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JOURNAL
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THE GENERA OF RUTACEAE IN THE SOUTHEASTERN UNITED STATES[1]

GEORGE K. BRIZICKY

RUTACEAE Jussieu, Gen. Pl. 296. 1789.

(RUE FAMILY)

Armed or unarmed trees or shrubs [sometimes scandent or xeromorphic], rarely herbs. Leaves alternate or more rarely opposite, simple or compound, usually glandular-punctate at least at the margin, exstipulate; petioles sometimes winged. Flowers bisexual and/or unisexual, the plants monoecious, dioecious, or polygamous, regular [rarely irregular], usually 3–5-merous, the insertion hypogynous, solitary and axillary or in various axillary or terminal, often cymose, inflorescences. Sepals distinct or connate, very rarely wanting, often glandular-dotted, usually imbricate in bud. Petals distinct [rarely connate or wanting], often glandular-dotted, imbricate or valvate. Stamens as many as the petals and in 1 series (haplostemonous) or twice as many to more numerous and in 2 series (diplo- or obdiplostemonous), those of the outer series often shorter than those of the inner [or occasionally reduced to staminodes]; filaments distinct or ± connate, often conspicuously dilated [or rarely appendaged] at base; anthers versatile, introrse, 2[4]-locular at anthesis, often gland-tipped, longitudinally dehiscent. Intrastaminal nectariferous disc ring-, cup-, or cushion-like, rarely wanting. Gynoecium of (1)2–5(–several),

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[1] Prepared for a generic flora of the southeastern United States, a joint project of the Arnold Arboretum and the Gray Herbarium of Harvard University which has been made possible through the support of George R. Cooley and the National Science Foundation. This treatment follows the pattern established in the first paper in the series (Jour. Arnold Arb. 39: 296–346. 1958) and continued through those in volumes 40–42 (1959–1961). It should be repeated that the area covered by this work is bounded by and includes North Carolina, Tennessee, Arkansas, and Louisiana. The descriptions are based primarily on the plants of this area, with any supplementary material in brackets. References which the author has not seen are marked by an asterisk.

The author is indebted to Dr. Carroll E. Wood, Jr., for his criticism and valuable suggestions, and to Mrs. Gordon W. Dillon, for her careful help in the preparation of the manuscript. The illustration has been made by Dorothy H. Marsh under the direction of C. E. Wood, Jr.

sessile or stipitate, distinct or incompletely to completely connate carpels; stigmas simple or lobed; styles basal, ± lateral or terminal, distinct, connivent or connate; ovaries 1-locular or 2–5(–several) locular, with axile placentae [very rarely 1-locular with parietal placentae]; ovules usually anatropous and epitropous [rarely apotropous], with 2 integuments and a thick nucellus, 1 or 2–many in each locule of the ovary. Fruit of (1)2–5(–several) follicles or drupes, or a capsule, berry, drupe, samara, or schizocarp; pericarp often glandular-pitted to -verruculose. Seeds with or without endosperm, sessile or funiculate, 1 or 2–several in a locule; embryo relatively large, straight or curved, with plano-convex, sometimes convolute [rarely plicate] cotyledons and a superior radicle. TYPE GENUS: *Ruta* L.

A family of about 150 genera and 1600 species, widely distributed in tropical and temperate regions, most abundant in tropical America, South Africa, and Australia, extremely scarce in Europe. Eight genera (five naturalized) in three subfamilies are represented in our area.

The presence of secretory cavities (or at least inner multicellular glands) containing an aromatic volatile oil in stems (in cortex, rarely in phloem), leaves, floral parts, and pericarp of fruits is a characteristic feature of the family, distinguishing Rutaceae from their morphologically very similar allies, especially Simaroubaceae and Meliaceae. Rutaceae are also closely related to Zygophyllaceae, Cneoraceae, and Burseraceae.

The family, in general, seems to be entomophilous, insects being attracted by the strong smell of the flowers and/or by usually abundant nectar, sometimes also by showy corollas (e.g., *Citrus* spp.). Ornithophilly has also been presumed for some genera. Cross-pollination seems to be the rule. In some genera self-pollination is prevented by dicliny, or (in monoclinous genera) by proterandry (e.g., *Ruta*, *Ravenia*, *Barosma*) and/or the position of the stigma in regard to the anthers (e.g., *Triphasia*, *Dictamnus*). In some genera, however, both cross- and self-pollination seem equally possible and effective (e.g., *Choisya*, *Skimmia*, *Murraya*, *Poncirus*, *Citrus*). Cleistogamy has been recorded in the New Zealand *Melicope simplex* A. Cunn. Nucellar embryony (apomixis) has been shown in several genera (e.g., *Zanthoxylum*, *Esenbeckia*, *Ptelea*(?), *Triphasia*, *Aegle*, *Murraya*, *Poncirus*, *Citrus*), but probably is of even wider distribution in the family. Zygotic (gametic) polyembryony seems to be very rare, having been recorded or presumed in only a few cases.

Chromosome counts have been made for about 50 genera and 150 species. On the basis of these counts, nine appears to be a basic number for the family. (Banerji [1954], however, suggested three as a basic number and nine as a result of secondary polyploidy for *Citrus grandis* (L.) Osbeck.) The family, in general, appears to be ± euploid, except the Australian aneuploid tribe Boronieae (which has chromosome numbers based on 7, 8, 9, 11, 13, 17, 19) and apparently some genera from other tribes. Polyploidy is widely distributed in Rutaceae and seems to be of importance in the evolutionary development of the family.

The family is of economic importance, notably for a number of important fruits (*Citrus* spp., *q.v.*), timbers, aromatic oils (e.g., *Citrus* spp., *Ruta graveolens* L.), various products of medicinal value, and ornamentals.

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KEY TO THE GENERA OF RUTACEAE

General characters: *leaves usually pinnate to 3–1-foliolate, alternate, rarely opposite; leaflets (at least at margin), perianth parts, and fruits glandular-, often pellucid-punctate.*

A. Plant a perennial herb or subshrub; leaves 2- to 3-pinnately divided; flowers greenish yellow, bisexual, 4–5-merous with 8–10 stamens; fruits 5-lobed, many-seeded capsules. . . . . 1. *Ruta.*

A. Plants woody, shrubs or trees.

  B. Flowers unisexual or uni- and bisexual, small, yellowish or yellowish white, 3–5-merous, sometimes without calyx; stamens as many as petals; gynoecium apo- or syncarpous, (1)2–5-carpellate; fruits dry; leaves alternate.

    C. Plants dioecious or monoecious, often prickly; leaves pinnate, usually 5 or more foliolate; flowers unisexual, with or without sepals; gynoecium apocarpous, (1)2–5-carpellate; fruits dehiscent, 1-seeded follicles. . . . . 2. *Zanthoxylum.*

    C. Plants polygamous, unarmed; leaves usually 3-foliolate; flowers uni- and bisexual; gynoecium syncarpous, 2-loculate; fruit a flat, indehiscent, 2-locular, 2-winged samara. . . . . 3. *Ptelea.*

  B. Flowers usually bisexual, small to large, usually white, 3–5-merous; stamens twice as many as petals, or more numerous; gynoecium syncarpous, 2–18-locular, rarely 1-carpellate; fruits fleshy drupes or berries; leaves alternate or opposite.

    D. Stamens twice as many as petals; flowers relatively small; ovary 1–5-loculate; fruits small, pulp without pulp-vesicles; petioles not winged.

      E. Ovary 1-carpellate; fruit a 1-seeded drupe; leaves opposite, 3-foliolate; flowers usually 4-merous, paniculate; unarmed, aromatic, resinous shrubs or trees. 4. *Amyris.*

      E. Ovary 2–5-carpellate; fruit a 1–3-seeded berry; leaves alternate.

        F. Flowers (4)5-merous, in short, spikelike axillary panicles; berry subglobular, sometimes depressed at apex and slightly oblique, white to pink, 1–3-seeded, edible; unarmed shrubs or trees with pinnate, usually 1–3(5)-foliolate leaves and large leaflets. . . . . 5. *Glycosmis.*

F. Flowers usually 3-merous, solitary or in 2's or 3's in the leaf axils; berry subglobular, sometimes apiculate, reddish orange to crimson, 1–3-seeded, insipid; shrubs with solitary or paired, axillary spines; leaves 3-foliolate, leaflets small. .... 6. *Triphasia.*

D. Stamens numerous (20–60); flowers relatively large; perianth usually 5-merous; ovary 6–18-loculate; fruits (hesperidia) greenish yellow, yellow, orange to reddish orange, large, pulp formed by pulp vesicles; usually thorny shrubs or trees, mostly with winged petioles.

G. Flowers on the previous year's branchlets; stamens distinct; ovary 6–8-loculate; fruits relatively large, pubescent, pulp with very sour and acrid juice; leaves 3-foliolate, deciduous. ... 7. *Poncirus.*

G. Flowers on new branchlets; stamens polyadelphous; ovary 8–18-loculate; fruits large, glabrous, pulp with sweet or sour not acrid juice; leaves 1-foliolate, persistent. .... 8. *Citrus.*

Subfam. RUTOIDEAE Engler

1. **Ruta** Linnaeus, Sp. Pl. **1**: 383. 1753; Gen. Pl. ed. 5. 180. 1754.

Heavy-scented perennial herbs, subshrubs [or shrubs]. Leaves alternate, usually glandular-punctate, compound [or simple], odd-pinnate to -bipinnate, with pinnae or pinnules respectively deeply cut (divided) into obovate-cuneate to oblanceolate or oblong segments. Flowers bisexual, 4- or 5-merous, in terminal, panicled cymes with simple or 3-fid bracts. Sepals ± connate at base, persistent. Petals yellow or greenish, glandular-punctate, spatulate-cochleariform with incurved, hooded apex, ± clawed, denticulate [fimbriate or entire], imbricate in bud. Stamens 8–10, in 2 series, the outer (antipetalous stamens) usually somewhat shorter than the inner whorl (antisepalous stamens); filaments filiform, broadened toward the base; anthers oblong. Gynoecium syncarpous, 4–5-carpellate, raised on an intrastaminal, cushion-like, nectariferous disc; stigma small; style central; ovary deeply 4- or 5-lobed, 4- or 5-locular, with [2 to] numerous ovules on axile placentae. Capsule glandular-punctate, 4- or 5-lobed, 4- or 5-locular, [few- to] many-seeded, dehiscent loculicidally inward (adaxially) at apex, [or split into indehiscent segments]. Seeds angled, brown, tuberculate; endosperm fleshy; embryo slightly curved, cotyledons sometimes 2-lobed. (Including *Haplophyllum* A. L. Juss.). LECTOTYPE SPECIES: *R. graveolens* L.; see P. Wilson, N. Am. Fl. **25**: 212. 1911. (Classical Latin name of the plant [since Cicero in literature], related to and questionably derived from Greek, *rhyte*, the name of the plant in Nicander; etymology obscure.) — RUE.

A genus of about 60 species, ranging from Macaronesia eastward through the Mediterranean region to central Asia and eastern Siberia. *Ruta graveolens* L., common rue, $2n = 72, 81$, native to the Mediterranean region but widely naturalized in temperate parts of the Old World, is introduced and more or less naturalized in the eastern United States. There are few reliable records from our area and further data regarding the distribution of this species in the southeastern United States are very desirable.

The species is proterandrous. The stamens execute peculiar nutation movements during the expansion of the flowers. Pollination agents recorded are small Hymenoptera, Coleoptera, and Diptera. Polyploidy seems to be of frequent occurrence in the genus, and at present diploid, tetraploid, and octoploid species are known. The occurrence of a nonaploid chromosomal race of the otherwise octoploid *Ruta graveolens* has also been recorded. However, no general conclusions can yet be drawn on the basis of the few counts.

The common rue is of ancient culture as an ornamental, spice, and medicinal plant. Because of a volatile oil ("oil of rue") it was formerly used in medicine, but at present, its use is quite limited because of very unpleasant secondary effects. The species should be regarded as ± poisonous. Contact with fresh leaves of the plant produces a dermatitis in some individuals. Poisoning by oil of rue is characterized by gastroenteritis. The Mediterranean *R. chalapensis* L. and some other species have also been used locally in much the same way as *R. graveolens*. The latter and a few other species are cultivated as ornamentals.

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See also under family references ENGLER (1931, pp. 243–246), GALLET (1913, pp. 23–27), NEGODI (1937, pp. 93–97, 101), URBAN (1883, pp. 372, 373, 401), WILSON (1911, p. 212).

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2. **Zanthoxylum** Linnaeus, Sp. Pl. 1: 270. 1753; Gen. Pl. ed. 5. 130. 1754.

Deciduous or evergreen trees or shrubs, often armed with prickles which sometimes become elevated on broad-conical or -pyramidal corky excrescences; bark aromatic. Leaves alternate, odd- or even-pinnate to 1-foliolate; leaflets opposite or alternate, frequently inequilateral, crenulate or entire, glandular-punctate, at least at the margin; petiole and rachis winged or wingless, unarmed or prickly. Plants dioecious, monoecious, [or polygamous]; flowers small, white to greenish yellow, unisexual [and/or bisexual], in axillary short spikes or cymose fascicles or in terminal, sometimes corymbiform, panicles. Sepals 3–5[10], distinct or ± connate, deciduous or persistent, or apparently wanting. Petals 3–5[8], imbricate [or valvate] in bud. Stamens 3–5[8], distinct, alternate with the petals, rudimentary (staminodial) or wanting (or sometimes transformed into carpels) in ♀ flowers; filaments filiform to subulate; anthers ovate, elliptic to subcircular in outline. Intrastaminal disc small, often pulvinate, or obscure. Gynoecium of (1)2–5 sessile or stipitate, distinct or partially united [very rarely completely connate] carpels, rudimentary in ♂ flowers; stigmas capitate, distinct or connate; styles sublateral, distinct, connivent or connate toward the summit; ovaries usually 1-carpellate and -locular [very rarely ovary compound, 2–5-carpellate and -locular] with 2 collateral, pendulous ovules in each carpel [or locule]. Fruits 2-valved follicles, distinct or connate at base, stipitate to sessile, firm-walled or fleshy, glandular-punctate, with separating (loose) or adherent endocarp, 1(2)-seeded. Seeds obovoid to subglobular [or ± lenticular], black [blue-black, brown, or dark red], shining, with a crustaceous testa and fleshy endosperm, at maturity often hanging from the carpels on slender funicles; embryo axial, straight or somewhat curved, with a short radicle and flat, almost circular cotyledons. (Including *Fagara* L., nom. cons., type: *F. Pterota* L.) TYPE SPECIES: *Z. americanum* Mill. ("Xanthoxylum") (*Z. fraxineum* Willd.); see F. R. Fosberg, Taxon 8: 103–105. 1959. (Name from Greek, *xanthos*, yellow, and *xylon*, wood.) — PRICKLY ASH.

A genus of about 215 species, primarily pantropical, extending with several species into the Temperate Zone of eastern Asia and North America. Two subgenera sometimes regarded as distinct genera are recognized in the present treatment.[2]

Subgenus ZANTHOXYLUM, with unisexual flowers with petaloid [or sometimes sepaloid], 4–5[10]-merous, "simple" perianth in a single series (presumably petals) and 4–5[8] stamens or [1]3–5 carpels, includes about 15 species, primarily of the Temperate Zone of eastern Asia and North America, but with at least two species in Central America. *Zanthoxylum americanum* Mill., common or northern prickly ash, $2n = 68$, 136, a shrub or small tree with odd-pinnate leaves, paired pseudostipular prickles (rarely prickleless) and yellow-green flowers in sessile, axillary, umbellate clusters, expanding before leaves, is the only eastern North American species of the subgenus, occurring from Georgia and Alabama northward beyond our area to North Dakota, Minnesota, Ontario, and western Quebec. *Zanthoxylum mazatlanum* Sandwith is known from

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[2] The occurrence of species apparently transitional in the character of the perianth between *Zanthoxylum* and *Fagara* is ample reason to regard both as components of a single genus. See "Taxonomic and Nomenclatural Notes on *Zanthoxylum* and *Glycosmis* (Rutaceae)" in the present issue of this *Journal.*

Mexico; *Z. Williamsii* Standl. and *Z. ferrugineum* Radlk. occur in Honduras and Costa Rica respectively.

Subgenus FAGARA (L.) Triana & Planch. (*Fagara* L.), with unisexual [or both uni- and bisexual] flowers with 3–5[–8]-merous perianth in two series (i.e., sepals and petals), 3–5[–7] stamens and/or 3–5 carpels, includes about 200 species, primarily of the tropics of both hemispheres, four in our area. *Zanthoxylum Clava-Herculis* L., southern prickly ash, Hercules' club, $2n$ = ca. 72, armed trees or shrubs with odd-pinnate leaves and usually 5-merous flowers in terminal panicles, occurs on the Coastal Plain from southern peninsular Florida to Texas and southeastern Virginia, northward to southern Arkansas and Oklahoma. The South American-West Indian *Z. Fagara* (L.) Sarg. (*Fagara Pterota* L.), an evergreen shrub or tree usually armed with pseudostipular prickles, with odd-pinnate leaves having relatively small leaflets and winged petioles and rachises, and 4-merous flowers in short axillary spikes, reaches its northern limit in central Florida and in southern and southwestern Texas beyond our area. The West Indian *Z. coriaceum* A. Rich., a ± prickly tree or shrub, usually with even-pinnate, coriaceous leaves and 3-merous flowers in terminal panicles, is known from southern peninsular Florida and the Florida Keys. The West Indian *Z. flavum* Vahl, yellow-wood, satinwood, an unarmed tree with odd-pinnate, occasionally 3–1-foliolate leaves and 5-merous flowers in terminal panicles, occurs on the lower Florida Keys.

Little is known regarding pollination, but bees and various Diptera have been recorded as the most frequent visitors of the flowers of *Z. americanum.* Nucellar polyembryony has been found in a few species (e.g., *Z. americanum,* "*Z. Bungei* Planch.," *Z. alatum* Roxb.), but probably is of wider distribution within the genus. The few published chromosome counts ($2n = 32, 64, 68, 70, 72, 136$) indicate polyploidy and perhaps aneuploidy. No interspecific hybrids have been recorded. A modern monograph is highly desirable.

The dried bark of *Zanthoxylum americanum* and *Z. Clava-Herculis,* "toothache bark," "prickly ash bark," or "xanthoxylum," has been applied as a stimulant, tonic, and sialagogue in the United States, and the bark of *Z. alatum* has been used against fever, dispepsia, diarrhoea, and cholera in India. *Zanthoxylum americanum* and some eastern Asiatic species are sometimes cultivated as ornamentals. Various other species have been used for timber, spices, and medicines.

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Subfam. TODDALIOIDEAE Engler

3. **Ptelea** Linnaeus, Sp. Pl. **1**: 118. 1753; Gen. Pl. ed. 5. 54. 1754.

Unarmed shrubs or small trees, with bitter bark and foliage disagreeably scented when crushed. Leaves alternate, usually 3-foliolate, rarely 4–5-foliolate, leaflets entire or toothed, glandular-punctate, glabrous to densely soft-hairy beneath. Plants usually polygamous, the flowers bisexual and/or unisexual, greenish or yellowish white, aromatic, in terminal corymbiform, cymose panicles. Sepals usually 4 or 5, distinct, imbricate. Petals usually 4 or 5, relatively narrow, surpassing the sepals, imbricate. Stamens usually 4 or 5, alternating with petals, hypogynous, inserted at base of a disc, very short, with imperfect sterile anthers in ♀ flowers; filaments subulate, hairy in the lower half; anthers ovate-cordate, introrse. Gynoecium syncarpous, usually 2-carpellate, inserted on a low disc in bisexual and ♀ flowers, very small, imperfect (lacking style and with rudimentary stigmas), raised on a conspicuous truncate-pyramidal to subglobular disc in ♂ flowers; stigma capitate, usually 2-lobed; style relatively short and slender; ovary compressed, usually 2-locular and narrowly 2-winged, with 2 superposed ovules (the lower usually sterile) on axile placenta in each locule. Fruit a flat, subcircular to obovate, glandular-punctate samara with 2 broad, thin, reticulate lateral wings completely encircling the indehiscent 2-locular and 1(2)-seeded body. Seeds laterally compressed, semiovate to semilanceolate in outline, acute at apex, rounded at base, dark reddish brown to black, densely papillose and glossy on the surface; seed coat thin, leathery; endosperm fleshy, thin; embryo large, straight, with oblong to ellipsoid cotyledons and short, stoutish superior radicle; germination epigeous. Lectotype species: *P. trifoliata* L.; see P. Wilson, N. Am. Fl. **25**: 208. 1911. (Classical Greek name of elm, *Ulmus*, transferred by Linnaeus to this genus on account of the similar fruit.) — Hop-tree, shrubby trefoil.

A genus of three (according to P. Wilson) or probably more species, of temperate North America. *Ptelea trifoliata* L. (including *P. microcarpa* Small fide Wilson), common hop-tree, stinking ash, $2n = 36, 42$, a shrub or small tree, very variable in regard to size, shape, and pubescence of the leaflets and size and shape of fruits, occurs from northern Florida, throughout our area, and beyond to Texas and northern Mexico, Nebraska, Iowa, Michigan, southern Ontario, New York, and Connecticut. Its variant var. *mollis* Torrey & Gray, regarded by Wilson as *P. tomentosa* Raf., with branchlets, lower surface of the leaflets and inflorescences subtomentose, ranges from Georgia to North Carolina and westward to Oklahoma, Arizona, and Mexico. *Ptelea serrata* Small, an irregularly branched shrub with shallowly serrate leaflets, probably belongs with the preceding. *Ptelea Baldwinii* Torrey & Gray, a shrub with leaflets smaller and narrower than in *P. trifoliata*, has been recorded only from northeastern Florida in our area but is apparently conspecific with *P. angustifolia* Benth., widely distributed in the western United States from southern Texas to Colorado, Utah, California, New Mexico, and Arizona, and southward into Mexico.

Vegetative reproduction by root sprouts has been recorded in *Ptelea trifoliata*. The occasional occurrence of 3- or 4-carpellate ovaries, sometimes accompanied by a few additional antipetalous stamens, is noteworthy. Polygamy seems to be a generic character. Although herbarium specimens usually are represented either by male or by female inflorescences, sometimes both bisexual and male flowers occur in the same inflorescence; more rarely a few female flowers (usually terminal) are found in the male inflorescence. Cross-pollination is the rule because of the predominance of unisexual flowers, but self-pollination seems to be possible in the bisexual flowers. Bees, especially short-tongued species, and a few other Hymenoptera and Diptera have been recorded as pollinators. The occurrence of a nucellar embryo has been recorded in *P. trifoliata* (Mauritzon, 1935), but the observations (made on scanty material) need verification. Only two chromosome counts are reported for the genus. No hybrids have been recorded, but, Desai (1960), investigating the cytology of *P. trifoliata* grown in England ($2n = 42$), observed meiotic irregularities resulting in high sterility and concluded a possible hybrid origin for the plant.

Over 60 species of *Ptelea* have been described, but these are apparently not well understood at present, and the reduction of all of them to two or three species is open to question. A modern monograph is urgently needed.

Ptelea trifoliata is a generally known ornamental plant. Its bitter fruits have sometimes been used in brewing as a substitute for hops, hence the English name of the genus. The bark is reputed to possess medicinal properties as a weak tonic.

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4. **Amyris** Linnaeus, Syst. Nat. ed. 10. 2: 1000, 1367. 1759.

Usually glabrous shrubs or trees with resinous, fragrant wood. Leaves opposite [subopposite or alternate], odd-pinnate, often 3–5[rarely 1]-foliolate, with glandular-punctate leaflets and unwinged [or winged] petioles. Flowers small, bisexual [rarely unisexual], usually 4[rarely 3 or 5]-merous, pediceled, in terminal or axillary panicled cymes. Calyx cuplike, 4-lobed, glandular-dotted, persistent. Petals 4, white, glandular-dotted, imbricate in bud. Stamens 8, in 2 series, inserted at base of a disc or of the ovary; filaments filiform; anthers ovate to oblong, introrse, 2-locular at anthesis. Intrastaminal disc pulvinate, gynophore-like, supporting gynoecium, or wanting. Gynoecium 1-carpellate; stigma capitate to discoid-subcapitate; style very short and stout or wanting; ovary 1-locular, with 2 collateral ovules suspended from the top of the locule. Drupes globular, ellipsoidal to obovate, black [or reddish], often glaucous, dotted with glands, aromatic, oily, the endocarp chartaceous, 1-seeded. Seed pendulous, with thin, membranaceous testa, lacking endosperm; embryo with plano-convex, fleshy, glandular-dotted cotyledons and a short, superior radicle. LECTOTYPE SPECIES: *A. balsamifera* L.; see P. Wilson, N. Am. Fl. **25**: 216. 1911. (Name apparently derived from Greek, *a*, with, abounding in, and *myron*, balsamic juice, resin, with reference to the balsamic properties of the genus.)[3] — TORCHWOOD.

A genus of about 20 species of the West Indies and especially of cis-Amazonian tropical America, extending southward (with one species?) to Peru and northward (with a few species) to Texas and Florida. The South American-West Indian *A. balsamifera* L., with 3–5-foliolate leaves, leaflets dull underneath, puberulous inflorescences, and puberulous, stipitate ovary, occurs in southern peninsular Florida and the Florida Keys. The primarily West Indian *A. elemifera* L., differing from the preceding especially in the glabrous inflorescences and glabrous, sessile ovaries, is

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[3] More frequently the Greek prefix *a* has been used in a reverse sense, *without, devoid of, not*. This has led Little (U.S. Dep. Agr. Handb. **41**: 57. 1953) to a different, hardly probable derivation: "not myrrh," "not true myrrh."

also known from southern peninsular Florida and the Keys, and the very similar *A. maritima* Jacq., with stipitate ovaries, has been recorded from Key West. Wilson and Small included this last species in *A. elemifera*, but Urban (1896, 1920) regarded it as distinct.

The genus is, in general, very imperfectly known. The species, especially the West Indian, are closely related, and their delimitation is often weak, sometimes being based on few, questionably specific characters. A modern revision based on field observations, experimental cultures, and cytology is very desirable.

The resinous timber, especially that of *Amyris balsamifera* and *A. elemifera*, is of excellent quality but is scarce and of small size. It is used locally for fuel, torches (fragrant when burned), small cabinet work, and to a limited extent as a source of an oleoresin, Mexican elemi, which is used locally in medicine.

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Subfam. AURANTIOIDEAE Engler

5. **Glycosmis** Corréa, Ann. Mus. Hist. Nat. Paris **6**: 384. 1805.

Unarmed, evergreen shrubs or trees. Leaves alternate [rarely opposite], odd-pinnate, often 1–3(5)-foliolate; leaflets pellucid-punctate, entire [serrate or crenulate], ± inequilateral at base; petiole articulated with the blade in 1-foliolate leaves. Flowers relatively small, fragrant, bisexual, (4)5-merous, with very short, stout pedicels, in rusty-villosulous, spike-like cymes arranged in axillary panicles. Sepals (4)5, nearly distinct [or ± connate], triangular-semicircular, ± fleshy, imbricate. Petals (4)5, elongate, somewhat concave, white, imbricate. Stamens (8)10, the antipetalous shorter than the alternipetalous, filaments flattish [or filiform], dilated upward [or downward] and abruptly narrowed into an acuminate tip; anthers relatively short, ovate-cordate, often apiculate, gland-tipped. Gynoecium 2–5-carpellate, syncarpous, raised on a cushion-like [or cylindrical] nectariferous disc; stigma broad, cushion-like (convex-disciform to semiorbicular), persistent; style often indistinct, short and very stout, merging into a subglobular or ellipsoidal 2–5-locular ovary covered with glands; ovules pendulous, one in each locule. Fruit a relatively small berry with thin pulp, ± globular, sometimes depressed at apex and ± oblique, 1–3-seeded. Seeds without endosperm, ellipsoid to subglobular, with a membranaceous testa; embryo with plano-convex cotyledons and a short superior radicle. Lectotype species: *G. arborea* (Roxb.) DC. (*Limonia arborea* Roxb.); see P. Wilson, N. Am. Fl. **25**: 215. 1911.[4] (Name from Greek, *glycys*, sweet, and *osme*, scent, odor, referring to the fragrant flowers of the genus.)

A genus of about 35 species of southeastern Asia, the East Indies, the Philippines, New Guinea, and northeastern Australia. The southeastern Asiatic *Glycosmis parviflora* (Sims) Little (*G. citrifolia* (Willd.) Lindl.), with white or pink subglobular berries, widely cultivated in the warm regions of both hemispheres, has become naturalized in the hammocks of Key West (Small, Manual, 1933; Everett, 1940). Wilson (1911) and some other authors have included this species in "*G. pentaphylla* (Retz.) DC." or "*G. pentaphylla* (Retz.) Corréa."

The present knowledge of the genus is very imperfect, and both taxonomy and nomenclature are complex. Tanaka has studied the genus critically for many years but has not yet published a monograph.

The genus is of no economic importance.

References:

See also under family references Engler (1931, pp. 316–318), Penzig (1887, pp. 194–209, *pls. 19–21*), Swingle (1943, pp. 153–158), and Wilson (1911, p. 215).

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6. **Triphasia** Loureiro, Fl. Cochinch. 152. 1790.

Evergreen shrubs with paired, or sometimes solitary, axillary spines. Leaves 3-foliolate [or simple], occasionally 1- or 2-foliolate; leaflets relatively small, subsessile, the terminal somewhat larger than the lateral, thickish, without evident reticulation, crenulate to crenate, glandular-dotted; petioles short, puberulous, not articulated with the leaf blade. Flowers 1–1.6 cm. long, bisexual, 3[5]-merous, fragrant, solitary or in 2- or 3-flowered cymes in the leaf axils, pedicels short, minutely 2-bracteolate. Calyx cuplike, 3[5]-lobed, persistent. Petals 3[5], linear to lanceolate-oblong, imbricate. Stamens 6[10] in 2 series; filaments slender, broadened toward the base; anthers small, oblong. Disc ringlike to short-cylindric, encircling the stipelike base of the ovary. Gynoecium 3[5]-carpellate, syncarpous; stigma ± capitate, 3[5]-lobed; style slender, deciduous; ovary ovoid to ellipsoid, narrowed toward the ends, 3[5]-locular, with a solitary ovule in each locule. Berry small, dull reddish orange or crimson, with

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[4] See also "Taxonomic and Nomenclatural Notes on *Zanthoxylum* and *Glycosmis* (Rutaceae)" in the present issue of this *Journal.*

glandular-dotted exocarp (peel), mucilaginous, pulpy flesh, and 1–3[–5] seeds. Seeds ellipsoid to subglobular, lacking endosperm, with fleshy or leathery testa; embryo straight, with plano-convex, sometimes unequal cotyledons and small radicle. (Including *Echinocitrus* Tanaka.) TYPE SPECIES: *T. Aurantiola* Lour. (= *T. trifolia* (Burm. f.) P. Wils.). (Name from Greek, *triphasios*, threefold, triple, referring to the usually trifoliolate leaves and trimerous flowers of the type species.) — LIMEBERRY.

A genus of three species, probably native in southeastern Asia, the East Indies, and the Philippines. *Triphasia trifolia* (Burm. f.) P. Wilson, common limeberry, $2n = 18, 36$, apparently indigenous to southeastern Asia and the East Indies, has been recorded as naturalized on the Coastal Plain from Florida to Texas. This species, much cultivated as an ornamental and hedge-plant in the warm regions of both hemispheres, is widely naturalized in the tropics. Flowers with 4-merous perianth and gynoecium sometimes occur in this species.

Cross-pollination by insects seems to be the rule, spontaneous self-pollination being prevented by the position of the stigma which considerably overtops the anthers. Nucellar polyembryony has been recorded in *Triphasia trifolia*. A spontaneous autotetraploid form of this species, with leaves thicker and flowers larger than in the diploid, typical form, has been found. Fruits of *T. trifolia* are edible.

REFERENCES:

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7. **Poncirus** Rafinesque, Sylva Tellur. 143. 1838.

Shrubs or much-branched small trees with green twigs armed with stout, axillary thorns often flattened at base; foliage spurs with extremely short internodes developing from dormant buds just above the thorns on the previous year's branches. Leaves deciduous, palmately 3-foliolate; leaflets sessile, shallowly crenulate to serrate above the middle; petiole articulated with the blade, narrowly winged. Flowers fairly conspicuous, 3–6 cm. in diameter, bisexual, subsessile, solitary or in pairs on the preceding season's twigs (just above the thorns). Sepals 4–7, usually 5, distinct, ovate, deciduous. Petals 4–7, usually 5, spatulate to obovate, with claw-like bases, white, soon deciduous. Stamens 20–60; filaments free, unequal in length, slender, broadened toward the base; anthers ovate to ovate-oblong in outline, gland tipped. Intrastaminal disc annular to shallowly cupular, hairy. Gynoecium 6–8(usually 7)-carpellate, syncarpous; stigma capitate; style short and stout; ovary subglobular, hairy, 6–8 (usually 7)-locular; ovules 4–8 in 2 collateral rows on axillary placentae in each locule. Hesperidium subsessile, globular to pyriform, 3–5 cm. in diameter, dull lemon-colored, fragrant when ripe, finely and densely pubescent, many-seeded; peel (exocarp and mesocarp) soft, 5–10 mm. thick, with numerous oil cavities, rather rough; pulp (forming together with the inner walls of the locules the endocarp of fruits) consisting of elongate, cylindric-conical, slender-stalked vesicles (outgrowths of the inner surface of the tangential walls of the locules) filled with a very acid juice and droplets of acrid oil in the center, and with minute, lateral, irregularly branched appendages (FIG. 1g, h) which presumably secrete a viscous fluid. Seeds lacking endosperm, plump, ovoid, the testa leathery; embryos often several in a seed, differing much in size, with 2 equal or unequal cotyledons and a short radicle; germination hypogeous, the young seedlings at first with bractlike cataphylls, then intermediate forms that soon merge into normal 3-foliolate leaves. TYPE SPECIES: *P. trifoliata* (L.) Raf. (*Citrus trifoliata* L.). (From French, *poncire*, of obscure origin but applied earlier to a variety of citron with large, tuberculate fruits [*C. Medica* var. *tuberosa* Risso], perhaps also to other similar varieties.) — TRIFOLIATE ORANGE.

The single species, *Poncirus trifoliata*, $2n = 18, 36$, native to central and nothern China, has become ± naturalized in our area on the Coastal Plain from Florida to Georgia and Texas. *Poncirus* shows only a few insignificant variations and seems to be the most stable species of the group of "citrus fruits" (including also *Fortunella*, *Eremocitrus*, *Clymenia*, *Microcitrus*, and *Citrus*) which have been cultivated for long periods by man (Swingle, 1943).

The floral biology of the species does not seem different from that of *Citrus*. Both cross- and self-pollination seem to be almost equally effective. Nucellar polyembryony, apparently of an induced type, has been proved. A small percentage of autotetraploids sometimes occurs among nucellar seedlings and those of open pollination. *Poncirus* hybridizes freely with species of *Citrus* and *Fortunella*, producing hybrids which usually are female-sterile but which occasionally produce some fertile pollen. Because of competition with nucellar embryos in a seed (and perhaps from other causes) the sexual embryo, when produced, seldom reaches maturity in most of the *Poncirus* × *Citrus* hybrids. This leads to the development of maternal-type seedlings, seriously interfering with the normal segregation and recombination necessary in plant breeding (Yarnell, 1942). Vigorous, variable trigeneric hybrids, some very complex, have also been produced. The citrangedin, involving *Citrus*, *Fortunella* and *Poncirus*, is extremely resistant to cold and is notable in that it shows clearly traces of all three genera, but is strikingly different from any species of those genera.

Generic distinctions in the Aurantioideae are weak and are much in need of further critical study. Although genetic evidence shows that *Citrus* and *Poncirus* are closely related, the latter has a number of differ-

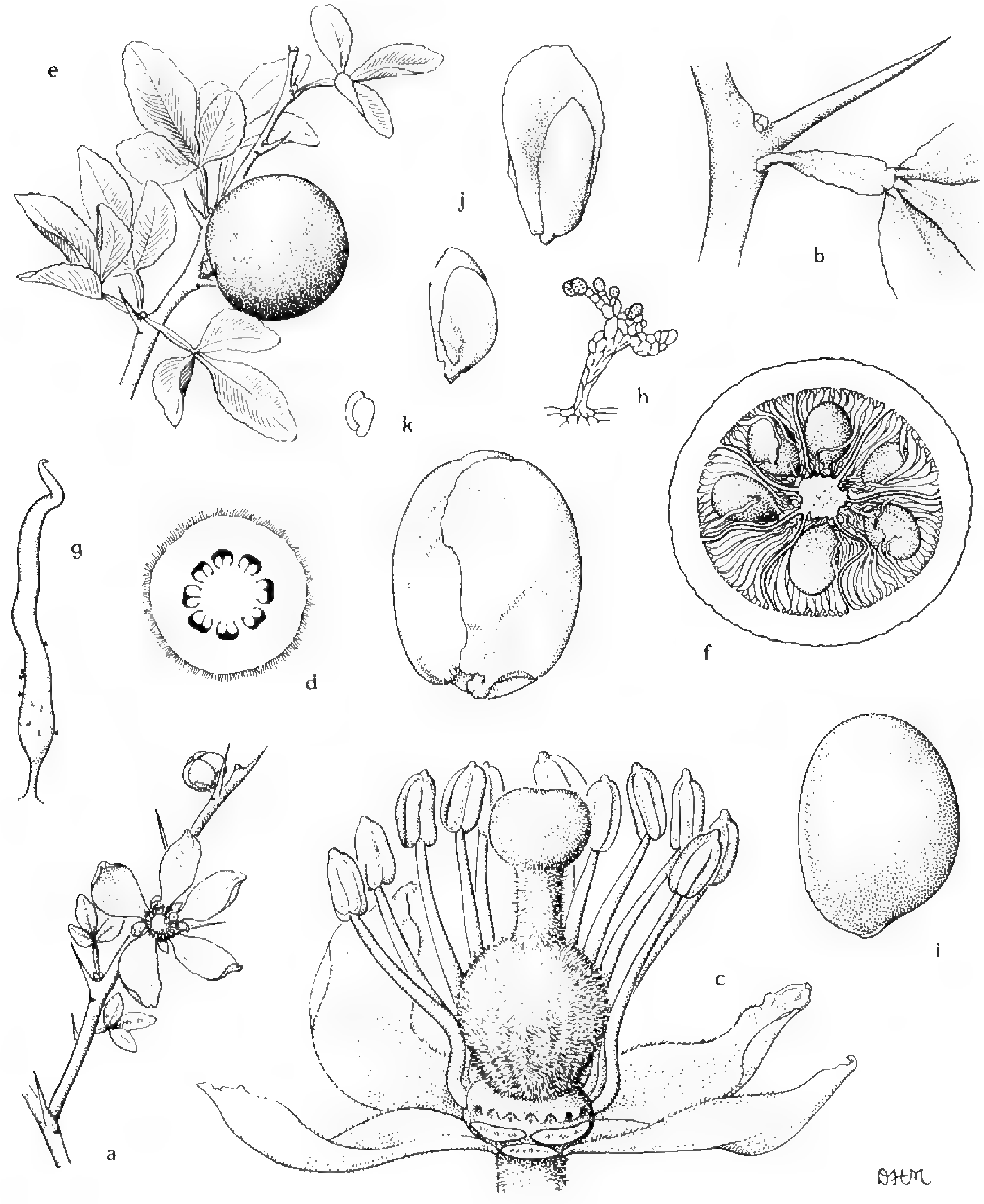

FIG. 1. **Poncirus.** a–k, *P. trifoliata*: a, flowering branchlet, × ½; b, portion of twig, showing winged petiole with base of leaf blade, axillary thorn, and bud, × 1; c, flower (two petals, one sepal removed), showing insertion of stamens, disc, and gynoecium, × 4; d, ovary, diagrammatic cross section, showing ovules on axile placentae, × 6; e, fruiting branch — note foliage spurs. × ½; f, mature 7-locular fruit, showing seeds embedded in pulp vesicles (many omitted), × 1; g, pulp vesicle with minute multicellular lateral appendages, × 3; h, appendage of pulp vesicle (after Penzig, 1887), × ca. 110; i, seed, × 3; j, k, four of nine embryos from a single seed (nucellar polyembryony), × 4 — note mostly unequal cotyledons and different sizes and shapes of embryos.

ential characters: deciduous 3-foliolate leaves; overwintering flower buds covered with bud scales; densely pubescent fruits; pulp vesicles with minute lateral appendages; pith with transverse plates of thick-walled cells; stomata of the green twigs situated at the bottom of deep, narrow pits; seedlings with spirally arranged cataphylls, which merge gradually into foliage leaves, as in *Eremocitrus*; and the presence in immature fruits of the glucoside ponciridin, analogous to hesperidin but not found in *Citrus*. (Cf. Swingle, 1943.) Since the generic problem is very complex, involving a number of other genera, current usage is followed here, and *Poncirus* and *Citrus* are maintained as distinct.

Poncirus has been used more or less extensively in many citrus-producing regions of the world as a rootstock for cultivated citrus fruit trees. The somewhat dwarfing effect on *Citrus* scions is noteworthy. The species is commonly grown as an ornamental in Asia, southern and central Europe, and North America, and is sometimes used for hedges. The fruits have been used in medicine in China. The juice and peel of fruits sometimes are used after special treatment for flavoring in baking and confectionary.

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8. **Citrus** Linnaeus, Sp. Pl. 2: 782. 1753; Gen. Pl. ed. 5. 341. 1754.

Glandular, aromatic shrubs or trees, usually with solitary, axillary thorns, the older branches often thornless. Leaves alternate, persistent, 1-foliolate; leaflet subcoriaceous, glandular-dotted, entire or toothed; petiole usually winged and clearly jointed with the blade (except in *C. Medica*). Flowers bisexual, sometimes also unisexual by abortion of the gynoecium, usually relatively large, 2–5 cm. in diameter, often fragrant, solitary or in pairs in the leaf axils or in short, axillary, corymbiform cymes. Calyx shallowly cup-shaped, 4- or 5-lobed. Petals 4–8, usually 5, linear-oblong, thickish, white, pink, or purplish pink, glandular dotted, imbricate in bud. Stamens 20–60, polyadelphous [or distinct]; filaments linear-lanceolate, subulate upward, white, usually variously connate; anthers oblong or somewhat sagittate. Disc annular to cushion-like, supporting the gynoecium. Gynoecium syncarpous; stigma ± capitate, sometimes slightly lobed; style cylindrical, deciduous; ovary ellipsoidal to subglobular, 8–18 (usually 10–14)-locular, with several, usually 4–8, ovules (arranged in 2 rows) on an axillary placenta in each locule. Hesperidium usually large to very large, ellipsoidal and often mammillate at apex or pyriform to subglobular, sometimes depressed at apex; pericarp differentiated into 3 layers: an outer, yellowish-green to orange, leathery exocarp (flavedo) dotted with very numerous oil glands, a middle, thick and spongy, white mesocarp (albedo), and an inner, membranaceous endocarp with juicy, stalked, fusiform, inner outgrowths (pulp-vesicles) filling the locules (segments of the fruit) and forming the "pulp"; the thin, membranaceous partitions (radial walls) of the locules often loosely coherent and easily separated one from another as well as from the spongy, white central column (core) of the fruit. Seeds ellipsoidal to obovoid, plump or flattened, sometimes beaked at apex, usually a few in each locule (segment), the testa leathery; endosperm lacking; embryos 1–several, greenish to white, with fleshy, plano-convex, often unequal cotyledons and short radicle. LECTOTYPE SPECIES: *C. Medica* L.; see P. Wilson, N. Am. Fl. **25**: 221. 1911. (Classical Latin name, originally used for the wood of *Tetraclinis articulata* (Vahl.) Mast., the African sandarac tree, and perhaps other conifers, but transferred to the citron in about the first century of the Christian Era; etymology of the word obscure.)

A polymorphic genus of an uncertain number of species (16–145), of southern and southeastern Asia and Malaysia. Several species with numerous cultivars are widely cultivated and often spontaneous in all warm regions of the world. Five species, *Citrus Medica* L., citron, $2n = 18$; *C. Limon* (L.) Burm. f. (*C. Limonum* Risso), $2n = 18, 36$; *C. aurantiifolia* (Christm.) Swingle, lime, $2n = 18, 19–21, 27$; *C. Aurantium* L. (*C. vulgaris* Risso), sour or Seville orange, $2n = 18$; and *C. sinensis* (L.) Osbeck (*C. Aurantium* [var.] *dulce* Hayne), sweet orange, $2n = 18, 27, 36, 45$, all presumably natives of southern or southeastern Asia, have been recorded as more or less naturalized in our area (primarily southern Florida and the Keys). Accurate and recent data, however, are scanty, and perhaps only *C. Aurantium* and *C. Limon* ("rough lemon") can with some certainty be regarded as extensively naturalized. Seedlings of all the above, as well as of *C. paradisi* Macf., grapefruit, $2n = 18, 27, 36$, are often found along roadsides, at the edges of woods, and in secondary woods in Florida. Further data as to the extent to which such seedlings persist and reproduce themselves are much needed.

Bisexual flowers usually occur regularly in *Citrus sinensis* (also in *C. grandis* (L.) Osbeck, pummelo, *C. paradisi* Macf., grapefruit, and *C. reticulata* Blanco, tangerine). Both bisexual and unisexual (staminate) flowers are common in *C. Medica*, *C. Limon*, *C. aurantiifolia*, *C. Aurantium*, and some cultivars of other species (polygamo-monoecious species and varieties). Cross-pollination and self-pollination (including pollination between individual trees of a clone) seem equally effective in the formation of embryos and seeds, with some exceptions involving absence or defective development of pollen, or self-incompatibility. Self- or cross-incompatibility has been recorded in some horticultural varieties of different species. Thrips, honeybees, bumblebees, and some other insects attracted by the conspicuous corollas, fragrance, and abundant nectar apparently are responsible for natural cross-pollination and for most self-pollination.

Polyembryony is common in *Citrus*. Gametic (zygotic) polyembryony (gamospermy) seems to be rare, but can arise either by embryonic fission (cleavage polyembryony) or sometimes by the development of two gametophytes (embryo sacs) in the same ovule. Nucellar (somatic) embryony (apomixis, agamospermy) is widely distributed within the cultivated species, apparently lacking only in *C. grandis.* (Some cultivars of *C. Limon* and *C. reticulata* are also mainly monoembryonic.) The number of embryos per seed (1–18) varies with species and variety, and there is no general consistency within the species. Often only a single seedling or rarely more than two or three seedlings develop from a polyembryonic seed. Although nucellar embryos sometimes occur in a fertilized ovule alongside a zygotic embryo, only pollination (not fertilization) seems to be necessary for their formation. The occurrence of autonomous nucellar embryony has not been positively demonstrated. Nucellar seedlings show increased vigor, larger leaves and fruits, and a luxuriant development of spines ("rejuvenation" or "neophyosis"). Parthenocarpy regularly occurs in some cultivars of *C. sinensis* (e.g., navel orange, Satsuma), *C. aurantiifolia* (e.g., 'Tahiti lime,' a triploid), and some others.

The species of *Citrus* generally are interfertile, and their hybrids are ± fertile. Only a few varieties may be cross-sterile, and many inter- and intraspecific hybrids are known. The F_1 progeny of such hybrids usually shows great variability, but less vigor, than nucellar offspring or hybrids from intergeneric crosses (e.g., with *Poncirus* and *Fortunella*). The great variabiltiy of F_1 of inter- and intraspecific hybrids is mainly explainable by parental heterozygosity, which is common. Bud mutants are frequent.

Polyploidy is frequent, triploids (of gametic origin) and tetraploids (somatic autotetraploids) having been recorded in various species, e.g., *C. aurantiifolia* and *C. Aurantium.* Penta- and hexaploids seem to be extremely rare. Aneuploidy and an unbalanced chromosomal complement, $2n = 28$, have been found in a few hybrids.

A mycorrhizal association with an endophytic fungus has been recorded for the genus, but the association seems to be facultative (perhaps ± parasitic), since the formation of root hairs has been observed in young seedlings grown in artificial cultures (Girton, 1927, Hayward & Long, 1942), as well as under field conditions (Bartholomew & Reed, 1943).

There is little unity of opinion on the generic delimitation of *Citrus.*

Although Swingle, who is followed here, regarded *Poncirus, Fortunella, Eremocitrus*, and *Microcitrus* as distinct genera, some taxonomists include *Poncirus* in *Citrus*, and Burkill (1931) united all of these. Much greater differences exist in the concept of the species. Swingle (1943) recognized 16, at least one, *C. paradisi* Macf., being considered a satellite (or doubtful) species, while Tanaka (1952) accepted 145 species. The difficulties in delimiting the species, subspecies, and varieties of *Citrus* seem to depend, for the most part, on the absence of sterility barriers between groups of related forms and their apparent heterozygosity; but the problem is further complicated by nucellar embryony, by rejuvenation by nucellar progeny of ± senescent varieties long propagated asexually, and by the spontaneous production of autotetraploids.

In addition to morphological and anatomical characters, the chemical composition, especially the presence of certain glucosides in the fruits (e.g., hesperidin and eriodictyol glucoside in *C. sinensis*, those plus hesperidin chalcone in *C. Limon*, hesperidin in *C. Medica*, aurantiamarin, naringin (?), and hesperidin in *C. Aurantium*), seems to be of importance in distinguishing the species. The presence or absence, as well as the number, distribution, and character of the acrid oil droplets in the pulp vesicles of *Citrus* (and relatives) may be of some taxonomic significance.

The diverse uses and application of citrus fruits in the food and beverage industries, in essential oil production and the perfume industry, and as sources of vitamin C and "vitamin P," are well known. The peel (flavedo) of sour and sweet oranges and lemons or the volatile oil extracted from the fresh peel are used in medicine as stimulants, aromatics, and flavoring agents.

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THE LEAF BASE IN PALMS
ITS MORPHOLOGY AND MECHANICAL BIOLOGY

P. B. Tomlinson

In preparing a summary account of the palms for the *Anatomy of the Monocotyledons* (Tomlinson, 1961a) the construction of the leaf base was described in a very cursory fashion, since little material had been available for detailed study. Also, this anatomical survey of palms had been carried out from the standpoint of systematic anatomy, and there seemed to be little information of taxonomic significance in the microscopic structures of the leaf base. More recently, having had access to abundant material from living palms, the problem has been reappraised. It has become evident that, although, from the point of view of systematic anatomy, the initial attitude may have been justified, the construction and behavior of the leaf base in palms is a complicated subject which is of considerable morphological interest. It is a problem which can only be understood by considering mechanical aspects of leaf development in relation to growth of the stem. This subject is virtually unexplored, since the mechanical behavior of the palm leaf has no parallel elsewhere in the plant kingdom, and the construction and growth of palms is itself little understood.

That there is considerable variety in the structure of the leaf base in palms is obvious at once when a large collection of living plants is studied. Some palms have smooth trunks because the leaves are early deciduous, each abscissing cleanly; other palms have a more dishevelled appearance because the leaf base persists on the stem, as fibers, shreds, spines, or solid stumps. The distribution of these visible characters is not random, for the appearance and behavior of the leaf base is very constant for each species. Sometimes a single type may occur throughout an entire genus or larger taxon. In this way the structure of the leaf base in palms affords good diagnostic features. However, in spite of the diagnostic usefulness of these features, they are rarely employed by taxonomists, or, if used, their description indicates a sad lack of understanding of the fundamental construction of the palm leaf on the part of the author. There are some exceptions. The notes given by Wallace (1853), although brief, often include sufficient information to allow the recognition of the type of leaf base which is described. Bailey (1941) considered characters of the stem surface to be a basis for the subgeneric division of *Acrocomia*; these characters are a result of differences in the behavior of the leaf base in the two proposed subgenera.

On the other hand, it is not surprising that these features are poorly understood since many taxonomic descriptions of palms have been made from fragmentary specimens in which the attachment of the leaf base to the stem is not visible. In addition, there is no accurate account of the morphology and anatomy of the leaf base in palms. But this problem is only one of the many aspects of palm structure in which our knowledge is sadly deficient. The reason for these deficiences can best be appreciated by the tropical botanist; living palms must be studied, and it is difficult to obtain material of plants which are scarce or inaccessible or too valuable to horticulture to be used for science. The problems are on a scale larger than that envisaged by most plant morphologists, and special techniques must be devised, for it is difficult to apply orthodox anatomical and morphological procedures to buds which may be up to half a meter in diameter.

The present account is intended as a general survey of the problem and fills in some of the larger gaps in our understanding without offering any comprehensive solution. The problem cannot be solved by casual examination of unmolested palms. Buds must be carefully dissected and leaves of all ages examined because structures visible in mature leaves may only be of mechanical significance in early stages of development. Conversely, structures may be visible in the young leaf primordium only to disappear as the leaf reaches maturity. Thus, a ligule is far more commonly developed by palms than an examination of their mature leaves would suggest. The ligule is present in the leaf primordium but shrivels, erodes away, or shreds as the leaf approaches maturity.

The only published work on the mechanical features of leaf development in palms is that of Schoute (1915) who described the morphology, anatomy, and mechanical behavior of the leaf base in *Hyphaene*. Schoute's work illustrates how the mechanical demands made on a cylindrical sheathing organ which encloses growing tissues are met by the development of vertical clefts or sutures which appear in precise regions as a result of anatomical modifications. The ultimate configuration of the leaf attachment is shown to be very efficient and to utilize available tissues in an economic manner.

However, the leaf base in *Hyphaene* represents only one method by which the mechanical problems of the leaf base are overcome. Other methods involve either the shredding or partial decomposition of certain tissues of the leaf base, or the complete disappearance of certain parts, or sometimes the abscission of the whole organ. I have recognized a number of distinct biological types and these are described subsequently. Schoute himself was well aware that there was much to be added to his own account, for he wrote, "Il est cependant sûr que le corps tout entier des palmiers n'a pas encore été étudié suffisamment sous ce point de vue et que l'examen attentif nous pourra révéler encore beaucoup de détails intéressants."

It is emphasized that this present article is only a preliminary essay and cannot hope to elucidate all the details. It deals with the problem entirely in a qualitative way and aims at providing information of use to the taxonomist who may wish to include notes on the diagnostic features of the leaf base in his description of palms. Since problems of growth are involved, future detailed studies must be based on quantitative observations.

As a preliminary aid, an account of the growth processes taking place within the leafy crown of a palm are given in order that the subsequent discussion of mechanical adaptations may be understood. These growth processes have been summarized elsewhere (Tomlinson, 1961a,b), so only a brief outline is presented here.

THE DEVELOPMENT AND MORPHOLOGY OF THE LEAF BASE IN PALMS

Leaves in a palm always originate within the terminal cluster. Most stages of leaf development take place within this leafy crown and are not visible without careful dissection of the bud. As in most monocotyledons, each leaf in the palm originates as a minute cowl-shaped primordium at the shoot apex. In its earliest stages, the primordium does not completely encircle the stem, but its two margins soon grow rapidly around the shoot apex so that the base of the primordium is sheathing almost from the first. Eventually the base develops into a closed tube, the future leaf sheath. The distal part of the primordium elongates to form the petiole and rachis, the blade being segmented by peculiar growth processes in the distal part of the primordium (cf. Eames, 1953). Since differentiation of organs and tissues within the leaf occurs in a basipetal direction, the distal parts mature early and complete their growth and expansion while the base is still meristematic. This basipetal order of maturation should be clearly recognized, since it is of considerable mechanical significance. In each successive leaf, at the time when the blade is fully differentiated and on the point of unfolding, the leaf base is still actively meristematic. Therefore, in its early stages of unfolding and assimilation the blade is borne upon a delicate leaf base in which cell division and cell expansion still continue and which is useless as a rigid supporting organ. Support for the open blades of the younger leaves is provided by older, surrounding leaves with rigid, mature sheaths.

Elongation of the parts of the leaf may take place neither at a uniform rate nor in the sequence in which the parts mature. For example, elongation of the petiole is often very tardy, but rapid once it begins. In some cocoid palms a true petiole is absent since there is no naked portion of the leaf axis between the insertion of the lowest leaflets on the rachis and the mouth of the leaf sheath. In these palms a pseudopetiole is developed, because as the leaf matures the marginal tissues of the distal part of the leaf sheath disappear. This pseudopetiole may be quite long, as in *Arikuryroba.* In yet other cocoid palms, as in species of *Orbignya,* the petiole is absent. Other palms with no petiole, or with a very short petiole include species of *Copernicia* (e.g., *C. torreana*) and some of the scandent lepidocaryoid palms.

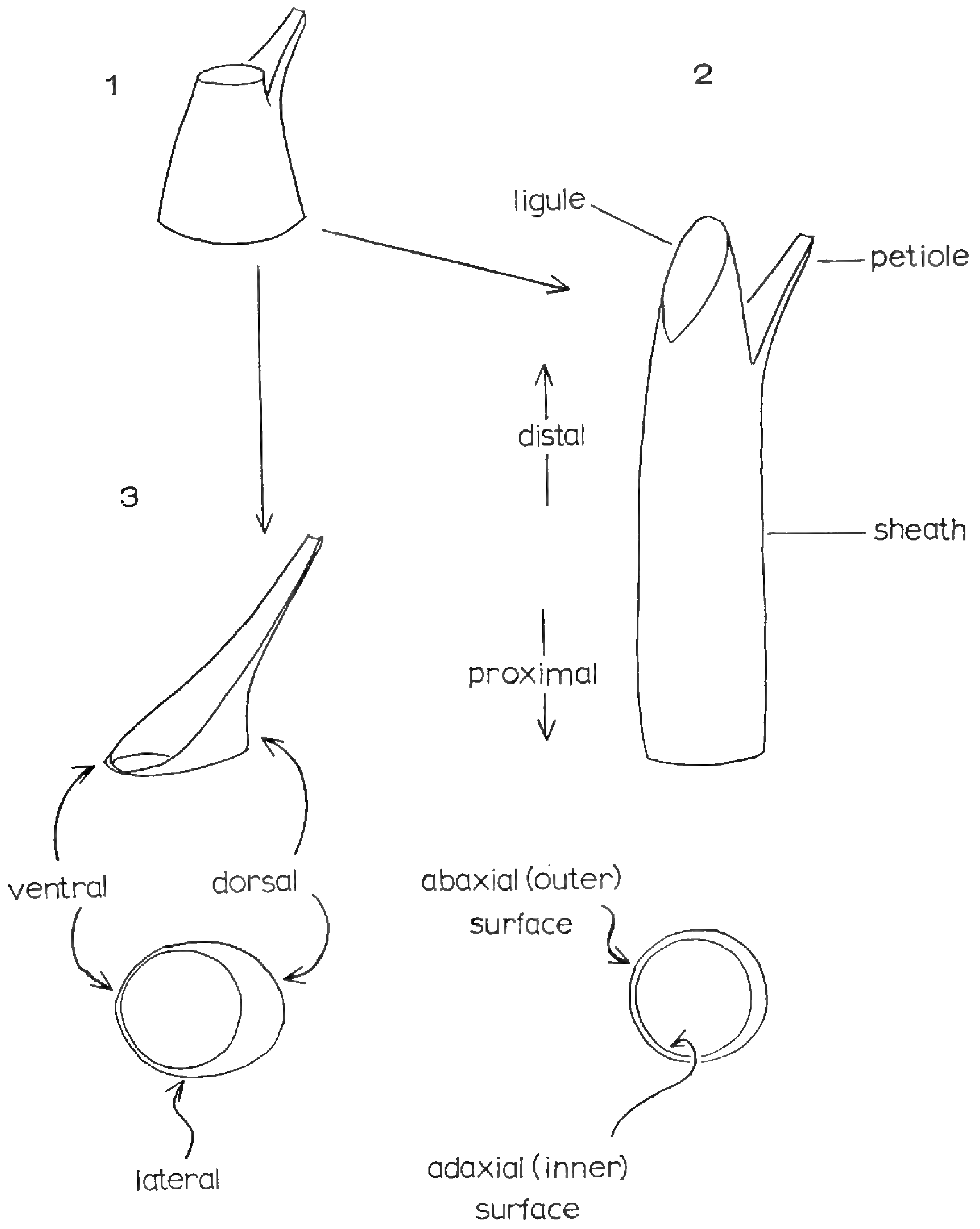
The basal, sheathing part of the leaf in all palms is always tubular in its early stages of development (FIG. 1). The tube is closed and the leaf insertion completely encircles the stem. In many palms the initial tubular state of the leaf base can be revealed only by dissecting the bud, because, as the leaf matures, decay and dissolution of certain tissues reduces its size considerably, and at maturity it may have only a narrow insertion.

A ligule is a characteristic feature of a number of palms. It is a tubular extension (rarely the tube is open as in *Rhapidophyllum* and *Zombia*) of the distal part of the leaf sheath above the insertion of the petiole. It is most conspicuous and persistent in many scandent palms of the lepidocaryoid alliance in which it may have a specialized function. Thus, in *Korthalsia* it is commonly occupied by ants. A ligule is also present in many, possibly all, palms of the bactroid and caryotoid groups, although it is visible only in young leaves, disorganizing as the leaf matures. In some arecoid palms, e.g., *Ptychosperma,* and some borassoid palms, e.g., *Latania,* there are small auriculate outgrowths on each side of the mouth of the sheath. These structures may be homologous with a true ligule.

In order that subsequent descriptions may be clearly understood, it is necessary to define certain terms which are used consistently in later sections (FIGS. 1–3). The abaxial surface of a tubular leaf sheath is its *outer* surface, the adaxial surface being the *inner.* In accordance with the terminology of Von Mohl (1824), which was also adopted by Schoute (1915), the part of the sheath on the side below the petiolar insertion is referred to as the *dorsal* side, the opposite side being the *ventral* side. This corresponds to the same use of these terms in descriptions of the carpel, itself a modified leaf. The tissues on each side of the dorsiventral plane may be described as *lateral.*

Although the leaf sheath in all palms is fundamentally a closed tube, it is convenient to recognize two main types of leaf base, according to the behavior of the sheath as it ages. In the first group the leaf base may be described as *obviously tubular* since the base persists and matures as a visible long, closed tube (FIG. 2). Leaf sheaths of this type are always long in proportion to the total length of the leaf. Up to one quarter of the leaf axis may be sheath. This type of leaf base occurs predominantly in members of the arecoid, chamaedoroid, and iriartoid groups and is also characteristic of scandent palms in other groups. In the second category the leaf base is *not obviously tubular* (FIG. 3). Only in the early stages of development does the sheath have the form of a closed tube. As the leaf base grows certain tissues disorganize and the cylindrical sheath disappears, the leaf sheath at maturity being represented by a broad clasping base which may or may not encircle the stem. Leaf bases of this type are always short and rarely exceed more than one-eighth of the total length of the leaf. It should be emphasized that there is no sharp distinction between these two classes and that intermediate types of leaf base, difficult to categorize, are quite common.

When the leaf base is examined at various stages of development it is



FIGS. 1–3. Types of leaf bases in palms. 1, Diagrammatic representation of young leaf primordium. 2, Mature leaf base of obviously tubular type, with representative cross section of sheath below. 3, Mature leaf base of not obviously tubular type, with representative cross section of sheath below.

obvious that it can only be described as a uniform cylinder in a very approximate sense. The leaf sheath is always somewhat conical upwards, and the walls of the tube are not of uniform thickness. The conical outline is a result of the basipetal sequence in maturation. The distal part of the sheath matures early, so its mouth is always narrow, enclosing younger leaves, the tissues of which are not yet bulky. Subsequent widening of the mouth of the sheath is to a large extent accomplished as a result of continued growth and expansion of younger leaves which are forced through the mouth by their own basal meristematic growth. Whereas the mouth of the sheath is widened mechanically, the base widens through activity of its own meristematic tissues. In ligulate leaves the loss of the ligule is to a large extent caused by internal expansion of younger leaves. The ligule, being the most distal part of the leaf sheath, is always much narrower than the rest of the leaf base, and its disappearance from the leaves of larger palms is essential if younger organs which it encloses are to expand without restriction. In fact, the mechanical function of a tubular ligule may be to direct and support the pointed apex of primordia of younger leaves, maintaining them in a vertical position in such a way that they meet no resistance from older leaves.

In the tubular type of leaf base, the walls of the sheath are fairly uniform except for slight thickening on the dorsal side (FIG. 2), a thickening which is most obvious in the distal region, close to the insertion of the petiole. There may also be slight constrictions in regions in which sutures subsequently appear. In the nontubular type of leaf base the differences between dorsal and ventral regions are more conspicuous (FIG. 3); the dorsal region is always thick, woody, and persistent, whereas, the ventral region is thin, membranaceous, and often ephemeral.

DEVELOPMENT OF THE LEAF BASE IN RELATION TO THAT OF THE STEM

Growth processes in the leafy crown of a palm are not comparable to those of a woody dicotyledon (Tomlinson, 1961a,b). The apical meristem region is minute and is situated at the base of a shallow depression which terminates the axis of the palm. Leaves originate in the apical meristem proper, and, as they grow, each in turn comes to occupy the center of this depression. Each leaf is, however, displaced from this position to allow the development of younger leaves within, its insertion widening at the same rate as the stem enlarges. Thickening growth of the stem is not induced by the apical meristem itself but by a primary thickening meristem, a tissue which forms the surface of the apical depression. Each annular leaf insertion therefore continually increases in circumference as a result of the thickening of the axis, itself brought about by the primary thickening meristem. The rest of the leaf sheath also increases in circumference at the same rate of enlargement as the leaf insertion. Initially this enlargement of the leaf sheath is effected entirely by cell division and cell expansion, but in the later stages cell division ceases. At the periphery of the apical depression thickening growth is no longer predominant, lengthening growth of the axis occurs, and adjacent leaves become separated by internodal elongation. It is in this predominance of thickening over elongation growth in the early stages of stem development that palms differ so strikingly from most dicotyledons.

The stem commonly continues to widen as elongation proceeds, but no longer by activity of the primary thickening meristem. Instead, there is continued growth and expansion of the ground parenchyma. This diffuse secondary thickening (Tomlinson, 1961a, p. 20) may be long continued and obvious, as in *Roystonea*, the trunk tapering upwards (FIG. 14). Otherwise, secondary growth is either limited or not obvious, since it is restricted to that part of the stem which is still enclosed by persistent leaf bases so that the distal tapering of the stem is not visible without removal of the expanded leaves. However, it is this phase of stem growth which has such a significant effect on the behavior of the leaf base.

It should be emphasized that, although growth of the palm stem can be envisaged as taking place in two distinct phases (an initial phase of thickening growth, followed by elongation growth), there is no marked disjunction between the two. Thickening growth continues well into the phase of elongation growth. In the smaller, canelike palms, and particularly in the scandent palms, elongation growth begins early and may be much exaggerated. It should also be emphasized that a true understanding of the growth processes at the stem apex in palms can only come from quantitative observations and not merely from a qualitative approach employed in this article. Apart from figures quoted by Schoute (1915) there are no relevant published measurements. It is hoped that these qualitative notes can be amplified by measurements in future work.

The general basipetal sequence of growth and differentiation has already been emphasized. Since growth of the leaf and its associated stem internodes is closely correlated, this basipetal sequence is continuous from leaf to stem. Consequently, growth of the internode, both in length and thickness, continues after the leaf base has ceased to enlarge. The mature leaf base thus is seen as a rigid envelope enclosing growing tissues. Mechanical stresses are set up in the leaf base. Several types of stress are imposed and these are indicated below.

MECHANICAL STRESSES IMPOSED UPON THE LEAF BASE

Four main mechanical stresses are exerted upon the leaf base. These stresses are not of equal significance, and their magnitude differs in different palms, largely as a consequence of the great variety in growth habit exhibited by palms.

(a) *Stresses due to growth of younger leaves.* During the early phases of growth the leaf sheath is subjected to internal stresses arising from the expansion of younger, enclosed leaves. These stresses are not of equal significance throughout a single leaf base because the distal part of the leaf sheath matures before the base. Thus, the still meristematic base is capable of accommodating internal expansion by cell division and cell enlargement. The narrow mouth of the sheath is, however, usually widened passively under the internal stress. This widening may involve splitting or loss of tissues at the mouth of the sheath, changes which are most obvious in the ligule, when present.

(b) *Stresses due to expansion of the stem.* The growing palm bud is to some extent in a state of dynamic equilibrium. Much of the stress set up by the growth and enlargement of the young stem internodes is resisted by the rigidity of the encircling, mature leaf bases. That these stresses are considerable is shown when the mature leaves around a palm bud are removed so that there is no restriction on internal expansion: the axis commonly splits vertically. The structural modifications described below are largely a result of changes induced by such internal expansive forces.

(c) *Stresses due to the weight of the leaf.* Stresses are imposed upon the leaf base by the weight of its own rachis and blade. In view of the great weight of the leaves in the larger palms, these stresses are likely to be enormous. "A single, entire leaf is a load for a man" (Wallace, 1853). Such forces can trap and kill a man. They are not constantly and uniformly distributed because the palm leaf moves in the wind. The distribution and moments of these forces have been indicated by Schoute (1915) for *Hyphaene.* Schoute considers that the mode of attachment of the leaf in *Hyphaene* is of maximum efficiency in catering to these forces. However, Schoute discusses the problem as that of a single leaf on the axis. This condition does not occur in palms, and much of the stability of the leafy crown must be a result of many leaves deriving mutual support as a consequence of their overlapping leaf bases being arranged on a spiral with a high phyllotactic fraction. This probably accounts for the scarcity of a distichous leaf arrangement in palms and for the relatively short internodes of the larger palms with persistent leaves. Some of the stresses set up in the dorsal part of the leaf axis by the weight of the blade sometimes have visible effects. The dorsal tissues may buckle under compression, as in the leaf base in *Cocos*, or a "geniculum" may be developed, as in many scandent palms.

(d) *Stresses due to the development of the inflorescence.* The inflorescence in palms is usually axillary, and its enlargement places some strain on the leaf base. This strain may be minimized in several ways. In many of the arecoid palms, for example, the inflorescence does not expand until the leaf has abscissed (FIG. 15). Commonly the inflorescence elongates considerably, and grows through the mouth of the leaf sheath before it expands. The inflorescence sometimes pierces the leaf sheath, or grows through an existing suture. In general, mechanical stresses imposed by the expansion of the inflorescence are less severe than those imposed during the normal processes of vegetative growth.

Of these four types of mechanical stress, that imposed by the expansion of the stem is undoubtedly the most significant for the behavior of the leaf base. Thus, the measurements given by Schoute (1915) for *Hyphaene* indicate that at least a 30% increase in diameter of the leaf base occurs passively, after its growth has ceased. My own measurements on *Sabal* indicate that the diameter of the leaf base must at least double as a result of stem expansion. This increase is accommodated entirely by splitting of the leaf sheath, since the sheath widens neither by addition of new tissues nor by stretching of old ones.

Anatomical observations indicate that the leaf sheath has only a limited capacity for expansion by passive stretching. Initially the leaf base widens to accommodate internal enlargement by cell division and cell expansion. After cell division ceases, tangential expansion of ground tissue cells continues, the cells often widening two- to threefold. This enlargement involves the cells of the ground parenchyma only, since the tissues of the vascular bundles complete their differentiation early and are incapable of passive expansion. Tangential expansion of ground tissue cells is most obvious close to the inner surface of the sheath. Here cells which were originally isodiametric may be widened up to tenfold in the tangential direction.

The limit of this passive enlargement is soon reached, however, and subsequent widening of the leaf base takes place entirely by means of certain mechanical contrivances for which the leaf is adapted in various ways. In this way the rigid leaf base is able to persist on a stem which is still widening. The main biological types which I have recognized are described below. There is no clear limit to these categories, and different types intergrade. Some palms may show mechanical features belonging to more than one class.

MORPHOLOGICAL TYPES OF LEAF BASES

The following observations are entirely my own, made on living palms either in cultivation or in their natural habitat. In each of the classes which I have recognized, the bud of at least one example has been dissected carefully. A few preliminary remarks should be made concerning observations on leaf base morphology in palms. The larger palms have a long period of growth in which only juvenile leaf characters are seen (Tomlinson, 1960). These juvenile characters may persist longer in the leaf sheath than in other parts of the leaf, and a leaf with the adult characters of the blade may still have juvenile features in the sheath. In *Mascarena*, for example, the leaves at the base of the plant are long persistent and not deciduous like the more distal leaves. In the following notes juvenile characters are ignored. Observations on palms in cultivation can also be misleading, since such palms are commonly leaf pruned at regular intervals and not allowed to show features they would develop if left undisturbed. These abnormal aspects also have been ignored.

The types of leaf base listed below are identified by the name of a genus in which typical features are clearly shown. These types are listed in two groups according to whether the leaf base is obviously tubular or not.

Leaf sheath obviously tubular. Palms in this category can be subdivided into two main types according to whether the leaf base is deciduous or not. However, these two types intergrade.

CALAMUS TYPE. *Leaf base long-persistent, little modified with age.* In palms of this type each leaf base is long, tubular, and wholly or partly covers the slender internode. Stem thickening is slight, and the leaf base compensates for internal stresses entirely by division and expansion of cells. The leaf sheath is subjected to little mechanical strain and shows no mechanical adaptations. Each leaf base dies, its tissues dry and shrivel somewhat, but the leaf is not abscissed. It is only lost in extreme age, by gradual erosion and decay. Where a ligule is present it also may persist, as in most of the scandent palms. Otherwise it may decay, as in *Bactris* species. The only change brought about in such leaf bases by mechanical means is a widening of the mouth of the sheath early in development.

This type of leaf base is found in the scandent palms which belong to several unrelated groups: lepidocaryoid palms (several genera), bactroid palms (*Desmoncus*), chamaedoroid palms (*Chamaedorea* spp.). It is also found in many of the smaller palms with erect, rigid but canelike stems as in species of *Chamaedorea, Geonoma* and *Pinanga*. In these last-mentioned genera, however, there is a tendency for the leaf to absciss in the manner described below.

VEITCHIA TYPE. *Leaf deciduous, developing distinct separation layers.* (FIG. 4). In this type the diameter of the stem continues to increase appreciably long after the tubular leaf sheath has achieved its maximum diameter through growth. The extent of this belated stem expansion may be considerable, and in *Roystonea* it may continue throughout most of the life of the palm (Schoute, 1912), although the trunk tapers obviously only close to the crownshaft (FIG. 14). The leaf sheath is not resistant to this expansion, but the whole leaf abscisses cleanly as a unit. This results from the development of separation layers in precise abscission regions. An annular separation layer at the node frees the leaf from the stem, but since the sheath is a closed tube, the leaf is not yet able to fall away from the stem. Complete release is effected by a vertical split on the ventral side through a narrow, but often conspicuous, separation layer which extends the full length of the leaf sheath (FIGS. 11, 12). In this region the leaf may be slightly constricted; rarely the constriction is so deep as to form a conspicuous ventral groove (FIG. 15). These separation layers are both anatomically specialized and, at maturity, represent weak areas. Under the strains imposed from within, the leaf sheath splits from above downwards through the ventral separation layer (FIG. 12) abscission then being completed by cleavage at the node (FIG. 13). The annular leaf scar is always clean and smooth, indicating that separation is predetermined and not merely a mechanical tearing and also that protective layers are developed before the leaf falls (FIG. 13). Anatomical aspects of this abscission require further study.

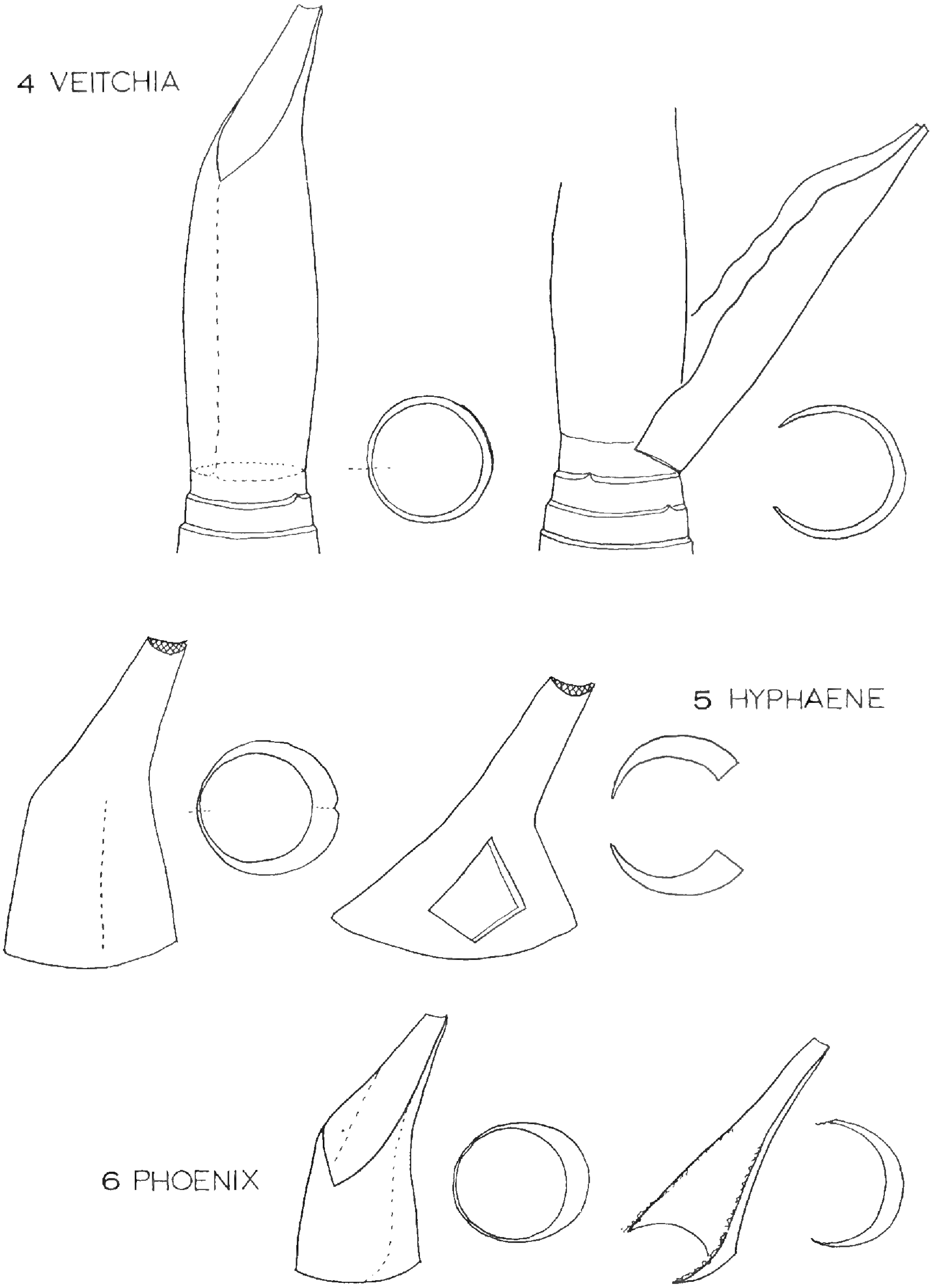
The ventral line of abscission is always present, although it is more conspicuous in some species than in others. It is probable, however, that its conspicuousness is a good specific diagnostic feature. It is easily seen in *Veitchia*, for example (FIG. 12), but is not obvious in *Roystonea*. This ventral separation layer apparently has been overlooked in taxonomic literature. Schoute (1915) certainly missed it in *Roystonea*, which was contrasted with *Hyphaene* as an example of a palm in which the leaf base was split in a haphazard manner. Admittedly this irregular tearing does occur in *Roystonea,* but usually only in young palms, and Schoute's observations may well have been made on young *Roystonea* plants. In adult specimens cleavage is almost invariably regular.

An additional morphological peculiarity, common in species with the *Veitchia* type of leaf base, is the presence of a small triangular notch at the node, the apex continuous upward into the ventral separation layer (FIG. 11). This structure must be formed early in leaf development and represents the region in the minute leaf primordium where the encircling halves of the future leaf sheath meet on the ventral side, touching but not fusing completely. This feature is probably a good specific diagnostic character, although it has apparently never been mentioned in taxonomic writing. For example, it is very conspicuous in some species of *Veitchia,* e.g., *V. montgomeryana,* but absent from others, e.g., *V. joannis.* Since the notch marks the exact ventral point of the leaf insertion and persists as part of the leaf scar, it is a very useful tag by which the original phyllotaxis can be determined on old trunks.

This type of leaf base, exemplified by *Veitchia,* is common throughout the arecoid, chamaedoroid and iriartoid groups. It is almost universally associated with an infrafoliar inflorescence. It does, however, intergrade with other types. In many small palms with canelike stems abscission is often imprecise and there is a transition to the *Calamus* type. In many palms of the arecoid alliance the inflorescence is either interfoliar or not consistently infrafoliar, and abscission layers are not well defined. There is thus a transition to other types of leaf base, and further study would probably reveal them as a new type. *Heterospathe* is an example of a palm the inflorescence of which is, with fair consistency, infrafoliar, but in which abscission of the leaf is irregular. This makes it difficult to categorize.

Leaf sheath not obviously tubular. This includes a number of distinct biological classes of which the type examples are quite clear cut. Some leaf bases may have characters of more than one type, however, and in many genera it is not easy to categorize the type of leaf sheath.

HYPHAENE TYPE. *Leaf base cleaving widely on the dorsal side.* (FIG. 5.) This type has been described by Schoute (1915), and the present summary of his observations adds little new information. In palms of this type the leaf base is at first shortly tubular. Allowance for the demands of stem expansion is made in two ways. Initially a ventral split (*fente ventrale* of Schoute) appears and its widening is accompanied by the loss of some ventral tissue. This split permits expansion of younger leaves and also causes the leaf as a whole to fall from a vertical position into a more pendant one. The second adaptation is more complex and accommodates the more extensive forces of stem thickening. These forces are exerted on the thick, woody dorsal tissues of the leaf base, and their effects are indicated by Schoute's measurements. They show that the circumference of the leaf base ceases to increase actively after it has reached a diameter of about 20 cm. Subsequent increase, up to a diameter



FIGS. 4–6. Behavior of leaf base, illustrated diagrammatically, immature stage to right, mature stage to left, with representative cross sections of both stages. Lines either of future dehiscence or of separating distinct tissue regions indicated by dots. 4, *Veitchia* type; 5, *Hyphaene* type; 6, *Phoenix* type.

of 38.5 cm. is largely due to the development of a dorsal cleft (*fente dorsale*) which widens at the same rate as the stem thickens and ultimately assumes a broad, rhombohedral shape (cf. FIG. 18). This cleft is not merely the result of mechanical cleavage. It is marked in the immature leaf by a slight constriction, the microscopic examination of which shows certain anatomical peculiarities. The cleft is mechanically weak so that separation occurs easily within it. In *Hyphaene* the margins of the cleft are clean, but in *Sabal* and some other palms with this type of leaf base there is some fraying of the margin and fibers frequently remain to connect the newly exposed surfaces.

This type of leaf base is usually distinct and easily recognized, but transitional forms exist in some small palms. Thus, in *Thrinax*, the dorsal cleft is rather indistinct, and the rest of the leaf base shows additional mechanical adaptations.

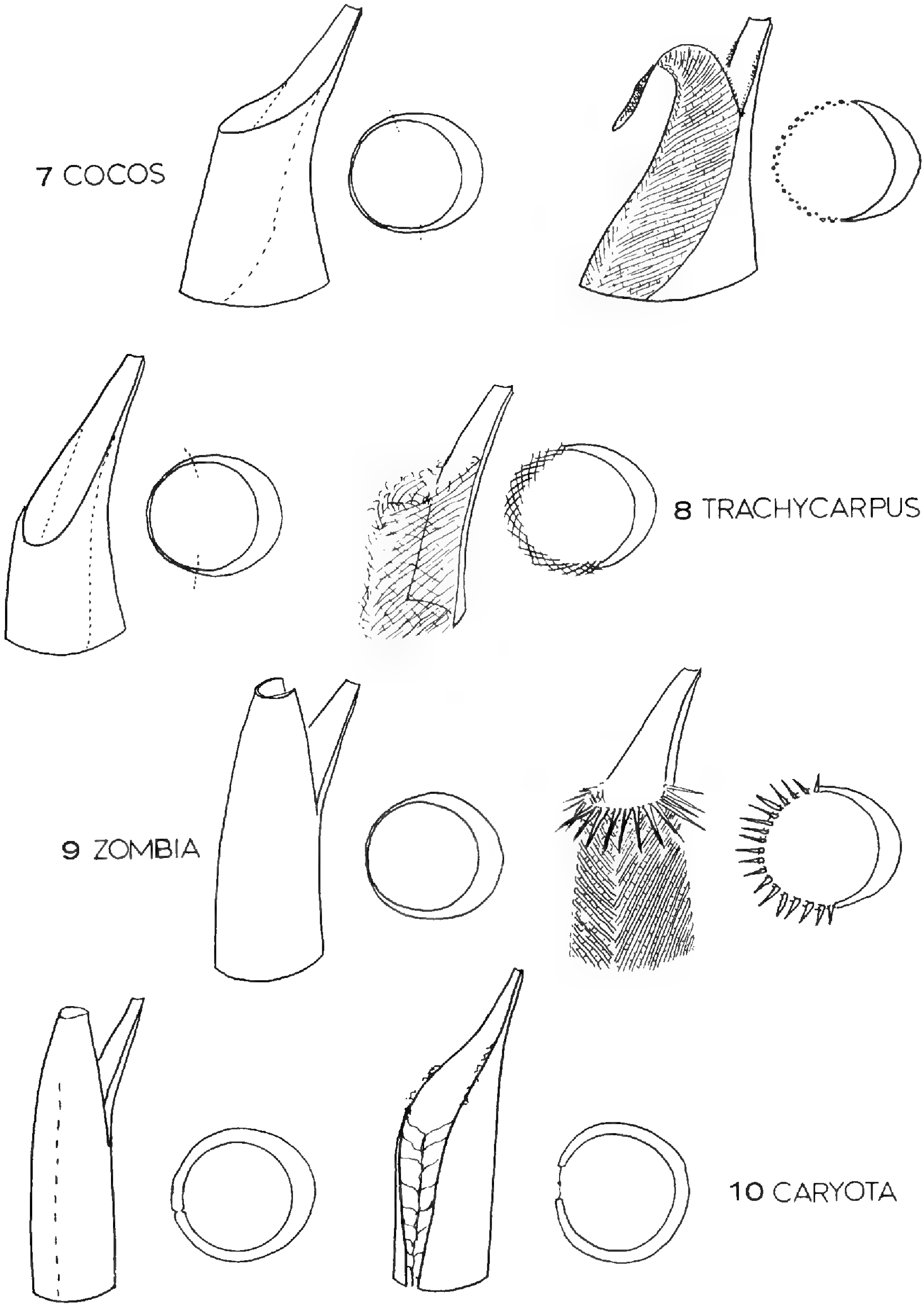
The overall result of the development of a dorsal cleft is the appearance of a broad diamond-shaped hole in the woody leaf base. Mature stems of palms with this type of leaf base are thus clothed with a crisscross pattern of overlapping leaf stumps, each "strand" in the pattern representing one half of a split leaf base. Schoute's mechanical analysis of *Hyphaene* indicates that the clefts do not weaken the leaf attachment since they appear in such a position that they offer mechanical advantages to the leaf insertion. In older leaves the distal part usually breaks away by a fracture of the petiole. Commonly the residual leaf base persists throughout the life of the palm, if undisturbed, as in *Hyphaene*. In *Sabal*, the leaf base itself soon falls to leave a fairly clean trunk. In *Washingtonia*, the whole leaf persists and the stem of an unmolested palm is a striking object, being clothed with a "skirt" of old leaves. In *Corypha* the extent of lateral movement of the leaf base is revealed by horizontal scratches, scored in the leaf base by the teeth on the margin of the petiole (FIG. 19).

This type of leaf base occurs in larger palms of the borassoid and sabaloid groups. The reason for the consistent correlation between a *Hyphaene*-type leaf base and a palmate blade is unexplained.

PHOENIX TYPE. *Ventral tissues of leaf base eroding without becoming conspicuously fibrous.* (FIG. 6.) The leaf base is initially shortly tubular, but resists stem expansion very little. The ventral tissues disorganize, decay, and erode, and only the thickened, woody dorsal part of the leaf base persists (FIGS. 16, 17). Otherwise, there are no specialized anatomical adaptations in this type. It is possible that expansion in the nodal region ruptures the ventral leaf traces so that the ventral tissues are deprived of food and water and die, subsequent decay being a passive process. The dead tissues show little tendency to persist as a fibrous material. The annular leaf scar, which is often rather indistinct, is the only indication of the original tubular state of the leaf base. The petiole fractures, and only the dorsal woody stump persists, sometimes throughout the life of the palm. Otherwise it is abscissed or decays gradually. The persistent dorsal part of the leaf base may occasionally show the effects of internal forces of expansion, in numerous small vertical splits, as in the larger species of *Copernicia* (FIG. 17). In the larger species of *Phoenix,* e.g., *P. canariensis,* in which the internodes are congested, the woody overlapping stumps of the leaf bases form a complete vesture on the trunk (FIG. 16). This may have some protective value, like the bark of a hardwood tree. In other species of *Phoenix*, as in *P. reclinata*, the internodes are longer, and the woody base is less persistent. *Copernicia cerifera* is an interesting example of the *Phoenix* type in which the leaf bases are more persistent on the older, lower parts of the stem than on the younger, upper part. Hence, mature specimens of this palm have old woody leaf stumps at the base of the trunk, below the relatively smooth upper trunk.

This type is common throughout the palms in many unrelated genera. Its limits are not easy to define and it intergrades imperceptibly with other types, particularly with the two next described. In *Phoenix* itself, for example, there is little tendency to form a persistent fibrous mass. In some of the cocoid palms which I have included in the *Phoenix* type, however, the ventral tissues tend to split into strips before they disappear. One feature which characterizes many cocoid palms is for a part of these strips to persist as blunt spines spaced at regular intervals along the margin of the leaf sheath, as, for example, in *Arikuryroba*, *Butia*, *Elaeis*, *Jubaea*, and *Syagrus*. The distal part of the petiole bears spines in *Phoenix* itself, but these are obviously modified leaflets and not homologous with the spines in the cocoid palms. Another diagnostic feature of the cocoid palms is the absence of a true petiole, the apparent petiole being the persistent thickened dorsal region of the leaf sheath, although this may be quite long. In *Attalea*, *Orbignya*, *Scheelea*, and *Maximiliana* there is neither petiole nor pseudopetiole. Only in *Cocos* itself is a naked petiole present.

COCOS TYPE. *Ventral tissues of leaf base long persisting as a continuous fibrous network.* (FIG. 7.) This class shows a complete intergradation with the previous class. The type example, *Cocos*, is, however, quite distinct. The ventral tissue decomposes only partly, and its remains persist and serve an important mechanical function. There is some loss of tissue and splitting in the distal part of the leaf sheath. The splits generally separate the thin, ventral tissue from the thickened dorsal tissue, this being necessary for the correct mechanical behavior of the leaf base. The ventral tissues undergo decomposition, the soft, parenchymatous ground tissue decaying and being lost. The fibrous strands and fibrovascular bundles persist and form a material which resembles coarse sacking, not only in appearance but, to some extent, in texture (FIG. 20). This material owes its texture to the peculiar disposition of the vascular and fibrous bundles. Towards the distal end of the leaf sheath the bundles of the ventral tissues are arranged so that they are not wholly parallel one with another, but form two or more systems (cf. FIGS. 23, 24). Bundles within each system form parallel lines, but the different systems are arranged so that they execute a shallow spiral, the spiral in adjacent systems running in opposite directions. There are frequent anastomoses and irregularities within this arrangement, but the general analysis de-



FIGS. 7–10. Behavior of leaf base, illustrated diagrammatically as in Figs. 4–6. 7, *Cocos* type; 8, *Trachycarpus* type; 9, *Zombia* type; 10, *Caryota* type.

scribes the system quite well. With the decay of epidermal and ground tissues, only this fibrous network persists. Internal expansion pulls the tissue laterally, but the peculiar arrangement of this network allows the angular divergence of bundles in different systems to be increased, without affecting the structure or strength of the whole tissue. The tissue thus comes to resemble a coarse cloth, but only in a superficial way. There is no regular interweaving of warp and woof as in a man-made fabric; the palm sacking shows interweaving between fibers in different systems in an irregular manner and only sufficient to hold the adjacent systems of strands tightly together.

Examination of this material shows that it can be stretched sideways, as the mechanical requirements of the palm bud demand, but it is also very elastic. Consequently, while offering no resistance to expansive forces, it functions as an elastic tissue, cushioning and damping the variable strains imposed upon the leaf base by the movement of the blade in the wind. A horizontal widening of this leaf tissue must be compensated by a vertical shortening. This probably accounts for the distal cleaving of the ventral tissues away from the rigid dorsal part of the leaf base, and this cleavage is probably entirely passive. The long, pendulous tongues of ventral tissue, each of which represents the remains of the distal part of the leaf sheath, are conspicuous objects in the leafy crown of a coconut (FIG. 20).

It should be pointed out that the anatomical peculiarities in the distribution of the strengthening tissues in the leaf sheath are not restricted to palms of the *Cocos* type, but that a similar arrangement is to be found throughout the whole family. This suggests that this construction has the same mechanical significance for all palms, but only in the *Cocos* type is the arrangement of major and obvious mechanical significance. Further detailed anatomical studies are needed to analyze this construction correctly.

The *Cocos* type can be recognized in many genera belonging to unrelated groups, but often only in a modified form. Intergradation with other types is frequent. For example, the texture of the elastic tissue varies considerably. Thus in species of *Coccothrinax* the fibrous strands are quite woody and the tissue is very rigid (FIG. 24). In *Livistona*, on the other hand, the fibers are fine and the tissue delicate and almost woolly. The leaf sheath of *Livistona* thus resembles the type of leaf base described as the next class.

In palms of the *Cocos* type, the useful life of this elastic mechanical device is often short, as in *Cocos* itself. The ventral tissues are lost and the woody, dorsal stump soon abscisses to leave a fairly clean trunk. Otherwise, the leaf base may be long persistent, as in *Paurotis* and many species of *Coccothrinax*.

TRACHYCARPUS TYPE. *Leaf-base tissue mostly persisting as fibrous material.* (FIG. 8.) This class represents only a modification of the previous type, and all intermediate stages of transition can be seen. In

Trachycarpus all the tissues of the leaf base, except the thickened dorsal region, persist as a fibrous mass which represents the fibrovascular system released by the decay of the ground parenchyma. This fibrous mass offers no resistance to internal expansion. The leaf bases are closely crowded on the trunk and persist, if undisturbed, throughout the life of the palm as a continuous fibrous mat out of which the dorsal stumps protrude (cf. Fig. 25). *Trachycarpus* itself is of some interest because it will grow at much higher latitudes than any other palm, even as far north as Scotland. One is tempted to correlate this cold tolerance with the shaggy coat, but it should be remembered that *Trachycarpus* is not a warm-blooded animal. *Coccothrinax crinita* has a similar shaggy coat but is not particularly cold-resistant.

Isolated examples of this class can be found in several unrelated genera, but it is often difficult to distinguish this type from the *Cocos* type with which it intergrades. A transition to another type is also shown by *Arenga* species. For example, in *A. pinnata* (Fig. 25) the fibrous remains of the larger vascular bundles protrude prominently from the fibrous mass as long, pliable, but not sharply pointed, spines, as in the next class.

Zombia type. *Leaf base shredding partly or wholly into protective spines.* (Fig. 9.) Examples of this class can be considered a modification of either the *Cocos* or the *Trachycarpus* type. The softer tissues of the ventral region decay but the fibrovascular bundles persist, either partly or wholly, as spines. These completely invest the stem and form a very effective armature (Fig. 23). In *Zombia*, the distal extremities of all those larger vascular bundles which have massive fibrous bundle sheaths end in a sharp point. These extremities become reflexed as the leaf matures and form the prominent stout spines. Anatomically the arrangement of the vascular bundles corresponds to the general pattern described for *Cocos*. Three systems of vascular bundles exist, but only the bundles of the outer system have massive fibrous tissues. Distally these extend beyond the insertion of the petiole into a long ligule which, unlike the ligule in most palms, is open on the dorsal side (Fig. 22). As the leaf base matures, the spaces between the vascular network are enlarged by internal expansive forces (cf. Figs. 22, 23), while the distal extremities of the future spines are freed by disappearance of the marginal tissues (Fig. 22). The reflexing of the spines is entirely a mechanical process, resulting from the effect of expansion on the peculiar mode of attachment of the ligular spines to the leaf sheath.

In *Rhapidophyllum hystrix* the mature leaf base has the same biological function as in *Zombia*, but a few morphological differences are obvious. A ligule is present, open on the dorsal side, the free margins overlapping somewhat. The spines are the larger vascular bundles of the ligule freed by the breakdown of the surrounding tissues. These spines do not become reflexed. In mature palms, the spines protrude from a mat of fibrous tissue, which represents the remains of the network of smaller nonspinous vascular bundles. *Arenga* is very similar to *Rhapidophyllum,* although not of the same class because no rigid spines are developed. *Trithrinax acanthocoma* is a third example of this class, although I have not studied it in detail. However, the spines seem to originate as in *Zombia.*

It is hoped in the future to make detailed histological studies of the leaf base in this peculiar biological group.

CARYOTA TYPE. *Leaf base splitting ventrally, split surfaces connected by persistent fibers.* (FIG. 10.) This type is found only in the smaller, caespitose species of *Caryota,* but seems sufficiently distinct to merit separate description. The leaf base is initially long, tubular and ligulate, the walls of the sheath being much thicker than is usual in tubular sheaths. The ligule shreds into fibers and disappears as the leaf matures. A slight constriction on the ventral side is visible externally as a vertical separation layer. This region is anatomically specialized. As a result of internal expansion, the sheath splits along this line. The two margins of the suture do not separate cleanly, being connected by persistent fibers which are pulled into a horizontal position as the suture widens. These horizontal fibers interweave in a complex and irregular manner along the line of the original suture (FIG. 21).

The leaf base in the *Caryota* type is quite long and more obviously tubular than in related palms. It is, therefore, intermediate between the tubular and nontubular type of leaf base.

DISTRIBUTION OF LEAF TYPES IN THE MAJOR GROUPS OF PALMS

The preceding account represents a summary of incomplete observations. The main biological classes I have described are quite distinct, but others may exist, and the present ones may be subdivisible. In the succeeding paragraphs the distribution of these types throughout the major tribes of palms is indicated. The taxonomic groups are those employed in Tomlinson (1961a, Table I), recognized partly on an anatomical basis. Only genera are listed, although it is evident that some genera include more than one leaf-base type. Where a record is based on personal observation, the name is followed by an exclamation mark. Otherwise the records are based on published descriptions and illustrations, and may not be accurate. The list is very provisional and incomplete. Many palm genera are omitted.

Palms in which the stem is more or less subterranean are not considered, since these form a group which has not been studied in detail. Such palms commonly show no mechanical response to the little stem expansion which occurs.

Arecoid palms

(a) Inflorescence infrafoliar

VEITCHIA TYPE: *Acanthophoenix, Actinorhytis!, Archontophoenix!, Areca!,* *Bentinckia!*, *Brassiophoenix!*, *Chrysalidocarpus* spp.!, *Clinostigma*, *Cyrtostachys!*, *Dictyosperma!*, *Drymophloeus!*, *Euterpe* spp.!, *Geonoma* spp.!, *Gulubia*, *Hedyscepe*, *Hydriastele!*, *Iguanura*, *Linospadix*, *Loxococcus*, *Neoveitchia*, *Nephrosperma!*, *Normanbya!*, *Oncosperma!*, *Pinanga* spp.!, *Ptychandra!*, *Ptychococcus!*, *Ptychoraphis!*, *Ptychosperma!*, *Rhopaloblaste*, *Rhopalostylis!*, *Roscheria* spp., *Roystonea!*, *Siphokentia!*, *Veitchia!*.

In the above genera the inflorescences are always infrafoliar and abscission of the leaf takes place unequivocably according to the *Veitchia* type.

(b) Inflorescence either interfoliar or inconsistently infrafoliar

Phoenix type: *Manicaria*.

Trachycarpus type: *Oenocarpus* spp.

Type of leaf base obscure: The following palms require detailed study: *Asterogyne*, *Balaka*, *Calyptrocalyx*, *Calyptronoma*, *Chrysalidocarpus* spp., *Dypsis*, *Geonoma* spp., *Heterospathe*, *Howeia*, *Hyospathe*, *Jessenia*, *Linospadix*, *Neodypsis*, *Neophloga*, *Oenocarpus* spp., *Phloga*, *Pholidostachys*, *Pinanga* spp., *Prestoea*, *Reinhardtia*, *Roscheria* spp., *Stevensonia*, *Vershaffeltia*, *Vonitra*.

In these genera the leaf base abscisses fairly early, but often in an irregular manner. The inflorescence may be frequently infrafoliar, although the leaf base differs somewhat from the *Veitchia* type, as in *Heterospathe*. In other examples the inflorescence is consistently interfoliar, the leaf base is quite different from that of *Veitchia* and abscission is long delayed, as in *Neodypsis*.

Bactroid palms

Calamus type: *Bactris* spp.!, *Desmoncus!*.

Phoenix type: *Acrocomia!*, *Aiphanes!*, *Astrocaryum*, *Bactris* spp., *Guilielma!*.

Borassoid palms

Hyphaene type: *Bismarckia*, *Borassodendron!*, *Borassus!*, *Hyphaene!*, *Latania!*, *Lodoicea*, *Medemia*.

It should be noted that this group of palms is the only one with the same type of leaf base in all species.

Caryotoid palms

Cocos type: *Wallichia* spp.!

Trachycarpus type: *Arenga!*, *Wallichia* spp.!

Caryota type: *Caryota* spp.!

Chamaedoroid palms

Calamus type: *Chamaedorea* spp.!

Veitchia type: *Chamaedorea* spp.!, *Mascarena!*, *Opsiandra!*.

In some *Chamaedorea* species and in *Gaussia* and *Synechanthus*, the inflorescence is commonly interfoliar, abscission is imprecise, and these palms are difficult to typify. They require further study.

Cocoid palms

PHOENIX TYPE: *Arecastrum!*, *Arikuryroba!*, *Attalea!*, *Butia!*, *Corozo*, *Elaeis!*, *Jubaea!*, *Maximiliana!*, *Orbignya!*, *Rhyticocos*, *Scheelea!*, *Syagrus!*.

COCOS TYPE: *Cocos!*.

It should be noted that, although most genera of this alliance have leaf bases of the *Phoenix* type, those of this type can be subdivided into two more or less distinct groups. *Arikuryroba*, *Butia*, *Corozo*, *Elaeis*, *Jubaea*, and *Syagrus* have a spiny margin to the pseudopetiole, whereas in *Arecastrum*, *Attalea*, *Maximiliana*, *Orbignya* and *Scheelea* the pseudopetiole is not spinous and is often absent.

Iriartoid palms

VEITCHIA TYPE: *Catoblastus*, *Catostigma*, *Iriartea* spp., *Socratea*, *Wettiniicarpus*.

In *Iriartea* species and *Iriartella* the inflorescence is commonly interfoliar, abscission of the leaf base may be imprecise and the palms are difficult to categorize.

Lepidocaryoid palms

CALAMUS TYPE: *Ancistrophyllum!*, *Calamus!*, *Calospatha*, *Ceratolobus*, *Cornera*, *Daemonorops!*, *Eremospatha!*, *Korthalsia!*, *Lepidocaryum* spp., *Myrialepis!*, *Plectocomia!*, *Plectocomiopsis!*, *Schizospatha*.

PHOENIX TYPE: *Coelococcus!*, *Mauritia* spp. (e.g., *M. setigera*), *Metroxylon!*, *Raphia* spp.!

TRACHYCARPUS TYPE: *Mauritia* spp. (e.g., *M. carana*), *Raphia* spp. (*R. taedigera*).

Sabaloid palms

HYPHAENE TYPE: *Corypha!*, *Cryosophila!*, *Nannorhops!*, *Sabal!*, *Thrinax* spp.!, *Washingtonia!*.

PHOENIX TYPE: *Copernicia!*, *Erythea* spp.!, *Pritchardia* spp.!

COCOS TYPE: *Coccothrinax* spp.!, *Colpothrinax*, *Erythea* spp., *Licuala* spp.!, *Livistona!*, *Paurotis!*, *Pritchardia* spp.!, *Rhapis!*, *Serenoa!*.

TRACHYCARPUS TYPE: *Chamaerops!*, *Coccothrinax* spp. (e.g., *C. crinita*!), *Trachycarpus!*.

ZOMBIA TYPE: *Rhapidophyllum!*, *Trithrinax* spp. (e.g., *T. acanthocoma*!), *Zombia!*.

Genera of uncertain taxonomic position

VEITCHIA TYPE: *Pseudophoenix!*

COCOS TYPE: *Leopoldinia* spp. (e.g., *L. pulchra*), *Pelagodoxa*.

TRACHYCARPUS TYPE: *Leopoldinia* spp. (e.g., *L. piassaba*).

The leaf base in *Ceroxylon*, *Orania*, and *Sclerosperma* needs further study.

DISCUSSION

In the present era of specialized and sophisticated botany with so much emphasis on experimental procedures, the plea for more research involving simple morphological observation is likely to go unheard. Descriptive botany is regarded as too unscientific and unprofitable a field for startling new discoveries. And yet, in the realm of tropical botany there is enormous scope for research which requires the simplest apparatus: an axe, a knife and a scalpel, a clear eye, and the patience and willingness to settle down and observe elemental things. The present article is based entirely on simple techniques of this caliber. The observations have been made on living palms, mostly in the field or outside the laboratory rather than within it. The palms are a tropical family, their morphology is imperfectly understood because it differs from most other plants in many peculiar ways. It cannot be understood by regarding palms as aberrant trees. They are a unique but neglected group, and their study demands an outlook unclouded by a knowledge of how hardwood trees behave and preconceived notions as to how palms should behave. In so far as the growth of palms can be said to be known at all, its peculiarities raise problems more easily comprehended by an engineer than a botanist. The palms have discovered many devices by which these mechanical problems can be overcome. If we could ascribe reasoning powers to plants, palms would certainly be granted a high intelligence quotient, for their "ingenuity" soon becomes apparent to a thoughtful observer. The success and persistence of palms through a long geological history and their size as a taxonomic group and wide present-day distribution bear witness to their success in experimenting with original, and often apparently ill-adapted, growth forms.

One of the most difficult tasks which may confront a morphologist is to recognize the existence of mechanical problems. The purpose of the present article has been to emphasize the question of mechanical behavior of leaf insertion in palms, just as much as it has been to indicate ways in which the problem has been overcome. Only by further detailed studies using the more elaborate and precise techniques of modern botany can more decisive answers be given.

There are many other aspects of palm morphology, in addition to the leaf base, which require study from a functional aspect. For example, the growth and expansion of the inflorescence enclosed by a leaf sheath needs sympathetic consideration. Some of the answers to these mechanical problems seem easy enough. The leaf may fall before the inflorescence expands. Usually the inflorescence grows through the open mouth of the sheath. Sometimes the inflorescence protrudes through a cavity developed for quite a different purpose, as it protrudes through the dorsal slit in the leaf sheath of *Latania* and *Lodoicea*. Commonly the sheath is pierced by the expanding inflorescence. But to what extent this break-through is facilitated by anatomical preadaptation, we do not know. Here is a profitable field for simple observation. The behavior of the spathe in palms is also a subject deserving careful study. Often the spathes are deciduous and conveniently fall so as not to hinder flowering. I know of no studies on the abscission of the spathe. The large woody spathe in cocoid palms deserves looking at with the eye of an engineer. One of its most common and striking features is the system of deep longitudinal grooves in its outer surface. They are of obvious mechanical significance when the life history of the spathe is considered.

None of these studies, however elementary, can be accomplished swiftly. It takes time to become familiar with the biology of the living palm. Palms in botanic gardens are to a large extent inviolate, and the gift of a palm bud for dissection may come only at long intervals and then, quite literally, as a windfall. However skillful a research botanist may be in planning a budget for the expenditure of large sums on laboratory equipment, he is usually much less adept at acquiring funds for travel and collecting. But a travel fund is an important item of research expenditure for the tropical botanist.

The study of some of these elementary problems in tropical biology may have wider implication than is at first apparent. Thus, the persistence or otherwise of the leaf base in palms may be a significant matter to the ecologist. The stems of palms with smooth, self-cleaning trunks are a common habitat for lichens and small bryophytes. Palms with rough, persistent leaf bases provide an important lodging place for many epiphytes — ferns, orchids, bromeliads, figs, and others. The shaggy fibrous coat of a palm stem is an excellent habitat for small animals — snakes, scorpions, frogs, beetles, ants, spiders, cockroaches, and a host of small insects. In dissecting the buds of palms the botanist should be prepared for constant zoological surprises.

SUMMARY

The problem of the leaf base in palms is introduced in this essay and solutions are offered only in a very general way. The leaf base in all palms is initially tubular, although it does not always mature as a closed tube. It completes tissue differentiation and matures as a rigid sheath long before the stem which it encloses has ceased its thickening growth. The rigid sheath, especially in the larger palms, is thus subjected to internal stresses which it cannot accommodate by further active growth and expansion. Instead, this accommodation is effected by various mechanical devices for which the sheath of the palm leaf is often remarkably preadapted. Several distinct biological groups are recognized, although intermediate types are common. The leaf may absciss as a unit due to the development of separation layers in clearly prescribed regions. Otherwise, expansion of the sheath may be permitted through the development of wide clefts. Yet again, tissues may break down and disappear before they can offer resistance to stem expansion. In other types, these same tissues may persist either as an elastic tissue, or as a

fibrous mass, or sometimes even as protective spines, thus serving a secondary, incidental, but important, function.

In order to emphasize the taxonomic value of these morphological characters, which are quite constant in each species, a provisional list of leaf base types throughout the family Palmae is included.

It is emphasized that there is much scope for this type of simple observation, not only in palms, but in other groups of tropical plants. These observations are likely to have wide significance.

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EXPLANATION OF PLATES

PLATE I

Figs. 11–13. Leaf bases of the *Veitchia* type. 11, *Ptychandra glauca*, leaf insertion, ventral aspect, separating layers and notch distinct. 12, *Veitchia johannis*, leaf insertion, ventral aspect, leaf sheath splitting from above downward along the ventral separation layer, notch not developed. 13, *V. johannis*, abscissing leaf, ventral aspect, the clean leaf scar indicating preformed protective layers.

PLATE II

Figs. 14–17. Palms with the *Veitchia* and *Phoenix* types of leaf base. 14, *Roystonea regia* (*Veitchia* type), falling leaf abscissed as a unit — note distinct tapering of stem below crownshaft indicating future extent of internal diffuse secondary growth. 15, *Mascarena vershaffeltii* (*Veitchia* type), crownshaft from below, separation region of outermost leaf sheath visible as conspicuous ventral groove. 16, *Phoenix canariensis*, stem surface with woody armor of overlapping, persistent, partly encircling leaf bases. 17, *Copernicia curbeloi* (*Phoenix* type), vertical splits in leaf base near insertion reflecting extent of internal expansive forces.

PLATE III

FIGS. 18–21. Palms with the *Hyphaene*, *Cocos*, and *Caryota* types of leaf base. 18, *Latania commersonii* (*Hyphaene* type), dorsal view of mature leaf base on young nonflowering specimen — in flowering specimens inflorescence commonly protrudes through large dorsal cleft. 19, *Corypha elata* (*Hyphaene* type), leaf bases showing horizontal scratches scored by marginal teeth of petiole. 20, *Cocos nucifera*, showing persistent ventral tissues of leaf base visible as tongues of material resembling coarse sacking. 21, *Caryota mitis*, ventral aspect of mature leaf sheath with peculiar fibrous configuration.

PLATE IV

FIGS. 22–25. Palms with leaf bases of the *Zombia*, *Cocos*, and *Trachycarpus* types. 22, *Zombia antillarum*, immature leaf base, with ligule (open on dorsal side) beginning to separate into individual vascular bundles. 23, *Zombia antillarum*, stem covered with persistent spinous leaf bases, spines reflexed — note separation of larger vascular bundles (as compared with FIG. 22) indicating extent of expansion. 24, *Coccothrinax acuminata* (*Cocos* type), showing woody and rigid remains of ventral tissue. 25, *Arenga pinnata* (*Trachycarpus* type), showing long, pliable spines originating from ligular tissues and initially standing vertically erect.

TOMLINSON, LEAF BASE IN PALMS


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TOMLINSON, LEAF BASE IN PALMS


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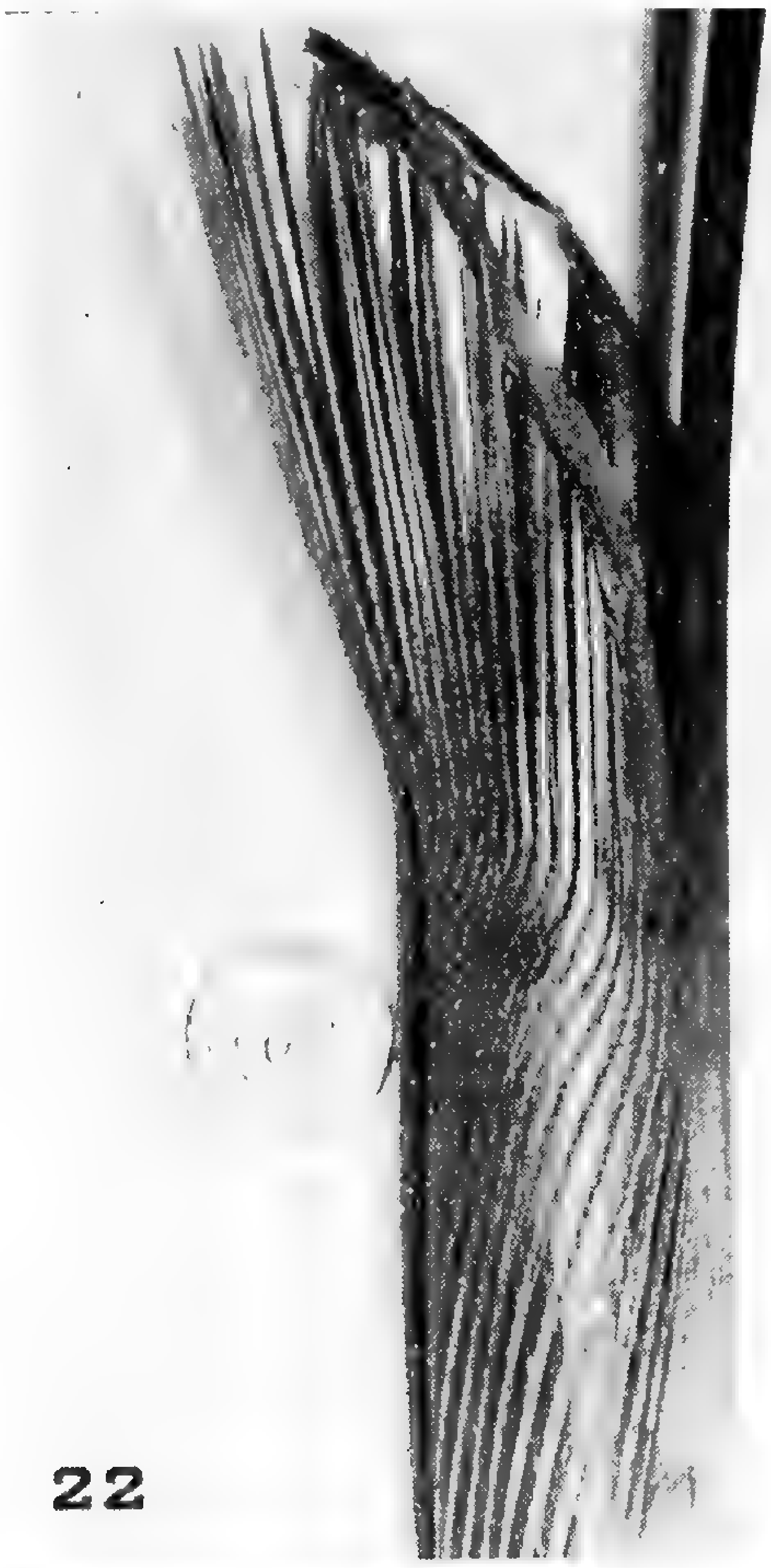
TOMLINSON, LEAF BASE IN PALMS



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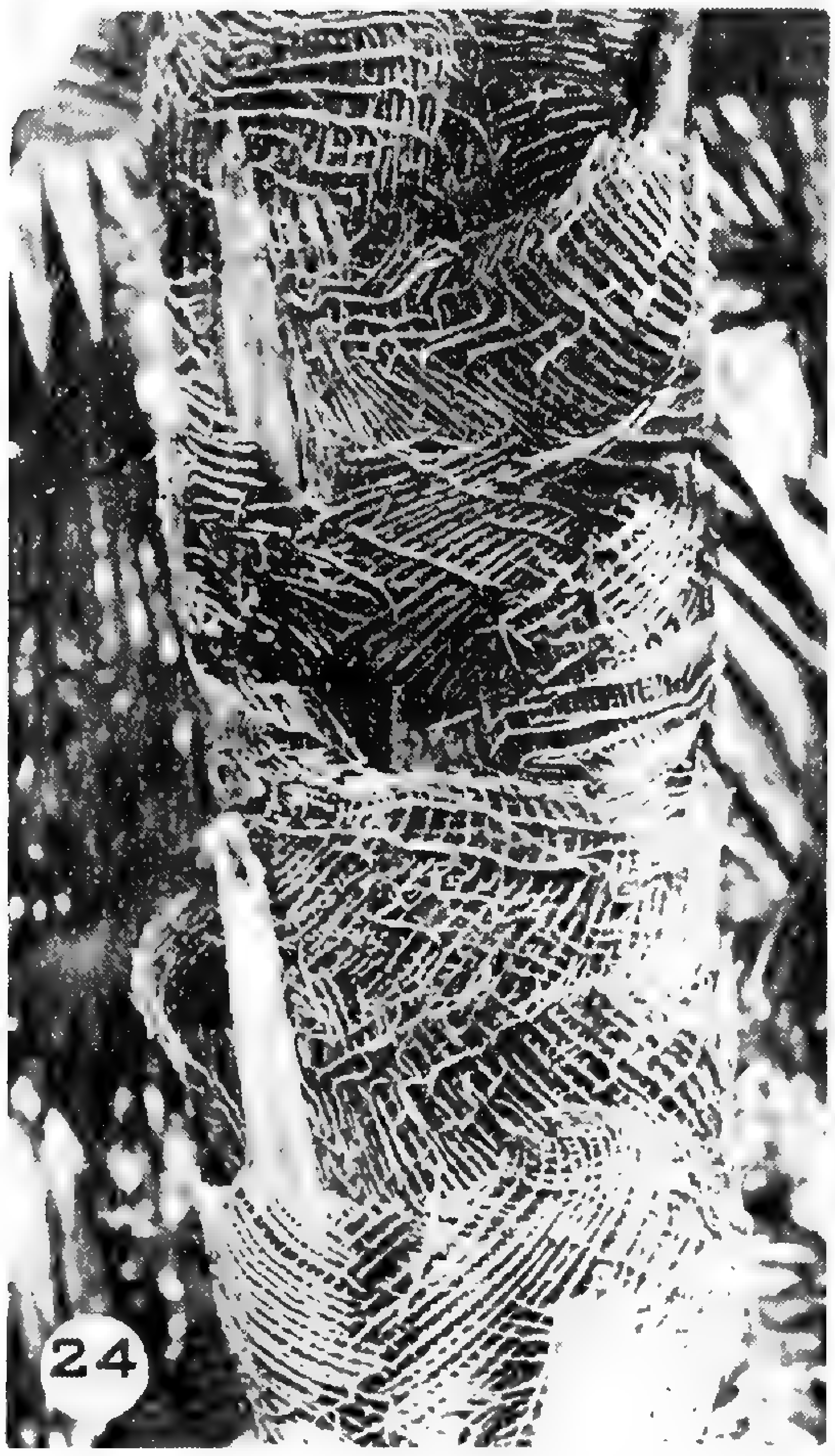

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Tomlinson, Leaf Base in Palms

BOTANICAL AND OTHER OBSERVATIONS ON REDONDA, THE WEST INDIES

RICHARD A. HOWARD

THERE ARE MANY SMALL ISLANDS in the West Indies, but none is so intriguing as Redonda to the traveler in the Leeward Islands. Isolated and pinnacle-like, Redonda is a landmark to the sailors who pass it. Since deep water surrounds the rock, one can approach it closely, only to learn that a landing appears to be difficult, if not impossible. From the east, Redonda appears to live up to its descriptive name as a round island, and as the descriptions of Redonda have varied little from the original supplied by Columbus, who named it, one suspects that few of the recent writers have done more than reword an earlier description. At one time, the island of Redonda supported a mining operation and had about 130 people living on it, but for the last half a century it has been uninhabited. The island, however, is reported to have a "king" representing a regency now in the second dynasty. There are only meager botanical records from Redonda, and only one other biologist, an entomologist, has climbed to the crest.

During several weeks of field work on Montserrat in January, 1961,[1] I saw Redonda daily in the distance. Finally, the temptation to visit it became overwhelming, and with the assistance of Mr. Kingsley Howes, my wife and I chartered the schooner "Melody" for a day and the trip to Redonda. Departure before the break of dawn allowed a smooth and rapid passage to the island, where we landed, climbed to the peak, explored the shaft of the phosphate mine, and collected some samples of the vegetation. Descending in midafternoon, we set sail and broke out of the lee of the island with some difficulty, returning to Montserrat before sunset through rougher seas. The diversity of the vegetation, although mostly of weedy species, was unexpected. This alone compensated for the physical difficulties of the trip. It is not to be recommended to a tourist.

Redonda lies about 25 miles southeast of Nevis, and 15 miles northwest of Montserrat. It is clearly visible from both of these larger islands. Redonda is recorded as being about 1.5 miles long and 0.3 miles wide, and the highest point is given by Martin-Kaye as 975 feet by aneroid reading (Reports on the geology of the Leeward and British Virgin Islands, p. 77. 1959). The island is obviously volcanic in origin, presumably of the post-Pliocene period, and a part of the volcanic chain of the Leeward Island group including Saba, St. Eustatius, St. Kitts, Nevis, and Montserrat. It is a fragment of a volcano, however, for the western two-thirds have been

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[1] The financial support of Grant No. G4441 from the National Science Foundation towards a Flora of the Lesser Antilles made this trip possible, and is therefore gratefully acknowledged.

lost in ocean depths, which reach 600 fathoms a short distance off shore. From the sea, the western face of the island is sheer, broken only by a mining scar at the northern end and one or two flume-like gullies farther south. In places, the vertical face appears to extend the full 975 feet. Various colored rocks and multiple layers of lava flows draw one's eye. Sea-eroded cliffs 100 feet high surround the remainder of the island, making the initial assault a formidable feat, impossible except in one place. Clearly some cataclysmic event split Redonda in the past to leave the fragment present today. The local story that this split occurred in the 17th century and was observed by a passing sea captain cannot be checked. One can only wonder when the discrepancy developed between the early descriptions of the island and its present condition.

Redonda was discovered and named by Columbus on November 11–12, 1493, on his second voyage. Morrison, in *Admiral of the Ocean Sea* (p. 410), relates that "from the northern end of Montserrat, Columbus sighted a large island to the northwestward but did not care to beat up to it against a trade wind. He named it Santa Maria la Antigua."

"Proceeding in a general northwesterly direction the fleet passed a small steep and rounded but inaccessible rock less than a mile long, which Columbus named Santa Maria la Redonda, St. Mary the Round. Redonda retains her name and her importance as a sea mark to this day; but she has never been worth inhabiting."

Other historians have about the same story. In the *Life of Christopher Columbus*, by his son Ferdinand (p. 125), it is reported that "from here he proceeded to Santa Maria la Redonda, to which he gave the name because it is so round and smooth that it is impossible to climb its sides without a ladder." Markham (*Columbus*, p. 152, 1892) reports Redonda to be "a round islet [that] was seen to the westward, so steep on all its sides that it seemed inaccessible without stairs or ropes thrown from the top." More recently, Sir Frederick Treves, in *The Cradle of the Deep* (1908), described Redonda (p. 196) as "a smooth pale fabric of stone rising out of the sea, like the dome of some immense submarine hall, whose span is a mile. It reaches to the height of 1,000 feet. It is bare as a pebble. . . ." Ober (*A Guide to the West Indies, Bermuda and Panama*, p. 343. 1920) says of Redonda, "It appears scarcely more than a rock pinnacle rising above the sea between Nevis and Montserrat, but it is a mile and a half in length by a mile in breadth, with an altitude of 1,000 feet. The Spaniards called it Redonda, or the Round Island, from its shape." Thus, the dimensions suggested by the chroniclers of Columbus do not vary from those of the present. It is not clear whether Columbus, viewing the island in the late evening, passed to the east and did not notice the steep western face, or whether the island has truly split since the time of discovery.

Although many naturalists passed the island of Redonda in the 17th, 18th, and 19th centuries, apparently not one of them reached it. Only Sir Hans Sloane appears to have noted the island, and even he fails to comment on its shape in his published writing. G. R. de Beer (*Sir Hans Sloane and the British Museum*, 1953) refers to a letter from Sloane which is now in the British Museum. Sloane wrote of his trip north from Barbados in September, 1687, "Between Montserrat and Nieves lies a very small Island called Redondo or Rotunda, discovered by Columbus in his

ABOVE: Redonda as seen from the southeast. BELOW: Redonda from the northeast. The wave-cut cliffs and the cirques are from one to several hundred feet high.

Second Voyage, who gave it the name Santa Maria Rotonda, from its Figure. It consists of one Rock, very Perpendicular and high, looking like a Pyramide, and if there were nothing but Rock, but I was inform'd by those who have been on it, that there is on its top an Acre or two of very good Ground, that it has a very good Landing-Place, and a Well of very good fresh Water. It has also a great store of Iquanas of black color. Many Boobies, and other Birds that come hither to lay their Eggs at proper Seasons."

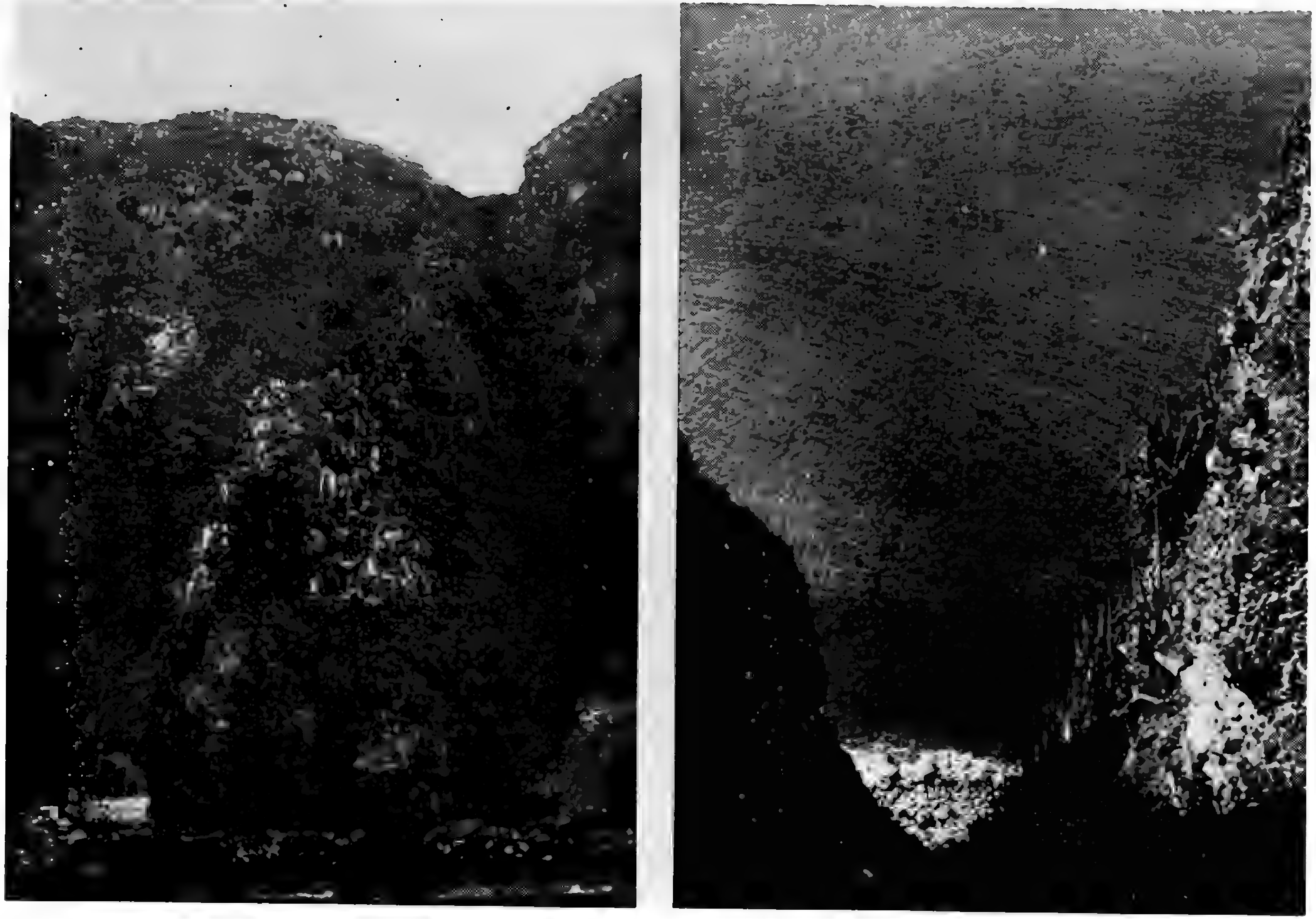
Redonda was not visited by a naturalist until the Smithsonian-Bredin expeditions of 1956 and 1958 stopped at the island. Waldo Schmitt related in the Smithsonian Report (457–8, *pl. 6.* 1957; 429–30. *pls. 9, 10.* 1959) of his visit to the shore and of the ascent of Redonda by J. F. Gates Clarke, who climbed the ridge on the first visit, and on the second made the ascent and spent the night collecting insects, while defending himself from the rats which infest the rock. Dr. Clarke gathered a few plant specimens, but some of these were lost, and others so ruined in the descent as to be of little use, and so were discarded. Dr. Clarke's photographs remain, to the present, the only published photographs of the island and its summit. Several comparisons between his photographs and my own or between our observations will be made.

Although currently uninhabited, Redonda has not always been so. At some unspecified period prior to 1860, ores containing phosphate were discovered on Redonda, and between 1865 and 1912 this material was mined. Shephard (Am. Jour. Sci. II. **47**: 428. 1869; **48**: 96. 1870) described this mineral as Redondite, a name later shortened to Redonite, and currently considered to be variscite. It is included in a porphyritic or felsparphyric olivine basalt. In 1891, Hitchcock (Bull. Geol. Soc. Am. 2: 7. 1891) reported an analysis to show concentrations of P_2O_5 as high as 42.9%, but a modern analysis of the residue remaining on Redonda yielded only 18% P_2O_5.

Mr. Fred W. Morse visited Redonda in the company of Prof. Charles H. Hitchcock in the summer of 1890, and reported on the trip (Popular Science Monthly **46**: 78–87. 1894). His colorful description of Redonda and the activities thereon is worth repeating. Redonda was reached after a sail of three hours from Montserrat, Mr. Morse related. "As we approached the pier, a boat manned by two negroes put off to meet us, with a strongly built man with a pleasant face and brown beard and dressed in white linen sitting in the stern. The man proved to be Captain H —, the superintendent of the mine, who welcomed us to Redonda and transferred us with our baggage to the shore.

"The beach was only a few yards in width, and above us towered the cliffs, over five hundred feet high. Groups of men stood on their brink, looking down at us and appearing like silhouettes against the clear sky. The ascent to the plateau above . . . was accomplished upon an aerial tramway.

"Two stout, heavy wire cables were stretched up the gorge and firmly anchored at both ends. Upon each cable ran a trolley, from which was



LEFT: Western escarpment of Redonda, showing remnants of the cable base and landing. An ascent must be made in the right-hand (southern) gully. RIGHT: View down the gully from the saddle. Plants of *Cephalocereus* and *Melocactus* are visible on the right. Notice the narrow coastal shelf and the deep water within a few yards of shore.

suspended a large iron bucket. To each trolley was attached the end of a light yet strong wire cable, which passed over a set of heavy pulleys at the top of the cliff, thus causing one bucket to ascend as the other descended. When passengers or freight were to be raised, the bucket at the top of the cliff was filled with water from a tank, and the lighter load at the bottom was quickly drawn up. The speed was regulated by means of brakes applied to the pulleys.

"The main cables were eight hundred feet long and the load was raised to the height of five hundred and twenty-five feet above the beach. In places the wires ran at a height of sixty feet above the uneven surface of the gorge.

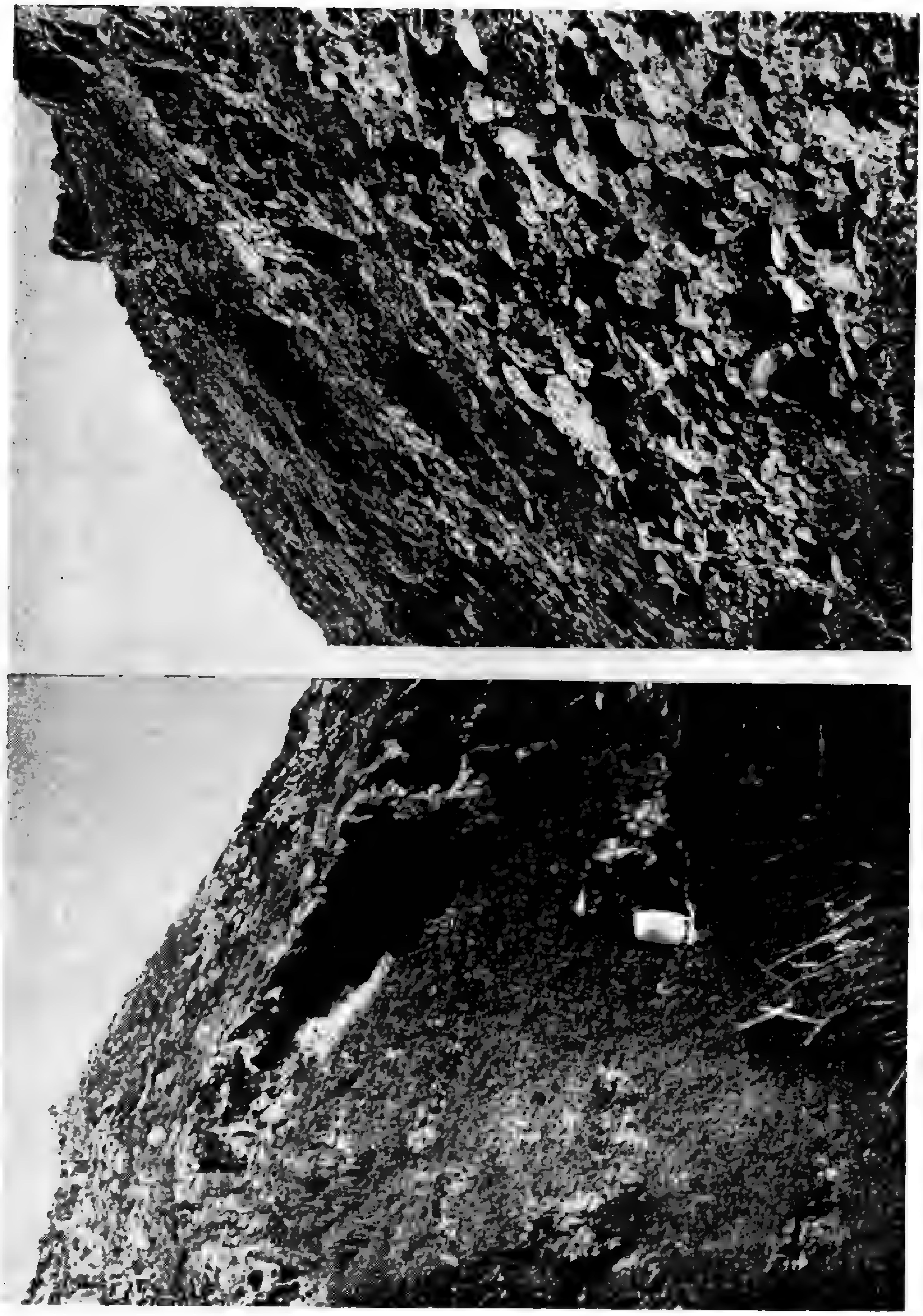
"We were invited to get into the bucket which was at the foot. Captain H — stood on the edge, clinging to the trolley, and we rapidly glided up between the steep walls of the gorge, from whose rocky sides peered round cactus plants like heads of gnomes and several strange shrubs threw down aerial roots as though in a vain effort to reach the thin soil at the bottom. On gaining the landing at the top, we were . . . conducted up the slope a hundred yards to the superintendent's house. The dwelling and office were really two separate buildings joined together by a wide veranda between them and along their front. . . . the buildings had been framed and ready for putting together, and were small cottages with two rooms and with roofs of corrugated iron. We were met at the house by Mrs. H — and her young daughter, Dorothea, who, with the captain, were the sole white inhabitants of the island. A small black boy called Chalmers showed us to our room, where we prepared for dinner. By this time, the short twilight of the tropics had been succeeded by darkness, and when we returned to the dining room with its bright light we could hardly believe that we were upon an almost inaccessible rock in the Caribbean Sea.

"The next morning, just before daybreak, while yet dark as night in the room, we were awakened by the cries of the sea birds, which made their homes by the hundreds in crevices and niches of the cliffs. Very soon a bell rang in front of the house to awaken the workmen in the huts below us."

Later Morse visited the mine. "The path to the mine led us along the eastern slope of the island to the northern face of the main peak, where a wide and deep ravine separated us from the smaller peak. The distance from the house to the mine was about three-fourths of a mile. The path was very steep in places as it ascended towards the summit in order to avoid a deep gorge, and sometimes so narrow that a misstep would give one a bad fall down the slope."

Morse reported on the birds and lizards around the house, and commented that "several sheep and goats, two dogs, some hens, two peacocks, and a white cat comprised the domestic animals of this Crusoe-like home. From time to time the sheep and goats had become wild and had taken to the almost inaccessible parts of the cliffs and gorges, where it was exciting sport to pursue them.

"After lunch, when the sun had begun to descend towards the west,



LEFT: View of western face of Redonda showing the rock pinnacle, the highest point of the island. A cirque formed by erosion and land slides is seen above the resting booby. RIGHT: Scree slope about the middle elevation on the eastern side. *Peperomia* and *Psilotum* were found in moist areas among the rocks.

Captain H— took us down to the plateau below the house to look at the quarters occupied by the workmen. The buildings consisted of two long sheds with close shutters instead of glass windows, and contained for furniture nothing but a tier of bunks or rather shelves, of rough boards along the walls. . . . Near the buildings were ovens where the baking was done. . . . Their fare was simple, consisting of bread and salt beef. The foremen and skilled workmen occupied two smaller houses, but lived in the same manner. Water for drinking was obtained by catching the rain on large inclined surfaces of corrugated iron, and collecting it in reservoirs. Such a reservoir was built at each end of the island for the use of the men, and the superintendent's dwelling was provided with capacious tanks connected with the roof. . . ."

Tempany (West Indian Bull. **15**: *22–25.* 1915) visited Redonda in 1915, after a disastrous hurricane on August 7, 1899, destroyed the buildings Morse had described. Tempany's descriptions, while less picturesque, give further details on the mining operations and on the living conditions of the workmen. Until the time of Tempany's visit, phosphate rock was mined in four places on the island. The rebuilt dormitories now had space for 180 men, and the working conditions, including the rations of food and water, indicate that life for the laborers from Montserrat was anything but serene. Breakfast and lunch were served at the mine areas. After the cable at the northern end of the island weakened and collapsed, all ore was carried over the treacherous trail in basket loads of 84 pounds each on the heads of the men to the remaining cable near the manager's house.

Although the last shipment of ore was made in 1912, ore was stockpiled at both ends of the cable until July, 1914. It cannot be definitely established when the island was evacuated, but it is known that a skeleton crew was maintained on the island until the hurricane of 1929 blew away the remaining buildings, and the company's lease was finally relinquished in 1930.

Martin-Kaye, in describing the resources of the Leeward Islands, suggests that "the outlook for Redonda, however, is poor. The reserves are not known and to determine them would be expensive. Reports have it that the material was becoming more difficult to win. . . . There is the possibility that important resources remain, and this is supported to some measure by the length of time for which the defunct company held on to the lease. If they thought that the island held little further reserves the lease would presumably have been abandoned earlier."

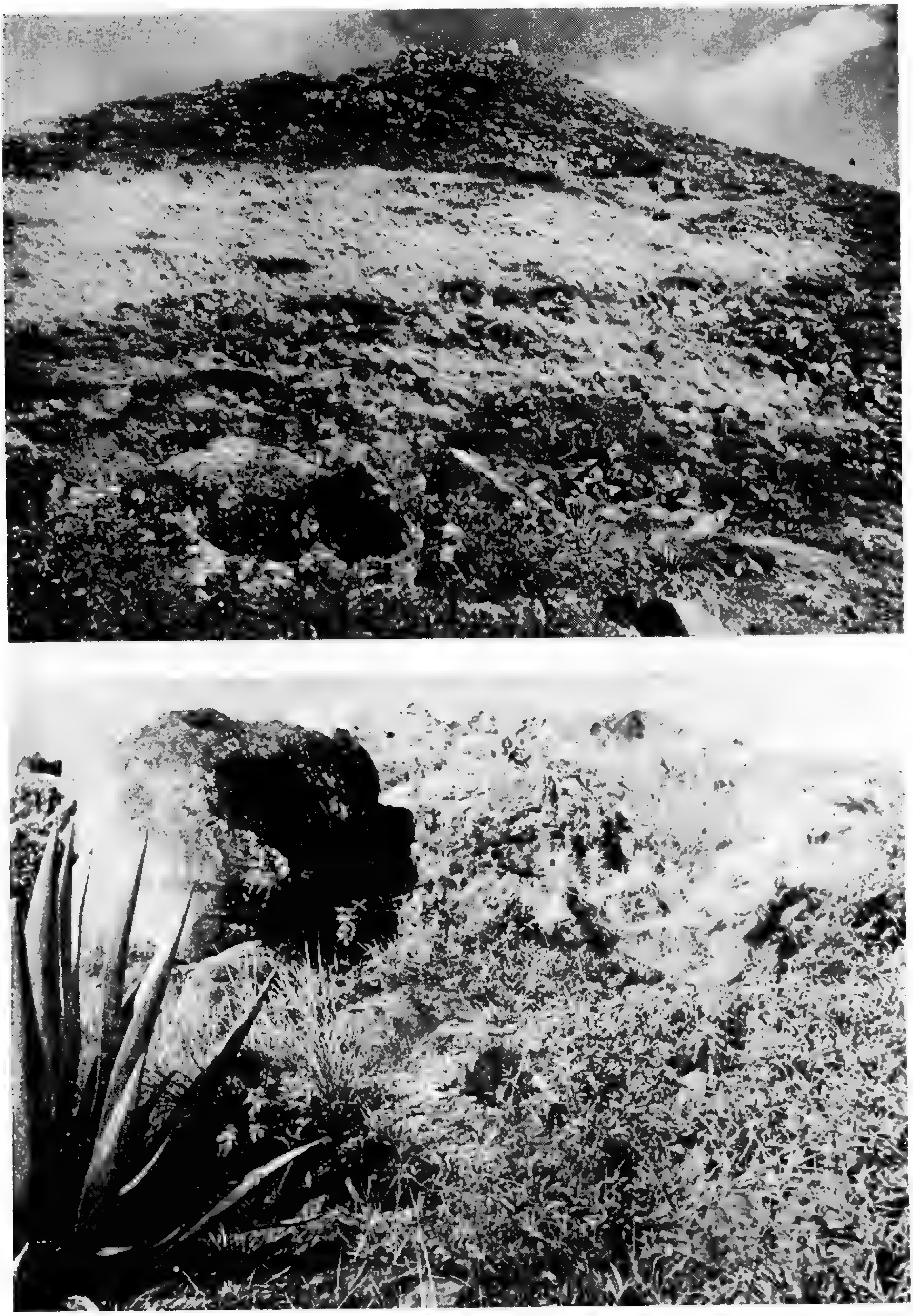
The story of the "King of Redonda" is worth reporting, for it is well known and often repeated by the residents of the nearby islands. The details vary a bit with the teller, and two published versions are also known. Bradley Smith, in his excellent book *Escape to the West Indies*, gives a straightforward account obtained from Charlesworth Ross, recently commissioner on Montserrat. Apparently the story began in 1865, when Matthew Dowdy Shiel claimed the island of Redonda, and a few years later had his son, Matthew Phipps Shiel, later better known as the writer M. P. Shiel, proclaimed King Felipe the First. Smith reports that the British Colonial office eventually "tacitly admitted" his claim, although today the island of Redonda remains under the administration of the government of Antigua. Eventually the younger Shiel passed his title to John Gawsworth through an ancient succession ceremony involving the mingling of blood through cuts on the wrist. After Shiel's death in 1947, Gawsworth became King Juan the First, and has since appointed many prominent figures Dukes of Redonda. A more glamorous version of this tale appeared in a recent issue of a popular magazine (Men Only [London] **75**: 58–60. 1960) under the title of "King of all the Seagulls." The coincidence of a disputed regency and a seemingly profitable mining operation makes one wish for more of the details of Shiel's claim.

THE VEGETATION

A visit to Redonda is becoming increasingly more difficult. Storms of recent years have all but destroyed the loading pier, the remnants of which mark the landing spot. Once on the narrow, boulder-strewn "beach," the only direction one can move is up. The ascent of Redonda is made along a cleft filled with volcanic gravel, which rises at a 60 degree angle. One climbs using all appendages, and the only resting place is the saddle, or ridge, fully 500 feet above the sea. In the afternoon, this valley assumes all of the characteristics of an oven, and, without a hint of a breeze on this, the leeward side, the rocks become too hot to touch. At the ridge, one finds a small level plateau on which are the foundations of former buildings and the rusting machinery of the old phosphate mine. A grassy appearing slope descends at an angle of 30 degrees to the east and the south. Broken water catchments, and the foundation of the manager's house, are on the slope to the north, which is capped with a pinnacle of large boulders. A disintegrating foot path follows a circuitous route of varying altitude to a mine shaft, a short tunnel, at the northern end of the island. In all directions there is a breath-taking view of the northern Caribbean.

Redonda supports a wild herd of nearly one hundred goats, some of the males massive and handsome specimens with beards nearly reaching the ground. Their hooves left prints the width of my hand. Myriads of sea birds nest on the island. During the peak of the laying season, the men from Montserrat visit the island and gather eighty dozen eggs a day for sale on adjacent islands. Rats persist on all parts of Redonda, and sleep is impossible along the shore or in the ruins of the buildings because of the attacks of these animals. Lizards and iguanas are commonly seen, but appear to be more agile than usual in avoiding capture.

The early accounts of the plant life of Redonda are meagre. Morse, who visited the island with Charles Hitchcock, reports of their interest in the minerals, as well as the flora and the fauna. In addition to the "round cactus plants like heads of gnomes" and "several strange shrubs which threw down aerial roots" seen on the west wall of the island, he mentions the "red and yellow blossoms of the cactus" around the manager's house. He reports that "a few air plants, a species of *Tillandsia*,



ABOVE: The grassy slope of Redonda as seen across the plateau (saddle) and site of the former barracks and mining buildings. The ruins of the manager's house are seen toward the upper right. BELOW: A closer view of the rocks and vegetation of the same slope. Volcanic "bombs" are infrequent. *Opuntia repens*, known locally as "suckers," is abundant. *Agave*, *Croton*, *Lantana*, and *Wedelia* species are dominant.

clung to the projections of the rocks and formed almost the sole vegetation at the extreme summit." He was also impressed that "one of the drawbacks to exploring the island was a variety of cactus which the workmen spoke of as 'suckers.' It resembles the prickly pear in form and had a yellow blossom. Its joints or sections were thickly covered with thorns or spines, which were from three-fourths of an inch to an inch and a half in length and barbed at the tip. The joints were easily broken off, and clung to anything upon which their spines could catch. The animals about the place were almost always seen with from one to a half a dozen of these 'suckers' clinging to them. When a barbed spine became imbedded in the flesh it produced a sore unless removed at once, and it was usually necessary to cut it out in order to remove it."

Although Morse wrote, "The remainder of our stay was spent in collecting and preparing specimens of the phosphate, and also of the plants and animals," no records of these collections can be located.

Mr. C. Steffens (Globus **67**: 49. 1895) reported that the island appeared treeless, but that near the peak were "Gold- und Silberfarne" and under other plants "Tillandsien."

In 1915, Trepany (*loc. cit.* 23) reported, "There is but little vegetation on the island, the surface being rock-strewn and barren, with no depth of soil. The principal vegetable forms which occur are species of Prickly pear (Opuntia) and Cacti, notably Cereus. It is, however, worthy of note that the silver fern (*Gymnogramme trifoliata*) and the gold fern (*Gymnogramme chrysophylla*) both occur fairly abundantly in places in sheltered crevices in the rocks."

More recently, Martin-Kaye (*loc. cit.* 77) states that Redonda possesses "scant vegetation beyond some coarse grass and extensive networks of particularly pugnaceous varieties of prickly pear. . . ." However, Clarke (Smithson. Rep. 430. 1959) reported, "The inclined plateau forming most of the top of the island is covered by coarse grasses, sedges, a slender narrow-leafed agave, several cacti in great abundance, lantana and several other scrubby shrubs." *Plates 9* and *10* associated with Clarke's report illustrate some of the plants I was able to collect.

Although early observers may have described Redonda to be "as bare as a pebble," plants exist on the island. Some ornamental or useful plants are remaining following cultivation, and a large number of "weeds" were obviously introduced. The typical strand plants of sandy beach and coral rock of the adjacent islands were missing; however, even the steep, wave-washed cliffs were abundantly populated with plants appearing to be perched in crevices or even on boulders soon to fall to the ocean below. The only level ground in the saddle, which formerly was occupied by mining buildings, had a wealth of grasses of wide-spread geographic distribution. The eastern slopes of Redonda were simply piles of boulders, yet on and between the stones were many plants so abundant that the footing was even more treacherous, as the stones were obscured by the growth of *Croton flavens*, *Lantana camara*, and *Wedelia calycina*, the broad-leaved species present.

By far the most memorable plants of Redonda are the "suckers," *Opuntia antillana*, *Opuntia repens*, and *Opuntia triacantha*. No description does justice to the audacity or tenacity of *Opuntia repens*. Truly its pads are delicately attached and its spines retrorsely barbed the full length. The slightest jar caused a fragmentation of the plant, and the pads penetrated with ease the canvas, leather, or heavy rubber footwear of various members of our party. On the rocky plateau, the plants were abundantly branched, extending in many directions, the segments stretching pad on pad over rocks and shrubs. On the cliff faces, plants of the same species seemed to develop a single stem structure. The plants hung in long festoons from the rocks, and single plants appeared to be as much as twenty feet in length. A slight touch with a stick or a falling rock would send the pads as individuals cascading down the slope on the unsuspecting climber below. If my records of the vegetation are inadequate or incomplete, the blame rests on this species alone.

Clarke reported that the only tree on Redonda was an introduced one, but failed to name it. *Casuarina equisetifolia* is clearly shown in his paper (*pl. 10, fig. 2*) near the ruins of the house of the manager of the mining company. In the vicinity are also introduced specimens of *Bougainvillea spectabilis*, its brilliant red flowers clearly visible from the schooner approaching the island; *Citrus aurantiifolia*, the lime; and *Annona squamosa*, the sugar apple. Since Clarke's visit in 1958, seedlings of *Ficus citrifolia* have been introduced by birds, for a nine-foot sapling is now flourishing from the apex of the central rock in Clarke's photo of the "very tiptop of Redonda" (*pl. 9, fig. 2*). Other abundant plants, obviously residual from the period of mining operation, are *Ricinus communis* and *Nicotiana tabacum*.

A spire-like cactus (*Cephalocereus royenii*) grew in profusion on the steepest slopes of the western escarpment, but nowhere could the plants be approached with safety in order to make a collection.

Although Clarke reported a cistern on top to be in "good condition," during our visit we found that all of them were dry and so cracked as to appear scarcely capable of holding water. No rainfall records are available, yet fortuitous showers must provide small pools or at least wet places deep in the piles of rock, and many of the scree slopes appeared damp and slippery. In damp, shady places on the eastern slopes, I was surprised to find several plants of *Psilotum nudum*, *Pityrogramma chrysophylla*, *Pilea microphylla*, and *Peperomia simplex*. Among the rocks, usually in slightly protected areas, were many plants of *Tillandsia recurvata*, but none was seen at the summit as Morse reported.

The following species represent the most complete account, to the present, of the vegetation of Redonda. All species cited by number are supported by vouchers deposited in the herbarium of the Arnold Arboretum. Regrettably, large collections could not be made, and several sight records are given for clearly recognized species which either could not be handled in my limited amount of collecting equipment, or just could not be reached over the edges of the precipices.

Lichenes

The determinations of this group were made by Dr. I. M. Lamb, of the Farlow Herbarium, where the supporting specimens are deposited. The unnumbered collections were some of the more colorful lichen-masses and were not separated in the field from the small rocks on which they grew.

Acarospora chrysops (*s.n.*)
Buellia prospersa (*s.n.*)
Calopaca sp. (*s.n.*)
Heppia bolanderi (*s.n.*)
Parmelia sp. (*s.n.*)
Ramalina subasperata (*15227*) — abundant in restricted areas of large boulders.
Roccella babingtonii (*15228*) — abundant, pendant from the underside of large boulders.

Psilotaceae

Psilotum nudum (*15220*) — a single clump found in a wet crevice under a large boulder.

Polypodiaceae

Pityrogramma chrysophylla (*15231*) — the silver form alone was found in a gulley on the east slope, but smaller clumps of both the silver and gold forms were growing in cracks on the walls of the cistern above and to the west of the ruins of the manager's house.

Gramineae

Chloris inflata (*15251*)
Digitaria sanguinalis (*15249*)
Eragrostis ciliaris (*15229, 15253*)
Panicum maximum (*15256*)
Pappophorum pappiferum (*15224*) — a clump grass with conspicuous inflorescences.
Paspalum laxum (*15252*) — a large clump grass, the largest and most common grass on the island.
Setaria setosa (*15250, 15257*)
Trichachne insularis (*15254*)
Trichachne sp. (*15234*) — a distinct species which, unfortunately has no available name. Specimens are known from a range extending from Mexico to Peru, and this collection must have been introduced as a weed. Dr. Jason Swallen, who supplied this information, will describe and name the species at a later date.
Tricholaena repens — a colorful and easily recognizable grass, but only locally abundant.

Cyperaceae

Cyperus ligularis (*15255*) — a heavy clump sedge essentially limited to the higher elevations, the edges of the western precipice, and found occasionally on the sheer faces. Only rarely does the plant assume its normal shape, for the clumps are the favorite nesting places of the boobies (*Sula* spp.). The birds apparently keep the plants trimmed into a cushion shape, and, at the time of our visit, only a few of the lateral shoots bore inflorescences. (See Clarke's illustration *loc. cit. pl. 10, fig. 1.*)
Cyperus sphacelatus (*15230*)

Bromeliaceae

Tillandsia recurvata (*15221*) — certainly not as abundant as Morse and Steffens implied. All plants were found growing on rocks at higher elevations.

Agavaceae

Agave montserratensis — although it was impractical to collect specimens of this large *Agave*, a complete set of photographs allows this determination. Trelease's monographic treatment may need revision, but his recognition of many species in the Leeward Island area seems sound. The Redonda specimen appears to be the same as the plants found on Montserrat. Clarke's photograph (*pl. 10, fig. 2*) shows the characteristic habit and the long narrow leaves of this species which it is strange that earlier visitors did not notice.

Agave sisalana — several plants of this species were seen near the ruins of the mine headquarters, suggesting that the plant may have been introduced as an ornamental or a possible crop plant.

Casuarinaceae

Casuarina equisetifolia (*15233*) — a single tree of this species was planted near the manager's house and is shown in Clarke's illustration (*pl. 10, fig. 2*). The specimen is pistillate, and no seedlings were to be found. The tree is a favorite nesting place for boobies, and all branches were heavily covered with guano.

Piperaceae

Peperomia simplex (*15222*) — Dr. T. G. Yuncker kindly identified this material and indicated that it is commonly known as *P. hamiltoniana* Miq., which is properly referred to *P. simplex* Ham. The present plants were abundant in damp areas under rocks and on the scree in gullies on the eastern side.

Moraceae

Ficus citrifolia (*15247*) — only three plants, all seedlings, were seen on Redonda. The largest grew in a crevice of the top-most boulder of the island, a rock covered with guano. Clarke's photograph of this same rock, taken in 1958, does not show this plant. The other specimens were in unapproachable locations on the steep western face of the island. Clearly the species has been introduced recently by birds.

Urticaceae

Pilea microphylla (*15219*) — this species occurred on rocks and the damp scree of the eastern gullies.

Amaranthaceae

Amaranthus dubius (*15245*) — a weed near the old building area.

Centrostachya indica — a weed along the old path to the mine.

Iresine angustifolia (*15235*) — a rampant herb among rocks at the summit.

Nyctaginaceae

Boerhaavia coccinea — on the plateau and on the western scree slope.

Bouganvillea spectabilis — a woody vine planted and persisting near the ruins of the manager's house.

Portulacaceae

Portulaca oleracea — a weed around the ruins and in the gully one ascends.
Portulaca halimoides (*15218*) — this, and the following two species, occur primarily on the scree slopes of the western face of the island.
Talinum triangulare (*15223*)
Trianthema portulacastrum

Annonaceae

Annona squamosa — a small shrub persisting following planting near the manager's house.

Capparidaceae

Cleome viscosa (*15241*) — a most common weed.

Leguminosae

Centrosema virginiana
Galactia sp. (probably *G. stricta*) — occurring commonly near the ruins, but all of the plants seen were sterile.
Tephrosia cinerea (*15237*) — an abundant herb found in many locations.

Rutaceae

Citrus aurantiifolia (lime) — a shrub persisting after cultivation near the manager's house.

Euphorbiaceae

Croton flavens (*15240*) — this species, *Wedelia calycina* and *Lantana camara* represent the most common broadleaved plants and dominant shrubs on the island. All of the plants, however, were of lower stature than the species assumes on other islands. Many of the flat-topped shrubs served as nesting places for the birds, and these plants appeared to be trimmed around the nests.
Croton lobatus (*15244*) — common herb in the western gully along which one ascends.
Euphorbia hirta (*15246*)
Euphorbia heterophylla
Jatropha gossypifolia — a weed around the ruins and in the scree of the western gullies.
Phyllanthus amarus — a weed around the ruins.
Ricinus communis — presumably persisting after cultivation; common in gullies on the west face of the island.

Malvaceae

Sida cordifolia (*15239*)

Cactaceae

Cephalocereus royenii — columnar cacti common on precipitous western escarpment.
Melocactus intortus — found primarily on the sheer western face of the island.
Opuntia antillana — a stout cactus of frequent occurrence.
Opuntia repens — "the sucker"; extremely abundant.
Opuntia triacantha — less frequent than *O. repens*, and less easily fragmented.

Plumbaginaceae

Plumbago scandens (*15248*) — abundant on the western escarpment.

Apocynaceae

Catharanthus roseus — occasional in mining area.

Asclepiadaceae

Cynanchum parviflorum (*15225*) — common vine on the plateau. A leafless form of this species hung in festoons from many rocks on the western face.

Verbenaceae

Lantana camara (*15236*) — an abundant shrubby species represented by the orange-yellow color form. All plants were spineless.

Lantana involucrata — found primarily at lower elevations above the cliffs on the windward side.

Stachytarpheta jamaicensis — infrequent.

Labiatae

Hyptis pectinata (*15226, 15242*) — frequent in occurrence, but usually browsed by goats.

Leonotis nepetifolia

Solanaceae

Nicotiana tabacum — occasional plants presumably persisting after cultivation.

Scrophulariaceae

Capraria biflora — a weed near the mine ruins.

Acanthaceae

Justicia periplocifolia (*15238*) — a narrow-leaved form usually browsed into abnormal growth forms. Determined by E. C. Leonard.

Rubiaceae

Oldenlandia corymbosa — occasional among rocks on the eastern slopes.

Compositae

Ageratum houstonianum

Emilia coccinea (*15233A*)

Pterocaulon virgatum (*15232*) — a few individuals at the northern end of the island.

Wedelia calycina — one of the common shrubs on the island.

After this article was set in type, I discovered a paper by Harold Box entitled "A Note on the Vegetation of Redonda, B. W. I." (Jour. Bot. 77, 311-313. 1939. Mr. Box, sailing from Antigua, visited Redonda on July 18, 1938. His observations were made from the landing place, since he was unable to climb the cliff. A list of 27 species, including *Talinum paniculatum* and *Lithophila muscoides* which I did not encounter, is given as the lithophyte flora of the island.

A TAXONOMIC REVISION OF PODOCARPUS, XIII SECTION POLYPODIOPSIS IN THE SOUTH PACIFIC

Netta E. Gray *

Section Polypodiopsis was established in 1874 by Bertrand (1) for *Podocarpus vitiensis* Seemann, then known only from Fiji. In 1903, Pilger (23) included this species and *P. minor* Parlatore as species of doubtful affinity in sect. Nageia, chiefly because of their opposite leaves. In 1926, he mentioned Bertrand's section and species synonyms briefly but did not change his interpretation. Florin (8) recognized the significant differences of these species from others in sect. Nageia and restored the use of sect. Polypodiopsis, to which he added *Podocarpus rospigliosii* Pilger, a South American species which had been described by then. This section now is firmly established in its use by Orr (22), Wasscher (32), and Buchholz & Gray (4).

The five living species now included in sect. Polypodiopsis are *Podocarpus vitiensis* Seemann, of Fiji, New Guinea, New Ireland, and the Solomon Islands; *P. filicifolius* sp. nov., newly described from the Moluccas; *P. comptonii* Buchholz and *P. minor* Parlatore, endemic to New Caledonia; and *P. rospigliosii* Pilger, of the Andes of Venezuela, Colombia, and Peru. Two fossil species (from Tertiary deposits) referred to this section are *P. araucoensis* (Berry) Florin, found in Chile, and *P. brownei* Selling, lately described from Tasmania.

This distribution is striking and becomes very significant in recent studies of regional floras (Smith 28), monographs (e.g., Van Steenis 30, Selling 26), conifer geography (e.g., Florin 9, Li 20), and phylogeny (Florin 14). An ancient vast southern continental land mass is emphasized by Van Steenis (30) in his consideration of the angiosperm genus *Nothofagus*, which is not only found both in the South Pacific and South America, but which has a subsection of twenty-one species limited to New Caledonia and New Guinea. Some of the land areas here included are southeastern Asia, Australia, New Guinea, New Caledonia, Fiji, and New Zealand. Since *Podocarpus vitiensis* was known first from Fiji, the section has tended to be associated mainly with those islands, but with the discovery of the closely related *P. comptonii* in New Caledonia and of *P. filicifolius* in the Moluccas, the New Guinea area of *P. vitiensis* becomes

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* The author wishes to express her appreciation to Dr. Rudolf Florin, of the Bergianska Trädgården, Stockholm, Sweden, for critically reading the introduction to this paper, and to Drs. Florin and J. Tengnér, for examination and evaluation of the wood anatomy of two critical specimens of *Podocarpus minor*. She also thanks Dr. A. C. Smith, of the Smithsonian Institution, for criticism of her Latin description of *Podocarpus filicifolius*.

of primary importance, with the Fijian specimens then representing an eastern extension of the species. There is a remarkably close similarity to the distribution of *Nothofagus* species. One would expect it to be possible to distinguish two separate species of *Podocarpus* from New Guinea and Fiji, but the specimens I have seen from New Guinea seem the same, and only ripe seeds are lacking from New Guinea. The close relationship of Fiji to these land areas, geologically and botanically, is shown especially well in the recent studies of the Fijian flora by Smith (28, 29).

The postulation of a great south land mass, often called Gondwanaland, would connect not only the continental islands of the South Pacific, but also Antarctica, Australia, Asia, South America and Africa.

The leaf anatomy of the species of sect. AFROCARPUS, endemic to Africa, shows the same twisting of the short petiole that is found in sect. POLYPODIOPSIS, even when the leaves are alternate instead of opposite. The species of both sections have amphistomatic leaves and the leaves lack accessory transfusion tissue; in the leaf epidermis of species of both sections, the subsidiary cells of the stomata show the Florin ring. The South American species, *Podocarpus rospigliosii*, is very like *P. vitiensis*, except that its branches are covered only with foliage leaves and we find scale leaves or bracts only on the fertile shoots; the seed usually is somewhat larger. Other gymnosperm genera with species in both South America and Australasia are *Araucaria*, *Dacrydium*, and *Austrocedrus*.

Florin (8, 11, 14) has concluded that *Podocarpus* is a southern genus which probably originated in the early Mesozoic, and we find fossil evidence in South America in *Podocarpus araucoensis* and in Tasmania in *P. brownei*. Florin's new fossil genus (11) from Australia belongs to sect. STACHYCARPUS of *Podocarpus* which has living species in South America, New Zealand, New Caledonia, and Australia. Buchholz (3) maintained the northern origin of all conifers.

The most significant change in recent gymnosperm systematics has been the separation of the taxads from the podocarps, leaving the latter with the conifers (Florin 10a,b, 12, 13, 14). Pilger (23), in his classical monograph of the Taxaceae, included the podocarps with the taxads. There was increasing indication that these should not be kept so close together, and, in 1926, Pilger arranged the gymnosperms in seven families with the Taxaceae and Podocarpaceae separated. This treatment was followed by Buchholz (2) in 1946, in spite of the growing realization that the taxads should not be included with other conifer families. Florin (14) compared these two groups morphologically in almost every way in which they could be investigated to uphold the elevation of a class Taxineae. This class has been based chiefly upon the evidence of the development of the female strobilus as found in fossils (Florin 10a,b, 13, 14). Wilde (33) limited her lengthy discussion to comparisons of the male and female strobili of many species of *Podocarpus*; she included many data, however, which were useful in deriving the interpretations and solutions given by Florin.

Only the two sections, POLYPODIOPSIS and NAGEIA, of *Podocarpus* regularly have opposite leaves; in sect. AFROCARPUS some specimens have all or only occasional branches with leaves opposite or subopposite. But all three of these sections show the peculiar twisting of the leaf bases and stem torsion In both sections POLYPODIOPSIS and NAGEIA, this may result in the leaves being spread in a single plane, as in the compound frond of a fern. This orientation has been described in detail by Florin (8), Orr (22), Gray & Buchholz (17), and Wasscher (32). Orr (22) recognized further similarities in sections POLYPODIOPSIS and AFROCARPUS in the leaf anatomy: the leaves are amphistomatic, with more or less hypoderm, transfusion tissue often extending more than half-way from the midrib to the margin of the leaf, no accessory transfusion tissue, and a single resin canal in all species except *P. rospigliosii.* The three resin canals below the vascular bundle, with additional ones in the blade of the leaf of *P. rospigliosii*, is an exception discussed by Gray & Buchholz (17) in relation to reports in the literature (e.g., Bertrand 1, Stiles 31, Mahlert 21) that *P. vitiensis* has more than a single vascular resin canal. The single resin canal which I have found in all transverse leaf sections of *P. vitiensis* is in agreement with the findings of Gibbs (16) and Orr (22) who emphasize this fact. Neither have I seen any accessory transfusion tissue in the mesophyll of the leaf blades such as is shown by Bertrand (1, *Pl. 6, fig. 12*). No mention has been made thus far that the notable difference in the leaves in sect. NAGEIA is in the many parallel veins extending the full length of the large leaf blades, in contrast to the single unbranched midrib of the species of sect. POLYPODIOPSIS.

Orr (22) used only three species in describing the leaf anatomy of sect. POLYPODIOPSIS: *Podocarpus vitiensis*, *P. rospigliosii*, and *P. minor.* The external appearance of the foliage of the two former is quite similar, and to these we may now add *P. filicifolius*, which has foliage most like that of *P. vitiensis*. The external appearance of *P. minor* differs in not showing the pinnate arrangement of the leaves in a single plane except in the foliage of seedlings and on occasional lower branches; the branches are otherwise fully covered with crowded, opposite, decussate, ascending, oval or elliptic leaves. The discovery in New Caledonia of *P. comptonii*, with transitional foliage, affirms the judgment that *P. minor* really belongs to this section. *Podocarpus comptonii* is a large tree, recognized by Compton (5) and others. It generally has the foliage which has been described in such detail, although the reproductive branches lose the pinnate arrangement and are covered with decussate, opposite, oval, or elliptic leaves, as seen in *P. minor*.

The only section of *Podocarpus* which has both bifacially flattened lanceolate leaves and scale leaves in the mature foliage is POLYPODIOPSIS. The two kinds of leaves in sect. DACRYCARPUS are scale leaves and the needle-like leaves on the pinnate twigs are tetragonal in transverse section. This remarkable dimorphism shown by the foliage on the main shoots and leafy branches was described by Florin (8) and Wasscher (32) for *Podocarpus vitiensis*, but it is also evident in the other species.

In his consideration of the external morphology of the coniferous leaves, De Laubenfels (6) described this section as having only Type II (bifacially flattened) leaves. The scale leaves (De Laubenfels Type III) have been found only in connection with mature foliage. This combination is rare among other gymnosperms, in fact, having been found only in seedlings of a *Dacrydium*; transitional foliage of *Chamaecyparis*, *Neocallitropsis*, and a *Dacrydium*; and mature foliage of *Athrotaxis*, *Taxodium*, and a group of *Juniperus*. *Podocarpus vitiensis* and *P. filicifolius* have scale leaves much as described by De Laubenfels, tapering sharply from the point of attachment and closely appressed to the stem in *P. vitiensis*. They are rarely crowded, except at the beginning of a growth period, but are usually spaced by internodes of about the same length as those between the foliage leaves. They are decurrent, and their arrangement is always decussate except at the one or two nodes immediately preceding distichous foliage leaves. *Podocarpus comptonii* and *P. minor* have some scale leaves of this kind but they become obtuse and ovate in shape, divaricate, often elliptic as they approach true leaves, even being abruptly narrowed at the base but not usually becoming more than 4 mm. in length. According to De Laubenfels, only in one group of *Dacrydium* do scale leaves follow juvenile leaves of his Type II, and, when scale leaves (Type III) are developed, they are never followed by any other leaf type. In sect. POLYPODIOPSIS, however, I find that all variations are exhibited in the alternation between scale leaves and foliage leaves. Main shoots may bear only scale leaves; a leafy branch which continues growth may first bear foliage leaves, then scale leaves. Leafy branches may have only one growth period with a dormant terminal bud or they may have at least one other burst of growth, as is evident in the leafy shoots where each growth period shows first an increase in leaf length to about the middle of the growth period, after which it again uniformly decreases; one to several pairs of scale leaves may separate the growth periods. The smallest of the leaves may be very similar to scale leaves and a pair of scale leaves is usually present in *P. comptonii* and *P. minor* at the first node of a leafy branch. Scale leaves have been found only on the special reproductive branchlets of *P. rospigliosii*.

The leaf anatomy, as seen in transverse sections of the foliage leaves, was described by Orr (22) for *Podocarpus vitiensis*, *P. minor*, and *P. rospigliosii*. The leaves are amphistomatic, and palisade parenchyma may be found on both sides or developed only on the side facing the light. The single vascular bundle is flanked by wings of transfusion tissue which sometimes extend fully half-way to the margin of the leaf. The extent of the transfusion tissue varies too much from one leaf to another for it to be used as a diagnostic character, but it is greatest in *P. minor* and *P. comptonii*. There is no organized accessory transfusion tissue, and isolated lignified cells with large lumina were detected only very rarely in the mesophyll, with none at all present in *P. rospigliosii*. I agree with Orr that *P. rospigliosii* has the greatest number of hypodermal fibers with often a continuous layer at the margin and midrib. In *P. vitiensis* and

P. filicifolius the hypodermal fibers are few, small, and often isolated even at the margin and midrib. In *P. minor* and *P. comptonii* the hypodermal fibers are larger and scattered, or grouped together, with the fewest in *P. minor,* except for an almost continuous layer at the margin. Vascular fibers are usually large and abundant above the midrib in all the species but are absent or rare below the midrib in *P. vitiensis*, *P. filicifolius*, and *P. rospigliosii.* The leaves of these latter species are thin, usually only between 0.3–0.6 mm. thick, those of *P. comptonii* are a little thicker (especially on fruiting branches), being from 0.5–0.8 mm., while *P. minor* has very thick leaves, from 0.6–1.2 mm.

The female strobili are remarkably similar in sections POLYPODIOPSIS, NAGEIA, and AFROCARPUS, even to the fertile bract adhering after the seed is separated from the axis at maturity. The detailed description of the ovule development of *Podocarpus vitiensis* by Gibbs (16) indicates a peduncle covered with imbricate scale leaves, succeeded by 6–10 bracts on the strobilus, the terminal one or two fertile. The portion of the peduncle covered by bracts might be designated as a woody receptacle, the uppermost 2–4 bracts subtending the ovule sometimes having definitely thickened adhering bases. This was not apparent to Gibbs in *P. vitiensis*, but that three sterile and one fertile bract unite to form a receptacle has been recognized in *P. minor* and *P. comptonii.* A thickened woody receptacle is very apparent on the mature seeds of *P. filicifolius*, where an additional pair of bracts may become involved.

In her observations on the wood structure of *Podocarpus*, Kaeiser (19) found that of species in sect. POLYPODIOPSIS usually like that of those in sections AFROCARPUS and NAGEIA.

In sect. POLYPODIOPSIS, Hair & Beuzenberg (18) counted the chromosomes of *P. vitiensis*, *P. comptonii*, and *P. minor* and found the $2n$ number to be 20. If one considers ten to be the basic number, this count affirms the suggestion that this section and sect. NAGEIA, in which $2n = 20$ in *P. blumei*, are the oldest groups in the genus.

KEY TO SPECIES OF SECT. POLYPODIOPSIS

A. All foliage leaves arranged pinnately on the twigs.
  B. Mature seed crested. . . . . *P. rospigliosii.*[1]
  B. Mature seed not crested.
    C. Mature seeds pear shaped. . . . . 1. *P. vitiensis.*
    C. Mature seeds spherical. . . . . 2. *P. filicifolius.*
A. Some twigs pinnately leaved, but fertile twigs not flattened, and always bearing decussate foliage.
  D. Large trees; foliage mostly flattened; twigs pinnately leaved. . . . . 3. *P. comptonii.*
  D. Small trees or shrubs; foliage mostly decussate; twigs rarely flattened. . . . . 4. *P. minor.*

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[1] This species treated previously in Jour. Arnold Arb. **29**: 118–122. 1948.

1. **Podocarpus vitiensis** Seemann, Bonplandia **10**: 366. 1862, Jour. Bot. 1: 33. 1863, Fl. Vitiensis 266. 1865–73; Van Tieghem, Bull. Soc. Bot. Fr. **38**: 169. 1891; Pilger, Pflanzenr. IV. 5(Heft 18): 63. 1903, Nat. Pflanzenfam. ed. 2. **13**: 245. 1926; Gibbs, Jour. Linn. Soc. Bot. **39**: 182. 1909, Ann. Bot. **26**: 533. 1912; Stiles, Ann. Bot. **26**: 455. 1912; Dallimore & Jackson, Handb. Conif. 58. 1923, 1931, 85. 1948; Florin, Sv. Vet-akad. Handl. III. **10**: 275. 1931; Wasscher, Blumea **3**: 425. 1941.

A large forest tree up to 43 m. high with trunk often over 1 m. in diameter (sometimes buttressed in New Guinea) and a crown of spreading branches. Young twigs decussate, usually in pairs at distances of 2.5–4 cm., spreading or erect-spreading, dimorphic; main twigs terete or slightly flattened below the ramifications, leafless, alternately bearing axillary decussate lateral leafy twigs and decussate, ovate to orbicular, deciduous bracts nearly 2 mm. long; lateral leafy twigs slender, usually unbranched, with the leaves usually smaller toward each end, decussate but turned in one plane, pinnately arranged, divaricate, the twigs up to 38 cm. long and terminated by small buds which may not develop. Terminal buds of main twigs globose or ovate, with decussate, ovate, orbicular, or obovate, obtuse scales, 1.5–2 mm. long. Leaves spread out in one plane by twisting at the base so that the adaxial sides are exposed on one side of the twigs and the abaxial sides exposed on the opposite side; leaf pairs 5–8 mm. apart; leaves sessile, lanceolate, rounded at the base and broadly decurrent, gradually narrowing toward the narrowly obtuse apices, amphistomatic, 1.5–3 cm. long by 3–5.5 mm. broad; midrib sometimes prominent on either surface and with stomata in the epidermis above and below. Leaves in transverse section with scattered hypodermal fibers on both sides, palisade mesophyll on upper, lower, or both sides, depending on the orientation of the leaf; a single median vascular bundle with a single resin canal (never 3) abaxial to the phloem and flanked by wings of transfusion tissue; vascular fibers conspicuous above the vascular bundle and no accessory transfusion tissue. Male strobili solitary or clustered 2 or 3, terminal on axillary leafy twigs or bracted pedicels, or on bracted main shoots often branching once or twice so that strobili or fertile branches may arise in bract or leaf axils, strobilus cylindrical, 12–20 mm. long and 2–2.5 mm. in diameter; microsporophylls triangular, with acute or obtuse tips, margins scarious. Female strobili terminal on peduncles in axils of bracts or normal leaves; peduncles 2–8 mm. long, sometimes branched, covered with 6–10 pairs of imbricate scale leaves; strobilus of 6–10 bracts, 1 or 2 fertile; receptacle not differentiated. Seed bluish red when ripe, to 2 cm. long, obliquely attached to receptacle, obovate, narrowed towards the base which may still bear the attached bract when the seed has fallen, apex obtuse; hard-coated inner seed terminated at the micropylar end by a sharp, sometimes recurved point.

DISTRIBUTION: In dense mixed forest, Fiji Islands, at altitudes between 100 and 900 m.; New Guinea, in the western part at altitudes of 1100–1200

m. and in the southeastern part at 1650–2000 m.; and Vanikoru, Solomon Islands.

Fiji Islands. VITI LEVU: Mba, Nandarivatu, *Degener 14483* (BISH, K, NY, US),[2] *14485* (MO), *14496* (A, NY), *Mead*, Sing. Field No. 1974 (K), *Parks 20653* (BISH, †UC), *Gibbs 674* (BM, K); valley of Singatoka River, *Gillespie 3273.2* (BISH), *3712* (BISH, DS, †UC), *3865* (BISH, K, NY, UC, US), *4308.1*, *4402.2* (BISH); Tailevu, e. of Wainimbuka River, *Smith 7076* (US). VANUA LEVU: Thakaundrove, Yanawei River, Mt. Kasi, *Smith 1796* (BISH, GH, NY, †UC, US). WITHOUT LOCALITY: *Horne 531* (GH, K), *Seemann 576* (Holotype, K; GH), *Graff* (K). **New Guinea.** NETHERLANDS NEW GUINEA: Idenburg River, Bernard Camp, *Brass 19534* (†A), *12787* (†A), *12787a* (A); Cyclops Mts., *Versteegh BW913* (LAE, †L); PAPUA: Alola, *Carr 14160* (A, †NY); Lala River, *Carr 15666* (†A, BM). **Solomon Islands.** Santa Cruz Group, Vanikoru, near Lemon River, *Walker B.S.I.P.212* (†A). **Cultivated.** AUSTRALIA: Bot. Gard. Sydney, *Boorman*, in 1908 (A), *Eames*, in 1937 (CU).

Even though *Podocarpus vitiensis* has been recognized as a species since 1862, an understanding of its relationships within the genus is quite recent. On the basis of the single vascular bundle in the leaf, stomata on both sides of the leaves, and supposedly two lateral resin canals as well as the one below the vascular bundle, Bertrand (1) put this species in a separate section, POLYPODIOPSIS. The confusion brought about by Bertrand and Mahlert (21) in ascribing the three vascular resin canals has been discussed previously (17) and referred to *P. rospigliosii* from South America which is now included in the same section.

Subsequently, Pilger (23) put *Podocarpus vitiensis* in his sect. NAGEIA on the basis of the opposite leaves which show the same characteristic turning of the leaf bases so that the lower surface is uppermost on one side of the twig and the upper surface on the other side of the twig when these decussate leaves orient themselves in the pinnate "fronds." Pilger's classification was followed by Gibbs (16) and Stiles (31) after Gibbs (15) had briefly considered sect. STACHYCARPUS. Florin (8) recognized the validity of Bertrand's sect. POLYPODIOPSIS for *P. vitiensis* as a separate group and added *P. minor*. This section is now well established.

All of these studies, including Gibbs' (16) description of the female

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[2] The following symbols indicate the location of the specimens cited: Arnold Arboretum, Cambridge (A); Bernice P. Bishop Museum, Honolulu (BISH); Botanic Museum and Herbarium, Brisbane (BRI); British Museum (Natural History), London (BM); Jardin Botanique de l'Etat, Bruxelles (BR); Herbarium of the University of California, Berkeley (UC); Wiegand Herbarium, Cornell University, Ithaca (CU); Dudley Herbarium, Stanford University, Stanford (DS); Herbarium of the University of Georgia, Athens (GA); Gray Herbarium, Cambridge (GH); University of Illinois, Urbana (ILL); Herbarium and Library, Royal Botanic Gardens, Kew (K); Rijksherbarium, Leiden (L); Missouri Botanical Garden, Saint Louis (MO); Department of Forests, Papua and New Guinea, Lae (LAE); New York Botanical Garden, New York (NY); Muséum National d'Histoire Naturelle, Paris (P); United States National Museum, Washington (US); National Herbarium of Melbourne, Melbourne (MEL).

A dagger (†) preceding the abbreviation of an herbarium signifies that the details of the leaves of this specimen have been examined in transverse section.

strobilus, were on Fijian specimens of *Podocarpus vitiensis.* In 1944, Wasscher (32) recognized specimens of this species from New Guinea and, for the first time, described the dimorphic foliage which had been overlooked in the Fiji material. It is interesting that the early specimens (*Seemann 576, Graff s.n.,* and *Gibbs 674*) all have only terminal male cones on leafy twigs, whereas recent male specimens (*Degener 14496, Parks 20653, Smith 7076*) definitely show the dimorphic foliage, main twigs with scale leaves, and lateral leafy branches bearing male strobili or fertile branches bearing scale leaves and strobili or axillary branches bearing strobili.

New Guinea specimens may still prove to represent a separate species, but the half-matured ovules which I have seen are still pear-shaped and obliquely attached to the receptacle, as in the Fijian *Podocarpus vitiensis.*

Both Seemann (25) and Gibbs (16) have waxed eloquent on the beauties of this species and I must quote from Seemann: "This is one of the finest Coniferae I have ever seen. . . It attains sixty feet in height, has a stem nine feet in circumference, and has drooping, extremely graceful branches, which would render the species a highly desirable acquisition to our living collections."

2. **Podocarpus filicifolius,** sp. nov.

Arbor 15 m. alta ramulis numerosis, divaricatis, spiralibus vel oppositis; alabastris in ramulis principalibus parvis, late ovatis, squamis paucis, late triangularibus decussatis, 1.5–2 mm. longis; alabastris in ramulis foliiferis permutatis, ovatis, plerumque constanter dormientibus; foliis dimorphis; squamis in ramulis principalibus, divaricatis, tenuibus; late triangularibus, 2 mm. longis, acutis vel obtusis; foliis ad ramulis pinnatis terminalibus vel axillaribus, sessilibus, divaricatis, oppositis, 6–24 mm. longis, 3.5–4.5 mm. latis, lanceolatis, tenuibus, planis, apice late acutis, basi late rotundatis, decurrentibus, costa non manifesta; strobilis masculis ignotis; strobilis femineis solitariis (?), pedunculis 10 mm. longis, squamas 4–6 binas decussatas vel cicatrices gerentibus; receptaculo parvo lignoso bracteis oppositis 2 late obtusis subtento, 7 mm. longo, 3 mm. lato, bracteis 3 coalescentibus equalibus, apice liberis composito, bractea unica fertili; semine maturo globoso, 1.5–1.8 cm. longo et lato, apice aequaliter rotundo, obtuso.

DISTRIBUTION: Morotai, in the Moluccas.

Moluccas. Morotai, *A. Kostermans*, in 1949 (Holotype, †L).

This tree differs from *Podocarpus vitiensis* in the spreading scale leaves, thinner foliage leaves, the distinct receptacle 7 mm. long supporting the seeds, and the spherical seeds. The dissected seed shows a smooth, brown outer coat 0.3 mm. thick, a hard, woody, light tan middle layer which is pointed at the micropyle, and a thin papery brown inner layer.

The name refers to the fern-like appearance of the pinnately leaved twigs, reminiscent of the royal fern, *Osmunda regalis.*

3. **Podocarpus comptonii** Buchholz, Bull. Mus. Hist. Nat. Paris II. **21**: 284. 1949; Guillaumin, Acta Horti Gothob. **19**: 8. 1952; Chevalier, Études Mélanésiennes II. **1**: 114. 1956.

A tree becoming 10–12 m. high with trunk up to 80 cm. or more in diameter, bearing few branches below but profusely branched above; bark brownish, longitudinally furrowed; young twigs green and showing decurrent leaf bases; branches erect or ascending, usually opposite while still young; terminal buds appearing naked but protected by special scales which become part of foliage but do not grow into leaves. Foliage dimorphic; scale leaves on main twigs decussate, broadly triangular, decurrent, 2 mm. long, becoming obtuse, then ovate-elliptic, divaricate, 3–4 mm. long; 1 pair opposite scale leaves usually at first node of leafy twigs; leaves decussate, emerging in 4 ranks from the twigs and, on vigorous branches, twisted at the base so that the pinnately leaved twigs bear opposite leaves, on one side all with the abaxial side exposed and on the other side the adaxial; on upper reproductive branches of mature trees, leaves held obliquely in 4 vertical ranks; leaves lanceolate to elliptic, obtuse, 7–15 mm. long, 2–5 mm. wide, thick, sessile, with decurrent leaf bases; single midrib not usually distinct, with the surface becoming dry in many longitudinal wrinkles. Usually only foliage leaves on small vigorous plants and seedlings becoming 30 mm. long, 6 mm. wide, very thin, acutish, and opposite on pinnate twigs. Leaves differentially amphistomatic, varying with the orientation; transverse sections showing hypoderm interrupted by the stomatal rows, single vascular bundle with single resin canal below phloem, transfusion tissue well developed, no accessory transfusion tissue, vascular sclereids abundant above the bundle with fewer below; palisade mesophyll on either or both sides depending on leaf orientation. Male strobili sessile and terminal on lateral twigs usually bearing regular foliage leaves, subtended by a pair of narrow, short foliage leaves or bracts; strobili ovoid, 5–6 mm. long, 3 mm. wide; microsporophylls broadly triangular, apices acute, margins thin and somewhat erose. Female strobili terminal on lateral twigs which may bear ordinary foliage leaves or spreading scale leaves; each strobilus bearing 3 or 4 pairs of small, opposite, sterile bracts on an axis 10 mm. or more long, with the two upper bracts unequal and forming a nonfleshy receptacle, one of the bracts fertile. Seed obovoid, 25 mm. long, 18–20 mm. diameter, fleshy, red (?) when ripe; kernel with two ridges to a straight or curved beak at the micropyle.

DISTRIBUTION: In forests on mountain slopes of New Caledonia above 1000 m. altitude.

New Caledonia. Mt. Ignambi, *Compton 1524* (†BM), *1587* (†BM); Mt. Mou, *Vieillard 1275* (†P), *3064* (†GH), *3264* (†P), *Buchholz 1085* (†ILL), *1421, 1452, 1474, 1578* (ILL), *1684* (Holotype, †ILL), *1697* (ILL), *MacDaniels 2323* (CU), *Virot* in 1938 (A), *White 2033* (†A, BRI), *De Laubenfels P129* (GA), *Compton 607* (BM); Mt. Humboldt, *Schlechter 15331* (†BR, †BM), Mt. Dzumac, *De Laubenfels 153* (GA), Montagne des Sources, *De Laubenfels 123* (GA); Koe, *Balansa 184* (†P); Plain des Lacs, Mons du Mai Forest, *Buchholz 1350, 1350a, 1697* (ILL); Bai des Piroques, *White 2120* (†A, 2 sheets); beside River Blanche, *Ingle I.66* (†MEL); River Tane & Bourail, *Balansa 1385* (K). No specified locality, *Buchholz 1539a* (†MO).

The twig dimorphism observed and described by Wasscher (32) for *Podocarpus vitiensis* is likewise very apparent in *P. comptonii.* The plant bears several kinds of foliage: definitely acute triangular scale leaves on vigorously growing main shoots; ovate or elliptic scale leaves on main shoots and lower parts of twigs; true foliage leaves lanceolate and arranged pinnately; and elliptic foliage leaves arranged on the twigs decussately. Variations, such as twigs bearing alternately scale leaves and foliage leaves for three growth periods with no branching, or branches bearing foliage leaves becoming main branches but subsequently bearing only scale leaves of either kind, are numerous.

This species has long been confused with *Podocarpus minor* which is a small tree along streams and in swamps at lower elevations. Compton (5), who strangely saw only the large trees, remarked on the inappropriateness of the name "*minor.*" All the specimens he assigned to *P. minor* belong here. The specimen *White 2120* from the Arnold Arboretum was labeled *P. vitiensis*, showing that it was recognized as being different from *P. minor.* Dr. J. T. Buchholz collected both species abundantly and the differences became clear to him. The specimen *Compton 1273*, listed as an undetermined species, belongs here.

4. **Podocarpus minor** (Carrière) Parlatore in DC. Prodr. **16**(2): 509. 1868; Brongn. & Gris, Bull. Soc. Bot. Fr. **16**: 326. 1869; Mahlert, Bot. Centralbl. **24**: 281. 1885; Pilger, Pflanzenr. IV. **5**(Heft 18): 62. 1903, Nat. Pflanzenfam. ed. 2. **13**: 245. 1926; Schlechter, Bot. Jahrb. **38**: 16. 1907; Compton, Jour. Linn. Soc. Bot. **45**: 425. 1922; Dallimore & Jackson, Handb. Conif. 51. 1923, 1931, 75. 1948; White, Wilson & Guillaumin, Jour. Arnold Arb. **7**: 78. 1926; Florin, Sv. Vet-akad. Handl. III. **10**: 278. 1931; Guillaumin, Acta Horti Gothob. **19**: 8. 1952; Chevalier, Études Mélanésiennes II. **1**: 114. 1957.

Nageia minor Carrière, Traité Gén. Conifères. ed. 2. 641. 1867.
Podocarpus palustris Buchholz, Bull. Mus. Hist. Nat. Paris II. **21**: 284. 1949; Chevalier, Études Mélanésiennes II. **1**: 114. 1957.

A dwarf tree or shrub, 2–3 m. high, trunk 15–30 cm. in diameter with numerous ascending branches; bark rough, brown or dark gray; twigs opposite on young stems or scattered, ridged by decurrent leaf bases; terminal buds normally small with few opposite scales, frequently abnormally enlarged due to infestation by insect larvae. Leaves dimorphic; scale leaves on main shoots often deciduous, decussate, triangular-obtuse, keeled, decurrent, 1 mm. long, becoming divaricate, elliptic, thick, to 4 mm. long, and usually 1 pair of elliptic scale leaves at the first node of leafy branches; foliage leaves crowded on short branchlets, opposite, decussate, ascending and held obliquely in 4 vertical ranks, oval or elliptic, obtuse, sessile, 10–20 mm. long. 3.5–5.5 mm. wide, thick and longitudinally wrinkled when dry, with broadly decurrent bases; midrib not evident. Leaves differentially amphistomatic with twice as many stomata on the adaxial side, stomata easily seen under low magnification on young leaves as minute white dots. Transverse sections of leaves showing rare hypodermal fibers on both sides but abundant at the margins, palisade mesophyll on both sides, a broad midvein due to extension of transfusion tissue half-way to the margin, single resin canal, usually abundant vascular sclereids above and below the vascular bundle. Male strobili terminal on short, bracted peduncles, 1–1.5 mm. long, in clusters of 3–5 or more at ends of short lateral leafy twigs; 5–8 mm. long, 2.5–3 mm. in diameter; microsporophylls broadly hastate with narrowly acute upturned apiculi. Female strobili terminal on lateral twigs, axis 4 mm. long; strobili of 3 or 4 pairs of decussate bracts 1–2 mm. long; immature ovules usually crested, long-pyriform; 1 terminal fertile bract (rarely 2), keeled, 2 mm. long and spread upon the back of the base of the large seed (away from the micropyle) with minute or suppressed apex, the 2 upper bracts fusing into a small receptacle 4 mm. long. Seed crested, obliquely conically pyriform, 2.8 cm. long, 1.7 cm. wide, becoming maroon-red when ripe; inner woody layer usually obtuse, with a beak formed at the micropyle, usually straight.

DISTRIBUTION: Along banks of streams and lakes on Plaine des Lacs and near Prony Bay, New Caledonia.

New Caledonia. Borders of Lac Arnaud, *Vieillard 1275* (Holotype of *P. minor*, †P; BM, †NOUMEA), *Vieillard* or *Deplanche 170* (†P); Plaine des Lacs, River des Lacs, *Buchholz 1719* (†ILL), *1729* (†ILL), *LeRat 607* (†BM), 22 km. Station, *Buchholz 1347* (†ILL), *1348* (ILL), *1421* (Holotype of *P. palustris*, †ILL; P), flooded lake shore, headwaters of Yate R., *De Laubenfels P112* (GA), Rio des Pirogues, *White 2261* (BRI, †UC, US); Lac en Huit, *De Laubenfels P115* (GA), *McKee 3382* (US); river sw. of Grand Lac, *Virot 658* (†A), *MacDaniels 2544* (†CU); Prony, *Frank 207 Ser. A* (†BM, BRI, †F, †UC, US); Baie du Sud, *Vieillard 1275* (A, BM). Without specific locality: *Levormand 9171* (†K), *Raoul s.n.* (†P), *Petit N138* (†P), *LeRat 1752* (†P).

At some sites these dwarf trees grow very slowly and become very old, their bases often growing in standing water and becoming buttressed. At times they may be entirely submerged beneath muddy, silt-laden water, reddish from the ferruginous soil carried down from the surrounding mountains during heavy rains. Dr. Buchholz (*ms.* data) believed there to be a related species, *Podocarpus palustris* which he described, but the differences he listed do not fall outside the normal range of variation in *P. minor*, and the difference in wood density is no more than expected from the slightly different ecological habitats.

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TAXONOMIC AND NOMENCLATURAL NOTES ON ZANTHOXYLUM AND GLYCOSMIS (RUTACEAE)[1]

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IN THE COURSE of surveying the genera of Rutaceae in the southeastern United States (see Jour. Arnold Arb. 43: 1–22. 1962), the author encountered several nomenclatural and taxonomic problems in *Zanthoxylum* L. and *Glycosmis* Corréa which require further comment. These include the generic limits of *Zanthoxylum*; the legitimacy of the name *Z. coriaceum* A. Rich., in view of the existence of a supposedly earlier homonym; and the correct name of the type species of *Glycosmis*. The problem of *Z. coriaceum* has led to further bibliographic research on the dates of publication of Achille Richard's work on the flora of Cuba in Ramón de la Sagra's *Histoire Physique, Politique et Naturelle de l'Île de Cuba*. These items are dealt with separately below.

THE GENERIC LIMITS OF ZANTHOXYLUM

The nomenclatural confusion concerning *Zanthoxylum* L. and *Fagara* L. seems to have been cleared up by the typification of the former by *Z. fraxineum* Willd. (= *Z. americanum* Mill.) by Fosberg (1959). (It is notable in this connection that Jussieu (1825, p. 505) and Triana and Planchon (1872, p. 310) indicated *Z. fraxineum* Willd. as the type of *Zanthoxylum* L. ("Zanthoxylum Colden — L. J. — Schreb.").) As the matter stands at present, the name *Zanthoxylum* L. has to be applied either *sensu stricto* to the genus with one perianth whorl (a simple or haplochlamydeous perianth, according to Engler, or one composed of petals, according to Eichler), or *sensu lato* to the combined genus, including *Fagara* L. (type, *F. Pterota* L.) with two perianth whorls (a double or diplo- and heterochlamydeous perianth). The recognition of two separate genera or of a single inclusive genus remains a matter of personal evaluation of the evidence. For the students of tropical African, South American, and West Indian floras the generic status of *Fagara* apparently does not seem questionable, since no species of *Zanthoxylum* L. *sensu stricto* have been recorded from these regions. But students of the floras of eastern and southeastern Asia and North and Central America, where species of both these taxa occur, face the problem of the recognition

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of *Fagara* as a segregate genus. Opinions have differed. Thus, Rehder (1945, p. 73) in his study of Asiatic species of *Zanthoxylum* and *Fagara* came to the conclusion that "the two genera are close and none of the characters are strong enough for generic separation, so it seems preferable to consider them subgenera or sections of one genus, as done by most authors." A different view is represented by Reeder and Cheo (1951, p. 68) who say, "After studying numerous specimens in this complex, it is our feeling that both these genera are worthy of recognition. Although there are no striking vegetative differences, flowering specimens are quite distinct. Accordingly we are accepting both *Xanthoxylum* and *Fagara*, an interpretation which is, we believe, in harmony with that of most modern students of the group."

Such disagreement in regard to the generic status of *Fagara* is based on differences in views as to the morphological nature of the perianth in *Zanthoxylum*. The earliest view, that formulated by Linnaeus in his generic descriptions, that the flowers of *Zanthoxylum* are apetalous while those of *Fagara* have sepals and petals, was followed by all taxonomists up to 1878 (e.g., Humboldt, Bonpland & Kunth, 1823; De Candolle, 1824; Jussieu, 1825; Triana & Planchon, 1872; Engler, 1874). This interpretation of the perianth favored considering *Fagara* a subgenus of *Zanthoxylum*, as was done by Triana and Planchon (1872), as well as by Engler (1874). Although maintaining the Linnaean view on the perianth of *Zanthoxylum*, Jussieu (1825, p. 505) noted, "Sepala interdum plura, sex aut etiam (teste Kunth) novem. Quorum analogia cum petalis confirmatur situ alterno staminibus ovariisque opposito, praetereaque metamorphosi ipsorum in stamina non infrequenti (observante C. Richard)." These features of the flowers spoke against the Linnaean interpretation of the perianth leaves of *Zanthoxylum* as homologous with the sepals, but Jussieu's note was disregarded or overlooked by his contemporaries.

In 1878, Eichler (p. 323), like Jussieu, taking into consideration the alternate position of the stamens and the opposite position of carpels (in the case of isomery) in respect to the perianth parts (leaves) in *Zanthoxylum americanum* ("*Z. fraxineum*"), concluded that the perianth leaves in this species are homologous with the petals and the flowers are asepalous. Eichler's view, accepted and followed by most American taxonomists, also was in favor of the inclusion of *Fagara* in *Zanthoxylum* as a subgenus or section of the latter.

Engler (1896, 1931), however, after reconsideration of his previous (Linnaean) view, came to the conclusion that the perianth of *Zanthoxylum* is simple (haplochlamydeous), not homologous with the sepals, of a primitive type which occurs in Rutaceae only in this genus, and that it cannot be derived from the double (diplo- and heterochlamydeous) perianth of *Fagara*. Consequently, *Zanthoxylum* and *Fagara* should be recognized as distinct genera. This view has been adopted by many taxonomists, especially in Europe. Engler's interpretation of the perianth in *Zanthoxylum* is objectionable on at least two bases.

First, there is no evidence that the simple perianth of *Zanthoxylum* really represents a primitive condition which is not the result of simplification. On the contrary, Saunders (1934, p. 660, *figs. 37–39*, & p. 661), analyzing the carpellate flowers of *Z. planispinum* Sieb. & Zucc. (= *Z. alatum* Roxb. var. *planispinum* Rehd. & Wilson), treated its eight-merous perianth as consisting of four sepals and four petals. She also noted that "exsertion of the two median sepals is delayed until after that of petals." The latter observation, if confirmed by more abundant material, may also suggest some complexity in ontogenetic development of the perianth expressed in delay, or perhaps discontinuation of development, of some or all of the sepals (or their homologues). In his considerations of phylogeny of the Rutaceae, based on Saunder's floral anatomical data, Moore (1936, p. 321) stated that his type "A" of vascularization of the floral parts (including *Zanthoxylum fraxineum* Willd., and apparently *Z. planispinum* Sieb. & Zucc., the species studied in greater detail by Saunders) "is more than likely the result of reduction."

Second, the occurrence in Mexico and Central America (perhaps also in South America) of species of *Zanthoxylum* which appear to be transitional to *Fagara* in their perianth structure supports Eichler's interpretation of the perianth in *Zanthoxylum*, rather than that of Engler. Thus, the perianth of carpellate flowers of *Z. ferrugineum* Radlk. (*Donnell Smith 6468*) from Costa Rica is described by Radlkofer (in Smith, 1897, p. 392) as, "perianthii foliola 9–10, linearia (2–3 mm. longa), alia (plus minus conspicue exteriora et sepalis respondentia) breviora et angustiora, alia (subinteriora, reliquiis subalterna) longiora et paullulo latiora, omnia tenuiter membranacea." The staminate flowers of *Hinton et al. 10136* (GH) from Mexico (identified at Kew as *Z. ferrugineum* Radlk., but perhaps representing a different species closely allied with the latter) possess five to ten, often eight to nine, perianth leaves, all similar in appearance, with one to five ± exterior and smaller than the others. The four to five stamens usually are opposite the smaller and alternate with the larger perianth leaves. (One five-merous flower which the author examined corresponded exactly with the *Fagara* type with only the difference that the minute sepals were of the same appearance as the petals.) Almost similar conditions were found in staminate flowers of *Z. mazatlanum* Sandw. (isotype, *Gonzales Ortega 5210*, GH), from Mexico, with 4–11-merous perianth and four to six stamens, and *Z. Williamsii* Standl. (isotype, *A. Molina 1078*, GH), from Honduras, with four to eight perianth leaves and usually four stamens. A few carpellate flowers (fruits) of *Z. Williamsii* exhibited six or seven persistent perianth leaves. It is also notable that Engler (1874, p. 180), having described *Zanthoxylum ciliatum* as a new species from Venezuela, remarked, "Species valde insignis et cum nulla alia Austro-Americana adhuc descripta confundenda. . . . Characteribus suis transitum inter *Zanthoxylum* et *Fagara* efformat." The present author's conclusion from the above is that the "simple" perianth of *Zanthoxylum* is most likely a secondary condition, derived by reduction from that of the *Fagara* type by abortion of some or all the sepals. The occurrence of species of *Zanthoxylum* which appear in their perianth structure to be transitional to *Fagara* not only supports this view, but also is ample reason to regard *Fagara* as a subgenus of *Zanthoxylum.*

ZANTHOXYLUM AMERICANUM MILL. VERSUS ZANTHOXYLUM FRAXINEUM WILLD.

Fosberg (1958, 1959), when discussing the problem of typification of *Zanthoxylum*, introduced an element of confusion into the nomenclature of the type species through the suggested replacement of *Z. americanum* Mill. (1768) by its later synonym, *Z. fraxineum* Willd. (1796). He reasoned, "Furthermore, according to Miller's description, his *X. americanum* could not be what is now called that as he says of it 'the flowers grow in loose panicles as on the first sort' rather than in axillary fascicles which is the case with the modern *Z. americanum* Mill. Lawrence, when photographing Miller's types in the British Museum in 1950, was unable to locate a specimen of *Xanthoxylum americanum* so we have no way of knowing what plant this name actually refers to. . . . As pointed out in Taxon 7(4): 95. 1958, the earliest available name for this is *Zanthoxylum fraxineum* Willd. (1805)." A number of items argue against Fosberg's proposition, however.

The general description of *Xanthoxylum americanum* given by Miller and his mentioning both the natural occurrence of the species in Pennsylvania and Maryland and its resistance to cold seem to show clearly that Miller's name referred to the plant of the northeastern United States, i.e., to the only species of *Zanthoxylum* which occurs north of Virginia and Arkansas. Furthermore, Aiton (1813, pp. 382, 383) mentioned only three species of *Zanthoxylum* which were introduced and cultivated by Miller in the Botanic Gardens at Kew. These were "*Z. emarginatum* Willden. . . . Cult. before 1739, by Mr. Philip Miller. Mill. dict. vol. 2 addenda, *Lauro affinis* 2."; "*Z. Clava Herculis* Willden. . . . Cult. 1739, by Mr. Philip Miller"; and "*Z. fraxineum* Willden. . . . Cult. before 1759, by Mr. Philip Miller. Mill. dict. ed. 7. n. 2." The last quotation indicates that the plant grown at Kew as *Z. fraxineum* Willd. was that introduced by Miller and described by him in the seventh edition (1759) of his *Gardeners Dictionary* as "*Xanthoxylum* no. 2." Since the latter, in turn, was the same entity as *Xanthoxylum americanum* of the eighth edition (1768) of Miller's work (the corresponding descriptions in both editions are identical), the conspecificity of the latter species with *Z. fraxineum* Willd. appears to be unquestionable. The circumstance that the type specimen of *X. americanum* has not been found among Miller's types but that the species was introduced into the Botanic Gardens at Kew prior to the appearance of the seventh edition of *Gardeners Dictionary* makes it probable that the description of this species was made from the living plant.

In 1771, Du Roi (pp. 57, 58) mentioned the species as *Xanthoxylum americanum* Mill., and provided it with a rather detailed Latin diagnosis, including the correct description of the inflorescence and staminate flowers (which he erroneously took for bisexual). He, however, regarded *X. americanum* as a variety of *Zanthoxylum Clava-Herculis* saying, "Cl. Millero species, mihi varietas *Zanthoxyli Clavae Herculis* L." In 1772, Du Roi (pp. 511, 512) again treated Miller's species in the same way, but the description was given in German. Wangenheim (1787, p. 116) treated *Xanthoxylum americanum* as a species, noting that perhaps it should be considered a variety of *Z. Clava-Herculis* L. Neither Du Roi nor Wangenheim had any doubts regarding the entity named and described by Miller.

Willdenow, in describing *Zanthoxylum fraxineum* (1796, p. 413), apparently was aware that his new species was identical with that of Miller, since he mentioned "*Zanthoxylum Clava Herculis* Du Roi" and "*Zanthoxylum americanum* Wangh." in the synonymy and also noted that "Der Herr von Wangenheim und Miller geben dieser Art ungezähnte Blättchen." Schkuhr (1803, pp. 467, 468, *pls. 323, 323b*), although he called the species *Z. fraxineum* Willd., remarked (p. 466) that this was the species which "auch Miller, Wangenheim und andere schon unter *Zanthoxylum americanum* bemerkt haben."

Since the entity described by Miller as *Xanthoxylum americanum* is known, neither the occurrence of an error in the description nor the lack of a type specimen makes this binomial illegitimate. Therefore, its replacement by *Z. fraxineum* Willd., as suggested by Fosberg, appears unjustifiable in the light of the present Code of Botanical Nomenclature.

ZANTHOXYLUM CORIACEUM A. RICHARD AND ITS DATE OF PUBLICATION

The legitimacy of *Zanthoxylum coriaceum* A. Richard in Ramón de la Sagra (Hist. Phys. Polit. Hist. Nat. Cuba. Bot.-Pl. Vasc. [Essai Fl. Cuba 1.] 326. *pl. 34*) is often questioned because of the existence of a supposedly earlier homonym, *Z. coriaceum* (Desv.) Walpers, Repert. **1**: 521. 1842 ("*coriacea*"). The former name refers to the species of southern Florida and the West Indies (absent from Jamaica and a few other islands); the latter is a synonym of the Jamaican *Z. spinosum* (L.) Sw. According to Urban (1894, p. 563) and Kuntze (1898, p. 162) the French edition of the Richard work appeared in 1845 and preceded the Spanish edition which bears the same year of publication. The publication date of the portion of this work that included *Z. coriaceum* A. Rich. was presumed by Wilson (1911, p. 185) to be 1842 and by Little (1953, p. 437) to be 1842 or 1843. Finally, Van Steenis-Kruseman (1960, p. 741), with reference to data given by Grisebach (1841, 1842, 1847, 1852) in connection with this work, stated, "Up to and including 1840, 28 parts were issued; in 1841 11 others followed. At that time the 1st part of the cellular cryptogams was out and the phanerogams were published up to the end of the Thalamiflorae (Cand. Syst.). In 1846 parts 1–54 had been published, probably no other parts appeared. The atlas, dated 1845 too, was not finished before 1851 (cf. Wiegmann's Repert. l.c. 1852, 387)." This statement, however, is not entirely clear and needs further explanation.

The Richard work consists of 42 signatures (printed sheets or *Bogen*) of 16 pages each, except the last with only 7 printed pages. Similarly, Montagne's *Plantes Cellulaires*, of the De la Sagra work, contained 35 such signatures, the last one of 15 pages. Usually several signatures formed an installment (a fascicle or an issue, *Lieferung*, *livraison*). It is unknown whether Grisebach's "Lieferungen" translated as "parts" by Van Steenis-Kruseman should be understood as installments (improbable because of their high number, e.g., 53 by 1846) or referred to the printed signatures (*Bogen*).

Richard's work was most likely published irregularly in relatively few, perhaps unequal, installments consisting of at least several signatures. Thus, a notice in Hooker's *London Journal of Botany* (1: 308–311), issued in June or July, 1842, mentioned receipt of "several of the first numbers" of the Richard work, accompanied with plates. At approximately the same time, Walpers apparently had at his disposal 192 pages (12 signatures) of this work, including Ranunculaceae through Buttneriaceae, since he included in the first volume of his *Repertorium* (1842) new taxa of this group of families (the last species mentioned being *Guazuma parvifolia*). Pages 193–336 (signatures 13–21) became available to Walpers sometime later in 1842 or 1843, since Richard's new taxa of Tiliaceae (e.g., *Belotia*) through Rutaceae (e.g., *Zanthoxylum coriaceum*) appeared in Supplementum 1 which was included in the second volume of the *Repertorium* (1843–1844). Endlicher, however, apparently had at his disposal both these portions in 1842, since Richard's new genera, including *Belotia*, were mentioned in the Addenda to the 2nd Supplementum to the *Genera Plantarum* (1842, after March). Grisebach (1842), recording the publication of Richard's work during 1841, mentioned Simaroubaceae as the last family treated by Richard in that portion. Therefore, one should assume that the part of Richard's work which appeared in 1841 consisted of pages 1–336 (signatures 1–21), and probably *Plates 1–35*, and included the families Ranunculaceae to Simarubeae (as well as one page of Ochnaceae with a portion of the generic description of *Gomphia*).

According to Grisebach's report of 1847, the part of Richard's work published during 1846 included the families Ochnaceae to "Portulacceae" up to page 624. Although it is unknown whether the corresponding *Plates 36–44(2)* also appeared at that time, there is no ground (at least at present) for the belief that the appearance of these plates was delayed. A relatively long interval between publication of this and the first part of the work is also evident from the Richard "Avant-propos" (p. vii) which is dated February 1, 1845. "Les circonstances tout à fait indépendantes de notre volonté ont singulièrment retardé la publication de la deuxième moitié de ce volume. Nous espérons que désormais cet ouvrage marchera avec plus de régularité vers la fin de sa publication." It is unknown whether this second part of Richard's work was issued in installments or whether it remained undistributed until the completion of the whole volume. One may assume that this part was either rare or not available at all to botanists for at least a few years after its publication.

Thus, Planchon (1846–1847) did not mention Richard's new species of *Gomphia* in his review of the genera and species of Ochnaceae; Naudin (1849–1852) did not include either *Pachyanthus* A. Rich. or *Naudinia* A. Rich., which was named after him, in the monograph of Melastomataceae; and only one new genus (*Belairia*, Leguminosae) of the second part of Richard's work was mentioned in the third edition of Lindley's *The Vegetable Kingdom* (1853).

Finally, in Grisebach's report of 1852 on phytogeographical and taxonomic works which were published during the preceding year, we read (p. 375), "Von R. de la Sagra's Werk über Cuba wurde der erste Band der von Richard bearbeiteten Gefässpflanzen (s. Jahresb. f. 1846. p. 53) vollendet [141]). Übersicht der seitdem bearbeiteten Familien: 5 Phytolacceen, 3 Cacteen, 4 Umbelliferen, 1 Araliaceae, 1 Hedera, 4 Loranthaceen" and (p. 387) "141) R. de la Sagra, Histoire physique, politique et naturelle de l'île de Cuba. Botanique. Plantes vasculaires, par A. Richard. al. tit. Essai d'une flore de l'île de Cuba. T. I. contenant les Dicotylédones polypetales. 663 pag. 8. Atlas. Paris 1845. (aber jetzt vollendet)." It is evident that the last parenthetical phrase referred to both the text and the atlas, not to the atlas alone. The circumstance that no new taxa of Phytolaccaceae (*Trichostigma* A. Rich., p. 627; *T. rivinoides,* p. 628; *Stegnosperma cubense*, p. 632), proposed by Richard in this last part, were mentioned by Moquin (1849) in his monograph of Phytolaccaceae (including "Addenda et Corrigenda"), seems to support the last Grisebach statement.

In summary, I assume the following probable dates of publication for Richard's work:

1841: Part 1 (in a few installments?), pp. 1–336 (signatures 1–21), probably *pls. 1–35*, Ranunculaceae to Simarubeae.

1846: Part 2 (in installments?), pp. 337–624 (signatures 22–39), probably *pls. 36–44*(*2*), Ochnaceae to Portulacceae.

1851: Part 3, pp. 625–663 (signatures 40–42) and i–viii, probably *pl. 44*(*3*), Phytolacceae to Loranthaceae.

Since 1841 may be accepted as the publication date for *Zanthoxylum coriaceum* A. Rich., the priority of this binomial over *Zanthoxylum coriaceum* (Desv.) Walpers (1842) is clear and the former is the correct name for the species of southern Florida and the West Indies.

THE TYPE SPECIES OF GLYCOSMIS

Much nomenclatural confusion, with resulting taxonomic discrepancies, surrounds *Limonia arborea* Roxb. (1798), the type species of *Glycosmis* Corréa. Tanaka considered this species to be identical with *Limonia pentaphylla* Retzius (1788) and applied to it the binomial *Glycosmis pentaphylla* (Retz.) Corréa. Narayanaswami (1941), however, came to the conclusion that *Limonia arborea* Roxb. and *Limonia pentaphylla* Retzius are entirely different species, *Glycosmis arborea* (Roxb.) Corréa and

G. pentaphylla (Retz.) Corréa, respectively. A brief history of the genus and the basic species involved is necessary for an understanding of the situation.

In 1788, Retzius (p. 24) proposed *Limonia pentaphylla* based on Koenig's specimen from the East Indies. The leaves of this species were described as "Folia plerumque in petiolo quina, alterna, ovata, acuta, integra, magnitudine foliorum *Citri Medicae*." Roxburgh (1798, p. 60, *pl. 84*) provided the plant which he believed to be *Limonia pentaphylla* Retzius with a more or less detailed description and drawings, and also described and illustrated a new species, *Limonia arborea* (p. 60, *pl. 85*). According to him, the former species possessed relatively small, entire leaflets and staminal filaments conspicuously dilated upwards, while the leaflets of the latter species were larger than in the preceding and toothed, the staminal filaments ± filiform. However, Tanaka (1928a, p. 159) pointed out that "Roxburgh unfortunately transposed the figures [of the flowers] in the two drawings given in his above mentioned book."

In 1805, Corréa founded the genus *Glycosmis*, basing it on *Limonia arborea* and *L. pentaphylla* as they were understood by Roxburgh. Corréa, however, did not make formal transfers of these species into his genus, but only remarked (1805, p. 386), "Le *Limonia arborea* et le *Limonia pentaphylla* de Roxburgh, pl. Coromand. vol. 1, fig. 85, 86 [sic] . . . m'ont furni le caractère du genre *Glycosmis*, qui se distingue aisément du reste de la famille." De Candolle (1824, p. 538) apparently was the first to make the formal transfer. *Glycosmis arborea* (Roxb.) DC. was based on *Limonia arborea* Roxb., and *Glycosmis pentaphylla* DC. was based on the plant identified and illustrated by Roxburgh as "*Limonia pentaphylla* Retzius" and only questionably on Retzius' species ("*G. pentaphylla*, . . . *Limonia pentaphylla* Retz. obs. 5. p. 24 ? Roxb. cor. 1. t. 84.").[2] Most taxonomists, however, subsequently used the binomial *Glycosmis pentaphylla* (Retz.) Corréa for this species.

Engler (1896, p. 185) introduced a new combination, *Glycosmis cochinchinensis* (Lour.) Pierre ex Engler, based on Loureiro's *Toluifera cochinchinensis* (1790) and including *G. pentaphylla* (Retz.) Corréa taken in a very broad sense. It is unknown for what reason Engler ascribed the authorship of this new combination to Pierre. As far as the present author has been able to determine, Pierre himself did not make the transfer of *Toluifera cochinchinensis* into *Glycosmis*. In 1893 (text to *pl. 285*), having described a new species, *G. montana*, from Cochinchina, he mentioned "le *Glycosmis pentaphylla* Corr. qui est la même chose que le *Toluifera cochinchinensis* (Lour. Fl. Coch., p. 262) ou *cam ruu* des Annamites. . ." From a brief description of *G. pentaphylla*, included in the note, it is clear that Pierre understood this species in a broad sense.

Tanaka, who studied extensively *Glycosmis* (as well as the other genera

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[2] Further evidence that *G. pentaphylla* DC. was indeed based on the nonexistent basionym *Limonia pentaphylla* Roxb. is found in the way in which De Candolle (1824, p. 538) cited the basionym of his *Clausena pentaphylla*, "*Limonia pentaphylla* herb. Lamb. non Roxb."

of Aurantioideae), visited European herbaria in the late 1920's in a search for generic types. In 1928, he reported finding, in the Lund Herbarium, a Koenig specimen which presumably was the authentic type specimen of *Limonia pentaphylla* Retzius.[3] An examination of this specimen showed that the true *Limonia pentaphylla* Retz. was conspecific with *L. arborea* Roxb. and different from the plant identified by Roxburgh as *L. pentaphylla.* Consequently, Tanaka reduced *G. arborea* (Roxb.) Corréa (= *G. arborea* (Roxb.) DC.) to the synonymy of *G. pentaphylla* (Retz.) Corréa. To Roxburgh's "*Limonia pentaphylla* Retz." Tanaka (1928b) applied another name, *Glycosmis mauritiana* (Lam.) Tanaka, based on *Limonia mauritiana* Lam. (1792). Narayanaswami (1941), apparently having overlooked Tanaka's article on the type of Retzius' species, came to the conclusion, based only on Retzius' description of *Limonia pentaphylla* which mentions the entire leaflets, that Tanaka's interpretation of *L. pentaphylla* was entirely incorrect and that *L. pentaphylla* Retz. and *L. arborea* Roxb. are different species.

Narayanaswami was also of the opinion that Corréa should be assigned the authorship of the combination *Glycosmis pentaphylla,* as well as that of *G. arborea.* "But when we take into consideration the facts regarding the origin of the genus *Glycosmis* and the species *G. pentaphylla* and their acceptance by all botanists up to this day, as having been created by Correa, it logically follows that Correa should be assigned the authorship of *G. arborea* also, since *Limonia arborea* Roxb. formed one of the components of the types of the genus *Glycosmis* of Correa. There appears to be no rule in the botanical nomenclature, that governs such cases where an author creates a new genus from two species of another genus, and leaves it without making the necessary transfer of the earlier species to the new genus. But when a subsequent worker assigns the two species in their new status to the author of the new genus, does it not become binding on all subsequent botanists to follow this adoption by the first botanist, subsequent to the publication of the genus" (Narayanaswami, 1941, p. 25). Narayanaswami was correct insofar as there apparently was no clear rule governing the transfers at that time. However, in 1952 at Paris, the Eighth Botanical Congress formulated a rule concerning validly published new combinations and illustrated it with very clear examples (Art. 32, Int. Code Bot. Nomencl. 1954). In the light of this rule, Corréa's mentioning "Le *Limonia arborea* et le *Limonia pentaphylla* de Roxburgh"

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[3] In 1932, Fischer reported on an examination of the Koenig collection of the Lund Herbarium, which was sent on loan to Kew. Interestingly, *Limonia pentaphylla* Retzius was listed neither among the 346 "Retzius specimens" examined nor among 33 species mentioned in Retzius' *Observationes* but not found in the Koenig collection. Nor was "the authentic Retzius' specimen of *Citrus decumanus,*" quoted by Tanaka (1928a) included in either of the two lists. The presence, however, in the Koenig collection of a number of other specimens which were recognized as authentic Retzius specimens by Tanaka (*Triphasia trifolia* (Burm. f.) P. Wils., *Pleiospermum alatum* (W. & A.) Swingle, and *Feronia limonia* (L.) Swingle ["*Limonia acidissima* L." of Retzius]) makes Tanaka's conclusion in regard to the authenticity of the specimen of *Limonia pentaphylla* Retz. very probable.

as the species on which the genus *Glycosmis* was based does not constitute publication of the new combinations in this genus. Therefore the use of Corréa's authorship for these combinations is against the rules. De Candolle (1824) seems to be "the first botanist subsequent to the publication of the genus" who made formal transfer of the above-mentioned species of *Limonia* into *Glycosmis* as *G. pentaphylla* and *G. arborea*, and his authorship for these binomials is indisputable.

As was mentioned above, Tanaka (1928a), on the basis of the presumed type specimen of Retzius' species, stated that *Limonia pentaphylla* Retzius and *L. arborea* Roxb. were conspecific and different from the plant described and illustrated by Roxburgh as Retzius' species. Then *Glycosmis pentaphylla* DC., based on Roxburgh's plant, not on that of Retzius, must be regarded not as a new combination, but as a new name in *Glycosmis* for the species for which Tanaka later (1928b) created the combination *G. mauritiana* (Lam.) Tanaka (based on *Limonia mauritiana* Lamarck, validly published in 1792, not in 1789 as Tanaka believed). Since *G. pentaphylla* DC. cannot be applied to Retzius' *Limonia pentaphylla*, the next available name for the latter species is *Glycosmis arborea* (Roxb.) DC.

The third species involved in the nomenclatural confusion was *Glycosmis cochinchinensis* (Lour.) Pierre ex Engler (1896, p. 185) which was nomenclaturally based on *Toluifera cochinchinensis* Loureiro (1890, p. 262). Creation of this combination was of no assistance to our knowledge of the entity described by Loureiro as *Toluifera cochinchinensis*, for the type of the latter is not extant. Merrill has helped to reveal its identity. "Although Engler in taking up Pierre's transfer [sic!] of Loureiro's specific name intended it to replace *G. pentaphylla* Corr. as a collective species, it is not the same as *Limonia pentaphylla* Retz. (Obs. **5**: 24. 1789) = *Glycosmis pentaphylla* Corr. Loureiro's species is represented by *Clemens 3363, 4448*, from thickets at Hue and Tourane [presumed classical localities for most of Loureiro's species from Cochinchina], and de Pirey's specimen of *cam ruou*, *Chevalier 41186*. Guillaumin's description of *Glycosmis cochinchinensis* (Lour.) Pierre applies only in small part to Loureiro's species as he treated it as a collective one, citing 14 synonyms, most of which have to be excluded with the restriction of specific limits to the form actually described by Loureiro. True *Glycosmis pentaphylla* (Retz.) Correa does not occur in Indo-China" (Merrill, 1935a, p. 221). Merrill commented further, "The Hainan specimens closely match *Chevalier 41186*, Anamese *com ruou* (Loureiro's *cay cam ruu*) from Anam, and I believe these to represent Loureiro's species. This form closely resembles *G. citrifolia* (Willd.) Lindl., but the leaves are constantly simple. *Chun 5722* from Hainan, which represents the same form as the specimens cited above, has been identified by Tanaka as representing *Glycosmis citrifolia* (Willd.) Lindl. var. *obtusa* (Miq.) Tanaka" (Merrill, 1935b, p. 17). The quoted notes suggest that *Toluifera cochinchinensis* Lour. is closely related to *Glycosmis parviflora* (Sims) Little

(*G. citrifolia* (Willd.) Lindl.) and perhaps should be included in the latter.

In conclusion, it is to be said that in the light of the current rules of botanical nomenclature and of our present knowledge of botanical bibliography, the nomenclature of the two basic species of *Glycosmis* appears to be the following:

Glycosmis arborea (Roxb.) DC. Prodr. 1: 538. 1824.

Limonia arborea Roxb. Pl. Coromand. **1**: 60. *pl. 85*. 1798.
Limonia pentaphylla Retz. Obs. Bot. **5**: 24. 1788.[4]
Glycosmis pentaphylla sensu Tanaka and many other authors, not *G. pentaphylla* DC. 1824.

Glycosmis mauritiana (Lam.) Tanaka, Bull. Soc. Bot. Fr. **75**: 708. 1928.

Limonia mauritiana Lam. Encycl. Méth. Bot. **3**: 517. 1792.
Limonia pentaphylla Retz. according to Roxb. Pl. Coromand. **1**: 60. *pl. 84*. 1798, not Retzius, 1788.
Glycosmis pentaphylla DC. Prodr. **1**: 538. 1824; incorrectly given as *G. pentaphylla* (Retz.) Corréa by Narayanaswami, Rec. Bot. Surv. India **14**(2): 12. 1941.

SUMMARY

With regard to the generic limits of *Zanthoxylum* L., especially in connection with the difference in perianth structure between *Zanthoxylum* L. *sensu stricto* and *Fagara* L., the "simple" perianth of the *Zanthoxylum* type is presumed to be a secondary condition derived by reduction from the double perianth of the *Fagara* type. The occurrence in Mexico and Central America (perhaps also in South America) of species of *Zanthoxylum* which appear to be transitional to *Fagara* in their perianth structure is considered ample reason to regard *Fagara* as a subgenus of *Zanthoxylum*, rather than as a distinct genus.

A number of lines of evidence show that Miller's binomial *Xanthoxylum americanum* (1768) referred to the northeastern American species which was later described by Willdenow (1796) as *Zanthoxylum fraxineum*. Since neither the occurrence of an error in Miller's description nor the

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[4] Tanaka's interpretation of *Limonia pentaphylla* Retzius, based on the presumed type specimen, seems preferable to the Narayanaswami's concept of the species. This is especially true if one also takes into consideration that the original description of *Limonia pentaphylla* Retz. is well applicable to *L. arborea* Roxb., except for the entire leaflets of the former species and the serrate to crenate ones of the latter. It should be remembered, however, that the serration of leaflets in some specimens of *L. arborea* is perceptible only with a lens. On the other hand, the Retzius' species differs from "*Limonia pentaphylla* Retz." of Roxburgh in acute leaflets ("never acute" in the latter according to Narayanaswami, 1941, p. 14) and their size, "magnitudine foliorum *Citri Medicae*," ("small" according to Narayanaswami, loc. cit., "from two to three inches long, and about one and a half broad" according to Roxburgh 1798, p. 60). The leaves of *Citrus Medica* are about 12–20 cm. long.

lack of the type specimen makes Miller's binomial illegitimate, the replacement of *Zanthoxylum americanum* Mill. by *Z. fraxineum* Willd., recently suggested by Fosberg, seems to be unjustifiable in the light of the present code of botanical nomenclature.

In the light of the publication dates of Achille Richard's work on the flora of Cuba (in Ramón de la Sagra), as reported by Grisebach (1842, 1847, 1852), the priority of *Zanthoxylum coriaceum* A. Rich. (1841) over its homonym *Z. coriaceum* (Desv.) Walpers (1842) appears indisputable. Thus, the former binomial is the legitimate and correct name of a well-known species of southern Florida and the West Indies.

A very complex situation in the nomenclature of the type species of *Glycosmis* Corréa, *Limonia arborea* Roxb. (1798), is shown, and a brief history of this genus and the basic species is given. Tanaka's assumption of the conspecificity of *Limonia pentaphylla* Retzius (1788) with *L. arborea* Roxb., based on the presumed authentic type specimen of the former, seems correct. Since *G. pentaphylla* DC., based on *Limonia pentaphylla* sensu Roxburgh (1798), not of Retzius (1788), cannot be applied to *Limonia pentaphylla* Retz., the next available name for the latter species is *G. arborea* (Roxb.) DC. The correct name for *G. pentaphylla* DC. is *G. mauritiana* (Lam.) Tanaka. The third species involved in the nomenclatural confusion was *G. cochinchinensis* (Lour.) Pierre ex Engler, which was based on *Toluifera cochinchinensis* Loureiro (1790). Merrill's notes on the latter species, quoted by the present author, suggest a close relationship of Loureiro's species with *G. parviflora* (Sims) Little (*G. citrifolia* (Willd.) Lindl.), rather than with *G. arborea.*

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THE TYPIFICATION OF DIOSPYROS EBENUM AND DIOSPYROS EBENASTER

RICHARD A. HOWARD AND TYCHO NORLINDH

IN THE LATE PART of the eighteenth century, botanists were uncertain of the identity of the trees which produced two valuable commercial timbers, red sandalwood and true ebony. John Gerhard Koenig is credited with the identification of each during a stay in India and Ceylon. Koenig was born in Polish Latvia in 1728. He moved to Denmark in 1748 and studied with Linnaeus from 1757 to 1759. As a physician, he joined a Danish mission to India in 1767 and died in India in 1785. The present paper concerns the typification of *Diospyros ebenum* (the source of the true ebony), the proper citation of the name, and its synonymy.

A paper with the Swedish title, "Diospyros Ebenum eller Äkta Ebenholz, beskrifvit af John Gerhard König" [*Diospyros ebenum* or true ebony, described by John Gerhard Koenig], was published in the first volume of the *Lund Physiographiska Sälskapets Handlingar*, printed in Stockholm in 1781.[1] In addition to a Latin description of *Diospyros ebenum*, the article contained in a footnote a discussion of the distribution of the plant, its characteristics and its use, the method of formation of the characteristic black wood, and, finally, an eulogy of Koenig for supplying the information. The article, in contrast to others in the Handlingar, does not indicate the author. The discussion is written in the third person and we shall show that an original article written by Koenig was translated, edited and published by A. J. Retzius, the founder and the secretary of the Lund Physiographiska Sälskapet and its publication. The correct citation of the name given the ebony tree should be *Diospyros ebenum* Koenig ex Retzius.

The original description apppears to be a composite one, including unisexual and hermaphrodite flowers and fruit. It was obviously based on a field knowledge of the plant in Ceylon. No specimens were cited, and the selection of a lectotype for the species is now necessary.

In the library of the Botanical Museum, in Copenhagen, there are a number of long letters from Koenig in India during the period 1777–1783

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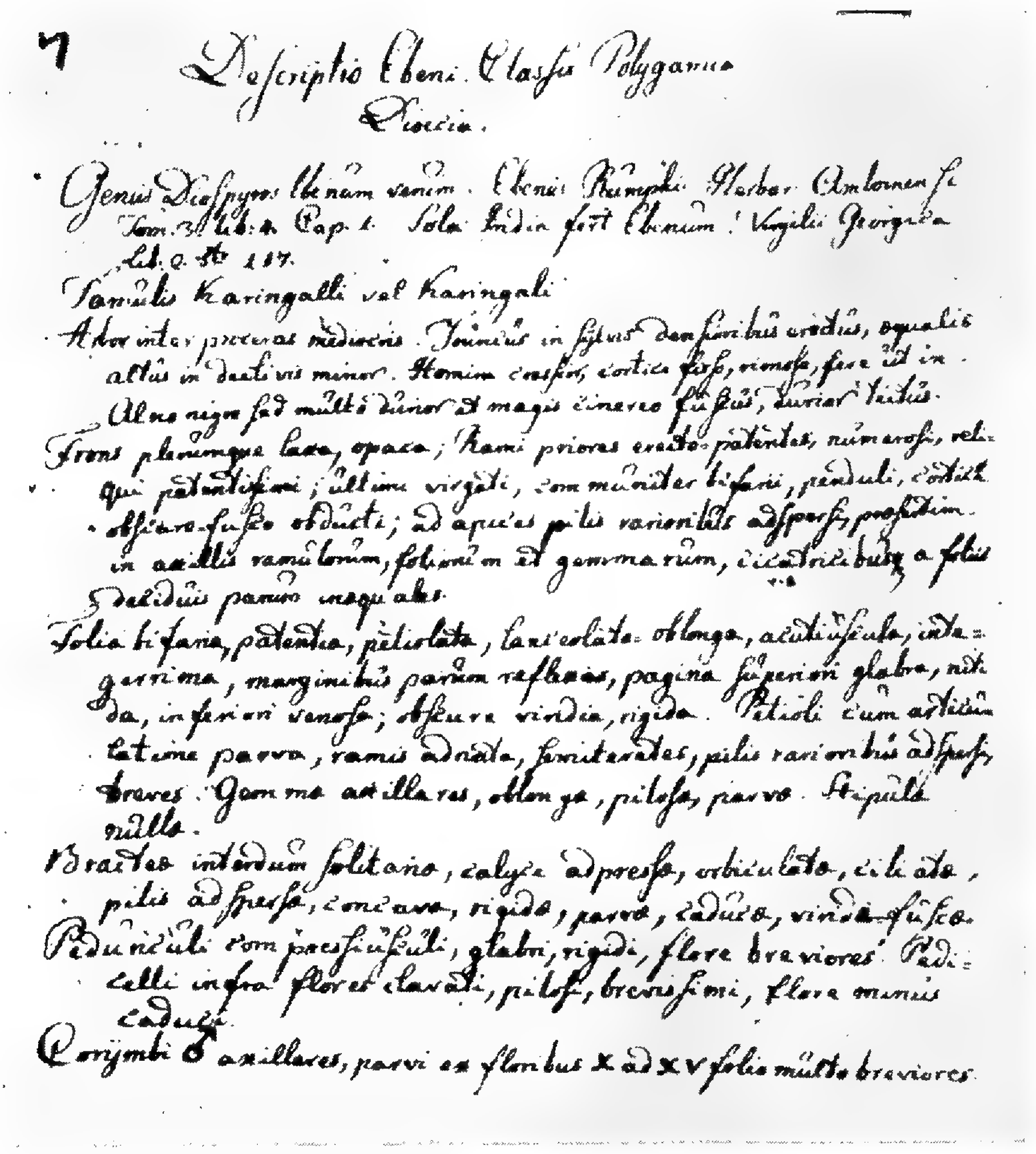
[1] The date of publication of *Diospyros ebenum* is given in Index Kewensis and by most recent authors as 1776, the date on the title page. The first volume of this journal was published in four parts. It is significant to note that Parts 1 and 2, pages 1–64 and 65–132 respectively, were published in 1776, but that Part 3, pages 133–220, containing the description of *Diospyros ebenum*, was published in 1781, and Part 4, pages 221–318, was issued in 1786. Otto Gertz (Kungl. Fysiogr. Sällsk. i Lund 1772–1940 Historisk Överblick, 16. 1940) reports that "the Secretary of the Society announced on May 2nd, 1781, that the printing of 'Handlingarna' Part 1:3 was finished."

to Rottboell who was chief of botany in the Chair of Medicine in Copenhagen until 1797. One letter, written on August 22, 1777, is fifteen pages long. Another pertinent to the present paper was written on February 5, 1778, and is eight folio-size pages in length. Koenig's letters are handwritten in an old-style German. The structure of the language he used is strange today, as is the spelling of many of the words. We are indebted to Mr. Sigurd Molander, of the Library of the Botanical Museum of Lund, for his assistance in the interpretation and translation of Koenig's script.

From Tranquebar, India, on February 5, 1778, Koenig wrote to Rottboell of his recently completed journey to Ceylon and his discovery of the true ebony. On May 10, 1777, the English warship "Seahorse," under Captain James' command and with Koenig aboard, sailed from Madras and arrived at Trincomalee, Ceylon, nine days later. Koenig wrote a brief



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Descriptio Ebeni. Classis Polygama
Dioecia.

Genus Diospyros Ebenum verum. Ebenus Rumphii Herbar. Amboinensi Tom. 3. Lib. 4. Cap. 1. Sola India fert Ebenum! Virgilii Georgica Lib. 2. Vs 117.

Tamulis Karingalli vel Karingali

Arbor inter proceras mediocris. Truncus in sylvis densioribus erectus, aequalis altus in declivis minor. Homine crassior, cortice fusco, rimoso, fere ut in Alno nigra sed multo durior et magis cinereo fuscus, durior textus.

Frons plerumque laxa, opaca; Rami priores erecto-patentes, numerosi, reliqui patentissimi; ultimi virgati, communiter bifarii, penduli, cortice obscuro-fusco obducti; ad apices pilis rarioribus adspersi, praesertim in axillis ramulorum, foliorum et gemmarum, cicatricibus a foliis deciduis parum inaequales.

Folia bifaria, patentia, petiolata, lanceolato-oblonga, acutiuscula, integerrima, marginibus parum reflexis, pagina superiori glabra, nitida, inferiori venosa; obscure viridia, rigida. Petioli cum articulatione parva, ramis adnata, semiteretes, pilis rarioribus adspersi, breves. Gemmae axillares, oblongae, pilosae, parvae. Stipulae nullae.

Bractea interdum solitario, calyce adpresso, orbiculato, ciliato, pilis adpressis, concavo, rigido, parvo, caduco, viridi-fusco.

Pedunculi compressiusculi, glabri, rigidi, flore breviores. Pedicelli infra flores clavati, pilosi, brevissimi, flore minus caduci.

Corymbi ♂ axillares, parvi ex floribus X ad XV folio multo breviores.

TEXT-FIG. 1. First page of Koenig's manuscript, "Descriptio Ebeni Classis Polygama Dioecia."

description of the Trincomalee Mountains, their geology and vegetation. He stated that their slopes were rugged and densely covered by many kinds of trees, among others very many ebony trees. The season was not well adapted for the collection of flowering material, but Koenig declared that he had been able to make a complete description of ebony which he enclosed and from which the addressee, Rottboell, could see that the ebony was a true *Diospyros*. The description Koenig sent was titled "Descriptio Ebeni Classis Polygama Dioecia" and is preserved today. The first page of this classic manuscript is reproduced here as TEXT-FIGURE 1. During a six-day stay in the area of Trincomalee, Koenig collected many new herbs and even concluded that he should very much like to live there. Later in his letter Koenig described another landing at Jaffna where the true ebony used to be cut. Here he said there were very tall and well-formed trees, many of which bore fruit. However, he was not able to find a single flower, though he offered rewards of much gold to the finder and many trees were thoroughly searched. In his presence two trees were cut down, and in these only the innermost part had turned black, showing beyond doubt that it was ebony. A forester on the spot told Koenig that holes were cut through the bark into the wood in order to encourage the development of pigmentation. He explained the white streaks found in ebony as incomplete mummification due to premature cutting and contrasted this with the uniformly colored woods obtained in the French and Mauritian islands. Koenig indicated in his letter that he had collected as many plants as possible and that these had been sent to Copenhagen ("von welchen allen ich im vorighten Jahr auch nach Copenhagen zureichende Exemplar überstandt habe. . .").

Although there is no correspondence to support the conclusion, it seems clear to us that Rottboell received the specimens sent by Koenig as well as the "Descriptio ebeni." He kept for himself a fruiting specimen and the wood specimen. He sent to Retzius a poorer fruiting specimen, and either the original manuscript, "Descriptio ebeni," which was later returned to Copenhagen, or a copy thereof. Retzius then edited Koenig's manuscript, for, when the original and the published documents are compared, we find several changes in Koenig's Latin constructions but no significant alteration of the diagnosis. The German text of the original manuscript was translated freely into Swedish for publication, and Retzius supplied only the footnote.

The selection of a lectotype, therefore, is a choice between the specimen Rottboell received from Koenig and sent to Retzius and the specimen which Rottboell retained. The specimen in the Retzius herbarium at Lund (PLATE I) bears only two annotations: "Diospyros ebenum," in Retzius' handwriting (PLATE Va), and "e coll. Retzii," which is probably the writing of Professor Agardh. There are fruits attached to this specimen but these are not associated with the leaves, which are only at the ends of the branches and probably represent a later period of growth. The leaves are thin in texture, pointed at the apex, and have dried a dark color.

In the Rottboell herbarium (Copenhagen) there is a specimen which we designate as the lectotype of *Diospyros ebenum* Koenig ex Retzius. This specimen (PLATE II), more ample than that sent to Retzius, has fruit associated with the leaves which, in turn, are thicker in texture, lighter in color, and less pointed at the apex than those of the specimen in the Retzius herbarium. On this sheet in the handwriting of Koenig are the annotations "Diospyros ebenum verum" and "habitat in vastissimis sylvis prope Jafnapatnam & ad latere montium Trinquemallensium" (PLATE Vb). Associated with this sheet is a piece of ebony wood and a section of a stem with both wood and bark.

A second sheet in the Vahl herbarium in Copenhagen bears a specimen in flower and an annotation partly in Koenig's handwriting (PLATE Vc). A label of more recent date designates this specimen as the "originaleksemplar" and indicates that the specimen was received from Koenig from "Trankebar ca. 1780." We do not know who supplied this particular label, but that botanist wrongly indicated its origin as "Trankebar." He failed to notice the annotation on the reverse side of the sheet which reads, "habitat in sylvis Zeylanicis copiose" (PLATE Vc). A sample of wood accompanies this flowering specimen. It is important to notice that this specimen has both older, coriaceous, light-colored leaves and younger, thinner textured, dark-colored leaves on the same shoot. It thus indicates the relationship between the types of foliage represented by the Retzius and the Rottboell collections. The more authentic label associated with the specimen in the Rottboell herbarium, the presence of two wood samples, the fruiting condition of the specimen, and the supporting correspondence have led us to accept the Rottboell specimen as the lectotype and to disregard the "originaleksemplar" label. A similar specimen is in the herbarium at Lund (PLATE IVb).

There is in the Linnaean herbarium in London a fruiting specimen with similarly shaped heavy leaves (PLATE IIIb). We have not been able to trace the origin of the Linnaean specimen in any correspondence from Koenig. The sheet is annotated "König 1777" and "Ebenum Verum ex vastis sylvis Zeylonae. Flores non vidi! an Diospyros?" We suspect that Koenig, a former student of Linnaeus, might well have sent a specimen of his important discovery directly to his former teacher. The chances are that it arrived after the death of the elder Linnaeus (January 10, 1778), for Linnaeus filius described *Diospyros ebenum* in his *Supplementum Plantarum Systematis Vegetabilium*, page 440, in 1781,[2] with

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[2] On the basis of the year of issue, *Diospyros ebenum* L. f. appears to compete with the same name attributed to Koenig. According to the date given in the preface, the *Supplementum* of Linnaeus was completed by October 1, 1780. Linnaeus states that his determination was confirmed by Thunberg, who worked with him at least in the early months of 1779 (Karsten, Jour. S. Afr. Bot. 5: 103. 1939). Stoever (*The Life of Sir Charles Linnaeus*, 295. 1794) quotes Ehrhart as stating that Linnaeus "sent me the manuscript in the autumn of 1779, to be printed. I perused it, set down my doubts and observations, and sent them to *Linnaeus*. A correspondence then began between us, which lasted almost the whole of the ensuing winter. After this, I had it copied afresh, and began to get it quite ready for the press; I was how-

the comment, "Hoc est verum Lignum Ebenum, cuius originem detexit König, confirmavit Thunberg." Linnaeus filius was obviously unaware of the nearly concurrent publication of the same epithet by Retzius in the *Lund Physiographiska Sälskapets Handlingar.* Certainly the date 1777 and the annotation on the Linnaean sheet, in further agreement with Koenig's letter to Rottboell, suggest that Koenig did send the specimen to Linnaeus after he had first seen ebony but while he was still uncertain of its identity as a species of *Diospyros.*

After his initial visit in 1777, Koenig returned to Ceylon several times. The majority of his visits were for but a few days. However, in 1781, he made extensive investigations of the flora. It is probable that Koenig continued to collect specimens of ebony, including ample flowering material, which he sent to Rottboell at Copenhagen. Rottboell was obviously aware of the two publications of the name *Diospyros ebenum* by Retzius and by Linnaeus, of the incomplete published description, and of the lack of an illustration of this important plant. In 1783, he published still another description of the plant, this time with an illustration, and changed the name to *Diospyros glaberrima* (Nye Samling K. Danske Videnskabers Selskabs Skrifter 2: 540. *tab. 5.* 1783). It is clear that Rottboell was renaming the plants described earlier. He points out that his description is largely compiled from Koenig's published description and from material Koenig sent him. Rottboell's own contributions, for which he takes full responsibility for errors, are based on dissections he made of the flowers, thus lending supporting to our conclusions that Koenig sent Rottboell additional material. Finally, in the explanation of the figures for the illustration he supplied, Rottboell notes, "Ramus Diospyri glaberrimi sive Ebeni." The upper portion of the illustration (PLATE IIIa) is clearly drawn from the Koenig specimen "Diospyros ebenum verum" in the Rottboell herbarium which we have designated as the lectotype (PLATE II). Rottboell did not annotate the sheet itself, but the outer cover is labeled *Diospyros glaberrima* in Rottboell's hand. The lectotype we have selected for *Diospyros ebenum* Koenig ex Retzius and the holotype of *Diospyros glaberrima* Rottboell are one and the same specimen. We believe this is what Rottboell intended.

The second specimen of *Diospyros ebenum* in the Retzius herbarium (PLATE IVb) at Lund is comparable to the specimens in the Rottboell (PLATE II), Vahl (PLATE IVa) and Linnaean (PLATE IIIb) herbaria. The Lund specimen, however, bears a copy of the description published by Linnaeus filius and the correct page reference to this work (PLATE Vd).

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ever, prevented, by the botanical tour through the electorate of Hanover, with which his BRITTANIC MAJESTY had expressly charged me. I got it ready at last, in the winter between 1780 and 1781. The work was to be printed at *Hanover*, under my immediate inspection; but it did not take place. I agreed afterwards for the printing of the work at *Brunswick*, in the asylum. The principals of the Orphan Asylum procured new types for this purpose, printed it off in the summer of 1781, and paid an honorary of two ducats per sheet, which I sent to Linnaeus after his return from *England*." Thus it appears that *Diospyros ebenum* Koenig has a priority of two or three months over *Diospyros ebenum* L. f. (See Footnote 1.)

The label also indicates that the specimen was collected by Koenig in Ceylon and sent to Vahl in 1781 ("misit Praeclar: Demonstr. D: Vahl, anno 1781"). Vahl may have sent this to Retzius at Lund. Vahl was attached to the Botanical Garden of Copenhagen as lecturer in 1779 and was appointed professor of botany there in 1801.

We conclude that Retzius had not seen this flowering specimen, which bears the name *Diospyros ebenum* L. f. as well as the description and reference, when he published *Diospyros ebenum* Koenig ex Retzius. We do not know whether it was this specimen from Vahl or whether Retzius saw the specimen which Linnaeus filius must have had at Uppsala, but it must have seemed to him that the heavier and bluntly pointed leaves of the two specimens (PLATES IVb & IIIb) characterized a different plant from the one he had on hand (PLATE I) when he published the Koenig manuscript. Therefore, in his *Observationum Botanicarum* (**5**: 31. 1789) Retzius published the following:

88. DIOSPYROS *Ebenaster* foliis ovali-oblongis coriaceis, gemmis glabris.
Diospyros Ebenum L. Supplem. p. 440.
Hebenaster Rumph. Amb. III. p. 13. t. 6.
Habitat in sylvis circa Calcuttam. KÖNIG.
Obs. Manifeste utrasque Diospyri species confundit *Nob. à* LINNÈ Fil. Descriptio hujus habetur in *Suppl. l.c.* quacum conferri meretur *Rumphius.*

89. DIOSPYROS *Ebenum* foliis ovato-lanceolatis acuminatis, gemmis hirtis.
Diospyros glaberrima Friis Rottb. in Novis Act. Hafn. II. p. 540. tab. 5.
Diospyros Ebenum Physiogr. Saelsk. Handl. V. I. P. 3. p. 176.
Habitat in Zeylonae sylvis.
Descriptionem ab inventore concinatum vide 1. cit.
Folia circiter tripollicaria, quoad consistentiam tenuia, flexilia, obscure viridia.

A translation of Retzius' comment under *Diospyros ebenaster* appears to be the following: "Obviously he (Linnaeus filius) mixes up both species of Diospyros. The description of this (*D. ebenaster*) is found in *Suppl. l.c.* with which place Rumphius deserves to be compared."

It seems clear, therefore, that Retzius was substituting a new name, *Diospyros ebenaster*, for *D. ebenum* L. f. and that this species probably was known to him at least by a specimen in his herbarium which he had received from Vahl in 1781. Regrettably, we have not been able to locate any specimens annotated as *D. ebenaster* by Retzius. Furthermore, it appears that Retzius made two mistakes in the protologue of *D. ebenaster*. The first is the description of the buds as glabrous. All of the specimens we have seen are more or less pubescent when viewed under the magnification of the usual hand lens. Mr. George Proctor examined for us the specimen in the Linnaean herbarium and confirms that the buds on that, too, are slightly pubescent. The second mistake appears to be Retzius' error in referring this species to a Koenig collection from Calcutta. Certainly the present specimen in the Linnaean herbarium is clearly marked from Ceylon. While Koenig did collect in India, we have not seen any specimens of *Diospyros ebenum* collected by him and reported to be from Calcutta.

It should also be noted that the Rumphius reference does not apply to specimens from Calcutta. Furthermore this name is pre-Linnaean (1743) and technically need not be considered in the synonymy. However, Retzius obviously based his new specific name on this mononomial. Bakhuizen van den Brink in a later publication described the Rumphius species as *Diospyros lolin* Bakhuizen van den Brink [3] (Gard. Bull. Straits Settl. 7: 175. 1933 and Bull. Jard. Bot. Buitenzorg III. **15**: 152. 1937).

There remains for consideration the difference in leaf shape given by Retzius in the protologues of the two species *Diospyros ebenum* and *D. ebenaster*. We have already indicated that the existing Koenig collections cited and illustrated show variation in single specimens comparable to that described by Retzius for the two species. During 1961, Mr. D. M. A. Jayaweera, director of the Royal Botanic Garden, Peradeniya, Ceylon, kindly obtained for us a suite of specimens of *D. ebenum*. A series obtained from a single tree clearly indicates that the size, shape, and texture of the leaves of the ebony do vary. The apex of the leaf blade may be acuminate, acute, obtuse, or emarginate on one branch. The texture of the blade in successive flushes of growth may be thin and membranaceous and black upon drying or the older leaves of the same branch may be coriaceous and of a lighter color after drying. The young buds on all the specimens examined were densely pubescent, while the buds in the axils of older leaves showed less pubescence.

We have concluded that *Diospyros ebenaster* is a synonym of *D. ebenum* and that the correct citation and synonymy should be:

Diospyros ebenum Koenig ex Retzius, Lund Physiogr. Sälsk. Handl. 1: 176. 1781.

Diospyros ebenum L. f. Suppl. Pl. Syst. Veg. 440. 1781.
Diospyros glaberrima Rottboell, Nye Saml. Kong. Dansk. Vidensk. Selsk. Skr. 2: 540. *pl. 5.* 1783.
Diospyros ebenaster Retzius. Obs. Bot. 5: 31. 1789.

The lectotype selected for *Diospyros ebenum* Koenig ex Retzius is the specimen in the Rottboell herbarium (Copenhagen).

Two monographs of the Ebenaceae published in the last century differ in their treatments of this species and its synonyms. Hiern (Trans. Cambr. Phil. Soc. 12(1, 2): 27–300. 1873) recognized *Diospyros ebenum* and *D. ebenaster* as distinct species. The treatment published by Bakhuizen is inconsistent and less than clear (Bull. Jard. Bot. Buit. III. **15**: 1–515. 1936–41). His first reference to the species was "*Diospyros*

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[3] It should be noted here *Diospyros lolin* Bakhuizen based on *Hebenaster* Rumphius might be considered a substitute name for *Diospyros ebenaster* Retzius, which is derived from *Hebenaster* Rumphius. We believe that Retzius used *Diospyros ebenaster* as a substitute name for *Diospyros ebenum* L. f. and that the Retzius epithet might be typified by the specimen in the Linnaean herbarium. Although Bakhuizen does not discuss this point, he does regard *D. ebenaster* Retzius as a synonym of *Diospyros ebenum*. By typifying *Diospyros ebenaster* Retzius with *Diospyros ebenum* L. f. the way is clear for the use of *Diospyros lolin* Bakhuizen.

Ebenum L." in an observation (*loc. cit.* 5. 1936). In the *Addenda et Corrigenda* (*loc. cit.* 369. 1941) this is corrected to read "Koen. et L. f." which is incongruous. In the body of the monograph (*loc. cit.* 216. 1937) he uses "Diospyros Ebenum Koen." and in the literature cited the reference "Linn. f., Suppl. Syst. Plant. (1781) 440, partim" is given. There is no discussion of this conclusion that Linnaeus filius had a mixed collection and no reference to the other part of the Linnaean concept can be found in the monograph. Bakhuizen also established as new two varieties for "D. ebenum Koen." The first variety "A. var. **glaberrima** (L.f.) Bakh. — *D. Ebenum* Koen. typica, *D. glaberrima* Linn. f."[4] if accepted today must be var. *ebenum* including as it does Koenig's type. The second variety is "B. var. **timoriana** (Miq.) Bakh. — ?*D. Ebenaster* Retz., *D. reticulata* Willd. var. *timoriana* A. DC., *D. timoriana* (A. DC.) Miq." In the following discussion Bakhuizen states, "*D. Ebenaster* is a very vaguely described species collected by Koenig in the forests of Calcutta. Hence it is most probable that the plant in question is only a form of *D. Ebenum* Koen. . . . It will be better to consider *D. Ebenum* Koen. and *D. Ebenaster* Retz. forms of the same species." The range of *D. ebenum* var. *timoriana,* however, is given by Bakhuizen as Timor, Celebes, and the Malayan Peninsula — and Calcutta, if one believes the Retzius reference on which this location is based. We have not examined material of Bakhuizen's *D. ebenum* var. *timoriana,* nor have we seen authentic specimens of *D. reticulata* Willd. var. *timoriana* A. DC. We call attention to this problem and leave for others the decision as to whether this is truly a variety of *D. ebenum* or some other taxon.

The taxon which Hiern called *Diospyros ebenaster* was reported to occur in the Philippines and the Celebes and to be in such "cultivated places in tropical America, perhaps introduced" as Mexico, Brazil, Cuba and Montserrat. Bakhuizen van der Brink renamed this *Diospyros nigra* (Gmel.) Perrottet. Many contemporary floras continue to use the name *D. ebenaster* Retz. for this widely distributed species. The senior author has pointed out in a previous paper (Jour. Arnold Arb. 42: 430–436. 1961) that Bakhuizen was in error in using the epithet *D. nigra* and that two species are represented by Hiern's *D. ebenaster* which is Bakhuizen's *D. nigra.* One is a native of the Lesser Antilles of the West Indies, and this species does not appear to be introduced into cultivation outside of the Western Hemisphere. Its correct name is *D. revoluta* Vahl, the type of which was collected in Montserrat. The other taxon involved is correctly named *D. digyna* Jacquin. This plant is a native of Mexico and Central America but has been introduced into many areas of Asia and is cultivated in many botanical gardens.

In addition to the individuals mentioned in the body of this paper, we wish to express our appreciation to Dr. A. Skovsted, of Copenhagen; Dr.

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[4] It should be noted that this reference is in error. Linnaeus filius did not publish "Diospyros glaberrima" but *Diospyros ebenum.* Bakhuizen either misread the Linnaean descriptive phrase (*q.v.*) or intended to credit Rottboell as the author of the basionym.

Frances Jarrett, of Kew; and Mr. T. B. Worthington, of Ceylon, for many instances of valuable assistance during the course of this study.

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AND
NATURHISTORISKA RIKSMUSEET,
STOCKHOLM

EXPLANATION OF PLATES

PLATE I

Diospyros ebenum in the Retzius herbarium. This specimen presumably received from Rottboell along with Koenig's original manuscript.

PLATE II

Lectotype of *Diospyros ebenum* Koenig ex Retzius in the Rottboell herbarium, Copenhagen. This specimen is also the holotype of *D. glaberrima* Rottboell.

PLATE III

a, Illustration published by Rottboell for *Diospyros glaberrima* Rottboell (Nye Saml. Kong. Dansk. Vidensk. Selsk. Skr. 2: *pl. 5.* 1783). Notice by comparison with Plate II accuracy with which this figure was prepared. b, Type specimen of *D. ebenum* L. f. in the Linnaean herbarium.

PLATE IV

a, Specimen of *Diospyros ebenum* in the Vahl herbarium, Copenhagen, annotated by an unknown hand as "Originaleksemplar." This specimen, incorrectly attributed to "Trankebar," is in flower. b, Flowering specimen in the Retzius herbarium, Lund. This specimen, bearing the description and reference of *D. ebenum* L. f. may well represent Retzius' concept of *D. ebenaster* Retzius.

PLATE V

Annotations from specimens of *Diospyros ebenum* illustrated in Plates I, II, and IV. a, Annotation in Retzius' handwriting from specimen in Plate I. b, Annotations from lectotype in the Rottboell herbarium (PLATE II). c, Annotation from specimen in the Vahl herbarium (PLATE IVa). d, Annotation from specimen in the Retzius herbarium (PLATE IVb).

HOWARD & NORLINDH, DIOSPYROS

Howard & Norlindh, Diospyros

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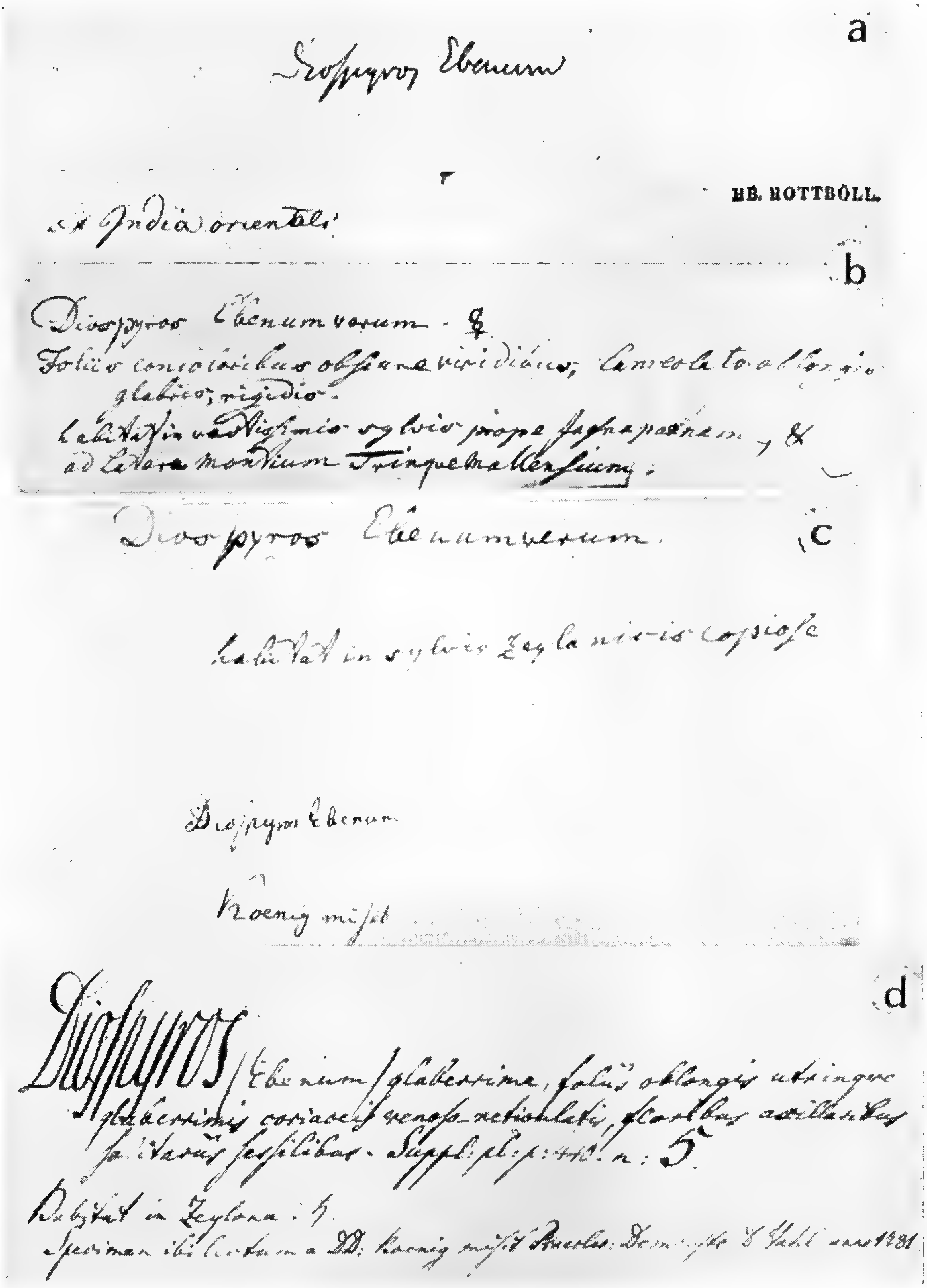

Diospyros Ebenum

ex India orientali:

HB. ROTTBÖLL.

Diospyros Ebenum verum. ♀
Foliis coriaceis obscure viridibus, lanceolato-oblongis
glabris, rigidis.
habitat in vastissimis sylvis prope Jaffnapatnam, & ad latera montium Trinquemallensium.

Diospyros Ebenum verum.

habitat in sylvis Zeylanicis copiose

Diospyros Ebenum

Koenig misit

Diospyros Ebenum glaberrima, foliis oblongis utrinque glaberrimis coriaceis venoso-reticulatis, floribus axillaribus solitariis sessilibus. Suppl. pl. p. 440. n: 5.
Habitat in Zeylona. ♄
Specimen ibi lectum a DD. Koenig misit Amplis: Dom: [illegible] & Vahl anno 1781

HOWARD & NORLINDH, DIOSPYROS

NOTE ON THE RELATIONSHIPS OF PINUS MERKUSII

NICHOLAS T. MIROV

IN HIS *Genus Pinus* (Publication No. 5 of the Arnold Arboretum, 1914), George Russell Shaw with some hesitation placed *Pinus merkusii* Jungh. & De Vriese in the group Lariciones. Shaw wrote, "Of the habit of this pine I know nothing. . . . In my specimens the pits of the ray-cells of the wood are both large [as in the group Lariciones] and small [as in the group Insignes]. In this particular it may belong in either of two groups of species. Its uniform leaf-hypoderm associates it with this group [Lariciones] or with P. halepensis of the Insignes. I have assumed the cone to be dehiscent at maturity and have placed it with the Lariciones, but if further information shows the cone to be serotinous, this species should be transferred to the serotinous group [of the Insignes]."

In February, 1961, I had occasion to observe *Pinus merkusii* in the field in Thailand, Indonesia, and the Philippines. I noticed that normally *P. merkusii* cones dehisce on maturity, shed their shiny ochre-yellow seeds, and remain open and attached to the trees. I could not help but admire Mr. Shaw's wisdom, his sound judgment, and intuition that caused him to place *P. merkusii* in the group Lariciones. Perhaps it is true that in certain characters, such as the uniform leaf-epidermis, *P. merkusii* resembles some pines of the Insignes group, but I think this pine has much more in common with the species of the group Lariciones.

The geographical distribution of the Insignes and the Lariciones pines is shown below:

REGION	PINES OF GROUP INSIGNES	PINES OF GROUP LARICIONES
Mexico	4	None
W. America	4 or 5	None
E. America	6	2
Europe	3 (incl. *P. brutia*)	3 (incl. *P. sylvestris*)
SE. Asia	None	7

It is seen from the above tabulation that the Lariciones pines are predominantly species of southeastern Asia (from Japan to Sumatra). On the other hand, the Insignes pines are not found there. Therefore, the occurrence of *Pinus merkusii* in southeastern Asia, where most of the Lariciones pines grow, seems to me to be one more point in favor of placing this southernmost pine in the group where Shaw placed it.

The Insignes are a rather heterogeneous group, perhaps the first one of the genus *Pinus* to be revised in the light of its genetic characteristics. But such a revision would chiefly concern pines of the eastern United States and would not affect pines of southeastern Asia. All pines of that part of the world most likely will remain in Shaw's group Lariciones.

CABOT FOUNDATION, HARVARD UNIVERSITY

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STUDIES IN THE GENUS JASMINUM, II THE SPECIES FROM NEW CALEDONIA AND THE LOYALTY ISLANDS *

P. S. GREEN

EXAMINATION OF THE EXTENSIVE MATERIAL of the family Oleaceae collected on the Franco-Swiss Botanical Expedition to New Caledonia, 1950–1952, and generously sent on loan from the Botanic Garden and Museum of the University of Zürich, soon indicated the need for a revision of the species of *Jasminum* recorded from New Caledonia. Even though Guillaumin published a key to the species as recently as 1948 in his *Flore de la Nouvelle-Calédonie* (p. 283), it soon became apparent that some species required reconsideration; and, in addition, two further species, *J. linearifolium* and *J. velutinum*, had been described since 1948. In this revision I have attempted to see as wide a range of material as possible, and although I have not seen all the specimens cited by Guillaumin in his numerous and valuable "Contributions to the Flora of New Caledonia," I have been enabled to examine the types of all the taxa concerned.

When considering specific delimitation in *Jasminum*, as in many genera, it is important to bear in mind the phenomenon of heterostyly. This was recorded in *Jasminum* as early as 1867 (Kuhn, Bot. Zeit. Leipzig **25**: 67), but unfortunately it appears to have been overlooked by Guillaumin in his studies of the New Caledonian species. *Jasminum artense* and *J. dzumacense* are separated in the key just mentioned by the relative positions of the anthers and style: the former with the anthers borne in the upper part of the corolla tube above the style and the latter with the reverse condition. Ignoring this as a specific distinction here, it becomes clear there are not two species but only one. The relative positions of the anthers and styles are mentioned in two or three other places in the key as well, and, in 1914, Guillaumin described a variety of *J. elatum* which he called *brevistylis*, based as it was upon the short or "thrum" condition of the style.

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* Results of the Botanical Expedition to New Caledonia 1950–52 (French-Swiss Mission). "Studies in the Genus *Jasminum*, I: Section *Alternifolia*" was published in Notes Bot. Gard. Edinb. 23: 355. 1961.

The immediate affinities of most, if not of all, species included in this revision lie with others outside New Caledonia, so it is not possible to arrange them in strict order of their suspected relationships. A rough grouping has been attempted, however, and, where two species are thought to be close enough in affinity, e.g., *Jasminum artense* and *J. linearifolium*, they have been arranged together.

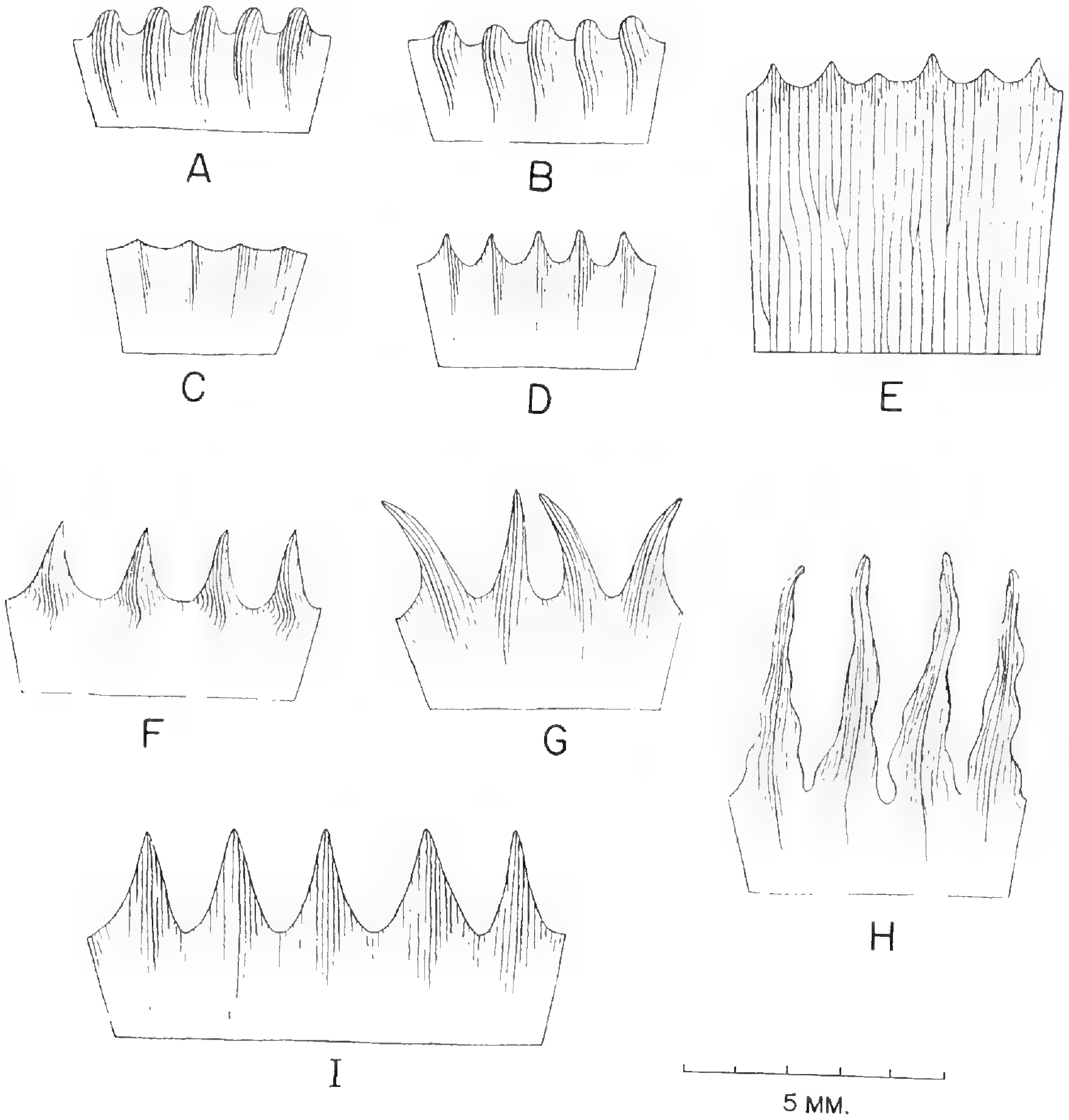

FIG. 1. Calyx types and range of variation in the New Caledonian species of *Jasminum*. *J. didymum*, C; *J. leratii*, F and I to G, rarely almost to D; *J. neocaledonicum*, G; *J. noumeense*, H; *J. artense*, C to D; *J. linearifolium*, C; *J. elatum*, A and B to, occasionally, almost C; *J. promunturianum*, A; *J. kriegeri*, E. (A drawn from *Pancher 316*; B, *Däniker 2270*; C, *Vieillard 913*; D, *Däniker 483*; E, *Vieillard 2937*; F, *Däniker 3089*; G, *Schlechter 15586*; H. *Pancher 315*; I, *Däniker 1333*).

It is perhaps significant that three out of the nine species are only known from a single collection. Furthermore, additional exploration may well indicate what can only be suspected at present; that *Jasminum lineari-*

folium may not be separable at specific rank from *J. artense* and that *J. promunturianum* is equally close to *J. elatum.* The calyces of these species, as pairs, appear identical, and in *Jasminum* the shape and dimensions of the calyx and its teeth, although somewhat limited in the possibilities of their variation, often give convenient characters for identification and a strong indication of affinities. *Jasminum kriegeri,* on the other hand, known only from the one somewhat scrappy specimen collected almost one hundred years ago, has a distinctive calyx. FIGURE 1 gives a diagrammatic representation of the calyces and their range of variation in the species under review.

Two alien species widely grown in the tropics throughout the world have been recorded from New Caledonia, and it is suspected that they have established themselves as escapes from cultivation. They are *Jasminum sambac* (L.) Ait. (see Guillaumin, Ann. Mus. Col. Marseille II. **9**: 191. 1911; Bull. Mus. Hist. Nat. Paris **25**: 500. 1919; Not. Syst. Paris **3**: 61, 65. 1914; and Fl. Nouv.-Caléd. 284. 1948) and *J. multiflorum* (Burm. f.) Andr. (as *J. pubescens* (Retz.) Willd.; see Guillaumin and Virot, Mém. Mus. Hist. Nat. Paris II (B). **4**: 48. 1953).

One or two native names are recorded for various species. From the Island of Lifou (Loyalty Islands) the name "queku" is noted for *Jasminum elatum* on the label of *Deplanch 82* (P) and the name "wechu" is reported by Däniker (Viert. Naturf. Ges. Zürich 78(Beibl. 19): 386. 1933) as being given to *J. didymum, J. elatum,* and *J. leratii* (as *J. simplicifolium*). From the adjacent Island of Maré, Däniker records the name "wekutsch" for *J. didymum* and *J. leratii* and Baumann-Bodenheim (*14770*) "wawekuce" for *J. didymum.* It would seem that these are general names for jasmines as a whole. Guillaumin (Candollea **5**: 151. 1932) quotes information from Bergeret, who had lived in the Loyalty Islands and knew the language, that on Lifou the name "wexu tremanji" is used for *J. leratii* and "wexu foë" for *J. elatum.*

I should like to express my grateful thanks and appreciation to the directors and curators of the cited herbaria for the loan of material or facilities for study. All material cited has been examined, and the respective herbaria are indicated by the abbreviations published in *Index Herbariorum,* Ed. 4, 1959. I should particularly like to mention Dr. Alicia Lourteig, of Paris; Dr. H. Hürlimann, of Basle; and Dr. H. A. Stauffer, of Zürich, to whom I am much indebted for their kind help and cooperation, and Miss Judith Kroll to whom I owe the drawings of calyces.

KEY TO SPECIES

1. Leaves trifoliolate; corolla tube up to 12 mm. long and lobes up to 2.5 mm. long. . . . . 1. *J. didymum.*

1. Leaves simple; corolla tube more than 12 mm. long (rarely as short as 8 mm. in *J. elatum*) and lobes more than 4 mm. long.
   2. Calyx teeth distinct, more than 1 mm. long (FIG. 1, F–I).

    3. Teeth of calyx narrowly lanceolate to subulate-filiform, up to 3 mm. long, usually less (FIG. 1, F to G or I); corolla tube 10–22 mm. long.
        4. Corolla tube up to 20 mm. long, usually less; leaves usually narrowly ovate but ranging from narrowly lanceolate to broadly ovate, (1–)2.5–5.5(–8) cm. long. . . . . 2. *J. leratii.*
        4. Corolla tube 20–22 mm. long; leaves broadly or very broadly ovate, (4–)6–9.5(–11) cm. long. . . . . 3. *J. neocaledonicum.*
    3. Teeth of calyx lanceolate, subfoliaceous, 2–5.5 mm. long (FIG. 1, H); corolla tube 24–33 mm. long. 4. *J. noumeense.*
2. Calyx teeth short or indistinct, up to 1 mm. long (FIG. 1, A–E).
    5. Leaf length not more than twice the breadth.
        6. Pedicels 5–20 mm. long; leaves usually less than 4 cm. long, rarely up to 5.2 cm., ovate to orbicular, more or less coriaceous, the margin more or less recurved and thickened. . . . . 5. *J. artense.*
        6. Pedicels 0–2 mm. long; leaves usually more than 4 cm. long, narrowly ovate, or if ovate to broadly ovate then always more than 4 cm. long, more or less chartaceous, the margin not usually recurved or noticeably thickened. . . . . 7. *J. elatum.*
    5. Leaf length more than twice the breadth.
        7. Length of leaf more than 3 cm.; leaves linear to narrowly lanceolate, apex obtuse or acute.
            8. Shape of leaf linear, not more than 6 mm. broad; calyx tube 1.25 mm. long. . . . . 6. *J. linearifolium.*
            8. Shape of leaf narrowly lanceolate, 6–11 mm. broad; calyx tube 4.5 mm. long. . . . . 9. *J. kriegeri.*
        7. Length of leaf up to 2.5 cm.; leaves oblanceolate or narrowly oblanceolate, apex retuse. . . . . 8. *J. promunturianum.*

Section TRIFOLIOLATA DC.

1. **Jasminum didymum** Forster fil., Prodr. 3. 1786; De Candolle, Prodr. **8**: 311. 1844; Drake del Castillo, Ill. Fl. Ins. Maris Pacif. 231. 1892, et Fl. Polyn. Franç. 120. 1893; Jeanneney, Nouvelle-Calédonie Agricole 121. 1894; Guillaumin, Ann. Mus. Col. Marseille II. **9**: 191. 1911, et Bull. Mus. Hist. Nat. Paris **18**: 40, 329. 1912; Guillaumin & Beauvisage, Ann. Soc. Bot. Lyon **38**: 102 ("Species Montrouzieranae," 28) 1914; Guillaumin, Not. Syst. Paris **3**: 61, 65. 1914, et Bull. Mus. Hist. Nat. Paris **25**: 291, 652. 1919, et in Sarasin & Roux, Nova Caledonia, Bot. 1: 207. 1921; Moore, Jour. Linn. Soc. Bot. **45**: 356. 1921; Guillaumin, Bull. Mus. Nat. Hist. Paris II. **4**: 701. 1932; Däniker, Viert. Naturf. Ges. Zürich **78**(Beibl. 19): 365. 1933; Guillaumin, Bull. Mus. Hist. Nat. Paris II. **6**: 458. 1934, *ibid.* **10**: 519. 1938, *ibid.* **14**: 455. 1942, et Not. Syst. Paris **11**: 55. 1943, et Bull. Mus. Hist. Nat. Paris II. **15**: 453. 1943, et Fl. Nouv.-Caléd. 283. 1948, et Mém. Mus. Hist. Nat. Paris II(B). **4**: 47. 1953, et Bull. Mus. Hist. Nat. Paris II. **27**: 475. 1955, *ibid.* **31**: 179. 1959, et Mém. Mus. Hist. Nat. Paris II(B). **8**: 161. 1959.

J. divaricatum R. Br. Prodr. 521. 1810; Labillardier, Sert. Austr.-Caled. *t. 27*. 1824–25; Endlicher, Wien Mus. Naturg. Ann. **1**: 177. 1836; De

Candolle, Prodr. **8**: 311. 1844; Montrouzier, Mém. Acad. Lyon **10**: 232. 1860; Jeanneney, Nouvelle-Calédonie Agricole, 121. 1894; Schlechter, Bot. Jahrb. **39**: 231. 1907; Guillaumin, Not. Syst. Paris **11**: 55. 1943.

J. didymum var. *stenophyllum* Däniker, Viert. Naturf. Ges. Zürich **78**(Beibl. 19): 366. 1933.

J. fitzgeraldii Knobl. ex Guillaumin, Bull. Mus. Hist. Nat. Paris II. **14**: 456. 1942, nomen pro syn.

Evergreen climber; stems puberulent, often minutely so, or more rarely glabrous. *Leaves* opposite, trifoliolate; common petiole 7–17(–22) mm. long, terminal petiolule (2–)4–12 mm. long, the lateral (1–)2–10 mm. long, puberulent, especially in the groove above, or glabrous; lamina thickish or more or less chartaceous, leaflets narrowly ovate, to narrowly lanceolate (or ovate) or more or less elliptic to narrowly elliptic, the terminal leaflet (0.8–)2–7(–9) cm. long by (0.4–)0.8–3.5(–7) cm. broad, the lateral (1–)1.5–5(–7) cm. long by (0.3–)0.6–2.5(–3.5) cm. broad; margin entire, sometimes slightly thickened, often slightly recurved; apex rounded, obtuse or acute, often with an apiculus or the remains of one; base rounded, subcordate or acute, not attenuate into the petiolule; venation more or less visible as a reticulation, with 4 or 5 (6) primary veins per side. *Inflorescences* axillary or terminal on side shoots, a contracted ternately branched panicle, with few to many flowers, puberulent or glabrous; bracts triangular-lanceolate or subulate, 0.5–2 mm. long; pedicels 0.5–1.5 (–2) mm. long. Flowers white, fragrant, heterostylous. *Calyx* glabrous, occasionally slightly puberulent towards the base, the tube 1.5–2 mm. long with 4–6 often obscure teeth 0–2.5 mm. long (FIG. 1, C), usually slightly ciliolate. *Corolla* hypocrateriform, tube 5–8(–10.5) mm. long, the lobes 4–7, ovate or broadly ovate, rounded to acute, 1.75–3 mm. long. *Stamens* 2, the anthers 2–3.5 mm. long, on filaments 0.5–1 mm. long. *Ovary* 0.75–1 mm. long, with style 2–2.5 mm. long in short-styled flowers or about 5 mm. long in long-styled. *Fruit* not seen in New Caledonian material.

New Caledonia. Gatope, *Vieillard 913* (A, E, GH); montagnes de Gomouen près Gatope, *Vieillard 2935* (BM, K); M'bée, *Vieillard 2936* (K); superieur de Koumac, *Balansa 2785* (E, K); im Tale der Koumac, am Weg von Koumac nach Ouegona, bei den Kalk Klippen, im Gëhölz am Bache, 23 May 1925, *Däniker 1717* (Z); Baie Banaré, *Balansa 3189* (BM, E, K); buissons, La Coulée, 28 March 1928, *Franc 2313* (A, US); bois de Port-Despointes (Nouméa), ±50 m. alt., bois secs des collines littorales, schistes nummulitiques, 21 Nov. 1942, *Virot 846* (A), *ibid.*, ± 40 m. alt., 6 Dec. 1942, *Virot 882* (A); Anse Vata, *Brousmiche 577* (A); Anse Vata, low calcareous hill, 23 Apr. 1955, *McKee 2428* (HULL, US); Oundjo, 1958, *McKee 6512* (HULL); bords de la Dumbéa, 50 m. alt., 6 June 1909, *Franc 1377* (NY); trail from Dumbéa towards Mt. Dzumac, 650 m. alt., mesophilous forest on serpentine soil, 28 Mar. 1951, *Hürlimann 1092* (A, Z); slope south of Paoué valley (Tipindjé), 500 m. alt., meso-xerophilous forest on rocky serpentine soil, 13 Apr. 1951, *Hürlimann 1166* (A, Z); upper Tipindjé valley, 150 m. alt., mesophilous forest on serpentine soil, 23 Apr., 1951, *Hürlimann 1307* (A, Z); base of Ouen Toro near Nouméa, 10 m. alt., dry forest on calcareous soil, 27 July 1950, *Baumann-Bodenheim 5032* (A, Z), 17 Sept. 1950, *Baumann-Bodenheim 6057* (A, Z), and 14 Oct. 1950, *Guillaumin & Baumann-Bodenheim 6842* (A, Z); Mt. Kouvelée (Dumbéa), forest on serpentine soil, 9 May 1951, *Guillaumin & Baumann-Bodenheim 13127* (A, Z); Mt. Kaféaté, 19 May 1951, *Guillaumin 13395* (A, Z); Mt. Mou, gully forest, serpentine, 450 m. alt., 1914, *Compton 455* (BM); bei Hieghène, Apr. 1921, *Heim 74* (Z): Tiebaghikuppen, am Nordostabhang, auf Serpentin, im Gebüsch auf Steinen, oft und verbreitet, 14 Mar. 1924, *Däniker 1436* (holotype, var. *stenophyllum*, Z).

ISLE OF PINES: *Le Rat 109* (K); near Kuto, on coral soil, 26 May 1951, *Baumann-Bodenheim 13454* (A, Z); Anse Kanumera, on coral soil, 27 May 1957, *Baumann-Bodenheim 13608* (Z); Kouibandiou Island, near Isle of Pines, *Araucaria cookii-Pandanus* forest on coral soil, 25 May 1951, *Baumann-Bodenheim 13436* (Z).

Loyalty Islands. LIFOU: Mou, oft an den felsigen Abhängen der Ostküste, 29 Nov. 1925, *Däniker 2465* (Z); Natalo, im Buschwalde, 2 Nov. 1925, *Däniker 2465a* (Z); Képénéé, in Wald, 17 Apr. 1912, *Sarasin 730* (Z). OUVÉA: May 1912, *Sarasin 890* (Z). MARÉ: Pénélo, on coral soil, 18 July 1951, *Baumann-Bodenheim 14770* (A, Z).

Easily distinguished amongst the jasmines of New Caledonia by its trifoliolate leaves, this species is nevertheless very variable. The variability is most obvious in leaflet size and breadth but also in corolla size, although the corolla tube and lobes are always smaller than in any of the other species. In 1933, Däniker described his variety *stenophyllum* based upon a small, narrow-leafletted variant (*Däniker 1436*) but, to judge from the considerable number of specimens I have examined, it falls into the range of the apparently continuous variation exhibited by the species. It is worth noting, too, that *Virot 846*, with leaflets similar to and perhaps a little narrower than *Däniker 1436*, is said, in the field notes on the label with the specimen, to be a "forme jeune", but I have no knowledge to what extent leaflet shape and size may vary with maturity. The name "*Jasminum fitzgeraldii*" attached by Knoblauch to the specimen of *Däniker 2465* at Zürich was never validly published, and Guillaumin, when drawing attention to the variability of *J. didymum* (in Bull. Mus. Hist. Nat. Paris II. **14**: 455. 1942), remarks that it is only an intermediate between the linear-leafletted expression, as exemplified in the extreme by *LeRat 1610* (not seen, also mentioned by Guillaumin in *ibid.* **6**: 458. 1934) and the almost orbicular-leafletted *Vieillard 2935*.

Jasminum didymum lies within a complex distributed over the Australasian and Malaysian areas; a complex which calls for investigation and treatment as a whole, with geographical distribution as only one of the characters taken into consideration. *Jasminum didymum* was the first species described in this complex; in addition to *J. divaricatum* R. Br., described from Australia and included in the synonymy above, the other species are: *J. dallachii* F. Muell. (Australia), *J. degeneri* Kobuski (Fiji), *J. domatiigerum* Lingelsh. (New Guinea), *J. gilgianum* K. Schum. (New Guinea), *J. lineare* R. Br. (Australia), *J. micranthum* R. Br. (Australia), *J. parviflorum* Decne. (Timor), *J. racemosum* F. Muell.

(Australia), *J. rupestre* Blume (New Guinea), *J. smithianum* Kobuski (Fiji), and *J. triphyllum* Merrill (Philippine Is.).

It appears that *Jasminum didymum* may exhibit a certain amount of androdioecism, for, despite the examination of several flowers, no styles have been found on some specimens (for example, *Franc 2313* and *Vieillard 913*), and the ovary, whilst normal in size, is presumably abortive. The anthers however, were normal and full of pollen. In other specimens both the style and stamens were normal, although exhibiting heterostyly.

Section UNIFOLIOLATA DC.

2. **Jasminum leratii** Schlechter, Bot. Jahrb. **40**(Beibl. 92): 32. 1908; Guillaumin, Ann. Mus. Col. Marseille II. **9**: 191. 1911, et Not. Syst. Paris **3**: 62. 1914, et Bull. Mus. Hist. Nat. Paris II. **6**: 458. 1934, *ibid.* **13**: 476. 1941, *ibid.* **15**: 454. 1943, et Fl. Nouv.-Caléd. 284, 1948, et Mém. Mus. Hist. Nat. Paris II(B). **4**: 47. 1953, et Bull. Mus. Hist. Nat. Paris II. **27**: 327, 475. 1955.

J. francii Guillaumin, Bull. Mus. Hist. Nat. Paris II. **5**: 323. 1933.
J. neocaledonicum Schlechter var. *angustifolium* Däniker, Viert. Naturf. Ges. Zürich **78**(Beibl. 19): 366. 1933.
J. daenikeri Knoblauch, Repert. Sp. Nov. **41**: 150. 1936.
J. paagoumenum Knoblauch, Repert. Sp. Nov. **41**: 150. 1936.
J. absimile L. H. Bailey, Gent. Herb. **4**: 346. 1940, Hortus Second 397. 1941, et Man. Cult. Pl. ed. 2. 797, 798. 1949: P. Riedal (Calif. Arboretum Foundation), Pl. for Extra-Trop. Regions 335. 1957.
J. noumeense Schltr. var. *microphyllum* Guillaumin, Bull. Mus. Nat. Paris II. **15**: 454. 1943.
"*J. simplicifolium* Forst. f." sensu Guillaumin, Ann. Mus. Col. Marseille II. **9**: 192. 1911, et Not. Syst. Paris **3**: 62, 65. 1914, et Bull. Mus. Hist. Nat. Paris **25**: 652. 1919, et in Sarasin & Roux, Nova Caledonia, Bot. **1**: 207. 1921; Moore, Jour. Linn. Soc. Bot. **45**: 356. 1921; Guillaumin, Candollea **5**: 151. 1932; Däniker, Viert. Naturf. Ges. Zürich **78**(Beibl. 19): 368. 1933; Guillaumin, Bull. Mus. Hist. Nat. Paris II. **5**: 323. 1933; *ibid.* **6**: 458. 1934, *ibid.* **15**: 454. 1943, et Fl. Nouv.-Caléd. 284. 1948.
"*J. australe* Pers." sensu Montrouzier, Mém. Acad. Lyon **10**: 231. 1866; Guillaumin & Beauvisage, Ann. Soc. Bot. Lyon **38**: 123 ("Species Montrouzieranae," 49) 1914.

Evergreen diffuse shrub, climber, or liane of variable length; the stem glabrous or minutely puberulent, especially when young. *Leaves* opposite, simple; petioles 1.5–10(–20) mm. long, glabrous or minutely puberulent, articulated ¼ to ½ way from base; lamina more or less chartaceous, (broad ovate to) ovate to lanceolate (to linear lanceolate), (1–)2.5–5(–8) cm. long by (0.4–)1.5–4(–5) cm. broad; margin entire, not or scarcely thickened, rarely slightly recurved; apex obtuse or acute, sometimes more or less rounded or apiculate; base rounded or obtuse, sometimes more or less truncate or acute or even angustate, often slightly attenuate into the petiole; venation more or less obscure or reticulate or with primary veins only visible above and below, 3–5(6) per side, the upper 3 or 4 often anastomosing towards the margin. *Inflorescences* terminal on side shoots or axillary, ternately paniculate with 3–9(–18) flowers per panicle, glabrous or minutely puberulent; bracts linear-filiform, 1–4 mm. long or occasionally approaching foliaceous and slightly longer; pedicels 2–20 mm. long. Flowers white, feebly to strongly fragrant, heterostylous. *Calyx* glabrous or minutely puberulent, tube (1.5–)2–2.5(–3) mm. long with 4–6, triangular-lanceolate teeth, (0.5–)2–3.5(–4) mm. long (FIG. 1, ranging from G, through I and F, to rarely almost D), more or less accrescent in fruit. *Corolla* hypocrateriform, tube 11–20 mm. long, lobes 5–7, lanceolate or narrowly lanceolate, acute, 7–12 mm. long. *Stamens* 2, anthers 3–4.75 mm. long on filaments 0.5–2 mm. long. *Ovary* 1–1.25 mm. long, style 3–6.5(–9) mm. long in short-styled flowers or 11–16 mm. long in long-styled. *Fruit* ellipsoid-ovoid, paired (or single by abortion) 6–8 mm. long by 5–6 mm. broad.

New Caledonia. Magenta, Jan. 1903, *Le Rat 172* (isotype, P); Nouméa, *Franc 1544* (syntype *J. francii*, P), *Franc 1544A* (syntype *J. francii* P; isosyntype, A); Port de France (Nouméa), 1855–60, *Vieillard 911* (A, G, K); Port Despointes, 50 m., bois secs des collines littorales, schistes nummulitiques, 6 Dec. 1942, *Virot 876, 881* (A), *ibid.*, 13 Dec. 1942, *Virot 922, 927, 929* (A); Prony, coteaux arides, roches ferrugineuses, 20 Feb. 1914, *Franc 1906* (A, Z); Koné, oft im niederen Gebüsch der Küstenhügel, 11 Feb. 1925, *Däniker 770a, 3088* (Z); an der Mündung des Flusses von Koné, zerstreut im Gebüsche der sumpfigen Flussdeltas, 10 Feb. 1925, *Däniker 1171* (holotype *J. neocaledonicum* var. *angustifolium* & *J. daenikeri*, Z); bei Paagoumen, im Grasbestand auf Serpentingebüsch, 22 March 1925, *Däniker 1518* (holotype *J. paagoumenum*, Z); Ile de la Table, bei Koumac, in Acaciengebüsch, 5 March 1925, *Däniker 1333, 1335* (Z); auf der Insel Neba, im Sumpfwäldchen bei dem Teiche, 8 April 1925, *Däniker 1599* (Z); am Anse longue bei Carticaté, St. Vincent, im Ufergehölz, 12 Dec. 1924, *Däniker 770* (Z); Anse Vata, low calcareous hill, remnant of dry forest with trees close together, 23 Jan. 1955, *McKee 1973* (A, HULL, US), *475* and *2342* (HULL); slope of Ouen Toro, 22 March 1955, *McKee 2251*, (A, US); Ouen Toro, promenade Pierre Vernier, 10 m. alt., climax littoral à *Acacia spirorbis*, nummulitique, terraine schisto-calcaire, 30 Jan. 1941, *Virot 442* (A); N.W. of Mt. Natégou, beneath the road to Yaté, shrubby forest on rocky serpentine ridge, 270 m. alt., 29 Jan. 1951, *Hürlimann 769* (A, Z); "Bois du Sud" (towards the Yaté valley), *Spermolepis* forest on serpentine, 29 March 1951, *Guillaumin & Baumann-Bodenheim 11663* (A, Z); south of Mt. Poindas (Tipindjé), mesophilous forest on serpentine ridge, 520 m. alt., 21 April 1951, *Hürlimann 1290* (A, Z); Mt. Koniambo, on serpentine soil, 21 Dec. 1950, *Guillaumin & Baumann-Bodenheim 9514* (A, Z); Mt. Kaféaté, on serpentine soil, 22 Dec. 1950, *Guillaumin & Baumann-Bodenheim 9665* (A, Z), *ibid.*, on calcareous soil, 10 April 1951, *Guillaumin & Baumann-Bodenheim 12043* (A, Z); Moro Island, on coral soil, 5 & 6 March 1951, *Guillaumin & Baumann-Bodenheim 11106, 11135, 11161* (A, Z); Col de Vulcain, xerophilous forest on serpentine soil, 900 m. alt., 12 Nov. 1950, *Baumann-Bodenheim 8285* (A, Z); Gatope, 1861–67, *Vieillard 2938* (A, G, GH, P) and *2935* (holotype *J. noumeense* var. *microphyllum*, P); Voh, March 1921, *Heim 49* (Z). ISLE OF PINES:

Germain 13 (A); Kuto peninsula, on calcareous soil, 28 May 1951, *Baumann-Bodenheim 13642* (A, Z).

Loyalty Islands. LIFOU: bei Képénéhé, im Buschwalde, 31 July 1925, *Däniker 1886* (Z), *ibid.*, 22 Oct. 1925, *Däniker 2269* (Z), 19 April 1912, *Sarasin 185* (Z); in der Umgebung von Natalo, oft im Gebüsch, 2 Nov. 1925, *Däniker 2388* (Z); zwischen Natalo und Tingeting, in der Savanne zerstreut, 2 Nov. 1925, *Däniker 2388a* (Z); Kiätheng, in der Savanne, 21 Nov. 1925, *Däniker 3089* (Z). OUVÉA: May 1912, *Sarasin 885* (Z); Fayaoué, in den Gebüschen, 4 Aug. 1925, *Däniker 1909* (Z). MARÉ: uberall auf dem Plateau von Maré, 29 Nov. 1911, *Sarasin 424* (Z); Eneni, oft in der inneren Ebene von Maré, besonders längs der Wege, 29 Dec. 1925, *Däniker 2626* (Z); Tadine, forest on coral soil, 12 July 1951, *Baumann-Bodenheim 14529* (A, Z); Rawa, mesophilous forest on coral soil, 17 July 1951, *Baumann-Bodenheim 14721* (A, Z) without locality, Jan. 1908, *Franc 1021* (NY).

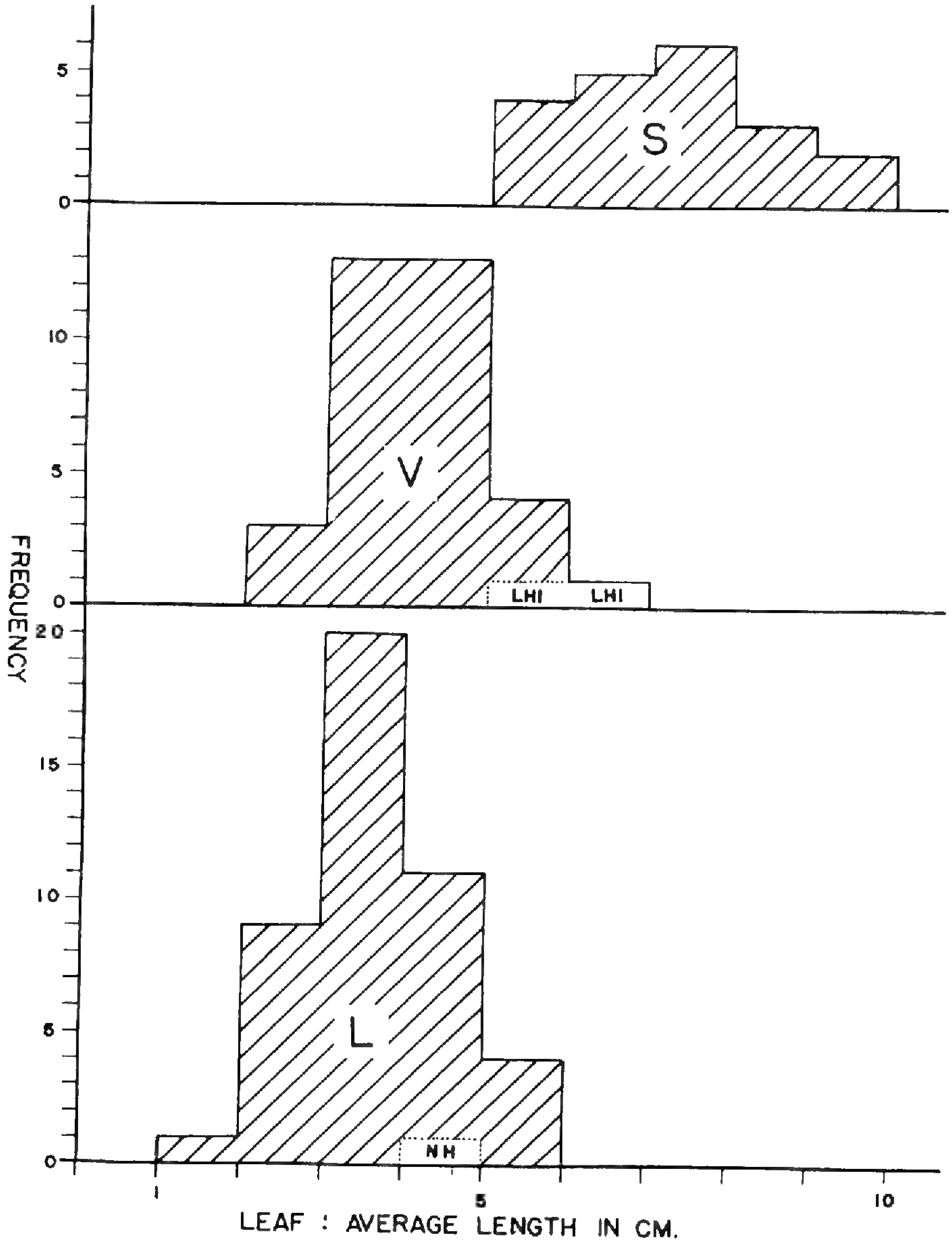

FIG. 2. Frequency histograms of leaf length in *Jasminum leratii* (L), *J. volubile* (V), and *J. simplicifolium* (S). LHI and NH indicate the position of the specimens examined from Lord Howe Island and the New Hebrides respectively.

Cultivated. United States of America, California: Santa Barbara, 27 July 1917, *Eastwood* (A); San Diego, Aug. 1919, *Woodcock 630* (holotype of *J. absimile*, BH); Golden Gate Park, San Francisco, 23 March 1927, *Bailey 9623* (BH); R. Menzie's place, Mill Valley, 24 July 1927, *Walter 65* (A).

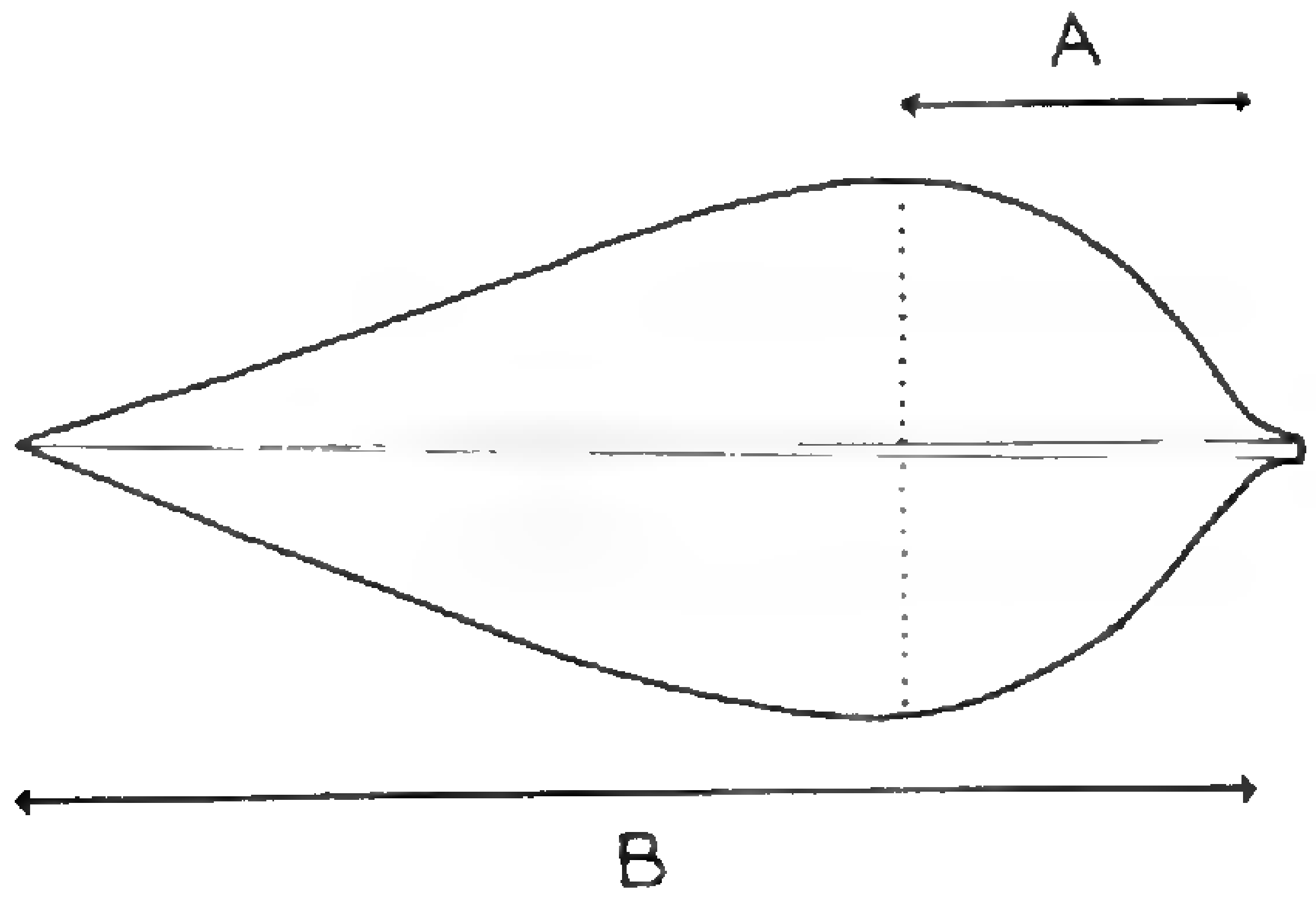

FIG. 3. Greatest leaf breadth factor: measurement B divided by measurement A (see text).

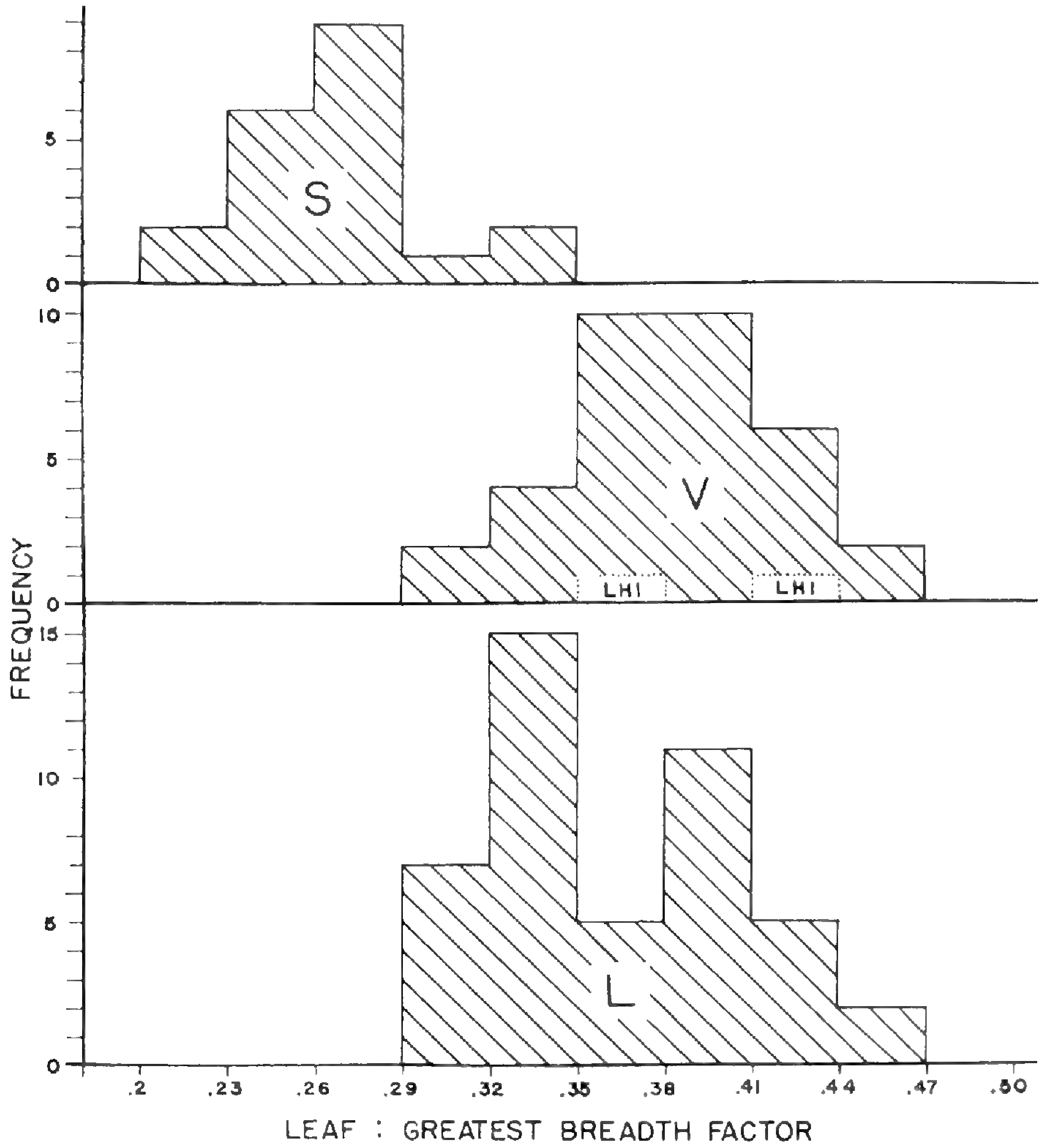

FIG. 4. Frequency histograms for greatest leaf breadth factors in *Jasminum leratii* (L), *J. volubile* (V), and *J. simplicifolium* (S). LHI and NH indicate the position of the specimens examined from Lord Howe Island and the New Hebrides respectively.

A close relationship exists between this species, *Jasminum simplicifolium* Forst. f. and *J. volubile* Jacq. (*J. gracile* Andr.), and, after considerable study of material of all three, I have come to the conclusion that, for the present at least, they should be treated as separate species. Without doubt all three lie very close together and it is not without significance that *J. leratii* was placed as a doubtful synonym under *J. simplicifolium* by Guillaumin in 1921 (in Sarasin & Roux, Nova Caled. Bot. 1: 207. 1921) and later by Däniker (Viert. Naturf. Ges. Zürich 78(Beibl. 19): 368. 1933), although the two were maintained as distinct in Guillaumin's relatively recent *Flore de la Nouvelle-Calédonie* 284. 1948. Bailey (Gent. Herb. 4: 342. 1940) separates *J. volubile* (as *J. gracile*) and *J. simplicifolium* and infers that the former is confined to Australia, an inference supported by this investigation. For this study a careful analysis has been made of leaf length, distance from the base to the greatest breadth of the leaf, length of calyx teeth, length of pedicel, and length of corolla tube; and each has been considered in relation to geographical distribution. The results may be expressed as follows: (i) LEAF LENGTH. The extra-Novo Caledonian *J. simplicifolium* (from Fiji & Tonga) has longer leaves than either *J. leratii* (from New Caledonia) or *J. volubile* (from Australia), although, using the average leaf length of a specimen, a slight overlap occurs around 5.5–6 cm. (FIG. 2). (ii) GREATEST LEAF BREADTH FACTOR. Bailey (*loc. cit.*) indicated the possible value of the position of greatest breadth of the leaf in distinguishing between these species. In this analysis a "greatest leaf breadth factor" was calculated by measuring the total length of a leaf, and dividing by the distance up the midrib to the position of greatest breadth (see FIG. 3; B divided by A). Using this method it was found that *J. simplicifolium* had the lowest factor, less than 0.3 whilst *J. leratii* and *J. volubile* both had factors ranging from 0.3 to 0.45 (FIG. 4). That is to say, *J. simplicifolium* has leaves which have their greatest breadth in the lower third and the other species between the lower third and middle of the leaf. (iii) LENGTH OF CALYX TEETH. *Jasminum volubile* is more or less separable from *J. leratii* and *J. simplicifolium* on this character. In the first species, the teeth range from practically nothing to no more than an average of 0.75 mm. in length, usually less, whilst in the latter two species they vary from an average of just under 0.75 mm. to 2 mm. in *J. simplicifolium* and to nearly 4 mm. in *J. leratii*, which is very variable in length of calyx teeth (FIG. 5). (iv) LENGTH OF PEDICEL. There is no clear cut separation of the taxa on this character but only a very slight tendency for *J. volubile* to have shorter pedicels than the other two species. (v) LENGTH OF COROLLA TUBE. *Jasminum volubile* is distinguishable by its shorter corolla tube which, in the material examined, ranges from about 8 to 11 mm., whereas in *J. leratii* and *J. simplicifolium* (which together seem indistinguishable on this character) it ranges from 11–20 mm. (FIG. 6).

These details may be summarized by saying that *Jasminum leratii* has leaves which are shorter and slightly more elliptical than those of *J.*

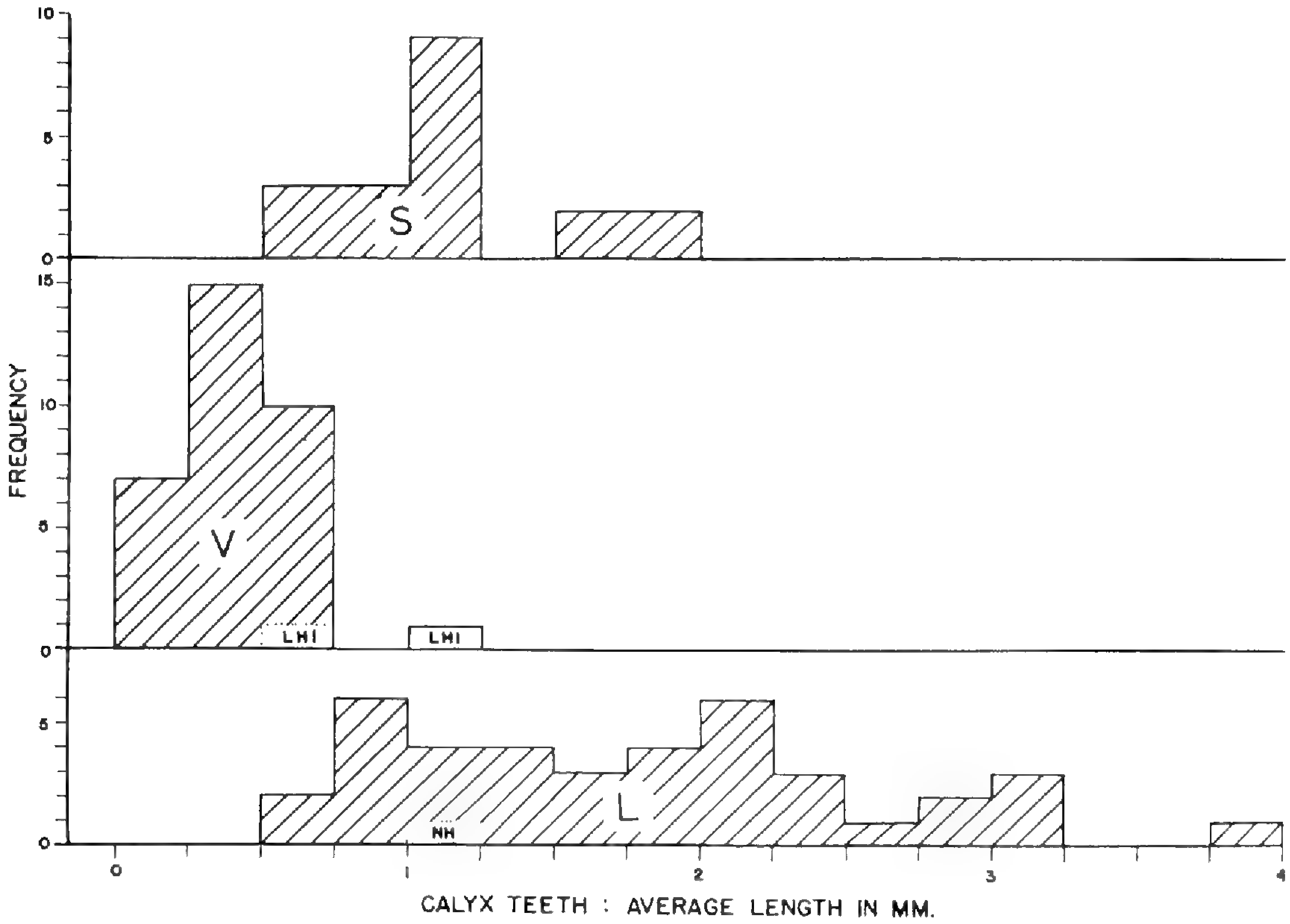

FIG. 5. Frequency histograms for length of calyx teeth in *Jasminum leratii* (L), *J. volubile* (V), and *J. simplicifolium* (S). LHI and NH indicate the position of the specimens from Lord Howe Island and the New Hebrides respectively.

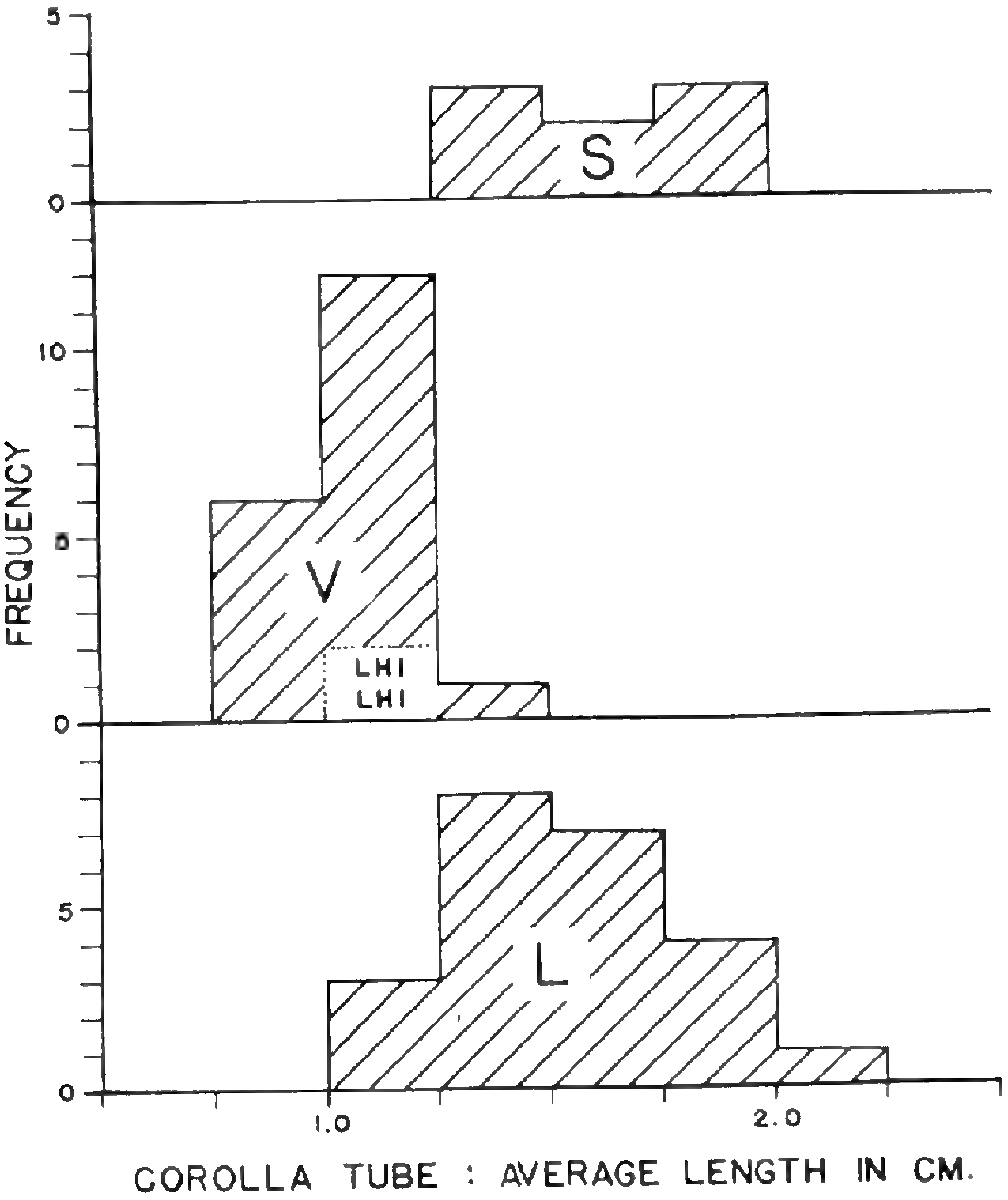

FIG. 6. Frequency histograms for length of corolla tube in *Jasminum leratii* (L), *J. volubile* (V), and *J. simplicifolium* (S). LHI indicates the position of the specimens examined from Lord Howe Island.

simplicifolium and generally has a larger corolla tube and calyx teeth than *J. volubile.*

Whilst not strictly observations on New Caledonian material, it is interesting to make two notes on allied material. The only specimen seen from the adjacent New Hebrides (*Kajewski 404*, A, NY) is *Jasminum leratii.* It was originally identified as *J. simplicifolium* (Guillaumin, Jour. Arn. Arb. 13: 17. 1932), but, although it has no corollas on it to examine and measure (being in fruit), in leaf dimensions and shape, and in calyx type, it falls into the range of *J. leratii.* The two specimens examined from Lord Howe Island in this investigation (*McCornish 4* [A] and "Phytologic Museum of Victoria, Government Botanist Melbourne" [E]) have leaves and calyx teeth which in length lie on the edge or outside the ranges of the Australian specimens of *J. volubile.* Yet in greatest leaf breadth factor and length of corolla tube they agree with the rest of the Australian material.

At the same time as *Jasminum leratii*, *J. volubile*, and *J. simplicifolium* were being investigated, the opportunity was taken to examine the cultivated species *J. absimile* L. H. Bailey, and a separate note about this will appear in *Baileya.* It is sufficient to point out here that *J. absimile* is conspecific with *J. leratii*, although in the former there are usually more flowers per inflorescence and the leaves are a little larger on the average. But both these differences can be accounted for by favorable conditions of growth in cultivation.

Jasminum leratii is very variable in leaf shape and size, and it is suspected that this may be a reflection of the habitat conditions under which the plants are growing. Some of the largest leaves (up to 7 cm.) are exhibited by a specimen of *Däniker 1909*; yet under this same number is a shoot with quite typical leaves half their size. *Däniker 1171* exhibits leaves which are consistently small and narrow. Because of this it was used as the type of both *J. daenikeri* and *J. neocaledonicum* var. *angustifolium*, but some of the leaves on *Le Rat 172*, the type of *J. leratii*, are an exact match, as are those of *Guillaumin & Baumann-Bodenheim 11663*, in which they range from broad-ovate to linear, although considerably larger than in *Le Rat 172.* Similarly, a small-leaved scrap (*Vieillard 2935*) was the basis of the published name *J. noumeense* var. *microphyllum* (although the type sheet at Paris bears only the name *J. neocaledonicum* var. *microphyllum* in Guillaumin's hand). The leaves are shorter than those of *Däniker 1171* but they can be matched exactly by the smallest leaves of several other specimens and in floral characters this specimen is identical with the rest of *J. leratii.*

Dr. Hürlimann has remarked in correspondence that it is uncommon for endemic species in New Caledonia to occur on calcareous as well as on serpentine soils, but using dried specimens I have been unable to discern any consistent differences between individuals from the two habitats. It is possible that there are differences which are masked in the herbarium by the limitations of the material and the wide variability of the species, and an examination of populations in the field with this point in mind might well prove profitable.

Although Guillaumin described *Jasminum francii* in 1933, he placed it in synonymy the following year (see Bull. Mus. Hist. Nat. Paris II. **6**: 458. 1934) after he had seen authentic material of Schlechter's species.

When describing *Jasminum kriegeri*, Guillaumin cited two numbers, one of which was *Vieillard 2938*; however, all the specimens of this number which I have seen, including one from Paris, are clearly *J. leratii*. This number is presumably a mixed gathering, for Guillaumin (in Bull. Mus. Hist. Nat. Paris II. **15**: 453, 454. 1943) referred *Vieillard 2938* to both *J. kriegeri* and *J. leratii*, adding "*pro parte*" to the citation under the latter.

3. **Jasminum neocaledonicum** Schlechter, Bot. Jahrb. **39**: 231. 1906; Guillaumin, Ann. Mus. Col. Marseille II. **9**: 191. 1911, Not. Syst. Paris **3**: 65. 1914, et Bull. Mus. Hist. Nat. Paris **25**: 652. 1919, *ibid.* II. **2**: 169. 1930; Däniker, Viert. Naturf. Ges. Zürich **78**(Beibl. 19): 366. 1933; Guillaumin, Bull. Mus. Hist. Nat. Paris II. **13**: 127, 1941, *ibid.* **20**: 371. 1948, et Fl. Nouv.-Caléd. 284. 1948, et Bull. Mus. Hist. Nat. Paris II. **27**: 475. 1955, *ibid.* **30**: 397. 1958.

J. pulchrefoliatum Guillaumin, Not. Syst. Paris **3**: 62, 65. 1914, et Bull. Mus. Hist. Nat. Paris **25**: 500. 1919, et in Sarasin & Roux, Nova Caledonia, Bot. **1**: 207. 1921, et Bull. Mus. Hist. Nat. Paris **27**: 560. 1921, *ibid.* II. **4**: 701. 1932; Däniker, Viert. Naturf. Ges. Zürich **78**(Beibl. 19): 367. 1933; Guillaumin, Bull. Mus. Hist. Nat. Paris II. **10**: 520. 1938, et Fl. Nouv.-Caléd. 284. 1948.

Evergreen liane; stem glabrous, even when young. *Leaves* opposite, simple; petioles 6–35 mm. long, glabrous, articulated ⅓–½ from the base, occasionally on the largest leaves an additional articulation toward the top; lamina broadly ovate to very broadly ovate, (4–)6–9.5(–11) cm. long by (3–)4–8.5(–10) cm. broad; margin entire, not noticeably thickened or recurved; apex acute or acuminate, more rarely obtuse or even retuse; base rounded, truncate or subcordate, only slightly attenuate into the petiole; venation more or less evident, especially above, primary nerves (4)5–7 per side. *Inflorescences* axillary and terminal on side shoots, ternately paniculate, (5–)7–50 flowered, glabrous; bracts more or less linear subulate, 2–7 mm. long; pedicels 3–10 mm. long. Flowers, white, fragrant, heterostylous. *Calyx* glabrous, tube 2–3 mm. long with 4–6 subulate-lanceolate teeth, 1–2.5 mm. long, often slightly recurved (FIG. 1 G). *Corolla* hypocrateriform, tube 20–22 mm. long, lobes 5–7, lanceolate, acute, about 13 mm. long. *Stamens* 2, anthers 4.75–5 mm. long on filaments 0.25–0.5 mm. long. *Ovary* 1.25–1.5 mm. long, style about 10 mm. long in short-styled flowers and 20 mm. long in long-styled. *Fruits* (one loose fruit only seen, *Baumann-Bodenheim 5881*), ellipsoid, 22 mm. long by 9 mm. broad.

New Caledonia. Bei Oubatche, in den waldern der Berge, c. 900 m. alt., 27 Dec. 1902, *Schlechter 15586* (holotype, B [destroyed, not seen]; isotypes, BM, E, K, Z); entre Bourail et Houailou, montagnes, c. 400 m. alt., 6 Feb. 1912, *Sarasin 525* (syntype *J. pulchrefoliatum*, P [photograph seen]; isosyntype, Z); Bourail, *Balansa 1299* (P); Prony, buissons du littorale, Jan. 1915, *Franc 1935* (P); road to Montagnes des Sources, 650 m. alt., 4 March 1955, *McKee 2198* (US); south of Mt. Kongouaouri, mesophilous forest on serpentine, 300 m. alt., 10 Sept. 1950, *Baumann-Bodenheim 5874*, *5881* (A, Z); Mé Amméri, 700 m. alt., on serpentine soil, 28 Nov. 1950, *Guillaumin & Baumann-Bodenheim 8883* (Z); Mé Aoui, hygrophilous forest on schistaceous soil, 500 m. alt., 7 & 8 Feb. 1951, *Guillaumin & Baumann-Bodenheim 10301*, *10440* (A, Z).

A handsome species with large leaves and usually numerous flowers to the inflorescence which must be very beautiful as a living plant. Vegetatively it is sometimes very similar to large-leaved examples of *Jasminum elatum*, but the two may easily be distinguished by their calyces and, to a limited extent, by the position of the petiolar articulation (see under *J. elatum*). To judge from some of the specimens examined, there is also a tendency for specimens of *J. neocaledonicum* to blacken on drying.

In his protologue for this species Schlechter cites his specimen no. *15585* but this must be a misprint, for *15586* is the number on all the Schlechter specimens examined, and, in the same publication (Bot. Jahrb. **39**: 224. 1906), he cites no. *15585* as the type of another of his species: *Leucopogon septentrionalis*.

4. **Jasminum noumeense** Schlechter, Bot. Jahrb. **40**(Beibl. 92): 33. 1908; Guillaumin, Ann. Mus. Col. Marseille II. **9**: 191, 1911, et Not. Syst. Paris **3**: 65. 1914, et Bull. Mus. Hist. Nat. Paris II. **6**: 458. 1934, *ibid.* **10**: 519. 1938, *ibid.* **15**: 454. 1943, et Not. Syst. Paris **11**: 55. 1943 (sphalm. *J. noumeanum*), et Fl. Nouv.-Caléd. 284. 1948, et Mém. Mus. Hist. Nat. Paris II(B). **4**: 48. 1953, et Bull. Mus. Hist. Nat. Paris II. **27**: 475. 1955.

J. bouquetii Jeanneney, Nouv.-Caléd. Agricole 121. 1894, *nom. nud.*; Guillaumin, Not. Syst. Paris **11**: 55. 1943, nom. pro syn.

J. magentae Guillaumin, Bull. Mus. Hist. Nat. Paris II. **2**: 169. 1930; *ibid.* **4**: 697. 1932.

Evergreen liane of variable length; stem puberulent or occasionally glabrous. *Leaves* opposite, simple; petioles 3–17 mm. long, puberulent or occasionally glabrous, articulated near the base; lamina more or less chartaceous, ovate to very broadly ovate, (2–)3–5(–6) cm. long by (1.5–)2–3.5(–5) cm. broad; margin entire, not thickened, occasionally very slightly recurved; apex rounded to obtuse, or retuse, occasionally acute, often with an apiculus; base truncate or occasionally rounded or subcordate, only slightly attenuate into the petiole; venation with primary nerves usually visible, sometimes more or less obscure, 3–5 per side. *Inflorescences* terminal or axillary on side shoots, ternately subcorymbose-paniculate, with up to about 20 flowers per panicle, usually pubescent, especially towards the base of the inflorescence, occasionally glabrous; bracts more or less foliaceous, especially the basal ones, and up to 2 cm. long, occasionally the upper ones ranging to subulate, 1–2 mm. long; pedicels 3–12 mm. long. Flowers white, fragrant, sometimes strongly so (*McKee 2728*) or inodorous (*Däniker 1846*), heterostylous. *Calyx* pubescent, occasionally glabrous, the tube 2–3(–4) mm. long, with 4 or 5 subfoliaceous teeth 2–5.5 mm. long, often wavy margined (FIG. 1,H), somewhat accrescent in fruit. *Corolla* hypocrateriform; tube 24–33 mm. long, lobes 5, lanceolate or broadly lanceolate, acute or very acute, 8.5–15 mm. long. *Stamens* 2; anthers (3–)4–5.5(–6) mm. long, on filaments 0.2–2 mm. long. *Ovary* 1–1.25 mm. long; style 10–11 mm. long in short-styled flowers or 20–30 mm. long in long-styled. *Fruits* (*Balansa 2232*, *Virot 842*) bilobed, united for about ⅔ length of each half, 8–9 mm. long by 7–8 mm. broad, occasionally single sided with a lateral projection 2–3 mm. in diameter representing the abortive loculus.

New Caledonia. Magenta (near Nouméa), June 1903, *Le Rat 574* (isosyntype, P) also, May 1903, *Le Rat 588* (isosyntype, P); bois de Port Despointes (Nouméa), ±50 m. alt., bois secs des collines littorale, schistes nummulitiques, 21 Nov. 1942, *Virot 842* (A); Port N'Gea (Nouméa), près du littorale, ±15 m. alt., bois secs des collines littorale, schistes nummulitiques, 26 Nov. 1942, *Virot 865* (A); Küstenhügel der Halbinsel Nouméa, in den Buschwäldchen am Abhang, 24 July 1925, *Däniker 1846* (Z); Nouméa, Aug. 1926, *Franc 2232* (holotype *J. magentae*, P; isotypes, A, NY, US); Nouméa, foot of Ouen Toro, just above beach, 6 July 1955, *McKee 2728* (A, HULL); Anse Vata, remnant of dry forest on low calcareous hill, 27 March 1955, *McKee 2298* (A, HULL, US). Without locality, *Franc 845* (A, BM, E, K, NY, P, US); *Vieillard 2936* (BM); *Pancher 315* (A) and *Pancher s.n.* (labeled *J. bouquetii*, A).

One of the most distinctive features of this species is the large, almost subfoliose, calyx lobes (FIG. 1,H). The corolla tube, too, is longer than in any other New Caledonian jasmine. Vegetatively it can be very similar to *Jasminum artense*; for vegetative characters which can be used to distinguish between them see under that species.

It was recognized as a distinct species as early as 1894 when, without description, Jeanneney used the name *Jasminum bouquetii*. In 1930, Guillaumin published his *J. magentae* with a short description in French, and two years later (in Bull. Mus. Hist. Nat. Paris II. 4: 697. 1932) he amplified the description and published it in Latin. Later (*ibid.* 6: 458. 1934), after having seen syntype material of Schlechter's species published in 1908, he placed it in synonymy under *J. noumeense*, where it undoubtedly belongs.

5. **Jasminum artense** Montrouzier, Mém. Acad. Lyon **10**: 231. 1860; Guillaumin, Ann. Mus. Col. Marseille II. **9**: 191. 1911, et Bull. Mus. Hist. Nat. Paris **18**: 468. 1912, et Not. Syst. Paris **3**: 61, 65. 1914; Guillaumin & Beauvisage, Ann. Soc. Bot. Lyon **38**: 102 ("Species Montrouzieranae," 28) 1914; Däniker, Viert. Naturf. Ges. Zürich **78**

(Beibl. 19): 365. 1933; Guillaumin, Fl. Nouv.-Caléd. 284. 1948, et Mém. Mus. Hist. Nat. Paris II(B). **8**: 161. 1959.

J. dzumacense Guillaumin, Not. Syst. Paris **3**: 63, 65. 1914; Däniker, Viert. Naturf. Ges. Zürich **78**(Beibl. 19): 366. 1933; Guillaumin, Fl. Nouv.-Caléd. 284. 1948, et Mém. Mus. Hist. Nat. Paris II(B). **4**: 47. 1953, *ibid.* **8**: 161. 1959.

J. velutinum Guillaumin, Mém. Mus. Hist. Nat. Paris II(B). **4**: 48. 1953, non Kobuski (1941); Virot, Vég. Canaque, 175. 1956.

Evergreen liane; stem glabrous or puberulent, rarely somewhat velutinous, especially when young. *Leaves* opposite, simple; petioles 3–20 mm. long, glabrous or puberulent, rarely velutinous, articulated ⅓–½ from the base, sometimes on larger leaves showing an additional articulation toward the top; lamina more or less coriaceous, glabrous or rarely puberulent, ovate to orbicular, rarely narrowly ovate, (1.2–)2–4.5(–5.5) cm. long by (1–)1.5–4(–5.2) cm. broad; margin entire, slightly thickened, usually recurved; apex rounded, obtuse or even retuse to acute, often with a small apiculus; base rounded or subcordate, rarely obtuse; venation with primary veins visible, sometimes obscure above, (2)3 or 4 per side, occasionally reticulate. *Inflorescences* axillary and terminal on side shoots, ternately paniculate, with 5–7(–15) flowers per panicle, glabrous or puberulent, rarely velutinous; bracts subulate, 1–1.5 (–3) mm. long; pedicels 5–20 mm. long. Flowers white, fragrant, heterostylous. *Calyx* glabrous or puberulent, rarely velutinous; tube 1.5–2.5 mm. long with 4 or 5 shallowly triangular teeth 0.1–0.7 mm. long (FIG. 1, C to D). *Corolla* hypocrateriform; tube 10–20 mm. long with 5–8 lanceolate or narrowly lanceolate, acute (to rounded) lobes 8–13 mm. long. *Stamens* 2; anthers 2.75–3.5 (–5) mm. long on filaments 0.5–1 mm. long. *Ovary* 1–1.25 mm. long; style about 7 mm. long in short-styled flowers or 9–17 mm. long in long-styled. *Fruit* (*Balansa 3629*) ovoid-ellipsoid, paired (or single by abortion) 10–11 mm. long by 7–8 mm. broad.

New Caledonia. Valleé du Diahot (Dothio), collines eruptive, Jan. 1872, *Balansa 3629* (syntype *J. dzumacense*, P; isosyntypes, BM, E, K); Mt. Dzumac, Jan. 1909, *Le Rat 165* (syntype, *J. dzumacense*, P); bords des creeks desechés, base des versants ouest du Mt. Kaala, ± 20 m. alt., maquis serpentineux, 10 Nov. 1943, *Virot 1302* (holotype *J. velutinum*, P); im Tale des vom Mt. Humboldt kommenden Zuflusses der Kalouéhola und an den Abhängen des Tontoutatales, im Serpentingebüsch, 18 Nov. 1924, *Däniker 483* (Z) and 10 Nov. 1924, *Däniker 588* (Z); am Mt. Bacon am äusseren Abhang des südlichen Serpentinmassivs gegen die Tontoutaebene, im Buschwalde, 15 Nov. 1924, *Däniker 700* (Z); Prony, 1890, *Bougier* (LY); Ile Art, in montanis et silvis, Sept. & March, *Montrouzier 143* (holotype, P); slope west of "Baie des Pirogues," on serpentine soil, 40 m. alt., 16 Dec. 1950. *Hürlimann 355* (A, Z), *ibid.*, meso-xerophilous shrubby forest on serpentine soil with rocks, 170 m. alt., 17 Dec. 1950, *Hürlimann 381* (A, Z); range of Mt. Podchoumié (Dumbéa), on rocky serpentine ridge, 180 m. alt., 23 July 1951, *Hürlmann 1625* (A, Z); Col de Plum (Mt. Dore), on serpentine soil, 200 m. alt., 22 Aug. 1950, *Baumann-Bodenheim 5577*, *5593A* (A, Z), *ibid.*, 8 Nov. 1950, *Guillaumin & Baumann-Bodenheim 7879*, *7933*

(A, Z); Col de Vulcain, serpentine bush, 900 m. alt., 11 Nov., 1950, *Baumann-Bodenheim 8178* (A, Z). ISLE OF PINES: south of Pic Nga, mesophilous forest on serpentine, 29 May 1951, *Baumann-Bodenheim 13699* (A, Z), and creek on the southwest slope of Pic Nga, mesophilous forest, 30 May 1951, *Baumann-Bodenheim 13786, 13789, 13816* (A, Z).

Jasminum artense is a distinct species which may perhaps be confused vegetatively with *J. noumeense*, but the leaves of the latter tend to be thinner in texture and the articulation of the petiole appears never to be more than 2 mm. from the base, even on the longer petioles. In *J. artense* the articulation is usually at least 2 mm. from the base, except in the case of very short petioles, where however, it is found at least between one-third and one-half of the way from the base of the petiole. When material bears an inflorescence there is no difficulty in distinguishing the two species, for the calyx lobes are quite distinct: in *J. artense* short and broadly triangular, in *J. noumeense* long and almost subfoliaceous.

Jasminum dzumacense was separated from *J. artense* on the relative lengths and positions of the style and stamens, but I cannot separate them as species in view of the frequency of heterostyly in the genus. In 1953, Guillaumin also distinguished and published the name of *J. velutinum*, but examination of the type (*Virot 1302*, not *1303* as cited in the protologue) shows that in everything but its velutinous indumentum the plant matches *J. artense*. Furthermore, *J. artense* has been found to be very variable in the amount of its pubescence, and *Virot 1302* is only the extreme expression of this character. Similar treatments of hairy variants as species have occurred in other species of *Jasminum*, e.g. *J. angulare*, *J. humile*, *J. subhumile*, and *J. floridum* (see Verdoorn, Bothalia **6**: 560. 1956, and Green, Notes Bot. Gard. Edinb. **23**: 355. 1961), and in each case an examination of more extensive collections than had been available earlier has shown that separation at specific rank cannot be justified.

In addition to the collections cited above, there is a specimen without sign of flowers or fruit (south slope of Ouen Toro, near Nouméa, on calcareous soil, 30 Oct. 1950, *Guillaumin 7414*, [A, Z]) which appears very similar to *Jasminum artense*. However it bears orbicular, retuse leaves which are especially small, varying from 0.8 cm. to 2 cm. in diameter, and was gathered from a plant growing on calcareous soil. All the specimens of *J. artense* of which there is mention of the soil type in their field notes are from serpentine soil and it would be interesting to see more material of this plant, especially flowering material.

6. **Jasminum linearifolium** Guillaumin, Mém. Mus. Hist. Nat. Paris II(B). **4**: 47. 1953; Virot, Vég. Canaque, 175. 1956.

Evergreen liane of variable length or diffuse shrub; stems glabrous, slender. *Leaves* opposite, simple; petioles (2–)3–5 mm. long, glabrous, passing imperceptibly into the lamina, articulated at approximately the middle; lamina linear or very narrowly lanceolate, (3–)3.5–5(–7) cm. long by (0.1–)0.2–0.4(–0.6) cm. broad; margin entire, slightly thickened;

apex acute; base narrowly attenuate into the petiole; venation obscure above and below with 3 or 4 primary veins per side. *Inflorescences* terminal on side shoots, ternately branched with about 5 flowers per inflorescence, glabrous; bracts subulate, 0.5–2 mm. long; pedicels 5–10 mm. long. Flowers white. *Calyx* glabrous; tube 1–1.25 mm. long with 4 or 5 shallowly triangular teeth, 0.1–0.2 mm. long (Fig. 1, C). *Corolla* hypocrateriform; tube 16 mm. long with 4 narrowly lanceolate, acute or obtuse lobes 10 mm. long. *Stamens* 2; anthers 3.75 mm. long on filaments 2.5 mm. long. *Ovary* globose (fide Guillaumin); style 5 mm. long (fide Guillaumin) in a short-styled flower. *Fruit* unknown.

New Caledonia. Sommet du Dôme de la Tiébaghi, ±600 m. alt., maquis serpentineux, 27 Oct. 1943, *Virot 1275* (holotype, P).

The specimen upon which this species is based is unique amongst all the material examined in this investigation. However, one gathering of *Jasminum leratii* (*Guillaumin & Baumann-Bodenheim 11663*) bears some shoots and leaves which approach (and in their extreme match) in slenderness and narrowness the stem and leaves of *J. linearifolium*. But a glance at the calyx shows that this species is not immediately related to *J. leratii*. Rather is the relationship with *J. artense* and, in fact, except for the leaves, the two species are identical, and further collections may perhaps produce intermediates. Yet the difference between linear leaves and ovate or orbicular ones is so great that, for the present at least, it is felt best to maintain this species, based though it is, upon a single few-flowered specimen with only one corolla.

7. **Jasminum elatum** Pancher ex Guillaumin, Not. Syst. Paris **3**: 63, 65. 1914, et Bull. Mus. Hist. Nat. Paris II. **1**: 217. 1929 et Candollea **5**: 151. 1932; Däniker, Viert. Naturf. Ges. Zürich **78**(Beibl. 19): 366. 1933; Guillaumin, Fl. Nouv.-Caléd. 284. 1948.

J. elatum var. *brevistylis* Guillaumin, Not. Syst. Paris **3**: 64, 1914, et in Sarasin & Roux, Nova Caledonia, Bot. **1**: 207. 1921, et Bull. Mus. Hist. Nat. Paris II. **15**: 453. 1943.

Evergreen climbing shrub; stems glabrous or puberulent, often minutely so and especially when young. *Leaves* opposite, simple; petioles 3–22 mm. long, glabrous or puberulent, articulated near the base; lamina more or less chartaceous, narrowly ovate to broadly ovate, or even very broadly so, (2.5–)4–8(–10) cm. long by (1.2–)2–7(–7.5) cm. broad, margin entire, not usually recurved or noticeably thickened; apex obtuse or acute, or more rarely slightly retuse, often with an apiculus; base truncate, rounded, obtuse or cuneate, often more or less attenuate into the petiole and rarely almost subcordate; venation usually with primary nerves only visible above and below, 4–7 per side. *Inflorescences* axillary or terminal on side shoots, dense, ternately subcorymbose, many flowered, glabrous to densely and minutely puberulent; bracts subulate, narrowly oblanceolate or elliptic, the lower ones subfoliaceous, 1–6 mm. long; pedicels short, 0–2 mm. long. Flowers white, fragrant, heterostylous. *Calyx* glabrous and ciliolate to densely and minutely puberulent; tube 1.5–2.5 mm. long with 4–6 stout, blunt, teeth 0.1–1 mm. long, which in the extreme are almost flattened laterally (FIG. 1, A & B, occasionally almost to C). *Corolla* hypocrateriform; tube 8–21 mm. long; lobes 4–6, broadly ovate or ovate, rounded or acute, 4–7.5 mm. long. *Stamens* 2; anthers (2.5–)3–4 mm. long on filaments 0.2–0.5 mm. long. *Ovary* 0.75–1.25 mm. long; style 3–6.5 mm. long in short-styled flowers or 12–22 mm. long in long-styled. *Fruit* (*Balansa 1298*) ovoid, paired (or single by abortion), 9–10 mm. long by 7–8 mm. broad.

New Caledonia. Environs de Nouméa, bosquets, Sept. 1868, *Balansa 578* (syntype, P; isosyntype, BM, NY); Port de France [=Nouméa], *Vieillard 907* (syntype var. *brevistylis*, P; isosyntypes, A, G); Kanala, *Vieillard 908* (syntype var. *brevistylis*, P); Mt. Canala, 650 m., Nov. 1911, *Sarasin 363* (Z); au Sûd de Canala, forêts, vers 1,000 m. alt., Nov. 1869, *Balansa 1702* (syntype var. *brevistylis*, P); près de Koe, bords de la Dumbéa, 14 Dec. 1869, *Balansa 1298* (syntype, P; isosyntype, K); bei La Foa an der Brücke über das Flüsschen La Foa, im Ufergebüsch, 27 Sept. 1924, *Däniker 131* (Z); Gatope, *Vieillard 2929* (BM, K); northwest slope of Mt. Mou, forest, 15 Oct. 1950, *Guillaumin & Baumann-Bodenheim 6958* (A, Z); Mé Amméri, on serpentine soil, 700 m. alt., 28 & 30 Nov. 1950, *Guillaumin & Baumann-Bodenheim 8770, 9066* (A, Z); above the "Ermitage" valley (Mt. Koghi), hygrophilous forest on serpentine, 400 m. alt., 4 July 1951, *Baumann-Bodenheim 14479* (A, Z); without locality, *Pancher 316* (=*Vieillard 2930*) (syntype var. *brevistylis*, P; isosyntype, BM), massifs sur les sols argilo-schisteux, March, *Pancher 313* (=*Vieillard 2941*) (lectotype, P).

Loyalty Islands. LIFOU: Képénéhé, im Buschwald in Küstennähe, 22 Oct. 1925, *Däniker 2270* (Z); Thosip, 10 Nov. 1925, *Däniker 2270a* (Z); without locality, *Deplanche 82* (syntype, P).

Jasminum elatum is distinguished amongst the simple-leaved New Caledonian species by its sessile or almost sessile flowers. The apparent "flatness" of the inflorescence branches and the size of the upper bracts are also distinctive. In length of calyx lobes it is similar to *J. artense*, but the lobes of the two species are nevertheless different: in *J. artense* they are flat, broadly triangular and acute, or at least with an angular apex, but in *J. elatum* they are blunt and thick, or even somewhat flattened laterally in those with the largest teeth. In addition, although the corolla tube in these two species is the same length, the lobes in *J. elatum* are shorter than those in *J. artense*. Large-leaved vegetative specimens of *J. elatum* may be confused with *J. neocaledonicum*, but in the former the petiolar articulation is usually found more or less towards the base and in the latter well up the petiole. Some purely vegetative specimens with large leaves can be difficult to identify and a good example is *Guillaumin & Baumann-Bodenheim 8732* (Mé Amméri, 700 m. alt., on serpentine soil, 28 Nov. 1950, Z) which is perhaps best left as "cf. *elato*."

With his original description Guillaumin cited five collections; it has been decided to select as lectotype the specimen of *Pancher 313* at Paris: it is the only Pancher specimen amongst the syntypes, and on the label with the Paris specimen he has written "Jasminum elatum — de la hauteur de la tige."

8. **Jasminum promunturianum** Däniker, Viert. Naturf. Ges. Zürich **78**(Beibl. 19): 367. 1933; Guillaumin, Bull. Mus. Hist. Nat. Paris II. **14**: 456. 1942, *ibid.* **15**: 454. 1943, *ibid.* **20**: 371. 1948, et Fl. Nouv.-Caléd. 284. 1948.

Evergreen shrub; stem puberulent. *Leaves* opposite, simple; petioles 1–2 mm. long, puberulent, articulated at the top; lamina thickish, oblanceolate or narrowly oblanceolate, (1–)1.5–2.5 cm. long by (0.2–)0.4–0.6(–0.7) cm. broad; margin entire, strongly recurved; apex retuse; base very narrowly cuneate, attenuate to the petiole articulation; venation more or less obscure, especially above, with 2 or 3 primary nerves per side. *Inflorescences* terminal on side shoots, single flowered; peduncle 1–1.5 mm. long, glabrous. Flowers white, ? heterostylous. *Calyx* glabrous; tube 2–3 mm. long with 5 or 6 stout, blunt, ciliolate teeth, 0.6–1.1 mm. long (Fig. 1, A). *Corolla* hypocrateriform; tube 20 mm. long; lobes 5, broadly lanceolate, acute, 7 mm. long. *Stamens* 2; anthers 4.25 mm. long on filaments 0.25 mm. long. *Ovary* 1 mm. long; style 7 mm. long in a short-styled flower. *Fruit* unknown.

New Caledonia. Insel Art der Belepgruppe, an den Küste, niedrigen Gebüschen, felsiger und exponierter Nordoststeilhang, 8 May 1925, *Däniker 1681* (holotype, z).

Vegetatively this species, with its small oblanceolate leaves, is very distinct. However, the calyx is extremely similar to that of *Jasminum elatum*, which itself is quite distinct from the other New Caledonian species in this respect. The field notes which accompany the one and only specimen state that it was collected on a rocky and exposed steep northeast slope on the coast, and it seems possible that *J. promunturianum* is really only a habitat form of *J. elatum*. Field observations and additional material may prove that the two ought to be united, but, since as yet I have seen no intermediate material, it seems best to maintain them for the present as separate species.

9. **Jasminum kriegeri** Guillaumin, Bull. Mus. Hist. Nat. Paris II. **15**: 453. 1943, et Fl. Nouv.-Caléd. 284. 1948.

Evergreen; stem glabrous. *Leaves* opposite, simple; petioles 6–12 mm. long, glabrous, articulated ⅓–½ from the base; lamina thickish, narrowly lanceolate, 3.5–5.5 cm. long by 0.6–1.2 cm. broad; margin entire, slightly thickened; apex obtuse or acute, subapiculate; base attenuate-obtuse, somewhat decurrent onto the petiole; venation clear and raised above and below, 2 (or 3) primary veins each side from near the base, the upper two prominent, running the length of the lamina and anastomosing, joined by 3 or 4 (5) slightly less prominent, short veins per side from the midrib, occasionally 1 or 2 of these being prominent. *Inflorescences* terminal on side shoots, ternately corymbose-paniculate, 5–12 flowers per inflorescence, glabrous; bracts subulate, 1–2 mm. long; pedicels 8–12 mm. long. *Calyx* glabrous, tube 4.5–5 mm. long (at least in dried material with about 20 longitudinal raised lines), with 5 acute or obtuse teeth, shallowly triangular, 0.2–0.5 mm. long (FIG. 1, E). *Corolla* hypocrateriform; tube (10–)20 mm. long with 5 or 6 lanceolate, acute, or obtuse lobes 11–13 mm. long. *Stamens 2*; anthers 4.5 mm. long, subsessile. *Ovary* 1.25 mm. long; style 18 mm. long in the long-styled flower examined. *Fruit* unknown.

New Caledonia. Gatope, leg. M. Krieger, *Vieillard 2937* (lectotype, P).

Jasminum kriegeri, although based on a scrappy specimen collected in 1867 by an infantry lieutenant named Krieger, was not described until 1943, and, despite the many collections that have been made in New Caledonia during the last forty years, the original, rather poor gathering is still the only example of this species in the herbaria I have examined.

When describing *Jasminum kriegeri*, Guillaumin cited two specimens, *Vieillard 2937* and *2938*, but all the material of the latter that I have seen, including one from Paris, is undoubtedly *J. leratii*. The specimen of the former number at Paris, with the name written in Guillaumin's hand and collected by Krieger, is the only one which the original description fits, and it is therefore selected as the lectotype.

The calyx is perhaps the most noticeably distinct feature of this species. In none of the other species is the calyx tube normally longer than 3 mm. at the most, although rarely in *Jasminum noumeense* it reaches 4 mm. but with large subfoliaceous lobes on top. Usually in the New Caledonian jasmines it is only 1.5–2.5 mm. long, whereas in *J. kriegeri* it is 4.5–5 mm. in length and contrasts with the very small comparatively obscure teeth. The calyces on the dried specimen which constitutes the type are furrowed throughout their length by shallow grooves which presumably correspond to the spaces between the veins. They are never so noticeable in the other species, and it is suspected that they appear only on drying.

The other part of this specimen which is noticeably distinct is the leaves. In shape they are very similar to a narrow-leaved expression of *Jasminum leratii*, but the venation is more or less unique amongst the New Caledonian species. In several species the main lateral and basal nerve runs the length of the lamina near the margin and joins up with the other lateral nerves given off by the midrib, but in this species two prominent nerves run the length of the lamina and the nerves joining them are fewer in number and more obscure. Nevertheless, this difference is only one of degree, and within the genus a whole range can be found from a regularly pinnately nerved leaf to the extreme as exhibited, for example, by *J. crassifolium* Blume where the only two prominent lateral nerves run the length of the leaf, one on each side of the midrib.

None of the intact flowers on the type specimen are quite mature, and it is feared that the measurements of the corolla given in the description above may be too short, for, judging from specimens of other species, it is believed that the corolla tube, for example, lengthens right up to the time of anthesis. (Observations on living plants would perhaps settle this point.)

INDEX TO EXSICCATAE

The list is arranged alphabetically by the last name of the collector. Numbers in parentheses refer to the corresponding species in the text.

Bailey *9623* (2)
Balansa *578*, *1298* (7); *1299* (3); *1702* (7); *2785*, *3189* (1); *3629* (5)
Baumann-Bodenheim *5032* (1); *5577*, *5593A* (5); *5874*, *5881* (3); *6057* (1); *8178* (5); *8285* (2); *13436*, *13454*, *13608* (1); *13642* (2); *13699*, *13786*, *13789*, *13816* (5); *14479* (7); *14529*, *14721* (2); *14770* (1)
Bougier *s.n.* (5)
Brousmiche *577* (1)
Compton, *455* (1)
Däniker *131* (7); *483*, *588*, *700* (5); *770*, *770a*, *1171*, *1333*, *1335* (2); *1436* (1); *1518*, *1599* (2); *1681* (8); *1717* (1); *1846* (4); *1886*, *1909*, *2269* (2); *2270*, *2270a* (7); *2388*, *2388a* (2); *2465*, *2465a* (1); *2626*, *3088*, *3089* (2)
Deplanche *82* (7)
Eastwood, *s.n.* (2)
Franc *845* (4); *1021* (2); *1377* (1); *1544*, *1544A* (2); *1906* (2); *1935* (3); *2232* (4); *2313* (1)
Germain *13* (2)
Guillaumin *7414* (under 5); *13395* (1)
Guillaumin & Baumann-Bodenheim *6842* (1); *6958* (7); *7879*, *7933* (5); *8732* (under 7); *8770* (7); *8883* (3); *9066* (7); *9514*, *9665* (2); *10301*, *10440* (3); *11106*, *11135*, *11161*, *11663*, *12403* (2); *13127* (1)
Heim *49* (2); *74* (1)
Hürlimann *355*, *381* (5); *769* (2); *1092*, *1166* (1); *1290* (2); *1307* (1); *1625* (5)
Le Rat *109* (1); *165* (5); *172* (2); *574*, *588* (4)
McKee *475*, *1973* (2); *2198* (3); *2251* (2); *2298* (4); *2342* (2); *2428* (1); *2728* (4); *6512* (1)
Montrouzier *143* (5)
Pancher *313* (7); *315* (4); *316* (7); *s.n.* (4)
Sarasin *185* (2); *363* (7); *424* (2); *525* (3); *730* (1); *885* (2); *890* (1)
Schlechter *15586* (3)
Vieillard *907*, *908* (7); *911* (2); *913* (1); *2929*, *2930* (7); *2935* (1); *2935* (2); *2936* (1); *2936* (4); *2937* (9); *2938* (2); *2941* (7)
Virot *442* (2); *842* (4); *846* (1); *865* (4); *876*, *881* (2); *882* (1); *922*, *927*, *929* (2); *1275* (6); *1302* (5)
Walter *65* (2)
Woodcock *630* (2)

A CYTOLOGICAL STUDY OF THE GENUS VIBURNUM[1]

DONALD R. EGOLF

THE GENUS VIBURNUM includes some 250 species from diverse habitats in Asia, Europe, North America, and South America. Though viburnums are varied in form, the ideal ornamental that combines fragrance, colored flowers, small stature, evergreen or brilliantly colored foliage, and luxuriant fruit does not exist. The present cytological study was initiated to establish a basis for genetical research that might yield interspecific hybrids combining in one plant the ornamental characteristics of several species. Such a study of chromosomes is obligatory for the plant breeder to initiate and pursue intelligently an interspecific hybridization program. Many *Viburnum* species and varieties involve complexes that have not been adequately covered by any comprehensive taxonomic treatment. The data obtained from such related disciplines as cytology and genetics when combined with taxonomy may help to resolve the species complexes and clarify the classification of the genus.

To the extent that this publication is a portion of more extensive cytogenetical and cytotaxonomical studies in progress, only that portion of the research concerned with cytology is reported. Although the literature has been frequently consulted to verify the identification and relationships of the taxa studied, this paper is not intended as a taxonomic study. The author has followed the taxonomic nomenclature of Rehder's *Manual of Cultivated Trees and Shrubs* (30) and *Bibliography of Cultivated Trees and Shrubs* (31).

REVIEW OF LITERATURE

All the chromosome counts reported by various authors are incorporated under the respective species in TABLE I. The earliest cytological study of *Viburnum* was that of Sax and Kribs (32), who reported that eleven species had a gametic chromosome number of nine ($n = 9$). The Asiatic

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[1] This study includes a portion of the research completed for the Ph.D. thesis in the Departments of Plant Breeding and Floriculture, Cornell University, Ithaca, N. Y., and later work in the United Kingdom and at the U. S. National Arboretum, Washington, D. C.

The author is indebted to all who have co-operated in supplying seeds, cuttings, or plants for this study. Appreciation is expressed to the Shell Oil Company for the Shell Fellowship in Plant Sciences, 1955–56, and to the U. S. Educational Commission for a Fulbright Scholarship in the United Kingdom, 1956–58. The many courtesies extended in the United Kingdom by the Royal Botanic Garden, Edinburgh; the British Museum (Natural History), London; the Royal Botanic Gardens, Kew; the Royal Horticultural Society's Gardens, Wisley; the John Innes Institute, Bayfordbury; and the University of London are gratefully acknowledged.

and American species studied included six of the nine taxonomic sections of Rehder (30). Sax and Kribs stated that the chromosomes are large, have an affinity for chromosomal stains, and consequently provide favorable material for study. A second basic chromosome number of eight ($n = 8$) was reported for *V. fragrans* by Simonet and Miedzyrzecki (35), who also published counts for seven additional species as $n = 9$. The gametic and somatic number of *V. tinus* was determined by Feng (15) to be $n = 18$ and $2n = 36$. Sugiura (38) reported $2n = 20$ for *V. awabuki* (syn. *V. odoratissimum*). In 1946, Poucques (27) listed the gametic chromosome counts for five species, four of which were previously unpublished; in a later publication (28) he listed two additional species.

Janaki Ammal determined the chromosome number $2n = 16$ for *Viburnum fragrans* and *V. grandiflorum*, and for *V. × bodnantense*, a hybrid produced from a cross between these species. The chromosomes of the two species paired normally in the hybrid, and the pollen fertility was as high as one hundred per cent (36). The extensive cytological study of Janaki Ammal (18) included thirty-seven determinations, of which twenty-one were reported for the first time. Her survey reported somatic chromosome numbers for species in cultivation at the Royal Horticultural Society's Garden, Wisley, England; the Royal Botanic Gardens, Kew, England; and the Jardin des Plantes, Paris, France. Seventeen of these counts are at variance with the somatic chromosome numbers of the present study; while three are at variance with previous reports. These differences are considered in the discussion. She has interpreted the $2n = 18$ of the hybrid *V. × juddii* (*V. carlesii*, $2n = 20$, × *V. bitchiuense*, $2n = 16$) as a synthesis of a plant with $n = 9$, and in addition, proposed that *V. carlesii* ($2n = 20$) arose as a backcross between a chance triploid ($2n = 24$) and the normal diploid ($2n = 16$) of *V. bitchiuense*. This was considered to be an example of the possible manner of evolution of *Viburnum* species in nature, which finally resulted in a large number of species with the basic number $n = 9$. A chromosome count of *V. lobophyllum*, $2n = 20$, determined by Enoch for a plant grown at Exbury, Southampton, England, was included in the publication of Janaki Ammal (18).

The cytological study by Thomas (40) included twenty-nine of the plants cultivated in the Arnold Arboretum. A few of these counts were obtained from root tips, but most were made from pollen mother cells; however, only partial designation is given as to which counts were gametic. Thomas concurs with the author that the origin of species with $n = 9$ as postulated by Janaki Ammal (18) is questionable. He states that it is more likely that species with basic chromosome numbers of eight and ten originated from species with a base number of nine by the loss or gain of a chromosome. His study indicates that translocations occur rather frequently, as evidenced by bridge formations observed in several of the species. He noted a relatively high percentage of aberrations in *Viburnum cassinoides*, *V. carlesii*, *V. dentatum*, *V. plicatum*, *V. × rhytidophylloides*, *V. sieboldii*, *V. trilobum* f. *compactum*, and *V. veitchii*.

MATERIALS AND METHODS

The seventy-seven species, sixty-one varieties and forms, thirteen hybrids, and two unidentified accessions of *Viburnum* investigated are presented with their sources, in TABLE I. Plant material was obtained as seed, cuttings, or plants from native habitats, botanic gardens, arboreta, and estate gardens throughout the world, exclusive of Central and South America. In all cases an effort was made to secure representatives of each taxon from three or more sources to provide a check on identification and chromosome counts of each taxon. Since commercial nurseries often propagate horticultural forms of *Viburnum* by grafting, all plant material for cytological study has been propagated from cuttings or from seed collected when possible in the native habitat of the species. Seed from native habitats have been used chiefly because seed from botanical collections may have been the result of cross pollinations with other species in the collection. The plants for cytological study were maintained during the summer months in frames or in a lath house. The remainder of the year the plants were grown under long-day conditions of twenty to twenty-two hours of light in a 70° F. greenhouse. Under these conditions it was possible to keep the plants actively vegetative and to avoid any dormant period.

In so far as feasible, plants propagated from seed and cuttings, and representatives of all sources, will be maintained at the Cornell Plantations and the U. S. National Arboretum for further study. Herbarium specimens, which are identified with the code accession numbers, were prepared for each collection that provided sufficient material. These are maintained as part of the permanent record and will be supplemented with flowering and fruiting material when the plants mature. Original descriptions and many of the type specimens have been studied to verify identifications. Photographs of type specimens and photostats of pertinent taxonomic literature were prepared to provide a basis for cytotaxonomic research. The identification of many of the plants previously studied (14) has been checked since they flowered and fruited. In those cases in which a positive determination was made, the alteration has been entered on TABLE I. However, the documentation numbers have not been altered and will be the same as in the previous list (14).

The root-tip smear technique was used exclusively in this study. Preliminary use of McClintock's permanent aceto-carmine (19) and La Cour's (20) acetic-orcein stain techniques revealed that the latter gave best results. In a portion of the early work the root tips were pretreated in aqueous paradichlorobenzene (22), fixed in Baldwin's modified Carnoy's (2), hydrolized in a solution of equal parts of 95% alcohol and concentrated hydrochloric acid, and smeared in acetic-orcein on the slide. After trial of numerous schedules and variations of these procedures a modification of La Cour's (20) technique was employed. Three- to five-millimeter-long root tips were pretreated in aqueous paradichlorobenzene for one to two hours. The root tips were placed in a watch glass containing one part 1.0 N. hydrochloric acid to nine parts 0.5% acetic-orcein stain. The watch glass with root tips was passed two or three times over the flame of an alcohol lamp to heat the mixture, but great care was taken to keep the solution under the boiling point. After the heated watch glass had cooled for several minutes, a root tip was placed in a drop of 0.5% acetic-orcein on a slide, smeared, and the cover slip applied.

The Feulgen technique (10) has been used in recent studies with excellent results. Root tips were collected and pretreated with 0.1% colchicine for two hours and fixed in La Cour's 2BD general fixative for twelve hours. The root tips were thoroughly washed with distilled water before immersion in a peroxide-oxalate bleach consisting of equal parts of ammonium oxalate in distilled water and hydrogen peroxide, and placed in direct sunlight or under a spot light for five minutes. After the root tips were washed again, they were hydrolized in 1.0 N. hydrochloric acid at 60° C. for twelve minutes, stained in leuco-basic fuchsin for 2 hours, and smeared. The edges of the cover slip were sealed with a mixture of gum mastic and paraffin in equal parts.

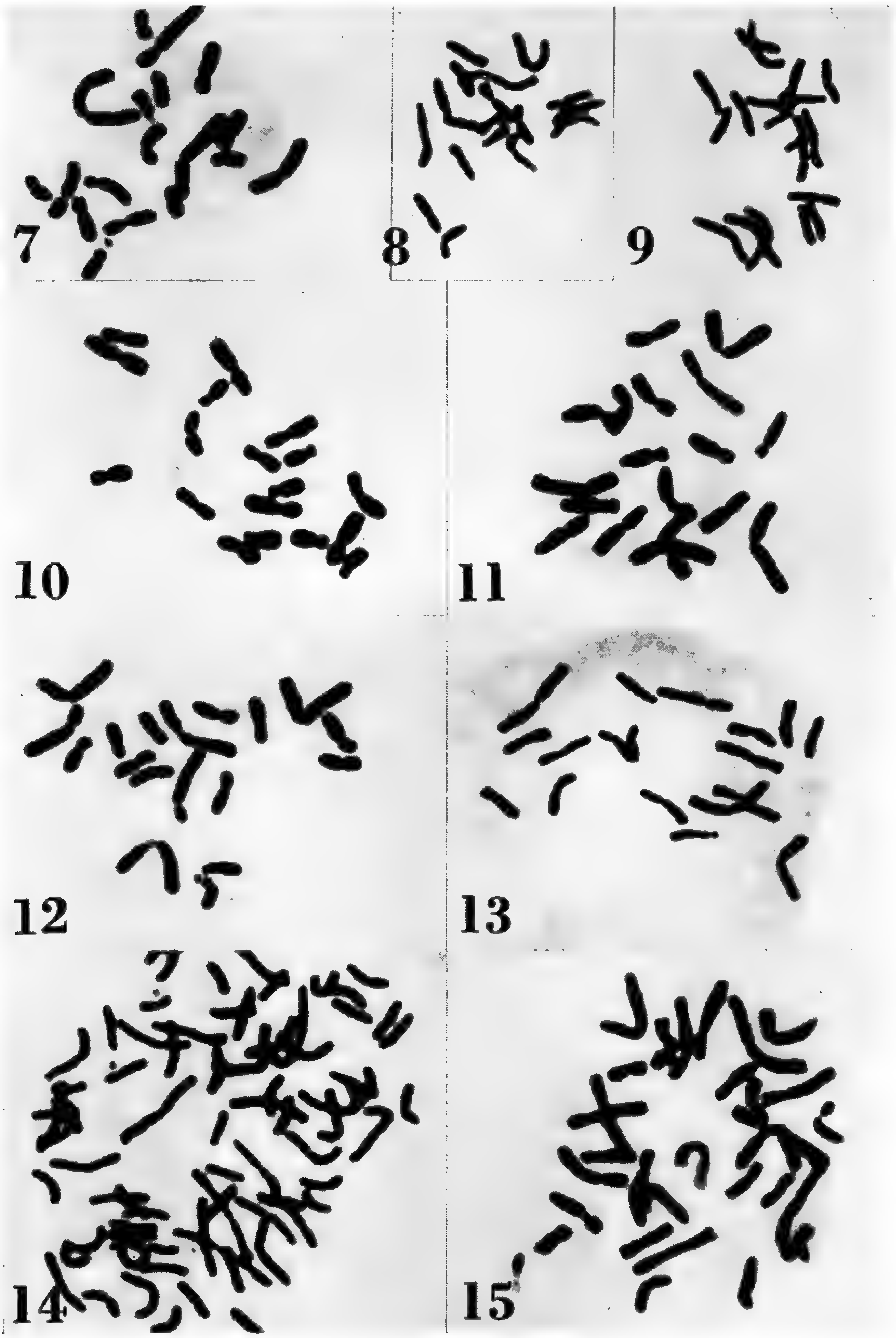
Slides were observed immediately or stored in a 40° F. refrigerator. After critical examination of the temporary smears was completed, camera lucida drawings made, and photomicrographs taken, selected slides were made permanent. The method of Conger and Fairchild (6) accomplishes the separation of the cover slip from the slide by freezing on dry ice. More recently, compressed carbon dioxide has been utilized for freezing slides to separate the cover slip from the slide. Immediately before thawing, the separated frozen slide and cover slip are placed in 95% alcohol which contains 5–10% acetic acid. After two or three minutes they are placed in absolute alcohol for another few minutes before mounting in diaphane. The permanent preparations made by this method are almost always equal in excellence and clarity to temporary slides and are superior for photomicrographs. Permanent slides of virtually all accessions here reported have been prepared.

Critical examination of the preparations was made with a binocular microscope equipped with 98 × fluorite objectives, N.A. 1.30, and 12.5 oculars. A minimum of ten countable cells was located before ascertaining the number of chromosomes in the somatic complement. Drawings were made with a camera lucida at table level, using 15 × oculars, giving the drawing a magnification of approximately 2400 ×. In addition to the drawings, photomicrographs were taken on 35 mm. microfilm at a magnification of approximately 1500 ×.

RESULTS

The somatic chromosome counts of the 153 taxa of *Viburnum* included in this investigation are presented in TABLE I. The species are arranged alphabetically within the taxonomic sections, as designated by Rehder (31). Under each taxon the chromosome counts published by other authors precede those from this study. The general geographic distribution and

FIGS. 1–6. Photomicrographs of chromosomes of *Viburnum* to show variations in chromosome complements, approximately × 1100. 1, *Viburnum erubescens*, $2n = 32$; 2, *V. lobophyllum*, $2n = 18$; 3, *V. sieboldii*, $2n = 32$; 4, *V. carlesii*, $2n = 18$; 5, *V. bracteatum*, $2n = 72$; 6, *V. scabrellum*, $2n = 72$.



Figs. 7–15. Photomicrographs of chromosomes of *Viburnum* to show variations in chromosome complements, approximately × 1100. 7, *V.* × *carlcephalum*, $2n = 18$; 8, *V. rigidum*, $2n = 18$; 9, *V.* × *rhytidocarpum*, $2n = 18$; 10, *V. cotinifolium*, $2n = 18$; 11, *V. schensianum*, $2n = 18$; 12, *V. macrocephalum* f. *sterile*, $2n = 18$; 13, *V. nudum*, $2n = 18$; 14, *V. dentatum* var. *pubescens*, $2n = 72$; 15, *V. odoratissimum*, $2n = 32$.

the source of material are given for each accession. A series of photomicrographs (FIGURES 1–15) illustrates variations in the chromosome complement.

In order to make the table more concise, the sources of material have been abbreviated as follows:

AA	Arnold Arboretum, Jamaica Plain 30, Mass.
AB	Arboretum des Barres, Loiret, France.
AN	Arturo Ansaloni, Bologna, Italy.
AR	Armstrong Nursery, Ontario, Calif.
B	Botanisches Museum, Berlin-Dahlem, Germany.
BB	Brooklyn Botanic Garden, Brooklyn 25, N. Y.
BC	Birr Castle, Birr, County Kings, Ireland.
BE	Collected near Bedford, Pa.
BG	Bodnant Garden, Tal-y-Cafn, Denbighshire, N. Wales.
BH	Borde Hill, Haywards Heath, Sussex, England.
BO	U. S. Botanic Garden, Washington, D. C.
BR	Collected near Brighton, Sussex, England.
BT	Boyce Thompson Arboretum, Yonkers, N. Y.
C	Botanic Garden of the University of Copenhagen, Copenhagen, Denmark.
CC	Caerhays Castle, St. Austell, Cornwall, England.
CG	Collected near Chattanooga, Tenn.
CH	R. Chenault, Orleans, France.
CL	W. B. Clarke & Co., San Jose 3, Calif.
CR	Crathes Castle, Crathes, Kincardshire, Scotland.
CU	Cornell Plantations, Ithaca, N. Y.
DA	Dominion Arboretum, Ottawa, Ontario, Canada.
DO	Collected near South Downs, England.
DS	J. T. Dawson, Nantucket, Mass.
DU	National Botanic Gardens, Glasnevin, Dublin, Ireland.
E	Royal Botanic Garden, Edinburgh, Scotland.
EN	Carl S. English, Seattle 7, Wash.
EX	Exbury, Southampton, England.
FN	Fruitland Nursery, Augusta, Ga.
G	Conservatoire et Jardin Botaniques, Geneva, Switzerland.
GA	Gardens of the Blue Ridge, Ashford, N. C.
GB	Göteborgs Botaniska Trädgård, Göteborg, Sweden.
GP	The Great Park, Windsor, Berkshire, England.
HA	N. G. Hadden, West Porlock, Somerset, England.
HB	Hattori Botanical Laboratory, Nichinan, Miyasaki, Japan.
HC	Headford Court, Kells, County Meath, Ireland.
HF	Henry Foundation for Botanical Research, Gladwyne, Pa.
HH	Hermann A. Hesse, Weener, Germany.
HI	Highdown, Worthing, Sussex, England.
HL	Hillier and Sons Nursery, Winchester, Hampshire, England
HM	Unknown Source, Hong Kong.
HN	Hong Kong Dept. of Agriculture, Hong Kong.
HP	Highland Park, Rochester, N. Y.
IC	Collingwood Ingram, Cranbrook, Kent, England.
JG	George Jackman & Son, Woking, Surrey, England.
JI	John Innes Institute, Bayfordbury, Hertfordshire, England.
JP	Jackson and Perkins Co., Newark, N. Y.
K	Royal Botanic Gardens, Kew, Richmond, Surrey, England.
KB	Botanic Gardens of Indonesia (Kebun Raya), Bogor, Indonesia.
KH	Henry Kohankie and Son, Painesville, Ohio.
KN	Kingsville Nurseries, Kingsville, Md.
KR	Kornik Gardens, Kornik, Poland.
LA	Collected east shore of Lake Cayuga, Ithaca, N. Y.
LE	V. Lemoine & Fils, Nancy, France.
LI	Linn County Nurseries, Center Point, Iowa.
LO	Los Angeles State & County Arboretum, Arcadia, Calif.
LS	Lu Shan Botanic Garden, Kiukiang, China.

MA	C. J. Marchant, Wimborne, Dorset, England.
MC	W. L. McAtee, Chapel Hill, N. C.
ML	McLean Bog, McLean, N. Y.
MR	Morris Arboretum, Philadelphia 18, Pa.
MT	Morton Arboretum, Lisle, Ill.
MY	Myddelton House, Enfield, Middlesex, England.
NB	Nanking Botanic Garden, Nanking, Kiangsu, China.
NN	R. C. Notcutt, Ltd., Woodbridge, Suffolk, England.
NS	Nymans Gardens, Haywards Heath, Sussex, England.
NY	New York Botanical Garden, New York 58, N. Y.
ON	Onarga Nursery Co., Onarga, Ill.
P	Muséum National d'Histoire Naturelle, Paris, France.
PE	Pennsylvania State University, University Park, Pa.
PI	U. S. Plant Introduction Garden, Glenn Dale, Md.
PN	Princeton Nurseries, Princeton, N. J.
PO	Unknown Source, Warsaw, Poland.
RE	Regel & Kesselring, Rome, Italy.
RF	Ringwood Forest, Ithaca, New York.
RH	Royal Horticultural Society's Garden, Wisley, Surrey, England.
RU	B. Ruys, Ltd., Dedemsvaart, Holland.
SN	Siebenthaler Co., Dayton 5, Ohio.
SO	Collected South Hill, Ithaca, N. Y.
SP	L. Späth, Berlin, Germany.
ST	Bergius Botanic Garden, Stockholm, Sweden.
SY	Swyncombe House, Oxford, England.
TA	Taiwan Forest Research Institute, Taipei, Taiwan, China.
TC	Taiwan Pineapple Corp., Taipei, Taiwan, China.
TG	Tokyo University Botanic Gardens, Tokyo, Japan.
UC	Univ. of California Botanical Garden, Berkeley, Calif.
UW	Univ. of Washington Arboretum, Seattle, Wash.
VN	Vaughan Nursery, Chicago 6, Illinois.
VO	Arnold Vogt, Erlenbach-Zurich, Switzerland.
WA	Wakehurst Place, Ardingly, Sussex, England.
WG	Wayside Gardens, Mentor, Ohio.
WL	Wildlife Research Laboratory, Delmar, N. Y.
WM	Isaac L. Williams, Exeter, N. H.
WW	Willowwood Farm, Gladstone, N. J.
WY	Wyman's Garden Centers, Inc., Framingham, Mass.
WZ	Wyoming Nurseries, Cincinnati 15, Ohio.

TABLE I. Chromosome Numbers of Viburnum

SPECIES	2n	AUTHORITY [a]	DOCUMENTATION [b]	SOURCE OF MATERIAL [c]	GENERAL DISTRIBUTION
Sect. I. **Thyrsosma** (Raf.) Rehd.					
V. × *bodnantense* Aberc. (*V. fragrans* × *grandiflorum*)	16	9	76E	CL	cult.
"	16	9	874E	UW539-50(HL) [d]	"
"	16	9	902E	RH	"
"	16	9	1007E	K660-48(BG)	"
"	16	9	1102E	HL	"
'Dawn'	16	6*	—	—	cult.
"	16	9*	1357E	BG	"
'Deben'	16	9*	1937E	NN	cult.
V. erubescens Wall.	48	6	—	—	Himal.
"	32	9	972E	AA7602-A	"
"	32	9	1149E	K	"
"	32	9*	1170E	EX	"
var. *gracilipes* Rehd.	32	9	100E	HP2158	Himal.
"	32	9	502E	RU	"
"	32	9	1092E	HL	"
"	32	9*	1594E	DU183P	"
V. foetens Decne.	16	6	—	—	Himal.
"	16	9	441E	RH	"
"	16	9	1061E	K	"
"	16	9	1091E	HL	"
"	16	9*	1571E	HA	"
V. fragrans Bge.	16	2	—	—	n. China
"	16	6*	—	HI	"
"	16	9	25E	CU	"
"	16	9	27E	PI-82380	"
"	16	9	174E	AA11588(K)	"
"	16	9	597E	MT1007-39	"
"	16	9	1074E	RH	"
"	16	9*	1154E	HA	"
var. *album* Krüss.	32	6	—	—	n. China
(as var. *candidissimum*)	16	8	AA55-50-B	AA55-50-B	n. China
"	16	9	250E	MT35-38	"
"	16	9	598E	MT235-38(VN)	"
"	16	9	896E	RH	"
"	16	9*	1419E	MY	"

[a] 1, Sax and Kribs (1930); 2, Simonet and Miedzyrzecki (1932); 3, Feng (1934); 4, Sugiura (1936); 5, Poucques (1946); 5*, *ibid.* (1949); 6, Janaki Ammal (1953); 6*, *ibid.* (1950); 7, Enoch (1953); 8, Thomas (1961); 9, Egolf (1956); 9*, *ibid.*, reported here for the first time.

[b] The numbers listed in this column are the accession numbers and voucher herbarium specimen numbers for the plants studied. Specimens of others are given as "AA" (Arnold Arboretum) and "K" (Kew).

[c] The number or designation after the code letters identifies specific plants. The abbreviation "sd." signifies that the accession was obtained as seed.

[d] Source of material reference in parentheses refers to the original source from which the seed or plants were procured.

TABLE I (*Continued*)

SPECIES	2*n*	AUTHOR-ITY	DOCUMEN-TATION	SOURCE OF MATERIAL	GENERAL DISTRIBU-TION
var. *nanum* Boom	16	9	431E	UW198–41	cult.
“	16	9	504E	RU	“
“	16	9	600E	MT685–50(CL)	“
‘Roseum’	16	9	438E	RH	cult.
“	16	9*	1422E	JG	“
V. grandiflorum Wall.	16	6*	—	—	Himal.
“	16	9	1022E	K	“
“	16	9	1082E	RH	“
“	16	9	1093E	HL	“
“	16	9*	1426E	GP	“
“	16	9*	1427E	BG	“
“	16	9*	1428E	E3025 (Cooper)	“
“	16	9*	1576E	NN	“
V. henryi Hemsl.	48	6	—	—	c. China
“	32	9	984E	C	“
“	32	9	1039E	K	“
“	32	9	1069E	DU	“
“	32	9	1097E	HL	“
“	32	9*	1168E	EX	“
“	32	9*	1175E	HI	“
“	32	9*	1435E	BH1398	“
“	32	9*	1441E	DU10–39 (Henry)	“
V. × *hillieri* Stern (*V. henryi* × *erubescens*) ‘Winton’	32	9*	1442E	HL	cult.
V. odoratissimum Ker-Gawl. (as *V. awabuki*)	40	4	—	—	Malaysia
“	40	6	—	—	“
“	32	9	68E	CU (Wash.)	“
“	32	9	119E	FN	“
“	40	9	293E	UW	“
“	32	9	371E	LO	“
“	40	9	392E	NY(BO)	“
“	32	9	427E	LO	“
“	32	9	919E	HL	“
“	32	9	983E	C	“
“	32	9	1011E	K	“
V. photinioides Fashiro	32	9	691E	KB	Malaysia
V. sieboldii Miq.	16	6	2454K	RH	Japan
“	32	8	AA616–6–B	AA616–6–B	“
“	32	9	62E	CU	“
“	32	9	105E	HP2161	“
“	16	9	270E	SN	“
“	32	9	656E	MT159–38(KH)	“
“	32	9	718E	MR2143	“
“	32	9	839E	AA616–6–B	“
“	32	9	903E	RH	“
“	32	9	1120E	P	“
f. *reticulatum* Rehd.	32	9	657E	MT281–51(AB)	Japan
“	32	9	878E	VO	“
“	32	9*	1056E	K986–36(LE)	“

TABLE I (*Continued*)

SPECIES	2*n*	AUTHOR-ITY	DOCUMEN-TATION	SOURCE OF MATERIAL	GENERAL DISTRIBU-TION
V. suspensum Lindl. (as *V. sandankwa*)	18	5	—	—	Malaysia
“	16	6	—	—	“
“	16	9	289E	UC	“
“	16	9	389E	NY	“
“	16	9	692	KB	“
	Sect. II. **Lantana** Spach.				
V. bitchiuense Makino	16	6	—	—	w. Japan
“	18	9	4E	PI–82381	“
“	18	9	70E	sd. PI–82381	“
“	18	9	307E	KR, sd.	“
“	18	9	522E	WZ, sd.	“
“	18	9	788E	AA (Wilson)	“
“	18	9	980E	MR3	“
“	18	9	998E	K	“
“	18	9	1078E	RH	“
“	18	9	1143E	CU	“
“	18	9*	1354E	K	“
“	18	9*	1355E	E430–29	“
V. buddleifolium Wright	18	2	—	—	c. China
“	20	6	—	—	“
“	18	9	7E	PI–111380	“
“	18	9	8E	CU	“
“	18	9	422E	BB	“
“	18	9	423E	KN	“
“	18	9	710E	MR	“
“	18	9	808E	AA7533 (Veitch)	“
“	18	9	1049E	K	“
“	18	9*	1328E	JI	“
“	18	9*	1360E	EX	“
V. burejaeticum Rgl. & Herd.	18	9	278E	GB, sd.	n. China
“	18	9	428E	LO	“
“	18	9	434E	UW160–46	“
“	18	9	585E	MT546–32 (AA, sd)	“
“	18	9	586E	MT475–40 (ST, sd.)	“
“	18	9	628E	MT1144–40	“
“	18	9	675E	KH	“
“	18	9	772E	AA4942 (RE)	“
V. × *burkwoodii* Burk. & Skip. (*V. carlesii* × *utile*)	18	8	AA815–41–B	AA815–41–B	cult.
“	18	9	11E	CU	“
“	18	9	518E	WZ, sd.	“
“	18	9	587E	MT295–36 (SN)	“
“	18	9	1006E	K1923HK	“
“	18	9*	1363E	SY	“
‘Park Farm Hybrid’	18	9	923E	HL	cult.
V. × *carlcephalum* Burk. ex. Pike (*V. carlesii* × *macrocephalum*)	18	8	AA618–53–A	AA–618–53–A	cult.

Table I (*Continued*)

Species	2*n*	Authority	Documentation	Source of Material	General Distribution
"	18	9	77E	CL	"
"	18	9	433E	UW	"
"	18	9	689E	WG	"
"	18	9	1023E	K	"
V. carlesii Hemsl.	18	2, 5*	—	—	Korea
"	20	6	—	—	"
"	18	8	AA17981–A	AA17981–A	"
"	18	9	112E	HP2193	"
"	18	9	421E	BB	"
"	18	9	521E	WZ, sd.	"
"	18	9	536E	JP, sd.	"
"	18	9	676E	KH	"
"	18	9	785E	AA17981(Gibbs)	"
"	18	9	1009E	K972–34(Trickett)	"
"	18	9	1144E	CU	"
"	20, 22	9	1145E	HN, sd.(Korea)	"
"	20, 22	9	1146E	TA, sd.	"
"	20, 22	9	1147E	HM, sd. (s. China)	"
"	18	9*	1369E	DU	"
"	18	9*	1596E	E529–38	"
V. × *carlotta* Hort. (*V.* × *burkwoodii* × *carlesii*)	18	9	78E	CL	cult.
V. × *chenaultii* Chenault	18	9	406E	RU	cult.
"	18	9	469E	MT741–50	"
"	18	9	519E	WZ, sd.	"
"	18	9	592E	MT218–51(SN)	"
"	18	9	1057E	K227–48(AB)	"
V. cotinifolium D. Don	18	5	—	—	Himal.
"	18	9	819E	AA1236–52(K)	"
"	18	9	871E	UW17493 L&S (Bhutan, sd.)	"
"	18	9	1037E	K56–81	Himal.
"	18	9	1040E	K1067–83	"
"	18	9	1067E	DU	"
"	18	9	1086E	HL	"
V. glomeratum Maxim.	18	9	817E	AA, W180–5(K, sd.)	China
"	18	9	992E	MT406–44	"
"	18	9	1052E	K	"
V. × *juddii* Rehd. (*V. carlesii* × *bitchiuense*)	18	6	—	—	cult.
"	18	9	81E	CL	"
"	18	9*	97E	MR	"
"	18	9	606E	MT451–48(AA)	"
"	18	9	756E	AA1107–27(Gibbs)	"
"	18	9*	823E	AA813–49	"
"	18	9*	824E	AA284–44	"
"	18	9	973E	HP	"
"	18	9*	1312E	RH	"
V. lantana L.	18	1	—	AA	Eur., w.As.

TABLE I (*Continued*)

SPECIES	*2n*	AUTHORITY	DOCUMENTATION	SOURCE OF MATERIAL	GENERAL DISTRIBUTION
“	18	5*, 6	—	—	“
“	18	9	31E	CU	“
“	18	9	239E	MT1010–39	“
“	18	9	301E	KR, sd.	“
“	18	9	385E	NY	“
“	18	9	607E	MT437–37 (PI–107644)	“
“	18	9	608E	MT640–34	“
“	18	9	722E	BT78–38	“
“	18	9	996E	K40–33	“
“	18	9	1041E	K	“
“	18	9	1142E	P	“
“	18	9*	1325E	DO	“
“	18	9*	1456E	BR	“
“	18	9*	1467E	E(B193–36)	“
‘Aurea Marginata’	18	9	609E	MT838–37(B)	cult.
‘Floribundum’	18	9	1138E	P	cult.
‘Lanceolatum’	18	9	612E	MT616–39	cult.
“	18	9	940E	P	“
‘Lees’	18	9	825E	AA(K)	cult.
‘Macrophyllum’	18	9	472E	MT	cult.
var. *rugosum* Lange	18	8	AA907–27–A	AA907–27–A	cult.
“	18	9	99E	HP2167	“
“	18	9	456E	MT352–46	“
“	18	9	615E	MT213–41(KH)	“
“	27	9	679E	KH	“
“	18	9*	775E	AA907–27(DA, sd.)	“
f. *variegatum* (West.) Rehd.	18	9	618E	MT1053–41	cult.
“	18	9*	1470E	E	“
V. macrocephalum Fort. f. *sterile* Dipp.	18	9	82E	CL	cult.
“	18	9	424E	KN	“
“	18	9	713E	MR47–121	“
“	18	9	975E	HP	“
“	18	9	1015E	K	“
“	18	9*	1597E	E	“
V. microphyllum (Oerst.) Hemsl.	18	9	624E	MT642–36	Mexico
V. mongolicum (Pall.) Rehd.	16	6	—	—	e. As.
“	18	9	277E	GB, sd.	“
“	18	9	673E	MT501–53	“
V. × *rhytidocarpum* Lemn. (*V. buddleifolium* × *rhytidophyllum*)	18	9	418E	RU	cult.
“	18	9	643E	MT503–53	“
“	18	9	806E	AA412–36(LE)	“
V. rhytidophylloides Suring. (*V. rhytidophyllum* × *lantana*)	18	8	AA711–36–A	AA711–36–A	cult.
“	18	9	102E	HP	“
“	18	9	426E	KN(WW)	“

TABLE I (*Continued*)

SPECIES	*2n*	AUTHOR-ITY	DOCUMEN-TATION	SOURCE OF MATERIAL	GENERAL DISTRIBU-TION
“	18	9	449E	NY	“
“	18	9	671E	MT265–37	“
“	18	9	754E	AA711–36(LE)	“
“	18	9	826E	AA1481–52(WW)	“
“	18	9	1038E	K387–29	“
V. rhytidophyllum Hemsl.	18	2	—	—	c. & w. China
“	18	6	2451K	RH	“
“	18	9	51E	CU	“
“	18	9	52E	PI–58813	“
“	18	9	91E	MR	“
“	18	9	304E	KR, sd.	“
“	18	9	1048E	K201–07(Veitch)	“
“	18	9*	1203E	E401–37	“
“	18	9*	1205E	E493–36	“
“	18	9*	1259E	RH	“
“	18	9*	1278E	HI(Wilson)	“
“	18	9*	1505E	E493–36(CR)	“
f. *roseum* (Gard. Chron.) Rehd.	18	9	295E	UW(CL)	cult.
“	18	9	800E	AA510–41(HL)	“
f. *aureovariegatum* Boom	18	9	822E	AA266–54	cult.
V. schensianum Maxim.	18	9	128E	AA15570	nw. China
“	18	9	397E	NY(HP)	“
“	18	9	465E	MT1051–401	“
“	18	9	652E	MT795–35(AA)	“
“	18	9	726E	NY	“
“	18	9	1014E	K(AA562–30)	“
“	18	9	1090E	HL	“
V. stellulatum Hemsl.	18	9	506E	DU	Himal.
“	18	9	1017E	K131–38(DU)	“
V. utile Hemsl.	18	6	—	—	c. China
“	18	9	214E	DA, sd.	“
“	18	9	425E	KN	“
“	18	9	507E	DU	“
“	18	9	694E	PI–111380	“
“	18	9	1008E	K	“
“	18	9*	1528E	BH	“
“	18	9*	1529E	WA	“
“	18	9*	1530E	E	“
V. veitchii Wright	18	8	AA7198	AA7198	c. China
“	18	9	113E	HP2177d	“
“	18	9	261E	MT1101–36	“
“	18	9	685E	KH	“
“	18	9	727E	NY67480	“
“	18	9	753E	AA7198(Veitch)	“
“	18	9	1005E	K101–13(Veitch)	“
“	18	9*	1560E	DU1288W	“

TABLE I (*Continued*)

SPECIES	2*n*	AUTHOR-ITY	DOCUMEN-TATION	SOURCE OF MATERIAL	GENERAL DISTRIBU-TION
Sect. III. **Pseudotinus** Clarke					
V. furcatum Bl. ex Maxim.	18	6	—	—	Japan
"	18	9	740E	AA17988(Wilson)	"
"	18	9	1099E	HL	"
V. lantanoides Michx. (as *V. alnifolium*)	18	1	—	AA	e. N. Am.
"	18	6	—	—	"
"	18	9	497E	RF	"
"	18	9*	1876E	GA	"
V. sympodiale Graebn.	18	9	451E	NY(LS)	China
V. urceolatum S. & Z.	18	8	AA876–51	AA876–51	Japan
"	18	9*	1645E	PI–227284	"
Sect. IV. **Pseudopulus** (Dipp.) Rehd.					
V. plicatum Thunb.	16	8	AA18016–1	AA18016–1	e. As.
"	18	9	92E	MR681	"
"	18	9	103E	HP2165	"
"	18	9	157E	AA18016–1	"
"	16	9	577E	PN	"
"	16	9	578E	PN	"
"	16	9	779E	AA933–4	"
"	16	9	1002E	K629(HH)	"
f. *glabrum* (Nakai) Rehd.	16	9	532E	TI, sd.(Ozegahara)	Japan
'Lanarth'	16	9	436E	RH	cult.
"	16	9	843E	AA134–53	"
f. *lanceolatum* Rehd.	16	8	AA6122–1	AA6122–1	cult.
"	16	9	658E	MT1204–41	"
"	16	9	763E	AA6122–1(Sargent)	"
f. *mariesii* (Veitch) Rehd. (as *V. tomentosum* var. *mariesii*)	18	6	2456K	RH	cult.
"	18	8	AA870–51–A	AA870–51–A	"
"	16	9	500E	RU	"
"	16	9	762E	AA19355(K)	"
"	16	9	1010E	K	"
"	16	9	1079E	RH	"
'Roseum'	16	9	580E	PN	cult.
f. *roseum* (Doney) Rehd.	16	8	AA856–34	AA856–34	cult.
"	16	9	737E	BB	"
"	16	9	742E	AA856–34(BB)	"
'Rowallane'	16	9	437E	RH	cult.
'St. Keverne'	16	9	505E	RU	cult.
f. *tomentosum* (Thunb.) Rehd. (as *V. tomentosum*)	18	1	—	AA	e. As.
"	18	6	2452K	RH	"
"	18	9	43E	CU	"
"	16	9	95E	MR1218	"
"	16	9	110E	HP2195	"

TABLE I (*Continued*)

SPECIES	2*n*	AUTHOR-ITY	DOCUMEN-TATION	SOURCE OF MATERIAL	GENERAL DISTRIBU-TION
"	18	9	484E	MT176–37, 1204–41	"
"	16	9	688E	KH	"
"	16	9	846E	CU	"
"	16	9	1001E	K257–33(NN)	"
"	18	9	1084E	RH	"
Sect. V. **Lentago** DC.					
V. cassinoides L.	18	8	AA17997	AA17997	e. N. Am.
"	18	9	12E	CU	"
"	18	9	106E	HP2790	"
"	18	9	575E	ML, sd.	"
"	18	9	590E	MT, 570–43	"
"	18	9	677E	KH	"
"	18	9	1000E	K	"
var. *nanum* Krüss.	18	9	1088E	HL	cult.
V. × *jackii* Rehd. (*V. lentago* × *prunifolium*)	18	9	257E	MT1037–40(AA)	cult.
"	18	9	965E	AA17992–1–B	"
V. lentago L.	18	1	—	AA	e. N. Am.
"	18	6	—	—	"
"	18	9	166E	AA18021–A	"
"	18	9	535E	CU	"
"	18	9	574E	SO	"
f. *sphaerocarpum* (Fern.) Rehd.	18	9	619E	MT892–35	e. N. Am.
"	18	9	968E	AA11316	"
V. nudum L.	18	6	—	—	e. N. Am.
"	18	9	570E	MC	"
"	18	9	681E	KH	"
"	18	9	988E	MT	"
"	18	9	1059E	K961–31(Gibbs)	"
"	18	9	1151E	CG	"
V. obovatum Walt.	18	9*	982E	C	se. U.S.
"	18	9*	1802E	HF(Fla.)	"
V. prunifolium L.	18	1	—	AA	e. N. Am.
"	18	6	—	—	"
"	18	9	46E	CU	"
"	18	9	47E	BE	"
"	18	9	156E	AA1805–2	"
"	18	9	223E	DA, sd.	"
"	18	9	960E	CU	"
"	18	9	1020E	K	"
V. rufidulum Raf.	18	9	517E	WZ	se. U.S.
"	18	9	569E	MC	"
"	18	9	645E	MT1012–39	"
"	18	9	1150E	PE	"

TABLE I (*Continued*)

SPECIES	2*n*	AUTHOR-ITY	DOCUMEN-TATION	SOURCE OF MATERIAL	GENERAL DISTRIBU-TION
Sect. VI. **Tinus** Maxim.					
V. atrocyaneum Clarke	18	9	918E	HL	Himal.
"	18	9	1043E	K566–48(HL)	"
"	18	9*	1173E	HI	"
"	18	9*	1267E	DU9198K.W.	"
V. calvum Rehd.	18	9	922E	HL	w. China
"	18	9	1054E	K(E23–48)	"
"	18	9*	1285E	E16–52(HL)	"
V. cinnamomifolium Rehd.	18	6	—	—	w. China
"	18	9	85E	CL	"
"	18	9	884E	UW163–41(AR)	"
"	18	9	895E	RH	"
"	18	9*	1270E	DU963W	"
"	18	9*	1276E	HC	"
"	18	9*	1372E	BH	"
"	18	9*	1374E	WA	"
V. davidii **Franch.**	18	6	—	—	w. China
"	18	9	86E	CL	"
"	18	9	181E	E2485, sd.	"
"	18	9	415E	RU	"
"	18	9	877E	VO	"
"	18	9	885E	UW	"
"	18	9	900E	RH	"
"	18	9	1029E	K	"
"	18	9*	1390E	E963W	"
"	18	9*	1391E	WA	"
'Femina'	18	9	503E	RU	cult.
"	18	9*	1315E	DU(MA)	"
V. harryanum Rehd.	18	5	—	—	w. China
"	18	9	917E	HL	"
"	18	9*	1165E	EX	"
"	18	9*	1194E	E56–42	"
"	18	9*	1275E	BC	"
"	18	9*	1314E	DU	"
V. propinquum Hemsl.	18	5	—	—	w. China
"	18	9	559E	K	"
"	18	9	875E	VO	"
"	18	9	886E	UW79–50	"
'Lanceolatum'	18	9	924E	HL	cult.
V. rigidum Vent.	18	9	556E	K	Canary Is.
"	18	9	858E	C	"
"	18	9*	1174E	HI	"
V. tinus L.	36	2, 3, 5, 6	—	—	Eur.
"	36	9	118E	FN	"
"	36	9	267E	AN, sd.	"
"	36	9	291E	UW	"
"	36	9	314E	C	"
"	36	9	1035E	K	"

TABLE I (*Continued*)

SPECIES	2*n*	AUTHOR-ITY	DOCUMEN-TATION	SOURCE OF MATERIAL	GENERAL DISTRIBU-TION
"	36	9	1064E	K	"
"	36	9*	1180E	E	"
"	36	9*	1260E	RH	"
'French White'	36	9	915E	HL	cult.
var. *hirtulum* Ait.	36	9	1028E	K22–11–47	Eur.
"	36	9	1100E	HL	"
var. *lucidum* Ait.	72	9	288E	UC	Eur.
"	72	9	292E	UW	"
"	72	9	343E	DU, sd.	"
"	72	9	997E	K	"
"	72	9*	1198E	E	"
'Variegatum'	72	9	999E	K	cult.
'Purpureum'	36	9	1046E	K1936	cult.
var. *variegatum*	36	9	1096E	HL	cult.
"	36	9	1181E	E	"
Sect. VII. **Megalotinus** Maxim.					
V. coriaceum Bl.	18	9	879E	VO	e. As.
"	18	9	1026E	K90–51(E)	"
"	18	9	1101E	HL	"
"	18	9*	1167E	EX	"
"	18	9*	1274E	BC	"
V. sempervirens Koch.	18	9	276E	HN, sd.	Malaysia
Sect. VIII. **Odontotinus** Rehd.					
V. *acerifolium* L.	18	1	—	AA	e. N. Am.
"	18	6	—	—	"
"	18	9	1E	CU	"
"	18	9	2E	SO	"
"	18	9	357E	DU	"
"	18	9	581E	MT202–38(WM)	"
"	18	9	799E	AA19181	"
"	18	9	1066E	K258–53(HP)	"
"	18	9	1144E	LA	"
V. betulifolium Batal.	18	6	—	—	c. & w. China
"	18	9	297E	UW(CL)	"
"	18	9	447E	NY	"
"	18	9	674E	KH	"
"	18	9	757E	AA550–26 (Rock 13476)	"
"	18	9	1003E	K61–08	"
"	18	9*	1187E	E346F	"
"	18	9*	1247E	RH	"
"	18	9*	1338E	NS	"
"	18	9*	1340E	WA	"
"	18	9*	1342E	HL	"
"	18	9*	1347E	DU238A–W	"
'Aurantiacum'	18	9*	283E	C	cult.

TABLE I (*Continued*)

SPECIES	2*n*	AUTHORITY	DOCUMENTATION	SOURCE OF MATERIAL	GENERAL DISTRIBUTION
V. bracteatum Rehd.	72	9	455E	MT960–37	se. U.S.
“	72	9	552E	K	“
V. dasyanthum Rehd.	18	9	294E	UW	c. China
“	18	9	736E	BB	“
“	18	9	1055E	K910–39(LE)	“
“	18	9	1386E	E910–39(LE)	“
V. dentatum L.	54	6	—	—	e. N. Am.
“	36	8	AA17985	AA17985	“
“	36	9	16E	CU	“
“	36	9	107E	HP2212	“
“	36	9	142E	AA17985–B	“
“	36	9	391E	NY(HP)	“
“	36	9	572E	SO	“
“	36	9	593E	MT639–34(ON)	“
“	36	9	890E	RH	“
“	36	9	1036E	K(JG)	“
“	36	9	1148E	BE	“
var. *deamii* (Rehd.) Fern.	72	9	144E	AA100–38–A	c. U.S.
“	72	9	636E	MT1006–39 (Deam)	“
var. *pubescens Ait.*	36	8	AA18008	AA18008	e. N. Am.
“	36	8	AA18009	AA18009	“
“	72	9	49E	CU	“
“	36	9	179E	AA18009	“
“	36	9	639E	MT355–46 (AA2106–4A)	“
“	36	9	743E	AA18008(DS)	“
“	72	9	777E	AA5070–1	“
“	72	9	974E	HP	“
“	72	9	1019E	K1938HK	“
V. dilatatum Thunb.	18	8	AA229–46–B	AA229–46–B	e. As.
“	18	9	19E	CU	“
“	18	9	23E	PI–76383	“
“	18	9	30	PI–C3R29	“
“	18	9	93E	MR4	“
“	18	9	525E	TG, sd. (Japan)	“
“	18	9	526E	TG, sd. (Japan)	“
“	18	9	564E	HB, sd. (Japan)	“
“	18	9	784E	AA7665–D(CH)	“
“	18	9	832E	AA137–52 (Japan, sd.)	“
“	18	9	835E	AA138–52	“
“	18	9	888E	UW248–49(E, sd.)	“
“	18	9	1021E	K	“
f. *hispidum* Nakai	18	8	AA17486–1–A	AA17486–1–A	e. Asia
“	18	9	146E	AA17986–1–A	“
“	18	9	386E	NY(TG)	“
“	18	9	731E	NY2311–36(TG, sd.)	“
“	18	9	818E	AA647–53 (Japan, sd.)	“

TABLE I (*Continued*)

SPECIES	2*n*	AUTHORITY	DOCUMENTATION	SOURCE OF MATERIAL	GENERAL DISTRIBUTION
“	18	9	828E	AA567–53 (Japan, sd.)	“
“	18	9	831E	AA569–53 (Japan, sd.)	“
“	18	9	833E	AA139–52 (Japan, sd.)	“
“	18	9	870E	UW91–46(NY, sd.)	“
f. *pilosum* (Thunb.) Nakai	18	9	446E	NY(TG)	e. As.
“	18	9*	534E	TG, sd.(Japan)	“
“	18	9*	562E	HB, sd.(Japan)	“
“	18	9	563E	“	“
f. *xanthocarpum* Rehd.	18	8	AA10140	AA10140	cult.
“	18	9	149E	AA10140	“
“	18	9	373E	NY	“
“	18	9	594E	MT457–45(KH)	“
“	18	9*	1397E	E(IC)	“
V. ellipticum Hook.	18	9	430E	LO	w. U.S.
“	18	9	1060E	K316–32(EN)	“
V. erosum Thunb.	18	9	24E	PI–4276P	e. As.
“	18	9	89E	MR2015	“
“	18	9	515E	HB, sd.(Japan)	“
“	18	9	595E	MT499–53(AA11596)	“
“	18	9	734E	NY179752	“
“	18	9	810E	AA11596 (Wilson)	“
“	18	9	881E	UW168–50(NY, sd.)	“
“	18	9	1081E	RH	“
“	18	9*	1398E	E15163 Yii	“
var. *punctatum* Franch.	18	9	511E	TC(Japan, sd.)	e. As.
“	18	9	512E	“	“
“	18	9	527E	TG, sd.(Mt. Tawa)	“
var. *taquetii* Rehd.	18	9*	1401E	E	Korea
V. flavescens W. W. Sm.	18	9*	202E	E2486, sd.	China
“	18	9*	882E	UW274–49(E, sd.)	“
“	18	9*	1407E	E	“
V. foetidum Wall.	16	6	—	—	Himal.
“	18	9	440E	RH	“
“	18	9	1087E	HL	“
var. *rectangulatum* (Graebn.) Rehd.	16	6	—	—	w. China
“	18	9*	1158E	HA	“
“	18	9*	1163E	EX	“
V. hanceanum Maxim.	72	9	477E	MT564–39	China
“	72	9	821E	AA1507–51(HL)	“
“	72	9	1033E	K124–26(AA)	“
“	72	9	1132E	P	“
V. hirtulum Rehd.	18	9	883E	UW264–49(LS, sd.)	China
“	18	9*	1784E	WY	“
V. hupehense Rehd.	18	1	—	AA	c. China
“	18	2	—	—	“
(as *V. hirtulum*)	18	8	AA708–37–B	AA708–37–B	“

TABLE I (*Continued*)

SPECIES	2*n*	AUTHOR-ITY	DOCUMEN-TATION	SOURCE OF MATERIAL	GENERAL DISTRIBU-TION
“	18	9	302E	KR, sd.	“
“	18	9	355E	DU, sd.	“
“	18	9	463E	MT, 390–39	“
“	18	9	678E	KH	“
“	18	9	711E	MR601A(Wilson)	“
“	18	9	738E	BB	“
“	18	9	765E	AA18020 (Wilson 601)	“
“	18	9	769E	AA708–37–B (LS, sd.)	“
“	18	9	978E	MR601A–5	“
“	18	9	995E	K650–10 (Wilson 601)	“
“	18	9	1080E	RH	“
V. ichangense (Hemsl.) Rehd.	18	9	80E	CL	c. & w. China
“	18	9	695E	PI–114819	“
“	18	9	838E	AA(KN)	“
“	18	9	1072E	RH	“
“	18	9	1085E	HL	“
“	18	9*	1162E	EX	“
“	18	9*	1319E	BC	“
V. japonicum (Thunb.) Spreng.	18	9	560E	K	Japan
“	18	9	566E	HB, sd. (Japan)	“
“	18	9	876E	VO	“
“	18	9	887E	UW631–50(HL)	“
“	18	9	1047E	K167–37(DA)	“
“	18	9*	1159E	CC	“
V. lobophyllum Graebn.	18	1	—	AA	c. & w. China
“	20	6	—	—	“
“	22	7	—	EX	“
“	18	9	108E	HP2152	“
“	18	9	131E	AA19494–C	“
“	18	9	351E	Du, sd.	“
“	27	9	620E	MT1303–35 (NB, sd.)	“
“	18	9	730E	NY67491(LS)	“
“	18	9	967E	AA19498–A	“
“	18	9*	1004E	K88–08(AA238w)	“
“	18	9	1128E	P	“
“	18	9*	1472E	HL	“
V. molle Michx.	36	9	391E	NY(HP)	c. U.S.
“	36	9	625E	MT1044–40	“
“	36	9	803E	AA18294–A (Palmer)	“
“	36	9	1016E	K104–35(DU)	“
f. *leiophyllum* Rehd.	18	8	AA4643–1–A	AA4643–1–A	c. U.S.
“	36	9	804E	AA4643(Bush)	“
“	36	9	985E	MT1097–36	“
V. ovatifolium Rehd.	18	1	—	AA	w. China
“	18	8	AA20078A	AA20078A	“

TABLE I (*Continued*)

SPECIES	2*n*	AUTHOR-ITY	DOCUMEN-TATION	SOURCE OF MATERIAL	GENERAL DISTRIBU-TION
“	18	9	290E	UW(MT, sd.)	“
“	18	9	764E	AA20078 (Wilson 590)	“
“	18	9	1025E	K1008–34(NN)	“
“	18	9	1076E	RH	“
V. parvifolium Hayata	18	9	889E	RH	Formosa
V. phlebotrichum S. & Z.	36	9	531E	TG, sd. (Japan)	Japan
“	36	9	723E	BT37–39	“
“	36	9	869E	UW38–49(HL)	“
“	36	9	1095E	HL	“
V. rafinesquianum Roem & Schult.	36	9	365E	K	e. N. Am.
“	36	9	573E	SO	“
“	36	9	576E	LA	“
var. *affine* (Schneid.) House	20	8	AA4622–2–B	AA4622–2–B	e. N. Am.
“	36	9	571E	MC	“
“	36	9	768E	AA17972(Bush)	“
“	36	9	1051E	K378–36	“
V. *recognitum* Fern.	36	9	707E	MR54–94	e. N. Am.
V. *scabrellum* Chapm.	72	9	96E	MR	se. U.S.
“	72	9	396E	NY(BT)	“
“	72	9	567E	MC	“
“	72	9	579E	PN(Va.)	“
“	72	9	714E	MR2200	“
“	72	9	745E	AA11549–B (Harbison)	“
V. setigerum Hance (as *V. theiferum* Rehd.)	18	2	—	—	c. & w. China
“	36	8	AA20189	AA20189	“
“	36	9	55E	CU	“
“	18, 36	9	57E	PI–104128	“
“	36	9	88E	MR11(Wilson)	“
“	36	9	654E	MT807–40(MR)	“
“	36	9	655E	MT522–50	“
“	36	9	709E	MR218A(Wilson)	“
“	36	9	744E	AA20189 (Wilson 236)	“
f. *aurantiacum* Rehd.	36	8	AA812–32	AA812–32	c. & w. China
“	36	9	59E	PI–023027	“
“	36	9	60E	PI–TN–R8	“
“	36	9	94E	MR12(Wilson 236)	“
“	36	9	815E	AA19085–2(Wilson 236)	“
V. wilsonii Rhed.	18	9	1053E	K262–23(HL)	w. China
“	18	9	1068E	DU	“
“	18	9*	1562E	E262–33(HL)	“
V. wrightii Miq.	16	6	2450K	RH	Japan
“	18	9	84E	CL	“
“	18	9	116E	HP2202	“
“	18	9	286E	C	“

TABLE I (*Continued*)

SPECIES	2*n*	AUTHORITY	DOCUMENTATION	SOURCE OF MATERIAL	GENERAL DISTRIBUTION
“	18	9	516E	HB, sd.(Japan)	“
“	18	9	667E	MT165–37	“
“	18	9	686E	KH	“
“	18	9	781E	AA18015(Sargent)	“
“	18	9	912E	RH	“
var. *eglandulosum* (Miq.) Nakai	18	9	565E	HB, sd.(Japan)	Japan
var. *hessei* (Koehne) Rehd.	18	9	402E	NY	Japan
“	18	9	1031E	K	“
Sect. IX. **Opulus** DC.					
V. edule (Michx.) Raf.	18	9	873E	UW1053–50 (White R.)	n. N. Am.
“	18	9*	1098E	HL	“
V. kansuensis Batal.	18	9	1083E	RH	w. China
“	18	9	1094E	HL	“
“	18	9*	1453E	GP13248 L&S	“
V. opulus L.	18	1	—	AA	Eur., n. Afr.
“	18	6	—	—	“
(as *V. sargentii*)	20	6	2459K	RH	“
“	18	9	39E	CU	“
“	18	9	191E	K2491, sd.	“
“	18	9	324E	PO	“
“	18	9	344E	DU	“
“	18	9	375E	NY	“
“	18	9	400E	NY(Austria)	“
“	18	9	459E	MT1189–35	“
“	18	9	545E	K	“
“	18	9	672E	MT49–52(AA)	“
“	18	9	687E	KH	“
“	18	9	741E	AA	“
“	18	9	786E	AA20736(E, sd.)	“
“	18	9	1013E	AA562–30	“
“	18	9	1030E	K53–46(RH)	“
“	18	9	1032E	K94–29(G)	“
“	18	9	1063E	K106–63	“
‘Aureum’	18	9	629E	MT1046–40(SP)	cult.
“	18	9	842E	AA997–52	“
“	18	9	892E	RH	“
“	18	9	1012E	K	“
‘Compactum’	18	9	417E	RU	cult.
“	18	9*	1485E	JG	“
var. *nanum* (David) Zabel.	18	9	524E	CU	cult.
“	18	9	630E	MT118–53(HL)	“
“	18	9	981E	C	“
‘Notcutt’	18	9	670E	MT211–51	cult.
“	18	9	747E	AA814–38(NX)	“

TABLE I (*Continued*)

SPECIES	2*n*	AUTHOR-ITY	DOCUMEN-TATION	SOURCE OF MATERIAL	GENERAL DISTRIBU-TION
f. *roseum* (L.) Heg. (as *V. tomentosum* var. *sterile*)	18	6	2463K	RH	cult.
"	18	9	41E	CU	"
"	18	9	246E	MT156–38	"
"	18	9	632E	MT1098–36(AA)	"
"	18	9	790E	AA26–47–A	"
"	18	9	1107E	P	"
"	18	9	1118E	P	"
f. *variegatum* (West) Zabel	18	9	316E	DA	cult.
"	18	9	633E	MT528–51(DA)	"
f. *xanthocarpum* (Endl.) Rehd.	18	8	AA1298–28–A	AA1298–28–A	cult.
"	18	9	104E	HP2157	"
"	18	9	403E	RU	"
"	18	9	634E	MT1099–36(HP)	"
"	18	9	791E	AA1298–28–A	"
V. orientale Pall.	18	9	175E	AA677–33	w. As.
"	18	9	296E	UW(MT, sd.)	"
"	18	9	837E	AA934–52	"
V. sargentii Koehne	18	1	—	AA	ne. As.
"	18	9	74E	PI–81798	"
"	18	9	300E	KR	"
"	18	9	337E	PO	"
"	18	9	404E	RU	"
"	18	9	794E	AA18012–B(Korea)	"
"	18	9	827E	AA571–53(Japan, sd.)	"
"	18	9	829E	AA572–53(Japan, sd.)	"
"	18	9	830E	AA570–53(Japan, sd.)	"
"	18	9	834E	AA646–53(Japan, sd.)	"
"	18	9	901E	RH	"
f. *calvescens* (Rehd.) Rehd.	18	8	AA467–26	AA467–26	ne. As.
"	18	9*	494E	AA467–26	"
"	18	9	797E	AA2144(Hers, sd.)	"
"	18	9	798E	AA467–26(Rock 13485)	"
"	18	9	1042E	K234–38 Marsh	"
f. *flavum* Rehd.	18	9	117E	HP2159	cult.
"	18	9*	130E	AA21419	"
"	18	9	647E	MT2195–22(HP)	"
"	18	9	795E	AA11037(HP)	"
'Puberulum'	18	9	649E	MT975–38(GB)	cult.
V. trilobum Marsh.	18	1	—	AA	n. N. Am.
"	18	6	—	—	"
"	18	9	327E	PO	"
"	18	9	659E	MT1228–38	"
"	18	9	816E	AA15673	"
"	18	9	1058E	K205–48(KR)	"

TABLE I (*Continued*)

SPECIES	2n	AUTHORITY	DOCUMENTATION	SOURCE OF MATERIAL	GENERAL DISTRIBUTION
'Andrews'	18	9	248E	MT1055–40	cult.
"	18	9	793E	AA292–42(LI)	"
"	18	9*	1663E	WLA66–104	"
'Compactum'	18	8	AA871–51	AA871–51	cult.
"	18	9	664E	MT216–53(KH)	"
"	18	9	684E	KH	"
'Hans'	18	9	661E	MT801–40	cult.
"	18	9	789E	AA293–42(LI)	"
'Wentworth'	18	9	663E	MT1057–40	cult.
"	18	9	783E	AA294–42(LI)	"
Unidentified species	18	9	693E	PI–22978	
"	18	9	700E	PI–111382	

CONTROVERSIAL CHROMOSOME COUNTS

Poucques (27, 28) reported $2n = 18$ in *Viburnum sandankwa,* a synonym of *V. suspensum,* while a somatic chromosome number of 16 is reported here. However, since several different evergreen forms have been referred to *V. sandankwa,* it is possible that Poucques' plant was not the same as *V. suspensum.* Simonet and Miedzyrzecki (35) reported a chromosome number $2n = 18$ for *V. setigerum* (*V. theiferum*). In the present study a single plant of this species was found with a chromosome number $2n = 18$; whereas other determinations, including that of Thomas (40), revealed a chromosome number of $2n = 36$.

The somatic chromosome counts reported in this study for thirteen species and four varieties differ from those reported by Janaki Ammal (18). In order to check Janaki Ammal's counts, and, if possible, to resolve the differences between our studies, an attempt was made to secure all the species grown at the Royal Horticultural Society's Garden, Wisley; at the Royal Botanic Gardens, Kew; and in the Jardin des Plantes, Paris. It is assumed that plants from these sources are similar to the material studied by her, but there is no assurance that the same plants were sampled. Since she published no record of the particular plants involved, it is uncertain whether she studied the same species in all three gardens or in only one. In any case, it seems logical to assume that some of the plants included in this study were the same as some of those she studied.

As with most cytological investigations, many of the studies must be made with cultivated plants that may be variants of the native species. The plant material used or the technique used could result in differences of chromosome counts. In a personal letter from Janaki Ammal it was stated that she had used the lacmoid leaf-bud technique (10), whereas in the present study root-tip smears were used. A critical comparison of her cytological study with the present one is impossible, for no slides, drawings, or photomicrographs and only a limited number of herbarium specimens were available. For clarity of discussion the differences between her and my counts are grouped into two classes: 1) species differing by a few chromosomes per complement and, 2) those differing in the number of sets of chromosomes in each complement.

In the first category, *Viburnum bitchiuense*, *V. foetidum* var. *foetidum*, *V. foetidum* var. *rectangulatum*, *V. mongolicum*, and *V. wrightii* were determined to have $2n = 18$ chromosomes, two more than reported by Janaki Ammal (18). Among the plants studied were *V. bitchiuense*, from Kew, and *V. bitchiuense*, *V. foetidum* vars. *foetidum* and *rectangulatum*, and *V. wrightii* from the R.H.S. Garden, Wisley. In the collection at Wisley is a plant identified as *V. foetidum* var. *rectangulatum* which is probably the plant studied by Janaki Ammal. Plant 1084E of this study, which was received from the R.H.S. Garden as *V. foetidum* var. *rectangulatum* and which has horizontally spreading branches, oblong-ovate leaves, and an inflorescence with fertile flowers surrounded by sterile marginal flowers, is correctly identified as *V. plicatum* f. *tomentosum*. Upon visiting the R.H.S. Garden the author further verified the identification of this individual plant.

The present study has revealed that *Viburnum carlesii* is composed of a complex $2n = 18$, 20, and 22 chromosome forms. All the plants studied that were obtained from cultivation, including a plant from Kew, had $2n = 18$ chromosomes, which agrees with the reports by Poucques (28) and by Simonet and Miedzyrzecki (35). Janaki Ammal (18) reported this species have $2n = 20$ chromosomes.

The present study agrees with the previously reported counts of $2n = 18$ in *Viburnum buddleifolium* (35) and in *V. lobophyllum* (32), but Janaki Ammal (18) reported $2n = 20$ and 22 (the count of Enoch) for *V. lobophyllum*. Included in my study was a plant of *V. lobophyllum* from Kew.

In this study both *Viburnum plicatum* f. *plicatum* and f. *tomentosum* were determined to have forms with $2n = 16$ and $2n = 18$. Janaki Ammal (18) reported both these and f. *mariesii* to have $2n = 18$. The plants of f. *mariesii* and f. *tomentosum* from Kew and of f. *mariesii* from the R.H.S. Garden used in this study have chromosome complements of $2n = 16$. The herbarium specimens deposited at Kew by Janaki Ammal clarify the discrepancies, and this documentation has been added to TABLE I. Specimen *2456K* of *V. plicatum* f. *mariesii* (*V. tomentosum mariesii*) has an annotation note "$2n = 16$?" which definitely indicates that her published count was questionable. The specimen of *V. plicatum* (*V. tomentosum sterile*), *2463K*, collected at the R.H.S. Garden, is identified by me as *V. opulus* f. *roseum*. Likewise, specimen *2459K* of *V. sargentii*, collected at the R.H.S. Garden, is *V. opulus*. The plants of *V. odoratissimum* from Kew were found to be of the $2n = 32$ variation. Janaki Ammal reports $2n = 40$ for this species. This last number, however, was found elsewhere in the *V. odoratissimum* complex in this study and has likewise been reported by Sugiura (38).

The number of genomes reported by Janaki Ammal (18) in the complements of four species and one variety differ from those found in this study. *Viburnum erubescens, V. henryi,* and *V. dentatum,* including in the present study specimens of all three from Kew and of *V. dentatum* from R.H.S., were found to be tetraploid, whereas Janaki Ammal reported them all to be hexaploid. Janaki Ammal's theory that the species evolved after spontaneous doubling of an unstable triploid obviously is not supported by this new evidence. *Viburnum sieboldii,* reported by Janaki Ammal (18) to be a diploid, was determined in this study to have both diploid and tetraploid forms, the tetraploid occurring much more frequently. The plant from the R.H.S. Garden studied was the tetraploid form. Janaki Ammal (18) reported *V. fragrans* 'Album' to be a tetraploid, but plants of this variety from R.H.S. Garden, and from other sources utilized in this study, were determined to be diploids. Thomas (40) also reports this variety to be diploid.

Among the 536 counts listed by the author (14) were a number of plants procured from the Arnold Arboretum. Thirteen of the plants studied by Thomas (40) are identical with those from which the author acquired material, while another six plants have the same Arnold Arboretum accession number but are not necessarily the same individual plant. The author lists the counts of an additional sixty-six plants from the Arnold Arboretum. Two of Thomas' counts, those for *Viburneum rafinesquianum* var. *affine* ($2n = 20$) and *V. molle* f. *leiophyllum* ($2n = 18$), differ significantly from the present work. *Viburnum rafinesquianum* var. *affine* was determined to be $2n = 36$ for all plants studied. A plant of *V. molle* f. *leiophyllum* bearing the Arnold Arboretum accession number 4643 was determined to be $2n = 36$, while Thomas reports $2n = 20$ for plant 4643–1–A, the latter having been propagated vegetatively from one of the original lot. Quite possibly, either a mixed lot or a mistake in labeling may be involved.

VARIATION IN CHROMOSOME NUMBERS WITHIN SPECIES AND VARIETIES

Differences in chromosome number were found within six species and five varieties. These differences can be placed in two classes for discussion: 1) those species that differ by a few chromosomes and, 2) those species that differ by a number of genomes.

The first category includes *Viburnum plicatum* and *V. carlesii.* Morphologically indistinguishable plants of *V. plicatum,* with $2n = 16$ and $2n = 18$, have been found. Comparison of the chromosome complements of these two forms reveals that the form with $2n = 18$ has an extra pair of metacentric chromosomes. This species will be discussed later in more detail. All plants of *V. carlesii* from cultivation have $2n$ chromosome complements of 18. However, among plants produced from seeds collected in Korea, the native habitat of the species, chromosome complements of $2n = 18$, 20, and 22 have been found.

Six species that differed in number of genomes were studied. One plant of *Viburnum lobophyllum* ($2n = 27$) was determined to be a triploid, with three cytologically identical genomes. All other specimens of this species studied were diploid, with $2n = 18$. Since the triploid plant appears identical with the diploid, it does not seem likely that this is a hybrid between the diploid *V. lobophyllum* and one of the tetraploid species. It is possible that this triploid could have resulted from the fertilization of an unreduced functional gamete by a normal gamete. Likewise, it could have originated as a cross between diploid and tetraploid plants of *V. lobophyllum*, although this does not seem probable since no tetraploid *V. lobophyllum* is known.

One species, *Viburnum odoratissimum*, is represented by tetraploid and pentaploid forms. These two forms, which have distinct vegetative differences, comprise a taxonomic complex that is given further consideration later. The pentaploid form, with $2n = 40$, has five similar genomes, each of which is morphologically identical with the genomes of the tetraploid. It is unknown whether the four pentaploids and seven tetraploids are representative of the variation that occurs in native populations.

Individual diploid plants of *Viburnum sieboldii* and *V. setigerum* were discovered in species that otherwise are tetraploid. The diploid plant of *V. setigerum* was isolated from a group of plants grown from seed obtained from the U. S. Plant Introduction Garden, Glenn Dale, Maryland. This plant probably resulted from parthenogenesis wherein an unreduced gamete developed without syngamy. The diploid plant of *V. sieboldii* was secured from a commercial nursery and it is not known whether the plant was propagated asexually or from seed. The diploid plants of these species are still immature, making it impossible to compare them critically with tetraploid plants. Although at this time they do not appear morphologically distinct from the tetraploid, they are obviously somewhat weaker, and growth has been slower. This may be partially or entirely due to environmental conditions, however.

Only six of the sixty-one varieties observed in this study had chromosome complements with numbers different from the species (i.e., the typical varieties). *Viburnum tinus* var. *lucidum*, *V. dentatum* var. *deamii*, and *V. dentatum* var. *pubescens*, all $2n = 72$, had double the number of genomes of the typical variety of the species. One of the five collections of *V. lantana* var. *rugosum* was found to be a triploid, $2n = 27$. Though there are three cytologically identical genomes in this particular plant, it does not appear to be morphologically distinct from the other collections. It is conceivable that this plant developed from a chance unreduced gamete that was fertilized by a normal gamete.

In *Viburnum plicatum* f. *tomentosum* and *V. plicatum* f. *mariesii*, as well as in *V. plicatum* f. *plicatum*, occur both $2n = 16$ and 18 chromosome forms which cannot be distinguished by vegetative characteristics. All other taxa of this species which have been examined (*V. plicatum* f.

glabrum, *V. plicatum* 'Lanarth,' *V. plicatum* f. *lanceolatum*, *V. plicatum* f. *mariesii*, *V. plicatum* 'Roseum,' *V. plicatum* 'Rowallane,' and *V. plicatum* 'St. Keverne') have chromosome complements of $2n = 16$. The forms with $2n = 18$ differ from those with $2n = 16$ by an additional pair of metacentric chromosomes. Since the $2n = 16$ plants produced the most abundant fruit, it is to be expected that these forms should have a higher rate of survival. The evidence indicates that most of the minor variations in *Viburnum* that have been given varietal rank are the result of genic or intrachromosomal changes, rather than the result of changes in chromosome numbers.

CYTOTAXONOMIC COMPLEXES

Differences in the chromosome numbers of different collections of *Viburnum odoratissimum*, *V. carlesii*, and *V. dentatum* suggest that each of these is a species complex.

VIBURNUM ODORATISSIMUM. Two distinct forms are evident in *V. odoratissimum*, the plants of which were secured from nine different sources. The one has smooth-barked branches; thin, coriaceous, elliptic-ovate leaves; and indistinct axillary buds. The other has stout, lenticular branches; thick, coriaceous, elliptic-obovate leaves; and prominent axillary buds. The illustrations of *V. odoratissimum* by Dippel (13) and of *V. awabuki* by Nakai (23) portray two types which are respectively similar to the two forms observed in the present study. Nakai (23) recognized *V. odoratissimum*, *V. liukiuense*, *V. awabuki*, and *V. awabuki* var. *serratum* in this complex, but other taxonomists generally have accepted only one species, *V. odoratissimum*. Because all the plants used in this study have not yet produced flowers, it is impossible to make a positive identification of these variants. Chromosome counts of $2n = 32$ (tetraploid) and $2n = 40$ (pentaploid) have been observed among both morphological forms of this species complex. Two of the three plants with $2n = 40$ are from the same original source and are of the variant with coriaceous leaves and stout, lenticular branches. Sugiura's (38) report of $2n = 40$ in *V. awabuki* also indicates that his *V. awabuki* may be different from *V. odoratissimum*. Do these represent species or are they variants of one species? Although the cultivated material studied probably does not differ from representatives of the native populations of this species complex, additional material from known populations and further study will be necessary to determine the relationships within the species.

VIBURNUM CARLESII. In this study all plants of *V. carlesii* received from cultivation have chromosome counts of $2n = 18$. However, seeds supposedly collected from native populations in China and Korea produced an array of plants with $2n = 18$, 20, or 22 chromosomes. It is difficult, if not impossible, to explain this variation if this is a true species. Of course, there is no assurance that this seed was from isolated plants and not from plants growing near other species with which there could be cross-pollination.

As previously noted, Janaki Ammal (18) proposed that *Viburnum carlesii* arose as a backcross between a chance triploid ($2n = 24$) and the normal diploid ($2n = 16$) of *V. bitchiuense.* In view of the present study, her explanation appears inadequate, for *V. bitchiuense* has $2n = 18$ chromosomes, rather than the 16 chromosomes required by her proposal. If triploid plants exist in nature, this variation in the chromosome complement of seedlings might be the result of self-pollination or cross-pollination between the triploid and diploid forms, which would produce progeny with additional chromosomes. It is doubtful, even if the triploid does exist, that fruit would normally result from self-pollination.

Most taxonomists consider *Viburnum bitchiuense* and *V. carlesii* to be closely related. However, few have gone to the extreme of Nakai (24), who not only reduced *V. bitchiuense* to a variety of *V. carlesii,* but also put both of these in a new genus *Solenolantana.* It is doubtful if this complex requires the latter action. Pollinations by the author of *V. bitchiuense* ($2n = 18$) × *V. carlesii* ($2n = 18$) produced no seed, while the reciprocal cross between these species produced, from ninety-nine flowers pollinated, forty-three seed which have yielded forty-one plants. A meiotic chromosome study of these plants should indicate more clearly the natural relationships of these species. Until a sporocyte study is made of authentic materials collected from native populations, this remains an unsolved cytotaxonomic complex.

VIBURNUM DENTATUM. *Viburnum dentatum* var. *dentatum* and *V. dentatum* var. *pubescens,* represented by $2n = 36$ and $2n = 72$, form the third cytotaxonomic complex. According to Rehder (31), *V. pubescens* is a synonym of *V. dentatum* var. *pubescens.* In the *V. dentatum–pubescens* complex specific delimitation has been based almost entirely on the presence and distribution of pubescence on petioles, leaf surfaces, and inflorescence branches or combinations of these. Blake (4), who examined Solander's manuscript of *Hortus Kewensis,* an early treatment of this complex, and who also studied native material, recognized *V. pubescens, V. pubescens* var. *canbyi,* and *V. pubescens* var. *longifolium.* Rehder (29) described two new varieties from Indiana, *V. pubescens* var. *deamii* and *V. pubescens* var. *indianense,* which have only minor differences from each other.

Svenson (39) commented on the variations of this group, which he separated on the basis of leaf shape and pubescence into *Viburnum dentatum, V. dentatum* var. *lucidum, V. dentatum* var. *pubescens* and *V. pubescens* var. *semitomentosum.* He also concluded that *V. pubescens* var. *deamii* probably is a separable variation.

Fernald (16) was in disagreement with Svenson's reduction of the glabrous-twigged form of *Viburnum dentatum* to varietal rank as *V. dentatum* var. *lucidum,* and elevated this glabrous variation to the rank of species with the specific name *V. recognitum. Viburnum recognitum* is distinguished from *V. dentatum* by its glabrous branchlets and cyme, glabrous or glabrate foliage, and flowers produced ten days to three weeks earlier. Fernald further stated that *V. dentatum* and its variations and *V. recognitum* "are both hopelessly variable in leaf outline and toothing of leaves, each of them with blades varying from lance-ovate to ovate-oblong to orbicular, with veins prominent beneath or obscure, with length from 2.5 to 10 cm. and breadth from 2 to 8 cm." *Viburnum recognitum*, *V. recognitum* var. *alabamense*, *V. crenatum*, *V. dentatum*, *V. carolinianum*, *V. carolinianum* var. *deamii*, and *V. pubescens* are entities recognized by McAtee (21) in this species complex.

The present study follows Rehder's treatment which reduces this complex to *Viburnum dentatum*, *V. dentatum* var. *pubescens*, and *V. dentatum* var. *deamii*. The material studied here was received under practically every one of the different names applied by past authors to these variations. Many of these collections were from cultivated plants, since materials from native populations were not available for all species or varieties. Therefore, it must be realized that the material studied is not necessarily an adequate sampling of variability of the native population, but it does give indications which may establish a basis for further research. The plants are being maintained for further study and identification.

Two chromosomal forms, $2n = 36$ and $2n = 72$, were located among plants of *Viburnum dentatum* var. *pubescens*. All plants of *V. dentatum* var. *deamii* had $2n = 72$. Are these plants of another variety or polyploid forms of the same species? Are these variations within a species the result of natural hybridization that has been followed by segregation and selection? The variations between *V. dentatum* var. *dentatum*, var. *pubescens*, and var. *deamii* have been described taxonomically but are only of minor magnitude. Likewise, *V. recognitum* is only slightly different from *V. dentatum*, though it has been elevated to specific rank. Are these cases in which speciation is resulting from natural hybridization but in which divergence of types is not yet great enough for complete delimitation? Is the glabrous-branched *V. recognitum* a plant of a segregating hybrid population or does it represent another species?

It has been suggested that *Viburnum dentatum* may have crossed with *V. rafinesquianum*, another related species, to produce by introgressive hybridization a different ecological population. Normally, however, these species are isolated by season of bloom, *V. dentatum* flowering approximately ten days later than *V. rafinesquianum*, and by habitat, *V. dentatum* being located on moist soil and *V. rafinesquianum* on dry upland. It is possible that a few late flowers of *V. rafinesquianum* may be shedding viable pollen when the first *V. dentatum* flowers open, and the distance between plants would not prevent cross-pollination. The offspring produced by such crosses could, over a period of time, produce a population of a type differing from the original species of the locale. In the particular area of South Hill, near Ithaca, N.Y., where plants were used for controlled pollinations in this study, there is no evidence of natural hybridization, but in similar situations elsewhere the densely pubescent *V. rafinesquianum* may have crossed with the nearly glabrous *V. dentatum* to produce a population with additional variations.

A further complication arises from the report by Janaki Ammal (18) that *Viburnum dentatum* has a chromosome number of $2n = 54$. In the present study, $2n = 36$ has been counted in all cases. It is logical to think that her plant was a hybrid, unless the count was incorrectly determined, since all of her work was done on cultivated plants growing in close proximity and hence subject to crossing. Since it is the custom of many botanic gardens to raise plants from seed, not realizing the seed may be from cross-pollination and not true for the species type, it is possible that the plants studied by her may have originated in this way.

One approach to the problem is experimental; that is, to reproduce a similar plant by controlled hybridization. All the possible pollination combinations between *Viburnum dentatum* var. *dentatum*, *V. dentatum* var. *pubescens*, and *V. rafinesquianum* were made in the present study. From 386 flowers of *V. dentatum* pollinated by *V. rafinesquianum* were produced 190 seeds from which 123 plants have been grown. From 130 flowers pollinated in the cross *V. dentatum* var. *dentatum* × var. *pubescens*, 49 seed and 15 plants were obtained. The only other combination to yield seed was *V. dentatum* var. *pubescens* × *V. rafinesquianum* which, from 329 pollinations, produced five seed that yielded two plants. The other combinations failed to produce seed, but this cannot be attributed necessarily to sterility or incompatibility, for climatic conditions and technique may have been variable factors. That seeds and plants were procured from crosses between these species and varieties indicates a relationship within the complex. As these plants attain flowering size, a study of the meiotic chromosome configurations of the sporocytes should reveal the interrelationships more definitely. It will be desirable to repeat those crosses that produced no seed and to attempt additional crosses with other related species from section ODONTOTINUS.

Because polyploids are found in this complex, a study of the native populations will be required to resolve the problem. Such experimental studies should not be concentrated within a few isolated populations but should cover the distribution range of this species complex so that differences and relationships between populations, as well as within populations, can be determined. With the union of the evidence from cytology, genetics, and taxonomy the intricate relationships of this complex should eventually be clarified further.

The section ODONTOTINUS of Rehder's classification includes other species that occur in the same geographical areas as members of the *Viburnum dentatum–pubescens* complex. Other taxa related to this complex and warranting study include *V. molle*, *V. scabrellum*, *V. bracteatum*, and *V. rafinesquianum*. The Chinese *V. hanceanum* appears to be allied closely to this complex. When the plants studied have produced fruit and the identification has been checked, a more valid interpretation of *V. hanceanum* may result.

This cytotaxonomic complex in eastern North America and the two complexes in Asia may be representative of those that exist in other species groups of this genus. The author is inclined to believe that a similar complex may exist with *V. cassinoides*, *V. nudum*, and *V. lentago* of eastern North America.

PHYLOGENETIC RELATIONSHIPS

The phylogenetic relationships within a genus can be accurately formulated only when the number, morphology, and behavior of chromosomes are correlated with anatomy, morphology, and taxonomy of the species. A tentative scheme for the species of *Viburnum* has been constructed utilizing all the available data (FIG. 16).

The genus *Viburnum* includes polyploid series with the basic numbers of eight and nine. Polyploidy can take place effectively only in one direction; the diploid must nearly always be the parent of the polyploid (11, 33). Stebbins (37) emphasizes the point that diploid members must be older than the polyploids, although they are not necessarily more primitive in the sense that they are less specialized in structure. Since higher polyploids (tetraploids, hexaploids, etc.) usually cannot revert to the diploid without abnormalities in the reproductive cycle, it is likely that one of the lower gametic numbers, i.e., 8 or 9, is primitive.

Wilkinson (44) presented additional evidence of the natural relationships of selected species in the genus. She reported on fourteen species, representing all but two of the sections of the genus, which were placed in five groups on the basis of their internal morphology and the vascular anatomy of their flowers. *Viburnum sieboldii* ($n = 8$) is the most primitive of those studied, with only two characteristics that might be considered advanced: reduction of peripheral bundles to five and the reduction of the sepal supply to a single unbranched trace. In no other species included in her study were so many primitive characteristics present. A group of relatively primitive species includes *V. carlesii*, *V. lantana*, and *V. dentatum*, all $n = 9$. Another group of less primitive species would include *V. lantanoides* ($n = 9$), *V. plicatum* f. *tomentosum* ($n = 9$), and *V. lentago* ($n = 9$). The group of more advanced nine-chromosome species includes *V. rhytidophyllum*, *V. nudum*, *V. cassinoides*, *V. dilatatum*, and *V. trilobum*. *Viburnum opulus* ($n = 9$) is considered the most advanced. Her work supports the theory that the species with the basic number of eight are primitive, while those with a basic number of nine are more advanced.

From a study of the stem anatomy, De Vos (12) concurred that *V. opulus*, *V. lentago*, and *V. cassinoides* are the most advanced and that *V. plicatum* f. *tomentosum*, *V. lantanoides*, and *V. sieboldii* are the most primitive.

To date, this is the extent of comparative morphological and anatomical studies of *Viburnum* species. *Viburnum sieboldii* ($n = 8$) is on these grounds considered to be the most primitive species of the genus. All other species with a basic number of eight have many characteristics in common with *V. sieboldii*, so that it can be assumed that this group is more primitive

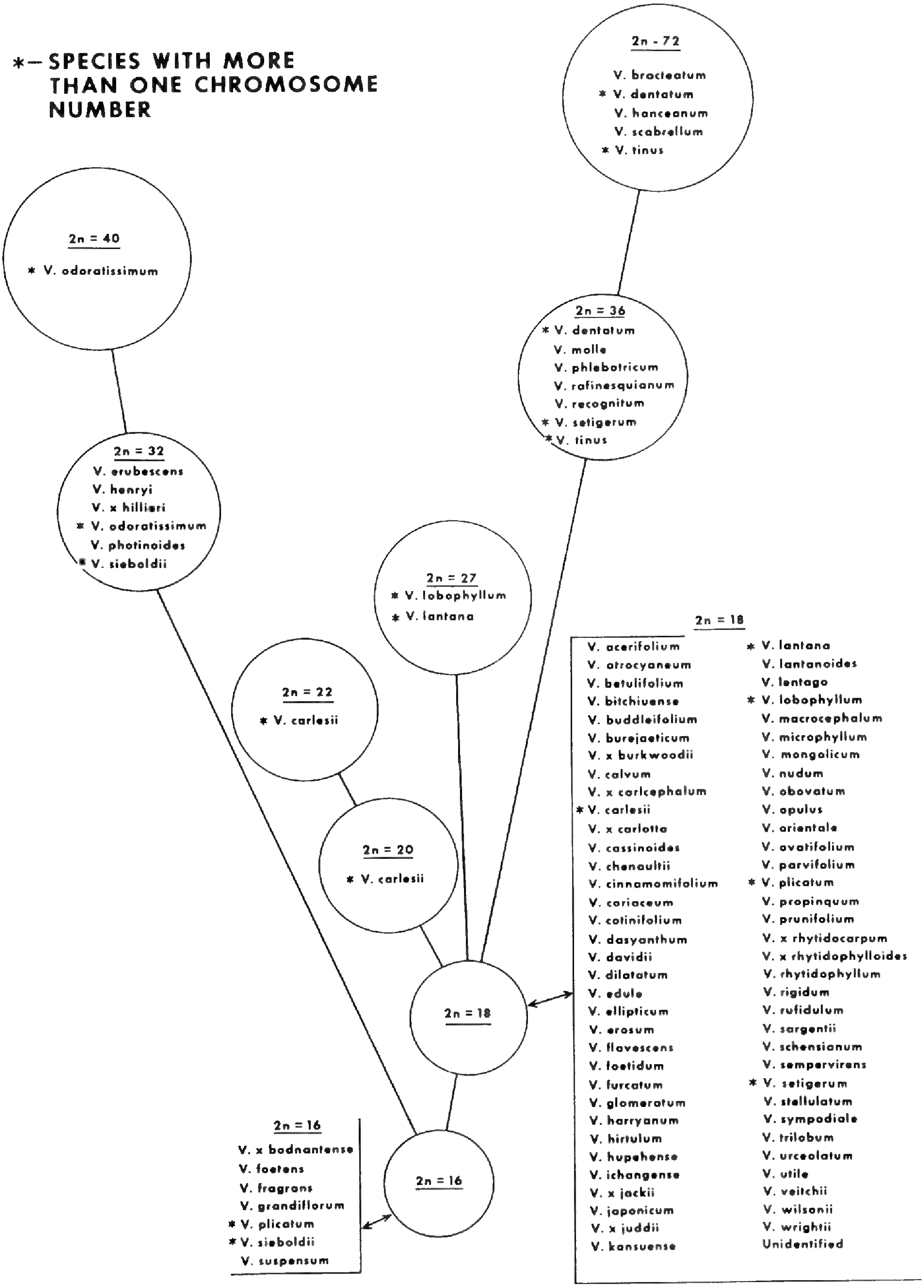


FIG. 16. Diagram based on chromosome complements to show interrelationships of species of *Viburnum*.

than those species with a basic number of nine. But the possibility remains that another species within the $n = 8$ group may be more primitive than *V. sieboldii*, and likewise that *V. opulus* need not necessarily be the most advanced species of the genus. Only a small sample of species and of the variation that exists in this widely distributed genus has been evaluated critically. Opinion concerning the relative position of species in regard to primitiveness may shift when additional evidence is available, but the basic cytological relationships of the various chromosome groups appear to be well established.

On the basis of floral anatomy Wilkinson (43, 45) postulates that there are in the Caprifoliaceae two lines of development. Through a form resembling the prototype postulated for *Viburnum* one line leads to *Viburnum* and *Sambucus*; the other stems through *Leycesteria* and branches separately to the Loniceraeae and Linnaeeae. The evidence at hand is inadequate to hazard an interpretation or conclusion as to what was the prototype for the family and from whence *Viburnum* arose, but the present evidence favors the $n = 8$ forms as the more primitive.

ALTERATION OF BASIC CHROMOSOME NUMBER

Evolutionary changes within a genus may be due to polyploidy, to the addition or subtraction of one or a few chromosomes of a complement, to gross structural rearrangements of the chromosomes, to submicroscopic changes, probably involving the chemistry of the chromosomal material, or to any combination of these. It can be assumed that all these changes have probably functioned in speciation in *Viburnum*. However, the genus has not been studied sufficiently to ascertain the evolutionary significance of each. For this reason, this discussion of phylogenetic relationships will be centered primarily around the evolutionary significance of the basic chromosome numbers of the genus.

Navashin (25) realized that changes in the basic number must involve loss or gain of the existing kinetochore, since kinetochores or kinetochore modifications cannot arise *de novo*. In this light, the increase or decrease in chromosome number attributed to "fragmentation" and "fusion" (7) could occur only when it involved a gain or loss of the kinetochore.

Darlington (8) presented a procedure favoring the loss or gain of a chromosome by means of an equal translocation between two different nonhomologous chromosomes with subterminal kinetochores. An interchange involving the long arm of one and the short arm of the other would produce one long metacentric chromosome and one very short chromosome or fragment. It has been pointed out that the consequences of unequal translocation depend on whether the regions about the kinetochore are genetically active or inert. An inert centric fragment may be eliminated, with a consequent reduction in chromosome number. If the fragment chromosome is genetically active it may persist as a univalent and be passed at meiotic metaphase to the same pole as the other interchange chromosome. This will yield, in addition to normal gametes, gametes with both or none of the interchange chromosomes. The union of gametes with additional chromosomes may yield trisomic or eventually tetrasomic plants which evolve into species with permanently increased basic numbers. Morphological differences may arise by virtue of either dosage effect or by divergent gene mutation in the duplicated chromosomes. Further cytological divergence may arise from reciprocal translocation between one of the new extra chromosomes and another chromosome of the complement (5, 37, 1).

Tobgy (41) confirmed Darlington's postulate with the demonstration that a reciprocal translocation between two chromosomes of *Crepis neglecta* ($n = 4$) gave rise to one chromosome of *Crepis fuliginosa*. Of the two chromosomes resulting from this translocation, the one with a genetically inactive region adjacent to the kinetochore was lost. Likewise, Sherman (34) obtained evidence that the origin of the *Crepis kotschyana* ($n = 4$) complement involved reciprocal translocation in the reduction from five to four pairs of chromosomes.

Chromosome number can also be increased or decreased by aberrations such as the translocations observed by Thomas (40) in the meiotic cycle. Asynapsis, desynapsis, nondisjunction, and chromosome lagging may be responsible for the production either of gametes with a single extra chromosome, several extra chromosomes, or with the entire unreduced complement, or of other gametes with chromosomal deficiencies. The union of such gametes may result in individuals deficient in or with additional chromosomes.

Chromosome numbers may be increased by supernumeraries or by misdivision of the kinetochore. White (42) considers the formation of supernumeraries, fragments produced by deletion or translocation, and fragmentation of the kinetochore to be probably the chief method whereby chromosome numbers have become increased in the course of evolution in animals. The fragment lacking the kinetochore region is lost in subsequent divisions unless it is translocated to another chromosome. Thus, fragmentation, in association with translocation, provides a mechanism for chromosome number increase. According to Darlington and Mather (11), misdivision of the kinetochore is the only single change that can affect both the number and structure of the chromosomes in a single stroke. The kinetochore, rather than dividing lengthwise, divides crosswise, resulting in two telocentric chromosomes which at a later division may produce two pairs of unlike isochromosomes (9). Races of *Campanula persicifolia* (11) have been found in which two telocentric chromosomes occur instead of a single chromosome and thus add an additional chromosome to the haploid number.

The backcrossing of a triploid, produced by a cross between a tetraploid and diploid plant, to a diploid has experimentally produced a great variety of segregant types, from among which have been recovered a small proportion of fertile types. Examples of such results have been reported in *Triticum* by O'Mara (26) and in *Gossypium* by Beasley and Brown (3) and have been summarized for *Nicotiana* by Goodspeed (17). This system of hybridization has artificially changed the basic chromosome number but has not been established as occurring in the natural evolution of species.

These examples individually, or in combination, illustrate numerous means whereby the basic chromosome number could increase or decrease as the taxonomic group evolved. Likewise, the progressive increase or decrease in basic number could be followed or accompanied by amphidiploidy to produce a complicated aneuploid series such as occurs in *Carex*, *Iris*, *Sedum*, *Viola*, and other genera. Stebbins' (37) summary of the types of aneuploid series in higher plants shows that the number of descending basic series is far greater than either the ascending basic or interchange amphidiploid series.

It is possible that in *Viburnum* the change in the basic chromosome number from eight to nine was adequate to keep the two types isolated and to allow each to evolve independently. As the types were exposed to new and changing environments the selection pressure further subdivided the major groups into minor groups with differential adaptability. It is conceivable that under certain circumstances the polyploid was favored over the diploid, or in others vice versa, thus increasing the variability. During this interval adaptive mutations could arise in certain subgroups. As the minor groups became further subdivided and isolated for survival in specific environmental niches, the variability within the genus expanded until today many *Viburnum* species have great morphological divergence. Although the phylogenetic relationships suggested by the chromosome numbers of *Viburnum* species provide a basic framework from which the specific differences evolved, the pathway remains obscure.

CHROMOSOMES AND THE TAXONOMIC SECTIONS

The nine taxonomic sections of the genus, based on morphological characters, as recognized by Rehder (30) may be correlated with the pattern of cytological relationships. Section THYRSOSMA, which includes *Viburnum sieboldii*, is composed entirely of species with a basic chromosome number of eight. This number occurs in only one other section, PSEUDOPULUS, in which, however, *V. plicatum* and *V. plicatum* f. *tomentosum* have forms with both $n = 8$ and $n = 9$. The question arises as to whether *V. plicatum* and *V. plicatum* f. *tomentosum*, both with cytological forms that are morphologically indistinguishable, represent the connecting link in the evolution of the genus between the basic numbers of eight and nine. Wilkinson (43) concluded from the study of floral anatomy and morphology that *V. plicatum* f. *tomentosum* was relatively primitive, but not as primitive as *V. carlesii*, $n = 9$, of sect. LANTANA, and *V. dentatum*, of sect. ODONTOTINUS. This does not support the proposition that *V. plicatum* forms an evolutionary bridge between the groups of species with $n = 8$ and $n = 9$. It is probable that $n = 9$ may have evolved more than once and in various places. However, with additional study this relationship may be clarified.

Only diploids are found in sects. PSEUDOPULUS, LENTAGO, MEGALOTINUS, OPULUS, and LANTANA, with the exception of *V. carlesii* ($2n = 18$, 20, 22) and *V. lantana* var. *rugosum* ($2n = 27$).

Tetraploids and higher polyploids are found in sects. THYRSOSMA, TINUS, and ODONTOTINUS. The scheme showing the relationship between chromosome complements is presented in FIG. 16, which shows the evolutionary trend to be from $2n = 16$ to $2n = 32$, and from 16 to 18 to 36 to 72. In the evolution of the genus the diploids probably have had the highest adaptive value and today are represented by the largest number of species. At the present time it appears impossible to separate the diploid species into taxonomic sections on the basis of chromosome morphology. The distinct gross morphological differences used by the taxonomist to divide the genus into sections appear to be the result of genic rather than structural chromosomal changes. When karyotype analysis has been completed for these species, differences of arm length, secondary constrictions, kinetochore position, satellites, and size of chromosomes may reveal natural relationships between species and sections.

A study of the chromosome complements of polyploid species reveals that the genome is duplicated. These species, preceded by an asterisk in FIG. 16, provide additional evolutionary information. For example, in sect. ODONTOTINUS the tetraploid *V. setigerum* has the same genomes duplicated that occur in the diploid. In the same section, *V. dentatum* var. *pubescens* and *V. dentatum* var. *deamii* are represented by octoploid forms with eight genomes duplicating the four genomes of the tetraploid. *Viburnum carlesii* (sect. LANTANA) and *V. plicatum, V. plicatum* f. *mariesii*, and *V. plicatum* f. *tomentosum* (sect. PSEUDOPULUS) are the only aneuploid species yet found in *Viburnum*. The forms with $2n = 20$ and $2n = 22$ can be considered to have developed from the $2n = 18$ form which is the most common. The plants with 20 and 22 chromosomes have, respectively, one and two pairs of chromosomes not found in the $2n = 18$ form, but at present the origin and relationship of these additional chromosomes to the usual 18 in *V. carlesii* is unknown.

The geographical distribution of polyploids is much more restricted than that of diploids. *Viburnum* species from all the major centers of distribution, except Central and South America, are well represented in this study. Since the origin of most of the varieties, whether natural or by man's selection, is uncertain, in many cases they cannot be assigned to a specific geographic area and are omitted in the following discussion. The greatest number of species studied is in the 18-chromosome group, and these are distributed over a wide geographic area. The diploid species include fifty from Asia, four from Europe, and twelve from North America, while the polyploids include eight species from Asia Minor, one from Europe, and six from North America.

From the foregoing it is obvious that the distribution of polyploids in *Viburnum* provides little evidence for one distinct center of origin of the genus. It is probable that polyploidy has evolved several to many times and in various places: eastern Asia, the Himalayan and Mediterranean regions and eastern North America. In eastern Asia occur all the species with the basic number of eight, along with a large number of diploids and a few polyploid forms with the basic number of nine. The Mediterranean species are few in number and belong to the group with a basic number of nine. The eastern North American species include the greatest number of octoploids, possibly indicating that this geographical niche has been more favorable for their evolution and establishment.

Only for certain sections does a relationship exist between the geographical distribution and the taxonomic sections of the genus. Sections THYRSOSMA and MEGALOTINUS are entirely of Asiatic distribution. *Viburnum plicatum* and its varieties, composing sect. PSEUDOPULUS, are native only to China and Japan. All species of sect. LENTAGO are limited to eastern North America. Representative species of sects. TINUS and LANTANA are distributed both in Asia and in Europe. Sections ODONTOTINUS and PSEUDOTINUS are represented both by North American and Asiatic species. The species of the sect. OPULUS occur both in Europe and in North America.

At present, the cytological evidence suggests that Rehder's sectional classification of *Viburnum* corresponds favorably with the natural relationships. It is hoped that as this study is continued and expanded a more accurate evaluation of the classification can be achieved.

PROPOSED RESEARCH

Portions of the preceding discussion are based principally on inference which indicates where the problems lie and suggests methods of approach. Definite conclusions cannot be drawn until much additional research is completed. Therefore, the present study is basic both for plant breeding and for cytological studies to be continued in the genus *Viburnum*.

To the present, it has been impossible to secure the species native to Mexico and Central and South America, but by expedition or otherwise, it is hoped that these may become available for future study. Within these areas are many species of diverse form which, when secured from higher elevations, should prove hardy and noteworthy ornamentals in this and other latitudes. These species not only may provide additional genetical variability for interspecific hybridization, but also are representatives of one of the centers of diversity in the evolution of the genus.

Cytological studies, in addition to providing a basis for plant breeding, have provided a useful tool for taxonomists in classifying certain plant groups, and there is every indication that such information can likewise be useful in studies of *Viburnum*. It is anticipated that a sporocyte study and karyotype analysis, associated with genetical and taxonomic studies, will aid materially in revealing natural relationships which can be utilized in the classification of the genus *Viburnum*.

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THE GENERA OF SIMAROUBACEAE AND BURSERACEAE IN THE SOUTHEASTERN UNITED STATES[1]

George K. Brizicky

SIMAROUBACEAE A. P. de Candolle,
Ann. Mus. Hist. Nat. Paris 17: 422. 1811, "Simarubeae."

(Quassia Family)

Trees and shrubs [rarely subshrubs], often with bitter bark. Leaves usually alternate, never glandular-punctate, pinnately compound or simple [rarely rudimentary], with predominantly entire margins, exstipulate [or stipulate]. Flowers usually small to minute, greenish or variously colored, hypogynous, regular, bisexual or unisexual by abortion, or both, with biseriate, [3]4–6[8]-, usually 5-merous perianth, in terminal and/or axillary many- or few-flowered cymose panicles or racemes, rarely solitary. Sepals distinct or united, imbricate or valvate. Petals distinct, imbricate or valvate, rarely wanting. Stamens distinct, as many or twice as many as the petals [rarely more numerous], usually inserted at base of an intrastaminal disc, rudimentary or wanting in ♀ flowers; filaments usually slender, sometimes appendaged at base on the ventral (adaxial) side; anthers usually versatile, 2- or rarely 4-locular at anthesis, introrse, longitudinally dehiscent. Intrastaminal nectariferous disc usually present, annular, cupular, cushion-like [to columnar], mostly lobed or crenate, rarely obscure or wanting. Gynoecium usually inserted on or encircled at base by the disc, sessile [or rarely raised on a gynophore], 2–6[8]-carpellate, apocarpous to syncarpous, rudimentary or wanting in ♂ flowers; stigmas distinct or united; styles basal, lateral or apical, distinct or partially to completely united; ovaries 1-carpellate and -locular (gynoecium apocarpous) or 2–3[4]-carpellate and -locular with axile placentae (gynoecium syncarpous); ovules anatropous or rarely orthotropous to campylotropous, usually epitropous, very rarely apotropous, 2- or rarely 1-integumented, with a thick nucellus, 1 or 2 (collateral or superposed) [very rarely more

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[1] Prepared for a generic flora of the southeastern United States, a joint project of the Arnold Arboretum and the Gray Herbarium of Harvard University which has been made possible through the support of George R. Cooley and the National Science Foundation. This treatment follows the pattern established in the first paper in the series (Jour. Arnold Arb. **39**: 296–346. 1958) and continued through the seventeen subsequent papers in volumes **40–43** (1959–1962). It should be repeated that the area covered by this work is bounded by and includes North Carolina, Tennessee, Arkansas, and Louisiana. The descriptions are based primarily on the plants of this area, with any supplementary material in brackets. References which the author has not seen are marked by an asterisk.

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numerous] in a locule, pendulous from the top or ascendant from the base of the latter. Fruit apocarpous, of 2–6[8] one-carpellate and -locular drupes, [berries] or samaras, or a syncarpous, 2–3[4]-carpellate and -locular (occasionally 1-locular by abortion) berry, samaroid capsule [drupe or schizocarp] with 1-seeded locules. Seeds with membranaceous or leathery testa; endosperm scanty or wanting; embryo rather large, straight or rarely curved, with narrow, mostly fleshy, plano-convex or flat cotyledons and usually a very short radicle. (Including Surianaceae.) Type genus: *Simarouba* Aublet.

A pantropical family of about 30 genera and 200 species, at least two species in temperate eastern Asia. Four of twelve genera indigenous to the New World occur in subtropical Florida. One species of *Ailanthus* is also naturalized in our area.

The rather heterogeneous family includes six sharply delimited subfamilies. Evidence from wood anatomy supports the segregation of at least some as distinct families, but, since data from gross morphology appear to be inconclusive and those from floral anatomy, embryology, and cytogenetics of the family are fragmentary, it seems preferable to retain the family in the larger sense.

Simaroubaceae are closely related to Rutaceae and Burseraceae, differing from the former mainly in the absence of multicellular glands (secretory cavities) with aromatic oils in leaves, axes, and floral parts, and from the latter in the absence of schizogenous resin ducts in the bark.

Wood and/or bark of some species (e.g., *Picrasma excelsa* (Sw.) Planch., "Jamaica Quassia"; *Quassia amara* L., "Surinam Quassia") yield a bitter principle employed as tonics and vermifuges, as an insecticide, and sometimes as a substitute for hops in brewing. Some genera produce timber of local importance; a few species are ornamentals.

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Key to the Genera of Simaroubaceae

General characters: *trees or shrubs with alternate, predominantly pinnate leaves; flowers small, uni- or bisexual, or both; perianth double, usually 5-merous; stamens 5 or 10, distinct; intrastaminal disc usually present; gynoecium apo- or syncarpous, 2–5-carpellate; ovules 1 or 2 in each locule.*

A. Leaves simple, small (not over 5 cm. long) and narrow; flowers bisexual, in short, terminal, few-flowered, corymb-like panicles, rarely solitary; stamens 10, the 5 antipetalous usually staminodial or rudimentary; intrastaminal disc wanting; carpels distinct; fruit of 5 or fewer achene-like drupelets; strand plant of subtropical Florida. . . . . 1. *Suriana*.

A. Leaves pinnately compound; flowers usually unisexual (occasionally also bisexual) in large, many-flowered, complex terminal panicles or racemes; intrastaminal disc distinct; carpels connate, sometimes only by the styles, rudimentary or wanting in ♂ flowers; fruits various, never achene-like drupelets.

  B. Stamens 10 in ♂ flowers, much reduced or wanting in ♀ flowers; carpels 4–6, usually 5; styles lateral, connate; ovaries distinct, connivent; fruits aggregate.

    C. Leaves usually even-pinnate, persistent; leaflets alternate, ± leathery, entire; staminal filaments appendaged at base; fruit of 5 or fewer olive-shaped drupes about 2 cm. long; hammocks of subtropical Florida. . . . . 2. *Simarouba*.

C. Leaves odd-pinnate, deciduous; leaflets usually opposite, thin, with a few glanduliferous teeth or lobules near the base; staminal filaments without appendages; fruit of 5 or fewer oblong samaras 3–5 cm. long, each with a flattened seed at the middle of the membranaceous wing; northern Florida and northward. .... 3. *Ailanthus.*

B. Stamens 5 and alternate with the sepals in ♂ flowers, reduced or wanting in ♀ flowers; carpels 2 or 3; styles terminal, connate or distinct; ovary compound; leaves odd-pinnate; hammocks of subtropical Florida.

D. Leaflets 5–9, 5–12 cm. long; ♂ and ♀ flowers with linear-lanceolate petals, in terminal panicles with slender racemose or spikelike branches; stigma 2-lobed; style one, very short and stout; fruit a 1- or 2-seeded berry. .... 4. *Picramnia.*

D. Leaflets 19–51, 1–3 cm. long; ♂ flowers with linear-filamentous petals, the ♀ flowers without petals, in terminal and axillary racemes; stigmas 3; styles 3, distinct, subulate, short; fruit a flat, papery, 1-seeded samaroid capsule. .... 5. *Alvaradoa.*

Subfam. SURIANOIDEAE Engler

1. **Suriana** Linnaeus, Sp. Pl. 1: 284. 1753; Gen. Pl. ed. 5. 137. 1754.

Shrubs or small trees 1–8 m. high with most parts more or less densely pubescent with simple and glandular hairs. Leaves sessile, simple, entire, narrow (seldom over 4 cm. long), thickish, with indistinct lateral veins and centric mesophyll. Flowers relatively small, bisexual, obdiplostemonous, with 2-bracteolate pedicels, in terminal, few-flowered, corymb-like cymose panicles (sometimes reduced to a solitary flower). Sepals 5, narrow (about 6–10 mm. long), connate at base, imbricate, persistent. Petals 5, yellow, broad, clawed, about as long as the sepals, imbricate. Stamens 10, distinct, the antipetalous usually antherless or rudimentary; filaments subulate, hairy below; anthers subcircular in outline, emarginate at both ends, introrse, 2-locular at anthesis; pollen grains medium sized, suboblate, 3-colpate, finely striate. Intrastaminal disc apparently wanting. Gynoecium apocarpous, 5-carpellate; stigmas distinct, capitellate; styles distinct, filiform, nearly basal; ovaries 1-locular, sessile; ovules 2 (collateral), ascending from the base of the ovary locule, 1-integumented, orthotropous, becoming campylotropous after fertilization. Fruits 1-seeded achene-like drupelets (not over 5 mm. long) with thin flesh and crustaceous endocarp (stone), obovoid-subspherical, pubescent. Seeds broadly obovoid, slightly flattened laterally, endospermless, with a thin membranaceous testa; embryo horseshoe shaped, with flat, oblong cotyledons and an elongate radicle descendent toward the micropyle which is side by side and in contact with the hilum. TYPE SPECIES: *S. maritima* L. (Named in honor of Joseph Donat Surian, a French physician and botanist, "Dioscorides Americanus futurus" [Plumier, Nov. Pl. Am. Gen. 37. 1703], companion and collaborator of Plumier.) — BAY CEDAR.

A monotypic genus represented by *Suriana maritima*, widely but sporadically distributed on the seashores of the New and Old World tropics, but apparently absent from the Pacific coasts of the Americas, the islands of the Central Pacific, and the Atlantic coast of Africa. It occurs in the coastal sand dunes and hammocks of the Florida Keys and of peninsular Florida northward to Brevard and Pinellas counties, and beyond our area in Bermuda, the West Indies, and from Yucatán south to Brazil. Millspaugh (Publ. Field Mus. Bot. **2**: 241. 1907) believed the fruits (stones) to be carried on the feet of sea birds, but according to Guppy they "could readily be carried in the crevices of floating logs, or in the cavities of floating pumice, such as is stranded on the beaches of tropical regions all over the world. But it is on their great floating powers, which fit them for dispersal by currents, that we must mainly rely." Buoyancy of the stones is produced by the unfilled space in the fruit locule (Guppy, Schimper).

Record & Hess (1943, p. 521), Small (Man. 761. 1933), Wilson (1911), and a few others thought the genus to represent a distinct, monotypic family Surianaceae; but, if a separate family is recognized, it should also include the closely related genera *Cadellia* F. Muell., *Guilfoylia* F. Muell., and perhaps also *Recchia* Sessé & Moc. ex DC. (*Rigiostachys* Planch.).

The branches exude some kind of "manna."

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Subfam. SIMAROUBOIDEAE

Tribe SIMAROUBEAE

2. **Simarouba** Aublet, Hist. Pl. Guiane Fr. 2: 859. 1775.[2]

Trees or large shrubs with bitter bark and wood. Leaves even-pinnate [or odd-pinnate], persistent; leaflets 3–21, mostly 8–16, alternate, rarely opposite, entire, ± coriaceous, shortly petiolulate. Plants polygamo-dioecious or dioecious. Flowers small, unisexual or uni- and bisexual, obdiplo-

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[2] Aublet's generic name should be conserved against its earlier homonym, *Simaruba* Boehmer, 1760 [nom. rejic. vs. *Bursera* Jacquin ex Linnaeus, 1762, nom. cons.]. See A. A. Bullock, Taxon **8**: 199. 1959.

stemonous, in large terminal and axillary complex panicles. Sepals 4–6, usually 5, rather small, connate at least at base, imbricate. Petals 4–6, usually 5, yellowish to yellow [or whitish], much longer than the sepals, imbricate. Stamens 8–12, usually 10, as long as the petals, reduced, rudimentary or absent in ♀ flowers; filaments subulate, broadened toward base, with an adaxial, liguliform, pubescent appendage at base; anthers oblong in outline, slightly emarginate, versatile, 2-locular at anthesis; pollen grains small, subprolate, 3-colpate. Intrastaminal disc ± cushion-like, depressed in ♂ flowers. Gynoecium (4)5(6)-carpellate, sessile on the disc, partially syncarpous, rudimentary or wanting in ♂ flowers; stigmas 4–6, usually 5, long, slender, and divergent in ♀ flowers, short, lobe-like in bisexual flowers; styles connate into a short column; ovaries distinct, 1-locular, cohering [or perhaps sometimes weakly connate] by their ventral sutures and thus resembling a compound deeply lobed ovary; ovules solitary in each carpel, pendulous from near the top of the inner angle of the locule, anatropous and epitropous, 2-integumented. Drupes 5 or fewer from each flower, ellipsoid to obovoid, slightly laterally compressed, usually 2-ridged, with thin flesh and a crustaceous stone. Seeds endospermless; testa thin, membranaceous; embryo straight, with fleshy, plano-convex cotyledons and a very short, superior radicle partly included between the cotyledons (retracted). TYPE SPECIES: *S. amara* Aublet. (Name derived from the Carib Indian name of the type species in French Guiana.)

A tropical American genus of about six species. *Simarouba glauca* DC., paradise tree, occurs in coastal hammocks on the Florida Keys and in southern peninsular Florida (Dade, Broward, and Palm Beach counties). It is widely distributed in the West Indies and in Central America from Costa Rica to southern Mexico. The ellipsoidal fruits, about 2 cm. long, are scarlet, changing to dark purple or black when ripe. A white-fruited form has been reported from El Salvador.

The timber of some species, especially the South American *Simarouba amara*, is of commercial importance. The bitter bark of roots of *S. amara* and *S. glauca* is said to be efficient against diarrhea and post-dysenteric disorders. Seeds of *S. glauca* yield about 60 per cent of edible oil and a crystalline glycoside, glaucorubin, which reportedly has amoebicidal properties and is now being introduced in most of the major tropical areas under the trade name of "Glaumeba."

The genus is a representative of a very natural group, Simarouboideae–Simaroubeae, and is closely related to the tropical South American *Simaba* Aubl. and *Quassia* L. (monotypic, according to Cronquist), as well as to the tropical African *Odyendea* (Pierre) Engl.

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Tribe PICRASMEAE Engler

3. **Ailanthus** Desfontaines, Mém. Acad. Sci. Paris **1786**: 265. 1788, nom. cons.

Trees, sometimes strong smelling. Leaves odd-pinnate, large, deciduous; leaflets opposite or alternate, thin, with a few glanduliferous, blunt teeth or lobules near base [or entire or rarely coarsely toothed to lobed throughout], petiolulate. Plants polygamo-dioecious. Flowers small, uni- and bisexual, obdiplostemonous, of unpleasant odor, pediceled, in large, terminal panicles. Sepals 5 (6), connate in the lower third or higher, imbricate. Petals 5 (6), longer than the sepals, greenish or yellowish, induplicate-valvate in aestivation. Stamens inserted at base of an intrastaminal disc, 10 (12) in ♂ flowers, sometimes fewer in bisexual, much reduced and sterile or absent in ♀ flowers; filaments subulate, without appendages; anthers oblong or oblong-ovate in outline, versatile, 2-locular at anthesis, subintrorsely dehiscent; pollen grains small to medium sized, subspheroidal, 3-colpate, reticulate. Intrastaminal disc annular, thick, usually deeply 5(6)- or 10(12)-lobed, or crenate, of receptacular origin. Gynoecium 5(6)-carpellate [rarely 3-carpellate], partially syncarpous [or apocarpous], sessile within the disc, rudimentary or absent in ♂ flowers; stigmas distinct, tongue-shaped and divergent or ± capitellate; styles lateral, filiform, usually connate [or distinct]; ovaries 1-carpellate and -locular, much compressed laterally, distinct but ± cohering by their sutures and resembling a compound, deeply lobed ovary; ovules anatropous, 2-integumented, solitary in each carpel, hanging from below the insertion point of the style. Fruit of (1)2–5(6) distinct, oblong to oblong-elliptic samaras, each with a flattened seed at the middle of the thin, veiny, adaxially emarginate wing. Seeds lenticular, with thin, membranaceous testa and sparse, fleshy endosperm; embryo with flat, obovate to orbicular cotyledons and a short, superior radicle. TYPE SPECIES: *A. glandulosa* Desf. (= *A. altissima* (Mill.) Swingle). (Name derived from the Moluccan name for *A. integrifolia* Lam., *ailanto*, tree-of-heaven, in allusion to the height of the trees.) — TREE-OF-HEAVEN.

A primarily tropical genus of about 15 species, distributed in eastern and southern Asia, the Philippines, Malaysia, Melanesia (east to the Solomon Islands), and northeastern Australia, extending into the Temperate Zone to northeastern China and Korea (to about 40° N. Lat.). The northernmost species, *Ailanthus altissima* (Mill.) Swingle, Chinese tree-of-heaven, stinkweed, $2n = 80$, introduced into North America in 1784 as an ornamental tree, has become naturalized in native woodlands of the southeastern United States as far south as northern Florida. Northward and westward beyond our area it seems to be primarily a "weed" tree of cities, but the exact extent of naturalization needs to be more carefully recorded. An irregularly branched, rapidly growing tree which reproduces by seeds, stump sprouts, and root suckers, it becomes a weed difficult to eradicate. However, it has sometimes been used for fastening sterile, sliding declivities and for aforestation of bare hill and mountain slopes (Alps, Caucasus) and of grasslands (Asia Minor). The leaves contain a substance toxic to seedlings of many species of gymnosperms and angiosperms. "It is possible that the toxic substance is washed from the [fallen] leaves by the rain and influences the composition of plant communities" (Mergen).

Small flies and beetles have been recorded as pollinators in *Ailanthus altissima*, but bees must participate since it is regarded as an undesirable honey plant. Wind pollination is also possible (cf. Wodehouse). Floral anatomy has been studied in this and a few other species, embryology only in the Indian *A. excelsa* Roxb., $2n = 62$. Apparently only two chromosome counts have been recorded.

Wood of *Ailanthus altissima* and the other species appears to be of relatively little value, being used mostly for fuel, occasionally for cabinet work, musical instruments, etc. It also seems to be fit for paper pulp. Leaves and bark of *A. altissima*, and bark of a few other species are used locally in Asia as anthelmintics or antidysenterics.

The genus occupies a somewhat isolated position in the tribe Picrasmeae of Simarouboideae, representing a subtribe of its own.

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Subfam. PICRAMNIOIDEAE Engler

4. **Picramnia** Swartz, Prodr. Veg. Ind. Occ. 2, 27. 1788, nom. cons.

Trees or shrubs, usually with slender, curving branches, the bark and wood often very bitter. Leaves odd-pinnate, persistent; leaflets [3]5–9[21], opposite or alternate, entire, chartaceous to ± coriaceous, petioluled. Plants dioecious [or occasionally polygamous]. Flowers minute, unisexual [occasionally also bisexual]. Inflorescences paniculate, terminal [sometimes opposite the leaves], with slender, raceme- or spikelike branches. Sepals 5 [3 or 4], connate from ¼ to ½ of their length, imbricate. Petals 5 [3 or 4, or wanting], narrowly linear-lanceolate [or lanceolate], as long [or twice as long] as the sepals, imbricate. Stamens as many as and opposite the petals, inserted below and between the lobes of a low intrastaminal disc, reduced to staminodia in ♀ flowers; filaments subulate; anthers basifixed, almost globular, with thick connective, introrse, 4-locular at anthesis. Gynoecium 2(3)-carpellate, syncarpous, rudimentary in ♂ flowers; stigma deeply 2-lobed, the lobes thick, divergent; style very short and stout, usually inconspicuous; ovary sessile, 2(3)-locular; ovules anatropous, epitropous, 2-integumented, pendulous from near the top of the carpels, 2 in each locule. Fruit a rather juicy, subglobular, ellipsoidal or obovoid berry, (3)2- or (by abortion) 1-locular, with 1-seeded locules. Seed ovoid, often plano-convex, filling the cavity of the locule, the testa membranaceous, adnate to the undifferentiated embryo; endosperm wanting. (*Pseudobrasilium* Adans., 1763; *Tariri* Aubl., 1775; nom. rejic.) TYPE SPECIES: *P. antidesma* Swartz. (Name derived from Greek, *pikros*, bitter, and *thamnos*, shrub, in allusion to the bitterness of the vegetative parts.) — BITTERBUSH.

A genus of about 40 species of tropical American distribution. *Picramnia pentandra* Sw., a shrub or small, slender tree, of the West Indies, Colombia, and Venezuela, occurs in our area in the coastal hammocks of southeastern peninsular Florida (Dade County) and on the Florida Keys. Berries of this species are olive-shaped, 9–15 mm. long, red, turning black when fully ripe; the seeds are light brown and lustrous. Leaves, bark, and roots of this and other species have been used locally in the tropics as febrifuges.

The genus, which represents a subfamily of its own, is in need of a revision.

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Subfam. ALVARADOIDEAE Engler

5. **Alvaradoa** Liebmann, Vid. Medd. Nat. For. Kjøbenh. **1853:** 100. 1854.

Shrubs or trees up to 15 m. high, with slender, terete, pubescent [or glabrous] branchlets and bitter bark. Leaves odd-pinnate, many-foliolate, crowded at the end of branches, apparently persistent; leaflets alternate, small (not over 5 cm. long), thin and firm [or leathery], entire, petiolulate. Plants dioecious. Flowers minute, unisexual, in slender, many-flowered, axillary or terminal racemes. Sepals 5, usually distinct in ♀ flowers and variously connate from near the base to the half of their length in ♂ flowers, valvate. Petals 5, linear-filamentous, present [or absent] in ♂ flowers, wanting in ♀ flowers. Stamens 5, alternate with the sepals, inserted below and between the lobes of the disc, wanting in ♀ flowers; filaments filiform, hairy in the lower part; anthers basifixed, oblong in outline, with a conspicuous, almost orbicular, swollen connective and introrse anther-halves, 4-locular at anthesis; pollen grains small, prolate-subspherical, 3-colpate. Intrastaminal disc thickish, deeply 5-lobed in ♂ flowers, thin and scarcely lobed in ♀ flowers. Gynoecium 3-carpellate (but only 1 carpel fertile), syncarpous, sessile on the disc, wanting in ♂ flowers; stigmas small, simple; styles 3, distinct, subulate, short, recurved; ovary densely villous, flattened, obtusely triangular in cross section, imperfectly 2- or 3-locular on account of 2 incomplete partitions (apparently deeply intruded parietal placentae) demarcating a sole fertile locule in the obtuse angle of the ovary; ovules 2 in the fertile locule, basal, ascendent, anatropous, apotropous, 2-integumented. Fruit a compressed, 2[3]-winged, ± papery samaroid capsule [or leathery samara], crowned by remnants of the styles, appearing 3- or 1-locular, with 1 seed in the lower half. Seeds ± terete, narrowly ellipsoidal (the shape of rice grains) [or rather compressed and broadly elliptical in outline]; testa membranaceous; endosperm wanting; embryo straight, with plano-convex [or flat], fleshy cotyledons and a short, inferior radicle. TYPE SPECIES: *A. amorphoides* Liebm. (Named in commemoration of Pedro de Alvarado, one of the chief aides of Hernando Cortez in the conquest of Mexico.)

A genus of about five species, the range disjunct, including southern Florida, the West Indies, Mexico, and Central America, Bolivia, and Argentina. *Alvaradoa amorphoides* occurs in a few hammocks in southern peninsular Florida (Dade County) and the Florida Keys and in the West Indies, Mexico, and Central America.

Although the genus was originally placed with the Sapindaceae, Radlkofer showed *Alvaradoa* to be simaroubaceous with the closest relationship to *Picramnia*. Engler, however, placed the two in separate unigeneric subfamilies.

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BURSERACEAE Kunth, Ann. Sci. Nat. 2: 346. 1824.
(TORCHWOOD FAMILY)

Trees or shrubs, the inner bark with resin ducts. Leaves alternate, usually once pinnate, deciduous [or persistent], usually exstipulate. Flowers small, hypogynous, regular, apopetalous, usually unisexual by abortion, 3–5-merous, in axillary [or terminal] cymose panicles. Plants mostly dioecious. Stamens 6–10, usually distinct, inserted below an intrastaminal [rarely extrastaminal] nectariferous disc; anthers versatile, introrse, longitudinally dehiscent, sterile in ♀ flowers. Gynoecium 3[2–5]-carpellate, syncarpous, rudimentary or wanting in ♂ flowers; ovary 3[2–5]-locular, with axile placentae; ovules anatropous, epitropous, 2 in each locule. Fruit usually drupaceous, with ± dry [or fleshy] exo- and mesocarp, dehiscent by valves [or indehiscent]; stones solitary [or 2–5], 3[–5]-, usually 1-locular by reduction or abortion of 2 locules. Seeds without endosperm, solitary in each locule; embryo straight [or curved], cotyledons contortuplicate [or flat], usually ± deeply lobed, radicle superior. TYPE GENUS: *Bursera* Jacq. ex L.

A pantropical family of 15 or 16 genera and about 600 species. Six genera (including *Bursera* and *Protium*) with about 200 species occur in the New World. The family is subdivided into the tribes Protieae Engl., Bursereae [H. J. Lam] (Boswellieae Engl.), and Canarieae Engl. The subdivisions, although based exclusively upon the structure of the fruits, seem to be rather natural ones.

Burseraceae are closely allied with Rutaceae, Simaroubaceae, and Meliaceae. A close relationship to Anacardiaceae, proposed by some taxonomists (e.g., Radlkofer), is supported by evidence from anatomy and palynology.

Resinous substances obtained from some species are of economic significance. The most important of these are myrrh, from *Commiphora molmol* Engl. and *C. abyssinica* (Berg) Engl., and olibanum or frankincense, from species of *Boswellia*, especially *B. Carteri* Birdw. Myrrh is used in perfumery, and both are used in medicine and as incense.

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1. Bursera Jacquin ex Linnaeus, Sp. Pl. ed. 2. 1: 471. 1762; Gen. Pl. ed. 6. 440. 1764, nom. cons.

Trees [or shrubs]. Leaves odd-pinnate [sometimes bipinnate], 3–9[–many]-foliolate [rarely 1-foliolate], usually crowded at the end of branchlets, deciduous; leaflets opposite, chartaceous to subcoriaceous [or coriaceous], entire [or toothed], manifestly petiolulate [to sessile]. Flowers very small, unisexual [and/or bisexual], in axillary, raceme-like panicles, appearing prior to or with [or after] the leaves. Plants dioecious [or polygamous?]. Sepals 3–5, minute, connate at least at base, imbricate in bud. Petals 3–5, whitish to creamy, much longer than the sepals, spreading and recurved, induplicate-valvate in bud. Stamens 6–10, nonfunctional in ♀ flowers; filaments subulate; anthers oblong in outline, dorsifixed near the base, shorter and without pollen in ♀ flowers; pollen grains medium-sized, 3-colpate, reticulate-striate. Intrastaminal disc annular, 6–10-lobed, orange or red. Stigma capitate, 3-lobed; style short, ovary sessile, ovoid, 3-carpellate and -locular, with 2 collateral, pendulous ovules in each locule, rudimentary in ♂ flowers. Drupes subglobular or obliquely ellipsoid, indistinctly triangular, with resinous, fleshy, leathery exo- and mesocarp detaching in 3 [or 2] valves when the fruit matures; stones (bony endocarp) covered with a thin, membranaceous, light-pink coat (probably the innermost layer of mesocarp remaining attached to the endocarp), usually solitary, attached to the persistent axis of the ovary, ovoid-trihedral, essentially 1-locular, but bearing 2 minute, sterile locules or rudimentary stones in the upper half on the adaxial (ventral) side, usually 1-seeded. Seeds without endosperm; testa membranaceous; embryo straight [or curved] with foliaceous, contortuplicate cotyledons and a short superior radicle. Germination epigeous, cotyledons 3-fid, the first leaf 3-foliolate. (*Elaphrium* Jacq., 1760; *Simaruba* Boehmer, 1760; nom. rejic.) TYPE SPECIES: *B. gummifera* L. (= *B. Simaruba* (L.) Sarg.). (Named in honor of Joachim Burser, 1583–1639, a German physician and botanist.)

A genus of about 100 species of tropical America. *Bursera Simaruba* (*Elaphrium Simaruba* (L.) Rose), gumbo-limbo or West Indian birch, of the West Indies, Mexico, Central America, and northern South America, occurs in coastal hammocks on the Florida Keys and in peninsular Florida about as far north as Brevard and Pinellas counties. Easily recognizable by its lustrous, smooth, copper-colored bark which exfoliates in thin, papery layers as in some species of *Betula*, in winter the tree (to 20 m.) is conspicuously leafless, in contrast with its evergreen associates. The species is a common "fence-post" tree in tropical America, for pieces of the trunk or branches set in the ground quickly develop roots and grow into trees. The Mexican *B. fagaroides* (HBK.) Engl. and *B. microphylla* Gray occur in southern Arizona, the latter in southeastern California as well.

Insect pollination has been presumed for the genus, but no data are available. *Bursera Simaruba* apparently is dioecious; records of polygamy are in need of verification. Staminate flowers in this species are 5-merous (or more rarely 4-merous), while the carpellate appear to be almost invariably 3-merous and only very rarely 4-merous.

The species of *Bursera* yield a fragrant glutinous resin which is locally applied in domestic medicine. The resin of *B. Simaruba* is also used as a substitute for glue and as cement for mending broken china and glass.

The genus seems to be most closely related to the paleotropic *Boswellia* Roxb. ex Colebr.

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COMPARATIVE ANATOMY OF THE LEAF-BEARING CACTACEAE, IV

THE FUSIFORM INITIALS OF THE CAMBIUM AND THE FORM AND STRUCTURE OF THEIR DERIVATIVES

I. W. Bailey [1] and Lalit M. Srivastava [2]

It has been demonstrated that in both dicotyledons and monocotyledons vessels originated by modification of long tracheids having scalariform pitting (Bailey & Tupper, 1918; Cheadle, 1942, 1943). In the case of the dicotyledons, highly advanced stages in the phylogenetic specialization of vessels occur in plants having short vessel members with simple perforation plates throughout both the primary and secondary xylem (Bailey, 1944). In such plants scalariform perforation plates are eliminated. During the evolutionary specialization of vessels there commonly tend to be concomitant changes in the ground mass of imperforate tracheary cells which, by elimination of the borders of their pits, become libriform fibers, which, in turn, may at times retain their living contents, become septate, and function in the storage of starch (Bailey, 1936).

In dicotyledons, the differentiation of sieve tubes in the secondary phloem has appeared to afford a phylogenetic parallel to the development of vessels in the secondary xylem (Esau, 1953, p. 275; Esau, Cheadle & Gifford, 1953). In both tissues, axial translocation seems to be facilitated by modification in the more or less extensively overlapping ends of adjacent cells in axial seriations: in the xylem by loss of pit membranes to form perforations and in the phloem by formation of sieve plates having larger connecting strands than those in the sieve areas of the lateral walls. Some investigators have suggested that there is a direct correlation between the degree of evolutionary spcialization of sieve plates in the end walls and decrease in conspicuousness of the sieve areas in the lateral walls (Cheadle & Whitford, 1941; Cheadle, 1948; Cheadle & Uhl, 1948; Esau & Cheadle, 1959). Zahur (1959), however, did not find such a correlation.

It should be strongly emphasized in this connection that huge volumes of anatomical data regarding the secondary xylem of dicotyledonous families have accumulated during the last half-century. Wood, in general, is adequately preserved by simple drying, and industrial pressures have stimulated the assembling and study of large collections of wood samples by institutions in various parts of the world. No comparable information is available at present regarding the secondary phloem of dicotyledons.

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Further, as explained by Cheadle (1956), this tissue is difficult to study because of its physiological and structural peculiarities. Even the most extensive reconnaissance to date (Zahur, 1959) deals with only a relatively few representatives of the 85 families sampled.

Furthermore, as one of us (Bailey, 1957) has emphasized: "There are certain details of the trends of specialization in the xylem which need to be more clearly and generally understood in shifting from a consideration of the dicotyledons *as-a-whole* to investigations of the taxonomy of individual taxa of restricted size. In revealing salient trends of evolutionary specialization by analyses of data obtained from the dicotyledons *as-a-whole*, variations due to obtaining specimens from different parts of the plant, from plants of different growth rates, from genetically different taxa, etc., tend to neutralize one another. In addition, various localized, divergent trends of specialization do not obscure or confuse the major trends of evolution in the dicotyledons *as-a-whole*. However, when one becomes concerned with taxa of decreasing size, viz. families, subfamilies, tribes, genera and species, such variations and deviations become increasingly significant."

For example, data from the dicotyledons as-a-whole clearly reveal evolutionary changes from scalariform to simple perforation plates, and from scalariform to alternate multiseriate intervascular pitting. In any randomly selected minor taxon, one of these trends may be retarded or accelerated in relation to the other. Therefore, with present inadequate information regarding the secondary phloem in most orders, families, and genera, it is not possible to determine with certainty what some of the more important trends of phylogenetic specialization in the dicotyledons as-a-whole may actually be. This is particularly the case in those parenchymatous cells that are physiologically and ontogenetically related to sieve elements.

During the phylogenetic specialization in the secondary tissue of dicotyledons, there is a progressive shortening of fusiform cambial initials which not infrequently culminates in storied forms of cambia, involving longitudinal rather than pseudotransverse anticlinal divisions and the elimination of intrusive elongation following such divisions (Bailey, 1923).

In general, the phylogenetic shortening of fusiform cambial initials is most closely paralleled in the secondary xylem and phloem by shortening of fusiform parenchymatous derivatives and by changes in the length of parenchyma strands (for *ordinarily* fusiform parenchymatous cells and the mother cells of parenchyma strands do not elongate during tissue differentiation). As a concomitant of shortening fusiform cambial initials, the parenchyma strands commonly tend to be composed of fewer and generally of shorter cells.

Statistical data obtained from the dicotyledons as-a-whole indicate that shortening of the fusiform initials likewise is closely reflected in the length of vessel members, there being only slight elongation at times during the maturation of primitive, long, slender vessel members, and a slight contraction at times during the differentiation of short, very broad, highly specialized ones. On the contrary, fiber-tracheids and libriform fibers become longer than the fusiform cambial initials from which they are derived owing to more or less extensive intrusive elongation during tissue differentiation.

In the secondary phloem of such vesselless gymnosperms as the Pinaceae, Taxodiaceae, and Cupressaceae, statistical averages indicate that sieve cells simulate fusiform cambial initials in length, there being no appreciable elongation, as occurs at times in tracheids, during their maturation from cambial initials. In the phylogenetically specialized dicotyledons having very short fusiform cambial initials, particularly those having storied cambia, the sieve-tube members in statistical averages closely simulate the fusiform initials in length. On the contrary, in some dicotyledons having less highly specialized cambia, the parallelism in length may be modified by more or less numerous divisions of mother cells prior to the formation of sieve-tube members, companion cells, and some parenchymatous cells (cf. Esau & Cheadle, 1955; Cheadle & Esau, 1958; Zahur, 1959). In such plants, the sieve-tube members tend statistically to be considerably shorter than fusiform cambial initials.

Statements in the literature regarding detailed structure of the xylem and phloem of leaf-bearing cacti are casual and fragmentary and are based largely upon *Pereskia aculeata* Mill. The occurrence of septate libriform fibers and porous vessels in the wood of this species is recorded by Schenck (1893) and Solereder (1899). If the most primitive living cacti occur among the leaf-bearing ones, as is generally assumed to be the case, it is essential to obtain comprehensive information regarding the levels of phylogenetic specialization that they have attained, particularly for future use in understanding trends of increasing structural specialization that occur in the Opuntieae and Cereeae.

In all of the putative species of *Pereskia*, *Pereskiopsis*, and *Quiabentia* that we have studied (mentioned in previous papers of this series [Bailey, 1960, 1961a, 1961b]) the fusiform initials of the cambium have attained a high level of evolutionary modification. They are comparatively short, commonly ranging in length from only 150 to 400 microns. Although they are not consistently in perfect storied or stratified arrangement, they frequently exhibit a tendency to become storied, at least in some parts of a mature plant. Where they approach a perfect storied arrangement, they have abruptly tapered ends and a hexagonal form as seen in tangential longitudinal sections of the cambium (FIG. 1) and the cells of one stratum do not extensively overlap those of higher and lower levels. On the contrary, where stratification is imperfect, the cells have more gradually tapered ends, and there is more overlapping of the cells of different levels (FIG. 4). It should be noted in this connection that where stratification occurs in the leaf-bearing cacti it tends to differ from that which occurs in plants of other dicotyledonous families in exhibiting a conspicuous tendency for the strata of fusiform initials to have a diagonal, rather than a transverse, orientation as seen in tangential longitudinal sections of the cambium.

In dicotyledons having very short, especially storied, cambial initials, where adequately preserved material of the cambium is not available, the length and the arrangement of fusiform initials may be detected both in certain of their derivatives in the xylem and in recently formed phloem.

The distribution of wood parenchyma in *Pereskia*, *Pereskiopsis*, and *Quiabentia* is of a specialized paratracheal rather than a primitive apotracheal form, but more or less extensive arcs of thick-walled lignified or thin-walled unlignified parenchyma occur at times and may prove to be associated in some manner with successive zones of growth in the enlargement of stems and roots. The fusiform parenchymatous cells and parenchyma strands are short, the latter being composed usually of two or three cells only. In tangential longitudinal sections of the secondary xylem, the fusiform parenchyma and parenchyma strands (where not deformed and displaced by excessive enlargement of vessels) closely simulate fusiform cambial initials in overall form. Furthermore, where parenchyma is sufficiently abundant, particularly in areas of zonal distribution, the arrangement of fusiform cambial initials, whether storied or nonstoried, is clearly revealed by the arrangement of the parenchymatous cells.

The vessels in stems and roots of the leaf-bearing cacti are of a highly advanced evolutionary form having simple perforation plates throughout the primary (FIG. 8) and secondary xylem (FIG. 5). In the secondary xylem, the vessels vary markedly in diameter from 20 microns to as much as 200 microns in certain cases. The vessels occur independently and in clusters of varying size and form. The smaller vessels, as seen in transverse sections, are angular, whereas the larger ones are more nearly circular or oval, except where they are modified by compression in clusters. Such variations in the vessels occur, not only in different species and different parts of a single plant, but also in closely adjacent areas of the secondary xylem. The members of the smallest vessels (i.e., those which do not expand appreciably in tangential diameter during maturation) resemble fusiform cambial initials in overall form when viewed in tangential longitudinal sections of the xylem. In such sections, the vessel members may be confused with vascular tracheids, but the perforations in their more or less abruptly tapered ends are clearly visible in radial longitudinal sections. Where sufficiently abundant, and particularly in association with parenchyma, such small vessel members reveal a storied (FIG. 2) or nonstoried arrangement of fusiform initials in the cambium.

In the secondary xylem of the leaf-bearing cacti, vessel members of the smallest diameter tend to have diagonally oriented perforation plates in their terminal radial walls. Larger vessel members, although as short or shorter than fusiform cambial initials, vary more or less markedly in form owing to excessive lateral enlargement during their maturation. The perforation plates, consisting of a circular or oval opening surrounded by a clear zone of unpitted wall, may be transversely (FIG. 5) or more or less diagonally oriented. Furthermore, where vessels are closely associated in larger clusters and where vessels deviate from a longitudinal course to pass diagonally through the broad multiseriate rays (FIGS. 6, 7), the vessel members may at times have perforation plates in their sides rather than in their more or less inclined ends.

The bordered pitting in the sides of adjoining vessels tends to be of the evolutionarily advanced alternate-multiseriate form (FIGS. 9, 11), but areas of scalariform pitting (FIGS. 12, 13) and of opposite-multiseriate pitting are of not infrequent occurrence. The bordered pits of multiseriate arrangements vary in size and considerably in form from circular to oval and to angular where the pits are closely crowded. (Compare FIGS. 9, 11, 13, 15, 16.) The pit apertures likewise vary from small, nearly circular (FIG. 9), to oval (FIG. 15), and to transversely slitlike (FIG. 13). Furthermore, the borders of the pits exhibit at times reduction in conspicuousness in relation to the size of the apertures. (Compare FIGS. 11, 15, 16.) In areas of scalariform pitting, unconformity in the pitting of the walls of adjacent vessels frequently occurs (FIGS. 12, 13), i.e., a transversely extensive pit in one wall being related to smaller pits in the adjoining vessel wall.

The pits of vessels in contact with wood parenchyma and rays exhibit a wide range of variability. At times, they closely resemble those of intervessel contacts in size, form, and arrangement. (Compare FIGS. 9, 10; 13, 14; 16, 18.) However, in the case of the leaf-bearing cacti, there commonly is a conspicuous tendency for vessel pits in contact with parenchyma to have enlarged apertures and to reduce or eliminate their bordering area (FIG. 20). In other words, the pits in the walls of vessels in contact with parenchyma become simple pits in conformity with the unbordered pits of adjacent parenchymatous cells. Where vessels are completely jacketed by wood parenchyma and have large, transversely elongated unbordered pits, the vessel members, when isolated by maceration, resemble vessel members of those parts of the primary xylem which have reticulate forms of wall thickening (FIG. 22).

The libriform fibers of the leaf-bearing cacti, unlike the vessel members, fusiform wood parenchyma, and parenchyma strands, elongate more or less extensively by intrusive elongation during tissue differentiation. Therefore, they (FIGS. 24–27) become longer than the fusiform cambial initials (FIG. 23) from which they are derived. However, the amount of elongation varies greatly, not only in different parts of a plant, but also in closely adjacent parts of the secondary xylem. In some cases, the elongation at one or both ends of the cell is only a few microns, whereas, in other cases, the elongation at both ends of the cell is extensive. Thus, libriform fibers may be only slightly longer than the fusiform cambial initials from which they are derived, i.e., 150–400 microns (FIG. 24) or they may attain maximum lengths of as much as 1000–1300 microns (FIGS. 26, 27). Some libriform fibers are relatively slender and taper gradually and uniformly toward their ends (FIG. 26); others are broader in their central part and taper abruptly at one or both ends into long narrow tips (FIGS. 25, 27). In both instances the small oval or slitlike simple pits tend to be concentrated in the central part of the fibers which corresponds roughly in length to that of the fusiform cambial initials. (Compare FIG. 23 with FIGS. 24–27.)

The slitlike pits usually are oriented more or less diagonally to the long axis of the cell but may at times be oriented parallel to its axis. This indicates that the orientation of cellulosic microfibrils in the central or S_2 layer of the secondary wall may, at least occasionally, deviate from helical to longitudinal.

The fibers in any particular part of the secondary xylem may be prevailingly septate (usually a single septum to each cell, FIG. 26), nonseptate, or in varying mixtures of septate and nonseptate. Both the septate and the nonseptate (FIGS. 17, 19, 21) fibers retain their protoplasts and nuclei and are capable, at least in certain parts of the plant or at certain seasons of the year, of storing abundant starch.

In the members of *Pereskia*, *Pereskiopsis*, and *Quiabentia* which we investigated, the phloem derivatives, viz., sieve elements and parenchyma, as seen in tangential longitudinal sections in close proximity to the cambium, commonly reflect the form and distribution of the fusiform cambial initials (FIGS. 3, 4). The fusiform parenchyma and parenchyma strands, however, are more reliable indicators of the overall form of fusiform initials than are the sieve elements. This is because the sieve-tube members commonly differentiate in one or more parts of a cell complex that results after longitudinal and sometimes transverse divisions in a single phloem mother cell. Therefore, although the length of sieve-tube members in statistical averages generally corresponds to that of the fusiform cambial initials, their overall form frequently does not. The phloem-parenchyma strands are usually composed of two or three cells arranged in a vertical file and appear to originate by divisions in a single phloem mother cell.

The sieve-tube members present features of advanced structural specialization. The sieve plates commonly occur in the more or less transverse (FIG. 28) or slightly oblique end walls (FIGS. 29, 30) but sometimes may be present in the lateral walls (FIG. 29). In certain cases, sieve plates may not be present at both ends of a sieve-tube element but may occur only at one end and in one of the lateral walls (FIG. 29). Usually the pores and the callose cylinders are distributed rather evenly throughout the sieve plate and the latter may be interpreted as a simple sieve plate. Occasional variations in sieve-plate structure occur, however. In some sieve elements with somewhat sloping end walls the pores and the callose cylinders may be distributed in two or more distinct groups in the sieve plate (FIGS. 30, 31). There is no strict uniformity with regard to the distribution of these two forms of sieve plates. They occur in different parts of the same plant and even at the two ends of a single sieve-tube member. These variations in sieve-plate structure are related in a general way to the orientation of the end walls in the sieve elements which, in turn, seems to be related to the character and orientation of end walls in the fusiform cambial initials (FIG. 23).

In addition to sieve plates which usually occur at or near their end walls, sieve-tube members have numerous small sieve areas that are scattered throughout both radial and tangential lateral walls (FIG. 32). The pores and their callose cylinders in these sieve areas are much smaller than those in the sieve plates. (Compare FIGS. 31, 32.) The size of these lateral sieve areas, as determined by the number of callose cylinders stained with lacmoid in one area, varies considerably. In the same sieve-tube member, some lateral sieve areas may be very small, composed of one or two strands and their callose cylinders only, whereas others may be composed of several strands and their callose cylinders.

Generally, one or more companion cells occur in association with a sieve-tube member (FIGS. 28, 29). In addition, one or more members of a cell complex, in which sieve-tube elements and companion cells arise, may differentiate as parenchymatous elements. The exact relationships between the different cells that originate after divisions in a single phloic mother cell and the sieve-area connections between them require detailed ontogenetic study.

During the transition from "functional" to "nonfunctional" phloem[3] the parenchymatous cells of both the axially oriented part and the rays retain their living contents, capacity for division, and commonly undergo more or less extensive changes in size and form. The most striking changes of taxonomic significance are those which occur in the nonfunctional phloem of *Pereskia*, these being absent in *Pereskiopsis* and *Quiabentia*. As one of us has shown (Bailey, 1961a) three distinct categories of pereskias can be segregated upon the basis of differences in the formation of sclereids in the nonfunctional part of the secondary phloem. In two of these categories of species, sclereid formation involves extraordinary enlargements of parenchymatous cells in both diameter and length. In the third category, the changes in size and form are more nearly comparable to those that occur in the formation of ordinary sclereids.

Although crystals are commonly present in the ray parenchyma of functional phloem in all three genera, they rarely, if ever, occur in axially oriented parenchyma. However, they do occur at times in axial parenchyma of nonfunctional phloem (Bailey, 1961b). Variations in the presence and form of these crystals may prove to be of some taxonomic significance when more adequate and extensive collections are available for detailed investigation.

DISCUSSION

It is evident from our reconnaissance of the secondary vascular tissues of *Pereskia*, *Pereskiopsis*, and *Quiabentia* that these tissues have attained highly advanced levels of evolutionary specialization. This is shown, for example, by the dimensions and form of the cambial fusiform initials and their derivatives, by the perforation plates and the lateral pitting in vessels, by the storage of starch in both septate and nonseptate libriform fibers, and by the distribution patterns of vessels and wood parenchyma.

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[3] Following Esau (1953, p. 299) "nonfunctional" phloem refers to that part of the phloem in which sieve elements and companion cells have ceased to function.

Such evidence at least suggests that the early leaf-bearing representatives of the Cactaceae (those of nearly typical dicotyledonous woody arborescent and shrubby form) had attained high levels of internal anatomical specialization before increasing succulence and other morphological changes led to the differentiation of the Opuntieae and Cereeae.

The ranges of anatomical variability in different parts of a single plant and in the same clone when grown under different environmental influences are very extensive. Potential diagnostic criteria, such as differences in the size, form, and distribution of the constituent cells of xylem, in the form and orientation of perforation plates; in pitting between vessels and between vessels and parenchyma; in the presence or absence of septa in libriform fibers, etc. (which have been utilized so commonly in the differentiation of taxa in other dicotyledonous families) appear, in general, in the leaf-bearing Cactaceae to be of a quantitative rather than a qualitative character. Likewise, in phloem, the orientation of the sieve plates near the ends of sieve-tube members may vary from more or less oblique to perfectly transverse, and the number of pore groups (viz., sieve areas) on the sieve plate may range from one to three or more. The difference between the size of pores and connecting strands in the lateral sieve areas *versus* the sieve plates is very great in all species of the three leaf-bearing genera. Therefore, in the case of these cacti, large volumes of material must be studied statistically in order to attain results of valid taxonomic significance.

In the past, unjustifiable phylogenetic and taxonomic inferences have resulted from comparisons between the frequency of diagonal and transverse orientations of terminal perforation plates in closely related taxa without taking into consideration various factors involved in the statistical differences. Important influences in this connection are the length of fusiform cambial initials, the amount of transverse enlargement of vessel members during tissue differentiation, the deformation when vessels occur in crowded clusters, and the aberrations produced in xylem of distorted or burly grain. In straight-grained xylem of the leaf-bearing cacti, the broader vessel members tend, on an average, to have transversely or nearly transversely oriented terminal perforation plates, whereas the narrowest vessels commonly have diagonally oriented ones. Where the grain of the xylem is distorted, as so frequently happens in stems and roots of the leaf-bearing cacti (owing in large measure to the frequent diagonal dissection of broad rays by conversion of ray initials to fusiform ones), steeply diagonal and even laterally placed perforation plates are of not infrequent occurrence. Similar aberrations occur in the orientation of sieve plates in the phloem. From the point of view of salient trends of phylogenetic specialization in the dicotyledons *as-a-whole*, the occurrence of simple perforation plates throughout both the primary and secondary xylem is of greater evolutionary significance than are deviations from a transverse orientation of perforation plates in the vessels of certain parts of the stems and roots of the leaf-bearing cacti.

The occurrence of septate libriform fibers in various dicotyledonous families has been based largely upon surveys made of dried wood samples. It should be recognized, in this connection, that a great many of the samples consist of heart-wood. Where specimens of undecayed sapwood are available, they are sectioned after boiling in water and frequently after softening treatment in hydrofluoric acid. Such sections do not contain starch, but the assumption is made, probably correctly, that the septate fibers in the sapwood retained their living protoplasts at functional maturity and were capable, at least for a time, of storing starch. The common occurrence of starch in nonseptate libriform fibers of the leaf-bearing cacti raises the question whether the storage of starch in nonseptate fibers of sapwood is not of much commoner occurrence in dicotyledons than has been realized. From physiological as well as phylogenetic points of view, the whole problem of retention of living protoplasts and storage of starch in nonseptate libriform fibers, whether confined to newly formed sapwood, whether capable of seasonal depletion and renewal as in the case of starch in ray tissue, etc., needs to be thoroughly investigated, not only in the Cactaceae, but also in other families of the dicotyledons.

In this paper, we have omitted discussion of ray initials in the cambium and of their derivatives in the xylem and phloem. The rays in the leaf-bearing Cactaceae are obviously of a highly specialized form, being prevailingly multiseriate, uniseriate rays having been eliminated. It seems best to discuss rays in subsequent papers of this series, dealing in greater detail with the structure of various putative species of *Pereskia*, *Pereskiopsis* and *Quiabentia.*

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EXPLANATION OF PLATES

PLATE I

Figs. 1–4. Tangential longitudinal sections of cambium, xylem and phloem, × 110. 1, *Pereskia cubensis* Britt. & Rose [Atkins Gard.], storied fusiform initials of the cambium. 2, *Pereskiopsis blakeana* Ortega [*Kimnach & Moran 82*], diagonally storied vessel members and wood-parenchyma strands. 3, *Pereskia autumnalis* (Eichlam) Rose [*Moore 8210*], storied sieve-tube members; terminal sieve plates are black. 4, *Pereskia* aff. *sacharosa* Griseb. [*Cárdenas*], imperfectly storied cambial fusiform initials (left of ray) and phloem derivatives (right of ray).

PLATE II

Figs. 5–8. Occurrence and orientation of simple perforation plates in vessel members. 5, *Pereskia grandifolia* Haw. [*Castellanos*], transverse section of the secondary xylem showing transversely oriented perforation plates, × 260. 6, *Pereskia colombiana* Britt. & Rose [*Romero*], radial longitudinal section of the secondary xylem showing laterally placed perforation plate, × 260. 7, *Pereskia nicoyana* Web. [*Rodríguez 662*], tangential longitudinal section of the secondary xylem showing divergence of vessel members through multiseriate ray; vessel members at right have perforation plates, as seen in sectional view at (X), in their lateral radial walls, × 180. 8, *Pereskiopsis aquosa* (Web.) Britt. & Rose [*Dressler*], radial longitudinal section of the primary xylem showing perforation plates in helically thickened vessel members, × 260.

PLATE III

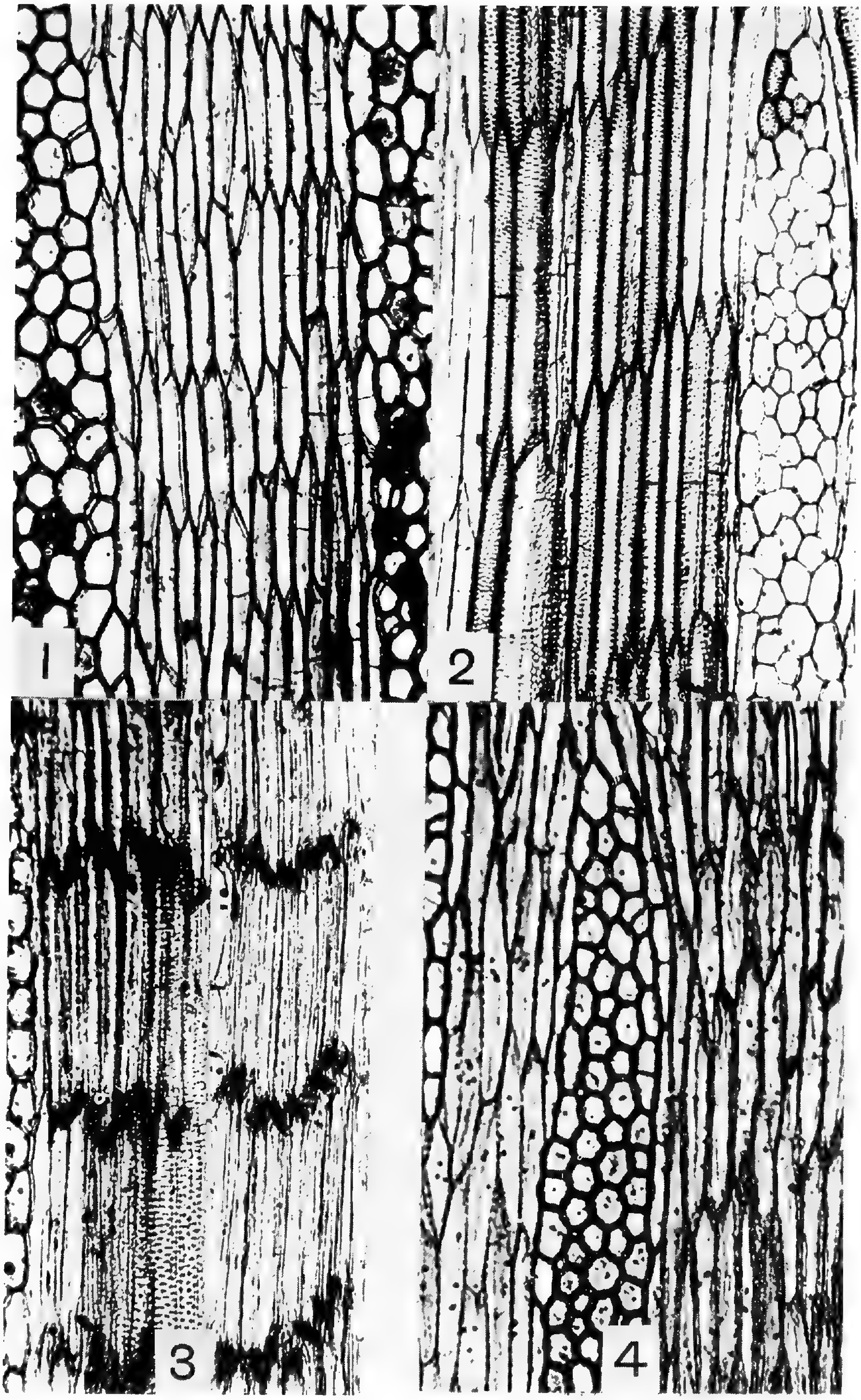
FIGS. 9–15. PITTING BETWEEN VESSELS AND BETWEEN VESSELS AND PARENCHYMA. 9, *Pereskia grandifolia* [*Castellanos*], crowded alternate-multiseriate pitting in walls of contact between vessel members, × 410. 10, *Pereskia colombiana* [*Romero*], pitting between vessel and ray parenchyma, × 410. 11, *Pereskia grandifolia* [*Castellanos*], variations in form of bordered pits and their apertures, × 1130. 12, *Pereskia colombiana* [*Romero*], unconformity in the pitting of vessels; many of the transversely elongated pits in the wall of one vessel are in contact with rows of shorter pits in the wall of the adjoining vessel, × 960. 13, *The same*, scalariform and transitional pitting in lateral walls of adjoining vessels, × 410. 14, *The same*, scalariform pitting between vessel and parenchyma, × 410. 15, *Quiabentia* aff. *chacoensis* Backbg. [Tucumán], bordered pits with large apertures in the lateral walls of adjoining vessels, × 410.

PLATE IV

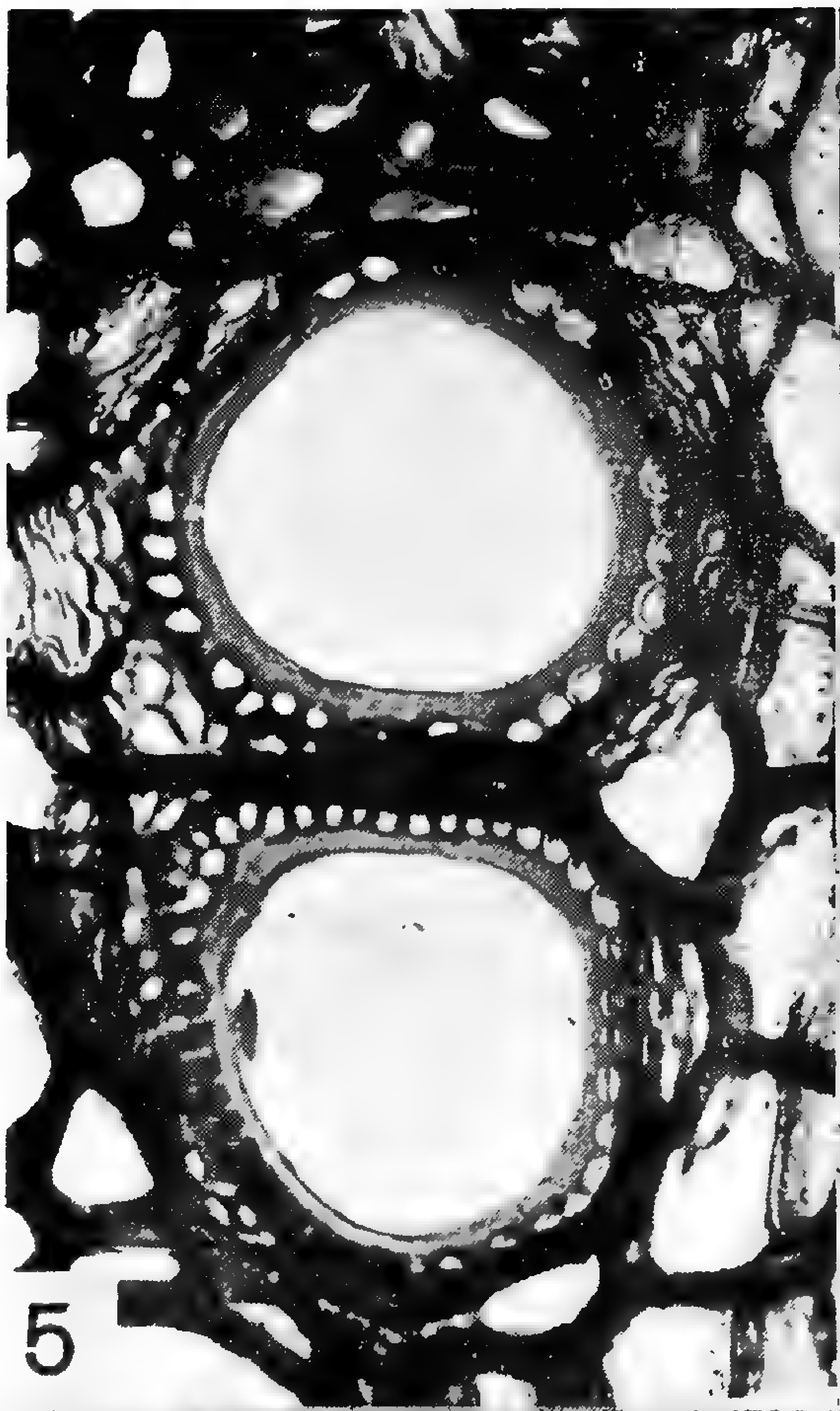
FIGS. 16–22. LONGITUDINAL SECTIONAL VIEWS OF VESSELS, PARENCHYMA AND NONSEPTATE LIBRIFORM FIBERS. 16, *Pereskiopsis blakeana* [*Kimnach & Moran 82*], reduction in the borders and increase in size of apertures in intervascular pitting, × 410. 17, *Pereskia aculeata* Mill. [Atkins Gard.], iodine stained starch in a nonseptate libriform fiber, × 750. 18, *Pereskia bleo* DC. [Atkins Gard.], reduction in borders and increase in size of apertures in pitting between vessel and ray parenchyma, × 410. 19, *Pereskiopsis chapistle* Britt. & Rose [*Boke B–3*], nuclei (black) and unstained starch in nonseptate libriform fibers, × 1000. 20, *Pereskiopsis blakeana* [*Kimnach & Moran 82*], pitting between vessels and parenchyma, × 410. 21, *Quiabentia* aff. *chacoensis* [Tucumán], nucleus with nucleolus in nonseptate libriform fiber, × 1000. 22, *Quiabentia pereziensis* Backbg. [*Cárdenas*], large unbordered pits between vessel and parenchyma, × 410.

PLATE V

FIGS. 23–32. DIAGRAMMATIC ILLUSTRATIONS OF CAMBIAL FUSIFORM INITIALS, LIBRIFORM FIBERS AND SIEVE-TUBE MEMBERS. 23, *Pereskia sacharosa* [Tucumán], fusiform cambial initials, drawn from tangential longitudinal section of cambium. 24, *Pereskia conzattii* Britt. & Rose [*Dressler*], libriform fiber drawn from maceration. 25, *Pereskia aculeata* [Atkins Gard.], libriform fiber drawn from maceration. 26, 27, *Pereskia conzattii* [*Dressler*], septate and nonseptate libriform fibers drawn from maceration. 28, *Pereskia sacharosa* [Tucumán], sieve-tube member and companion cells, drawn from tangential longitudinal section of phloem. 29, *Pereskiopsis* aff. *chapistle* [*Boke B–3*], sieve-tube member and companion cell, drawn from tangential longitudinal section of phloem. 30, *The same*, sieve-tube member drawn from radial longitudinal section. 31, *The same*, part of a sieve plate, drawn from radial longitudinal section of phloem. 32, *The same*, lateral sieve areas, drawn from radial longitudinal section, companion cell on right. Figures 23–30, × 175; figs. 31, 32, × 875.



BAILEY & SRIVASTAVA, LEAF-BEARING CACTACEAE, IV



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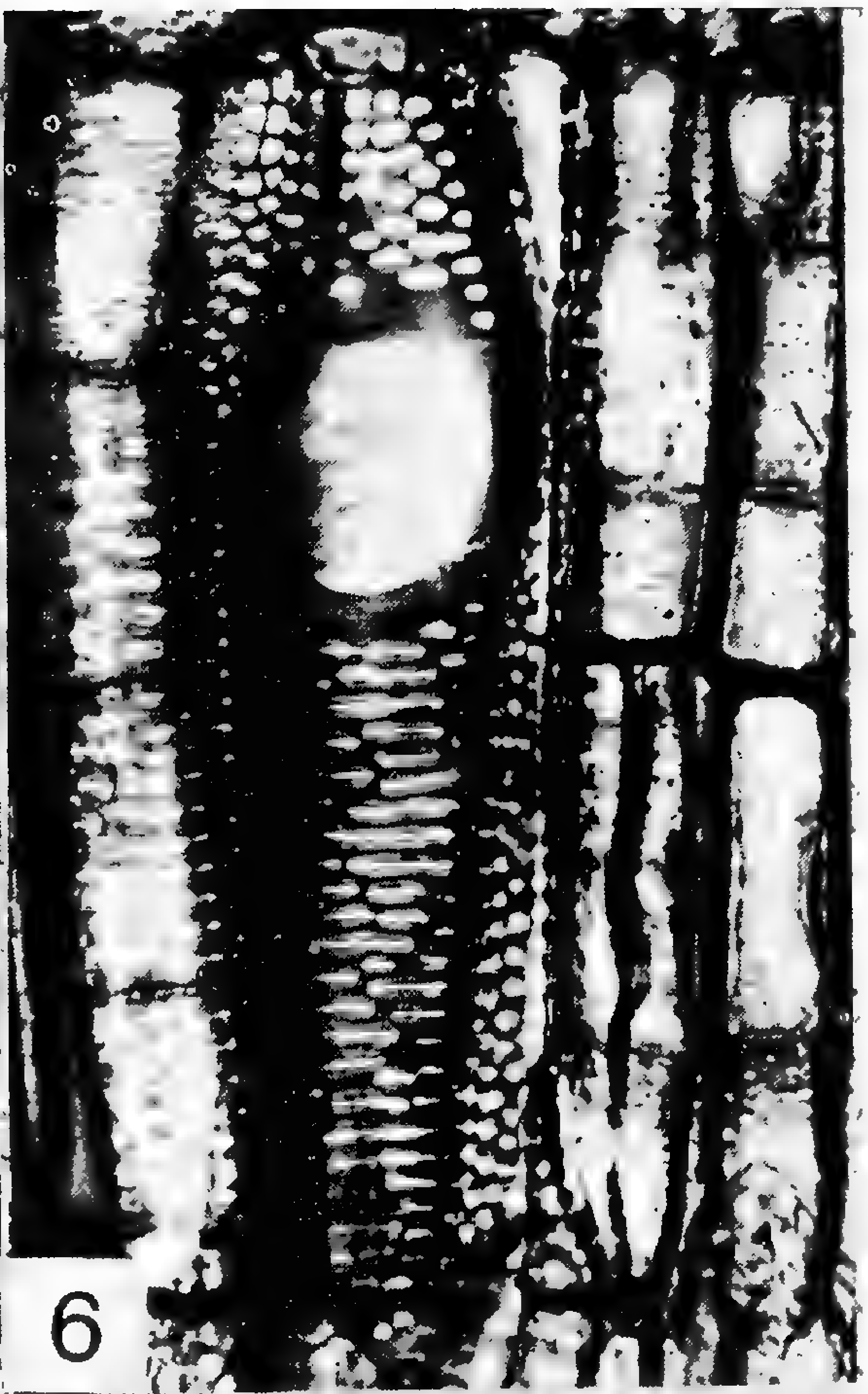

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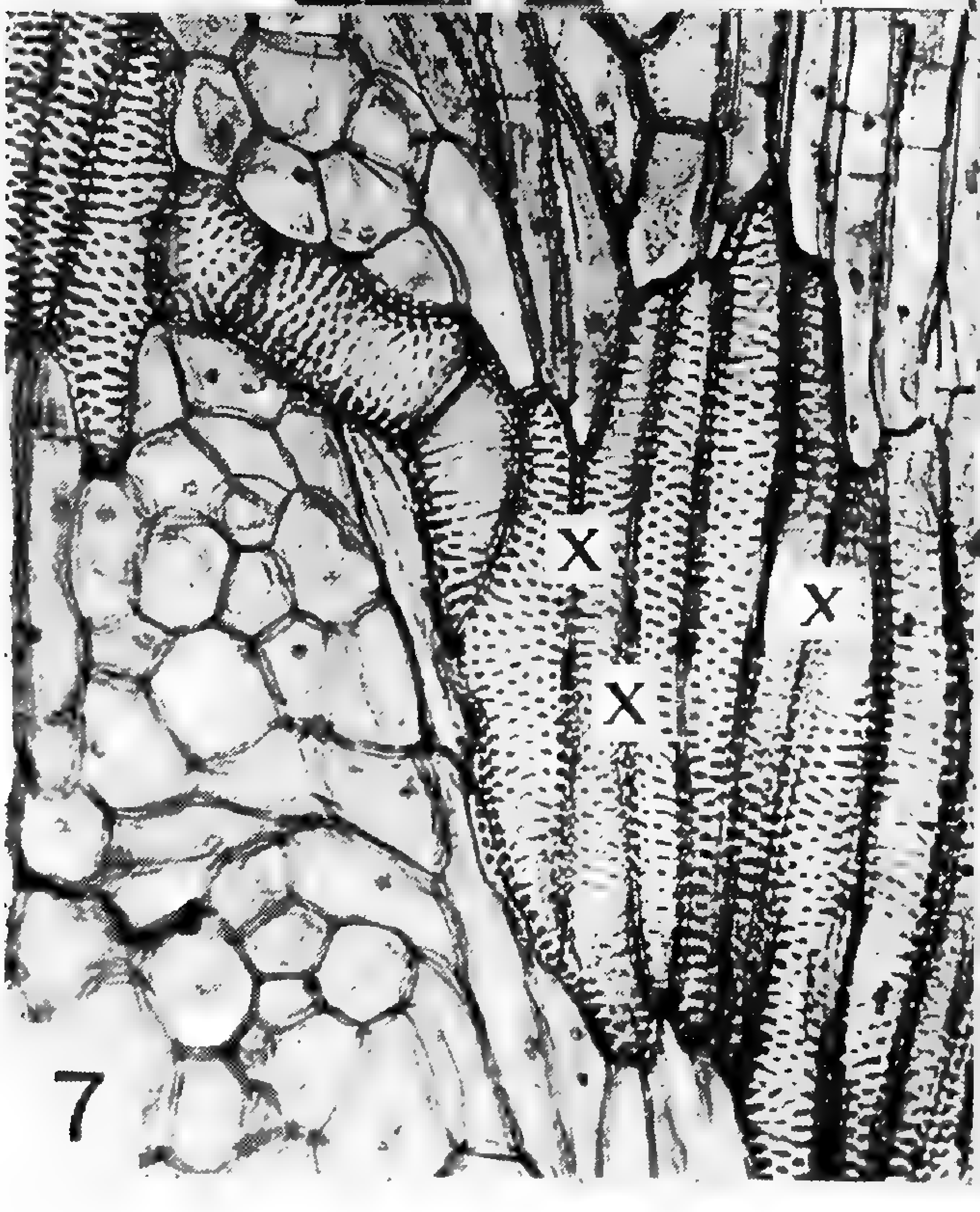

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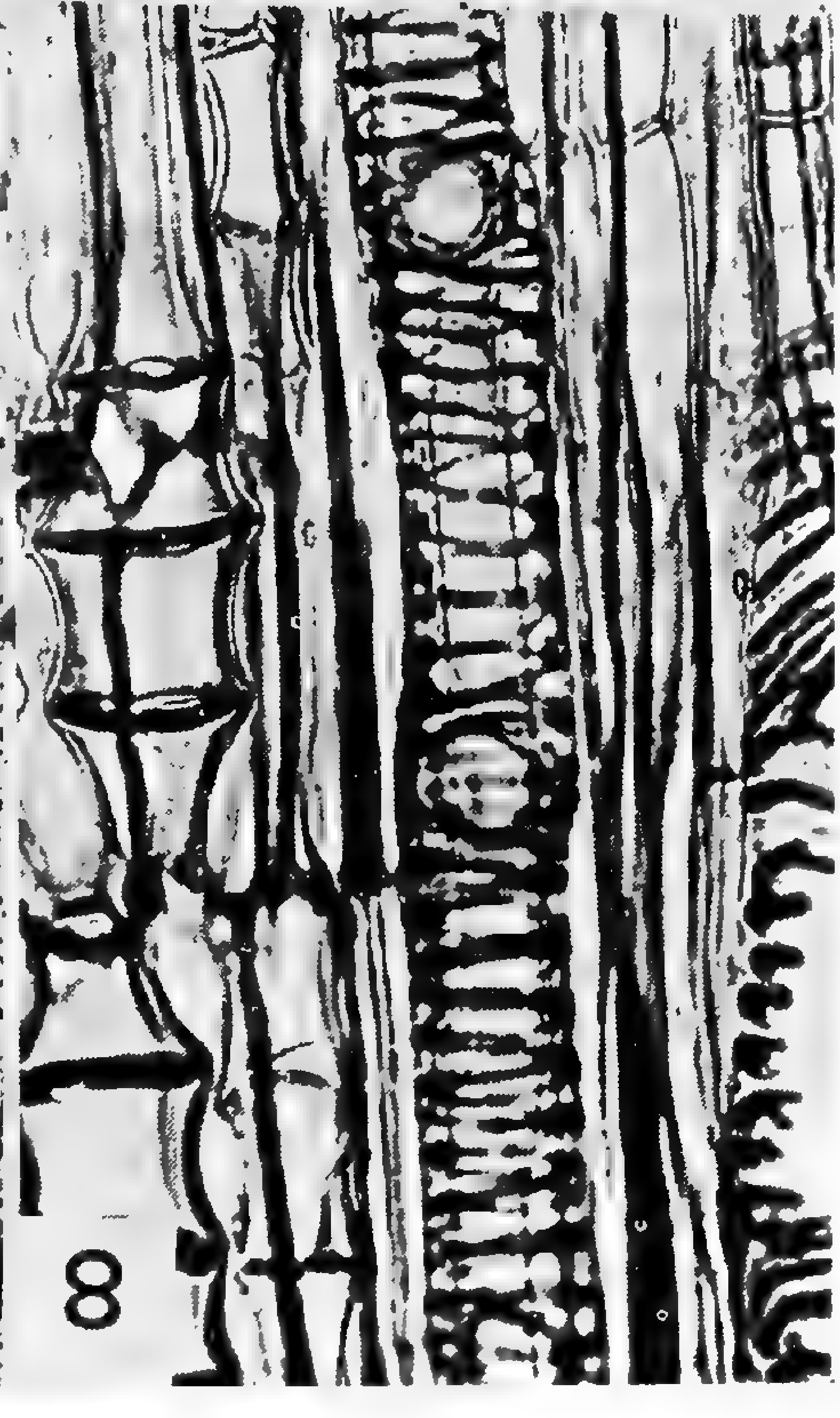

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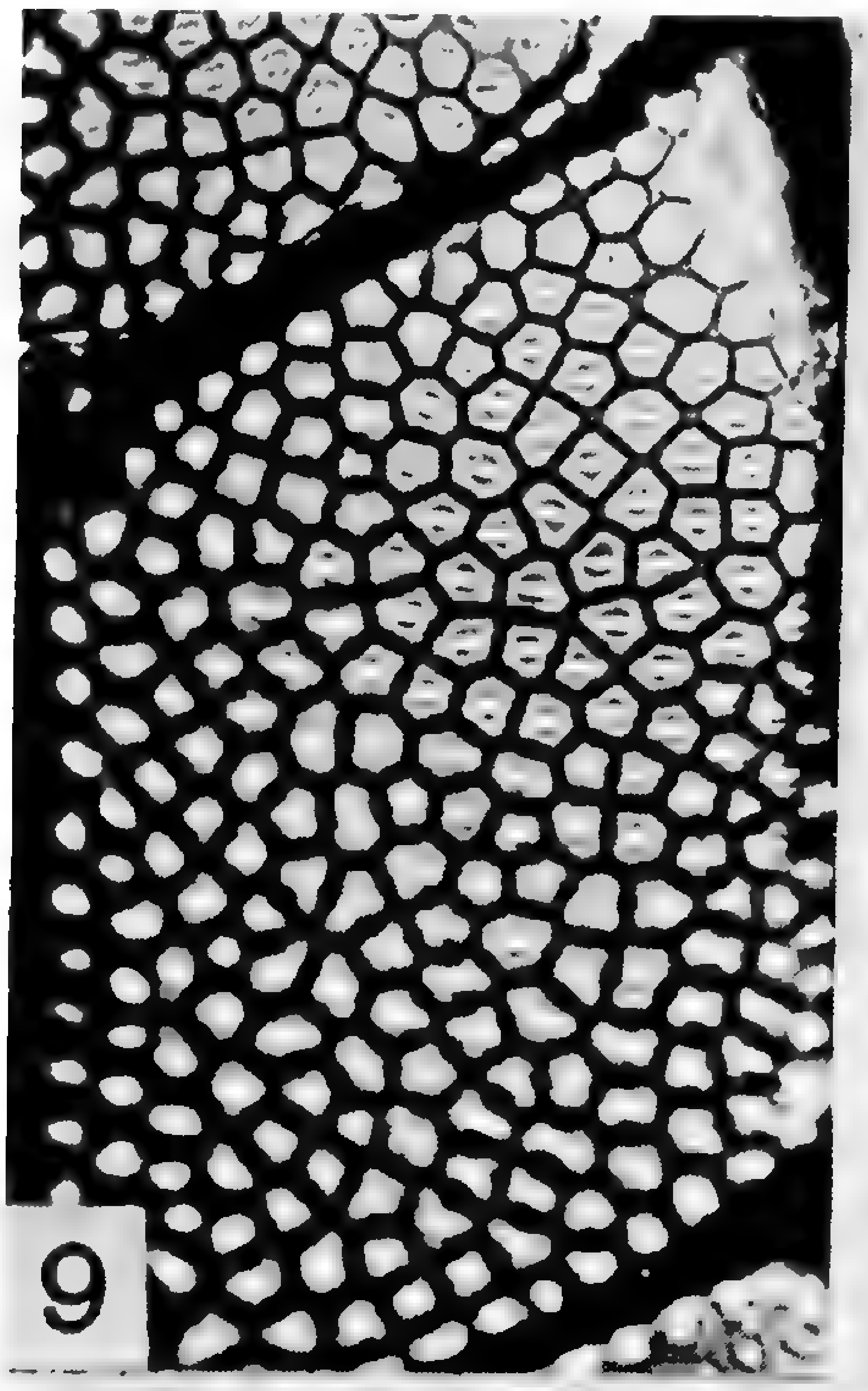
Plate III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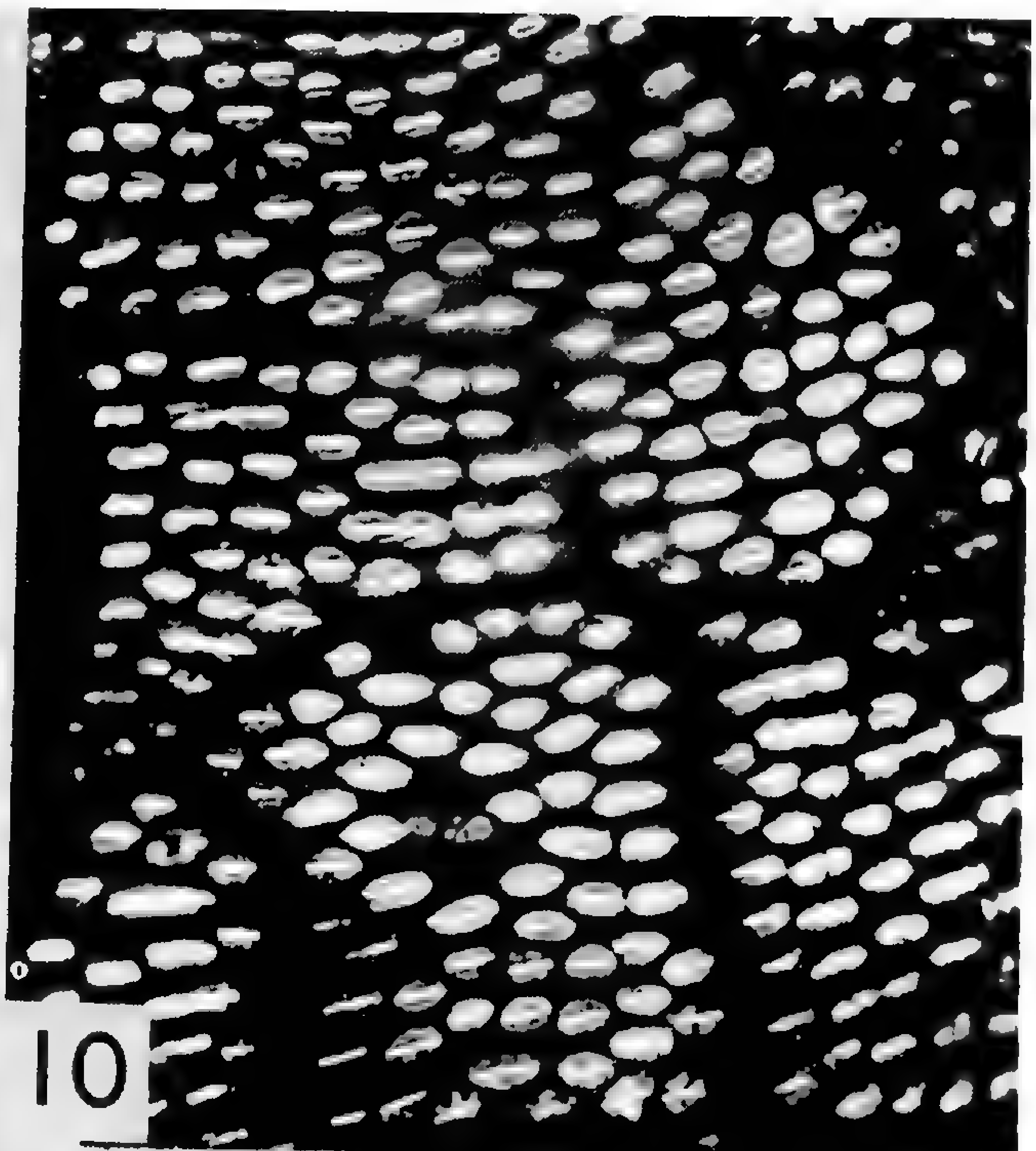
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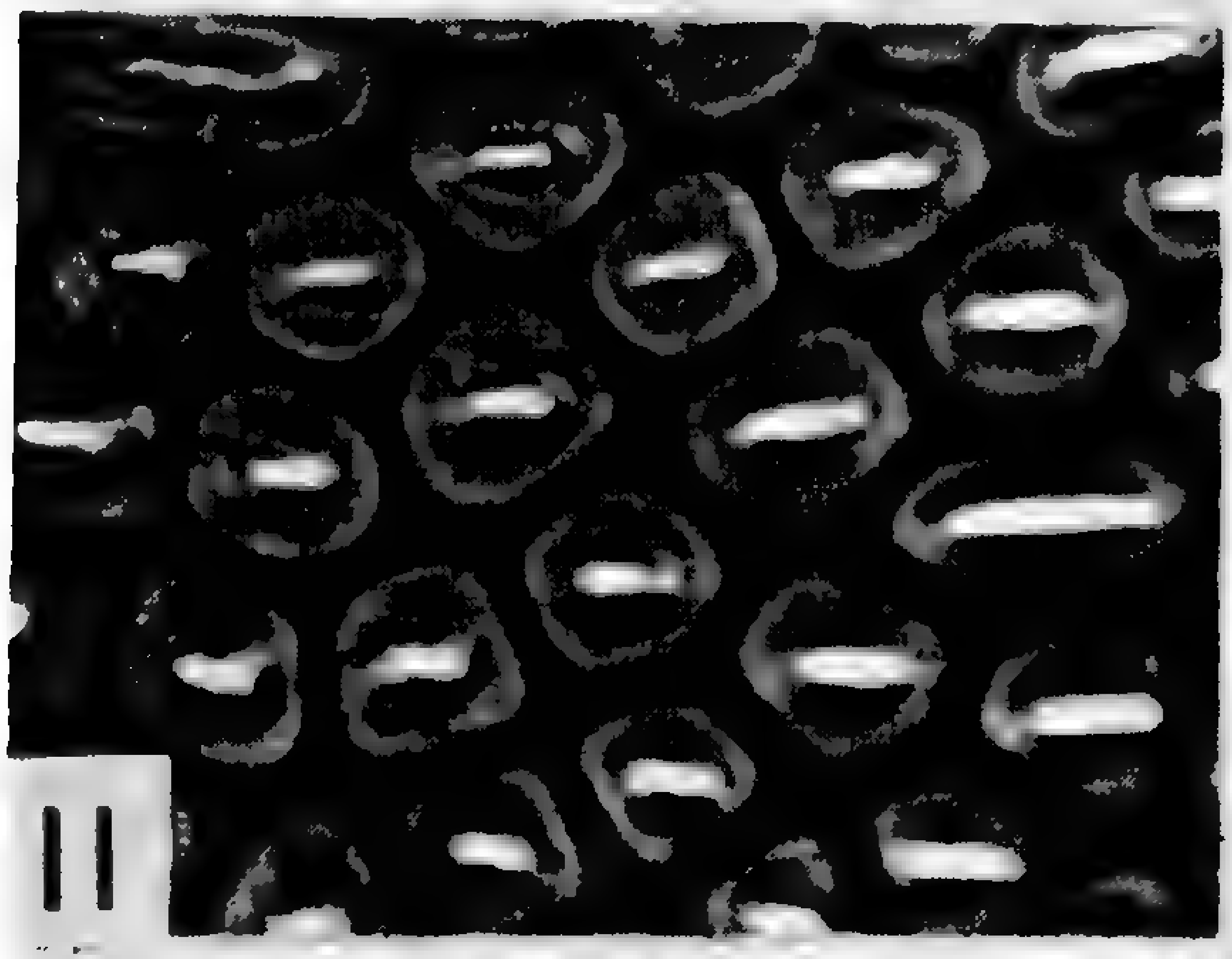
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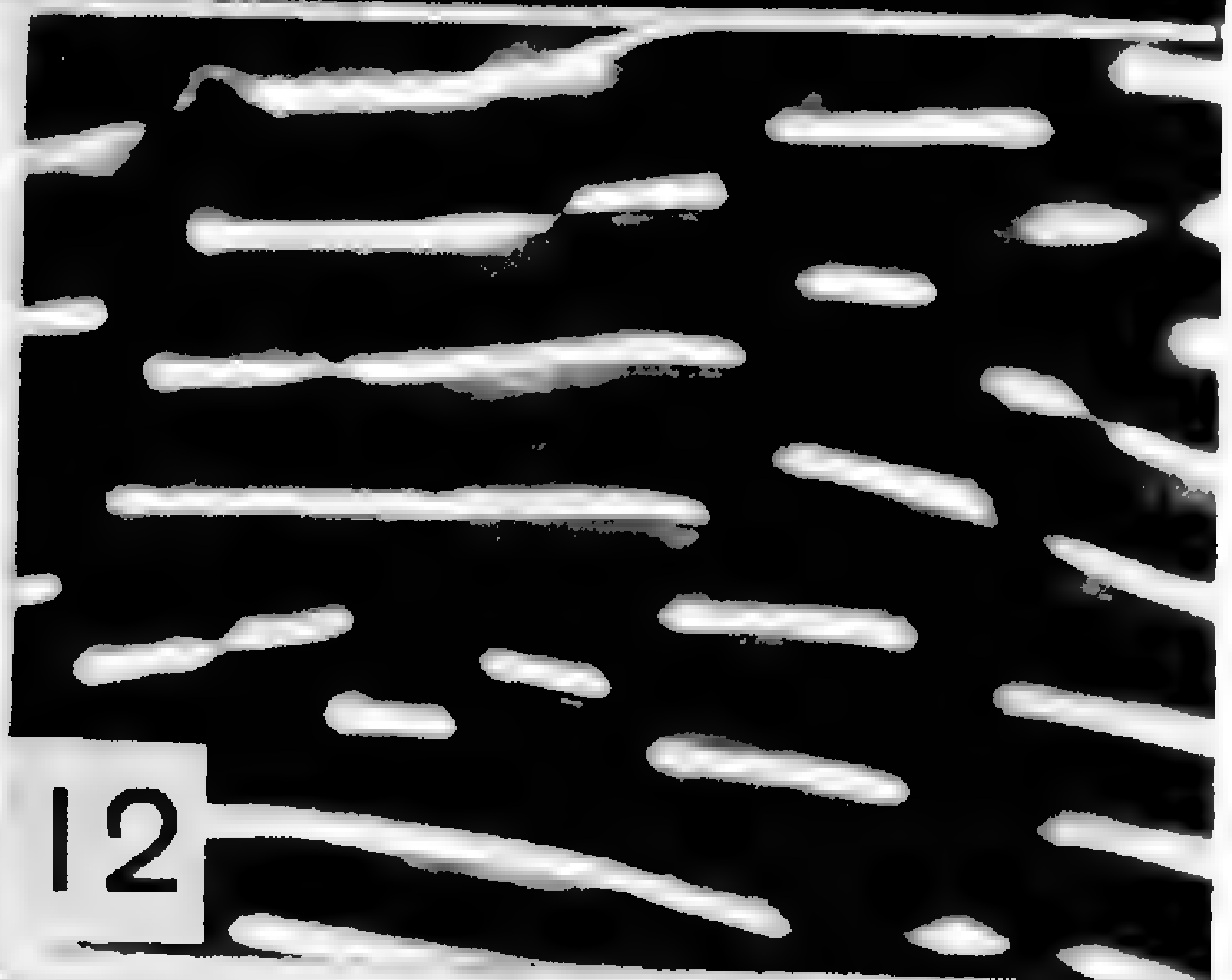
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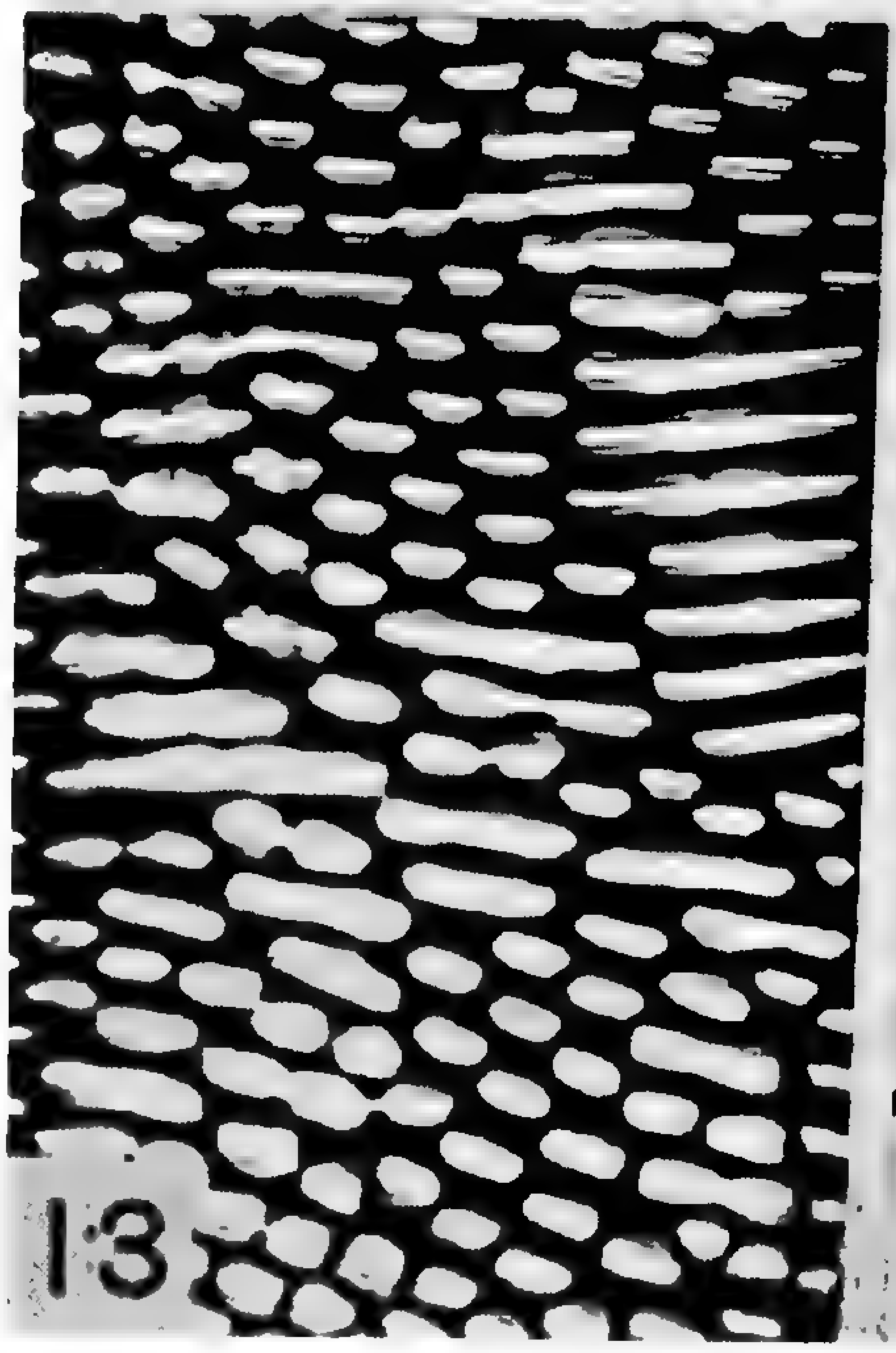
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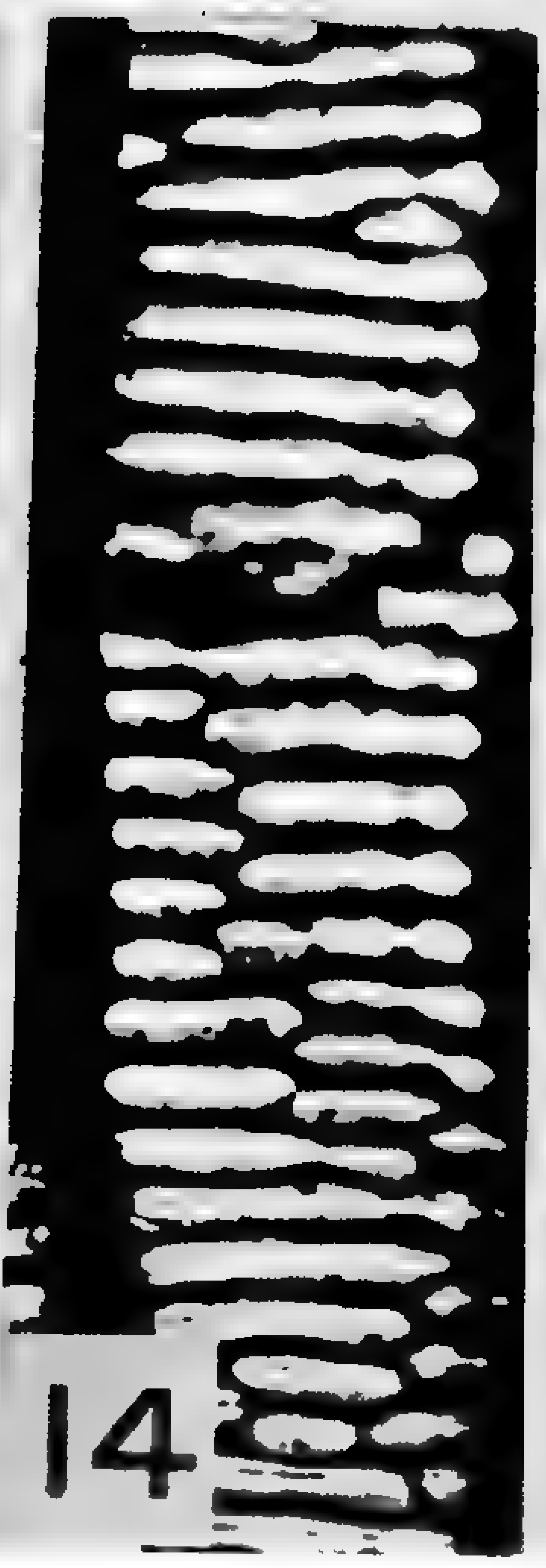
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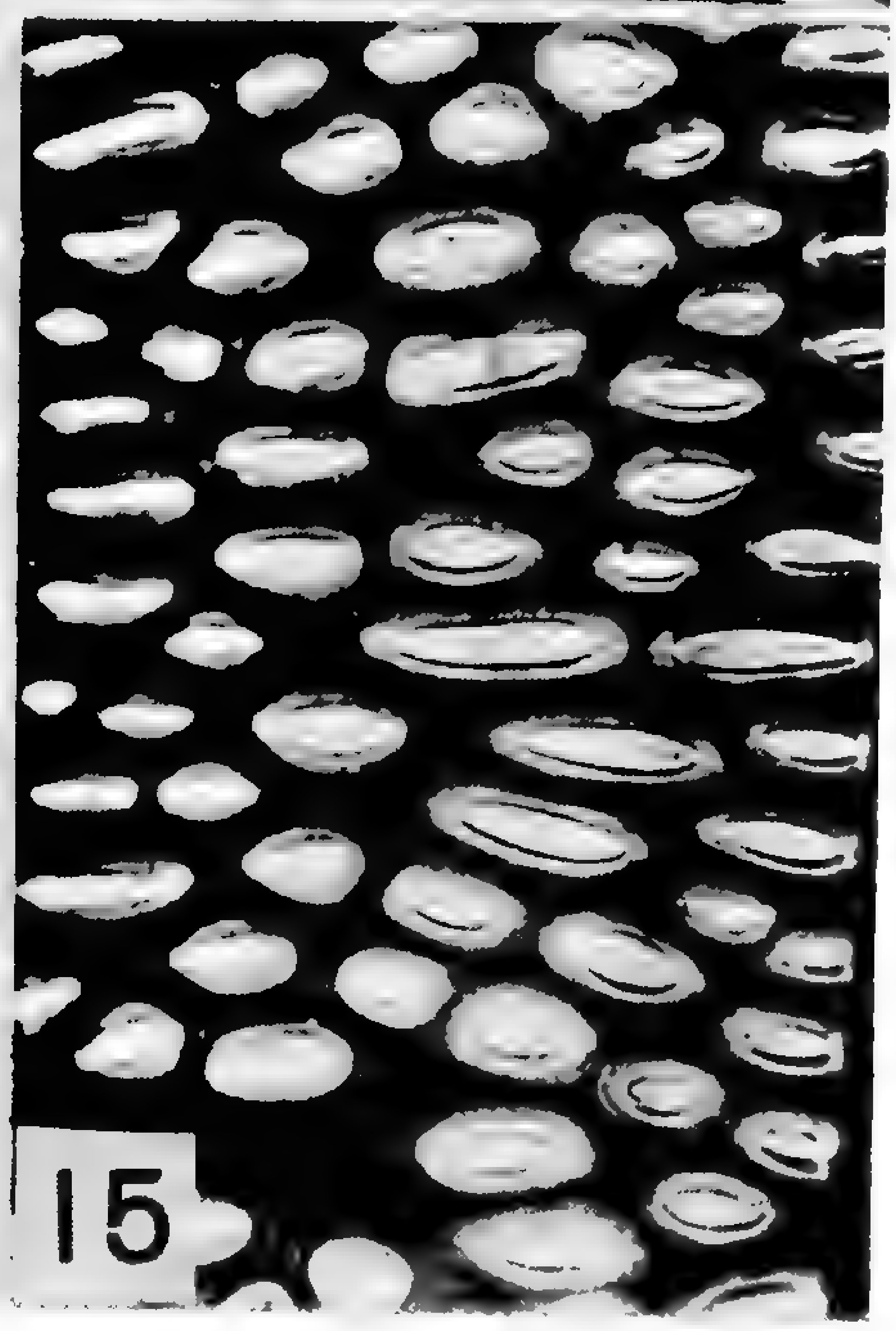
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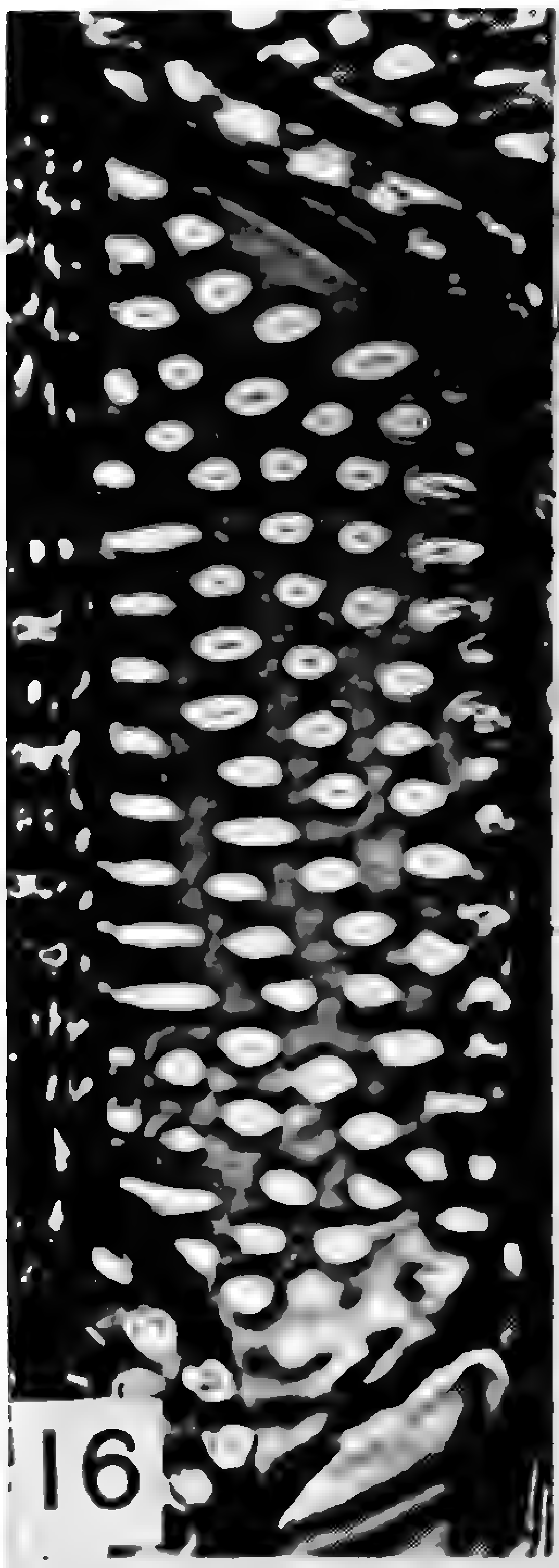
Bailey & Srivastava, Leaf-bearing Cactaceae, IV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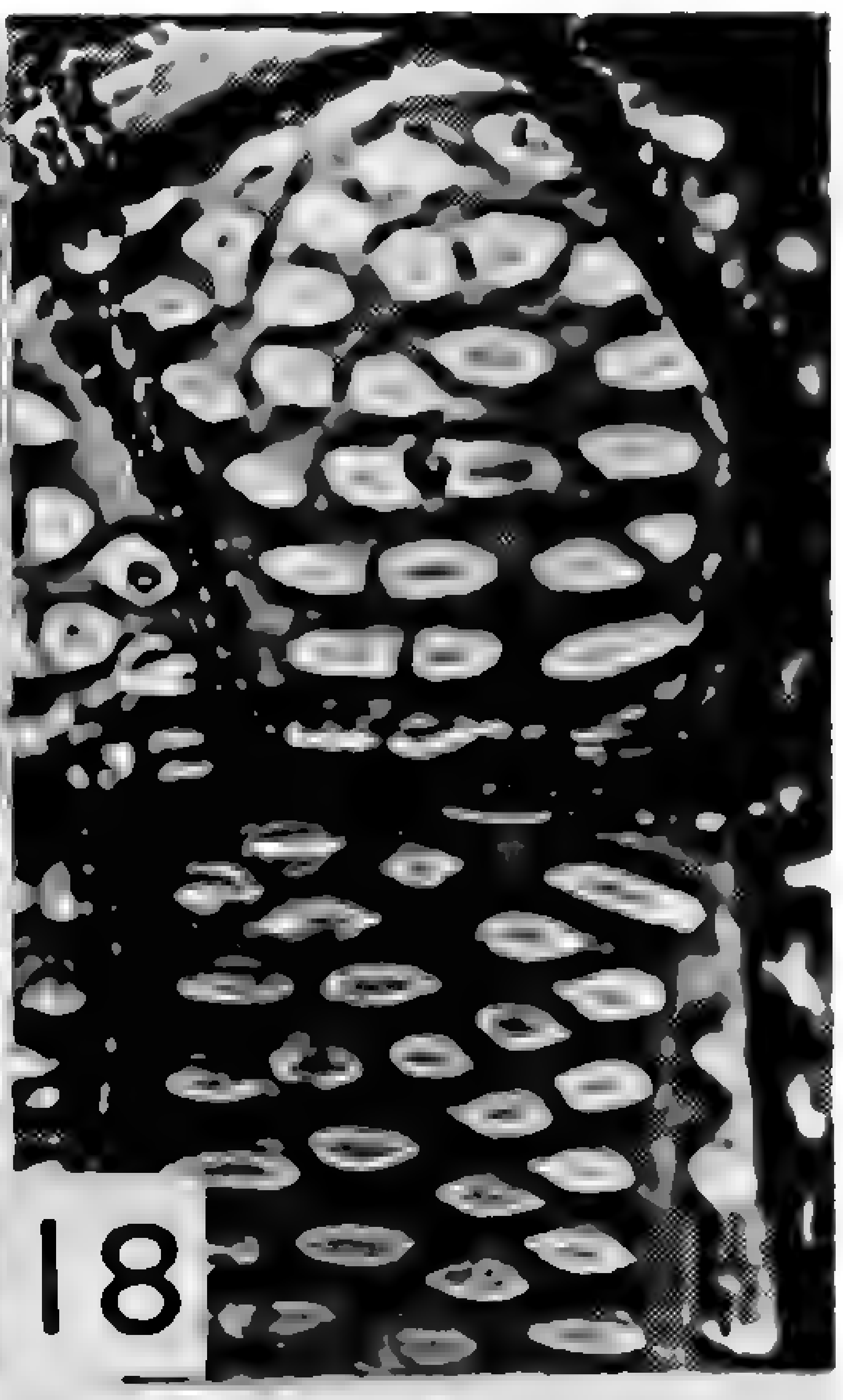
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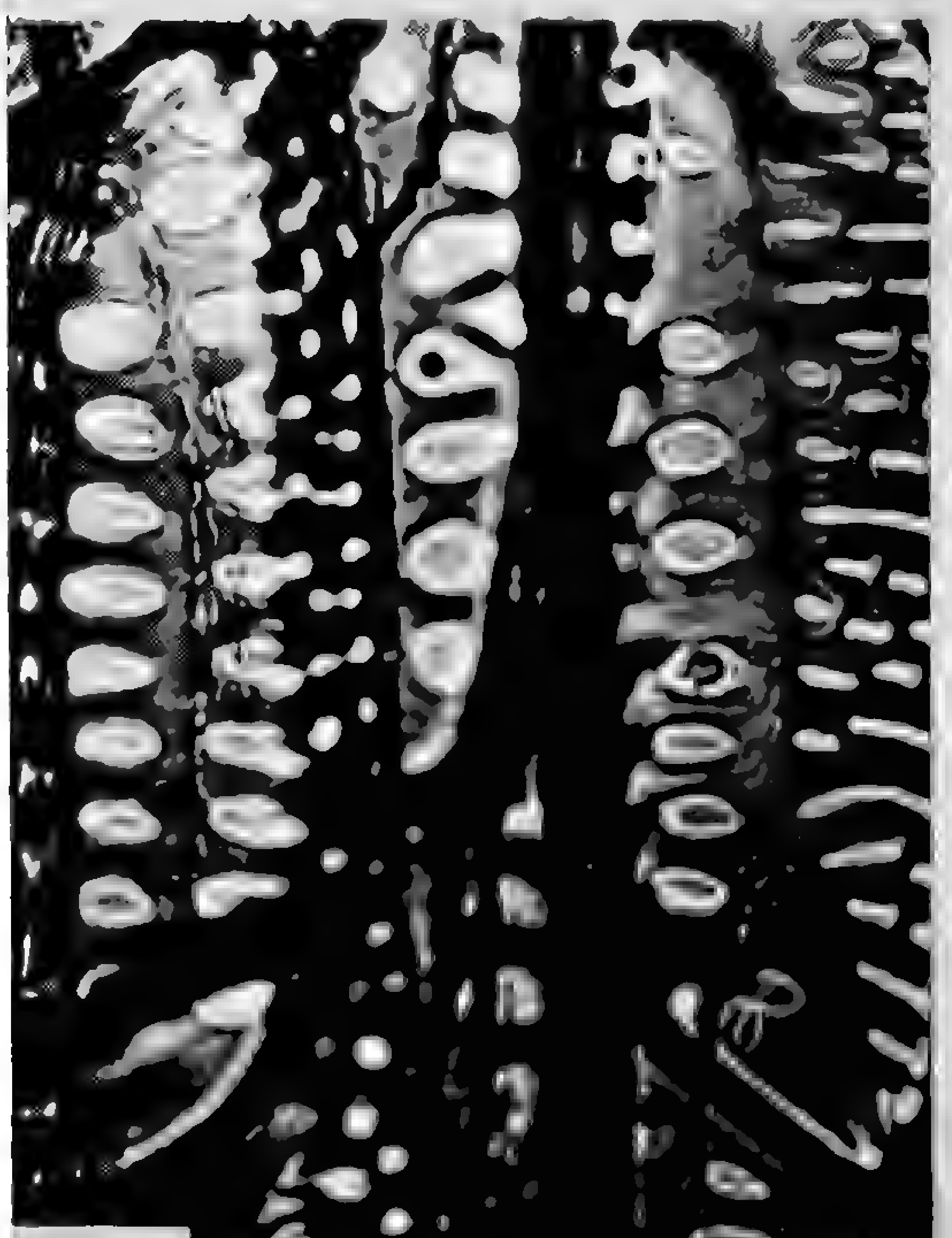
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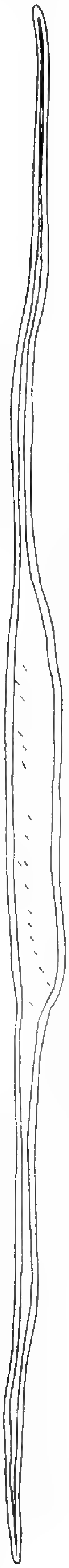

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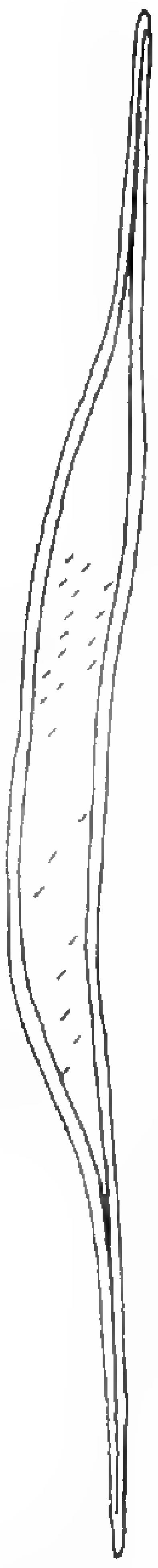

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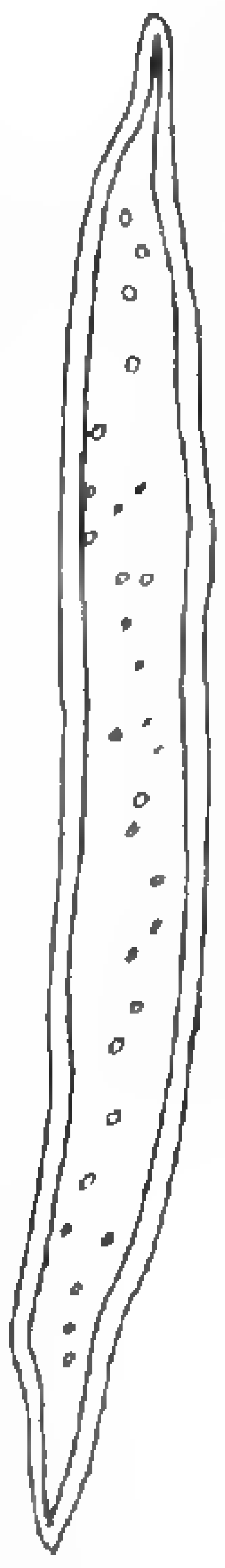

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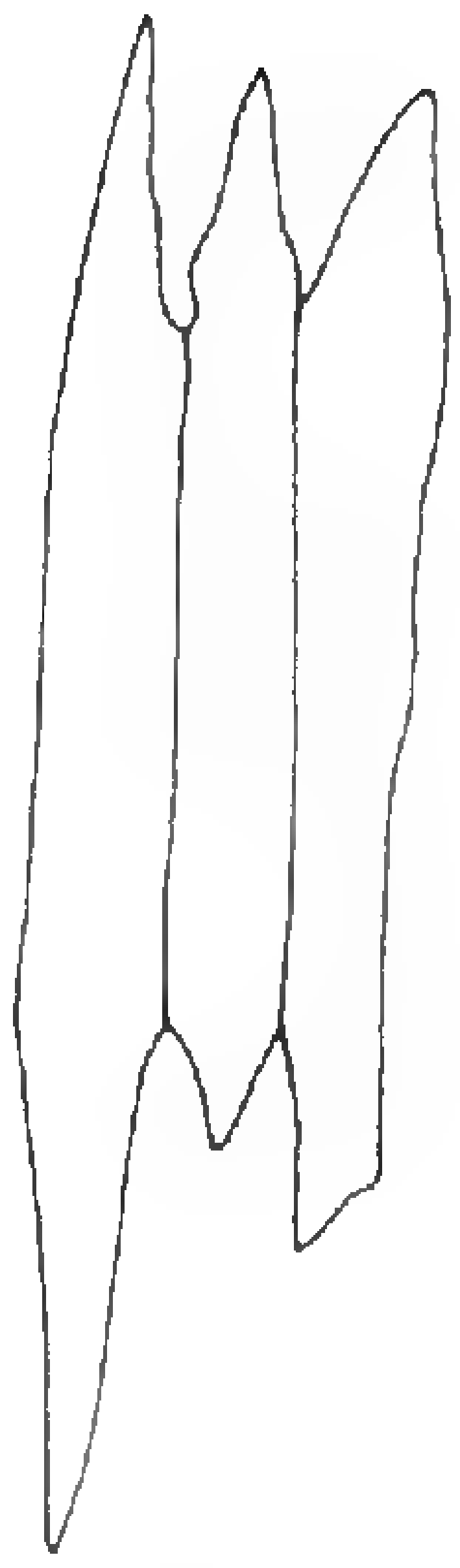

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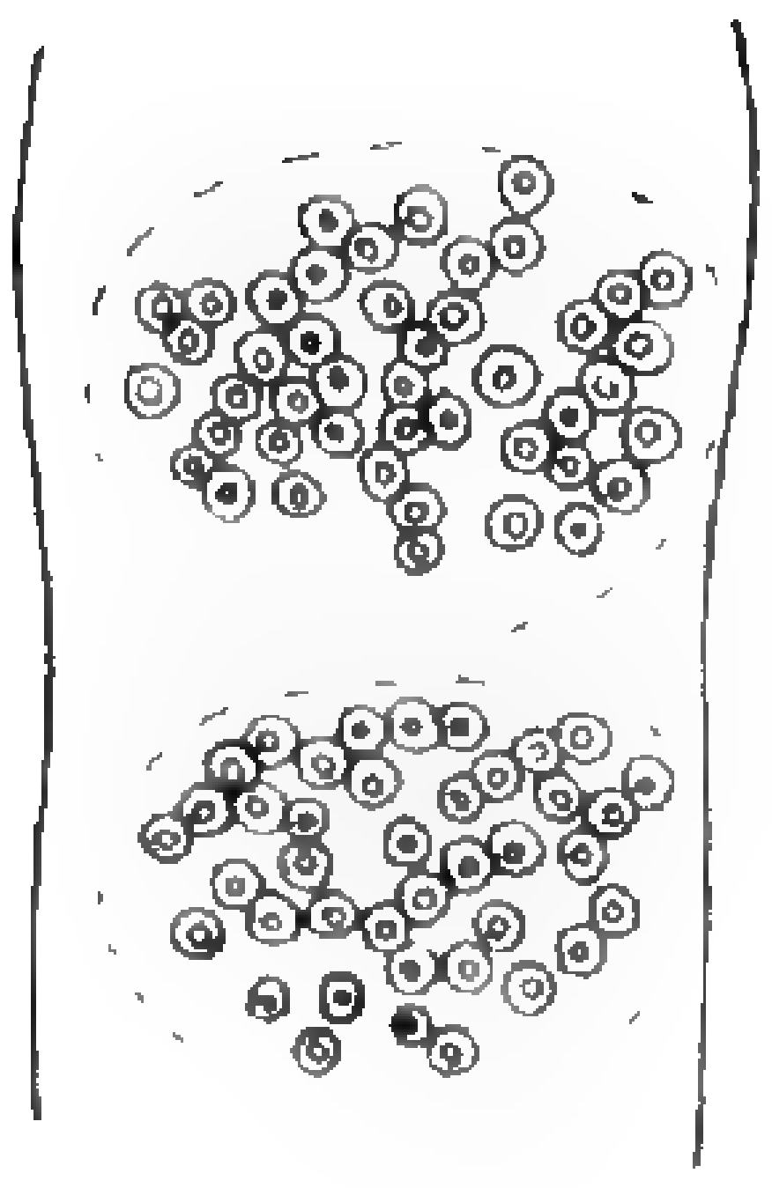

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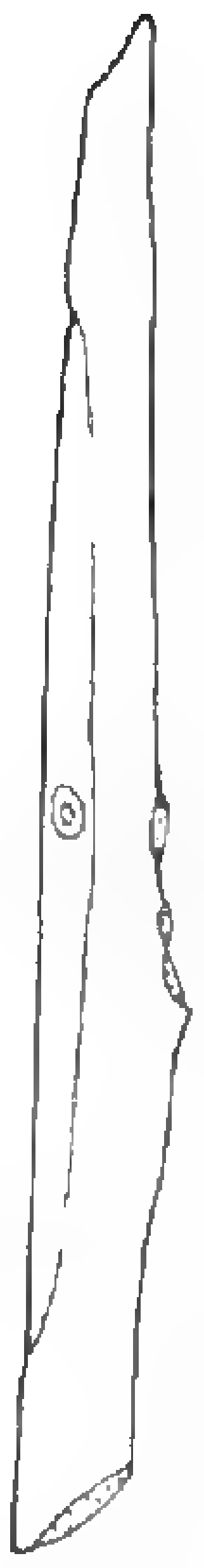

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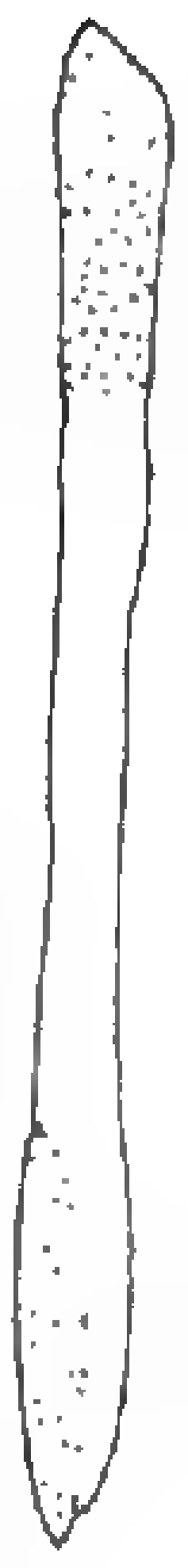

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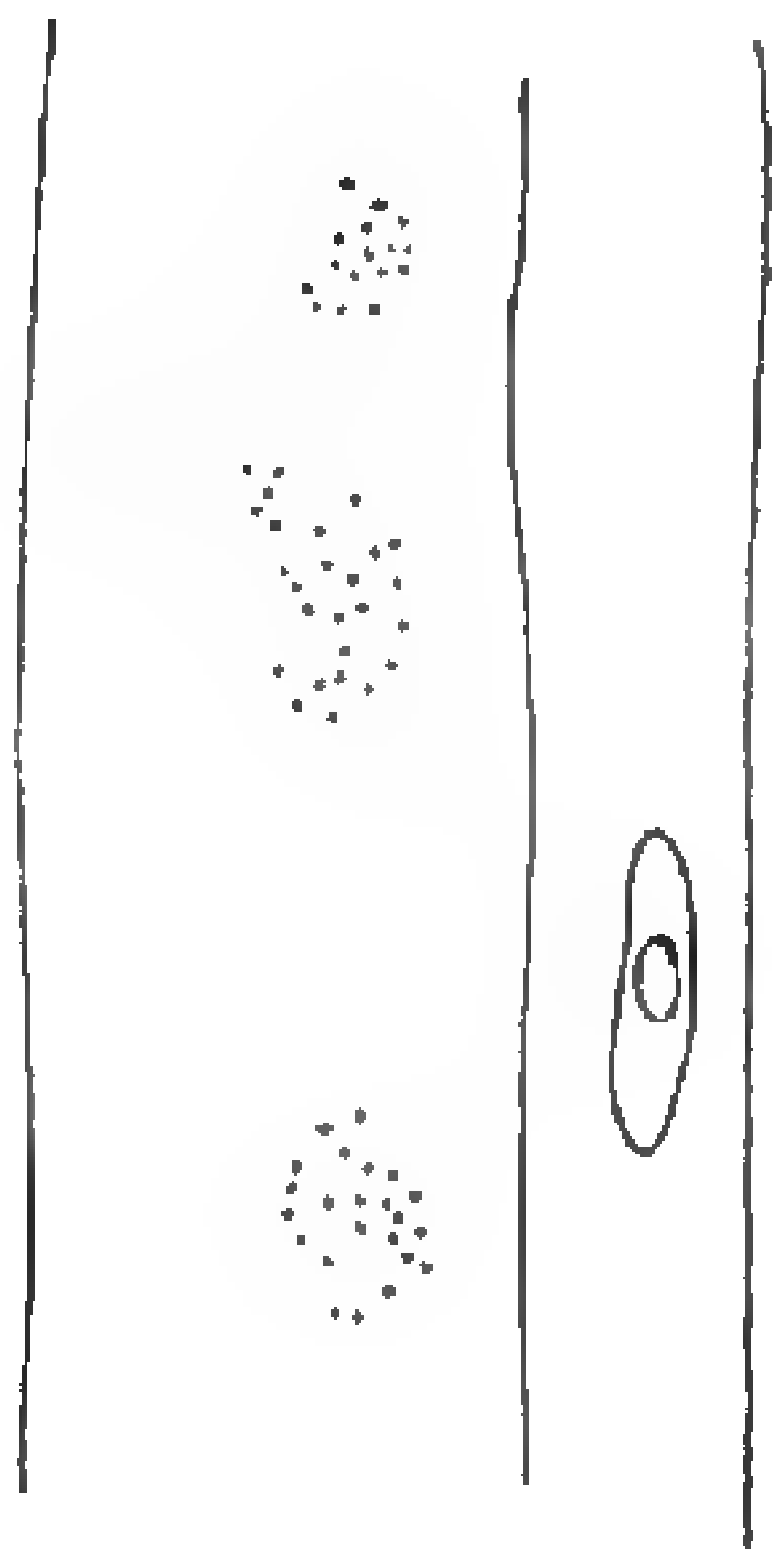

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BAILEY & SRIVASTAVA, LEAF-BEARING CACTACEAE, IV

ON THE ORIGIN OF CARAGANA SINICA[1]

RAYMOND J. MOORE

THE SHRUB LONG KNOWN as *Caragana chamlagu* Lam. probably was introduced to Europe by Father Pierre d'Incarville, who sent seed of many plants collected near Peking, China, to the Jardin des Plantes, Paris, in the period 1740–1756 (Bretschneider, 1898). Loudon (1844) stated that the species was introduced to Great Britain in 1773. Apparently it has remained since the eighteenth century one of the less commonly cultivated shrubs. Rehder (1941) has pointed out that the overlooked epithet *Robinia sinica* of Buc'hoz has priority over that of Lamarck and, to avoid confusion, the name *Caragana sinica* (Buc'hoz) Rehder will be used exclusively hereafter, although Komarov, Pojarkova, *et al.* have treated this entity under the name *C. chamlagu.* Chiefly on the basis of flower and calyx size, Pojarkova (1945) has divided *C. sinica, sensu lato,* into *C. sinica* and *C. ussuriensis.*

Caragana sinica, sensu lato, occurs widely in eastern China and far-eastern Siberia. It is a shrub 1–2 m. tall, apparently common in dry, rocky, or other well-drained sites. The leaves consist of 2 pairs of leaflets, usually pinnately arranged, but often so close together as to appear almost palmate; the leaflets are obovate, 10–35 mm. long, 5–15 mm. broad, rather coriaceous, glaucous above, the base cuneate, the apex retuse, mucronulate. The leaf rachis thickens and develops into a spine up to 25 mm. long which persists after the leaflets drop. The persistent rachises and the spiny stipules (5 mm.) give the bush its conspicuous spiny character. The flowers are large, 20–30 mm. long; the calyx 9–14 mm. long, 5–6 mm. broad, with lobes 2–3 mm. long; the pedicel attachment asymmetrical; and the calyx almost gibbous. The flowers are borne one or two per node on stalks 10–20 mm. long, articulated in the middle between pedicel and peduncle. The corolla is pale yellow, usually with a rose or bronze tinge which deepens with age.

It is generally agreed that *Caragana frutex* and related species comprise the only species-group to which *C. sinica* is clearly related. Komarov (1908) placed *C. sinica* in his series FRUTESCENTES. He recognized its unique character and regarded it (*loc. cit.*, p. 370) as the closest claimant to the position of generic prototype. He based this view on its leaf character, noting that at an early age the leaf is palmate but later becomes pinnate. This transition he held to be a phylogenetic recapitulation, apparently regarding palmate leaves as ancestral to pinnate. Although not clearly stated, it appears that Komarov did not refer to the form of early seedling leaves but to the varying forms seen on adult plants. He believed

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[1] Contribution No. 128 from the Plant Research Institute, Canada Department of Agriculture, Ottawa.

(p. 371) that different environmental conditions then had resulted in the evolution from *C. sinica* of both palmate-leaved species (FRUTESCENTES) and pinnate-leaved species (ALTAGANAE) and subsequently from these, all the other series. *Caragana sinica* thus assumes special importance as the foundation of Komarov's phylogenetic scheme. Doubtless as a result of this opinion, he designated east Asia (range of *C. rosea*, *C. fruticosa*) as the primary center of species formation.

To show specific relationships more exactly, Pojarkova (1945) divided the series FRUTESCENTES Kom. into three more homogeneous but related series: CHAMLAGU, FRUTESCENTES *emend.*, and GRANDIFLORAE. The series CHAMLAGU Pojark. consists of *C. sinica* and *C. ussuriensis* (Regel) Pojark. The latter taxon had been described by Regel as *C. frutex* var. *ussuriensis*, and, as such, was placed in the synonymy of *C. sinica* by Komarov (1908).

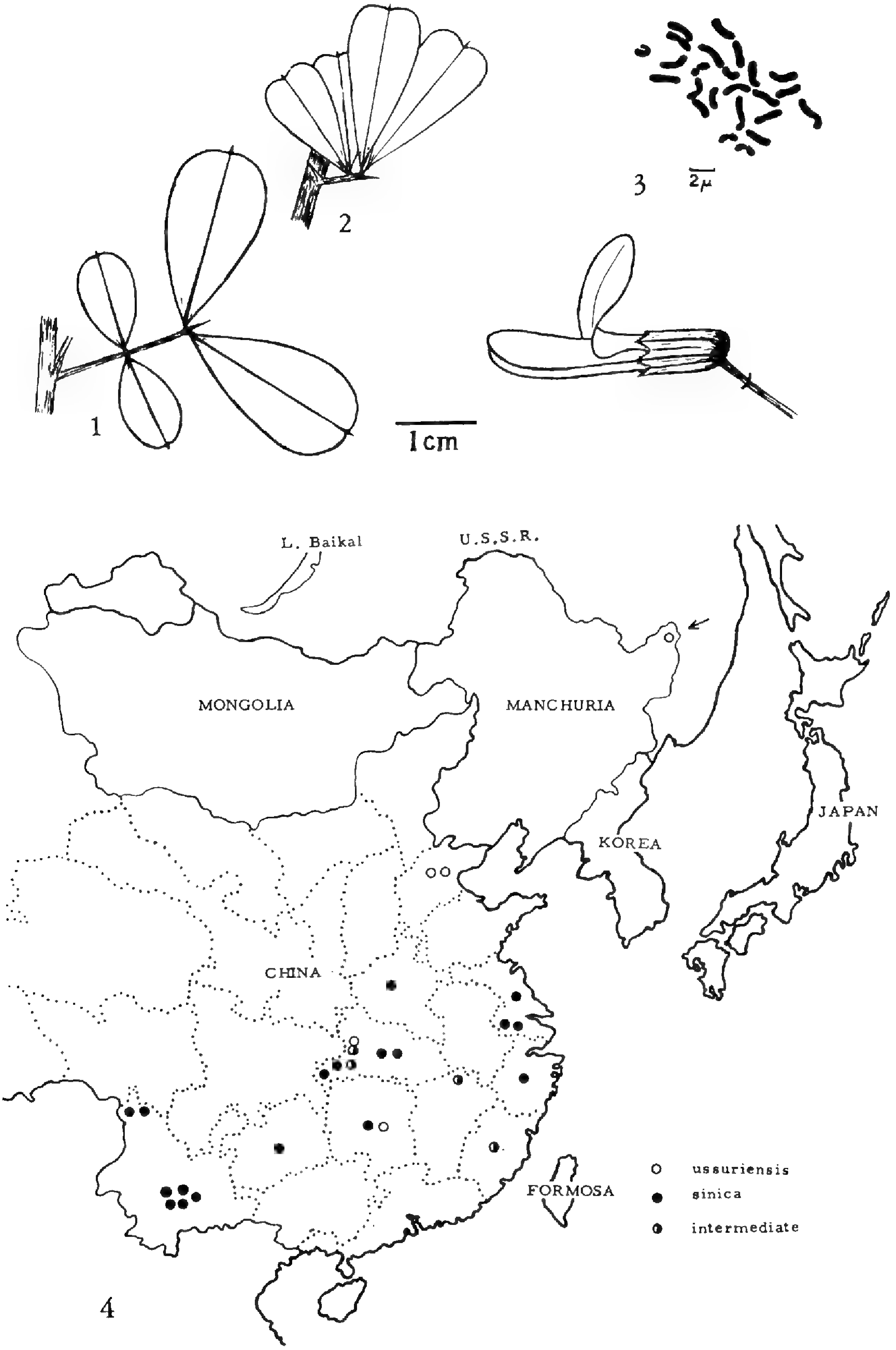
Pojarkova separates *Caragana ussuriensis* and *C. sinica* chiefly on floral characters: flower length, 23–25 mm. *vs.* 28–30 mm.; and calyx size, to 9 mm. long × 5 mm. broad *vs.* 12–14 mm. long × 6 mm. broad. The leaflets of *C. sinica* are said to have a broader, obovate blade and broader base, giving a more rounded outline, whereas those of *C. ussuriensis* are narrow with a narrowly cuneate base. Only *C. ussuriensis* occurs in the U.S.S.R. (region of the river Ussuri just north of Manchuria) from whence it extends southward into Manchuria and northern China. It is reported that *C. sinica* has a more southerly distribution in China: Hopeh (Chili) to Yunnan. The impression is conveyed by Pojarkova that the range of *C. ussuriensis* is more northerly than that of *C. sinica* and that, although they overlap in northern China, *C. sinica* alone occurs in southern China. The two taxa are illustrated in FIGS. 1 and 2.

The illustration accompanying Buc'hoz's (1779) description of *Robinia sinica* is apparently drawn life-size and shows the larger-flowered plant. Mature open flowers are 30 mm. long, the calyx being 11–12 mm. long and 6 mm. broad, measurements which fall within the limits indicated by Pojarkova for *C. sinica*.

MATERIALS AND METHODS

In the course of a survey of chromosome numbers in *Caragana*, a special attempt has been made to obtain living material of *C. sinica*. Seeds have been received under this name from twelve botanic gardens (eleven European) but the resulting seedlings proved to be not the desired species but typical plants of *C. frutex*, *C. arborescens*, *C. pygmaea*, or *C. aurantiaca*. Some of these species are not closely related to *C. sinica*; all are readily distinguished from it and it is considered that the error is due solely to incorrect identification of the seed parent. In two cases, leaflets in the seed packet indicated that the source of the seed was *C. arborescens* and *C. pygmaea*, as were the resulting seedlings.

Living plants of *Caragana sinica* have been obtained from only one source: F. J. Grootendorst & Sons, Boskoop, Holland. The species has been propagated asexually in this nursery. It was received there at some



FIGS. 1–4. Morphological details and distribution of *Caragana sinica*. 1, Leaf and flower of *C. sinica*. 2, Leaf of *C. ussuriensis*. 3, Somatic chromosome complement of *C. sinica* (cultivated triploid). 4, Distribution of *C. sinica, sensu lato*.

time before 1928, but the source is unknown (H. J. Grootendorst, personal communication, 1961).

Cuttings of the rare species *Caragana rosea* were received from the Arnold Arboretum, Harvard University, where there is a single shrub grown from seed collected by William Purdom (seed lot 9a), in 1909, in Weichang, Chili (Hopeh) Province, China. This collection was determined as *C. rosea* by Rehder (1926).

Herbarium material of *Caragana sinica* from the Arnold Arboretum (A) and the Gray Herbarium (GH) of Harvard University and from the United States National Museum (US), as well as that in the Herbarium, Canada Department of Agriculture (DAO) has been examined. Particular attention has been paid to the characters which separate *C. sinica* and *C. ussuriensis* and to the condition and size of the pollen. Pollen was mounted in 45% acetic acid and stained with dilute cotton blue. Grains with a protoplast which completely filled the cell and stained blue were counted as viable. The grains are thin walled and smooth; the diameter stated is the measurement to the outer surfaces.

MORPHOLOGY, POLLEN CONDITION, AND NATURAL DISTRIBUTION

Little variation was found in the size of the flower on any single herbarium specimen, and it is believed that these size-characters are reasonably constant for any individual. A similar opinion has been formed from observation of numerous living plants of various species of *Caragana* over a number of years, and it is believed that the size-characters used by Pojarkova reflect genetic differences and are reliable for systematic purposes.

Following the floral and leaf characters designated by Pojarkova, 34 of 38 herbarium specimens were referred either to *Caragana ussuriensis* or to *C. sinica*. The determination of the remaining four, all wild Chinese collections, was less certain. Two had the flower size of *C. sinica* with a smaller calyx, and two had the smaller flower of *C. ussuriensis* with a calyx similar in size and appearance to that of *C. sinica*.

The localities of the Asiatic collections are plotted on the map of eastern Asia (FIG. 4) and are listed below. A few collections were omitted, either because of uncertainty about the location or because only a general area was indicated. Symbols were placed in the center of a province when data or knowledge were insufficient to place them more accurately.

It is concluded, in agreement with Pojarkova, that the small-flowered plant occurs from northern China to Siberia and that the large-flowered plant is dominant in southern China. The small-flowered plant seems to extend as far south as approximately 27° N, well into the range of the large-flowered entity, and a few intermediates were found in the zone of central China in which both entities occur.

Pollen of 34 herbarium specimens, 27 of these wild Asiatic collections, was examined, and in none was the pollen 100% normal. The samples consisted of mixtures of normal grains with full, densely staining protoplasts; grains full but with a thinner, lightly staining content; grains only partially filled with a thin protoplast; grains empty and collapsed; and empty micro-grains. Difficulty was experienced in classifying some grains since the first two classes intergrade. Only grains with a full, dense protoplast were classed as normal in the following counts. The micro-grains probably were formed from lagging chromosomes excluded from the tetrad nuclei and indicate a high degree of meiotic irregularity.

The maximum percentage of normal pollen found among the herbarium specimens was 80, the minimum, 3; 12 lay in the range 0–39%, 14 had 40–50%; 8 had over 50%. The size of the normal grains ranged from 18 to 30 μ but this range was not found in any single sample. The modal range was 20–40 μ (13); in 6 samples the lower limit was 18–20 μ, and the upper limit was lowered correspondingly. The range in 10 samples was from 20 μ to 25–27 μ, and in 6 the smallest grains were 23 μ, the largest 27–30 μ.

Pollen measurements (unpublished) made on other *Caragana* species do not show a correlation between the diploid and tetraploid chromosome number and pollen size. The samples are almost invariably 100% normal. Pollen of seven diploid species falls in the range 20–27 μ; two additional diploids measured 23–29 μ and 28–30 μ. Pollen of one tetraploid species (*C. frutex*) measured 20–27 μ, of another (*C. spinosa*) 24–34 μ. No correlation between pollen size, probable chromosome number, or morphological features is believed to exist in *C. sinica*, and the pollen size variability is attributed to gene differences between the various populations. The significant feature lies in the consistent absence of wholly good pollen and the similarity of the condition of all samples. No difference was found in the range of size or of fertility between specimens classed as *C. sinica*, *C. ussuriensis*, or intermediate. Pollen samples of the latter group fall in the range of 40 to 60% normal and thus were no more "hybrid" than those of the more typical groups. No certain correlation was found between the degree of pollen fertility and geographical location, although there may be a tendency for plants with the higher percentages (70% plus) to occur on the extremes of the range (Northern China and Yunnan).

Caragana sinica (Buc'hoz) Rehder, Jour. Arnold Arb. 22: 576. 1941.

Robinia sinica Buc'hoz, Pl. Nouv. Decouv. 24. *t. 22.* 1799.

Flowers 27–30 mm. long, calyx 11 mm. or more, leaflets broadly obovate.

China. Chekiang: without location, *Barchet 146* (us). Fukien: Diongloh Hsien, *Chung 1239*, Apr. 5, 1923 (a). Hopeh (Chili): Hsi Yu Ssu, *Liu 2286*, June 8, 1929 (a). Hunan: Tschangscha, *Handel-Mazzetti 638*, Apr. 14, 1918 (a). Hupeh: W. Hupeh, *Wilson s.n.*, Apr. 1900 (us); W. Hupeh, *Wilson 2203*, May 1907 (gh); without location, *Henry 5378* (gh), *3812* (us). Kansu(?): Fengwangschan, *Forbes 113*, Apr. 22, 1877 (a). Kiangsu: without location, *Tsu 436*, Apr. 26, 1920 (a): Yun Dai Shan, Nanking, *Tso 79*, Apr. 17, 1926

(A): without location, Faber *s.n.* (A). KWEICHOW: Kweiyang, *Teng 90079*, Apr. 15, 1936 (A). YUNNAN: East of Tengyueh, *Forrest 19343*, Apr. 1921 (A, US); Yunnanfu bei Puchli, *Schneider 214*, Mar. 7, 1914 (A); zwischen Ssiao und Schin lung, *Schneider 4046*, Mar. 9, 1914 (A, GH); without location, *Bonati* or *Maire 7286* (US); Yunnanfu, *Smith 1582*, 8/3, 1922 (A).

Cultivated. JAPAN. Hondo: Musashi, *Teizo 1648*, July 2, 1904 (A); without location or collector, May 13, 1910 (US 1311798); Nagasaki, *Maximowicz s.n.*, 1863 (GH). FRANCE: Paris, *Gay*, *s.n.*, 1822 (GH). Bavaria, Scherzer *s.n.*, Apr. 1, 1906 (DAO). UNITED STATES: Washington, D.C., Apr. 24, 1886 (US 137850); Washington, D.C., 1915 (US 786433); Chico, Calif., Apr. 25, 1922, S.P.I. 22981 (originally collected in Soochow, Kiangsu, China) (A). CANADA: Royal Botanic Gardens, Hamilton, Ont., *Rhodes* & *Florian 3587*, June 11, 1952 (DAO); Dominion Arboretum and Botanic Garden, Ottawa, Ont. *Moore*, 53-249-1, May 27, 1960 and *Moore*, 60-231-45, May 29, 1961 (DAO); Experimental Station, Morden, Man., *Rhodes* & *Vitens 4583*, Sept. 10, 1953 (DAO).

Caragana ussuriensis (Regel) Pojark. Flora U.S.S.R. **11**: 395. 1945.

Caragana frutescens β ussuriensis Regel, Mem. Acad. Sci. St. Petersb. ser. 7. **4**(4): 44. 1861.

Flowers 23–26 mm., calyx to 9 mm., leaflets narrowly obovate with cuneate base.

China. HOPEH (Chili): Western Hills, Peiping, *Chiao 21361*, May 7, 1929 (A); Nankow, Peiping, *Chiao* 21253, May 11, 1929 (A). HUNAN: Yi Chang District, *Tsang 23430*, Mar. 21–29, 1934 (A). MANCHURIA: Ussuri super, *Maximowicz s.n.*, 1860 (US). NORTH CHINA: without location, *Bunge s.n.* (GH).
Cultivated. JAPAN: without location, *Zuccarini s.n.*, 1842 (GH).

Specimens intermediate between *Caragana sinica* and *Caragana ussuriensis*.

China: HUPEH: W. Hupeh, *Wilson 2203*, May 1907 (US); Patung, *Wilson s.n.*, Apr. 1907 (A). KIANGSI: Kipkiang, *Bullock 151*, Apr. 20, 1892 (US). FUKIEN: Diongloh Hsien, *Chung 1239*, Apr. 5, 1923 (A).

CULTIVATED CARAGANA SINICA

The five plants purchased from the Grootendorst nursery are identical in appearance, doubtlessly having been propagated asexually from a single plant. Flowers are 30 mm. long, with the calyx 11–12 mm. long and 6 mm. broad. The leaflets are broadly obovate, to 20 mm. long, 9 mm. broad, coriaceous, and glaucous. On the basis of flower and calyx size and leaflet shape, the plants are to be classed as the larger-flowered species, *C. sinica* sensu Pojarkova. In all characters they are indistinguishable from collections of other cultivated and wild Asiatic plants.

CYTOLOGY. The chromosome number was determined from leaf squashes to be $2n = 24$ (FIG. 3). The basic number of the genus is 8: hence this number is triploid. Meiosis was studied in one plant growing outdoors at Ottawa. The configurations at Metaphase I could be fully analyzed in only eight cells but these seem to be representative. The minimum pairing seen was 16 univalents and 4 bivalents; 8 bivalents and 8 trivalents were seen in two cells. The trivalent was the largest association found, and three trivalents was the maximum number found in a single cell. The average pairing for eight cells was $8^{I} + 6.7^{II} + 0.86^{III}$.

Approximately 40% of mature pollen grains are normal in appearance. Grains judged to be normal have a full, dense protoplast and measure 20–24 μ in outer diameter. Pollen was spread on a mixture of 2% agar plus 5% sucrose, and germination of at least 50% of these full grains was observed. This agar medium has been found to give good germination of pollen of many species of *Caragana*.

Flower Biology. At Ottawa, the shrubs flower from late May to mid-June, meiosis occurring in buds 5–6 mm. long in the period May 10–17. Over the past ten years it has been observed that varying weather conditions cause little variation in the onset of flowering in *Caragana* species, at most, two to three days.

Small aborted pistils were noted, but probably not over 10% of the flowers are defective. No other abnormality was observed. The style elongates markedly and extends approximately 2 mm. beyond the keel at anthesis. This feature favors cross-pollination and probably makes insect action necessary even for self-pollination. The plants studied were located approximately 100 feet from other *Caragana* bushes (*C. arborescens*, *C. frutex*, *C. aurantiaca*) and separated by various other trees and shrubs. It is highly probable that the 5 plants of *C. sinica* were not pollinated from other species. Most flowers dropped without ovary enlargement; some showed slight enlargement but dropped in two to three days. A smaller number, estimated at 8–10%, developed conspicuously enlarged ovaries (25–28 mm.) which turned green and for a week appeared to be forming seed. However, all turned brown and fell. Some of the shrubs have been observed for three years and no seed has been formed. Plants from the same source grown at the Experimental Farm, Morden, Manitoba also are sterile (personal communication). Pollen of *C. sinica* was used to pollinate shrubs of *C. arborescens*, *C. microphylla* and *C. frutex* but no seed resulted. Two of 38 flowers of *C. frutex* pollinated by *C. sinica* showed slight ovary enlargement before dropping.

Ovule Histology. Ovaries of various sizes, pre- and post-flowering, were fixed for histological study of the ovules. Several different types of ovule development were observed, but in all cases all ovules within a single ovary were similar.

Ovaries which lacked ovules or contained abnormal and partially developed ovules were found. Undeveloped ovules consisted of a small nucellus partially enclosed by a tissue two or three cells thick which presumably represented the outer, or perhaps both integuments. This integument did not enclose the micropylar end of the nucellus. No sporogenous tissue was differentiated and all tissues appeared unhealthy. Such ovules were found in mature open flowers, a stage when mature embryo sacs should have been present.

Structurally normal ovules were found in ovaries of some mature flowers. These ovules, approximately 525 μ long and 375 μ broad consisted of two integuments and nucellus, all apparently normal. Cell formations suggestive of aborted embryo sacs were observed in the nucellus. A linear formation of three compact cells, the micropylar one of which was the largest, was probably the product of meiosis. The innermost of the three was the most healthy and normally probably would be the functional megaspore. A large two-nucleate cell surrounded by disorganized tissue seemed to be an aborted early embryo sac. A four-nucleate cell (75 μ long, 15–20 μ broad) also was apparently an immature embryo sac. The most advanced structure seen was interpreted as a disintegrating mature embryo sac. This structure was 125 μ long, 20 μ broad and contained five recognizable nuclei and remnants of at least two antipodal cells. In all the above examples both sporophytic and gametophytic tissues were obviously in an unhealthy condition and incapable of continued development. Many ovules were so disorganized that the stage of embryo sac development could not be determined.

The large ovaries mentioned above (to 28 mm.) contained ovules that were enlarged by some 50% beyond the size of the most normal mature ovules. However, none of these contained embryos. Counts of the cell layers and measurements of representative cells indicated that ovule enlargement was due solely to cell enlargement in both the integuments and nucellus. By the time such ovaries drop, breakdown of the nucellus is advanced. A patch or narrow zone of empty collapsed cells in the area in which an embryo would normally be found is first seen. Dissolution of cell contents and collapse of the walls progresses through the middle of the nucellus from the micropylar to the antipodal end. It was usually observed that the two-celled peripheral layer of the nucellus at its micropylar end remained longest in apparently healthy condition. A zone of the inner integument adjoining the micropylar end of the nucellus appeared more active than the remainder of the integument endodermis. These observations together suggest that the integument cells at this point were absorbing the contents of the nucellus. In the final stage of ovule collapse only remnants of walls remained of the nucellus. No evidence of apomictic seed formation was observed and there is no reason to believe that these plants would ever set seed through either sexual or apomictic processes.

DISCUSSION

The occurrence of a major amount of aborted pollen in the living cultivated (Grootendorst) plant and in all known collections of *Caragana sinica* from the wild suggests that the species is of hybrid origin. Whether the species in nature is triploid, like the cultivated plant studied, cannot be decided with the available evidence.

Morphology of the species alone suggests a hybrid origin. That the leaf, which is pinnate with two pairs of leaflets, frequently appears to be palmate due to the lack of elongation of the rachis suggested to Komarov that the species was ancestral to both the pinnate and the regularly palmate series. An alternative explanation of this phenomenon is that *C. sinica* is a hybrid between a pinnate- and a palmate-leaved species. The variable-leaf type occurs otherwise only in the series SPINOSAE and DASYPHYLLAE, groups of central Asia morphologically very unlike *C. sinica*. It seems obvious that these do not bear on the present problem.

All authors agree that *Caragana sinica* is most closely related to *C. rosea* Turcz. The affinity appears in the number, shape and texture of the leaflets, the persistent spiny leaf rachis, the large flower (more than 2 cm.) which is pale yellow with a rosy tinge, and the large calyx which is longer than broad. The rose flower color is not known in other species of eastern China. *Caragana rosea* has a range in eastern Asia (Manchuria, Hopeh, Honan, Kansu, Chekiang [Rehder, 1926]) very like that of *C. sinica*.

If the hybrid nature of *Caragana sinica* is accepted, *C. rosea* must be proposed as one parent. A pinnate-leaved species of eastern China is required as the other parent, but the exact species cannot be named with an equal degree of assurance. The large flowers of *C. sinica*, larger even than those of *C. rosea*, point to another large-flowered species as the second parent. Such is to be found in *C. microphylla* Lam. (flowers 25 mm., calyx 9–12 mm.) a species of suitable leaf type and range as well.

It is therefore postulated that *Caragana sinica, sensu lato* (including *C. sinica* (Buc'hoz) Rehd. and *C. ussuriensis* (Regel) Pojark.) is a hybrid between *C. rosea* Turcz. and a pinnate-leaved species, probably *C. microphylla* Lam. In the opinion of the author it would be preferable to recognize the entities *sinica* and *ussuriensis* at infraspecific level under *C. sinica* (Buc'hoz) Rehd. It seems obvious that they have shared a common origin and are separated by characteristics of a minor order, quantitative rather than qualitative. The two populations have achieved geographic separation, and taxonomic recognition is justified.

A variation within *Caragana rosea* in flower and calyx size and leaflet shape, parallel to that used by Pojarkova to split *C. sinica* was noted in thirteen specimens (US) examined. These could be divided into large-flowered (flower 25–27 mm., calyx 9–11 mm.) and small-flowered (flower 20–24 mm., calyx 6–8 mm.) plants. The more rounded leaflet shape was not invariably associated with the greater flower size, nor was there an evident geographical correlation. The range in pollen size in *C. rosea* was 20–27 μ. The variation within a single plant was not more than 4 μ. However, no correlation between larger pollen size and flower size was found. The existence in *C. rosea* of variation of the same type as that seen in *C. sinica* is an additional indication of their close affinity.

The chromosome number of the single available accession of *Caranga rosea* was found to be $2n = 16$. This diploid number is surprising, since it might be expected that this species would be tetraploid like the closely related *C. frutex*. The latter was reported to be tetraploid ($2n = 32$) by

Tschechow (1930, as *C. frutescens*), and only this number has been found in nine accessions in the present work. *Caragana rosea* appears to be morphologically a more advanced species than *C. frutex*. The persistent thickened petiole seen in *C. rosea* is apparently developed from the deciduous petiole of *C. frutex*. Throughout the genus there is an evolutionary trend toward transformation of the deciduous petiole, first, to a persistent but essentially unthickened petiole and, finally, to a persistent and much thickened organ. The latter is the stout spine seen in many species. This trend is found in both the pinnate- and the palmate-leaved series.

The lower chromosome number of *Caragana rosea* can be reconciled with the view that the species is derived from *C. frutex* by postulating that diploid populations of *C. frutex* do or did exist. It is, indeed, not improbable that the series FRUTESCENTES arose at the diploid level from a pinnate-leaved ancestor. All pinnate-leaved species yet examined are diploid (Moore, 1958 and unpublished). The series FRUTESCENTES Kom. *em.* Pojark. contains six species which extend from the Black Sea to central Mongolia. Three other Chinese species not treated in the *Flora of the U.S.S.R.* but which should doubtless be referred to the series, extend the range of the series across northern China and Manchuria to the Pacific. *Caragana frutex* has by far the largest range of any single species (Black Sea to northwest Mongolia). Four species of relatively narrow distribution are found in Central Asia, south of Lake Balkhash. It seems possible that ancestral diploid "frutex" has spread from central Asia eastwards, developing in the most eastern part of the series range into *C. rosea*. The morphologically more primitive "frutex" stock may have become autotetraploid in central Asia, and, enjoying an advantage, accomplished the present wide distribution, particularly to the west and north from Central Asia. It seems probable that *Caragana frutex* in cultivation has come from the European part of the range, the western extreme, and thus is tetraploid. Diploid populations may still exist in Central Asia. Unfortunately the chromosome numbers of the more limited species of Central Asia are unknown. The range of *C. rosea* is second only to that of *C. frutex*, suggesting considerable age for the former species.

The triploid number of the Grootendorst plant of *Caragana sinica* suggests a hybrid origin between a diploid and a tetraploid species. Two serious difficulties at once arise. The tetraploid number is not known in either postulated parent species. A triploid hybrid, if at all like the Grootendorst plant, will be seed sterile, and it seems impossible that the extensive range of *C. sinica* was accomplished by any means other than by seed dispersal. Moreover, it is known that the species in China does set seed.

These difficulties may be relieved by suggesting that *Caragana sinica* in eastern Asia is diploid, a hybrid between diploid *C. rosea* and *C. microphylla*. A reduced, but still appreciable, seed fertility will then be possible. The triploid condition of the Grootendorst plant may have arisen in cultivation. The plants are morphologically indistinguishable from wild collections, and it is therefore improbable that a cross with a different tetraploid species has occurred in cultivation. The triploid condition may, however, have developed from the fertilization of an unreduced egg. Indeed, the different climactic conditions of Europe acting on a somewhat unstable hybrid genome may have caused the formation of an unreduced gamete. By random chromosome segregation, the additional haploid set could add an equal number of chromosomes from each parent to the diploid hybrid complement, converting some former bivalents into trivalents. The presence of equal numbers from each parental species might maintain the gene balance to such a degree that the triploid appears identical with the diploid. The absence of a noticeable difference in pollen grain size between diploid and triploid may be disregarded since no correlation between chromosome number and pollen size has been observed in the genus, and it is believed that pollen size depends solely on the genes governing this character.

It may be pointed out in conclusion that the widespread occurrence of pollen abortion in *Caragana sinica* is explained better by the hybridity hypothesis than by the prototype hypothesis of Komarov. It seems improbable that an ancestral stock would have retained a condition of abortive pollen, presumably due to meiotic irregularities, which had been eliminated from its descendants.

SUMMARY

It has been possible to obtain *Caragana sinica* (Buc'hoz) Rehd. from only one source in cultivation. The plant is triploid ($2n = 24$), pollen is 40% normal, no seed is set. All herbarium specimens, of wild and cultivated collections, have partially aborted pollen. It is postulated that *C. sinica* is a hybrid between *C. rosea* Turcz. and probably *C. microphylla* Lam. The hybrid in nature is probably diploid; the triploid cultivated clone may have arisen in Europe by the production of an unreduced gamete. The chromosome number of *C. rosea* Turcz. is $2n = 16$.

The author wishes to express appreciation to the curators of the herbaria from which material was borrowed and particularly to members of the staff of the Arnold Arboretum and Gray Herbarium with whom the author has corresponded. Dr. J. L. Thomas, formerly of the Arnold Arboretum, was most co-operative in making observations and procuring specimens and cuttings of the *Caragana rosea* in the Arboretum. At the author's request, Mr. H. J. Grootendorst looked into the source of the *Caragana sinica* sold by their nursery. Dr. T. Koyama, University of Tokyo, has informed the author that collections of *C. sinica* from Japan are undoubtedly introductions.

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SHIUYINGHUA, A NEW GENUS OF SCROPHULARIACEAE FROM CHINA

J. PACLT

IN HER MONOGRAPH of the genus *Paulownia* Sieb. & Zucc. (Scrophulariaceae), Hu (1959, p. 47) excluded *P. silvestrii* Pampanini & Bonati (1911) from that genus and transferred it to *Catalpa* Scop. (Bignoniaceae). I have had the opportunity of examining a photograph of the type specimen, *P. C. Silvestri 3286* (PLATE I), which shows characters of a tree clearly different from *Catalpa*. The characters which do not permit one to classify this plant as a member of the genus *Catalpa* may be summarized as follows:

1. The conspicuously dimorphic shape of leaves which are broadly ovate (cordate) in the axial position and elliptically lanceolate in the abaxial position on flowering branches.
2. The flowering branches which bear both leaves and almost laterally situated (axillary) loose cymes of flowers, as in *Paulownia fortunei* (Seem.) Hemsl. and substantially all other species of *Paulownia*. In *Catalpa*, the inflorescences are formed terminally and correspond to racemes or true panicles (thyrses).
3. The calyx which is five lobed and patelliform, as in *Paulownia* but not *Catalpa* in which the calyx is gamosepalous, splitting into two strongly convex lobes at anthesis. Also, the flower buds are generally oblong in *Paulownia silvestrii*, instead of showing the typically subglobular shape of the bud of *Catalpa*.

Although the fruit of *Paulownia silvestrii* is unknown, the original description of this species by Pampanini and Bonati leaves, in my opinion, no serious doubts about its correct position in the system. This place is to be found in the tribe PAULOWNIEAE Pennell of the family Scrophulariaceae.

However, the general shape and consistence of the flower buds of *Paulownia silvestrii* alone separate this species sufficiently from all known members of *Paulownia*. This character also seems to be Hu's basic reason for excluding *P. silvestrii* from *Paulownia*. In addition, her analysis of a flower bud of *P. silvestrii* revealed another difference concerning the structure of the young stigma (Hu 1959, p. 47). Some apparently less important differences between *P. silvestrii* and the other species of *Paulownia* may be found in the general appearance of the flowering branches and in the size of flowers. Accordingly, *Paulownia silvestrii* is best interpreted as the type of a distinct new genus which I have the pleasure of naming in honor of Dr. Shiu-ying Hu, of the Arnold Arboretum, to whom botany is indebted for her contributions to the knowledge of Chinese plants.

HOLOTYPE OF PAULOWNIA SILVESTRII (*Silvestri 3286*)

Shiuyinghua, gen. nov.

Plantae lignosae foliis simplicibus oppositis vel etiam ternatim verticillatis. Inflorescentia axillaria cymosa. Alabastra oblonga. Calyx lobis 5 membranaceis vel ± crassis. Corolla gamopetala quinquefida tubo inflato, lobis subaequilongis. Stamina didynama basi tubi inserta. Stigma (in alabastro visum) bilamellatum. Fructus ignotus. — Hab.: Asia temperata.

TYPUS GENERIS: **Shiuyinghua silvestrii** (Pamp. et Bonati), comb. nov. *Paulownia silvestrii* Pampanini et Bonati in Pampanini, Nuov. Giorn. Bot. Ital. II. **18**: 177. 1911. *Catalpa silvestrii* (Pampanini et Bonati) S. Y. Hu, Quart. Jour. Taiwan Mus. **12**: 47. 1959.

TERRA TYPICA: China, provincia Hupeh, praeter ripam fluminis Yang-tze Kiang (et praecipue fluvii Han Kiang), alt. 700 m., 20–30 Juni 1907, *P. C. Silvestri 3286* in hb. FI (et fragmentum, A).

The new genus *Shiuyinghua* becomes now the second known genus of the tribe PAULOWNIEAE. However, another genus, *Wightia* Wallich, is sometimes considered to belong here also. *Wightia* is likewise a woody genus and is represented in the Himalayan, Burmese, Chinese (Yunnan), Vietnamese (Tonkin), and Malayan floras. The relatively limited knowledge of the morphology of *Shiuyinghua* does not make it possible to elaborate for the time being more than the following key to the practical identification of the three genera.

Stamens surpassing the top of corolla; calyx entire, tight-fitting. .... *Wightia.*
Stamens not surpassing the top of corolla; calyx with 5 ± outstanding lobes.
    Flower buds oblong and slender, with stigma appearing bilamellate at this stage of immaturity; corolla not longer than 3 cm. .... *Shiuyinghua.*
    Flower buds broadly ovate and robust, with stigma appearing punctiform at this stage of immaturity; corolla at least 3 cm. long, mostly much longer. .... *Paulownia.*

My warmest thanks are due to Professor Richard A. Howard, director of the Arnold Arboretum, for his valuable help in sending me a photograph of the type specimen for study, as well as to Dr. Carroll E. Wood, Jr., editor of this journal, for his very kind criticism.

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PHENOLOGY OF TROPICAL PINES[1]

NICHOLAS T. MIROV

IN THE TEMPERATE ZONE pines shed their pollen during the season of the year vaguely designated as spring. At that time pollination occurs, and the ovulate strobili begin to develop slowly and, in warmer parts of the zone, continue to develop throughout the ensuing winter.[2] Ovules are fertilized the next spring, the cones develop throughout the second growing season, and the seeds ripen in the fall. Time elapsed between pollination and ripening of the seed thus is equal to about 15 or 16 months and embraces two summers and one winter. The farther south, the earlier pine pollen flies. Of course, many local environmental and genetic factors determine the time of pollen shedding. *Pinus radiata* D. Don sheds pollen in March both in its natural environment on the Pacific Coast and in low elevations of the Sierra Nevada. It is interesting that when *Pinus radiata* is planted in the southern hemisphere, for example, in New Zealand where it is known as *Pinus insignis* Douglas, it sheds pollen when it is spring there, i.e., during August or September.

It should be noted that photoperiod *sensu stricto* does not affect flowering of pines; they are photoperiodically neutral. That is, when a northern (long day) pine is moved to a more southern (shorter day) location, its flowering pattern is not changed. When a tropical (short day) pine is cultivated in a more northern (longer day) latitude, it continues to flower as freely as in its southern home.[3]

The closer to the Equator, the more distorted is flowering in pines. Even in the southern parts of the United States, pines, for instance *Pinus elliottii* Engelm. in southern Texas or in northern Florida, shed their pollen sometimes as early as the end of January. When you go farther south to the highlands of Mexico, early "flowering" of pines becomes a widespread phenomenon, and its relation to the four seasons of the year becomes really distorted.

I had occasion to observe *Pinus oocarpa* Schiede at the southernmost limits of pine distribution in Nicaragua. It was on a south slope of the mountains at an elevation of 4000 feet above sea level. It was the middle of February; the trees had just completed blooming (probably at the end of January), and numerous female strobili were still pink and tender, just having passed their "receptive stage." But the trees also possessed many full-sized cones, still green in color but already containing ripe seeds.

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[1] Regarding definition of the term "tropical pines" see my paper on "Some taxonomic problems of tropical pines," Proceedings, 13th Congress of the International Union of Forest Research Organizations, Vienna, 1961. (In press.)

[2] Gifford, Ernest M. Jr., and N. T. Mirov. Initiation and ontogeny of the ovulate strobilus in ponderosa pine. Forest Sci. **6**: 19–25. 1960.

[3] Mirov, N. T. Photoperiod and flowering of pines. Forest Sci. **2**: 328–332. 1956.

Squirrels were busy cutting the cones and eating the fresh seeds. There it was evident that the timetable of events leading to the production of seeds was somewhat distorted.

Springtime in Nicaragua is not an upsurge of life as in the North; tropical pines never cease to grow. We cannot make the statement that in the mountains of Nicaragua it takes two growing seasons, or two calendar summers, for seeds to mature. The ovulate strobili continue to develop, apparently without much winter slowing, for there is no winter; and it takes them only a little over one year to mature. That is why a Honduran botanist told me once that in his country it takes only one year for *Pinus oocarpa* to produce seed.

In Indonesia, late in February and early in March of 1961, I observed even more distortion in the flowering of pines. The pine there was *Pinus merkusii* De Vriese, moved from the mountains of northern Sumatra (about 3° N. Lat.) to the mountains and lowlands of Java (about 6° S. Lat.). I am not familiar with the flowering habits of this pine in Sumatra, but I suspect, judging from its performance in the mountains of northern Thailand, that it sheds pollen in January.

In the mountains of Java (elev. 4900 ft.) near Bandung, *Pinus merkusii* sheds its pollen twice a year: in January–February, and in July–August. Better seeds are obtained from the latter pollination.

A 20-year-old pine plantation at sea level was visited February 25, 1961. The forest ranger procured phenological records taken for several years. These records showed that *Pinus merkusii* pollen had been produced and dispersed intermittently all year round; the ovulate strobili emerging from the buds, as well as the mature cones, were also recorded throughout the year. But *Pinus kasya* Royle, a pine of Burma and Indo-china, growing naturally at elevations higher than those of *P. merkusii*, neither produced pollen nor developed ovulate strobili in the plantation. Apparently high air humidity is detrimental to the normal seed production of this pine in the humid and hot lowlands of Java.

These cursory observations suggest that a more comprehensive study of the phenology of tropical pines would be interesting and profitable. Both Central America and Indonesia are well suited to such a study. In Central America there are several institutions in Honduras, Nicaragua and Guatemala where such work could be done. In Sumatra, where the southernmost of all pines, *Pinus merkusii* grows naturally (about 2° south of the Equator) travel is at present hazardous; but in Java there are many easily accessible pine plantations where phenological records have been diligently kept. There a phenological project could be conducted either in the world renowned Herbarium Bogoriense, in Bogor, where the Forest Research Institute is also located, or in the Division of Biology of the Institute of Technology at Bandung.

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ON THE STATUS OF PSILAEA (THYMELAEACEAE)

LORIN I. NEVLING, JR.

THE GENUS PSILAEA was described, with a single species *P. dalbergioides*, by Miquel in 1861 [1] (Fl. Ind. Bat. Suppl. 355). The full combined generic-specific description was based upon a single Teysmann collection from "Sumatra occid., ad littus prope Siboga." Nine years later, Kurz (Jour. As. Soc. Beng. **39**(2): 83) placed *Psilaea dalbergioides* as a synonym of *Linostoma pauciflorum* Griffith, and, consequently, *Psilaea* was treated as a generic synonym of *Linostoma*. In 1922, *Psilaea* was used by Hans Hallier (Med. Rijksherb. **44**: 28) to typify his section *Psilaea* of *Linostoma*. The typification of the section, based on Miquel's taxon, is indicated by parenthetical credit i.e., "Sect. Psilaea (MIQ.) m." Under section *Psilaea*, Hallier described two new species, *L. leucodipterum* and *L. longiflorum* (both synonymous with *L. pauciflorum*).

Following Kurz's publication, in which he expressed the belief that *Linostoma pauciflorum* and *Psilaea dalbergioides* were conspecific, it appears as though subsequent authors accepted his determination without re-examining the Teysmann specimen. In my recent revision of *Linostoma* (Jour. Arnold Arb. **42**: 295–320. 1961) I placed *P. dalbergioides* and the names based upon it in a category of undetermined status. This procedure was followed because the Teysmann type apparently never had been re-examined taxonomically in the one hundred years since Kurz's publication; Kurz recognized only a single genus (*Linostoma*) where today we recognize two (*Linostoma* and *Enkleia*); recent revision of the generic limits of the two genera has produced some shifting of species from one genus to the other; and, finally, the genus *Enkleia* is known from several collections from Sumatra, but *Linostoma* is not (excluding the Teysmann type), although it is found on the neighboring Malay Peninsula.

To resolve my hesitancy to accept the validity of Kurz's determination of the Teysmann type required first locating and then examining the specimen. This proved more difficult than anticipated. Many of Miquel's types (particularly Teysmann specimens) are deposited currently at Utrecht. The specimen was not located at Utrecht or at any of the other major American or European herbaria. However, from Kurz's brief remarks on *Psilaea* it is evident that he had seen authentic Teysmann specimens during his curatorship (1864–1878) at the Royal Botanic Garden, Calcutta (now Indian Botanic Garden); and in addition, Teysmann Sumatran material is deposited at Calcutta (see M. J. van Steenis-Kruseman, Flora Malesiana 1: 525. 1950). After considerable effort, it was established, through Dr. H. Santapau, S.J., that the Teysmann specimen

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[1] For date of issue see Steenis, C. G. G. J. van, Flora Malesiana **4**: ccii. 1954.

was extant, and a black and white photograph of it has been sent to me through the courtesy of Mr. Basu, the specimen itself being judged too fragile to be loaned. It is unquestionably the holotype (*Teysmann s.n.*) of *Psilaea dalbergioides*, and, further, is referable to *Linostoma pauciflorum* Griffith. Thus, Kurz's identification is confirmed and the faith with which subsequent authors have accepted his determination is justified. A photograph of the holotype has been deposited in the herbarium of the Arnold Arboretum.

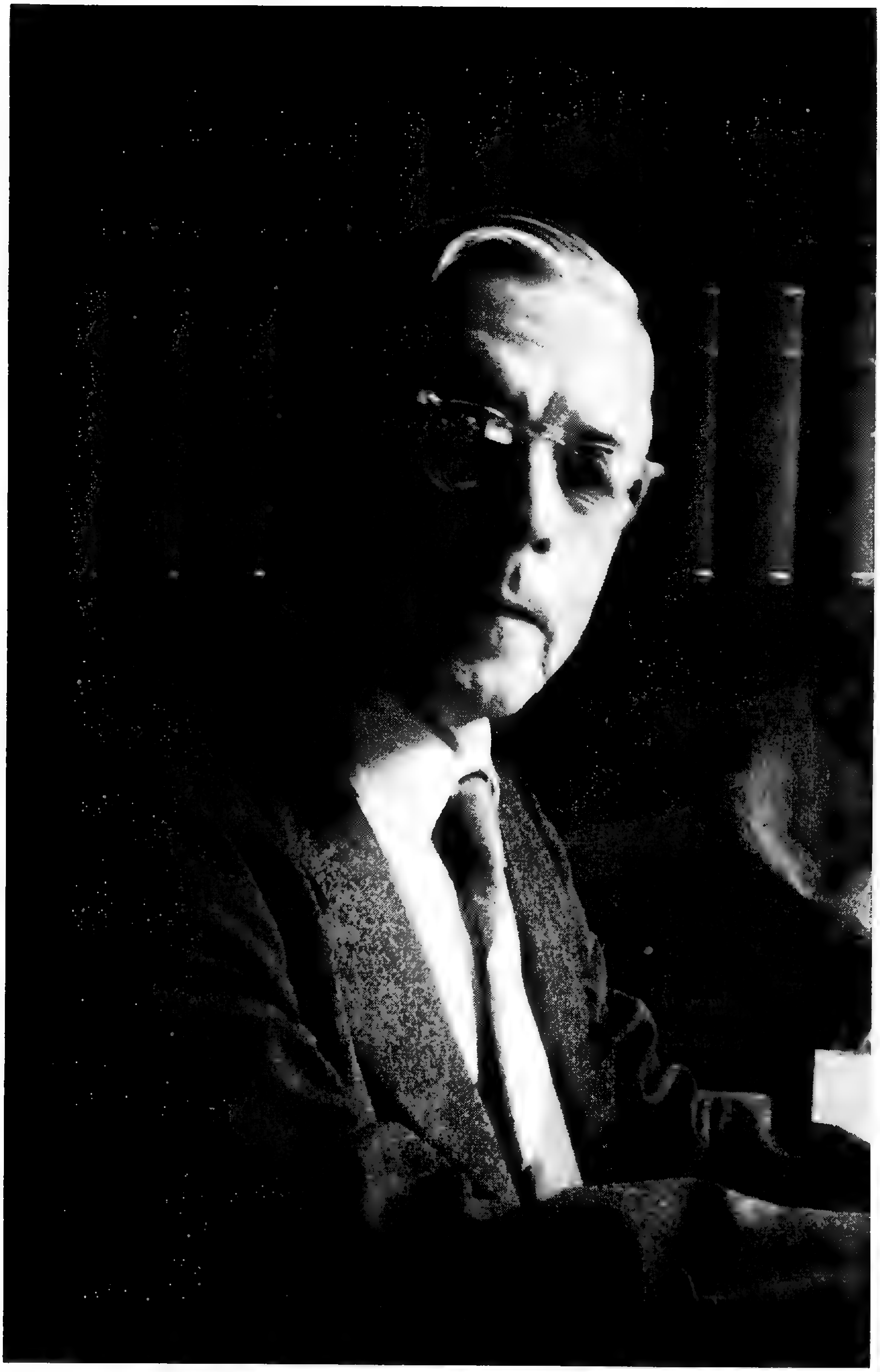
The full synonymy of *Linostoma* and of *L. pauciflorum* is emended to read:

Linostoma Wall. ex Endl. Gen. 331. 1837 (TYPE: *L. decandrum* (Roxb.) Wall. ex Endl.).

Linostoma Wall. Cat. n. 4203. 1831, sine descript.
Linostoma sect. *Eulinostoma* Meissn. in Mart. Fl. Bras. **5**(1): 72. 1855 (TYPE: *L. decandrum* (Roxb.) Wall. ex Endl.).
Psilaea Miquel, Fl. Ind. Bat. Suppl. 355. 1861 (TYPE: *P. dalbergioides* Miq.).
Linostoma subg. *Nectandra* Kurz, Jour. As. Soc. Bengal **39**(2): 83. 1870 (TYPE: *L. decandrum* (Roxb.) Wall. ex Endl.).
Linostoma sect. *Psilaea* Hallier f. Med. Rijksherb. **44**: 28. 1922 (TYPE: *Psilaea dalbergioides* Miq.).

Linostoma pauciflorum Griffith, Calcutta Jour. Nat. Hist. **4**: 234. 1844 (TYPE: *Griffith 4376*).

Psilaea dalbergioides Miquel, Fl. Ind. Bat. Suppl. 355. 1861 (TYPE: *Teysmann s.n.*).
Linostoma leucodipterum Hallier f. Med. Rijksherb. **44**: 28. 1922 (TYPE: *Hallier f. B.2261*).
Linostoma longiflorum Hallier f. *ibid.* 29 (TYPE: *Haviland 1759*).



Joseph Horace Faull

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JOSEPH HORACE FAULL, 1870–1961

ANNA F. FAULL

With portrait *

JOSEPH HORACE FAULL was born in L'Anse, Michigan, on May 3, 1870, the eldest son of James and Catherine (Bennetts) Faull. He died June 30, 1961, at his home in Cambridge, Massachusetts, Professor of Forest Pathology, *Emeritus,* at the Arnold Arboretum, Harvard University. His studies of plant pathogens had led him from the Arctic Circle to the Tropics in North America, filled his classrooms with students, and won for him world-wide recognition as an authority on forest diseases and in particular the rust fungi.

His early life and training can be summarized quickly. Born in the pine forests of Michigan, he grew up as a minister's son on the nothern shore of Lake Ontario. Here he often drove long distances through the farm and forest lands with his father talking about Charles Darwin whose theories on evolution James Faull was inclined to accept. He began to teach before finishing high school, interspersing study with teaching until he had earned three Normal School certificates and the first degree in Arts from the University of Toronto, where he had enrolled at Victoria College with the class of 1898. From 1898 to 1900, he taught mathematics in Belleville, Ontario, at Albert College, where he had completed his preparation for the University some years earlier.

He married Annie Bell Sargent, of Bellwood, Pennsylvania, late in 1903. They had met during the summer in Cold Spring Harbor, Long Island, New York, where he replaced Albert F. Blakeslee as assistant to Dr. Duncan S. Johnson, of Johns Hopkins University in the summer botany course. Miss Sargent, as a candidate for the doctorate, was studying life-histories of spiders. She had obtained her A.B. degree from the University of Pennsylvania, as one of the first small group of young women ever to be admitted to the regular courses of study at that institution. Together until her death in 1953, she shared with him an unabated interest in natural history, as well as a great love for students and all children. Of their own three, Cath-

* This portrait was taken by J. Horace Faull, Jr., in 1949 at the Pathological Laboratory of the Arnold Arboretum, Jamaica Plain, Boston, Massachusetts.

erine Sargent died at the age of sixteen, an invalid following an attack of influenza in early infancy; Anna Forward followed her father into botany; while J. Horace, Jr., has made a name for himself in chemistry.

Dr. Faull's career in botany began in 1900 when he returned to the University of Toronto to study with Edward Charles Jeffrey, Lecturer in Biology, whose sectioning of lignites (coal), along with the application of Darwin's theory of evolution to research on the anatomy of woody plants, was already attracting attention. Mr. Faull's problem was the vascular structure of the *Osmunda* ferns. His first paper was published by the *Botanical Gazette* in 1901. More important, Dr. Jeffrey told him about William Gilson Farlow and Roland Thaxter at Harvard, the two American pioneers in the new field of mycology.

Mr. Faull went to Harvard in 1901–1903 as an Austin Fellow to begin under Professor Thaxter the studies on the cytology of the Ascomycetes which were to be the major subject of his published research until 1913. His papers on the formation of the ascus and its spores are still standard references in this field. In 1904, he received his doctorate from Harvard.

In 1903, Dr. Faull had already accepted a lectureship in botany at the University of Toronto, the same lectureship (under a changed name) left vacant by Dr. Jeffrey's appointment to Harvard. He remained with his wife and family in Toronto until 1928, with sabbatical leave in 1909–1910 for a brief visit to Harvard and a year's study abroad, mostly with Robert Hartig at the Forst Botanische Institut of the University of Munich, Germany. Botanically he found the trip abroad somewhat disappointing, although he profited in prestige, in an increased facility with the German language, and in a deepened interest in forest pathology. He had been made an associate professor at Toronto in 1907. In 1918, this was changed to a full professorship while he continued as head of the department which he had created. Before he left, his department taught students in the general (liberal) arts, applied science, household science, pharmacy, and forestry; his classrooms were crowded; his graduate students and assistant staff were increasing in numbers, and a new building for botany alone was being proposed in the Provincial Parliament.

Summers at the University, with an early closing date in April or May, were long and, for Professor Faull, varied. He continued his research with publications on the Ascomycetes and other fungi, a natural history of the Toronto region and a paper on Charles Darwin. He built a large collection of lantern slides, photographs, and preserved material for teaching. He attended courses in forestry at the College of Forestry, Syracuse University, New York. He taught in the summer schools at Cornell University, Ithaca, New York (1915–17), and at Harvard (1925). He also taught his own students in Toronto. He collected in the Adirondacks with G. F. Atkinson, in the Allegheny Mountains of Pennsylvania with his wife (1913–1917), in the country a few miles or more from his Toronto home, and in the forest lands of Ontario and Quebec (Timagami, Algonquin Park, the Rideau Lakes, Georgian Bay, the Laurentians). Wherever he went he collected fungi and pathological specimens. These impressive collections of teaching, research, and reference material are one of his legacies to botany.

Apart from the University and at the request of the Canadian Government, Dr. Faull established a department of forest pathology with a field laboratory in the coniferous forests on Bear Island in the Lake Timagami Forest Reservation of Ontario. Commencing in 1918, much of his summer time was spent in the development of this laboratory, in long-range experiments there, and with one of his students, Wade Watson, in the compilation of a check list of the Timagami flora. At the same time his services as a consultant were in increasing demand by lumber companies and others with forest or tree problems. These requests, although remunerative, were to him often annoying interruptions to his major interests at the University and in the field laboratory. When he left, the Government laboratory and department, as well as a shade-tree laboratory, were as firmly established as the department at the University, while his students were beginning to appear as responsible men and women in botany and forestry in the universities, schools, and government laboratories and departments throughout the Dominion. He had indeed earned the citation of "Father of Canadian Botany" given him in 1959 at Montreal in the opening address at the IX International Botanical Congress.

In 1928, he came to Harvard University as Professor of Forest Pathology to take part in the expanding program of research envisioned by Charles Sprague Sargent and Oakes Ames for the Arnold Arboretum. For Professor Faull this meant freedom from the increasingly heavy teaching and administrative load at Toronto and a chance to devote most of his time to writing, research, and the advancement of forest pathology. He brought with him his collections of research and reference material, his graduate students and his reputation as a consultant. The Arboretum provided a laboratory and greenhouse built to his specifications on the adjacent Bussey Institution grounds; the Farlow Herbarium gave working space there; and, later, after their completion, the Biological Laboratories provided additional laboratory rooms.

Professor Faull's conception of the new appointment and of forest pathology can best be stated in his own words taken from letters to Edward C. Jeffrey and to Oakes Ames at this time. He wrote: "My mind is set on advancing Forest Pathology — completing and writing up accumulated researches of which there is a good stock in hand, taking up others in mind, organizing the position at the Arboretum on a broad and sound basis and perhaps working towards a treatise of the Hartig type — these are possibilities within reasonable expectation of attainment." Again, "The field is a broad one for it involves the study of the etiology of arboreal diseases and of the principles of their control. As for etiology only a beginning has been made in America; there exists a host of diseases the causes of which are yet unstudied and unknown, and in several instances that come to mind wrongly ascribed. Intelligent control is possible only when causes are known, but even then there are principles to be worked out. This is particularly true of our untamed and abused American forests where the solution seems to lie along prophylactic lines frequently based on a knowledge, mostly not yet acquired but acquirable, of the relation of the age of the hosts to susceptibility, of the rate of progress of the pathogens and the relative amount of destruction caused. There is likewise a phase in connection with the utilization of immense quantities of waste diseased living timber. All these aspects constitute a vast field within which researches may be undertaken and if you subscribe to these limits your project will be as broadly based as the one in taxonomy which has been so long and so successfully developed."

Scarcely pausing to settle into the new laboratory, Dr. Faull began at once the program that he had laid out for himself: the completion of earlier research, the study of "immediate pathological problems presented by trees in the Arboretum" and "of any or all diseases of all kinds of trees wherever found and whether in plantations or in the forests." The latter was to lead him far afield from one end of the continent to the other, while his days in Cambridge were filled with writing, research, students, and visitors from all over the world. One can trace his collecting and travel in his accessions books.

The first summer found him in Timagami in August checking on the experiments he had last seen in June just before coming to Harvard; returning to old locations at Proulx, Quebec; and extending his range into the Gaspé. A month later he was in Maine examining nursery spruce and white pine for the Brown Company. His first paper appeared in the *Journal of the Arnold Arboretum* in 1929, "A Fungous Disease of Conifers Related to Snow Cover." It was based on the work at Proulx, Quebec, begun some years earlier, and on observations made at the Brown nurseries.

From 1929 to 1933, he continued this program of revisiting old locations and experiments, adding new ones, advising and co-operating in experiments with the lumber companies and others. He also gave the undergraduate half-course in pathology agreed upon. In 1929, he made collections at the Arnold Arboretum; at the Kelsey nurseries, in Boxford; at Oqussoc, in Maine; and again at Proulx, in Quebec, and at Lake Timagami. He extended his trips into Nova Scotia at the request of the Provincial forester where he notes finding "*Milesina polypodophila* (Bell) Faull on *Abies* and *Polypodium* side by side." He repeated the June trips in the fall and again in 1930. He visited the West and the Pacific Coast in 1931, collecting in the Yellowstone National Park, in Wyoming; at the North Priest River Forest Station, in Washington; in Oregon; in California; in Idaho; and in Illinois. He concentrated on the New England mountains in 1932: Vermont, the Presidential Range, the Berkshires. In 1932–1934, the Arboretum published the first of his monographs on rusts, that on *Milesia*.

From 1933 to 1940, Dr. Faull included a winter trip to the tropics in his regular program for the year. In December and January, 1933–34, he visited the mountains of Jamaica, Panama, and the Canal Zone. He returned to Jamaica in February and March, 1935, and again in 1935–36, after a three week stop in Cuba. He wrote in the records of the Harvard Botanical Garden at "Soledad," near Cienfuegos, Cuba: "Arrived Dec.

17, 1935. Departed Jan. 5, 1936. Activities: 1) Made a pathological reconnaissance of the Arboretum and of the forest tree plantations at and near Soledad. 2) Examined critically a disease of Marabu [*Dichrostachys cinerea*] between Soledad and San Blas, a disease of *Ficus* in Soledad and several heart rot diseases of trees; assembled some relevant material. 3) Collected Pucciniastreae in the Trinidad Mts." The following winter he went to Guatemala where, in addition to rusts, he collected material of an *Abies* growing at 10,000 feet which Rehder later described as *A. guatemalensis*. In November, 1937, he was in Mexico with Professor Maximino Martínez collecting in the remote areas of the states of Michoacán, Mexico, Morelos, Hidalgo, Veracruz, and Chiapas, as well as in the Federal District. He returned to Mexico in 1938 to visit Oaxaca and in 1939 to collect again in Chiapas and Hidalgo, as well as in the northern states of Chihuahua and Durango. In the meantime, his summer trips continued: the Gaspé, Maine, New Brunswick, Long Island, and Chicago, in 1933; Quebec, Mt. Washington and Maine, in 1934; Maine and Metis, Quebec, in 1936; Vermont, Maine, and Long Island, in 1937; Vermont and Connecticut, in 1938; New Hampshire, in 1939; Massachusetts every year.

In 1938, the Arboretum published the second of his monographs on rusts, that on *Uredinopsis*. Actually, this was the third of his long papers on the rust fungi dealing with the taxonomy, morphology, physiology, host relations, etc., which he considered not only knowledge of general botanical interest but basic for control of plant diseases specifically or in principle. In 1926, two years before his Harvard appointment, he had presented a long paper on the Puccineastreae at the International Congress of Plant Sciences, Ithaca, New York. While not themselves "treatises of the Hartig type" contemplated in his letter to Dr. Jeffrey, they undoubtedly were working towards it. One more monograph was intended but never written, although he had collected the material and begun the necessary studies. Like all of his work, these papers are the scholarly presentations of careful study and experiment in field and laboratory by a man with a capacity for detail combined with breadth of vision and a keen insight.

Simultaneously with the field work, Dr. Faull organized the laboratory at the Arboretum. By September, 1928, the small building was ready with its own library "of several thousand pamphlets," periodicals, and reference books; the important collections of diseased plants (about 1000 specimens); and the usual apparatus for work with cultures and microscope. Addition of the experimental greenhouse in 1929 or 1930 completed the small laboratory, while more space for students was provided as needed at the nearby Bussey Institution, at the Farlow Herbarium in Cambridge, and, later, in the new Biological Laboratories there. On July 1, 1929, Dr. Faull reported on a reconnaissance of the living collections of the Arboretum, in addition to five major projects under active investigation by himself, his assistant (G. D. Darker, from Toronto), and the first of his Harvard graduate students: (1) rusts of fir and spruce, (2) *Phacidium* blight and snow cover, (3) lilac disease, (4) needle-cast diseases of conifers, (5) browning of white-pine transplants. The first two were a continuation of work begun at Toronto, in the Timagami forests, and at Proulx, Quebec. The last two came from field work with lumber companies in Maine or from general collecting. The lilac was an Arboretum problem.

By 1931, the pathological laboratory envisioned by Oakes Ames and Dr. Faull and established in fulfilment of "the expressed wish of the late Director, Charles Sprague Sargent, and as part of Dr. Sargent's conception of the Arboretum as an institution for the study of woody plants in all fundamental aspects" was in full swing with the functions of the laboratory defined "as comprising interest in the Arboretum's living collections, extension services, instruction and research." With the propagating houses next door and the living collections of the Arboretum itself within hand's reach it was ideally located both for his own researches and for friendly co-operation with the rest of the Arboretum group. Contact with the undergraduate College was maintained through the half-course in plant pathogens, while graduate students, postgraduates, and scholars continued to come in twos and threes and sevens. The United States and foreign governments from Canada to Jamaica, estate owners, forest interests, and others called with increasing frequency for extension services. This, in turn, offered not only new problems but often supplementary financial support for their study and for the postgraduate work which Dr. Faull encouraged his students to do both in his own laboratory and abroad.

For the next ten years the laboratory continued to operate under Dr. Faull's direction with the same efficiency and devotion. The problems brought in by field work, collecting trips, extension services, and the Arboretum itself were numerous and specific. Many of them were quickly answered. But many involved much broader botanical issues: "the host of unknown and unstudied" causes of plant disease; "the principles of control yet to be worked out"; the relationships of host, parasite, and environment; morphology; anatomy; physiology; and even some aspects of genetics — in short, the entire range of botanical science. At least twenty-two such studies were carried through to the publication of significant conclusions, a broadly based beginning in the "vast field" of unstudied arboreal pathology for which the laboratory had been organized. Of most popular interest is the Dutch elm disease, which Dr. Christina Buisman, of Holland, found for the first time in the United States at the end of a year's work (1929–30) on American elm-diseases. Early hope of eradication faded when some years after its elimination from Ohio it reappeared in New Jersey; thereafter, the Arboretum effort was directed at control. Equally or more important both botanically and practically were other studies: a disease of *Fagus*, lilac blight (a graft incompatibility leading to work on viruses), taxonomy of *Ganoderma* (initially a question of classification), morphology of rust spermogonia as taxonomic criteria, mycorrhiza (morphology and physiology involving mineral nutrition of pine), wilt diseases of elm (other than Dutch), etc. The record of the laboratory can be traced in the annual reports and papers published in the Arboretum's *Journal* or as one of its *Contributions*, a series inaugurated by two papers from the pathology laboratory: Dr. Darker's Ph.D. thesis on needle-cast fungi and Professor Faull's monograph on "*Milesia*." That the laboratory was not continued and his position remained unfilled after his retirement was a disappointment to him.

Professor Faull retired in 1940, a world figure in forest pathology and the world's authority on rust fungi associated with ferns. His students have gone on to make names for themselves in the botanical world and to serve in responsible teaching, administrative, and research positions both in the United States and Canada. The extension services have been taken over mostly by government agencies, but the broad and comprehensive kind of research begun at the Arboretum seems not to have been continued in this country.

For several years, Dr. Faull himself remained in his laboratory, assisting with Arboretum affairs, helping in the fight against Dutch elm disease, serving as an associate editor of the *Journal*, organizing his collections, advising at the Farlow Herbarium, and welcoming the scientists who came to see him. The visits of two of these gave him particular satisfaction. One was that of Professor Maximino Martínez, of Mexico, who had arranged for his earlier collecting in the Mexican forests and had accompanied him on some of the trips. The other was Dr. Krishnadas Bagchee, from the Forest Service in India, who shared Dr. Faull's love of the forests and his interest in fungi. Dr. Bagchee brought with him a collection of Indian rusts to my father's delight. In 1956, the *Journal of the Arnold Arboretum* published his last paper. Shortly thereafter, Dr. Faull gave up his last small room in the Cambridge laboratories.

The proper disposal of his large collections of pathological material occupied much of his time in these later years. Some, of course, had been left at the University in Toronto. But the thousand specimens brought with him to Harvard had grown through exchange, communication, and his own collecting trips and field work and that of his students and associates to nearly fourteen thousand. The small room where the earlier collections had at first been kept had become inadequate long before his retirement. In 1939, he had placed a thousand duplicates of wood destroying fungi in the Farlow Herbarium and three hundred in the Bureau of Plant Industry in Washington (later transferred to the National Herbarium). In 1940, he noted in his report the deposition of his large collection of polypores at the Farlow Herbarium. Finally before his death, he placed a collection of fern rusts (type specimens and material documenting his publications) in the U.S. National Herbarium, where he hoped it would be both adequately cared for and available for reference and future investigations. The large remainder of the collections with duplicates has been placed in temporary storage at the Farlow Herbarium and the Arnold Arboretum awaiting more permanent quarters. A few are still at his home in Cambridge.

As his health failed, Dr. Faull spent more and more of his time with his family, partly in Texas, but most of it at their home in Cambridge. Here he enjoyed his garden, his neighbors, a little carpentry, a great deal of reading, a little cribbage, and a voluminous correspondence with friends and students dating back to those whom he had taught as little children in the Canadian rural schools. As a student at Toronto, he had been the gold medalist in his graduating class of 1898. Now he reread the entire works of Dickens and Shakespeare, along with his other books. As a young man, too, he had played ice hockey on the Victoria College team. Now he listened to the sports broadcasts on the radio. He never lost his interest in the schools or in the education of women or his sympathy for the underprivileged. At his death, a volume of Dickens was near his chair by the radio along with a copy of the Cambridge School Report, a box of fern rusts near his desk.

As a teacher and a scientist, Joseph Horace Faull enriched the two countries in which he lived. His students continue to do so.

Professor Faull had been a member of the American Academy of Arts and Sciences, the American Association for the Advancement of Science, the American Phytopathological Society, the American Society of Naturalists, the Mycological Society of America, the National Agricultural Chemicals Association, the New England Botanical Club, the Royal Canadian Institute, the Royal Society of Canada, the Society of American Foresters, the Society of the Sigma Xi, and the Sociedad Botánica de México.

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COMPARATIVE ANATOMY OF THE LEAF-BEARING CACTACEAE, V

THE SECONDARY PHLOEM

LALIT M. SRIVASTAVA [1] AND I. W. BAILEY [2]

IN AN EARLIER PAPER (Bailey and Srivastava, 1962), it was indicated that the vascular cambium, tracheary tissue, and sieve elements in the leaf-bearing Cactaceae show structural features that suggest an advanced level of evolutionary specialization. The arrangement of fusiform initials in the cambium and their derivatives in xylem and phloem, and the structure of xylem tissue were described in detail in this paper. In contrast, the account of phloem was cursory and restricted mainly to the form of sieve elements and their sieve plates and sieve areas. In order to understand the structure of phloem tissue, particularly the relationship between sieve elements and parenchyma cells associated with them, an ontogenetic study of the tissue was considered essential. This study forms the subject of the present paper.

Three species of leaf-bearing Cactaceae, *Pereskia sacharosa* Griseb. [Tucumán], *Pereskiopsis* aff. *chapistle* Britt. & Rose [Boke B-3], and *Quiabentia* aff. *chacoensis* Backbg. [Tucumán] were selected for detailed ontogenetic work. The material was killed in FAA. Small pieces from the stems of these species were embedded in paraffin and sectioned on a rotary microtome. Some additional material was embedded in celloidin and sectioned on a sliding microtome. Serial transverse, radial, and tangential sections were obtained and, later, stained by a combination of tannic acid, iron chloride, and lacmoid as described by Cheadle, Gifford & Esau (1953).

In order to determine the origin of phloem elements, several tiers (that is, radial files of derivatives of single cambial initials) were studied in detail for each of the three species. Tiers were drawn from serial cross sections with the use of a camera lucida attachment. The cells in each tier were reconstructed from these drawings. The entire height of a tier was examined in order to determine the exact relationship between sieve elements and the parenchymatous cells associated with them. The results obtained from a study of cross sections were later substantiated by a study of tiers from serial tangential sections. Radial sections were only of limited use in the present study, partly because of the difficulty of obtaining good radial sections and partly because of the irregular planes of divisions in the phloic initials and the small size of some of the phloem derivatives.

As is well known, sieve elements and the associated companion cells

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[1] Mercer Fellow of the Arnold Arboretum.

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usually function for a limited period only. They die in old phloem and, in most cases, are eventually crushed by the expanding parenchyma cells and the pressures resulting from new growth (cf. Esau, 1953, pp. 299, 300). As a result, the arrangement of phloem derivatives, typical of young phloem, is distorted and the study of tiers cannot be pursued with accuracy in very old phloem. The tiers drawn in the present study, therefore, represent the functional phloem and only as much of nonfunctional phloem [3] as had not yet been distorted.

The terms used here are common in literature on phloem (cf. Esau, 1950, 1953; Esau & Cheadle, 1955; Cheadle & Esau, 1958), but some of them are explained again for clarity. A *phloic initial* is the daughter cell formed towards the phloem after a periclinal division in the cambial initial. The phloic initials either directly, that is, without any further divisions, or after a few divisions produce the various cell types in the phloem. For instance, a phloem-parenchyma strand is formed after one or more horizontal divisions in the phloic initial. The term *precursor* refers to a cell that would either differentiate directly as a definitive phloem element or in which further divisions would occur; in any case, it denotes an undifferentiated cell in which further changes are going to occur. Thus a phloic initial may behave as a precursor of a fusiform phloem-parenchyma cell, or one of the daughter cells after a division in the phloic initial may behave as a precursor of the sieve-tube mother cell and a parenchyma cell. The term *sieve-tube mother cell* refers to a cell in which one or more divisions occur and within the confines of which a sieve element and its companion cells are formed. Occasionally a sieve-tube mother cell may differentiate directly as a sieve element and no companion cells may be formed. The terms *sieve element* and *sieve-tube member* are used interchangeably. Various kinds of parenchyma cells occur in phloem. In the present paper, the terms used to describe them have an ontogenetic implication. Thus, a *fusiform phloem-parenchyma cell* is derived directly from a phloic initial; and a *phloem-parenchyma strand* is formed after one or more horizontal divisions in the phloic initial. Some other parenchyma cells and companion cells are formed in association with a sieve element after divisions in a single phloic initial. For convenience of description, these cells ontogenetically related to the sieve elements are often referred to as *parenchymatous cells* or *elements.*

ORIGIN OF PHLOEM ELEMENTS IN PERESKIA

Analysis of Tiers

A cross section through the phloem of *Pereskia sacharosa* is shown in FIG. 32, in which the cell types present in the tissue and their general arrangement are seen. Another cross section is drawn in FIG. 1, but the individual tiers are separated tangentially for a better illustration of

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[3] Nonfunctional, in contrast to functional, phloem refers to that part of phloem in which sieve elements are no longer conducting (cf. Esau, 1953, p. 299).

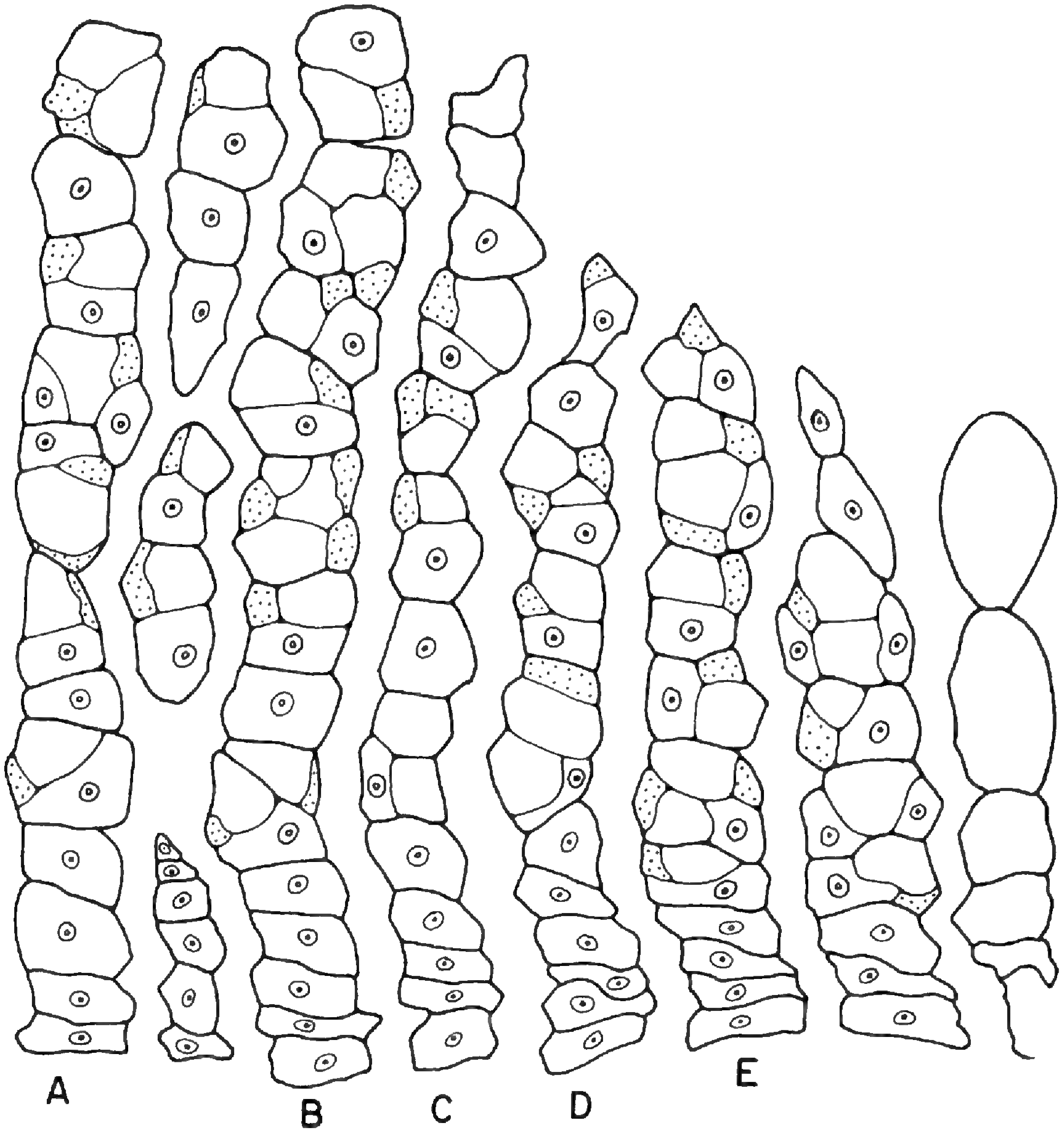


FIG. 1. *Pereskia sacharosa,* transection of cambial zone (below) and phloem, × 495. Tiers separated from one another to show radial extent of each; sieve elements unmarked; companion cells stippled; parenchyma cells with nuclei; ray cells on extreme right without nuclei. Tiers A-E analyzed in detail in FIGS. 2–6 and in text.

their radial extent. A study of similar drawings from serial cross sections reveals the axial extent of each tier and the cell types that compose it. Tiers A, B, C, D, and E in FIG. 1 are analyzed in detail. The cross section drawn in FIG. 1 did not pass through the middle (in terms of axial extent) of all the five tiers selected for study. The cross sectional views at different levels in the axial extent of these tiers are illustrated in FIGS. 2–6, a–e; the levels at which these cross sections were taken are indicated along the margins of FIGS. 2–6, f. In FIGS. 2–6, a–e, sieve elements are unmarked except for sieve plates which, when present, are indicated by hatched areas; companion cells are stippled; and parenchyma cells ontogenetically associated with sieve elements are shown with nuclei. Fusiform phloem-parenchyma cells and phloem-parenchyma strands are shown with a circle drawn with a heavy pen. Cells internal to the cell complex in which sieve element 1 occurs are not considered — they are assumed to be undifferentiated cells. Some of them may have differentiated as fusiform phloem-parenchyma cells or phloem-parenchyma strands, but we were not certain about this. They are shown without nuclei. FIGURES 2–6, f, represent schematically the axial extent of the sieve elements and the parenchymatous elements ontogenetically associated with them in tiers A–E; the sieve elements are drawn with numbered solid lines, the companion cells with dotted lines, and parenchyma cells with broken lines. Lines representing companion cells and parenchyma cells are placed arbitrarily on the left and right, respectively, of the lines representing sieve elements. If a strand of companion or parenchyma cells is formed in association with a sieve element, it is represented by a single line; but the individual cells in the strand are demarcated by short oblique lines intersecting the vertical line that represents the strand. All cells that are ontogenetically related and derived from a single phloic initial are included within pairs of horizontal lines drawn at the upper and lower limits of the complex of cells. The numbers 0–225 or –300 at left in each drawing represent the length in microns. The purpose of this schematic representation is twofold. First, it shows at a glance how many and what kinds of cells are ontogenetically related with one another. Second, the combined length of the cells in a complex of cells, barring the overlap of cells, reflects the length of the phloic initial (and, hence, that of the fusiform cambial initial). The lengths of different phloic initials in a tier represent approximately the axial extent, or the height, of the tier. Fusiform phloem-parenchyma cells and phloem-parenchyma strands are not considered in FIGS. 2–6, f.

TIER A: Seven sieve elements, indicated by arabic numerals, are present in tier A (FIG. 2, c, f). Sieve element 1 is associated with two companion cells and one parenchyma cell, sieve element 2 with one companion and one parenchyma cell, sieve element 3 with three companion and two parenchyma cells, sieve element 4 with two companion and two parenchyma cells, sieve element 5 with one companion and one parenchyma cell, and sieve elements 6 and 7 with one companion cell each. Two fusiform phloem-parenchyma cells occur in the tier and were derived directly from their phloic initials.

Each of the sieve elements 1–5 with their associated parenchymatous cells and the sieve elements 6 and 7 with their companion cells originated by divisions within the confines of a single phloic initial. The origin of these elements is considered in detail.

The phloic initial within the confines of which sieve element 1 is present divided obliquely and longitudinally. Of the two daughter cells formed, the one towards cambium was the precursor of a parenchyma cell, the other away from the cambium was the mother cell for sieve element 1 and its companion cells. In this mother cell a longitudinal,

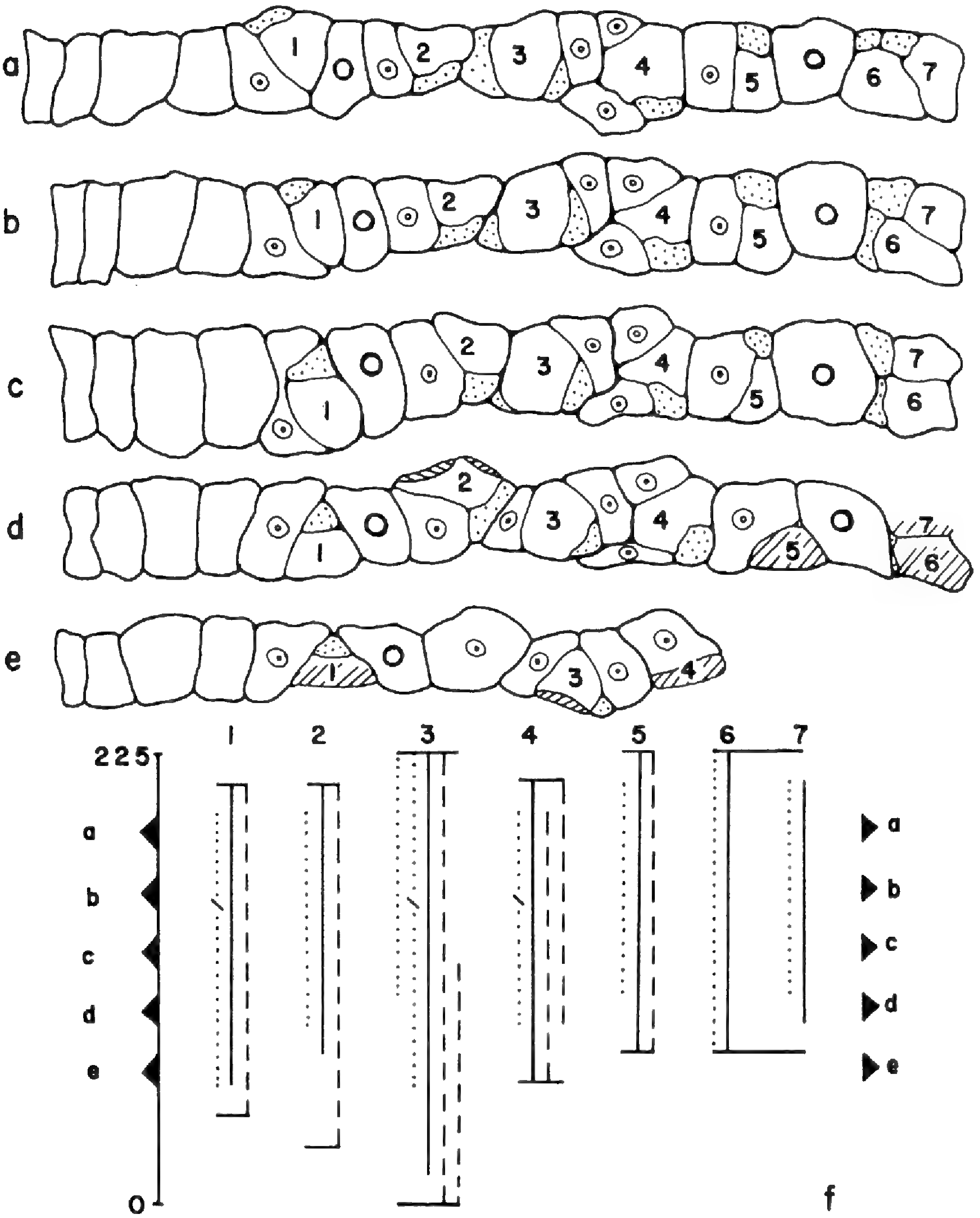


FIG. 2. *Pereskia sacharosa*, TIER A of FIG. 1: a–e, cross sections of tier at levels indicated in schematic representation of certain members of tier (f) by arrowheads opposite a–a, b–b, etc., respectively; a–e, × 495.

For details of drawings in FIG. 2 *and in* FIGS. 3–6, 10–14, 21–25, *see text*, p. 236.

more or less radial division separated a narrow cell from a larger cell. The narrow cell divided horizontally and formed a strand of two cells that differentiated as companion cells; the larger cell matured as sieve element 1.

The sequence of divisions in the phloic initials responsible for sieve elements 2 and 5 and their parenchymatous cells was similar to that in the phloic initial for sieve element 1 — the first oblique longitudinal wall separated the precursor of a parenchyma cell from the sieve-tube mother cell, and a subsequent division in the sieve-tube mother cell produced a small and a large cell; the small cell differentiated as a companion cell, the large cell as a sieve-tube member.

The order of divisions in the phloic initials within the confines of which sieve elements 3 and 4 occur is more complicated. The cell complex with sieve element 3 is analyzed as follows. A more or less tangential division extending through most of the length of the phloic initial resulted in two daughter cells, one away from the cambium was the precursor of a parenchyma cell (Fig. 2, a–e), the other towards the cambium was the precursor of a second parenchyma cell and the mother cell of sieve element 3. An oblique longitudinal division in the lower half of this latter precursor formed two daughter cells: one was the precursor of the second parenchyma cell (Fig. 2, d–e), the other, a larger cell, was the sieve-tube mother cell for element 3. A longitudinal division along the right radial and outer tangential walls of the sieve-tube mother cell produced a narrow precursor that divided horizontally to form a strand of two companion cells (Fig. 2, a–e); another longitudinal division along the inner tangential wall, but confined to the upper half of the sieve-tube mother cell, produced a third companion cell (Fig. 2, a–c). The larger cell left after these divisions in the sieve-tube mother cell differentiated as sieve element 3. The following sequence of divisions is visualized for the origin of sieve element 4. Two successive oblique longitudinal divisions in the phloic initial, one along left radial and the other along right radial wall, separated two precursors of parenchyma cells from the sieve-tube mother cell. A more or less radial longitudinal division in the sieve-tube mother cell produced a narrow cell, which divided horizontally and formed two companion cells (Figs. 2, a–d), and a larger cell that differentiated as sieve element 4.

Sieve elements 6 and 7 are ontogenetically related. A more or less radial longitudinal division in the phloic initial separated two sieve-tube mother cells, each of which divided subsequently and formed a sieve-tube element and a companion cell.

Tier B: Twelve sieve elements (indicated by arabic numerals) with their associated parenchymatous cells and one fusiform phloem-parenchyma cell occur in tier B (Fig. 3, c, f). The divisions in phloic initials responsible for sieve elements 3, 7, and 12 are least complicated and, hence, are analyzed first. A tangential longitudinal wall laid down in the phloic initial of sieve element 3 separated two daughter cells, one (towards cambium) was the precursor of a parenchyma strand, the other (away from cambium) was the sieve-tube mother cell. A radio-longitudinal wall divided the sieve-tube mother cell into a narrow precursor, which divided horizontally and formed a strand of two companion cells, and a larger cell that matured as sieve element 3. The pattern of divisions in the phloic initials of sieve elements 7 and 12 is similar except that the precursor of companion cells did not divide horizontally. In the cell complex including sieve element 12, the precursor of the parenchyma cell also did not divide horizontally to form a strand of parenchyma cells (FIG. 3, f).

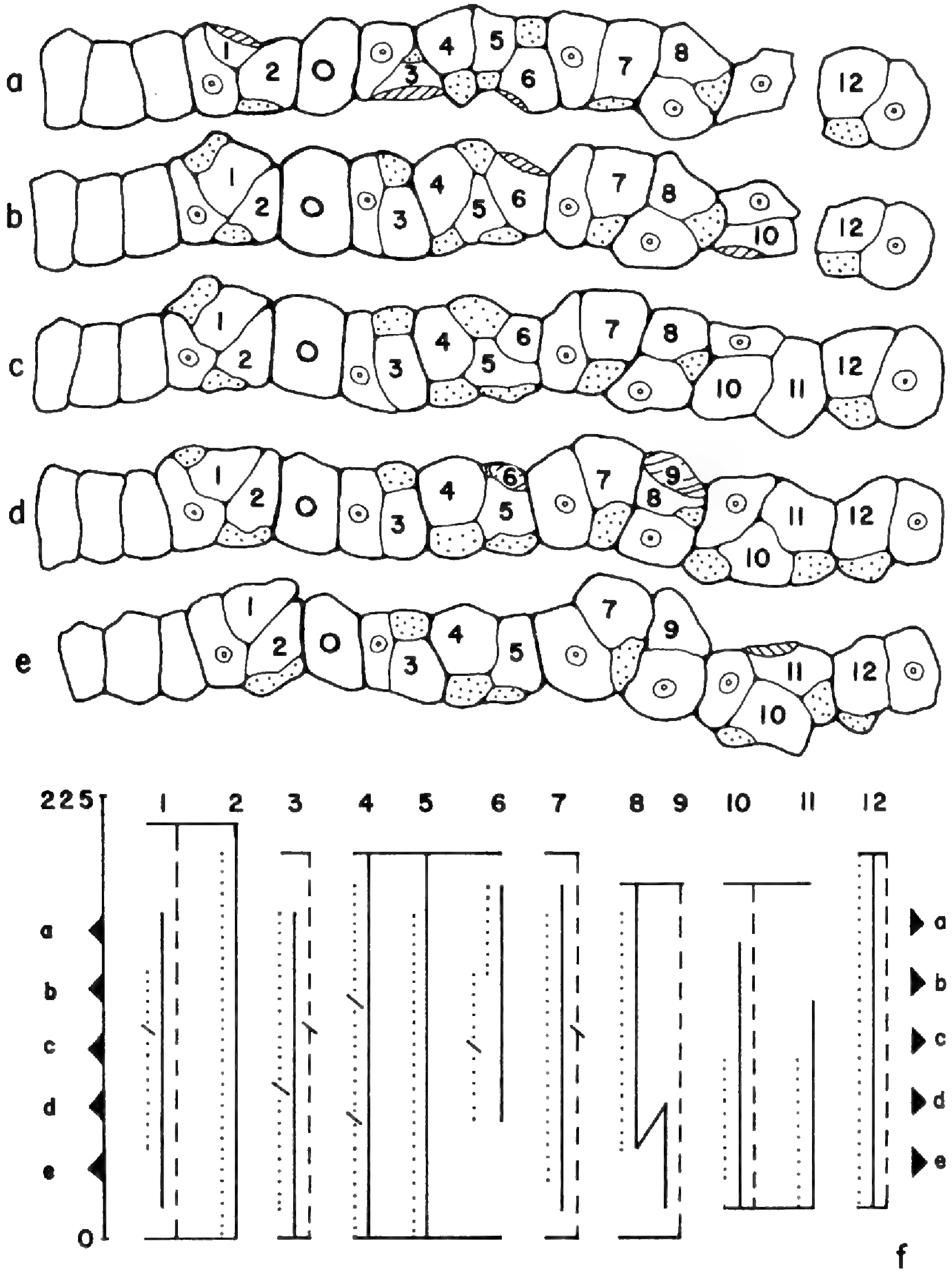


FIG. 3. *Pereskia sacharosa*, TIER B of FIG. 1: a–e, cross sections of tier at levels indicated in schematic representation (f), as in FIG. 2; a–e, × 495. Oblique line connecting sieve elements 8 and 9 in diagram (f) shows that the two originated after division in a single mother cell. For details of drawings, see text.

Sieve elements 1 and 2; 4, 5, and 6; 8 and 9; and 10 and 11 are ontogenetically related and were formed with their associated parenchymatous cells after divisions in single phloic initials. One parenchyma cell occurs in common association each with sieve elements 1 and 2, 8 and 9, and 10 and 11. Sieve elements 4, 5, and 6 do not seem to have any parenchyma cell. The sequence of divisions in the phloic initials in all these instances is more complicated than in the case of sieve elements 3, 7, and 12. It appears that in the phloic initial responsible for the cell complex in which sieve elements 1 and 2 occur, an oblique anticlinal wall was laid down. Of the two resulting daughter cells, one towards the cambium, the precursor of a parenchyma cell and the mother cell of sieve element 1, divided obliquely, but the dividing wall did not extend to the cell tips (FIG. 3, f). The longer cell formed after this division was the precursor that matured as the parenchyma cell; the shorter was the sieve-tube mother cell for element 1. In this sieve-tube mother cell an oblique wall was laid down that separated a narrow precursor (left and above), which divided horizontally and formed two companion cells, from a larger cell that matured as sieve element 1. The cell away from the cambium, formed after the first anticlinal division in the phloic initial, was the mother cell for sieve element 2 and its companion cell. In this mother cell a more or less radial division separated the precursor of a companion cell from a precursor that matured as sieve element 2. In the interpretation of the origin of this cell complex, it has been assumed that the parenchyma cell was more closely related to sieve element 1 than to sieve element 2. It is possible, however, that the first division in the phloic initial of this cell complex was not the one that separated the sieve-tube mother cell of element 2 from the precursor of the mother cell of element 1 and the parenchyma cell, but it was one that separated the parenchyma cell from a precursor in which later divisions formed sieve elements 1 and 2. In the latter interpretation the parenchyma cell would be equally related to the two sieve elements.

In the analysis of the cell complex in which sieve elements 4, 5, and 6 occur, it appears that a more or less tangential longitudinal division of the phloic initial resulted in two daughter cells. The daughter cell towards the cambium was the sieve-tube mother cell of element 4; a radial longitudinal division in this mother cell followed by two transverse divisions in the narrower of the two cells resulted in three companion cells and the sieve-tube member 4. In the daughter cell away from the cambium an oblique division extending through the upper half of the cell set off the sieve-tube mother cells of elements 5 and 6. The mother cell of element 6 was shorter than that of element 5 (cf. FIG. 3, a–f). A longitudinal division in the mother cell of element 5 produced a long, narrow companion cell and the sieve-tube member 5. Two successive divisions occurred in the mother cell of element 6 and formed two precursors of companion cells and a precursor that matured as sieve element 6. In one of the precursors of companion cells a horizontal division resulted in two companion cells; the other precursor matured directly as a companion cell. As a result, sieve element 6 is associated with three companion cells.

In the phloic initial that formed the cell complex including sieve elements 8 and 9, an oblique radio-longitudinal division formed two daughter cells. One was the precursor of a parenchyma cell; the other divided obliquely near its lower end and produced two mother cells, one each for sieve elements 8 (FIG. 3, a–d) and 9 (FIG. 3, d–e). An oblique division in the mother cell of element 8 formed a narrow cell that differentiated as a companion cell and a larger cell that matured as the sieve element 8. The precursor of sieve element 9 differentiated as a sieve-tube member without any divisions. The sequence of divisions in the phloic initial within whose confines elements 10 and 11 appear is similar to that in the phloic initial of elements 1 and 2.

TIER C: Nine sieve elements with their associated parenchymatous cells and one fusiform phloem-parenchyma cell occur in tier C (FIG. 4, c, f). The origin of the cell complexes including sieve elements 5 and 9 is simple and followed the pattern described for sieve elements 1, 2, and 5 in tier A, and 3, 7, and 12 in tier B. A strand of four companion cells was formed in association with sieve element 5.

Sieve elements 1–4 and 6–8 with their associated parenchymatous cells were derived from single phloic initials. A new feature is seen in the origin of sieve elements 1–4. A more or less transverse division in the phloic initial formed two daughter cells. An oblique, more or less tangential division in the upper daughter cell formed two precursors, the one away from the cambium matured without any further divisions as sieve element 2, the other towards the cambium divided radially and formed a parenchyma cell and sieve element 1 (FIG. 4, a–b). No companion cells were formed in association with either sieve element 1 or 2. In the lower daughter cell (formed after the first, transverse division in the phloic initial) an oblique longitudinal division separated the mother cell of sieve element 4 from the precursor of the mother cell of sieve element 3 and a parenchyma cell (FIG. 4, c–e). An oblique division in the mother cell of element 4 separated a narrow cell that differentiated as a companion cell (lower right corner) and a larger cell that matured as the sieve element 4. In the precursor of the mother cell of sieve element 3 and the parenchyma cell, a tangential division produced two daughter cells: one towards the cambium was the parenchyma cell, the other away from the cambium was the sieve-tube mother cell of element 3. In this mother cell a tangential longitudinal division separated a precursor of two companion cells from a precursor that differentiated as the sieve element 3 (FIG. 4, c–e). In the origin of sieve elements 6–8, two successive oblique divisions, one somewhat anticlinal and separating the phloic initial into an upper and a lower cell (cf. FIG. 4, a–e), the other somewhat tangential and oblique and separating the lower cell into an outer and an inner daughter cell (FIG. 4, d–e), resulted in three mother cells, one each for elements 6, 7, and 8. The mother cell of element 6 was the

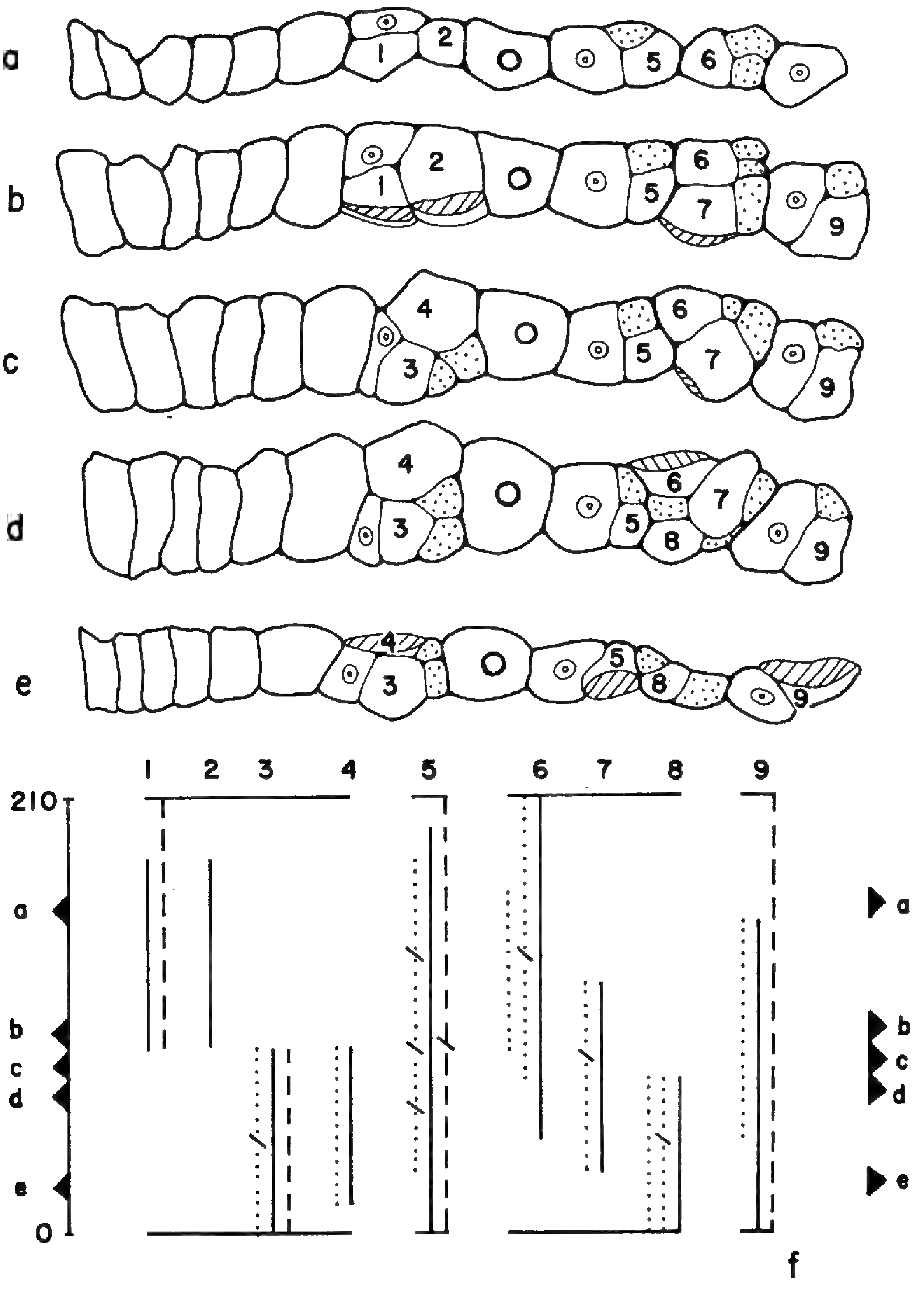


FIG. 4. *Pereskia sacharosa*, TIER C of FIG. 1: a–e, cross sections of tier at levels indicated in schematic representation (f), as in FIG. 2; a–e, × 495. Details as given in text.

longest and extended from the top end of the phloic initial to well below its middle, that of element 7 was in the lower half of the phloic initial but did not extend to its lowermost tip, and that of element 8 extended through lower one-third of the phloic initial (FIG. 4, f). Two successive longitudinal divisions along the outer tangential wall of the mother cell of element 6 produced two precursors of companion cells and a precursor that matured as sieve element 6. In one of the precursors of companion cells a horizontal division yielded two cells. As a result, three companion cells were formed in association with sieve element 6. In the mother cell of element 7 a longitudinal division along the outer tangential wall produced a narrow precursor of two companion cells and a large cell that matured as sieve element 7. In the mother cell of element 8 two longitudinal divisions, one along the radial wall on left and the other along the outer tangential wall, produced two precursors of companion cells and a precursor that matured as sieve element 8. The precursor of companion cells along the outer tangential wall divided horizontally. Eventually three companion cells were formed.

That the sieve elements 1–4 originated by divisions in a single phloic initial is shown clearly in FIG. 4, f, where the combined lengths of the parenchyma cell associated with sieve element 1 and the sieve element 3 (which are the longest derivatives of the upper and lower daughter cells formed after the first horizontal division in the phloic initial) approximately equal the length of other phloic initials in the tier. Likewise, the combined lengths of elements 6, 7, and 8, barring the overlap, is the same as that of the phloic initials responsible for the complexes of cells including elements 5 and 9.

TIER D: Six sieve elements with their associated parenchymatous cells and one fusiform phloem-parenchyma cell occur in tier D (FIG. 5, c, f). Sieve elements 3 and 6 and their associated companion and parenchyma cells originated in the usual manner described for sieve elements 1, 2, and 5 in tier A; 3, 7, and 12 in tier B; and 5, and 9 in tier C, and are not considered. Sieve elements 1 and 2, and 4 and 5 are ontogenetically related. In the phloic initial within the confines of which sieve elements 1 and 2 occur, a longitudinal wall was laid down. This wall has a somewhat radial orientation in the upper half of the phloic initial (FIG. 5, a–c), but in the lower half it is somewhat tangential (FIG. 5, d) and finally oblique (FIG. 5, e). (It would appear that the resultant daughter cells were placed somewhat radially in relation to one another near their upper end and somewhat tangentially near their lower end. Such arrangements were commonly seen in tangential sections, cf. FIGS. 7–9.) Of the two cells thus formed, one (below and right) was the mother cell of element 2. A longitudinal division along the outer tangential wall of this mother cell separated a narrow cell from a larger cell; the former divided horizontally thrice and formed a strand of four companion cells, the latter matured as the sieve element 2. In the other cell (above and left) was laid down a wall which had a tangential orientation in the upper end of the cell (FIG. 5, a–c) and a more or less radial orientation in the lower end (FIG. 5, d–e) and which separated the mother cell of sieve element 1 from a precursor of a parenchyma cell. A longitudinal division along the outer tangential wall of the sieve-tube mother cell of element 1 produced a short, narrow cell, which divided horizontally and formed two companion cells, and a larger cell that differentiated as sieve

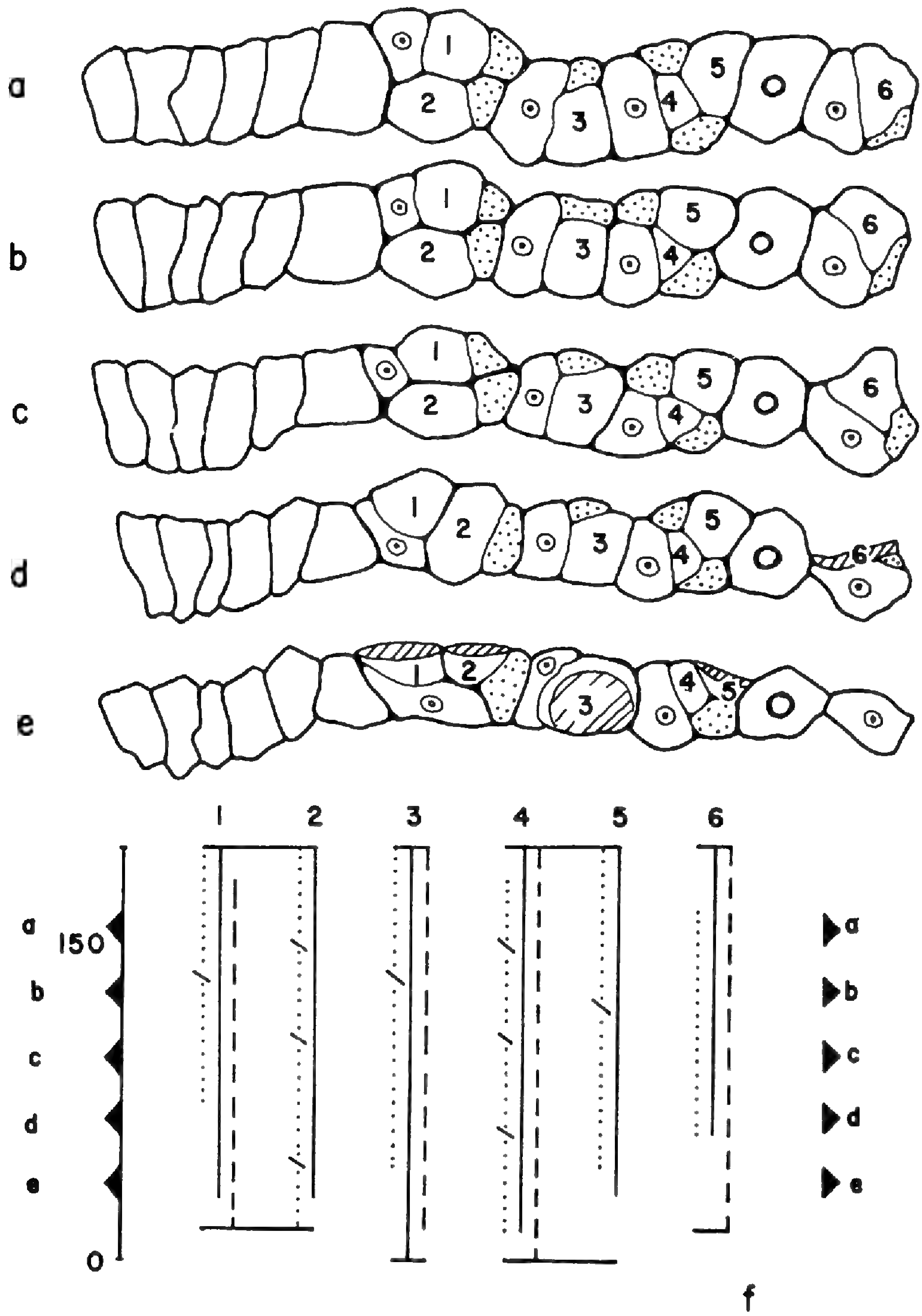


FIG. 5. *Pereskia sacharosa*, TIER D of FIG. 1: a–e, cross sections of tier at levels indicated in schematic representation (f), as in FIG. 2; a–e, × 495. Details as given in text.

element 1. Sieve elements 4 and 5 and their associated parenchymatous cells originated in a similar manner.

TIER E: In tier E there are eight sieve elements with their associated companion and parenchyma cells (FIG. 6, c, f). Sieve elements 1, 4, 5, and 8 originated in the usual manner — a tangential or a radial longitudinal division in the phloic initial separated the precursor of a paren-

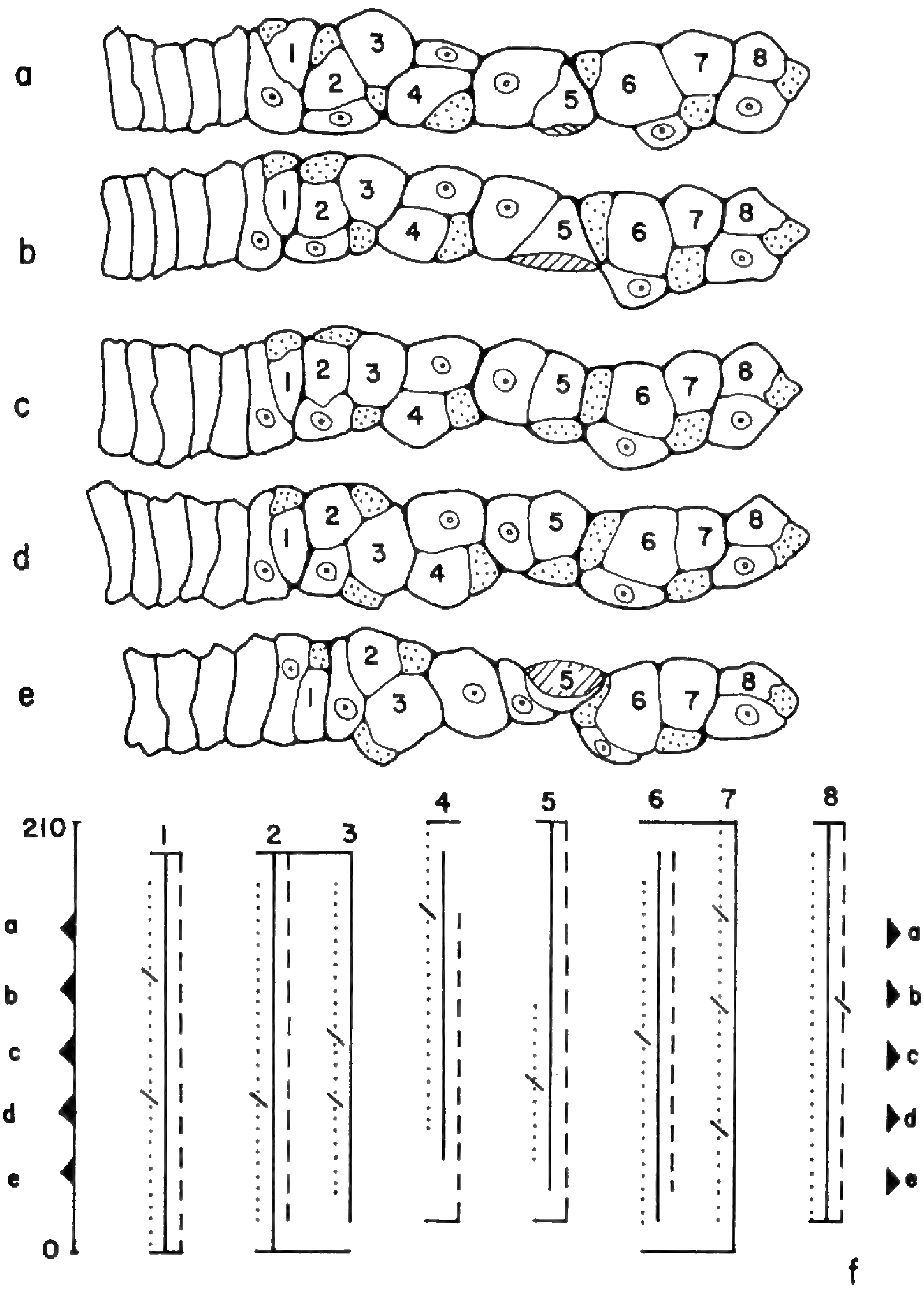


FIG. 6. *Pereskia sacharosa*, TIER E of FIG. 1: a–e, cross sections of tier at levels indicated in schematic representation (f), as in FIG. 2; a–e, × 495. Details as given in text.

chyma cell (or strand) from the sieve-tube mother cell. In the sieve-tube mother cell itself a longitudinal division separated the precursor of one or more companion cells from the precursor of the sieve-tube member. Sieve elements 2 and 3, and 6 and 7 are ontogenetically related and originated in the manner common to that of sieve elements 1 and 2, and 10 and 11 in tier B; and 1 and 2, and 4 and 5 in tier D.

Discussion

The five tiers studied from cross sections reveal some patterns about the method of origin of sieve elements and related parenchymatous cells in *Pereskia sacharosa*. In the following, this information is summarized and confirmed from a study of tangential sections.

In the five tiers examined, a total of 32 phloic initials was studied. Cells internal to the cell complex in which sieve element 1 occurred are excluded from this discussion. As mentioned earlier, they may have been fusiform phloem-parenchyma cells or phloem-parenchyma strands, but we were not certain that these cells had differentiated. Of the 32 phloic initials, 5 had matured directly as fusiform phloem-parenchyma cells; the remaining 27 phloic initials had divided in various planes and had formed cell complexes in which one or more members had differentiated as sieve elements. Most commonly, the first division in the phloic initial is longitudinal and radial, oblique, or tangential. The resultant daughter cells may be unequal in size, but one is the precursor of a parenchyma cell, the other the precursor in which the sieve element and its companion cells arise (sieve-tube mother cell). This method of the origin of parenchyma cells, sieve elements and companion cells was encountered in 14 of the 27 phloic initials studied (cf. Figs. 2–6, f).

Less commonly, the first division in the phloic initial, which again is longitudinal, but may vary from radial, oblique, to tangential, separates two daughter cells, one of which behaves like the phloic initial, the other like the sieve-tube mother cell mentioned in the previous paragraph. As a result, two sieve elements, at least one parenchyma cell (or strand), and some companion cells are formed within the confines of a single phloic initial (cf. Figs. 2–6, f). As mentioned during the analysis of the cell complex including sieve elements 1 and 2 in tier B, the sequence of the first two divisions is not very clear in such instances.

Occasionally, two successive oblique divisions in the phloic initial separate three cells. The dividing walls may be oriented in different planes but usually one is somewhat radial, the other somewhat tangential. Also, one or both walls may not extend to the tips of the phloic initial, thus producing cells shorter than the initial. (Compare the lengths of sieve elements 3 and 4 and their associated parenchyma cells in Fig. 2, f; sieve elements 4, 5, and 6 in Fig. 3, f; sieve elements 6, 7, and 8 in Fig. 4, f.) Of the three cells that are formed, all three may behave as sieve-tube mother cells or one may behave as a sieve-tube mother cell and the other two as precursors of parenchyma cells, or strands. As a result, three sieve elements with their companion cells (sieve elements 4–6, Fig. 3, f; sieve elements 6–8, Fig. 4, f), or one sieve element with its companion cells and two parenchyma cells (sieve elements 3 and 4, Fig. 2, f) are formed within the confines of a single initial.

Three other patterns of divisions in phloic initials were recorded. A longitudinal division in the phloic initial may separate two cells. Each daughter cell may then behave as a sieve-tube mother cell (sieve elements

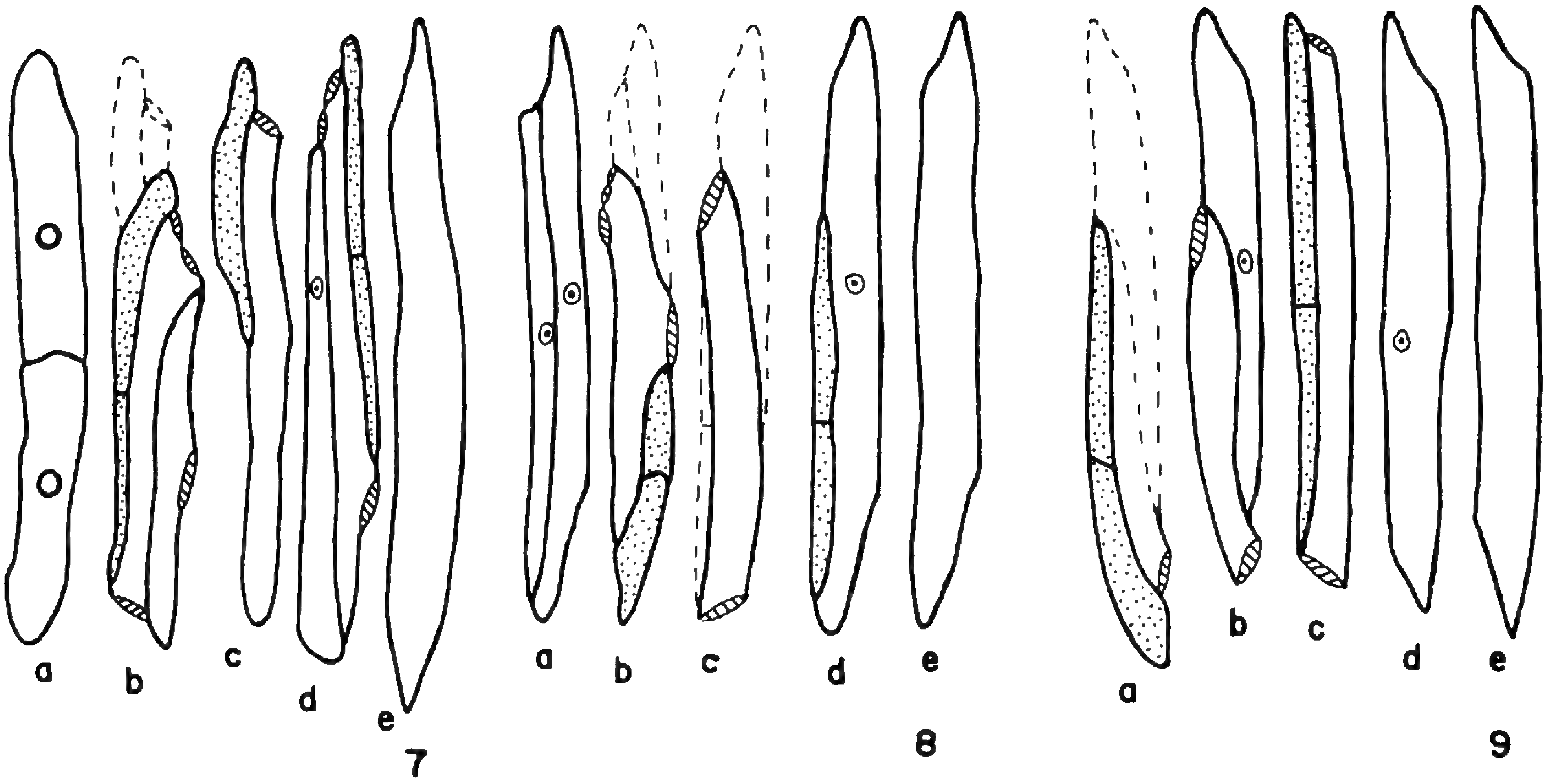
6 and 7, FIG. 2, f), or one may behave as a precursor of a parenchyma cell (or strand) and the other as the precursor of two sieve-tube mother cells (sieve elements 8 and 9, FIG. 3, f). Finally, a phloic initial may be divided almost horizontally into two daughter cells. The upper and lower daughter cells may then behave as more or less "independent" phloic initials producing sieve elements and parenchymatous cells in manners described above (sieve elements 1–4, FIG. 4, f).

In order to confirm some of the conclusions drawn from a study of cross sections, several tiers were also studied by use of tangential sections. As is clear from FIGS. 2–6, a–e, the planes of divisions in the phloic initials and their daughter cells are often irregular, with the result that, even in almost perfect tangential sections, the outlines of cells appear at different levels of focus in the same section and even in different sections. Another difficulty with tangential sections is that the tangential walls of derivatives (and, hence, the tangential limits of phloic initials) are not easy to determine. Because of these complications serial sections must be studied.

Three representative tiers are drawn in FIGS. 7–9. Although partly corrected, these figures show the outlines of cells at different levels of focus as truly as was necessary for a clear understanding of the planes of divisions. Only a few derivatives in each tier are shown; the last cell in each set of drawings represents the fusiform cambial initial. The sieve cells are left unmarked, except for the sieve plates which are hatched; companion cells are stippled; parenchyma cells ontogenetically related to sieve elements are shown with nuclei; and parenchyma cells ontogenetically unrelated to sieve elements are shown with a circle drawn with a heavy pen.

A phloem-parenchyma strand occurs in FIG. 7, a. It was derived by a single transverse division in the phloic initial. The derivatives shown in FIG. 7, b–c, d; and at a–b, and c–d in FIGS. 8 and 9, are ontogenetically related and originated after divisions within the confines of a single phloic initial. One parenchyma cell, a sieve element and a strand of two companion cells occur in the cell complexes shown in FIG. 7, d; FIG. 8, c–d; and FIG. 9, a–b, c–d. In the cell complex shown in FIG. 7, b–c, three sieve elements and their companion cells were formed; whereas in the cell complex in FIG. 8, a–b, two parenchyma cells were formed in association with the sieve element. The planes of divisions leading to the formation of cell complexes shown in FIG. 7, d, FIGS. 8 and 9, c–d, are easily understood. Others are somewhat more complicated but can be explained on the basis of our information obtained from the study of cross sections.

The wall separating the sieve element from the strand of two companion cells in FIG. 9, a–b, appears radial at the lower end, tangential at the upper end. This is shown by the fact that these elements are placed radially to each other at their lower end but appear in different planes of focus near their upper end. Similar orientations of derivatives were encountered in the study of cross sections (cf. cell complex including sieve elements 1 and 2 in FIG. 5, a–e). It would appear from these illustra-



FIGS. 7–9. *Pereskia sacharosa*: a–e, in each figure, successive phloem derivatives from outer to inner phloem (a–d) and fusiform cambial initial of each tier (e), in tangential view, × 325. Derivatives at (a), (b–c), and (d) in FIG. 7, and those at (a–b) and (c–d) in FIGS. 8 and 9 are ontogenetically related. Broken lines indicate cell outline seen more clearly at another focal level. *Details of figures and of* FIGS. 15–20, 26–31 *given in text*, p. 248.

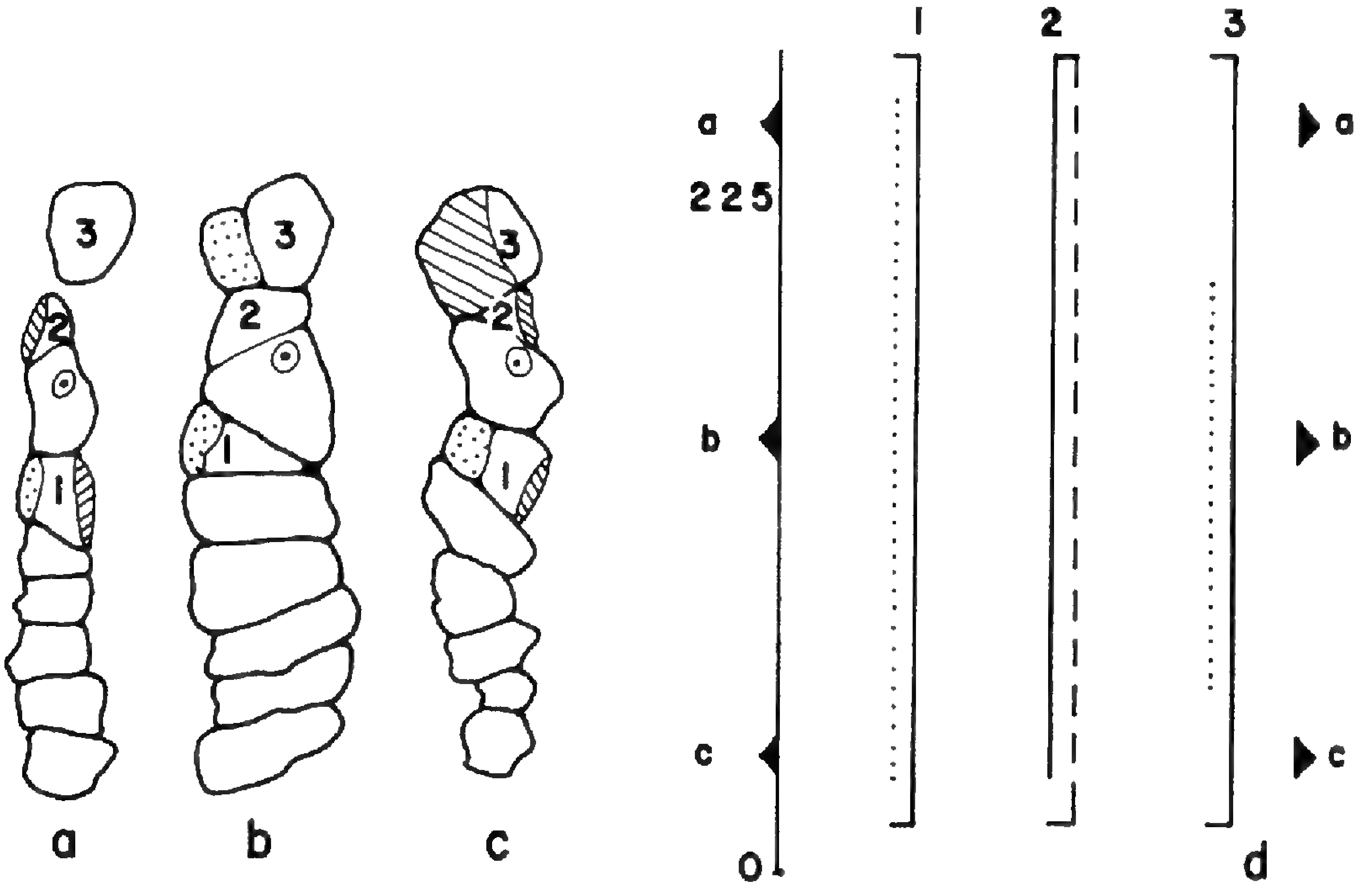
tions that, during cytokinesis in phloic initials and their daughter cells, the cell plates may, in their upper and lower extensions, intersect different walls of the mother cell. Possibly, also, the cells formed after divisions within the confines of a phloic initial expand differentially in mutual adjustment with the related cells derived from the same phloic initial and with the cells in neighboring tiers, so that the shape of the mature cells and the orientations of the walls that separate them are different in final stages from those in early stages of ontogeny. These factors may account for the peculiar configurations of cells seen in FIG. 7, b–c; 8, b; and 9, a–b, and for the lateral intrusion of cells in one tier into neighboring tiers (FIG. 1).

ORIGIN OF PHLOEM ELEMENTS IN PERESKIOPSIS AND QUIABENTIA

Tiers in *Pereskiopsis* aff. *chapistle* and *Quiabentia* aff. *chacoensis* were studied from serial cross sections in the same manner as in *Pereskia sacharosa*. Five tiers from each of these species are analyzed in detail in FIGS. 10–14, a–d, and FIGS. 21–25, a–d. The cross sectional views of the tiers and the schematic representation of sieve elements and related parenchymatous cells in them are drawn in the same manner as in *Pereskia sacharosa*. However, the cross sections are drawn only at three levels in the axial extent of each tier, because the difference in the structure of the tier from one level to another was not very marked. These figures are mostly self-explanatory and do not need much comment. In the following, therefore, only the important points concerning the occurrence of fusiform phloem-parenchyma cells and phloem-parenchyma strands, and the number and planes of divisions in phloic initials (and their daughter cells) preceding the formation of sieve elements and related parenchymatous cells are mentioned.

Altogether, 18 phloic initials in *Pereskiopsis* aff. *chapistle* and 35 in *Quiabentia* aff. *chacoensis* were studied in the five tiers examined for each species. (Cells internal to the cell complex including sieve element 1 in all tiers, except that in FIG. 24, are omitted from this consideration. In the tier shown in FIG. 24, three cells internal to sieve element 1 were considered as fusiform phloem-parenchyma cells, because the cells in neighboring tiers at that distance from the cambium appeared mature.) Two of the 18 phloic initials in *Pereskiopsis* aff. *chapistle* had given rise to one fusiform phloem-parenchyma cell (FIG. 13, a–c) and one phloem-parenchyma strand (FIG. 14, a–c), and 15 of the 35 phloic initials in *Quiabentia* aff. *chacoensis* had matured as fusiform phloem-parenchyma cells (FIGS. 21–25, a–c). The remaining 16 phloic initials in *Pereskiopsis* aff. *chapistle* and 20 in *Quiabentia* aff. *chacoensis* had formed cell complexes with at least one cell in each case differentiating as a sieve element.

As in *Pereskia sacharosa*, the most common mode of origin of sieve elements and related parenchymatous cells is one in which the phloic initial divides longitudinally and radially, obliquely, or tangentially. Of



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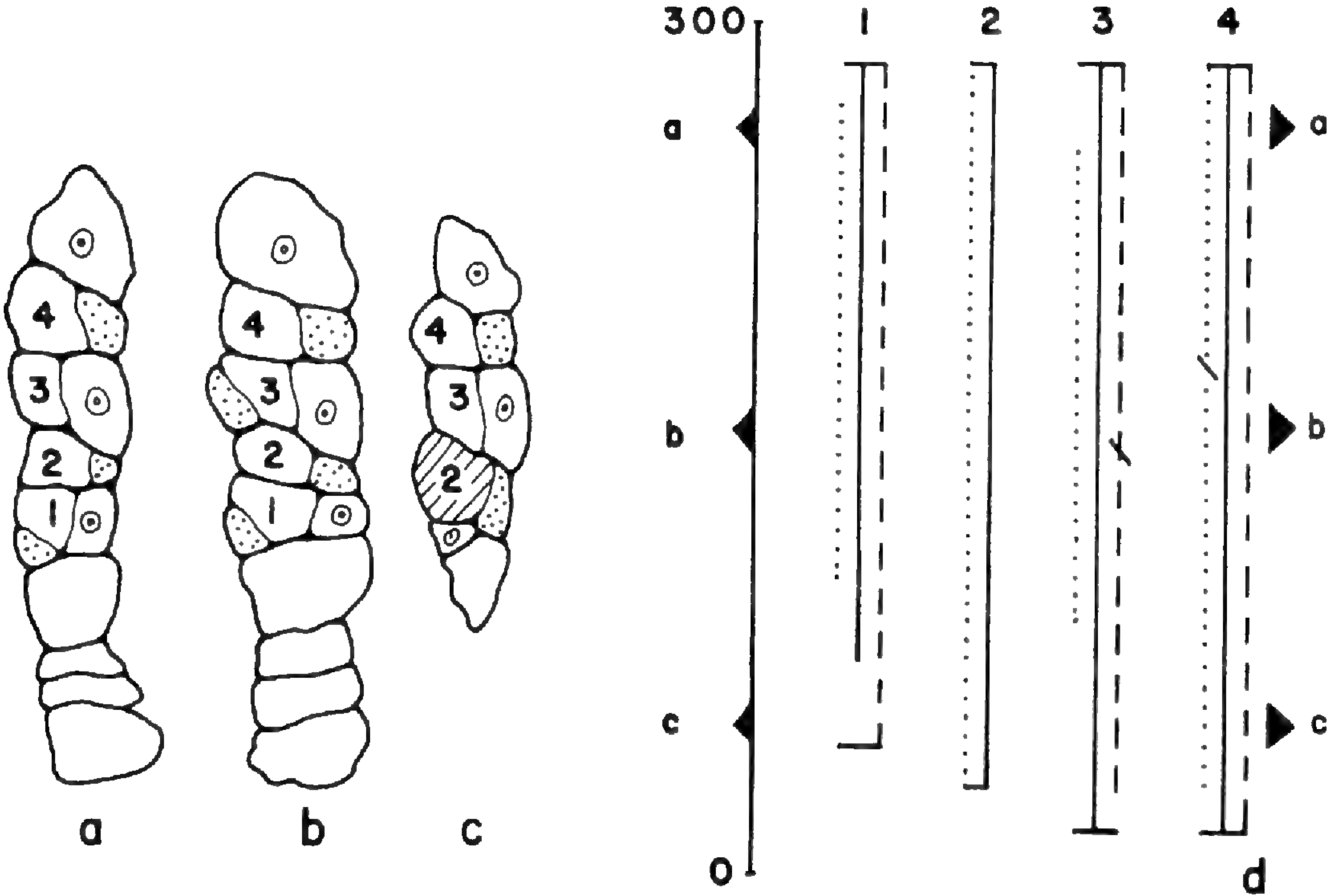

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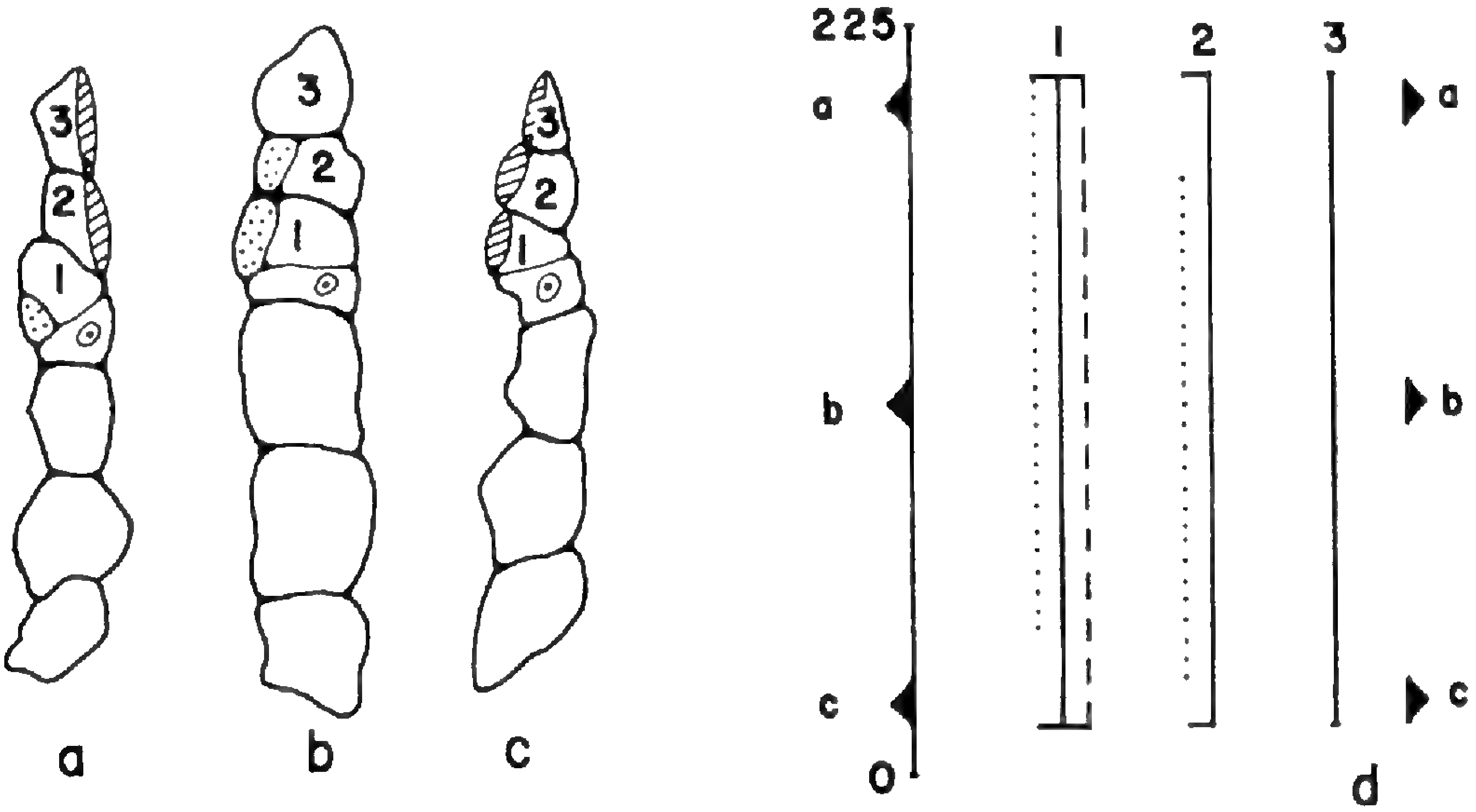
FIGS. 10, 11. *Pereskiopsis* aff. *chapistle*: a–c, cross sectional views of two tiers at levels shown in diagrams (d), schematic representations of some members of the two tiers, as in FIG. 2; a–c, × 390. See explanation in text.

the two resultant daughter cells, one cell behaves as a precursor of a parenchyma cell, or strand, the other cell as a sieve-tube mother cell. Such an origin of sieve elements and related parenchymatous cells was recorded in 8 of the 16 phloic initials in *Pereskiopsis* aff. *chapistle* (FIGS. 10–14, d) and 15 of the 20 phloic initials in *Quiabentia* aff. *chacoensis* (FIGS. 21–25, d).



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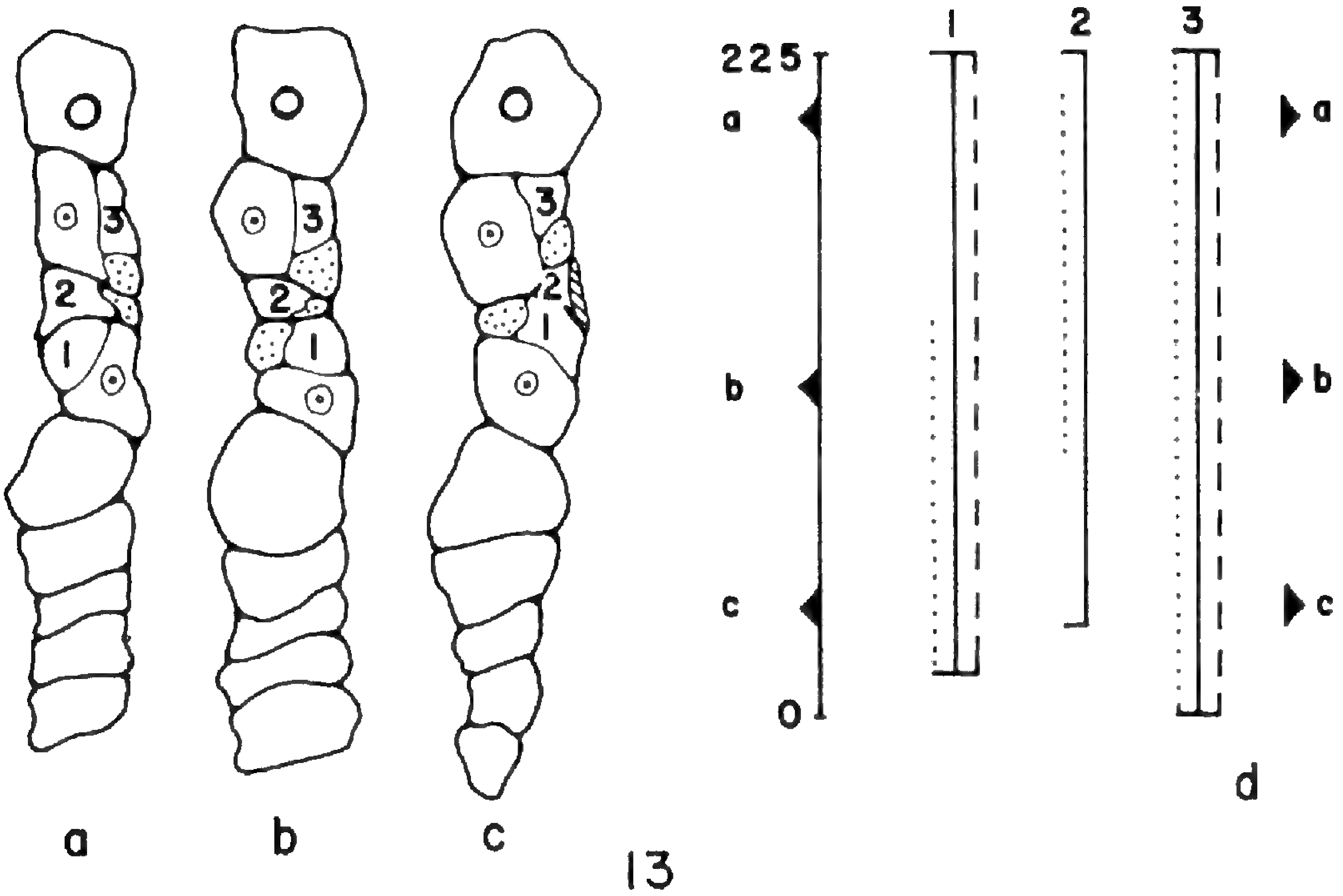

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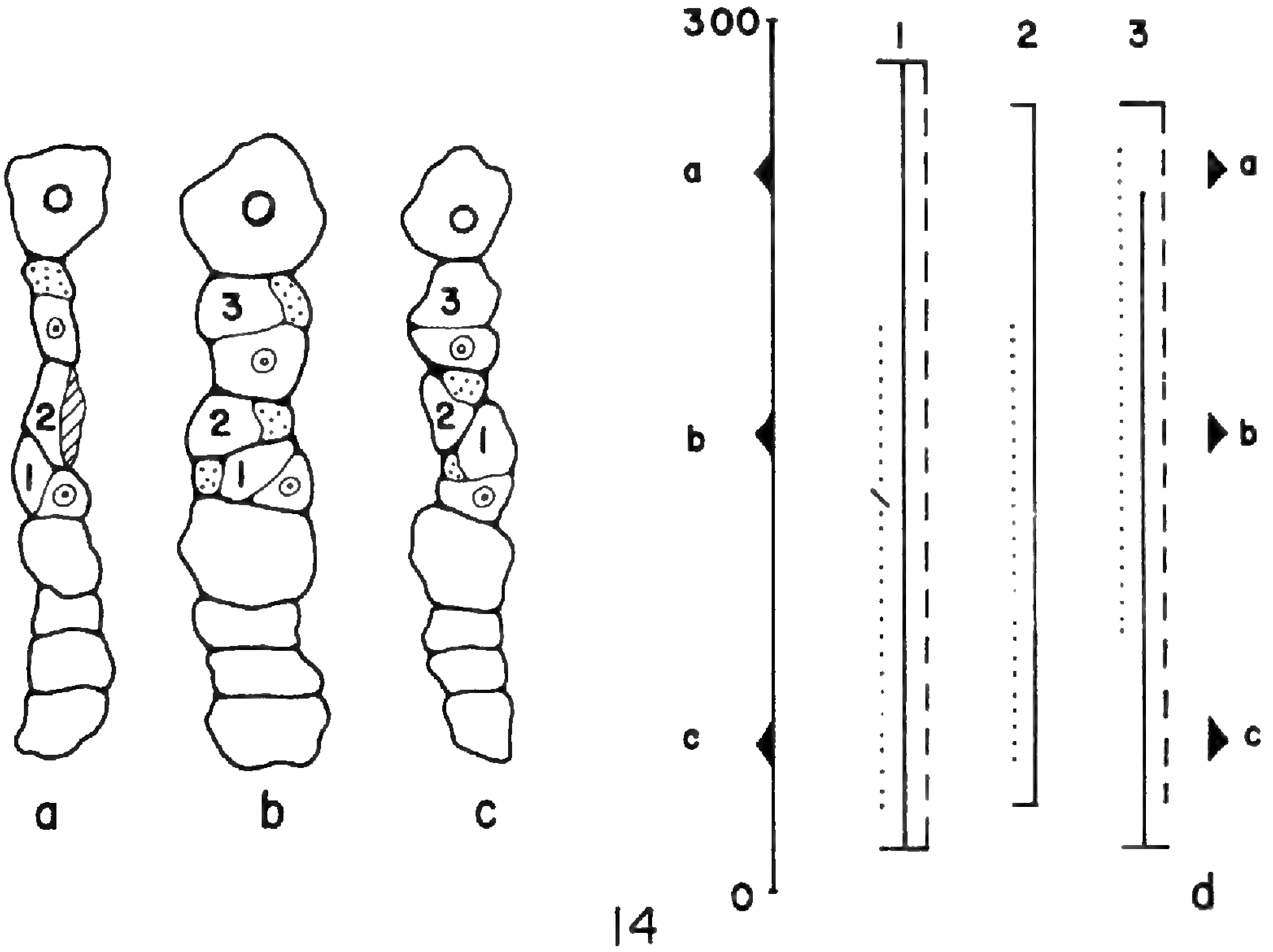
FIGS. 12, 13. *Pereskiopsis* aff. *chapistle*: a–c, cross sectional views of two tiers at levels shown in diagrams (d), schematic representations of some members of the two tiers, as in FIG. 2; a–c, × 390. For details, see text.



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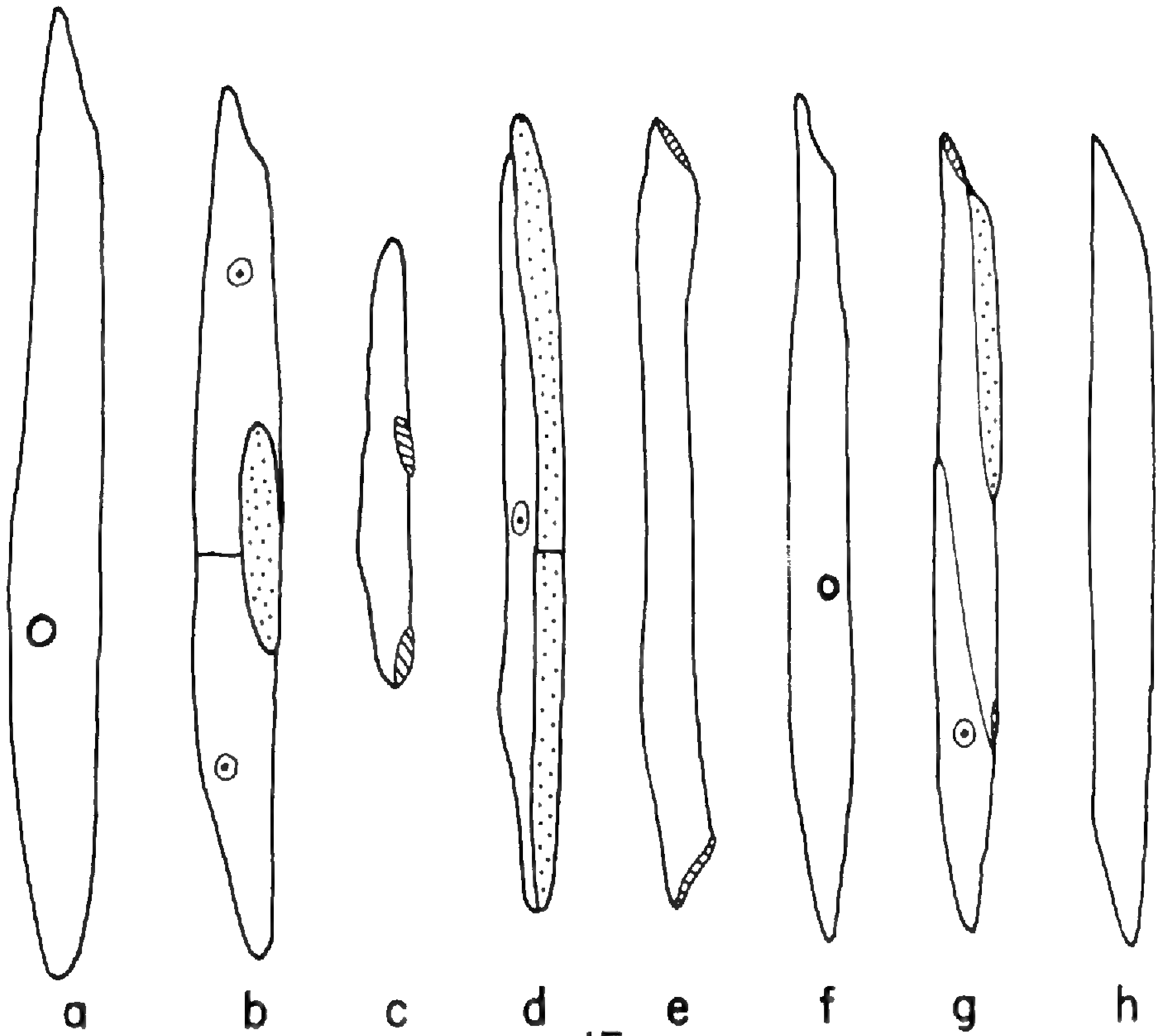

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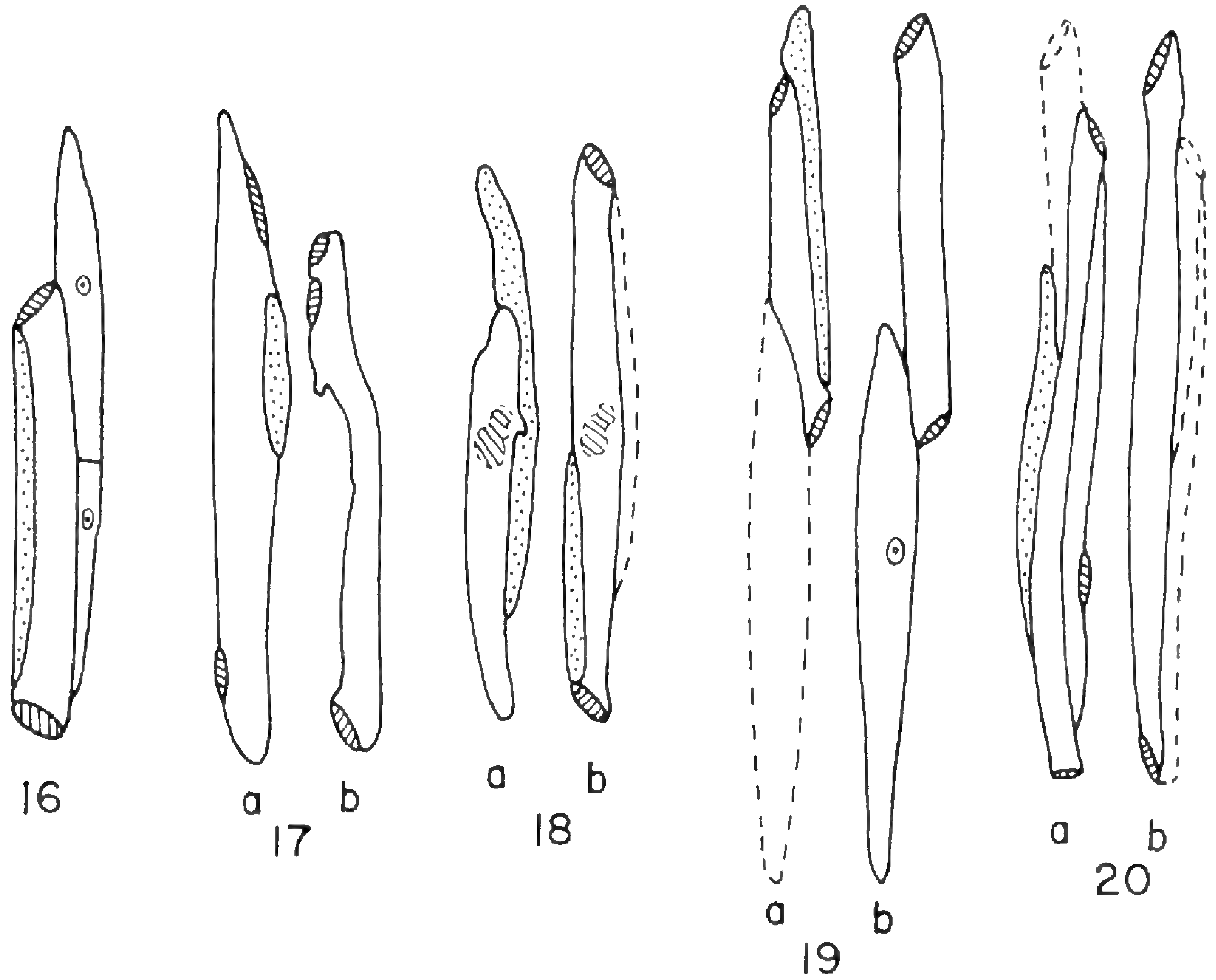
FIGS. 14, 15. *Pereskiopsis* aff. *chapistle*. FIG. 14, a–c, cross sectional views of a tier at levels indicated in diagram (d), a schematic representation of some members of tier, × 390. For details, see text. FIG. 15, successive phloem derivatives (a–g) and the fusiform cambial initial (h) of a tier in tangential view, × 220. Derivatives at (a), (b–c), (d–e), (f), and (g) are ontogenetically related. Symbols explained in text.



FIGS. 16–20. *Pereskiopsis* aff. *chapistle*: representative sieve elements and associated parenchymatous cells, drawn from tangential sections, × 220. Derivatives in each figure originated after divisions in a single phloic initial; some derivatives separated in FIGS. 17–20 for better illustration; sieve elements in FIG. 18 with a sieve plate on their common lateral wall. Broken lines represent outlines of cells seen more clearly at a different focal level; other symbols explained in text.

Two other patterns of divisions in phloic initials recorded in *Quiabentia* aff. *chacoensis* were similar to those seen in *Pereskia sacharosa*. In one method two successive, oblique longitudinal divisions in a phloic initial resulted in three daughter cells, one of which matured as a sieve element, the other two as parenchyma cells (sieve elements 3 and 4, FIG. 22, a–d). Such an origin of sieve elements and parenchyma cells seems to be a variation of the same method as was recorded for sieve elements 3 and 4 in FIG. 2, f, except that in this instance the sieve-tube mother cell differentiated directly as the sieve element without forming any companion cells. Sometimes the phloic initial divided obliquely and the resulting daughter cells behaved as sieve-tube mother cells of two elements (sieve elements 2 and 3, FIG. 23, a–d; cf. also sieve elements 6 and 7, FIG. 2, f).

In some other patterns recorded in *Pereskiopsis* aff. *chapistle* and *Quiabentia* aff. *chacoensis* the number of divisions in phloic initials preceding the differentiation of sieve elements and parenchymatous cells was much less. Sometimes the sieve-tube mother cell, formed after the first longi-

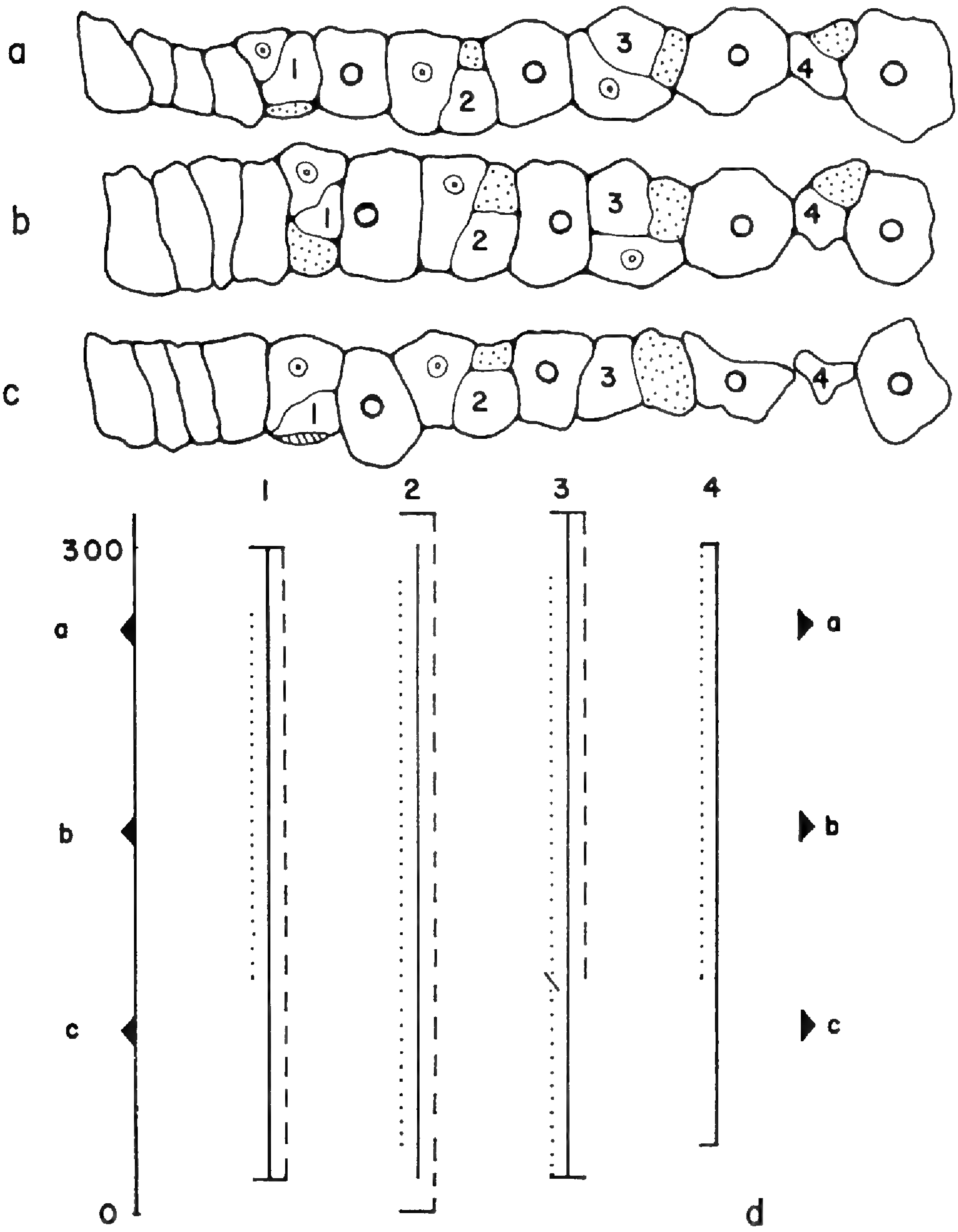


FIG. 21. *Quiabentia* aff. *chacoensis*: a–c, cross sectional views of a tier at levels indicated along the margins of diagram (d), a schematic representation of some members of the tier, as in FIG. 2; a–c, × 390. For details, see text.

tudinal division in the phloic initial, matured directly into a sieve element. A parenchyma cell (or strand) was formed in association with the sieve element but no companion cells were formed (sieve element 2, FIG. 10, d). In a few instances, the phloic initial behaved as the sieve-tube mother cell, the first division setting off a precursor of one or more companion cells and a precursor that matured as a sieve element. No parenchyma cells were formed in these cell combinations (sieve elements 1 and 3, FIG. 10, d; sieve element 2, FIGS. 11–14, d; sieve element 4, FIG. 21, d; and sieve element 5, FIG. 22, d). In still other cases, the phloic initial did not divide at all and matured directly into a sieve element (sieve element 3, FIG. 12, d).

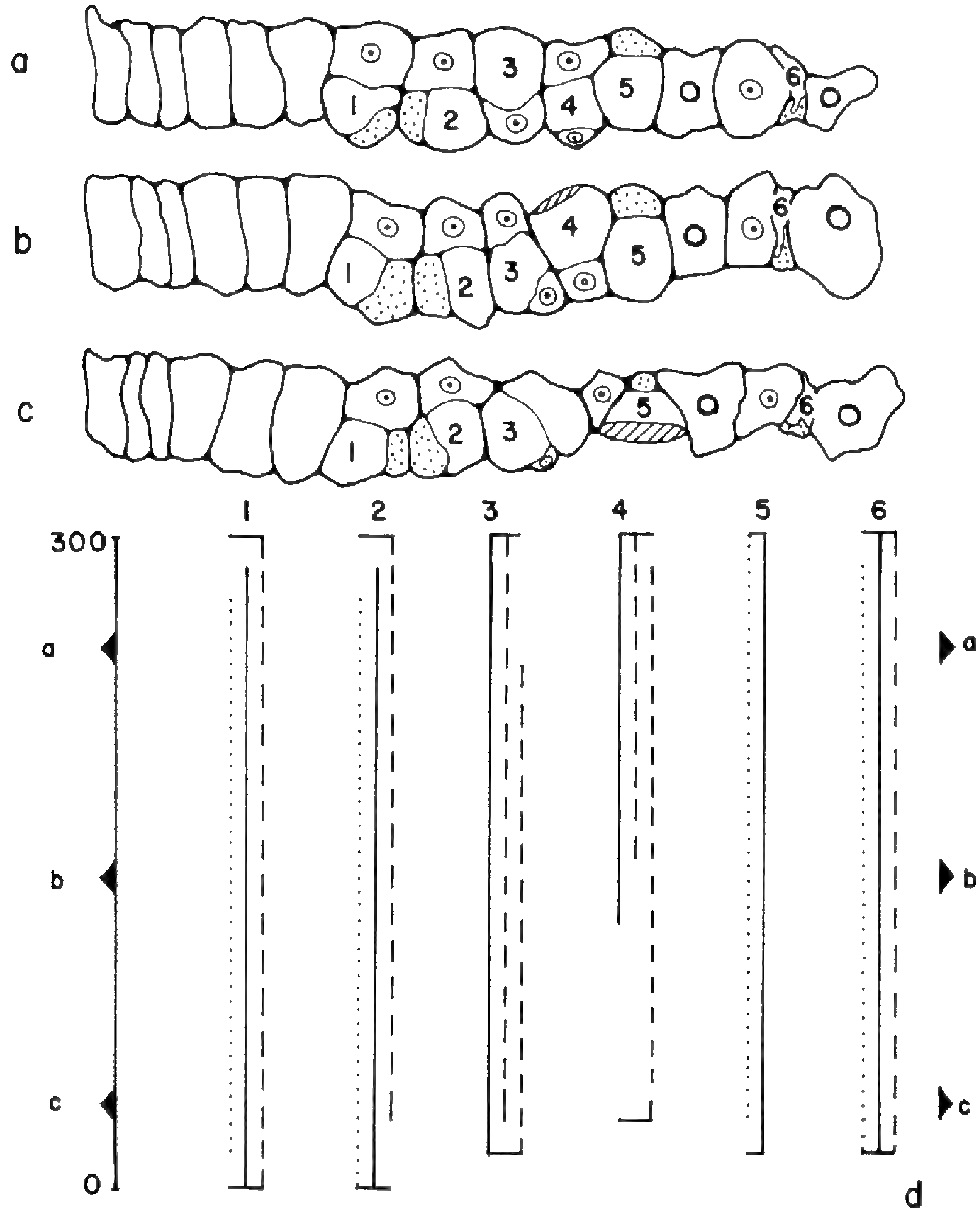


FIG. 22. *Quiabentia* aff. *chacoensis*: a–c, cross sectional views of a tier at levels indicated along the margins of diagram (d), a schematic representation, as in FIG. 2; sieve element 6 and associated companion cell partly crushed; a–c, × 390. For details, see text.

Several tiers in *Pereskiopsis* aff. *chapistle* and *Quiabentia* aff. *chacoensis* were studied from serial tangential sections. The results obtained from this study generally confirmed the observations made from cross sections (cf. FIGS. 15, 26). Some cell complexes including sieve elements and ontogenetically related parenchymatous cells selected from different tiers of these two species are shown in FIGS. 16–20 and 27–31. These figures emphasize the variations in number and planes of divisions in different phloic initials, and also give an indication of the number of sieve elements that may be formed within the confines of a single phloic initial.

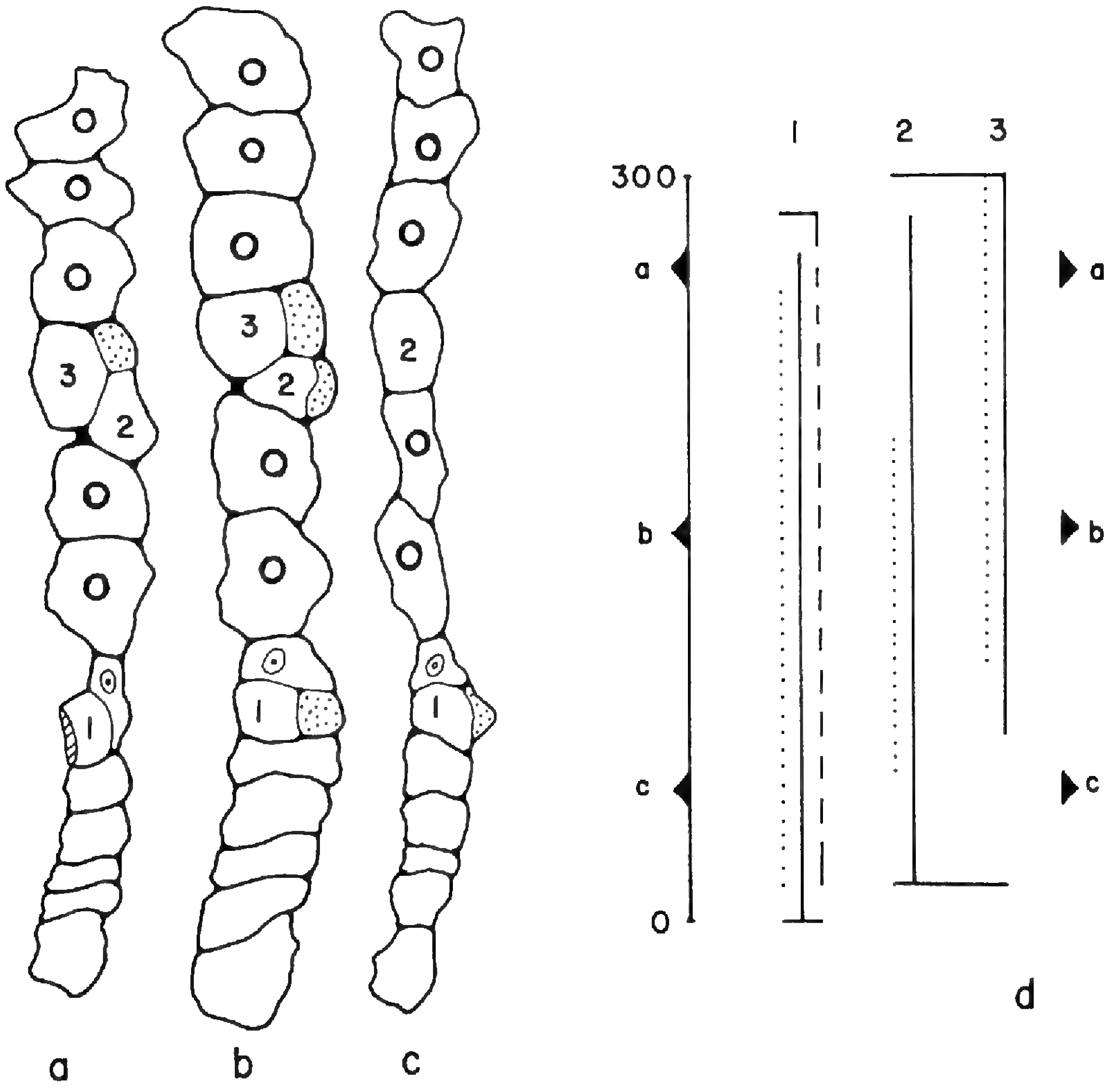


FIG. 23. *Quiabentia* aff. *chacoensis*: a–c, cross sectional views of a tier at levels indicated along the margins of diagram (d), a schematic representation of some members of tier, as in FIG. 2; a–c, × 390. For details, see text.

It may appear from our analysis of tiers that in *Pereskiopsis* aff. *chapistle* and *Quiabentia* aff. *chacoensis,* as compared to *Pereskia sacharosa*, relatively few divisions occur in the phloic initials and relatively few parenchymatous cells are formed in association with the sieve elements. It would also seem that the planes of divisions are lesss irregular and confusing in the first two species than in the last. It must be stated, however, that 2 or 3 sieve elements and related parenchymatous cells are frequently formed from a single phloic initial in *Pereskiopsis* aff. *chapistle* and *Quiabentia* aff. *chacoensis* (FIGS. 17–20, 30), and sieve elements with no ontogenetically related parenchymatous cells may be formed in *Pereskia sacharosa*, particularly in the neighborhood of rays (FIG. 35). Also, the planes of divisions in the phloic initials and their daughter cells in *Pereskiopsis* aff. *chapistle* and *Quiabentia* aff. *chacoensis* (FIGS. 17, 18, 20, 30) are often as irregular and confusing as in *Pereskia sacharosa.* If quantitative differences exist between these species, only a wider sampling of tiers and material would reveal them and make the results statistically significant.

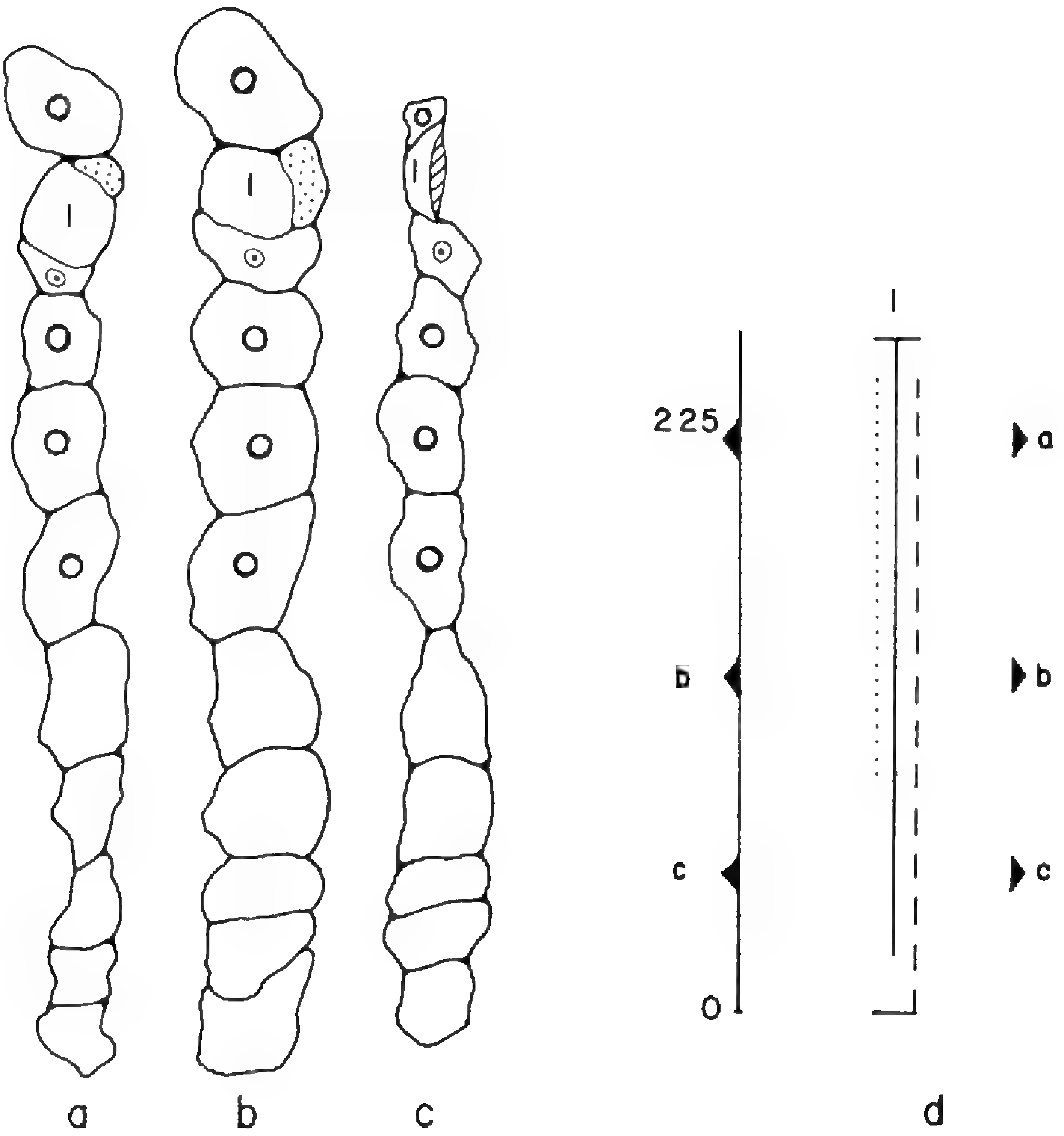


FIG. 24. *Quiabentia* aff. *chacoensis*: a–c, cross sectional views of a tier at levels indicated along margins of diagram (d), a schematic representation of some members of tier, as in FIG. 2; a–c, × 390. Three cells internal to cell complex including sieve element 1 considered to be fusiform phloem-parenchyma cells. Details of drawings in text.

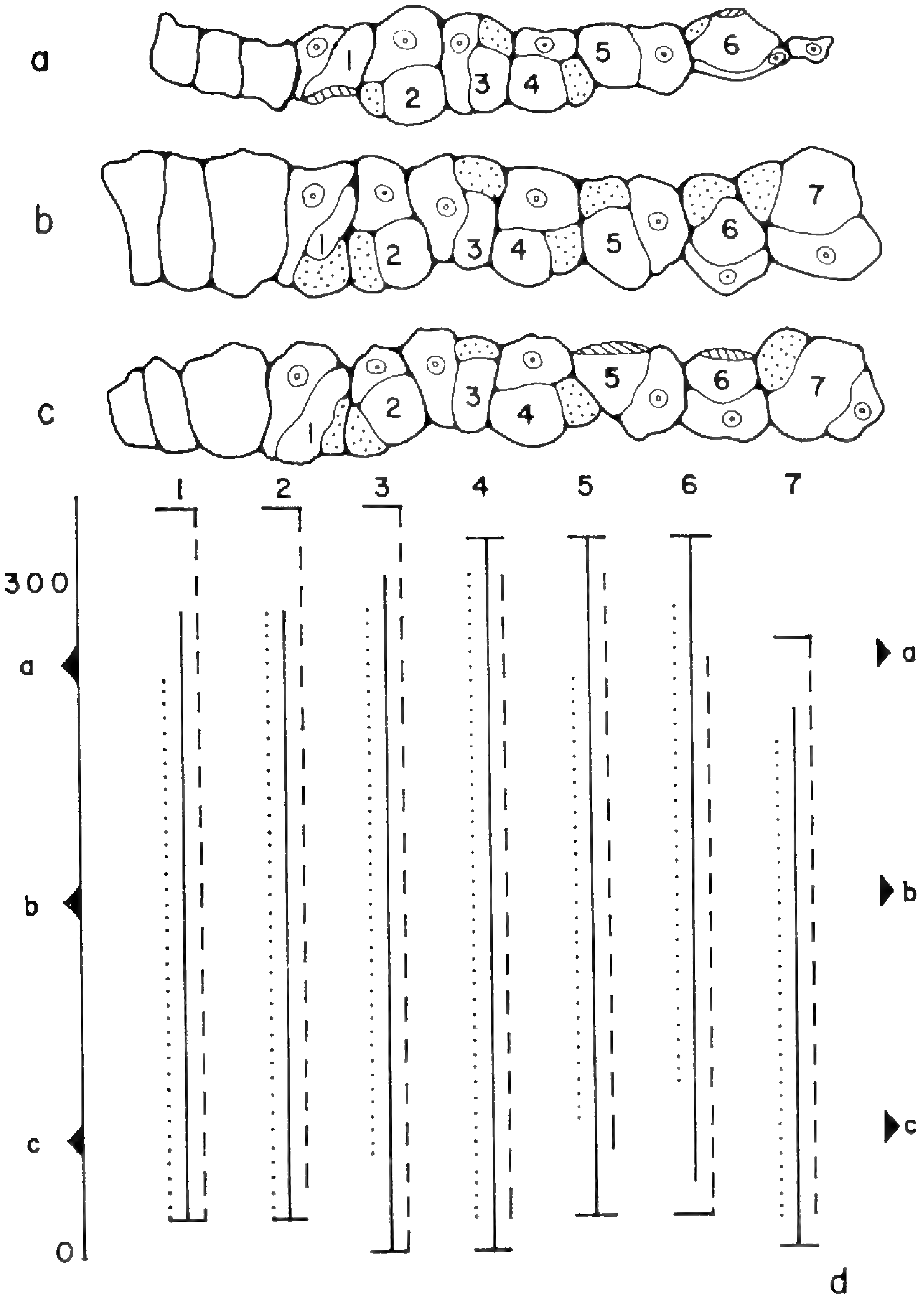


FIG. 25. *Quiabentia* aff. *chacoensis*: a–c, cross sectional views of a tier at levels indicated along margins of diagram (d), a schematic representation of some members of tier, as in FIG. 2; a–c, × 390. Details of drawings in text.

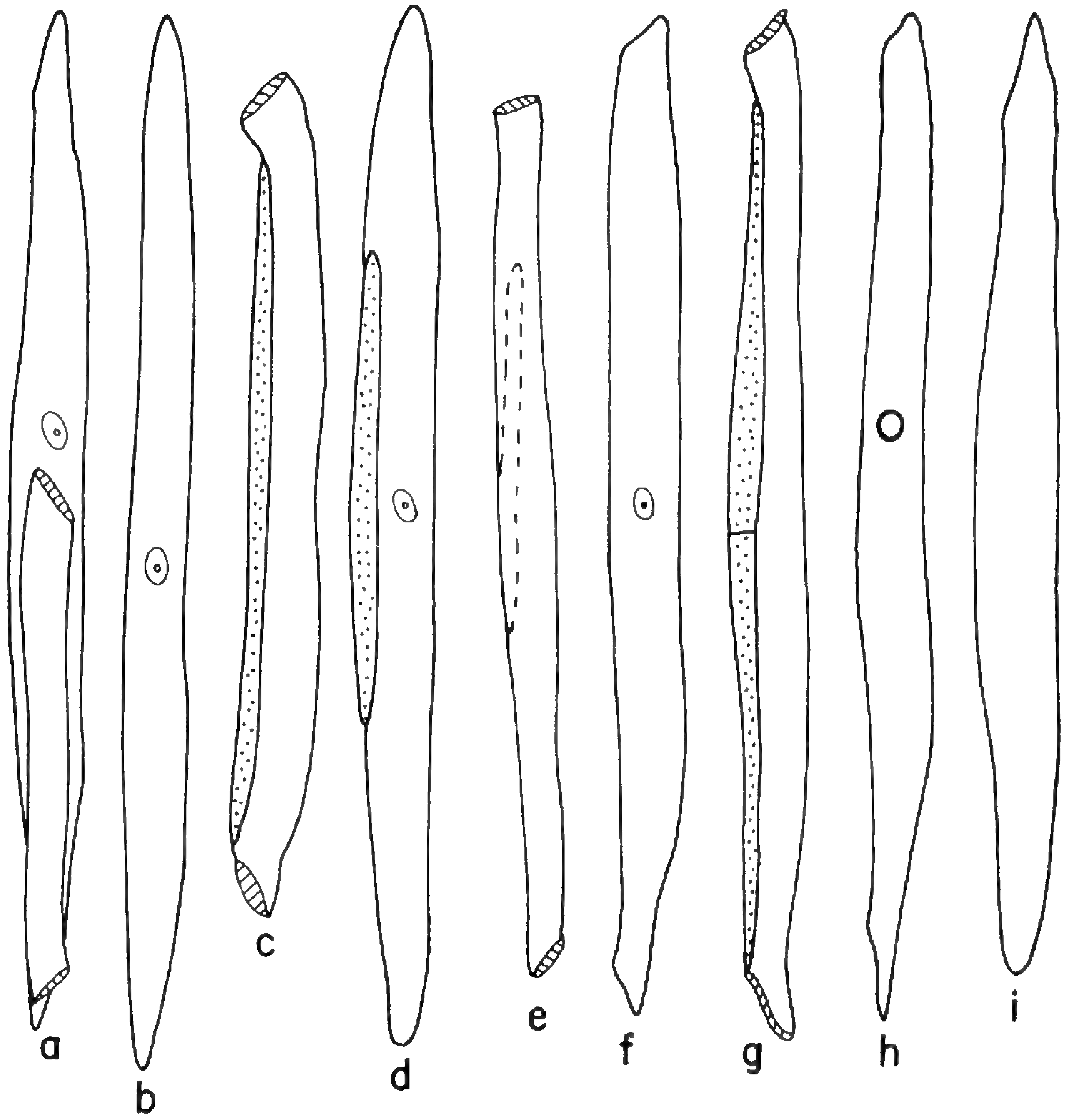
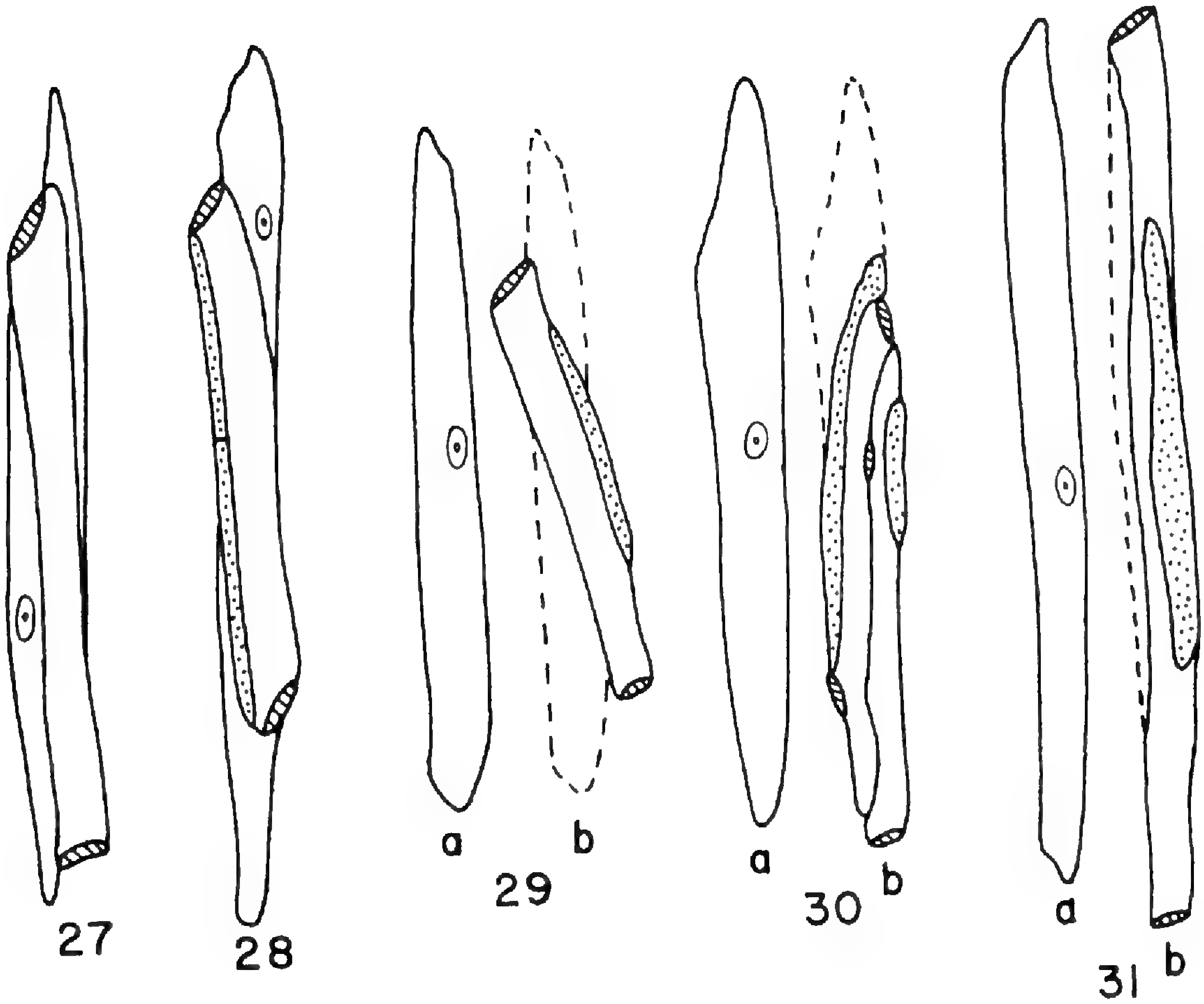


FIG. 26. *Quiabentia* aff. *chacoensis*: successive phloem derivatives (a–h) and the fusiform cambial initial (i) of a tier in tangential view, × 220. Derivatives at (a), (b–c), (d–e), (f–g), and (h) derived from single phloic initials. Symbols explained in text.



FIGS. 27–31. *Quiabentia* aff. *chacoensis*: representative sieve elements and associated parenchymatous cells in tangential view, × 200. Derivatives in each figure originated after divisions in a single phloic initial. In FIGS. 27 and 28, parenchyma cell is seen both above and below sieve element with which it is associated. Sieve elements in FIG. 30, b, are connected by a lateral sieve plate. Symbols explained in text.

SIEVE ELEMENTS

Sieve elements are considered to be the principal conduits through which carbohydrates and other food materials are transported within a plant. Their structural peculiarities are important, therefore, not only to physiologists concerned with problems of translocation, but also to morphologists interested in the evolutionary aspects of the phloem tissue as a whole. Esau, Cheadle, and Gifford (1953) suggested some possible trends of specialization in the phloem. In recent years, some new information, particularly about the length of sieve elements in relation to that of the phloic initials from which they are derived and about the association of sieve elements with parenchymatous cells, has been added through detailed ontogenetic work (Esau & Cheadle, 1955; Cheadle & Esau, 1958; Evert, 1960). In the following paragraphs some structural features of the sieve elements in leaf-bearing Cactaceae, their contents, wall structure, sieve areas, and length, are emphasized for a better understanding of their physiologic and evolutionary specialization.

As is typical of this type of cell, the sieve elements in the leaf-bearing Cactaceae are enucleate in their functionally mature state. The fixative and the staining procedures used by us were not conducive to a critical cytological study. However, numerous, doughnut-shaped bodies, probably carbohydrate granules, were seen in the sieve elements. These granules aggregated in large numbers near the sieve plates and sieve areas (FIGS. 39, 41). In addition, the material described in the literature as "slime" was often present in copious quantities. It was usually deposited on one side of a sieve plate in the form of a plug and extended like a strand through most of the cell lumen (Figs. 35, 41). In longitudinal sections, this feature was often useful in determining the extent of a particular sieve element. It was rather scanty in *Pereskiopsis* aff. *chapistle* (FIG. 39).

Nacreous walls, reported in the sieve elements of various dicotyledons by Esau and Cheadle (1958), were uniformly lacking in the material studied by us (cf. Figs. 32, 38, 40). In permanent slides the walls of sieve elements appeared rather thin, but they were birefringent under polarized light.

The common walls between two sieve elements bear numerous sieve areas, some of which are more specialized than others and are termed sieve plates (cf. Cheadle & Whitford, 1941; Esau, 1950). Sieve areas occur on radial as well as tangential walls (FIGS. 44, 48); and their size, as determined by the number of callose cylinders stained by lacmoid, varies considerably (FIG. 51). The difference in size of connecting strands and pores in sieve areas that occur in the sieve plates on the one hand and those that occur elsewhere on the walls is very marked (FIGS. 50, 51). The sieve plates are generally of the simple type with a single sieve area, but sieve plates with two or more sieve areas are present also (FIG. 50). As a rule, every sieve element has two sieve plates (cf. FIGS. 7–9, 15–20, 26–31); but some sieve elements may have as many as 3 or 4 sieve plates

(FIGS. 18, b; 30, b) others may have only one (FIGS. 7, b, c; 18, a; 20, a). The position of sieve plates in the sieve elements varies likewise. Commonly, the sieve plates occur at or near the ends of the sieve elements, but sieve plates on lateral walls are not unusual (FIGS. 7, b; 8, b; 18, a, b; 30,b). The final shape, size, and orientation of the mature sieve elements is often different from that of the phloic initials from which they are derived. Some sieve elements may be rather grotesque in shape (FIGS. 7, b; 8, b; 17, b); and the long axis of some may be placed slantingly in relation to the vertical axis of the phloic initial and, hence, that of the stem (FIGS. 9, b; 20, a; 28; 29, b; 41). Such slantingly placed sieve elements are often connected through sieve plates with sieve elements in laterally adjacent (rather than vertically adjacent) tiers (FIG. 41). Often, two sieve elements derived from the same phloic initial form parts of two different sieve tubes, one with a vertical, the other with a diagonal orientation in relation to the long axis of the stem. Laterally placed sieve plates are encountered rather frequently in areas where diagonally placed sieve elements abut on the lateral walls of adjacent sieve elements.

The length of a sieve element depends not only on the length of the phloic initial from which it arises, but also on the number and planes of divisions in the phloic initial and its daughter cells and on the number and planes of divisions in the sieve-tube mother cell.[4] The length of sieve elements as measured from transections (FIGS. 2–6, f; 10–14, d; 21–25, d) is subject to an error which must be mentioned. When the sieve plates occur near but not at the end of the sieve element (e.g., FIGS. 7, d; 17, a; 30, b), the tapering end of the cell may be missed from calculations. The following statements about the lengths of sieve elements and the phloic initials from which they are derived are, therefore, liable to some error.

Since the phloic initials in a tier are usually derived by symmetric periclinal divisions in a fusiform cambial initial, one normally expects them to be of approximately equal length (e.g., FIGS. 4, f; 10, d). The fluctuations in the lengths of phloic initials in several tiers (e.g., FIGS. 2, f; 6, f; 25, d) are, therefore, somewhat unusual. A possible explanation for the different lengths of the phloic initials in a tier would be that the individual phloic initials elongated intrusively in varying degrees. But this explanation is contrary to the commonly held belief that the phloic initials, in contrast to fusiform cambial initials, do not elongate intrusively. It appears that in the leaf-bearing Cactaceae the periclinal divisions in the fusiform cambial initials are often not strictly longitudinal and the dividing walls fall short of one or both tips of the mother initial. The daughter cells formed after such an asymmetric periclinal division may be equal or unequal in length, but they are vertically displaced (at one or both ends) in relation to one another. If a number of such asymmetric periclinal divisions occur in the daughter cell that be-

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[4] This reasoning is based on the assumption that the sieve elements do not undergo intrusive elongation during their differentiation from the phloic initials or their daughter cells. Several studies on the phloem of gymnosperms and dicotyledons support this assumption (Bannan, 1950; Cheadle & Esau, 1958; Evert, 1960; Srivastava, 1962).

haves as the fusiform cambial initial after each division and if such divisions are interpolated among others that are symmetric, the net result as seen in mature tissue would be comparable to that shown in FIGS. 2,f; 6,f; 15; 25,d; and 26. In its radial extent, the tier would show fluctuations in height that would be independent of the intrusive growth of the fusiform cambial initial. The intrusive growth of the fusiform cambial initial, if it occurred after a periclinal division, would further complicate the pattern.

In instances where the phloic initial matures directly as a sieve element and no parenchymatous cells are formed (FIG. 12,d, sieve element 3), the length of the sieve element is approximately the same as that of the phloic initial. Also, if the phloic initial behaves as a sieve-tube mother cell, that is, one or more precursors of companion cells are formed as sister cells of the precursor that matures as the sieve element but no parenchyma cells are formed (FIGS. 10,d, sieve elements 1 and 3; 11 14,d, sieve element 2; 21,d, sieve element 4; 22,d, sieve element 5), the length of the sieve element closely reflects the length of the phloic initial. In other instances, the length of the sieve element bears no predictable relationship to that of the phloic initial — it may be the same (cf. FIGS. 9, c; 15, d–e; 26, f–g) or it may be much less (cf. FIGS. 7, b; 8, b, c; 9, b; 15, b–c, g; 26, a).

In concluding this section on sieve elements, a few remarks must be made about the relative lengths of the sieve-tube members and the parenchymatous elements ontogenetically associated with them. The length of parenchyma cells (or strands) may be equal to, or more than, or less than that of the sieve element with which they are associated (cf. FIGS. 2–6,f; 10–14,d; 21–25,d). The divisions that separate the precursor of the companion cell (or strand) from that of the sieve element are usually longitudinal with reference to the long axis of the sieve-tube mother cell, but the dividing walls are laid down in such a manner that the precursor of the companion cell (or strand) may be almost as long as that of the sieve element or it may be shorter (cf. FIGS. 7–9; 15–20; 26–31). Occasionally, the dividing wall is laid obliquely and short of the cell tips at either end; as a result, the precursor of the companion cell (or cells) at one end projects a little beyond the end of the precursor that matures as the sieve element (e.g., FIGS. 7, c; 9, a; 19, a; 30, b; 33). Exceptionally, the precursor of the companion cell (or cells) may be a little longer than the precursor of the sieve element (e.g., FIGS. 5, f, cell complex including sieve element 2; 9, c).

PARENCHYMA CELLS

Although the parenchyma cells in the phloem of leaf-bearing Cactaceae differ in their ontogeny, we were not able to discern any *significant* cytological differences between them with the fixing and staining procedures that we used. The fusiform phloem-parenchyma cells and the individual cells in phloem-parenchyma strands, which in other plants commonly store starch, oil, tannins, etc. (cf. Esau, 1953, p. 284), did not show any such inclusions in the functional phloem. The parenchymatous cells ontogenetically related to the sieve elements also did not show any of these inclusions. It is commonly held that companion cells have a denser cytoplasm and, in general, stain more deeply than other parenchyma cells in phloem (cf. Esau, 1953, p. 283). We utilized this feature in identifying companion cells and were partially successful. But it was not always possible to use this criterion because the deeply staining appearance of a companion-cell protoplast depends partly on the size of the companion cells and partly on the plane of the section with reference to the cell lumen. For instance, if a longitudinal section passes close to a lateral wall rather than through the middle of the cell, the protoplast may appear lightly stained. Because of these features it was difficult for us to be certain about the identity of individual parenchymatous cells in isolated cross and tangential sections. With the use of serial sections one can normally distinguish between fusiform phloem-parenchyma cells and phloem-parenchyma strands, on the one hand, and the parenchymatous cells ontogenetically related to the sieve elements, on the other. It is also possible in most cases to distinguish between companion cells and parenchyma cells ontogenetically associated with the sieve elements, because the length of the companion cells (or strand of companion cells) usually does not exceed that of the sieve element, whereas that of the parenchyma cells (or strands) frequently may. Still, in several cell configurations (e.g., those including sieve elements 3 and 4, FIG. 22, a–d) it was almost impossible to tell whether one was dealing with companion cells or parenchyma cells or both. (In this instance, the cells were interpreted as parenchyma cells.)

Sieve elements are usually connected with their associated companion cells through one-sided sieve areas. Such sieve areas have densely staining connecting strands and callose cylinders only in the wall belonging to the sieve element; in the companion cell wall there is only a primary pit field. Cheadle and Esau (1958) and Evert (1960) reported such one-sided sieve-area connections between sieve elements and the parenchyma cells ontogenetically associated with them also. In the material of leaf-bearing Cactaceae that we have examined, sieve-area connections were common between sieve elements and companion cells and between sieve elements and ontogenetically associated parenchyma cells (Figs. 45, 46, 49). Although no counts were made, our general impression is that the number of sieve-area connections between sieve elements and companion cells is usually higher than that between sieve elements and ontogenetically associated parenchyma cells. Cheadle and Esau (1958) made a similar observation. One notable feature about the sieve-area connections between sieve elements and ontogenetically related parenchyma cells was that the connections occurred in those portions of the common wall that bulged somewhat in the lumen of the parenchyma cell (FIGS. 46, 52). In contrast, the common wall between the sieve elements and their companion cells, although covered with numerous sieve areas, was usually straight (FIG.

45). Sieve-area connections usually occur between sieve elements and parenchymatous cells derived from the same phloic initials; but occasionally sieve elements derived from one phloic initial may be connected to a parenchymatous cell that forms part of a cell complex derived from a different phloic initial. Such connections were recorded especially in those parts of a parenchymatous cell that projected beyond the end of the sieve element to which it was ontogenetically related.

Sieve-area connections were also observed between sieve elements and some fusiform phloem-parenchyma cells (FIG. 47). The sieve areas occurred in those portions of the common wall that bulged into the lumen of the parenchyma cell. The fusiform phloem-parenchyma cells that were so connected with sieve elements occurred in the same tier as the sieve element or in neighboring tiers, but their number was relatively very small and relatively few sieve-area connections occurred on the common wall. Fusiform phloem-parenchyma cells in such intimate contact with the sieve elements were more common in *Pereskiopsis* aff. *chapistle* and *Quiabentia* aff. *chacoensis* than in *Pereskia sacharosa*.

In the nonfunctional phloem, sieve elements and companion cells lose their living contents, collapse, and sooner or later are crushed (FIGS. 36, 37). It is our impression that the parenchyma cells ontogenetically related to the sieve elements survive for a longer time than the related sieve elements and companion cells, but eventually they also lose their protoplast, collapse, and are crushed. The fusiform phloem-parenchyma cells and the individual cells of phloem-parenchyma strands seem to survive and sometimes store starch and even accumulate druses of calcium oxalate. However, in the absence of any definite cytological differences between the parenchyma cells ontogenetically related to sieve elements and those that are not so related, and because of a general distortion of the tissue, it is difficult to determine in nonfunctional phloem which cells or strands may or may not have been ontogenetically related to the sieve elements. Consequently, we are not sure whether *all* fusiform phloem-parenchyma cells and phloem-parenchyma strands continue to live in the nonfunctional phloem; we are also not sure whether *all* parenchyma cells and strands ontogenetically related to sieve elements die and collapse in the nonfunctional phloem.

DISCUSSION AND CONCLUSIONS

Our studies on the phloem of leaf-bearing Cactaceae were restricted in scope, partly because of the difficulty of obtaining and sectioning the material of cacti and partly because of the fixative used to kill it. Only those species were selected for a detailed study which could be sectioned in a satisfactory manner, and only those aspects of cellular detail were followed which were not directly related to seasonal changes and the elucidation of which did not require elaborate cytological techniques. For these reasons we did not concern ourselves with such aspects of phloem study as the development and maturation of sieve elements, the cytological inclusions in companion cells and parenchyma cells ontogenetically related and unrelated to sieve elements, and the longevity of sieve elements. We also did not study the changes from functional to nonfunctional phloem in any detail, and our investigation of ray tissue was only cursory.

The secondary phloem of the three species that we investigated is relatively simple. Sieve elements and parenchyma cells of various types were the only constituents in the axial tissue. Oil cells, mucilage cells, fibers, etc., were absent from the functional phloem of these species. In the nonfunctional phloem several parenchyma cells accumulated druses of calcium oxalate and, in *Pereskia sacharosa*, some were modified as sclereids (Bailey, 1961a, b). Intercellular spaces were commonly seen in functional and nonfunctional phloem (Figs. 32, 38, 40). The rays are typically high and multiseriate and include, especially near the ray margins, some upright cells that may be almost as long as some of the fusiform derivatives. High and broad rays are often dissected by a conversion of ray initials into fusiform initials. In the early stages of such conversion the sieve elements that are formed are often of the same size as other ray cells and frequently lack companion cells (Fig. 35). Fusiform initials are converted into ray initials also, with accompanying changes in the nature of their derivatives.

Ontogenetic studies of phloem yield valuable data about the origin and interrelationships of different phloem elements. Our analysis of tiers in the phloem of leaf-bearing Cactaceae revealed several possible ways in which sieve elements and parenchymatous cells may arise from phloic initials. Most of these methods of origin have been discussed in detail elsewhere in this paper. In the following some of the main conclusions are summarized.

The three representatives of the leaf-bearing Cactaceae studied, *Pereskia sacharosa*, *Pereskiopsis* aff. *chapistle*, and *Quiabentia* aff. *chacoensis*, do not seem to differ basically in the method of origin of phloem elements. Fusiform phloem-parenchyma cells and phloem-parenchyma strands arise either directly from or after a few horizontal divisions in the phloic initials. In contrast, the differentiation of sieve elements and parenchymatous cells ontogenetically related to them is usually preceded by several divisions in the phloic initials and their daughter cells. Evidence of such divisions was seen not only in mature tissue (cf. Figs. 33, 34), but also in immature tissue close to the cambium (cf. Figs. 42, 43). Commonly, a parenchyma cell (or strand) is formed in association with a sieve element and its companion cells; but sometimes the companion cell, or the parenchyma cell, or both are lacking, and sometimes several parenchyma cells, sieve elements, and companion cells are formed within the confines of a single phloic initial. Apparently, the phloic initials and their daughter cells show varying degrees of mitotic activity before cells are differentiated. Such variations among different phloic initials may be encountered, not only among different tiers of the same species, but also within the same tier. Also, one tier may be composed predominantly of fusiform phloem-parenchyma cells and phloem-parenchyma strands and may have very few sieve elements (FIG. 24, a–c), whereas a neighboring tier may have numerous sieve elements and ontogenetically related parenchymatous cells and relatively few fusiform phloem-parenchyma cells and phloem-parenchyma strands (FIG. 25, a–c). We do not know what factor or factors may be responsible for these variations in the behavior of phloic initials in the same tier and in neighboring tiers.

Although the final number of parenchyma cells, sieve elements, and companion cells arising within the confines of a phloic initial varies considerably, the sequence of divisions seems to be such that the precursors of parenchyma cells arise as sister cells of precursors that behave as sieve-tube mother cells, and the precursors of companion cells arise as sister cells of the precursor that matures as a sieve element. Two observations support this assumption. First, in cross sections, the wall separating the parenchyma cell from the complex of sieve element and companion cells seems to be the first wall laid down in the phloic initial (or its daughter cell) and the wall separating the sieve element from the companion cell seems to be laid down in one of the daughter cells formed after the first division (FIG. 40). Second, the length of the associated parenchyma cells may frequently exceed that of the sieve element, but that of the companion cells rarely does (FIG. 41). If our interpretation of the sequence of divisions within the confines of a phloic initial is correct, the parenchyma cells in their ontogenetic relationship would be somewhat more distantly related to the sieve elements than the companion cells. But this interpretation is applicable only if parenchyma cells, as well as companion cells, are formed in association with a sieve element.

It is significant that the sieve elements in the leaf-bearing Cactaceae have sieve-area connections, not only with ontogenetically related, but also with ontogenetically unrelated parenchyma cells. These connections are numerous between sieve elements and companion cells, less numerous between sieve elements and ontogenetically related parenchyma cells, and are only infrequently observed between sieve elements and the parenchyma cells that are derived from independent phloic initials. Apparently, the varying degrees in which the parenchyma cells are ontogenetically related to sieve elements are paralleled by the degree of their physiological affinity to sieve elements: those with the closest ontogenetic association are also those that have the most intimate physiological association. For future research, it will be of extreme interest to determine the cytological features of these parenchyma cells and to see in what important ways they differ from one another.

From an evolutionary viewpoint, the parenchyma cells physiologically associated with the sieve elements present a complicated picture. The albuminous cells of gymnosperms, although physiologically comparable to companion cells of angiosperms, generally have no ontogenetic association with the sieve elements (cf. Strasburger, 1891; Srivastava, 1962). Companion cells are lacking in *Austrobaileya scandens*, a primitive dicotyledon (Bailey & Swamy, 1949); and it is possible that some parenchyma cells derived from independent phloic initials serve as companion cells in this plant. Holdheide (1951) reported some parenchyma cells in the secondary phloem of dicotyledons that he compared to albuminous cells of gymnosperms, thus implying that these cells originated from independent phloic initials. Other reports include varying degrees of specialization among companion cells themselves (Resch, 1954). In view of these findings and the ontogenetic studies carried out by Cheadle and Esau (1958), Evert (1960), and in the present work, it may seem that the evolution of the parenchyma cells physiologically associated with the sieve elements has progressed in the direction of a closer ontogenetic association with the sieve elements. But the presence of sieve-area connections between sieve elements and parenchyma cells ontogenetically unrelated to them in a family as highly specialized as Cactaceae presents serious impediments in the acceptance of this idea. It is clear that more and detailed ontogenetic and cytological studies of the phloem of vascular plants need to be carried out before any valid generalizations about the evolution of parenchyma cells physiologically associated with the sieve elements can be made.

In the preceding paper of this series (Bailey & Srivastava, 1962), based upon the study of numerous putative species of *Pereskia*, *Pereskiopsis* and *Quiabentia*, we demonstrated that the fusiform initials of the cambium and their derivatives in phloem have attained a high level of phylogenetic specialization. This is shown by their short length and their tendency to occur in stratified arrangements as seen in tangential longitudinal sections. The well-developed structure of the sieve plates in the sieve elements of the leaf-bearing Cactaceae and the marked difference in the size of pores and connecting strands in the sieve plates, on the one hand, and the lateral sieve areas, on the other (FIGS. 50, 51), also suggest an advanced degree of evolutionary specialization.

In this paper we have been concerned primarily with the phenomenon of cell divisions in phloic initials and their daughter cells and the interrelationships between sieve elements and different kinds of parenchyma cells. It is evident from our studies that the ontogenetic changes in the differentiation of sieve elements, companion cells and parenchyma cells are diversified and variable. They obviously are qualitatively similar in the three genera that we examined. Although there are some evidences of possible quantitative differences in these forms, it is clear that a great deal of material must be critically studied before valid taxonomic conclusions can be drawn. This is in marked contrast to the structure of nonfunctional phloem, where, as one of us (Bailey, 1961a) has shown, *Pereskia* differs from *Pereskiopsis* and *Quiabentia* by the presence of sclereids, and where three groups of species of *Pereskia* may be differentiated upon the basis of form and distribution of such sclerenchymatous elements.

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EXPLANATION OF PLATES

The following symbols have been used consistently in all the plates: C, cambial zone; CS, companion cell or strand; FP, functional phloem; Gr, carbohydrate granules; IS, intercellular space; NP, nonfunctional phloem; P, parenchyma cell or strand ontogenetically related to sieve elements; Par, fusiform phloem-parenchyma cell or phloem-parenchyma strand; R, ray; S, sieve element; SA, sieve areas; Sl, slime; SP, sieve plate.

PLATE I

FIGS. 32–34. Transverse and tangential views of phloem and cambium of *Pereskia sacharosa.* 32, Transverse section, × 455. 33, Tangential section of phloem showing a strand of parenchyma cells (P) and companion cells (CS) in ontogenetic association with a sieve element (S), × 220. A strand of companion cells (indicated by arrow) projects below the end of the sieve element with which it is associated. Fusiform phloem-parenchyma cells (Par) give an idea about the length and size of phloic initials. 34, Tangential section of the cambium, × 220.

PLATE II

FIGS. 35–37. Tangential and radial views of phloem of *Pereskia sacharosa.* 35, Tangential section through functional phloem. 36, Radial section of functional (right) and nonfunctional (left) phloem. 37, Tangential section of nonfunctional phloem. All figures × 455.

PLATE III

FIGS. 38–40. Transverse and tangential views of phloem. 38, *Pereskiopsis* aff. *chapistle*, transverse section of phloem and cambium. 39, *The same*, tangential section of phloem. 40, *Quiabentia* aff. *chacoensis*, transverse section of phloem and cambium. Cell complexes including a parenchyma cell (P), sieve element (S) and companion cell (CS) are shown. All figures × 455.

PLATE IV

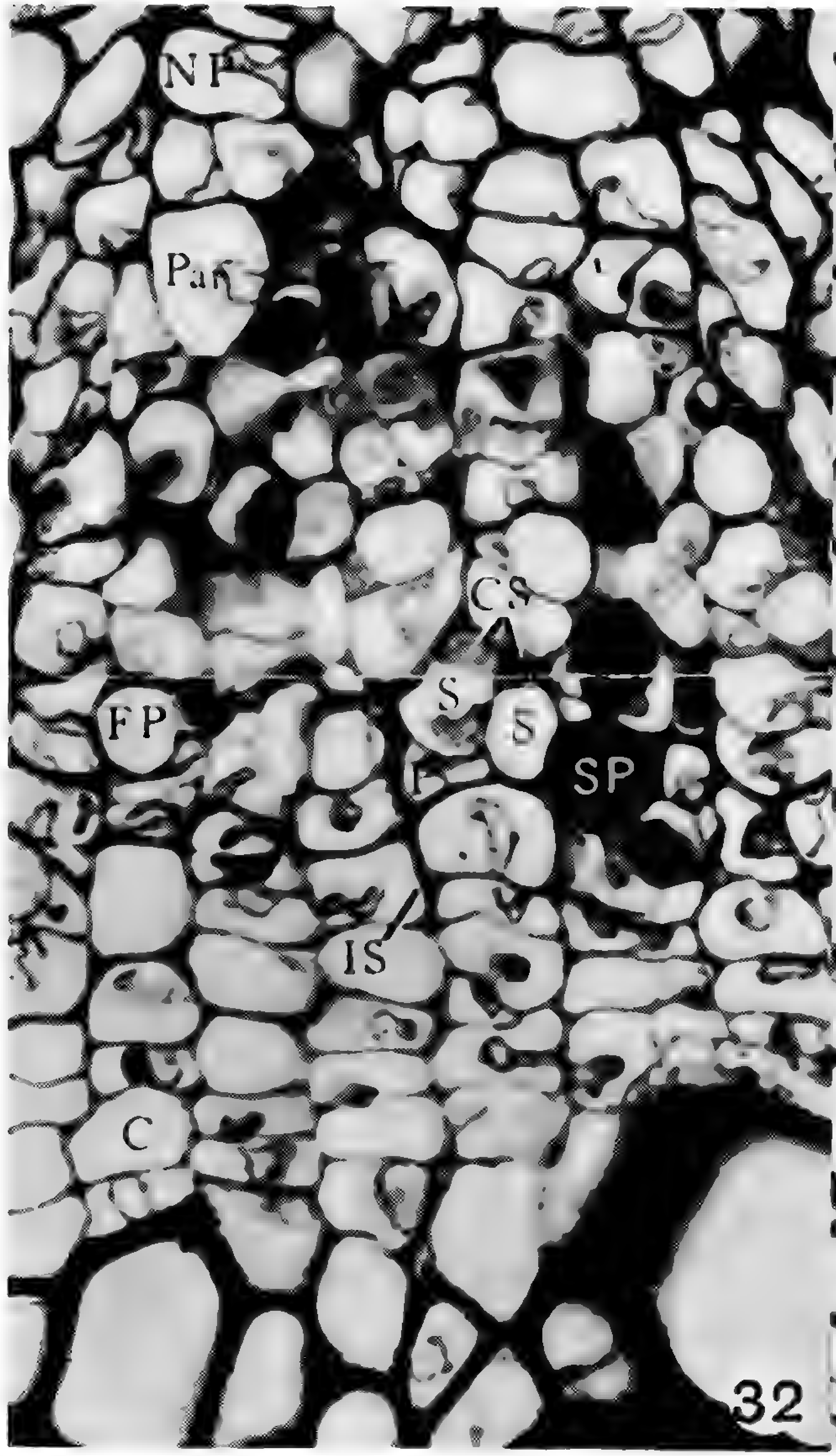
FIGS. 41–43. Tangential sections of phloem and cambium of *Quiabentia* aff. *chacoensis.* 41, section through mature phloem. The sieve element on lower left is slantingly placed in relation to the parenchyma cell which occurs in association with it. 42, section through immature phloem showing divisions in phloic initials marked with (x). 43, section through cambium. FIGS. 42 and 43 are photographs of successive sections in a tangential series; the cambial initials that produced the phloic initials in FIG. 42 marked with (x) are similarly marked in FIG. 43. All figures × 220.

PLATE V

FIGS. 44–47. Tangential sections of phloem showing sieve areas between sieve elements, sieve elements and companion cells, sieve elements and ontogenetically related parenchyma cells, and sieve elements and ontogenetically unrelated parenchyma cells. 44, *Pereskia sacharosa,* × 910. 45–47, *Quiabentia* aff. *chacoensis*, × 910.

PLATE VI

FIGS. 48–52. Sieve plates, lateral sieve areas and sieve-area connections between sieve elements and related parenchymatous cells. 48, *Pereskia sacharosa*, transverse section showing a sieve area (indicated by arrow) on the tangential wall between two sieve elements, × 1140. These sieve elements formed part of a cell complex that had originated from a single phloic initial. 49, *Quiabentia* aff. *chacoensis*, transverse section showing one-sided sieve-area connections (indicated by arrows) between a sieve element and the companion and parenchyma cells that are associated with it, × 910. 50, *Pereskiopsis* aff. *chapistle*, sieve plate in radial view, × 1140. 51, *Quiabentia* aff. *chacoensis*, lateral sieve areas between two sieve elements in tangential view, × 1140. 52, *The same*, tangential section showing one-sided sieve-area connections between a sieve element and related parenchyma cell, × 1140. The sieve areas occur in those portions of the common wall that bulge into the lumen of the parenchyma cell.



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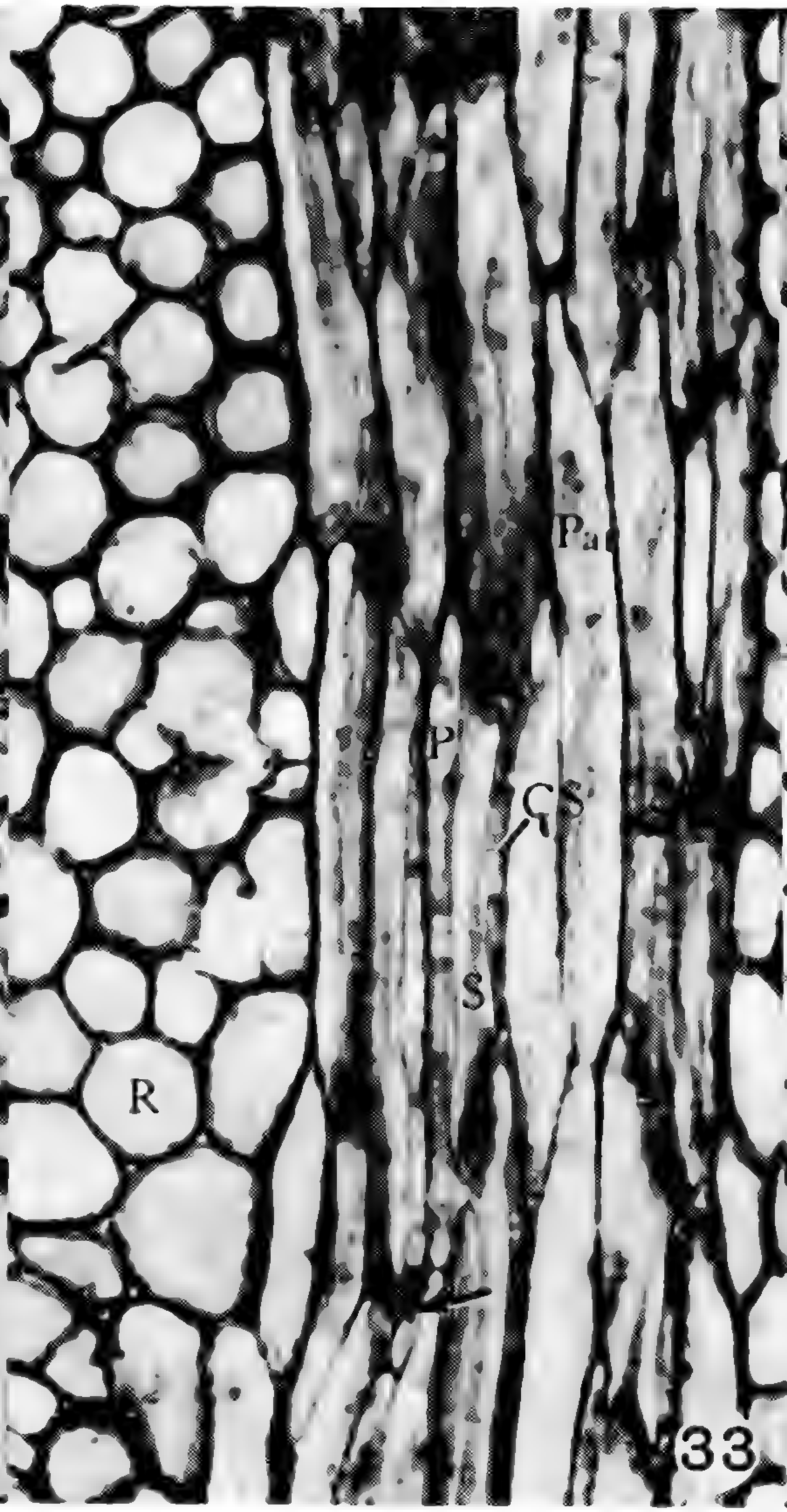

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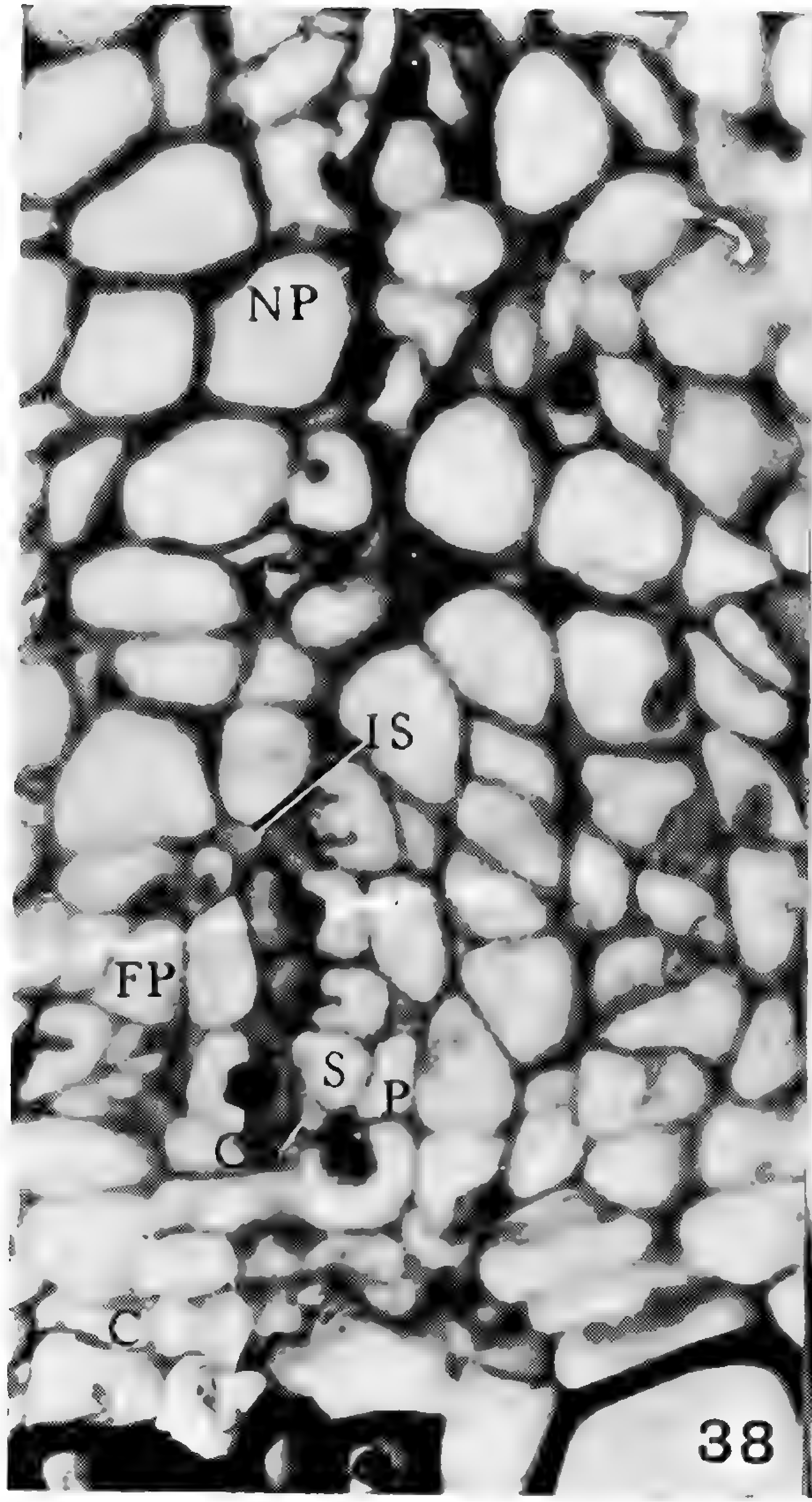
Srivastava & Bailey, Leaf-bearing Cactaceae, V

Srivastava & Bailey, Leaf-bearing Cactaceae, V



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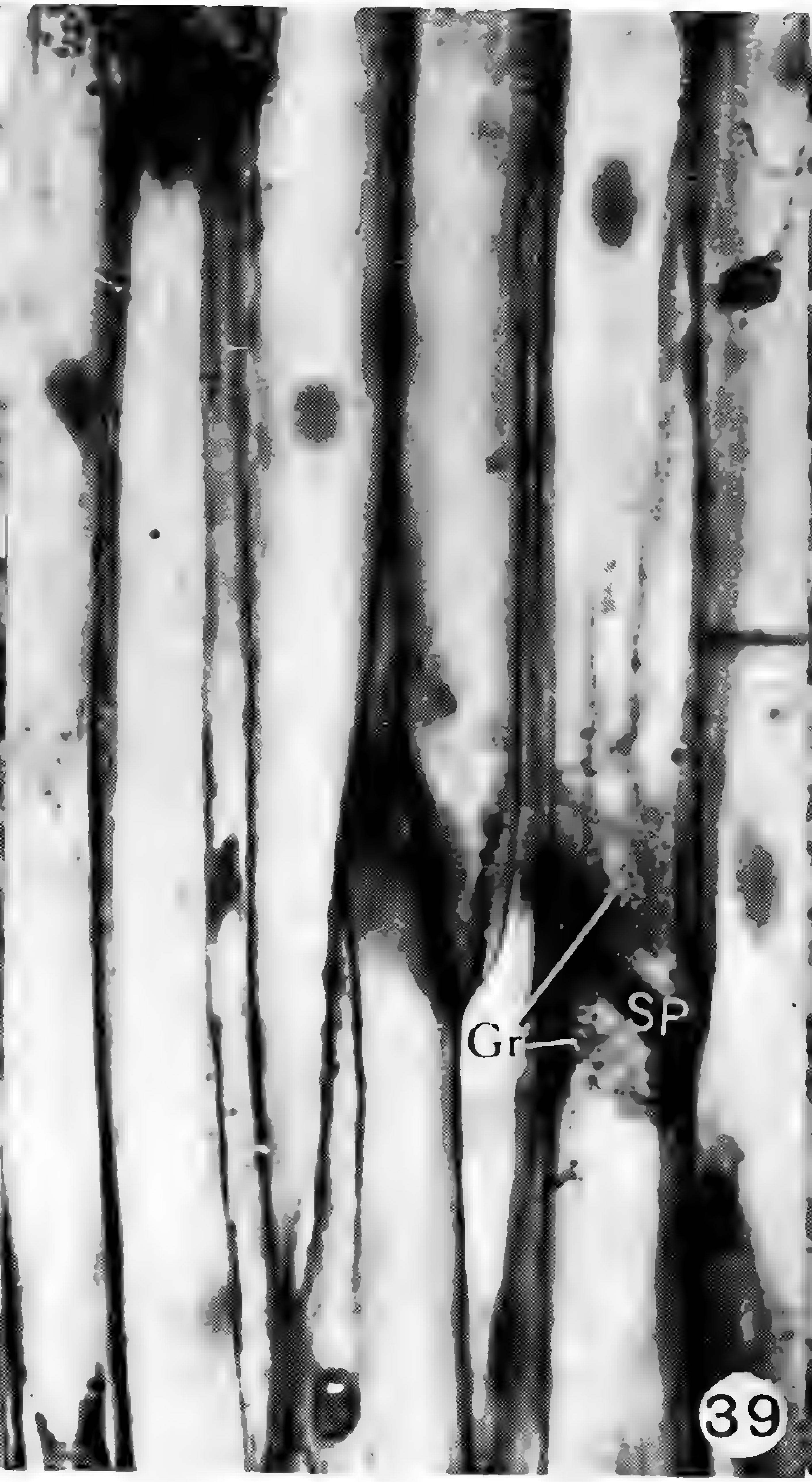

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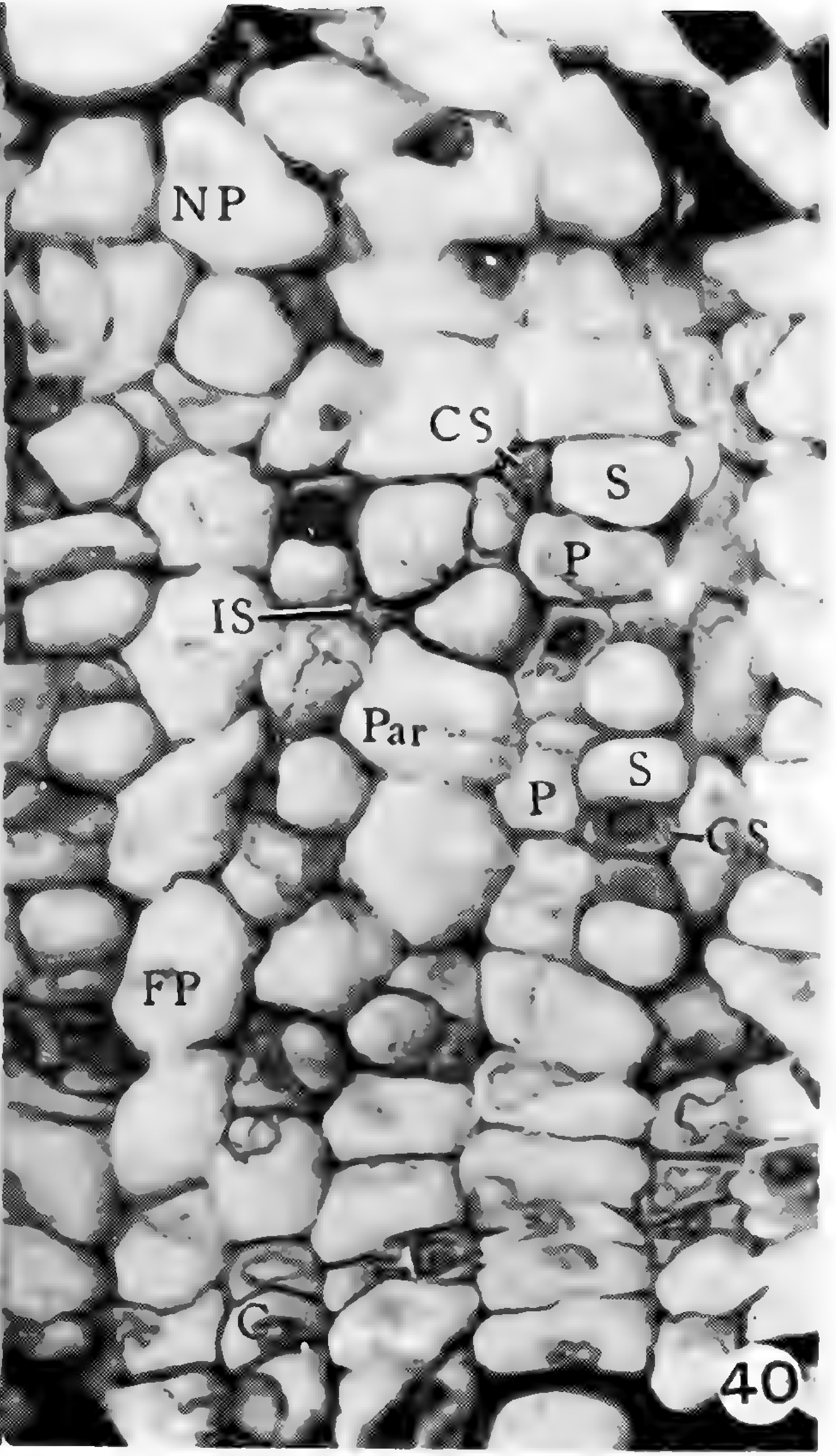

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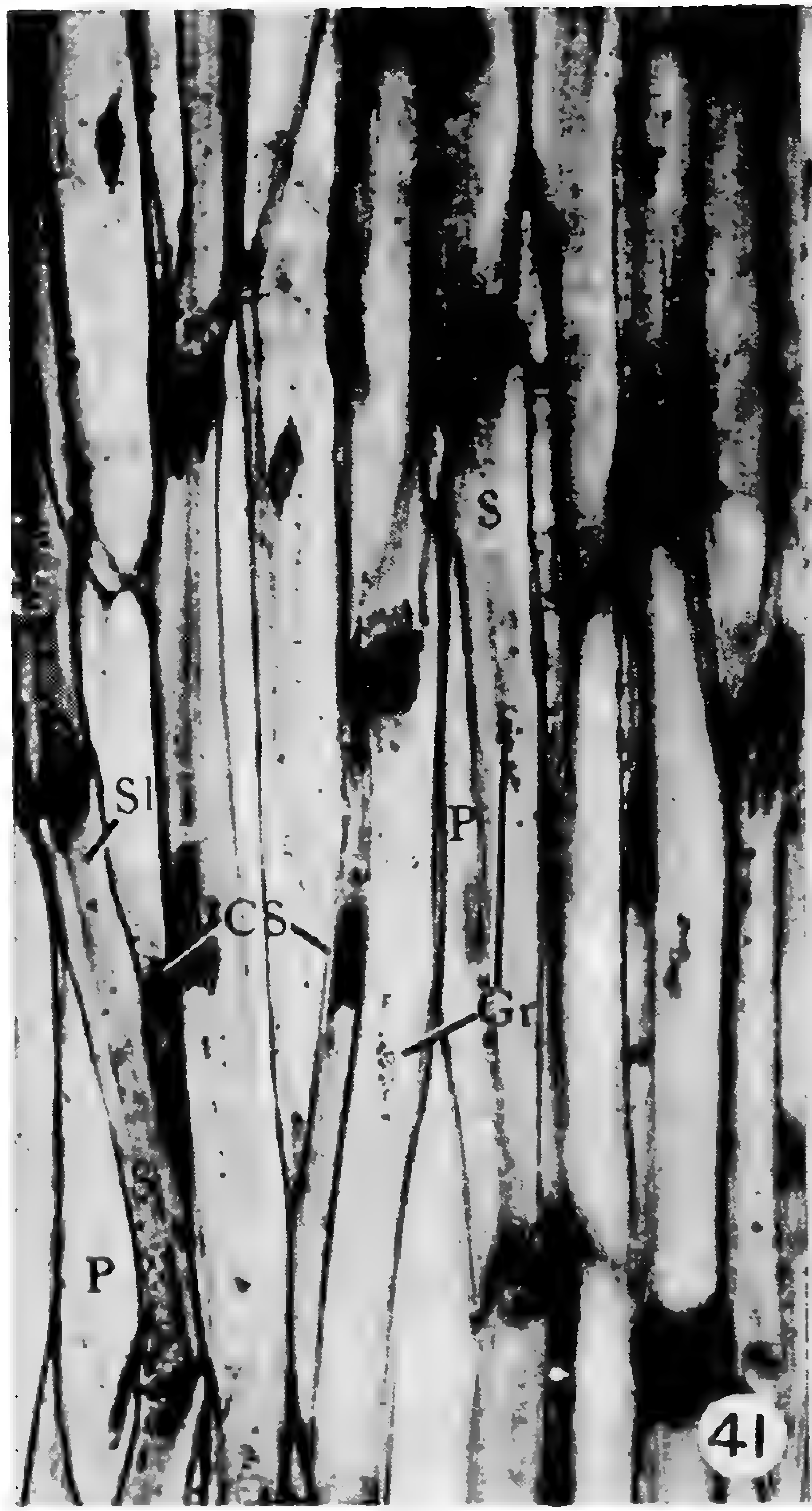

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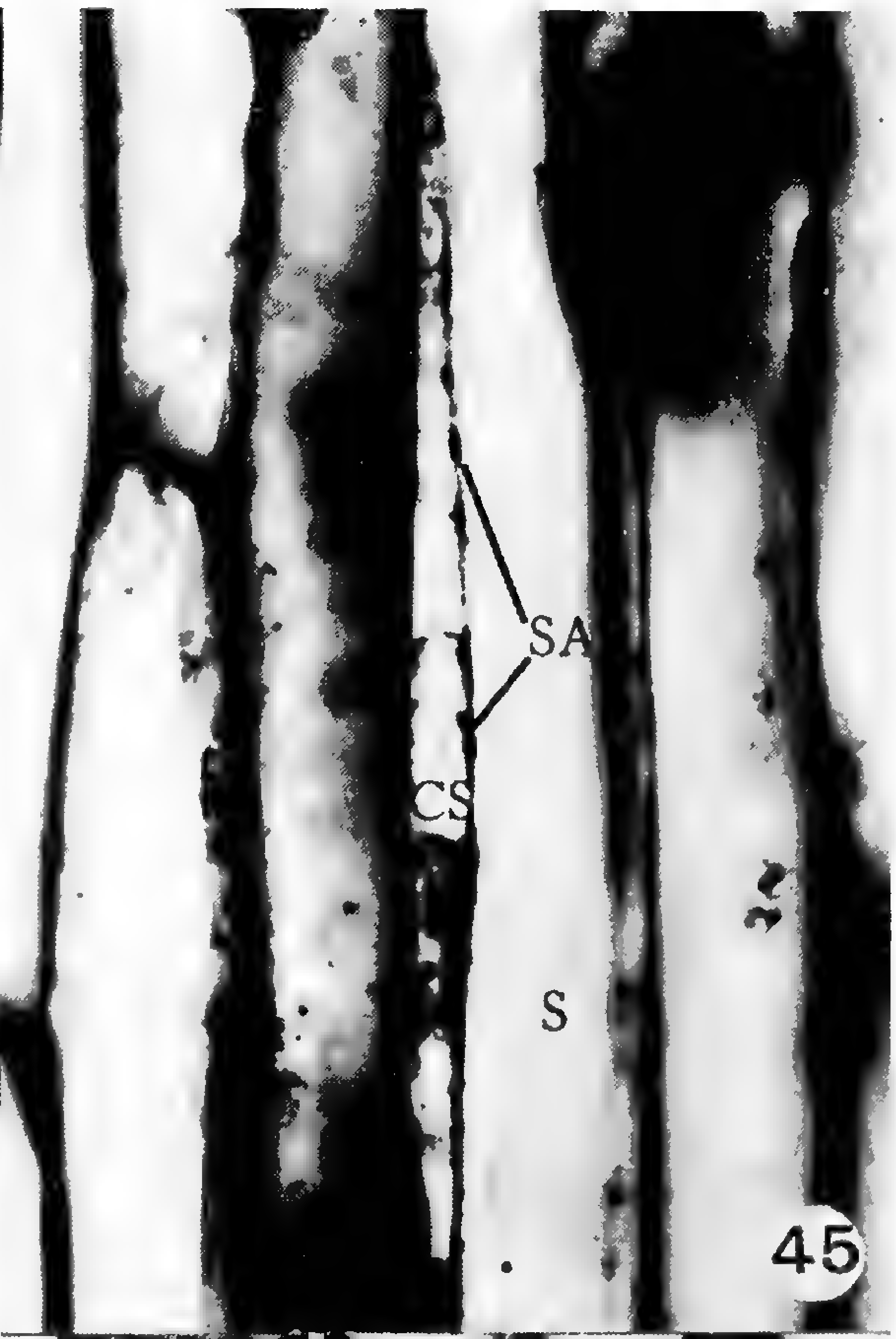

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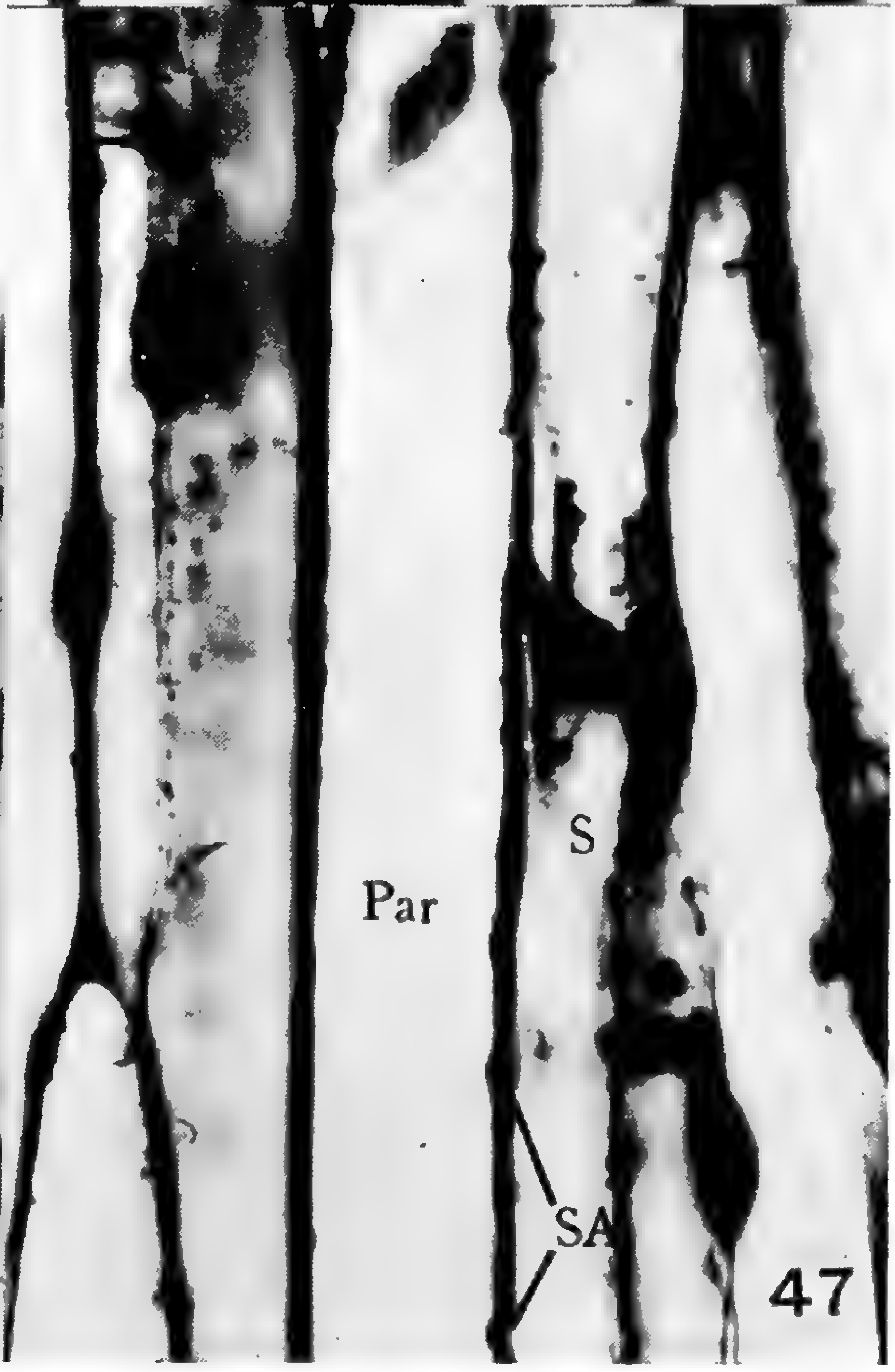

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SRIVASTAVA & BAILEY, LEAF-BEARING CACTACEAE, V


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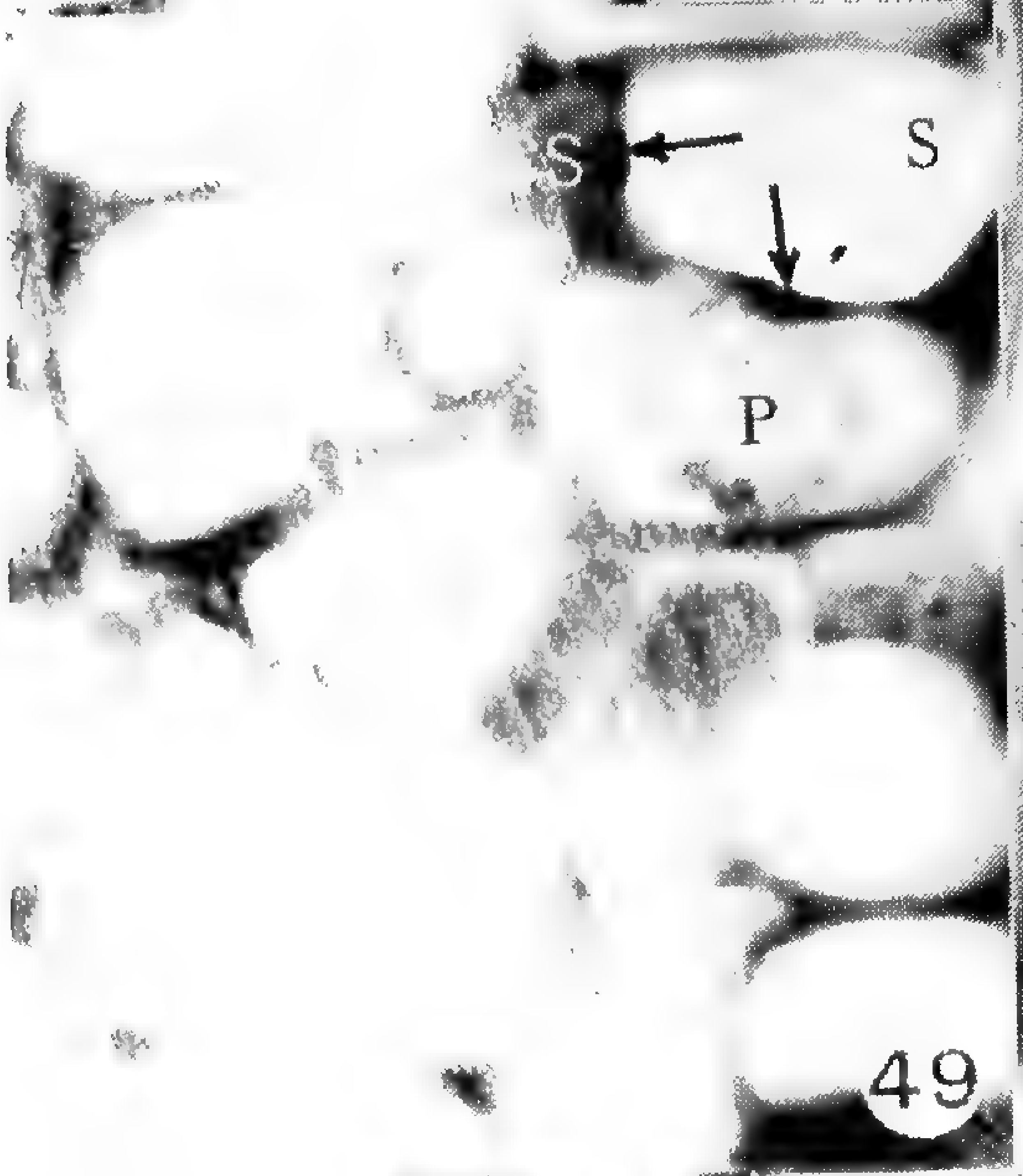

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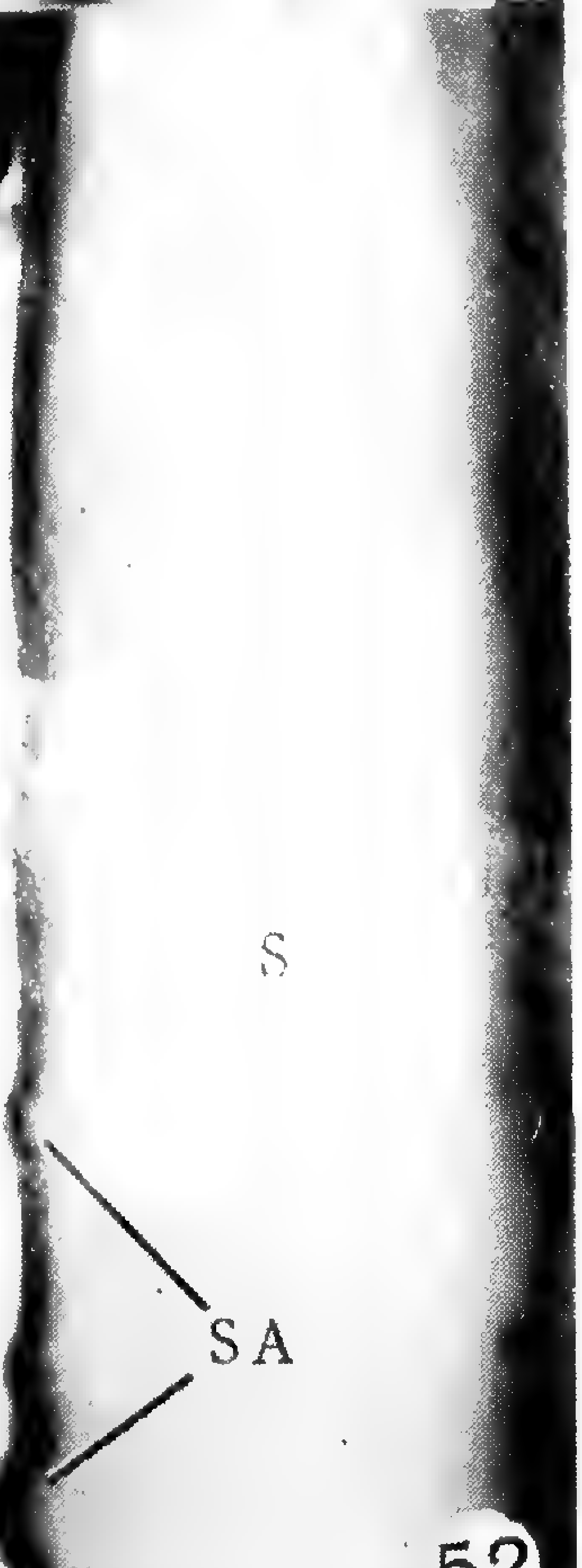

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SRIVASTAVA & BAILEY, LEAF-BEARING CACTACEAE, V

VOLCANISM AND VEGETATION IN THE LESSER ANTILLES

RICHARD A. HOWARD

THE MAJORITY OF THE ISLANDS of the Lesser Antilles in the Caribbean archipelago are volcanic in origin. Two of the islands have active volcanoes which currently are dormant. However, Mt. Pelée on Martinique erupted in 1902 and 1930, and the Soufrière on St. Vincent erupted in 1902. Nine of the islands from Grenada, in the south, to St. Kitts, in the north, have active fumaroles or soufrières, indicating residual volcanic activity. Of the few volcanic islands without historic volcanic activity, Saba, Redonda, Union, and others show the classic forms of their volcanic origin and prehistoric volcanic activity (11, 13, 48, 60).

The eruptions of the twentieth century on Martinique and St. Vincent have been well observed, studied, and recorded. An extensive descriptive literature is available for the volcanic and seismic activities of the area. The literature regarding the geological phenomenon of fumaroles in the Lesser Antilles is less complete, although a specialized interest in utilizing the thermal power of one, the Qualibou soufrière in St. Lucia, has been recorded recently (8, 49, 50).

In nearly all of the geologic studies, as well as in many floristic, phytogeographical and ecological papers on the area, some mention is made of the effects of volcanoes and soufrières on the vegetation. These range from Perret's mention of the attempted use of the sensitive plant, *Mimosa pudica*, to record earthquakes, to the papers by Stehlé and Beard considering the progressive changes in the regrowth of vegetation on devastated volcanic slopes. The present paper, a survey of the nature of volcanic activity and its effects on the vegetation in the Lesser Antilles, is based on observations made in 1950 during a field trip which began in Trinidad, extended to the northern and western islands, and ended in Jamaica. Data and specimens were collected in and around many sites of past and present volcanic activity. More recent visits to the Lesser Antilles, particularly to Montserrat in 1961, have allowed comparative observations after an elapsed time, as well as the gathering of specific information. For comparison with the West Indies, I have had the opportunity of studying the effects of the recent eruptions of Kilauea and Kilauea-iki and of the various fumaroles on Mauna Loa, in Hawaii.

These trips, observations, and collections form part of a continuing study of the vegetation of the Lesser Antilles. I acknowledge with gratitude the support of the American Philosophical Society during the 1950 trip and that of the National Science Foundation for grants which have aided more recent work. Many people in the Lesser Antilles have aided my work in

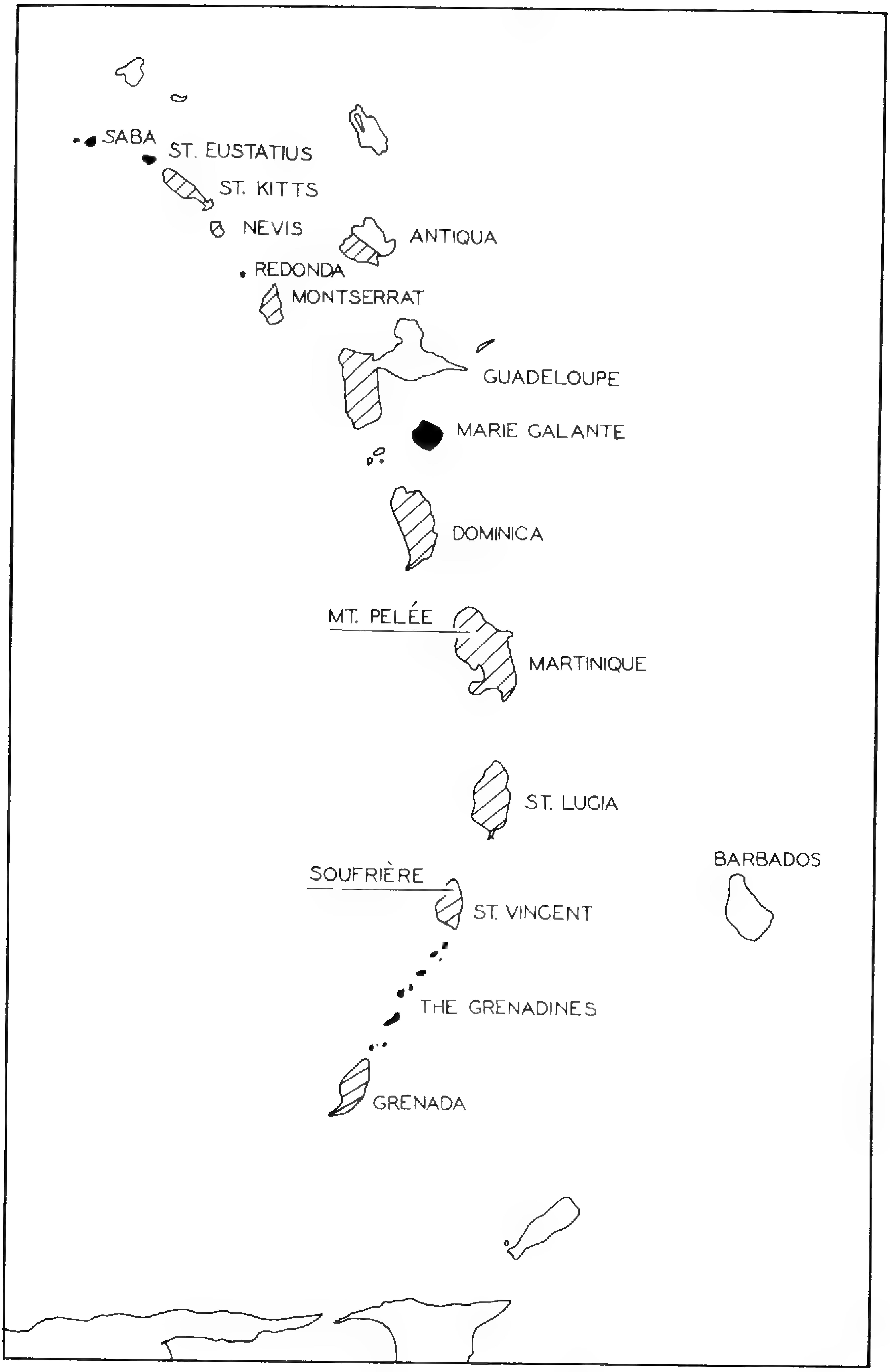
various ways. I mention in particular the assistance of Hugh McConnie, of St. Vincent; James Ross, of Grenada; Frank Delisle, now of Antigua; Kingsley Howes, of Montserrat; Harold Simmonds, of St. Lucia; John Knowlton, formerly of Dominica; and the late Malcolm Smith, of St. Kitts.

HISTORY OF VOLCANISM IN THE LESSER ANTILLES

Perret (46) has recorded the volcanological history of the Lesser Antilles. A chronology of the important eruptions is the following:

1692 – earthquakes followed by eruption on Mt. Misery, St. Kitts.
1694 – earthquakes followed by eruption on the Soufrière, Guadeloupe.
1718 – first recorded eruption of the Soufrière, St. Vincent.
1765 – earthquakes and gas emission on Dominica.
1766 – eruption of the Qualibou soufrière, St. Lucia.
1798 – earthquakes and eruption of the Soufrière, Guadeloupe.
1812 – great eruption of the Soufrière, St. Vincent.
1838 – eruption of the Soufrière, Guadeloupe.
1851 – earthquake and lateral outbreak of Mt. Pelée, Martinique.
1880 – ash eruption on Dominica.
1898 – start of three years of earthquakes and gas emission on Montserrat.
1902 – most destructive eruptions of Mt. Pelée, Martinique, and the Soufrière, St. Vincent.
1929 – eruption of Mt. Pelée, Martinique.
1934 – start of four years of earthquakes and gas emission on Montserrat.

The occurrence of earthquakes and actual eruptions is usually well recorded. Nevertheless, some of the earlier dates cited above have been questioned. Anderson (2), for example, cites both the picturesque report of the 1718 eruption of the Soufrière on St. Vincent, as given by Defoe (37), and the subsequent questions raised by the report. To the present day, the 1718 eruption is a questionable one. However, the geologists apparently have overlooked the work by Rev. Mr. Smith (64) who, while on Nevis, "heard six or seven dull bounces of noise resembling those of Cannon at a great distance pretty quickly following each other at the exact time of this Explosion: as the Sky was quite clear in the eye of the Wind, and as none of my acquaintance there took the same notice of the thing, I durst not venture to insist much upon hearing those dull bounces till I had seen Mr. Boyd." Mr. Boyd was previously identified as the captain of a merchant ship en route from St. Kitts to Barbados who noted that the sky grew dark and a horrible noise "far surpassing the loudest thunder" and a "falling likewise instantaneously so thick a Shower of Ashes, that the Sloop's Deck was covered two or three inches deep with them. . . . They in fright enough turned back homewards [and] . . . it was soon after found out, That a large Mountain in the Island of Saint Vincent . . . abounding in Veins of Sulphur and Brimstone blew up at once, viz. Woods, Rocks &c. all together, which must be allowed to cause a most dreadful Explosion." By contrast, the 1902 erup-



VOLCANIC AREAS OF THE LESSER ANTILLES. Diagonal lines indicate islands with active fumaroles. Mt. Pelée (Martinique) and the Soufrière (St. Vincent) are currently dormant but have erupted in the present century. Solid black areas are volcanic in origin. Unmarked areas are nonvolcanic islands.

tions of Mt. Pelée and the St. Vincent Soufrière were observed by parties of scientists from eight different countries, and, today, modern seismological stations record the minute signs of activity of these two dormant volcanoes.

The occurrence and duration of fumarole activity have been less accurately reported. Nugent's account of 1810 (42) is regarded as the original scientific observations for soufrières on Montserrat and other islands. Earlier accounts of hot springs do appear, with the emphasis generally placed on their curative medical properties or the ability to coagulate the protein of eggs. Père Labat (35), a French missionary to the Antilles between 1694 and 1705, recorded in six volumes his recollections of the Lesser Antilles. In 1696, he visited the Ance de Goyave in Guadeloupe and described the boiling fountains (*fontaines boüillantes*) in the bay, as well as in a neighboring swamp. He reported the water within a few feet of the coast to be warm enough to cook an egg held in his handkerchief. He attempted to determine the source of the heat and reported that, although the surface of the beach sand was without heat, when he dug to the depth of a foot he encountered sand and water too hot for his hand. This layer, he reported, smoked "comme on voit fumer la terre qui couvre le bois dont on fait le charbon." The fumes of sulphur were nearly unbearable. In a neighboring swamp he found a lake approximately 45 feet in diameter which boiled at the edges and also more strongly but less frequently in the center. The quiet periods, Labat reported, were of a duration sufficient to allow one to say both a *Pater* and an *Ave*. Odors of sulphur were strong here, too, and a sulphurous taste was present in the water. Even today, previously unknown areas of prehistoric soufrière activity are discovered in remote places on most of the Lesser Antilles, and new outbreaks of fumarole activity have been recorded in the last decade on Nevis and Montserrat. In general, the most active areas are well known, and the locations of the principal soufrières are to be indicated in summary for the various islands.

TYPES OF VOLCANIC ACTIVITY

Two basic types of volcanic activity occur in the Lesser Antilles. The most spectacular is the eruptive form so well recorded for Martinique and St. Vincent. Lava eruptions on these and other islands apparently occurred only in prehistoric times. The historic eruptions have been characterized by the forming of *nuées ardentes,* plus ash fall and mud flows. Hill (20) has described Mt. Pelée as an ash pile, a description which applies equally well to the Soufrière on St. Vincent.

Less spectacular, but of longer continuous duration in activity, is the fumarole. The fumarole is generally defined as a hole or vent (in or near a volcano) from which fumes are emitted. Subterranean as well as surface noise is present at most fumaroles. The gases produced may be saturated, ejecting with them large quantities of water, or they may be dry and either hot or cold. The dry, hot gases seem to condense atmospheric moisture some distance from the orifice, producing steam or clouds of vapor, thereby giving fumarolic areas an eerie appearance. With one exception, the gases and liquids produced by fumaroles in the Lesser Antilles are acid in reaction. This acidity is responsible for the chemical alteration, the coloration, and the physical decomposition of the soil and rocks characteristic of the areas around fumaroles.

A cluster of fumaroles is called a "soufrière," although in the Lesser Antilles this term is loosely applied to solitary as well as clustered vents, to mountains, and even to towns near sulphur-producing vents. A fumarole producing an odor of sulphur compounds is occasionally called a "solfatara" in this area. Technically, fumaroles are also classified according to their location as crateral fumaroles, when located in a volcanic crater, and noncrateral, when the point is lateral to a volcanic mass. Noncrateral fumaroles may be primary or secondary, depending on their association with the magmatic heat source. Representatives of all these types are to be found in the area. When the fumarole is depressed, surface waters may collect, and the dissolution of rock forms a mud pond or lake. Such bodies are also produced by the damming of valleys below fumarole areas by land slides, as in the case of the Boiling Lake in Dominica. Clear-water hot springs commonly found in alkaline areas elsewhere in the world have not been found in the Lesser Antilles.

VOLCANIC ERUPTIONS AND THE VEGETATION

The two active volcanoes on Martinique and St. Vincent are unique in producing only ash accumulations and a characteristic eruptive form termed *nuées ardentes* during the eruptions observed in modern times. The few lava flows or blocks recorded from the Lesser Antilles are of great age.

The recent and observed volcanic activity in the Lesser Antilles began with earthquakes and noise, the emission of gas and steam, and the ejection of ash and boulders. Some of the steam was derived from the vaporization of a crater lake from the caldera, at or near the summit. In the eruptions of the Soufrière in St. Vincent in both 1812 and 1902, either an eruptive force or a break in the crater wall produced a cascade of boiling water which descended the slopes to the sea. While this boiling torrent followed the established valley patterns on the mountain slope, its heat, volume, and speed killed and removed the vegetation. During its descent, it scoured the river valleys clear of accumulations of ash which thickened the consistency of the water and led to the reports of a lava flow. Anderson (2), who studied the 1812 deposits, concluded that it was a mud flow of accumulated ash and not a true lava flow.

The most destructive of the eruptive features of West Indian volcanoes have been the *nuées ardentes*. (See *Figs. 1, 2.*) The French seismologist Lacroix (36) proposed this term for the eruptions of Mt. Pelée and the Soufrière, and it has now become a standard term in all languages, although it is occasionally translated into English as "incandescent ash."

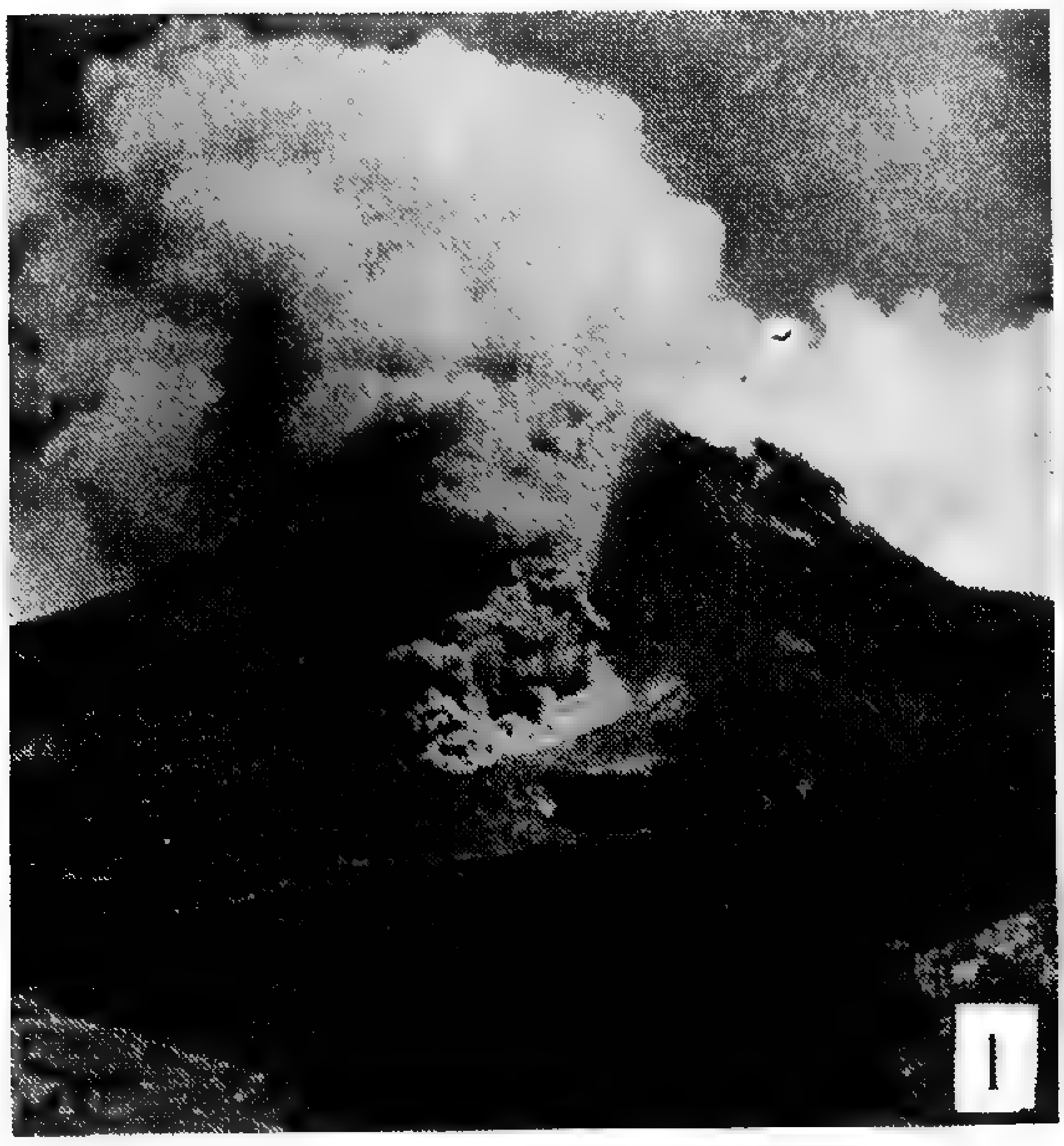


FIG. 1. *Nuée ardente* descending slopes of Mt. Pelée, April 13, 1931. Photo reproduced from Perret (44). FIG. 2. Initiation of *nuée ardente* on Mt. Pelée, 1930. Photo reproduced from Perret (46). FIG. 3. Ash accumulation on Wallibu fields, St. Vincent, 1902. Photo reproduced from Anderson and Flett (4).

Smith (63) has described the phenomenon as a "strange black cloud, which, laden with hot dust, swept with terrific velocity down the mountainside, burying the country in hot sand, suffocating and burning all living creatures in its path, and devouring the rich vegetation of the hill with one burning blast." Perret (46) explains its formation as follows: "In the acidic type [of volcano] its conduit normally closed because of the relative infusibility of the lava . . . the lava will have become surcharged with gases rising slowly from below, with possible assimilation from meteoric precipitation from above . . . the accumulated gas charge will, with eventual rupture of whatever restraint may have been imposed, go into paroxysmal explosive manifestation in the early stages of an eruption. A good instance of this is seen in the *nuée ardente*. . . . The viscous liquid has, through its own high gas content now coming out of solution in distributed gas vesicles, become autoexplosive as a whole and thus capable, on release, of lifting itself . . . clear out of its pocket, in a stupendous en masse expansion. It will be evident that this will convert what had been a liquid into an infinitely subdivided mass; in a word, largely into a cloud of vapor and solidifying particles. Its great weight will precipitate this upon the mountain flanks in a down rushing avalanche of very heavy materials at high temperature, emitting gas from every pore amid rising clouds of ash, and constituting what has been termed *nuée ardente.* This phenomenon was not described prior to 1902, the date of the destruction of St. Pierre, Martinique. . . . The velocity of the onrushing avalanche is phenomenal, and this fact is not unrelated to the continuing evolution of gas. Vapor films between all solid particles — from which particle the gas continues to be emitted during the 'life' of the *nuée* — effectively prevent all solid contacts, leaving the moving mass quite frictionless and capable of flowing upon the slightest inclines. . . . The original temperature (certainly on the order of more than 1,000 degrees C.) tends to be maintained by this insulating atmosphere." Perret also indicates that in a *nuée ardente* there is little if any free oxygen. As a result, no combustion occurs during its passage and materials are therefore carbonized and not burned.

The effects of a *nuée ardente* are localized but lethal to the life of the narrow belt over which it progresses. *Nuées ardentes* have been photographed from close range and have even been entered by volcanologists. Lava flows in Hawaii may leave little islands of vegetation (kipukas) undisturbed but surrounded with incandescent molten rock. Thus, too, in the case of a *nuée ardente,* areas adjacent to the descending cloud may be unaffected by the passage of the "incandescent avalanche." A study of the slopes of the Soufrière in St. Vincent today will show forests of massive trees cleft cleanly by the passage of a *nuée ardente.* On one particular slope there are 50–80-foot trees with trunks 2 to 3 feet in diameter and within a few yards the ash and scoria of the *nuée ardente* still barely colonized after 60 years. The *nuée ardente* carbonizes the vegetation in its path, while the residue of scoria left behind (in some cases 80 feet thick) retains its heat and kills the subterranean parts of the plants and the seeds and fruits on the ground. (See *Fig. 3.*)

Quite in contrast is the effect of the free fall of ash which may precede or follow the *nuée ardente.* The volume of free ash is tremendous and the distance it may be carried by the wind difficult to believe. Anderson and Fleet (3, 4) cite reports of a fall of ash on ships 830 miles east-southeast of Barbados, following the eruption of the St. Vincent Soufrière. Ash fell on Barbados, 100 miles away, at the rate of 3.94 tons per acre. Nearly all of St. Vincent was dusted or submerged in free ash from the eruption.

The term "volcanic ash" carries the popular connotation of a lightweight material. Perret states that this is not so, particularly in the ash derived from a *nuée ardente.* The crushing effect of the masses of ash is clearly documented, and the flattening effect on the vegetation implied. In the case of free-fall ash, the weight of individual particles may be less, but the cumulative weight equally great on any given area. Fields of arrowroot and other crops in St. Vincent buried under inches or feet of the cold free-fall ash did not recover. The accumulation of ash on leaves and branches caused defoliation and breakage of plants throughout the island. Although the size of the ash particles may have been small, the abrasive effect was noted in the puncture of leaves of crop plants and the removal of bark. A more modern report following the eruption of Parícutin in Mexico appropriately termed this "plutonic sandpaper" (47). The effects of the free ash on the vegetation is limited to abrasion, crushing, and smothering. The ash is generally chemically inert and without heat. The plants affected may recover or sprout from the base. Underground portions of the plants are not killed, and seeds germinate and may push up through the covering of ash.

The days which followed the eruptions of Pelée and the Soufrière have been reported as stormy. Heavy rain showers occurred. Perhaps the activity of the volcanoes caused the formation of the heavy rain clouds; but in any case, violent rain storms swept the area, and exceptionally heavy rain descended on the ash-covered slopes. Russell (52) noted that "instead of being a protection to the surface on which it rests, the fresh debris is in many instances of assistance in its more rapid erosion. On steep slopes, and even when the surface is nearly level, the rills formed during the numerous tropical showers quickly cut through the loose surface material, and aided by the angular particles in suspension, corrode the soil or rocks beneath. The rains, as it seems, are heavier than usual, owing to two causes: first, the great amount of water contributed to the atmosphere as steam, and second, the vast amount of dust blown into the air, each particle of which serves as a center for condensation." Riverbeds filled with ash and scoria were swept clean, scoured to new depths and often altered from their previous courses. As the ash deposits were removed, the lower soil areas, too, were eroded in sheets of mud which were deposited along the coast in fans recorded as 70 to 80 feet wide and seven miles in length. Subsequent earthquakes caused landslides in shaken and loosened terrain. North of Châteaubelair in St. Vincent, Russell reported "strips of nearly flat alluvial land, adjacent to the sea, have disappeared leaving fresh bluffs of loose debris some 30 or 40 feet high."

The revegetation of areas affected by volcanic activity has been the basis for classic studies in the case of Krakatoa. For the West Indies, Perret (44, 46) and Anderson (2) made initial studies and Stehlé (66) and Beard (6, 7) some recent summaries. A more detailed study is still required, with consideration given to the specific nature of the disturbance in each area. Perret noted the occurrence of "several mosses and fungi" within two years of the 1930 eruption of Mt. Pelée in an area affected by a *nuée ardente.* Judging from his photographs, the "fungi" are lichens of the genus *Stereocaulon.* Perret also noted the invasion of the "golden back fern" and a plant with "tiny blue blossoms, said to be invariably yellow in other localities." As both gold and silver forms of *Pityrogramma calomelanos* and *P. chrysophylla* occur in the Lesser Antilles, the scientific determination of plants cited in the geologists' reports are not to be trusted. Perret also commented that while the golden form of the fern occurred at lower elevations, only the silver form was found at higher level on the disturbed areas. Although the plant with blue blossoms can not be identified, *Pitcairnia spicata* is represented by the yellow-flowered var. *sulphurea* near craters and by the red-flowered typical form where volcanic fumes are not present.

Both Anderson (2) and Sands (53) visited the St. Vincent Soufrière in 1907, five years after the last eruption, and noted the species which invaded the area. Although Beard cites Anderson's paper, he quotes only from Sands' less critical report in which 154 species of plants were collected from low-altitude areas badly devastated by the eruption. Anderson, who was present during the eruptions, differentiates between areas affected by the *nuée ardente* and those affected by an ash fall. He states, "The incandescent avalanche swept down the Wallibu valley and spread out over the old fan or plateau at its mouth. It then turned south round the lower end of the Richmond Ridge and destroyed the Richmond Works and all the vegetation near them. The ash still remains to a depth of two to six feet in different parts, and the old roots are completely buried and thoroughly destroyed, but the avalanche was confined to the bottom of the valley and none of its effects are visible on either side. . . . The surface of the ash near the Works has not consolidated, but is rapidly breaking up under the influence of plant roots, and humus is being formed. . . . The chief new plants are Castor Oil (*Ricinus communis*), which grows in luxuriant masses along and around the ruins of the Works, and a plant, Cattle Tongue (*Pluchea odorata*) which has already formed flourishing bushes taller than a man. Besides these, Indigo (*Indigofera anil*), Sensitive Plant (*Mimosa pudica*), Guinea Grass (*Panicum maximum*), *Eupatorium odoratum*, and two grasses were also noted." Where the surface of the ash was consolidated, no vegetation can spring up; where it was broken by water or the hooves of animals the first invaders proved to be silver fern, grasses, and *Pluchea*. For areas covered with free fall ash, Anderson also related, "On the south slope leading up to the Morne Garu range the return has been considerable. The surface is still studded with the charred and bleached skeletons of trees, which appear to have been killed universally with the single exception of a small lateral valley north of the lower part of the Richmond Ridge, where a few palm trees in a sheltered position have recovered. The shrubs and herbaceous vegetation, which were all burnt level with the ground, are gradually returning, in many cases from the old roots, since the removal of the thin covering of ashes by the rain.

"The top of the Wallibu plateau was entirely devastated. The trees remain only as bleached trunks except a few which have recovered in sheltered positions at the ends and south edge of the plateau. The dead trunks show that the ash was never more than a few feet thick at the most, and the whole is now covered with a luxuriant growth chiefly from the old roots.

"At about 800 feet Tree Ferns (*Cyathea arborea*) become very abundant and large sheets of them are common, and generally it may be said that vegetation is luxuriant up to a height of about 1,000 feet, abundant up to 1,500, and very sparse above that height, with only a few grasses and silver ferns; higher up nothing but mosses and lichens are found.

"At the lower lip of the crater and just inside it mosses and lichens only are found. The mosses have been identified at Kew as: *Pogonatum tortile*, P. Beauv. and *Philonotis tenella*, Jacq. and the lichen as *Stereocaulon sp.*"

Beard (6) presented a study of the altitude zonation of vegetation types in undisturbed areas and, in comparison, the types he found on the slope of the Soufrière in 1940, approximately 40 years after the eruption. Beard found at 2,400 feet altitude that the "plants are knee high only, still composed of silver fern with now very stunted *Charianthus* and *Cyathea*, *Pitcairnia*, *Lobelia*, ferns and grasses.

"At 820 m. *Charianthus* and silver fern begin to thin out, and *Cyathea* is only 60 cm. high. Towards 900 m. the vegetation is simulating 'paramo' and is distinctly alpine in appearance. The ground is entirely and thickly covered with lichens, thallose, foliose and crustose. Higher plants are scattered and tufted and include the *Lobelia* and *Pitcairnia*, several grasses, a *Lycopodium* and a few ferns. *Cyathea* is now at most 30 cm. high, and the general vegetal covering is ankle deep only.

"At the highest levels one finds a tundra only. The stony ground is thickly covered with lichens and, in between, a few clumps of *Lobelia* and *Pitcairnia*. The lichens vary greatly in colour, being predominantly grey or orange, and having a striking appearance at a little distance."

It is interesting that the inside walls of the crater are covered with larger plants, right down to the water line nearly 1,000 feet below. Here *Baccharis cotinifolia*, *Gleichenia*, *Lycopodium*, ferns, grasses, and a few *Cyathea* occur in greater stature than at comparable levels on the outer slope of the crater.

Stehlé (66) described the revegetation of the slopes of Mt. Pelée and also determined that the altitudinal zonation existing before the eruption was re-established afterwards. On both Mt. Pelée and the Soufrière it was apparent that the *nuée ardente* completely removed all plants and their propagules. The ash fall, however, may have killed the portions of plants above the ground but allowed subterranean root and stem systems, as well as seeds, to survive and grow. In both cases, the revegetation was more rapid at lower elevations where a weedy flora was the first type to be established. At all but the highest elevations, lateral invasion from the areas of vegetation unaffected by the *nuée ardente* was apparent. At the highest elevations where no unaffected areas were present and the soil was isolated both vertically and horizontally from seed sources which would tolerate those environmental conditions, the reinvasion and re-establishment was slow, and often an unexpected composition was created. Lichens and mosses were the first and most successful invaders. Wind-blown spores of ferns were introduced, and the plants created pure stands of many individuals. Although spores of *Lycopodium* were eventually introduced, only scattered plants were found. The seeds of *Pitcairnia, Cladium,* and various grasses could have been distributed by wind to these new areas. Stehlé suggests that the fruits of *Charianthus, Lisianthus, Lobelia, Tibouchina, Ilex, Weinmannia,* and *Clusia* are distributed by birds or bats, and these plants are slow to become established in the devastated areas of high elevation. At lower altitudes birds, cattle, and man have played a role in starting new plants. Stehlé, for example, noticed the invasion of sugar cane on the slopes of Martinique and suggested that a wind-blown seed allowed this plant to be established on the scoria. Perhaps a node dropped by a wandering cane-chewing sightseer might be a more logical interpretation. The seeds of *Acacia* and *Mimosa* observed by Sands, Perret, and others were spread by cattle wandering over the newer ash accumulations.

It is of some interest to note that in all cases the growth of invading species appeared to be more rapid inside the crater of the volcano than at comparable levels on the outside. This growth can probably be associated with the greater protection afforded within the crater walls, as well as the more abundant moisture available on the less porous soil surface.

FUMAROLES AND THEIR EFFECTS

The occurrence of fumaroles, either singly or clustered as soufrières, can be reported for all the major islands of the Lesser Antilles from Grenada, in the south, to St. Kitts, in the north. The fumaroles are found at many elevations — submarine near Nevis, coastal on Montserrat, at low elevation on Grenada, and at the summit of the Soufrière (4800 feet) on Guadeloupe. The fumaroles are present in many vegetational types, including the thorn scrub of Grenada, old field vegetation on Dominica, mesophytic forests on Montserrat, and the volcanic facies on Guadeloupe. Active fumaroles can be determined from some distance by the production of heat, steam, and fumes laden with sulphur compounds. Near by, they show a characteristic destruction or absence of adjacent vegetation, if the fumes contain sulphur compounds, or an equally characteristic alteration of the rock texture and color. Extinct or dormant fumaroles may be recognized in open areas where mosses, algae, or perhaps a few higher plants cover the surface or where the softened rock in a restricted area reveals the former fumarole and its activity.

The activity of the fumarole may vary considerably in intensity over a long period of time or even in relation to the annual rainy or dry seasons. Some recurrence of fumarolic activity has been noted and associated with active volcanism on adjacent islands or with earthquakes of considerable geographic latitude. Within the Lesser Antilles are dormant fumaroles, those with long records of continuous activity, new ones, and those sporadic in their action.

Nearly all fumaroles are characterized by the emission of heat. Stehlé

(67) gives temperatures of the crateral fumaroles of Mt. Pelée as high as 700° C. Robson and Willmore (50) have published the most recent studies of heat emission from fumaroles in the Lesser Antilles. They have suggested as a base point the temperature of 24° C. for meteoric water or ordinary cold springs and for the air temperature. Steam temperatures from the Qualibou soufrière in St. Lucia have been measured as high as 185° C., while water outflow temperatures from ponds in the same soufrière varied from 63° to 96° C. On Montserrat, Robson and Willmore recorded the flow of water from Gages Upper Soufrière at temperatures of 34–86° C. from three sources and at Galway's Soufrière from 56° to 97° C. from two sources. Crater lakes, which may not show violent actions typical of fumaroles may show the effects of their proximity to sites of volcanism. The mean lake temperatures for the crater lake in the Soufrière of St. Vincent was 27.1° C., indicating at least a 4° rise in temperature due to the heating effect of submerged fumaroles. There is only one record of plant life in the boiling lakes of the Lesser Antilles, but this has never been verified in more recent observations. No animal life has been reported. Crater lakes, by contrast, have an algal or higher plant flora, and the crater lake on St. Vincent's Soufrière has recently been stocked with fish. The heat of water flowing from fumaroles or boiling lakes is soon dissipated. Blue-green and green algae, diatoms, and even sedges have been collected from outflows with temperatures of 56° to 85° C. within five feet of vents on several islands. Unfortunately, no identifications have ever been received from specialists who might name these collections of plants properly.

The direct emission of steam could have a noticeable destructive effect on the surrounding vegetation. Few plants could stand blasts of temperatures of 100° to 185° C. However, the direct blast of steam heat probably is of minor importance or none at all in comparison with soil heat, toxic gases, and cumulative acidity. Although MacGregor (39) gives in tabular form records of heat from soufrières on Montserrat, he also points out that the maximum temperature recorded depends on how far the thermometer can be pushed down the orifice against the gas pressure. Temperatures are higher below than at the surface, and such heat as is emitted is dissipated rapidly in the atmosphere.

For many of the West Indian fumaroles there appear to be few if any toxic substances included in the air being forced out at the present time. Around the fumaroles of Wotten Waven, in Dominica, the vegetation, instead of being adversely affected or killed, appears to grow more luxuriantly in the local area of higher heat and humidity. However, in many fumaroles there must be toxic substances, for the fumes have a definite effect on the vegetation. MacGregor and other authors have stated that the fumes kill the local vegetation. Even the names of the fumaroles and their areas suggest the toxicity. The largest soufrière on St. Lucia is known as "Qualibou," a name meaning "place of death," and some soufrières in Dominica are located in the "Valley of Desolation." It is clear that the fumes are often noxious and toxic to men and to plants. The death of two visitors to the Boiling Lake of Dominica has been substantiated. The geologist Perret was overcome by fumes while residing in his field station within Gages Lower Soufrière, and workmen on an earlier project in the same area were overcome. Although several geologists have attempted to collect and analyze the gases, the results are inconclusive. Romer (51) has reported the fumes from fumaroles on Mt. Pelée to contain only carbon dioxide, sulphur dioxide, and traces of hydrogen chloride; however, some fumaroles on Montserrat failed to give positive tests for carbon dioxide. Obviously the composition of the gases may vary with the nature of the activity of the fumaroles. Most fumaroles of the Lesser Antilles produce hydrogen sulphide, but all characteristically reveal an absence of fluorine, relatively few chlorides, and negligible amounts of boron. Perret described the gas of Gages Lower Soufrière and concluded it was "a gas having a traitorously pleasant odor, but extremely irritating to the eyes and respiratory passages. . . . It was highly unstable and decomposed into hydrogen sulphide and sulphur. It may have been one of the persulfides of hydrogen." Willmore (71) stated, "These vents emit a mixture of steam and sulphur gases which, during quiet periods, usually have a temperature a little below that of boiling water. During periods of abnormal activity the temperature of the exhalations often rises, and the predominant sulphur constituent may change from hydrogen sulfide to sulphur dioxide. — The tendency for the temperature to become stabilized near boiling point is readily explained on the assumption that the soufrière is supplied by hot juvenile gases which bubble through meteoric water on their way to the surface. The change in gaseous constitution during active periods is presumed to occur because the original magmatic gases undergo reactions on their way to the surface, so that the end products depend on the temperature and velocity of the flow." The absence of fluorides and the relatively small amounts of chlorides and boron support the conclusion that meteoric and not juvenile water is involved in most soufrières of the Lesser Antilles, at least most of the time.

The destruction of the vegetation around fumaroles, therefore, is apparently not caused by the chemical elements of the fumes or the water but by their nature as compounds. The various sulphur compounds in the presence of water can produce a series of acids. Litmus papers and "pHydrion" papers respond quickly, giving acid reactions. Perret reported that during the seismic crisis on Montserrat egg shells dropped in the fumarolic waters give rapid effervescence. Another mildly acid constituent of the fumarole fumes is hydrogen sulphide. The presence of this compound is evident, not only in the odor, but in the tarnishing of all silver brought into the vicinity. The town of Soufrière in St. Lucia is unfortunately in the lee of the Qualibou soufrière, and one is continuously aware of the derivation of the name of the town. Silverware tarnishes in the town of Plymouth in Montserrat which is downwind from the Gages soufrières. Perret depended on the reaction of lead-acetate paper to sulphur to record the intensity of such emission from the Gages soufrières, and during the same seismic crises even the lead paint blackened on ships in the roadstead.

The acids derived from the various sulphur compounds also affect the soil and rocks in the vicinity of the fumaroles. MacGregor (38, 39) concluded that "mineral changes brought about in the country rock render it locally pale to pure white in color." The pale color of soufrière areas renders them conspicuous and easily recognizable from a considerable distance. Accompanying the color change in the rock is a loss of structural hardness. Rocks in fumarole areas may retain their original shape and texture but become soft and nearly putty-like in consistency. The novice learns quickly of the treacherous footing in areas of fumaroles, where even the largest stones are not to be trusted.

When both hydrogen sulphide and sulphur dioxide are present, a chemical reaction may take place oxidizing the former and reducing the latter to produce water and crystalline sulphur. The deposits of sulphur crystals around the vents of Lesser Antillean fumaroles are colorful. Local needs for sulphur are easily met and at times small quantities of sulphur have been exported from the area. The commercial extraction of sulphur as a by-product of the use of steam for thermal power has been proposed (8).

EFFECTS OF FUMAROLES ON VEGETATION

During a visit to many of the fumaroles in the Lesser Antilles, it became apparent that there were areas around most fumaroles where no vegetation survived; that leeward from the vents certain plants were affected or killed by the emissions of the vent, while to the windward the same species approached or persisted much more closely; that certain species tolerate the effects of the fumaroles longer than others; that certain species invaded an affected area more readily than others; that some physiological change took place in the species which did grow successfully near the fumaroles in comparison with the same species elsewhere; and that the effects of the fumaroles on the vegetation were greater at certain periods than others. A review of the literature reveals that the earliest descriptions of the Boiling Lake on Dominica do not vary from observations made recently, and that Sapper's sketch (57) of the limit of devastation of vegetation at Galway's Soufrière on Montserrat differs little from a sketch map made last year. As long as the fumarole remains active and reasonably constant the effects on the vegetation are noticeable to a distance limited primarily by the terrain. Furthermore, the chemically altered rock and soil near the fumarole remain an inhospitable area for plants for decades, and revegetation is an extremely slow process.

However, new vents do open and I have had the opportunity of recording a sequence in the change of the vegetation near a new fumarole over a ten-year period on the island of Montserrat. In 1950, I visited both Gages Lower Soufrière, studied by Perret in 1934–37, and Gages Upper Soufrière, which was reactivated by an earthquake in 1937 when Gages

Lower Soufrière was dormant. Gages Upper Soufrière was active, but the vegetation around it appeared to have been stabilized in relation to the vents. Photographs were taken at both soufrières, notes were made, and specimens were collected approaching and adjacent to the devastated area. I returned to the area in 1961 expecting to determine the identity and the role of the plants which had successfully invaded during the past decade. At Gages Lower Soufrière I was not disappointed. Several four-foot plants of *Clusia alba*, as well as other weeds, were growing in the center of the ruins of Perret's field station. Young plants of *Andropogon*, *Philodendron giganteum*, and *Pitcairnia* were seen, and a coating of mosses colored many of the rocks.

The situation at Gages Upper Soufrière was another matter. New vents had opened in a thicket downstream from the previously affected area, affording an opportunity of determining the initial effects of a fumarole on previously undisturbed vegetation. The exact date of the inception of this vent is not known. Martin-Kaye (40) observed the area affected by Gages Upper Soufrière in 1954. A marker tree, a large buttressed rooted specimen of *Sloanea massonii* from which I had collected a specimen in 1950 was now dead, and only the stump remained some 50 feet inside the devastated area (*Fig. 13*). A vent had opened in the last decade directly under that tree, the base of which was now discolored white and yellow. The remaining stump was hot from the steam and wet and rotted, so that an 18-inch machete penetrated easily to its hilt, while "pHydrion" paper pressed against the sodden wood showed a pH of 1.5. The activity of the Gages Upper Soufrière had not only been extended downstream but up the hillside nearly to the ridge (*Fig. 12*). It apparently will be only a short time before the fumarole activity breaks through the crest of the ridge and effects a new drainage system.

In the newly affected area readings of temperature and the pH were taken on occasions between 8 A.M. and 5 P.M. over a period of two weeks with no significant variation in the figures. The vent of greatest interest (*Fig. 18*) was in a thicket composed of species of *Blechnum*, *Charianthus*, *Clusia*, *Cyathea*, *Ficus*, *Ilex*, *Miconia*, *Palicourea*, *Philodendron*, and *Symplocos*. No noticeable hole or pore had developed, and the steam appeared to be issuing from an area of dry soil about four inches in diameter. Outside of this small focal point some organic material was present but this was extremely dry. The diameter of the area of dry duff was approximately four feet. Outside of this area the debris on the soil surface was noticeably warm and moist, and dead and dying plants were obvious and readily identifiable. The effects of this new vent extended for a distance of only 20 feet. The temperature reading in the vent area was 94–96° C., a measurement obtained by inserting to a depth of three inches a laboratory thermometer calibrated to 250° C. In the area of dry and barren soil around the vent the temperature was 84° C. at a depth of three inches. The most tolerant plants in the area of wet, warm soil nearest the vent were *Blechnum*, *Clusia*, and *Philodendron*.

Beneath these plants the soil temperature was 54° C. Progressing outward on several radii, it was determined that species of *Ficus* and *Lycopodium* grew in soils at 48° C., while *Miconia* and *Palicourea* withstood 40° C. Beyond this point the soil temperature dropped to 30° C., and no killing was evident. The dead or nearly dead plants in soil temperatures of 40° C. and above were *Charianthus*, *Cyathea*, *Ilex*, *Miconia*, *Palicourea*, and *Symplocos*. About 100 yards away from this vent in the undisturbed forest, soil and air temperatures varied between 24° and 26° C. at different times of the day. It is apparent that one previously unrecognized factor in the death of plants around new fumaroles is the heating effect of the soil. Although the fumes from this small vent did discolor lead acetate paper they gave no reading on "pHydrion" paper. Litmus paper gave an acid reaction very slowly. The same papers used on the moist soil zone where plants had been killed gave readings of pH 1–1.5. The vegetable material present in the dry zone crumbled easily in my fingers. That of the moist zone, by contrast, was slippery or almost mucilaginous. The structure of the duff had been altered, and I judged from the ease with which my feet slipped that a heavy shower of rain would cause severe erosion. The areas unaffected by heat or low pH were more fibrous to the touch and more resistant under foot. Readings taken in the vegetable material in the unaffected forest showed pH 4–4.2. Hardy, Rodrigues, and Nanton (19) report that the majority of agricultural soils on Montserrat range from a pH of 6.1 to 7.4. Their two sets of figures for forest sites indicate pH readings of 4.3–4.8 (for lower montane rain forest soil on Frenchman's Hill) to a pH of 5.2–6.6 (for soils in a palm brake on Chance's Mountain). The initial killing effect of fumaroles may well be, first, soil temperatures beyond the range of tolerance of many species and, secondly, high acidity.

General observations were made on the vegetation within a few yards of the older area of devastation around Gages Upper Soufrière. Although the heat of the steam emissions could be felt in this area, it was not oppressive, and temperature readings were only a degree or two above those recorded deeper in the forest. The odor of hydrogen sulfide was noticeable, as was a higher humidity. Wet litmus paper did not indicate an acid reaction during a 30-minute exposure. Nevertheless, plants were dying and a slowly cumulative toxic effect of the fumes is the only explanation. The genera most susceptible appeared to be *Cyathea*, *Freziera*, *Hirtella*, *Licania*, *Palicourea*, *Peperomia*, *Philodendron* (except *P. giganteum*), *Psychotria*, *Symplocos* and *Weinmannia*. Species of *Gonzalagunia*, *Ilex*, and *Sloanea* appeared more tolerant and those of *Clusia* and *Ternstroemia*, as well as *Philodendron giganteum*, most resistant.

The oldest areas of Gages Upper Soufrière showed scattered plants of *Clusia alba*, *Cyperus ligularis*, *Philodendron giganteum*, and *Pitcairnia spicata*. It is not clear whether these plants were residual from the former vegetation or more recent invaders. They grew both as individuals and in groups. In numbers they were more abundant on the fumarole affected soil than in comparable areas of the undisturbed forests. Vents of two types were present in the areas where these plants grew. One type issued only fumes while the other had steam so laden with moisture that it condensed around the orifice and ran off, forming a small stream. The air issuing from the dry vents was recorded as high as 93° C., but the soil temperature immediately around the vent was 37° C. Incrustations of crystalline sulphur lined such orifices. The moist steam vents, however, gave readings of 37° to 70° C. taken in a comparable manner, and the "pHydrion" paper gave a reading of pH 1.5. Barren soil temperatures around these vents were 30° C. Temperatures recorded from around the root systems of *Philodendron* and *Pitcairnia* were 32° C. and the pH was 3. The highest water temperature recorded in any of the small pools within Gages Upper Soufrière was 94° C.

The Qualibou soufrière in St. Lucia afforded an example of vegetation stabilized to the long-term effects of fumes from fumaroles. This soufrière is located in a valley with a high hill on the windward side so that fumes from the fumaroles tend to rise along the hill face. The vegetation of this hillside consisted of stunted low plants of *Blechnum*, *Clusia*, *Cyperus*, *Gleichenia*, *Lycopodium*, and *Pityrogramma*. Just over the crest, in an area where the fumes were dissipated by the prevailing winds, the native forest flourished in an unaffected manner. The species which tolerated the fumes on the hillside were those with heavy cuticles, for the wax-rigid nature of the foliage was conspicuous in contrast to that of the same species growing in an area where they were unaffected by the fumes. The waxy coating on the leaves apparently made this vegetation more susceptible to burning, for a large fire scar dominated the face of the hill. In a few places a clear line of demarcation was evident between the plants which burned and those which only wilted down. This demarcation appeared to be associated with the plants exposed to the fumes and those protected from it.

An example of the periodicity of activity of fumaroles and the killing effect on the vegetation can be found on the slopes of the Soufrière on Guadeloupe. Stehlé (65) has described the units of vegetation which have been established at successive altitudes to the summit. His "Clusietum," "Lobelietum," "Pitcairnietum" represent, in part, tolerance of the component species to temperature, wind, and cloud cover but also to the pH of the ash terrain and to the effects of the fumaroles at the summit. During periods of little fumarole activity, the shrubs and trees may develop normally. When the fumaroles become active, the acid fumes will kill many of the branches and occasionally entire plants. Generally these plants recover by sprouting from the lower branches or the base, but the upper branches remain dead and leafless.

A unique fumarole area, perhaps more properly termed a hot springs, is found in Chambourg section of St. David's parish in northern Grenada. The twelve small bubbling hot springs apparently are influenced by the old volcanic mass below the crater lake, Lake Antoine. The soils appear to be coral limestone and a sandstone which includes volcanic ash. During certain seasons the waters of the springs overflow and several sizeable cones have been created. An alkaline litmus reaction was obtained from the waters collected in overflow pools. This, to my knowledge, is the only alkaline fumarole in the Lesser Antilles. No plants from the surrounding scrub of *Acacia*, *Acrostichum*, *Avicennia*, *Chrysobalanus*, and *Laguncularia* have encroached on the rock areas built up by the hot spring.

The Grenada hot-spring area is the only one in the Lesser Antilles venerated by the local people. One vent had an animal sacrifice placed there by religious cultists. Several springs had fresh or wilted bunches of flowers in the orifices. Candles and coatings of wax were present in the largest vent, along with a painting of the Sacred Heart. The late Father Bryan Proudman, who was my host in this area attributes the tokens to "shandoo" ceremonies.

CATALOGUE OF THE FUMAROLE AREAS OF THE LESSER ANTILLES

Grenada

THE GRAND ETANG. This crater lake is in the caldera of an old volcano. Beard (7) has described and illustrated this area and its vegetation. The lake temperature indicates the presence of some heat source. Sulphur odors are noticeable at times, and particles of sulphur occasionally appear on the surface of the lake. No effect of the heat or acidity can be noticed on the surrounding vegetation.

LAVERA HOT SPRINGS. (*Figs. 4, 5.*) About twelve small vents or pot holes near Lake Antoine produce an occasional weak odor of hydrogen sulfide. These are the only alkaline reacting springs that I have encountered. The vegetation has not encroached on the sheets of hard rock formed by the overflow from these springs.

St. Vincent

THE SOUFRIÈRE. Interest in the eruptive volcano on St. Vincent centers on the accuracy of the reports of its eruption in 1902. Prior to that time, eruptions have been recorded for 1718 and 1812. Reports of the former eruption have been considered by Anderson and Flett (4). They point out that while Huggins (32) discredits such reports, Defoe (37) only in part exaggerates in his story, which may indeed have been based on fact. The letters of Rev. Smith (64) may be considered corroborative evidence that the Soufrière did erupt in 1718.

Mr. James Anderson apparently was the first white man to ascend the volcano. In an account published in 1785 (1) he described the summit. "We found very little obstruction in our way up until we got to the place where I returned, and there, for about a quarter of a mile, we had considerable difficulty to clear our way through grass and ferns. After we came within a quarter of a mile from the top, we found ourselves in another climate all at once, the air very cold, and the vegetable productions changed; here was nothing but barrenness over the whole summit of the mountain. On the confines of the grassy region and the barren I found some beautiful plants. Moss grows here in such plenty that I frequently sunk up to my knees in it. This is the only place in the West Indies that produced any moss that I have seen. About noon we gained the top of the peak . . . when in an instant, we were surprised with one of the grandest and most awful scenes I had ever beheld." For the crater Anderson reported, "In the centre of the bottom is a burning mountain, of about a mile in circumference, of a conic form, but quite level. . . . From the external appearance of this mountain, I imagine it has only begun to burn lately, as on several parts of it I saw small shrubs and grass, which looked as if they had been scorched and burnt. . . . On two opposite sides of the burning mountain, . . . are two lakes of water."

An anonymous account published in the *Evening News* of July 30th, 1812, is reprinted by Anderson and Flett (4). This account described an ascent of the Soufrière on April 26th, only a few hours before its eruption at noon on the 27th. On viewing the crater, the anonymous report stated, "Exactly in the centre of this capacious bowl rose a conical hill, about 250 or 300 feet in height, and about 200 in diameter, richly covered and variegated with shrubs, brushwood, and vines about half-way up, and for the remainder powdered over with virgin sulphur to the top. . . . The precipitous sides of this magnificent ampitheatre were fringed with various evergreens and aromatic shrubs, flowers, and many alpine plants. On the north and south sides of the base of the cone were two pieces of water, one pure and tasteless, the other strongly impregnated with sulphur and alum." A comparison of the two reports indicates a secession of the activity of the cone and a re-establishment of the vegetation. The eruption changed all this, for as Shephard (62) stated, "all the former beauty of the Soufrière was, of course destroyed; the conical mount disappeared, and an extensive lake of yellow-coloured water, whose agitated waves perpetually threw up vast quantities of black sand, supplied its place." Hooper's account in 1886 (24) suggests that a single lake remained in the crater. Anderson and Flett (4) reported that the crater "contained three small lakes of water, greenish and turbid, that in the southeast corner was throwing up jets of mud and steam with a hissing noise." In the years which followed, an accumulation of rain water apparently raised the surface of the three lakes and made them confluent. Beard (6) found only one lake in the crater during his visit in 1940, and such is the situation today. The southeast corner of the lake, however, is often discolored with suspended material and flakes of sulphur, indicating that all is not quiet in the fumarole area.

Beard has described the progress of plant succession on the Soufrière in a paper published in 1945. A new study, now that an additional two decades have passed, appears to be in order. I visited the summit of the Soufrière in 1950 and found sufficient differences from Beard's description to suggest that the initial invasion of plants had been successful, that a favorable environment had been created, and that rapid changes were then taking place. At that time, the floral composition of the summit was closer to that described by Hooper prior to the 1902 eruption, with the sole exception of an abundance of fleshy liverworts unmentioned by either Hooper or Beard.

St. Lucia

THE QUALIBOU SOUFRIÈRE. (*Figs. 20, 21.*) This appears to be the only active soufrière on the island of St. Lucia and is situated about a mile and a half southeast of the town of Soufrière. Hooper visited the area in 1886 and reported briefly that "the exhalation . . . has reduced the vegetation on both sides within reach to a carpet of brake fern." In 1903, Sapper (56) and, in 1904, Hovey (26) described the area as between two and three acres in extent, but neither made reference to the vegetation. In 1949, Beard (7) noted that a specialized vegetation was found around the Sulphur Springs (the Qualibou vents). "Clumps of *Pitcairnia* are as usual found nearest to the vents with some *Cyperus ligularis.* Farther out, these are joined by various species of ferns, principally *Blechnum serrulatum* dominated by large clumped bushes of *Clusia plukenetii* and *C. alba.* The whole hillside above the Springs is carpeted with *Blechnum* ferns with an occasional *Clusia.*"

The vegetation around the Qualibou soufrière appears to be completely stabilized. Algae are found in dense mats in the drainage of the hot springs. *Cyperus* and *Eleocharis* plants are common in shallow warm pools of seepage areas. None of the larger plants seen in the area showed any damage from the constant emissions of the fumaroles.

Recent interest has centered in the possible utilization of the thermal heat for generating electricity. The reports of Bodvarsson (8) and of Robson and Willmore (49) are pertinent to this problem.

Martinique

MT. PELÉE. The destructive eruption of Mt. Pelée in 1902 eliminated the town of Saint Pierre, killing all but one person. The latter stages of this eruption, as well as that which occurred in 1930, are well described by numerous authors (2, 3, 29, 36, 39, 44, 52). Bibliographies of significant publications are given by Hovey (28) and Russell (52). Few specific data are available on the regrowth of the vegetation, and a modern survey seems desirable. Stehlé visited the area and published in 1938 a general consideration of the regrowth (66). He recognized conditions comparable to those of Guadeloupe, excepting the sulphur fumes, and suggested that the vegetational zones were a "Clusietum martinicense," a "Lobelietum martinicense," and a "Pitcairnietum martinicense." Stehlé attributed to larger animals the introduction of *Mimosa pigra* and *Acacia tortuosa* to the areas of recent lavas. Birds, he felt, accounted for the introduction of *Ficus*, *Melia*, *Trema*, *Tetrazygia discolor*, and *Miconia striata.* At the lowest elevations on new lavas, Stehlé found common weedy species of *Crotalaria*, *Cassia*, *Emilia*, *Euphorbia*, *Bidens*, *Ageratum*, *Indigofera*, *Pluchea*, etc. Slightly higher and probably introduced by wind were plants of *Ochroma pyramidale*, *Ceiba antillana*, and *Tecoma stans*. Near the top of Mt. Pelée, Stehlé reports the occurrence of two species of *Desmodium* and single species each of *Stenotaphrum*, *Erigeron*, *Sauvagesia*, *Mikania*, *Arthrostemma*, *Hypoxis*, *Cuphea*, *Rubus*, *Phenax*, and *Cyperus*. The majority of these are not found at higher altitudes in undisturbed vegetation on Martinique or nearby islands. No information is available on the length of their persistence. Stehlé indicated that the most powerful colonizers were *Pitcairnia bracteata*, *Guzmania plumieri*, *Tibouchina chamaecistus*, *Baccharis cotinifolia*, *Pityrogramma calomelanos*, and two species of *Epidendrum*.

Thermal springs are recorded from the vicinities of the towns of Frégate and La Redoute, along the coast near Marigot, and on the slopes of Mt. Pelée above Macouba. I have not located descriptive literature regarding their activity as fumaroles or the vegetation around them.

Dominica

The earliest record of fumaroles on Dominica appears in Atwood's account of the island published in 1791 (5). His vivid, but questionably accurate description stated, "These sulphurous mountains are certainly among the most wonderful phaenomena of nature, and command our astonishment and admiration. To see vast tracts of land on fire, whose smoke, like clouds, stretches far around; brimstone in flames, like streams of water issuing from the sides of precipices; in the vallies large holes full of bituminous matter, boiling and bubbling like a caldron; the earth trembling under the tread, and bursting out with loud explosions, are objects truly terrefic to the beholder; who, on the spot, are struck with awe and admirations, on viewing such dreadful works of the Almighty, who causes them to exist, for purposes only known by him." Edwards (15) also reported about Dominica that "several of the mountains contain unextinguished volcanoes, which frequently discharge vast quantities of burning sulphur. From these mountains also issue springs of hot water. . . ." There are no reports of eruptions on Dominica in historic times, and these two early descriptions can not be definitely located geographically. It is possible that these both refer to the imposing Valley of Desolation and its famous Boiling Lake, and represent its earliest record. The discovery of the Boiling Lake is generally credited to Dr. H. A. Nicholls around 1880. Nicholls' route was soon followed by Ober (43), Johow (33), and others, all of whom comment in one way or another on the nature and composition of the vegetation in the Valley of Desolation and around the Boiling Lake.

Hovey (30) and Earle (14) were the first to consider the geology of the area. Later in the twentieth century Domin (13a) and Hodge (21, 22) studied the vegetation of Dominica, and both wrote extensively on this subject. Hodge has said of the Valley of Desolation, "The combined sulphurous fumes of all the vents and fumaroles have had a blighting effect far up the slopes, wherever they have come against the vegetation.

The end result has been the formation of what is known locally as the Valley of Desolation.' [See *Fig. 6.*] Along the ridges above lies Elfin woodland but in the valley only patches of it remain and in these *Clusia venosa* and an *Ilex* seem best able to tolerate the noxious gases. In the proximity of the fumaroles vegetation is absent or sparse and except for the colorful algae to be seen in the warm water of the streams, is apparently unable either to tolerate the noxious fumes or to root in the mineral-impregnated soil. The only pioneer species observed close to the vents were the bromeliad *Pitcairnia spicata* var. *sulphurea,* a grass, *Ischaemum latifolium,* and occasional plants of *Dicranopteris bifida.*" Hovey (30), Sapper (56), and Robson and Willmore (51) give data on the water temperatures of the Boiling Lake.

Earle (14) reported additional soufrières in Dominica at Ravine D'Or (Layou Valley), Morne au Diable (Portsmouth), Laudat and Soufrière villages, and Wotten Waven. He states, "All of these are insignificant besides the Grande Soufrière, though the Wotten Waven springs are quite numerous and besides a few violent fumaroles also display small mud volcanoes."

At Wotten Waven I was able to visit the fumarole area which is located in an old field now devoted largely to pasture. The fumaroles at the time of my visit were noisy and emitting steam, but almost without sulphurous odors. The high humidity and heat appeared to encourage plant growth, and the shrubs of *Clusia alba* were more luxuriant than specimens we had passed a few yards away (*Fig. 7.*)

The fumarole area behind Soufrière village was represented by an enormous scar on the hillside where landslides had recently exposed fresh surfaces and obscured some of the vents. The fumaroles were not noticeably active, and although the odors of sulphur dominated the air, there was no evident destruction of the vegetation. The area was well stabilized, but few plants other than species of *Blechnum*, *Dicranopteris*, and *Cyperus* had invaded the areas.

Guadeloupe

THERMAL SPRINGS. The island of Guadeloupe is reported to have thermal springs along the coast at the towns of Boüillante, Monchy, and Pigeon; somewhat inland near La Lise and Dolé; on the slopes of the Soufrière near Baines Jaunes; and at the summit of the Soufrière. All of these are on Basse Terre and probably are associated with the volcanic massif of the Soufrière. I have not visited the thermal springs at low altitude and have been unable to find any descriptive literature regarding them or the vegetation surrounding them.

The oldest reference to hot springs and fumaroles is found in Père Labat's writings. His description of the thermal springs of "Ance de Goyave" presumably refer to the area currently called Boüillante and not to Goyave on the west coast. Labat also climbed the Soufrière and described the stunted vegetation near the summit. A trip from St. Claude to Baines Jaunes and along the old carriage trails past the warm and cold baths to the summit of the Soufrière suggests that few changes have occurred in the intervening 260 years (*Figs. 8, 9*).

Stehlé (65, 67, 68) has published several admirable treatments of the vegetation of the slope of the Soufrière. He indicates that the effects of high altitude and of the sulphur vapors cause a limitation in height of plants but seem to encourage the development of many lateral branches. He also states, "Les gaz sulfureux émis par la Soufrière sont néfastes à la végétation environnante, qu'ils détruisent peu à peu." Stehlé concludes that the species which exist in this environment are particularly interesting and rare. Many are thought to be endemics, but as more is known of the vegetation of the high mountain peaks from St. Kitts to St. Vincent it becomes increasingly difficult to separate those species which are restricted to high elevations on the ash of volcanic ejecta and those which are there because of their tolerance to fumarole emissions. However, the red-flowered form of the bromeliad *Pitcairnia spicata* occurs at high altitudes on St. Kitts, Guadeloupe, Dominica, Martinique, and St. Vincent, while the yellow-flowered form, *P. spicata* var. *sulphurea*, has not been found on St. Kitts and occurs on the other islands in areas influenced by the crateral fumaroles. The endemic species of these high mountains are not the most distinct of species, and recent collections from other islands have indicated that their distribution is wider in the Lesser Antilles than has been previously reported.

Montserrat

GALWAY'S SOUFRIÈRE. (*Fig. 15.*) One of the earliest accounts of the soufrières on Montserrat was made by Dr. Nicholas Nugent, an honorary member of the Geological Society of London who visited Montserrat in 1810. His point of view in visiting Galway's Soufrière was entirely geological, but his description applies to the present as well. "A rugged horse-path was traced along the brink of the ravine, which we followed amidst the most beautiful and romantic scenery. At the head of this ravine is a small amphitheatre formed by lofty surrounding mountains, and here is situated what is termed 'The Sulphur.' Though the scene was extremely grand and well worthy of observation, yet I confess I could not help feeling a good deal disappointed, as there was nothing like a crater to be seen, or anything else that could lead me to suppose the place had any connexion with a volcano. On the north, east and west sides were lofty mountains wooded to the tops, composed apparently of the same kind of porphyry we had noticed all along the way. On the south, the same kind of rock of no great height, quite bare of vegetation, and in a very peculiar state of decomposition. And on the south-eastern side, our path, and the outlet into the ravine. The whole area thus included, might be three or four hundred yards in length and half that distance in breadth."

Karl Sapper visited Montserrat in 1903 (57) and visited both Gages and Galway's soufrières. He published a sketch map of Galway's Soufrière indicating the principal fumaroles where he recorded temperatures of 34.2–93.2° C. and commented on the production of hydrogen sulfide by each. Sapper estimated the area of destruction of vegetation as between three and four hectares. MacGregor (39) reproduced Sapper's sketch-map and concluded that the site of fumarole activity had changed by the time of his visit in 1936. Perret also visited Galway's Soufrière during the volcanic crisis in Montserrat in 1934. His description of the area is meager, for he concluded that, "Galways Soufrière was a more ordinary solfatara having less chemical activity and water of less acidity — altogether, a vent less capable of serving as an indicator of increasing volcanic activity than the more accessible Gages Soufrière." He did note that the water from Gages Soufrière had an acid content ten times as great as that from Galway's. My tests in 1961 with "pHydrion" paper gave a reading of pH 5 for the waters in Galway's fumaroles and 1.5 for those in Gages.

Sapper commented only on the dead and dying vegetation in the vicinity of Galway's Soufrière, and his outline map of the area of activity and destruction has recently been questioned by Martin-Kaye (40), who felt from seeing MacGregor's reproduction of Sapper's map that the main stream was in reality the southeast stream as drawn by Martin-Kaye (40). I find it difficult to agree with this conclusion and suggest that Sapper and MacGregor are correct. Certainly the locations of the principal vent are similar on the two maps in relation to the area of destroyed vegetation.

Martin-Kaye has reproduced temperature records at Galway's Soufrière taken by the Montserrat Department of Agriculture from 1936 to 1952. My own reading taken in January, 1961, showed a vent temperature of 96° C. (200° F.) and pool temperatures 83° and 77° C. (180° and 170° F.), respectively, for the pools where, I was told, the temperatures were generally recorded.

The vegetation at Galway's appears to be completely stabilized. The prevailing winds blowing down the mountain gorges across the soufrière and towards the sea apparently have carried the toxic fumes for years at definite elevations. Plants have developed in the lee of fans, piles of scree, and even behind boulders. To the windward, the vegetation is unaffected, and not at all stunted. The principal plants nearest the soufrière were *Clusia*, *Freziera* and *Ternstroemia*. Within the soufrière proper the existing and often flourishing plants belong to the genera *Andropogon*, *Clusia*, *Cyperus*, *Philodendron*, *Pitcairnia*, *Pityrogramma*, and *Ternstroemia*.

GAGES LOWER SOUFRIÈRE. (*Fig. 14.*) Nugent does not mention Gages soufrières and Shafer's (61) description of his visit to Montserrat speaks so generally of the three soufrières that one can not place his actual visit. Gages Lower Soufrière is said to have originated in 1896 following a cloudburst and to have been moderately active during an earthquake series in 1898. Perret's visit to and study of Gages Lower Soufrière during its period of renewed activity beginning in 1933 is well recorded. Gages Lower Soufrière consists of two parallel valleys, one old and inactive, the other a "new rift" which opened around 1930. The one valley remained active through 1935, but by the 6th of May, 1937, the gas phase had subsided and the water from the gorge was nearly chemically inert. I visited this area in 1950 and again in 1961. Little change was observed in the first visit from the condition shown in Perret's photographs. In 1961, only minor fume emissions were noticeable with faint odors of hydrogen sulfide with sufficient heat and steam to cloud one's glasses. Fume temperatures at the most active vents were 94–96° C. The area of devastation, which Perret judged to be 600 feet long and 350 feet wide, had not increased, but by 1961 an occasional patch of green from prothallia or young gametophytes of mosses was evident, with an occasional plant of *Andropogon*, *Capraria biflora*, *Clusia*, or *Cyperus* present in the valley. On the limonitized zone at the head of the valley grasses and sedges were becoming more abundant, apparently developing from seed sources above the devastated area.

GAGES UPPER SOUFRIÈRE. (*Figs. 10–13, 18, 19.*) Accurate dating is not available for the age of Gages Upper Soufrière. Sapper (57) visited it in 1903, and Perret indicates that it was dormant prior to the earthquake of November 11, 1935, when its activity increased enormously. Perret does not go into detail on his observations on Gages Upper Soufrière, although he delayed his departure from Montserrat to study this new outbreak. He does indicate that the temperatures were 99° C. in the steam vent and 96° and 98° C. in the pools. His illustrations, and particularly *Fig. 31* reproduced here, are noteworthy for the remnants of the vegetation shown. Clearly, the area of Gages Upper Soufrière had been relatively small prior to the 1935 activity, for the density of the vegetation indicates a recent kill. Perret noted that there was a threat for Gages Upper Soufrière to "extend its domain by reason of gas emission and rain erosion." Martin-Kaye's observations and map for his visit in October, 1954, led to the conclusion that "much of this area has comparatively recently opened up as many rotted tree stumps are still to be seen more or less in the position of growth." My own comparative observations already mentioned were made in 1950 and again in 1961 and lead only to the conclusion that Gages Upper Soufrière is not only as active as it has been in the past but is continuing to increase to the southwest and may well cross the ridge into the next valley. The area devastated at present is about eight acres at an altitude between 1300 and 1400 ft. along the stream bed, but extending up the hill to around 1700 ft.

TAR RIVER SOUFRIÈRE. MacGregor (39) has illustrated in his *Figure 37* the appearance of the "New Cow Hill soufrière" (Tar River) shortly after its inception in 1936. The fumaroles apparently appeared in the center of a banana plantation. When Martin-Kaye and Willmore visited the area the fumarole was relatively quiet, and only about an acre of vegetation was affected by the fumes. In 1961 steam and fumes were not apparent from a convenient observation point on the slopes leading to English's Mountain.

LANG'S SOUFRIÈRE. (*Figs. 16, 17.*) With the expert guidance of Kingsley Howes we visited the recently discovered Lang's Soufrière on the north flank of the Soufrière Hills above Paradise Estate. The soufrière itself is essentially dormant, giving only occasional indication of hydrogen sulfide and some degree of heat. It is located at the head of a deep ravine, and landslides not of recent time have covered the actual fumaroles. The decomposition of the rock in the area, plus the occurrence of one large dead specimen of *Sloanea* and the abundance of *Philodendron giganteum* attested to the past activity of this fumarole.

OTHER SOUFRIÈRES. Through the Soufrière Hills are other indications of dead or dormant fumarole areas. Several were seen in Gages Gut en route to Gages Upper Soufrière. Neither fumes nor heat is emitted from these areas at the present. The older ones were green with mosses and lichens, and the younger ones still showed the color of the altered rocks. These fumaroles were apparently never of major importance, for the surrounding vegetation was neither affected nor characterized by the genera usually found in active areas. Mulcair Soufrière was known by reputation to the local people, but, as Martin-Kaye discovered, it seems to be inaccessible, for no local individual was capable of guiding me to it.

HOT WATER POND. This coastal pond is thought to be heated by subterranean springs, possibly the drainage from the Gages soufrières. It did not support any unusual plant life nor was the surrounding vegetation affected in any way.

St. Kitts

Martin-Kaye (40) supplies the only references I have encountered to fumarole activity on the island of St. Kitts. My visits have been at times when the cloud cover made any ascent of Mt. Misery of doubtful value. Martin-Kaye reports however, that the crater of Mt. Misery is between one-half and three-fourths of a mile in diameter at the rim, 500 to 600 feet deep, and possesses a small shallow lake in the southwest part of the floor, which "except in the vicinity of two small areas of fumarole activity, is otherwise covered with vegetation." Martin-Kaye also reports that "now defunct fumarolic activity has caused rock alteration at Rainbow Cliff, Frigate Bay where variously colored ochres are associated with yellowish, brownish and grey clays, kaolin, some gypsum and probably opal powders and alunite as are associated with the active soufrières in Montserrat, Nevis, Mt. Misery itself and elsewhere in the Lesser Antilles." Regrettably no data on the surrounding vegetation are available.

Nevis

The Rev. Mr. Smith (64) in a series of letters presents some of the earliest records of the natural history of Nevis. In his second letter he refers to a hot river and to baths "supposed to flow from the sulphur ground which is not above three quarters of a mile higher in the country." He also notes that "In my parish of St. John in the Island of Nevis, there is a considerable spot of sulphurous ground on the south side, at the upper end of a deep rupture in the earth vulgarly called Sulphur Gut, which is so excessive hot . . . as to make us immediately feel it through our Shoe Soals." Rev. Smith refers to another at a "place two miles and half south-ward of Charles Town" and reports that "a new hot spring was in 1718, discovered in Windward Parish, upon clearing of a wood . . . just above Camp-ground."

Bryan Edwards (15) said for Nevis, "That the island was produced by some volcanic explosion, in ages long past, there can be no doubt; for there is a hollow, or crater, near the summit, still visible, which contains a hot spring strongly impregnated with sulphur; and sulphur is frequently found in substances, in the neighboring gullies and cavities of the earth." In his excellent treatment of the geology of the Leeward Islands, Martin-Kaye has reported two active soufrières on Nevis at Farm's Estate and Cades Bay, the latter first noticed in 1953. In addition there is some gas seepage noticeable in the Belmont area and thermal pools at Bath Springs near Charlestown and in the Camp Springs area. The thermal pools apparently are those described by the Rev. Smith, indicating an activity of nearly 250 years.

The Farm's Estate Soufrière is both old and relatively quiet. Hydrogen sulphide odors and wisps of steam are noticeable. Willmore recorded temperatures of 42–44° C. in small fissures and temperatures of 96° C. in a vent. Apparently the vegetation has been affected by the activity of the fumaroles but has now become stabilized.

The Cades Bay Soufrière, according to Martin-Kaye, was first noted in 1953 when the "vegetation began to die and hydrogen sulfide was evident." In six months an area twenty by thirty feet containing sunken boiling steam holes had developed and odors of sulphur dioxide were evident. Shortly thereafter several areas became confluent by the loss of vegetation and a barren area of about 1.5 acres was produced containing small pools with water registering a temperature of 118° F. Martin-Kaye reports that in 1958 the vents "seem to have mainly concentrated in one small bubbling pool a few feet across" and that the "vegetation had re-established itself over the western part." Regrettably no specific information on the nature of the vegetation of the area is available.

SUMMATION AND COMPARISONS

Volcanism, either eruptive or fumarolic, is destructive to vegetation, as ample examples show in the Lesser Antilles. *Nuées ardentes*, characteristic of recent eruptions, are totally destructive of plant life, and ash falls less so. The revegetation of ash-covered areas is related to the type of destruction but also to the altitude of the area considered and its proximity to sources of new plants. At lower elevations or adjacent to undisturbed areas invasion by weedy species is rapid. Plants covered only with free-fall ash appear to sprout rapidly from the basal portions and quickly supply a covering vegetation. At highest elevations where a specialized vegetation occurs the re-establishment of vegetation is much slower. Even when the proper seeds are introduced from adjacent mountain tops the environment is inhospitable, and decades pass before the original introductions have formed an even moderately complete cover.

New areas of fumarolic activity appear to act first through a heating effect of the soil to which the native species are selectively tolerant. The emission of sulphur compounds creates an acid environment in the soil and air-borne acidic fumes. Natives species appear to be killed off in direct relationship to their ability to stand increasing acidity. The air-borne acid particles appear to be cumulative in their action on the surrounding vegetation. Ferns with leaves of delicate textures and broad-leaved plants without heavy cuticles are most sensitive to these fumes. Plants with coriaceous leaves or heavy cuticles are most resistant. At the highest elevations on soils composed of volcanic ash it is difficult to determine the role of fumarole emissions in the establishment and persistence of the species present.

In the Lesser Antilles the species which appear to be most tolerant of fumarolic gas emissions and soil acidity are the following: *Andropogon pertusus*, *Blechnum indicum*, *Cladium restioides*, *Clusia alba*, *Clusia mangle*, *Clusia plukenetii*, *Cyperus ligularis*, *Cyperus planifolius*, *Dicranopteris bifida*, *Guzmania plumieri*, *Lycopodium cernuum*, *Lycopodium meridionale*, *Lycopodium tortum*, *Philodendron giganteum*, *Pitcairnia angustifolia*, *Pitcairnia albucifolia*, *Pitcairnia spicata* var. *sulphurea*, *Pityrogramma calomelanos*, *Pityrogramma chrysophylla*, and *Ternstroemia peduncularis*.

A comparison of the plant species from other geographic areas which are tolerant of fumarolic environments or which are invaders of volcanically disturbed areas is interesting yet difficult due to the differences in composition of the floras. Much has been written of the thermal springs of the United States, particularly the area of Yellowstone National Park where emphasis has been given to heat tolerant algae and to the animal life of the hot springs. Similar studies are available for the hot-spring areas of Iceland. In both cases, the families, genera, and species of the plants can not be compared with those of the Lesser Antilles. The extensive fumarole areas of Indonesia and of Japan have received some study. Mizushima (41) studied the plant community of the fumarole areas of the Idzu Islands, midway between Tokyo and the Bonin Islands. He found that the plants tolerant of fumarole conditions were: *Chamaesyce hirta*, *Chrysanthemum pacificum*, *Cyperus polystachyos*, *Fimbristylis dichotoma* f. *floribunda*, *Imperata cylindrica* var. *koenigii*, *Lindernia crustacea*, *Lycopodium cernum*, *Lygodium japonicum*, *Ophioglossum petiolatum*, *Paspalum orbiculare*, and *Pouzolzia zeylanica* (Urticaceae). He noted that plants of *Lindernia crustacea* are of interest as the individuals gain in stature as they approach the fumaroles. *Hedyotis*, *Paspalum* and *Pouzolzia* were limited in their distribution on the island to the areas of the fumaroles. *Cyperus*, *Fimbristylis*, *Imperata*, *Lycopodium*, and *Lygodium* were indicated as abundant near the fumaroles.

The locations of the numerous areas of volcanism in Indonesia are effectively shown in a map published by Ter Braake (9). Braun-Blanquet (10) indicates that *Pteris incisa* thrives on the soft, sulphurous soils adjacent to springs that are rich in alum. *Polypodium vulcanicum* has been reported to survive on rocks which are occasionally flooded by waters with temperatures as high as 75° C. According to Holtermann (23), the dominant shrubs in such areas are *Agapetes vulgaris* and *Rhododendron retusum.*

Braun-Blanquet suggests that the plants of such fumarole areas are mesophytic in nature. Schimper (59) however, indicates that the flora of the solfatara areas is composed of xerophilous species. Zollinger (72) and later Junghuhn (34) were the first to observe in Java that the vegetation close to fumaroles was composed of alpine species, even when the fumarole was 1000 to 1500 meters below the natural alpine region. Schimper described the fumarole area as follows: "Where these pools are collected, usually in large numbers and of different sizes, the soil is a wet white clay, which is said by Junghuhn to arise by the action of sulphuric acid on trachyte; it is usually covered by a yellowish efflorescence of sulphur. The ground is frequently so hot that to remain standing on it is impossible. From all the crevices and pools there escape hot vapors of suffocating odour, sometimes of sulphuretted hydrogen, at other times of sulphurous acid. The water has an acid taste and sets the teeth on edge." He noted further that "the bushes of the solfataras are much lower in stature than the surrounding forest and quite sharply marked off from it. None of the small trees and shrubs that form the underwood in the high-forest appear among them; of forest herbs only a few species represented by detached individuals occur; plants that occur elsewhere in the open situations of the same region are entirely absent."

In the vicinity of solfataras Schimper indicates there are always numerous plants of *Ficus diversifolia, Rhododendron javanicum,* and *Vaccinum varingiaefolium.* In solfataras of lower regions some other species, notably *Gaultheria leucocarpa, Medinilla javanensis, Myrsine avenis, Rhododendron retusum,* and *Rhododendron tubiflorum,* occur, and, in addition, "isolated ferns with leathery leaves and lycopods are always present in such spots." Plants of the Melastomataceae and Myrsinaceae, although abundant in the Lesser Antilles, do not tolerate fumarolic environments. The Ericaceae are poorly represented in the Lesser Antilles, and the genera do not occur in areas where fumaroles are active.

Junghuhn noted that in solfatara areas the shrubs are swept clear of all epiphytic vegetation, including mosses and lichens. This is also true throughout the Lesser Antilles. A new fumarole seems to be most toxic to the epiphytic moss, liverwort, and lichen flora of trunks and branches of the adjacent vegetation. In dormant fumarole areas, however, mosses are among the first invaders.

The steam vents on Mauna Loa, Hawaii, contain minimal amounts of sulphur and do not seem to be influential in determining the vegetational components around them. Ferns, particularly *Nephrolepis,* are abundant, while *Dodonea*, *Styphelia*, *Vaccinium*, and many rubiaceous genera grow more vigorously in the humid environment of the vent than at a distance.

The revegetation of surfaces disturbed by volcanic eruptions has been the subject of a classic study in the case of Krakatoa (69). Fosberg (16) has outlined the nature of the invasion and revegetation of lava flows and ash-cinder areas of Hawaii. Only preliminary studies are available for the Parícutin eruptions in Mexico. Calvert and Calvert (12) discuss the effects of volcanic activity and subsequent fumarolic activity for Volcán Irazú, Costa Rica. However, the altitude and the species involved in all these areas do not permit comparisons with similar areas of the Lesser Antilles.

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EXPLANATION OF PLATES

PLATE I

FIG. 4. Cone of fumarole at Lavera Hot Springs, Grenada. FIG. 5. Path of mineral deposit from cone in *Fig. 4,* Grenada. FIG. 6. Valley of Desolation, Dominica. FIG. 7. Steam vent at Wotten Waven, Dominica. FIG. 8. "Clusietum guadelupense" on windward slopes of La Soufrière, Guadeloupe. *Dicranopteris bifida* and *Cladium restioides* are seen in foreground, *Clusia mangle* in middle, and *Ilex* species on distant slope. FIG. 9. *The same* on leeward slopes, showing killing by periodic emissions of sulfur fumes. Dead plants are *Clusia*, *Ilex*, and *Freziera*; living plants are *Philodendron giganteum*.

PLATE II

FIG. 10. Gages Upper Soufrière, Montserrat, after its reactivation on November 11, 1935. Photo reproduced from Perret (45). FIG. 11. Gages Upper Soufrière, Montserrat, as it appeared in June, 1950. FIG. 12. Gages Upper Soufrière, Montserrat, as it appeared in January, 1961. FIG. 13. Dead and acid-rotted stump of *Sloanea dentata* at Gages Upper Soufrière in January, 1961. A fumarole had opened under this tree within the last decade, for the tree was alive in 1950. FIG. 14. Gages Lower Soufrière, Montserrat, in January, 1961. Vegetation has descended on the limonitized area from above. FIG. 15. Main steam vent at Galway's Soufrière, Montserrat, in January, 1961. Effect of the prevailing winds from the mountain is shown by the path of the steam. Effects of the fumes are visible on the hillsides by the reduction of vegetation.

PLATE III

FIG. 16. Lang's Soufrière, Montserrat, as seen from Paradise Ridge. Point of arrow locates the dead *Sloanea* trunk shown in FIG. 17. Rear of the arrow marks dense growth of *Philodendron giganteum*. FIG. 17. Point of emission of fumes from Lang's Soufrière, Montserrat. A dead trunk of *Sloanea* is on the left. Recent rock fall shows the depth of the effects of the acidity on the rock face. FIG. 18. A new area of fumarole activity at Gages Upper Soufrière, Montserrat, January, 1961. Plants of *Clusia alba* are in the foreground. *Cyathea* and other components of adjacent woodland are shown in the background, as yet, not affected by fumes of the new fumarole. Destructive effects to the present are due to heat and soil acidity. FIG. 19. Gages Upper Soufrière, Montserrat, January, 1961. The upper valley of this soufrière showing the proximity of the undisturbed woodland on the windward side of the fume area. FIG. 20. Qualibou Soufrière, St. Lucia. Boiling lakes and steam vents with acid-softened rock are in the foreground. The profile of the hill in the background shows the absence of shrubs or trees. FIG. 21. Qualibou Soufrière, St. Lucia. A face view of the hill shown in *Fig. 20*. The hillside vegetation is of *Blechnum* and *Lycopodium* where affected by the fumes of the soufrière. The edge of the affected area is shown on the right.

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HOWARD, VOLCANISM IN THE LESSER ANTILLES

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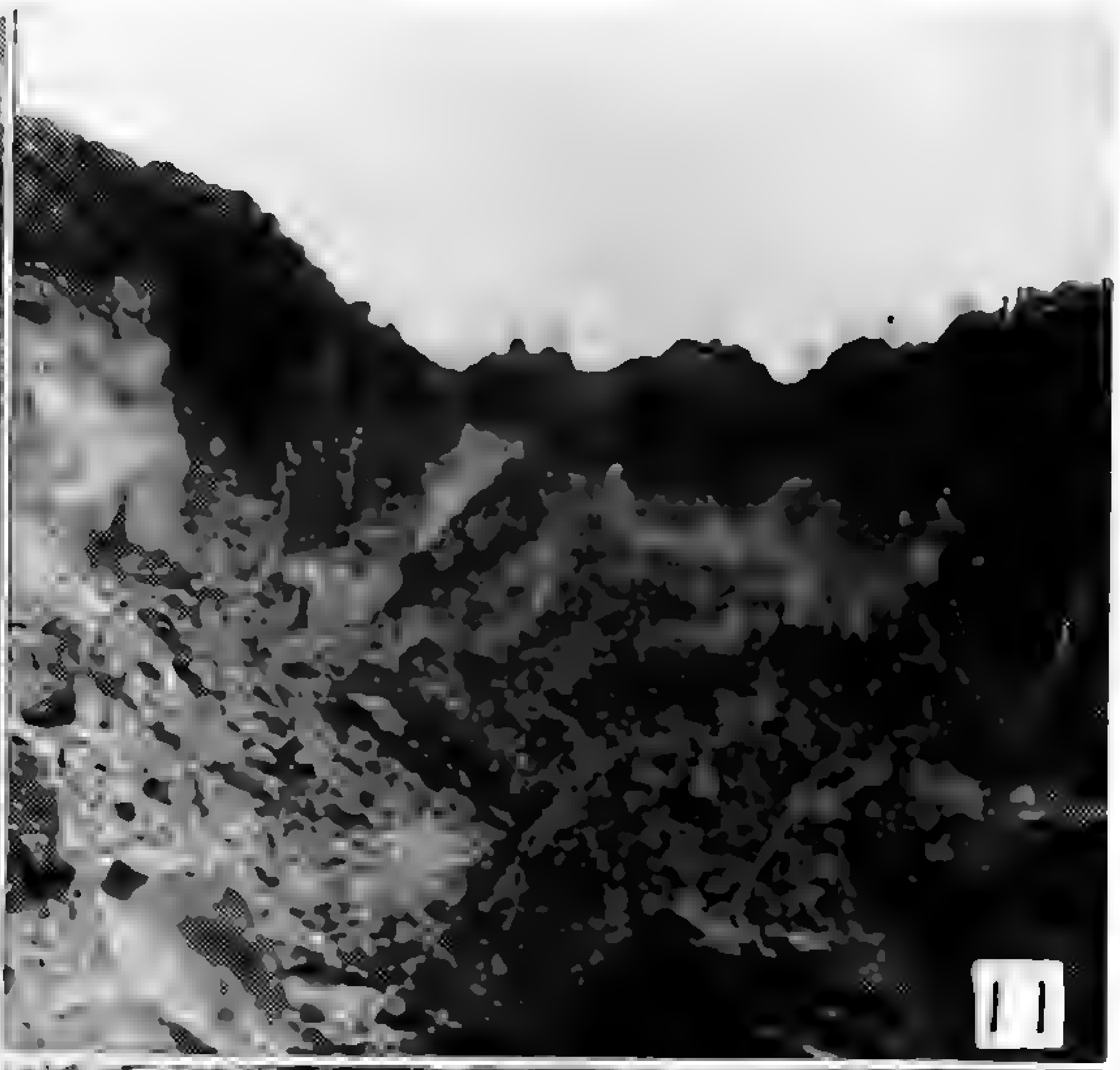

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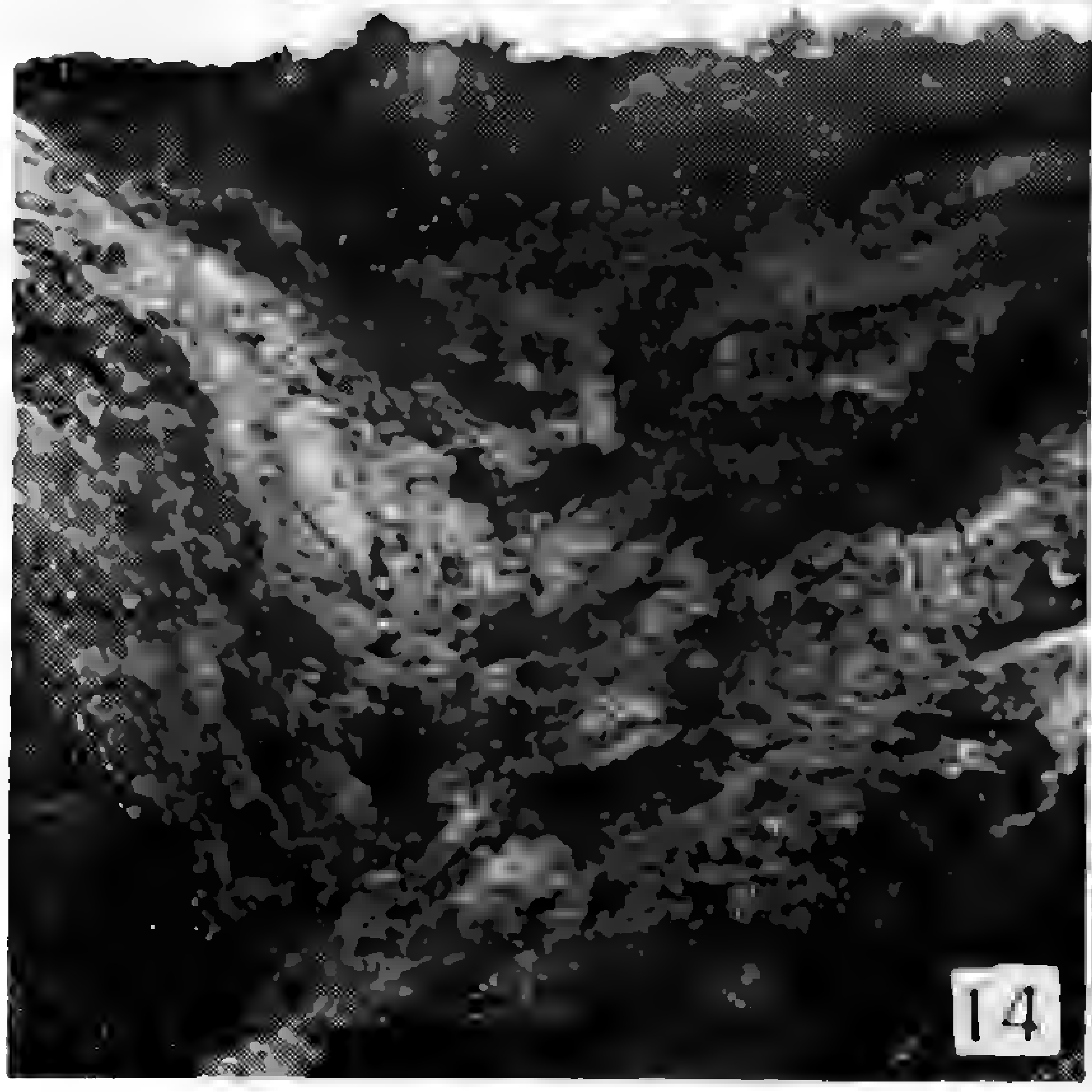

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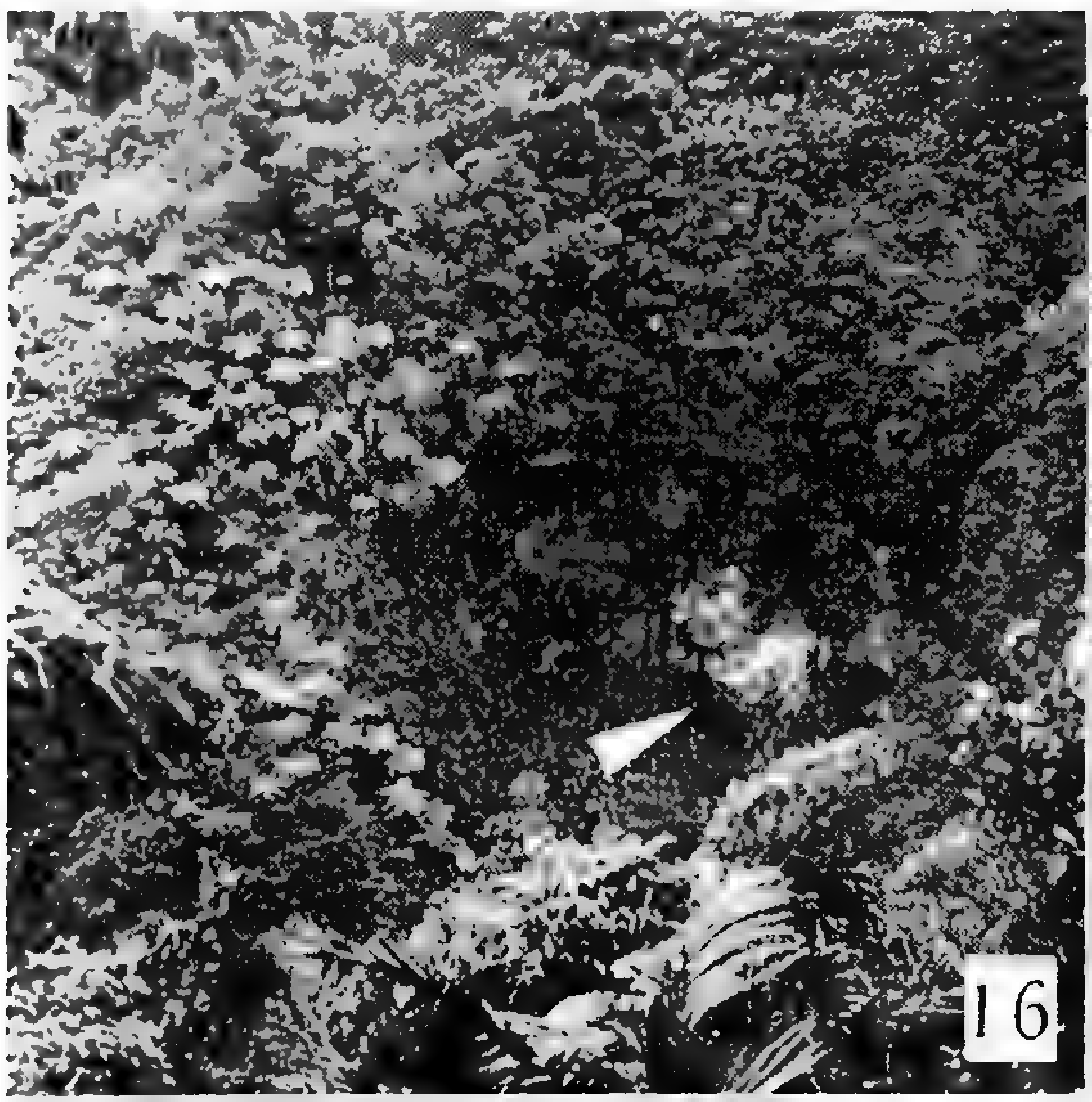
Howard, Volcanism in the Lesser Antilles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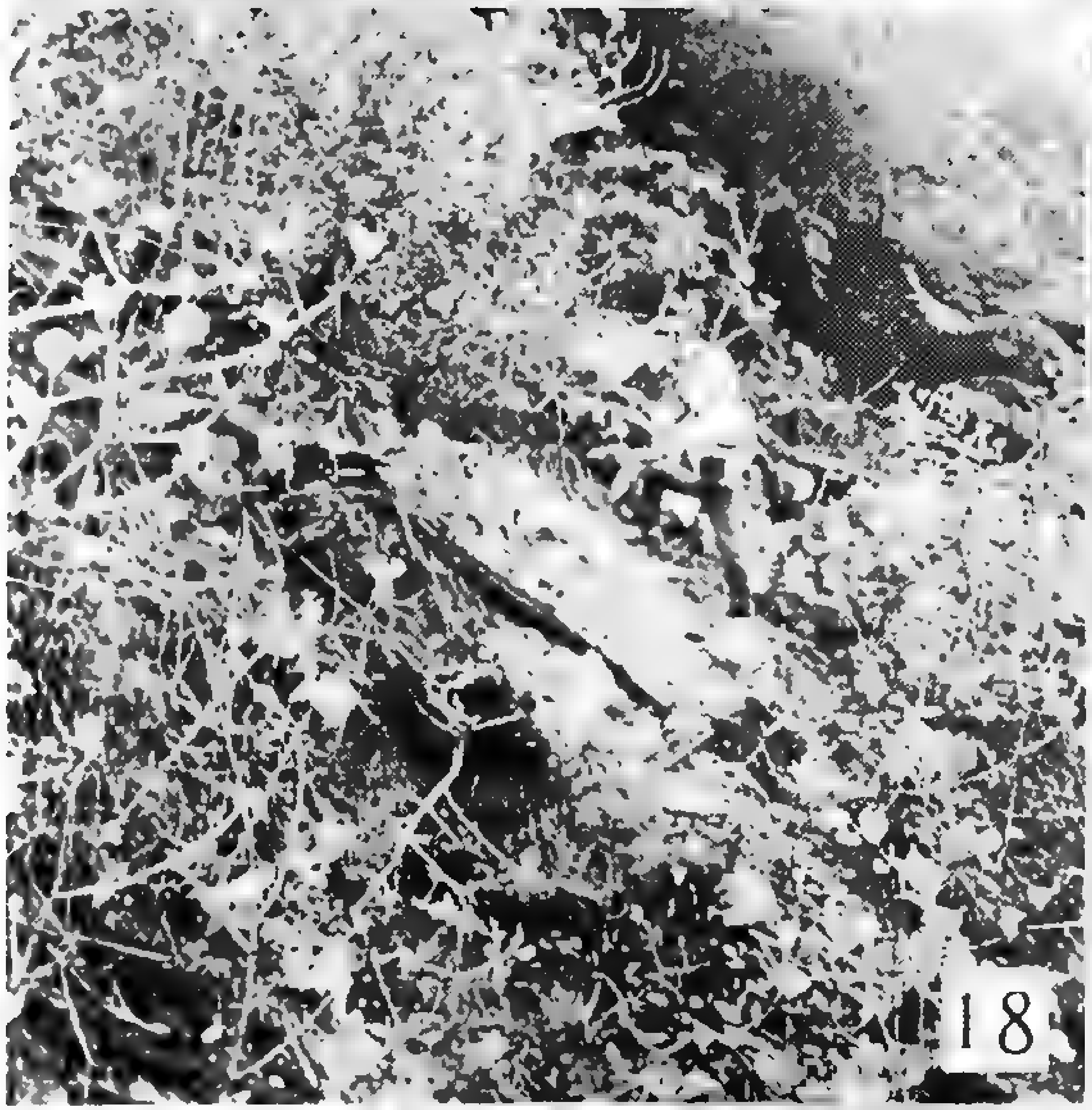
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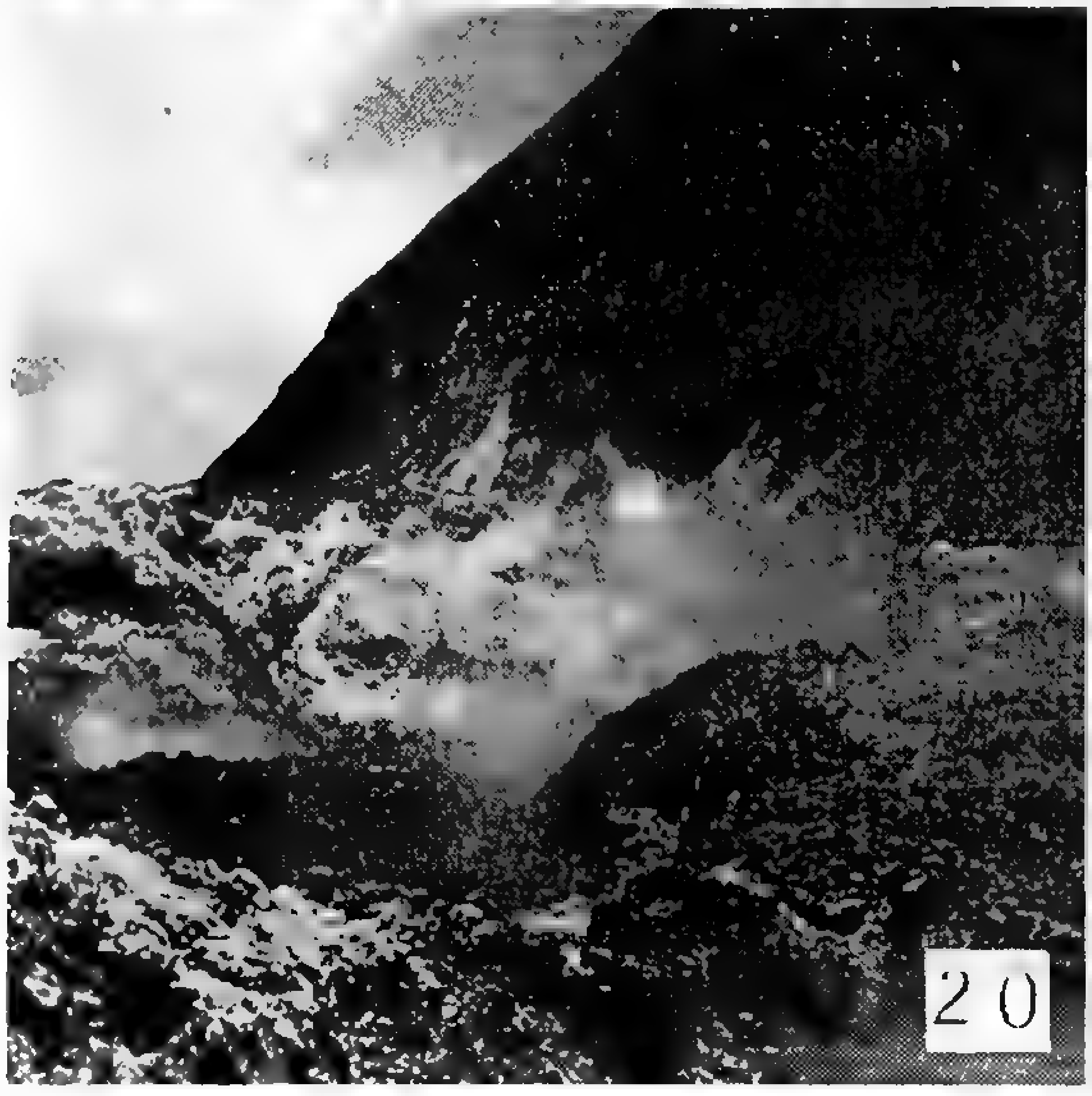
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HOWARD, VOLCANISM IN THE LESSER ANTILLES

THE GENERA OF PAPAVERACEAE AND FUMARIACEAE IN THE SOUTHEASTERN UNITED STATES [1]

Wallace R. Ernst

PAPAVERACEAE A. L. de Jussieu, Gen. Pl. 235. 1789, nom. cons.
(Poppy Family)

Annual or perennial, sometimes rhizomatous herbs [shrubs, or small trees], often glaucous and pubescent with multicellular [or unicellular] hairs or glabrous, usually with acrid, reddish-orange to yellow [or white] sap. Leaves rosulate and/or cauline, usually alternate, reduced upward, exstipulate, petiolate or sessile, pinnately (seldom palmately) [or ternately] veined, lobed, or dissected [or entire]. Inflorescences terminal and determinate, 1–many-flowered, usually cymose [or rarely paniculiform]; buds erect [or nodding], subtended by a leaf or bract. Flowers erect, bisexual, open, essentially regular and hypogynous [seldom perigynous]. Perianth cyclic, imbricate, usually 3-seriate, 2- or 3-merous. Sepals 2 or 3 [seldom synsepalous], usually with dissimilar left-right-oriented margins [seldom reversed], tightly inclosing the buds until anthesis, then caducous. Petals usually 2-seriate and twice as many as sepals (sometimes polypetalous) [or seldom apetalous], opening diurnally,

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This presentation is based, in part, on a survey of the floral morphology of Fumariaceae and a doctoral dissertation on the floral morphology of Papaveraceae. The subfamilies described here, discussed in detail in the above dissertation, represent a re-evaluation of the generic affinities. Altogether, these four subfamilies constitute the subfamily Papaveroideae, as used by Fedde, their names and included genera more or less corresponding to four of his five tribes. In the terminology of Fedde, the Romneyeae Benth. & Hook. (including *Romneya* Harv. and *Arctomecon* Torr. & Frém.) are placed with the Papavereae, and *Glaucium* Mill. has been removed from the Papavereae and placed with the Chelidonieae Reichenb.

The Russian literature citations were translated by Dr. G. K. Brizicky; the eloquent Latin descriptions were prepared by Dr. R. C. Foster; Dr. G. W. Gillett and Mr. R. C. Bean provided material for cytological study; Mrs. H. Francia Hommersand verified some distribution records in the herbarium of the University of North Carolina; and Dr. C. E. Wood, Jr., has given much expert advice.

sometimes wrinkled, usually fugacious; the outer series larger and alternate with the sepals. Stamens usually many, indefinite, varying in number with the size of the flower, usually shorter toward the petals; the filaments sometimes expanded [or toothed] and often constricted below the anther; anthers basifixed, 2-locular at anthesis, usually extrorse, dehiscent by longitudinal slits; pollen often 3-colpate, sometimes polyporate [polycolpate or rugate]. Gynoecium syncarpous, of 2 to many carpels; stigmas laterally confluent [or discrete], as many as and alternate with the placentae, the margins of adjacent stigmas often conspicuous over the placentae [see *Eschscholzia*]; style definite to absent; ovary 1-locular [locule rarely occluded; or rarely multilocular; or rarely the carpels conduplicate about a central cavity]; ovules usually numerous [seldom 1], obovoid, amphitropous, 2-integumented, the micropyle beneath the funiculus; placentation parietal, sometimes intruded into the locule. Fruit dehiscent by 2 to many valves alternate with the persistent placentae [or fruit nonvalvate and dehiscent through the placentae]; dehiscence usually incomplete, acropetal or basipetal. Seeds [1 to] many, obovoid to ± reniform, free [or rarely fruit fragmenting into 1-seeded joints], variously sculptured or smooth, sometimes arillate and attractive to ants; endosperm present, often oily; embryo small, straight or somewhat curved. Seedling cotyledons linear [very rarely bifid] or expanded and petiolate. (Excluding Fumariaceae DC. and *Hypecoum* L.) TYPE GENUS: *Papaver* L.

About 25 genera and at least 200 species, widely distributed in the Northern Hemisphere from sea level to ca. 5800 m. (19,000 ft.); *Papaver*, local in both South Africa and Australia, extends northward into the Arctic; *Bocconia* and *Argemone* occur in the New World tropics. Of the 13 genera indigenous to the United States, only three occur in our area.

The genera may be divided conveniently into four subfamilies. The Chelidonioideae Ernst,[2] the most heterogeneous of the subfamilies, tending to have multicellular-uniseriate hairs, 2-merous perianths, 3-colpate or polyporate pollen, 2-valved gynoecia (3–5-valved in *Stylophorum diphyllum*) with well-developed median carpellary traces, and arillate seeds, are represented in our area by *Sanguinaria* and *Stylophorum*, and by *Chelidonium majus*, a naturalized weed. *Glaucium flavum* Crantz (2*n*

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[2] **Chelidonioideae,** subfam. nov. Papaveraceae pilis mollibus, laevibus, multicellularibus, terminaliter uniseriatis, septis perpendicularibus (in *Bocconia* ramosis, in *Macleaya* ramosis, fastigatis et imbricatis); perianthio dimero (in *Eomecone* synsepalo; in *Sanguinaria* polypetalo; in *Macleaya* et *Bocconia* apetalo); gynoecio biplacentato et bivalvato (valvis 3–5 in *Stylophoro diphyllo*); vena carpellare mediana bene explicata; valvis acropetaliter vel basipetaliter dehiscentibus, sed dehiscentia plerumque laterale et subcompleta; seminibus saepe arillatis (arillus deest in *Glaucio*, *Dicranostigmate*, et *Macleaya microcarpa*); polline tricolpato vel polyporato. Herbae perennes, saepe rhizomatosae vel in *Bocconia* arborescentes, in hemisphaerio septentrionale. TYPUS GENERICUS SUBFAMILIAE: *Chelidonium* L. GENERA ALIA: *Bocconia* L., *Coreanomecon* Nakai, *Dicranostigma* Hook. & Thoms., *Eomecon* Hance, *Glaucium* Mill., *Hylomecon* Maxim., *Macleaya* R. Br., *Sanguinaria* L., *Stylophorum* Nutt.

= 12, 24) and *Macleaya cordata* (Willd.) R. Br. ($2n = 20$) are reported as garden escapes or weeds to the north of our area. The dehiscence of the valves is acropetal in *Sanguinaria* and *Chelidonium* but basipetal in *Stylophorum*, *Glaucium* Mill., and *Macleaya* R. Br.

The Papaveroideae,[3] represented with us by *Argemone* and at least three introduced species of *Papaver*, tend to have multicellular-multiseriate hairs, 2- or 3-merous perianths, 3-colpate [or several-aperturate] pollen, and usually more than 3-valved gynoecia; the median carpellary traces tend to be absent and are replaced, in *Papaver* and some other genera, by pseudomedian traces originating from the placental bundles; dehiscence of the valves is basipetal, and the seeds usually lack arils.

The Eschscholzioideae Ernst,[4] occasionally represented in our area by *Eschscholzia californica*, are glabrous or have unicellular hairs, usually 2-merous perianths, polycolpate pollen, and 2-valved, conspicuously ribbed gynoecia with well-developed median carpellary traces; the dehiscence of the valves is acropetal and violent; the seeds usually lack arils.

The Platystemonoideae Ernst,[5] vernal herbs of the western United States, have multiseriate hairs, 3-merous perianths, 3-colpate pollen, 3- or several-carpellate gynoecia with median carpellary traces, and discrete stigmas; the fruits open by splitting through the placentae without the formation of valves, and the seeds lack arils.

The family is rich in alkaloids, some of them important narcotics, with both medicinal and poisonous properties claimed. The alkaloid protopine, originally thought common and unique to both Papaveraceae and Fumariaceae, has been identified in the Berberidaceae; berberine, having the same empirical formula, is reported for Papaveraceae and six other families (see Willaman & Schubert). The acrid sap, usually colored and

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[3] **Papaveroideae,** subfam. nov. Papaveraceae pilis multicellulari-multiseriatis; perianthio di- vel trimero (aliquando polypetalo); gynoecio triplacentato vel placentis valvisque numerosioribus; vena carpellare mediana plerumque deest, saepe vena pseudomediana de fasce placentale substituta; fructu basipetaliter dehiscente; in *Arctomecone humile* seminibus arillatis; polline tricolpato vel pluri-aperturato. Herbae annuae vel perennes (raro sublignosae), praecipue in hemispherio septentrionale. Typus genericus subfamiliae: *Papaver* L. Genera alia: *Arctomecon* Torr. & Frém., *Argemone* L., *Canbya* Parry, *Meconopsis* Vig. (*Cathcartia* Hook. f.), *Roemeria* Medic., *Romneya* Harvey, *Stylomecon* G. Tayl.

[4] **Eschscholzioideae,** subfam. nov. Papaveraceae plerumque glabrae, vel pilis unicellularibus et papillatis; perianthio trimero vel plerumque dimero (in *Eschscholzia* synsepalo); gynoecio biplacentato et bivalvato, longitudinaliter conspicue nervato; vena carpellare mediana bene explicata; valvis acropetaliter violenterque dehiscentibus; in *Dendromecone* seminibus arillatis; polline polycolpato. Herbae annuae vel perennes breve victi, vel lignosae, Civitatium Consociatorum occidentalium et Mexiconis septentrionalis orientalisque. Typus genericus subfamiliae: *Eschscholzia* Cham. Genera alia: *Dendromecon* Benth., *Hunnemannia* Sweet.

[5] **Platystemonoideae,** subfam. nov. Papaveraceae pilis multicellulari-multiseriatis; foliis angustis et integris, saepe verticillatis; perianthio trimero; gynoecio tri- vel pluri-placentato, vena carpellare mediana aliquando tarde explicata; fructu semi-apocarpico, carpellis partim vel in toto divisis per placentis sine formatione valvarum; seminibus exarillatis; polline tricolpato. Herbae vernales Californiae, etiam Oregonis et Washingtonis. Typus genericus subfamiliae: *Platystemon* Benth. Genera alia: *Hesperomecon* Greene et *Meconella* Nutt. ex Torr. & Gray.

darkening after exposure, apparently contained in articulated tubes or nonarticulated sacs, is an important characteristic of the family.

The interpretation of the gynoecial structure has been hotly contested by morphologists, some concluding, for example, that the 2-valved fruits are the equivalent of four carpels arranged in two series (see Bancroft), while Arber favored the classical 2-carpel interpretation. The latter view, both simple and appealing, is applicable with equal success to all members of the Papaveraceae and the Fumariaceae. The 2-valved fruits in Papaveraceae seem less specialized in some respects than the multivalved fruits.

It seems generally agreed that the Papaveraceae are to be placed near the Ranales, on the one hand, and near Fumariaceae, Cruciferae, and Capparaceae, on the other. Papaveraceae and Fumariaceae have 2-seriate corollas of twice as many petals as sepals, while the corollas of Cruciferae and Capparaceae are ± uniseriate and the petals as many as, and alternate with, the sepals. The insertion of the perianth segments is fundamentally similar in Fumariaceae and Papaveraceae, but the patterns of the traces to the perianths are ± different. The sepals of Papaveraceae inclose the buds until anthesis, while those of Fumariaceae being mere scales, sometimes without traces, do not.

Chromosome numbers are reported for many species ($2n = 12, 14, 16, 18, 20, 22, 24, 28$, ca. $32, 34, 36, 38, 40, 42, 44, 56$, ca. $58, 70, 80, 84$, ca. 112). Gametic numbers of 6, 7, or multiples thereof are ± common, while 8–11, 16, and 19 are uncommon and usually from rather exceptional taxa in the family. Species small in habit and usually annual tend to have low chromosome numbers, while those large in habit, among them the woody members of the family, tend to have higher numbers.

Economically the family is important as the source of showy garden plants; edible poppy seed, poppy-seed oil, and opium and its derived alkaloids are obtained from *Papaver somniferum*.

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KEY TO THE GENERA OF PAPAVERACEAE

General characters: *plants herbaceous, sometimes rhizomatous, with acrid, usually colored sap; leaves rosulate or usually alternate (rarely opposite); inflorescence terminal and cymose [rarely paniculiform]; flowers solitary or clustered, subtended by a leaf or bract, bisexual, hypogynous (or rarely perigynous), essentially regular; perianth cyclic, 2- or 3-merous; sepals inclosing the buds until anthesis, then caducous; petals twice as many as sepals and 2-seriate (occasionally polypetalous) [rarely apetalous]; stamens many; gynoecium 1-locular with 2 or more parietal placentae; fruit dehiscent by 2 or more valves.*

A. Inflorescence scapose or cymose, flowers solitary or several and clustered; petals 4–6 or more.
  B. Gynoecium with 2 placentae and valves.
    C. Leaf blades palmately veined and lobed, glabrous; flowers solitary on scapes; dehiscence of valves acropetal; seeds arillate; low perennial from thick rhizome. .... 1. *Sanguinaria.*
    C. Leaf blades pinnately veined, lobed or dissected.
      D. Flowers hypogynous, aposepalous; leaves pubescent, broadly pinnately dissected.
        E. Inflorescence subumbellate, flowers subtended by small, narrow bracts; dehiscence of valves acropetal; seeds arillate. .... 3. *Chelidonium.*
        E. Inflorescence an expanding cyme, flowers subtended by broad bracts; locule occluded, dehiscence of valves basipetal; seeds nonarillate; fruit linear, becoming 10 cm. or more long; foliage gray. .... [*Glaucium.*]
      D. Flowers perigynous, synsepalous; leaves pinnately finely dissected,

glabrous (or hairs unicellular); fruits longitudinally ribbed, dehiscence acropetal. . . . . 4. *Eschscholzia.*

B. Gynoecium with 3 or more placentae and valves; dehiscence basipetal.

  F. Flowers on ± weak pedicels subtended by small bracts and 2 or 3 ± opposite leaves on a naked shoot; hairs soft, multicellular-uniseriate; fruits nodding, dehiscence ± complete; seeds arillate; herbaceous perennial. . . . . 2. *Stylophorum.*

  F. Flowers on rigid pedicels subtended by leaves or foliaceous bracts on leafy shoots; hairs multicellular-multiseriate; fruits erect, dehiscence incomplete; seeds nonarillate; annuals.

    G. Flowers on short pedicels; stigmas undulate, style short; leaves harshly prickly. . . . . 5. *Argemone.*

    G. Flowers on long pedicels; stigmas appearing radiate and embedded in a cartilaginous disc, style absent; leaves not prickly. 6. *Papaver.*

A. Inflorescence paniculiform, flowers numerous, apetalous; fruits 2-valved, flattened, nodding, dehiscence basipetal; tall herbaceous perennials with broad, long-petiolate leaves. . . . . [*Macleaya.*]

Subfam. CHELIDONIOIDEAE Ernst

1. **Sanguinaria** Linnaeus, Sp. Pl. 1: 505. 1753; Gen. Pl. ed. 5. 223. 1754.

Low, glabrous, perennial herb with red-orange sap, from a thick rhizome. Leaves few, with broad, basically reniform-sagittate, palmately veined and variously lobed blades, long-petiolate, subtended by 2–6 ovate to spatulate bracts. Flowers solitary on naked scapes (or very rarely 2 or 3, each subtended by a bract); scape at first enfolded by a leaf. Sepals 2, thin, ± notched apically. Corolla often appearing quadrate, 2 (or more)-seriate, with 8 (rarely 6–12), narrow, white or pale-pink, sometimes irregularly inserted petals. Stamens many; anthers oblong; pollen polyporate with 9–16 apertures. Stigma 2-lobed; style ± definite; placentae 2. Fruit broadly fusiform, 2-valved; dehiscence ± acropetal, usually incomplete apically. Seeds few to many, black or reddish-orange with a conspicuous aril along the upper surface. Seedling cotyledons hypogeal, oblong, short-petiolate. TYPE SPECIES: *S. canadensis* L. (Name from Latin, *sanguinarius*, bleeding, from the color of the sap.) — BLOODROOT, PUCCOON.

A monotypic genus of eastern North America. *Sanguinaria canadensis,* $2n = 18$,[6] with autumnal meiosis of the pollen mother cells, is among the earliest vernal herbs of deciduous woodlands, often occurring on limestone or calcareous soils, from Texas to northern Florida north to Nova Scotia and Manitoba. The leaf shape is variable; the seeds are reported to be attractive to ants.

The closest affinity is with the monotypic *Eomecon* Hance, of eastern Asia, which shares with *Sanguinaria* a preference for the forest habitat,

[6] Original determination by the author from squash preparations of microsporocytes from plants cultivated in the Beal-Garfield Botanic Garden, Michigan State University, East Lansing, Michigan (*Gillett 1264*, collected 1 November 1961); nine pairs of chromosomes were observed in several cells.

palmately veined, long-petiolate leaves with broad blades, white petals, 2-valved, fusiform fruits, arillate seeds, and polyporate pollen; but the leaves of *Eomecon* are cordate and sparsely pubescent, the calyx is synsepalous, and the inflorescence is a branched scape with each of the several flowers pedicellate and subtended by a small bract.

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2. **Stylophorum** Nuttall, Gen. N. Am. Pl. 2: 7. 1818.

Low, pubescent, perennial herbs with yellow to orange sap, developing a stout rhizome; hairs multicellular, terminally uniseriate. Leaves rosulate, petiolate, deeply 5–7-pinnatifid, pale beneath. Inflorescence umbelliform, few flowered, bracteate, and subtended by 2 or 3 ± opposite leaves terminating an elongated naked shoot. Sepals 2, attenuate, apically involute and reflexed, the upper left margin lobed. Petals 4, 2-seriate, yellow. Stamens many; filaments narrow, often constricted below the oblong anthers; pollen usually with several ± obscure apertures. Stigma truncate with 3 or 4 shallow lobes; style conspicuous; placentae 3 or 4 [or placentae 2, stigma deeply 2-lobed, and style short]. Fruits ellipsoid, usually 4-valved [or ± linear and 2-valved], pubescent and nodding; dehiscence basipetal and ± complete. Seeds few to many, with a conspicuous aril along the upper surface. LECTOTYPE SPECIES: *S. diphyllum* (Michx.) Nutt.; see Britton & Brown, Illus. Fl. No. U. S. ed. 2. 2: 140. 1913. (Name from Greek, *stylos*, style, and *phoros*, bearing, "from the distinct and conspicuous style which distinguishes this plant from all the rest of the Papaveraceae," a distinction no longer true.)

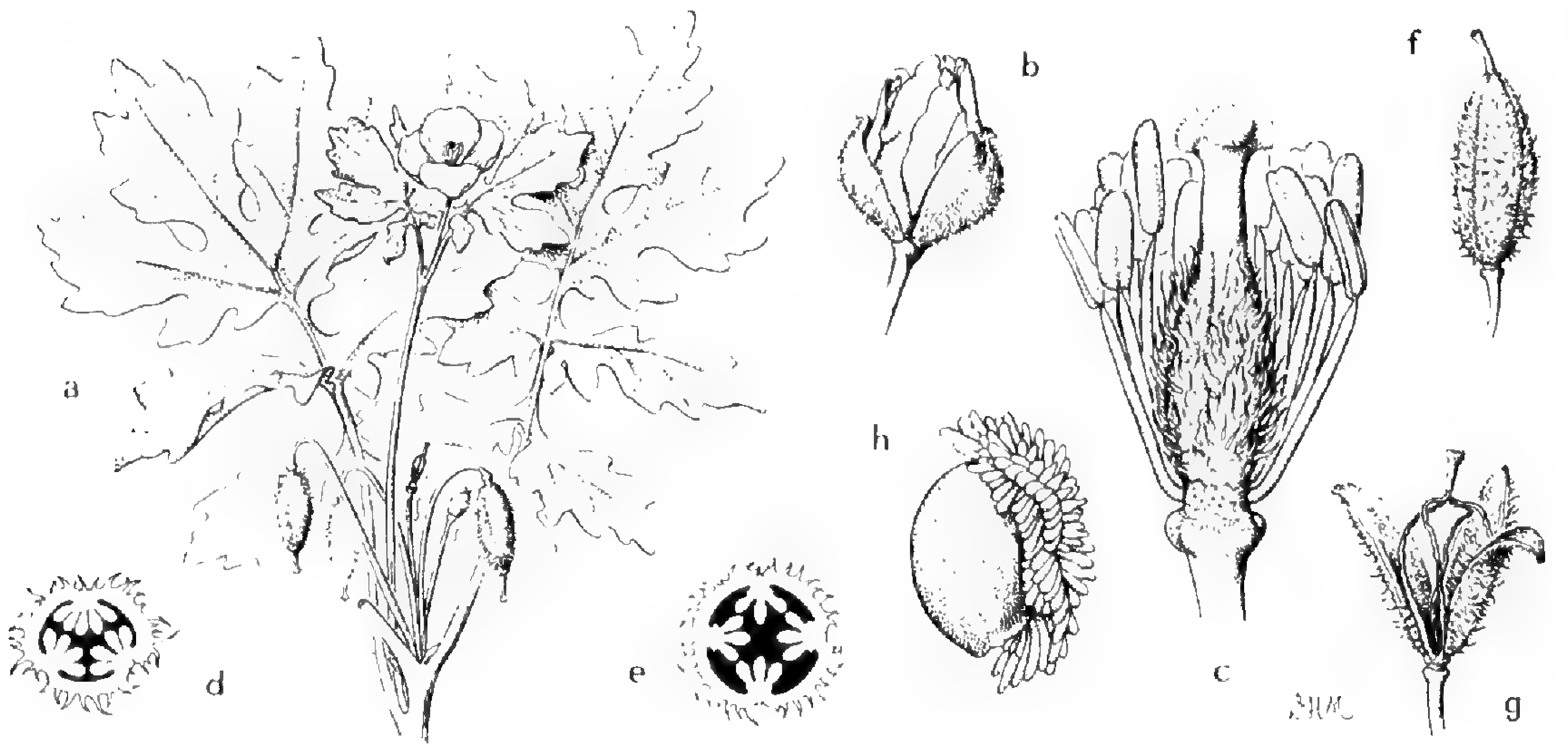

FIG. 1. **Stylophorum.** a–h, *S. diphyllum*: a, flowering and fruiting shoot from a very vigorous plant, × ¼; b, flower bud, × 1; c, androecium and gynoecium at anthesis, perianth and some stamens removed, × 3; d, e, three- and four-carpellate ovaries, in cross section, diagrammatic, × 4; f, mature fruit, × ½; g, four-valved fruit after dehiscence, one valve removed, × ½; h, arillate seed, the micropyle below, × 7.

A genus of two or three species of eastern North America and eastern Asia. *Stylophorum diphyllum*, celandine poppy, wood poppy, mock poppy, or yellow poppy, $2n = 20$,[7] occurs in rich woods and on bluffs, sometimes on calcareous soil, from northern Arkansas and Tennessee to Pennsylvania and Wisconsin. The degree of dissection of the leaves is variable. Our species, described by Michaux as a species of *Chelidonium* and reunited with *Chelidonium* by Prain (1895), is remarkably similar in the vegetative

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[7] Original determinations by the author from squash preparations of microsporocytes from a plant cultivated at Stanford University, California (grown from seeds from the Royal Botanical Garden, Uppsala, Sweden), and from a plant cultivated at Waverley, Massachusetts (*Ernst 800* [GH]); twenty chromosomes were observed in the former and ten pairs were observed in several cells of the latter.

stage to the Old World *C. majus*. *Stylophorum*, with characteristic compact inflorescences usually subtended by two ± opposite leaves on a naked shoot, pubescent fruits with basipetal dehiscence, and pollen with several ± obscure apertures, contrasts markedly with *Chelidonium majus*, in which the subumbellate inflorescences arise from branched, leafy stems, the dehiscence of the glabrous fruits is ± acropetal, and the pollen is 3-colpate. The closest affinities of *S. diphyllum*, characterized by ellipsoidal, usually 4-valved fruits and ± rounded divisions of the leaves, is with *S. lasiocarpum* (Oliver) Fedde (described by Oliver as a species of *Chelidonium*) which has elongated, almost linear, 2-valved fruits, and ± pointed divisions of the leaves.

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3. **Chelidonium** Linnaeus, Sp. Pl. 1: 505. 1753; Gen. Pl. ed. 5. 224. 1754.

Low, branched, pubescent, biennial or perennial herb with yellow sap, developing a stout rhizome or taproot; hairs multicellular, terminally uniseriate. Leaves rosulate and cauline, ± petiolate below, deeply 5–7 (or more)-pinnatifid, with rounded [or laciniate] divisions. Inflorescences subumbellate, with several flowers, bracteate, terminal and axillary, arising from branched, leafy shoots. Sepals 2, somewhat hooded, the upper

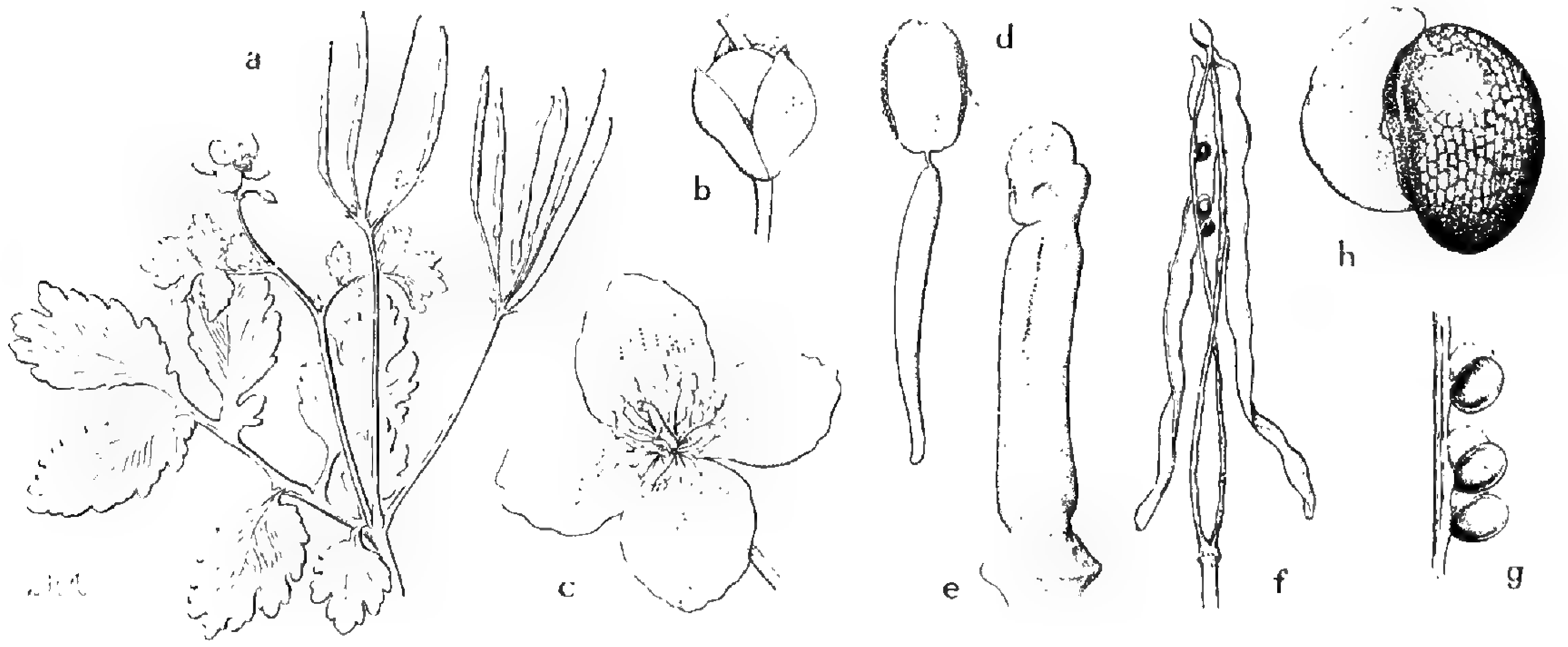

FIG. 2. **Chelidonium.** a–h, *C. majus*: a, flowering and fruiting shoot, × ½; b, opening flower bud, showing emerging stigma, × 3; c, flower, × 3; d, stamen, × 10; e, gynoecium from flower bud just before anthesis, × 10; f, two-valved fruit after dehiscence, × 2; g, portion of persistent placenta showing attachment of seeds, × 4; h, arillate seed, × 20.

left margin lobed. Corolla appearing cruciform; petals 4, 2-seriate, yellow. Stamens several to many; anthers elliptical; filaments narrow, usually constricted below the anther; pollen 3-colpate. Stigma 2-lobed; style short or indefinite; placentae 2. Fruit narrowly oblong or linear, sometimes curved, 2-valved; dehiscence ± acropetal, usually incomplete apically. Seeds few to many, with a conspicuous aril on the upper surface. Seedling cotyledons petiolate. LECTOTYPE SPECIES: *C. majus* L; see Britton & Brown, Illus. Fl. No. U. S. ed. 2. 2: 141. 1913; typified by removal of other Linnaean species to other genera. (Name from Greek, *chelidon*, swallow, because, according to Aristotle and other scholars, the mother-swallows bathed the eyes and thereby strengthened the sight of their young with the saffron-colored sap.) — CELANDINE, SWALLOWWORT, ROCK POPPY.

An Old World genus, probably monotypic. *Chelidonium majus*, $2n = 12$, usually of damp, shady areas, roadsides, rock walls, and waste places, widely naturalized in eastern North America, occurs in northwestern North Carolina and probably elsewhere in our area. Forms with large flowers or with variously dissected or laciniate leaves are occasionally seen in collections from both Europe and Asia.

Linnaeus (1753) included two species of *Glaucium* and one of *Roemeria* Medic. in his *Chelidonium*. Later, Prain united *Stylophorum*, *Hylomecon* Maxim., and *Dicranostigma* Hook. & Thoms. with *Chelidonium*; but *Glaucium*, its generic distinction from *Dicranostigma* debatable, was not included. The vegetative stages of *Chelidonium majus* and *Stylophorum diphyllum* (*q. v.*) are similar.

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Subfam. ESCHSCHOLZIOIDEAE Ernst

4. **Eschscholzia** Chamisso in Nees, Horae Phys. Berol. 73. *pl. 15.* 1820.

Low, annual or perennial herbs with thin yellow to orange sap, sometimes developing a stout taproot; usually glabrous (or hairs 1-celled). Leaves rosulate and/or cauline, alternate or subopposite, petiolate, ± ternately finely dissected [or rarely entire]. Flowers and fruits erect on long pedicels; early flowers usually terminating short shoots, later flowers often terminal and axillary on long shoots; receptacles perigynous. Calyx synsepalous, usually attenuate. Petals usually 4, 2-seriate, yellow or orange [sometimes pinkish or white]. Stamens usually many, often adhering to base of petals; filaments thick, sometimes with a dark spot; anthers usually narrowly oblong; pollen polycolpate with 5–7 [10] slitlike [sometimes confluent] apertures. Stigmas 2 to several (the secondary stigmas over the placentae); style absent; placentae 2. Fruit columnar, constricted below the apex, conspicuously ribbed, 2-valved; dehiscence acropetal, incomplete, usually violent. Seeds many, reticulate [papillate or variously pitted]. Seedling cotyledons linear, bifurcate [but usually entire]. TYPE SPECIES: *Eschscholzia californica* Chamisso. (Named for J. F. Eschscholtz,[8] 1793–1831, zoologist of Dorpat, friend and companion of Chamisso on the Kotzebue expedition which visited California in 1816 on the *Rurick.*) — CALIFORNIA POPPY.

At least 14 species of northwestern Mexico and the western United States, concentrated in California. Perhaps half of the 123 species listed by Fedde are referable to *Eschscholzia californica*, $2n = 12$, cultivated for its attractive flowers, adventive in many parts of the world, and collected in our area at least in North and South Carolina; it is distinguished by the apparently unique bifurcated cotyledons and the fleshy receptacle rim. In nature, as in cultivation, the species is exceedingly variable.

The 2-valved, deeply ribbed fruits of *Eschscholzia*, sometimes described as polycarpellate, are most easily interpreted as the equivalent of two carpels. The longest stigmas are centered over the median carpellary traces; secondary stigmas, perhaps a peculiarity of reduction in the vasculature, often develop over the placentae. The combination of synsepaly, perigyny, and stigmatic structure suggest that *Eschscholzia* is relatively specialized.

The genus is allied most closely with the monotypic *Hunnemannia* Sweet, $2n = 56$, of eastern Mexico, in which the flowers are somewhat perigynous but aposepalous. Synsepaly is also characteristic of *Eomecon*,

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[8] The name of the man is usually given thus, but the generic name was rendered *Eschscholzia* in the original description (misspelt *Escholzia* on the plate) and in the later reprint (Linnaea **1**: 553–555. 1826), seemingly confirming the intended orthography.

of eastern China, but the affinities of the latter are with *Sanguinaria* and other Chelidonioideae.

Chromosome numbers of $2n = 12, 14, 22, 24, 34$, and 36 have been reported.

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Subfam. PAPAVEROIDEAE

5. **Argemone** Linnaeus, Sp. Pl. 1: 508. 1753; Gen. Pl. ed. 5. 225. 1754.

Stout, prickly, annual [or biennial] herbs [rarely shrubs] with yellow [or white to reddish-orange] sap; prickles and hairs multicellular-multiseriate, harsh, smooth and polished [or rough and/or branched]. Leaves rosulate and cauline, pinnately veined and lobed, sessile, clasping, or somewhat decurrent, sometimes narrowed into a petiole-like base. Inflorescence an expanding cyme, few to several flowered and bracteate. Sepals 2 or 3, ± hooded, usually attenuated into a sharp prickle. Corolla 2-seriate, with twice as many petals as sepals (occasionally polypetalous), yellow or white [bronze or lavender]. Stamens numerous; filaments narrow; anthers narrowly oblong, apically revolute after anthesis; pollen 3-colpate. Stigmatic region deeply undulate, the lobes 3 – several (margins of adjacent stigmas forming conspicuous lobes over the placentae); style short or obscure; placentae as many as stigmatic lobes. Fruit usually more than 3-valved; dehiscence basipetal and incomplete. Seeds numerous, reticulate. Seedling cotyledons linear-lanceolate. LECTOTYPE SPECIES: *A. mexicana* L.; see Britton & Brown, Illus. Fl. No. U. S. ed. 2. 2: 138. 1913. (Name of an herb mentioned by Pliny; perhaps "from the Greek, *argema*, the cataract of the eye for which the juice of a poppy-like plant of the same name was a supposed remedy" [Ownbey].) — PRICKLY POPPY.

About 28 species (Ownbey) lacking clear subgeneric groupings, often of disturbed habitats in the New World; one presumed endemic in the Hawaiian Islands. *Argemone mexicana*, devil's fig, $2n = 28$, with yellow petals and leaves usually blotched with white along the main veins, occasional (mostly in the Coastal Plain) in our area, is a cosmopolitan weed of warmer climates, and may be native to the West Indies, Central America, and Florida (Ownbey). Forma *leiocarpa* (Greene) G. B. Ownbey, of southwestern peninsular Florida, where perhaps introduced from Key West (Ownbey), is prickly only on the margins of the leaves. It is infrequently collected, and the chromosome number is unreported. *Argemone albiflora* Hornem. (*A. alba* of authors), with white petals, occasionally polypetalous, is reported from Florida to Texas and discontinuously northward to Illinois and Connecticut. Subspecies *albiflora*, $2n = 28$, with oblong to oblong-elliptic capsules and uniform, evenly spaced spines, primarily of the Coastal Plain, is perhaps native only to northern Florida and introduced northward; subsp. *texana* G. B. Ownbey, $2n = 28$, with narrowly elliptical capsules and unequal spines and prickles, is native only to eastern Texas and is introduced in Arkansas. The two subspecies are completely interfertile or nearly so (Ownbey).

The degree of prickliness, often inconsistent and difficult to describe, is apparently of diagnostic importance. Interspecific hybrids, possible between many species, can, if the original parents were of the same polyploid level, be carried beyond the first generation, but show a decline in vigor and fertility. Sterility barriers probably have not played the primary role in speciation (Ownbey). Chromosome numbers of $2n = 28$, 56, 84, and ca. 112 have been reported.

The characteristic hooded sepals terminated by a harsh prickle are rarely found outside of *Argemone*. As in *Arctomecon* Torr. & Frém., *Papaver, Roemeria, Stylomecon* G. Tayl., some species of *Meconopsis* Vig., and usually in *Romneya* Harv., the median carpellary traces are lacking, the fruits are at least three-valved, and the continuous margins of adjacent stigmas become conspicuous over the placentae.

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6. **Papaver** Linnaeus, Sp. Pl. 1: 506. 1753; Gen. Pl. ed. 5. 224. 1754.

Annual [biennial or perennial] herbs, usually with white sap and pubescent with multicellular-multiseriate [rarely prickly] hairs. Leaves rosulate and/or cauline, pinnately veined and lobed or dissected, usually without a distinct petiole. Buds nodding [or erect]; flowers on long peduncles subtended by a leaf or bract [or rarely sessile between a pair of foliaceous bracts on a scape, or in a cymose spike]. Sepals 2 or 3, somewhat hooded. Corolla 2-seriate, with twice as many petals as sepals (occasionally polypetalous) white to purple or scarlet [or yellow], often with a dark spot toward the base. Stamens many; filaments filiform, often constricted below the elliptical or oblong anthers; pollen often 3-colpate [or seldom with several apertures]. Stigmatic furrows, usually more than 3, appearing radiate, embedded in a flattened or ± conical, cartilaginous, disclike structure [or disc rarely absent]; placentae as many as stigmas. Fruit globose to clavate, truncate, usually more than 3-valved; dehiscence basipetal and incomplete. Seeds numerous, somewhat reniform or obovoid-falcate, usually reticulate. Seedling cotyledons ± linear. LECTOTYPE SPECIES: *P. somniferum* L.; see Britton & Brown, Illus. Fl. No. U. S. ed. 2. 2: 136. 1913. (Name Latin, *papaver*, poppy, apparently derived from *papa*, pap, thick milk.) — POPPY.

At least 40 species of the Northern Hemisphere, including in the New World the Arctic, the Rocky Mountains, and western California; also reported locally in South Africa and Australia. Representatives of three of nine sections recognized by Fedde, adventive from Europe or garden escapes, are to be expected in our area. These include *Papaver Rhoeas* L. (§ Orthorhoeades Fedde), $2n = 14$, or its cultivated derivative, "Shirley Poppy," with deeply dissected, pubescent leaves and smooth fruits about as wide as long; *P. dubium* L., $2n = 42$, resembling *P. Rhoeas*, with fruits about twice as long as wide; and *P. somniferum* (§ Papaver, § *Mecones* Bernh.), opium poppy, $2n = 22$, with smooth, globose fruits and usually glabrous, broad, clasping, shallowly dissected or incised leaves. *Papaver Argemone* L. (§ Argemonorhoeades Fedde), $2n = 42$, with clavate, sparsely pubescent fruits, has been collected immediately to the north of our area.

Several weedy species of *Papaver* often associated with the cultivation of cereal crops may inhabit the same or nearby habitats in Britain and have common insect visitors, but interspecific hybrids are rarely found. The relatively self-incompatible diploid, *P. Rhoeas*, and the relatively self-compatible hexaploid, *P. dubium*, can be hybridized experimentally in either direction, the hybrids showing anomalous variation and reduced fertility (McNaughton & Harper); bees sometimes discriminate between these species.

The absence of a style and the more than three stigmatic furrows (i.e., the margins of adjacent deltoid stigmas) usually embedded in a disc characterize the genus. In most species of *Papaver*, as in those of *Roemeria*, in *Meconopsis cambrica* (L.) Vig., and in the monotypic *Stylomecon*, the median carpellary traces are absent and replaced by pseudomedian traces originating from the placental bundles; the vascular bundles of the pedicels of some species are ± scattered.

Chromosome numbers of $2n = 12, 14, 15, 21, 22, 28, 40, 42, 44. 56, 70$, and 84 have been reported.

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FUMARIACEAE A. P. de Candolle,
Reg. Veg. Syst. Nat. **2**: 105. 1821, nom. cons.

(FUMITORY FAMILY)

Annual, biennial, or perennial, sometimes scandent herbs from taproots, bulblets, or rhizomes [or tubers]; plants usually glaucous, rarely pubescent with unicellular [or multicellular] hairs. Leaves rosulate and/or cauline, usually alternate, reduced upward, exstipulate, petiolate, or sessile, pinnately or ternately veined, lobed, or dissected. Inflorescences terminal and/or axillary, determinate or indeterminate, cymose or racemose, scapose or branched, few [rarely 1] to many flowered; buds erect or nodding, bracteate. Flowers erect to nodding, bisexual, hypogynous, usually ± closed by the apical connation of the inner petals (sometimes cleistogamous), bilaterally symmetrical or irregular; perianth cyclic, 3-seriate, 2-merous. Sepals 2, bractlike, often ± peltate, with ± similar margins, not inclosing the buds at anthesis [seldom persistent]. Petals 4, in 2 series, imbricate (very rarely sympetalous); outer petals alternate with the sepals, 1 or both [rarely neither] ± saccate basally; inner petals opposite the sepals, characteristically connate over the stigmas [or seldom free]. Stamens 6, diadelphous, the phalanges alternate with the sepals, sometimes spurred basally and/or nectariferous; anthers dimorphic, 2- and 1-locular at anthesis, applied to the stigmatic region [or stamens 4, free, anthers 2-locular]; pollen 3-colpate or several-rugate [rarely 2-colpate or polyporate]. Gynoecium syncarpous, of 2 carpels; style narrow, persistent [or articulated and deciduous], usually flattened apically in the nonplacental plane into a 2- to several-lobed structure bearing the stigmatic surface [or seldom attenuated into 2 simple stigmas]; ovary 1-locular [rarely occluded]; placentae parietal, ovules few to many, 2-integumented, usually campylotropous, lenticular and ± reniform [rarely anatropous and obovoid]. Fruit 2-valved [seldom inflated], the inner wall of valves often transversely ribbed; dehiscence usually incomplete, acropetal or basipetal, the placentae persistent [or fruit indehiscent, or very rarely dimorphic]. Seeds 1–many, free [or fruit rarely fragmenting into 1-seeded joints], ± flattened, reniform or orbicular [rarely obovoid], often lustrous, arillate, and attractive to ants; endosperm present; embryo small, straight or somewhat curved. Seedling cotyledons 2 [1], often petiolate (seldom ± linear-lanceolate). (Papaveraceae subfam. Fumarioideae Endl. Gen. Pl. 858. 1839, "Fumariaceae"; including *Hypecoum* L. and *Pteridophyllum* Sieb. & Zucc.) TYPE GENUS: *Fumaria* L.

About 19 genera and perhaps 425 species, primarily of the Northern Hemisphere, concentrated in Asia where the species are poorly known, occurring also in Africa. The family has not been monographed in detail. Of the three subfamilies recognized on the basis of floral structure, the monotypic Pteridophylloideae Murbeck (restricted to Japan), and the monogeneric Hypecoideae Prantl & Kündig (Eurasian), are distinguished by free petals and four free stamens. The genera of subfam. Fumarioideae, characterized by diadelphous stamens applied to the stigmatic mechanism and the apical connation of the inner petals, fall into two tribes. The Corydaleae Reichenb., of worldwide distribution in the Northern Hemisphere, represented in our area by indigenous species of *Dicentra*, *Adlumia*, and *Corydalis* have persistent, nonarticulated styles; the more specialized Fumarieae, of limited Old World distribution, represented in our area by at least one species of *Fumaria*, have articulated, deciduous styles. The character of the styles seems more important than either the dehiscence or indehiscence of the fruits or the number of seeds in the fruits, the criteria by which the two tribes are usually separated. Some of the Old World species now referred to *Corydalis* have deciduous styles, suggesting that their taxonomic status should be reconsidered.

The Fumariaceae, with some medicinal and poisonous properties claimed, appear to be as rich in alkaloids as the Papaveraceae, sharing about ten per cent of their approximately 140 known alkaloids (Willaman & Schubert). Of their common alkaloids, eight are reported only for these two families, two (with identical empirical formulas) are found in six other families, and three (with identical empirical formulas) are found in four other families. The sap of the Fumariaceae, somewhat acrid, watery, and apparently colorless, is contained in nonarticulated sacs; some authors consider the family devoid of laticifers.

The Fumariaceae and Papaveraceae share bracteate inflorescences, two-seriate corollas of twice as many petals as sepals, and similar two-valved fruits, the latter most easily understood as the equivalent of two carpels; however, the patterns of the vascular traces to the perianths and the nature of the sepals, stamens, and seeds usually are different. Hutchinson has suggested that the Fumariaceae, nearly as closely allied with some Berberidaceae as Papaveraceae, probably have not arisen directly from the ancestors of the present Papaveraceae. The least specialized Fumariaceae do not closely resemble Berberidaceae, however.

Chromosome numbers reported for Fumariaceae include $2n = 12$, 14, 16, 18, 20, 24, 28, 32, 48, 56, 64, and ca. 150; somatic numbers of 18 and ca. 150 are exceptional. Gametic numbers of 8 and multiples thereof are common, while 6 and 7, or multiples thereof, are rare or have not been verified in recent years (cf. Papaveraceae); only one report of $2n = 28$ is verified (Ryberg).

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KEY TO THE GENERA OF FUMARIACEAE

General characters: *plants herbaceous, with watery sap, sometimes rhizomatous or with bublets (rarely scandent); leaves rosulate or alternate, glabrous. Inflorescence terminal or axillary, bracteate, racemose or cymose; flowers bisexual, hypogynous, bilaterally symmetrical or irregular; perianth cyclic, 2-merous; sepals not inclosing the buds at anthesis; petals 4, two-seriate (very* *rarely sympetalous), 1 or both outer petals ± saccate basally, the inner petals connate apically; stamens 6, diadelphous, 1 or both median stamens basally spurred and/or nectariferous; anthers applied to the lobed and flattened stigmatic mechanism; gynoecium 1-locular with 2 parietal placentae; fruit 2-valved [rarely indehiscent].*

A. Flowers bilaterally symmetrical, nodding, usually bracteolate and bracteate; petals usually ± free (or sympetalous); outer petals identical; inner petals symmetrical.
  B. Plants acaulescent or rhizomatous; petals ± free basally; stamen filaments usually ± partially free basally; valves of fruit dehiscent basipetally, only the median vein persistent apically. .... 1. *Dicentra.*
  B. Plants caulescent and scandent; petals united through half their length, spongy and persistent; stamen filaments united basally and adnate to corolla; valves of fruit dehiscent acropetally, free at the base. 2. *Adlumia.*
A. Flowers irregular, variously ascending or descending, bracteate; petals ± free at base (or adnate to the stamens); outer petals dissimilar, the upper petal conspicuously saccate, the lower sometimes gibbous; inner petals similar but asymmetrical.
  C. Style persistent; fruit elongate, several seeded, dehiscent ± acropetally; annuals or biennials. .... 3. *Corydalis.*
  C. Style articulated and dehiscent; fruit globose, hard, 1–seeded, indehiscent; adventive annuals. .... 4. *Fumaria.*

Tribe CORYDALEAE Reichenb.

1. **Dicentra** Bernhardi, Linnaea 8: 457, 468. 1833. nom. cons.

Perennial [sometimes scandent] herbs from rhizomes, bulblets [tubers or taproots], glabrous [or very rarely with a few multicellular-multiseriate hairs] and occasionally glaucous. Leaves few to many, rosulate [or cauline and alternate], pinnately or ternately dissected [petioles very rarely subterranean and absorptive]. Inflorescence terminal, simple or branched [sometimes axillary or leaf-opposed], determinate [or rarely indeterminate], cymose or racemose [very rarely with solitary, 1-flowered scapes]. Flowers usually nodding [or seldom erect], bilaterally symmetrical, usually bracteolate as well as bracteate. Sepals ovate to lanceolate, nonpeltate. Outer petals identical, ± saccate basally and reflexed apically; inner petals symmetrical and identical, ± spatulate, externally crested and apically connate. Stamens in 2 similar phalanges with filaments fused or usually partly free basally; median stamens spurred basally and/or nectariferous; pollen 3-colpate or 12-rugate. Style narrow, persistent, flattened apically into a lobed stigmatic structure. Fruit nodding [or seldom erect], 2-valved, elongate, dehiscence basipetal, incomplete basally, the median carpellary vein persistent apically [or dehiscence acropetal, free at the base and incomplete apically]. Seeds few to many, reniform-suborbicular, flattened, usually lustrous and ± arillate. (*Bikukulla* Adans. [= *Bicuculla* of authors], nom. rejic.) TYPE SPECIES: *D. Cucullaria* (L.) Bernh. (Name from Greek, *dis*, twice, and *kentron*, a point.) — BLEEDING HEART.

About 19 species and three subgenera distributed in North America and eastern Asia. Subgenus DACTYLICAPNOS (Wall.) K. R. Stern, is scandent and confined to northern India and adjacent China; CHRYSOCAPNOS Engelm. occurs in California and eastern Asia; DICENTRA, with one species in eastern Asia and several in North America, is represented in our area by three species. *Dicentra Cucullaria,* Dutchman's breeches, $2n = 32$, occurring from South Carolina to Arkansas, north to Minnesota and Nova Scotia, and discontinuously in the Pacific Northwest, is distinguished by white to pink, asymmetrical bulblets and basally fused stamen filaments with the nectariferous spur directed diagonally; *D. canadensis* (Goldie) Walp., squirrel-corn or turkey-corn, $2n =$ ca. 64, flowering somewhat earlier and sympatric almost throughout the eastern distribution of the above, has yellow, pea-shaped bulblets and filaments partially free basally with the short nectariferous spur oriented vertically. These two, seemingly most closely related to each other, have similar scapose, racemose inflorescences terminating blindly in a linear lobe, an aborted bud, or a flower. A strictly racemose inflorescence, also occurs in *D. spectabilis* (L.) Lem., $2n = 16$, of Asia. *Dicentra eximia* (Ker) Torr., bleeding heart, $2n = 16$, with cymose, usually branched inflorescences, strongly allied with *D. formosa* (Haw.) Walp., $2n =$?24, of the Pacific States, is distributed from eastern Tennessee and western North Carolina and northward to New Jersey and Pennsylvania.

The flowers of *Dicentra,* as in most Fumariaceae, are somewhat tubular and closed by the apical connation of the inner petals over the anthers and stigmas. Although abundant pollen is shed directly on the stigmas and adheres to them, the germinating pollen tubes barely penetrate the stigmatic tissue in a number of species (Stern, 1961). In some, ovaries abort if protected from the visits of insects; bees sometimes gain direct access to the nectaries by biting through the base of the corolla.

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2. **Adlumia** Rafinesque ex A. P. de Candolle, Reg. Veg. Syst. Nat. **2**: 111. 1821, nom. cons.[9]

Delicate, taprooted biennial vine usually with a single, indeterminate leader. Leaves pinnately divided, at first rosulate, then cauline and alternate, the petiolules ± opposite, distally tendriliform. Inflorescences many, 1 or 2 in a leaf axil, cymose, often branched, usually with many nodding, bracteate flowers. Sepals somewhat peltate. Corolla sympetalous, white to purplish, persistent and spongy, bilaterally symmetrical, basally ± saccate alternate with the sepals, apically with 2 reflexed outer lobes, and 2 connate inner lobes. Stamens 6, diadelphous, but basally ± monadelphous and united with the corolla; median stamens nectariferous basally but not spurred; pollen 3-colpate or 6-rugate [9–12-rugate]. Style narrow and persistent, terminating in a flattened, ± 2-lobed stigmatic region. Fruits ± linear, 2-valved, dehiscence acropetal, the valves free basally. Seeds few, flattened, suborbicular, lustrous, nonarillate. Seedling cotyledons 2, petiolate. TYPE SPECIES: *A. cirrhosa* Raf. ex DC. = *A. fungosa* (Ait.) Greene ex BSP. (Named for John Adlum, 1759–1836, soldier of the Revolution, major under the elder Adams, later brigadier general of the Pennsylvania Militia; enthusiastic advocate of American viticulture.)

A genus, probably monotypic, of eastern North America and Korea. *Adlumia fungosa,* Allegheny vine, mountain fringe, or climbing fumitory, $2n = 32$, distributed from adjacent North Carolina and Tennessee to Ontario, Quebec, and New England, was reported from Korea by Komarov (1904, p. 343), who stated that his specimens, insofar as he could determine, were identical to the American species, a conclusion substantiated by his description. Ohwi (1931, p. 387), described *A. asiatica*, but the description and plate are indistinguishable from the American plant. The name *A. Komarovii* was used by Popov (1937, posthumous).

The unique, sympetalous corolla of *Adlumia* may culminate a trend toward the tubular condition evident in the scandent species of *Dicentra* and in the analogous, long-spurred petals of some species of *Corydalis*. The affinities of *Adlumia* are with *Dicentra* subg. DACTYLICAPNOS, which also has tendrilliform leaflets, scandent growth, and acropetal dehiscence of the fruits, the valves becoming free basally. Current growth of other species of *Dicentra* is not scandent, lacks tendrilliform leaflets, and is terminated by an inflorescence; and dehiscence of the fruits is basipetal, the valves remaining attached apically only by the filamentous median carpellary vein and basally where no abscission zone forms. Stern favored the retention both of *Adlumia* (indeterminate-monopodial growth with axillary, cymose inflorescences, sympetalous corolla and nectariferous but nonspurred median stamen filaments) as a genus and of DACTYLICAPNOS (indetermi-

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[9] *Adlumia* was unnecessarily conserved over *Bicuculla* Borckh., a later homonym of *Bikukulla* Adans. which is equal to *Fumaria Cucullaria* L. and now equivalent to the type species of the conserved *Dicentra* Bernh. (See Rickett & Stafleu, Taxon **8**: 274. 1959.)

nate-sympodial growth with leaf-opposed, racemose inflorescences, apopetalous corollas, elaborately spurred and nectariferous median stamen filaments) as a subgenus of *Dicentra*.

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3. **Corydalis** Ventenat, Choix de Plantes. *pl. 19.* 1803, nom. cons.[10]

Annual, biennial [or perennial, very rarely scandent] herbs, from taproots [tubers or rhizomes], often glaucous, usually glabrous (or very rarely with 1-celled hairs). Leaves variously pinnately or ternately dissected, rosulate or cauline, alternate, petiolate toward the base. Inflorescence terminal, simple or branched, few to many flowered [or scapose], usually racemose (or very rarely cymose); flowers irregular, often ± horizontally oriented, bracteate. Sepals ovate, ± peltate. Outer petals dissimilar, the upper conspicuously saccate, the lower sometimes ± gibbous; inner petals similar but asymmetrical, connate apically. Stamen filaments fused in 2 dissimilar phalanges, the upper median stamen spurred and nectariferous; pollen 3-colpate or 6–12-rugate. Gynoecium elongate, usually upwardly curved; style persistent [or seldom articulated and deciduous], apically flattened into a lobed stigmatic structure. Fruit erect or nodding [sometimes geniculate at the receptacle], usually elongate, 2-valved, sometimes falcate, often torulose [or very rarely inflated], dehiscence ± acropetal, the valves free at the base and often transversely ribbed between the seeds. Seeds few to many, flattened, reniform or ± orbicular, lustrous, and usually arillate. Seedling cotyledons 2 [or 1], usually long-petiolate. LECTOTYPE SPECIES: *C. sempervirens* (L.) Pers. (Name from Greek, *korydos,* or *korydallis,* the crested lark of Greece, and presumably the name of a plant with a corolla spur resembling the spur of the lark.)

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[10] When first conserved, *Corydalis* was attributed to Medicus who applied the name to *Fumaria vesicaria* L., now *Cysticapnos vesicarius* (L.) Fedde. To preserve the modern concept of *Corydalis*, the authority was changed to Ventenat who stated in a footnote, while illustrating and describing only *Fumaria fungosa* Ait. (now *Adlumia fungosa* (Ait.) Greene ex BSP.), that his *Corydalis* was the same as *Capnoides* of Tournefort and Gaertner. Tournefort cited *Fumaria siliquosa sempervirens* of Cornuti, presumably now equivalent to *Corydalis sempervirens* (L.) Pers., the lectotype species. Gaertner presumably illustrated *Corydalis lutea* (L.) DC.

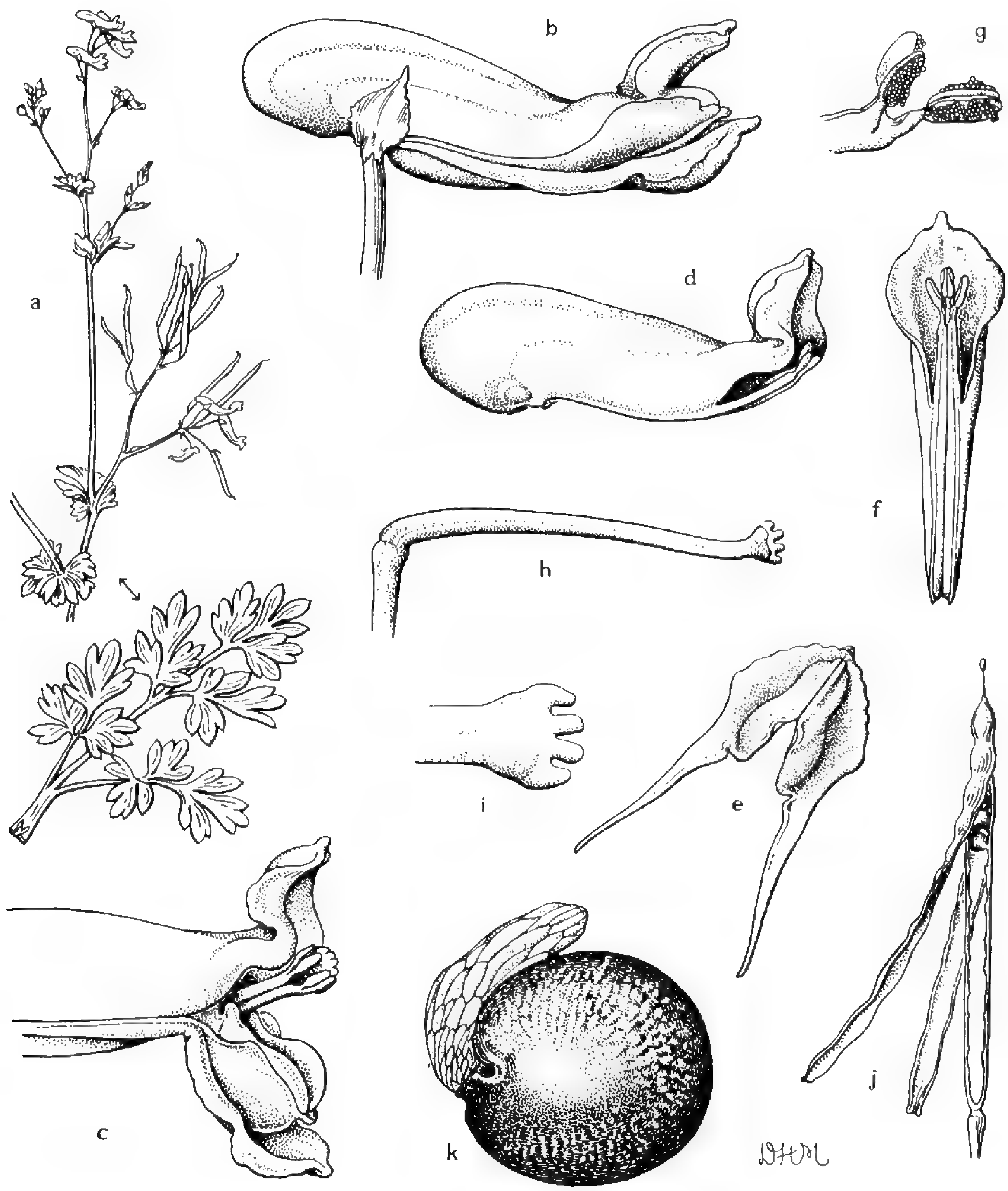

FIG. 3. **Corydalis.** a–k, *C. sempervirens*: a, flowering and fruiting shoot and basal leaf, × ½; b, flower, lateral view — note peltate sepal, × 4; c tip of flower with lower petal and two inner petals depressed to show stamens surrounding style, × 4; d, upper petal, lateral view, with upper phalange of stamens, × 4; e, two inner petals apically connate, from above, × 4; f, lower petal, from above, with lower phalange of stamens, × 4; g, anthers of lower phalange of stamens, the lower two-locular, the two upper one-locular, × 10; h, gynoecium and pedicel, lateral view, × 4; i, lobed stigmatic region, lateral view, × 10; j, fruit after dehiscence, showing persistent style, placentae, and attachment of seeds, × 1½; k, arillate seed, the micropyle at left edge below aril, × 20.

A genus of the Northern Hemisphere, probably of fewer than 300 species, concentrated in south-central Asia (where poorly known), with one species in East Africa, variously segregated without agreement into several sections and subsections.

In our area, five taxa of sect. CORYDALIS (§ *Eucorydalis* Prantl) are widely distributed (Ownbey). *Corydalis sempervirens*, $2n = 16$, pink or pale corydalis, rock fumeroot, or roke harlequin, a biennial distributed from northern Georgia to Newfoundland and central Alaska, tentatively reported from Siberia (Fl. USSR.), is distinguished by its branched, leafy shoots, pinkish flowers, and apparently unique cymose inflorescences. Four winter annuals bearing a general resemblance to *C. aurea* Willd., $2n = 16$, the latter widespread to the west and north of our area, were defined by Ownbey (1947): *C. crystallina* Engelm., with conspicuously pubescent fruits, occurring in Arkansas and the states immediately west and north; *C. micrantha* (Engelm.) Gray subsp. *micrantha*, $2n = 16$, slender fumewort, with erect fruits, occurring in northwestern Arkansas northward and westward; *C. micrantha* subsp. *australis* (Chapm.) G. B. Ownbey, intergrading with subsp. *micrantha*, usually with ± longer racemes and flowers, and longer, narrower fruits, occurring from Arkansas southeastward along the Gulf Coast, across Florida, and north along the Atlantic Coast to North Carolina; and *C. flavula* (Raf.) DC., yellow fumewort or yellow harlequin, similar to *C. micrantha* subsp. *australis*, with nodding fruits, occurring from Louisiana to Missouri eastward to North Carolina and Connecticut.

The taxon *Corydalis micrantha* subsp. *australis*, first described as *C. aurea* var. *australis* Chapm., was considered conspecific with *C. micrantha* (Engelm.) Gray (originally *C. aurea* var. *micrantha* Engelm.), and redescribed as *Capnoides Halei* Small (with part of the original material referable to *Corydalis crystallina*), later *Corydalis Halei* (Small) Fernald & Schubert.

Both *Corydalis micrantha* (including subspp. *micrantha* and *australis*) and *C. flavula* are complicated biologically by the occasional occurrence of individual, or whole inflorescences of, cleistogamous flowers, apparently sometimes correlated with certain vegetative peculiarities. Normal flowers in this instance are closed by the permanent apical connation of the inner petals, and the stamens shed pollen on the stigmatic mechanism to which they are appressed. In some species the stigmatic region can be exposed suddenly by probing along the path leading to the nectariferous spur.

Chromosome numbers of $2n = 12, 14, 22, 24, 34$, and 36 have been reported.

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Tribe FUMARIEAE

4. **Fumaria** Linnaeus, Sp. Pl. 1: 699. 1753; Gen. Pl. ed. 5. 314. 1754.

Low, glabrous, compact or diffuse herbs from taproots. Leaves rosulate and/or cauline, alternate, variously pinnately or ternately dissected [sometimes ± tendriliform]. Inflorescences many flowered, terminal or axillary, indeterminate, and racemose; flowers irregular, bracteate. Sepals small, peltate-ovate, variously dissected. Outer petals dissimilar, the upper saccate at the base; inner petals similar but asymmetrical, connate apically. Stamen filaments fused in 2 dissimilar phalanges, somewhat adnate laterally with the base of the petals; upper median stamen spurred and nectariferous; pollen polyporate with 6–12 apertures. Style narrow, ± ascending, articulated and dehiscent, apically flattened into ± 2 lobes; ovary short, ± ovate; ovules 4, ± reniform. Fruit subhemispheric, often with 2 shallow depressions apically, hard, indehiscent, filled with the single nonarillate seed. Seedling cotyledons linear-lanceolate, nonpetiolate. TYPE SPECIES: *F. officinalis* L. (Name from Latin, *fumus*, smoke, perhaps alluding to the odor of the plant.) — FUMITORY, EARTH-SMOKE, FUMEROOT, FUMEWEED, FUMEWORT.

A genus of cosmopolitan weeds, concentrated in the Mediterranean region, with many species and infraspecific taxa; represented in our area by *Fumaria officinalis*, $2n = 32$ (also ?14 and ?16), occurring from western Florida along the Coastal Plain into North Carolina. Other species, the differences appearing trivial in view of the apparent edaphic plasticity of the genus, may occur in our area. The environment readily modifies the character of the vegetative organs and, under some conditions, the frequency of cleistogamous flowers which are paler or whitish in color, reduced in size and lacking nectaries but producing fruit. Hybrids in the Old World are uncommon, isolated, and sterile (Pugsley). Chromosome numbers of $2n = 14, 28, 32$, ca. 48, 56, and 64 have been reported.

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NOTE ON DAPHNOPSIS CRASSIFOLIA (THYMELAEACEAE)

LORIN I. NEVLING, JR.

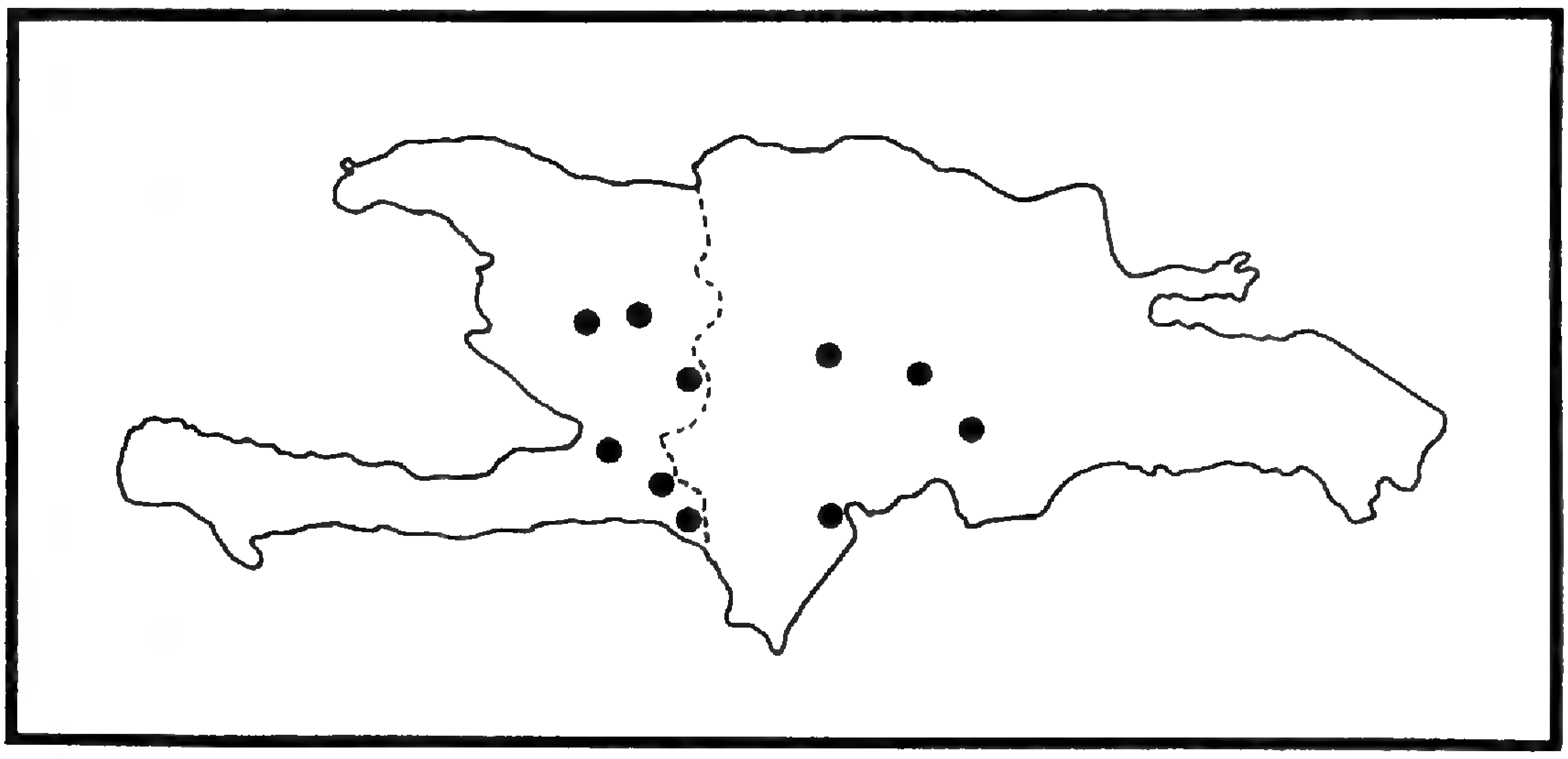
AMONG A NUMBER OF SPECIES which were poorly or incompletely known at the time of my revision of the genus *Daphnopsis* (1959) was *D. crassifolia* (Poiret) Meissner. The description of this species necessarily was sketchy and incomplete because of the availability of relatively few and fragmentary specimens. I was not able to see fruiting material, for example, although it had been described previously. Since my publication, a relatively large number of specimens referable to this species have been rediscovered and examined. On the basis of new data drawn from recently examined herbarium material, the description has been recast and completed. In addition, these collections give the first precise knowledge of the range of the species (see MAP).

Daphnopsis crassifolia (Poir.) Meissn. in DC. Prodr. **14**: 524. 1857.

Daphne crassifolia Poir. Encycl. Méthod. Bot. Suppl. **3**: 316. 1813 (TYPE: *Nectoux s.n.* [♂]!).
Daphnopsis crassifolia var. *eggersii* Krug & Urb. Bot. Jahrb. **15**: 350. 1892 (TYPE: *Eggers 2317* [♀]).
Hyptiodaphne crassifolia (Poir.) Urb. Symb. Ant. **2**: 454. 1901.
Hyptiodaphne crassifolia var. *β. eggersii* (Krug & Urb.) Urb. *ibid.* 455.

Dioecious shrubs or trees, to 4 m. tall, the young branches terete, densely ochraceous-hirsute and glabrescent, rugose. Leaves simple, approximately whorled by irregular condensation of internodes or rarely alternate on very vigorous shoots, usually 3 or 4 per whorl; leaf blades rarely narrowly elliptic to elliptic to oblanceolate to obovate or very reduced and bractlike, the expanded blades 3–6(–13.5) cm. long, 1–3.5 cm. broad, acute to acuminate or rotund and mucronulate at the apex, cuneate to subauriculate at the base, coriaceous, (sparsely) to densely ochraceous-sericeous and early glabrescent above and beneath, the costa plane to immersed above, elevated beneath, the primary lateral veins obscure above, prominent beneath, arcuate-ascending and forming a prominent submarginal vein; petiole 2–4 mm. long; exstipulate. Inflorescences borne terminally (but appearing axillary or extra-axillary) from young bracteate stems, umbelliform to subracemiform, hirsute, the primary peduncle 10–40 mm. long, the rachis 1–3 mm. long, the secondary peduncles 3–7 mm. long. Flowers unisexual, 4-merous, perigynous. Staminate flowers: 2–5 per inflorescence, white; pedicel obsolete to 0.5 mm. long; calyx tube tubular to broadly obconic, 7–10 mm. long, 2–4.5 mm. broad at the orifice, hirsute without, glabrous within; calyx lobes subequal, indefinitely papillate within, 2.5–4 mm. broad; petals connate into an obscure faucal annulus; antisepalous stamens inserted at the orifice, subexserted, the alternisepalous inserted 2–3 anthers' lengths below the orifice, included, the anthers oblong, about 1 mm. long, 0.5 mm. broad, sessile; disc of irregular lobes, free, 1–3.5 mm. tall, glabrous; pistillode tenpin-shaped, 0.75–1.5 mm. tall, glabrous. Pistillate flowers: 2 or 3 per inflorescence, white; pedicel 1–1.5 mm. long; calyx tube more or less tubular, 4–8.5 mm. long, 2 mm. broad at the orifice, hirsute without, glabrous within; calyx lobes unequal, indefinitely papillate within, the outer 3–4.5 mm. long, 2.5–3.5 mm. broad, the inner 2.5–3 mm. long, 2 mm. broad; petals connate into an obscure faucal annulus; staminodia 8, papilliform, minute; disc of 4 lobes, the lobes irregularly shaped, free, 1–2 mm. tall, glabrous; gynoecium single, tenpin-shaped, 4.5–5.5 mm. long, the ovary 1-locular, glabrous, the single ovule anatropous, the style ca. 1.5 mm. long, thick, the stigma capitate, obscurely bilobed, included or very rarely exserted. Drupe ellipsoid, ca. 15 mm. long, 10 mm. in diameter, glabrous.

Endemic to the island of Hispaniola where it is abundant on lateritic soils, according to Ekman. It has been collected along river banks, in thickets and woods from 600 to 2000 m. altitude. Flowering is known from January through May and October; fruiting in April and May. The tough fibrous bark is used, according to Holdridge, for making rope. It is known locally as *mahaut* (Holdridge) and *jayao* (Jaquez).



Map of Hispaniola showing distribution of *Daphnopsis crassifolia.*

Dominican Republic. AZUA: Sierra de Ocoa, San José de Ocoa, Loma del Rancho, *Ekman H11641* (US, ♂). BARAHONA: Barahona, *Fuertes 891* (A, sterile); Firme Noche Buena, *Fuertes 1433* (A, NY, ♂), *1498* (A, NY, US, ♂). BENEFACTOR: Piedra del Aguacate, n. of Río Arriba, *Howard & Howard 9436* (A, ?). LA VEGA: prope Constanza, *Von Türckheim 3103* (GH, ?; NY, ♂, ♀; US, ♂, ♀). Without precise locality: Pico de Igua, *Jaquez 2028* (US, ♀). **Haiti.** ARTIBONITE: Massif du Nord, Hinche, *Ekman H11641* (NY, ♂); Massif des Bahos, Pte- Rio de l'Artibonite, Perodin, bridge above Ingrand, *Ekman H3454* (US, ♂). OUEST: vicinity of Mission, Fonds Varettes, *Leonard 3905*

(GH, NY, US, ♂); Massif de la Selle, Petionville, top of Mt. Tranchant, *Ekman H1159* (US, ♀); Massif des Cahas group, Las Caobas [Cahobas], Belladire [Belladère], Morne Lagoume-Hire (?), *Ekman H5627* (NY, ♂); Massif de la Selle, group Crête-a-Piquants, Port-au-Prince, Morne, Bercy, erupt., *Ekman H5910* (NY, ♂); Gros Cheval, Mornes des Commissaires, *Holdridge 951* (GH, MO, NY, US, ♀). Without precise locality: La Revellue (?), collector unknown *s.n.* (C, ♀); "Saint-Domingue," *Nectoux s.n.* (P-holotype of *Daphne crassifolia*, ♂).

The precise locality at which the holotype of this species was collected by Nectoux is unknown; consequently, it has not been mapped. Nectoux was "Jardinier en chef du Jardin du Roi" (Nectoux, 1791) in what is now Haiti. I have been unable to ascertain to what extent he travelled and collected.

Ekman's number *H11641* is a split collection, part collected in the Dominican Republic and part in Haiti. Both localities have been mapped.

The included stigma is an unusual feature of the pistillate flower of this species. The only exception I have seen, in which the stigma is exserted, is on *Von Türckheim 3103* (US). In this specimen the gynoecium is of average size, but the calyx tube is relatively short for the species, and this may account for the exsertion of the stigma.

Krug and Urban's *Daphnopsis crassifolia* var. *eggersii* is based on an Eggers specimen (*2317*) which is larger in respect to petiole length and leaf size than var. *crassifolia*. They give the following measurements for var. *crassifolia:* petiole 2 mm. long; leaf blade 3–3.5 cm. long, 1.3–1.7 cm. broad. In contrast, for var. *eggersii* they give: petiole 3–4 mm. long; leaf blade 5–8 cm. long, 2–3 cm. broad. These are the only contrasts, for var. *crassifolia* was known from staminate material and var. *eggersii* only from fruiting material. The measurements of leaf and petiole may be applied successfully to separate *Nectoux s.n.* (type of var. *crassifolia*) from a few specimens (the holotype of var. *eggersii* (*Eggers 2317*), was destroyed at Berlin and I have not located an isotype); but many specimens display enough variability on a single branchlet to overlap significantly the measurement ranges given for the two varieties. I believe that the leaf variation exemplified by this species is of a phenotypic, rather than of a genotypic nature.

In 1901, when Urban erected the genus *Hyptiodaphne* to accommodate *Daphne crassifolia* Poir. (= *Daphnopsis crassifolia* (Poir.) Meissn.), he indicated as one of the main features of the new genus the orthotropous ovule attached basally in the ovary. Unfortunately, there was (and is) little or no information available concerning ovule position and attachment within the genus *Daphnopsis* except that the ovules are anatropous. Domke has figured (1934, *figs. 39a,b,c*) several ovules from plants referable to *Daphnopsis crassifolia* which show, quite strikingly, considerable variation in ovule attachment. The ovules, however, are always of the anatropous type. A pistillate flower (*Holdridge 951*, GH) was cleared and stained to recheck this point. The ovary wall is heavily vascularized with veinlets composed of short and sinuous tracheary elements. The ovular trace is developed poorly, but the trace and ovule position is nearly identical with that figured by Domke in *Fig. 39b.* If Urban based his observation on sectioned material he may have sectioned the ovule at right angles to the attachment, thus leading to the false impression of an orthotropous ovule (demonstrated in Domke's *fig. 39c*). Regardless of these difficulties, a slight shift in ovule position alone is not enough to warrant recognition of *Hyptiodaphne.*

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TWO NEW ASIATIC PANDANACEAE

BENJAMIN C. STONE

DURING A SHORT VISIT to the Harvard University Herbarium I was enabled, through the courtesy of the directors, to study the collections of Pandanaceae. Among the specimens studied were two which represent undescribed species, one in the genus *Freycinetia*, the other in *Pandanus*. Descriptions of these follow.

Freycinetia kostermansii B. C. Stone, sp. nov. (Sect. FREYCINETIA), (FIG. 1).

Planta scandens, caulibus subrobustis subteretibus, plerumque 8–9 mm. crassis, internodiis 5–15 mm. longis; foliis obovato-oblanceolatis, basi breviter contractis, apice abrupte acuminatis breviter caudatis, vulgo 10–15 cm. longis et 12–28 mm. latis, margine basim versus serrato-dentatis, dentibus ad 2 mm. longis, et apicem versus serrato-denticulatis (dentibus ad 0.5–1 mm. longis), costa media ad apicem et in acumine denticulata; syncarpiis terminalibus cylindricis usque ad 8 cm. longis et 3 cm. latis, pedicellis in angulis et distaliter scabridulis; baccis rubris, 14–16 mm. longis, circiter 4 mm. latis, lageniformibus, apice rostrato-contractis, truncatis (areola stigmatica minima 1–2 mm. lata), parte inferiore succulentibus, stigmatibus (5–)6–9, seminibus circiter 1.6–1.9 mm. longis linearibus rhaphide et strophiolo instructis.

HOLOTYPE. **Moluccas:** Morotai, 1000 m. alt., May 27, 1949, *A. J. G. H. Kostermans 1193* (A).

This new species is apparently related to *Freycinetia oblanceolata* Martelli, of New Guinea, and perhaps also to *F. hemsleyi* Warb., of Borneo.

Pandanus gressittii B. C. Stone, sp. nov. (Sect. ACROSTIGMA).

P. Gressittii Merr. ex G. F. Sauer, List Pl. Lingnan Univ. Campus 94. 1947, nomen nudum.

Frutex foliis circiter 30–101 cm. longis et (7–)11–14 mm. latis, margine robuste armatis dentibus antrorsis acicularibus, costa media dorsaliter armatis dentibus robustis antrorsis, apicem versus adpressibus; syncarpium solitarium, ellipsoideum, circiter 5–7 cm. longum et 3.5–5 cm. diametro; pedunculo erecto bracteato; drupis anguste obclavatis circiter 14 mm. longis et 2–3 mm. latis, apice rotundato-conicis, pileo 2–3 mm. longo; stigmate breviter erecto-curvato, aceroso, circiter 2 mm. longo et 0.75 mm. lato, endocarpio supramediale, semen unicum.

DISTRIBUTION: endemic to Hainan Island.

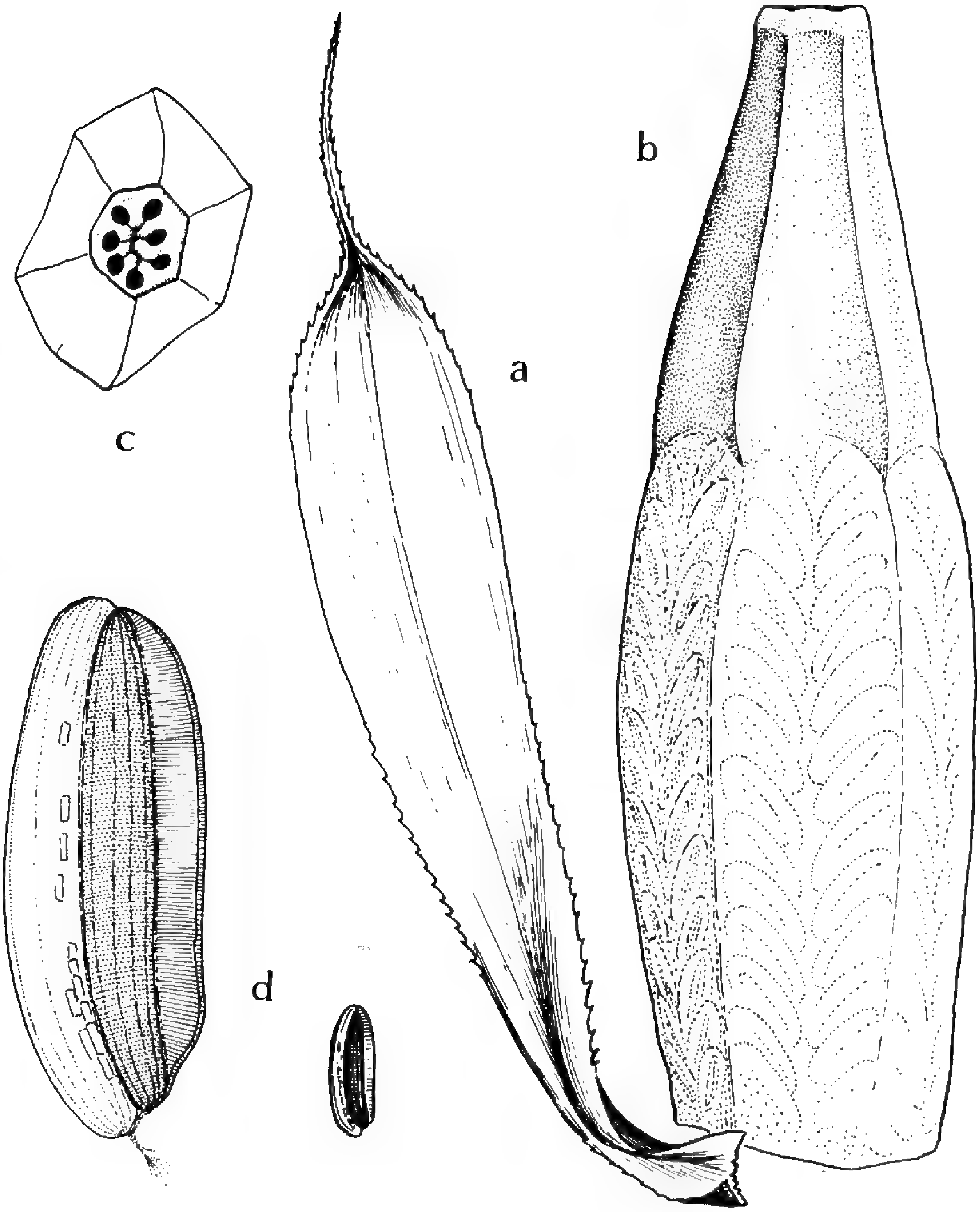

FIG. 1. FREYCINETIA KOSTERMANSII: a, leaf, × 0.8; b, c, berry, lateral and top views, × 8; d, seed, × 8 and × 35. (Drawn from the holotype.)

HOLOTYPE. **Hainan Island:** small jungle stream at Liamui, 400 m. alt., June–July 1935, *J. Linsley Gressitt 1185* (A). ADDITIONAL SPECIMENS EXAMINED. Lokwui, near stream, 15 May 1935, *F. C. How 72350* (A); Bo-Ting, in thickets, 17 Oct. 1936, *S. K. Lau 28026* (A).

The existence of this species was first called to my attention by Dr. J. Linsley Gressitt, who collected the type specimen. The name conferred by Merrill and long carried in manuscript appears never to have been formally published. I take pleasure in bringing into use the name honoring Dr. Gressitt, now Entomologist and Head of the Entomology Department of the Bernice P. Bishop Museum, Honolulu, whose labors in the two fields of insect taxonomy and zoogeography of the Pacific are of more than casual interest to the botanist.

The new species may be recognized by its shrubby habit; solitary syncarp set on a long or slightly nodding peduncle furnished with bracts; and the unilocular drupes with conoid pilei about 2–3 mm. long produced into a short acerose stylose stigma slightly curved or hooked in form, with the stigmatic groove uppermost. Gressitt's notes indicate that the type plant was about 1 m. tall, with a trunk 1.5 cm. in diameter; the fruits were green. The leaves, which are quite small and narrow for the genus, are evenly tapered to a sharp, elongated apex.

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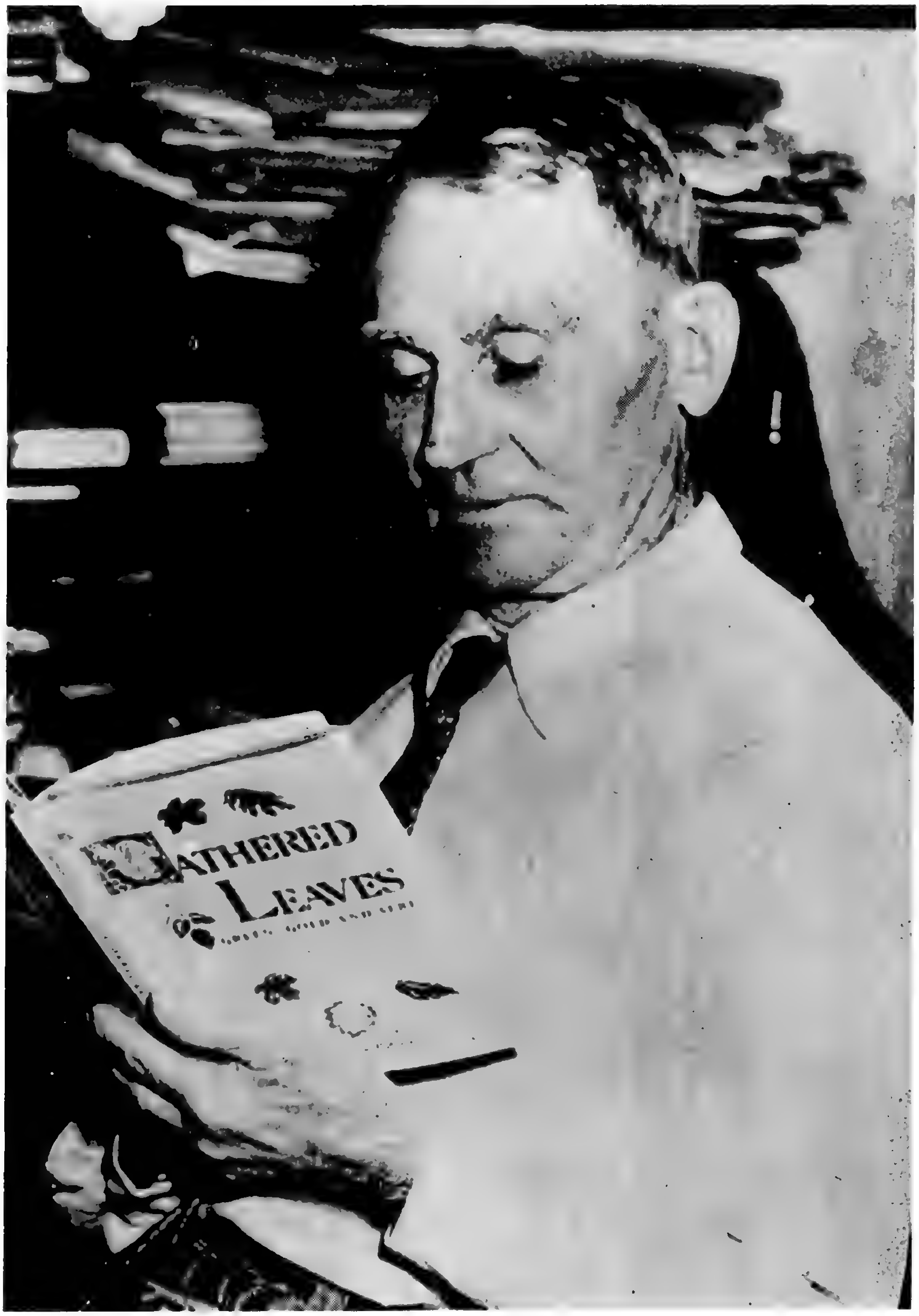
Agana, Guam



Ernest Jesse Palmer

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ERNEST JESSE PALMER, 1875–1962

Clarence E. Kobuski [1]

With portrait

Ernest Jesse Palmer died at Webb City, Missouri, on February 25, 1962, in his 87th year. This marked the end of a long and in many ways remarkable career in the fields of botany and allied sciences.

He was born in Leicester, England, April 8, 1875, and, in 1878, when he was three years old, he and his sister, Louise, were brought to this country by their parents, Amos and Annie Palmer, who settled temporarily near Warrensburg, in Johnson County, Missouri. When he was 14, his father, responding to the stories of quick wealth offered by the mining opportunities in the southwestern part of Missouri, moved the family to Webb City and built a home for them at 321 South Main Street. The wealth never materialized! Throughout the rest of his life, although he spent many of his years away from Webb City, the Palmer home was maintained, and after retirement, Ernest Palmer moved with his family and lived out the rest of his life there.

In this mining area, young Palmer did find a wealth of his own liking. It was here that he began his studies of natural phenomena. In the piles of waste material from the mines, fossils of plants and animals caught his fancy, and as in all boys of his age the collecting instinct came to the fore. He developed a great keenness for unearthing most interesting artifacts. In later years at the Arnold Arboretum he was always "picking up" Indian arrowheads and other Indian deposits. This was easy for him, but not necessarily for others. I can recall his telling me of a spot in the Arboretum where arrowheads were in abundance. I hurried to the exact location but found nothing. The next day we went out together — and sure enough, he picked up several more artifacts. Eventually two attractive trays of Palmer's finds in the Arboretum were mounted and have been on display there ever since.

His formal education was broken off suddenly while he was attending high school. A physical collapse of his father made it necessary for him to leave school and seek employment. This was undoubtedly a severe

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[1] This article on Mr. Palmer will be published also in the current volume of *Rhodora*, but without the bibliography. C.E.K.

blow to his pride because he wanted an education above all things. He loved study and research — and he intended to continue it at all costs. Just recently I learned from an article by Marcia W. Kershaw, a Special Correspondent of the St. Louis Post-Dispatch, that Palmer managed to study Latin and Greek at old Webb City Baptist College. I had often wondered where he obtained his profound knowledge of these languages, especially Latin which he used so ably in his original technical descriptions of new species of plants. Mrs. Kershaw's article brought to light many other facets of Mr. Palmer's career which were previously unknown to me and I am very thankful to her for her assistance.

All his life he had managed to study not only the natural sciences but also English literature, mathematics, economics, and poetry until he was considered very proficient in each of them.

The portrait which accompanies this article was taken in 1958 and shows Mr. Palmer at his desk with a copy of his published book of poems entitled, "Gathered Leaves, Green, Gold and Sere." These poems, I understand, are truly gathered leaves, "leaves" which had been lying around in various places during the years and were gathered together by his wife and published through her efforts when Palmer was eighty-three years old.

His scientific papers were noted not only for his Latin descriptions but also for the fine phrasing which he always employed. He wrote so well and so easily that often he found it necessary to delete whole paragraphs from his papers because he considered the contents "unscientific." It was a pity because everyone would have enjoyed reading them.

Although he was dedicated to the life of a naturalist it was not until his meeting with Benjamin Franklin Bush, also from Missouri, that he tried his wings and ventured away from his home setting. When Bush died in 1937, Palmer published a resumé of his life in *The American Midland Naturalist.* On re-reading this biography one cannot help but be struck by the similarity in the early backgrounds, the interests, and, in fact, the entire careers of the two men.

In 1901, Bush, then a collector for the Arnold Arboretum, visited the Palmer home and spent a week there using it as a base for his botanical collections. Bush was especially interested in obtaining specimens of *Crataegus* for C. S. Sargent, then director of the Arnold Arboretum, and when he departed from Webb City he left with Palmer a supply of driers for further collections. Thus at the age of 25 Palmer began his lifelong interest in *Crataegus* and his association with Sargent and the Arnold Arboretum. For the next twelve years he collected extensively in his home area, concentrating on the flora of Missouri, and it was not until 1913, when he was 38, that he became associated with the Missouri Botanical Garden. Two years later at the age of 40 he began his many collecting trips to the Southwest under the aegides of both the Missouri Botanical Garden and the Arnold Arboretum.

Palmer began publishing as early as 1910, at which time his first paper, "Flora of the Grand Falls Chert Barrens" appeared in the *Trans-*

actions of the Academy of Science, St. Louis. During the next ten years he published seven papers, mostly on ferns. In 1920, while still a collector-at-large he sent in from Webb City to the newly organized *Journal of the Arnold Arboretum* his first of many papers to be published by this Harvard University publication. Two more papers were published in this journal before he came to Jamaica Plain in 1921 as a regular staff member. He retained this status at the Arnold Arboretum for twenty-seven years, until he retired in 1948.

My personal association with Palmer began in 1927. By that time he was firmly established at the Arboretum as a collector-botanist. Since he was away so much of the time on his many collecting trips and since he was still a bachelor he maintained personal quarters in a rooming house.

He was a very busy man during this period. He managed to make a collecting trip nearly every year, usually alone, occasionally with a single companion. Upon his return from these trips his time was spent identifying his specimens, making up sets for distribution, and writing occasional papers — and getting ready for his next trip. He once mentioned to me that he had hopes of collecting in all the states of the Union. At the time he had nearly accomplished his intention. If I recall correctly he said that there were only two states in which he had not made "official" collections — and, as one might suspect, one of them was surprisingly close by!

The greater portion of his collections was made in the southwestern United States. However, he always maintained his interest in the Missouri flora, and, in 1935, there appeared in the *Annals of the Missouri Botanical Garden* the 385-page article by Palmer and Steyermark, "An Annotated Catalogue of the Flowering Plants of Missouri." This catalogue is more complete than is usual in such a publication. The first seventy-five pages are devoted to the botanical history, terrain, climate, plant regions, etc., of the state. Under the actual listing of the taxa may be found the habitat and a record of the counties wherein specimens of each entry had been collected. A footnote states that an earlier publication on the ferns and fern allies of Missouri published by the same authors three years earlier in the *American Fern Journal* should be considered supplementary to the 1935 Catalogue.

A recent letter to me from Julian Steyermark, the junior author of the above two publications, mentions that his latest publication, *Flora of Missouri,* which has been in press since 1959 is being dedicated to E. J. Palmer. Palmer had hoped to see the book and knew of the proposed dedication.

In 1930, when he reached the age of 55 he surprised us all by getting married. We had thought of him as a confirmed bachelor. He married Elizabeth McDougal, a bacteriologist at the Massachusetts State Laboratory which is located alongside the Arnold Arboretum. Naturally, a great change took place in Palmer's life. He eventually set up a fine home in one of the houses belonging to the Arnold Arboretum in Jamaica Plain. He and his wife had three children: Ernest Macdougal Palmer, born in 1931; Grace Elizabeth Palmer, in 1932; and Theodore Windle Palmer, in 1935.

Palmer possessed a physique that defied age. He was the slender, wiry type and at the time of his retirement and departure from Jamaica Plain for Webb City could outlast any of us on a collecting trip. Although I did not see him again, I understand from his long letters and from various conversations with others that he continued his same brisk manner in everything which he undertook. His letters show that when he retired he merely transferred his activities from Massachusetts to Missouri. In a letter to me in February 1955 he says: "Of course we miss many friends there [Jamaica Plain], and I miss many of the associations at the Arboretum. But I have never been sorry that I retired when I did, for my life on the whole has been quite happy here. I have never been busier at any time or interested in more things. In April I will pass another anniversary — and you can figure it out as the records show that I was born in 1875. It is hard for me to believe it as I still feel as strong in body and mind — so far as I can tell — as I did at fifty. I can easily walk ten miles any day; and I think I could climb a good sized tree, if there was anything at the top of it that I wanted badly enough. . . Steyermark and I are still working actively on the Flora of Missouri . . . Specimens of Crataegus, Quercus and other genera keep coming to me for determination or revision. . . Other collections in my museum also occupy much time. . . I have agreed to talk to a joint meeting of all the Garden Clubs of Carthage at the public library. While I do not solicit or particularly enjoy speaking engagements, I fill them occasionally. . . It is so fine and warm today that I think I will go fossil hunting this afternoon." For a man retired and eighty years old he certainly was enjoying life to the fullest, doing exactly what he wanted to do — and he seemed so well equipped to do it!

During his life time Ernest Palmer joined many scientific organizations, among them: the American Fern Society, the American Association for the Advancement of Science, the American Society of Plant Taxonomists, the Boston Mineral Club, the Botanical Society of America, the Missouri Archaeological Society, the New England Botanical Club (President, 1944–1945), and the St. Louis Academy of Science.

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

GEORGE K. BRIZICKY

ANACARDIACEAE Lindley, Intr. Nat. Syst. 127. 1830. nom. cons.
(CASHEW FAMILY)

Trees or shrubs, rarely subshrubs or vines, with resin ducts in bark and often in leaves, flowers, and fruits. Leaves alternate [very rarely opposite or verticillate], simple, 3-foliolate, or pinnate, deciduous or persistent, exstipulate. Flowers small, usually regular, hypogynous [rarely perigynous or epigynous], usually unisexual by abortion or both uni- and bisexual [rarely bisexual throughout], in axillary and/or terminal thyrses or panicles, more rarely in solitary or panicled spikelike racemes; bracts deciduous or persistent, bractlets 2, deciduous or persistent, or wanting. Perianth double [rarely simple or absent], usually 5-merous. Sepals usually connate at least at base, imbricate [or valvate]. Petals usually distinct, imbricate [or valvate]. Stamens 5–10 [or very rarely more], sometimes only 1 or 2 fertile in ♂ flowers, distinct [or basally connate], reduced and sterile [or wanting] in ♀ flowers; anthers versatile, 2-locular at anthesis, introrse, longitudinally dehiscent. Intrastaminal (or rarely extrastaminal) nectariferous disc usually 5- or 10-lobed [sometimes produced into a gynophore, rarely absent]. Gynoecium syncarpous [or apocarpous], 3[–5]-carpellate or 1-carpellate by reduction, rudimentary [or absent] in ♂ flowers; stigmas 1–3[–5]; styles 1–3[–5]; ovary 1[3–5]-locular; ovules anatropous, apotropous, solitary in a locule, the funicle usually elongate with a basal, parietal, or apical insertion. Fruit usually drupaceous, with ± resinous and sometimes waxy or oily mesocarp and crustaceous or bony endocarp (stone). Seeds with scanty endosperm or endospermless; embryo ± curved [or straight]. (Terebinthaceae Juss., 1789; Spondiaceae Kunth, 1824.) TYPE GENUS: *Anacardium* L.

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[1] Prepared for a generic flora of the southeastern United States, a joint project of the Arnold Arboretum and the Gray Herbarium of Harvard University, made possible through the support of George R. Cooley and the National Science Foundation and under the direction of Reed C. Rollins and Carroll E. Wood, Jr. This treatment follows the pattern established in the first paper in the series (Jour. Arnold Arb. **39**: 296–346. 1958) and continued through those in volumes **40–43** (1959–1962). It should be repeated that the area covered by this work is bounded by and includes North Carolina, Tennessee, Arkansas, and Louisiana. The descriptions are based primarily on the plants of this area, with any supplementary material in brackets. References which the author has not seen are marked by an asterisk.

The author is indebted to Dr. Carroll E. Wood, Jr., for his criticism and valuable suggestions, and to Mrs. Gordon W. Dillon, for her careful help in the preparation of the manuscript.

A family of about 70 genera with nearly 600 species, primarily pantropical, extending with several genera into the temperate zones of both hemispheres. Of the five tribes, only Rhoëae (Rhoideae) and Anacardieae (Mangifereae Marchand emend. Engler) are represented in our area, the former by three indigenous genera and a naturalized species of *Schinus*, the latter by a species of *Mangifera* naturalized in southernmost Florida. Since generic lines in the Rhoëae are often weak and differently interpreted, various authors have recognized one to five indigenous genera in our area.

The family, with a few exceptions (e.g., *Pistacia* L.), is considered to be entomophilous. Since the species are mostly dioecious or polygamo-dioecious, cross-pollination should be the rule. Apomixis (adventitious polyembryony) has been found in some species of *Mangifera*, parthenocarpy in several genera. Cytological data presently known for about 25 species in ten genera ($2n$ = 24, 28, 30, 32, 40, 42, 48, 60) suggest polyploidy. Resin of many species is poisonous on contact.

The family is believed to be closely allied with Sapindaceae and Julianaceae. Wood-anatomical and palynological evidence seems to support the assumption of a close relationship with Burseraceae, from which Anacardiaceae differ essentially in the uniovulate ovary locules and in apotropy of the ovules.

Anacardiaceae are economically important for edible fruits (e.g., *Mangifera indica*, mango; *Spondias* spp., mombin) or nuts (*Anacardium occidentale* L., cashew; *Pistacia vera* L., pistachio), for resins (e.g., *Pistacia Lentiscus* L., mastic) and lacquers (*Rhus verniciflua*), for tannins (*Cotinus Coggygria*, *Rhus* spp., *Schinopsis* spp.), and for timbers (*Schinopsis* spp., red quebracho; *Astronium* spp., zebrawood or kingwood). Some species are ornamentals.

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KEY TO THE GENERA OF ANACARDIACEAE

General characters: *woody plants with resin ducts in bark, leaves, flowers, and fruit; flowers small, usually hypogynous, unisexual or uni- and bisexual, in axillary and/or terminal thyrses or panicles; perianth double, usually 5-merous; stamens 5–10; nectariferous disc intra- or rarely extrastaminal; gynoecium 1–3 [–5]-carpellate, ovary usually 1-locular by abortion; fruit drupaceous.*

A. Flowers ♂ and bisexual; petals with longitudinal ridges; disc extrastaminal; stamens 5, only 1 or 2 fertile; gynoecium 1-carpellate; drupes large to very large, with copious juicy flesh; leaves simple; naturalized tree of subtropical Florida. . . . . 1. *Mangifera.*

A. Flowers usually unisexual; petals not ridged; disc intrastaminal; stamens 5 or 10, all fertile in ♂, all reduced and sterile in ♀ flowers; gynoecium 3-carpellate; drupes small, not exceeding 15 mm. in length, with meager drying flesh; leaves various.

  B. Stamens 10; drupes spicy-aromatic, containing oil cavities adherent to stone; leaves pinnate, with winged rachises; naturalized shrubs or small trees of southern Florida. . . . . 2. *Schinus.*

  B. Stamens 5; drupes not aromatic, without oil cavities; leaves various, if pinnate, rachises not winged, except in *Rhus copallina.*

    C. Stigma 1, 3-lobed; style 1, very short, stout; drupes 10–15 mm. long, ellipsoid to obovoid, scarlet to orange, glabrous; endocarp thin, crustaceous; leaves odd-pinnate, leaflets long petioluled; poisonous trees or shrubs of subtropical Florida. . . . . 3. *Metopium.*

    C. Stigmas and styles 3; drupes 3–8 mm. long, subglobular or subreniform (covered with glandular club-shaped hairs if red or orange); endocarp thick, bony; leaves various (if pinnate, leaflets sessile or short petioluled).

      D. Styles appearing sublateral in flowers; drupes obliquely subreniform, usually much compressed laterally, prominently reticulate, glabrous, the remnants of styles lateral; mesocarp very scanty; pedicels of aborted flowers becoming plumose-villous; leaves simple; innocuous trees or shrubs. . . . . 4. *Cotinus.*

D. Styles terminal; drupes subglobular, usually slightly compressed laterally, not reticulate, sometimes with simple and/or glandular hairs; mesocarp thickish, resinous and sometimes also waxy; pedicels never plumose; leaves 3-foliolate or odd-pinnate; trees, shrubs, or vines, some poisonous. 5. *Rhus.*

Tribe ANACARDIEAE

1. **Mangifera** Linnaeus, Sp. Pl. 1: 200. 1753; Gen. Pl. ed. 5. 93. 1754.

Mostly large evergreen trees, the leaves alternate [rarely verticillate], simple, entire, membranaceous to coriaceous, petiolate, persistent. Plants polygamous, usually andromonoecious. Flowers small, ♂ and bisexual, in terminal [and/or axillary] thyrses; pedicels articulated; bracts and bractlets deciduous. Sepals 5 (4 or 6), deciduous. Petals 5 (4 or 6), distinct [or adnate to the disc at base], the veins thickened into [1–]3–5 prominent ridges, deciduous. Disc extrastaminal, tumid [or minute, sometimes stipelike, or wanting], 5-lobed. Stamens usually 5 [rarely 10–12], inserted just within [or on] the disc, distinct [or connate at base], usually 1 or 2 [rarely 5 or 6] fertile, the rest remaining sterile with imperfect small anthers [or reduced to toothlike projections]; pollen 3-colpate, small to medium sized, ellipsoidal, finely reticulate. Gynoecium 1-carpellate (exceptionally 2-carpellate, apo- or syncarpous), rudimentary or wanting in ♂ flowers; stigma simple; style sublateral; ovary obliquely subglobular, 1-locular, sessile; ovule solitary, funicle subbasal. Fruit a large [or relatively small] drupe of various shapes and colors; exocarp ± leathery; mesocarp thick, fleshy, sweet [to acid], sometimes resinous; stone compressed, usually hard, woody, coated with fibers. Seed large, compressed; testa papery; endosperm lacking (or scanty?); embryo subreniform with plano-convex, often unequal and lobed cotyledons and small ascendent radicle; germination hypogeous. TYPE SPECIES: *M. indica* L. (From Portuguese, *mango*, the common name for this fruit, and Latin *-fera*, bearing, i.e., "bearing mangoes.")

An Indo-Malayan genus of about 40 species. *Mangifera indica* (including *M. laurina* Bl.), common mango, $2n = 40$, presumably native to India (and perhaps to Indochina and the Sunda Islands), widely cultivated throughout the tropics for its edible fruits, has become naturalized in hammocks of southern Florida and the Florida Keys. A tree with relatively large, narrow leaves and large to very large, ovate to subreniform or subcylindrical, yellowish or greenish fruits sometimes flushed with scarlet or crimson, the species has been in cultivation in the tropics of the Old World for over four thousand years and shows a wide range of variation, about a thousand wild forms and cultivars occurring in India.

Mangifera indica is the only economically important species. Its fruits, mangoes, are said to be eaten by at least one-fifth of the world's population. In India the astringent flowers, seeds, and bark find medicinal application, especially in diarrhoea. Bark and leaves yield a yellow dye used locally in southern Asia. The wood, said to be of excellent quality, is used extensively in India for carpentry, cabinet-work, boat-building, etc.

Short-tongued insects, especially Diptera, Hymenoptera, and Coleoptera, seem to be the principal pollinators of *Mangifera indica*. Cross-pollination seems to be the rule. Since self-pollination has not been recorded, one may assume that the morphologically bisexual flowers are (at least in most cases) functionally (physiologically) carpellate. The somatic chromosome number $2n = 40$ has been recorded for 23 grafted varieties and one wild race of *Mangifera indica,* as well as for *M. sylvatica* Roxb., *M. caloneura* Kurz, *M. caesia* Jack, and *M. foetida* Lour. Although no polyploid series has been found in the genus, Mukherjee (1950) suggested on the basis of his cytological analysis that *M. indica* and its allies are allopolyploids. No records of natural or artificial interspecific hybrids have been available, but Mukherjee (1957) remarked that "similarity in the chromosome number and morphology and in the pollen size and morphology . . . indicates that there may be close compatibility among the species during hybridization and in stock-scion relationship in grafting . . ."

Apomixis (adventitious polyembryony) has been recorded in *Mangifera indica* and in *M. odorata* Griff., the embryos originating either from the nucellus or by budding from the cotyledons and hypocotyl. While Indian "seedling races" and "horticultural [grafted] varieties" are almost exclusively monoembryonic, the "seedling races" common in culture in some other countries ("Philippine" or "Manila" races) mostly are polyembryonic. There are, however, records indicating that some "Indian races" considered monoembryonic in India yielded a considerable percentage of polyembryonic seeds when grown in the Philippines.

Although *Mangifera indica* is usually innocuous and dermatitis caused by its resin is infrequent, several wild species (e.g., *M. caesia*, *M. foetida*, *M. odorata*, and *M. lagenifera* Griff.) sometimes cultivated in the Malaysian region for their edible fruits are regarded as positively poisonous.

The genus seems to be related to the Malayan *Bouea* Meisn. and to the tropical American *Anacardium* L.

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Tribe RHOËAE Marchand, "Rhoideae"

2. **Schinus** Linnaeus, Sp. Pl. 1: 388. 1753; Gen. Pl. ed. 5. 184. 1754.

Trees or shrubs [rarely subshrubs, sometimes thorny]. Leaves odd-pinnate or rarely even-pinnate [or simple]; the leaflets membranaceous to subcoriaceous [or coriaceous], (3)5–13[–41], usually opposite [or alternate], relatively small to medium sized, entire or toothed, sessile or subsessile, the rachis often winged. Plants usually dioecious. Flowers usually unisexual, small, pediceled, in axillary [and terminal] thyrses [or in contracted raceme-like inflorescences]; bracts small, bractlets 2, minute, deciduous. Sepals 5 [4], persistent. Petals 5 [4], white [or yellow], considerably longer than the sepals. Stamens 10 [8], in 2 series, the antipetalous shorter than the antisepalous, inserted below and between the lobes of a saucer-shaped 10[8]-lobed intrastaminal nectariferous disc, reduced and sterile in ♀ flowers; pollen 3-colpate, medium sized, ellipsoidal, finely reticulate. Gynoecium 3-carpellate, rudimentary in ♂ flowers; stigmas 3 [1], capitellate; styles 3 [1], connate at least at base; ovary sessile, 1-locular by abortion; ovule solitary, 2-integumented, with a thick nucellus, suspended from near the top of the locule. Drupe small, pea-like, bright red [pink or lavender]; exocarp thin, chartaceous, shining; mesocarp resinous, the innermost layers (adherent to endocarp) with large cavities containing an aromatic oil; stone laterally compressed, cartilaginous to bony. Seed sublenticular; testa thin, membranaceous; endosperm fleshy, scanty; cotyledons flat; radicle elongated, incurved upwards. (Including *Duvaua* Kunth). LECTOTYPE SPECIES: *S. Molle* L., $2n = 28, 30$; see A. S. Hitchcock, *in* Int. Bot. Congr. 1930. Nomencl. Propos. Brit. Bot. 153. 1929. (An ancient Greek name for the mastic tree, *Pistacia Lentiscus* L., applied by Linnaeus to this genus.) — PEPPER-TREE.

A genus of about 28 species of warm-temperate and tropical South

America, from Chile, Argentina, and Uruguay, north to Venezuela and Colombia. *Schinus terebinthifolius* Raddi, Brazilian pepper-tree or Christmas-berry, with 5–13 oblong-ovate leaflets, and *S. Molle*, Peruvian pepper-tree, with 15–41 very narrow leaflets, are frequently cultivated in the warmer parts of the Eastern and Western hemispheres as ornamentals. Both are grown in Florida, and the former, a shrub, has become naturalized in southern Florida and the Keys where it seems to be spreading rapidly; the exact extent of naturalization needs to be determined. *Schinus Molle* has become naturalized in California and Mexico. The infructescences are often used as Christmas decorations. In Mexico and South America the fruits are used in various beverages, the seeds are sometimes used to adulterate pepper, and the resin, bark, and fruits are used locally in medicine.

The genus seems to be most closely related to the South American *Lithraea* Miers and the East Australian *Rhodosphaera* Engl. The group is entomophilous, and honeybees have been reported as frequent visitors of flowers of *Schinus Molle.* No hybrids have been recorded.

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3. **Cotinus** Miller, Gard. Dict. Abr. ed. 4. 1754.

Small trees or shrubs with orange-yellow wood and strong-smelling, resinous sap. Leaves simple, entire, medium sized [or small], membranaceous, deciduous, the petioles short to long. Plants usually dioecious [occasionally polygamo-dioecious or -monoecious]. Flowers small, usually unisexual [rarely also bisexual], many abortive, in loose terminal thyrses, the slender pedicels much elongated after flowering, those of abortive flowers becoming plumose-villous; bracts narrow, ± scarious, in part persistent. Sepals 5, persistent. Petals 5, yellowish- or greenish-white [rarely crimson], twice as long as the sepals. Stamens 5, distinct, inserted below an annular, shallowly 5-lobed intrastaminal disc, alternate with and shorter than the petals, reduced and sterile in ♀ flowers; filaments subulate; anthers broadly ovate in outline, somewhat shorter than the filaments, 2-locular at anthesis; pollen 3-colpate, medium sized, subspherical, striate-reticulate, with round to slightly oblong, smooth germ pores. Gynoecium 3-carpellate, rudimentary in ♂ flowers; stigmas 3, small, subcapitate; styles 3, appearing sublateral, unequal, that of the fertile carpel conspicuously longer than the 2 sterile ones; ovary 1-locular by abortion, obliquely obovoid, sessile; ovule raised on a basal funicle. Drupes small (4–5 mm. long), obliquely obovate to subreniform, usually much compressed, conspicuously reticulate veined, the style-remnants lateral; exocarp membranaceous; mesocarp very scanty; stone (endocarp) bony, subreniform, 1-seeded. Seed reniform; testa thin, membranaceous; endosperm wanting (?); embryo with flat, elliptic cotyledons and an elongate radicle incurved upwards (toward the hilum). TYPE SPECIES: *Rhus Cotinus* L. = *Cotinus Coggygria* Scop. (Derived from Greek, *kotinos*, an ancient name for wild olive, used by Pliny for an unidentified shrub of the Apennines, but applied by some pre-Linnaean botanists, e.g., Tournefort, to *C. Coggygria.*) — SMOKE-TREE.

A genus of three or more species, primarily of warm-temperate Eurasia (southern France to the eastern subtropical Himalaya and central China) and eastern North America. *Cotinus obovatus* Raf. (*C. americanus* Nutt., *Rhus americanus* (Nutt.) Sudworth), American smoke-tree,[2] a tree, sometimes a low shrub, with obovate-cuneate leaves turning orange to crimson in autumn, occurs sparingly on wooded, rocky cliffs and river bluffs, usually on limestone, in disjunct populations in the mountains of northern Alabama and adjacent Tennessee (Franklin County); in Daviess County, Kentucky (introduced?); in southwestern Missouri, northwestern Arkansas, and eastern Oklahoma; and on the Edwards Plateau, Texas. "Its rarity, discontinuous distribution, lack of related species in the New World, and occurrence as a pioneer on rocky cliffs all suggest that [it] is an old species formerly of general distribution but now approaching extinction" (Little, p. 23). Trees to about 10 m. tall have been recorded, but Sargent (1892) wrote that "during the War of Secession nearly all the large specimens were cut down for the dye which the wood yields . . ."

Most observations on the genus have been made on the Eurasian *Cotinus Coggygria*, Venetian sumac or smoke-tree,[2] in which polygamo-dioecism and monoecism, as well as flowers with 3-locular ovaries, have been observed occasionally. Short-tongued Hymenoptera and Diptera apparently are the principal pollinators. Parthenocarpy seems to be of common occurrence, since many fruits fail to develop seeds. Although birds have

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[2] Since the above was written, chromosome numbers of three taxa of *Cotinus* have been determined by Dr. Otto T. Solbrig, of the Gray Herbarium, from staminate material collected by Dr. C. E. Wood from the living collections of the Arnold Arboretum: *C. obovatus* (Arnold Arb. No. 1814-B, from seed, Charles Mohr, Mobile, Alabama, July 5, 1882; *Wood 9427* [AAH]), $2n = 15^{II}$; *C. Coggygria* (Arnold Arb. No. 276, from Harvard Bot. Gard., 1876; *Wood 9428* [AAH]), $2n = 15^{II}$; and *C. Coggygria* 'Atropurpureus' (Arnold Arb. No. 708–49–A, from seed, New York Bot. Gard., 1948; *Wood 9429* [AAH]), $2n = 15^{II}$.

been mentioned, wind is assumed to be the principal means of seed dispersal by transport of the whole infructescence. Asexual reproduction takes place by root- and stump-sprouts.

In spite of many similarities with *Rhus,* from which *Cotinus* differs mainly in the asymmetrical ovaries and fruits, unequal styles appearing sublateral in flower and lateral in fruit, very scanty mesocarp, and peculiar infructescences, the two genera do not seem to be very closely related. According to Engler, *Cotinus* represents a branch of a line of evolution different from but with a common origin with that of *Rhus.* Some relationship to the South African genera *Laurophyllus* Thunb., *Smodingium* E. Mey., and *Loxostylis* Spreng. f. ex Reichenb. (*Botryceras* Willd.) seems possible.

The leaves and bark of *Cotinus Coggygria* are important sources of tannin and have been employed extensively in the tanning industry in southern Europe. Leaves and flowers yield an aromatic oil. The orange-yellow dye (fustic, "young fustic") extracted from the heartwood of *C. Coggygria* and *C. obovatus* was formerly used extensively for dyeing silk, wool, etc. Both species are ornamental.

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4. **Metopium** P. Browne, Civ. Nat. Hist. Jamaica 177. 1756.

Trees or shrubs with resin ducts in bark and wood. Leaves odd-pinnate, (1)3–7-foliolate, stoutly petioled, usually clustered near the tips of branches, persistent; leaflets long-petioluled, ± leathery, entire, lustrous, veins and veinlets prominent. Plants usually dioecious. Flowers small, usually unisexual; pedicels short, stout, and articulate near base, in loose, ascending, determinate axillary panicles; bracts and bractlets minute, in part persistent. Sepals 5, connate into a ± cupuliform 5-lobed calyx; lobes broadly ovate to almost semicircular [or truncate], ± unequal, thin-leathery with scarious margins, persistent. Petals 5, twice as long as sepals, yellow-green, with brownish to blackish veins. Stamens 5, distinct, alternate with and shorter than the petals, inserted at base and between the glandlike lobes of an intrastaminal nectariferous disc, reduced and sterile in ♀ flowers; anthers oblong in outline, nearly as long as [or longer than] the subulate filaments, 2-locular at anthesis; pollen 3-colpate, medium sized, ellipsoidal, reticulate-striate, with round, smooth germ pores. Gynoecium 3-carpellate, rudimentary in ♂ flowers. Stigma 3-lobed; style very short, stout; ovary 1-locular by abortion, obovate to subglobular; ovule raised on a basal funicle. Drupe ellipsoidal to somewhat obovoid, about 1–1.5 cm. long, glabrous, shining, orange to scarlet when ripe, tipped with the remnant of the style; exocarp membranaceous, mesocarp resinous, endocarp thin, crustaceous, all permanently united (coherent). Seed compressed, almost quadrangular in outline, the broad funicle covering one of its margins; testa thin, smooth, dark brown; endosperm scanty or wanting; embryo oriented vertically, the cotyledons accumbent, flat, the radicle long, incurved upwards toward the hilum. TYPE SPECIES: *Terebinthus Brownei* Jacq. = *M. Brownei* (Jacq.) Urban. (An ancient name for some oriental plant [perhaps some species of *Ferula*], yielding the gum resin galbanum, applied by Browne to his genus; etymology obscure.)

A genus of three species, of the West Indies, southern Florida, British Honduras, Guatemala, and southern Mexico. The West Indian *Metopium toxiferum* (L.) Krug & Urban, poisonwood or coral sumac (also hog gum, doctor gum), occurs in hammocks, pinelands, and coastal sand dunes in southern Florida (about as far north as Martin County) and on the Florida Keys. A large tree in hammocks, a shrub in pinelands, in its appearance the species resembles *Bursera Simaruba*, with which it is often confused.

The genus is very closely related to *Rhus*, but the combination of the single style and stigma, the thin, crustaceous endocarp, the vertical embryo, and anatomical characters (diffuse-porous wood; abundant, often banded, vasicentric parenchyma; septate wood fibers) seems to support the maintenance of *Metopium* as distinct.

All species are poisonous, and all parts of the plants act as a contact skin-poison. Leaves and resin were formerly used in local medicine in the West Indies. The floral biology probably does not differ much from that of *Rhus*. Birds apparently are responsible for seed dispersal.

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See also under family references BARKLEY (1937, pp. 303–309), ENGLER (1881, p. 378; 1883, pp. 367–369; 1892, p. 167), HEIMSCH (1940; 1942, pp. 139–141), RECORD (pp. 28, 29), SARGENT (pp. 658, 659), and WEST & ARNOLD (p. 112).

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5. **Rhus** Linnaeus, Sp. Pl. 1: 265. 1753; Gen. Pl. ed. 5. 129. 1754.

Trees, shrubs [sometimes thorny], subshrubs, or vines climbing by aërial, clinging, adventitious roots, often pubescent with glandular and/or nonglandular hairs, some poisonous by contact. Leaves 3-foliolate [rarely palmately 5-foliolate] or odd-pinnate (occasionally even-pinnate) [or simple], petioled, deciduous [or persistent]; leaflets usually opposite, entire or toothed, sometimes lobed, sessile or ± distinctly petioluled, rachis sometimes winged. Plants usually dioecious. Flowers small [to minute], usually unisexual by abortion, pediceled [or sessile], in terminal [and]/or axillary thyrses [or panicles], or in solitary or panicled racemes [or spikes]; bracts deciduous or persistent, bractlets 2, at base of pedicel, deciduous or persistent, or wanting. Sepals 5, connate at base [or higher], usually persistent. Petals 5, longer than the sepals, greenish-white to yellow [or rarely pink], inserted at base of disc, imbricate. Stamens 5, alternipetalous, inserted below a 5–10-lobed, annular, patelli- or cupuliform intrastaminal nectariferous disc, reduced and sterile in ♀ flowers; anthers ovate to oblong in outline, usually shorter than the ± subulate filaments; pollen 3-colpate, medium sized [or small], ellipsoidal to spherical, reticulate, reticulate-striate or striate, more rarely smooth, with oblong, mostly irregular to ragged, germ pores. Gynoecium 3-carpellate, rudimentary in ♂ flowers; stigmas 3, capitellate, sometimes slightly depressed; styles 3, terminal, distinct or partly [rarely ± completely] connate; ovary 1-locular; ovule raised on an elongate ascendent basal funicle. Drupe subglobular to globular, 3–8 mm. [rarely over 1 cm.] in diameter, often somewhat laterally compressed, white, tan to brown, or red [or black], smooth or sometimes striate [rarely verruculose], glabrous or pubescent with glandular and/or nonglandular hairs; exocarp membranaceous, sometimes fragile and bursting irregularly; mesocarp thin or thick, ± resinous, sometimes also waxy; stone ± laterally compressed, smooth or ridged, sometimes bumpy, with thick, bony endocarp. Seed ± laterally compressed, ovate to subreniform in outline; testa membranaceous; endosperm scanty or wanting; embryo large, generally transverse, with flat transverse cotyledons and a ± elongate radicle incurved upwards toward the hilum. (Including *Lobadium* Raf. [*Schmaltzia* Desv. ex Small emend. Greene], *Toxicodendron* Mill.). LECTOTYPE SPECIES: *R. Coriaria* L.; see E. L. Greene, Leafl. Bot. Obs. Crit. 1: 114.

1905. (Name Latin, from Greek, *rhous* or *rhoys*, an ancient name for the Sicilian sumac, *R. Coriaria*; etymology obscure.)

A genus of over 150 species, primarily of the warm-temperate areas of both hemispheres, but extending into tropical and cold-temperate regions. The genus seems to be somewhat heterogeneous, and its taxonomy is difficult and confused. Both the four sections of Engler, based mainly on fruit morphology, and some fractions of the sections have been treated by Barkley as distinct genera. Although thorough investigations may perhaps justify at least some of these segregations, a complete study of the entire complex is necessary. The relationships appear to be reticulate, with species showing transitions in respect to most characteristics used for delimiting genera, and many supposed differences are based on incomplete observations or on insufficient material. At present it appears preferable to regard *Lobadium* Raf. and *Toxicodendron* Mill. as subgenera of *Rhus.*

Subgenus RHUS (subg. *Sumac* Torr. & Gray, 1838; § *Trichocarpae* Engler, 1881, in part), includes about ten species (primarily of warm-temperate North America and Eurasia) with flowers in terminal thyrses expanding after the leaves; thin, narrow, caducous bracts and bractlets; reddish drupes covered with ± club-shaped hairs and sometimes also with slender red to colorless nonglandular hairs; exocarp adherent to the resinous mesocarp and both easily detachable from the smooth, bony stone; and odd-pinnate leaves. All (at least in our area) are innocuous trees or shrubs. The northeastern American *Rhus typhina* L. (*R. hirta* (L.) Sudw.); the wide-ranging *R. glabra* L.; the very local *R. Michauxii* Sarg., of the Piedmont of North Carolina and Georgia; and the widely distributed *R. copallina* L. (including *R. leucantha* Jacq. and *R. obtusifolia* Small) represent the subgenus with us. Presumed natural hybrids of *R. glabra* × *typhina* have been known as *R. glabra* var. *borealis* Britt. (*R. borealis* (Britt.) Greene, *R. pulvinata* Greene), while *R. Ashei* (Small) Greene, recorded from the Piedmont of North Carolina, appears to be *R. glabra* × *Michauxii.* A careful study of variation in *Rhus copallina* (including vars. *copallina*, *latifolia* Engler, *leucantha* (Jacq.) DC., *obtusifolia* (Small) Fern. & Grisc., and *lanceolata* Gray [the last supposedly beyond our range] is much needed.

Subgenus LOBADIUM (Raf.) Torr. & Gray, 1838 (*Lobadium* Raf., 1819; *Schmaltzia* Desv. ex Small emend. Greene, 1905; *Rhus* § *Trichocarpae* Engler, 1881, in part; including *Styphonia* Nutt. and *Rhoeidium* Greene) includes species with flowers in short, dense, spikelike racemes usually forming terminal panicles expanding before the leaves (more rarely in axillary and/or terminal panicles expanding after the leaves); leathery, broad, persistent (rarely caducous) bracts and bractlets; drupes essentially as in subg. RHUS (but in some with the inner layers of mesocarp, striate by numerous resin ducts, remaining attached to the stone); and leaves 3-foliolate (in ours). The nearly 35 species, all innocuous shrubs [or trees], are centered in Mexico, extending north to Alberta and Quebec and south to Costa Rica. The northeastern *Rhus aromatica* Ait. var. *aromatica* (*Schmaltzia crenata* (Mill.) Greene), fragrant sumac, with precocious flowers, is of frequent occurrence on calcareous soils through our area southward to northwestern Florida and westward and northward beyond our limits. The var. *serotina* (Greene) Rehd. (*R. trilobata* Nutt. var. *serotina* (Greene) Barkley), with coetaneous flowers, occurring north and west of our region has been recorded from Arkansas. Hybridization between *R. aromatica* and the largely western American *R. trilobata*, as well as between some other species of the subgenus in areas of overlap, is believed possible (Barkley, 1937).

Subgenus TOXICODENDRON (Mill.) K. Koch, 1853, emend. Gray, 1856 (§ *Venenatae* Engler; § *Trichocarpae* Engler, as to *R. trichocarpa* Miq.; *Toxicodendron* Mill., 1754), comprises species with flowers in axillary thyrses expanding after the leaves; caducous bracts; no bractlets; yellow-white to -brown, usually smooth drupes, glabrous or pubescent with nonglandular hairs; usually thin, fragile exocarp which finally breaks, exposing the whitish, waxy mesocarp striate with black resin ducts; stones bony with a few riblike longitudinal ridges (or more rarely smooth); and leaves 3-foliolate or odd-pinnate [rarely simple]. The nearly 15 species, including trees, shrubs, or woody vines climbing by aërial roots and all producing a contact dermatitis, are largely of temperate North American–eastern Asiatic distribution, but with at least *R. striata* Ruiz & Pavon in tropical South America (Colombia, Venezuela, Peru). Our representatives are *R. Vernix* L. (*Toxicodendron Vernix* (L.) Kuntze), poison sumac, a shrub or small tree with odd-pinnate leaves, chiefly of the Coastal Plain; *R. radicans* L. (*T. radicans* (L.) Kuntze), poison ivy, $2n = 30$; and *R. Toxicodendron* L. (*T. Toxicodendron* (L.) Britt., *T. quercifolium* (Michx.) Greene), poison oak. *Rhus radicans* is both widely distributed and variable, and a number of varieties and forms have been recognized. According to Gillis (1962, p. 21), the eastern Asiatic *R. orientalis* (Greene) Schneider is conspecific with *R. radicans*. The external and internal morphology of *R. diversiloba* Torr. & Gray, western poison oak, $2n = 30$, is better known than that of other species.

The genus seems to be rather uniform in regard to floral morphology and biology. Flowers are usually unisexual and the species dioecious, but the occasional occurrence of bisexual flowers, and consequent polygamy, is probable. Various Hymenoptera (especially short-tongued bees) and Diptera have been recorded as the most frequent visitors. Chalazogamy has been found in all the species thus far investigated. The chromosome number $2n = 30$ has been recorded for three or four species of subg. TOXICODENDRON, $2n = 32$ for the North African *Rhus oxyacantha* Schousb. ex Cav. (*Searsia* Barkley; § *Gerontogeae* Engler). Seed dispersal by animals, especially by birds, apparently may be assumed for the genus as a whole.

Dried leaves of *Rhus glabra*, *R. typhina*, and *R. copallina*, and especially of *R. Coriaria*, are important sources of tannin. Leaf galls produced on *R. javanica* L. (*R. chinensis* Mill., *R. semialata* Murr.) yield tannin which is also sometimes used in making ink. The Asiatic *R. verniciflua* Stokes and sometimes *R. succedanea* L. are sources of natural lacquer. Commercial vegetable wax is obtained from the mesocarp of fruits of the last and some allied species.

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COMPARATIVE ANATOMY OF THE LEAF-BEARING CACTACEAE, VI

THE XYLEM OF PERESKIA SACHAROSA AND PERESKIA ACULEATA

I. W. BAILEY[1]

THE MOST PRIMITIVE living representatives of the Cactaceae have been considered to be *Pereskia sacharosa* Griseb. and *P. aculeata* Mill. Such a conclusion is based largely upon the claim that the flowers of these species have "superior" ovaries (Berger, 1926; Buxbaum, 1953). It is of interest to determine whether evidence from other parts of the plants supports such a phylogenetic generalization. Evidence from the xylem is considered in this paper. Additional evidence from other parts of the plants will be considered subsequently.

PERESKIA SACHAROSA

During its earlier stages of growth, this species is considered to be a shrub which ultimately may become a small tree eight meters high. As in the case of other wide-ranging putative species of *Pereskia*, plants from different localities exhibit more or less conspicuous differences in their leaves, general habit of growth, spination, and floral characters. At present, it is uncertain whether such differences are produced by different environmental influences or are due to genetic differences at racial or specific levels.

My anatomical specimens of this species have been obtained from the following sources: 1) From a wild plant collected by Carenzo and Legname in Jujuy Province, Argentina; 2) from a wild plant collected by Cárdenas in the Department of Cochabamba, Bolivia; 3) from a plant growing in the Missouri Botanical Garden; and 4) from a plant growing at the New York Botanical Garden. The ranges of variability in the xylem of the four plants are so closely similar as to provide no reliable anatomical criteria for differentiating one plant from the others.

In the outer secondary xylem of larger stems the vessels occur singly and in small clusters (FIGS. 1, 3), but tend at times in their overall arrangement to exhibit more or less conspicuous concentric patterns (FIG. 1). The wood parenchyma is scanty paratracheal (FIG. 3), having lignified walls. The multiseriate rays are composed of cells of varying size, form, and orientation which likewise have comparatively thick lignified walls

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(FIGS. 3, 5). Where crystals of calcium oxalate are present in ray cells they occur singly or as several independent ones, druses being absent. The distribution of vessels and wood parenchyma in comparable secondary xylem of roots is similar (FIG. 2) but the multiseriate rays are broader (FIGS. 2, 6). The rays, as in those of the stem, may be composed, throughout their radial extension, of cells with lignified walls. In some cases, however, the first-formed multiseriate rays in the center of the root are composed at first of cells having thin, unlignified walls. These cells differ from subsequently formed lignified ones in containing isotropic granular contents, rather than starch.

It is evident that the secondary xylem in stems and roots of *Pereskia sacharosa* is of a phylogenetically highly evolved structure such as occurs in trees and shrubs of normal form in a number of other dicotyledonous families. For a discussion of pitting, perforation plates, and other structures visible under higher magnification, the reader is referred to the fourth paper of this series (Bailey & Srivastava, 1962).

There are certain ontogenetic changes in rays that should be considered in dealing with the secondary xylem of the leaf-bearing Cactaceae. The multiseriate rays of dicotyledons commonly exhibit significant changes in passing from the first-formed to the later-formed secondary xylem (Chattaway, 1933; Barghoorn, 1940, 1941a). The first-formed part of multiseriate rays adjacent to gaps in the primary body (particularly of stems having elongated internodes) frequently tend to be narrow and vertically extensive as seen in tangential longitudinal sections (FIG. 8). During subsequent radial extension of such rays they tend to become wider and dissected sooner or later into vertically less extensive parts which ultimately may assume fusiform outlines (FIG. 6). Of the various cytological changes involved in the modification of such rays the transformation of ray initials into fusiform cambial initials is particularly significant. Furthermore, the dissected parts of the original rays tend to be laterally displaced during increase in girth of the cambium. In addition, the cells of the rays generally vary more or less in form and orientation during successive modifications of the multiseriate rays, the cells in the first-formed part of the rays tending to have a longer vertical axis (i.e., being "erect"), whereas in subsequently formed parts of the rays they become more or less isodiametric or even radially extensive (i.e., "procumbent"). Such changes in multiseriate rays vary in degree, and may be precocious and relatively abrupt, gradual, or considerably delayed, varying at least in part with different rates of growth and the enlargement of stems.

In roots of *Pereskia sacharosa*, the first-formed multiseriate rays broaden conspicuously during their radial extension outward (FIG. 2). In their first-formed part they are not only much narrower, but also more extensive vertically. During their radial extension outward they tend to become dissected into lower derivatives which assume fusiform outlines as seen in tangential longitudinal sections (FIG. 6). In stems from some parts of a mature plant, the first-formed parts of the rays are narrower and more extensive vertically, but subsequent widening and dissection of the rays is much less conspicuous than in roots (compare FIGS. 1 and 2, 5 and 6). In other stems from the same plant, the first-formed rays of the secondary xylem are broader, subsequently becoming narrower (FIG. 4) and then broadening somewhat in the later-formed xylem (FIG. 3).

Such variations in the form of the multiseriate rays appear to be correlated with differences in the development of the primary body. The diameter of the primary vascular cylinder and pith commonly varies in different stems of the same plant from three millimeters to one centimeter. As seen in transverse sections, the two extreme forms of eusteles may be composed of the same number of fascicular and interfascicular parts. Although there is some variation in the breadth of fascicular parts, the conspicuous differences in circumference of the eusteles appears to be due largely to differences in the width of interfascicular parts (i.e., parenchymatous gaps). In the case of the smaller young stems, cambial activity develops precociously in the parenchyma of the narrow gaps, and the multiseriate rays of the secondary xylem are relatively narrow when first formed. On the contrary, in the larger young stems the parenchymatous gaps tend to widen by division and transverse expansion of their constituent cells for a considerable time after cambial activity is initiated in the fascicular parts of the eustele (FIG. 4). It should be noted in this connection that the widening of the interfascicular parts and the delayed initiation of cambial activity within them leads, not only to a conspicuous increase in the circumference of the eustele, but also permits a marked increase in the diameter of the pith. Furthermore, when multiseriate rays of the secondary body are initiated they tend at first to be considerably broader than in the case of smaller stems (FIG. 4).

In both stems and roots of *Pereskia sacharosa*, the parenchymatous cells of the first-formed part of the multiseriate rays are of "erect" form but are shorter than the fusiform initials of the cambium. Subsequent changes in the size, form, and orientation of the ray cells, as seen in radial longitudinal sections of the xylem, are precocious and abrupt. Most of the cells become more or less isodiametric, except on the sides of the rays and their upper and lower margins where they may retain an erect form. In addition, some radial tiers of slender cells of procumbent orientation tend to occur within the rays.

PERESKIA ACULEATA

This species is widely distributed in the West Indies and in eastern and northern South America. Because of the edibility of its fruits and leaves, its ornamental value in gardens, and its use in hedges, its original range has been considerably extended by man. It is therefore difficult at times to determine with certainty whether plants now growing in the wild (e.g., Florida or Mexico) are native or were introduced and escaped from cultivation.

The species is commonly described as a shrub, frequently producing long clambering branches and forming vines three to ten meters long (cf. Britton & Rose, 1919). The larger, older stems may have a diameter of two to three centimeters with a primary vascular cylinder and pith five to six millimeters in diameter. The ultimate terminal branches of mature plants are, in general, more numerous and more slender than those of *Pereskia sacharosa*, grading down in many cases to as little as two millimeters in diameter with correspondingly slender primary vascular cylinders and pith. Furthermore, in branches of comparable diameter, the eusteles of *P. aculeata* are composed of fewer fascicular strands and comparatively broader parenchymatous gaps. This conspicuous difference in the primary bodies of the two species appears to be correlated with the tendency of *P. aculeata* to have two-trace unilacunar nodes, whereas *P. sacharosa* commonly has four to six vascular strands at its unilacunar nodes. (For illustrations see Bailey, 1960.)

The young branches of *Pereskia aculeata* are commonly of two different forms: slender woody ones and broader, very succulent ones, referred to in Boke's (1954) developmental investigations as long shoots and spur shoots respectively. In the former stems cambial activity and the formation of secondary xylem are precocious, whereas in the latter stems the formation of secondary xylem is delayed and the thickness of the pith and cortex is relatively greater. At times, the most slender woody stems bear short, broad, highly succulent laterals. In such cases the slender woody stems have long internodes, whereas the succulent laterals have short internodes. These abrupt differences in external form and internal structure resemble those between long shoots (pycnoxylic [2]) and short shoots (manoxylic [2]) that occur in *Ginkgo biloba* L. (Gunckel & Wetmore, 1946a, 1946b) in *Cercidiphyllum japonicum* Sieb. & Zucc. (Titman & Wetmore 1955), and a number of other plants.

The structure of the secondary xylem of *Pereskia aculeata* varies markedly in different parts of a mature plant. As so frequently happens in scandent representatives of other dicotyledonous families, e.g., Hippocrateaceae, Icacinaceae, Schisandraceae, etc., many stems exhibit more or less abrupt transitions from first-formed, denser, more nearly normal secondary xylem to phylogenetically highly modified, softer, more porous forms of tissue. The denser, earlier-formed secondary xylem (illustrated in FIG. 7) resembles the secondary xylem of *P. sacharosa* (FIG. 7). The vessels, allowing for higher magnification, are of comparable size, form, and distribution. The wood parenchyma is scanty paratracheal and has strongly lignified walls. The multiseriate rays, although somewhat narrower than those of *P. sacharosa,* have thick, strongly lignified cell walls. On the contrary, the later-formed secondary xylem has much enlarged vessels, as well as radial rows of much smaller ones. In addition to scanty wood parenchyma about vessels in the denser parts, it has arcs or concentric zones of unlignified parenchyma. The cells of the broadened rays (compare FIGS. 2 and 3) are very thin, unlignified, and many of them contain druses (FIG. 16). Furthermore, the number of thick-walled libriform fibers is greatly reduced.

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[2] Using these terms as redefined by Titman and Wetmore.

In other stems, even from the same plant, the transition from normal dense to modified secondary xylem occurs at varying distances from the pith. The transition to xylem containing huge vessels may be abrupt or gradual (FIG. 11). Furthermore, the volume and distributional patterns of the unlignified[3] parenchyma varies markedly from stem to stem. In the xylem illustrated in FIG. 10, the unlignified parenchyma occurs in broad concentricities alternating with zones of strongly lignified tissue. The relatively narrow multiseriate rays, unlike those of FIG. 7, have lignified walls, except where they pass radially through the broad zones of unlignified parenchyma. In contrast to this, the outer secondary xylem in FIG. 11, although exhibiting a conspicuous enlargement of vessels has unlignified parenchyma that is confined to narrow arcs and concentricities.

The roots of *Pereskia aculeata* superficially resemble those of *P. sacharosa*, having numerous rapidly broadening multiseriate rays (compare FIGS. 2 and 14), but the ray cells of *P. aculeata*, many of which contain druses of calcium oxalate, differ in having thin, unlignified walls (FIG. 14). It should be noted in this connection that the first-formed ray cells in the center of some roots of *P. sacharosa*, although having thin unlignified walls, contain no druses and little if any starch. Furthermore, in roots, as in stems (FIGS. 8, 9), of *P. aculeata*, the multiseriate rays tend to remain vertically extensive, and in passing radially outward do not exhibit precocious and conspicuous dissection into laterally displaced parts as illustrated for *P. sacharosa* in FIG. 6. The unlignified rays of both roots and stems of *P. aculeata*, not only contain abundant druses (FIG. 16) but also at times varying numbers of mucilage cells (FIG. 17).

In many stems of *Pereskia aculeata*, owing to the breadth of the parenchymatous gaps in the eustele, the multiseriate rays tend to be broader when first formed than in the subsequently formed secondary xylem. As indicated in FIG. 11, this reduction in ray width resembles that which occurs in very stout young stems of *P. sacharosa* (FIG. 4). However, in the case of *P. aculeata*, the cells of the first-formed ray tissue tend to resemble fusiform cambial initials in their vertical extension (FIG. 12). In other words, the first-formed ray initials of the cambium resemble fusiform initials in size and orientation. Subsequent transverse divisions of the ray initials lead to the formation of less "erect" ray cells (FIG. 13) and ultimately to more or less isodiametric or somewhat procumbent ones. It should be noted in this connection that similarities between ray initials and fusiform initials occur in the first-formed cambium of some other dicotyledonous families (Barghoorn, 1941).

Tyloses are of sporadic occurrence in the vessels of *Pereskia aculeata*. In some stems, they are not only abundant but contain starch (FIG. 15).

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[3] The unlignified primary walls of leaf-bearing Cactaceae give a red coloration in sections stained with Haidenhain's haematoxylin and safranin. Therefore, in testing for lignification it is advisable to use the phloroglucin-HCl and Mäule reactions where unlignified walls remain colorless, as in FIGS. 10 and 14.

DISCUSSION

In the fourth paper of this series (Bailey & Srivastava, 1962) we discussed the finer structural details in derivatives of the fusiform initials of the cambium. We found that the ranges of variability of potential diagnostic criteria in the leaf-bearing genera *Pereskia*, *Pereskiopsis*, and *Quiabentia* are extensive, not only in different collections of the same taxon and in the same clone grown under different environmental influences, but also in different parts of the same mature plant. It is evident that the grosser anatomical features of *Pereskia aculeata* (e.g., size and distribution of vessels, abundance, distributional patterns. and internal structure of wood parenchyma, and the size, form and internal structure of the multiseriate rays) likewise vary markedly even in different parts of a single plant.

Anatomical surveys of the dicotyledons as a whole demonstrate that the xylem of vines and lianas commonly exhibits trends of highly advanced phylogenetic modification, i.e., in comparisons with the structure of related trees and large woody shrubs of the same genus, family, or order. This obviously occurs in *Pereskia aculeata* in contrast to *P. sacharosa*. Thus, although *P. sacharosa* may have retained a form of xylem characteristic of ancestral leaf-bearing cacti, the internal structure of stems and roots of *P. aculeata* negates any possibility of considering this species to be the most primitive living representative of the Cactaceae. Therefore, in searching for such a primitive representative, it will be of interest in succeeding papers of this series to compare the internal structure of *P. sacharosa* with that of other arborescent and woody, shrubby species of *Pereskia*.

The tendencies in the xylem of *Pereskia aculeata* toward the formation of parenchymatous cells having thin, unlignified walls, with concomitant inclusions of druses, are extensively developed in roots of Andean pereskias and in stems of *Pereskiopsis* and *Quiabentia*. They seem to be correlated in some manner with increasing succulence and merit detailed investigation. Furthermore, the tendency in some stems of both *P. sacharosa* and *P. aculeata* toward increase in circumference of the primary vascular cylinder and in diameter of the pith after cambial activity is initiated in the fascicular parts of the stele is a phenomenon which becomes greatly exaggerated in many representatives of the Cactaceae. It is a conspicuous feature in dealing with the larger basal stems of pereskias from Southern Mexico and Central America and in stems of certain species of *Pereskiopsis* and *Quiabentia*.

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EXPLANATION OF PLATES

PLATE I

FIGS. 1–3. Transverse sections of the secondary xylem of *Pereskia sacharosa*. 1, Outer xylem from stem 7 cm. in diameter, × 11. 2, Xylem from root 3 cm. in diameter, × 11. 3, Xylem of FIG. 1 more highly magnified, × 88.

PLATE II

FIGS. 4–6. Transverse and tangential longitudinal sections of *Pereskia sacharosa* showing structure of multiseriate rays. 4, Transverse section of inner xylem from a stem 7 cm. in diameter, × 34. 5, Tangential section from outermost xylem of FIG. 1, × 43. 6, Tangential section of outermost xylem of FIG. 2, × 43.

PLATE III

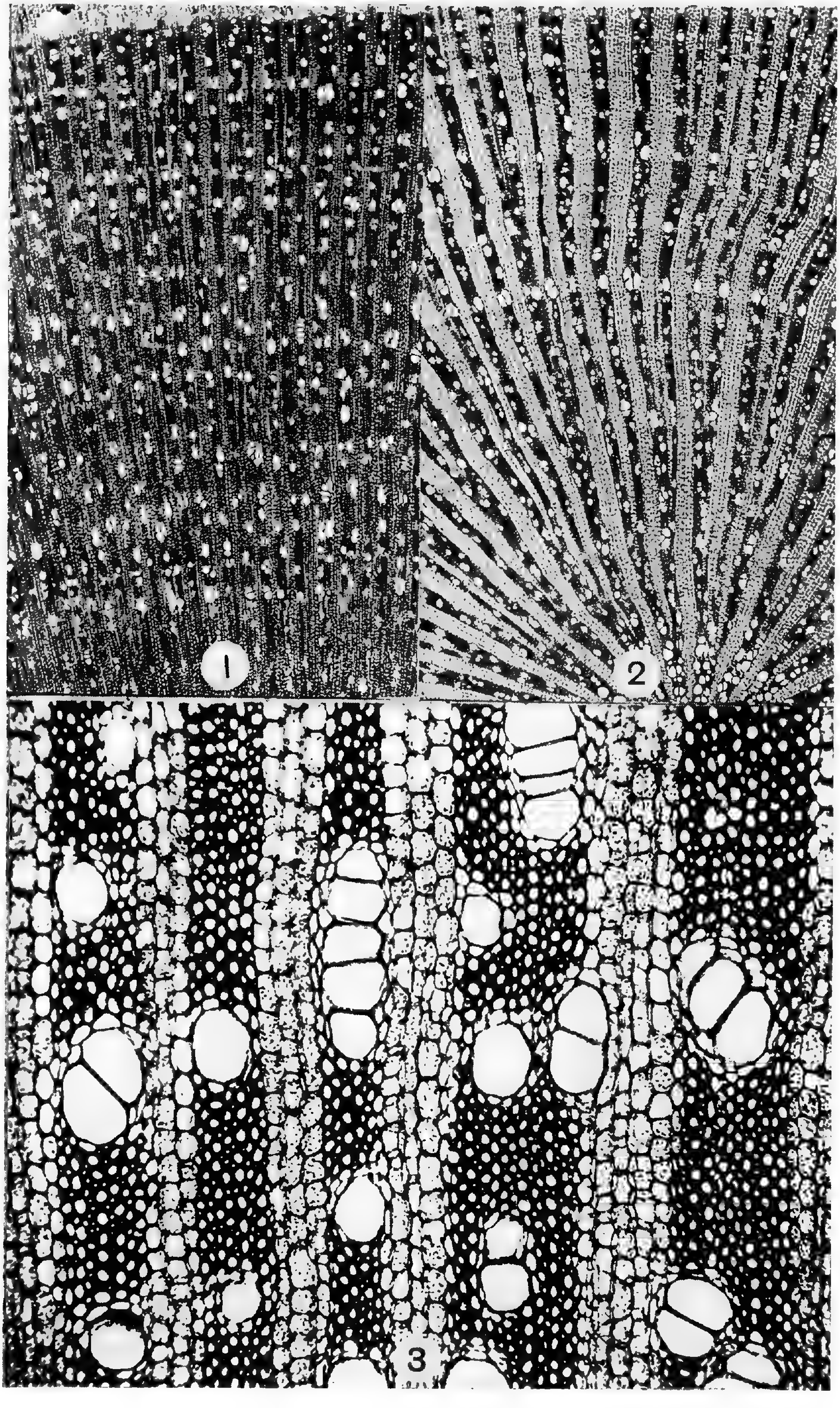
FIGS. 7–9. Transverse and tangential longitudinal sections of *Pereskia aculeata* from stem 2.5 cm. in diameter. 7, Transverse section of xylem, × 34. 8, Tangential section of denser xylem, × 43. 9, Tangential section of outer, softer xylem, × 43.

PLATE IV

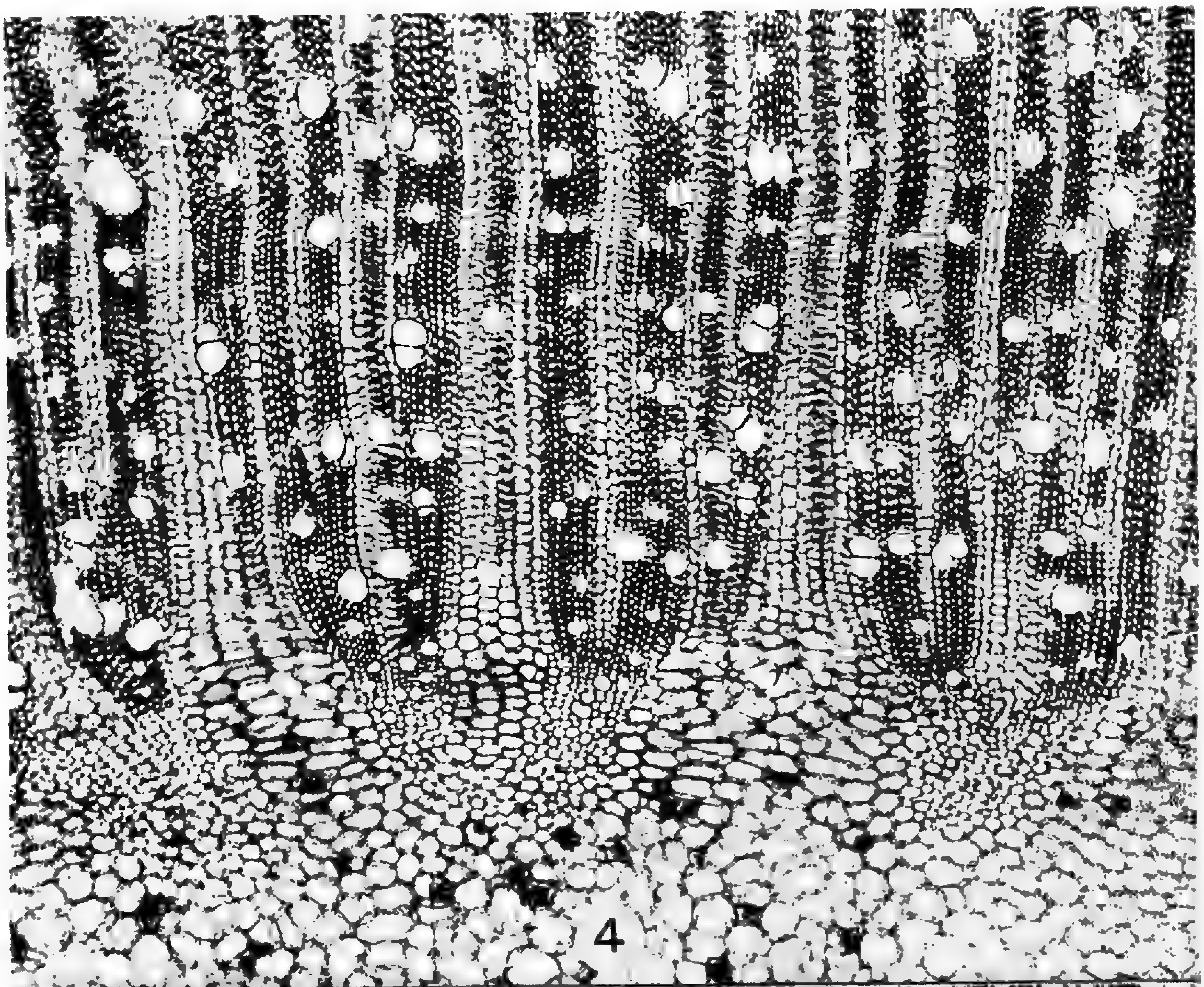
FIGS. 10–13. Transverse and longitudinal sections of the xylem from stems of *Pereskia aculeata*. 10, Transverse section treated with phloroglucin-HCl, showing concentric zones of unlignified parenchyma (white), × 34. 11, Transverse section of inner xylem, showing changes in ray structure and narrow arcs of thin-walled wood parenchyma, × 43. 12, Tangential section of first-formed secondary xylem, × 88. 13, Radial section showing transitional changes in the height of ray cells, × 88.

PLATE V

FIGS. 14–17. Transverse and tangential longitudinal sections of *Pereskia aculeata*. 14, Transverse section of root, treated with phloroglucin-HCl, showing unlignified multiseriate rays (white), × 34. 15, Transverse section of vessel, showing starch in tyloses, × 107. 16, Part of FIG. 9, more highly magnified, showing druses in multiseriate ray, × 107. 17, Tangential section of xylem, showing mucilage cells (arrows) in multiseriate ray, × 107.



Bailey, Leaf-bearing Cactaceae, VI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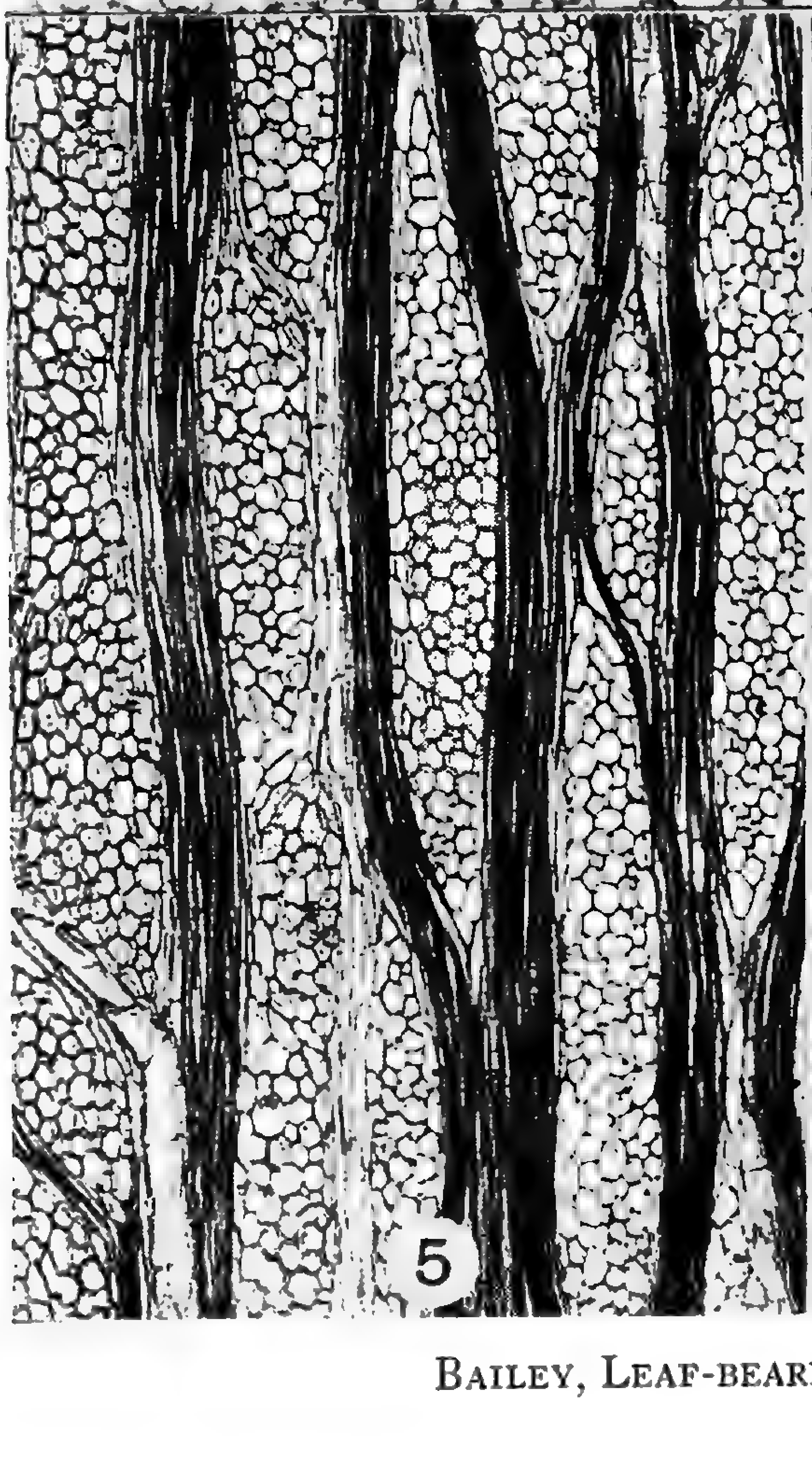
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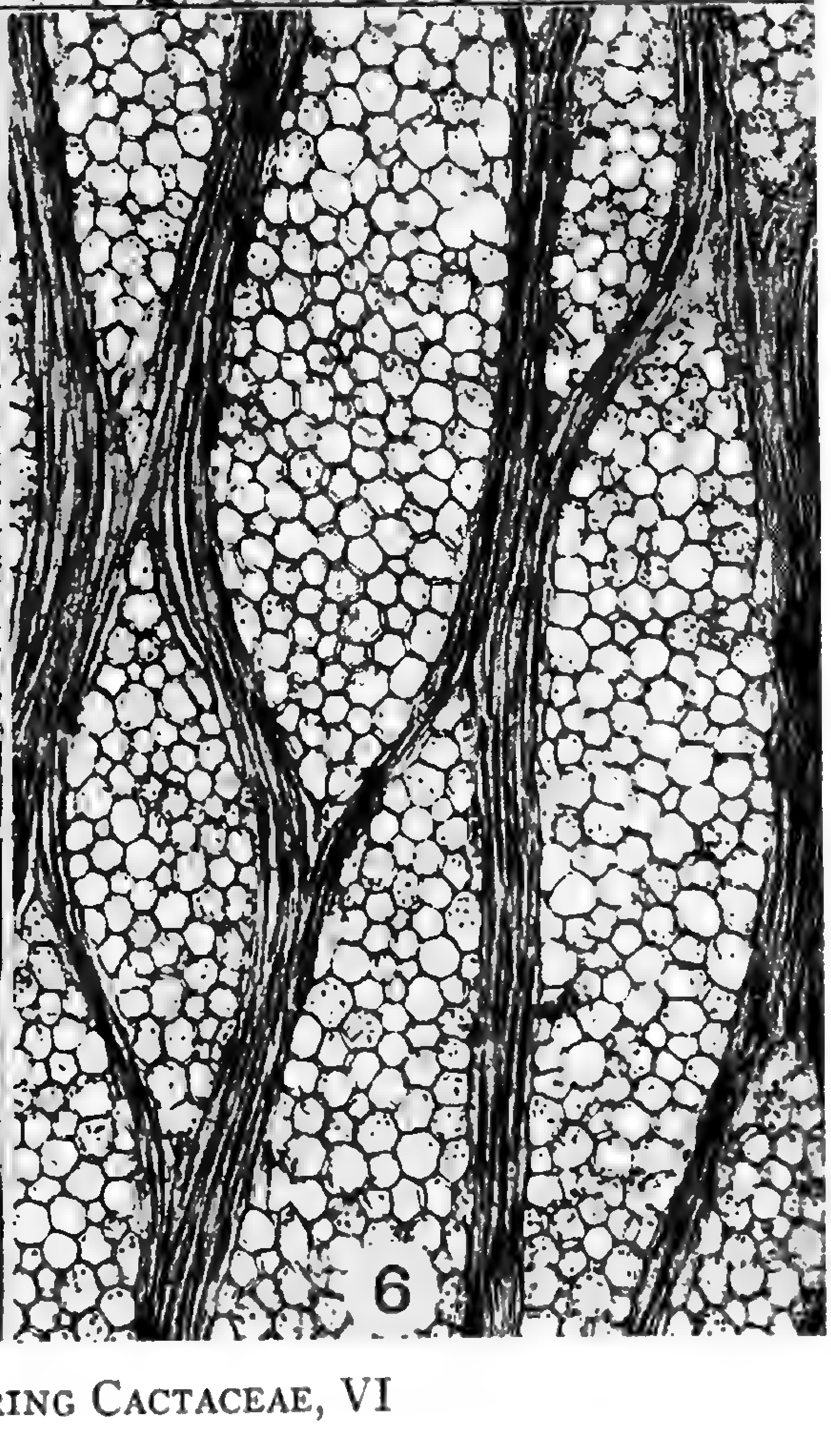
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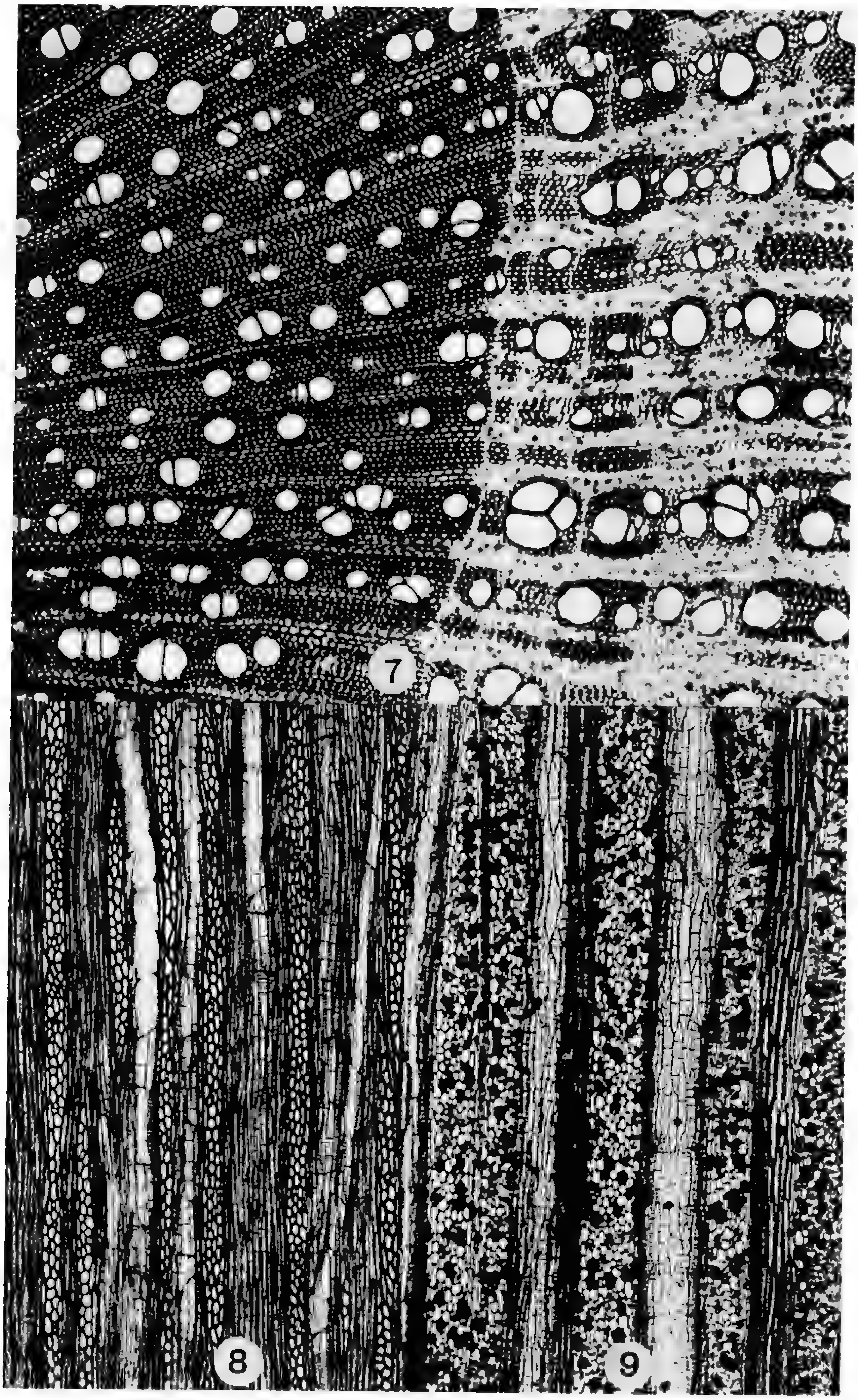

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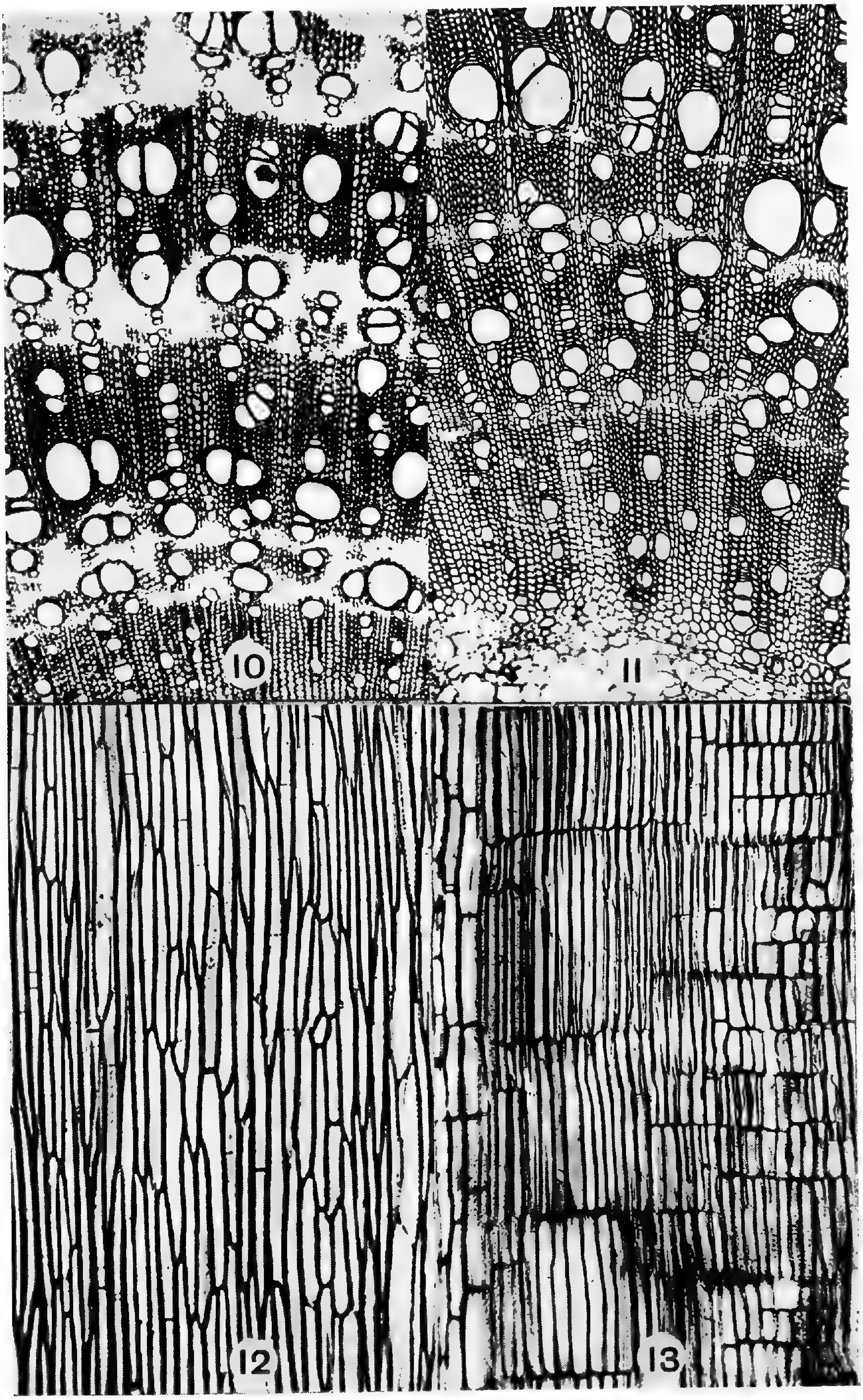

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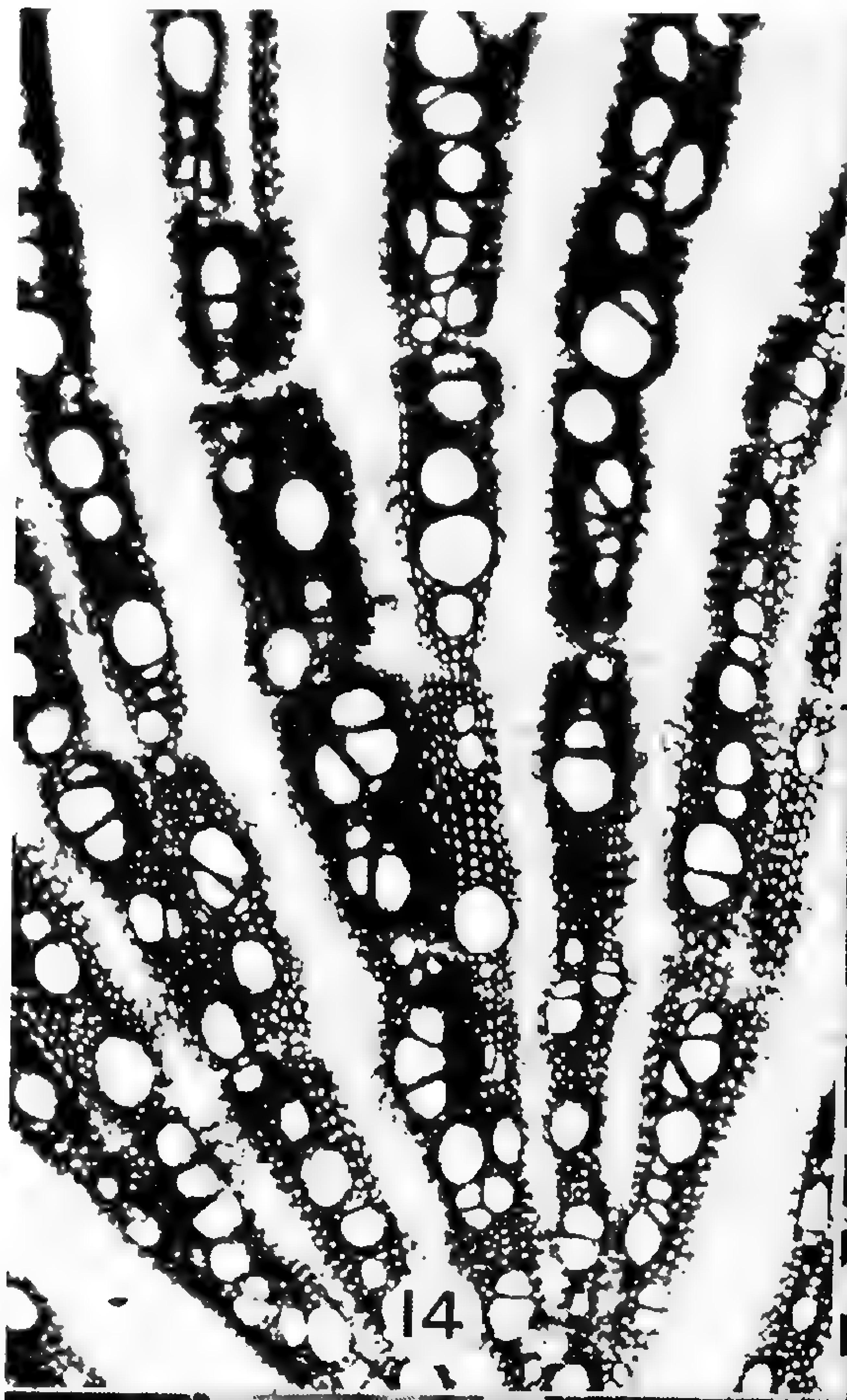
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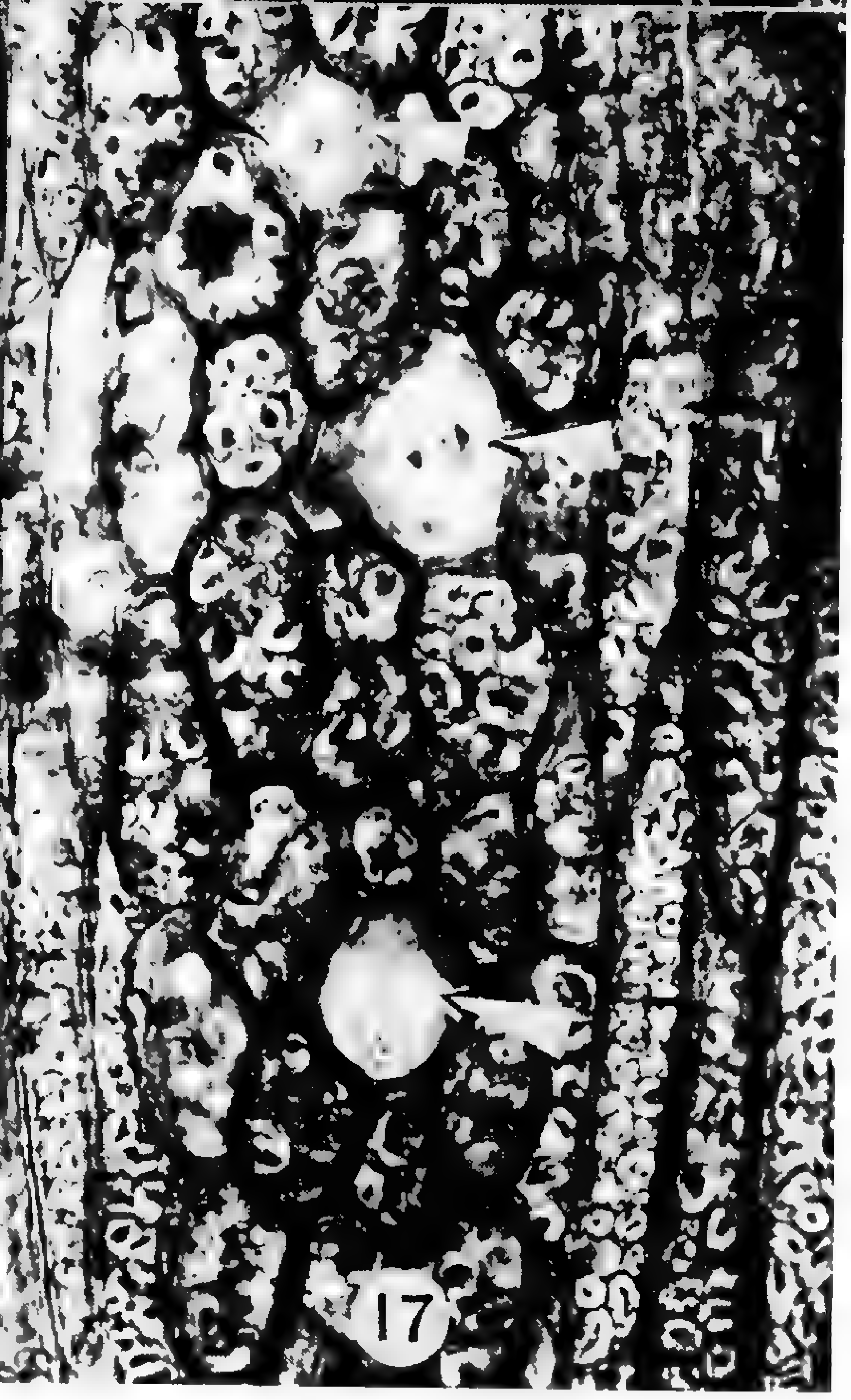
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BAILEY, LEAF-BEARING CACTACEAE, VI

SOME GUTTIFERAE OF THE LESSER ANTILLES

RICHARD A. HOWARD

IN THE COURSE of preliminary work leading towards the preparation of a flora of the Lesser Antilles, I have encountered several nomenclatural problems in the genera *Clusia*, *Calophyllum*, and *Rheedia*. The following notes are presented as discussion and clarification of these problems.

I have received most generous assistance from Miss Alicia Lourteig, Mr. George Proctor, and Mr. James Dandy in checking historic specimens and illustrations in European herbaria. It is also with gratitude that I acknowledge the support of this work through a grant from the National Science Foundation.

CLUSIA

Britton and Millspaugh (Bahama Fl. 281. 1920) and Hitchcock and Green (Prop. Brit. Bot. 160. 1929) selected *Clusia major* L. as the type species of the genus. More recently the *Index Nominum Genericorum* formalized this status. Unfortunately, *Clusia major*, proposed by Linnaeus in the first edition of *Species Plantarum*, was abandoned by him in the second edition and has not been used in floras or monographs in the intervening 209 years. In the interest of stability of well known specific names, one questions the value and the necessity of resurrecting such an epithet. There is, however, no option in the present rules of nomenclature, and so *Clusia major* L. must replace the better known *Clusia alba* Jacq. In the process of this investigation, it became apparent that the nomenclature of nearly every species of *Clusia* in the Lesser Antilles was involved, and several others in the Greater Antilles presented one or more additional problems. These will be discussed in the following paragraphs.

Clusia major L.

In the first edition of *Species Plantarum* (p. 509. 1753), Linnaeus described two species of *Clusia*, namely, *C. major* and *C. minor*. The protologue of *C. major*, with the modern equivalents of its supporting literature given in brackets, is the following:

> 1. CLUSIA foliis aveniis. *major.*
> Clusia flore albo, fructu coccineo. *Plum. gen.* 21. [*C. alba* Jacq.]
> Cenchramidea arbor saxis adnascens, obrotundo pingui folio, fructu pomiformi. *Pluk. alm.* 92 *t.* 157. *f.* 2. [*C. plukenetii* Urb.]
> Terebinthus folio singulari non alato rotundo succulento, flore pallide luteo. *Sloan. jam.* 167. *hist.* 2. *p.* 97 *t.* 200. *f.* 1 [*C. flava* Jacq.] *Raj. dendr.* 51 [unknown]

β. Clusia flore roseo major, fructu subviridi. *Plum. gen.* 21.
[*C. rosea* Jacq.]
γ. Clusia alia minor: flore albo, fructu virescente. *Plum. gen.* 21. [possibly *C. plumieri*, or not known according to Planchon & Triana]

In considering this species, the specimens in the Linnaean herbarium are of little assistance. There are five sheets included under the name of *Clusia*. Sheet 1224.1 does not appear to be a *Clusia*. Sheet 1224.2 is annotated, "*Clusia alba* H. Aublet vix Linnaei J. E. S." The specimen is probably a *Clusia*. Sheet 1224.3 bears only two detached leaves. One is obviously sessile and is probably *Clusia mangle* L. C. Rich. ex Planch. & Triana. The other leaf has a petiole and is annotated as *Clusia flava* ex Herb. Jacq. The remaining two sheets, 1224.4 and 1224.5, represent *Mammea americana* and *Chrysobalanus icaco* respectively.

In 1760, in his *Enumeratio Systematica Plantarum*, Jacquin described four species of *Clusia* but made no reference to *Species Plantarum*. The species are briefly but validly described and each carries a reference to an illustration. *Clusia rosea* has the reference "*Catesb. Car. 2. t.* 99."; *C. alba* carries "*Plum. ic.* 87. *f.* 1."; *C. flava* bears "*Sloane hist. Jam.* 2. *t.* 200. *f.* 1."; and *C. venosa* is supported by a reference to "*Plum. ic.* 87. *f.* 2." The species published in Jacquin's *Enumeratio* were normally based on material he collected in the West Indies. Mr. Dandy has pointed out in correspondence that Jacquin sometimes cited published figures from Browne, Sloane, Catesby, and others, but in doing this his intention was to provide the reader with what he supposed was an illustration of his own plant. In his later *Selectarum Stirpium Americanarum Historia* the same species were usually described at length, more complete references were given, type localities were cited, and often a figure drawn from his own material was published.

Unfortunately, Jacquin's herbarium was badly damaged while in the West Indies. Although the remains were purchased by Sir Joseph Banks and are in the herbarium of the British Museum, there is no material of *Clusia* available. Jacquin, in his *Selectarum*, in 1763, did publish complete descriptions of the four species of *Clusia*, along with illustrations of two of them, previously briefly described in the *Enumeratio* of 1760. It is necessary to accept 1760 as the date of publication of Jacquin's species but to typify them with the data and illustrations of 1763. Three of Jacquin's species, *C. alba*, *C. rosea*, and *C. flava* represent segregates from Linnaeus' *C. major*. The fourth species, *C. venosa*, appears to be identical with Linnaeus' *C. minor* and will be discussed later. In the *Selectarum* in 1763 Jacquin gave for his *C. alba* the basic polynomial "Clusia foliis aveniis" and the reference "*Linn. sp. pl.* I. *p.* 509," as well as the reference "Clusia flore albo, fructu coccineo. *Plum. gen.* 21. *ic.* 87. *f.* I." although he did not use the Linnaean specific epithet. Jacquin's illustration clearly indicates the same plant as in Plumier's unpublished plate (FIG. 1) which was copied (with alterations) for the Burmann edition.

Fig. 1. Lectotype of *Clusia major* L. Fig. 85, Dessin aquarellé "Clusia flore albo, fructu coccineo" from Manuscript No. 6, Plumier, *Botanicum Americanum*, *t. VI*. Courtesy of the Muséum National d'Histoire Naturelle, Paris.

There is no doubt in my mind that Jacquin was renaming *Clusia major* by dividing this composite species and assigning new names to all three parts of it. In the second edition of *Species Plantarum*, also published in 1763, Linnaeus accepted Jacquin's divisions of *Clusia major*, used Jacquin's specific names, credited him, and cited Jacquin's publications. By this act *Clusia major* disappeared and was never again used until Britton and Millspaugh cited it as the type species of the genus.

In 1860, Planchon and Triana (Ann. Sci. Nat. IV. 13: 318–376. 1860) published a detailed treatment of *Clusia* in a larger work considering the Guttiferae as a whole. They concluded that *Clusia major* should be regarded as a *nomen confusum* and cited *C. major* in part under each of the three species mentioned by Jacquin and accepted by Linnaeus. Other monographers have followed suit.

Although Hitchcock and Green (*loc. cit.*) selected *Clusia major* as the type species of the genus, they qualified this by stating "senus *C. rosea* Jacq." The *Index Nominum Genericorum* refers to the Hitchcock and Green selection. The qualification is obviously incorrect, for Jacquin's application of the basic references and illustration of *C. major* is to *C. alba* Jacq.

The typification of *Clusia major* must rest on Jacquin's selection of the Linnaean reference to Plumier's work. The plant in the Linnaean herbarium annotated by J. E. Smith as "Clusia alba H. Aublet vix Linnaeus" is neither the plant Jacquin described, nor does it correspond to the earlier Plumier description. Specimens collected by Plumier exist but none is available for the genus *Clusia*. Planchon and Triana selected as basic material an unpublished plate of Plumier (FIG. 1) but noted that the Burmann reproduction of this plate contained inaccuracies and excluded the flower and the analytical drawing. Thus the choice of a type then is between a previously unpublished plate and the illustration of *C. alba* published by Jacquin. I prefer the former, now published in this paper, to detract a bit from the long established status of *C. alba*.

Clusia major L. (syn. *C. alba* Jacq.) appears to be characterized by the elongate fruits borne on a cymose inflorescence which has a short peduncle. The species is represented by recent collections of material of the Lesser Antillean islands from St. Eustatius, St. Kitts, Montserrat, and Antigua, southward to St. Vincent. Urban's *C. plukenetii* is similar in having a much elongated peduncle to the cymose inflorescence and a globose fruit. Urban cited a collection from Martinique (*Duss 1829*) which I have not seen. I have seen more recent material from Barbados (the type locality) and St. Lucia which agrees with Urban's description. Regrettably, considerable variation is found in the shape of the fruits of *Clusia major*. Although the length of the peduncle appears to be a reliable difference between these species, additional field study is necessary to determine if two taxa are truly represented.

Clusia flava Jacq.

There is no confusion in the use of this name. Linnaeus (Sp. Pl. 509. 1753) included a Sloane reference (Hist. Jam. 2. *t.* 200, *f.* 1.) in the literature cited with the original publication of *Clusia major.* Jacquin (Enum. 34. 1760; Select. 272. 1763) cited the same reference under the name *C. flava.* In the second edition of *Species Plantarum* (p. 1495. 1763) Linnaeus credited the epithet to Jacquin and cited as supporting literature references to Jacquin (1763), Sloane, and Browne. Fawcett and Rendle (Fl. Jam. **5**: 193, 194. 1926) selected as the lectotype the Browne specimen in the Linnaean Herbarium. Presumably this is part of sheet 1224.3 and is the solitary detached leaf on the right-hand side.

Fawcett and Rendle cited the distribution of *Clusia flava* as Jamaica, Barbados, Grand Cayman, and the Florida Keys. The species is indeed well represented by recent collections from Jamaica and has been recollected recently by George Proctor on Grand Cayman (*Proctor 15141* [GH]). The occurrence of this species in Barbados is not supported by specimens in any herbarium collections I have seen. The reference to its occurrence in the Florida Keys is apparently obtained from the writings of Nuttall (N. Amer. Sylva 2: 58. *pl. 77.* 1859) who stated of *Clusia flava,* "This singular and splendid tree is a native of Jamaica, and Cayenne in South America, where it is found among rocks on the declivities of mountains. We have now also to record it as a native of Key West in Florida, where it has recently been found, with so many other tropical productions, by Dr. Blodgett." The illustration given by Nuttall is clearly that of *C. flava*; however, there are no supporting herbarium vouchers cited and one wonders if the illustration was not made from other herbarium material. Blodgett's collections are preserved in the herbarium of the New York Botanical Garden where there are two sheets labelled "Clusia flava" collected by Dr. Blodgett. One sheet bears the common name "Bull Bay" and is from Pine Key. The other sheet without a common name was collected on Key West. Both specimens are sterile; however, both have heavier leaf blades than does *C. flava* and both specimens, I believe, should be referred to *C. rosea.* In further reference to Nuttall's statement, I have seen no material of *C. flava* from Cayenne. *Clusia flava* appears to be restricted to Jamaica and Grand Cayman.

Fawcett and Rendle and authors of other modern floras of the Antilles do not accept the two varieties of *Clusia flava* proposed by Planchon and Triana (*q.v.*).

Clusia rosea Jacq.

This species was described briefly by Jacquin (Enum. 34. 1760) with the supporting citation "*Catesb. car.* 2, *p.* 99. *t.* 99." In the *Selectarum* (270. 1763) Jacquin supplied the additional references of "*Plum. gen.* 21." and "*Pluk. alm.* 92. *t.* 157. *f.* 2." and gave a full description. In the first edition of Catesby's work (1743), the plant is described and illustrated with white petals. In the second edition (1754), the illustration shows rose-colored petals. The text refers to the petals as "white with rose streaks." Jacquin did not illustrate the species in his *Selectarum*, but he reported it to be from Santo Domingo. In 1926, Fawcett and Rendle selected as the "type" the Bahama specimen collected by Catesby and now in the herbarium of the British Museum.

In modern floras, *Clusia rosea* is reported to occur in Florida, the Bahamas, the Greater and Lesser Antilles, Trinidad, Central America, and Venezuela. I have not seen all of the specimens cited by various authors for this species but a study of many specimens labeled *C. rosea* led to the conclusion that it occurs only in Southern Florida, the Bahamas, the Greater Antilles (Cuba, Jamaica, Hispaniola, and Puerto Rico), and the Virgin Islands (St. Thomas, St. Martins, St. Jan, and Anguilla). All of the material I have seen from Trinidad is best referred to *C. palmicida* L. C. Rich., although I have some doubt about the application of that name. The specimens labeled *C. rosea* from northern South America and from Central America do not represent that species as typified by the Catesby plant from the Bahamas.

Clusia plukenetii Urb.

Both Jacquin (Select. 270. 1763) and Linnaeus (Sp. Pl. ed. 2. 1495. 1763) cited the polynomial by Plukenet in the references given for *Clusia rosea*. Fawcett and Rendle (Fl. Jam. **5**: 192. 1926) did the same. Urban, in 1908 (Symb. Antill. **5**: 432.), described *C. plukenetii*, gave the Plukenet reference and polynomial, and cited specimens from Martinique, St. Lucia, and Barbados, but did not designate a type. The Plukenet reference is to a poor illustration of a plant reported to occur in Barbados. It shows a branch with alternate leaves except for two very small leaves at the apex of the stem. Mr. George Proctor has informed me that a specimen of *Clusia* credited to Plukenet is in the Sloane Herbarium (Vol. 95, p. 152, upper right). It consists of only three leaves but is probably the holotype of Plukenet's polynomial and therefore of Urban's species. The common name of "Balsam apple" reported by Plukenet is appropriate for the genus *Clusia*. This species has been discussed under *C. major*. It is not comparable to *C. rosea*, and the name should not be used in the synonymy of that species as it has been by many recent authors.

Clusia minor L.

The protologue of this species as given by Linnaeus is the following:

2. CLUSIA foliis venosis, *minor*
Clussa, flore roseo, minor, fructu flavescente, *Plum. gen.* 21.
Habitat in America *meridionali.* ♄
Arbor *foliis venosis*. Racemus *florum terminalis*.

Jacquin in his *Enumeratio* described *Clusia venosa* as "C. foliis venosis" and cited "*Plum. ic.* 87. *f.* 2." The Plumier references used by Linnaeus and Jacquin are comparable, although the latter (Ic. 87. *f.* 2) expands on

FIG. 2. Lectotype of *Clusia minor* L. FIG. 88, Dessin à la plume "Clusia flore roseo minor, fructu e viridi rubra" from Manuscript No. 6, Plumier, *Botanicum Americanum, t. VI.* Courtesy of the Muséum National d'Histoire Naturelle, Paris.

the former (Gen. 21) and is accompanied by an illustration. One can conclude, therefore, that Jacquin in his *Enumeratio* supplied an illegitimate substitute name for *C. minor* L. In the *Selectarum*, however, Jacquin refers to "Clusia (*venosa*) foliis venosis. *Linn. sp. pl. 2. p.* 510." but supplements this with a vague description which some subsequent authors felt represented a different species. It is clear from Jacquin's use of *Clusia venosa* in 1760 that this name must be considered a synonym of *C. minor* L. In the second edition of *Species Plantarum* (p. 1495. 1763) Linnaeus accepted the specific epithet "venosa" given by Jacquin and abandoned his own "minor," but did not use Jacquin's name nor refer to Jacquin's publication as he did for the three segregate species of *Clusia major*. This action seems to indicate that Linnaeus felt *C. venosa* Jacq. was the same as his *C. minor*.

Planchon and Triana typified *Clusia minor* by the unpublished plate numbered 88 in the Plumier manuscript. They recognized that this drawing was not finished in the characteristic manner of Plumier's other drawings but stated that with alterations it was comparable to *fig. 2* of *plate 87* in the Burmann edition of *Plantae Americanae*. Planchon and Triana, to clarify this species, printed the original, previously unpublished description and commentary by Plumier and compared these with existing herbarium specimens available to them. Either the original Plumier drawing, reproduced here as FIG. 2, or the Burmann version with corrections will serve to typify the species. *Clusia minor* L. is clearly defined in modern floras.

Clusia venosa Jacq. (1763 not 1760)

Planchon and Triana (*loc. cit.* 369) were troubled by the description of *Clusia venosa* supplied by Jacquin in the *Selectarum* (273. 1763). In their manuscript, they described *Clusia mangle*, crediting the name to L. C. Richard on the basis of a manuscript notation. In a discussion of this species they state, "D'après le nom de *Palétuvier de montagne* que porte à la Martinique le *Clusia venosa* de Jacquin (non L.) on pourrait croie que cette espèce est identique avec celle que nous décriverons ici. Mais la description de la plante de Jacquin ne justiferait en aucun point une telle détermination." Planchon and Triana do not otherwise place *C. venosa* Jacq. (1763).

In 1893 J. Vesque (DC. Monographiae Phanerogamarum **8**: 140, 57. 1893) listed both *C. venosa* Jacq. (1763) and *C. mangle* Rich. ex Planch. & Triana. For *C. venosa* Vesque stated, "Il est impossible de classer avec certitude la plante visée par Jacquin. C'est probablement une espèce de la section *Anandrogyne*, voisine du *Cl. Mangle* qui, à ce qu'il paraît, porte le même nom vulgaire de 'palétuvier de montagne'." Vesque placed as supporting literature the polynomial and plate references which Planchon and Triana had used in defining *C. minor*. Vesque did not cite Jacquin's *Enumeratio* of 1760, but listed only the *Selectarum* of 1763. There is an implication in the work of these men that *C. venosa* Jacq. as used in 1760 and defined in 1763 represent two different plants. The description Jacquin used in 1763 does not clearly define either *C. minor* L. (*C. venosa* Jacq. 1760) or *Clusia mangle* L. C. Rich. ex Planch. & Triana, except as the common name applies to the later species.

Engler (Nat. Pflanzenfam. **21**: 201. 1925) considered *Clusia mangle* to be a synonym of *Clusia venosa* Jacq. This decision can not be accepted. Grisebach (Flora Brit. W. Indies 107. 1859) used *Clusia venosa* Jacq. "exclus. syn. Plum." and the Imray collection he cited is *Clusia mangle*. This treatment, too, is invalid. *Clusia mangle* L. C. Rich. ex Planch. & Triana is typified by a Richard collection from the Soufrière in Guadeloupe. The species is known from Martinique, Dominica, and Guadeloupe. It is characterized by long peduncled cymes, small globose fruits about 2 cm. in diameter and by subsessile or short-petioled leaves. The identity of *Clusia venosa* Jacq. 1763 remains unsolved but the epithet is a later homonym of *Clusia venosa* Jacq. 1760 which is a synonym of *Clusia minor* L. of 1753.

Clusia grisebachiana (Planchon & Triana) Alain

Grisebach described *Tovomita clusioides* for a plant from Cuba (*T. clusioides* Griseb. Mem. Amer. Acad. II. **8**: 166. 1860, not *T. clusioides* [Choisy] Cambessèdes, 1828). Planchon and Triana recognized the earlier homonym and renamed the species in honor of Grisebach. They retained the species in the genus *Tovomita*, but expressed some doubt as to its proper assignment (*Tovomita* (?) *grisebachiana* Planch. & Triana, Ann. Sci. Nat. IV. **14**: 284. 1860). Alain correctly transferred the species to the genus *Clusia* (Fl. Cub. **3**: 314. 1953).

Urban described *Clusia krugiana* (Repert. Sp. Nov. **20**: 340. 1924) from Puerto Rico and *C. abbottii* (Symb. Antill. **1**: 367. 1899) from the Dominican Republic. Schmidt indicated on the herbarium labels of several Ekman collections that he believed *C. abbottii* belonged in the synonymy of *C. krugiana*. In as much as Schmidt's work was never published, this lead was reexamined on the basis of more recent collections and the type collections of each species. Only minor differences in leaf size, those partly of age, separate these three supposedly endemic species and they should be considered as one.

CALOPHYLLUM CALABA

A common tree of the Lesser Antilles, often used as a wind break, has a widely used common name of "galba." Regrettably, the scientific name used in modern floras is less consistent. Grisebach (Flora Brit. W. Indies 108. 1859), Urban (Symb. Antill. **8**: 438. 1920), and Duss (Ann. Inst. Colon. Marseille **13**: 103. 1896) use *Calophyllum calaba* L. Britton & Wilson (Sci. Surv. Porto Rico **5**: 584. 1924) and Williams (Fl. Trinidad & Tobago **1**: 62. 1929) use *Calophyllum antillanum* Britt. Fawcett and Rendle (Fl. Jam. **5**: 200. 1926) use *Calophyllum jacquinii* Fawc. & Rend., while Moscoso (Cat. Fl. Dom. 378. 1943) and Leon and Alain (Fl. Cub. **3**: 309. 1953) use *Calophyllum brasiliense* Camb. var. *antillanum* (Britt.)

Standl. Recently Furtado (Gard. Bull. Straits Settlements 11: 258–260. 1941) suggested the typification of *Calophyllum calaba* L. and his proposals seem acceptable.

Linnaeus (Sp. Pl. 514. 1753) proposed the name *Calophyllum calaba* citing four earlier references and referring to the origin of the plant as in "Indiis," thereby implying that the plant occurred in both the Old World and the New World. The first generic description is given by Linnaeus in 1754 (Gen. Pl. ed. 5. 229.) where only the reference to Plumier's *Calaba* is given. The Plumier reference is not given as such in the first edition of *Species Plantarum*, but is included in the reference Linnaeus gave to his Flora Zeylanica (90. 1747). In 1763, Jacquin elaborated on Linnaeus' description (Select. Stirp. Amer. 269. *t. 165*. 1763), citing both the works of Plumier and Linnaeus, thereby implying a New World origin. In the sixth edition of *Genera Plantarum* (p. 266. 1764), Linnaeus accepted Jacquin's treatment. The monographers Planchon and Triana (Ann. Sci. Nat. IV. **15**: 249. 1861), Vesque (DC. Monogr. Phan. **8**: 588. 1893), and Engler (Nat. Pflanzenfam. **21**: 196. 1925) restricted *Calophyllum calaba* in application to plants of the New World but credit the name to Jacquin.

Hitchcock and Greene (Prop. Brit. Bot. 161. 1929) suggested that the species be typified by Jacquin's interpretation of Linnaeus' name. More recently, Swartz in preparing the *Index Nominum Genericorum* cards cited as the lectotype for *Calophyllum* L. (Sp. Pl. 513. 1753) "*C. calaba* Linnaeus vide Gen. Pl. ed. 5. 229. 1754; etiam vide M. L. Green, Prop. Brit. Bot. 161. 1929)."

The acceptable synonymy therefore is:

Calophyllum calaba L. Sp. Pl. 514. 1753; Gen. Pl. ed. 5. 229. 1754; Jacquin, Sel. Stirp. Amer. 269. *t. 165*. 1763.

Calophyllum antillanum Britt. in Britton & Wilson, Sci. Surv. Porto Rico **5**: 584. 1924.
Calophyllum jacquinii Fawc. & Rendl., Fl. Jam. **5**: 584. 1924.
Calophyllum brasiliense Camb. var. *antillanum* (Britt.) Standl. Trop. Woods **30**: 6. 1932.

Britton had rejected the Jacquin interpretation of *Calophyllum calaba* as a species of the New World and had proposed the name *C. antillanum* for the American elements. Fawcett and Rendle reached the same conclusion, proposing *C. jacquinii* in apparent unawareness of Britton's earlier publication. Standley felt that the West Indian plants represented only a geographical extension of a Brazilian species and proposed several varieties including the combination *Calophyllum brasiliense* var. *antillanum*. If the Antillean material is different from that of Central and South America at the varietal level, many of Standley's varieties must be transferred to the older specific name *Calophyllum calaba* L. typified by plants in the Antilles.

RHEEDIA LATERIFLORA

Linnaeus (Sp. Pl. 1193. 1753) based this species on the work of Plumier (Gen. 45. 1703). Plumier did not specify the country of origin of the plant, but Lamarck (Encyc. 2: 245. 1786) noted the plant to be abundant in the Cul-de-sac aux Frégates in Martinique, an area visited by Plumier. Urban cites the distribution of the species as Jamaica, Hispaniola, Montserrat, Guadeloupe, Dominica, Martinique, St. Vincent, and Trinidad (Repert Sp. Nov. Beih. 5: 98. 1920). In spite of a study of recent collections from Guadeloupe, Dominica, Martinique, Marie Galante, Grenada, and Jamaica the species remains poorly understood. There have been no recent collections from Hispaniola and even the assignment of plants from Jamaica to this species is questionable.

The synonymy of this species is the following:

Rheedia lateriflora L. Sp. Pl. 1193. 1753.

Mammea humilis Vahl, Eclog. Amer. 2: 40, *t. 20.* 1798.
Mammea humilis var. *macrophylla* (Mart.) Duss, Ann. Inst. Col. Marseille 13: 102. 1897.
Mammea humilis var. *vahlii* Griseb. Fl. Brit. W. Indies 108. 1859.
Mammea humilis var. *plumieri* Griseb. *Ibid.*

Vahl's species is based on a Ryan collection from Montserrat. Grisebach's two varieties are based respectively on the Vahl and Plumier types. Grisebach described var. *vahlii* as shrubby with the leaves pointed at both ends. His var. *plumieri* was a tree with the leaves rounded or subcordate at the base. The specimens I have seen are variable in leaf shape and both types of leaf-bases can be found on one branch. Usually the leaves of young plants and of the lateral or axillary branches of older plants have the acute leaf bases.

Most modern workers consider *Garcinia macrophylla* Mart., the basionym of *Rheedia macrophylla* (Mart.) Planchon & Triana and of Duss' var. *macrophylla*, to be a distinct species. The specimens Duss cited are to be referred to *Rheedia lateriflora.*

DATES OF PUBLICATION OF THE JOURNAL LINNAEA

ROBERT C. FOSTER

THE NINETEENTH CENTURY GERMAN periodical *Linnaea* is of considerable importance to American taxonomy because of the large numbers of New World plants described in it. For some time it has been known that certain title-page dates were incorrect. Suspicion was also felt that others might well be incorrect. When the Gray Herbarium Card Index began to include varietal names from *Linnaea*, it became imperative to establish the dating as accurately as possible. Between my own investigations and those of six previous workers, it has been possible to do this for many of the volumes. It seems desirable to combine these results in one publication to obviate the necessity of searching in seven different places. The earlier references are as follows:

BLAKE, S. F., Jour. Wash. Acad. Sci. **46:** 192. 1933.
KUNTZE, O. Rev. Gen. **3**(2): 158, 159. 1898.
MOORE, H. E., Gent. Herb. **8:** 375. 1954.
STEENIS-KRUSEMAN, M. J. VAN, Fl. Males. ser. 1. **4:** cxcviii–cxcix. 1954.

VOLUME	DATE	COMMENTS AND SOURCES
Volume 1.		
TITLE-PAGE DATE: 1826.		
Heft 1: 1–165		P. 65: paper dated Oct. 1825.
Heft 2: 166–332		P. 279: ref. to Mart. Nov. Gen. fasc. 4, publ. before Apr. 1826 [?].
Heft 3: 333–511	After Aug. 1826	P. 468: reviewed Pohl, Pl. Bras. Ic. Heft 6; this appeared in Aug. 1826.
Heft 4: 512–677		
Volume 2.		
TITLE-PAGE DATE: 1827.		
Heft 1: 1–144		
Heft 2: 145–276		
Heft 3: 277–540	After Aug. 1827 ?	P. 527: reviewed Lindl. Orch. Scelet.; copy given by Lindl. to Brit. Mus., Aug. 1827.
Heft 4: 541–738		
Volume 3.		
TITLE-PAGE DATE: 1828.		
Heft 1: 1–114		P. 69: paper dated Aug. 1827.
Heft 2: 115–198		P. 173: paper dated Dec. 1827.
Heft 3: 199–308		
Heft 4: 309–440		

VOLUME	DATE	COMMENTS AND SOURCES
Volume 4.		
TITLE-PAGE DATE: 1829.		
Heft 1: 1–128	Jan. 1829	Hook. Bot. Misc. 3: 1. 1832.
Heft 2: 129–288		
Heft 3: 289–450		P. 358: paper dated 16 Mar. 1829.
Heft 4: 451 to end		P. 598: note dated Oct. 1829.
Volume 5.		
TITLE-PAGE DATE: 1830.		
Heft 1: 1–176	Jan. 1830	
Heft 2: 177–337	Apr. 1830	
Heft 3: 338–496	July, 1830	
Heft 4: 497–688	Oct. 1830	
Heft 5: 689–756	[1830]	All dates from Van Steenis-Kruseman.
Volume 6.		
TITLE-PAGE DATE: 1831.		
Heft 1: 1–208	After Mar. 1831	P. 65: ref. to Mar. 1831.
Heft 2: 209–384		
Heft 3: 385–544		
Heft 4: 545–736		
Heft 5: 737–796		
Volume 7.		
TITLE-PAGE DATE: 1832.		
Heft 1: 1–144		
Heft 2: 145–272		
Heft 3: 273–400		
Heft 4: 401–560		
Heft 5: 561–688		
Heft 6: 689–778		
Volume 8.		
TITLE-PAGE DATE: 1833.		
Heft 1: 1–112		
Heft 2: 113–256		
Heft 3: 257–384		
Heft 4: 385–512	After July, 1833	P. 395: ref. to July, 1833.
Heft 5: 513–624	After 27 July 1833	P. 529: ref. to 27 July 1833.
Heft 6: 625–684		
Volume 9.		
TITLE-PAGE DATE: 1834; 1835 at bottom of page.		
Heft 1: 1–144	After Jan. 1834	P. 124: letter dated 20 Jan. 1834.
Heft 2: 145–272		
Heft 3: 273–402		P. 331: counts 216 Annonaceae known in 1834.
Heft 4: 403–514	Early 1835	P. 506: manuscript dated 27 Dec. 1834.
Heft 5: 515–642		P. 566: notes dated 7 Feb. 1835.
Heft 6: 643–758		

VOLUME	DATE	COMMENTS AND SOURCES
Volume 10.		
TITLE-PAGE DATE: 1836; 1835–1836 at bottom of page.		
Heft 1: 1–128	After July, 1835	P. 123: paper dated 1 July 1835.
Heft 2: 129–224		
Heft 3: 225–368		P. 289: paper dated 25 Oct. 1835.
Heft 4: 369–464	After Apr. 1836	P. 463: see date of letter.
Heft 5: 465–608	After Apr. 24, 1836	P. 484: see date of letter.
Heft 6: 609–758		
Volume 11.		
TITLE-PAGE DATE: 1837.		
Heft 1: 1–128		P. 108: paper dated 16 Oct 1836.
Heft 2: 129–256		P. 164: paper dated 23 Nov. 1836.
Heft 3: 257–432		P. 280: paper dated Feb. 1837.
Heft 4: 433–544		P. 486: letter dated 15 Apr. 1837.
Heft 5: 545–608		
Heft 6: 609–728		P. 650: paper dated July, 1837. At end of volume, Cat. Pl. Exsicc. Afr. Austr., p. 13, dated 20 Mar. 1838.
Volume 12.		
TITLE-PAGE DATE: 1838.		
Heft 1: 1–128		P. 119: paper dated Jan. 1838.
Heft 2: 129–256		P. 200: paper dated 16 Feb. 1838.
Heft 3: 257–352		
Heft 4: 353–496		
Heft 5: 497–576		
Heft 6: 577–700		P. 686: ref. to plants collected in June, 1838.
Volume 13.		
TITLE-PAGE DATE: 1839.		
Heft 1: 1–112		
Heft 2: 113–272		
Heft 3: 273–336		
Heft 4: 337–448		P. 377: paper dated 7 Aug. 1839.
Heft 5: 449–560		
Heft 6: 561–744		
Volume 14.		
TITLE-PAGE DATE: 1840.		
Heft 1: 1–160		
Heft 2: 161–240		P. 178: paper dated 31 Dec. 1839 (Old Style).
Heft 3: 241–304		P. 277: paper dated 12 Apr. 1840.
Heft 4: 305–384		
Heft 5: 385–528		
Heft 6: 529–728	Early 1841	P. 706: bears date Feb. 1841.

Volume	Date	Comments and Sources
Volume 15.		
Title-page date: 1841.		
Heft 1: 1–160		P. 160: paper dated Jan. 1841.
Heft 2: 161–288		P. 282: paper dated 15 Apr. 1841.
Heft 3: 289–384		P. 384: paper dated May, 1841.
Heft 4: 385–480		P. 442: paper dated 1 July, 1841.
Heft 5: 481–704		P. 703: paper dated Oct. 1841.
Volume 16.		
Title-page date: 1842.		
Heft 1: 1–112		P. 112: paper dated 4 Jan. 1842.
Heft 2: 113–224		
Heft 3: 225–336		P. 336: note, dated June, 1842.
Heft 4: 337–400		P. 388: paper dated 9 Aug. 1842.
Heft 5: 401–512		P. 512: paper dated Sept. 1842.
Heft 6: 513–592		Noticed, Bot. Zeit. **1**: 288. 28 Apr. 1843. Introduction to volume dated March, 1843.
Volume 17.		
Title-page date: 1843.		
Heft 1: 1–128		Vol. 16, p. iv, dated Mar. 1843, says Vol. 17, Heft 1, will soon appear.
Heft 2: 129–256		P. 244: paper dated May, 1843.
Heft 3: 257–384		
Heft 4: 385–512		P. 446: paper cites material collected 29 Aug. 1843.
Heft 5: 513–640		P. 577: paper dated Dec. 1843.
Heft 6: 641–764	Early 1844	P. 676: paper dated Jan. 1844.
Volume 18.		
Title-page date: 1844.		
Heft 1: 1–112		P. 50: paper dated May, 1844.
Heft 2: 113–256		1st paper dated Sept. 1844.
Heft 3: 257–384		P. 301: paper dated Oct. 1844.
Heft 4: 385–512		P. 505: review dated 1 Dec. 1844.
Heft 5: 513–640	Mid-1845	P. 626: preface to paper dated May, 1845.
Heft 6: 641–774		P. 717: paper read 12 June 1845.
Volume 19.		
Title-page date: 1847.		
Heft 1: 1–128	Jan. 1846	Kuntze, Rev. Gen. 3(2): 158. 1898.
Heft 2: 129–256	Feb. 1846	Kuntze, *loc. cit.*
Heft 3: 257–384	1846	Before 18 Dec. 1846; noticed Bot. Zeit. **4**: 875, of that date.
Heft 4: 385–512	Dec. 1846	Kuntze, *loc. cit.*
Heft 5: 513–640	Feb. 1847	Kuntze, *loc. cit.*
Heft 6: 641–765	Apr. 1847	Kuntze, *loc. cit.*

Volume	Date	Comments and Sources
Volume 20.		
Title-page date: 1847.		
Heft 1: 1–128	May, 1847	All dates from Van Steenis-Kruseman.
Heft 2: 129–256	June, 1847	
Heft 3: 257–384	July, 1847	
Heft 4: 385–512	Aug. 1847	
Heft 5: 513–640	Oct. 1847	
Heft 6: 641–781	Dec. 1847	
Volume 21.		
Title-page date: 1848.		
Heft 1: 1–128		
Heft 2: 129–256		P. 202: paper dated Jan. 1848.
Heft 3: 257–384		
Heft 4: 385–512		
Heft 5: 513–640		Hefte 1–5 noticed, Bot. Zeit. **6**: 870. 15 Dec. 1848.
Heft 6: 641–780		Noticed, Bot. Zeit. **7**: 750. 19 Oct. 1849.
Volume 22.		
Title-page date: 1849.		
Heft 1: 1–128		P. 113: note ref. to Bot. Zeit. 10 Nov. 1848.
Heft 2: 129–256		P. 144: paper dated 20 Dec. 1848.
Heft 3: 257–384		
Heft 4: 385–512		P. 464: paper dated 24 Mar. 1849.
Heft 5: 513–640		
Heft 6: 641–768		
Heft 7: 769–898		
Volume 23.		
Title-page date: 1850.		
Heft 1: 1–128		
Heft 2: 129–256		P. 212: paper dated 30 Mar. 1850.
Heft 3: 257–384		
Heft 4: 385–512		
Heft 5: 513–640		
Heft 6: 641–770		P. 736: note dated 18 Sept. 1850.
Volume 24.		
Title-page date: 1851.		
Heft 1: 1–128		
Heft 2: 129–256		
Heft 3: 257–384		P. 300: paper dated July, 1851.
Heft 4: 385–512		
Heft 5: 513–640		
Heft 6: 641–804	Early 1852	P. 649: paper dated Jan. 1852.
Volume 25.		
Title-page date: 1852.		
Heft 1: 1–128	June, 1852	All dates from Kuntze, Rev. Gen. 3(2): 158. 1898.
Heft 2: 129–256	Dec. 1852	

VOLUME	DATE	COMMENTS AND SOURCES
Heft 3: 257–384	Feb. 1853	
Heft 4: 385–512	Apr. 1853	
Heft 5: 513–640	June, 1853	
Heft 6: 641–772	Dec. 1853	
Volume 26.		
TITLE-PAGE DATE: 1853.		
Heft 1: 1–128	Feb. 1854	All dates from Kuntze, Rev. Gen. 3(2): 159. 1898.
Heft 2: 129–256	Apr. 1854	
Heft 3: 257–384	Aug. 1854	
Heft 4: 385–512	Feb. 1855	
Heft 5: 513–640	May, 1855	
Heft 6: 641–807	Sept. 1855	
Volume 27.		
TITLE-PAGE DATE: 1854.		
Heft 1: 1–128	Nov. 1855	Engl. Bot. Jahrb. **19**: 562. 1894.
Heft 2: 129–256	Jan. 1856	*Ibid.*
Heft 3: 257–384	Jan. 1856	*Ibid.*
Heft 4: 385–512	Feb. 1856	*Ibid.*
Heft 5: 513–640	[1856]	
Heft 6: 641–799	Aug. 1856	Gent. Herb. **8**: 375. 1954.
Volume 28.		
TITLE-PAGE DATE: 1856.		
Heft 1: 1–128	Aug. 1856	All dates from Blake in Jour. Wash. Acad. Sci. **46**: 192. 1933.
Heft 2: 129–256	Sept. 1856	
Heft 3: 257–384	Jan. 1857	
Heft 4: 385–512	June, 1857	
Heft 5: 513–640	Aug. 1857	
Heft 6: 641–767	Feb. 1858	
Volume 29.		
TITLE-PAGE DATE: 1857–1858.		
Heft 1: 1–128	Feb. or later, 1858	See cover of Vol. 28, Heft 6.
Heft 2: 129–256	June, 1858	Engl. Bot. Jahrb. **19**: 526. 1894.
Heft 3: 257–384	Sept. 1858	Engl. Bot. Jahrb. **19**: 526. 1894.
Heft 4: 385–512	Feb. 1859	Gent. Herb. **8**: 375. 1954.
Heft 5: 513–640	Apr. 1859	Gent. Herb. **8**: 375. 1954.
Heft 6: 641–764	June, 1859	Bull. Soc. Bot. Fr. **7**: 118. 1860.
Volume 30.		
TITLE-PAGE DATE: 1859–1860.		
Heft 1: 1–128		
Heft 2: 129–256		Before 25 Nov. 1859; cf. Bull. Soc. Bot. Fr. **6**: 742. 1859.
Heft 3: 257–384		
Heft 4: 385–512		Before 23 Nov. 1860; cf. Bull. Soc. Bot. Fr. **7**: 867. 1860.

VOLUME	DATE	COMMENTS AND SOURCES
Heft 5: 513–640		Before 25 Jan. 1861; cf. Bull. Soc. Bot. Fr. **8**: 24. 1861.
Heft 6: 641–779	Mar. 1861	Engl. Bot. Jahrb. **19**: 562. 1894.
Volume 31.		
TITLE-PAGE DATE: 1861–1862.		
Heft 1: 1–128		Before 11 Apr. 1862; cf. Bull. Soc. Bot. Fr. **9**: 194. 1862.
Heft 2: 129–256		Before 11 Apr. 1862; cf. Bull. Soc. Bot. Fr. **9**: 194. 1862.
Heft 3: 257–384		Before 13 Mar. 1863; cf. Bull. Soc. Bot. Fr. **10**: 122. 1863.
Heft 4: 385–512		Before 14 Nov. 1862; cf. Bull. Soc. Bot. Fr. **9**: 419. 1862.
Heft 5: 513–640		Before 13 Mar. 1863; cf. Bull. Soc. Bot. Fr. **10**: 122. 1863.
Heft 6: 641–751		Before 13 Mar. 1863; cf. Bull. Soc. Bot. Fr. **10**: 122. 1863.
Volume 32.		
TITLE-PAGE DATE: 1863.		
Heft 1: 1–128		Before 13 Nov. 1863; cf. Bull. Soc. Bot. Fr. **10**: 459. 1863.
Heft 2: 129–256		Before 11 Dec. 1863; cf. Bull. Soc. Bot. Fr. **10**: 539. 1863.
Heft 3: 257–384		Before 11 Dec. 1863; cf. Bull. Soc. Bot. Fr. **10**: 539. 1863.
Heft 4: 385–512		Before 1 Apr. 1864; cf. Bull. Soc. Bot. Fr. **11**: 87. 1864.
Heft 5: 513–640		Before 13 May 1864; cf. Bull. Soc. Bot. Fr. **11**: 149. 1864.
Heft 6: 641–801		Before 13 Jan. 1865; cf. Bull. Soc. Bot. Fr. **12**: 4. 1865.
Volume 33.		
TITLE-PAGE DATE: 1864–1865.		
Heft 1: 1–128		Before 31 Aug. 1864; reviewed in Flora, Repert., Halfbogen 3–4, 31 Aug. 1864.
Heft 2: 129–256		Before 14 Dec. 1864; reviewed in Flora, Repert., Halfbogen 5, 14 Dec. 1864.
Heft 3: 257–384		Before 24 Mar. 1865; cf. Bull. Soc. Bot. Fr. **12**: 144. 1865.
Heft 4: 385–512		Before 24 Mar. 1865; cf. Bull. Soc. Bot. Fr. **12**: 144. 1865.
Heft 5: 513–640		Before 20 May 1865; reviewed in Flora, Repert., Halfbogen 10, 20 May 1865.
Heft 6: 641–770		Before Sept.–Oct., 1865; cf. Bull. Soc. Bot. Fr. **12**: 227. 1865.

VOLUME	DATE	COMMENTS AND SOURCES
Volume 34.		
TITLE-PAGE DATE: 1865–1866.		
Heft 1: 1–128		Before Mar. 1865; cited in DC. Prodr. **15**(2): 543. 1865.
Heft 2: 129–256		Before 22 Dec. 1865; cf. Bull. Soc. Bot. Fr. **12:** 409. 1865.
Heft 3: 257–384		Before 22 Dec. 1865; cf. Bull. Soc. Bot. Fr. **12:** 409. 1865.
Heft 4: 385–512		Before 23 Jan. 1866; reviewed in Flora, Repert. (1865), Halfbogen 3, 23 Jan. 1866.
Heft 5: 513–640		Before 11 May 1866; cf. Bull. Soc. Bot. Fr. **13:** 253. 1866.
Heft 6: 641–752		
Volume 35.		
TITLE-PAGE DATE: 1867–1868.		
Heft 1: 1–128		Before 13 Oct. 1867; reviewed in Flora, Repert. 13 Oct. 1867, p. 7.
Heft 2: 129–256		Before 13 Oct. 1867; reviewed in Flora, Repert. 13 Oct. 1867, p. 7.
Heft 3: 257–352		Before June, 1868; reviewed in Flora, Repert. Mid-June, 1868, p. 26.
Heft 4: 353–384		Before June, 1868; reviewed in Flora, Repert. Mid-June, 1868, p. 26.
Heft 5: 385–512		
Heft 6: 513–637	Nov. 1868	Date from Van Steenis-Kruseman.
Volume 36.		
TITLE-PAGE DATE: 1869–1870.		
Heft 1: 1–128	Late 1869	Reviewed in Flora, Repert. 15, Jan. 1870, p. 9.
Heft 2: 129–256	Late 1869	Reviewed in Flora, Repert. 15, Jan. 1870, p. 9.
Heft 3: 257–384	Jan. 1870	Van Steenis-Kruseman.
Heft 4: 385–512	Apr. 1870	Van Steenis-Kruseman.
Heft 5: 513–640		
Heft 6: 641–790	Dec. 1870	Van Steenis-Kruseman.
Volume 37.		
TITLE-PAGE DATE: 1871–1872.		
Heft 1: 1–128	[Early 1872]	
Heft 2: 129–256	Apr. 1872	Jour. Bot. **10:** 220. 1872.
Heft 3: 257–432	July, 1872	Jour. Bot. **10:** 382. 1872.
Heft 4: 433–512	July, 1872	Jour. Bot. **10:** 383. 1872.

VOLUME	DATE	COMMENTS AND SOURCES
Heft 5: 513–544	Oct. 1872	Jour. Bot. **11:** 61. 1873.
Heft 6: 545–663	Sept. 1873	Jour. Bot. **12:** 125. 1874.
Volume 38.		
TITLE-PAGE DATE: 1874.		
Heft 1: 1–144	Dec. 1873	Jour. Bot. **12:** 125. 1874.
Heft 2: 145–256	Jan. 1874	Jour. Bot. **12:** 125. 1874.
Heft 3: 257–384	May, 1874	Van Steenis-Kruseman.
Heft 4: 395–512	July, 1874	Van Steenis-Kruseman.
Heft 5: 513–640		Noticed, Bot. Zeit. **32:** 751. 13 Nov. 1874.
Heft 6: 641–753		
Volume 39.		
TITLE-PAGE DATE: 1875.		
Heft 1: 1–128	Feb. 1875	Jour. Bot. **13:** 253. 1875.
Heft 2: 129–224	June, 1875	Jour. Bot. **13:** 253. 1875.
Heft 3: 225–256	June, 1875	Bot. Zeit. **33:** 455. 2 July 1875.
Heft 4: 257–352		Noticed, Bot. Zeit. **33:** 769. 19 Nov. 1875.
Heft 5: 353–448		
Heft 6: 449–526		Noticed, Bot. Zeit. **33:** 790. 26 Nov. 1875.
Volume 40.		
TITLE-PAGE DATE: 1876.		
Heft 1: 1–96		Noticed, Bot. Zeit. **34:** 64. 28 Jan. 1876.
Heft 2–3: 97–192		Noticed, Bot. Zeit. **34:** 352. 2 June 1876.
Heft 4: 193–288		Noticed, Bot. Zeit. **34:** 480. 25 July 1876.
Heft 5: 289–384	Aug. 1876	Svenson, Rhodora **41:** 313. 1939.
Heft 6: 385–468	Dec. 1876	Svenson, Rhodora **41:** 313. 1939; noticed, Bot. Zeit. **35:** 16. 5 Jan. 1877.
Volume 41.		
TITLE-PAGE DATE: 1877.		
Heft 1: 1–117	Dec. 1876	All dates from original covers bound in a volume in the Oakes Ames Orchid Herbarium Library.
Heft 2: 113–192	Feb. 1877	
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Heft 4: 289–384	Aug. 1877	
Heft 5: 385–576	Oct. 1877	
Heft 6: 577–655	Feb. 1878	

VOLUME	DATE	COMMENTS AND SOURCES
Volume 42.		
TITLE-PAGE DATE: 1878–1879.		
Heft 1: 1–112	Feb. 1878	Jour. Bot. **16:** 123. 1878.
Heft 2: 113–192		Noticed, Bot. Zeit. **36:** 318. 17 May 1878.
Heft 3: 193–288	1879	Van Steenis-Kruseman.
Heft 4: 289–384	1879	Van Steenis-Kruseman.
Heft 5: 385–480	1879	Van Steenis-Kruseman.
Heft 6: 481–667	Nov. 1879	Van Steenis-Kruseman.
Volume 43.		
TITLE-PAGE DATE: 1880–1881.		
Heft 1: 1–66	Sept. 1880	All dates from Van Steenis-Kruseman.
Heft 2: 67–138	July, 1881	
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GRAY HERBARIUM,
HARVARD UNIVERSITY

A MONOGRAPH OF THE GENUS PLATYDESMA (RUTACEAE)[1]

BENJAMIN C. STONE[2]

THE GENUS PLATYDESMA was described by Horace Mann, Jr. (1866), to accommodate an unusual rutaceous species collected by him and William Brigham "on the mountains behind Honolulu" on the island of Oahu in the Hawaiian Islands. Mann presented a rather full description of the genus and its single species, which he named *Platydesma campanulata*. A few years later (1869) he again wrote of the genus and species, with almost unchanged descriptions, but added a few sentences pertaining to the circumstances of the discovery, and a fine full-page half-tone plate illustrating its habit and flowers. The species was noted by Heinrich Wawra (1873) without further description or commentary. In 1888, however, Wilhelm Hillebrand, in his great *Flora of the Hawaiian Islands*, added three species to the genus, two of them, *P. cornuta* and *P. rostrata*, described as new, and a third to which Hillebrand applied the name *P. auriculaefolia*, based on *Pelea auriculaefolia* A. Gray. As has previously been pointed out (Rock 1913, 1918; Stone 1961, 1962), Hillebrand erred in considering Gray's species to be a *Platydesma*, for it is a true *Pelea* of the typical section. However, the specimens which led Hillebrand to include a fourth species in *Platydesma* are, in fact, members of the genus. Rock (1913) named the taxon represented by these specimens *Platydesma campanulatum* var. *sessilifolia* (sic). This taxon is here considered to be of specific rank, agreeing essentially with Hillebrand's treatment, but clearly less distinct from *P. spathulatum* (the correct name of Mann's *P. campanulata*) than either *P. cornutum* or *P. rostratum* which Hillebrand first described.

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[1] Studies in the Hawaiian Rutaceae, VI.

[2] The field work for this revision was accomplished while the writer was Research Assistant, Department of Botany, University of Hawaii, Honolulu. Some studies of borrowed herbarium specimens were performed at the Herbarium, Department of Botany, U. S. National Museum, Washington, D. C. I am grateful to the officers of several institutions for making the material available. These include: Sir George Taylor, Royal Botanic Gardens, Kew; Dr. J. E. Dandy, British Museum (Natural History); Dr. Bertil Lindquist, Göteborg Botanical Garden; Dr. R. T. Clausen, Herbarium, Department of Botany, Cornell University; Dr. Alicia Lourteig, Mme. Tardieu-Blot, and Dr. J. Léandri, of the Laboratoire de Phanérogamie, Muséum National d'Histoire Naturelle, Paris; and Dr. Otto Degener, Waialua, Oahu, Hawaii, who supplied both herbarium material and fresh collections. I also wish to thank Dr. L. B. Smith of the U. S. National Museum for his kind assistance. At the Bishop Museum, Honolulu, where a rather large number of collections of the various species has been accumulating, I was provided with all necessary facilities for study. I am much indebted to Marie C. Neal and to E. H. Bryan, Jr., of the Museum staff, for their assistance and encouragement. At Harvard, Dr. R. A. Howard and Dr. L. M. Perry provided generous assistance in my studies of the materials in the herbarium of the Arnold Arboretum and of the Gray Herbarium, for which I am most grateful.

The name now applied to this species has a curious history. Material collected by Jules Remy was provisionally determined by H. Baillon in Paris as *Claoxylon insigne* sp. nov. (*Claoxylon* is a genus of Euphorbiaceae, the fruits of which [in the Hawaiian species] bear a slight resemblance to those of *Platydesma.*) Remy's specimen bears only fruit. The name *C. insigne* was never validly published, but was listed (without description and only a herbarium reference) by Drake del Castillo (1890). Many years later, while revising the Hawaiian members of *Claoxylon*, E. E. Sherff happened to see the Remy collection and, relying all too heavily on the authority of Baillon, published the name *Claoxylon Remyi* Sherff sp. nov., with a full description. Recently the real identity of this "Claoxylon" became apparent to Dr. Otto Degener, who received confirmation from the Muséum National d'Histoire Naturelle of Paris that the plant was rutaceous. A lifelike drawing of the specimen was prepared (see FIG. 4) in which the character of *Platydesma* may readily be seen. The proper transfer of the name was made in Degener's *Flora Hawaiiensis* (1960), where the present writer was able to show that this species is identical with the one intended by Hillebrand to include his specimens from Kohala, Hawaii, to which he had appended the name *Platydesma auriculaefolia*. The species is now called *Platydesma Remyi* (Sherff) Deg., Sherff & Stone.

Only two other names must be considered in the genus, both published by H. Léveillé, whose erratic work, discussed at some length both by Rock and Rehder in recent years, scarcely needs further mention. The first is *Platydesma oahuensis* Lévl. (1911), which is simply a synonym of Mann's original species. The second, *Platydesma Fauriei* Lévl. (1911) is borne by a plant not a member of the Rutaceae, but of the Solanaceae, *Nothocestrum longifolium* A. Gray, as was first pointed out by Rock (1914).

Recently it was found necessary to take up an older specific epithet for Mann's original species (Stone, 1962), which must now be called *Platydesma spathulatum* (A. Gray) Stone. The basionym is *Melicope spathulata* A. Gray, published a decade earlier than Mann's species. Gray also described *Melicope ? grandifolia* in the same work (1854), which is the same species. Photographs of the type specimens were published in a preceding paper (Stone, 1962).

Platydesma H. Mann,[3] Proc. Boston Soc. Nat. Hist. **10**: 317. 1866; Mem. Boston Soc. Nat. Hist. **1**: 529. 1869. Hillebrand, Fl. Hawaiian Is. 71. 1888. Rock, Indig. Trees Hawaiian Is. 241. 1913. Engler, Nat. Pflanzenfam. ed. 2. **19a**: 240, *fig. 101, A–G.* 1931.

Shrubs or small trees with opposite or subopposite, simple, punctate,

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[3] Mann attributed feminine gender to the generic name, and was followed in this usage by most later authors. The name, however, like several others taken from Greek (such as *Geniostoma*) is of a class which, although ending in the apparently Latin feminine *-a*, takes neuter modifiers. Therefore the specific and varietal epithets are corrected, where necessary, to neuter gender.

elongate, nonstipulate leaves; wood when freshly broken with a pepsin-like odor, somewhat brittle; inflorescences axillary, cymose or subsessile and contracted; flowers hermaphrodite, with 4 broad, rounded sepals in imbricated pairs; petals 4, white, but slightly imbricated; disk plane, obscurely 4–8-lobate; stamens 8, connate into a staminal tube, white, only the anthers and a short, broad, deltoid filament (adnate to the connective) free, the anthers narrow, elongate, subhastate at the base, with linear thecae; ovary of 4 carpels, rounded above, adnate to the apex, each with 5–8 pendulous ovules on short, broad funiculi; style central, of 4 connate elements, columnar, the linear, erect, united stigmas somewhat thickened at apex; fruit capsular, dry, 4-lobed, the carpels remaining connate, loculicidally (sometimes tardily) dehiscent, rounded or horned at apex, the endocarp thin, glabrous, finally separable, the seeds subovoid or ellipsoid with angles and faces (if any) from mutual pressures, the testa black and shining, the wall osseous, the cotyledons of the embryo thin, broad, rounded, the hypocotyl very short, the embryo enclosed by endosperm.

TYPE SPECIES: *Platydesma campanulatum* H. Mann = *P. spathulatum* (A. Gray) Stone.

DISTRIBUTION: Endemic to the Hawaiian Islands; four species: *Platydesma spathulatum*, widespread in the archipelago, with insular varieties and forms; *P. cornutum*, endemic to Oahu; *P. rostratum*, endemic to Kauai; and *P. Remyi*, apparently endemic to the Kohala Mountains, Hawaii.

RELATIONSHIPS: *Platydesma* is placed by Engler in the subfamily Rutoideae, tribe Xanthoxyleae, subtribe Choisyinae, as genus 28 between *Choisya* HBK., a Mexican and southwestern American genus, and *Dutaillyea* Baill., a small genus of two species endemic to New Caledonia. Neither of these genera, however, appears to be either very close in relationship or similar in superficial or technical characters. *Medicosma* Hook. f., a monotypic Australian genus, is closer in appearance, and possibly in affinity, although placed before (as genus 25) the above-mentioned genera. It is perhaps more plausible to consider that *Platydesma* may be ultimately an Old World derivative, but to exclude American affinities would be premature.

ECOLOGY: *Platydesma spathulatum*, and its subtaxa, are both more common and more widely distributed in the Hawaiian group than the other species. None, however, could be considered dominant or even frequent members of the vegetation. The species are to be found chiefly in the rainforests at moderate elevations, from roughly 2000 to 5000 feet, and also on windswept crests in low, stunted vegetation. *Platydesma cornutum* and *P. rostratum* usually occur as single plants or in small groups, often along streams or gullies under heavy shade, while *P. spathulatum* may be found under open or closed canopy forests, or exposed on slopes, and can apparently tolerate drier situations. In a few localities (such as around Kokee, Kauai) *P. spathulatum* may be found so frequently as to constitute a considerable, though never dominant, component of the association.

HABIT: *Platydesma spathulatum* is a polymorphic species, but older individuals in more protected areas become small trees. In forests such as those about Kumuwela, Kauai, trees of five to eight meters in height form an understory in a forest containing species of *Psychotria*, *Pelea*, *Bobea*, *Pleomele*, *Pritchardia*, and other genera. In exposed, windswept areas such as open crests along the Koolau Range, Oahu. a form of the same species may be found occurring as a small shrub. Both *Platydesma cornutum* and *P. rostratum* are shrubby, with erect, usually slender stems and erect or ascending branches. They can accurately be called "Schopfbäume" with their rather large leaves clustered toward the ends of the branches (see FIG. 1). *Platydesma Remyi* has the habit of *P. spathulatum*.

LOCAL NAME AND USE: The Hawaiian name for all species is "Pilo kea," meaning "white pilo." If the Hawaiians had a particular use for the plant, it is not presently known. Certain species have recently been the subject of chemical investigations by P. J. Scheuer and his associates at the University of Hawaii. Evidence has been found that some species contain appreciable amounts of alkaloids and essential oils. In this connection, it is worthy of note that Rock (Indig. Trees 242. 1913) reported that the odor of the plant when bruised is like pepsin. The wood, when broken, emits a starchy odor.

SPECIFIC CHARACTERS: Characters of taxonomic value are found chiefly in the structure, shape, and size and presence or absence of indument of the fruits; the structure of the inflorescence; the shape and size of the leaf, especially the petiole; the habit; and, to a lesser extent, the amount of pubescence both on leaves and parts of the inflorescence. The other indigenous genera of Rutaceae, *Fagara* (*Zanthoxylum*) and *Pelea*, are greatly different both in appearance and in technical characters, although seedling stages of *Pelea* and *Platydesma* could perhaps be confused with one another.

KEY TO THE SPECIES

1. Carpels in fruit rounded, the capsule subglobose; habit shrubby or usually arborescent, small trees with several to many irregularly arranged spreading or ascending branches. Section PLATYDESMA.
    2. Petioles conspicuous, 1–6 cm. long; fruits glabrous, Kauai, Oahu, Maui, Hawaii (probably also Molokai). . . . . 1. *P. spathulatum*.
    2. Petioles obsolete or at most 5 mm. long, flattened; fruits with a more or less persistent minute pubescence; Hawaii. . . . . 2. *P. Remyi*.
1. Carpels in fruit rostrate, cornute, or sharply pointed, and somewhat divaricate; habit shrubby, with erect, sparsely branched or simple stems closely foliose toward the apices. Section CORNUTIA.
    3. Carpels in fruit conic-pointed or shortly attenuate; leaves elongate, spath-

ulate, narrowed at base to a small rounded or decurrent lamina; Oahu. . . . . 3. *P. cornutum.*

3. Carpels in fruit tapered into a slender, elongate beak; leaves narrowly oblong or subspathulate, the base broad and abruptly truncate or obtuse; Kauai. . . . . 4. *P. rostratum.*

Section PLATYDESMA

1. **Platydesma spathulatum** (A. Gray) B. C. Stone, Madroño **16**: 165. 1962.

Melicope spathulata A. Gray, Bot. U. S. Expl. Exped. **15**: 352. 1854.
Melicope? grandifolia A. Gray, *op. cit.* 354.
Platydesma campanulata H. Mann, Proc. Boston Soc. Nat. Hist. **10**: 317. 1866; Mem. Boston Soc. Nat. Hist. **1**: 529–531. *pl. 22.* 1869. Hillebrand, Fl. Hawaiian Is. 71. 1888, *"companulata."* Heller, Minn. Bot. Stud. **1**: 841. 1897. Rock, Indig. Trees Hawaiian Is. 241. 1913 (including f. *coriaceum*). Skottsberg, Acta Horti Gothob. **10**: 120. 1936; *ibid.* **15**: 388. 1944.
Platydesma campanulata γ var. *macrophylla* Hillebrand, *loc. cit.*
Platydesma oahuensis Léveillé, Rep. Sp. Nov. **10**: 153. 1911.

A shrub or small tree to about 12 m., with spreading branches foliose toward the ends, trunk straight, to about 20 cm. thick, glabrous throughout or with fulvous pubescence on the new leaves and inflorescence (and in some varieties the mature leaves pubescent beneath); juvenile branches greenish, at last clothed with pale grayish bark; all parts copiously glandular, emitting odor of pepsin; wood, when broken, with a starchy odor; leaves variable in size, distinctly petiolate, the petiole 10–60 mm. long, the blades usually 10–50 cm. long (sometimes less), 5–20 cm. wide (sometimes less), spathulate, lanceolate, obovate-lanceolate, or sometimes elliptic, generally about 2.5 to 4.5 times longer than broad, coriaceous or thickly so, sometimes the margins revolute, rounded to obtuse, acute, or even slightly acuminate at apex, rounded, obtuse, or acute at base, entire, moderately to very dark green above, usually paler beneath, pinnately veined, the lateral nerves subopposite, ascending from the dorsally prominent ventrally sulcate costa, straight for about ¾ their length, thereafter dividing but not uniting into a distinct marginal vein; inflorescences axillary, initiated among the leaves, pedunculate, cymose, usually 3–5-flowered; peduncles about as long as the petioles, nodose, with ovate-subulate or narrowly deltoid acute bracts; pedicels up to 1 cm. long, bracteolate; flowers about 15–20 mm. long, the 4 calyx lobes imbricate in pairs, green, glabrous except for the ciliolulate margins, or sparsely to densely puberulent with appressed hairs, ovate-orbicular, about 8–10 mm. long, minutely carinate apically without, more or less persistent into fruiting; petals 4, clear somewhat creamy white, somewhat (never widely) spreading at anthesis, slightly obovate-oblong to ovate-oblong, minutely thickened unguiculate within at apex, sometimes obscurely emarginate and mucronulate in the notch, about 14–21 mm. long; stamens 8, united into a tube, white, the tube 12–13 mm. long, the anthers connivent on short deltoid oblong processes adnate to the connective; ovary 4-locular,

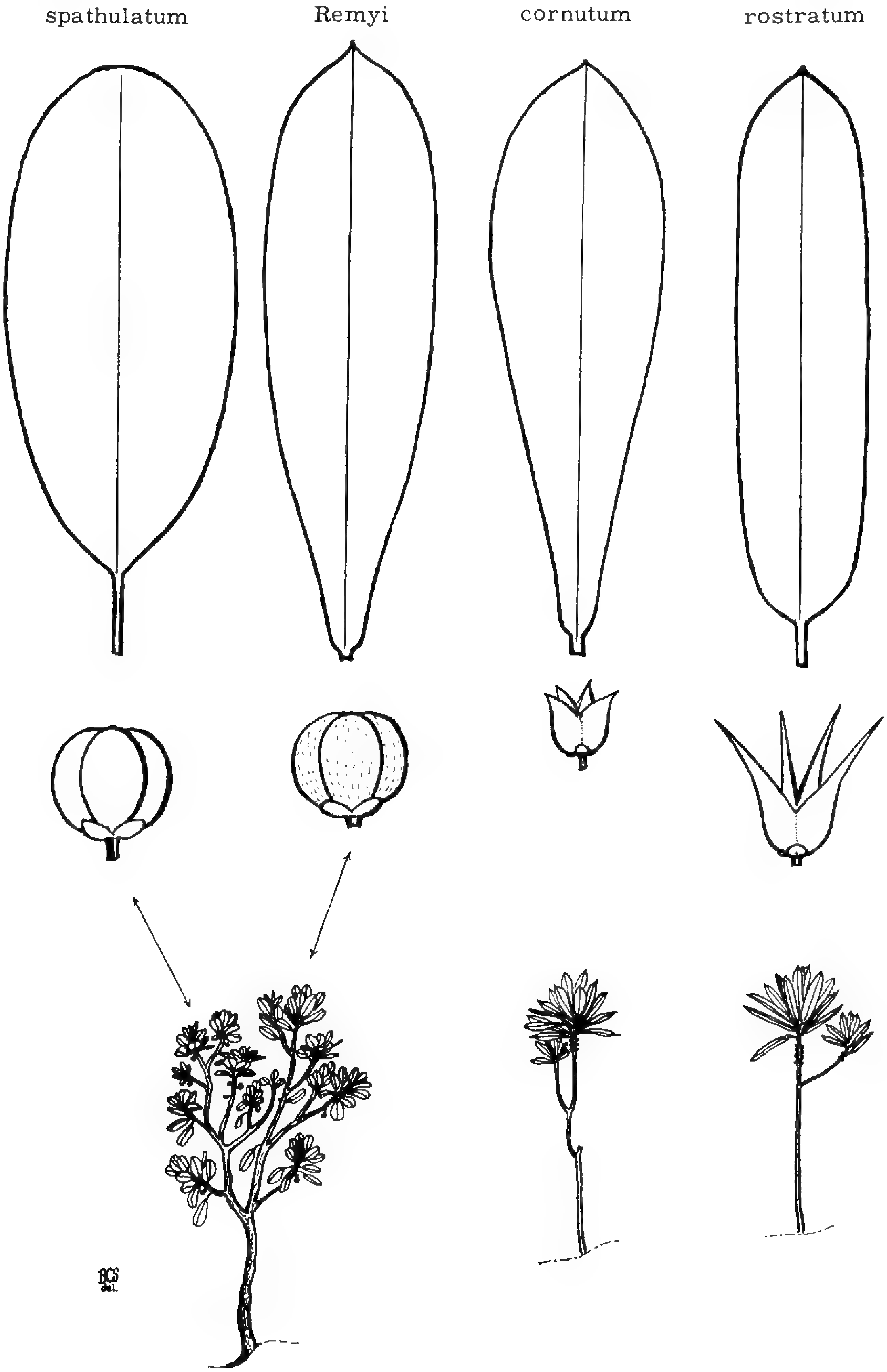

FIG. 1. Leaves, fruits, and habit sketches of the four species of *Platydesma*; semi-diagrammatic.

4-lobed, at first minutely puberulous; style about 9 mm. long, whitish, slightly clavate and greenish at apex, with linear stigmas; fruit globose, slightly 4-lobed, to 26 mm. in diameter, the carpels adnate to the summit, in age slightly separating laterally, at last dehiscent; seeds 5–8 per locule, with a shining black testa, attached by short funicles to the glabrous endocarp.

HOLOTYPE: United States Exploring Expedition, 1838–1842, island of Kauai (US) (*Melicope spathulata* A. Gray).

KEY TO SUBTAXA OF PLATYDESMA SPATHULATUM

1. Calyx glabrous or very sparsely puberulent only at extreme base.
    2. Leaves glabrous beneath.
        3. Petioles slender, elongate, usually 2–6 cm. long; blades ample, oblong-spathulate or obovate-spathulate, 3–4 times longer than wide, mostly rounded at apex; Kauai, Oahu, Hawaii; perhaps also elsewhere. . . . . var. *spathulatum* (typical form).
        3. Petioles shorter, somewhat flattened, about 1–2 cm. long.
            4. Leaves usually less than 15 cm. long, spathulate but tapered and acute or even acuminate at apex, tapered at base, pale, rigid, the margins often revolute, the blade usually 3–4 times longer than wide; Oahu. . . . . var. *spathulatum*, form b.
            4. Leaves generally 20–50 cm. long or more, relatively broader (about 2–3 times longer than wide), generally rounded or obtuse at both ends, dark; Kauai. . . . . var. *spathulatum*, form c.
    2. Leaves pubescent beneath, densely villous at least on the midrib, the laminar surface sometimes glabrescent; blades large, dark, rather broadly spathulate; Kauai, Oahu. . . . . var. *pubescens*.
1. Calyx densely cinereous-puberulent; leaf-blades usually somewhat pubescent beneath; Oahu, Maui, Hawaii. . . . . var. *pallidum*.

Platydesma spathulatum var. spathulatum.

Platydesma campanulatum f. *coriaceum* Rock, Indig. Trees Hawaiian Is. 242. 1913.

Glabrous throughout; petioles slender, elongate, usually 2–6 cm. long; blades ample, oblong-spathulate or obovate-spathulate, usually 3–4 times longer than wide, mostly rounded at apex, often somewhat rounded at base.

Kauai. Hanalei, *Faurie 241* (A); Makaweli, *Faurie 246* (A); Waimea, *Faurie 245* (A, BISH), *Forbes 911.K.* (BISH); Kokee, *Rock*, 1956 (BISH); Kaholuamanu, *Forbes 328.K.* (BISH); *Rock 1968*, *1976*, *5338* (GH), *1978*, *5344*, *5969* (BISH), *6021* (A); Kaunuohua ridge, Kaluapuhi trail, *Wichman* (GB); Kokee Camp, *Degener 8640* (A); Kokee-Kilohana, *Skottsberg 981* (BISH, GB); Lehuamakanoe-Kilohana, *Cranwell et al. HBS. 2938* (BISH, GB); Halemanu, *Rock 2298* (BISH), *2314* (GH); *Neal*, 1929, 1930 (BISH), *Kusche* (GH); Kumuwela, *Cranwell et al. HBS. 2841* (BISH, K), *2847* (GB), *Stone 3360* (BISH, BM, CU, E, GH, P), *3395* (BISH, GB); Awa'awapuhi trail, *Lane 56–614* (BISH), *Stone 1609* (BISH, K), *3330* (BISH, P, US); Kohua ridge, *Degeners & Hansen 23919* (BISH); without locality, *Forbes* (BISH).

Oahu. WAIANAE RANGE: Piko trail, Makua, Mokuleia forest reserve, *Davis*, 1932 (BISH). KOOLAU RANGE: Northern end: near summit 1 mi. se. of Black Junction, Kahuku, *Degener & Carroll 20554* (BM); Kahuku, *Degener 8624* (A); Punalu'u and vicinity, *Faurie 242* (A), *Forbes*. 1908, 1909 (BISH); *Rock 459, 640, 657, 8834* (BISH); *MacDaniels 382* (BISH), *Hume 76, 106* (BISH); Kaliuwa'a, *Rock 65* (BISH); Waipio-Waiawa, *MacDaniels 16, 53* (BISH); Waiawa, *Anon*., 1930 (ex Herb. Bd. Comm. Agric. For. Terr. Hawaii) (BISH); Kawailoa, *Bryan 867* (BISH); Kahana, *Lyon*, 1926 (BISH); Wahiawa-Kahana, *Forbes 2202.0.* (BISH); back of Wahiawa, *Swezey*, 1920 (BISH); *Budd & Emerson 1155* (BISH); Waikane-Schofield trail, *St. John 10161* (BISH); Kipapa gulch trail, *Cowan 700* (BISH); Anahulu trail, *Degener 10092* (A). Southern end: Pauoa, *Hillebrand* (BISH); Konahuanui, *Forbes*, 1908 (BISH), *Heller 2373* (GH), *Mann & Brigham 94* (CU, type of *Platydesma campanulata*; BISH, GH, K); Mt. Olympus, *Rock 10225* (BISH, GH), *Forbes 1637.0.* (BISH); Koolau range, without locality, *Hillebrand 242* (K); *Rock 134* (GH).

Hawaii. Kohala, *Rock*, 1957 (BISH), *Rock 8367* (GH); Hualalai (?), *Rock 3800* (BISH); Ola'a flume, *Forbes 652.H.* (BISH); Ten-Miles, *Fullaway & Gifford*, 1919 (BISH); Glenwood, *Faurie 244* (A, BISH), *Rock*, 1918 (BISH), 1914 (BISH); Kilauea, *Rock 12999* (BISH); "Sandwich Isl.," *U. S. Exploring Expedition* (GH).

Platydesma spathulatum var. **spathulatum**, form b. (FIG. 2.)

Shrubby, with slender branches and small, narrowly spathulate, pale, rigid leaves tapered at both ends, the margins often revolute; petiole 1–2 cm. long.

This form is the one most commonly found on the summit crests of the Koolau Range, Oahu, where the vegetation is low, stunted, and windswept.

Oahu. KOOLAU RANGE: Punalu'u, summit of Castle trail, *Stone 3551* (BISH) (see FIG. 2), *1142* (BISH), *Degener, Park & Nitta 8633* (US); Laie, Malaekahana trail, *Degener et al. 10093* (CU); ridge above Kahana, *Skottsberg 1853* (BISH, GB); near summit of Poamoho trail, *Degener 27328* (US); Punalu'u, *Faurie 243* (A, BISH); *Rock 460* (A).

Platydesma spathulatum var. **spathulatum**, form c.

Arborescent, with thick, often rugulose branches and ample leaves up to 50 cm. long, usually 7–25 cm. wide, obtuse at apex and rounded at base, dark green, quite glabrous.

This form appears to be limited to Kauai, where it occurs in the high forested tableland around the rim of Kalalau Valley.

Kauai. Honopu, Awa'awapuhi trail, *Lane 56–586* (BISH); east rim of Kalalau Valley, *Degeners & Cadenheads 27150* (BISH, GB, K, US).

Platydesma spathulatum var. **pubescens** (Skottsberg) B. C. Stone, Madroño 16: 165. 1962.

Platydesma campanulata var. *pubescens* Skottsberg, Acta Horti Gothob. **15:** 388. 1944.

Arborescent; petioles distinct, up to 5–6 cm. long; blades ample, relatively broad, pubescent beneath (on the lamina sometimes glabrescent, but

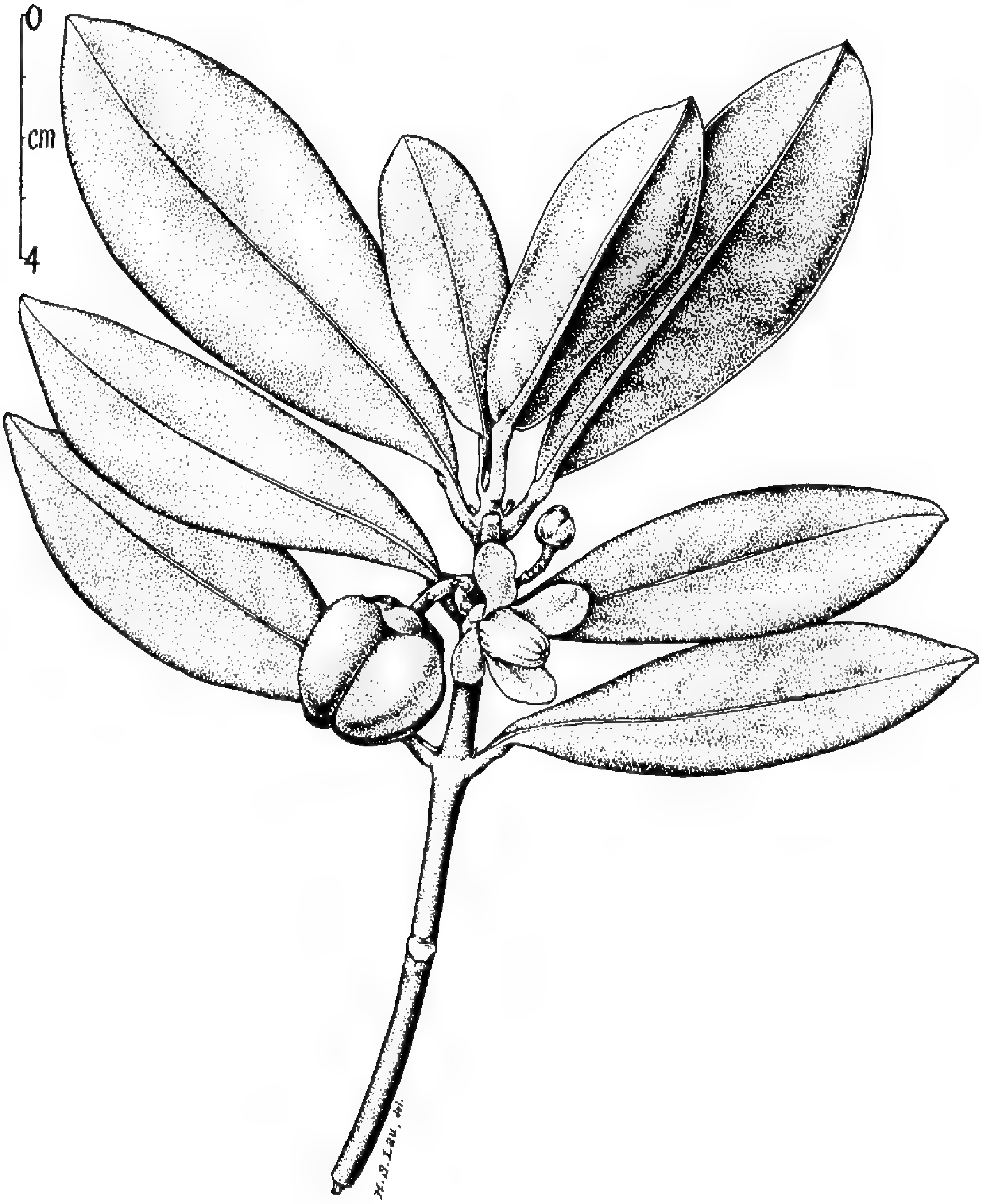

FIG. 2. Habit, with flower and fruit, of *Platydesma spathulatum* var. *spathulatum* form b. (From Punalu'u, Oahu.)

the costa with a persistent villosity), broadly spathulate to subelliptic, dark above (the lower surface paler); calyx glabrous or nearly so.

HOLOTYPE: Oahu: Waianae Mountains, slope of Kaala, *O. Selling 3710* (GB).

Kauai. Wahiawa Mountains, *Forbes 231.K.* (BISH); Waimea drainage basin, west side, *Forbes 782.K.* (BISH); Halemanu, *Rock 2318* (BISH); Kalalau trail, *Forbes 1046.K.* (BISH); Kaholuamanu, *Rock 5339, 10226,* (BISH), *5340* (A); Kumuwela plateau, *Stone 3358* (A, BISH, BM, E, GB); Hanalei-Lihue powerline trail, *Forbes*, 1909 (BISH); Hanapepe, *Faurie 240* (A). **Oahu.** Waianae Mountains, slopes of Kaala, Mokuleia, *Morley*, 1934 (BISH).

Platydesma spathulatum var. **pallidum** (Hillebrand) B. C. Stone, Madroño **16**: 165. 1962. (FIG. 3.)

Platydesma campanulata β var. *pallida* Hillebrand, Fl. Hawaiian Is. 71. 1888.

Similar in most respects to the typical variety, but with densely cinereous-puberulent calyx lobes (sometimes also the outer surfaces and

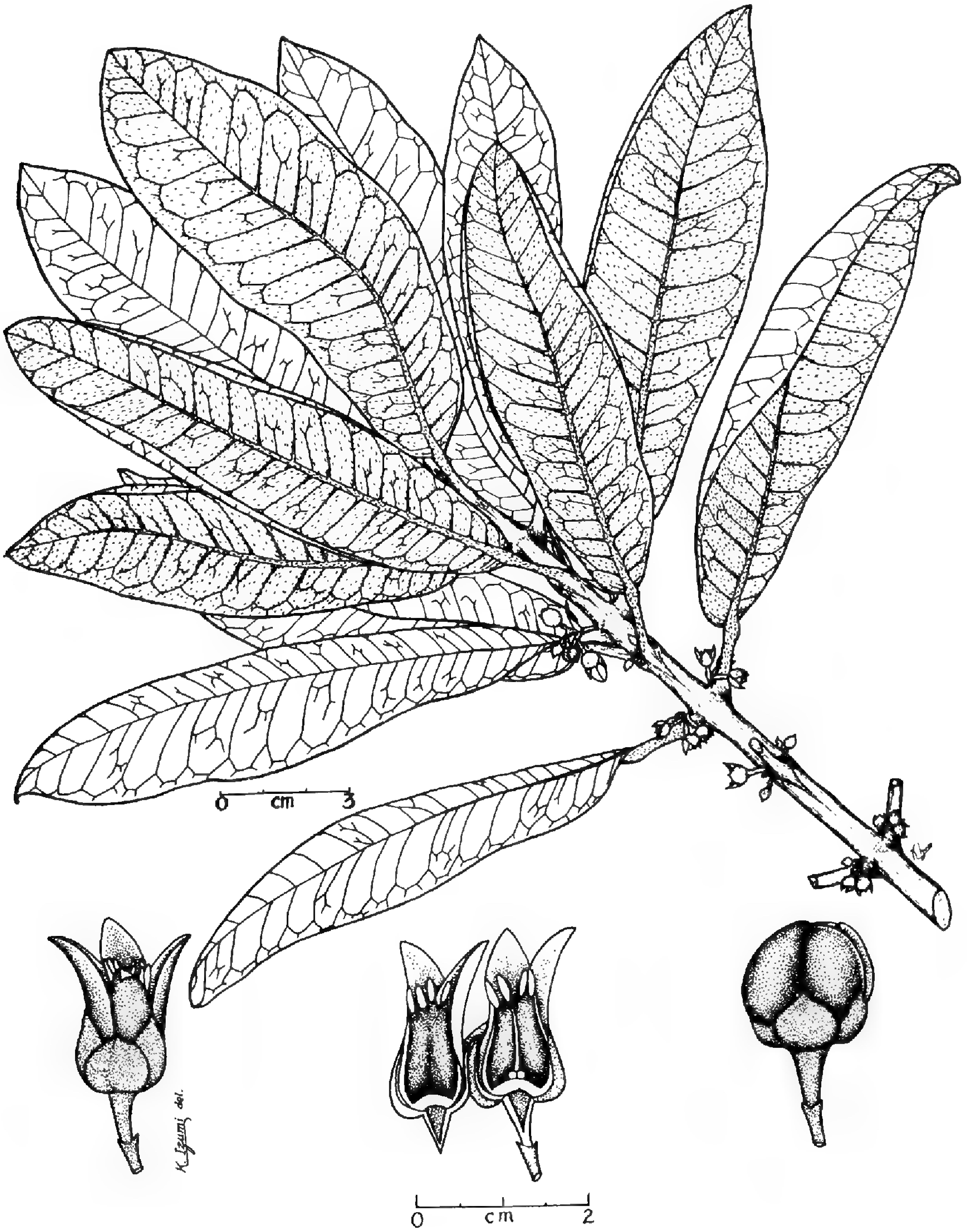

FIG. 3. Habit, flowers, and fruit of *Platydesma spathulatum* var. *pallidum*. (From Olinda, Maui, coll. *Degener*; courtesy of Dr. Degener.)

margins copiously ciliolulate), the pubescence extending to the mid-region of the petals; leaf blades pubescent beneath; hairs pale or fulvous, erect to somewhat spreading, about 0.2–0.4 mm. long, those on the calyx (and axes of the inflorescence) appressed, those of the leaves more erect.

SYNTYPES: Oahu, Kaala, *Hillebrand*; Maui, Hamakua, *Rev. John Lydgate*; both formerly at Berlin, but destroyed in World War II. NEOTYPE: *Topping* (*Degener 8615*) (BISH), cited below.

Oahu. WAIANAE MOUNTAINS: *Hillebrand*, 1869 (GH); Peahinaia trail, *Degener 12771* (A). KOOLAU RANGE: Pupukea, *Degener, Park & Nitta 8622* (A, NY); Poamoho trail, *Degener et al. 10859* (A). **Maui.** Woods near Ukulele, above Olinda, *Forbes 205.M.* (BISH); Olinda, *Rock 8534* (BISH, GH); *Topping* (*Degener 8615*) (BISH, CU, K); Kaea, *Forbes 2552* (BISH); Nahiku, *Forbes 240.M.* (BISH); below Kula pipeline, *Munro 796* (BISH); Kipahulu valley, ridge on left side, *Forbes 1642.M.* (BISH); ridge between west and east Wailuailai, *Forbes 2664.M.* (BISH); Honomanu, east bank of gulch, *Forbes 2658.M.* (BISH); west trail behind Honomanu, *Forbes 2587.M.* (BISH); Honomanu trail, *Rock 10228* (BISH), *Rock*, 1911 (BISH); Kailua, *Rock*, 1908 (BISH); without definite locality other than "East Maui," *Rock*, 1911 (BISH); without locality, *Forbes*, 1920 (BISH). **Hawaii.** Kohala, Honokanenui, *Rock 8367* (A, BISH); Papaikou near Honomu, *Bryan*, 1937 (BISH).

2. **Platydesma Remyi** (Sherff) Deg., Sherff, & Stone, Fl. Hawaiiensis, fam. 179. 1960. Stone, Adansonia II. 1: 98, 99. 1961. (FIG. 4.)

Claoxylon Remyi Sherff, Publ. Field Mus. Bot. 17: 557. 1939.
Claoxylon insigne H. Baillon ex Drake del Castillo, Illustr. Fl. Ins. Mar. Pac. 291. 1892 (*nomen nudum*).
Platydesma campanulatum var. *sessilifolia* Rock, Indig. Trees Hawaiian Is. 243. 1913.
Platydesma auriculaefolia sensu Hillebrand, Fl. Hawaiian Is. 72. 1888, not *Pelea auriculaefolia* A. Gray, 1854.

A sparingly branched light-wooded shrub or laxly branched small tree up to 2 or 3 m. tall, with branches loosely foliose and leaves subdistant, opposite; habit similar to that of preceding species; leaves sessile or subsessile, the short obsolete petiole broad, flattened, up to 5 mm. long, sparsely hispidulous; blades obovate or broadly spathulate, elongate, 14–38 cm. long, 4.5–18.5 cm. broad, often about 30 × 12 cm. (2–3 times longer than broad), punctate-glandular, entire, rounded or bluntly obtuse to subacute at apex, narrowed and at last rather abruptly rounded, subtruncate, or even subauriculate at base, glabrous above, sparingly puberulent beneath at least when young, the costa sulcate above and raised beneath; inflorescences axillary, 1–3(–5?)-flowered, on short peduncles and axes, the pedicels up to 2 cm. long, the axes nodose with opposed ovate bracts 1–2 mm. long; flowers as in *Platydesma spathulatum*, but the calyx lobes puberulent on both faces; capsule about 25 mm. in diameter, minutely puberulent, with rounded carpels.

HOLOTYPE: Hawaii. Location unknown, *Jules Remy 604*, 1851–55 (P).

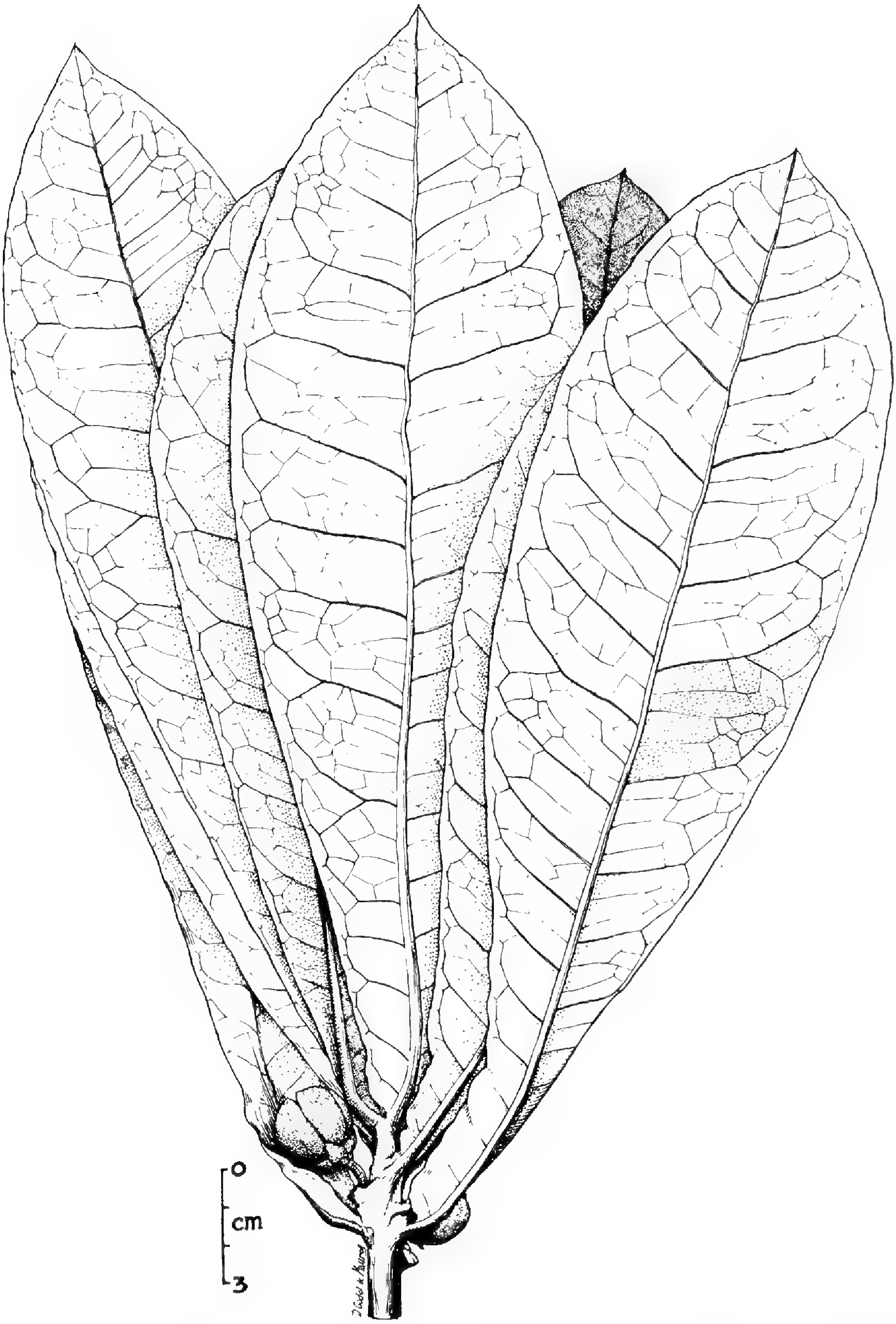

FIG. 4. Holotype of *Platydesma Remyi.* (Illustration by Mme. Godot de Mauroy, commissioned by O. Degener; courtesy Muséum National d'Histoire Naturelle, Paris, and Dr. Degener. Coll. *J. Remy 604*, Hawaii, 1851–55.)

Hawaii. Kohala Mountains, *Hillebrand 244* (GH, K; this collection is the basis of Hillebrand's *Platydesma auriculaefolia*); upper Hamakua ditch trail, above Koiawe valley, *Cranwell & Skottsberg HBS. 3192* (BISH, GB); Kohala, *Forbes 499.H.* (BISH); mauka of Waipio valley (inland side), *Lyon*, 1919 (BISH); Kohala, *Rock 8354* (BISH, GH), *4222* (GH, type of var. *sessilifolia*), *Rock*, 1912 (A).

This species is very close to *Platydesma spathulatum*, differing mainly in the obsolete petioles, the pubescence of the leaves and calyx (similar to that of *P. spathulatum* var. *pallidum*) and the puberulence of the fruits.

The drawing of the holotype given here (FIG. 4) was made at the request of Dr. Otto Degener, and has been published previously in *Flora Hawaiiensis*.

A specimen from Kauai (Alakai, *MacDaniels 781*) may belong here, but it is fragmentary and somewhat dubious. The locality would not be implausible in relation to the type of habitat, but the wide distributional gap would be most unusual. At present it seems apparent that this species is endemic to the Kohala region of Hawaii. Because of the number and recentness of some collections there seems to be no basis for considering it extinct, but new collections would be desirable. It may be possible eventually to show that this taxon should better be considered as a subspecies of *Platydesma spathulatum*.

Section CORNUTIA, sect. nov.

Carpidii maturitatem divaricati cornuti vel rostrati.
TYPE SPECIES: *Platydesma cornutum* Hillebrand.

3. **Platydesma cornutum** Hillebrand, Fl. Hawaiian Is. 72. 1888. (FIG. 5.)

Melicope grandifolia sensu Wawra, Flora **56:** 138. 1873, non A. Gray, Bot. U. S. Explor. Exped. **15:** 354. 1854.

Erect unbranched or sparsely branching shrub with soft wood up to 7 m. high, the main stem about 2 cm. diameter, the few branches erect or ascending, closely foliose near the ends, the youngest branches green, soon clothed with a pale grayish bark, the wood when freshly broken having a starchy odor; glabrous throughout except for the leaf buds and the proximal parts of the inflorescences, these sparsely hirtellous, but glabrate; leaves petiolate, petioles short, broad, flattened, 2–10 mm. long; blades glabrous, dark green when mature, linear-spathulate or narrowly obovate, 12–40 cm. long, 5–13 cm. broad, commonly about 30 × 9 cm., tapering gradually to the base, decurrent or finally obtuse, rounded or more commonly bluntly obtuse or acute at apex, the costa sulcate above, prominent beneath, the lateral nerves similar, ascending from the costa, merging distally with the deeply arched connecting vein. Inflorescences axillary, borne among the leaves but maturing on the lower stems after the leaves fall, fasciculately cymose, (3–)9–15-flowered, the peduncle and axes obsolete, pedicels thus subsessile, bractlets and bracteoles at first hirtellous, pedicels glabrous or nearly so, 5–10 mm. long, flaring into the base of the calyx; sepals glabrous except for the ciliolulate margins, broadly rounded, 3–4 mm. long and 5–6 mm. broad, imbricate in pairs, the inner pair slightly smaller; petals white, glabrous except for the minutely ciliolulate margins, 9–12 mm. long; stamens 8, connate into a staminal tube, the anthers on very short deltoid filaments, unequal, 4 somewhat larger, equalling the corolla, 4 slightly shorter; tube at base very slightly connate with base of corolla; ovary 4-lobed. on an obscurely 8-lobed disk, the styles at first connate, with 4 linear stigmas, later separating as the fruit matures; capsule with thin, chartaceous walls, glabrous, about 12 mm. long, the carpels united along their mutual faces nearly to the apex or free down to the middle, the distal portions divergent, each carpel terminating in a sharply acuminate horn-like tip; carpels usually 8-seeded; seeds with a shining black crustaceous testa.

KEY TO VARIETIES OF PLATYDESMA CORNUTUM

Leaves abruptly truncate or obtuse at base, petiole distinct. var. *cornutum*.
Leaves tapered and gradually, evenly decurrent at base. . . . . . . var. *decurrens*.

Platydesma cornutum var. **cornutum.**

Leaves tapering toward the base but at last briefly but abruptly truncate or obtuse, the petiole distinct.

HOLOTYPE: Oahu. Without definite locality except "Helemano, Wailupe, and Pauoa" (Koolau Range), *Hillebrand* (K; isotype, GH).

Oahu. KOOLAU RANGE: Northern end: Pupukea, *Skottsberg 1815* (BISH, GB); Pupukea-Malaekahana, *Lyon*, 1926 (BISH); south Opaeula gulch, Pa'ala'a, *St. John 10642* (A, BISH); Pupukea-Kahuku, *Degener 8623* (A, CU); Paumalu, *Hosaka 123* (BISH); Punalu'u, *Rock 8833* (BISH), *Rock and Forbes*, 1908 (A), *Rock*, 1908 (GH), *Anon.*, 1908 (Herb. Bd. Agric. For. Terr. Hawaii) (BISH); between Kaipapau and Punalu'u, *Forbes*, 1908 (BISH); Kaluanui, summit and beyond, Castle trail, Punalu'u, *Webster 1610* (BISH); Wahiawa gulches, *Forbes 1712.0.* (BISH); southern end, Puu Konahuanui, *Forbes 1010.0* (BISH); head of Manoa valley, *Rock & Shaw*, 1912 (BISH).

The typical variety, easily distinguished by the leaf characters noted, appears to occur only in the Koolau Range, the main eastern chain of mountains of Oahu. There does appear, however, to be some contact between the varieties, since var. *decurrens*, though mostly restricted to the Waianae mountains, has been found once or twice on the western slopes of the Koolau Range nearest the Waianae mountains. It is here that intermediate forms, if any are to be found, could be expected to occur.

Platydesma cornutum var. **decurrens,** var. nov.

Folia longe spathulata, base attenuata laminis in petiolam decurrens.

HOLOTYPE: Oahu. Waianae Range, Pu'u Kanehoa, southeastern side,

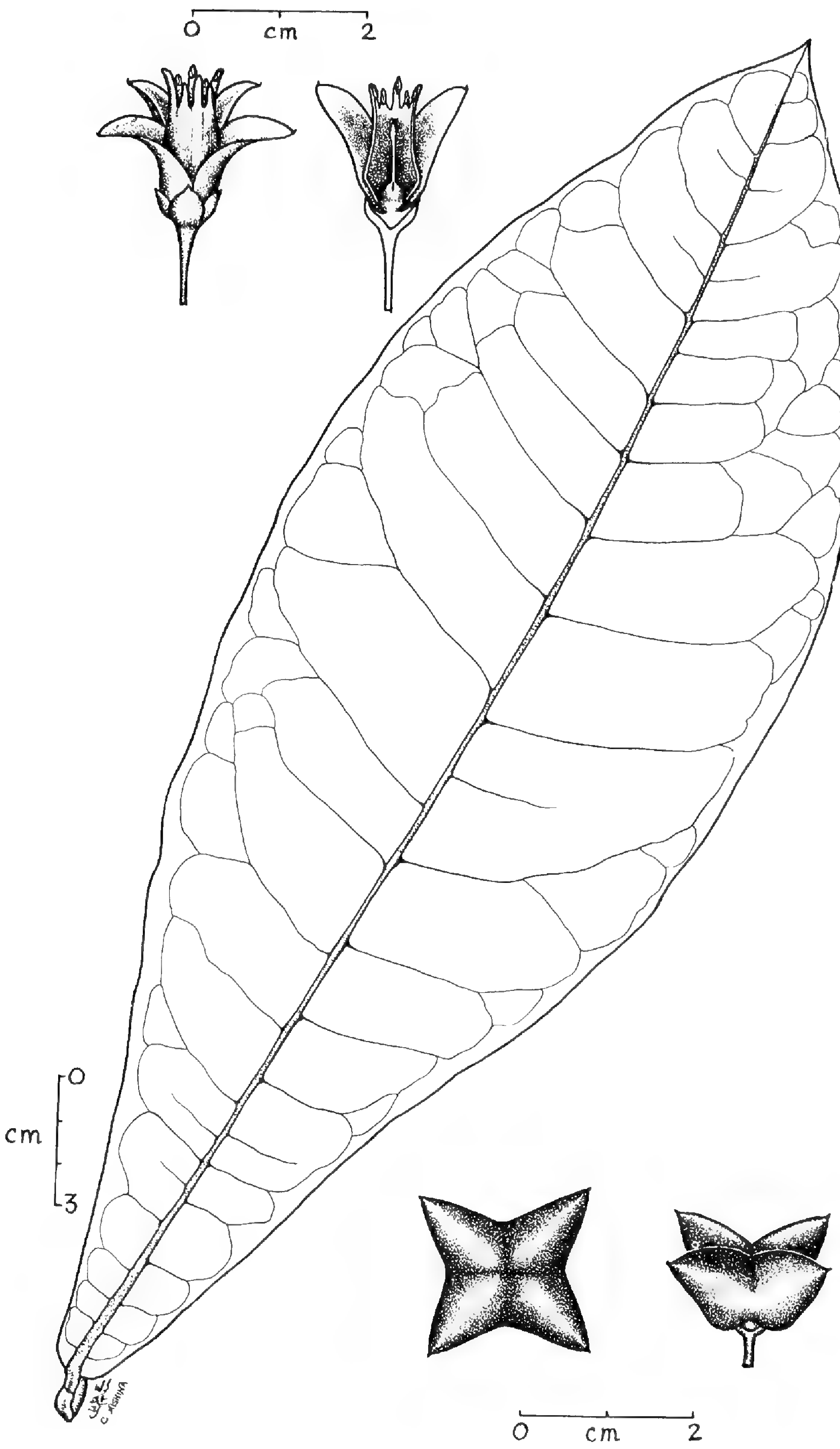

FIG. 5. Leaf, flower, and fruit of *Platydesma cornutum* var. *cornutum*. (From Punalu'u, Oahu; courtesy of Dr. Degener.)

on steep moist banks of stream in valley about 200 m. below summit at altitude of about 700 m., March 26, 1960, *B. C. Stone & G. Pearsall 3263* (BISH).

Oahu. Makaha valley, ridges of Mt. Kaala, *Forbes*, 1909 (BISH); Mokuleia valley, *Forbes 1822.0.* (BISH); Pahole gulch in Mokuleia, *Degener & Hatheway 20664* (BM); Makaleha valley, *Russ*, 1929 (BISH); valley south-east of trail to Pu'u Kanehoa, type locality, *Stone 3430* (BISH, US); Mt. Kaala, *Degener, Park, Topping & Swezey 8631* (A).

This variety is still another of the many examples of taxa endemic to the Waianae mountain range of western Oahu. This range, which is geologically much older than the larger Koolau Range, may be about the age of the island of Kauai. Several examples are known of taxa restricted to Kauai and to the Waianae Mountains, as well as species with distinct varieties in the Waianae Mountains and in Kauai. The specimens cited above are mostly sterile or in flower, but *Forbes*, 1909, bears an immature fruit. There are no apparent differences in floral or fruit characters between the two varieties, but the difference in the leaves is both obvious and constant. The holotype and *Stone 3430* are both from the same location, where a small group of these tall, erect, unbranched shrubs was growing in a moist, rocky habitat near a stream, in company with species of *Urera*, *Touchardia*, *Cyrtandra*, *Alectryon*, *Straussia*, *Morinda*, *Pelea*, and *Athyrium*. The flowers, like those of the next species, *Platydesma rostratum*, are borne on the slender trunks and mature at some distance below the leaves. The sepals are green, the petals and staminal tube clear white.

4. **Platydesma rostratum** Hillebrand, Fl. Hawaiian Is. 72. 1888. (FIG. 6.)

Erect unbranched or sparsely branching shrub with soft wood, branches ascending, juvenile stems green, later clothed in thin, pale, grayish bark, trunks to one or two (or more) meters high, 1–2 cm. thick, freshly broken wood with a starchy odor; leaves clustered near the ends of the branches, opposite, subsessile or with short, flattened petioles about 3–18 mm. long; blades linear-oblong or long, narrowly elliptic to subspathulate, mostly 20–40 cm. long, and 4–12 cm. broad at maturity, usually about 33 × 7 cm., at base broadly and abruptly truncate or obtuse (rarely subcordate), scarcely or not attenuate, at apex bluntly acute to coarsely acuminate (the tip bluntly acute) or somewhat rounded, in bud hirtellous but soon glabrate, glabrous at maturity; costa sulcate above, raised beneath, the lateral nerves numerous, subopposite or subalternate, almost at right angles to the costa, united distally 3–10 mm. from the margin by a deeply and symmetrically arching connecting vein; inflorescences axillary, at first hidden among the leaves, maturing below the leaves on defoliate young branches, cymose, the cymes 3–9-flowered (and sometimes fasciculate, two or three together), less than 2 cm. long overall, the peduncle stout, 1–3 mm. long and 1–1.3 mm. broad, the axes and pedicels up to 9 mm. long, the pedicels with an opposed pair of bractlets near the flaring apex at base of calyx, the axes with 1–3 pairs of decussate bractlets, these, with the bracteoles, axes, and peduncle, hirtellous when young, soon glabrescent; calyx slightly puberulent, the lobes imbricate in pairs, the outer pair larger, each lobe about 3 mm. long and 5 mm. wide, the inner pair with each lobe slightly smaller; petals clear white, glabrous, oblong, obtusely rounded at apex, about 5-nerved, valvate, about 12–13 mm. long and 5 mm. broad; stamens united into a staminal tube about 11 mm. long, anthers on brief deltoid filaments, these alternating in size, 4 about 2.5 mm. long, 4 about 2 mm. long, versatile, the anther affixed in the middle of the dorsal side; ovary 4-lobed, on a disk about 5 mm. broad, the carpels free distally, about 1.8 mm. high, subconic and shortly attenuate into a brief style; capsule of 4 carpels, each with a distal rostrum about 8 mm. long, connate nearly their whole length but the beaks free; capsule about 4 mm. long, excluding beaks; carpels 8-seeded; seeds black with a shining crustaceous testa.

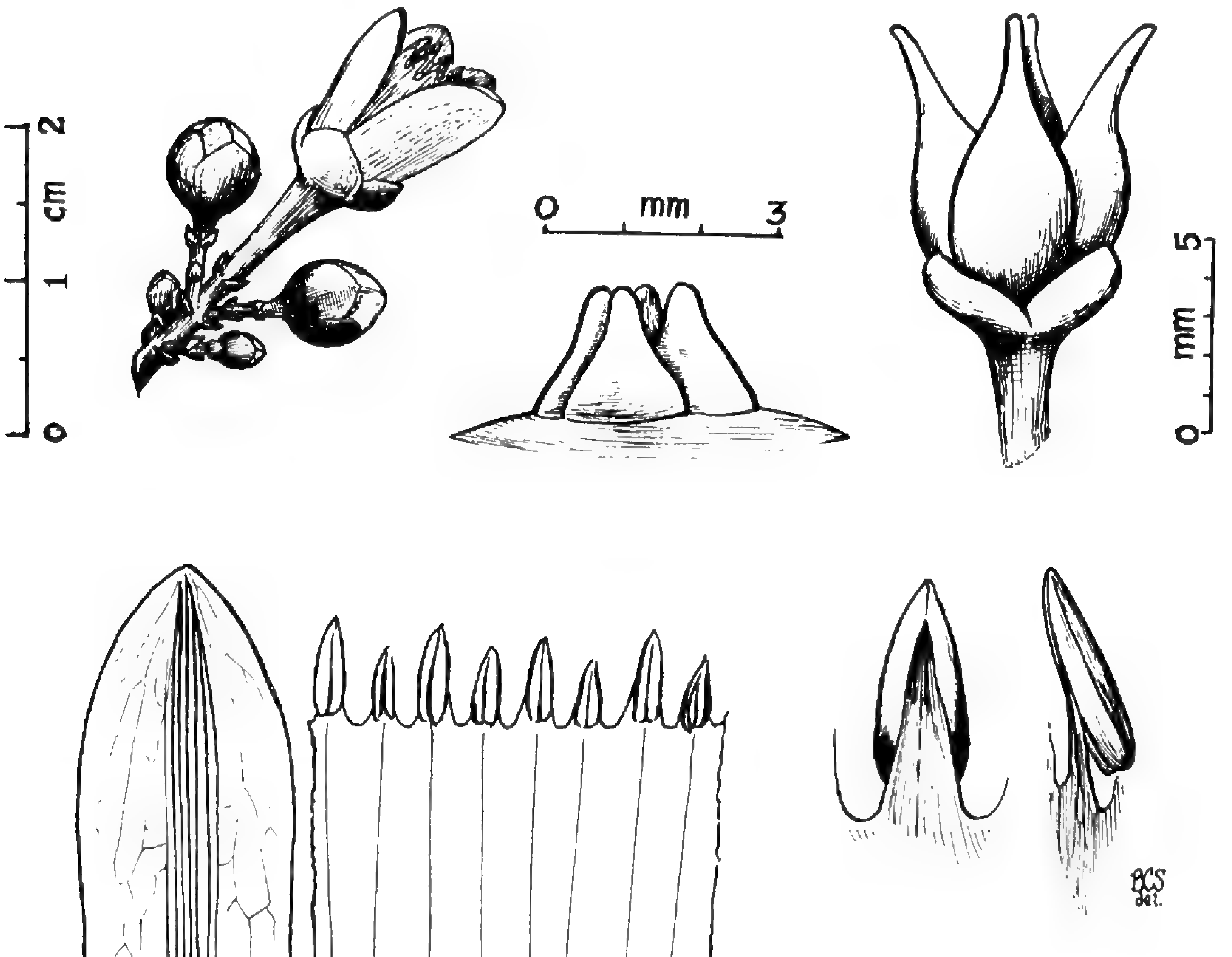

FIG. 6. Floral details of *Platydesma rostratum*. (Three upper figures from *Skottsberg 3100*, Kauai. Petals and stamens from *Rock 6081*. Original.)

HOLOTYPE: Kauai, without locality, *Knudsen 68* (Berlin, probably destroyed).

Kauai. Waimea, Kokee-Kalalau trail, *Cranwell, Selling & Skottsberg HBS. 3100* (BISH, GB); Kaunuohua ridge, Kaluapuhi trail, *Wichman* (*Skottsberg 2937*) (GB); Halemanu, *Rock 2000, 1999* (A), *2323, 6081, 6084* (GH); Awa'awapuhi trail, *Stone 1599* (BISH, K, US); *Lane*, 1956 (BISH); *Pearsall*, 1956 (BISH); *Stone 3329* (BISH); Hanalei valley, *Forbes 133.K.* (BISH); upper Lihue ditch trail, *MacDaniels 837* (BISH); without locality or date, *Rock 17302* (A).

This species is to be found in the mesic to wet forests of the high plateau region of Kauai, where it is well distributed but not common. The leaves are usually rather dark green and glossy above, the flowers clear white. The small, erect, sparingly branched shrubs form an understory element in rain-forest associations.

The relationship of the species is clearly with *Platydesma cornutum*, but the two are easily distinguished by both vegetative and fruit characters. If (as seems probable) evolutionary divergence closely followed the sequence of island formation, this species may antedate *P. cornutum*; or the two may be derived from a common ancestor. The relationship of these species to the arborescent, globose-fruited *P. spathulatum* and *P. Remyi* is obvious, but not particularly close, despite the small size (in number of species) of the genus.

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COLLEGE OF GUAM
AGAÑA, GUAM

THE THYMELAEACEAE IN THE SOUTHEASTERN UNITED STATES [1]

LORIN I. NEVLING, JR.

THYMELAEACEAE A. L. de Jussieu, Gen. Pl. 76. 1789, "Thymelaeae," nom. cons.

(DAPHNE FAMILY)

Erect shrubs [sometimes dwarf or climbing; trees, lianas, rarely herbaceous annuals]; stems generally with a layer of tough cortical fibers, often with internal phloem. Leaves alternate [approximate, opposite or irregularly pseudowhorled], simple, entire, laminar [to needle-like or scalelike], deciduous [or evergreen], dorsiventral [or isolateral, sometimes glandular-punctate]; petiolate or sessile, exstipulate. Inflorescences terminal at shoot apex, extra-axillary [axillary, or cauliflorous], pedunculate or sessile, racemose [spicate, umbelliform, or capituliform], simple [or compound]; bracts and bracteoles present or absent, [sometimes resembling an involucre]; pedicel articulated when present. Flowers bisexual [or unisexual by abortion and the plants polygamo-dioecious or dioecious], regular or rarely somewhat irregular. Calyx lobes free or, more generally, connate and adnate to the corolla and androecium to form a variously shaped calyx tube, open [or imbricate, valvate], 4[6, 5 or 3]-merous, often greenish yellow [but sometimes brightly colored, sometimes articulated at the middle]. Corolla nonpetaloid; petals adnate to the calyx, the lobes alternisepalous, free [or connate into a faucal corona, either simple or variously divided, of various shapes, or absent, generally inserted near the orifice of the calyx tube]. Androecium generally diplostemonous [rarely haplo- or very rarely poly- or hemistemonous, in ♀ flowers reduced to staminodia or absent], in 1 or 2 whorls, the upper whorl antisepalous and the lower alternisepalous; anthers filamented [or sessile], longitudinally dehiscent, introrse [extrorse or horseshoe-like], basifixed

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[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 C. E. Wood, Jr., and R. C. Rollins. The scheme follows that outlined at the beginning of the series (Jour. Arnold Arb. 39: 296–346. 1958) except that the family description and bibliography are more extensive than usual. 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 the species of this area is placed in brackets. References which have not been verified are designated by an asterisk. The figure of *Dirca* was drawn by Dorothy H. Marsh under the supervision of R. B. Channell and C. E. Wood, Jr.

[or dorsifixed, the connective sometimes thickened or produced beyond the pollen sacs]; pollen globose, polyporate. Disc annular [cupular, tubular, scalelike, or absent], free [or sometimes adnate to the calyx tube], surrounding the base of the gynoecium. Gynoecium syncarpous, [12-, 8-, 5-, 2- or] 1(pseudomonomeric)-carpellate, [reduced to a pistillode in ♂ flowers]; stigma usually capitate; style 1, [terminal or] eccentric, sometimes obsolete, [rarely with parastyles]; ovary superior; ovules 1 in each locule, mostly pendent from the locule apex, anatropous and with ventral funicles [or rarely hemi-anatropous to nearly orthotropous], 2-integumented, [often carunculate, often with an obturator at the base of the style]. Fruit a berry [loculicidal capsule, nut, or drupe, often accompanied by an accrescent calyx]. [Seeds sometimes arillate;] embryo straight, with flat or thickened, narrow or broad cotyledons; endosperm present [or absent]. TYPE GENUS: *Thymelaea* P. Miller, nom. cons.

Approximately 55 genera, with some 500 species now recognized, all tropical or temperate, with the greatest speciation in tropical and subtropical regions. It is expected that the number of genera will be reduced by nearly one-fifth in the near future, and a further reduction could be realized by the elimination of a number of genera of "convenience." A single genus composed of two species, only one in our area, is native to the United States. *Thymelaea Passerina* (L.) Coss. & Germ., an annual weed, has been reported in Iowa and Nebraska; and *Daphne Mezereum* L. is a more or less common escape from cultivation in the northeastern United States.

The family is divided into four subfamilies, according to Domke's system which is followed here. Some authors exclude the three genera of subfam. Gonystyloideae Domke and the three of subfam. Aquilarioideae Gilg, tribe Microsemmatideae Domke, treating them as a separate family, Gonystylaceae Gilg, a segregation which seems both unnecessary and unwise, contradicting as it does both anatomical and palynological evidence. A third subfamily, Gilgiodaphnoideae Domke, is monogeneric. The Thymelaeoideae, to which our genus belongs, contains the bulk of the genera and species of the family, although a number of genera still remain unplaced in the family system. American genera of uncertain position are *Goodallia* Bentham, *Lasiadenia* Bentham, and *Linodendron* Grisebach.

On the basis of the few and scattered chromosome-number reports, a base number of nine is assumed. The majority of the species are diploid; the only known exceptions are a triploid *Daphne* and polyploid series in *Edgeworthia*, *Pimelea*, and *Wikstroemia*. Apomixis has been demonstrated in one species of *Wikstroemia* and is suspected in others.

The family is of little general economic importance except, perhaps, in very localized areas. The genus *Daphne* is of considerable horticultural interest and is grown in many temperate regions for its sweetly scented flowers. In local areas, almost the world over, the tough extraxylary fibers of various species are employed as cordage and in the manufacture of paper or "cloth." The heartwood of some Asian species is highly prized as incense wood. The fruits, which seem to have some poisonous principle, are used as a purgative or emetic in primitive areas. Unidentified alkaloids are reported from plants of a number of genera.

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1. **Dirca** Linnaeus, Sp. Pl. 1: 358. 1753; Gen. Pl. ed. 5. 167. 1754.

Slow-growing, deciduous shrubs with slender, flexible branches swollen at the nodes. Mature plant-parts usually containing simple or compound crystals of calcium oxalate. Leaves ovate, broadly elliptic, or obovate, sparsely sericeous and glabrescent, the petioles calyptrate over the axillary bud. Flowers appearing before or simultaneously with the leaves, borne in few-flowered, nodding racemes from the axils of last years' leaves, the primary and secondary peduncles conspicuous [or nearly obsolete]; bud scales woolly. Sepals connate into an infundibuliform or narrowly campanulate calyx tube, straight [or strongly bent], yellowish green to yellow, glabrous, the lobes connate, the sinuses shallow and becoming obscure with age (in our species). Petals minute, lobes inserted on the calyx tube between the insertion of the filaments. Stamens 8, in 2 closely adjacent whorls; filaments filiform, inserted between the lower and upper one-third of the calyx tube, glabrous; anthers exserted even in bud. Disc a minute, irregularly lobed annulus surrounding the base of the ovary. Gynoecium pseudomonomeric, glabrous; stigma punctate, exserted; style filiform, glabrous; ovary 1-locular with a single anatropous ovule. Fruit a bilaterally symmetrical berry, yellow or yellowish green to white, becoming reddish or purplish. Seeds with a fleshy outer and hard inner seed coat; endosperm scanty; embryo with thick, plano-convex cotyledons. TYPE SPECIES: *D. palustris* L. (Name from Greek mythology, after Dirce, second wife of Lycus, who was bound by Amphion and Zethus, sons (by Zeus) of Lycus' first wife, Antiope, to the horns of a wild bull to be killed and who then was transformed into the fountain of Dirce near Thebes.) — LEATHERWOOD.

Two species of temperate North America, of obscure affinities, distinguished from other American genera by the 4-merous, bisexual flower with eccentric style. *Dirca occidentalis* Gray is restricted to six counties in the San Francisco Bay area of California, while *D. palustris* ranges sporadically from New Brunswick, Quebec, and Ontario, southward to northwestern Florida and Alabama, and westward to Minnesota, Iowa, Missouri, and Oklahoma. The two generally are considered to be closely related, and in some instances their distinctness has been questioned.

Our species is generally restricted to rich woods where considerable moisture is available. It is found, however, in a variety of habitats and seems to be a facultative calciphile. Although of sporadic occurrence, local populations often are extensive.

There is considerable disagreement in the literature concerning color of the fruits, which, being eaten by birds as soon as ripe, are rarely seen in the wild. The color is described as reddish or purplish in some studies and yellowish or yellow-green in others. The large majority of field observations favor the yellow or yellow-green color, with the fruit often turning white and then purplish after falling or during the preparation of specimens for the herbarium. Further field observations are in order.

The extreme flexibility of the stems of *Dirca* (as well as of many other Thymelaeaceae), well known to field botanists, is due largely to the slight degree of lignification, as determined by chemical tests, of the secondary wood. Poor lignification is found sporadically throughout the entire family. The wood is very light, with a specific gravity of about 0.41, as compared to 0.21 in *Leitneria floridana* Chapm., the lightest native wood of the United States. The low density of the wood in *Leitneria* is due to extensive amounts of parenchyma, but in *Dirca* the bulk of the wood is composed of fibers. The stems of *Dirca*, as well as many other Thymelaeaceae, have an extensive development of extraxylary fibers which accompanies all vascularization. Although these fibers can be considered as an added supporting device, they, too, are nonlignified (in *Dirca*).

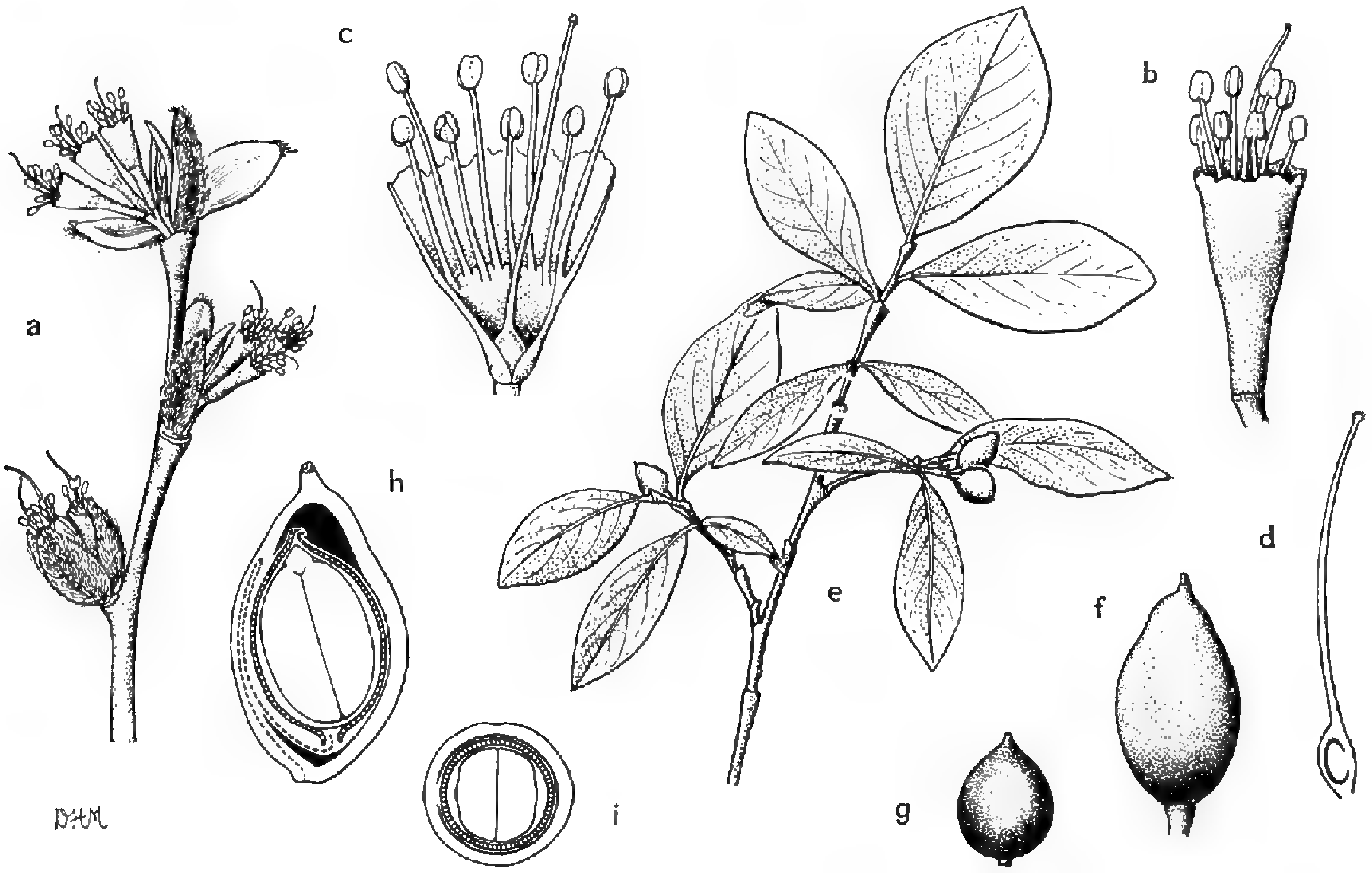

FIG. 1. **Dirca.** a–i, *D. palustris*: a, flowering twig, × 1; b, flower, × 3; c, flower, calyx tube opened lengthwise, to show insertion of stamens and minute petals between filaments, × 3; d, gynoecium, in vertical section, diagrammatic, × 3; e, fruiting twig, × ½; f, mature berry, × 2; g, seed, with fleshy outer seed coat removed to show bony inner coat, × 2; h, fruit, with single seed in vertical section — semidiagrammatic; note ovary wall, fleshy outer seed coat, stony inner seed coat (hatched), thin layer of endosperm (white) surrounding large embryo, ovular trace (broken line), × 3; i, fruit in cross section to show seed attachment, seed coats, endosperm, and cotyledons, × 2.

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THE LEITNERIACEAE IN THE SOUTHEASTERN UNITED STATES[1]

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

LEITNERIACEAE Bentham in Bentham & Hooker, Gen. Pl. 3: vi, 396. 1880, "Leitnerieae," nom. cons.

(CORKWOOD FAMILY)

A monotypic family distinguished by secretory canals in the pith and leaves, nonaromatic foliage, erect catkins, single-styled gynoecium with a superior, 1-locular ovary, single parietal anatropous ovule, and seed with a large embryo and thin, fleshy endosperm.

1. **Leitneria** Chapman, Fl. So. U. S. 427. 1860.

Dioecious deciduous shrub or small tree to 6 m. tall, up to 15 cm. in diameter; current stems hairy; bark brown; wood very light in weight. Leaves alternate, 5-ranked, simple, exstipulate, pubescent; blades 10–15 cm. long, lanceolate to elliptic-lanceolate, acute, entire, somewhat coriaceous and glossy in age, finally rugose; petioles half-cylindric, ca. 2.5 cm. long; nodes with 3 traces from 3 gaps. Flowers appearing before the leaves in erect, preformed aments with weak axes. Staminate catkins curving outward, the axis lax, with 40–50 cymules in the axils of spirally deltoid-ovate scales, each cymule of (3–)10–12(–15) free stamens (apparently representing about 3 flowers); bracteoles and perianth absent; filaments short, slightly dilated at the base; anthers oblong, 2-locular at anthesis, slightly versatile, nearly extrorse, dehiscing longitudinally; pollen nearly globose, smooth, 3–6-colpate. Carpellate catkins stiffly erect, spikelike,

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[1] Prepared for a 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. This treatment was prepared originally by the first author while he was associated with the Arnold Arboretum and the Gray Herbarium; it has been edited by the second author in the style developed since that time and has been modified through the incorporation of additional information. The scheme follows that outlined at the beginning of the series (Jour. Arnold Arb. 39: 296–346. 1958). As in former treatments, the area covered is bounded by and includes North Carolina, Tennessee, Arkansas, and Louisiana. References which we have not verified are marked with an asterisk. The illustration was prepared by Dorothy H. Marsh from living plants cultivated at the Arnold Arboretum and from fresh material kindly collected for us on the Apalachicola River by Dr. Robert K. Godfrey, of Florida State University. We are further grateful to Dr. Wilbur H. Duncan, of the University of Georgia, for information on the occurrence of *Leitneria* in Georgia, and to Dr. Delzie Demaree, of Hot Springs, Arkansas, for data from that state and from Missouri.

relatively few flowered; carpellate flowers sessile, solitary in the axils of the spirally arranged primary bracts, each with 2 bractlets at the base and surrounded by a perianth (involucre) of (3) 4(–8) minute tepals (scales?) (2 often somewhat larger than the others); style linear-lanceolate, reddish, deciduous, the grooved stigmatic surface facing the bract; ovary superior, ovoid, green, 1-locular with a single parietal, pendulous, anatropous, 2-integumented ovule on the side toward the bract; embryo sac of the "Polygonum" type. Fruit an erect, smooth, oblong-ovoid, somewhat compressed, dry drupe (the thin flesh heavily reticulated with vascular bundles), chestnut-brown, green when young, with a terminal stylar scar. Seed with a thin layer of endosperm and a large, straight embryo. TYPE SPECIES: *L. floridana* Chapm. (Named for Dr. E. T. Leitner, –1838, a German naturalist who traveled in Florida and was killed during the Seminole War.) — CORKWOOD.

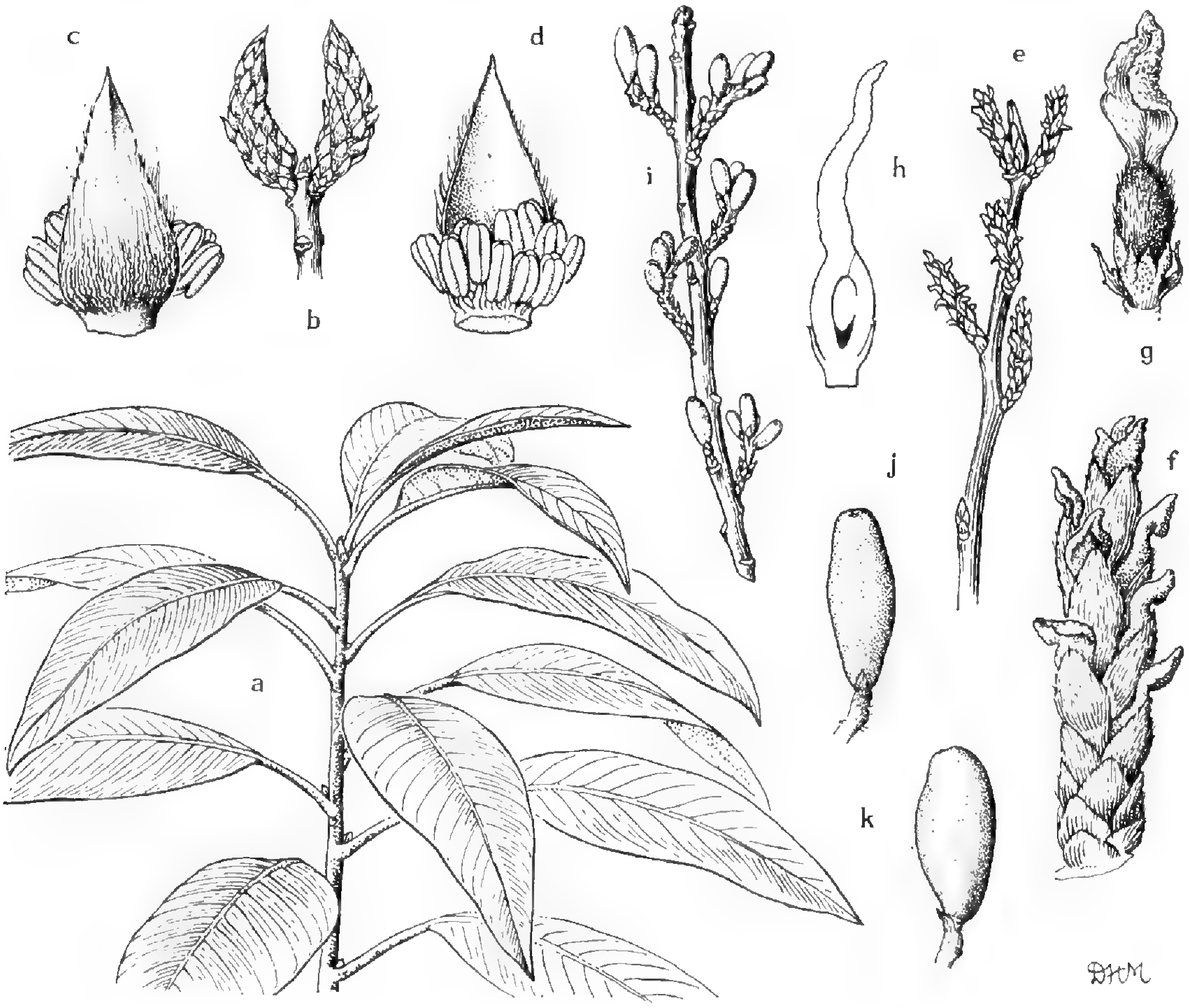

FIG. 1. **Leitneria.** a–k, *L. floridana*: a, vegetative shoot, × 1/4; b, twig with staminate catkins, × 1/2; c, d, bracts of staminate catkin from without and within, showing stamens, × 4; e, twig with carpellate catkins, × 1/2; f, carpellate catkin, × 3; g, carpellate flower with subtending bract removed, stigmatic surface toward viewer — note tepals and two lateral bractlets, × 4; h, carpellate flower in vertical section, stigmatic surface to the right, micropyle of ovule at top, diagrammatic, × 4; i, twig with immature fruits, × 1/2; j, k, mature fruits, × 1.

A single species, *Leitneria floridana*, known from muddy, brackish tidal shores, river swamps, swampy prairies, and sloughs[2] in scattered localities in three widely separated areas: southern Georgia (McIntosh and Dougherty counties) and northern Florida (Clay, Franklin and Levy counties); southeastern Missouri (Butler, Dunklin, Pemiscot, and Ripley counties) and eastern Arkansas (Arkansas, Clay, Craighead, Jackson, Jefferson, and Lincoln counties); and southeastern Texas (Brazoria and Chambers counties).

According to the literature, the species is variable in respect to height, leaf shape, length of catkins, and fruit size, but no comprehensive study of variation has been made, and no formal taxonomic segregates have been proposed.

Individual plants spread clonally, apparently from adventitious buds on the shallow root system. Pollination is by wind, and fruits are not set in the absence of pollination. Sometimes cultivated as an ornamental oddity in appropriate wet situations, the Missouri form is hardy as far north as Boston, Massachusetts, and Rochester, New York. The soft, only slightly porous wood, the lightest of any North American plant (sp. gr. 0.21) has sometimes been used locally for floats on fishing nets.

Generally admitted to be highly specialized (reduced) in structure, *Leitneria* shows few features which assist in determining its relationships. It has been associated with Ranales, Rosales, Geraniales, Sapindales, Parietales, and Myricales, and in most modern works it is placed in the "Amentiferae," usually as a separate order in a position close to Myricales, despite various lines of evidence to the contrary. Comparative morphological, anatomical, and embryological studies indicate that the closest relationships may be with the primitive Rosales (including Hamamelidaceae) or Geraniales, but more diagnostic evidence from these groups is needed. The development of the male gametophyte and fertilization have not been studied, and the chromosome number is unknown.

Vascular and other evidence suggests that the flower of *Leitneria* is derived from a bisexual ancestral form with a perianth of two cycles, at least one cycle of stamens, and a 2-carpellate, perhaps apocarpous, gynoecium. The staminate inflorescence apparently represents a many-flowered compound ament with a cymule of three florets in the axil of each primary bract.

The secondary xylem is so advanced in various respects, including the simple perforation plates and the alternate pit arrangement on the side walls of the vessel elements, that there would be little difficulty in deriving it from that of the primitive types of any of the groups with which

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[2] Dr. Delzie Demaree has written to Channell (April 1, 1962) of an exceptional colony of *Leitneria* in valley farmland on the property of Mr. Ronney G. Mattics about 2¼ miles east of Senath, Dunklin County, Missouri. "The area has been cleared of large *Taxodium* trees. Waste areas and fence rows are covered by *Leitneria*. These plants are a troublesome weed to this farmer. . . . I have watched this area for over ten years and before any of it was cleared thousands of plants were present. The soil is sandy loam and fertile." The plants in the area are three to five feet tall and were in abundant flower.

Leitneria has been associated. The most distinctive anatomical feature is the presence of secretory canals in the outer part of the pith which extend in association with the vascular bundles throughout the leaves. This and the stratified phloem led Solereder to note the similarity to Dipterocarpaceae, from which, however, it must be excluded on other grounds. (See Metcalfe & Chalk; Heim; Van Tieghem & Le Conte.)

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THE DIRECTOR'S REPORT

The Arnold Arboretum During the Fiscal Year Ended June 30, 1962

In recording the activities of the staff of the Arnold Arboretum during the past year, the event that stands out most vividly is the completion of the Charles Stratton Dana Greenhouses and the associated "open house" days for the Friends of the Arnold Arboretum and interested public. The planning of this new facility has occupied the staff for several years and the actual construction of it for much of the present one. The contractors finished their work in March, leaving April and early May for the tasks of moving the contents of the old greenhouses and laboratory to the new location and of preparing the surrounding grounds. The complete cooperation and the hard work of the horticultural staff of the Arnold Arboretum, best described as dedicated, made it possible to meet our schedule. For once, the fickle New England climate cooperated with our plans, producing excellent weather for the moving operations and also one of the most extended flowering seasons in the recent history of the Arboretum. The frequent newspaper notices and radio announcements of the progress of the flowering season were also helpful in giving us the largest weekly attendance since before the last war. The general response to the publicity culminated in an historic traffic tie-up on surrounding streets during lilac weekend with an estimated 25,000 visitors on the grounds between two and three P.M. on Sunday, May 20.

Staff:

New appointments to the staff during the year were Dr. Bernice G. Schubert and Dr. Wallace R. Ernst. Dr. Schubert, formerly with the U. S. Department of Agriculture, at Beltsville, Maryland, joined the staff on January 1st as Associate Curator. Dr. Ernst, a recent graduate of Stanford University, was appointed jointly with the Gray Herbarium to work with Dr. Wood on the generic flora of the southeastern United States. Two scholars were appointed Mercer Fellows during the year. Mr. Don M. A. Jayaweera, Director of the Royal Botanic Gardens, Peradeniya, Ceylon, held a Rockefeller Foundation Fellowship during the last year and was appointed a Mercer Fellow to complete his work on the genus *Mussaenda*. Dr. Lalit Mohan Srivastava, a graduate of the University of California at Davis, was appointed a Mercer Fellow to work with Dr. I. W. Bailey on further studies of the cambium and secondary phloem of vascular plants.

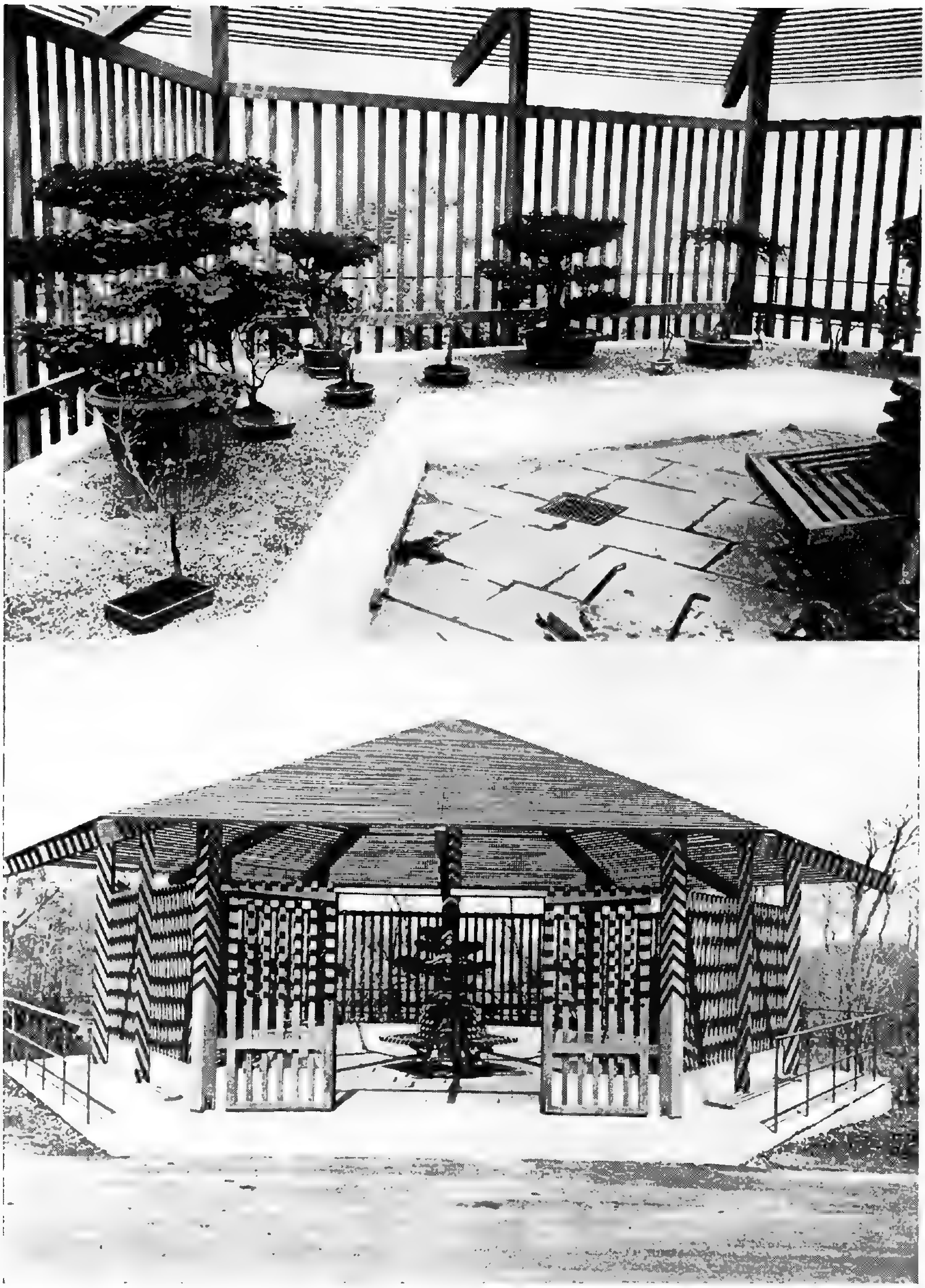
The resignations of Dr. Joab L. Thomas and Dr. Burdette L. Wagenknecht were accepted at the beginning of the year. Dr. Thomas accepted a position at the University of Alabama and Dr. Wagenknecht one at Norwich University.

It is a pleasure to record the horticultural award of the Colman Medal to Dr. Sax by the American Association of Nurserymen in recognition of the work which he accomplished at the Arnold Arboretum. Dr. Ernst was awarded the George R. Cooley Prize for the best paper presented at the annual meeting of the American Association of Plant Taxonomists. This paper, entitled "The Familial Status of the Fumariaceae," summarized his morphological comparisons of this family with its relatives, the Papaveraceae. Dr. Wyman completed his term as President of the American Horticultural Society and was elected to the Board of Directors of the Society at its annual meeting.

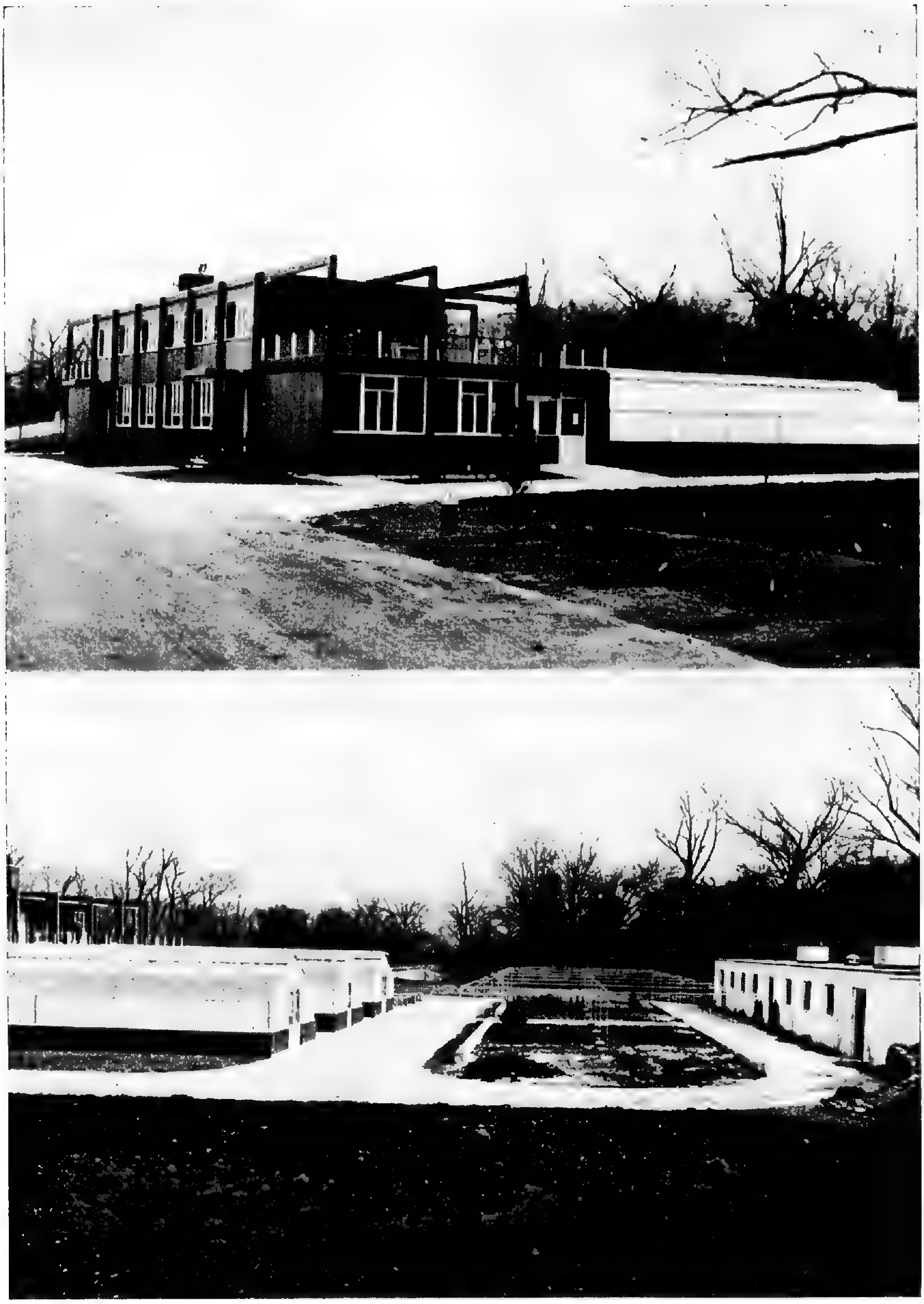
Horticulture:

The completion of the Charles Stratton Dana Greenhouses and the transfer of the propagation work to these new quarters summarize in large measure the activities of the staff in horticulture during the past year. Previous reports have indicated the nature of the physical plant proposed, and a full description of these greenhouses was published in *Arnoldia*, volume 22, combined issues 5 and 6. The new greenhouses are built on land owned by Harvard University for the Arnold Arboretum and adjacent to the city-owned land occupied by the main collections. The development consists of four units of construction, a main building with three attached greenhouses, a cold storage house built into an earthen bank, a free-standing slat house of modern design to house the Larz Anderson *bonsai* collection, and a pipe-frame construction to be covered with saran cloth to function as a shade house for nursery stock. In the surrounding area, over an acre of ground is devoted to nursery stock; additional space is for planned future expansion, appropriate landscaping for the buildings, bank plantings of suitable materials, as well as a demonstration area for many varieties of such plants, a collection of genetically dwarf plants near the *bonsai* collection, and a new location for the Arboretum hedge collection. The entire location is fenced and can be locked, thus affording for the first time excellent protection to the greenhouse and nursery areas.

The Dana Greenhouses have a main building, the headhouse, 36 × 111 feet with full basement and first floor and a smaller second floor with an apartment 22 × 68 feet for a resident guard. Included in the main building, in addition to ample areas for the work of the propagation staff, are a small conference-lecture room, a laboratory for anatomical or cytological work, two walk-in cold rooms for controlled temperature experiments in ranges of plus 40° to minus 20° F., and abundant storage space. Three greenhouses, each 17 × 51 feet, are attached, and there is space for a fourth. Expansion of each is possible on standard modules. The heating



Two views of the new lath house for the Japanese *bonsai* of the Larz Anderson Collection of the Arnold Arboretum. The lath house is opposite the main building of the Charles Stratton Dana Greenhouses and overlooks the hedge collection.



The Charles Stratton Dana Greenhouses of the Arnold Arboretum.
ABOVE: Main building and greenhouses.
BELOW: Greenhouses, shade houses, and cold storage house.

plant is designed to handle twice the present glass area. An auxiliary generator was installed to provide automatic take-over when the line voltage drops below 70 per cent of normal. This generator will operate both the heating and refrigeration units for an extended emergency. Ease of maintenance and operation were the primary considerations in the design of the building and are exemplified by the uniform floor levels throughout the building, the ample aisles for trucks, an electric elevator for transport of supplies to the basement storage, glazed tile walls for cleanliness, chutes to an incinerator or bins for debris, washable floors which can be hosed and then dried with "squeegees," and soil bins which are filled from the outside and are unloaded from the inside.

The cold storage house is another feature of the experimental opportunities made possible through the new construction. This building, 15 × 100 feet, is of concrete block construction and is insulated with slabs of "styrofoam." The house has heating as well as refrigeration units. One section will house the *bonsai* collection during the winter months, and a separate section can be used to produce an early cold season or extend a winter season for plants larger in size than are usually cared for in a greenhouse. Nursery stock normally subjected in New England to unseasonable early warm periods followed by a late freeze now can be maintained in a dormant condition until all frost danger is over.

The erection of the new greenhouses, named for Charles Stratton Dana, was made possible through a generous bequest by his daughter, Martha Dana Mercer. This development has met a long-standing need of the Arboretum for modern greenhouses with experimental facilities. Their completion and occupancy make possible continued contributions by the staff to the study of the ornamental plants hardy in New England.

To move from the old greenhouse area as quickly and as completely as possible required long planning and hard work on the part of the staff. During the fall, plants to be moved were planted in cans or were root pruned. Accumulations of many years were sorted and discarded or packed for the move. Soil was conditioned to receive the transplants. New equipment and supplies had to be anticipated and ordered. Finally, in March when construction was completed the move took place. During May and again during commencement week the greenhouse area was on display. New lawns were planted, newly transplanted materials had to be watered, mulches were spread, much pruning was required, and, finally, the ever-present weeds of newly developed areas required attention. At the time of this report operations are about back to normal, and much of the work which remains to be done can be fitted into a regular schedule. A special word of appreciation is due Dr. Wyman, horticulturist, who worked with the architects and contractors throughout the planning and the completion of this construction; Mr. Williams, superintendent, for his own efforts combined with those of the grounds crew; and Mr. Fordham, propagator, and his staff. The good job expected was done.

The weather of the past year was extremely favorable to the living collections. The season was marred only by the passage of hurricane

"Esther" on September 21st. Moderate damage to branches resulted from gale-force winds, which also destroyed our only specimen of *Juglans mandshurica* in a localized gust. A replacement specimen has since been obtained from Finland, but the loss emphasizes the value of the efforts of the greenhouse staff to propagate plants now represented in our collections by single individuals which have proven extremely difficult to reproduce by the usual propagating techniques. The heavy snow coverage of February gave adequate protection to the plants during the month of most violent weather, and little or no killing of flower buds or branches was experienced. The beneficial result of natural winter protection was revealed in a most floriferous spring season of moderate temperatures which saw the major collections remain in flower for longer periods than usual.

The labor requirements associated with the new greenhouses caused a reduction in the cultural efforts in the main collections during the year. Very little planting was done during the fall or spring season, and the regular distribution of plants to cooperating nurserymen was omitted this year. Materials for both programs are on hand and both will be reactivated during the transplanting season in the fall.

The Department of Parks and Recreation of the City of Boston continued its regular attention to the Arboretum road system. A major road unit from the Forest Hills gate to the pond area and a second unit from the forsythias past the lilac collection to the rockery were resurfaced, the drains relocated, and the sidewalks repaired. This is a major improvement which will facilitate snow plowing during the winter and make many areas more accessible for winter-time work. With the cooperation of the representatives of the Department of Parks and Recreation, the City of Boston scheduled a hearing concerning necessary repairs to a storm sewer which passes through the new greenhouse area. Since this land belongs to Harvard University and not the city of Boston, a division of the costs of repairs has been agreed upon, and it is expected that the needed repair will be completed in the next year.

At the annual meeting of the American Association of Botanical Gardens and Arboretums, the Arboretum staff was asked to serve for another two-year period as registration authority for cultivated woody plants not represented by special societies. Although no additional registration lists of cultivars were published during the year, several lists have been completed, and work is in progress on others. Dr. Wyman completed the registration list for *Fagus* and Mr. Green that for *Ulmus*.

Dr. Howard, with the assistance of Miss Carroll, Miss Herron, and Mrs. Walsh, completed the compilation of a directory of botanical gardens of the world which is to be published by the International Association for Plant Taxonomy as a volume of *Regnum Vegetabile*. A grant from the International Union of Biological Sciences will assist in the publication of this directory which lists the physical characteristics, staff members, and the research and resources of over 500 botanical gardens.

During the past year the staff of the propagation department received

The Charles Stratton Dana Greenhouses of the Arnold Arboretum.
Left, above: Office and conference room; below: Research laboratory. Right, above and below: Apartment for greenhouse guard.

Two views of the work area for plant propagation in the Charles Stratton Dana Greenhouses of the Arnold Arboretum.

164 shipments of plant materials representing 579 species and varieties from 23 different countries. One hundred and thirty of these lots (representing 458 taxa) came as plants or cuttings, while only 30 shipments (121 taxa) consisted of seeds and fruits. By contrast, 214 shipments comprising

852 taxa were distributed on request to botanists in nine countries. Of these, 157 shipments (645 taxa) were as plants or cuttings and 57 shipments (207 taxa) as fruits or seeds. In addition to these, we were able to fill 52 requests for pollen, leaf samples, soil samples, fruits, or wood specimens obtained from the living collections in support of research requests of scientists in thirteen countries, not including the United States.

The requirements of the projected plantings around the greenhouses and the development of new groups in the Arboretum collection necessitated the propagation of 467 taxa. Outside requests for materials from the Arboretum collections not available elsewhere numbered 62 items which have been propagated for distribution at the proper stage of development. The Arboretum staff requested the propagation of 74 taxa for taxonomic, cytological, or morphological studies. Finally, 84 taxa were handled by the propagation staff to obtain or to check propagation data.

Experimental work in the greenhouses, although interrupted by the move, continued on problems concerned with winter survival of rooted cuttings, methods of rooting species which defy normal procedures, techniques of handling and breaking seed dormancy, methods of obtaining more complete and uniform germination of seeds, and viability studies in the storage of scions. The results of these studies appear as notes or more comprehensive papers in *Arnoldia* and other horticultural journals.

Case Estates:

The Case Estates in Weston continue to serve as a nursery testing, and demonstration area, a quarantine zone, and a place to retain under conditions of easy maintenance plant material not desired in the main collections in Jamaica Plain. Plants propagated in the Arboretum greenhouses are held in Weston until they reach flowering size. During this period their growth habits, hardiness, and flowering characteristics can be determined. The best plants from the cultural or ornamental points of view later are planted in Jamaica Plain. Less desirable plants, the distribution of which may be restricted by law (e.g., *Ribes* or *Berberis*), or plants marginally hardy may be retained in permanent non-display plantings in Weston. Of the demonstration areas, the perennial garden, the ground cover plots, and the small stature trees attract the greatest attention from visitors. Increased interest is seen in the test plantings of *Narcissus* varieties contributed by Dr. Helen Scorgie and other members of the New England Section of the American Daffodil Society. Plants received from abroad, subject to plant quarantine restrictions, are maintained in special sections and screened houses on the Case Estates prior to their clearance for distribution by representatives of the Department of Agriculture. In addition, certain areas of the various plantings on the Case Estates can be used experimentally for trial of new horticultural practices. For example, the search continues for safe, yet effective, chemical weed killers for use in display nurseries. One of the most promising materials tried during the past year was "Simazine" which, when applied in the fall, made hand hoeing unnecessary in nursery rows until mid-June.

The Arnold Arboretum display of dwarf conifers at the Spring Flower Show of the Massachusetts Horticultural Society, Revere, Massachusetts, April 17–25, 1962.

The grounds of the Case Estates are used for teaching activities of the staff. In addition to an "open house," field classes have been held for the general public in the spring and the fall. Special tours are arranged for interested groups which can be shown certain plants, plantings, and practices not demonstrable in Jamaica Plain, and the grounds are used for field work in biology classes of Harvard University and the Weston Public Schools. In addition, staff members of the Bussey Institution, the Department of Biology, the Cabot Foundation, and the Gray Herbarium, of Harvard University, have been allowed to use small plots of land for experimental studies. Currently, three high-school and private-school students have "science fair" projects under way on the grounds.

Herbarium:

During the year, 16,467 specimens were mounted and added to the herbarium, bringing the total collection to 742,811 specimens on June 30, 1962. During the same period, 10,920 specimens were received as accessions. Of these 9292 were in exchange, 1277 through subsidy, and the remainder as gifts or for identification. In conformity with the joint policy of having the Gray Herbarium maintain all exchanges with countries and institutions of the New World and the Arnold Arboretum those of the Old, the above accessions represent plants of the Eastern Hemisphere. All collections of cultivated plants are credited to the Arnold Arboretum and, whatever their source, are added to the horticultural herbarium in Jamaica Plain. Only 438 specimens were sent out as exchange during the year, although many collections are being prepared for exchange in the near future.

The staff filled 117 requests for loans of herbarium material, amounting to 12,056 specimens sent to 69 institutions — 48 in the United States and 21 to other countries. For their study, the staff requested 94 loans comprising 7278 specimens from 20 American herbaria and 22 foreign institutions. Outgoing loans averaged 103 specimens per loan and included materials from the Arnold Arboretum and the Gray Herbarium. Incoming loans averaged 80 specimens per loan, again emphasizing the wealth of material in our herbaria. It is of interest to note that of the outgoing loans, 29 per cent, representing 38 per cent of the specimens sent, were for the use of advanced students, the remainder for professional taxonomists.

Forty-three steel herbarium cases were purchased from the Art Metal Company for installation in the Administration Building in Jamaica Plain. Two additional cases were purchased for staff use in Cambridge. After the installation of the new cases, the entire horticultural herbarium was shifted to allow room for expansion throughout the collection and to provide case space for individual staff members and for the use of the mounters. It is gratifying that there is a gradual increase in the number of specimens of cultivated plants being sent for identification and in exchange. These have been received from many individuals in the United States and offer more exact evidence of the distribution of plants under cultivation. Our colleagues in foreign countries are also cooperating in response to our request for specimens from cultivation in addition to those from the wild.

Although the publications cited in the bibliography speak for the scientific achievements of the taxonomists, it is also desirable to record work in progress: Mr. Green, studies in the Oleaceae, particularly *Notelaea* in New Caledonia, Australia, and New Zealand; Dr. Howard, studies on the anatomy of the petiole of the dicotyledons and floristic studies of the West Indies, particularly in the Guttiferae and Leguminosae; Dr. Hu, studies of the Compositae of China, as well as the Commelinaceae and Juncaceae of the same region; Mr. Jayaweera, studies on Asiatic *Mussaendae* and the orchids of Ceylon; Dr. Kobuski, the Theaceae of Asia, particularly the genus *Ternstroemia*; Dr. Nevling, studies of the Thymelaeaceae; Dr. Perry, with the assistance of Mrs. Metzger, studies of the medicinal plants of Southeast Asia; Dr. Schubert, the genus *Desmodium* in tropical East Africa and in Panama, as well as studies toward a monograph of the American species of *Dioscorea*; and Drs. Wood, Brizicky, and Ernst, studies of families and genera of seed plants in the southeastern United States. During the year Mrs. Metzger visited libraries in England and Germany, while Dr. Perry consulted libraries in New York and Washington to lend completeness to many of the medical references being reviewed by them. Mr. Jayaweera completed revisions of the rubiaceous genus *Mussaenda* in India and Ceylon and in the Philippine Islands.

In addition to many visitors who studied in the herbarium during short visits, we have had two scholars working for longer periods of time. Dr. Shun Ching Lee, Professor of Botany, National University of Taiwan, is a Fulbright Fellow working on a revision of his book on the forests of China. Lieutenant Robert Bird, U. S. Army, undertook special studies of the vegetation of several countries of southeastern Asia, using the library and herbarium.

Members of the botanical field trip after the 10th Pacific Science Congress at the summit of Haleakala, Maui, Hawaii.

Library:

The librarians continued their regular services during the year, since the shifting of books described in previous reports has been completed. Three hundred forty-seven volumes obtained by purchase, gift, and binding were added to the library, making the total number of volumes 51,453 on June 30, 1962. A total of 624 pamphlets was also catalogued and added to the collection, making a total of 18,926. The work of cross-indexing the main catalogue continues, with 2088 such cards being added, including the new acquisitions. Four issues, totalling 3000 cards, were added to the Gray Herbarium Card Index of American Plants. The Torrey Index to American Botanical Literature was enriched with the addition of 2600 cards, and issue number 15 was added to the Index Nominum Genericorum.

In response to requests, sixty-six volumes were sent on interlibrary loan. This represents about one half the number of volumes lent in previous years. The staff is filling a larger number of requests by the use of "contura," "xerox," or microfilm reproduction methods to avoid lending old volumes. It was necessary to request only eight volumes from outside sources to meet the research needs of the staff, so extensive are the libraries of the Arboretum and the Gray Herbarium and of the neighboring departments of Harvard University.

The librarian, Mrs. Schwarten, along with Dr. Howard, attended the dedication of the Rachel McMasters Miller Hunt Botanical Library at the Carnegie Institute of Technology, Pittsburgh, Pennsylvania.

Comparative Morphology:

Irving W. Bailey, Professor of Plant Anatomy, *Emeritus*, has continued to serve as curator of the wood collection. During the year, Professor Bailey continued his research on the leaf-bearing cacti of the genera *Pereskia*, *Pereskiopsis*, and *Quiabentia*. Additional preserved specimens were received from tropical America and prepared for anatomical studies of xylem and phloem. As a Mercer Fellow, Dr. Lalit M. Srivastava has worked with Professor Bailey in studying the cambium and phloem of these genera. Dr. Srivastava completed his doctoral dissertation on the secondary phloem in the Abietineae, and the manuscript has been submitted to the University of California Press for publication. At present, he is continuing his studies involving ontogenetic and histochemical investigations of the vascular cambium and its derivatives on other genera within the collections of the Arboretum.

Since the wood collection of the Arnold Arboretum is one of the best in existence, frequent requests, which are filled as materials are available, are received for study samples. During the past year, wood samples were sent to 26 investigators in 14 countries. Where specimens have not been sectioned previously for our own slide collection duplicate slides are requested in return, adding to the available slides for local study. The wood samples supplied on request are acknowledged in published papers, for in many cases supporting herbarium vouchers are preserved in the Arboretum herbarium.

Education:

No formal classes were offered by members of the staff during the past year. Informal classes on horticultural topics were represented by the field classes held in the fall and the spring at Weston and Jamaica Plain. The staff members also took part in two seminar series held weekly and biweekly in Cambridge and open to all students. The weekly series dealt with botanical problems in Latin America, while the biweekly one comprised a discussion of the research projects of staff members and students of the Arboretum and Gray Herbarium. A series of lectures open to the public was given evenings during the fall at the administration building in Jamaica Plain. Attendance varied at these meetings depending on the topic and the weather. It seems unlikely that evening programs in Jamaica Plain will ever be completely successful due to the remote location and difficulty of public transportation.

We again experienced an increase in the number of groups visiting the Arboretum and the Case Estates and requesting guided tours. There was an unexpected increase in the number of requests by mail for information on the Arboretum and in individual requests for information on or the location of specific plants in the Arboretum. These can be explained only in terms of the recent increased publicity given the Arboretum in newspapers, national magazines, and on local radio programs. The Arboretum's exhibit at the Massachusetts Horticultural Society's Spring Flower Show was mentioned and complimented in the March 30th issue of *Time*, which drew attention to the dwarf plants. *Life* of May 4th listed the Arnold Arboretum first in a column on American arboreta and referred to our introduction of *Metasequoia*. The *Harvard Alumni Bulletin* of February 17th had a cover illustration of the Arboretum, drawing attention to the conifer collection. The *New York Times* of April 22nd published an article by Dr. Walter Hodge on botanic gardens which contained an illustration of our lilac collection and comment that "Harvard University's Arnold Arboretum, America's best known arboretum, has been rated since Ernest Wilson's day as 'America's greatest garden'." Dr. Wyman's timely articles in the *Boston Herald* feature the plants in flower at the Arnold Arboretum and the flowering calendar in the Sunday edition of the *New York Times* lists the plants in bloom at the Arnold Arboretum each week during the spring season. Such publicity is welcome for the interest it focuses on the contributions of the staff and the educational values of the living collections.

The increase in requests for Arboretum staff members as speakers for individual garden club meetings now poses a real problem. Whenever possible requests are filled, but largely at the discretion of the staff member invited as speaker. Joint meetings of garden clubs are one way of utilizing speakers more efficiently. In order to compensate in some measure for the loss of working or research time, it is necessary to charge a standard fee for speaking engagements of staff members. Such receipts are used to further the work of horticultural education.

Dr. Howard appeared on the science lecture series of the Royal Canadian Institute in Toronto and that of the American Association for the Advancement of Science at Franklin and Marshall College. He gave the evening address on Hawaiian botany at the 16th Congress of the American Horticultural Society and at the annual meeting of the Massachusetts Dietetic Association spoke on the economic uses of plants. Following the Pacific Science Congress, Dr. Howard was invited to address an open meeting of the Garden Club of Honolulu. Dr. Wyman addressed meetings of nurserymen in Iowa and Michigan. He took part in short courses in horticulture sponsored by the Oregon State University and the University of Massachusetts. Dr. Wyman also appeared on the lecture program of Longwood

Gardens. Mr. Green described the work of the Arboretum at Pine Manor Junior College and reported on methods of vegetation mapping for the New England Botanical Club. He also talked about the plant introduction and distribution program at the annual meeting of the American Association of Botanical Gardens and Arboretums. Mr. Fordham discussed dwarf

Strollers in the Arnold Arboretum on lilac weekend, May 20, 21, 1962.

and abnormal conifers at the nurserymen's short course at the Waltham Field Station and spoke on methods of accelerating seed germination at a meeting of the New England Nurserymen's Association. Mr. Heman Howard is aiding the development of Bartlett Park in Chelmsford as a local arboretum and spoke about the selection of plants to its supporters. Dr. Wyman and Mr. Williams conducted a day-long demonstration lecture on pruning methods for the New England Electric Public Utility Services which was attended by over forty line superintendents involved in maintenance of electric lines.

Radio programs often involving telephone interviews and audience questions have included several members of the staff. Dr. Wyman and Mr. Williams have also appeared on local television stations. The majority of these programs take place in the spring, when interest in gardening practices is highest.

Exhibits and Displays:

The living collections of the Arnold Arboretum are planted on 400 acres in Jamaica Plain and Weston. Only the professional horticulturists or the most determined visitors take time to see all of the plants of a given group. In some areas the many representatives of a group may be quite loosely associated, but more often the individual plants are widely distributed and located where they will show the best growth. A flower show, by contrast, offers an opportunity for displaying small plants or branches or portions of plants in a small area, conveniently displayed and studied. Such displays may be seen by more people in a few hours than may visit the living collections in a full week. As a part of its effort in horticultural education, the staff of the Arboretum will prepare educational displays of plant materials. Regrettably, we cannot fill all requests or accept all invitations which, during the past year, were received from seven states, including Hawaii, from Canada, and from Europe. A display of ornamental fruiting shrubs and trees was shown at the Fall Show of the Massachusetts Horticultural Society attended by about 5000 people and at the comparable show of the Worcester County Horticultural Society which had about 9000 visitors. The staff cooperated with members of the Massachusetts Horticultural Society in preparing a Christmas Show which drew 3000 visitors to Horticultural Hall in Boston. The Arboretum received a silver medal for its display of cones and evergreens. A separate exhibit area featured a display of fruiting branches of selected hollies native to New England.

During the spring season our largest exhibit was at the Massachusetts Horticultural Society's Spring Flower Show at Revere, Massachusetts. This display, awarded a first prize and a gold medal, featured a collection of dwarf evergreen plants which will eventually be located near the Dana Greenhouses. Eighty-six thousand people attended this exhibition. At the request of the New York Horticultural Society the Larz Anderson collection of *bonsai* was taken to New York for the New York International Flower Show. A final exhibit, again by request, was a demonstration of methods of pruning trees and shrubs at the Jordan Marsh Spring Show sponsored by the Garden Club Federation of Massachusetts and seen by an estimated 50,000 people. The various exhibits were designed and executed by Dr. Wyman, Mr. Williams, and Mr. H. Howard. Considerable time was spent this year in the preparation of permanent labels engraved in colored plastic for these displays, in an attempt to have a type of exhibit more easily assembled in the future.

Japanese *bonsai* of the Larz Anderson Collection of the Arnold Arboretum on exhibition at the International Flower Show, New York City, March 10–18, 1962.

Travel and Exploration:

The Arboretum was represented by staff members at various professional meetings including those of the American Association of Botanical Gardens and Arboretums, the American Institute of Biological Sciences, the American Horticultural Society, the Plant Propagators Society, the Pacific Science Congress, the National Shade Tree Conference, the American Nurseryman's Association, and the American Society of Horticultural Sciences.

Dr. Howard collected some special plant materials for his research while in Hawaii for the Pacific Science Congress. The expedition to Burma of Mr. James Keenan, of the Royal Botanic Garden, Edinburgh, Scotland, sponsored in part by the Arnold Arboretum, was completed during the year, and the arrangement of materials collected is under way. Mrs. Claude Weber made a special trip to gardens and nurseries in Ohio and Illinois to study cultivars of *Chaenomeles* in flower. The trip was rewarding in the discovery of several old cultivars previously not known to be still in cultivation. Mrs. Weber also participated in a class in tropical botany which spent a month in Costa Rica. This trip, financed by a grant from the Fernald Fund, allowed her to make general and special collections of plant materials for the herbarium and special collections for several staff members with research problems involving plants in that area. Dr. Wyman travelled extensively in the United States during the year, visiting many gardens and arboreta during peak seasons to continue his studies of ornamental plants and to obtain new plants for trial at the Arnold Arboretum. Dr. Ernst left in late June for field work in Texas with Dr. Henry J. Thompson, of the University of California at Los Angeles, related to their joint research interests.

Gifts and Grants:

The Friends of the Arnold Arboretum who contribute regularly to the work of the Arboretum responded generously to an appeal during the spring. To these contributors we again express our continuing appreciation.

Through the initiative of Mr. Seth Kelsey, of East Boxford, a member of the Committee to Visit the Arnold Arboretum, eight Massachusetts nurseries contributed over 1300 plants of various types and sizes to be used in establishing the basic landscape plantings around the Dana Greenhouses. Through their generosity, the greenhouses lost immediately a portion of the bleak appearance so characteristic of new buildings and freshly moved soils.

One group of plantings proposed for the fenced-in area of the Dana Greenhouses was a collection of native hollies with most attractive fruits. A selection was offered the Arboretum in the fall of 1961 by Mr. Wilfrid Wheeler, of Hatchville, Massachusetts. Although Mr. Wheeler died on Christmas Day, 1961, his wishes were carried out by his sons, Wilfrid, Jr., Richard, and Charles. We regret that Wilfrid Wheeler could not see his collection of outstanding cultivars in their new location, and we are grateful to his family for this gift of plants which so well represent his long interest in and his contribution to horticulture in New England.

Portions of the research of six staff members involving the services of six assistants continue to be supported by grants from the National Science Foundation, the National Institutes of Health, and the gifts of Mr. George R. Cooley.

Publications:

Four quarterly issues of the *Journal of the Arnold Arboretum* including most of the scientific publications of the staff were distributed during the year, as were the twelve numbers of *Arnoldia* which appear at irregular intervals. These comprise the regular publications of the Arnold Arboretum. An issue of *Arnoldia* titled, "The Walter Street 'Berrying' Ground" was prepared by Mrs. Mary Lehmer, formerly of the Arboretum staff. This reviewed the history of the Walter Street Church and its adjacent cemetery now included within the boundaries of the Arboretum. Although remains are visible of the church, a memorial plaque, along with thirteen old headstones and a crypt, mark the Revolutionary War dead and are decorated each Memorial Day by the historic commission of Boston. This article, which drew attention to a remote section of the Arboretum, is one of a projected series of articles on the history of the land we occupy. Another number of *Arnoldia* issued at the dedication of the Dana Greenhouses has been requested frequently by other botanical gardens and by architectural students.

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