brazil. BAHIA: without location, *Blanchet 2421* (P–holotype of *C. ramosissima*, B, G). RIO DE JANEIRO: without location, *Glaziou 11444* (B–holotype of *C. laxiflora*, C, K).

Coccoloba recurva Newman ex Lindau, Bot. Jahrb. 13: 180. 1890.

Lindau indicated that this epithet was a manuscript name on a specimen in the herbarium at Geneva and published the name in the synonymy of *Coccoloba nitida*. The specimen came from Brazil but the exact locality is not known. A specimen in the general herbarium at Geneva, *Newman 158*, may be the one to which Lindau referred. This is clearly the same as *Coccoloba marginata* Bentham.

Coccoloba riedelii Lindau, Bot. Jahrb. 13: 137. 1890.

Lindau cited only *Riedel 613* in the Leningrad herbarium in his original description, so this specimen must be considered the holotype. A full sheet is now in the Berlin herbarium. The type collection was made at Ilheos, Bahia, Brazil. Lindau distinguished this species from *Coccoloba rosea* Meisner, another species represented by a single collection from the same location as *C. riedelii,* on the size and shape of the leaves. The type specimen of *C. riedelii* appears to represent the mature leaf form and that of *C. rosea* a younger leafy branch; therefore I refer *Coccoloba riedelii* to the synonymy of *C. rosea* Meisner.

Coccoloba rigida Meisner, Fl. Bras. 5(1): 29. 1855.

Coccoloba parvifolia Schott, in Sprengel, Syst. Veg. 4(2): 405. 1827; Lindau, Bot. Jahrb. **13**: 175. 1890, not *C. parvifolia* Poiret in Lam. Encycl. **6**: 64. 1804.

When *Coccoloba rigida* was described by Meisner, he cited only *"Schott 5538 (912)"* from "Sebastianopolitana" in the Vienna herbarium. The materials of *Coccoloba* in the Vienna herbarium were destroyed during World War II, but a packet containing several leaves and a short piece of the inflorescence from the Meisner herbarium is now at the New York Botanical Garden. The packet bears the annotation "Brasilia (loco non indicato) Schott n 5538 (912) in Hb. Mus. Vindobon." This is the only material of this collection known to me and should be considered the lectotype. The fragments are comparable to material of *St. Hilaire 138*, which is more widely distributed.

The name *Coccoloba parvifolia* Schott in Sprengel which Lindau accepted for this species, citing *C. rigida* in synonymy, is a later homonym of *C. parvifolia* Poiret. Poiret's species is correctly identified as *C. microstachya* Willd. I am not certain what is the type of *C. parvifolia* Schott, since no specimens were cited in the original description. Lindau later mentioned four specimens in his treatment of the species but did not designate a type. After the publication of his monograph the Berlin herbarium acquired the Kurt Sprengel herbarium. A scanty specimen from that herbarium bears the annotation "C. parvifolia Schott." Lindau did not annotate this specimen and possibly never saw it. I believe this to be the holotype of *C. parvifolia* Schott. The fragmentary material is comparable to the equally fragmentary holotype of *C. rigida* and it is possible that both species are based on the same collection.

Coccoloba rigida is similar to *C. brasiliensis* but is distinguished from it, at least on the basis of present collections, by its smaller leaves which are obtuse at the base and borne on thin petioles. A dense inflorescence is distinctive in *C. rigida* and the rachis is densely and persistently puberulent.

Brazil. RIO DE JANEIRO: Cabo Frio, *Riedel 683* (TO), *Glaziou 19766* (P), *Schenck 3939* (B); without specific location, *St. Hilaire 138* (B, P). State not known: *Schott 5538* (NY–lectotype of *C. rigida*), *s.n.* (B–holotype of *C. parvifolia* Schott).

Coccoloba rigida Willd. ex Lindau, Bot. Jahrb. 13: 188. 1890.

The epithet "*Coccoloba rigida* Willd." has appeared in several lists of species from South America. Fortunately it has no validity. Lindau cited this epithet as a manuscript name in the synonymy of *C. humboldtii*, a species from Mexico. He indicated that it was based on a specimen numbered 7705 in the Willdenow herbarium. I have not seen this name validly published and certainly hope it never was.

The collection in the Willdenow herbarium numbered 7705 is *Humboldt 4484*, which I have designated as the lectotype of *C. humboldtii* (Howard, Jour. Arnold Arb. 40: 198. 1959). Another specimen of the same number in the Paris herbarium, clearly the same species, bears a label indicating the origin as Vera Cruz and was annotated by Lindau as "*Coccoloba nutans.*"

Coccoloba rosea Meisner, Fl. Bras. 5(1): 33. *pl. 14, fig. 2.* 1855.

Coccoloba riedelii Lindau, Bot. Jahr. 13: 137. 1890.

The holotype of *Coccoloba rosea* was collected by Luschnath at Ilheos, Bahia, Brazil, on October 27, 1839. It is the only specimen cited by Meisner and is currently preserved in the Brussels herbarium. The specimen consists of one shoot, obviously a young branch with immature leaves. Considerable artistic liberty was taken in preparing the illustration published, but there is no question of its being of the Brussels specimen.

The specimens of *Riedel 613* on which Lindau based *Coccoloba riedelii* are more mature and vigorous shoots. They are comparable to *C. rosea* in all details of the inflorescence, pubescence and leaf venation. Only the leaves of *C. riedelii* are larger than those of *C. rosea*. Lindau listed these species successively in his monograph and indicated that *C. rosea* is smaller and more graceful than his new *C. riedelii*. In his key he distinguished them on the conspicuousness of the secondary venation. It is clear to me that the age of the specimens represents the only difference between them and that *C. riedelii* must be considered a synonym of *C. rosea*.

A sterile specimen in the Berlin herbarium, *Sellow 3120* from Brazil, was annotated by Lindau as "*Coccoloba* aff. *pubescens* vel *latifolia*." The specimen has extremely long, hollow internodes. The ocreae are 4–5 cm. long and the petioles arise 1.5–2 cm. above the base. The petioles are 4 cm. long and bear oblong blades 25 cm. long and 18 cm. wide. This specimen appears to me to be an adventitious shoot which should be referred to *C. rosea*.

Brazil. BAHIA: Ilheos, *Luschnath s.n.* (BR–holotype of *C. rosea*, B), *Riedel 613* (LE–holotype of *C. riedelii*, B, BM).

Coccoloba rubiginosa Martius ex Meisner, Fl. Bras. **5**(1): 33. 1855.

This epithet was published in the synonymy of *Coccoloba acrostichoides* Cham. by Meisner. The associated collection must be the collection by A. Niermann made in 1832 in Minas Geraes, Brazil. A specimen from the Martius herbarium bearing this name is now in the Brussels herbarium.

Coccoloba rubra L. B. Smith, Jour. Wash. Acad. **45**: 197, *figs. 1–4.* 1955.

Smith attempted to use Lindau's faulty key in comparing his new species with *Coccoloba schwackeana*. A more correct comparison would be with *C. warmingii*. I have seen the types of both species and conclude that *C. rubra* is to be referred to the synonymy of *C. warmingii*. The type of *C. rubra* is the collection made by R. Klein in Santa Catarina, Brazil, bearing the number *Institute of Malariology 33*.

Coccoloba ruiziana Lindau, Bot. Jahrb. **13**: 215. 1890.

Lindau did not indicate a type when he described this species. He cited three collections, *Ruiz & Pavon 228*, which he stated was from Peru, and *Spruce 6340* and *Andersson s.n.*, from Ecuador. The Ruiz & Pavon specimen in the Barbey-Boissier herbarium at Geneva should be designated as the lectotype. It is clearly from the Guayaquil area of Ecuador and not Peru.

Lindau placed this species in his section *Campderia*. However, *Coccoloba ruiziana* is not well defined and field studies are deemed necessary to determine the range of variation to be expected. The specimens cited below are suggestive of *C. obtusifolia* and *C. cujabensis*. From the former, *C. ruiziana* differs in the complete lack of pubescence on the lower leaf surface and in the broader leaf shape. The latter species is defined by the cordate leaf bases and the heavy primary venation. Additional collections are needed to clarify the relationship of these species.

A very pubescent specimen, *Eggers 15526*, is represented by two specimens in the herbaria of the Chicago Natural History Museum and the Berlin Botanical Garden. The specimen from Berlin bears Gross' annotation label with an unpublished specific name referring to "false stipules." The ocreae of the young shoots are often recurved and appear as stipules in this collection and in material of *Coccoloba ruiziana* and *C. spinescens*. The material on hand is inadequate for a reliable description and for the present is considered a pubescent phase of *C. ruiziana*. As such, it becomes intermediate between *C. meissneriana*, *C. obtusifolia* and *C. ruiziana*. It was collected either at Agua Amarga or El Recreo in Ecuador. The two labels carry different data as to location and date of collection.

Ecuador. GUAYAS: Guayaquil, *Ruiz & Pavon 228* (G–lectotype); between Guayaquil & Salinas, *Hitchcock 19989* (GH, NY); Isla Puná, *Andersson s.n.* (B); Posorja, *Mille 786* (F). MANABI: Caracas Bay, *Lehmann BT 748* (NY); El Recreo at Río Mudincho, *Eggers 14929* (F, M, P, US). Locality uncertain: Chanduy, *Spruce 6340* (F, LE, NY, P), Balao, *Eggers 14567* (A, B, LE, M). **Peru.** LAMBAYEQUE: Supo, *Townsend A–135* (F). PIURA: Chulucanas, *Weberbauer 6435* (F, GH); Negritos, *Haught F15* (F). TUMBES: Haciendas Casitas & Ricaplaya, *Weberbauer 7738* (F). Locality uncertain: Talara, *Haught 87* (NY).

Coccoloba sagittata Larranaga, Pub. Inst. Hist. Geog. Uruguay, Escritos 2: 147. 1923.

There is some doubt in my mind whether this was intended to be a new species. Larranaga stated only, "Yo he encontrado la siguiente: 1.a *Coccoloba sagittata* — foliis oblongis sagittatis, angulis posticis brevibus, racimis erectis, compositis. Sp. n. Marzo 19 de 1814." He followed this brief description with a discussion of the properties and uses of the plant which he referred to as climbing and common, and ended with a sentence on the culture of the species. No specimens were cited and none comparable to this description have been seen from Uruguay. The date "1814" may be a typographical error for "1914." The species cannot be identified from the description given and the name cannot be used since there is an earlier homonym by Poiret.

Coccoloba sagittata Poiret, in Lam. Encycl. 6: 64. 1804.

In considering the species excluded from *Coccoloba* for his treatment in Flora Brasiliensis, Meisner cited "COCCOLOBA SAGITATA *Poir.*" and

"COCCOLOBA SAGITTIFOLIA *Orl.*" (Fl. Bras. 5(1): 44. 1855). Both were referred to *Muhlenbeckia sagittifolia* (Ortega) Meisner. I have not seen authentic material but agree that the Poiret species does not belong in *Coccoloba*.

Coccoloba sagittifolia Ortega, Plant. Horti Reg. Bot. Matrit. 60. 1798.

Ortega described fully a specimen growing in the botanical garden at Madrid. Although the native country was given as Brazil, the seed was obtained by Broussonet in Africa. Meisner (Pl. Vasc. Gen. 2: 227. 1843) first tentatively suggested that the species belonged in his new genus *Muhlenbeckia* and later reaffirmed the placement (DC. Prodr. 14: 148. 1846).

Coccoloba sagotii Lindau, Bot. Jahrb. 13: 184. 1890.

The material which Lindau described as *Coccoloba sagotii* is the mature leaf form of *C. lucidula* Bentham. A *Sagot s.n.* collection was cited in the original description and although two specimens of it, both of which are fragmentary, were seen by Lindau in herbaria at Berlin and Stockholm, there is an ample sheet in the Paris herbarium which is an isotype.

Coccoloba salicifolia Weddell, Ann. Sci. Nat. III. 13: 259. 1850.

This species, which grows as a woody vine, appears to be distinct on the basis of its narrow, lanceolate leaves, although the full range of leaf variation is not known. The type (*Claussen 4*) is in flower. Lindau cited additional Claussen specimens which I have seen and *Schwacke 5801* which I have not seen. Lindau also added a description and illustration of a fruit which may be that of the Schwacke collection. Two additional sterile collections, *Glaziou 3086* and *3090*, have been identified by Lindau as this species. The first collection has larger leaves, considerably different in shape and appearance from the Claussen type. Additional collections and field study of the species is needed.

Brazil. RIO DE JANEIRO: Nuovo Friburgo, *Claussen 4* (P–holotype, B, BR, F, NY), *2002* (NY), *2094* (G); Rio de Janeiro, *Glaziou 3086* (BR), *3090* (BR).

Coccoloba sarmentosa S. Moore, Trans. Linn. Soc. II. 4: 446. 1895.

The type collection of this species is *Moore 1038* from Paraguay. It is regarded as a very pubescent phase of *Coccoloba spinescens* Morong and is referred to synonymy there.

Coccoloba savannarum Standley in A. C. Smith, Lloydia 2: 177. 1939.

This species is still known only from the type *Smith 2225* collected in a scrub savanna in the basin of the Rupununi River in British Guiana. The species appears to be similar to *Coccoloba rosea*, differing in the smaller ocreae and in having a lax inflorescence with the flowers borne on short pedicels. Both species are inadequately known at present. The type is at the Chicago Natural History Museum with isotypes at the Arnold Arboretum and the New York Botanical Garden.

It is possible that the material collected by Schomburgk from the Upper Rupununi which Bentham referred to *Coccoloba pubescens* (Hook. London Jour. Bot. **4**: 264. 1845), may represent adventitious leaves of this species.

Coccoloba scandens Casaretto, Nov. Stirp. Bras. **8**: 70. 1844.

Lindau (Bot. Jahrb. **13**: 184. 1890) cited this species in the synonymy of *Coccoloba sticticaulis*. Apparently, however, he did not see the type (*Casaretto 76*), for this specimen is cited neither under *C. sticticaulis* nor in his list of specimens studied. The Casaretto herbarium is extant at Turino, but I have not been able to see this specimen. Since Lindau was in error in several other instances where he cited Casaretto species, reducing them without seeing the specimens involved, it seems advisable to list this species without placement at the present time. This reference appears to be the earliest valid publication of the name *Coccoloba scandens*. The specific epithet has been used at least four times in the genus, mostly as *nomina nuda*, for four different species.

Coccoloba scandens Poeppig ex Lindau, Bot. Jahrb. **13**: 181. 1890.

Lindau published this epithet (a manuscript name found in the Vienna herbarium) in the synonymy of *Coccoloba peltata* Schott. He did not discuss the disposition of the name, but merely cited the collection *Poeppig 2670* from Ega, Amazonas Province, Brazil. The collections of *Coccoloba* in the Vienna herbarium having been destroyed, it seems worthwhile to call attention to another specimen of *Poeppig 2670* in the Leningrad herbarium. This consists of three detached leaves and a short piece of stem with two very short inflorescence axes, both without flowers. It can be referred to *Coccoloba parimensis* Benth.

Coccoloba schomburgkii Meisner, Linnaea **21**: 265. 1848.

Meisner mentioned only *Schomburgk 640* in the original description, but indicated that several specimens were in the Shuttleworth herbarium. Specimens and fragments of this collection are now widely distributed, and a study of a great many of them suggests a variation within the species in the size of leaves and the length of the inflorescences. Numerous recent collections by Steyermark and by Maguire and his associates are available for study and these indicate that, for the present, a very great variation in the habit of the plant and an apparently associated variation in the size and shape of the leaves must be recognized. It is hoped that some future collector in the table-mountain area will be able to determine the range of variation on one plant.

Coccoloba schomburgkii is variously described on collectors' labels as "shrub 1 foot tall," "small recumbent shrub," "shrub with simple or spreading stems, 3–5 feet tall," "depressed shrub 4 dm. tall," "tree 5–8 m.," "sprawling ligneous vine" or "liana." All of the specimens cited below were collected between 1100 and 2400 meters above sea level. The smaller specimens are reported from "rocky elevations in savannah," while those described as "trees" or "lianas" are reported from the forested edges of savannas, along rivers or on forested slopes. There is a suggestion of a correlation between habitat and leaf size, the plants of the savanna areas or rocky outcrops having the smaller leaves and those of the forested areas having larger leaves. Meisner stated in the original description that the leaves are 1.5–2.5 inches long and 0.75–2 inches wide and heteromorphic on the same branch. Lindau increased the dimensions to 6–10 cm. long and 3–5 cm. broad. The specimens cited below have, within single collections, leaves of the following dimensions: 1.5 × .8 to 4.5 × 2 cm.; 3.5 × 2 to 7.5 × 4.5; 4 × 2.7 to 7 × 5; 8 × 5 to 13 × 8 cm. long and broad. The small leaf-measurements are from the small plants with compact branches and short internodes. The largest leaf-sizes were taken from arching shoots with long internodes, described as a liana. All leaves are coriaceous and in most cases the margin is slightly inrolled. The primary veins depart at right angles, bifurcating near the margin, or are arcuate at slight angles from the midrib. Only one collection has fruit and these are immature. *C. schomburgkii* must be recognized as an extremely variable species as far as leaf size and shape is concerned. The length of the inflorescence appears to vary in proportion to the size of the leaf.

Brazil. AMAZONAS: Territory Rio Branco, Serra Sabang, *B. & C. Maguire 40302* (A, NY), *40433* (A, NY). **British Guiana.** Roraima, *Schomburgk 640* (*981*) (K–holotype, B, F, G); Upper Mazaruni river, Imbaimadai Savanna, *Maguire & Fanshawe 32188* (A, NY); between Chinowieng & Chi-Chi landing, *B. & C. Maguire 40663* (A, NY). **Venezuela.** BOLIVAR: Ilu-tepui, Gran Sabana, Mesa Ridge, *Maguire 33402* (A, NY), *33549* (NY); between Enemasic and San Rafael, *Maguire 33596* (A, NY); N.W. of Kavanayen Mission, *Maguire 33741* (A, NY); Ptari-tepui, *Maguire & Wurdack 33900* (A, NY), *33918* (A, NY), *Steyermark 59678* (F), *59712* (F), *60339* (F), *60618* (F); Mount Roraima, *Steyermark 58640* (F), *58676* (F).

Coccoloba schwackeana Lindau, Bot. Jahrb. **13**: 200. 1890.

Coccoloba erecta Glaziou, Bull. Soc. Bot. Fr. IV. **11** (Mem. 3f): 572. 1911, nomen nudum.

This species is readily recognized by the obovate leaves borne on petioles which are inserted well above the base of the ocreae. I have seen no collections, other than the original, which are in fruit. Lindau cited only *Glaziou 14219*, with specimens in the Berlin and Delessert herbaria. This collection has proved to be a mixture with *Glaziou 14220* which is *Coccoloba peltata*. *Glaziou 14219* in the Berlin herbarium is designated as the lectotype.

Brazil. RIO DE JANEIRO: without specific location, *Glaziou 14219* (B–lectotype, C, G, K), *14220* in part (LE, P).

Coccoloba senaei Lindau ex Glaziou, Bull. Soc. Bot. Fr. IV. 11(Mem. 3f): 571. 1911.

This epithet was used by Glaziou in a list of determinations of his collections. The name was not published by Lindau, so far as I can determine. Glaziou's description is brief and of no value in the genus. The name should be considered a ***nomen nudum*** and the species should be referred to the synonymy of *Coccoloba brasiliensis* Nees & Martius (*q.v.*). *Glaziou 19762* and *19763* from Rio dos Pedras, Valu, Minas Geraes, Brazil, were cited by the collector and a specimen of *Glaziou 19763* in the herbarium at Copenhagen has been labeled the cotype. In the Berlin herbarium *Glaziou 19763* and *Schwacke 8005* are both labeled "*Coccoloba senaei* Lindau, n. sp."

Coccoloba sparsifolia Lindau, Bot. Jahrb. 13: 195. 1890.

Lindau based this species on *Don 144* from the state of Maranhão in Brazil. Only a single specimen is indicated and that is in the herbarium at Brussels, although Lindau acquired a fragment which is currently in the Berlin herbarium. I have seen the holotype, which consists of a stem with several short inflorescences and two detached leaves. These leaves are of thin texture, called membranaceous by Lindau, with slender, short petioles. In all aspects the type suggests young specimens of *Coccoloba ascendens.* Lindau separated *C. sparsifolia* and *C. ascendens* in his key to the species on the basis of the glabrous inflorescence axis in the former and the puberulent axis in the latter. However, the type specimen of *C. sparsifolia* does not support this distinction, for the inflorescence axes are as puberulent as those of *C. ascendens.* While additional material may prove it necessary to assign *C. sparsifolia* to the synonymy of *C. ascendens*, I prefer to maintain them as separate species for the present.

Gleason 349 (GH, NY) from the bank of the Potaro River, Tumatumari, British Guiana, is also referred to *C. sparsifolia.* This has ovate leaves, coriaceous in texture, with short, stout petioles. The secondary venation is impressed in the dried condition and the leaf base is conspicuously cordate. Such a combination of characteristics is not familiar to me from the many collections of *C. ascendens* I have seen and from the plants I have studied in the Antilles.

Coccoloba spec. an nova? Herzog, Rijks Herb. Meded. 46: 3. 1922.

The collection *Herzog 1480* made along the Río Piray near Santa Cruz de la Sierra, Bolivia, is completely sterile. Herzog suggested that it might be a new species. The broadly lanceolate leaves are acute at the apex and narrowed to an obtuse base. The petiole is only 2–4 mm. long.

Tufts of brown hairs occur in the axils of the primary veins along the midrib. The specimens are best assigned to *Coccoloba peruviana* (*q.v.*), even though that species is poorly defined at the present.

Coccoloba sphaerococca Lindau, Bot. Jahrb. 13: 185. 1890.

This species was considered to be similar to *Coccoloba densifrons* Mart. ex Meisner. Both Lindau in his monograph and Macbride (Flora of Peru, Publ. Field Mus. Bot. 13: 458. 1937) distinguished the two on the basis of venation. The upper leaf surface of *C. sphaerococca* is essentially smooth with the minute venation finely reticulate. The primary veins are not evident. In contrast, the primary venation of *C. densifrons* is evident and when dry the ridged veins are conspicuous by being slightly depressed in the leaf surface.

None of the previous workers has compared this species with *Coccoloba padiformis* Meisner, but while Meisner's species is based on a staminate plant and *C. sphaerococca* is based on a fruiting specimen, it appears to me that only one species is represented. I therefore refer *C. sphaerococca* to the synonymy of *C. padiformis* Meisner. The type is an unnumbered Spruce collection in the Kew Herbarium collected near Tarapoto, Peru.

Coccoloba spinescens Morong, Enum. Pl. 212. 1892; Ann. N.Y. Acad. 7: 212. 1893.

Coccoloba sarmentosa S. Moore, Trans. Linn. Soc. II. **4**: 446. 1895.
Coccoloba paraguariensis f. *intermedia* Hassler, Repert. Sp. Nov. **14**: 163. 1915.
Coccoloba paraguariensis var. *grandifolia* Hassler, *ibid.*
Coccoloba paraguariensis var. *spinescens* Hassler, *ibid.*
Coccoloba paraguariensis f. *ovatifolia* Herzog, Rijks Herb. Meded. **46**: 3. 1922.
Coccoloba chacoensis Standley, Publ. Field Mus. Bot. **17**: 239. 1937.

This species is typified by *Morong 882* of which I have seen several specimens. In the original description Morong noted that the plant was thorny, the thorns consisting of the sharp, indurated ends of the short branches and branchlets. The leaves are described as oval and elliptic and it is important to note that the petioles were described as "downy." An examination of the type material shows also a characteristic rigidity to the leaves which, when dry, have lighter-colored veins and leaf margins. The pedicels recurve strikingly in fruit and the perianth segments enclose the achene.

Hassler incorrectly associated the species with *Coccoloba paraguariensis*, reducing Morong's species to varietal status. As I have pointed out in the discussion of *C. paraguariensis*, that species must be typified by *Balansa 2060* in the herbarium at Göttingen. The Balansa collection is a mixture and only the Göttingen specimen agrees fully with the original description. The material of *Balansa 2060* in the other herbaria as cited below corresponds with *Morong 882* and therefore must be called *C. spinescens*. There are definitely two species involved.

Hassler described several varieties and forms of "Coccoloba paraguariensis." The typical *C. spinescens* has the smallest leaves. Hassler's forma *grandifolia* (*Fiebrig 4237*) has the largest. Both leaf sizes can be found in single collections and most variations on single specimens. The varieties and forms are of doubtful value unless further field study proves their validity. Gross has annotated other sheets with unpublished varietal names in the Berlin herbarium and such specimens are included in the citations below.

I have assigned *Coccoloba sarmentosa* Moore to the synonymy of *C. spinescens*. The type of Moore's species (*Moore 1038*) is densely pubescent on the lower leaf surface and the inflorescence. The "downy" petioles mentioned by Morong for *C. spinescens* are typical of the species. However, the pubescence extends along the midrib and onto the lamina, as well. Specimens with the amount and density of pubescence on both leaves and rachises to make them intermediate between the types of *C. sarmentosa* and *C. spinescens* are cited below and indicate that *C. sarmentosa* cannot be maintained as a distinctive species.

Buchinger and Sanchez (Bol. Soc. Argent. Bot. 7: 253. 1959) maintain *Coccoloba chacoensis* Standley as a distinct species, separating it from *C. spinescens* in their key by the absence of lateral branches terminating in spines and by the presence of glands on the lower leaf surface. A tendency to produce terminal spines by modification of the shoot apex is seen on many specimens cited below. The presence of "glands" in *Coccoloba* appears to be inconsistent and unreliable. The "glands," in all cases examined, are either blocked stomata or residual hair bases. Glands comparable to those found on the type of *C. chacoensis* are also on material formerly called *C. paraguariensis* f. *ovatifolia* (*Herzog 1070*), *C. paraguariensis* (*Balansa 2060* in part), *C. paraguariensis* f. *intermedia* (*Hassler 12327*) and *C. paraguariensis* var. *spinescens* (*Rojas 180*).

Bolivia. Chaco, Cururenda, *Cardenas 2529* (FM–holotype of *C. chacoensis*, G); Gran Chaco, Río Pilcomayo, Camoteras, *Herzog 1070* (B–type of *C. paraguariensis* f. *ovatifolia*). **Paraguay.** Asuncion, *Morong 197a* (NY); Chaco, Bahia Negra, *Rojas 13757* (W); Corumba, *Moore 1038* (type collection of *C. sarmentosa*, B, NY); Gran Chaco, Loma Clavel, *Hassler 2486* (A, B, NY); Gran Chaco, *Moore 1049* (NY); Laguna Ypacaray, *Fiebrig 968* (A, M); Puerto Casado, *Pedersen 4027* (A, C); between Río Apa & Río Aquidabán-mi, *Fiebrig 4237* (type collection of *C. paraguariensis* var. *grandifolia*, A, B, GH, M); Río Paraguay, *Balansa 2060* in part (B, P); Río Pilcomayo, *Morong 882* (NY–lectotype, US), *Rojas 180* (B); Ypacaray, *Hassler 11476* (A, GH, NY), *12327* (type collection of *C. paraguariensis* f. *intermedia*, A, GH, NY).

Coccoloba spruceana Lindau, Bot. Jahrb. 13: 162. 1890.

This species was distinguished by Lindau on the basis of its subcoriaceous, subobovate leaves and long ocreae. Since the type collection has only submature leaves, additional collections are necessary to define this species accurately. No recent collections have been identified with the type collected by Spruce along the Casiquiari in Venezuela. However, the collections cited below are referred to this species. The collection *Maguire, Wurdack and Bunting 36756* was obtained from the classic area of Spruce and was described by the collectors as a tree 8 m. tall. The inflorescences are in bud, yet the leaves appear to be more mature than those of *Spruce 3185*. Considerable variation in leaf size and shape is to be seen on a single branch and the largest leaf can be described as broadly elliptic-oblong with a blade 16 cm. long, 13 cm. broad, rounded at the base and rounded but short-apiculate at the apex. The collections by Ducke, Silverio Level and by Wurdack and Adderley represent still another aspect of the same species. These are all from trees and consist of relatively stout branches of slow growth habit. The leaves, showing considerable variation in size and shape, are well expanded but membranaceous in texture and associated with staminate inflorescences in full flower. It appears that the type collection of Spruce with its obovate leaves represents only one phase of the final concept of this species. The relationship of *Coccoloba spruceana* to *C. striata*, for example, must be re-examined when pistillate flowers and fruiting material are available.

Venezuela. AMAZONAS: rivers Casiquiari, Vasiva and Pacimoni, *Spruce 3185* (GH–lectotype, BR, LE, NY, P); uppermost Río Yatua, *Maguire, Wurdack and Bunting 36756* (A, NY), between Tama-Tama and San Antonio, *Wurdack and Adderley 43652* (A), Cano Yagual on Río Orinoco, *Silverio Level 112* (A). **Brazil.** AMAZONAS: Manaos, *Ducke 21367* (F, NY, Y).

Coccoloba squamosa Martius ex Colla, Herb. Pedemontanum **5**: 48. 1836.

The original description is brief: "7. *C. squamosa* = Mart: in sched: (*Brasil:*) '*C.* caule laeviusculo, foliis brevi-petiolatis ellipticis (longit: 1. latit: ½ pollic:), basi inaequilateris membranaceis integerrimis glabris subtus pallidioribus, racemis axillaribus spicatis nutantibus.' NOB:" Neither Meisner nor Lindau considered this name in their treatments of the genus and I have been unable to locate any specimens, by Martius or others, which bear such a name. The only Brazilian species with leaves of comparable size is *Coccoloba pipericarpa* Mart. ex Meisner, but none of the five Martius collections I have seen of this species bears such a manuscript name. For the present *C. squamosa* cannot be identified.

Coccoloba sticticaulis Weddell, Ann. Sci. Nat. III. **13**: 260. 1849.

Coccoloba longependula Martius ex Meisn. Fl. Bras. **5**(1): 27. *pl. 9*, 1855.

A comparison of the authentic specimens of these species indicates that they are identical and that *Coccoloba longependula* should be referred to the synonymy of *C. sticticaulis*. When Meisner described *C. longependula* he referred to Weddell's *C. sticticaulis*, but indicated that he had not seen material of the type, *Claussen 280*. Lindau also stressed the occurrence of

2 styles in "*C. longipendula*" (sic) in contrast to three styles in *C. sticticaulis*. Unfortunately, such characters are of no value in this genus. Lindau (Engl. Bot. Jahrb. **13**: *pl. 5, figs. 34, 37.* 1890) illustrated fruits of both species, describing *C. sticticaulis* as having an ovoid, shortly stipitate fruit, in contrast to the fruit of *C. longependula*, which he described as globose. I have examined all of the specimens cited by Lindau, but not from all the herbaria he listed. There are no fruits available for the specimens I have seen; hence I question Lindau's description of the fruit of *C. sticticaulis*. A study of additional and more recently collected material supports the conclusion that only one species is involved.

A name honoring Claussen is also applied to the Claussen collections I have seen, many of which are without numbers. This name attributed to Weddell, apparently was never published.

Lindau (Bot. Jahrb. **13**: 184. 1890) placed the name *Coccoloba scandens* Casaretto (*q.v.*) in the synonymy of *C. sticticaulis* and referred to Meisner's treatments in the *Flora Brasiliensis* and DeCandolle's *Prodromus*. Neither Lindau nor Meisner saw or cited Casaretto's collection. Both authors cited a Riedel collection from Parahyba which I have not seen. Lindau cited *Riedel 2681* and Meisner, *Riedel s.n.* If Lindau is correct in considering *C. scandens* Casaretto identical to *C. sticticaulis* Weddell, then the Casaretto epithet must be used for this species.

Brazil. MINAS GERAES: Bello Horizonte, *L. O. Williams & Assis 6046* (GH); Bento Pires, Bello Horizonte, *L. O. Williams 5285* (GH); Capoeiras, Ouro Preto, *Damazio 1539* (G); Faria, *Glaziou 18427* (A, LE); Lagoa Grande, Municipio Nova Lima, *L. O. Williams & Assis 6577* (GH); Lagoa Pampulha, Municipio Bello Horizonte, *L. O. Williams & Assis 6096* (GH); between Porte do Paraopeba & Chapada, *Martius 759* (M–type of *C. longependula*); without specific locality, *Claussen 280* (P–lectotype of *C. sticticaulis*, (G), *s.n.* (A, GH); *Glaziou 21979* (BR). RIO DE JANEIRO: Caxoeira do Campo, *Lund 35* (B); Caxoeira do Campo, Lazoa Sta., *Warming 130* (C, LE); Restinga do Jacarépaguá, *Brade 77* (GH); Serra do Piedada, *Warming 126* (NY); Sta. Luzia do Rio das Velhas, *Schwacke 11431* (B).

Coccoloba striata Bentham in Hooker, London Jour. Bot. **4**: 626. 1845.

Coccoloba grisebachiana Lindau, Bot. Jahrb. 13: 195. 1890.
Coccoloba pittieri R. Knuth ex Pittier, Man. Pl. Usuales Venez. 355. 1926.

Bentham based this species on a collection by Schomburgk from British Guiana. Although a specific locality is not given, Lindau thought it to be near Roraima and one herbarium label refers to the "savannah." The collection was made in April, 1843, and bears the second collection numbers 929 or 1265.

Coccoloba grisebachiana Lindau, based on *Crueger s.n.* from Trinidad, and *C. pittieri*, based on *Pittier 8880* from Venezuela, were placed in the synonymy of *C. striata* in an earlier paper (Jour. Arnold Arb. **40**: 89. 1959).

The relationships of *Coccoloba glaziovii*, *C. parimensis*, and *C. spruceana* with the present species are not clear. Additional material and field study may show these to be representatives of only one species.

British Guiana. Roraima area, *Schomburgk 929* (P), *1265* (B, P). **Venezuela.** ANZÓATEQUI: El Amparo de Chive, *Pittier 15025* (US); Guaremalos, Punta Cabello San Felipe, *Pittier 8880* (type collection of *C. pittieri*, A, GH, LE, NY). FEDERAL DISTRICT: Carruao, *Pittier 11847* (A, GH, NY).

Coccoloba stricta Klotzsch in Schomburgk, Fl. Faun. Br. Guy. 934. 1848; Lindau, Bot. Jahrb. 13: 167. 1890.

Lindau referred this name, published without description, to the synonymy of *Coccoloba lucidula*. Of the Schomburgk collections I have seen and identified as *C. lucidula*, none has such a manuscript name.

Coccoloba strobilulifera Meisner, Fl. Bras. 5(1): 25. 1885; Howard, Jour. Arnold Arb. **40**: 185. 1959; Lindau, Bot. Jahrb. 13: 193. 1890.

Coccoloba strobilulifera was based on *Moritz s.n.* (*type*–P), collected in Colombia but without a known specific locality.

Meisner recognized that *Coccoloba strobilulifera* was similar to *C. acuminata* HBK., but stressed the differences in pubescence, shape of leaf bases and length of inflorescences in establishing and maintaining the species. Lindau placed the species in the synonymy of *C. acuminata*, but described a new variety to accommodate it. The numerous collections I have cited previously (*loc. cit.*) as *C. acuminata* (*q.v.*) show gradations to indicate that *C. strobilulifera* cannot be maintained as a distinct species or variety.

Coccoloba sublobata Heimerl, Denkschr. Akad. Wiss. Wein. 79: 244. 1908.

This species has been referred to the synonymy of *Coccoloba glaziovii* (*q.v.*) and discussed there. The type was in the collections at Vienna and was lost during World War II. However, a photograph of this specimen is in the collections of the Chicago Natural History Museum and a duplicate specimen bearing the same number but a different unpublished binomial attributed to Heimerl is in the Berlin herbarium. The type collection is *M. Wacket 12*, made in 1902 near Santos, Serra do Cubatão, São Paulo, Brazil.

Coccoloba swartzii Meisner, DC. Prodr. **14**: 159. 1856; Howard, Jour. Arnold Arb. 37: 324. 1956.

The type locality of this species is Jamaica. Continuous but slight variations occur in collections made in the Antilles, from Jamaica southward to St. Lucia and Barbados, and in Central America, specifically in British Honduras and Honduras. The species has not been collected in Grenada, Trinidad, or Tobago or in Central America south of Honduras. The following collections from Curaçao, Aruba, and mainland Venezuela fit into the known range of morphological variation but represent a disjunction of the range of the species. Future field studies of the populations represented by the specimens cited may indicate a hybrid situation or that a subspecific category is desirable.

Aruba: *Boldingh 6384* (NY). **Bonaire:** *Boldingh 7051, 7489* (NY). **Curacao:** *Boldingh 4882, 5070* (NY); *Britton & Shafer 3082* (NY); *Curran and Haman 150, 234* (NY); *Realino 18* (NY). **Venezuela.** PARAGUANÁ: Cerro Santa Ana, *Curran & Haman 525, 539* (GH), *702* (GH, NY); Pueblo Nuevo, *Tamayo 930* (GH).

Coccoloba tenuiflora Lindau, Bot. Jahrb. 13: 190. 1890.

Lindau described this species and mentioned that he saw a specimen in the Leningrad herbarium. He noted that the specimen was in flower in April, that it had been collected in Brazil, and that neither the specific location nor the name of the collector was indicated. In the material on loan from Leningrad I find a single sheet bearing the name "C. tenuiflora Lindau." The three fragments on this sheet are from the Fischer herbarium and one of the three labels on the sheet suggests that the plant may be cultivated. Nearly all of the material of the genus which I have seen from the Fischer herbarium has been of cultivated plants. Although several words cannot be deciphered, no date is given on any of the labels. There is also a second sheet in the Leningrad herbarium which was not annotated by Lindau but which is clearly the same plant. The label on this sheet states that the specimen is from a cultivated plant. The typification of this species is difficult. Lindau apparently obtained a fragment from the Leningrad sheet which he cited and the fragment plus a drawing is in the Berlin herbarium, though this was not cited in the original description. The sheet in Leningrad which Lindau cited has several fragments, plus additional material in packets; these could have come from one plant or from several or could have been taken at different times. However, it appears necessary to designate the sheet in Leningrad as the holotype.

Coccoloba tenuiflora Lindau is poorly understood. The species appears to be similar to *C. longipes* from the Matto Grosso, but the effects of greenhouse cultivation on *C. tenuiflora* are difficult to evaluate. The plants are obviously deciduous in cultivation, for some specimens show a flush of immature and delicate membranaceous leaves and ocreae on elongated shoots. Lindau concluded that the oblong to obovate leaves with long, acuminate apices and the elongated pedicels distinguish the species.

Coccoloba tiliacea Lindau, Bot. Jahrb. 13: 198. 1890; Buchinger & Sanchez, Bol. Soc. Argent. Bot. 7: 255. 1959.

Coccoloba peltata Griseb. Symb. Fl. Argent. 508. 1879, not Schott.

This species is easily recognized and is well represented in herbaria by material from northeastern Argentina and Bolivia. The plants are small trees with broadly ovate leaves which are commonly crenate or undulate at the margins. The leaves vary from peltate to non-peltate on the same specimens. The base of the blade may be obtuse and slightly to deeply cordate. The blades may show all gradations from attachment at the margin to peltation, with as much as 2.5 cm. of lamina between the petiole point of attachment and the margin. The inflorescence may be simple or much branched. The inflorescence branches usually arise from the base and may give the appearance of a cluster of racemes of equal length. The fruit has imbricate, but non-coronate perianth lobes one-third the length of the fruit.

In the original description Lindau cited several specimens without indicating a type. *Lorentz & Hieronymus 499* (B) has been designated as the lectotype.

Argentina. JUJUY: Ledesma, Sierra de Calilegua, *Venturi 5355* (A, F, GH); San Pedro, Sierra Santa Bárbara, *Venture 9655* (A, GH, LE, NY); San Antonio near San Lorenzo, *Lorentz & Hieronymus 378* (B, GOET), *Schulz 8169* (B, NY). SALTA: Orán, Badahonda, *Lorentz & Hieronymus 446* (GOET, NY, S), *499* (B–lectotype, GOET), Cuesta de Santa Rosa, *Lorentz & Hieronymus 658* (B, NY), El Bananal, *Meyer 658* (B, NY), Quinta del Río Santa María, *Willink 127* (W), Río Bermejo, *Schreiter 218* (F), Río Colorado, Paso Hondo, *Meyer 6492* (W), Tartagal, *Schreiter 3696* (GH), *8462* (GH), *11471* (A), *Venturi 5176* (A), Vado Hondo, *Devoto & Alberti 2223* (A). TUCUMÁN: Capital, cultivated, *Meyer 15813* (BR, W). **Bolivia.** LA PAZ: Sierra de Aguaragra, *Troll 304* (B). SANTA CRUZ: Between Santa Cruz and Samaipata, *Cardenas 4631* (US). TARIJA: La Merced, near Bermejo, *Fiebrig 2178* (A, M).

Coccoloba trianaei Lindau, Bot. Jahrb. **13**: 213. 1890.

This species is known only from the type collection, *Triana 974*, with the holotype in the Berlin herbarium and one isotype at Brussels. The collection was made in Colombia but no specific location or altitude data are given. The specimens are from staminate plants and the inflorescence tends to produce several shorter branches from near the base.

Coccoloba trianaei is similar to both *C. lehmannii* and *C. venosa*. It differs from *C. lehmannii* in having more lanceolate to ovate-lanceolate leaves with abruptly rounded bases and much shorter petioles. The stems, leaves and inflorescences are slightly more pubescent than in comparable material of *C. lehmannii*. In size and shape, the leaves of *C. trianaei* are similar to many specimens of *C. venosa*; however, the amount of pubescence and the laxly flowered inflorescence differs from that of *C. venosa*. Additional collections of *Coccoloba* are needed from coastal areas of Colombia to determine whether *C. trianaei* is only a pubescent phase of *C. venosa* or a truly distinct species.

Coccoloba uvifera (Linnaeus) Linnaeus, Syst. Nat. ed. 10. 1007. 1759.

Polygonum uvifera L. Sp. Pl. 365. 1753.

The common "sea grape" or "uva" is a well-known tropical American tree of the seacoast areas. It is abundant in the Caribbean, yet it has been overlooked there by many collectors so that herbarium records of its distribution show many gaps where it might be expected to occur.

In the present study it is of interest to note that the species is not represented in collections from Brazil or southern South America. Meisner mentioned the species in his treatment for *Flora Brasiliensis* (5(1): 42. 1855) without seeing specimens and questioned the identification of specimens to that species cited by other authors.

Colombia. ANTIOQUIA: Medellín, *Daniels s.n.* (NY). ATLÁNTICO: Puerto Colombia, *Barkley & Gutiérrez 1859* (F). BOLÍVAR: Boca Grande near Cartagena, *Killip & Smith 14092* (A, GH, NY); Torrecilla near Turbaco, *Killip & Smith 14418* (A, GH, NY). MAGDALENA: Barranquilla, *Holton s.n.* (NY); Santa Marta, *H. H. Smith 2102* (A, NY). Department not indicated: Gaira, *Castañeda 54* (F). **Curaçao.** *Curran & Haman 53* (A). **Dutch Guiana.** Without location, *Weigelt s.n.* (LE); *Regel 984* (NY). **Venezuela.** FALCÓN: Cumarebo, *Curran & Haman 491* (GH, NY), *492* (GH). FEDERAL DISTRICT: Caracas, *Pittier 10343* (GH, NY); La Guaira, *Fendler 840* (GH, NY); Macuto, *Pittier 11791* (A, NY). SUCRE: Cristóbal Colón, *Broadway 594* (GH, NY). Without location: *Mocquerys 800* (A, NY, P).

Coccoloba uvifera Salzman ex Lindau, Bot. Jahrb. 13: 186. 1890, not Linnaeus.

This epithet is a manuscript name on several Salzman collections, although Lindau referred specifically to the one in the Delessert herbarium. Lindau appears to have been the first to publish the name in the synonymy of *Coccoloba laevis* Casaretto. I have discussed the Salzman collections under *C. laevis.*

Coccoloba vellosiana Casaretto, Nov. Stirp. Bras. 70. 1844; Howard, Jour. Arnold Arb. **41**: 43. 1960.

In an earlier study (*loc. cit.*) I placed this epithet in the synonymy of *Coccoloba arborescens* (*q.v.*). Although Casaretto cited an unnumbered Riedel collection in the original description, he also indicated that his new species was a transfer of *Polygonum frutescens* Vellozo. *Coccoloba vellosiana,* therefore, must also be rejected as an illegitimate name.

Coccoloba venosa Linnaeus, Syst. Nat. ed. 10. 1007. 1759.

The complexities of this name, along with the problems of the morphology and distribution of the species, have been discussed by Fawcett and Rendle (Jour. Bot. **51**: 123. 1913) and by me (Jour. Arnold Arb. **30**: 398. 1949; **40**: 217. 1959). The specimens cited below are typical of the Lesser Antillean expression of the species, with the sole exception of *Velez 2668* which is similar to material from Central America formerly called *Coccoloba floribunda.*

Colombia. META: Puerto López, *E. L. & R. R. Little 8416* (NY). **Venezuela.** APURE: Puerto Páez, *Velez 2668* (US). SUCRE: Cristóbal Colón, *Broadway 431* (GH), *664* (GH, NY). YARACUY: Aroa, *Curran 323* (NY).

Coccoloba virens Lindley, Bot. Reg. 21: *pl. 1816.* 1835; Howard, Jour. Arnold Arb. **41**: 41. 1960.

This species was based on greenhouse material of unknown origin presumed to be from the West Indies. As I have pointed out, Lindau placed the species incorrectly. The correct disposition is to regard *Coccoloba virens* as a synonym of *C. coronata* Jacq.

Coccoloba warmingii Meisner in Warming, Symbollae 128. 1870.

Coccoloba rubra L. B. Smith, Jour. Wash. Acad. Sci. **45**: 197, *figs. 1–4.* 1955.

This species of southeastern Brazil is recognized by the obovate leaves which are bullate between the veins. The leaf apex is rounded, emarginate or abruptly mucronate in immature leaves but all mature leaves showed abnormal development of the apex.

No specimens are cited by number in the original description where Meisner stated, "Hab. in Serra da Gamba et in prov. Rio de Janeiro, m. Maio legit Warming." Lindau (Bot. Jahrb. **13**: 200. 1890) cited only specimens in the Warming herbarium but referred to these by numbers *125* and *128*. There is a fragment of an inflorescence, a single detached leaf and a sketch of an attached leaf of *Warming 125* in the Berlin herbarium. The origin of this fragment is not given. Specimens of both *Warming 125* and *128* are to be found in the Copenhagen herbarium where the first sheet is labelled "co type" and its origin indicated as "Rio." *Warming 128* (collected at Serra da Gamba) in the Copenhagen herbarium should be the lectotype.

Smith suggested that his new species *Coccoloba rubra* would be near to *C. schwackeana* in Lindau's key to the genus. Lindau's key, however, is faulty and it is difficult to reach *C. warmingii* with the material Lindau preserved in the Berlin herbarium. It is clear that *C. rubra* is a synonym of *C. warmingii.*

A single sterile specimen of *Burchell 3982* in the Kew herbarium appears to represent the adventitious leaf form of this species. Although Lindau referred this collection to *Coccoloba latifolia*, the elevated origin of the petiole on the ocrea indicates that the collection is better assigned here. *Dusen 17225* cited below is a similar sterile collection.

Brazil. MINAS GERAES: Piedade a Santa Luzia, *Glaziou 20438* (B, LE, P); Santa Luzia do Rio das Velhas, *Schwacke 11430* (P). RIO DE JANEIRO: Rio de Janeiro, *Warming 125* (B, C); Serra da Gamba, *Warming 128* (C–lectotype, B). SANTA CATARINA: Mato do Hoffmann, Brusque, *Klein s.n.* (Instituto de Malariologia 33) (US–type of *C. rubra*). SÃO PAULO: Jacarehy, *Dusén 17225* (GH).

Coccoloba williamsii Standley, Publ. Field Mus. Bot. **11**: 148. 1936.

The type of this species in the Chicago Natural History Museum is *Llewelyn Williams 4803* from Peru. I have referred this species to the synonymy of *Coccoloba lehmannii* Lindau in an earlier paper (Jour. Arnold Arb. **40**: 200. 1959).

Coccoloba zernyi Standley, Publ. Field Mus. Bot. 22: 18. 1940.

The type and apparently the only specimen of this species was collected by Ginzberger and Zerny between Taperinha and Santarem in Amazonas, Brazil, Aug. 13, 1927. It consists of two flowering branches and a few detached leaves in a packet. The inflorescence is very pubescent and all the flowers examined were staminate, lacking even the rudiments of a pistil. There is little doubt that this species is more properly assigned to the genus *Ruprechtia*; * however, the material available is inadequate for reference to any known species. It is hoped that some future monographer of *Ruprechtia* may find the correct assignment for this specimen.

---

* **Ruprechtia zernyi** (Standley) Howard, comb. nov. *Coccoloba zernyi* Standley, Publ. Field Mus. Bot. 22: 18. 1940.

VEGETATION ON GIBBSITIC SOILS IN HAWAII

J. C. Moomaw and M. Takahashi

Studies of the vegetation of an area of highly aluminous soils on the island of Kauai were initiated early in 1958. The soils were being considered by several aluminum companies as a commercial source of bauxite and the studies on rehabilitation of land denuded by strip mining were undertaken at the request of the then Territorial Legislature by the Hawaii Agricultural Experiment Station.[1] The purpose of the studies was to accumulate the ecologic, soil, and agricultural information that would enable the Legislature to enact suitable and just laws governing the reclamation of the mined area following removal of the mineral. It is the purpose of this paper to report studies of the initial vegetation of the reclamation study site made before the simulated mining and reclamation studies were begun. These studies represent the basic floristic and ecologic data with which comparisons of the reclamation treatments and results will be made. Coöperation in parts of the research was provided by several other departments of the Territorial government, especially the Board of Commissioners of Agriculture and Forestry, the Territorial Commissioner of Public Lands, and the B. P. Bishop Museum. Voucher specimens of the plants collected were deposited in the Bishop Museum and retained for study in the University of Hawaii Department of Agronomy and Soil Science.[2]

The site of the major investigations is an area of about 2500 acres located six miles WSW of Kapaa, Kauai, in the Wailua Game Refuge and adjacent lands. (The elevation varies from 500 to about 2000 feet.) Brief reference will be made to areas on Maui and Hawaii that were briefly examined and from which plant collections were made for determinations of tissue aluminum levels (Moomaw *et al.*, 1959).

Major studies of the vegetation of aluminous soils have been made in Australia–New Guinea (Webb, 1954) and in Jamaica (Howard & Proctor, 1957). In the Australia–New Guinea flora, 69 of 1154 dicotyledonous species examined were classified as accumulators of aluminum, as were 11 of 87 pteridophytes and *Lycopodium*. No monocotyledons or gymnosperms were so classified of 69 and 14 species respectively examined. The information developed by Webb in this study was used primarily for taxonomic deductions concerning the flora and the evolutionary status

---

[1] Published with the approval of the Director of the Hawaii Agricultural Experiment Station, University of Hawaii, as Technical Paper No. 483.

[2] Appreciation is expressed to Marie C. Neal, Curator of the B. P. Bishop Museum Herbarium, and to E. Y. Hosaka, Hawaii Agr. Extension Service, for help with the identification of some of the specimens.

of its members and secondarily for biochemical and ecologic discussions. Aluminum accumulating plants were never found on alkaline soils but were restricted to leached, acid soils from a variety of parent materials. Most of the species were inhabitants, with exceptions, of the closed mesic forest formation in eastern Australia which is in accord with the work of others (Chenery, 1948, 1949), who have observed the high frequency of aluminum accumulator species in the floras of the moist tropics. Webb states aluminum accumulators to be striking examples of what Crocker (1952) calls "pedogenetically effective biotypes" in that they favor laterization by the accumulation and retention of aluminum in the surface layers of the soil and in the litter and organic matter. Evidence from Webb (1954) and from Chenery (1948, 1949) indicates that accumulation is relatively rare in the monocotyledons but the information from Hawaii's gibbsitic soils given by Moomaw *et al.* (1959) shows substantial levels of the element in the dominant grasses, (especially *Paspalum orbiculare*), several other grasses, and the ground orchid *Spathoglottis plicata.*

The extensive work of Howard and Proctor in Jamaica (1957) led to conclusions that the Jamaican bauxite soils supported few species of aluminum accumulators and that the bauxite flora consisted of plants unaffected by aluminum and tolerant of its presence. They found no species characteristic of bauxite soils and did not find any species on adjacent soils that would not grow in the bauxite deposits. Their examination of a large flora in an area of active mining included successional studies on fallow mining pits and replanting plots with woody and pasture species.

GEOLOGY AND SOILS

The parent rocks of the Wailua Game Refuge are part of the Koloa volcanic series which flowed from vents in the mountain range to the north (MacDonald *et al.*, 1954) and the soils derived from these low-silica melilite and nepheline basalts have been described by Sherman (1958) and Cline *et al.* (1955) as belonging to the Aluminous Ferruginous Latosol and Ferruginous Humic Latosol great soil groups. The principal soil series in the area are the Halii, Puhi and the Haiku. The Halii series, in the Honolua family, is described by Cline *et al.* (1955) as being three to four feet in depth with dark brown, strongly granular, gravelly, silty clay at the surface grading into reddish and yellowish-red, blocky, silty clay at the depth where weathered rocks that have retained most of their original structure are frequently encountered. The soils are strongly acid (pH 3.5 to 5.0) and generally occur on long, smooth, narrow ridges of gentle (3–8%) slope but with steep-sided (40–50% slope) narrow gullies between them.

The chemical weathering of these soils from their porous, fine-grained parent rock is stated to be typical of many of the bauxite areas of the world and has been exceedingly rapid (Sherman, 1958; Mohr & Van Baren, 1954) because: (1) easily soluble minerals are present that are relatively free from combined silica and almost totally free from quartz;

(2) the topographic position, high effective rainfall at the higher elevations, combined with the high infiltration rate, free circulation and lateral movement of the percolating water favor the reduction and leaching of the iron oxides; (3) the humus of the forest floor produces an acid soil solution (Sherman & Kanehiro, 1948) which hastens the leaching process; and (4) a long period of chemical weathering has brought about the decomposition of silicates and the subsequent desilication of the weathering zone. The product of this intense and lengthy weathering process is a group of strongly leached soils depleted of bases and silica (0–5% SiO_2) with high concentrations of iron (25–60% Fe_2O) and alumina (20–50% Al_2O_3) and with at least small amounts of titanium (3–6% TiO_2). The principal mineral in the clay fraction developed under these conditions has been identified as gibbsite (Sherman, 1958).

Much evidence of mineral deficiency, especially of phosphorus, is observed in the vegetation. The surface soils are low in total bases but high in total nitrogen and organic matter. Physically the soils are classed as clays but do not in general display the physical properties usually associated with clays. Even when moist the soils present no physical problem in tillage operations.

THE CLIMATE

The mean annual rainfall has not been accurately measured on the main research site but it is known from adjacent areas to vary between 50 and 150 inches and to be well distributed. In general, the mean rainfall is greater than three inches per month and more than five inches per month during seven to twelve months of the year, with more than ten inches falling during two to seven months. The effectiveness of the rainfall is high and the soils are dry for only a few months in the lower areas. The rainfall exceeds evaporation and transpiration, especially during the winter months, partly because of a high degree of cloudiness. Relative humidity is high. Data for the nearest long-term weather station, Kapaa Stables, are given in Table I.

The average air temperature at sea level is about 73° F. in this zone, which is two or three degrees lower than that in the dry regions and, of course, it decreases with elevation. Extreme temperatures seldom exceed 90° F. or fall below 55° F. A long-term record of temperature for the northeast shore of Kauai is shown in Table I.

Wind blows almost constantly from the northeast at 10 to 20 miles per hour and exerts a drying influence on the exposed ridge-tops but frequently brings the trade showers to these same parts of the landscape. Hurricanes have been known in the area only recently and wind velocities of 75 or 80 miles per hour have been recorded. In the Islands the trade winds diminish and sometimes fail completely during and just after the autumnal equinox.

Daylength at 21° N. Latitude varies about 2.7 hours from June to December.

TABLE I. **Mean Monthly Temperature and Rainfall Data for Nearby Stations** (Weather Bureau, 1959).

STATION	Kapaa Stables	Kealia
ELEVATION	175 feet	9 feet
YEARS OF RECORD	18	47
	PRECIPITATION	TEMPERATURE
January	6.36 inches	70.9° F.
February	5.91	71.1
March	6.14	71.6
April	4.47	73.2
May	2.64	75.0
June	2.03	77.1
July	2.46	78.1
August	2.82	78.9
September	2.41	78.6
October	4.81	77.4
November	5.95	74.9
December	6.21	72.7
Annual	52.21 inches	75.0° F.

LAND USE AND HISTORY

At present, most of the land in the Honolua soil-family is used for either pasture or forest production. In neither case is the production potential high. The forest is composed mostly of *Meterosideros collina* ssp. *polymorpha* (ohia lehua) which is not of merchantable size. The forage produced is considered to be of inferior quality because of apparent low dry-matter production, low palatability, and probable mineral deficiencies. Shrubby weeds are a constant source of trouble in these areas. There is evidence that applications of lime and fertilizer will greatly improve production and nutritive value of the forage. The pastures are generally used for breeding herds and not for fattening cattle except when improved species such as *Digitaria decumbens* (Pangola grass), *Pennisetum clandestinum* (Kikuyu grass), or *Pennisetum purpureum* (Napier grass) have been planted. Paspalums, especially *P. conjugatum*, are naturalized pasture species of fair value. Very little land area of this type is cultivated at present, the high degree of cloudiness limiting sugarcane production and the wetness restricting its use for pineapple culture. Since the climate is continually moist, the control of diseases, insects, and weeds is extremely difficult. Little of the area is used for vegetable crops or fruit production but current research shows that this can be changed in many cases by improving fertility.

The land-use history of the Game Reserve of Kauai is one of hard use and abuse with a relatively recent attempt at reclamation through reforestration and game-food planting. The primeval vegetation was almost certainly forest but the composition of the forest is difficult to reconstruct after nearly 200 years of agricultural use by European and American settlers. The 900–1000 years of Hawaiian settlement had relatively little effect on this area since their settlements were normally confined to the beaches and the broad open valleys at low elevation. No remnant of terraces or native artifacts was encountered in the Game Reserve and such important native food plants as breadfruit, cooking banana and *Alocasia macrorrhiza* (ape) were absent.

The three major phases in the history of the Hawaiian flora were: (1) the arrival of the Hawaiians with their food plants and limited cultivation; (2) the introduction of European agriculture, forestry (especially the sandalwood trade) and cattle about 1790; and (3) the continued introduction of useful and weedy plants that have readily naturalized in the Hawaiian Islands. Especially the second and third of these influences have had a major effect on the Hawaiian vegetation in all ecologic zones and have led to replacement of the indigenous vegetation to a major degree by exotic species (Degener, 1932–date; Neal, 1948).

The vegetation of the Game Refuge of Kauai is classed in zone D_2 by Ripperton and Hosaka (1942) and was originally forested. The vegetation is dominated by *Metrosideros collina* subsp. *polymorpha* (ohia lehua) which is associated with *Acacia koa* (Hawaiian koa) and *Psidium guajava* (guava) in most places. Ferns such as *Dicranopteris linearis* (false staghorn), *Sadleria cyatheoides* (amaumau), *Nephrolepis exaltata* (Boston fern), and the tree fern *Cibotium chamissoi* are frequent. *Pandanus sp.* (hala) and *Aleurites moluccana* (kukui) are abundant in some areas and *Stachytarpheta cayennensis* (joee) is a weed of nearly universal occurrence. Open areas are dominated by grasses, sedges, herbs and several of the smaller ferns mentioned above. *Paspalum conjugatum* (Hilograss), *P. orbiculare* (ricegrass), *Setaria geniculata* (yellow foxtail) and a few others are found, and *Axonopus affinis* (carpetgrass) and *Sporobolus capensis* (rattail grass) are becoming more widespread. *Cyperus spp.* (sedges), *Centella asiatica* (Asiatic pennywort), *Mimosa pudica* (sensitive plant), and *Cuphea carthagenensis* (tarweed) are among the usual herbs.

The original forest on the reclamation site was probably a *Metrosideros* overstory with the tree fern *Cibotium chamissoi* either as the ground cover or at least well represented in the understory. The tree cover was probably relatively open on the ridge-tops. Whether the *Acacia koa* or *Santalum freycenetianum* (sandalwood) were ever represented here cannot be determined from present evidence, but is unlikely. The *Acacia* may have extended to this low elevation at one time. *Aleurites moluccana* (kukui) and *Eugenia malaccensis* were dominant in the valley-bottoms and drainages, but during the past hundred years these have been largely replaced by the more aggressive *Psidium guajava*, introduced in 1835. They show evidence of regeneration as does the *Metrosideros* on higher slopes.

The date of the first destruction of the forest cover on the Game Refuge is difficult to place but it can be said with certainty that since World War I the area has been repeatedly burned and at least lightly grazed. From 1918 to 1938, a major part of the area was leased as public grazing land, prior to which it had been in the Forest Reserve. There is no evidence of pasture improvement practices other than fencing, and it is known that the carrying capacity for livestock was very low. Species of improved pasture grasses and legumes are absent.

In 1939 the Wailua Game Refuge was created and management passed to the Division of Fish and Game of the Board of Agriculture and Forestry. Grazing was immediately prohibited and attempts were made to improve the cover and food supply for introduced species of game birds. During World War II, the Refuge was turned over to the military for a training area and was used for maneuvers, bivouac, and as an artillery range. Coral sand was brought in for camp sites and many of the ridges were travelled by military vehicles. The higher elevations were used as the impact area for an artillery range, which caused repeated fires. The lower, drier parts of the Refuge were much more easily fired than the higher parts but even on the slopes of Mount Waialeale to the west, where the annual rainfall probably exceeds 250 inches, the burned snags of *Metrosideros* trees of 18-inch diameter can be seen.

The area of study is traversed by an irrigation-ditch system involving a series of tunnels and ditches in some of the valleys but no direct influence on the vegetation is involved.

About ten years ago, after the end of the war, the Board of Agriculture and Forestry instituted a trial planting on a part of the area involving macadamia nut, Norfolk Island pine, and the variegated *Pandanus variegatus* (hala). Some of the planted trees have survived and are making slow growth. On a small plot of about an acre, the Board planted *Cajanus cajan* (pigeon pea) after plowing, liming with 500 pounds of crushed coral and fertilizing with 150 pounds of superphosphate per acre. The effect of this treatment is still visible on aerial photographs and can be seen on the ground from a distance of about a mile.

It is also interesting to conjecture on the role of wild goats in the destruction of native forest in this area and its subsequent displacement by introduced species.

VEGETATION OF GIBBSITIC SOILS

Methods

After an initial reconnaissance and examination of aerial photographs, the immediate surroundings of the test area were analyzed by examining a series of seventeen 100-foot line transects. Seven of the transects were oriented parallel with the center-line of the main ridge and on it, two were transverse transects on the ridge top, and eight of the transects were in pairs on the generally north- and south-facing slopes about one-third of the slope distance from the ridge-top and the valley-bottom respectively.

On each transect, *cover* was estimated on 50 two-square-foot plots evenly spaced along the line. Cover was estimated directly for each species present to the nearest five per cent and *frequency* was calculated from the cover data. Cover and frequency are commonly used ecologic measures of the importance of species in the plant community and of their distribution and dominance (Braun-Blanquet, 1932; Brown, 1954).

As used in this study, cover is best defined as the percentage of the total soil area covered by living plant material when it is projected downward into the plane of the soil surface from its natural growing position. It is always taken as the maximum spread of the plant involved, ignoring minor discontinuities in the crown or aerial portions. Since the objective of the method is to give a measure of the relative dominance of the species among its competitors, foliar spread is accepted as a good relative measure of root spread which is also an important factor in competitive domination.

Frequency is simply the percentage of the total number of plots in which the species occurred. This frequency of occurrence is a better measure of distribution within a subsample than is cover since it tends to be independent of plant size and dominance.

The parts of the Reserve not included in the quantitatively measured associations, such as the valley-bottoms and stands of pure *Dicranopteris* on steep slopes, were examined with long walking transects or jeep traverses resulting in species lists on which the only notations were of observational frequency, dominance, age, size, and general habitat and distribution.

Species Distribution

From the transect data in Table II and the general reconnaissance of the much wider area, including other ridges, the valley bottoms, and the higher elevations of the study site, it is possible to arrange the vegetation into three distinct and more or less homogeneous plant communities. The first and most general of these is the *Setaria–Paspalum* (weedy grass–shrub) association on the ridge-tops and exposed south slopes. On the northeast slopes extending nearly to the bottoms and occupying the northeast edge of the ridge is a community of weedy grasses and ferns designated as *Setaria–Nephrolepis* association. In the valley-bottom, a riparian, or at least much more mesic association of small trees, ferns and associated species is found. None of these communities approaches a climax type and each of them is a degraded representation of a collection of introduced species, each on a different habitat type.

The *Setaria–Paspalum* association of the ridge-top is a common one in the high-rainfall zone in the Hawaiian Islands and is similar to the vegetation associated with another known bauxite area on Maui (Haiku). As shown in Table II, this association is dominated by several common weedy grasses, *Setaria geniculata*, *Paspalum orbiculare*, and herbs such

TABLE II. **Mean Cover and Frequency Percentage in Two Associations on Gibbsitic Soils of Kauai.**

SPECIES	ASSOCIATIONS			
	SETARIA–PASPALUM (13 transects)		SETARIA–NEPHROLEPIS (4 transects)	
	Cover	Frequency	Cover	Frequency
Grasses				
Setaria geniculata	62%	99%	82%	99%
Paspalum orbiculare	38	82	20	58
Sacciolepis contracta	17	58	30	71
Chrysopogon aciculatus	7	21	2	6
Paspalum conjugatum	6	17	1	3
Ferns				
Nephrolepis exaltata	0	0	30	56
Stenoloma chinensis	5	14	14	34
Sadleria cyatheoides	0	0	2	4
Pteridium aquilinum	0.4	0.4	1	4
Shrubs				
Stachytarpheta cayennensis	12	50	18	61
Psidium guajava	1	4	2	7
Lantana camara	5	11	5	14
Eugenia cumini	4	5	0	0
Melastoma malabathricum	1	1	12	25
Psidium cattleianum	1	2	0.5	1
Herbs				
Elephantopus mollis	26	63	2	5
Centella asiatica	4	36	11	56
Cassia leschenaultiana	1	16	2	34
Spathoglottis plicata	5	14	4	13
Mimosa pudica	2	6	0	0
Passiflora foetida	1	6	0.5	2
Cuphea carthagenensis	1	4	0.5	2

as *Stachytarpheta cayennensis* (joee) and *Elephantopus mollis*, a declared noxious weed (FIG. 5). Also represented in the community with a high degree of constancy are *Paspalum conjugatum*, *Centella asiatica*, *Lantana camara*, *Cassia leschenaultiana*, *Sacciolepis contracta*, and the Philippine ground orchid, *Spathoglottis plicata*. All are introduced species and of no agricultural value except for the low grazing value of the dominant grasses. The one possibly indigenous species, *Chrysopogon aciculatus* (pilipiliula), has value as a soil binder and appears on about half the plots in the association, usually on very dry, exposed, and partially eroded areas. This is considered a true pioneering species in the successional trend following disturbance.

The habitat occupied by this association is the driest of the three described, but it still receives in excess of 80 inches of precipitation annually. It includes the ridge-top where an unimproved road was clearly marked by the growth of *Sporobolus capensis* and *Axonopus affinis* (FIG. 1), and the southwest-facing slope where the *Eugenia cumini* (Java plum) was found among the planted cultivars of *Macadamia*, *Araucaria*, and *Pandanus*. This association occupied one-half or more of the area of any given ridge in the Game Refuge.

The second association, *Setaria–Nephrolepis* (grass–fern), is slightly less extensive and occupies the northeast-facing slopes and the north sides of the ridges (FIG. 2). This area (about one-third of the total) is dominated by the same two weedy grasses: *Setaria geniculata* and *Paspalum orbiculare*. It is also well supplied with *Stachytarpheta* (TABLE II), *Centella*, *Cassia*, *Sacciolepis contracta*, and the *Spathoglottis*. *Paspalum conjugatum*, *Chrysopogon aciculatus*, and *Elephantopus* are much less common, but there is a substantial degree of dominance of the *Nephrolepis exaltata* and *Stenoloma chinensis*, the lace fern. The smaller Hawaiian tree fern or amaumau, *Sadleria cyatheoides*, also occurs. The noxious weedy shrub *Rhodomyrtus tomentosa* was gaining a foot-hold on this area at the time of first examination, spreading from its focus of introduction near the Kilohana Crater into favorable habitats at even greater distances. *Metrosideros* growth is vigorous in this habitat and given enough time without disturbance would eventually dominate even the *Melastoma* in most of the situations observed. Older specimens of *Metrosideros* show a marked production of aerial roots which apparently is associated with high moisture and favorable growing conditions. It should be pointed out that, in this instance, the combination of steep slope and its position athwart the northeast trade winds is thought to be responsible for the more mesic environment in this habitat type and *not*, as in more temperate climates, the protection of the north and east slopes from the effects of direct insolation, although this may play a minor role here also.

In the lower edge of this *Setaria–Nephrolepis* association there are frequent occurrences of solid stands of *Dicranopteris linearis*, the false staghorn fern (FIG. 3). *Dicranopteris* (*Gleichenia*) has been recognized as an accumulator of aluminum by several authors and has been analyzed in Hawaii (Moomaw *et al.*, 1959) where it was found to contain consistently high concentrations of aluminum. In addition to its relation to the aluminum levels in soils, *Dicranopteris* is usually associated with a mesic environment, as are most ferns. In this case the fern communities occur on the lower slopes of the ridges just above the valley-bottoms. Since free flowing water is observed in the valleys most of the year, it may be inferred that the hydrology of the area is such that the false staghorn patches coincide with the area of effluence of ground water leaching through the upper aluminous horizons. The outflow of water may not be great but it is reasonable to expect a water table not far below this level and also to expect that this percolation water is low in dissolved bases and silica and high in aluminum content. In addition, of course, the moist drainage ways and valley bottoms are protected from the fires that have swept the ridges at frequent intervals.

The plant association in the wooded valley-bottom (FIG. 4) was not examined quantitatively as were the upper areas on the aluminous soils but a thorough reconnaissance and collection was made. This semi-riparian community is dominated at present by an overstory of *Psidium guajava* (guava) with an occasional specimen of *Pandanus odoratissimus*, *Eugenia malaccensis* (mountain apple) and *Aleurites moluccana* (candle-nut tree). The latter two species show vigorous signs of reproduction in the understory and many fallen logs indicate the former importance of these trees in the community. The trees and rocks in this moist habitat support a number of epiphytic species of lichens, mosses, liverworts, and ferns as well as climbing vascular plants. The ground cover as well, is made up of ferns in especially moist places, the dominant or frequently occurring species are *Phlebodium aureum*, *Elaphoglossum reticulatum*, *Athyrium microphyllum*, *Dryopteris dentata*, *Blechnum occidentale*, and others. The lianes include a native *Peperomia* and *Dioscorea bulbifera*. The *Zingiber zerumbet* (awa'puhi), a *Lobelia*, and *Sida acuta* occur with some regularity, and, in places where drainage is good, the ground is covered with *Oplismenus hirtellus* (basket grass) in the open shade of the dominant guava. In more moist situations, the sedges, *Cyperus alternifolius* and *Cladium meyenii*, are frequent unless completely shaded by the *Hibiscus tiliaceus* (hau tree) or unless permanent water favors a semiaquatic community with rushes, *Jussiaea suffruticosa* var. *ligustrifolia*, and *Dryopteris gongylodes*.

Effects of Fire

During the course of the studies of the Kauai bauxite area, an excellent opportunity was afforded to study the effects of fire when the Territorial Division of Fish and Game embarked on a program of burning the area adjacent to the study site in an attempt to improve the cover and food supply for game birds. Most of the area within the Game Reserve was burned over a period of months beginning in December, 1958. This was eight months after the initial vegetation examination and after eight months following the burn, a reëxamination was made of some of the same transects. The results of this detailed examination are shown in TABLE III where the kind and degree of change is shown as a "consensus" of the five transects examined.

The more marked effects of fire, eight months following the burn are the increase in some of the broad-leaved weeds, the decrease in cover of the woody plants and *Stenoloma*, and the predictable reduction in litter and organic matter on the surface of the soil (or increase in bare soil cover) (FIG. 5). Principal increasers were *Elephantopus mollis*, *Cassia leschenaultiana*, *Cuphea carthagenensis*, *Chrysopogon aciculatus*, *Emilia sonchifolia*, and *Pteridium aquilinum*. Of these, the change in *Emilia* was the most striking, since its presence was not noted at the time of the first

TABLE III. **Comparative Cover of Major Species in Two Associations on Gibbsitic Soils of Kauai Before and After Fire.**

SPECIES	ASSOCIATIONS					
	SETARIA–PASPALUM (3 transects)			SETARIA–NEPHROLEPIS (2 transects)		
	Before Fire		After Fire	Before Fire		After Fire
Grasses						
Setaria geniculata	78%	>	60% *	84%	>	64%
Paspalum orbiculare	27	=	32	25	=	29
Sacciolepis contracta	11	=	14	27	=	28
Chrysopogon aciculatus	9	<	20	2	=	2
Paspalum conjugatum	6	>	0.3	0	=	1
Ferns						
Nephrolepis exaltata	0	=	0	6	=	6
Stenoloma chinensis	4	>	0	2	>	0
Pteridium aquilinum	0	=	1	1	<	3
Shrubs						
Stachytarpheta cayennensis	15	=	15	24	=	26
Psidium guajava	0	=	2	4	=	4
Lantana camara	9	>	3	8	=	7
Melastoma malabathricum	4	>	0	8	>	3
Psidium cattleianum	5	>	0.1	0	=	1
Herbs						
Elephantopus mollis	32	=	31	2	=	4
Centella asiatica	3	=	5	10	=	8
Cassia leschenaultiana	1	<	5	1	<	4
Spathoglottis plicata	5	>	1	5	=	4
Passiflora foetida	1	=	1	1	=	1
Cuphea carthagenensis	0	=	1	1	<	4
Emilia sonchifolia	0	<	5	0	<	2
Bare soil	0	<	12	0	<	12

* **Trends:** >, decrease; <, increase; =, no change.

examination except as a casual occasional plant on disturbed areas. The increase in *Elephantopus* is not impressive, partly because of the biennial habit of the plant and partly because the change was more pronounced in the more moist *Setaria–Nephrolepis* habitat type. Not all the plants appeared to be of biennial habit since some had flowered at the time of examination. The increase of *Cassia* following fire is large and involves both numbers of plants and size of individuals. It is possible that a slight seasonal effect tends to reinforce this difference. *Cuphea* was only mildly stimulated by the burning. *Chrysopogon* has been observed to thrive on the exposed and eroded south slopes and was predictably improved in its competitive position by fire. *Passiflora foetida* increased slightly in frequency in both associations.

Species showing a strong tendency to decrease in cover or frequency following fire in the two associations studied were *Lantana camara*, *Stenoloma chinensis*, *Melastoma malabathricum* (FIG. 6), and *Paspalum conjugatum*. To a lesser degree, *Spathoglottis plicata* showed a decrease in frequency while *Setaria geniculata* declined in cover only. *Stenoloma* was completely obliterated by the fire in places where it had been recorded a year before, while the woody *Lantana* and *Melastoma* were markedly reduced in cover but observation revealed that they were by no means killed.

Species that were little affected by burning include guava, which was found only in the *Setaria–Nephrolepis* community and which was observed elsewhere to be severely damaged by fire, *Centella asiatica*, *Sacciolepis contracta*, *Paspalum orbiculare*, and *Stachytarpheta cayennensis* which increased much less than expected.

Following the simulated strip-mining and planting of the stripped area with forage, field and fruit crops, a number of species new to the area were observed. An inventory of plants new to this area and appearing in the disturbed areas was taken and these are designated as "invaders" in the APPENDIX. Since all the fruit and ornamental plants were brought in from elsewhere, some as potted plants, undoubtedly some of the invaders came in with the plants. Others such as *Solanum nigrum* (popolo) may have already been in the soil in dormant condition awaiting proper conditions before breaking their dormancy and making their appearance. Stripping, followed by field preparation, apparently supplied the necessary conditions for the germination of long dormant seeds.

SUMMARY AND CONCLUSIONS

The evidence from the present study points to conclusions similar to those from the Jamaican study of Howard and Proctor (1957) in that none of the species studied shows a definite affinity for ecologic niches characterized by high aluminum content of the soil. The species present are nearly all those adapted to a generally moist environment with warm equable temperatures, acid, infertile soils, and a shallow root zone. Since the aluminum content of the soil increases with depth while the rooting of the dominant plants is unusually shallow, it must be inferred that they are not dependent on high levels of aluminum for survival, but rather are restricted in their root development to the organic and more fertile upper horizons. In addition, the major changes in the vegetation pattern apparently are not governed by alterations in the soil profile, but rather are related to slope, exposure and effective rainfall. The high degree of disturbance of the natural pattern through fire, grazing and manipulation of the cover has further removed the expression of the natural vegetation determinants. Despite the fact that several of the species encountered are known to contain high levels of aluminum (*Dicranopteris linearis, Paspalum orbiculare, Melastoma malabathricum* and sometimes *Nephrolepis exaltata*) and are growing on soils classed as aluminous, it can only be said that they are tolerant of the condition and are capable of accumulating the aluminum ion.

The most important single factor in the present distribution of species in the area is the locus and date of introduction of each of them and their competitive relationship both to the endemic species which they have replaced and to each other. A tabulation of the species present reveals only 5% to be endemics, while 30% are indigenous species of fairly wide Island distribution (see species list), and the remainder are introductions. The indigenous and endemic species occur more frequently in the gulch bottoms and protected areas than on the exposed and disturbed slopes and ridges, clearly indicating their remnant nature.

Other vegetation anomalies, such as the presence of *Scaevola frutescens* (beach naupaka) and other invaders, can be attributed to the importation of sand, coral and cinders at various times for road and building purposes.

Few of the species in the initial stages of succession on the Jamaican bauxites are the same as those observed on the Kauai site, but the later, more persistent weedy plants include *Lantana*, *Stachytarpheta*, and *Sida* which were present in Jamaica also. Several of the grasses used for revegetation in Jamaica are the same ones favored in the Wailua Reserve, such as *Digitaria decumbens* (Pangola grass), *Melinis minutiflora* (molasses grass), and *Panicum purpurascens* (Para grass). *Panicum maximum* (Guinea grass) was useful in the Jamaican study, while the site on Kauai was considered too wet for the successful establishment of any large-scale planting of Guinea grass. The overburden removed from the mining sites was observed to be unusually fertile in Jamaica, as it was in Hawaii, partly owing to the high content of organic matter and partly owing to the content of weed seeds, roots and living plant parts.

Studies with the major plantation and pasture crops in Hawaii have shown that successful production can be attained with applications of fertilizer in fairly large amounts. Six to eight hundred pounds per acre of complete fertilizer, with or without lime, will give good results with *Digitaria decumbens* and *Desmodium intortum* on either the mined substrate or the returned topsoil and produce a rapid vegetative cover. Sugar cane and pineapple can be grown at plantation levels of production or above, if well fertilized.

REFERENCES CITED

BRAUN-BLANQUET, J. 1932. The study of plant communities. McGraw-Hill Book Co.

BROWN, D. 1954. Methods of surveying and measuring vegetation. Comm. Bur. Past. and Field Crops Bull. **42.**

CHENERY, E. M. 1948. Aluminium in the plant world. Kew Bull. **1948:** 163–173.

———. 1949. Aluminium in the plant world. *Ibid.* **1949:** 433–466.

CLINE, M. G., *et al.* 1955. Soil survey of the Territory of Hawaii. U. S. D. A. Soil Survey Series 1939, No. **25.**

CROCKER, R. 1952. Soil genesis and pedogenic factors. Quart. Rev. Biol. **27**(2): 139–168.

DEGENER, O. 1932–date. Flora Hawaiiensis **1–5.** Published by the author.

HOWARD, R. A., and PROCTOR, G. R. 1957. The vegetation on bauxitic soils in Jamaica. Jour. Arnold Arb. **38:** 1–41, 151–169.

MACDONALD, G. A., DAVIS, D. A. and COX, D. C. 1954. Kauai, an ancient Hawaiian volcano. Volcano Letter No. **526:** 1–3.

MOHR, E. C. J., and VAN BAREN, F. A. 1954. Tropical soils. Interscience Publishers Inc.

MOOMAW, J. C., NAKAMURA, M. and SHERMAN, G. D. 1959. Aluminum in some Hawaiian plants. Pacific Science **13:** 335–341.

NEAL, MARIE C. 1948. In gardens of Hawaii. B. P. Bishop Museum Spec. Publ. **40.**

RIPPERTON, J. C., and HOSAKA, E. Y. 1942. Vegetation zones of Hawaii. Hawaii Agr. Exp. Sta. Bull. **89.**

SHERMAN, G. 1958. Gibbsite-rich soils of the Hawaiian Islands. Hawaii Agr. Exp. Sta. Bull. **116.**

———. and KANEHIRO, Y. 1948. The chemical composition of Hawaiian forest floors. Hawaii Agr. Exp. Sta. Bien. Rep. **1946–48.**

WEATHER BUREAU. 1959. Hawaii, annual summary, 1958. Climatological data **54**(13): 154–160.

WEBB, L. J. 1954. Aluminium accumulation in the Australian–New Guinea flora. Austr. Jour. Bot. **2:** 176–196.

EXPLANATION OF PLATES

PLATE I

FIG. 1. The *Setaria–Paspalum* association of the ridge-top, Wailua Game Refuge, Kauai. *Sporobolus capensis* is seen along the roadway. Shrubs in the background include *Eugenia cumini*, *Pandanus odoratissimus*, *Psidium guajava*, and *Melastoma malabathricum*, an aluminum accumulating species. FIG. 2. The *Setaria–Nephrolepis* association on a north-facing slope. The "Ama'uma'u" tree fern, *Sadleria cyatheoides*, is seen in the middleground. *Setaria* and *Paspalum* are the dominant grasses.

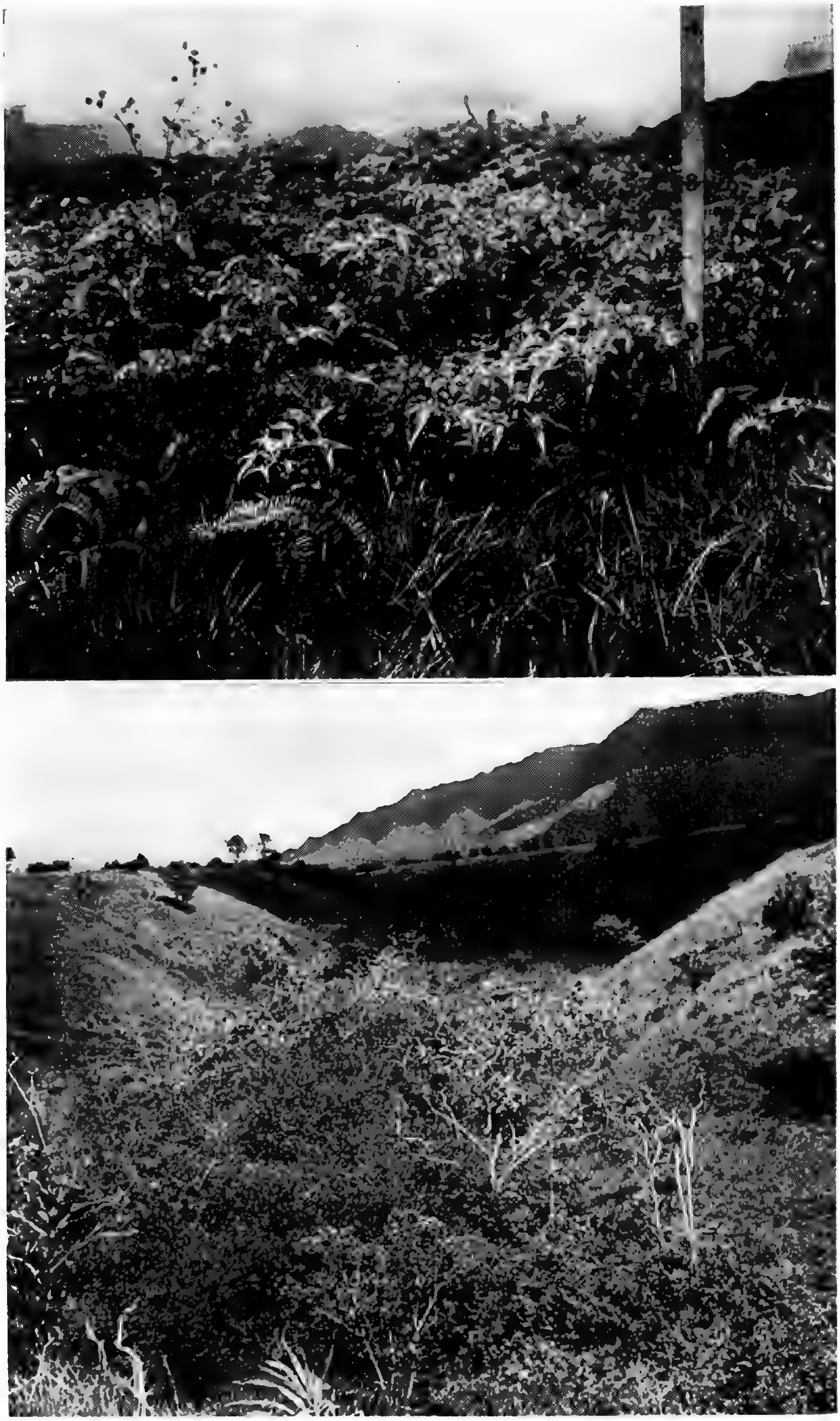
PLATE II

FIG. 3. *Dicranopteris linearis*, known to be an aluminum accumulating fern, occurs primarily on the lower slopes and valley bottoms. FIG. 4. The vegetation of the protected valleys is dominated by *Psidium guajava* and *Pandanus odoratissimus*. The understory contains high percentages of ferns (*Dryopteris*) and *Oplismenus hirtellus*, the shade-tolerant "basket grass." Most of the indigenous species were found in this association.

PLATE III

FIG. 5. A plot in the *Setaria–Paspalum* association following fire. A young orchid plant, *Spathoglottis plicata*, occurs on the left side of the plot, while the broad leaves are those of *Elephantopus mollis*. The stoloniferous grass on the bare soil is *Chrysopogon aciculatus*. FIG. 6. Regeneration of *Melastoma malabathricum* six months following fire. Top growth is completely killed back. Note that the *Setaria* has already produced mature inflorescences.

Moomaw & Takahashi, Vegetation on Gibbsitic Soils



MOOMAW & TAKAHASHI, VEGETATION ON GIBBSITIC SOILS

MOOMAW & TAKAHASHI, VEGETATION ON GIBBSITIC SOILS

APPENDIX. Species List with Occurrence and Origin Indicated.

Symbols: A, abundant; C, common; U, uncommon; R, rare; I, indigenous; E, endemic; *, known in Hawaii at that date; P, planted (usually by Board of Agriculture and Forestry); +, invader of stockpiled topsoil or of exposed subsoil.

SPECIES	OCCURRENCE			ORIGIN	
	RIDGE	SLOPE	VALLEY	INDIGENOUS OR ENDEMIC	INTRODUCED
FERNS AND FERN ALLIES					
Asplenium insiticium			U	?	
Athyrium microphyllum			U	?	
Blechnum occidentale			U		1923 Trop. Am.*
Cibotium chamissoi		U	U	E	
Dicranopteris linearis		C		I	
Diplazium sandwichianum			R	E	
Dryopteris dentata			C	I	
Dryopteris gongylodes			R	?	
Elaphoglossum reticulatum			U	E	
Lycopodium cernuum		U		I	
Microlepia setosa			U	I	
Microsorium scolopendria			U	?	
Nephrolepis biserrata var. *furcans*		U	U	I	
Nephrolepis exaltata	C	A	U	I	Pantropic
Nephrolepis hirsutula		R		I	
Phlebodium aureum			U		Trop. Am.
Pleuropeltis thunbergiana			U	I	
Psilotum nudum	U	U		I	
Pteridium aquilinum var. *decompositum*	U	U		I	
Sadleria cyatheoides	?	U		I	
Stenoloma chinensis	C	C		I	
GYMNOSPERMAE					
Araucariaceae					
Araucaria excelsa	U				P, Norfolk Island
MONOCOTYLEDONEAE					
Araceae					
Colocasia esculenta			U	I	
Commelinaceae					
Commelina diffusa			C		1888, Pantropic *
Cyperaceae					
Carex sp.	U			?	
Cladium meyenii			U	?	
Cyperus cylindrostachyus			U		1898, Madagascar *
Cyperus kyllingia f. *humilis*	U				1900, Pantropic *
Cyperus rotundus	C				+ 1850 *
Fimbristylis diphylla		U	U		Widespread

Species List (*Continued*)

SPECIES	OCCURRENCE			ORIGIN	
	RIDGE	SLOPE	VALLEY	INDIGENOUS OR ENDEMIC	INTRODUCED
Rhynchospora lavarum			R	E	
Scirpus validus			U		1888, N. Am.*
Dioscoreaceae					
Dioscorea bulbifera			R	I	
Gramineae					
Axonopus affinis	C	C			1912, Trop. Am.
Chloris inflata	U				+ 1906, Trop. Am.*
Chrysopogon aciculatus	U	C		I	
Coix lacryma-jobi			U		1888, Indonesia *
Cynodon dactylon	U				+ 1835, Old World *
Digitaria henryi	U				1932, Formosa
Digitaria violascens	U				+ 1917, Trop. Asia
Eleusine indica	U				+ 1840, India *
Oplismenus hirtellus			C		1841, Trop. Am.
Panicum purpurascens			U		1902, Africa
Paspalum conjugatum	C	C	C		1840, Dutch Guiana*
Paspalum orbiculare	A	A	U		1888 Asia *
Paspalum urvillei	U				1906, S. Am.
Sacciolepis contracta	C	A			+ 1906, Indonesia
Setaria geniculata	A	A			1851, Europe *
Setaria verticellata	U				+ 1860, Europe *
Sporobolus capensis	U				1903, Africa
Liliaceae					
Cordyline terminalis		U		I	
Orchidaceae					
Spathoglottis plicata	C	C			? Asia–Malaya
Pandanaceae					
Freycinetia arborea			U	E	
Pandanus odoratissimus		C	C	I	
Pandanus variegatus		U			P
Taccaceae					
Tacca leontopetaloides			U	I	
Zingiberaceae					
Zingiber zerumbet		U	U	I	India
DICOTYLEDONEAE					
Amaranthaceae					
Amaranthus hybridus	U			I	+ Pantropic
Amaranthus spinosus	U				+ 1900, Trop. Am.
Amaranthus viridus	U				+ Trop. Am.
Anacardiaceae					
Schinus terebinthifolius	U				+ 1917, S. Am.
Caryophyllaceae					
Drymaria cordata			U		1900, Asia–Malaya

Species List (*Continued*)

SPECIES	OCCURRENCE			ORIGIN	
	Ridge	Slope	Valley	Indigenous or Endemic	Introduced
Casuarinaceae					
Casuarina equisetifolia		U			P 1895, Malaya
Convolvulaceae					
Ipomea pes-caprae	R			I	+
Compositae					
Bidens pilosa	U				+ 1864, Trop. Am.*
Eclipta prostrata	U				Widespread
Elephantopus mollis	A	A	C		+ 1931, Trop. Am.
Emilia sonchifolia	C				+ Trop. Asia
Erechtites valerianifolia	U				+ 1870, N. Am.
Erigeron canadensis	C	R			+ ? N. Am.
Pluchea odorata	U				1931, S. Am.*
Sonchus oleraceus	U				? Europe
Vernonia cinerea	U				+ Trop. Afr., Asia
Euphorbiaceae					
Aleurites moluccana			U	I	
Euphorbia hirta	U				+ 1888, Pantropic *
Euphorbia hypericifolia	U				+ Pantropic
Euphorbia thymifolia	U				+ Widespread
Goodeniaceae					
Scaevola frutescens var. *sericea*	U	U		I	
Scaevola gaudichaudiana	U	U		I	
Lauraceae					
Cinnamomum camphora	R				? China
Leguminosae					
Albizzia moluccana		U			1917, Malaya
Cajanus cajan	U				P 1909, India
Canavalia sericea			U	I	
Cassia leschenaultiana	C	C			1888, India *
Crotalaria incana	U				+ Trop. Am.
Desmodium canum	U				P 1916, Trop. Am.*
Desmodium uncinatum	R				Trop. Am.
Mimosa pudica	C	C			1800, Trop. Am.*
Vigna marina			U		Pantropic
Lobeliaceae					
Lobelia sp.			R	E	
Lythraceae					
Cuphea carthagenensis	C				+ 1900, Trop. Am.
Malvaceae					
Hibiscus tiliaceus	U	U	C	?	?
Sida acuta		U			?
Melastomaceae					
Melastoma malabathricum	C	C			1916, India

Species List (*Continued*)

SPECIES	OCCURRENCE			ORIGIN	
	Ridge	Slope	Valley	Indigenous or Endemic	Introduced
Myrtaceae					
Eugenia cumini	U	C			1866, Trop. Afr.
Eugenia malaccensis			U		
Metrosideros collina subsp. *polymorpha*	U	C		E	
Psidium cattleianum	C	U			P
Psidium cattleianum f. *lucidum*	U				1888, Trop. Am.*
Psidium guajava	C	C	A		1800, S. Am.*
Rhodomyrtus tomentosa	C	C			1920, Asia
Onagraceae					
Jussiaea suffruticosa var. *ligustrifolia*			U		1888 Pantropic *
Oxalidaceae					
Oxalis corniculatus	U				1888, N. Am.*
Passifloraceae					
Passiflora edulis	U	U	U		1880, S. Am.
Passiflora foetida var. *gossypifolia*	U	U			1888, Trop. Am.
Phytolaccaceae					
Phytolacca acinosa	U				+ Asia
Piperaceae					
Peperomia membranacea var. *waimeana*			R	E	
Portulacaceae					
Portulaca oleracea	U				+ 1888, Pantropic *
Primulaceae					
Anagallis arvensis	U				+ Europe
Proteaceae					
Grevillea robusta	U	U			Australia
Macadamia ternifolia		U			P 1890, Australia
Rubiaceae					
Richardia scabra	R				1888 Trop. Am.*
Solanaceae					
Solanum nigrum	R			?	+
Sterculiaceae					
Waltheria americana		U			1819, Trop. Am.*
Umbelliferae					
Centella asiatica	C	C			1888, Asia *
Verbenaceae					
Lantana camara	C	A	U		1858, Trop. Am.
Stachytarpheta cayennensis	A	A			Trop. Am.

NOMENCLATURAL CHANGES IN DAPHNOPSIS (THYMELAEACEAE)

LORIN I. NEVLING, JR.

TWO NOMENCLATURAL ERRORS have come to light since the publication of a revision of the genus *Daphnopsis* (Nevling, 1959). These involve (1) the illegitimacy of the subspecific name *Daphnopsis americana* ssp. *tinifolia* (Sw.) Nevl. and (2) the combination *Daphnopsis anomala* (HBK.) Nevl. which should have been ascribed to Domke.

The subspecific combination *Daphnopsis americana* ssp. *tinifolia* (Sw.) Nevl. (1959, p. 313) is an illegitimate name and must be replaced. *Daphnopsis americana*, originally described by Miller (1768) as *Laurus americana*, was based upon a Houston specimen and Houston's "Manuscript Catalogue of the Plants which he had observed growing in the islands of Jamaica and Cuba; as also at Campeachy and La Vera Cruz, in the years 1728, 1729 and 1732" (introductory comments). In the subsequent edition of the *Dictionary* (Miller, 1797), *Laurus americana* was treated as a synonym of *Daphne tinifolia* Swartz, and Miller states that it was discovered at La Vera Cruz but is also a native of Jamaica.

Swartz's name *Daphne tinifolia* (1788, p. 63) is possibly based on Miller's earlier epithet as evidenced by the inclusion of *Laurus americana* as a synonym. Swartz's publication was concerned with new species of the Antillean flora and gives the habitat only as Jamaica. There is a real question as to whether or not Swartz was aware of the occurrence of the species in Mexico, a fact which he could not know without seeing the specimen of Houston. As a result of his citation of Jamaica only, the workers postdating Swartz, having benefit of information concerning the type and type locality contained in the 9th edition of Miller's *Dictionary*, assumed that a second species quite distinct from the Mexican *D. americana* existed, even if not realized by Swartz, and treated it as such. Three combinations were made, some of them several times, involving the specific epithet *tinifolia*, and all were based on the concept that it was a distinct species restricted to various islands of the Antilles. The subspecies under consideration is restricted to Cuba, Jamaica and Hispaniola and I proposed the subspecific combination, *Daphnopsis americana* ssp. *tinifolia* (Sw.) Nevl. indicating the basionym of Swartz. However, the combination is illegitimate because it is based on Swartz's illegitimate name (Article 64. International Code of Botanical Nomenclature. 1956). Thus a new subspecific epithet must be chosen to replace ssp. *tinifolia*. It seems proper to choose Meissner's indefinite infraspecific epithet *cumingii* (*D. tinifolia β. cumingii* Meissn. [1857, p. 523]) which is based upon a staminate specimen (*Cuming 56*) now on deposit in the Naturhistorisches Museum, Wien, and place it at subspecific rank. In addition, the names based on the Swartz basionym are transferred to ssp. *americana*. Accordingly, the nomenclature is emended to read:

Daphnopsis americana ssp. **americana**

Daphnopsis americana (Mill.) J. R. Johnston, Proc. Boston Soc. Nat. Hist. **34**: 242. May 1909; Contr. Gray Herb. ser. 2. **37**: 242. June 1909.
Laurus americana Mill. Dict. ed. 8. *Laurus* no. 10. 1768. (T.: *Houston s.n.*)
Daphne tinifolia Sw. Prodr. Veg. Ind. Occ. 63. 1788.
Daphne obovata Humb. & Bonpl. ex Wikstr. Diss. Daphne ed. 2. 40. 1820. (T.: *Humboldt & Bonpland 7549*.)
Daphne bonplandiana Kunth, Syn. Pl. **1**: 447. 1822.
Daphne lagetto Bonpl. ex Kunth, ibid. 1822, pro syn.
Nordmannia tinifolia (Sw.) Fisch. & C. A. Meyer, Ann. Sci. Nat. ser. 2. **20**: 49. February 1843; Bull. Acad. St. Pétersb. Classe Physico-Math. **1**: 355. June 1843.
Hargasseria mexicana Schiede & Deppe ex C. A. Meyer, Ann. Sci. Nat. ser. 2. **20**: 51. February 1843 (based on *Daphne bonplandiana* sensu Cham. & Schlechtd. non Kunth); Bull. Acad. St. Pétersb. Classe Physico-Math. **1**: 356. June 1843.
Hargasseria tinifolia (Sw.) Endl. Gen. Suppl. **4**^{2}: 68. 1847.
Hargasseria schiedeana Endl. ibid. 1847 (based on *Daphne bonplandiana* Kunth).
Daphnopsis bonplandii (Kunth) Meissn. DC. Prodr. **14**: 521. 1857.
Daphnopsis tinifolia (Sw.) Meissn. ibid. 523. 1857.
Daphnopsis lindenii Meissn. ibid. 1857. (T.: *Linden 95* (♀).)
Daphnopsis bonplandiana (Kunth) Standl. Contr. U.S. Natl. Herb. **23**: 1013. 1924.

Daphnopsis americana ssp. **cumingii** (Meissn.) Nevl., comb. & stat. nov.

Daphnopsis tinifolia β. cumingii Meissn. DC. Prod. **14**: 523. 1857. (T.: *Cuming 56* (♂).)
Daphnopsis americana ssp. *tinifolia* (Sw.) Nevl. Ann. Missouri Bot. Gard. **46**: 313. 1959.

An additional change involves the combination *Daphnopsis anomala* (HBK.) Nevl. (1959, p. 323). This combination was previously made by Domke and should be credited to him. *Daphnopsis anomala* (HBK.) Domke, Bibliotheca Bot. **111**: 57. 1934, in discussion.

LITERATURE CITED

MEISSNER, K. F. Thymelaeaceae. DC. Prodr. **14**: 493–605. 1857.
MILLER, P. The Gardners Dictionary, ed. 8. 1768.
———. The Gardners Dictionary, ed. 9. 1797.
NEVLING, L. I., JR. A revision of the genus *Daphnopsis*. Ann. Missouri Bot. Gard. **46**: 257–358. 1959.
SWARTZ, O. Prodr. Veg. Ind. Occ. 1788.

SEEDLING LEAVES IN PALMS AND THEIR MORPHOLOGICAL SIGNIFICANCE

P. B. TOMLINSON

IN MOST PLANTS the first plumular leaves, or leaves which are produced in succession to the cotyledons, differ from normal foliage leaves in shape and size. They are referred to as "juvenile" leaves (Primärblätter of German authors) in contrast to the "adult" leaves on the older parts of the plant. Normally where adult leaves of a plant are compound or much divided the juvenile leaves are much simpler in outline. Succeeding leaves (Folgeblätter of German authors) are increasingly complex and a gradual transition from juvenile to adult foliage takes place. Exceptions to this generalization are known, as, for example, in certain members of the Quiinaceae (Foster, 1951) and *Ficus alba* (Corner, 1951; p. 681) in which adult leaves are less complex than seedling leaves.

The adult leaves of most palms are large and compound, so it is not unexpected to find that their first foliage leaves are small and usually simple. Although there is considerable variety in the shape of the first foliage leaf, it is very constant for each species and so is of considerable diagnostic importance. A practical result of this, of value to nurserymen, is that it is possible to identify, or at least find evidence of misidentification, in palms at a very early stage of growth. Unfortunately, however, records of the diagnostic characters of seedling palm leaves are not often included in taxonomic writings but they are available for *Howeia* (Cook, 1926), *Roystonea* (Cook, 1935), and *Veitchia* (Moore, 1957). The present paper describes the main shapes exhibited by juvenile palm leaves.

A second major observation is that the series of increasingly complex leaf types which occur in the transition between the first foliage leaf and later adult forms is constant and characteristic for each species. Six main series are described here, and by comparing them it is possible to arrive at certain interesting conclusions about evolutionary trends in juvenile palm foliage.

Significant correlations are also found between the type of juvenile foliage and the adult foliage in palms and it has been found possible to explain these correlations on an evolutionary basis.

There is an extensive literature dealing with the morphology and anatomy of the palm seedling (Gatin, 1912; Boyd, 1932), but, except in the writings of Micheels, Pfitzer and Drude, little attention has been paid to later stages of growth in which juvenile foliage is exhibited. Micheels (1889) and Pfitzer (1885) both emphasize the diagnostic value of seedling leaves in palms. Micheels (1889) and Drude (1889) both describe some of the series of leaves developed by young palms.

Germination of palm seeds and a new term. A brief résumé of the morphology of the palm seedling as a whole is necessary for an understanding of the observations recorded below. Excellent accounts of this subject have been written by Gatin (1906, 1912). Germination of palm seeds is hypogeal. The cotyledon is never expanded as a green, aerial photosynthetic organ because its apex remains embedded in the endosperm of the seed and becomes modified into an absorptive organ or haustorium. This converts the reserve food material of the endosperm into a soluble form. The food material is then transmitted to the rest of the embryo via a tubular "middle piece" which represents the petiole and sheath of the cotyledon. In many palms the middle piece elongates considerably and buries the seedling some distance below the seed. In other palms, in which the cotyledon does not elongate, the seedling develops next to the seed, as, for example, in the coconut.

In examining palm seedlings it must be realized that the first green leaves are not immediate post-cotyledonary leaves because one or more of the first plumular leaves are bladeless and appear as sheathing scale-leaves. Their number seems to be fixed in each species of palm. They apparently have a protective function since they envelop the subsequent bladed leaves and are therefore mechanically useful in permitting buried shoots to break through to the soil surface without damage to the enclosed foliage leaves.

The present account deals largely with the morphology of the first foliage leaves. In this account it is proposed to apply the term *eophyll* (Greek *eos*-early; *phyllon*-leaf) to the first few leaves with a green expanded lamina developed by the seedling. This term seems necessary in order to identify these organs which are only one of a series of leaf forms to which the term "juvenile" can be applied. In the present paper "eophyll" is used with reference to palms, but it may have a wider application.

OBSERVATIONS

The first eophyll of palm seedlings. In most palms the first eophyll is simple, although it may be either entire or bifid, i.e., with a deeply emarginate apex. Within these two main types there is a considerable range of form, although for a given species the shape and size is very constant. Other diagnostic eophyll features are the type and distribution of armature and indumentum. As a consequence, it is often possible to identify at least the genus to which a palm belongs from its first eophyll. In all, three main categories of eophyll may be distinguished.

Entire eophylls. These are usually linear or linear-lanceolate (Figs. 1a, 2a). Sometimes their apices are truncate as in *Corypha*, *Licuala* (Fig. 3) and *Livistona*. In the caryotoid palms *Arenga*, *Didymosperma* and *Wallichia* the first eophyll is flabellate (Fig. 4), the margin and apex being irregularly and distantly toothed.

BIFID EOPHYLLS. The depth of the apical incision varies considerably. In species of *Drymophloeus* and *Iriartea* the apical incision is so inconspicuous that the leaflet appears to be entire at a casual glance. Normally, however, the segmentation is so complete that the leaf is evidently composed of two opposite, terminal leaflets (FIGS. 7b, 8a). The apex of each segment is either acute or, as in *Hyospathe* and many of the Ptychospermate palms, truncate (FIG. 10). In *Aiphanes* the margin is irregularly toothed (FIG. 9).

COMPOUND EOPHYLLS. Many palms have a first eophyll which is always compound. This is palmate in fan-palms such as *Borassodendron*, *Latania* (FIG. 5) and *Lodoicea* but pinnate in feather-palms such as *Hedyscepe*, *Metroxylon*, *Nephrosperma*, *Phytelephas* and *Raphia*. In several genera of feather-palms certain species have simple first eophylls whilst those of other species are compound, as in *Calamus*, *Chamaedorea*, *Euterpe*, and *Howeia*. The significance of compound first eophylls is discussed later.

When the distribution of types of first eophyll throughout the whole family Palmae is considered, certain significant correlations between the shape of this organ and the morphology of the adult foliage become apparent.

Comparisons between the first eophyll and adult foliage in palms. The following arrangement of the tribes corresponds to that given by Drude (1889).

A. INDUPLICATE PALMS (segments V-shaped in section).

Phoeniceae: Adult leaves imparipinnate, terminal leaflet always distinct; first eophyll entire, lanceolate.

Sabaleae: Adult leaves palmate or costapalmate; first eophyll entire, lanceolate, apex truncate in *Corypha*, *Licuala* and *Livistona*.

Borasseae: Adult leaves palmate or costapalmate; first eophyll entire, lanceolate but with a truncate apex in *Borassus* and *Hyphaene*; digitately compound in *Borassodendron*, *Latania* and *Lodoicea*.

Caryoteae excluding *Caryota*: Adult leaves imparipinnate, terminal leaflet often inconspicuous; first eophyll entire, somewhat flabellate.

Caryota: Adult leaves bipinnate; first eophyll bifid.

B. REDUPLICATE PALMS (segments Λ-shaped in section).

Lepidocaryineae: Adult leaves mostly paripinnate, pair of terminal leaflets often obscure; costapalmate in *Lepidocaryum* and *Mauritia*; first eophyll usually bifid, but pinnately compound in *Metroxylon*, *Raphia* and species of *Calamus* and *Daemonorops*.

Areceae and Geonomeae: Adult leaves mostly paripinnate, terminal pair of leaflets usually conspicuous and equal, rarely adult leaves persistently bifid as in species of *Geonoma*, *Hyospathe* and *Reinhardtia*; first eophyll mostly bifid, but pinnately compound in species of *Acanthophoenix*, *Euterpe*, *Hedyscepe*, *Howeia* and *Nephrosperma*, and entire, lanceolate in *Roystonea* and *Stevensonia*.

Iriarteae: Adult leaves paripinnate, terminal pair of leaflets usually conspicuous and equal, apices of segments usually irregularly toothed; first eophyll bifid, almost entire in *Iriartea* because of a very shallow apical incision; entire and lanceolate in the anomalous genus *Ceroxylon.*

Morenieae: Adult leaves usually paripinnate, adult leaves persistently bifid in some *Chamaedorea* species; first eophyll usually bifid, rarely pinnately compound in some species of *Chamaedorea*; entire and lanceolate in the anomalous genus *Pseudophoenix.*

Attaleae and Elaeideae: Adult leaves irregularly pinnate, terminal leaflets arranged irregularly, often obscure; first eophyll entire, lanceolate, but bifid in *Cocos nucifera.*

Bactrideae: Adult leaves paripinnate, terminal leaflets conspicuous and equal; rarely adult leaves persistently bifid in species of *Astrocaryum* and *Bactris*; first eophyll always bifid.

Phytelephas and *Nypa*: Adult leaves pinnate; first eophyll in *Phytelephas* pinnately compound. The morphology of the seedlings in these two genera is not well understood and they are not considered further in this account.

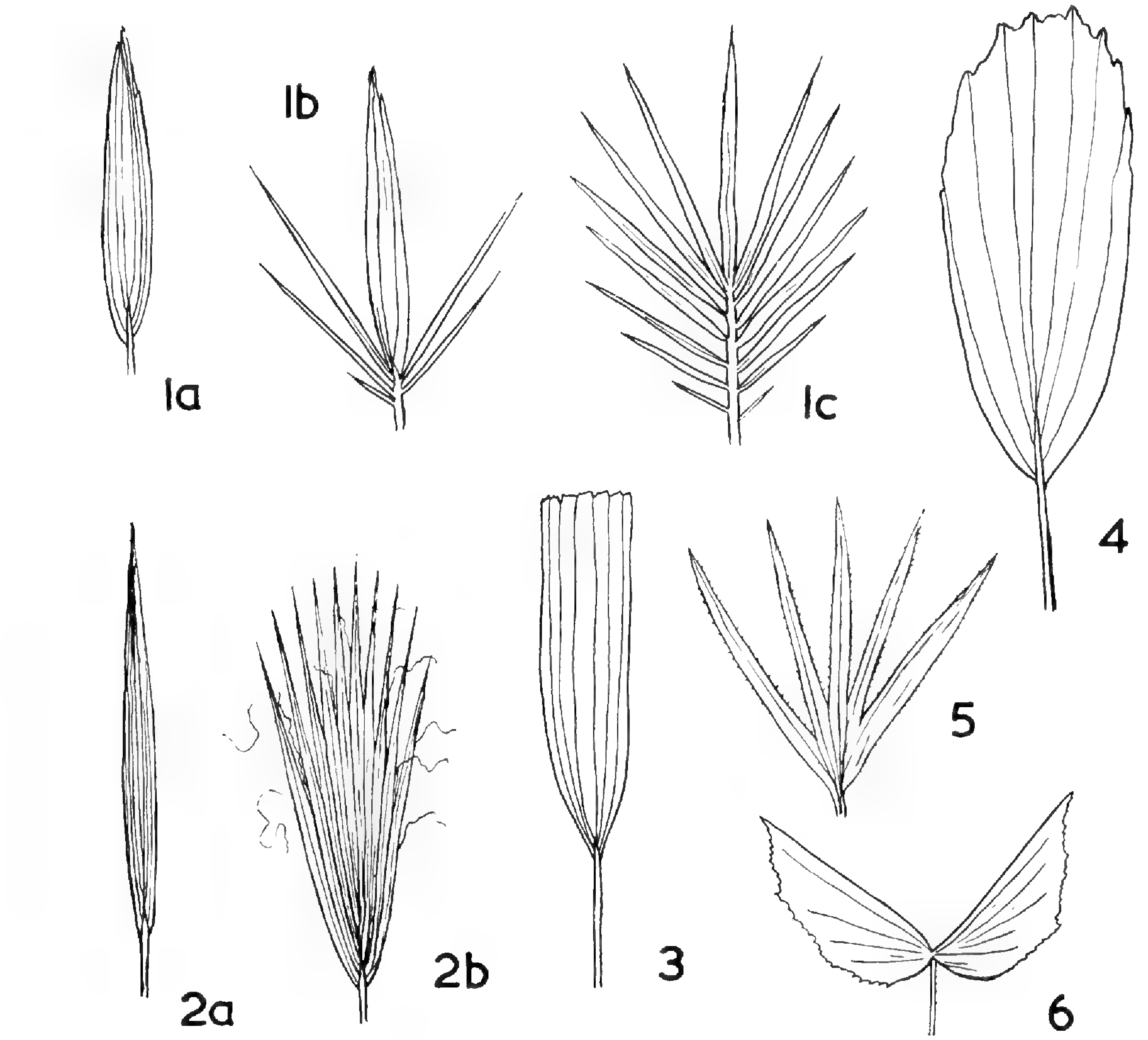
It may be noted that the first leaves of basal suckers of caespitose palms are usually simple, i.e., they revert to the juvenile condition.

Transitions to the adult foliage. In most palm seedlings, after one or more leaves of the same shape as the first eophyll have been produced, a long series of transitional leaves of increasing complexity is developed until the type of foliage characteristic of the adult plant appears. Although each species of palm produces its own characteristic series of transitional leaves, six main classes can be recognized. These are described below in relation to both the first eophyll and the adult type of leaf.

A. INDUPLICATE PALMS.

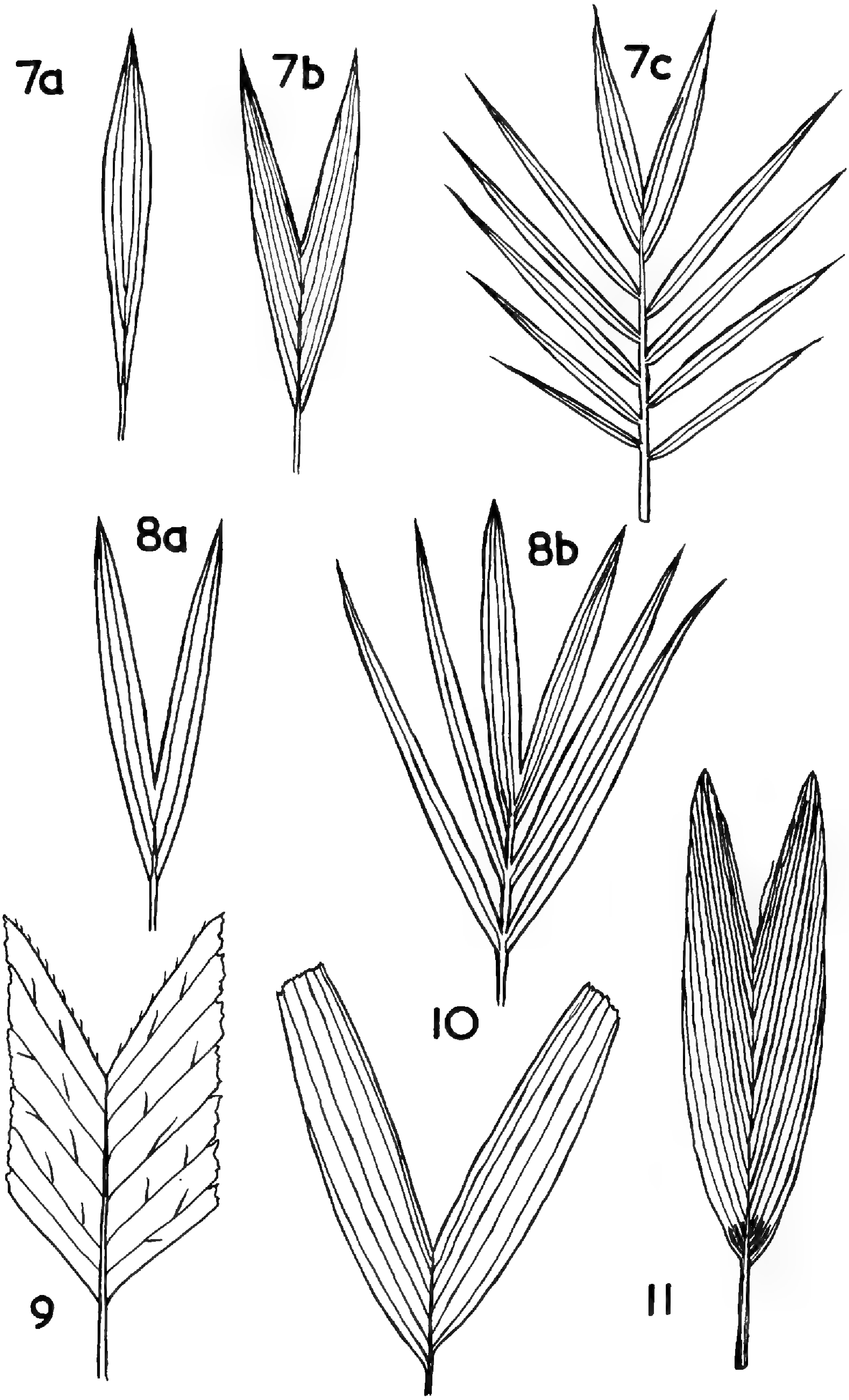
CLASS 1. *First eophyll entire*; *adult foliage leaves imparipinnate* (FIGS. 1a–c). The eophylls (FIG. 1a) are succeeded by imparipinnate leaves of increasing size in which the odd terminal leaflet resembles the whole lamina of the first eophyll (FIGS. 1b, c). This type occurs in *Phoenix* and in all the Caryotoid palms except *Caryota.* In *Phoenix* the odd terminal leaflet can always be recognized in undamaged adult leaves but often in the Caryoteae the situation is less regular so that the imparipinnate condition is only clear in small transitional leaves.

CLASS 2. *First eophyll entire; adult foliage leaves palmate or costapalmate* (FIGS. 2a, b). This class is confined to the fan-leaved tribes Sabaleae and Borasseae. The first, linear foliage leaves (FIG. 2a) are followed by broader leaves in which the lamina is incompletely split into a number of narrow segments (FIG. 2b). Later leaves are broader still and with more segments as the adult foliage is gradually approached. Normally the segmentation of these transitional leaves is not symmetrical, although rarely an odd terminal segment can be recognized, as in *Coccothrinax*, *Livistona* and *Trachycarpus*. In *Cryosophila* and *Sabal* the transitional leaves are often bifid as a result of a deep median split. This split persists in mature leaves of *Cryosophila*, the blades of which consequently have equally segmented halves. In all fan palms it is assumed that the terminal leaflet has been displaced.



FIGS. 1–6. Lamina of eophylls in induplicate-leaved palms. 1, *Phoenix pumila*: a, first eophyll, b, c, succeeding transitional eophylls. 2, *Washingtonia filifera*: a, first eophyll, b, transitional juvenile leaf. 3. *Licuala peltata*, first eophyll. 4, *Arenga pinnata*, first eophyll. 5, *Latania sp.*, first eophyll. 6, *Caryota urens*, first eophyll.

Caryota. First eophyll bifid; adult foliage leaves bipinnate. This type is anomalous. In the adult foliage the primary rachis ends in a pair of leaflets comparable to the bifid lamina of the first eophyll (FIG. 6). The transition series between juvenile and adult foliage is long and complex. Some of the intermediate stages in which the leaves are once-pinnate with basal leaflets tending to become secondarily segmented resemble the adult foliage of species of *Didymosperma* and *Wallichia*.



FIGS. 7–11. Lamina of eophylls in reduplicate-leaved palms. 7, *Roystonea regia*: a, first eophyll, b, c, succeeding transitional juvenile leaves. 8, *Chrysalidocarpus lutescens*: a, first eophyll, b, transitional juvenile leaf. 9, *Aiphanes* sp., first eophyll. 10, *Ptychosperma macarthurii*, eophyll. 11, *Cocos nucifera*, eophyll with basal perforations.

B. REDUPLICATE PALMS.

CLASS 3. *First eophyll entire; adult foliage leaves paripinnate* (FIGS. 7a–c). The first lanceolate eophylls (FIG. 7a) are succeeded by bifid eophylls (FIG. 7b) and then by paripinnate compound leaves of successively larger size (FIG. 7c). This transition series is the longest exhibited by reduplicate-leaved palms since it includes all possible types of first eophyll which they are capable of producing. It is known only in *Roystonea* and *Stevensonia*.

CLASS 4. *First eophyll bifid; adult foliage leaves paripinnate* (FIGS. 8a, b). The bifid eophylls (FIG. 8a) are eventually succeeded by pinnate leaves bearing a pair of terminal leaflets which resemble the whole lamina of the first eophyll (FIG. 8b). This last may be striking in palms in which the terminal leaflets are broader than the remaining leaflets. Sometimes, however, the arrangement of distal leaflets in the adult foliage is not regular and the adult foliage leaf is then not obviously paripinnate. This series corresponds to the previous one but for the omission of the initial lanceolate eophyll. It is found in the majority of palms belonging to the tribes Areceae, Bactrideae, Iriarteae, Lepidocaryineae and Morenieae together with *Cocos* of the Attaleae.

CLASS 5. *First eophyll entire; adult foliage irregularly pinnate.* In this class there is great variation in the shape of transitional leaves within a single species and even within a single individual. It is impossible to describe the juvenile leaves as either paripinnate or imparipinnate since they are not segmented regularly. Often the later eophylls have incomplete splits so that the blade is irregularly fenestrate. Other examples are common in which one half of the blade is entire whilst the other is partly or wholly segmented. The same irregularity and obscurity characterizes the terminal segments of adult leaves because the most distal leaflets are often filamentous and difficult to distinguish from the filament which terminates the rachis. This class characterizes most members of the Elaeideae and Attaleae and probably also occurs in *Ceroxylon* and *Pseudophoenix*. *Cocos*, together with other rare exceptions from the above mentioned tribes (e.g., *Attalea allenii*), has uniform paripinnate leaves and exhibits the series of Class 4.

C. MIXED REDUPLICATE AND INDUPLICATE PALMS.

CLASS 6. *First eophyll compound; adult foliage leaves either pinnate or palmate.* The occasional and mostly unrelated genera in which the first eophyll is compound have a transitional series which includes no new leaf forms, there being merely an increase in size until the adult type of foliage is produced.

DISCUSSION

A fairly constant correlation between the shape of the first eophyll and the morphology of the adult foliage is apparent in the information presented above. It is that the induplicate (V-folded) palms normally have an entire, lanceolate first eophyll and that the adult leaf is imparipinnate. On the other hand the reduplicate (Λ-folded) palms normally have a bifid first eophyll and an adult leaf which is paripinnate, whereever this condition can be recognized with certainty. It is suggested below how this correlation could arise and also how to account for apparent exceptions.

From the above it might also appear that there is a primary connection between fan-leaves and an entire first eophyll. However, it is generally regarded (see Eames, 1953) that the palmate leaf is merely a pinnate leaf with a condensed rachis or, more precisely, is equivalent to a pinnate leaf in which the rachis fails partly or wholly to elongate. It so happens that this trend has occurred mainly in the induplicate-leaved palms so that the two major tribes of this group, the Sabaleae and Borasseae, are entirely palmate. On the other hand only *Lepidocaryum* and *Mauritia* of the reduplicate-leaved group have developed palmate leaves.

Although palmate leaves of the borassoid and sabaloid tribes are thus morphologically equivalent to imparipinnate leaves, the development of an odd terminal leaflet, even in juvenile foliage or in costapalmate leaves which have a short but distinct rachis, is infrequent. In these palms it is assumed that the terminal leaflet has been displaced.

Before these correlations can be satisfactorily explained it is first necessary to account for the variation in eophyll morphology.

Phylogenetic trends in eophyll shape. The considerable range of eophyll shape and type in transitional juvenile foliage in palm seedlings (see Fig. 12) seems to result from certain evolutionary trends. It is assumed that a long and gradual transition between the first eophyll and the adult foliage leaf, including an extensive series of intermediate forms, is a primitive one, and that in more recently evolved palms one or more of the members of this series is omitted during seedling development. Essentially the same suggestion has been made by Dufour (1910) for some members of the Ranunculaceae in a paper describing juvenile foliage in *Anemone* and *Ranunculus* which was brought to my attention during the preparation of this article. The situation is somewhat complicated in palms because two main series of leaves are present: those with reduplicate and those with induplicate vernation. Parallel evolutionary trends have occurred independently within each series, and most possible stages of eophyll elimination occur.

Reduplicate palms. The longest series of different eophyll forms in this group are those exhibited by *Roystonea* and *Stevensonia* which form Class 3 (Fig. 12, lower left). This is assumed to be the primitive condition. The large Class 4 to which most reduplicate palms belong has been derived by omission of the initial entire eophyll (Fig. 12, lower middle left). In Class 6 are found those species in which both simple types of eophyll are omitted so that the first foliage leaf is pinnately compound (Fig. 12, upper middle left). This represents the most advanced condi-

12

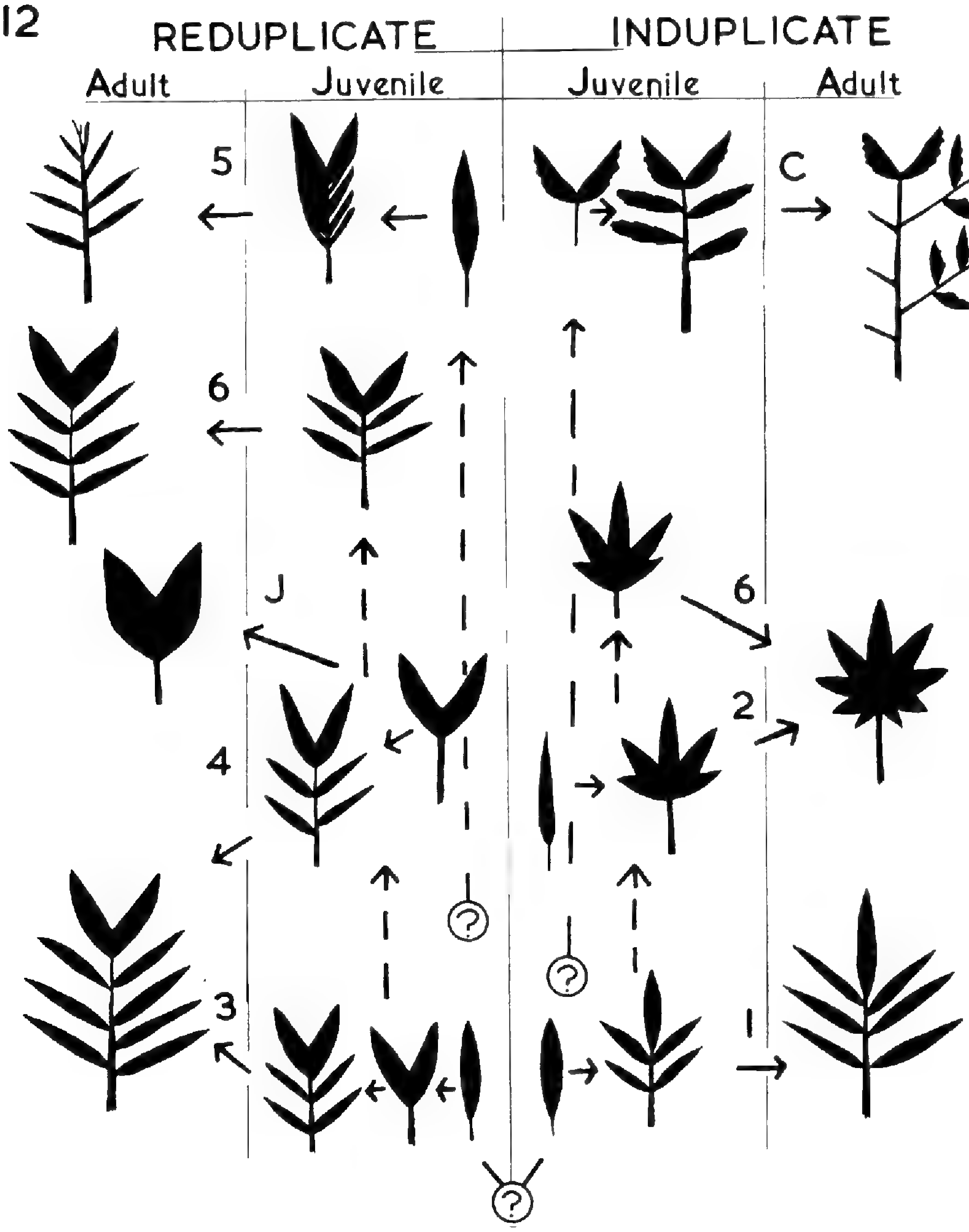


FIG. 12. Diagrammatic representation of blade shape in adult and juvenile palm leaves. Further explanation in text. Solid arrows indicate ontogenetic series. Broken arrows indicate presumed phylogenetic series. Numbers refer to classes described in text.

tion. It is evidently a derived and not a primitive condition since it has appeared quite independently in unrelated genera.

The cocoid palms of Class 5 (FIG. 12, upper left) are anomalous. The first eophyll is entire and certainly represents a primitive condition but the subsequent irregularly pinnate transitional leaves which are characteristic of this class indicate a special evolutionary trend. A possible explanation of this trend is given below.

INDUPLICATE PALMS. Class 1, exemplified by *Phoenix* represents the primitive condition in this group (FIG. 12, lower right). Since only two types of eophyll are present, only one derivative type is possible. This is found in the three borassoid genera in which the initial entire eophyll is omitted so that the first eophyll is palmately compound (FIG. 12, upper middle right). None of the sabaloid palms show this advanced condition. One other possibility has never been realized because none of the pinnate induplicate palms possess a pinnately compound first eophyll.

Caryota is obviously a derived type although it is difficult to account for its bifid first eophyll, a type of leaf not otherwise found in the induplicate palms (FIG. 12c, upper right). This genus merits a detailed developmental study.

Permanent juvenile foliage. In the evolutionary trend described above, certain types of juvenile foliage are omitted from the ontogenetic series. The converse trend, in which the adult type of foliage is never produced, is common, usually being found in palms with a reduced habit in which the stems are short and the internodes narrow. In these palms the juvenile foliage persists throughout the life of the plant (FIG. 12j, upper middle left), or at the most compound leaves with very few segments are produced. This feature has had a polyphyletic origin since it is exhibited by several unrelated genera.

Amongst the fan palms some species of *Licuala* and *Teysmannia* have an undivided, orbicular lamina, or at the most segmentation consists of shallow marginal incisions. In the feather palms more obvious juvenile foliage is retained in several species of the genera *Astrocaryum*, *Chamaedorea* and *Geonoma*. In these species the simple foliage leaves resemble the first eophylls of related species with reduplicately pinnate adult foliage. In *Bactris militaris*, *B. wendlandiana*, and *Hyospathe concinna* the leaves are always simple, unlike the pinnate adult leaves of the remaining species in these genera. Normally these persistent juvenile leaves are small, although in *Bactris militaris* the undivided leaves may be ten feet long.

The genus *Reinhardtia* is of special interest. *Reinhardtia elegans* has pinnate leaves and is considered by Moore (1957) to be the most primitive member of the genus. Other species are smaller and have fewer leaflets. *Reinhardtia latisecta* and varieties of *R. gracilis* have either simple leaves or at the most leaves with two or three segments. An additional peculiarity in these last two species is the presence of small perforations at the base of the lamina, close to its insertion on the rachis. These perforations are evidently incomplete splits. Somewhat homologous "fenestrate" leaves occur among the juvenile foliage of many cocoid palms and they are particularly striking in seedling coconuts (FIG. 11). Evidently it is common for *Reinhardtia* to have persistent juvenile foliage.

The general conclusion is that where simple leaves characterize the adult foliage of palms, they represent a derived and not a primitive condition.

Possible origin of the palm leaf. On the basis of his studies on the development of the palm leaf, Eames (1953) makes the following statement: "The compound leaf of the palm has been derived from the simple leaf by the dissection of the blade into leaflets attached to a rachis which represents the midvein of the ancestral leaf. The number and form of the leaflets are controlled by the venation pattern of the ancestral simple leaf." It is doubtful, as has just been shown, that any of the simple leaves in existing palms represent this ancestral type. The only primitive simple leaf in palms is the lanceolate first eophyll of *Phoenix* and *Roystonea*. However, it would be unwise to compare this juvenile leaf with archaic adult forms, although it is very probable that the ancestors of existing palms had a first eophyll essentially the same as that in *Phoenix* and *Roystonea*.

On the other hand, it is possible to construct mentally an ancestral palm leaf from which all existing leaf types can be derived by the splitting processes described by Eames. This archetype leaf would have a regularly plicate, entire lamina, with numerous lateral major veins in the form of ribs occupying the dorsal and ventral crests of the folds. Each vein would have a somewhat sigmoid course, its end in the leaf margin either passing to the apex or fusing with the ends of lower veins to form a marginal commissure. The thickened midrib would extend to the apex of the leaf and there become an abaxial rib (FIG. 13a). This is essentially the type of leaf envisaged by Eames. The nearest approach to it in living palms is found in such genera as *Manicaria, Mascarena, Stevensonia*, and *Vershaffeltia* in which the congested leaflets often are persistently coherent along the margins. From a distance leaves of these genera appear to be entire.

It is appropriate to mention at this point that the leaf of a fossil plant (*Sanmiguelia lewisii* Brown) has recently been described and interpreted as that of a primitive palm (Brown, 1956). Whilst this leaf does not bear all the essential features listed above, the chief difference being the absence of a midrib, it could still serve as a fundamental type from which modern compound palm leaves have evolved by the methods suggested below. The age of this plant is also noteworthy since, if it is interpreted correctly, it would be the remains of the earliest known flowering plant.

The splitting which produces individual segments may occur in three possible ways. First, the leaf may split along the ventral (abaxial) crests of the folds (FIG. 13b). This would produce reduplicate segments. At the leaf apex there could be either two equivalent splits, one on each side of the rachis, or a single split could bisect the rachis. In both examples a pair of equal terminal leaflets would result, but in the former type of splitting the free end of the rachis would persist as a whip-like filament, a feature not uncommon in paripinnate palms but particularly prominent in *Cocos* (Venkatanaryana, 1957). This situation accounts satisfactorily for the paripinnate, reduplicate leaf but it will only arise if there is a regular arrangement of ribs at the leaf apex. In contrast the cocoid palms of class 5 apparently owe their irregularly pinnate leaf to the fact that the ribs, at least at the leaf apex, are not equally spaced and that splitting is not regular. The segments here are reduplicate and the leaf is essentially paripinnate as is revealed by the few rare examples in which the arrangement of distal leaflets is regular.

The second possibility is that the splits which separate adjacent segments take place along the dorsal (adaxial) crests (FIG. 13c). This produces induplicate leaf segments and an odd terminal leaflet so that the leaf is automatically imparipinnate. This is the type of leaf found in *Phoenix* and the Caryoteae. The palmate leaf of the Borasseae and Sabaleae is a similar leaf with a partly or wholly condensed rachis in which it is assumed that the terminal leaflet is normally displaced and is no longer recognisable.

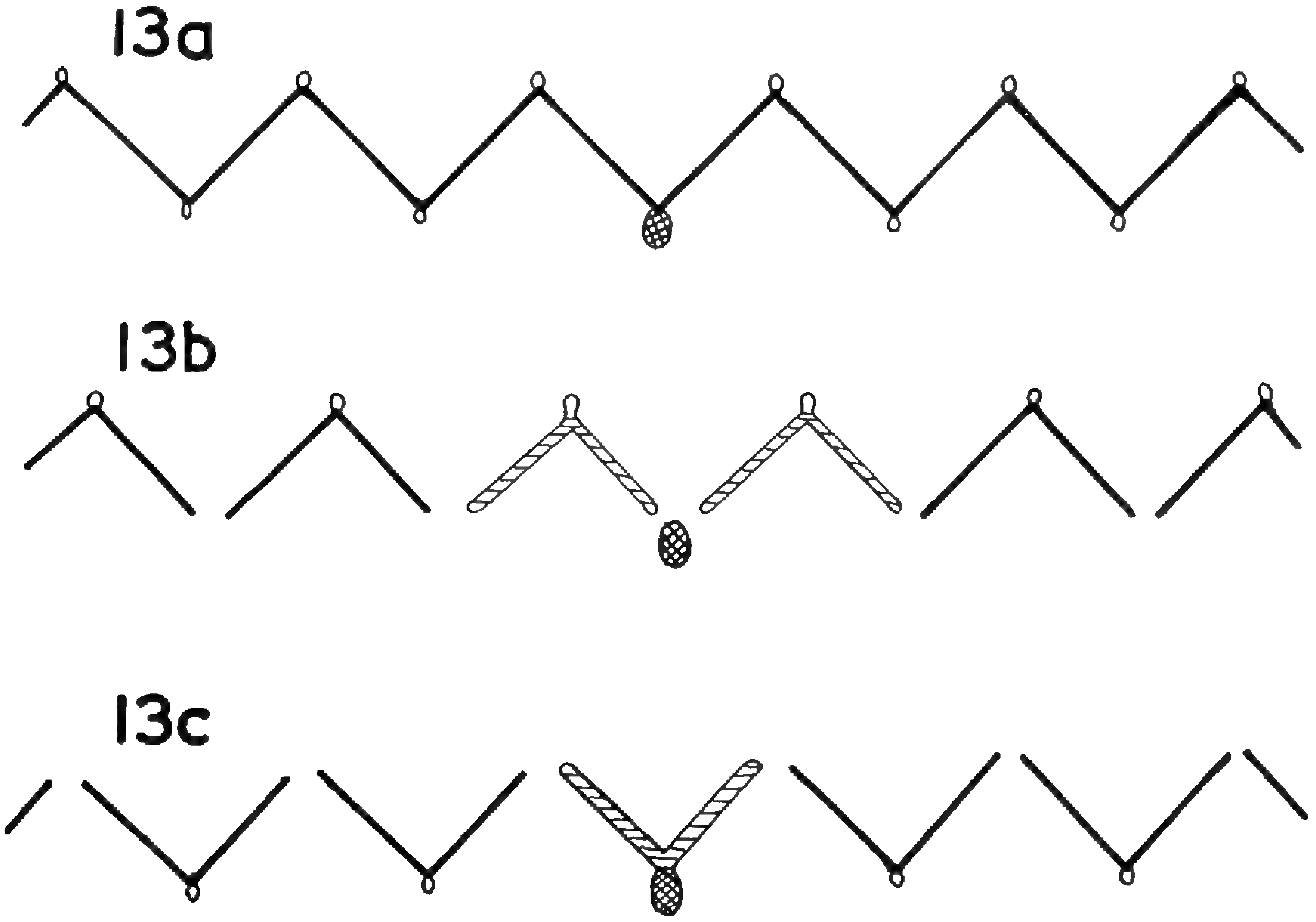


FIG. 13. Suggested origin of reduplicate and induplicate leaves from a hypothetical unsegmented ancestral leaf. a, Diagrammatic transverse section through apex of ancestral leaf with plicate but unsegmented lamina. b, Origin of reduplicate segments by cleavage along ventral crests. c, Origin of induplicate segments by splitting along dorsal crests. Rachis crosshatched, terminal segments lined. Splits are assumed to eliminate the ribs, otherwise the ribs themselves could be divided and the segments would then have marginal half-ribs.

The third possibility is for splits to occur without reference to the folds. This condition is known only in the small fan palm *Rhapis* which as a consequence has unequal and irregular segments (Naumann, 1887).

Although this theory accounts for the correlation between leaf shape and vernation it is an over-simplification of the situation. Eames, in confirmation of the observations of several early workers has clearly shown that the plication of palm leaves is a result, not of simple folding, but of a cleavage and invagination of a solid tissue.

This process is completed before the leaf primordium is more than a few millimeters high and results in a plicate blade, the margin of which is connected by a continuous strip of tissue. The splitting that results in the separation of adjacent segments occurs later and, according to Naumann, may take place in a variety of ways. However, this complex developmental process does not invalidate the above argument, since it is possible that the primitive palm leaf developed an entire, plicate lamina by the same initial cleavage process. On the other hand, the view of Arber (1922) that the palm leaf is a modified phyllode may mean that at no stage in its phyletic history was there an entire unsegmented blade.

The diagram constructed by Eames (1953, FIG. 11), based on *Roystonea*, showing the origin of equally-spaced folds in the leaf primordia will only result in mature leaves in which the segments are equal, uniformly spaced and either opposite or regularly alternate on the two sides of the rachis. This regularity is relatively uncommon in palms. Many palm leaves may be described as irregularly pinnate (since the leaflets are not evenly spaced) or unequally segmented (since the leaflets are not all of the same width) and combinations of these two types are common (Tomlinson, 1961). In irregularly pinnate leaves the initial clefts must be irregularly spaced in the primordium. The most difficult situation to account for is one in which the pinnae are fasciculate, individual clusters being separated by long, naked portions of the rachis, and in which clusters of leaflets are subopposite or even alternate. It is easier to account for unequally segmented leaves which evidently arise because splits separating individual segments occur at irregular intervals and along only a few furrows. Even so, the enormous range in the morphology of individual leaflets has still to be accounted for and only detailed studies of the development of the more outstanding leaf forms will reveal the mechanism of their origin. It is clear, on the other hand, that the fundamental process described by Eames takes place in the early stages of development of all adult palm leaves. The palms are undoubtedly an ancient group with a long phylogenetic history so it would not be unexpected to find minor divergence from the fundamental mechanism of leaf development inherited from primitive forms. Much of the controversy which exists in the literature dealing with the development of the leaf in palms is likely to be a consequence of this diversity.

Morphogenetic considerations.

From the account given by Eames it is apparent that three essential processes are responsible for the development of the palm leaf:— (i) a cleavage and folding of solid tissue during very early stages of leaf ontogeny, (ii) elongation of the rachis to a greater or lesser extent during the later stages, (iii) a splitting whereby adjacent leaf segments become free. The vast range of leaf forms in palms is a result of variation in the intensity of these processes. Consequently, if any one of them could be influenced experimentally it should be possible to modify the final leaf shape. Leaves vary considerably in the extent to which external influences modify their ultimate shape (Ashby, 1948) but the susceptibility of the palm leaf to changes in environmental conditions has never been explored. There are obvious technical difficulties involved in using palms as experimental objects. However, this account has shown that the essential morphology of the palm leaf is established very early during the production of juvenile foliage and therefore the possibility of carrying out experiments on palm seedlings grown in greenhouses in a cool temperate climate is not excluded.

One suggested experiment would be to establish whether failure of the rachis to elongate in typical palmate leaves is the result of an inhibition process which could be overcome by application of growth substances and, if so, whether it would be possible to recreate a presumed ancestral leaf.

SUMMARY

In the development of the palm seedling there is a gradual transition from small, usually simple leaves to the large compound leaves of the adult foliage. It is suggested that in the evolution of palms, one or more of the simple types of leaf which were present in the transitional series in the primitive palm and which are still extant in *Phoenix* and *Roystonea,* have been omitted and so the different types of transition series in existing palms produced. The most highly evolved seedlings have a compound first foliage leaf. A reverse trend is one in which the juvenile foliage persists and is present throughout the life of the palm.

There is found to be a significant correlation between (a) the shape of the first foliage leaf (first eophyll), (b) the series of transition forms between juvenile and adult foliage, (c) the morphology of the adult leaf, (d) the type of folding in the individual leaf segments. Palmate leaves are not essentially different from pinnate leaves. Two main groups exist in palms, the induplicate-leaved palms being imparipinnate, the reduplicate palms being paripinnate. It is suggested that these two forms are a result of a simple difference in the way in which a hypothetical entire, plicately-folded prototype palm leaf has been segmented.

The great variety in the morphology of adult palm leaves can be accounted for on the basis of variation in three fundamental processes which occur during their development. It is possible that these processes can be influenced artificially.

The present article is partly the outcome of several long discussions with Dr. H. E. Moore, of the Bailey Hortorium, Cornell University. I should like to thank him for clarifying many details and for correcting me on many points.

BIBLIOGRAPHY

Arber, Agnes. On the development and morphology of the leaves of palms. Proc. Roy. Soc. London. B. **93**: 249–261. 1922.

Ashby, E. Studies on the morphogenesis of leaves. I. An essay on leaf shape. New Phytol. **47**: 153–176. 1948.

BOYD, LUCY. Monocotylous seedlings. Trans. Bot. Soc. Edinburgh **31**: 1–224. 1932.

BROWN, R. W. Palmlike plants from the Dolores Formation (Triassic), S. W. Colorado. U. S. Geol. Surv. Prof. Paper **274H**: 205–209. 1956.

COOK, O. F. A new genus of palms based on *Kentia forsteriana*. Jour. Wash. Acad. Sci. **16**: 392–397. 1926.

———. Juvenile characters of royal palms. Science **81**: 590. 1935.

CORNER, E. J. H. Wayside trees of Malaya. ed. 2. vol. **1**. 1951.

DRUDE, O. Palmae. *In* Engler and Prantl, Die natürlichen Pflanzenfamilien II. **3**: 1–93. 1889.

DUFOUR, L. Études des feuilles primordiales de quelques plantes. Rev. Gén. Bot. **22**: 367–384. 1910.

EAMES, A. J. Neglected morphology of the palm leaf. Phytomorphology **3**: 172–189. 1953.

FOSTER, A. S. Heterophylly and foliar venation in *Lacunaria*. Bull. Torrey Bot. Club **78**: 382–400. 1951.

GATIN, C. L. Récherches anatomiques et chimiques sur la germination des palmiers. Ann. Sc. Nat. Bot. IX. **3**: 191–314. 1906.

———. Les palmiers: histoires naturelles et horticoles des different genres. Paris. 1912.

MICHEELS, H. Récherches sur les jeune palmiers. Mém. Cour. Acad. R. Belg. **55**: 1–126. 1889.

MOORE, H. E. Synopses of various genera of Arecoideae. Art. 21. *Veitchia*; Art. 23. *Reinhardtia*. Gent. Herb. **8**: 481–536, 541–576. 1957.

NAUMANN, A. Beiträge zur Entwicklungsgeschichte der Palmenblätter. Flora **70**: 193–253. 1887.

PFITZER, E. Ueber Fruchte, Keimung und Jugendzustände einiger Palmen. Ber. Deutsch. Bot. Ges. **3**: 32–52. 1885.

TOMLINSON, P. B. Anatomy of the Monocotyledons. Vol. **2**. Palmae. 1961 (*In press*).

VENKATANARYANA, G. On certain aspects of the development of the leaf of *Cocos nucifera* L. Phytomorphology **7**: 297–305. 1957.

DEPARTMENT OF BOTANY
UNIVERSITY OF LEEDS

THE DIRECTOR'S REPORT

THE ARNOLD ARBORETUM DURING THE FISCAL YEAR ENDED JUNE 30, 1960

The Staff:

It is with regret that the sudden death of Dr. Ivan M. Johnston on May 31, 1960, is recorded. Dr. Johnston, Associate Professor of Botany and a member of the staff of the Arnold Arboretum since 1931, was known in the botanical world for his monographic studies on the Boraginaceae and for his floristic work in the deserts of the United States, Mexico and South America. A biographical report of his life and professional career, as well as a bibliography of his published works, will appear in the next number of the *Journal of the Arnold Arboretum.*

Dr. Karl Sax, Professor of Botany, retired on August 30, 1959 and has served as Visiting Professor of Botany at the Gibbs Research Laboratory, Yale University, for the remainder of the year.

Three staff resignations also were accepted. Dr. Frances M. Jarrett, Botanist, resigned October 31st to accept a post at the Royal Botanic Gardens, Kew, England. Mrs. Claude Weber, Botanist, resigned September 1st to enter the graduate school of Radcliffe College. Mrs. Mary Lehmer, Business Secretary, resigned June 15th and will live in Albuquerque, New Mexico. Each contributed devoted and valuable services to the Arnold Arboretum and each carries with her our appreciation.

Two new scientists were appointed to the staff. Dr. Lorin I. Nevling was appointed Assistant Curator, beginning October 15. Dr. Nevling, who received his Ph.D. degree from Washington University in St. Louis, has been working on the Thymelaeaceae of the New World. Dr. Joab L. Thomas, a graduate of Harvard University, was appointed Cytotaxonomist as of July 1. Dr. Thomas, whose doctoral thesis dealt with the Cyrillaceae, will work primarily on the cytology and genetics of the cultivated plants in the living collections of the Arboretum.

During the year Mr. Henry Draper was appointed Superintendent of the Case Estates at Weston, Miss Ann Waterman was appointed jointly with the Gray Herbarium as Assistant Librarian, and Miss Ann Close became Business Secretary.

The Ninth International Botanical Congress was held in Montreal, Canada, between August 19th and 29th, 1959. Approximately three thousand botanists, representing many fields of research, plus wives and children attended these meetings. We were pleased that approximately 100 foreign scientists visited the combined herbaria and the living collections before, during and after the meetings. Eleven members of the Arboretum staff attended the pre-congress nomenclatural meetings. During the congress Dr. Howard presented an invitational paper titled "The Vascular

Anatomy of the Petiole as a Taxonomic Character" at a symposium on plant anatomy. Dr. Hu reported on "The Taxonomy, Geography and Economic Importance of the Genus *Fraxinus* in China" at a session on plant taxonomy. Dr. Wood was appointed to the Subcommittee for Family Names of the Committee for Spermatophytes. Dr. Howard was elected President and Dr. Wagenknecht, Secretary of the International Association of Botanical Gardens, both to serve for five years.

The annual meeting of the American Association of Botanical Gardens and Arboreta, held in conjunction with that of the American Horticultural Council at Rochester, New York, in October, was attended by Drs. Howard, Wagenknecht and Wyman. Following this meeting Dr. Wyman was appointed chairman of the committee on Plant Registration for the Association.

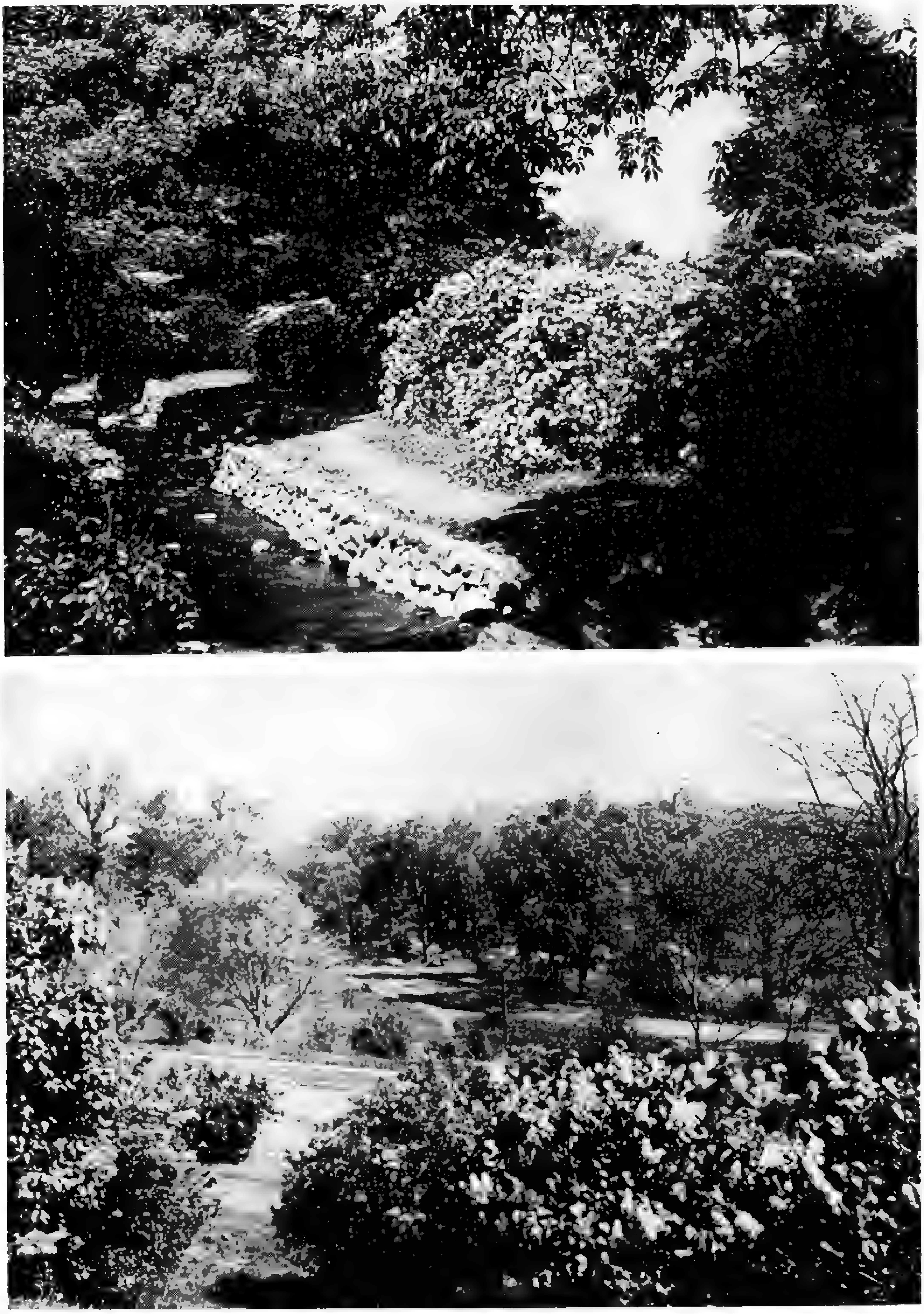
The Arboretum staff was represented at the annual meeting of the Plant Propagators Society by Mr. Fordham. The staff again made the necessary arrangements for the annual meeting of the New England section of the American Society of Horticultural Sciences which was held in Cambridge. Five staff members attended these meetings with three presenting technical papers. Dr. Howard was a participant in the Tropical Botany Conference sponsored jointly by the National Academy of Science and the National Research Council and held at the Fairchild Tropical Garden, May 5–7, 1960.

During the year the combination of the American Horticultural Society and the American Horticultural Council was effected. Dr. Wyman served for five years as Secretary of the latter organization which maintained its business office at the Arnold Arboretum. Following the union of the two groups as the American Horticultural Society, Dr. Wyman resigned as Secretary of the Council and was then elected First Vice-President of the new society, the headquarters of which will be in Washington, D. C.

Awards of recognition came to Drs. Wyman and Sax during the year. A special award to a professional horticulturist for outstanding accomplishments and contributions was given to Dr. Wyman by the Horticultural Society of New York. Dr. Sax received the Jackson Dawson Medal from the Massachusetts Horticultural Society and was named "Horticulturist of the Year" at the University of Massachusetts students' horticultural show.

Horticulture:

The winter of 1959–60 was unusually mild with only a single heavy snowfall. These conditions allowed for nearly continuous out-of-door work in the cleaning of many shrub plantings and in the pruning and removal of dangerous trees. Much of this work was necessitated by the extreme weather conditions of the previous year. The effects of the severe winter of 1958–59 became more evident in many plants as the season progressed and were again visible in the spring of 1960. The most conspicuous damage occurred on some, but not all, plants of the hardy strain of *Albizzia julibrissin* var. *rosea.*



The Arnold Arboretum in June, 1960. Above: Bussey Brook as it flows through the *Rhododendron* collection. Below: A view across the lilac collection toward the torch azaleas in the oak woods.

The spring season of 1960 appeared to be a short one. It was not possible to complete all the transplanting from the nursery in Weston to the permanent plantings in Jamaica Plain, but 214 species, varieties and cultivars were moved. Some of these were used to augment existing group plantings and others replaced weak or poorly grown plants. Many were new, representing additions to the permanent plantings.

Several plantings received special attention during the year. The collection of tree peonies, moved the previous year, is being pampered until it is well established in its new area. Approximately 1700 bulbs of *Narcissus* cultivars were added to the naturalized area being created along Bussey Brook. The mass planting of torch azaleas along the South Street bank was pruned, cleared and fertilized. The *Taxus* and *Juniperus* collections which had become crowded during recent years were given special attention, several of the large yews and junipers were moved, and some duplicate plants taken out. New specimens have been added to the main collection and the general appearance is much improved with favorable growth conditions again present in the area.

The city of Boston through its Department of Parks and Recreation continued the annual program of improvement of the roads, paths and benches which is its responsibility. A new surface was placed on the full extent of the road between South Street and Bussey Street in the area of the *Rhododendron* and conifer collections. The meadow road from the Arborway passing in front of the administration building to the maple collection was also resurfaced. These two areas not only represented the most serious deterioration of the roadways, outside of the Peters Hill area, but were also the sections most heavily travelled by visitors and by Arboretum equipment. It is hoped that additional areas may be resurfaced as city funds permit. The Department of Parks and Recreation also completed the last portion of the work of clearing the cobblestone gutters within the Arboretum. The area of Peters Hill is now clear and the whole roadway much improved. The dirt which had accumulated in the gutters had become overgrown and was salvaged for fill. Chemical sprays are now used to keep the cobblestones free of weeds.

During the year Mr. Williams, the superintendent, worked out a simple system of spraying with "Dowpon" to edge sharply and effectively the many plantings and beds in the shrub collection. Experiments continue on chemical methods of weed control as a means of improving the appearance of the grounds and of reducing the amount of hand labor required. This experimental program involves the type of chemical, the rate and frequency of application. The results are measured in cost of application, the control obtained and the effects on different woody plants.

In previous reports the use of large quantities of organic material as mulch on the Arboretum collections has been indicated. At various times the Arboretum has had available at low cost or simply for the hauling adequate supplies of spent hops, sawdust, wood chips, buckwheat hulls, or coffee grounds. The mulch used most recently has been cocoa shells for which there had been no commercial demand. The cocoa-shell mulch was used experimentally at first but with notable success. The mulch is fire proof, retains moisture, remains in place, i.e., does not float or blow away, has good fertilizing value which is released slowly, and is attractive in appearance. Through staff comments to classes, publications, and the questions of many visitors a horticultural demand for this product has now been created so that gratis supplies are no longer available to us in the quantities needed. Thus, during the year it has been necessary to locate new sources of mulching material; it now appears that animal manures from local horse stables and the city zoo will be available for our needs.

In an attempt to have within the collections representatives of genera, species, varieties and cultivars offered by the nursery trade within our area, an attempt was made to locate sources for 480 advertised taxa not currently in our living collections. Many of these taxa have been tried on previous occasions and have not proved hardy; others represent new selections or new cultivars. It is desirable, however, to have information on the growth and habits of such plants, even though previous experience has shown that many may not be botanically distinguishable from already known plants or that the commercial source is unwise in offering for sale a plant which is not hardy or desirable for the Boston area. The small plants which have been obtained will be held at Weston for growth and initial hardiness tests.

One of the striking features of the Arnold Arboretum living collections is the completeness and accuracy of the labeling and mapping systems. Both of these are maintained only by constant effort. Many staff members coöperate in the continuous work of checking identifications, to insure the accuracy of the names. During the past winter a complete inventory of the plants in the living collections at Jamaica Plain and Weston was made and the nomenclature checked against Rehder's *Bibliography*, as well as more recent monographs. The work of verifying plants in the living collections from which type specimens were collected by Sargent, Rehder, and others has been continued. A special label has been prepared to identify such plants properly.

During the fall the Arboretum was approved as the National Registration authority for cultivars of woody ornamental plants not now handled by special societies. This delegation is from the American Association of Botanical Gardens and Arboreta and the American Horticultural Society and is for a two-year trial period. In this work the Arboretum staff coöperates with any individual or organization wishing to register specific groups of plants. To the present, about a dozen individuals and organizations have expressed an interest in or a willingness to carry on such registration activity. For groups not delegated to others, the members of the Arboretum staff, in an effort coördinated by Dr. Wagenknecht, will register cultivar names and compile registration lists as interest is expressed. A set of registration regulations and forms was prepared and is distributed on request. The return of these forms, plus a small registration fee, a representative herbarium specimen, and a living plant establishes the registration of a name. If a check of the literature shows that the cultivar name has not been used previously and the name is in accordance with the International Code of Nomenclature for Cultivated Plants, the sender is so notified. Most of the plants received for registration during the first few months of this work had been given original and valid names. A few names were not acceptable, being either pre-occupied or incorrectly formed according to the Code. In each instance the sender agreed to alter the cultivar name in accordance with suggestions made. The Arboretum has no responsibility for the distinctness of the cultivar registered and legally none for the identification, although both points are of immediate concern to the staff. Where necessary, additional correspondence often has clarified the relationships of cultivars, producing information of lasting value which will be kept with the type specimen. The living plants will be kept in a special area of the Arboretum for reference and testing. If it is obvious that the species is not hardy in this area most of the registered plant material is sent to a coöperating arboretum in a more appropriate environment. The presence of authentic living and herbarium material of cultivars will facilitate the work of the staff in horticultural plant taxonomy. The end of the two-year trial period will coincide approximately with the 1962 International Horticultural Congress when steps may be taken to coördinate registration activities for all ornamental woody plants at the international level.

In the 1959 session of the Massachusetts Legislature a bill was passed to obtain from the Bussey Institution several acres of land, including that on which the Arnold Arboretum maintains its greenhouses, nursery area, hedge collection, and collection of *bonsai*. Although the bill was incorrectly filed, a new bill will be prepared. For this reason the staff has spent considerable time during this fiscal year drawing plans for new greenhouses and the necessary accessory buildings. A site was selected on land owned by Harvard University for the Arnold Arboretum along Centre Street and a program of fertilization and soil preparation is under way in this area. The new greenhouse plans will improve research facilities by providing experimental cold chambers, laboratory space and modern head-house equipment. A small classroom for graduate students and adult classes is also contemplated. The overall increase in greenhouse space will be approximately thirty-three per cent while the nursery area will be increased threefold. The President and Fellows of Harvard College, as trustees of the Arnold Arboretum, approved the plans in principle and it is expected that an architect will be selected during the summer with construction possible during the next year.

During the year the staff of the plant propagation department made a special study of the plants represented in the living collections by single specimens and those which were not in the best of condition. The unique taxa were selected for immediate propagation. Published information is lacking for the vegetative propagation of many of these and an experimental approach is necessary. In all, 257 taxa are to be considered. Initial propagation efforts have not been successful with all of these and this program will continue. Many of the plants represented by single specimens in the collections are desirable ornamental shrubs and it is the difficulty of propagation that presumably has limited both the number of specimens which we have and their availability in trade sources.

The routine work of filling requests for plant materials and of handling shipments of seeds and plants received may occupy a large percentage of the department's work time. During the past year 245 shipments were made by air mail or air freight, parcel post and express within the United States and to twelve countries beyond. A regular exchange is maintained with most of the institutions represented. Thus, during the year, the Arboretum received 235 shipments of living material of 693 species and varieties from the same or other sources in the United States and eleven other countries. A total of fifty-two shipments of seeds representing 186 taxa was received and processed from seventeen countries, in addition to the United States. Included were many oaks and related plants and several species of blueberries from higher altitudes of southeastern Asia. A collection of seeds of *Acacia drummondii*, said to be one of the hardiest and most attractive of the acacias, was received from New South Wales. The seeds germinated well and seedlings have been distributed to locations in the South and Far West.

During the past season trees of the hardy strain of *Cedrus libani* fruited heavily. Although these plants have grown in the Arboretum for many years this clone is relatively rare in cultivation. It was possible to distribute the seed in quantity to twenty-eight locations in fourteen of the colder northern states, with shipments also going to Canada and northern Europe for trial. A replicate experiment with these seeds has shown that two months of stratification at 41° F. allowed 80% germination within four days. The seedlings are extremely susceptible to damping-off organisms, but with the rapid germination obtained it was possible to separate seedlings quickly and to minimize the spread of these diseases.

The dawn redwood, *Metasequoia glyptostroboides*, is an Arboretum introduction which has become a popular tree for general planting. While none of the plants grown from seed introduced in 1948 has yet produced staminate inflorescences, many reports of ovulate cones have been received. With no fertile seeds available the species must be reproduced by cuttings. Work during the past year revealed that cuttings taken on August 5th rooted earlier and in far better percentages than those taken on June 5th. Winter hardwood cuttings of the same plant rooted poorly.

In an experiment to determine the viability of scions in storage, crabapple scions which had been collected in December 1958 and kept in a polyethylene bag with a small amount of moistened sphagnum moss at a temperature of 41° F. were finally grafted onto appropriate stock in March 1960. Although a small number of scions was involved, the viability and successful union of most of these suggest that many materials of this kind can be stored under appropriate conditions and retained from one grafting season to the next.

The use of sulphuric acid baths to break seed coats and dormancy is well known. Seeds of *Koelreuteria paniculata* germinated in six days following such treatment or could be stored (as in this instance) in a refrigerator for sixty days before planting. In all cases there was no evidence of the reported secondary dormancy. Seeds of *Cytisus nigricans* produced general germination in ten days following treatment in sulfuric acid for one hour. It is worth reporting that a flat of seeds of this species which had received the normal hot water treatment the previous year had failed to germinate. When these seeds were recovered and treated with sulfuric acid they, too, germinated in ten days.

Case Estates:

The house at 101 Wellesley Street in Weston adjacent to the groundcover demonstration area was made available to the Arboretum during the summer of 1959. This house, one of the oldest in Weston, was given to the Arboretum by Miss Marian Case but has been occupied by Miss Case's former gardener for a number of years. The house was reconditioned and a new heating system was installed. It is now occupied by the superintendent at the Case Estates.

The New England Daffodil Society expressed an interest in obtaining space for a test garden for *Narcissus* varieties at the Case Estates and beds were prepared for trial plots of these bulbs. The Case Estates have in various areas many naturalized bulbs which are not only colorful but draw considerable attention in the spring. A trial garden will be of value to the staff in relation to its teaching programs and to its work in cultivar registration. The New England Daffodil Society has agreed to plant and maintain the beds.

Work has continued in a general program of cleaning plantings and rejuvenating some of the older trees. Thirty old apple trees were removed during the year to reduce maintenance costs of this area and to allow for an expansion of other shrub and tree collections. Large amounts of manure were obtained without charge and many of the temporary nursery beds were fertilized following the removal of small plants.

Again this year the surplus plants were offered to the Department of Buildings and Grounds in accordance with the terms of the Arboretum trust. Approximately 430 plants of 144 taxa were offered and most of these were utilized on the Harvard campus and in conjunction with the Harvard building program.

Education:

None of the Arboretum staff was scheduled to offer formal courses at Harvard University during the past year. Several staff members assisted in the guidance of graduate students at Harvard and Radcliffe. A series of luncheon seminars for graduate students and staff was continued in which various staff members and students presented papers which were followed by discussion.

The popular classes in horticulture and botany, conducted by the staff, were eleven in number. The field classes at Jamaica Plain and Weston continued to draw the largest numbers. Plant propagation was again enrolled to the limit of the facilities. More technical courses on plant geography, plant ecology, the gymnosperms, economic botany and a course in French on the contributions of French horticulture to American gardens drew qualified students. A course in economic botany which visited restaurants offering foreign foods proved to be a novel and appealing method of teaching. After an enjoyable meal, the class studied and discussed the plants and plant parts used for food. This course has received considerable newspaper publicity, one report even returning from Caracas, Venezuela.

Another expression of the educational activity of the Arboretum staff is found in the outside lectures which they are requested to give. Such lectures are offered at various levels. On occasion the Arboretum staff has through lectures or guided tours dealt with students from the elementary grades of the Weston schools to the graduate students of many colleges. Many requests for speakers are received from Garden Clubs and similar groups interested in horticulture. Such lectures can be both entertaining and instructive and the staff speakers attempt to make them so. Again this year approximately fifty groups numbering at least twenty-five persons were given conducted tours of the living collections in Jamaica Plain or Weston. Dr. Wood represented the Arboretum on the program of the annual Williamsburg Garden Symposium, speaking on "Birds, Bats, Bees and Botany: the Story of Pollination." Dr. Howard was a speaker on the campuses of Duquesne and Pittsburgh universities and the State University Teachers College, Oneonta, New York, under the sponsorship of the American Institute of Biological Sciences. He was the American Association for the Advancement of Sciences speaker at Franklin and Marshall College in Lancaster, Pennsylvania, and was the principal speaker for the Pennsylvania Catholic Round Table of Science at its annual meeting in Pittsburgh. Dr. Wyman was the principal speaker at the annual meetings of the Colorado Nurserymen and the Arborist Association, the Michigan Nurserymen's Association, and the Pennsylvania Nurserymen's Association. He was also the horticultural speaker at the University of Maine's Farm and Home Week and took part in the nurseryman's short course offered by the Waltham Field Station.

Exhibits and Displays:

The annual Spring Flower Show of the Massachusetts Horticultural Society was held at a new location, Wonderland Park in Revere, Massachusetts. As display space was limited, the Arboretum staff was asked to display again a pruning exhibit which was used five years ago. This exhibit, demonstrating the methods and equipment of pruning shrubs and trees, also contained examples of plants showing both correct and improper pruning. While the exhibit lacked the color of forced flowers it was awarded a gold medal. Interest in the exhibit was such that it was again set up in the lecture hall in Jamaica Plain for the use of visitors and classes during the spring.

An open house was held at the Case Estates on May 1st to allow inspection of the nursery area, ground-cover and small-tree demonstration plots and other plantings. During the day staff members were on the grounds to answer questions. A rainy day reduced the crowds which nevertheless created a parking and traffic problem in the vicinity. As a result of such demonstrations the number of visitors and the number of tours in Weston increase each year.

A portion of the Arnold Arboretum exhibit on the grounds of the United States exhibition at the Floriade, in Rotterdam, the Netherlands, June, 1960.

From March to September, 1960, an International Horticultural Exposition, the Floriade, is being held in Rotterdam, the Netherlands. The American exhibit is under the sponsorship of the Foreign Agricultural Service of the Department of Agriculture and the American Horticultural Council. The latter organization requested the Arnold Arboretum to prepare an exhibit of plants introduced to American horticulture by the Arboretum. Dr. Wyman prepared a list which, with few exceptions, consists of plants available in European nurseries. A few plants not available in Europe were secured from our own nurseries or from commercial sources and shipped to Holland. The Arboretum plants in the American exhibit comprised part of a private arboretum as well as established landscape plantings around a typical American home. The selection of sixty-four taxa was made to afford some bloom or point of attraction throughout the six month period of the Floriade. Elsewhere in the exhibit, the American Association of Botanic Gardens and Arboreta prepared a display of Kodachrome transparencies, photographs, and technical data, illustrating and describing American arboreta and botanic gardens. Dr. Howard served on the organizing committee, and the staff supplied pictures and details concerning the Arnold Arboretum.

The lecture hall in Jamaica Plain was again the location for temporary displays of flowering plants for classes and various special meetings. The 24th Inter-scholastic Judging and Identification Contest in Floriculture and Ornamental Horticulture was held there in April. Nearly 100 students took part in the team and individual competitions. Special displays of Arboretum plants were also prepared both at Jamaica Plain and at the Harvard Club in Boston for the annual meeting of the Associated Harvard Clubs. A special display of ornamental crab apples was prepared and exhibited at the Fall Show of the Massachusetts Horticultural Society.

Comparative Morphology:

Professor I. W. Bailey, Professor of Plant Anatomy, Emeritus, continued to serve as curator of the wood collection of the Arnold Arboretum. In addition, Professor Bailey is continuing his investigations on the comparative anatomy of the Cactaceae under a three-year grant from the National Science Foundation. Thus far, he has devoted his attention largely to the leaf-bearing genera *Pereskia*, *Pereskiopsis* and *Quiabentia*. If these putatively primitive representatives of the Cactaceae are to be utilized as an initial fundamental basis in studying salient trends of phylogenetic specialization within the family, and in obtaining evidence of valid taxonomic significance, it is essential that both the exomorphic and the endomorphic structures of all organs and parts of the three genera be thoroughly investigated.

Dr. Uttam Prakash, of the Birbal Sahni Institute of Palaeobotany, Lucknow, India, has been a visiting scholar during the year and has utilized the wood and slide collections of the Arboretum in connection with his investigations of the fossil floras of central India.

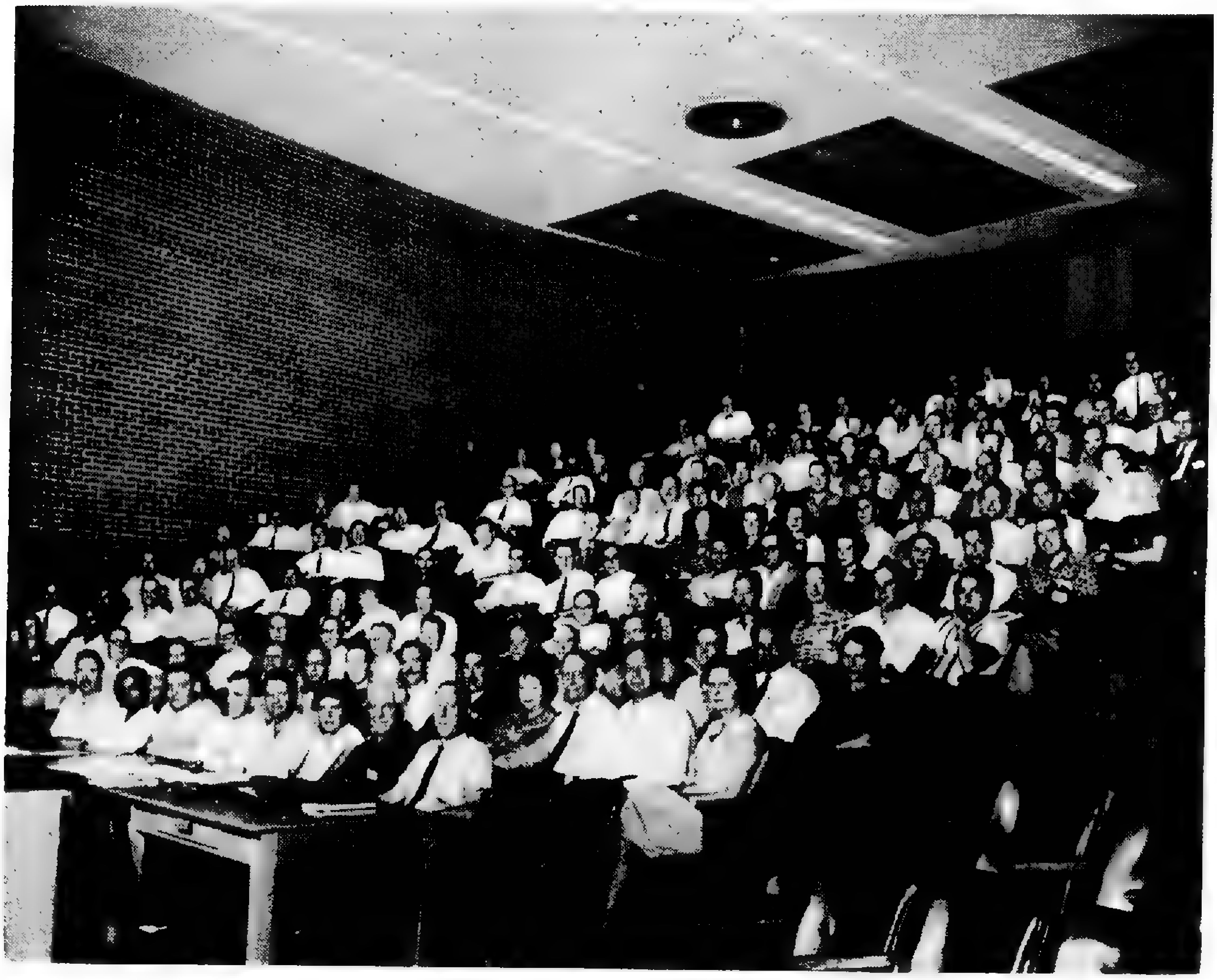
Library:

The efforts of the library staff were again concentrated on classifying and cataloguing the extensive reprint and pamphlet collection. This collection, formerly alphabetized by author as a separate unit, has now been distributed among the various library categories (e.g., monographs, floras, forestry, etc.). Three hundred fifty-six pamphlets were added to the collection, making the total number 17,340 on June 30, 1960. Two hundred sixty-eight books were added to the bound volumes bringing the total of 50,783 volumes. Fourteen hundred cards were added to the main catalogue, an indication of the extensive system of cross referencing of pamphlets and volumes now being developed.

Requests for the interlibrary loan of books remained high and 177 volumes were sent on loan from the combined libraries. An equal number of requests was handled by supplying contura copies, microfilms or photostats. The cost of such reproduction is charged to the person or institution making the request whenever possible. Filling requests in this manner requires more effort on the part of our own staff but reduces the wear on the books and allows them to remain available to our own staff.

The Gray Herbarium Index to American Plants, maintained in Jamaica Plain, received 3000 new entry cards during the year.

The Linnaean Society of London made available 825 microfiche reproductions of the Linnaean Herbarium. A set of these cards was purchased jointly with the Gray Herbarium and will be available in the library.



Meeting of the General Session on Nomenclature of the IX International Botanical Congress, which was attended by Arboretum staff members, photographed at McGill University, Montreal, Canada, on August 18, 1959.

Herbarium:

During the year 8,766 specimens were mounted and added to the herbarium, bringing the total collection to 714,136 specimens on July 1, 1960. The specimens added were in part received during the year and in part collections on hand from previous years that required study or preparation before mounting. During the past year 11,767 specimens were received: 10,585 in exchange, 1074 by gift, 54 for special identification, and a similar number by special subsidy. The largest numbers of specimens came from institutions or collectors in Asia with 2931, 2523 and 1458 specimens from Eastern Asia, Western Malaysia and Papuasia respectively. During the year the Arboretum staff sent 1,664 specimens in exchange to other American institutions and 6,277 to institutions in other countries.

The staff filled ninety-eight requests for loans which comprised 10,903 specimens from the combined Arnold Arboretum and Gray herbaria borrowed by fifty-three different institutions, thirty-six in the United States and seventeen foreign countries from Canada to Argentina and from England to Japan. For their own work or that of students, the staff of the combined herbaria borrowed sixty loans of 5290 specimens from thirty-five institutions, sixteen in the United States and nineteen abroad. The outgoing loans averaged 111 specimens, while the incoming loans averaged 88 specimens. These figures clearly indicate the relative wealth of the herbarium collections in the Harvard herbaria and the desire of other botanists to consult this material.

The research of the herbarium staff, in part supported by special gifts and grants, involves floristic, monographic and anatomical studies. Work is in progress on the floras of the Lesser Antilles, the southeastern United States and several areas of Asia. Monographic studies of genera in Chloranthaceae, Polygonaceae, Theaceae, Thymelaeaceae and Urticaceae are progressing. Three staff members are using detailed anatomical studies for taxonomic purposes in broad surveys of plant structures and in specific scientific problems. The results of this work will be reflected in future papers similar to those cited in the bibliography of the staff.

Travel and Exploration:

During July 1959, Dr. Howard made a final trip to Hawaii in order to record growth data on some experimental projects established on the island of Kauai. On this trip he completed a report on the use and rehabilitation of agricultural lands following strip mining for aluminum ores. The report was submitted to the Commissioner of Public Lands and was used for reference in preparing mining-rehabilitation legislation for the state of Hawaii. During two weeks of December and January, Dr. Howard and Dr. Wagenknecht collected in Florida, Jamaica and the Cayman Islands. The primary purpose of this trip was to observe agricultural and forest plantings on mined-out bauxite lands in Jamaica. The opportunity was taken to collect specimens of cultivated ornamental shrubs and trees in all three areas.

The Arboretum contributed to the support of the expedition of Drs. Ernst and Lucy Abbe, of the University of Minnesota, to Thailand, Cambodia, the Malay Peninsula, and Borneo. The purpose of this expedition was a study of the Asiatic oaks and their relatives. Dr. Abbe sent acorns and other fruits from the mountain areas for trial at the Arboretum where some species from the area are now under cultivation. Approximately a thousand collection-numbers of herbarium specimens were gathered by this expedition.

Gifts and Grants:

During the spring the Arboretum was notified that it had been designated as one of three beneficiaries of a perpetual charitable trust fund established under the will of Mrs. Martha Dana Mercer, of Doylestown, Pennsylvania, a long-time friend of the Arboretum, who died February 21, 1960. The fund is being handled by the Old Colony Trust Company of Boston with the income to be paid to the Arnold Arboretum. The use of this generous gift is unrestricted, and the income when available will be applied to improvement of the physical facilities and for increases in the staff of the Arboretum.

Again this spring the "Friends of the Arnold Arboretum" were generous in their response to the annual appeal for gifts to support the horticultural activities of the Arboretum. Even though such gifts are, with few exceptions, unrestricted they have been used for the most part in the areas of plant propagation and the care of the living collections.

Special gifts or grants from individuals and foundations were received to support the research of various staff members. A gift from Mr. George R. Cooley will support the collaborators of Dr. Wood on the flora of the southeastern United States. In addition, Dr. Reed C. Rollins, Director of the Gray Herbarium, and Dr. Wood received a three year grant from the National Science Foundation for the preparation of a biologically oriented generic flora of the southeastern United States. Dr. Perry received a one year grant from the Public Health Service for investigations on the native medical uses of plants of southeastern Asia. This grant, which may be renewed twice, is utilizing the extensive herbarium collections of the Arnold Arboretum from that area. Grants from the National Science Foundation to Dr. Bailey and Dr. Howard for their research have been continued.

Publications:

Under the editorship of Dr. Wyman, Volume 20 of *Arnoldia* was issued during the year. As a policy the articles in *Arnoldia* are of timely horticultural interest. The issues appear at irregular intervals with twelve numbers comprising each volume. The *Journal of the Arnold Arboretum*, by contrast, is issued quarterly on a regular basis with technical articles largely representing the research of the staff members. Volume 40 of the *Journal* was issued during 1959.

Dr. Wyman advised and coöperated with the Electric Council of New England in the publication of a twenty-four-page booklet, "Trees in Your Community — A Handbook of Selected Trees for New England." The recommendations were often based on growth habits of trees observed in our own small-tree demonstration plot in Weston and on the Arboretum grounds in Jamaica Plain. The booklet is being distributed by New England wire-using utilities to home owners interested in the subject. Orders for 156,000 before printing indicate the need and popularity of such handbooks.

Bibliography of the Published Writings of the Staff and Students

July 1, 1959 — June 30, 1960

BAILEY, IRVING WIDMER. Some useful techniques in the study and interpretation of pollen morphology. Jour. Arnold Arb. **41**: 141–148. 1960.

HOWARD, RICHARD ALDEN. An additional note on *Tillandsia paniculata*. Bromeliad Soc. Bull. **9**: 54–56. 1959.

———. The Director's Report. The Arnold Arboretum during the fiscal year ended June 30, 1959. Jour. Arnold Arb. **40**: 420–436. 1959.

———. Studies in the genus *Coccoloba*, VII. A synopsis and key to the species in Mexico and Central America. Jour. Arnold Arb. **40**: 205–220. 1959.

———. Studies in the genus *Coccoloba*, VIII. Nomenclatural changes. Jour. Arnold Arb. **41**: 40–46. 1960.

———. Studies in the genus *Coccoloba*, IX. A critique of the South American species. Jour Arnold Arb. **41**: 213–229. 1960.

HU, SHIU-YING. Chinese hollies. Tsing Hua Jour. Chinese Stud. Spec. No. Nat. Sci. **1**: 150–184. 1959.

———. A monograph of the genus *Paulownia*. Quart. Jour. Taiwan **12**: 1–54. 1959.

———. A revision of the genus *Clethra* in China. Jour. Arnold Arb. **41**: 164–190. 1960.

JOHNSTON, IVAN M. Some noteworthy American Borages (Studies in the Boraginaceae, XXX). Wrightia **2**: 13–22. 1959.

KOBUSKI, CLARENCE E. A revised key to the Chinese species of *Jasminum*. Jour. Arnold Arb. **40**: 385–390. 1959.

NEVLING, LORIN I., JR. Araliaceae. *In*: Woodson, R. E. *et al.* Flora of Panama. Ann. Missouri Bot. Gard. **46**: 223–242. 1959.

———. A revision of the genus *Daphnopsis*. Ann. Missouri Bot. Gard. **46**: 257–358. 1959.

SAX, KARL. The cytogenetics of facultative apomixis in *Malus* species. Jour. Arnold Arb. **40**: 289–297. 1959.

———. Meiosis in interspecific pine hybrids. Forest Sci. **6**: 135–138. 1960.

———. Standing room only. (Revised paperback edition.) Boston. 1960.

SCHWARTEN, LAZELLA. Index to American botanical literature. Bull. Torrey Bot. Club **86**: 147–157, 206–217, 270–282, 353–365. 1959; **87**: 73–83, 161–171, 229–245. 1960.

THOMAS, JOAB. A monographic study of the Cyrillaceae. Contr. Gray Herb. **186**: 1–114. 1960.

WAGENKNECHT, BURDETTE L. Christmas plants around the world. Arnoldia **19**: 59–77. *pl. 10–13*. 1959.

———. Note on *Elaeagnus commutata*. Rhodora **62**: 29. 1960.

———. Revision of *Heterotheca*, section *Heterotheca* (Compositae). Rhodora **62**: 61–76, 97–107. 1960.

WATERMAN, ANN H. The mints (family Labiatae) of Michigan. Mich. State Univ. Biol. Ser. **1**: 271–302. 1960.

WEBER, CLAUDE. Botanical motifs of the coats of arms on stamps. Topical Times **11**: 14–19. 1959.

———. National flowers and trees on stamps. Topical Times **10**: 200–202. 1959.

———. Palms on postage stamps. Principes **4**: 9–16. 1960.

WILSON, KENNETH A. The genera of Hydrophyllaceae and Polemoniaceae in the southeastern United States. Jour. Arnold Arb. **41**: 197–212. 1960.

———. The genera of the Arales in the southeastern United States. Jour. Arnold Arb. **41**: 47–72. 1960.

———. The leptosporangium of the New Zealand fern *Anarthropteris dictyopteris*. Contr. Gray Herb. **187**: 53–59. 1960.

———. The sporangia of three problematic species of *Polypodium*. Am. Fern Jour. **49**: 147–151. 1959.

——— (with C. E. WOOD, JR.). The genera of Oleaceae in the southeastern United States. Jour. Arnold Arb. **40**: 369–384. 1959.

WOOD, CARROLL E., JR. The genera of Sarraceniaceae and Droseraceae in the southeastern United States. Jour. Arnold Arb. **41**: 149–163. 1960.

———. The genera of Theaceae in the southeastern United States. Jour. Arnold Arb. **40**: 413–419. 1959.

——— (with R. B. CHANNELL). The genera of the Ebenales in the southeastern United States. Jour. Arnold Arb. **41**: 1–35. 1960.

———. The genera of Plumbaginaceae in the southeastern United States. Jour. Arnold Arb. **40**: 391–397. 1959.

———. The genera of the Primulales of the southeastern United States. Jour. Arnold Arb. **40**: 268–288. 1959.

——— (with K. A. WILSON). The genera of Oleaceae in the southeastern United States. Jour. Arnold Arb. **40**: 369–384. 1959.

WYMAN, DONALD. The dwarf evergreens. Horticulture **37**: 472, 473, 485, 486. 1959.

———. Few hawthorns selected from numerous species. Am. Nurseryman **110**(9): 10, 11, 98–101. 1959.

———. Firs contribute stately specimens to northern gardens. Am. Nurseryman **110**(11): 12, 13, 70–72. 1959.

———. Hydrangeas include old favorites in limited list of garden species. Am. Nurseryman **110**(3): 14, 15, 53–55. 1959.

———. Magnolias hardy in the Arnold Arboretum. Arnoldia **20**: 17–28. 1960.

———. Many forms and uses rank maples high among shade trees. Am. Nurseryman **110**(7): 10, 11, 88–94. 1959.

———. Maples liven the autumn scene. Horticulture **37**: 512, 513, 541. 1959.

———. Plant introduction by the Arnold Arboretum. Bull. Univ. Wash. Arb. **22**: 74–76, 100. 1959.

———. Plants of possible merit? Arnoldia **20**: 9–16. 1960.

———. Shrub honeysuckles with pink to red flowers. Arnoldia **20**: 29–32. 1960.

———. Sorting the woody ornamentals — Dogwoods yield varied foliage, flowers, fruits. Am. Nurseryman **111**(9): 10, 11, 105–111. 1960.

———. Sorting the woody ornamentals — Few spireas popular despite range in height and blooming time. Am. Nurseryman **111**(11): 10, 11, 71–76. 1960.

———. Sorting the woody ornamentals — Magnolias provide flowering trees for almost all sections. Am. Nurseryman **111**(7): 12, 13, 69–80. 1960.

———. Sorting the woody ornamentals — *Philadelphus* popular for spring white. Am. Nurseryman **111**(5): 14, 15, 68–73. 1960.

———. Sorting the woody ornamentals — A second look at the popular elm. Am. Nurseryman **111**(1): 12, 13, 78–82. 1960.

———. Sorting the woody ornamentals — The variable *Euonymus*. Am. Nurseryman **111**(3): 16–18, 93–96. 1960.

———. These make spring focal points. Horticulture **38**: 207. 1960.

———. Viburnums. Arnoldia **19**: 47–56. 1959.

———. Viburnums valued for varied species useful in gardens. Am. Nurseryman **110**(5): 14, 15, 61–71. 1959.

———. *Weigela* list reflects changing styles. Am. Nurseryman **110**(1): 12, 13, 30–33. 1959.

———. Why not plant many viburnums? Horticulture **37**: 34, 35, 41. 1960.

RICHARD A. HOWARD, *Director*

Staff of the Arnold Arboretum
1959–1960

RICHARD ALDEN HOWARD, Ph.D., Arnold Professor of Botany, Professor of Dendrology, and Director.

IRVING WIDMER BAILEY, S.D., Professor of Plant Anatomy, *Emeritus.*
JOSEPH HORACE FAULL, Ph.D., Professor of Forest Pathology, *Emeritus.*
KARL SAX, S.D., Professor of Botany, *Emeritus.*

MICHAEL ANTHONY CANOSO, M.S., Curatorial Assistant.*
ANN CLOSE, A.B., Business Secretary.**
HENRY DRAPER, Superintendent, Case Estates.
ALFRED JAMES FORDHAM, Propagator.
HEMAN ARTHUR HOWARD, Assistant Horticulturist.
SHIU-YING HU, Ph.D., Botanist.
FRANCES MARY JARRETT, Ph.D., Botanist.
IVAN MURRAY JOHNSTON, Ph.D., Associate Professor of Botany.
CLARENCE EMMEREN KOBUSKI, Ph.D., Curator.*
MARGARET CATHERINE LEFAVOUR, Herbarium Secretary.
MARY SCANLAN LEHMER, Ed.M., Business Secretary.***
SUSAN DELANO MCKELVEY, A.B., Research Associate.
LORIN I. NEVLING, JR., Ph.D., Assistant Curator.
LILY MAY PERRY, Ph.D., Botanist.
LAZELLA SCHWARTEN, Librarian.*
JOAB LANGSTON THOMAS, Ph.D., Cytotaxonomist.
BURDETTE LEWIS WAGENKNECHT, Ph.D., Horticultural Taxonomist.
ANN H. WATERMAN, M.S., Assistant Librarian.*
CLAUDE WEBER, Botanist, Special Project.*
KENNETH ALLEN WILSON, Ph.D., Botanist, Southeastern Flora Project.*
ROBERT GEROW WILLIAMS, B.S., Superintendent.
CARROLL EMORY WOOD, JR., Ph.D., Associate Curator and Editor.
DONALD WYMAN, Ph.D., Horticulturist.

* Appointed jointly with the Gray Herbarium
** Appointed June 15, 1960
*** Resigned June 15, 1960

INDEX