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B. G. SCHUBERT
EDITOR

L. I. NEVLING, JR.　　C. E. WOOD, JR.

LAZELLA SCHWARTEN
CIRCULATION

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VOL. 47 JANUARY 1966 NUMBER 1

ARISTEYERA, A NEW GENUS OF GEONOMOID PALMS[1]

HAROLD E. MOORE, JR.

THE GEONOMEAE CONSTITUTE A DISTINCTIVE TRIBE of monoecious arecoid palms (Palmae-Arecoideae) restricted to the Western Hemisphere. The most recent treatments of Burret (1930) and Burret and Potztal (1956) recognize seven genera — *Asterogyne, Calyptrogyne, Geonoma, Kalbreyera, Pholidostachys, Taenianthera,* and *Welfia* — to which *Calyptronoma* may be added as a genus distinct from *Calyptrogyne* as noted by Bailey (1938). Material recently received from Venezuela provides the basis for recognition of still another genus described herein as *Aristeyera.* The generic name is coined from the surnames of Lic. Leandro Aristeguieta and Dr. Julian A. Steyermark of the Instituto Botánico at Caracas, who have most kindly loaned or given specimens and provided preserved materials of flowers and fruits for anatomical study. This fine material has provided the writer and Doctors Uhl and Tomlinson, whose articles accompany this one, an opportunity to present a standard morphological description in concert with anatomical studies.[2]

The Geonomeae are marked by some 12 characteristics common to all the component genera. The generic distinctions, however, are found chiefly in the androecium, in the number of locules and ovules in the pistil at anthesis, in the fibers of the mesocarp of the fruit, in the arrangement of floral pits on the flowering axis or axes, and to some extent in the structure of the inflorescence. The synoptic key that follows is intended to suggest the combinations of characteristics that separate genera and the relative levels of their specialization. *Geonoma* is the largest, most widely distributed, and, so far as the unilocular, uniovulate pistil is concerned, the most advanced genus in the tribe. Burret (1930) recognized 172 species in the genus plus a few not well known, and some 26 species have been described since. If *Taenianthera* is to be included within the genus, as

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[1] This study has been supported in part by National Science Foundation Grant GB-1354.

[2] UHL, N. W. Morphology and anatomy of the inflorescence axis and flowers of a new palm, *Aristeyera spicata.* Jour. Arnold Arb. **47**: 9–22. 1966.

TOMLINSON, P. B. Notes on the vegetative anatomy of *Aristeyera spicata* (Palmae). Jour. Arnold Arb. **47**: 23–29. *3 pls.* 1966.

seems reasonable, then the number of recognized species slightly exceeds 200. The remaining genera are small or monotypic and are characterized, so far as known, by a trilocular, triovulate pistil in combination with various modifications of the androecium and inflorescence.

Although the tribe is being studied morphologically and anatomically as part of a program to produce a broadly based revision of the Palmae at the generic level, it seems desirable to describe *Aristeyera* separately and to put on record now some observations on the complex anatomy of the inflorescence axis as well as certain features of floral morphology and anatomy, and vegetative anatomy. The genus is of especial interest because of the structure of the anthers which parallels that of anthers in *Asterogyne, Geonoma*, and *Kalbreyera*, though in other respects the staminate and pistillate flowers are basically similar to those of *Welfia* with which it seems most clearly allied.

KEY TO GENERA OF GEONOMEAE

1\. Staminate flowers with numerous stamens (21–42); pistillate flowers with numerous staminodes (15–18); pistil trilocular, triovulate at anthesis; mesocarp with a layer of closely placed slender fibers surrounding the endocarp; bracts subtending the inflorescence inserted basally; floral pits arranged in vertical series on the inflorescence axes.

  2\. Anthers erect in bud, sagittate, the thecae united laterally with the connective; inflorescence of several massive unbranched axes from a short dorso-ventrally compressed decurved peduncle and very short rachis, subtended by massive broad woody bracts; seed with the raphe sparingly branched basally and apically; large palms with stout stems and long pinnate leaves; leaf with 2-layered colorless hypodermis abaxially and adaxially. . . . . *Welfia.*

  2\. Anthers inflexed in bud, the thecae separate and terminal on arms of a bifid connective; inflorescence spicate, erect, long-pedunculate, subtended by thin narrow bracts; seed with raphe unbranched, furcate, or of few parallel branches; small palms with elongate-cuneate pinnately nerved leaves divided only at the bifid apex or if irregularly divided laterally then the bases of the segments continuous along the rachis; leaf with colorless hypodermis 1-layered abaxially, absent adaxially. . . *Aristeyera.*

1\. Staminate flowers with 6 or rarely 3 stamens; pistillate flowers with staminodes united in a truncate, 6-crenulate or -toothed or prominently 6-lobed tube; pistil trilocular or unilocular at anthesis; fibers of the mesocarp various; insertion of bracts and arrangement of floral pits various.

  3\. Anthers erect in bud, sagittate, the thecae united laterally with the connective; pistil trilocular, triovulate at anthesis with terminal styles loosely united; fruit with few stout curved or anastamosing fibers in the mesocarp; floral pits arranged in vertical series; inflorescence and insertion of bracts various.

    4\. Upper bract of the inflorescence inserted at the base of the peduncle or somewhat above the base, never at the base of the flowering axis or axes.

      5\. Inflorescence once- or twice-branched; bracts subtending the floral pits with margins not overlapping adjacent bracts; staminodia of pistillate flowers united in a solid receptacle below the spreading lobes; fruit with wrinkled exocarp when dry but the fibers of the mesocarp not clearly outlined. .... *Calyptronoma.*

5. Inflorescence spicate; bracts subtending the floral pits with margins overlapping the bases of adjacent bracts; staminodia united in a hollow tube below the spreading lobes; fruit with fibers of the mesocarp prominently outlined when dry. ...... *Pholidostachys.*

4. Upper bract of the inflorescence terete, inserted at the base of and enclosing the spicate flowering axis in bud, caducous at anthesis, leaving a ring-like scar at apex of the long peduncle, the lower bract inserted at the base of the peduncle. .... *Calyptrogyne.*

3. Anthers inflexed in bud, the thecae separate and terminal on arms of a bifid connective; pistil various; fruit with numerous thin mostly unbranched closely placed longitudinal fibers surrounding the endocarp (unknown in *Kalbreyera*); bracts subtending the spicate to paniculately branched inflorescence inserted near or at the base, never at the base of the flowering axis; floral pits variously arranged.
    6. Pistil trilocular, triovulate at anthesis with elongate terminal styles loosely united (*Kalbreyera*?); floral pits arranged in more or less clearly defined vertical rows.
        7. Stamens 6; pistillode nearly as long as the stamens; staminodial tube with 6 spreading lobes; floral pits in 7 vertical rows; inflorescence long-pedunculate with 2–7 subfasciculate flowering axes. .... *Asterogyne.*
        7. Stamens 3; pistillode short, trifid; staminodial tube truncate; floral pits in 4 vertical rows and nearly decussate; inflorescence short-pedunculate, terminating in a diffuse panicle of flowering axes. .... *Kalbreyera.*
    6. Pistil unilocular, uniovulate at anthesis with lateral or basal styles loosely united; floral pits spirally arranged or verticillate; inflorescence spicate to diffusely paniculate. ...... *Geonoma* (incl. *Taenianthera*).

Aristeyera H. E. Moore, gen. nov. [Palmae-Arecoideae-Geonomeae].

Genus Geonomearum *Welfiae* affinis sed folia praeter apicem bifidum indivisa pinnate nervata, inflorescentia spicata bracteis tenuis, florum masculorum staminibus 21–24 antheris in gemma inflexis thecis disjunctis in connectivo bifido, semine rapha indivisa vel furcata instructo.

Solitary, slender, unarmed, monoecious, protandrous undergrowth palms. Leaves entire except for the bifid apex or rarely ruptured but scarcely divided laterally, pinnately nerved; sheath short, at first closed but soon rupturing opposite the petiole, this rounded below, shallowly grooved above, with sharp entire margins. Inflorescences interfoliar, erect, solitary at the nodes, subtended by 2 closely sheathing basally inserted bracts, the lower ancipitous, opening apically, the upper longer, rounded, acute and at first enclosing the spike in bud; peduncle elongate, terminating in a thick undivided spicate flowering axis, the flowers borne in triads of 2 lateral staminate and a central pistillate (or paired or solitary staminate through abortion of the pistillate toward the apex of the axis) sunken in prominent pits, these covered with a prominent bract in bud and arranged in 8 verti-

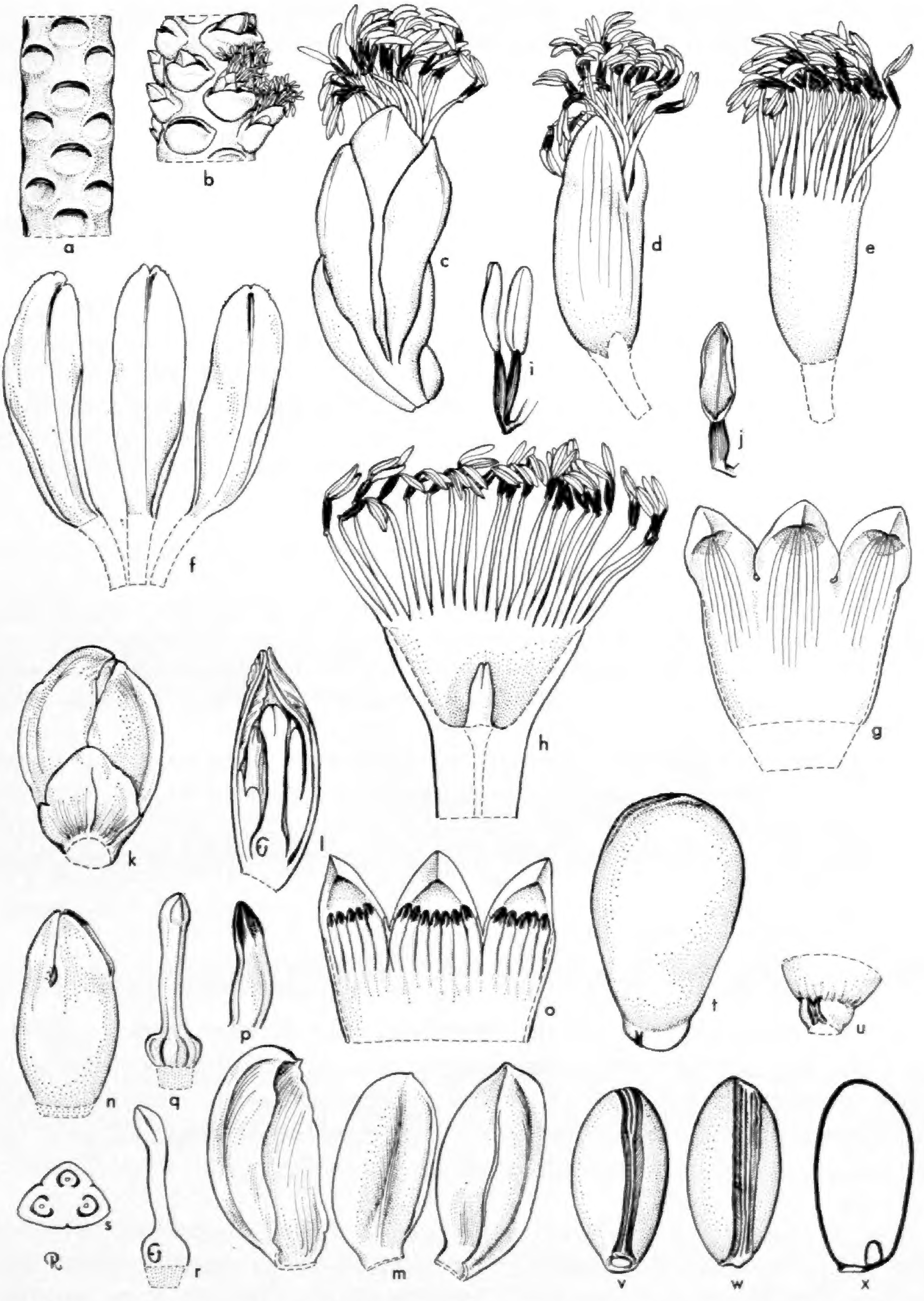

FIGURE 1. *Aristeyera spicata.* a, portion of young spike before anthesis showing bracts covering pits, × 1; b, pits and staminate flowers at anthesis, × 1; c, staminate flower and bracteole, × 4; d, staminate flower with calyx removed, × 4; e, androecium, × 4; f, sepals, × 4; g, corolla expanded, × 4; h, androecium expanded and pistillode, × 4; i, anther, × 8; j, theca and connective, × 8; k, pistillate flower with bracteole in bud, × 4; l, pistillate flower in vertical section, × 4; m, sepals, × 4; n, corolla, × 4; o, corolla expanded and staminodes, × 4; p, staminode, × 8; q, pistil, × 4; r, pistil in vertical section, × 4; s, ovary in cross-section, × 8; t, fruit, × 2; u, base of fruit and stigmatic residue, × 2;

cal rows, bracteoles subtending the flowers 3, anatomically one per flower but in the pit placed so that superficially one appears to subtend one of the staminate flowers and two surround the base of the pistillate flower. Staminate flowers about 1/3 exserted at anthesis, the 3 sepals distinct above a short attachment to the receptacle, glumaceous, imbricate at least basally in bud; petals 3, connate, sometimes unequally so, for 1/3–3/4 their length in a soft tube, the free, slightly asymmetric lobes deltoid, glumaceous, valvate above briefly imbricate bases; stamens 21–24, exserted at anthesis, the filaments united with the base of the pistillode and with the corolla-tube about 1/4 their length in a fleshy solid receptacle, then expanded and connate in a tube about equally long surrounding a fleshy, shallowly and acutely, often irregularly 3-lobed pistillode, the free portions of the filaments only slightly shorter than the connate portions, erect, the anthers inflexed in bud, the thecae separate, longitudinally dehiscent, terminal on arms of a bifid connective, the arms of the connective and thecae becoming erect or nearly so at anthesis. Pistillate sepals 3, glumaceous, distinct, imbricate in bud; petals 3, connate for about 2/3 their length in a soft fleshy tube, the deltoid free glumaceous lobes valvate in bud, probably spreading at anthesis; staminodes 15–18, connate basally and adnate to the corolla-tube about 1/2 their length, then free, angled-linear, often with shallow adaxial grooves and sometimes thickened apically, the apices dark and connective-like; pistil trilocular, triovulate, the ovary with 3 rounded lobes; styles terminal, elongate, loosely united; stigmas 3, prominent and probably recurved at anthesis; ovules hemitropous, axile, pendulous, attached near the top of the locule, only one normally maturing. Fruit ellipsoid-ovoid in outline, slightly compressed laterally (in relation to the flower but appearing dorso-ventrally compressed in relation to the axis) and slightly keeled apically when dry, the residual stigmas and abortive carpels basal; exocarp smooth; mesocarp dry with longitudinal fibers closely placed around the endocarp, this thin, crustaceous, shining, not adherent to seed; seed ellipsoid to obovoid and slightly compressed laterally; hilum small, excentrically basal; raphe encircling the seed from hilum to excentrically basal embryo, somewhat impressed and unbranched to furcate or with a few parallel branches; endosperm homogeneous.

TYPE SPECIES: *Aristeyera spicata.*

Aristeyera spicata H. E. Moore, sp. nov.

Caules solitarii ad 8 m. alti. Folia elongato-cuneata petiolo 35–36 cm. longo rachidi 68–70 cm. longa lamina utrinque 27-nervata. Inflorescentia 70–86 cm. longa spica dense fulvo-tomentosa 25–40 cm. longa. Flores masculi 7 mm. longi feminei in gemma 6 mm. longi. Fructus atroruber 12–14 mm. longus 6–7 mm. latus 6 mm. crassus.

Trunk short, 2–8 m. high, to 3.5 cm. in diameter or perhaps more,

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v, w, seed in adaxial and abaxial views, × 2; x, seed in vertical section, × 2. All from preserved material: *L. Aristeguieta*, Dec. 28, 1962.

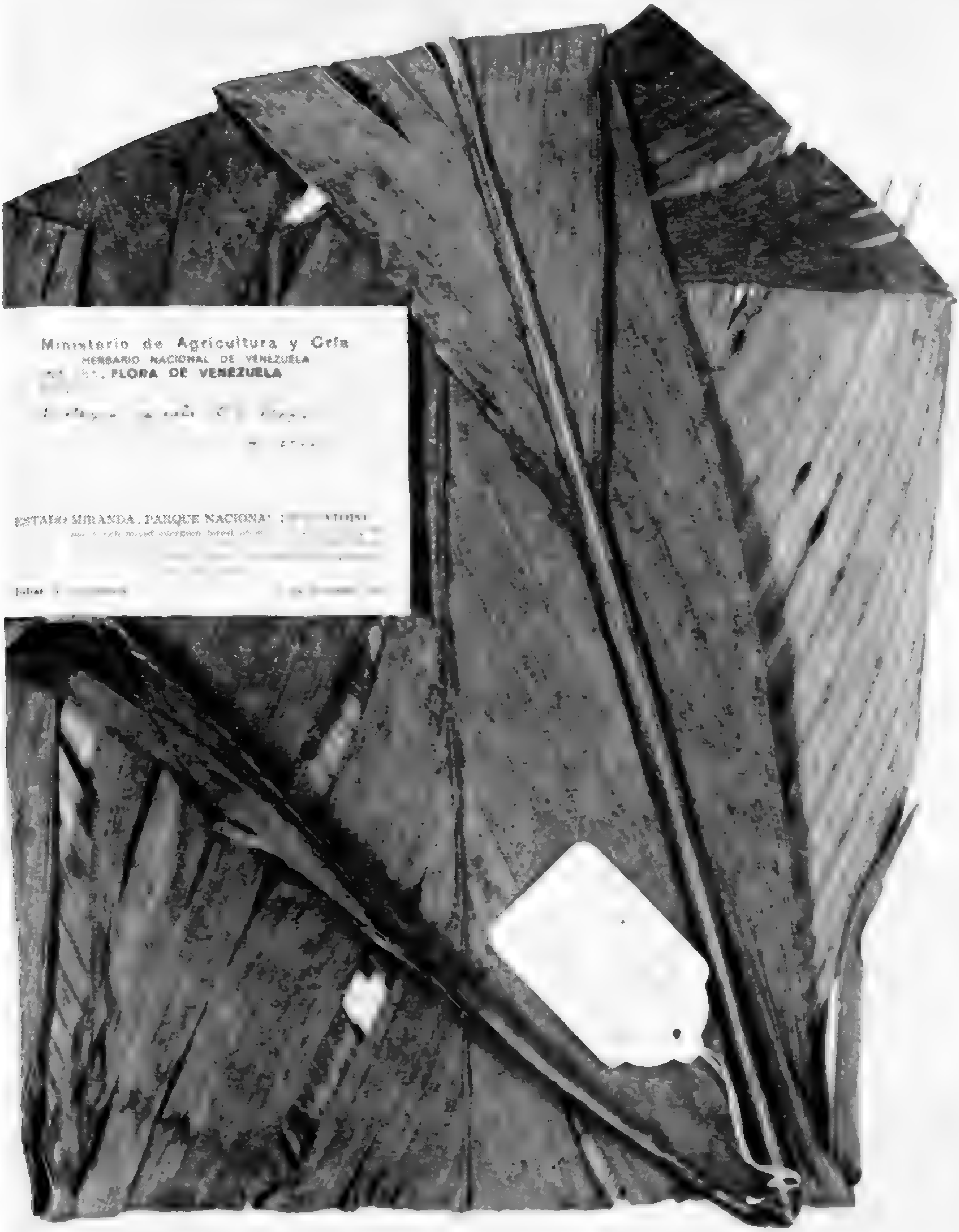

FIGURE 2. *Aristeyera spicata.* Leaf from holotype, × ca. ¼.

rather closely ringed with oblique leaf-scars. Leaves elongate-cuneate in outline, erect, subcoriaceous, deep green above, silvery green below, undivided except for the caudately bifid apex, or the blade sometimes irregularly split but the segments scarcely separated, the rachis terminating in a short filament; sheaths at maturity open to or nearly to the base, frayed into a few stiffish fibers marginally, densely dull red-brown, lepidote-tomentose, ca. 15 cm. long and narrowed to a petiole ca. 36 cm.

Figure 3. *Aristeyera spicata.* Part of stem with base of inflorescence and portions of inflorescences in fruit, at anthesis, and in bud, from holotype. × ca. ¼.

long, this deeply concave above, convex below, dark-brown-lepidote at least laterally below or becoming merely dark-puncticulate in age; rachis 6.8–7 dm. long, concave at base above but becoming triangular and elevated toward apex, rounded and brown-lepidote or -puncticulate below; blade ca. 30 cm. wide at apex of rachis, the caudate tips 19.5–33 cm. long on the inner margin, nerves ca. 27 per side, not elevated above, yellowish and prominent below when dry, brown scurfy toward base and with scattered brown mostly medifixed membranous scales to 6 mm. or more long on basal half, intermediate secondary nerves 2, tertiary nerves 7 or more, often minutely lepidote, the surface with numerous translucent dots. Inflorescence 70–86 cm. long; lower bract ca. 24 cm. long, upper ca. 39 cm. long, both more or less densely brown-lepidote-tomentose as the sheath; peduncle ca. 46 cm. long, densely fulvous-tawny lepidote-tomentose; spike 25–40 cm. long, densely fulvous-tawny lepidote-tomentose in bud and darker tomentose in fruit, usually narrowed to a sterile spinose tip ca. 2.5 cm. long. Staminate flowers with bracteole ca. 5 mm. high; sepals adnate basally to the receptacle for ca. 0.5 mm., nearly or quite as long as the petals, 6.5–7 mm. long, keeled, entire, and acute to emarginate at apex; petals 7 mm. long, united to receptacle for about 1.5 mm. then connate to 2/3 their length, the lobes 2.5–3 mm. long; stamen-filaments adnate to receptacle ca. 2 mm., then expanded in a tube ca. 2 mm. long, free filaments to 3 mm. long, connective to 1.5 mm. long, thecae to 1.5 mm. long; pistillode ca. 1 mm. high. Pistillate buds ca. 6 mm. high; sepals strongly keeled and about 6 mm. long, equalling the petals. Fruit dark red, 12–14 mm. long, 6–7 mm. wide, 6 mm. thick; seed 9–10 mm. long, 5 mm. wide, 4–5 mm. thick, 3 mm. across base.

VERNACULAR NAMES: *palma, palmito.*

USES: fruit said to be edible, leaves used for durable thatch supposed to last ten years.

DISTRIBUTION: on steep slopes of mixed evergreen forest.

Venezuela. ESTADO MIRANDA: Parque Nacional de Guatopo; moist rich mixed evergreen forest on steep slopes bordering Río Santa Cruz, between Santa Teresa and Altagracia de Orituco, 14.5 kms. from Los Alpes, 12 kms. from Ranchería Mi Querencia, alt. 520 m., 23 Nov. 1961, *J. A. Steyermark 90010* (BH, holotype; VEN, isotype); carretera Sta. Teresa-Altagracia de Orituco, June 1953, *L. Aristeguieta 1772* (VEN); selva de Guatopo, June 1958, *L. Aristeguieta 3185* (VEN); without definite locality, 20 Dec. 1961, *G. Agostini S. 00010* (VEN).

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MORPHOLOGY AND ANATOMY OF THE INFLORESCENCE AXIS AND FLOWERS OF A NEW PALM, ARISTEYERA SPICATA[1]

Natalie W. Uhl

A description of the internal structure of the unusual inflorescence and flowers of *Aristeyera spicata* is presented here to accompany the generic description (Moore, 1966) and an account of the vegetative anatomy (Tomlinson, 1966).

In the palms, branching of the major inflorescence axes is monopodial (H. E. Moore, Jr., personal communication), but in the ultimate flowering clusters, several different patterns of branching occur. Flowers have been described as solitary (*Sabal*), in pairs (*Calamus*), in triads (*Aristeyera*), in glomerules (*Livistona chinensis*), in acervulae (*Mascarena*), and in cincinni (*Borassus*). More than half the known genera of palms bear flowers arranged in triads. Work is presently under way on the structure and relationships of these different flowering units.

The anatomy of the Geonomoid palms (Palmae-Arecoideae-Geonomeae) has not been studied previously. In this tribe, 3-flowered clusters (triads) are completely or partially sunken in pits in the inflorescence axes. This paper presents an anatomical analysis of the flowers and of the branching pattern of the triad as found in *Aristeyera spicata*.

MATERIAL AND METHODS

The material studied, which was kindly collected and fixed in FAA by Lic. L. Aristeguieta on December 28, 1962, included inflorescences in bud, at anthesis, and in fruit. Material was softened by treatment for two weeks in one-third strength commercial (52 per cent) hydrofluoric acid. Serial sections of flowers and parts of the inflorescence, prepared by the usual paraffin method, and cut at 10 and 15 microns, were stained with safranin and fast green. Although tannins made complete clearing difficult, some flowers and portions of axes were cleared satisfactorily by treatment overnight in 5 per cent sodium hydroxide in an oven at 59° C., followed by two to four hours in one-third strength commercial sodium hypochlorite, and approximately 12 hours in a saturated solution of chloral hydrate.

INFLORESCENCE AXIS

The spicate inflorescence axis of *Aristeyera* (Fig. 1) consists of eight vertical rows of pits, each pit containing a cluster of three flowers (a

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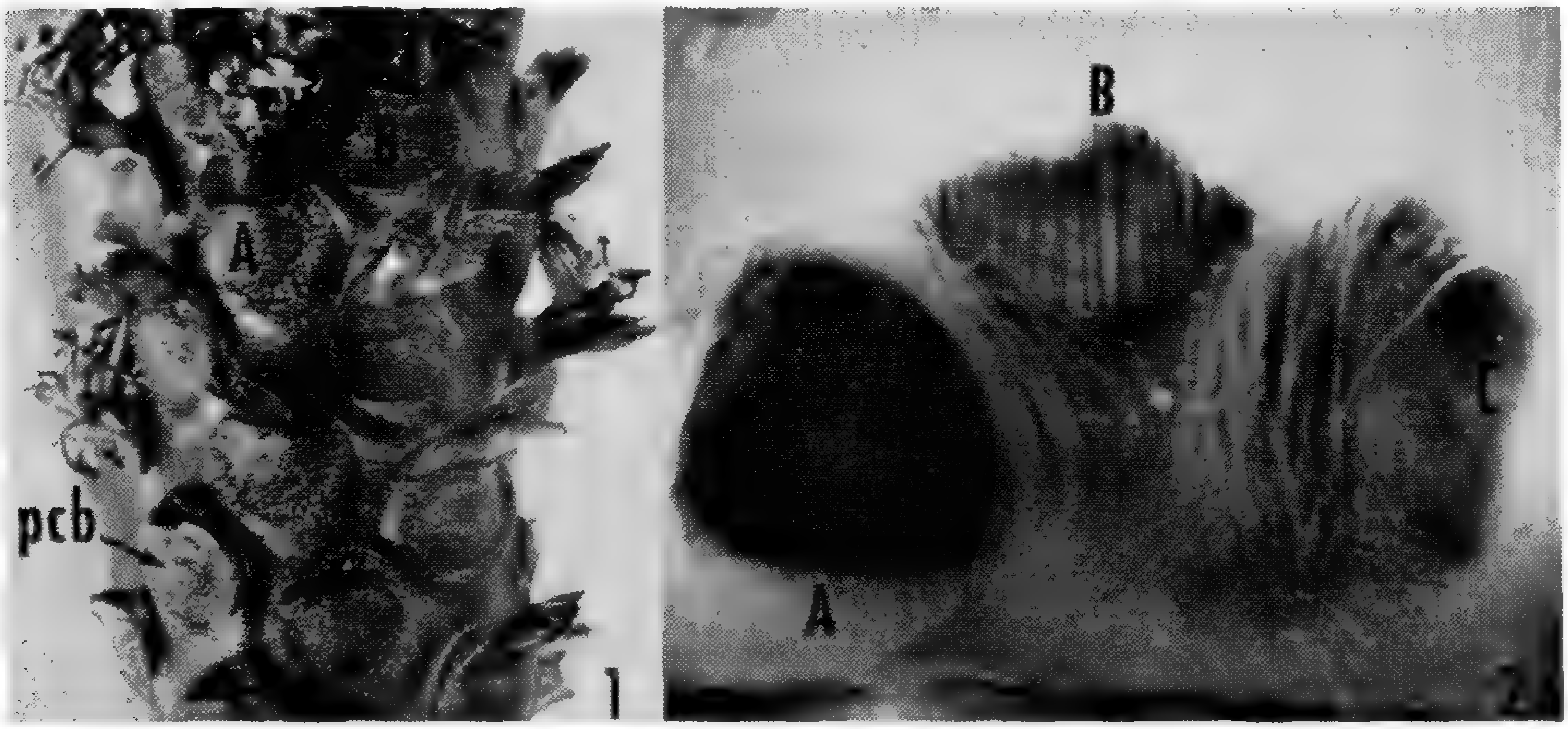
[1] From work supported by National Science Foundation grant GB-1354.

triad), and closed completely in bud by an obovate bract. In FIGURES 3 and 4, the letters A-H indicate successively higher pits in the phyllotactic succession (usually corresponding in mid-axis to an irregular 3/8 phyllotaxy) of a young inflorescence axis with buds. Below each pit, the vascular strands to each triad (at the level A in FIGS. 3 and 4) are arranged in a single group. Slightly higher (represented by the vascular plexus at B), these bundles are divided into two groups. In the pit at C, the section passes through a pit cavity containing flower bases and bracteoles. A pit including flowers and bracteoles at a slightly higher level is cut at D. The four pits, E, F, G, and H are sectioned above the flowers, at successively higher levels.



FIGS. 1 and 2. *Aristeyera spicata*. FIG. 1. Part of a spike with staminate flowers at anthesis; pcb, pit-closing bract, × 2. FIG. 2. Cleared preparation showing three pits: A, B, and C. Refer to pits A, B, and C in FIG. 1 for orientation, × 8.

Enclosed in each pit are two lateral staminate flowers (FIGS. 3 and 4, fs and ss), an inner central pistillate flower (pf), and three bracteoles (FIGS. 3 and 4, ob, mb, ib). Flower clusters may be designated as left-handed or right-handed depending on whether the first staminate flower (FIGS. 3, 4, and 9, fs), borne outside all bracteoles, is on the left or right side of the triad. Left-handed and right-handed triads are mirror images of each other and generally alternate in spiral succession.

The sequence of the floral axes in a pit may be deduced from the position of the three bracteoles associated with the flowers. It appears that the initial axis (FIG. 10, broken line) of the 3-flowered group arises in the axil of the bract that covers the pit (pcb, FIGS. 1, 3, 4, and 9). This axis bears the outer (FIG. 10, ob) bracteole of the triad and terminates with the first staminate flower (FIG. 10, fs). Arising in the axil of the outer bracteole (FIG. 10, ob) is a secondary axis that bears the bicarinate middle bracteole (FIG. 10, mb) and ends with the second staminate flower (FIG. 10, ss). A third-order branch arises in the axil of the bicarinate bracteole (FIG. 10, mb), bears the uppermost (inner) bracteole (FIG. 10, ib), and ends with the pistillate flower. No vascular bundles are present in any of the three bracteoles, but each has an adaxial row of fibrous bundles having no connection with any other veins. The branching pattern of the triad here corresponds to that of a monochasium, as defined by Rickett (1955, p. 444).

Thus, on the basis of general form and the pattern of bracteoles and flowers in each pit, the inflorescence of *Aristeyera* is interpreted as an indeterminate main axis bearing eight rows of determinate 3-flowered units (FIG. 10), each unit enclosed in a pit sunken in the main axis and covered by a subtending bract.

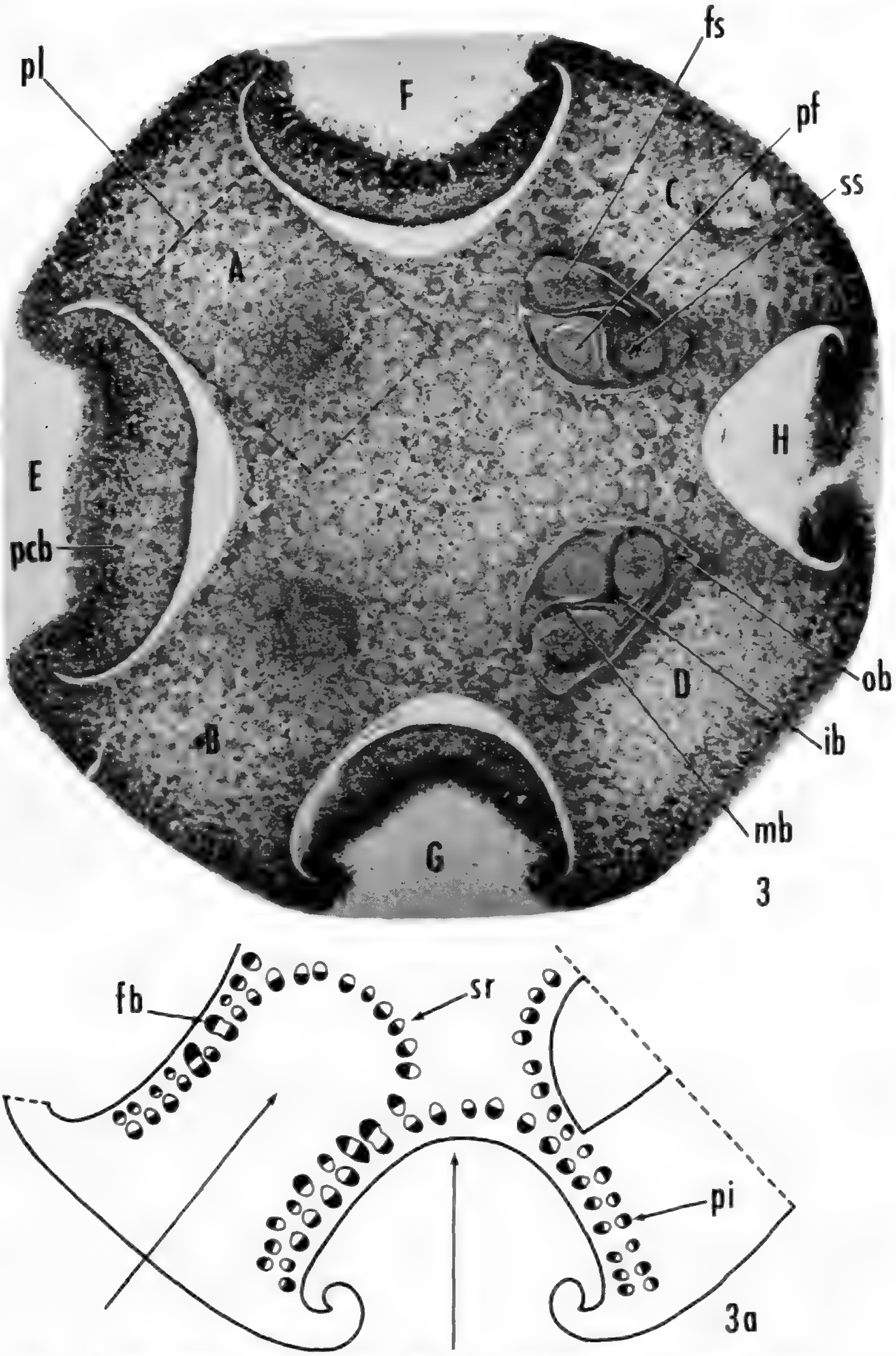
Histological features. The inflorescence axis is densely covered with profusely branched, dendroid trichomes containing tannin and originating from columnar epidermal cells. The hypodermis is a single layer of short, isodiametric cells. In the periphery of the inflorescence axis, just inside the hypodermis, many small (5 to 10 cells in transection) bundles of fibers form an anastomosing system.

The large bundles of the axis are arranged in a low spiral and oriented with the xylem toward the center of the axis. They gradually decrease in size from the largest, which occur in the second row inside the pits, to a few small vascular or entirely fibrous strands in the center. The xylem of the large vascular bundles consists of two large vessels and several smaller elements. Xylem and phloem meet in a straight line (type 3A, Cheadle and Uhl, 1948). The large vessels, often immature even in old axes, have long oblique, compound perforation plates with many (40 to 50) scalariform bars. Smaller xylem elements are helically thickened. A fibrous sheath, generally two cells in width, but sometimes wider (3–4 cells) around the phloem, surrounds each bundle. Two adjacent phloem areas in the same bundle occur below a bundle branch.

Pits. Each cluster of three flowers and the associated bracteoles are deeply sunken in a pit. Around the inner edge of each pit is a single row of bundles (FIG. 3a, sr). Bundles in the centripetal part of this row are oriented as are the central bundles of the axis, with the xylem toward the center, but between adjacent pits (FIG. 3a, pi), the bundles appear partially inverted with reference to the center of the axis. This orientation of axis-bundles adjacent to the pits indicates that pits represent depressions or invaginations in the surface of the axis (FIG. 3a, arrows).

Where vascular bundles between adjacent pit cavities (FIG. 3a) are crowded together, back to back, fusion sometimes occurs between the xylem (FIG. 3a, fb) of bundles extending around the edge of one pit and the corresponding row around the adjacent pit. The xylem of these fusion bundles is large, sometimes two-lobed, and between two opposite phloem groups. Distally, where the pit cavities are smaller in size and the vascular strands are less crowded, the bundles are usually separate.

Each pit is covered by a bract with a fleshy, tapering proximal half which is completely embedded in the axis (FIG. 4, stippled areas, A, B,



FIGS. 3, 3a. *Aristeyera spicata*. FIG. 3. Transection of a young spike. Phyllotactic succession indicated by letters: A, B, C, D, E, F, G, and H. Centripetal to A and B are vascular complexes below pits. Pits at C and D show flower bases and bracteoles. Pits E, F, G, and H sectioned above flowers. Details: pcb, pit-closing bract; fs, first staminate flower; pf, pistillate flower; ss, second staminate flower; ob, outer bracteole; mb, middle bracteole; ib, inner bracteole;

C, D). Distally, where the bract is free, the edge of the axis (FIG. 3, G) is involute and the upper edge of the bract is revolute. When the inflorescence is in bud, the inrolled edges of the axis "lock" the bract into position over the pit. Later, when the upper half of the bract becomes disengaged, the flowers are exserted through a mouth-like opening (FIG. 1). In fruit the bract is pushed farther away making a larger opening. These observa-

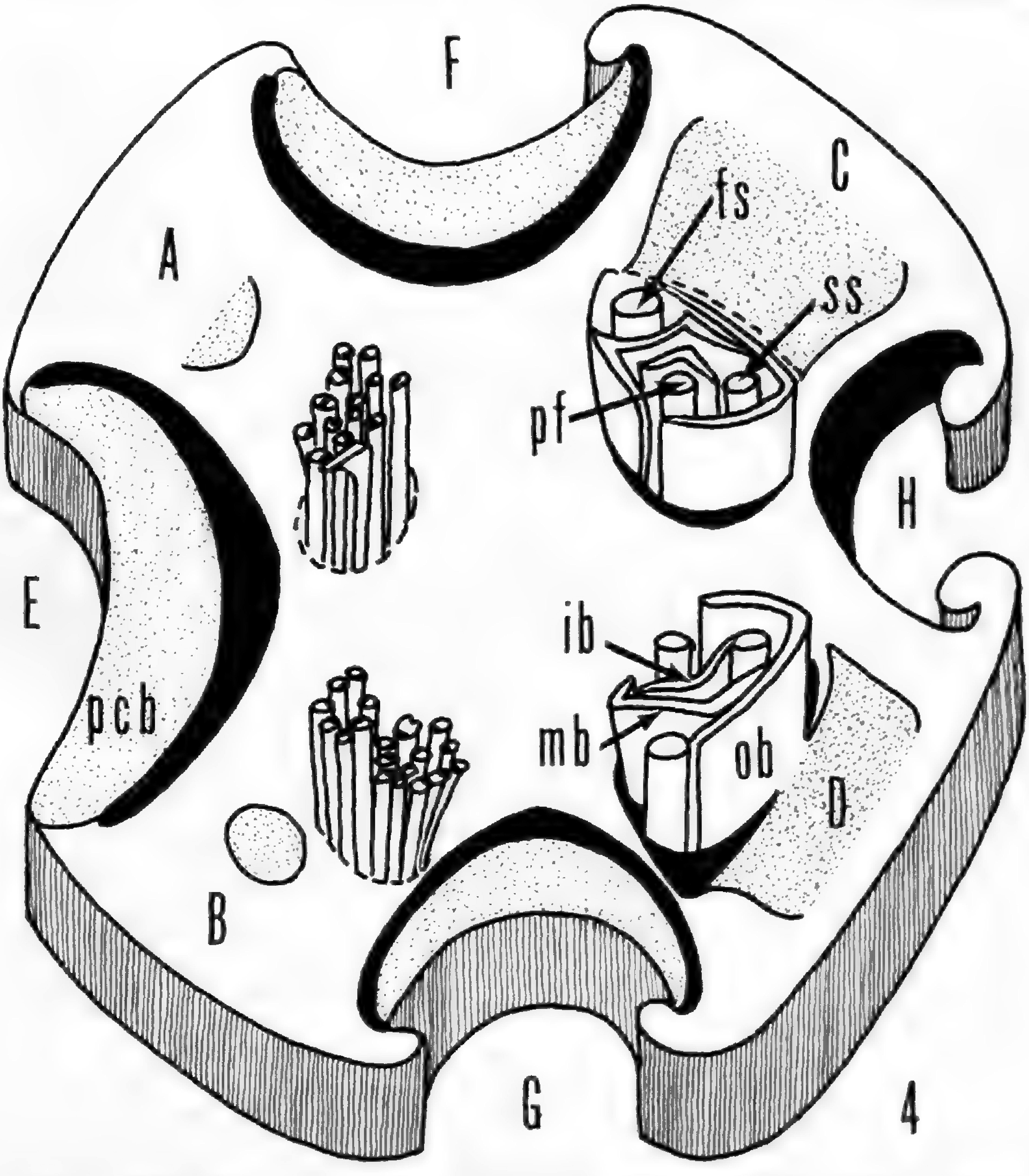


FIG. 4. *Aristeyera spicata.* Three-dimensional diagram of transection of young spike illustrating structures seen in FIG. 3. Vascular bundles seen in FIG. 3a not represented. [Traced from material represented in FIG. 3 and a section 60 microns lower.]

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pl, approximate position of polarized light pictures (FIGS. 5–8), × 12. FIG. 3a. Diagram of lower part of transection (FIG. 3) to show orientation of bundles around pits. Details: sr, single row of bundles around contour of a pit; pi, partially inverted bundle; fb, fusion bundle; phloem, black; xylem, white. Unlabeled arrows indicate the direction of invagination of the axis.

tions also support the conclusion that the pit represents an invagination of the surface of the axis.

Subtending bract. The limits of the obovate bract covering each pit are easily recognized histologically. Except for an adaxial row of parallel vascular bundles (FIG. 2, B) the bract is composed entirely of parenchyma cells that are somewhat larger than those of the axis proper (FIG. 3, D).

In cleared preparations, it is possible to remove the epidermal and outer fibrous systems of the axis and the thick outer parenchymatic part of the bract and thereby reveal the longitudinal shape of the bract and the vascular skeletons of bract and axis. A group of three pits (FIG. 2, A, B, and C, corresponding to pits A, B, and C in FIG. 1) were prepared in this manner. The bract bundles, shown in transverse section, abaxial to the pits at C and D in FIG. 3, are shown in longitudinal view below B in FIGURE 2. These traces originate from bundles of the main axis, usually as branches of the row of strands (FIG. 3a, sr) that, at a lower level, curve around the pit cavity beneath. Near the tapered base of the bract, some of these veins may enter the bract directly, or they may divide to form an inner branch to a floral axis and an outer branch to the bract. The shape and extent of the lower part of the bract can be further verified by comparing the longitudinal view (FIG. 2, B) with different levels of the bract as seen in transverse section (FIG. 4, stippled areas). In FIGURE 3, the letters A and B are in the approximate centers of small areas of large parenchyma cells representing transverse sections of the lower, tapered bases of the bracts. Slightly higher, the bracts are larger (FIG. 4, C and D, stippled areas).

Vascular patterns below pits. The configuration of bundles below the three flowers in a pit is illustrated by photomicrographs taken in polarized light (FIGS. 5–8) in which the early metaxylem is anisotropic and appears as bright spots. The relative size and position of the areas in these pictures is indicated by the broken lines in FIGURE 3, pl. The fibrous sheaths of the bundles in this young axis were not mature and did not exhibit birefringence.

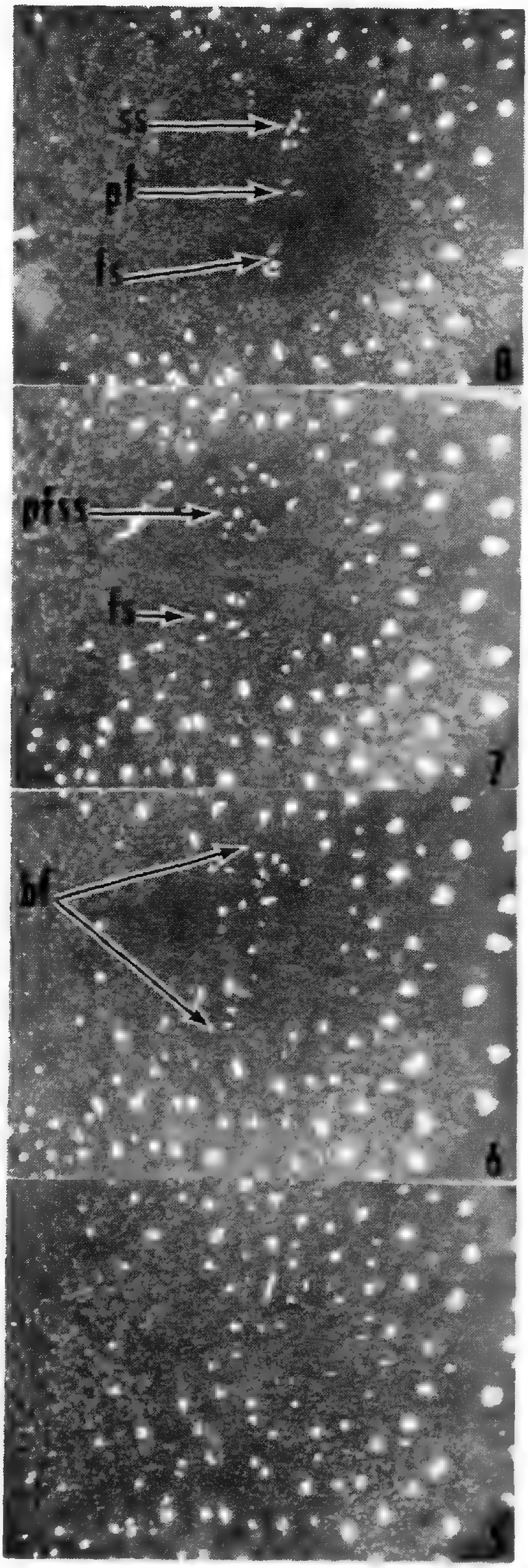
The first evidence of a pit appears as a bundle-free central area with small peripheral bundles (FIG. 5), approximately two-thirds to three-fourths the vertical distance above the top of the pit below. These small bundles originate as centripetal branches of the single row of strands around the pit. Slightly above the level in FIGURE 5, those small bundles which at a higher level supply the pit triad are arranged in an oblong group (FIG. 6, bf). This group of bundles divides into a larger (FIG. 7, pfss) and a smaller cluster of strands (FIG. 7, fs). The veins of these two groups become oriented so that the xylem of each bundle faces the center of each group. The smaller cluster supplies the first staminate flower (FIGS. 7–10, fs). At a higher level (FIG. 8), the second and larger group of bundles divides again to form two groups, the inner (pf) supplying the pistillate flower and the outer the second staminate flower (ss).

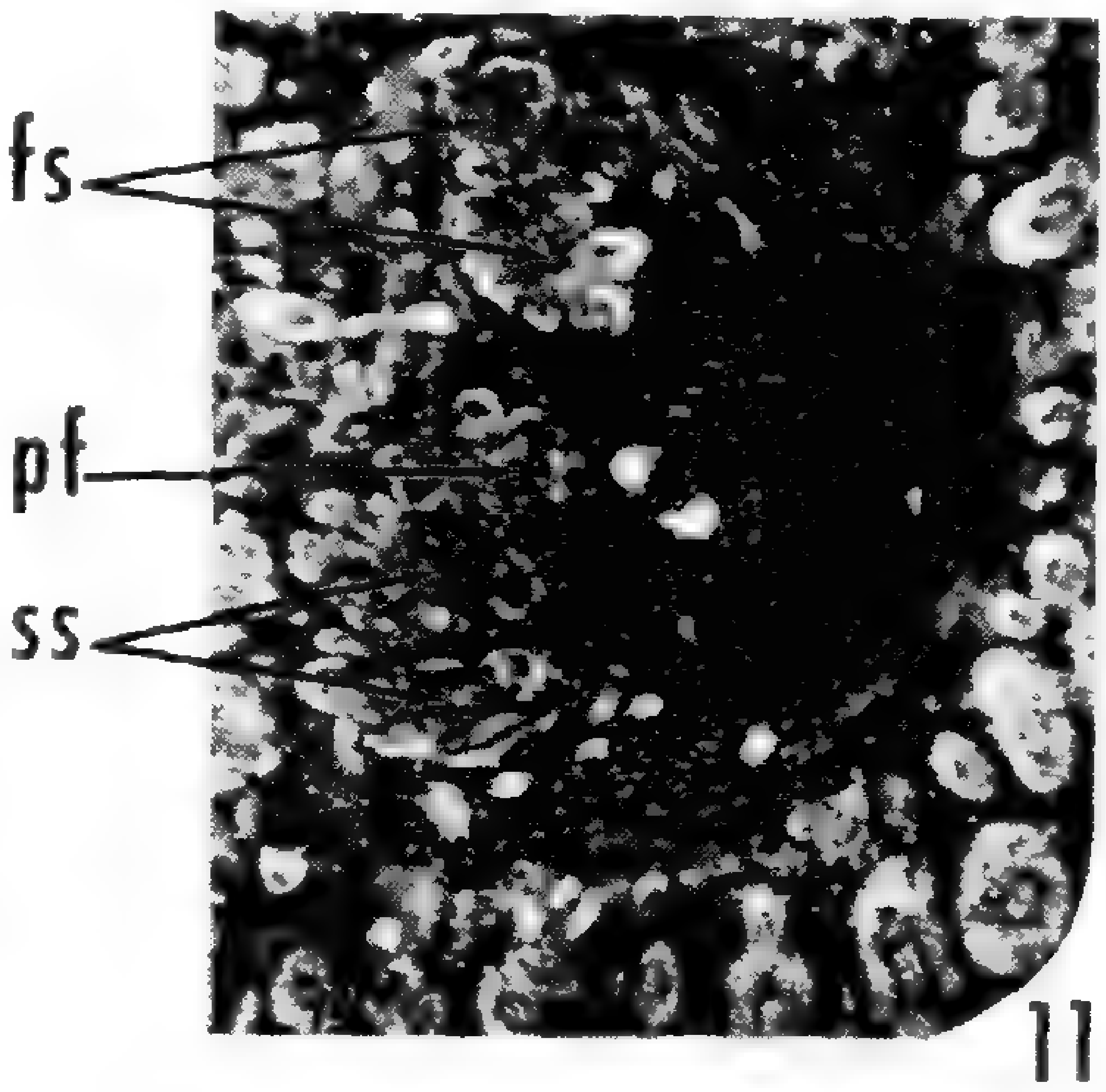
Thus anatomy confirms an arrangement of the flowers in the triad which was suggested by the position of the bracteoles (Figs. 9 and 10). The group of irregularly arranged bundles (Fig. 6, bf) represents the base of the branch subtended by the pit-closing bract and is shown as a dotted line in Figure 10. This group of bundles divides (Fig. 7 and Fig. 10, level ob), forming the vascular cylinder of a submerged branch on which the first staminate flower is terminal and a second branch which is represented by the vascular bundles in Figure 7, pfss. The second branch terminates in the second staminate flower (ss) and bears a lateral branch (the cluster of bundles, Fig. 8, pf) terminating in the pistillate flower.

Detailed study of the vascular bundles shows evidence of additional branching. The vascular supply below the first staminate flower always divides to form two, usually unequal, groups of bundles (Figs. 8 and 11, fs), each oriented with the xylem toward its center. In a mature axis, two vascular cylinders of approximately 9 bundles each can be seen surrounding the ends of the arrows (Fig. 11, fs). The same may also occur below the second staminate flower (Fig. 11, ss). The supply to the pistillate flower is often separated into two groups without forming two completely reoriented circles of vascular bundles. Each of the two groups of bundles at this level resembles the vascular supply that eventually enters the receptacle of the individual flower, but above this level, some (2–4) of the bundles fuse, others (1–4) end blindly and the two vascular cylinders become reoriented into one. The new cylinder is composed of ten to twelve vascular bundles just below the insertion of the perianth parts of each flower. This abortive branching of the vascular supply below a flower is evidence that, ancestrally, additional flowers may have been present in each triad. In *Aristeyera* this unit seem to have originated from a more ramified type of inflorescence.

FLOWERS

In the following sections certain structural aspects common to both staminate and pistillate flowers are first discussed briefly and then details peculiar to each are described. Vascular bundles in the flowers are very small, the xylem containing no large vessels and consisting of a few helical elements. The number of traces to perianth parts is variable. Two other features are worthy of note: (1) in the petal tube of the staminate flowers and in the sepals of pistillate flowers, some of the traces appear to differentiate over a long period of time and as a result the number of traces increases with the age of the flower; (2) the traces developing later do not become connected to the vascular strands in the floral receptacles. Unconnected lateral traces have also been found in perianth parts of *Borassus* (unpublished) and in *Chamaerops* (Morrow, 1965). There is evidence in monocotyledons that the procambium of lateral leaf traces develops basipetally (Sharman, 1942). In certain palms this is also true for some lateral bundles of sepals and petals.





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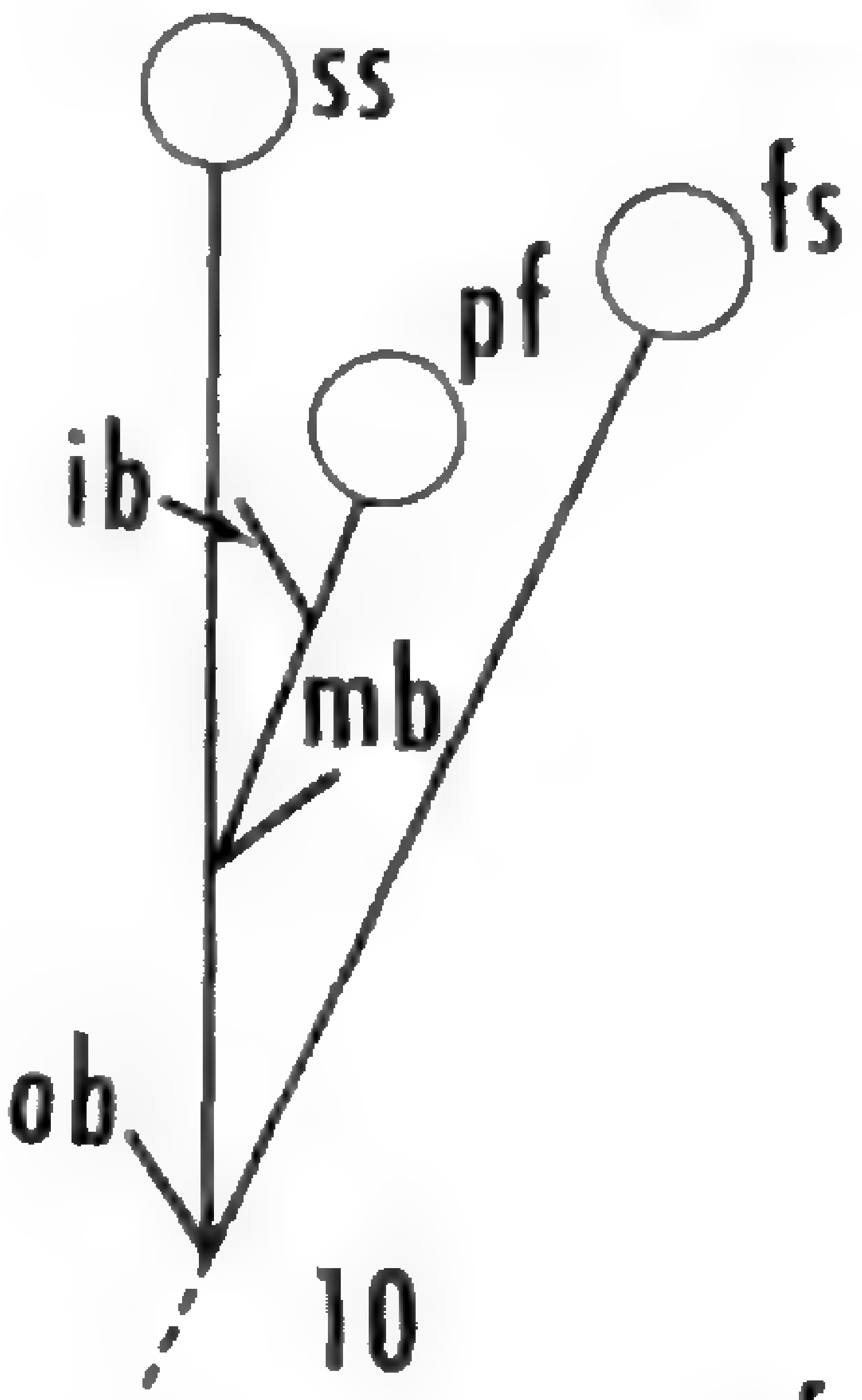

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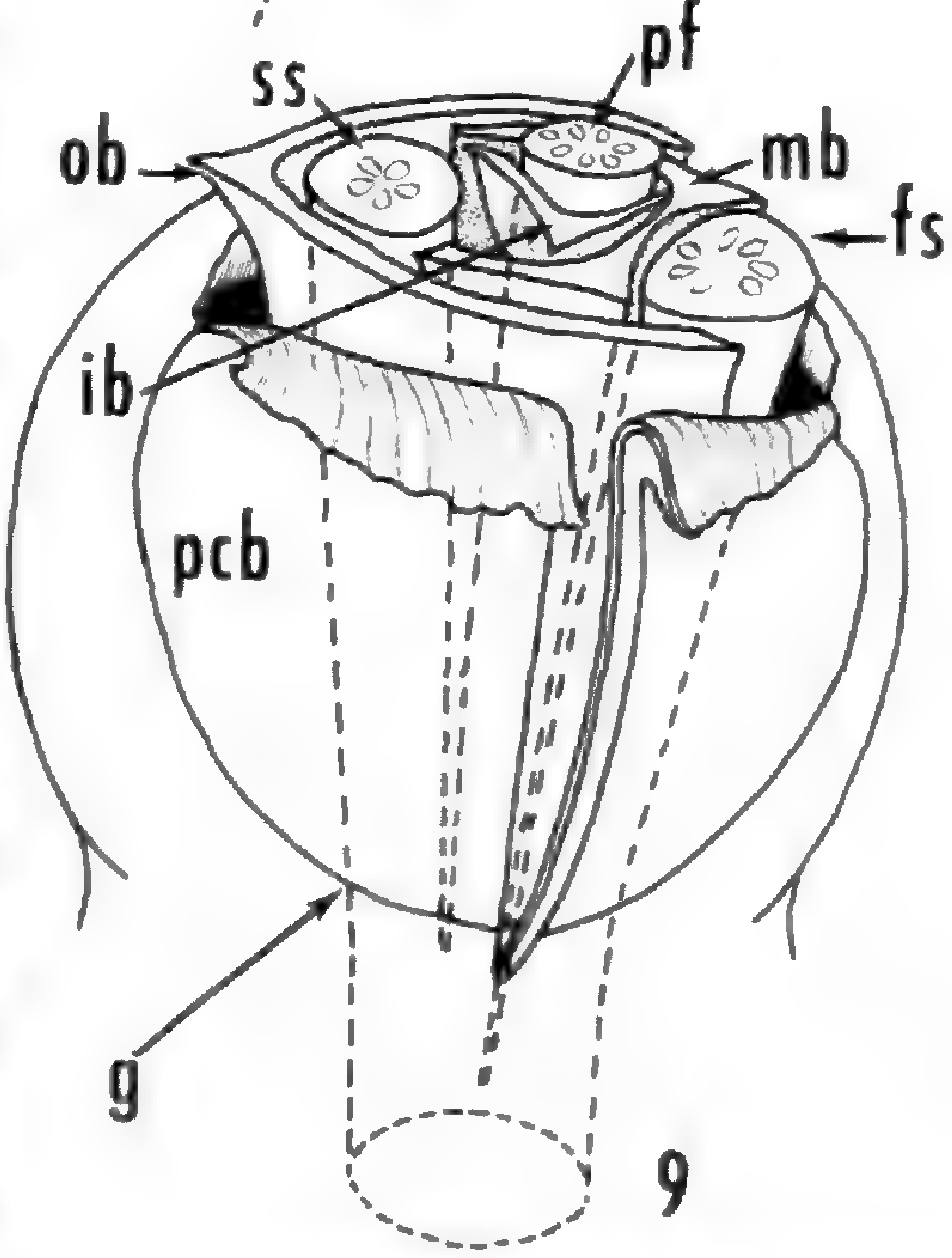

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FIGS. 5–11. *Aristeyera spicata*. FIGS. 5–8. Serial transections of a part (FIG. 3, pl) of the axis below a pit, taken in polarized light; bright spots are the early metaxylem; the late metaxylem and fibrous sheaths are immature and do not polarize. Center of the main axis is to the right, outer edge to left, all × 25. FIG. 5. Approximately 720 microns above the pit below. FIG. 6. 170 microns above FIG. 5; bf, bundles which, at a higher level, supply the three flowers in the

Staminate flowers. In staminate flowers the stalk has a wide parenchymatic cortex and a small central vascular cylinder of a varying number of bundles (5, 6, 7, and 11, observed). Traces of all floral organs arise in a spiral pattern as branches of these few receptacular bundles (FIG. 18). The stalk elongates until at anthesis the upper one-third of the flower with its exserted stamens is pushed out between the pit-closing bract and the axis (FIG. 1). Anthesis of both staminate flowers occurs before the pistillate flower in the same pit is receptive; as the pistillate flower matures, the staminate flowers wither in the pit or are shed by rupture of the stalks.

The sepals are attached spirally, their few vascular bundles arising as branches from receptacular bundles opposite their bases (FIG. 18, S1, S2, S3). In each flower, the sepals are imbricate and progressively smaller. Corresponding to this sequence, the lowest sepal receives three, four, or five vascular traces and the second and third sepals, one, two, or three traces. In the adaxial row in each sepal most of the bundles are fibrous strands which alternate with the few vascular bundles (above), and extend from the sepal bases nearly to the tips, but these do not extend into the stalk nor have any connection with bundles of the floral receptacle.

The petals of staminate flowers are connate for about one-third to three-fourths their length; above this they are imbricate for a short distance, then becoming valvate. Traces to the corolla arise from receptacular bundles in three successively higher groups (FIG. 18, p1, p2, p3; FIG. 17, pe), indicating a spiral arrangement of the petals. Some of the vascular bundles differentiate basipetally and are not connected to the floral receptacle. In the upper three-fourths of the petals many unconnected fibrous strands occur in the adaxial row of bundles.

The morphology of the 21 to 24 stamens is unusual (Moore, 1966); the anatomy, however, is straightforward. Bundles of the receptacle branch above the origin of the petal traces in a flat and irregular spiral pattern to form a single trace to each stamen. In FIGURE 17, traces to 23 stamens (st) surround the remaining three bundles of the floral receptacle (center).

The pistillode resembles the gynoecium of the pistillate flowers, consisting of a central axis with three rudimentary carpels. Bundles (3, 4, or

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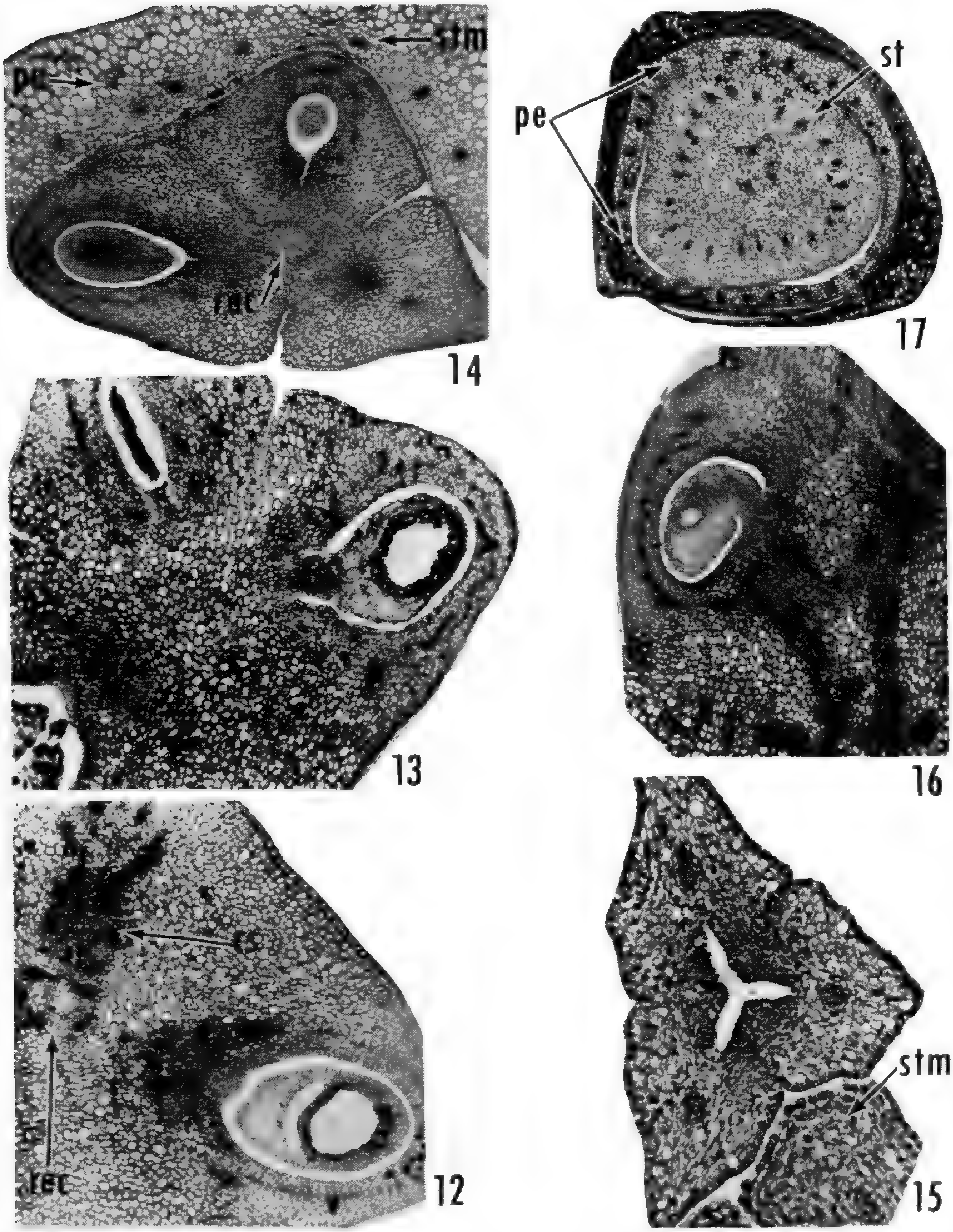
pit. FIG. 7. 120 microns above FIG. 6; fs, supply to the first staminate flower; pfss, supply to the second staminate flower and the pistillate flower. FIG. 8. 320 microns above FIG. 7; fs, supply to the first staminate flower, divided into two groups at this level; pf, supply to the pistillate flower; ss, supply to the second staminate flower. FIG. 9. Diagrammatic drawing of a pit. Details: g, flower bases and bracts occur at approximately this level but are extended to facilitate showing bracteoles; pcb, pit-closing bract; ob, outer bracteole; mb, middle bicarinate bracteole; ib, inner bracteole; fs, branch bearing first staminate flower; ss, branch bearing second staminate flower; pf, branch bearing pistillate flower. FIG. 10. Diagram showing relation of branches, flowers, and bracteoles *within* a pit. For details see legend, FIG. 9. FIG. 11. Transection of same area as FIGS. 5–8 (FIG. 3, pl) but of an older axis. Details: fs, ends of arrows indicate two vascular cylinders below the first staminate flower; ss, two vascular cylinders below the second staminate flower; pf, group of bundles which supply the pistillate flower, × 20.



FIGS. 12–17. *Aristeyera spicata.* FIG. 12. Transection of part of the ovary showing the locule of one carpel with ovule; rec, floral receptacle above separation of the traces to all three carpels; cs, lateral traces to uppermost carpel, × 61. FIG. 13. Transection of parts of the three carpels at the level of attachment of the ovule in the middle carpel, × 61. Observe the difference in the length of the slits beside the funiculus. FIG. 14. Transection of part of the pistillate flower including the ovary and a portion of the corolla-staminode tube; pe, petal trace; stm, trace to a staminode, × 40. FIG. 15. Transection of the style and part, stm, of one staminode, × 78. FIG. 16. Longitudinal section through one carpel showing the pendulous ovule, × 44. FIG. 17. Transection of a staminate flower; pe, arrows indicate one group of petal traces; st, stamen trace, × 44.

7 observed) remaining above the stamen traces (center bundles, FIG. 17) supply the pistillode. In one flower, the seven traces to the pistillode formed three groups and the xylem of each group coalesced, resembling the pattern found in the supply to the carpels of pistillate flower. Usually a single trace, sometimes formed by fusion of two or more receptacular strands, supplies each vestigial carpel.

Pistillate flowers. In bud, the pistillate flower, situated below and adaxial to the male flowers, is attached by a short, thick base which extends adaxially between the stalks of the staminate flowers to the inner central region of the pit. The vascular supply of the axis bearing the pistillate flower usually consists of a cluster of ten to 12 bundles. Several (2–4) of these fuse or end blindly and the remaining extend into the flower (FIG. 19).

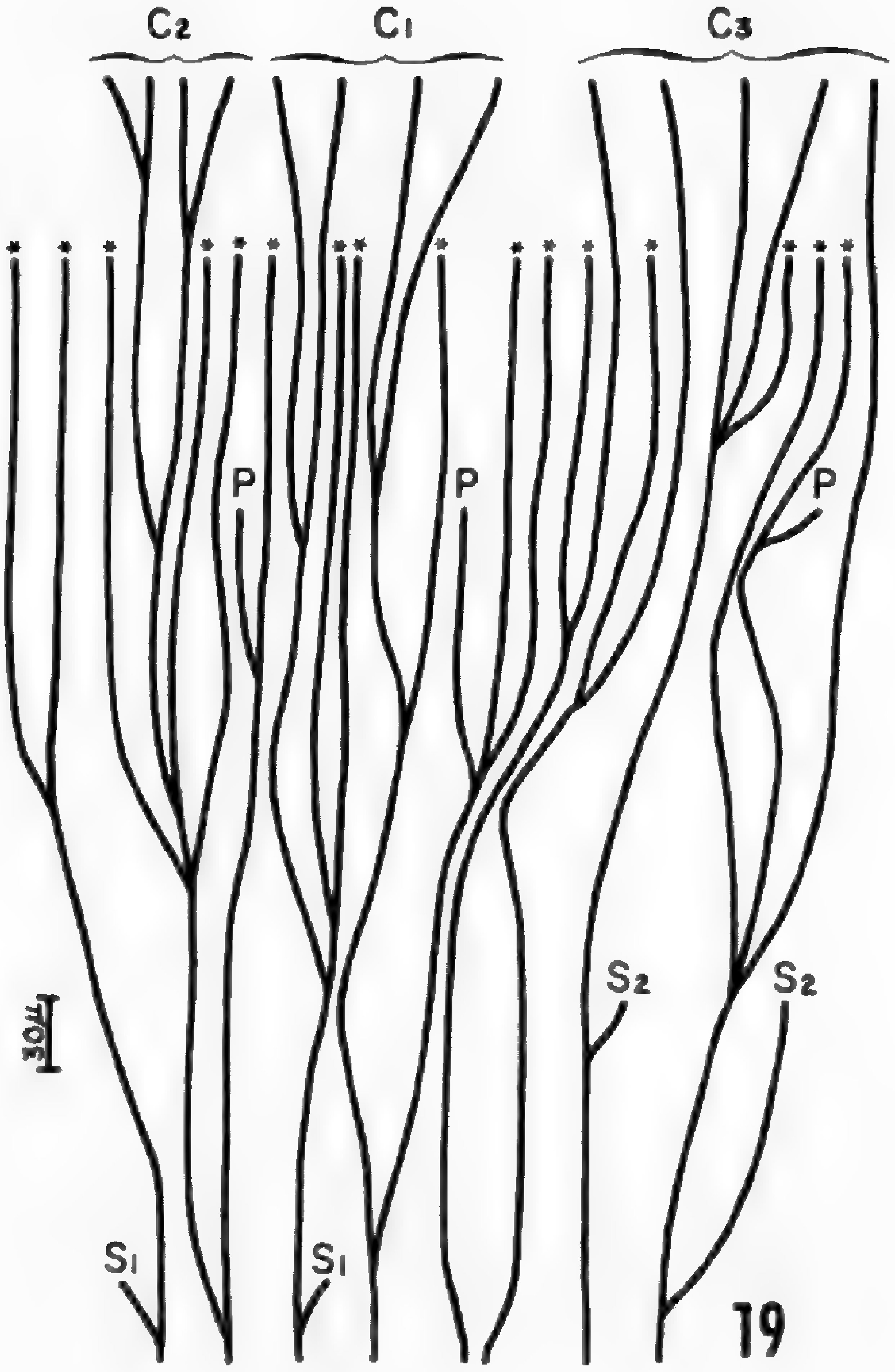
Vascular traces to the sepals are somewhat fewer than in the staminate flowers; two or three strands to the first sepal, two to the second, and one or none to the third were observed (FIG. 18, S1, S2). As in the staminate flowers, each sepal is successively smaller and the few vascular traces alternate with unconnected fibrous strands in an adaxial row of bundles.

The petals are connate for about two-thirds their length, then briefly imbricate, and the free tips valvate. The corolla tube is supplied by three very small traces (FIG. 19, P; FIG. 14, pe). These are the smallest bundles in the flowers and consist of one or two xylem elements and one or two sieve elements. In the upper valvate region of the petals are many unconnected fibrous bundles.

The 15 or 16 staminodes (FIGS. 14 and 15, stm) are adnate to the connate petals for about one-fourth the length of the corolla tube. Each receives one small bundle, that arises as a branch of a receptacular strand (FIG. 19) and ends between the vestigial anther sacs. Occasionally a trace to one staminode branches to provide the bundle to an adjacent one.

The floral axis extends approximately to the top of the locule of the highest carpel (FIG. 14, rec). This extension of the floral receptacle above the origin of all carpel traces is evident in the group of small bundles remaining in the center (FIG. 12, rec) and, at a higher level, as a parenchymatic tip (FIG. 14, rec). The gynoecium (Moore, 1966, *Fig. 1, q*) is composed of three carpels that are spirally arranged and closed basally, where they are adnate to the central axis. Near the upper end of the central axis (FIG. 14), the three carpels become free from each other and from the axis. Above the attachments of the ovule, the ventral sutures of each carpel are open; epidermal cells can be seen between individual ventral carpel sutures (FIG. 14). In the long stylar region (Moore, 1966, *Fig. 1, q*), the carpels are open and the degree of connation varies. At some levels glandular epidermal cells extend part way between adjacent carpels (FIG. 15).

Above the origin of the traces to the staminodes, the floral receptacle consists of a ring of eight to 13 bundles (FIG. 19). Just below the ovary, these bundles separate into three groups and the xylem of the bundles in



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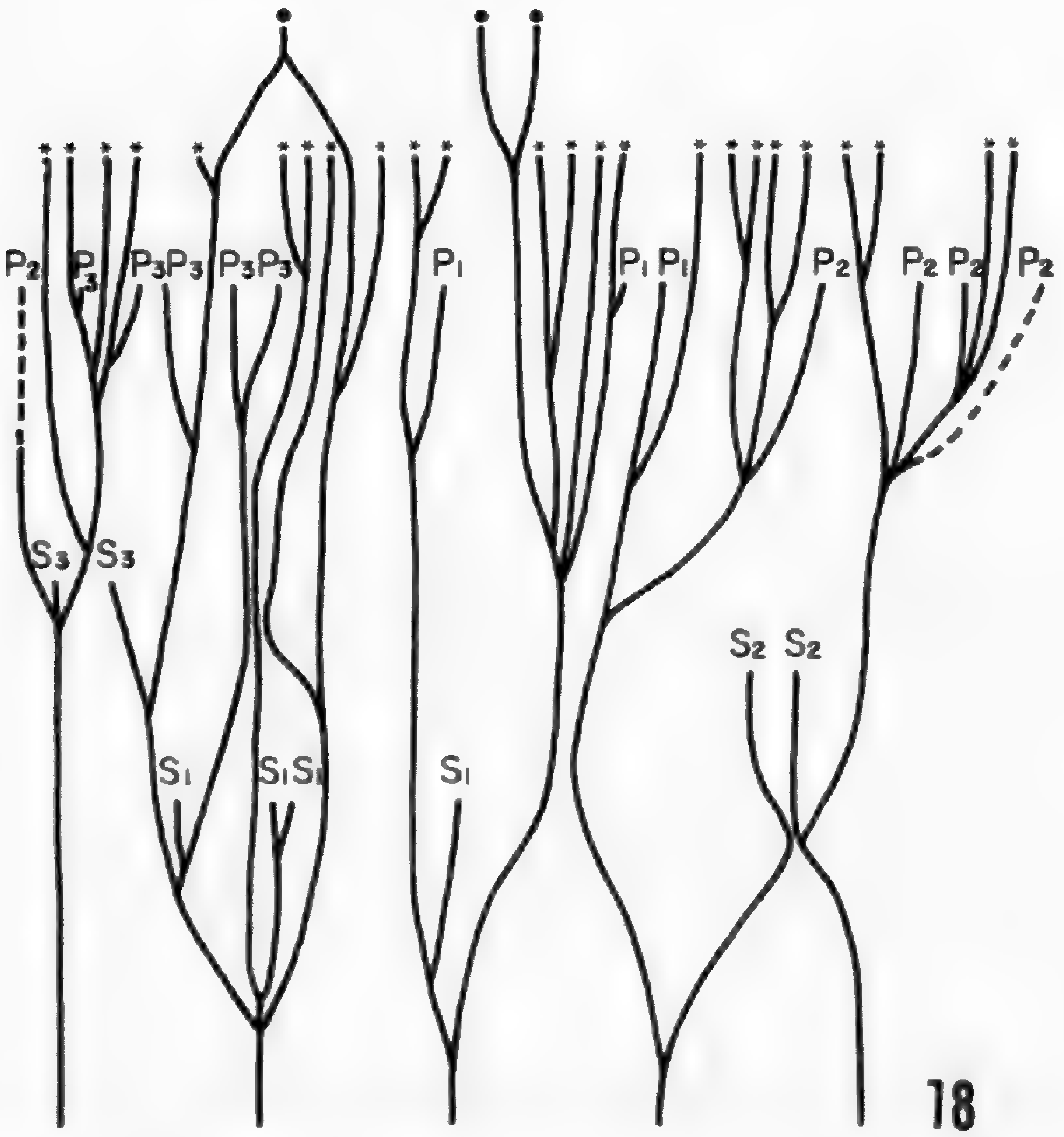

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FIGS. 18 and 19. *Aristeyera spicata.* FIG. 18. Diagram of the origin of floral traces in a young staminate flower. Details: S1, traces to lowest sepal; S2, traces to second sepal; S3, traces to highest sepal. P1, P2, and P3, groups of successive petal traces. Asterisks, stamen traces; black circles, traces to the pistillode.

each group is united, forming a fusion bundle with one large central xylem area and three to five outer patches of phloem. The central part of each of these compound bundles extends radially across the syncarpous base of the ovary and becomes a dorsal carpel bundle which curves upward around the locule and divides tangentially at the base of the long style. One of the branches crosses the top of the locule for a very short distance, the other extends through the style to the stigmatic lobe. At the base of each carpel, some 20 lateral bundles diverge from the two opposite sides of the fusion bundle and form a complete ring of bundles which extend around each locule. Two of these lateral traces extend into the style. Several (2–4) of the lateral bundles fuse to form a large bundle which supplies the ovule. In certain other palms (Morrow, 1965) the ovules are supplied by several ventrally situated bundles which do not fuse but extend into the ovule.

The carpel margins (FIG. 14, centripetal to locules) are very wide. The word "margin" is arbitrarily chosen for the descriptive purposes of this paper. Whether this thick area represents wide carpel margins, Puri's "lateral face" (Puri, 1961), or a closely appressed region of the ventral surface, as would be postulated by the conduplicate concept (Swamy and Periasamy, 1964), may become clarified as more palms are studied. The single, pendulous ovule (FIG. 16) is attached near the top of the locule on one of the carpel margins. (Note the difference in the length of the slits beside the funiculus in FIGURE 13.) The attachment of the ovule between closely appressed carpel margins is unusual. With the exception of the Cocoideae, where the ovules are sessile, and sometimes (*Elaeis*), embedded in the ventral carpel walls, most palm ovules appear to be submarginal. A better understanding of the ovule attachment in *Aristeyera* should result from work in progress on other palm genera (Moore, 1966).

SUMMARY

1. Flowers in *Aristeyera* occur in "triads" and are deeply sunken in pits, which are regarded as invaginations of the axis.
2. The relation of the three bracteoles to the three flowers in each pit suggests that each triad represents a monochasial branching unit.
3. The vascular supplies of the three axes, each terminating in a flower, are enclosed in the axis below each pit.
4. Anatomical evidence of additional aborted flowers or branches was found on the branches terminating in each staminate flower and possibly also on the branch ending with the pistillate flower. This suggests that the *Aristeyera* triad has originated from a more ramified type of inflorescence.
5. Perianth parts of both staminate and pistillate flowers are supplied by a variable number of traces which arise in a spiral pattern as branches from bundles of the floral receptacles.

FIG. 19. Diagram showing the origin of the traces to a young pistillate flower. Details: S1 and S2, bundles to the first two sepals; third sepal of this flower received no traces. P, petal bundles; asterisks, traces to staminodes; C1, lowest carpel; C2, middle carpel; C3, upper carpel.

6. In the petals of the staminate flowers and the sepals of the pistillate flowers some of the lateral veins appear to differentiate basipetally and never become connected to the bundles of the floral receptacles.

7. Fibrous bundles having no connection to floral receptacles occur in definite patterns in perianth parts. Such bundles extend the entire length of the sepals and petals in staminate flowers, and of the sepals in pistillate flowers, but occur only in the distal, valvate part of the petals in the pistillate flowers.

8. The usual vascular supply to stamens, staminodes, and rudimentary carpels consists of one small vascular bundle.

9. The gynoecium is composed of three spirally inserted carpels. At the base they are closed and congenitally adnate to the extended central axis. In the upper part of the ovary, above the extension of the floral receptacle, the carpels are free and ventral sutures can be distinguished. Through the long stylar region, each carpel is open and connate at its margins with the other two carpels forming a 3-pronged stylar canal.

10. A single, pendulous, hemitropous, bitegmic ovule is attached to one margin of each carpel. The ovular supply is a large trace formed by the fusion of 2 or 3 bundles.

ACKNOWLEDGEMENTS

I wish to express my appreciation to Dr. H. E. Moore, Jr., Cornell University, for directing this study; to Doctors H. W. Blaser, University of Washington, and P. B. Tomlinson, Fairchild Tropical Garden, for reviewing the manuscript critically; and to my husband, Dr. C. H. Uhl, Cornell University, for assisting in all possible ways.

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NOTES ON THE VEGETATIVE ANATOMY OF ARISTEYERA SPICATA (PALMAE)[1]

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THE FOLLOWING ACCOUNT OF THE ANATOMY of leaf and stem of *Aristeyera spicata* H. E. Moore forms an appendix to the taxonomic description by Dr. Moore and the study of the morphology and anatomy of the inflorescence axis and flowers by Mrs. Uhl being published simultaneously with this paper.[2]

MATERIAL AND METHODS

Small dried fragments of leaf-blade, petiole, and stem, without precise indication of their position, from the type collection (*Steyermark 90010*) were available for study. Material of the lamina was revived, and preparations in which the surface layers and internal tissues could be studied in various planes were made according to techniques outlined in Tomlinson, 1961 (p. 4). Dried fragments of petiole and stem were infiltrated directly with celloidin solvent (ethanol : ether in equal volumes) under a slight vacuum. Celloidin impregnation involved transference through a graded series of celloidin solutions (2–12%) in a 60° C oven in tightly stoppered bottles. Longitudinal and transverse sections of the hardened celloidin blocks were cut on a Reichert sliding microtome. Maceration of tissues with 10% KOH and 20% chromic acid provided isolated elements, particularly of the xylem. Most observations and drawings were made from sections mounted in glycerine; some permanent preparations stained in safranin and Delafield's haematoxylin were also examined.

ANATOMY

Lamina. Dorsiventral. Adaxial epidermis smooth; abaxial epidermis prominently ribbed, ribs irregularly spaced and with a graded series from largest, prominent ribs to large veins of lamina not producing ribs (FIGS. 12 and 18–21). Margin ribbed (FIG. 11). HAIRS (FIGS. 3, 9, 10, 24, 25) restricted to costal regions, most frequent below large ribs, least frequent in adaxial costal regions; solitary, irregularly scattered or rarely in pairs.

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[1] This study has been carried out with support from the National Science Foundation, Grant GB-506.

[2] MOORE, H. E. *Aristeyera,* a new genus of Geonomoid Palms. Jour. Arnold Arb. **47**: 1–8. 1966.

UHL, N. W. Morphology and anatomy of the inflorescence axis and flowers of a new palm, *Aristeyera spicata*. Jour. Arnold Arb. **47**: 9–22. 1966.

Each hair a more or less uniseriate adpressed filament, always pointing distally, not or scarcely sunken, arising from a single epidermal cell; basal cells conspicuously pitted, slightly lignified with a transition to thin-walled, delicate distal cells; filament probably much longer in immature leaves, but shortened in mature leaves by disappearance of terminal ephemeral cells. Adaxial somewhat thicker-walled than abaxial hairs, tending to become multiseriate by transverse segmentation of filament cells. ADAXIAL EPIDERMIS (FIG. 1) uniform, cells above veins not or scarcely differentiated from those elsewhere; cells in longitudinal files but markedly obliquely extended, more or less rhombohedral in surface view, without sinuous walls. Outer wall somewhat thicker than remaining walls with a thin cutinized layer penetrating somewhat between anticlinal walls. ABAXIAL EPIDERMIS somewhat shallower and thinner-walled than adaxial (14–15μ compared with 20–22μ); subdivided irregularly into costal bands of varying width below veins (FIG. 3) and wider intercostal bands (FIG. 2) between veins. Costal cells more or less rectangular in surface view, smaller than intercostal; intercostal cells obliquely extended but more irregular than adaxial cells. STOMATA (FIGS. 2 and 6–8) restricted to abaxial surface, diffusely distributed in intercostal regions, not in distinct longitudinal files. Terminal subsidiary cells somewhat shorter than, but otherwise not differentiated from normal epidermal cells. Lateral subsidiary cells wide, thin-walled and more conspicuously distinguished from remaining epidermal cells. Guard cells not sunken, equal in depth to abaxial epidermis, each with two prominent cutinized ledges (FIG. 8). Wall beneath ledges somewhat thickened; cell lumen wide and otherwise unrestricted (FIG. 7). EXPANSION CELLS developed as longitudinal bands of enlarged cells at intervals below each surface (FIG. 21 *exp.*). COLORLESS HYPODERMIS absent adaxially; represented beneath abaxial surface by a compact layer of thin-walled, colorless, more or less cubical cells (FIG. 13), those below largest veins smaller than cells elsewhere. Hypodermis interrupted by wide substomatal chambers each surrounded by 4 cells appearing more or less L-shaped in surface view (FIG. 4). ASSIMILATING MESOPHYLL without distinct palisade layers; adaxial cells compact (FIGS. 5, 14), somewhat transversely extended; middle mesophyll layers looser, aggregated into indistinct transverse diaphragms, forming a well-developed intercellular space system obvious only in longitudinal sections (cf. FIGS. 13 and 14). FIBERS up to 18μ wide, with wide septate lumina, unlignified walls; abundant throughout mesophyll, most common in adaxial layers; solitary or 2–3 forming narrow fibrous strands (FIG. 13). Adaxial fibers commonly in contact with adaxial epidermis, abaxial fibers rarely interrupting hypodermis and in contact with abaxial epidermis. VASCULAR BUNDLES (veins) either compound and situated in prominent ribs (FIG. 21) or smaller, simple and not producing pronounced ribbing of lamina (FIG. 18), with a complete transition between infrequent large ribs and numerous small vascular bundles (FIGS. 18–21). Vascular bundles independent of and equidistant from surface layers except largest bundles continuous with abaxial epidermis. Bundles each with a continuous uniseriate outer parenchymatous sheath of colorless, tabular cells elongated somewhat along the vein; outer sheath incomplete below larger veins. Inner sheath of somewhat thicker-walled cells, uniseriate and indistinct in smaller veins, more pronounced in larger bundles and including lignified abaxial fibers forming a distinct phloem sheath. Fibrous phloem sheath best developed in largest ribs. Largest veins including adaxial sheathing fibers (FIGS. 20, 21). Vascular tissues reduced in smaller veins (FIG. 13); collateral with a wide metaxylem vessel in larger veins (FIGS. 18, 22), large veins with several separate phloem strands (FIGS. 19, 20); largest veins compound with additional lateral vascular bundles resembling isolated small veins of lamina (FIGS. 21, 23). Protoxylem well developed only in larger veins; phloem of smaller veins often divided into two incipiently separate strands by a narrow medium sclerotic isthmus. TRANSVERSE COMMISSURES at irregular intervals connecting longitudinal veins; each with very reduced vascular tissues sheathed by uniseriate slightly sclerotic parenchyma (FIG. 15). MARGINAL RIB including a broad, compound vascular bundle representing fusion product of major longitudinal veins (FIG. 11). CELL CONTENTS not well preserved, no crystalline deposits observed. STEGMATA (silica cells) abundant next to mesophyll and vascular fibers, each with a massively thickened basal wall enclosing an irregularly spherical, spinulose silica body (FIGS. 16 and 17). Bodies 9–12μ wide in stegmata next to veins; smaller, 5–7μ wide next to mesophyll fibers.

Leaf axis (petiole) (FIGS. 26–29). HAIRS common abaxially, resembling those of lamina. EPIDERMIS shallow, outer wall somewhat thickened, wholly cutinized; cells more or less rectangular in surface view, slightly elongated. Abaxial epidermis somewhat papillose towards margin. STOMATA occasional. GROUND PARENCHYMA uniform, cells compact, somewhat elongated; only hypodermal layers slightly modified. Abaxial hypodermal ground parenchyma somewhat sclerotic; adaxial ground parenchyma cells somewhat anticlinally extended, thin-walled, their walls plicately collapsed in a concertina-like manner. Hypodermal ground parenchyma including small fibrous or fibro-vascular strands (e.g. FIG. 27). VASCULAR BUNDLES in two distinct series: (1) Single ADAXIAL SERIES of large INVERTED mostly compound bundles (FIGS. 26, 27), each including a large vascular strand towards the center of the petiole, the vascular tissues with inverted orientation, and one or more small strands embedded in the most fibrous part of the bundle towards the outer surface of the petiole; the vascular tissues of these supplementary strands with oblique or inverse orientation and often represented by phloem alone. (2) Remaining bundles with normal orientation occupying bulk of petiole, divisible into: (a) ABAXIAL SERIES of alternately large and somewhat smaller bundles each with a massive fibrous phloem sheath, the largest bundles compound and including one or more supplementary strands of vascular tissue, often phloem alone, within the fibrous sheath (FIG. 28); (b) CENTRAL SERIES of uniformly constructed bundles with normal orientation, more or less irregularly arranged but forming two distinct horizontal series in adaxial part of petiole (FIG. 26). Each bundle (FIG. 29) simple with a smaller fibrous sheath than in superficial bundles, including well developed protoxylem, usually two wide metaxylem vessels; the phloem subdivided into at least two separate strands by a medium sclerotic isthmus. Bundles of adaxial and remaining series partially fused in leaf margin to form a large commissure. TRANSVERSE COMMISSURES connecting longitudinal bundles occasional throughout petiole. Stegmata, crystals as in lamina.

Stem.[3] PERIDERM formed by suberisation of outer layers augmented by etagen meristematic activity in outer cortex. CORTEX narrow, up to 2 mm. wide including numerous narrow fibrous strands transitional internally to larger strands including either phloem or both xylem and phloem tissues. No distinct limiting layer for inner cortex. CENTRAL CYLINDER with peripheral congested vascular bundles, each bundle with well developed fibrous phloem sheath, the bundles often somewhat rhombohedral in transverse section. Obvious leaf traces frequent. Central vascular bundles somewhat less congested but with scarcely reduced fibrous sheaths. VASCULAR BUNDLES (FIG. 32) almost invariably with one wide metaxylem vessel, with or without protoxylem; two vessels appearing in bundles close below their exsertion as leaf traces. GROUND PARENCHYMA cells slightly thick-walled, conspicuously pitted, including abundant starch. Stegmata abundant next to vascular fibers (FIG. 34).

Secretory and conducting cells. RAPHIDE-SACS infrequent in all parts. STEGMATA (silica cells) abundant next to fibers in all parts, silica bodies smallest (5μ diameter) in cells next to mesophyll fibers of lamina, largest (12μ diameter) in cells next to vascular fibers of stem. STARCH abundant in ground parenchyma of stem; grains simple, more or less spherical, up to 15μ diameter. VESSELS present in metaxylem of stem, rachis and large ribs of lamina; larger elements in leaf mostly more than 2 mm. long, 70μ wide with scalariform perforation plates with many thickening bars (FIGS. 30, 31) on oblique or very oblique end walls; elements in stem (FIG. 33) average 860μ long, 120μ wide with scalariform perforation plates with 4–10 thickening bars on slightly oblique or oblique end walls. SIEVE-TUBES in stem with slightly oblique compound sieve-plates coinciding with vessel-element end walls; diameter 15–20μ.

DISCUSSION

A limited amount of information on vegetative anatomy of some other genera of Geonomeae: *Calyptrogyne*, *Calyptronoma*, *Geonoma*, *Pholidostachys* and *Welfia* is available in Tomlinson (1961), and suggests that the group shares a few diagnostic anatomical features. Most distinctive is the filamentous uniseriate (rarely biseriate) hair, commonly restricted to

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[3] General stem construction corresponds to that described for *Rhapis* by Zimmermann and Tomlinson, 1965.

costal regions and most frequent on the abaxial surface of the lamina. Those illustrated for *Aristeyera* (FIGS. 9, 10, 24 and 25) are quite typical. Hairs are more uniformly dispersed in *Calyptrogyne* and *Welfia*. Those in *Calyptronoma* and *Welfia* are somewhat distinctive in being sunken and this is associated with enlargement of the basal cell. Elsewhere in palms uniseriate filamentous hairs are rare. They occur in the bactroid palms which on morphological and anatomical grounds, however, show no special affinity with the Geonomeae. *Reinhardtia* and *Sclerosperma* may have hairs somewhat similar to those in *Calyptronoma* and *Welfia*.

Other anatomical features which are common to those geonomoid palms which have so far been examined and which are illustrated for *Aristeyera* above are: (1) shape of epidermal cells which are always thin-walled except in *Calyptronoma*, (2) structure and distribution of stomata, (3) structure and distribution of stegmata and to a certain extent the structure of assimilating mesophyll, veins, and ribs. The degree of differentiation of hypodermal mesophyll layers as specialized colorless layers varies from: (1) *Welfia* with a distinct 2-layered colorless hypodermis below each surface, to (2) *Calyptronoma* and, less conspicuously, *Pholidostachys* with a 1-layered hypodermis below each surface, to (3) *Aristeyera* with a 1-layered abaxial hypodermis, to (4) *Calyptrogyne* and *Geonoma* with no colorless hypodermis. Non-vascular fibers vary in their distribution. They are (1) absent from some *Geonoma* species, (2) solitary or in small strands scattered more or less throughout the mesophyll as in *Aristeyera*, *Calyptrogyne*, *Calyptronoma*, and some *Geonoma* species, (3) infrequent as small strands in a single series in *Pholidostachys*, and (4) distinctive in *Welfia* as large strands pectinating with the vascular bundles. Mesophyll fibers throughout the alliance tend to be septate, unlignified and with a wide cell lumen.

It is quite clear, therefore, even from the limited information available, that although the members of the Geonomeae share some common features they are anatomically quite diverse. *Welfia* seems rather isolated. *Aristeyera* shows no special anatomical affinity with *Welfia* although these two genera are most alike in floral morphology. Without further information on many more species of this tribe further speculation about generic affinity on an anatomical basis is pointless.

Nevertheless, the above account has demonstrated that there are anatomical features of diagnostic value in this tribe and continued investigation should reveal more. In view of the size of this assemblage, in the region of 200 species according to Dr. Moore, and considering the small sample for which anatomical information is available (about 10 species and for these mostly fragments of the lamina), one feels justified in stating that the anatomy of the Geonomeae is largely a *terra incognita*.

SUMMARY

A description of the anatomy of lamina; petiole and stem of *Aristeyera spicata* based on small fragments from the collection *Steyermark 90010*

supplements the formal taxonomic treatment and the account of floral anatomy. *Aristeyera* shows anatomical features which hitherto have appeared to be diagnostic for the Geonomeae. Without information about many more species from this tribe it is impossible to comment on the affinities of *Aristeyera* from an anatomical point of view except that it shows less resemblance to *Welfia* than to other geonomoid genera.

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EXPLANATION OF PLATES

(The abbreviations used on the figures are cited here with their equivalents: chlor. = chlorenchyma; exp. = expansion cells; f. (solid black) = fibers of bundle sheaths; hyp. = hypodermis; mes. f. = mesophyll fibers; mxy. (open circles) = metaxylem; phl. (dotted) = phloem; pxy. (open circles) = protoxylem; sc. par. (lined) = sclerotic parenchyma of bundle sheath; scl. = sclerenchyma; xy. = xylem; xy. par. (white) = xylem parenchyma.)

PLATE I

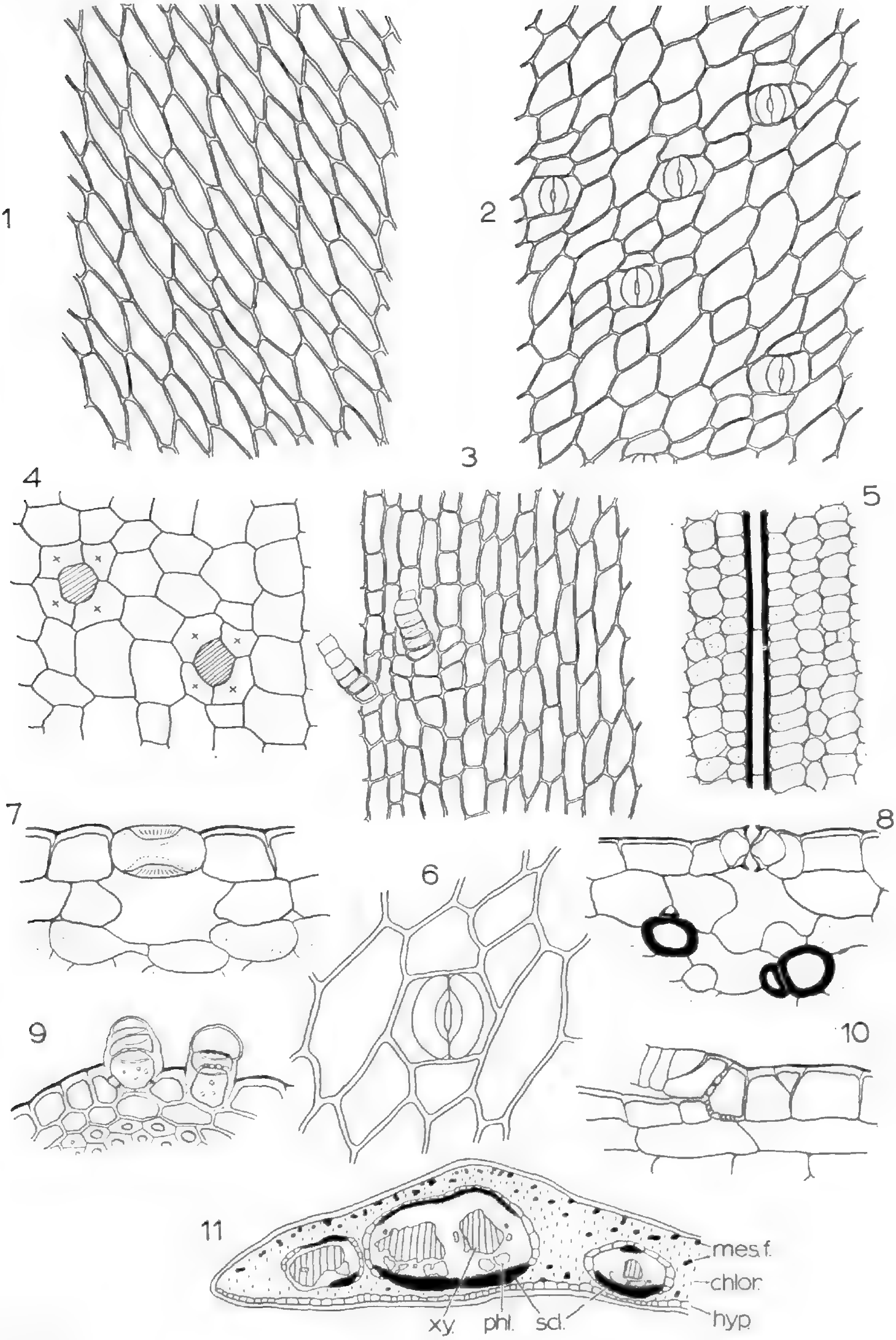
FIGURES 1–11, Lamina of *Aristeyera spicata*. FIGS. 1–5, Surface views, × 220. FIG. 1, Adaxial epidermis. FIG. 2, Abaxial epidermis, intercostal region. FIG. 3, Abaxial epidermis, costal region. FIG. 4, Abaxial hypodermis. FIG. 5, Adaxial mesophyll, hypodermal layer. FIGS. 6–8, Stomata, × 440. FIG. 6, Surface view. FIG. 7, Longitudinal section. FIG. 8, Transverse section. FIGS. 9 and 10, Abaxial hairs, × 440. FIG. 9, Transverse section. FIG. 10, Longitudinal section. FIG. 11, Lamina margin, transverse section, × 32 (cf. FIGS. 18–21).

PLATE II

FIGURES 12–25, Lamina of *Aristeyera spicata* (continued). FIG. 12, Transverse section, × 32, diagrammatic representation of the distribution of veins (solid black). FIG. 13, Transverse section, × 220, enlargement of portion of FIG. 12, inset showing details of cuticle. FIG. 14, Longitudinal section, × 220. FIG. 15, Transverse commissure, × 220, in transverse section from longitudinal section of lamina. FIGS. 16 and 17, Stegmata, × 440, next to isolated mesophyll fibers. FIGS. 18–21, Transverse section, × 32, of veins of increasing size; vascular and mesophyll fibers shown in solid black, xylem lined, phloem dotted, chlorenchyma as short lines. FIG. 22, Transverse section of vein, × 220, enlargement of vein shown in FIG. 18. FIG. 23, Transverse section of small vascular bundle, × 220, enlargement of small lateral bundle from FIG. 21. FIGS. 24 and 25, Hairs shown in surface view, × 440. FIG. 24, Abaxial hair. FIG. 25, Adaxial hair.

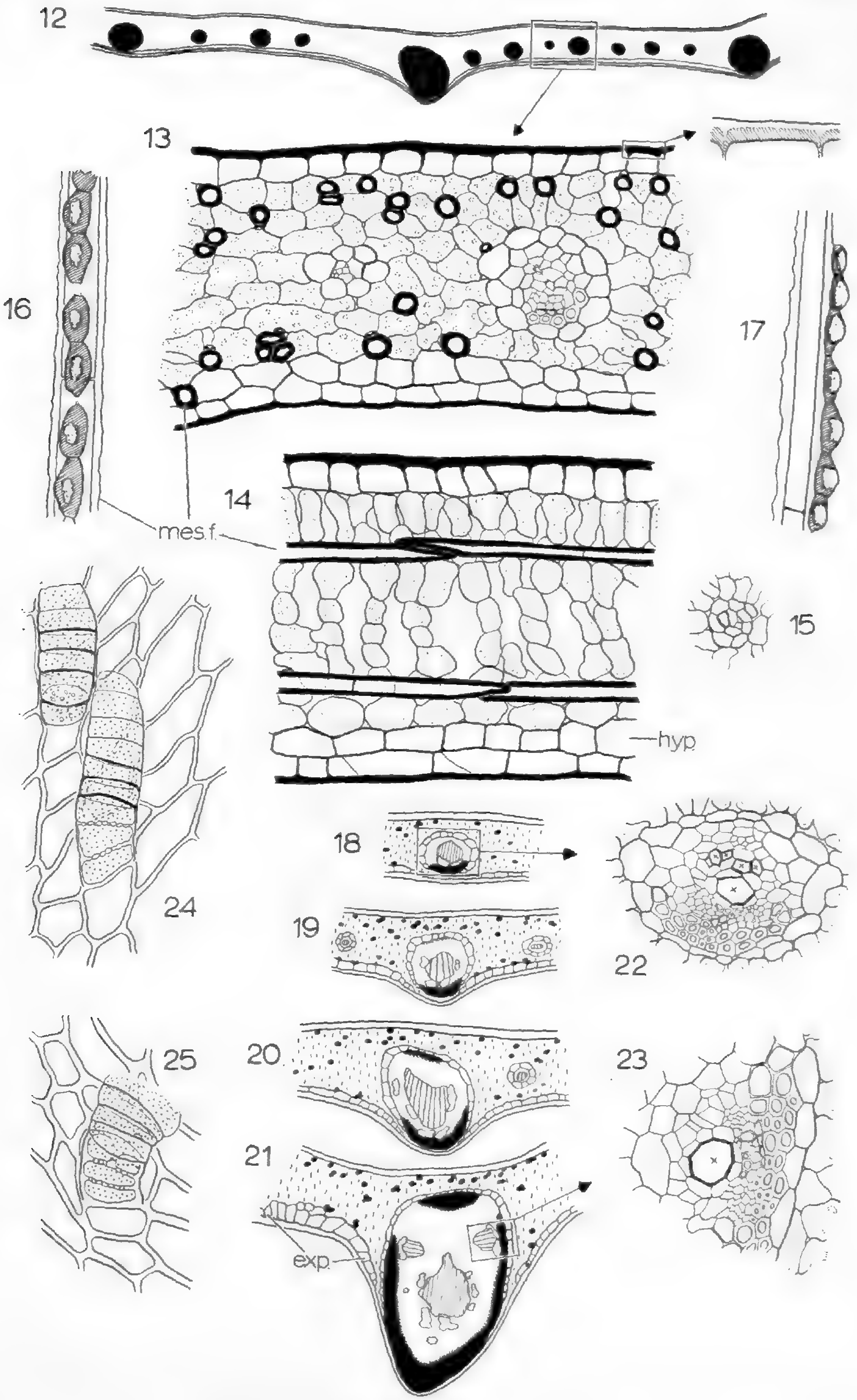
PLATE III

FIGURES 26–34, Petiole and stem of *Aristeyera spicata*. FIGS. 26–31. Petiole. FIG. 26, Transverse section, × 6, incomplete, complete outline indicated by dotted line. Inverted bundles shown in solid black, normally oriented bundles lined. FIGS. 27–29, Enlarged details, × 60, of vascular bundles from FIG. 26. FIG. 27, Adaxial, inverted bundles. FIG. 28, Abaxial bundle. FIG. 29, Central bundle. FIGS. 30 and 31, Metaxylem vessel element. FIG. 30, Outline of end wall, × 80. FIG. 31, Details of perforation plate, × 440. FIGS. 32–34, Stem. FIG. 32, Transverse section of peripheral vascular bundle, × 60. FIG. 33, Metaxylem vessel elements from stem, × 80, perforations seen directly represented by solid black; perforations seen through an imperforate wall represented by lines. FIG. 34, Stegmata next to stem fiber, × 440.

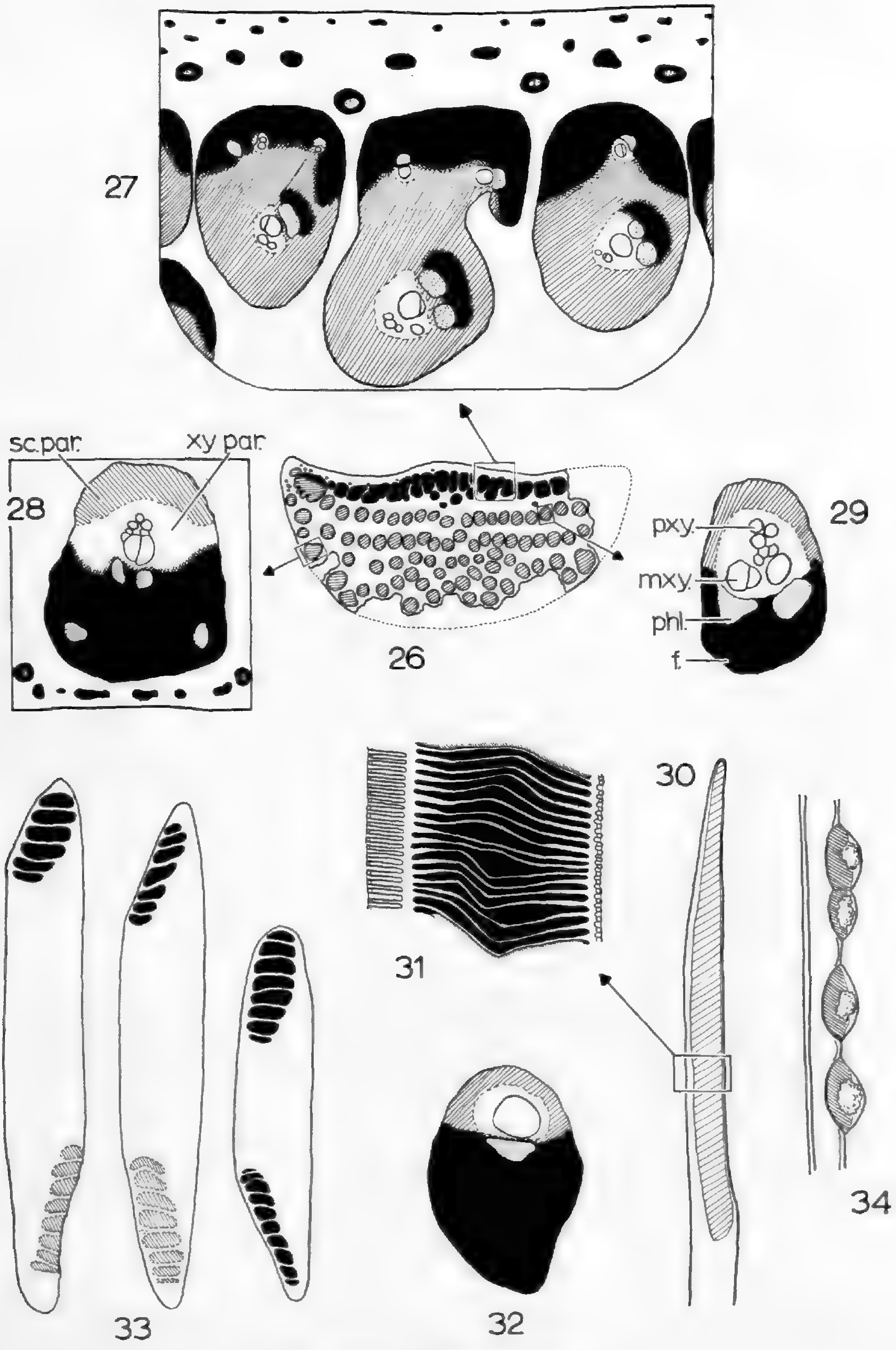


TOMLINSON, ARISTEYERA SPICATA

PLATE II



TOMLINSON, ARISTEYERA SPICATA



TOMLINSON, ARISTEYERA SPICATA

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

I. K. FERGUSON

CAPRIFOLIACEAE A. L. de Jussieu, Gen. Pl. 210. 1789, "Caprifolia," nom. cons.
(HONEYSUCKLE FAMILY)

Deciduous [or evergreen] shrubs, sometimes small trees or vines, rarely herbs, with opposite [or alternate], entire or divided, exstipulate or stipulate leaves. Inflorescence a corymb, cyme, thyrse, or spike of whorls, or flowers solitary or in pairs, usually bracteate and bracteolate. Flowers regular or irregular, epigynous, bisexual, rarely some sterile. Floral tube adnate to the ovary, with a distinct constriction at the level of the 3–5 usually small calyx lobes. Corolla sympetalous, 3–5-lobed, salverform, rotate, campanulate, funnelform, or tubular, often bilabiate, sometimes gibbous at or near the base; aestivation usually imbricate. Stamens 5 [4], epipetalous, alternate with the corolla lobes; filaments long or short; anthers 2-locular, longitudinally dehiscent, oblong or linear, versatile, dorsifixed, introrse or rarely extrorse; pollen tricolpate. Gynoecium 1–5-carpellate, syncarpous; style 1 or wanting; stigmas as many as the carpels, distinct or united; ovary inferior, 2–5-locular; locules with solitary to numerous, pendulous, anatropous ovules; placentation axile or parietal. Fruit a berry or drupe, rarely a capsule [or achene], 1–5-locular, with 1-∞ seeds or as many stones (pyrenes, nutlets) as locules. Endosperm copious, solid or ruminate; embryo straight, small, situated near the

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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 Carroll E. Wood, Jr., and Reed C. Rollins. 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 40–46 (1959–1965). The area covered includes North and South Carolina, Georgia, Florida, Tennessee, Alabama, Mississippi, Arkansas, and Louisiana. The descriptions are based primarily on the plants of this area, with supplementary material in brackets. References which the author has not seen are marked by an asterisk.

The author is indebted to Dr. Wood for his aid and valuable criticisms; to Dr. George K. Brizicky for his guidance and suggestions; to Dr. Rolla M. Tryon for his advice on some of the nomenclature; to Dr. Richard A. Howard for sharing some of his unpublished data on petiolar anatomy in *Viburnum*; and to Mrs. Gordon W. Dillon for her help in the preparation of the typescript. The illustrations, with the exception of *Fig. 3a* & *b*, which is the work of the late Dorothy H. Marsh, were prepared by Arnold D. Clapman. Parts of the materials used for illustration were collected by R. J. Eaton, P. S. Green, M. Lefavour, and C. E. Wood, Jr.

hilum, radicle terete, cotyledons ovoid or oblong. (Including Sambucaceae Link, Handb. 1: 662. 1829, "Sambucinae.") TYPE GENUS: *Caprifolium* Mill. = *Lonicera* L.

A family of about 18 genera and 500 species, primarily of the North Temperate Zone but extending to the mountains of the Tropics, South America, Australia, and New Zealand; seven genera native in North America; six in our area.

Caprifoliaceae are distinguished from most other families by the syncarpous, inferior ovary and opposite leaves. The presence of stipules is probably the most useful character for distinguishing the very closely related Rubiaceae, but there are exceptions, and there seems to be no single character which separates the two families consistently. Airy-Shaw has attempted to differentiate them on the basis of the scaly buds of the Caprifoliaceae *versus* the naked buds of Rubiaceae, but there are numerous exceptions in *Viburnum*. Some authors favor uniting the two families, but Kern & Van Steenis do not think this desirable without a full investigation, since many of the genera of the Caprifoliaceae would be placed in different tribes of the Rubiaceae and the identity of the family lost. These authors have drawn attention to small but important characters common to all Caprifoliaceae: the presence of enlarging calyx lobes, a distinct constriction below the limb of the calyx, dorsifixed anthers, and the absence of colleters (glandular trichomes) which occur on the inner surface of the stipules of many rubiaceous genera. The Asiatic genera *Carlemannia* Benth. and *Silvianthus* Hook. have been assigned to both the Rubiaceae and the Caprifoliaceae, but doubtfully belong to either family (see Airy-Shaw, 1965). It is problematical whether the New Zealand *Alseuosmia* Cunn. and the New Caledonian *Pachydiscus* Gilg & Schlechter and *Memecylanthus* Gilg & Schlechter belong to the Caprifoliaceae where they have been placed. *Viburnum* and, to a lesser extent, *Sambucus* show affinities with the Cornaceae, a relationship supported by pollen morphology. These genera also appear to be related to the Valerianaceae, valerianic acid occurring in both. In addition, the leaves of *Sambucus* closely resemble those of many of the Valerianaceae. The tribe Linnaeeae may also show affinities with the Valerianaceae, for *Abelia* resembles the Asiatic genus *Nardostachys* in some anatomical characters.

The Caprifoliaceae have been subdivided variously. Bentham & Hooker placed *Viburnum* and *Sambucus* together in the tribe Sambuceae HBK. ex DC. and the remainder of the genera in the tribe Lonicereae R. Br. ex DC.; and pollen morphology and biochemical studies do indeed indicate a close relationship between *Sambucus* and *Viburnum*. A better treatment, however, appears to be that of Fritsch, who separated the two, recognizing the tribes Sambuceae, Lonicereae (= Caprifolieae), Linnaeeae Fritsch, and Viburneae Fritsch. Meyer had previously segregated *Diervilla* and *Weigela* as tribe Diervilleae, and Wagenitz followed this course.

Reduction in the number of carpels and ovules seems to have been a feature in the evolution of the genera of the Caprifoliaceae. The basic chromosome numbers appear to be eight and nine, and changes in chromosome number presumably have played only a minor role in differentiation of the genera. The cytogenetics of *Lonicera* and *Viburnum* have been investigated quite extensively, but other genera have been neglected. No chromosome counts are available for *Triosteum*, *Leycesteria*, and *Alseuosmia* and few for *Symphoricarpos* (two of 16 species) and *Abelia* (two of 30 species). Pollination is primarily by insects which are attracted by the conspicuous corollas, the flowers aggregated into heads, and the usually abundant nectar.

The family is of little economic importance, aside from the many species of *Lonicera, Weigela, Viburnum, Leycesteria, Abelia, Symphoricarpos*, and *Sambucus* cultivated as ornamentals. *Abelia* × *grandiflora* (André) Rehd. (*A. chinensis* × *A. uniflora*) is one of the most widely cultivated ornamental shrubs of the southeastern United States.

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KEY TO THE GENERA OF CAPRIFOLIACEAE

General characters: *shrubs or trees, rarely herbs, mostly with opposite, exstipulate or occasionally stipulate leaves; flowers usually 5-merous, the floral tube with a distinct constriction below the limb of the calyx; gynoecium syncarpous, with a 2–5-locular, inferior ovary; endosperm copious, embryo small, straight.*

A. Corolla rotate or subrotate, deeply 5-lobed; style very short or absent; stigmas 1–5.
  B. Leaves pinnately compound; drupe with 3–5 stones. . . . 1. *Sambucus.*
  B. Leaves simple (sometimes lobed); drupe with 1 stone. . . 2. *Viburnum.*
A. Corolla campanulate, tubular, funnelform, or bilabiate; style elongate; stigma capitate.
  C. Plants coarse, erect, herbaceous perennials; fruit a dry drupe with 3 stones. . . . . 3. *Triosteum.*
  C. Plants shrubs or woody vines; fruit a capsule, fleshy drupe, or berry.

- D. Corolla companulate; ovary 4-locular; fruit a drupe with 2 stones. .... 4. *Symphoricarpos.*
- D. Corolla funnelform, tubular, or bilabiate; ovary 2- or 3(–5)-locular; fruit several- or many-seeded.
  - E. Ovary slender; calyx lobes linear-lanceolate; fruit a capsule. .... 5. *Diervilla.*
  - E. Ovary globular to ovoid; calyx lobes short-triangular; fruit a berry. .... 6. *Lonicera.*

Tribe Sambuceae HBK. ex DC.

1. **Sambucus** Linnaeus Sp. Pl. 1: 269. 1753; Gen. Pl. ed. 5. 130. 1754.

Rank-smelling deciduous shrubs or small trees [rarely perennial herbs]. Stems with a large pith. Winter buds with several pairs of scales. Leaves pinnately or bipinnately compound and usually with serrate leaflets, exstipulate or stipules small [or conspicuous] or reduced to glands. Inflorescence a corymb, cyme, or thyrse, usually terminal, bracteolate, the pedicels articulate at apex. Flowers small, white or yellowish, regular, bisexual. Calyx lobes 5 [3], small. Corolla rotate, 5[3 or 4]-lobed, lobes imbricate [rarely valvate], ovate [to oblong-lanceolate]. Stamens 5, inserted toward the base of the corolla; filaments slender, subulate; an-

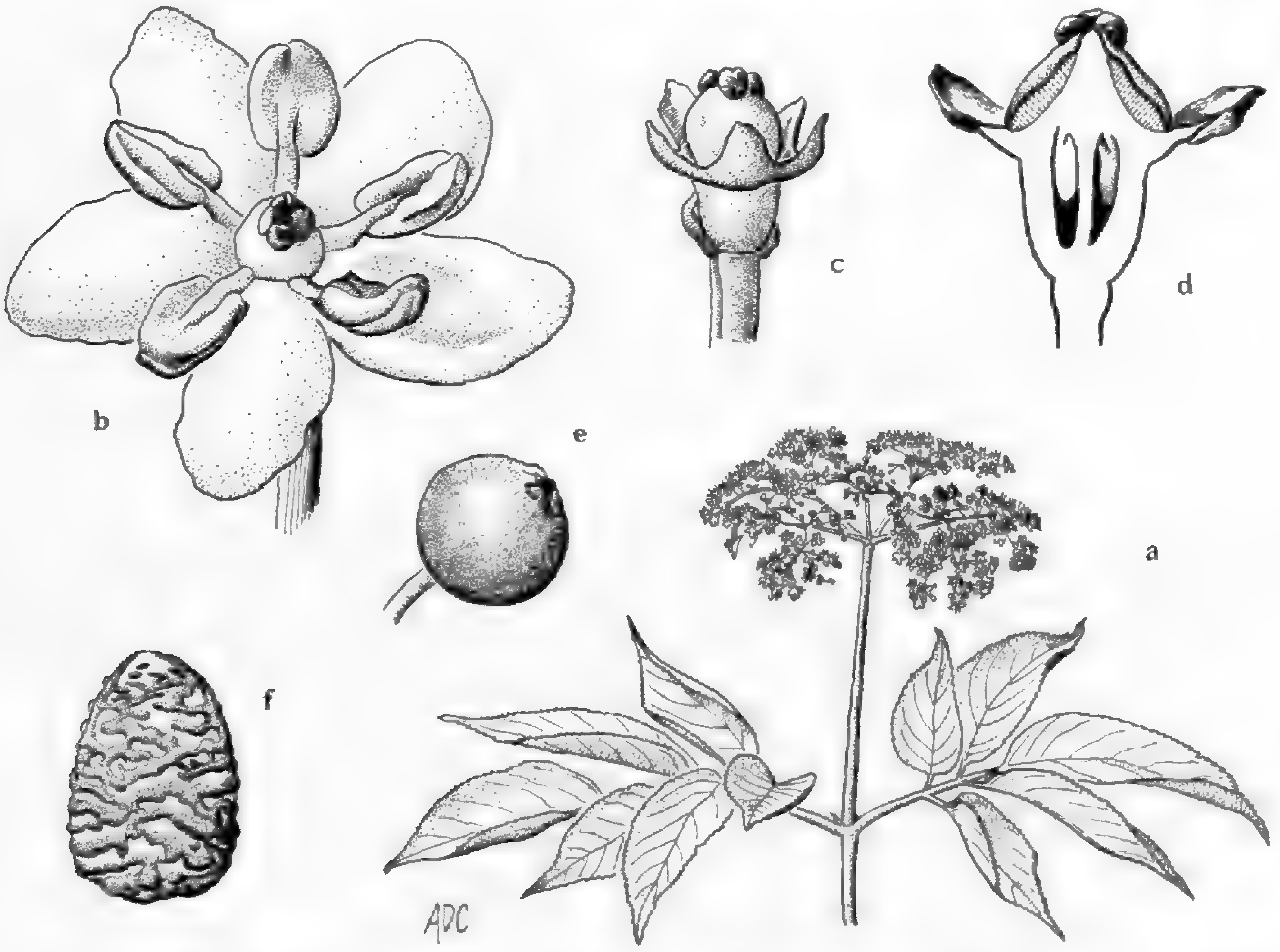

FIG. 1. **Sambucus.** a–f, *S. canadensis*: a, flowering branchlet, × 1/4; b, flower, × 6; c, flower with corolla and stamens removed to show bracteoles and calyx lobes, × 6; d, semidiagrammatic vertical section of flower with corolla and stamens removed to show solitary, pendulous, anatropous ovule in each locule, × 10; e, fruit, × 3; f, stone, × 9.

thers short, oblong, extrorse; pollen small to medium sized, reticulate. Stigma sessile, red or white, 3–5-lobed; ovary 3–5-locular with a solitary, pendulous ovule in each locule. Fruit a small ovoid or globular drupe with 3–5 cartilaginous, 1-seeded stones; stones oblong, compressed, rugulose or smooth. Seeds with a membranaceous testa and fleshy endosperm. Embryo sac development of the Adoxa type. LECTOTYPE SPECIES: *S. nigra* L.; see Britton & Brown, Illus. Fl. No. U. S. ed. 2. 3: 268. 1913. (Classical Latin name for the plant; believed to be from Greek, *sambuké*, a stringed musical instrument supposed to be made of the wood of the elder, *S. nigra.*) — ELDER.

A widespread genus of about 20 species, centered chiefly in the temperate regions of the Northern Hemisphere but extending south to the mountains of the Tropics and to East Africa, South America, Australia, and New Zealand; about ten species in North America, including the introduced *Sambucus nigra* and *S. Ebulus* L.; two or three species in our area.

Sambucus racemosa L. is widespread in cool-temperate regions of the Northern Hemisphere. In North America it is represented by subsp. *pubens* (Michx.) Hultén (*S. pubens* Michx.), $2n = 36$, which occurs throughout much of Canada and the northern United States and southward in the mountains to North Carolina, Tennessee, and northern Georgia. The paniculate inflorescences, red fruits, brown pith, and early spring flowering are characteristic. It is closely related to the European subsp. *racemosa*, $2n = 36$, separated by its denser inflorescences and glabrous leaves, and to the Japanese subsp. *Sieboldiana* (Miq.) Hara, distinguished by its reddish stigmas and small fruits. Some authors have treated these taxa as distinct species; their status needs further investigation.

Sambucus canadensis L., $2n = 36$, widespread in our area and extending throughout the greater part of North America, contrasts with *S. racemosa* in its umbelliform inflorescences, black fruits, white pith, and later flowering time in areas where both occur. *Sambucus Simpsonii* Rehd., a variant which occurs from the West Indies to Florida and north to southern Georgia, Alabama, Mississippi, and Louisiana, is very doubtfully distinct from *S. canadensis*. Rehder distinguished this species by its treelike habit, smooth bark, narrow pith, and usually five-locular ovary, in contrast with *S. canadensis* with shrubby habit, rough bark, wide pith, and usually four-locular ovary. Investigation of some of Rehder's material shows that the number of locules in the ovary may vary from three to five but is predominantly four. The other differences are perhaps a result of more favorable climatic conditions. Later authors have called attention to the pinnately divided lower leaflets of *S. Simpsonii*, a characteristic which is common in peninsular Florida, although northward numerous intermediates with a variable number of leaflets occur. Brown reports the frequent occurrence in Louisiana of specimens which have occasional leaves with the lower leaflets divided as in *S. Simpsonii* but with most of the leaves on the same branch like those of *S. canadensis*.

The pinnate leaves and extrorse anthers, as well as numerous small anatomical characters, make *Sambucus* a very distinct genus, but its taxonomic position is not clear. It shows affinities with *Viburnum* in floral characters, and some authors (e.g., Bentham & Hooker and Fernald) associate these genera as the tribe Sambuceae. Others (e.g., Fritsch and Wagenitz) regard *Sambucus* as constituting a separate tribe, while Höck has segregated it as the family Sambucaceae. Van Steenis has drawn attention to a marked structural resemblance between *Sambucus* and *Turpinia* Vent. and suggested that a fuller investigation should be made of the relationships between *Sambucus* and the Staphyleaceae.

Pollination is probably by insects, although few pollinators have been reported for some species and floral nectaries are absent. Both proterandry and proterogyny have been observed, and both self- and cross-pollination may occur. Chromosome numbers of $2n = 32$, 36, and 38 have been reported.

Several species are grown as ornamentals, and ripe fruits of some, including *Sambucus canadensis,* are used for making jellies and wines. The hard wood of *S. nigra* has been used in making musical instruments, as a source of pegwood and charcoal in Europe, and in various other ways. The large pith has been used both as a cleaning agent for the pivots of delicate machinery and for holding botanical specimens in the preparation of freehand sections.

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Tribe Viburneae Fritsch

2. **Viburnum** Linnaeus, Sp. Pl. **1**: 267. 1753; Gen. Pl. ed. 5. 129. 1754.

Deciduous [or evergreen], erect or decumbent shrubs or small trees. Winter buds naked or with scales. Leaves membranaceous to subcoriaceous, opposite or rarely whorled, entire, crenate, dentate, or lobed, glabrous or hairy (often with stellate tomentum), petiolate, exstipulate or stipulate, or the stipules partially adnate to the petiole [or sometimes reduced to glands]. Inflorescences terminal or axillary, compound, umbel-like or paniculate, cymose; bracts and bracteoles usually small, caducous. Flowers regular, bisexual, sometimes the marginal flowers of the inflorescence radiate, slightly irregular, and neutral. Calyx lobes 5, persistent.

Corolla rotate or subrotate [to campanulate], 5-lobed, white (rarely cream or pink), imbricate in bud. Stamens 5, inserted at the base of the corolla; filaments long or short, slender; anthers oblong, introrse, 4-lobed; pollen small to medium sized, reticulate. Style short, conical, glabrous or hairy; stigma 3-lobed; ovary with 2 abortive locules and 1 fertile locule with a single pendulous ovule. Fruit an ellipsoid, ovoid, or globose, 1-seeded drupe crowned by the persistent calyx lobes and style; mesocarp with bitter or sweet flesh; stone globose or laterally compressed, oblong-elliptic to ovate, often grooved or furrowed, the edges inflexed or undulate. Seed with copious, fleshy, solid or ruminate endosperm; embryo minute, linear, situated near the micropyle. Embryo sac development normal (Polygonum type). LECTOTYPE SPECIES: *V. Lantana* L.; see Hitchcock & Green, Int. Bot. Congr. Cambridge 1930. Nomencl. Propos. Brit. Bot. 142. 1929.[2] (Classical Latin name for the genus, thought to refer to *V. Lantana*; also said to be from Latin, *viere,* to bind, because of the pliability of the branches of some species.) — ARROW-WOOD.

A complex genus of about 250 species, mainly of the North Temperate Zone, but occurring south to Central and South America, Java, and Timor; approximately 25 species in North America, including three naturalized from Asia; about 13 (in four sections) native in our area.

Rehder distinguished nine sections based primarily on the shape and furrowing of the stone, number of scales on the winter buds, and leaf venation. Unpublished data from studies of petiolar anatomy by R. A. Howard support the separation of some of these sections. Rehder's treatment, however, does not include the species of Central and South America and Malesia, and a full investigation of the genus is needed.

Section PSEUDOTINUS Clarke ("*Alnifolia*" Small), distinguished by the presence of radiate flowers, naked winter buds, and ruminate endosperm, includes three species of eastern Asia and one of eastern North America. *Viburnum lantanoides* Michx. (*V. alnifolium* Marsh.),[3] $2n =$

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[2] Britton (N. Am. Trees 853. 1908) apparently was the earliest author to select a lectotype species for *Viburnum*. His choice of *V. Tinus* L., also adopted by Abrams & Ferris (Illus. Fl. Pacif. States **4**: 46. 1960), cannot be accepted, for *V. Tinus* is a constituent of the segregate genus *Tinus* Miller (Gard. Dict. Abr. ed. 4. 1754). Rehder (Bibliogr. Cult. Trees Shrubs 602. 1949) also gives *V. Lantana* L. as the lectotype species.

[3] *Viburnum alnifolium* Marshall (*Arbustrum Americanum* 162. 1785) must be typified by the description, for there is no known Marshall specimen. This description is almost a verbatim copy of the informal English description of Miller's *V. americanum* (Gard. Dict. ed. 8. 1768) and must be considered to be the same (cf. K. K. Mackenzie, Torreya **27**: 81–83. 1927). The Miller specimen in the British Museum (Natural History) labeled *V. americanum* is *Hydrangea arborescens* L. in early fruiting condition. Miller's diagnosis of 1768 [*Viburnum* (*Americanum*) foliis cordato-ovatis acuminatis serratis, petiolis longissimis laevibus. *Wayfaring tree with heart-shaped, oval, acute-pointed, sawed leaves, growing upon very smooth foot-stalks*] can apply entirely to *Hydrangea arborescens*, but his further informal account can only be interpreted as a mixture of *V. lantanoides* Michx. and *Hydrangea arborescens.* In the latter Miller refers to the leaves as having long, slender petioles and "deeply sawed" edges, characters of *Hydrangea arborescens*, not *V. lantanoides*, while he

18, is widespread in cool forests of the northeastern United States and adjacent Canada and extends southward in the higher mountains to North Carolina, Georgia, and Tennessee.

Section LENTAGO DC. ("*Prunifolia*" Small, "*Obovata*" Small), represented by some six species in North America, is characterized by winter buds with one pair of scales and leaves with anastomosing veins. *Viburnum cassinoides* L., $2n = 18$, is widespread from Newfoundland to Ontario but southward is confined mainly to the mountains in the Carolinas, Tennessee, northern Alabama, and Georgia. Characteristically with obscurely dentate to denticulate leaves, grooved stones, and shortly exserted anthers, it is usually distinguishable from the closely related and more polymorphic *V. nudum* L., $2n = 18$, which has entire or only crenulate leaves, flat stones, and long filaments. *Viburnum nudum* occurs at lower altitudes throughout much of the southeastern United States, north to Kentucky and southern Connecticut, and west to Texas. The interrelationships of these species may merit further study.

Viburnum rufidulum Raf. (*V. rufotomentosum* Small), $2n = 18$, usually easily recognized by its rusty tomentum and serrate leaves and widespread throughout our area (although absent from peninsular Florida), ranges to Texas, Indiana, Illinois, Missouri, and Ohio. *Viburnum prunifolium* L., $2n = 18$, which lacks the rufescent tomentum, occurs from the Carolinas, Georgia, Tennessee, and Arkansas, north to New York and Connecticut, and west to Kansas and Texas. Some authors have regarded the populations from Arkansas and Missouri as a separate species (*V. Bushii* Ashe) or variety (var. *Bushii* (Ashe) Palmer & Steyerm.), but Steyermark has shown that the leaf characters involved are so variable that these populations should not be treated as a distinct taxon. Some specimens seen from North Carolina appear intermediate between *V. prunifolium* and *V. rufidulum*. Another closely related species, the more northern *V. Lentago* L., $2n = 18$, has been reported from North Carolina and upland Georgia, but no confirming specimens have been found. The remaining species of the section is *V. obovatum* Walt. ("*Obovata*" Small), $2n = 18$, which has included stamens and usually small leaves. It occurs throughout most of Florida (apparently absent from the Keys), north to southern Georgia

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describes the plant as eight or ten feet tall and the fruits as oval red berries. The other details of the description can apply equally well to either species.

If the *Viburnum* element in Miller's description is used to typify *V. americanum*, this unfamiliar and long unused name must be taken up in preference to either *V. alnifolium* or *V. lantanoides*. The course followed here is to continue to typify *V. americanum* Mill. (and *V. alnifolium* Marsh.) by the *Hydrangea* element and to maintain as correct under the International Code *V. lantanoides* Michx., a name which has been used for the *Viburnum* element for a long time by many authors. This procedure follows that proposed by Mackenzie (*loc. cit.*), Suringar (Mitt. Deutsch. Dendrol. Ges. **43**: 216, 217. 1931), and Rehder (Jour. Arnold Arb. **28**: 446. 1947) and avoids another change in the name of this very characteristic species of *Viburnum*.

I am grateful to Dr. N. K. B. Robson, of the British Museum (Natural History) for examining and commenting upon Miller's specimen of *Viburnum americanum*.

and southwestern South Carolina. *Viburnum Nashii* Small appears to be only a robust form of this species.

Section ODONTOTINUS Rehder ("*Dentata*" Small), the species of which have coarsely dentate or lobed leaves and winter buds with two pairs of outer scales, has about six North American representatives, all of which occur in our area. A careful biosystematic study of this taxonomically difficult and confused group is needed. There is no general agreement on the delimitation of the species; the treatment followed here is that proposed by Fernald. *Viburnum Rafinesquianum* Schultes var. *Rafinesquianum* (*V. affine* var. *hypomalacum* Blake), $2n = 36$, distinguished by small, short-petioled or almost sessile stipulate leaves, is widely distributed from Quebec to Manitoba and south to upland Georgia and North Carolina. The glabrous var. *affine* (Bush ex Schneid.) House (*V. affine* Bush ex Schneid.) reaches our area in Arkansas. Closely related, *V. molle* Michx., $2n = 18$ and 36, with its long-petioled, deeply cordate leaves and flat stones, ranges from Indiana to Missouri, south to northern Arkansas. *Viburnum dentatum* L., $2n = 36$, 54, and 72, including *V. scabrellum* Chapm. (*V. semitomentosum* (Michx.) Rehd.) and *V. Ashei* Bush, a highly polymorphic complex characterized by rounded leaf bases, coarsely dentate leaf margins, long, usually exstipulate petioles, and hairy styles, is widespread throughout our area (except peninsular Florida) and beyond, reaching Texas and Massachusetts. *Viburnum bracteatum* Rehd., distinguished from *V. dentatum* by its long bracts and bracteoles and larger corolla, is known only from northwestern Georgia. *Viburnum recognitum* Fern., $2n = 36$, very closely related to *V. dentatum*, is considered by some authors as var. *lucidum* Ait. It is separated by its glabrous young shoots and leaves, and ranges from New Brunswick to Ontario south to the Carolinas, Tennessee, northern Alabama, and Arkansas in our area. In contrast to this difficult group, *V. acerifolium* L., $2n = 18$, throughout its wide range from Minnesota to Quebec, south to the Carolinas, northern Georgia, Tennessee, Alabama, northern Florida, and Louisiana, is immediately recognized by its palmately lobed leaves. *Viburnum densiflorum* Chapm., described from northern Florida and reported to occur in southern Georgia, Alabama, and Louisiana, appears at best to be only a variety (var. *densifolium* (Chapm.) McAtee) of this species.

Viburnum is a well-defined genus distinguished by its single-stoned drupe, usually regular flowers, nearly sessile stigma, and simple leaves. It shares with *Sambucus* regular flowers, uniovulate locules, and the occurrence of stipules in some species. Although various authors have associated the two, others have placed *Viburnum* and *Triosteum* together. A very close relationship with either seems doubtful, however, and the genus should probably by regarded as the only member of a separate tribe. *Viburnum* also shows affinities with *Abelia* and *Symphoricarpos*.

Seed germination, anatomy, and the pharmaceutical properties of the wood and bark of many species have been extensively investigated, but there is a need for further ecological information. Volatile oils and associated unpleasant odors resembling those found in *Valeriana* are characteristic.

Pollination is by insects, especially Hymenoptera and Diptera. Chromosome numbers of $2n = 16, 18, 20, 22, 27, 32, 36, 40, 48, 54$, and 72 have been reported.

Many species are widely cultivated as ornamentals. An extract from the bark of *Viburnum prunifolium* has been used in medicine for its antispasmodic properties.

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3. **Triosteum** Linnaeus, Sp. Pl. 1: 176. 1753; Gen. Pl. ed. 5. 81. 1754.

Perennial herbs with coarse, erect, glabrous or hairy stems. Leaves opposite, entire [divided], obovate to oblanceolate to panduriform, connate or united by a ridge around the stem, sessile, exstipulate, usually hairy. Flowers bisexual, irregular, sessile, solitary or in clusters of 2–4 in the axils of leaves [or in short, terminal, whorled spikes], bracteate and sometimes bracteolate. Calyx lobes 5, linear-lanceolate, foliaceous, persistent. Corolla 5-lobed, imbricate, a little longer than the calyx, greenish yellow to dull red, tubular, usually hairy within, slightly gibbous at the base, with a nectary of sessile or very short-stalked glands. Stamens 5, inserted about halfway up the corolla tube, usually included; filaments short, hairy; anthers oblong or linear, introrse, united for most of their length; pollen medium to large, echinate. Stigma capitate, 3–5-lobed; style usually hairy below, included or shortly exserted; ovary 4-locular, 3 locules with solitary ovules, 1 empty. Fruit a dry drupe containing 3 ribbed stones with a thick, bony endocarp. Seeds with well-developed endosperm; embryo minute, situated near the micropyle. Embryo sac development normal (Polygonum type). LECTOTYPE SPECIES: *T. perfoliatum* L.; see Britton & Brown, Illus. Fl. No. U. S. ed. 2. 3: 274. 1913. (Name an abbreviation of Dillenius's *Triosteospermum,* derived from

Greek, *treis*, three, *osteon*, bone, and *sperma*, seed, in allusion to the three stones; see Linnaeus's comments about sesquipedalian generic names in Crit. Bot. 133–135. 1737 [pp. 104–107 in English ed., A. Hort., transl., 1938].) — FEVERWORT, HORSE-GENTIAN.

A genus of about eleven species of the Himalaya, eastern Asia, and eastern North America; three species in North America, all occurring in our area. *Triosteum angustifolium* L., recognized by its hispid-setose indumentum, solitary flowers, and paired bracts, ranges from Connecticut to Illinois and south to the Carolinas, Tennessee, Georgia, and Alabama, and is reported to occur in Louisiana. *Triosteum perfoliatum* L. extends from Massachusetts to Wisconsin and Minnesota south to the Carolinas, Tennessee, Georgia, and Alabama. It is characterized by the lower leaves with broad connate leaf bases, soft indumentum, and 1–4-flowered inflorescences, with a single bract and paired bracteoles. Both this and the preceding seem to be associated with basic soils. *Triosteum aurantiacum* Bickn. is a polymorphic species considered to be doubtfully distinct from *T. perfoliatum* by some authors and treated as var. *aurantiacum* (Bickn.) Wiegand. Separated from the other species by the lower leaves tapering to the base, soft indumentum, shorter style, and earlier flowering time, it occurs throughout the northeastern United States, southward to the mountains of North Carolina, Tennessee, and Georgia.

Triosteum is a well-defined genus readily distinguished by its tubular corolla, herbaceous habit, and dry drupaceous fruit. Its uncertain affinities need investigation. Associated by various authors with both Viburneae and Caprifolieae (Lonicereae), *Triosteum* seems to have closer affinities with the Caprifolieae than with *Viburnum*. Fritsch thought that it probably lies between the tribes Viburneae and Linnaeeae. The mode of pollination is unknown, the cytology of the genus has not been investigated, and ecological information is needed. A study of dormancy, weathering of the bony endocarp, and germination might yield interesting data.

Triosteum is of no economic importance. The dried and roasted fruits have been used as coffee. The roots of *T. perfoliatum* are a mild cathartic.

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Tribe LINNAEEAE Fritsch

4. **Symphoricarpos** Duhamel, Traité Arbres Arbustes 2: *295. pl. 82.* 1755.

Deciduous, erect [or decumbent] shrubs. Winter buds with 2 pairs of outer scales. Leaves opposite, usually entire but sometimes toothed or lobed, glabrous or hairy, exstipulate, short petiolate. Inflorescences terminal or axillary racemes or spikes of paired, opposite, sessile or short-pediceled flowers [or flowers solitary]. Flowers bisexual, slightly irregular, subtended by bracts and paired bracteoles. Calyx lobes 5 [4], persistent. Corolla 5[4]-lobed, campanulate [salverform or tubular-funnelform], sometimes slightly gibbous at the base, with a nectary of sessile glands [or with 5 distinct nectaries]. Stamens 5 [4], inserted near top of corolla tube, included or exserted; filaments short, sometimes villous; anthers oblong or linear, introrse, united for most of their length; pollen echinate. Style glabrous or hairy, shorter than the corolla; stigma capitate or slightly 2-lobed; ovary 4-locular, usually with 2 fertile 1-ovulate locules and 2 sterile several-ovulate locules, the placentation axile. Fruit a globose, ovoid or ellipsoid drupe with 2 more or less compressed stones with a bony endocarp. Seeds oblong; endosperm copious, fleshy; embryo minute. Embryo sac development normal (Polygonum type). TYPE SPECIES: *Lonicera Symphoricarpos* L. = *S. orbiculatus* Moench. (Name from Greek, *symphorein*, to bear together, and *karpos*, fruit, in allusion to the clustered fruit.) — SNOWBERRY.

A genus of about 15 species of North America, two occurring in our area, and *Symphoricarpos sinensis* Rehd. in central China. The species fall into two groups treated either as sections or subgenera: sect. SYMPHORICARPOS (subg. *Eusymphoricarpos* G. N. Jones), in which the lobes of the shortly campanulate corolla are as long as or longer than the tube, and sect. MERIDIONALES Gray ex Schneid. (subg. *Anisanthus* (Willd. ex Roem. & Schult.) G. N. Jones), in which the lobes of the tubular or salverform corolla are shorter than the tube. These differences hardly seem to be of subgeneric value. Both species in our area belong to sect. SYMPHORICARPOS.

Symphoricarpos orbiculatus Moench (*S. Symphoricarpos* (L.) MacMillan), $2n = 18$, ranges from New York south to Florida, west to Texas, Colorado, and northern Mexico. The species seems to be a calciphile. The short, hairy styles and abundant small, purplish-red fruit contrast with the longer, glabrous styles and white fruit of *S. albus* (L.) Blake (*S. racemosus* Michx.). The var. *albus* is of wide range in the northern United States; the western American var. *laevigatus* (Fern.) Blake (*S. rivularis*

Suksdorf), widely cultivated as an ornamental shrub, is sporadically naturalized in our area. The characters of glabrous leaves and young shoots, large berries, and erect habit used to separate var. *laevigatus* from var. *albus* do not seem to be constant. Experimental studies are desirable.

Pollination appears to be chiefly by Hymenoptera. There seems to be no mechanism to limit self-pollination. Cleistogamous flowers have been reported in cultivated specimens of *Symphoricarpos orbiculatus*. The structure of the pericarp and dormancy and after-ripening of the seeds have been extensively investigated. It is reported that the root development of some species suggests a mycorrhizal association. The cytology of the genus is not well known; chromosome numbers have been reported only for *S. albus*, $2n$ = ca. 54, and *S. orbiculatus*.

Symphoricarpos is usually placed in the tribe Linnaeeae, which is distinguished by its four or three carpels with one-seeded fertile locules and two sterile locules. It is probably closely related to *Abelia*, in which the ovary is three-locular and the fruit an achene. It also shows affinities with *Kolkwitzia* and *Linnaea*.

A number of species, including both of ours, are cultivated as ornamentals.

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Tribe DIERVILLEAE C. A. Meyer

5. **Diervilla** Miller, Gard. Dict. Abr. ed. 4. 1754.

Deciduous, erect, often stoloniferous shrubs. Winter buds with several pairs of pointed scales. Leaves opposite, entire or serrate, glabrous or hairy, sessile or short petiolate, exstipulate. Inflorescence of terminal or axillary 3- to several-flowered, short-pedunculate, bracteate cymes sometimes forming a terminal thyrse. Flowers bisexual, slightly irregular, short pediceled, bracteolate. Floral tube slender; calyx lobes 5, linear-lanceolate, persistent or deciduous late in fruit. Corolla 5-lobed, bilabiate, with a 4-lobed upper lip, the lower lip and inner surface of the funnelform tube densely hairy; tube slightly gibbous at the base, with a large subglobular nectary. Stamens 5, inserted near the top of the corolla tube; filaments pubescent; anthers linear, usually exserted, introrse, dorsifixed, anther-halves free at the base, united above; pollen medium to large, echinate. Stigma capitate; style long, slender, densely pubescent below, equal in length or a little longer than the tube; ovary elongate, 2-locular, with numerous ovules, placentation parietal. Fruit a thin-walled septicidal capsule very weakly or tardily dehiscent, bivalvate, crowned with the persistent calyx. Seeds small, ovoid, with a reticulate testa; endosperm

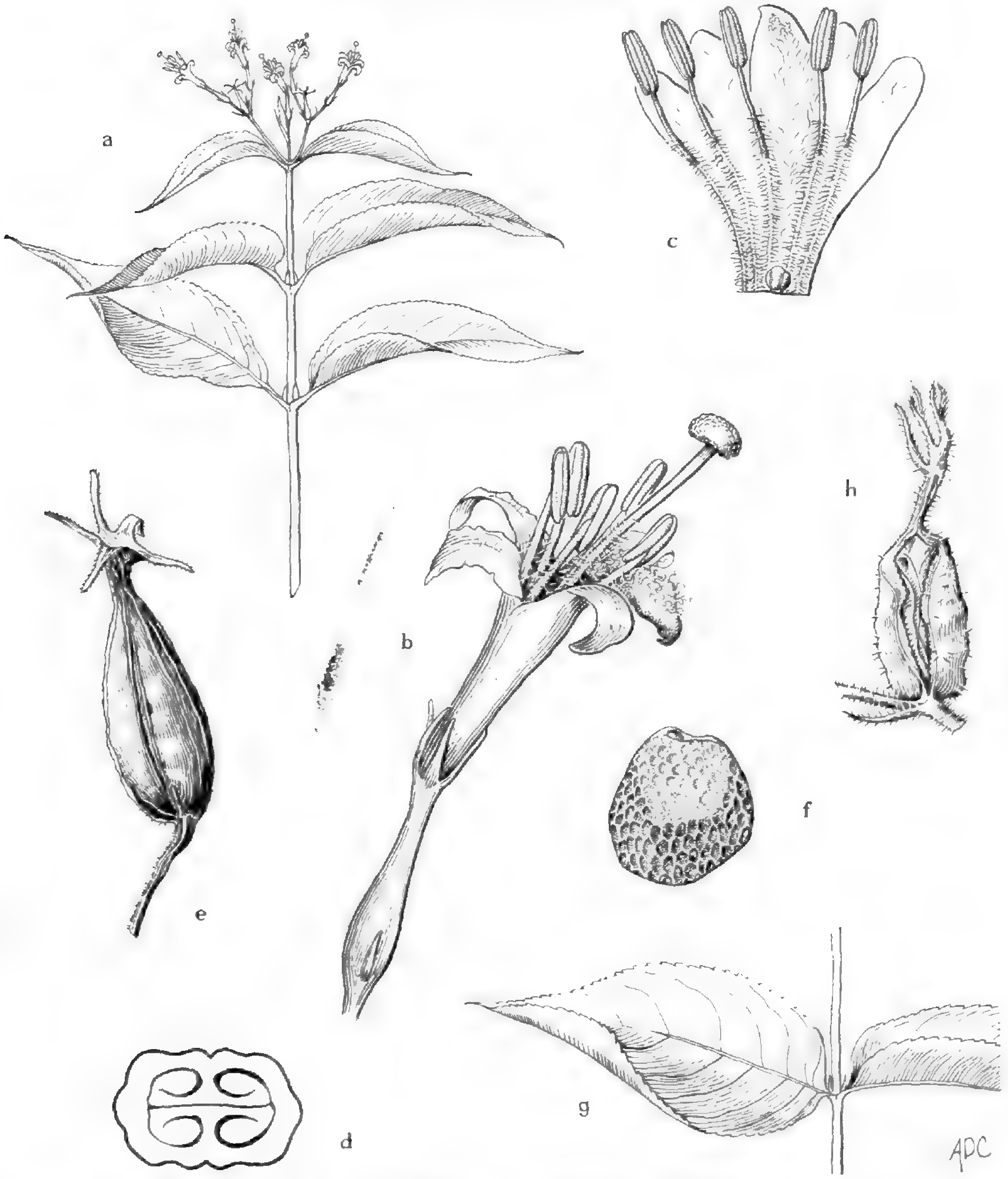

FIG. 2. **Diervilla.** a–f, *D. Lonicera*: a, flowering branchlet, × 1/2; b, flower, × 3; c, corolla opened lengthwise to show attachment of stamens, distribution of hairs, and subglobular nectary, × 2 1/2; d, ovary in semidiagrammatic cross section to show parietal placentation, × 20; e, capsule crowned with persistent calyx, × 4; f, seed, × 24. g, *D. sessilifolia*: node with sessile leaves, × 1/2. h, *D. rivularis*: dehisced capsule to show two valves and persistent calyx, × 3.

fleshy; cotyledons large, superior. Embryo sac development normal (Polygonum type). TYPE SPECIES: *Lonicera Diervilla* L. = *D. Lonicera* Mill. (Named after Diéreville or Dierville, a French surgeon who traveled in eastern Canada (Acadia), 1699–1700, and introduced the plant into France.) — BUSH-HONEYSUCKLE.

A genus including either three species of eastern North America or about

12 more of eastern Asia, depending upon the generic concept. *Diervilla Lonicera*, $2n = 18$, characterized by its petiolate rather than sessile leaves, occurs from Newfoundland to Saskatchewan, southward in the mountains to North Carolina and Tennessee. *Diervilla sessilifolia* Buckl., $2n = 36$, of mountain woods in North Carolina, Tennessee, Georgia, and Alabama, is distinguished from the closely related *D. rivularis* Gattinger (*D. sessilifolia* var. *rivularis* (Gattinger) Ahles), $2n = 36$, which occurs over about the same range, by its longer capsules and glabrous leaves.

The flowers are reported to be proterogynous and are adapted for pollination by Hymenoptera. The color of the corolla changes in the North American species from yellow to orange or red after anthesis.

The generic concept of *Diervilla* has been varied. A distinctive group of Asiatic species has been treated as a separate genus, *Weigela* Thunb., or as either a section (*Weigela* (Thunb.) Koehne) or subgenus (*Weigela* (Thunb.) K. Koch) of *Diervilla*. The Asiatic species are characterized by large, regular, pink to red corollas, woody capsules with a well-developed columella extending beyond the ends of the valves, and seeds with short wings, with the exception of the Japanese *W. Middendorfiana* Verschaffelt, which differs in its yellow corolla, capsule without a well-developed persistent columella, irregular bilabiate calyx, pilose anthers connected by hairs in a ring about the style, and long-winged seeds. This last species has been variously treated as a separate genus, *Macrodiervilla* Nakai, or as sect. *Calyptrostigma* Koehne of *Diervilla*. Another Japanese species, *W. Maximowiczii* (S. Moore) Rehd., intermediate in its yellow flowers, pilose anthers connected in a ring about the style, and capsule with a short, persistent columella equal in length to the valves, has also been treated as a separate genus (*Weigelastrum* (Nakai) Nakai) or as a section (*Weigelastrum* Nakai) of *Diervilla*. Further investigation is needed to determine the status of these groups.

Both *Diervilla* and *Weigela* have affinities with *Lonicera*, *Leycesteria*, and *Abelia*.

Species of *Weigela* are important as ornamental shrubs; the small-flowered North American species of *Diervilla* are rarely cultivated.

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Tribe CAPRIFOLIEAE [Lonicereae R. Br. ex DC.]

6. **Lonicera** Linnaeus, Sp. Pl. 1: 173. 1753; Gen. Pl. ed. 5. 80. 1754.

Deciduous or, more rarely, evergreen shrubs or woody climbers. Winter buds with several or 2 outer scales. Leaves usually entire, sometimes lobed or pinnatifid when young, opposite, short petiolate, sessile or connate, sometimes glaucous, glabrous or hairy, exstipulate. Inflorescence of simple, 2-flowered axillary cymes or of 3-flowered cymes either axillary or aggregated in terminal heads or whorls, bracteate. Flowers mostly conspicuous, regular or irregular, bisexual, subtended by paired, often connate [rarely wanting] bracteoles. Calyx 5-lobed [or truncate], the limb persistent [or deciduous]. Corolla 5-lobed, bilabiate, with a 4-lobed upper lip, or regular, imbricate, tubular or funnelform with a long or short tube, sometimes gibbous and with a nectariferous area of many sessile glands at the base. Stamens 5, inserted near the top of the corolla tube; filaments long, slender; anthers oblong or linear, usually exserted, introrse; pollen medium to large, echinate. Stigma capitate; style slender, equaling or a little longer than the corolla tube; ovary 2–3 [rarely to 5]-locular with 3–8 ovules [the walls of the ovaries of 2-flowered cymes sometimes united], placentation axile, the septa becoming free toward the top of the ovary. Fruit a few-seeded fleshy berry. Seeds ovoid, with a smooth or reticulate [or granular] testa; endosperm fleshy. Embryo sac development normal (Polygonum type). LECTOTYPE SPECIES: *L. Xylosteum* L.; see Rehder, Bibliogr. Cult. Trees Shrubs 614. 1949.[4] (Named in honor of Johann

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[4] The lectotype species of *Lonicera* has been incorrectly cited as *L. Caprifolium* L. by Britton & Brown (Illus. Fl. No. U. S. ed. 2. **3:** 277. 1913), Britton (Fl. Bermuda 372. 1918), and Hitchcock & Green (Int. Bot. Congr. Cambridge 1930. Nomencl. Propos. Brit. Bot. 131. 1929). Rehder's choice of *L. Xylosteum* appears to be correct.

Early authors treated *Lonicera* in various ways, recognizing one or more genera. Linnaeus (Sp. Pl. 173–175. 1753) placed all the species known to him in one genus, *Lonicera*, with two informal groups, "Periclymenum" and "Chamaecerasus." In contrast, Miller (Gard. Dict. Abr. ed. 4. 1754) distinguished the genera *Caprifolium, Lonicera, Periclymenum,* and *Xylosteon.* The species of Miller's *Caprifolium* correspond closely with those of Linnaeus's informal group "Periclymenum," and Miller's species 7, *C. Italicum* Dod., the Italian honeysuckle, is cited by Linnaeus in the synonymy of *L. Caprifolium.* In 1759 (Gard. Dict. ed. 7), Miller combined *Caprifolium* with *Periclymenum.* In 1768 (Gard. Dict. ed. 8), the full description of *Periclymenum italicum*, as it is called, corresponds exactly with the description of *L. Caprifolium* in *Species Plantarum.* Thus, while maintaining *Lonicera* as a distinct genus, Miller effectively segregated *L. Caprifolium* from *Lonicera* by placing it in his genus *Caprifolium.* This species therefore cannot be used to typify *Lonicera.* In

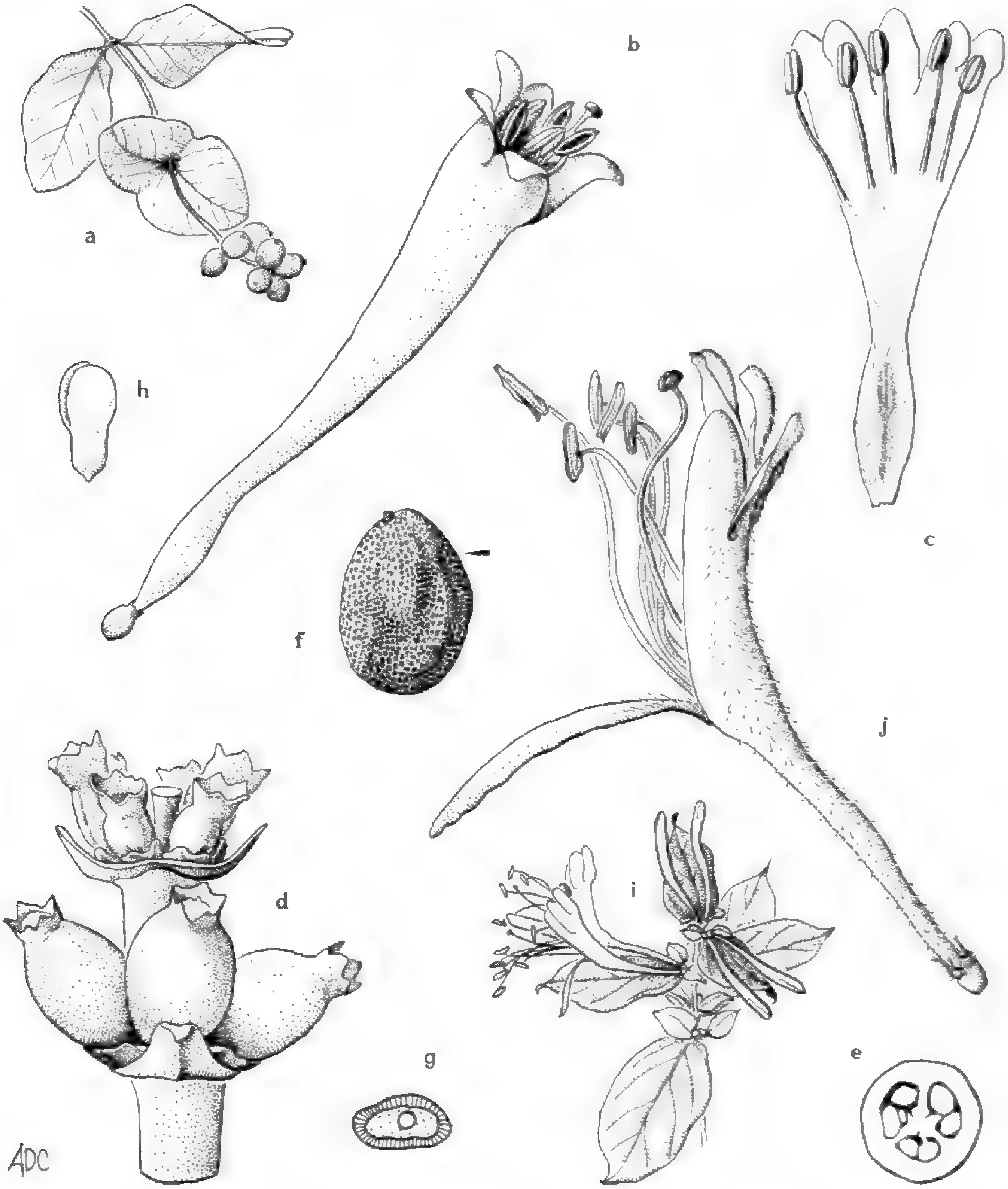

FIG. 3. **Lonicera.** a–h, *L. sempervirens*: a, fruiting branchlet, × 1/2; b, flower, × 2; c, corolla opened lengthwise to show attachment of stamens and distribution of hairs and nectar glands, × 1 1/2; d, portion of the inflorescence to show flowers borne in threes — note bracts, bractlets, and ovaries of flowers and buds (corollas removed), × 8; e, ovary in semidiagrammatic cross section to show axile placentation, × 10; f, seed, × 6; g, seed in diagrammatic cross section, showing testa (hatched), endosperm (stippled), and hypocotyl of embryo (unshaded), × 6; h, embryo, × 12. i–j, *L. japonica*: i, flowering branchlet, showing flowers in pairs, × 1/2; j, flower, × 2.

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contrast, *L. Xylosteum* was retained by Miller in *Lonicera* throughout. His species 3, "*Lonicera pedunculus bifloris ovatis acutis integris* Lin. Hort. Cliff. The Fly Honeysuckle, vulgo," (Gard. Dict. Abr. ed. 4. 1754) fits Linnaeus's description of *L. Xylosteum* (Sp. Pl. 174. 1753). This was further clarified in 1768 (Gard. Dict. ed. 8), when Miller used the binomial *Lonicera Xylosteum* for this species.

Lonitzer, latinized Lonicerus, 1499–1569, a German herbalist and physician, not Adam Lonitzer, 1528–1586; see Linnaeus, Crit. Bot. 93. 1737.) — HONEYSUCKLE.

A genus of about 180 species of temperate and tropical regions of the Northern Hemisphere. About 25 species occur in North America; about seven are native in our area and five are introduced. Although Small recognized *Phenianthus* Raf., *Xylosteon* Mill. (*Xylosteon* Juss.), and *Nintooa* Sweet as genera separate from *Lonicera*, there do not seem to be sufficient grounds for adopting this treatment.

The species fall into two well-marked subgenera: LONICERA (subg. *Chamaecerasus* Rehd.[5]), distinguished by axillary inflorescences with the flowers in pairs and the leaves free, and CAPRIFOLIUM (Mill.) Pers. (subg. *Periclymenum* L., of Rehd.[5]), with terminal, whorled inflorescences of three-flowered cymes and the upper leaves usually connate. The subgenera may be further divided into sections by the regular or irregular corolla, the length of the corolla tube, the climbing or erect habit, and the free or connate bracteoles.[6]

One indigenous and about four introduced taxa of subg. LONICERA occur in the southeastern United States. *Lonicera canadensis* Marsh. (*Xylosteon ciliatum* (Muhl.) Pursh), $2n = 18$, a northeastern species extending southward in the mountains to North Carolina, Tennessee, and Georgia, is distinguished by a short, nearly regular corolla distinctly gibbous at the base and by red fruit. *Lonicera japonica* Thunb. (*Nintooa japonica* (Thunb.) Sweet), $2n = 18$, introduced from Asia and now widespread in eastern North America, has become a pernicious and dangerous pest in woodlands, on roadbanks, and in hedgerows, overwhelming and strangling the native flora. An exuberant woody vine, it is readily distinguished by its bilabiate corolla, long-toothed calyx, and black fruits. *Lonicera fragrantissima* Lindl. & Paxton (*Xylosteon fragrantissima* (Lindl. & Paxton) Small), $2n = 18$, a Chinese shrub widely cultivated in the south-

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[5] Rehder (Missouri Bot. Gard. Rep. **14**: 27–232. 1903) recognized two subgenera: *Chamaecerasus* L. and *Periclymenum* L. As shown in the preceding footnote, however, these were informal categories, not subgenera, under Linnaeus's *Lonicera*. Persoon (Syn. Pl. **1**: 213. 1805), who appears to be the earliest author to establish subgenera as formal categories in *Lonicera*, distinguished three subgenera: *Xylosteum*, *Caprifolium*, and *Symphoricarpos*. The species placed in subg. *Xylosteum* were very similar to those assigned by Rehder to subg. *Chamaecerasus* and include the lectotype species, *L. Xylosteum*. This should therefore become subg. *Lonicera*. The species in Persoon's subg. *Caprifolium* correspond closely with those in Rehder's *Periclymenum* and include *L. Caprifolium*. *Caprifolium* is the earliest name used in the correct sense at the rank of subgenus and should be adopted.

[6] Rehder recognized five sections, four within subg. *Lonicera*, but some authors divide the genus only into sections, rather than into subgenera or both subgenera and sections. The sections then usually recognized are *Lonicera*, *Caprifolium* DC., and *Nintooa* (Spach) Maxim., but Warburg (in Clapham, Tutin, & Warburg, Fl. Brit. Isles, ed. 2. 790, 791. 1962) mistakenly regarding *L. Caprifolium* as the type species of *Lonicera*, gives the sections as *Xylosteon* (Mill.) DC., *Lonicera*, and *Nintooa* (Spach) Maxim.

eastern United States; *L. Maackii* (Rupr.) Maxim., $2n = 18$, from eastern Asia; and *L.* × *bella* Zabel (*L. Morrowii* Gray × *L. tatarica* L.), $2n = 18$, are reported to spread from cultivation in our area.

The remaining species in the Southeast are members of subg. CAPRIFOLIUM. *Lonicera sempervirens* L. (*Phenianthus sempervirens* (L.) Raf.), $2n = 36$, of wide range throughout our area, extending north to Maine and west to Nebraska, Ohio, Iowa, and Texas, is distinctive in its slender trumpet-shaped, regular, bright-red corolla. *Lonicera dioica* L., a polymorphic species occurring from Quebec and Maine to British Columbia, Kansas, and Missouri and extending south to North Carolina, Tennessee, and Georgia, is readily recognized by its bilabiate corolla gibbous at the base and uppermost connate leaves green above. The very doubtfully distinct *L. glaucescens* Rydb. is treated as a variety [7] of *L. dioica* by most authors. *Lonicera flava* Sims, a variable species occurring in the Carolinas, northern Georgia and Alabama, and Tennessee, Kentucky, Missouri, Arkansas, and Oklahoma, is distinguished by its bright orange-yellow bilabiate corolla and elliptic or rhombic, connate uppermost leaves. The paler, somewhat smaller-flowered *L. flavida* Cockerell ex Rehd. is probably best treated as *L. flava* var. *flavescens* Gleason (cf. Steyermark). *Lonicera prolifera* (Kirchner) Rehd. (*L. Sullivantii* Gray), $2n = 18$, closely related to both *L. flava* and *L. dioica*, occurs from Ontario to Wisconsin, Kansas, and Missouri, south to Arkansas and Tennessee. Its nearly orbicular connate uppermost leaves with a glaucous dorsal surface, its extended spicate inflorescence, and its bilabiate pale-yellow corolla gibbous at the base are characteristic. *Lonicera albiflora* Torr. & Gray was described from Fort Towson, Arkansas. Small (in both editions of *Flora of the Southeastern United States*) and Rehder recorded this species from Arkansas, but Fort Towson is today in southeastern Oklahoma, and there appears to be no other record of this species in Arkansas. The European *L. Caprifolium*, $2n = 18$, is reported as an escape from cultivation.

Many of the species are proterandrous. Species with long corolla tubes are pollinated by long-tongued insects or by hummingbirds, while those with short tubes are visited by various Diptera and Hymenoptera. Chromosome numbers of $2n = 18$, 36, and 54 have been reported; most species appear to be diploids ($2n = 18$). A large number of species are grown as ornamentals, and many hybrids (some of them complex) have arisen spontaneously in cultivation.

Lonicera is closely related to *Diervilla* and *Leycesteria*, the three genera showing their affinities in their two- or three-flowered cymes and ovaries with several ovules. *Lonicera* is distinguished from *Leycesteria* by its two- or three-locular *vs.* five-locular ovary and from *Diervilla* by its fleshy fruit.

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[7] Gleason (New Britt. & Brown. 1952) recognized both var. *glaucescens* (Rydb.) Butters and var. *dasygyna* (Rehd.) Gleason. In the event that these varieties are combined (as in Gray's Manual, ed. 8. 1950), the latter name is correct, for it is the older name in the rank of variety, having been described in 1903 under *Lonicera glaucescens*, which itself was not reduced to varietal status until 1913.

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

GEORGE K. BRIZICKY

STERCULIACEAE Bartling, Ord. Nat. Pl. 255, 340. 1830, nom. cons.

(STERCULIA FAMILY)

Trees, shrubs, or herbs [rarely vines]; pubescence of stellate and/or simple hairs; inner bark usually fibrous; mucilage cells and/or cavities and/or ducts in the axis and/or leaves and reproductive organs. Leaves alternate, usually simple and palmately veined at base, petioled [rarely sessile]; stipules caducous or persistent. Inflorescences bracteate cymes or thyrses, axillary and/or terminal, rarely opposite the leaves, sometimes reduced to fascicled or solitary flowers. Flowers bisexual or unisexual by abortion, regular, usually hypogynous, pediceled to sessile, usually bracteolate, sometimes with an involucel of 3 or 4 distinct bract(let)s. Sepals usually 5, connate [rarely distinct], often nectariferous at base within, valvate. Petals usually 5, distinct, sometimes adnate at base to the staminal tube, usually clawed, sometimes hooded (with a terminal appendage), convolute, or absent. Stamens 5–15[–45], usually connate into a staminal tube, often on an androgynophore, sterile in ♀ flowers, the antipetalous ones 5 (or in 5 fascicles of 2 or 3), fertile, the antisepalous ones 5, usually sterile or wanting, rarely fertile; anthers extrorse, usually dorsifixed, 2- or rarely 3-locular, the locules parallel or divergent [rarely separated, or exceptionally superposed], sometimes of unequal size, longitudinally dehiscent; pollen usually small to medium sized, oblate to prolate, often nearly spherical, 3–8-colp(oidor)ate, mostly reticulate. Gynoecium 5-carpellate [rarely up to 60-carpellate], syncarpous, rarely apocarpous, or 1-carpellate, rudimentary in ♂ flowers;

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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 Carroll E. Wood, Jr., and Reed C. Rollins. 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 40–46 (1959–1965). The area covered includes North and South Carolina, Georgia, Florida, Tennessee, Alabama, Mississippi, Arkansas, and Louisiana. The descriptions are based primarily on the plants of this area, with any supplementary material in brackets. References which the author has not seen are marked by an asterisk.

The author is indebted to Dr. Wood for his many editorial suggestions and helpful criticisms in the course of this work; to Dr. R. K. Godfrey for flowering material of *Firmiana*; and to Mrs. Gordon W. Dillon for her help in the preparation of the typescript.

stigmata 1–5; styles as many as carpels, distinct or variously connate; ovary superior, usually 5-locular with axile placentae, or rarely 1-locular with a submarginal placenta; ovules [1] 2 to many in a locule, ascendent to pendulous, hemianatropous to anatropous, epitropous to apotropous, 2-integumented, with a thick nucellus. Fruit various, often capsules, follicles, or schizocarps, with many- to 1-seeded locules. Seed [sometimes arillate or winged] with [or without] endosperm; embryo axial, straight or curved, the cotyledons plane or plicate and/or coiled around the radicle. Germination epigeous [or hypogeous]. (Including Byttneriaceae R. Br.). TYPE GENUS: *Sterculia* L.

An almost exclusively pantropical family of 65 or 70 genera (about 1000 species), with a few extensions into warm-temperate areas; six of 12 genera indigenous to tropical America restricted to that region; four genera (one naturalized) in our area; three additional genera extending northward from Mexico to Texas or California and Arizona.[2]

The family has usually been subdivided into eight to ten tribes. Evidence from wood and petiole anatomy favors the establishment of two subfamilies: Sterculioideae (including only Sterculieae) and Byttnerioideae (including the remaining tribes), with at least one tribe intermediate in petiolar anatomy. Floral anatomy emphasizes the great uniformity of the family in regard to the development and structure of the androecium. In contrast, "Pollen morphology is in favour of referring Erioleneae and Dombeyeae to Malvaceae, Fremontodendreae [Fremontieae] to Bombacaceae and parts of the rest of Sterculiaceae to Tiliaceae" (Erdtman, p. 421). Thus emended, the Sterculiaceae would be very homogeneous palynologically, but the limits between the families of the Malvalves would become even weaker and more uncertain than they are at present. It seems desirable, at least for the present, to treat the family within the generally accepted limits, with its subdivision into tribes.

Sterculiaceae are closely related to Tiliaceae, Malvaceae, and Bombacaceae. Evidence from floral anatomy and embryology suggests that the family is the most primitive in the Malvales. On the same basis the Sterculieae (with pentacyclic flowers, numerous stamens fertile in both series, apocarpous gynoecia, and many-ovulate locules) are regarded as the most primitive, and Hermannieae (with tetracyclic flowers, a reduced number of stamens and ovules, and a tendency to perigyny) the most advanced tribe of Sterculiaceae. In respect to perianth structure the Helictereae DC. (with irregular almost two-lipped flowers) and Byttnerieae DC. (with hooded and terminally or ± abaxially "appendaged" petals of complex structure) appear to be the most highly specialized tribes of Sterculiaceae.

Data on floral biology are few, but the family in general appears to be adapted to insect-pollination. Nectaries, when present, seem to be located

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[2] In addition, *Guazuma ulmifolia* Lam. (as *G. tomentosa* HBK.) has been recorded from one locality in Dade County, Florida (Moldenke). This record is in need of verification and insufficient as a basis for the inclusion of *Guazuma* Adans. in our flora.

at the base of the sepals (Brown) where they sometimes form an extrastaminal disc lining the calyx base and the receptacle around the ovary or the androgynophore. Foetid, indol- or scatol-scented flowers, usually dark purple or chocolate in color, are apparently pollinated by flies. Some of these flowers are of the "lantern type," with fly-traps for small flies. The nectariferous, irregular flowers of *Helicteres Isora* L. are supposedly pollinated by large Apidae or by small honey birds. In *Theobroma Cacao* L. pollination by thrips, ants, midges, and aphids has been recorded. Proterandry and the relative positions of the extrorse anthers and stigmata, characteristic of the family, seem to secure cross-pollination. Heterostyly is known in *Melochia* and *Waltheria* (*q. v.*). Cleistogamous flowers occur in a few species of *Ayenia* (Cristóbal). In *Theobroma Cacao*, individual trees are either self-incompatible, or cross-incompatible, or self-incompatible but cross-compatible only with the pollen of self-compatible trees (cf. Cope in Cuatrecasas).

The androecium in Sterculiaceae is basically obdiplostemonous. The traces for the antipetalous stamens, arising conjointly with those of the petals, divide first into three bundles each, a median and two laterals, which sometimes undergo a further secondary division (multiplication). Consequently, there are usually three (sometimes more or fewer) stamens opposite each petal (alternate with the sepals in apetalous flowers). The traces for the antisepalous stamens usually remain unbranched (single), sometimes becoming nonfunctional. Correspondingly, there characteristically are only five stamens (usually sterile), one opposite each sepal. All members of the androecium usually are connate into a staminal tube of various lengths. Thus, the androecium in Sterculiaceae seems to have evolved along the lines of cohesion and reduction (Rao, 1952).

The most significant embryological features of the family include the secretory type of anther tapetum; the multicellular archesporium of the ovule, with only one functional cell; Polygonum-type embryo sac; hooked synergids and usually ephemeral antipodals; nuclear endosperm becoming cellular at a late stage of seed development; and embryo development of the Urtica (exceptionally Polygonum) variation of the Asterad type. Polyembryony has been recorded in *Cola nitida*. Apotropous ovules occur at least in *Melochia* and *Waltheria*.

Chromosome counts recorded for about 20 genera (40 species) are $2n = 14, 16, 20, 24, 32, 36, 38, 40, 46$, ca. 50, and 120, suggesting that disploidy, polyploidy, and aneuploidy have been of importance in the evolution of Sterculiaceae. It is notable that chromosome numbers of 20 or 40 occur in 60 per cent of the genera investigated. The lowest number, $2n = 14$, has been found in *Melochia* and *Waltheria*.

Theobroma Cacao, native to tropical America and widely cultivated there and in the Tropics of the Old World, especially in West Africa, yields seeds which are the source of cocoa, chocolate, and cocoa butter. The seeds contain the alkaloid theobromine, as well as traces of caffeine. Species of the tropical African *Cola* Schott & Endl., mainly *C. nitida* (Vent.) Schott & Endl. and *C. acuminata* (Beauv.) Schott & Endl., furnish edible seeds, kola nuts, which contain caffeine and a heart-stimulating glucoside, kolanin, and which are used in medicine as a cerebral, cardiac, and nerve stimulant and in industry for beverage purposes. Some species of several genera yield bast fibers and/or lumber of local importance (e.g., *Guazuma*, *Sterculia* L., *Cola*). A few species of *Dombeya* Cav., *Fremontia* Torr. (*Fremontodendron* Cov.), *Brachychiton* Schott & Endl., *Sterculia*, and some other genera are grown as ornamentals in southern Florida.

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FAIRCHILD, D. Florida plant immigrants. A tree that is famous for its smell. Occ. Pap. Fairchild Trop. Gard. **12:** 4–6. 1943. [*Sterculia foetida* L., odor of flowers very offensive.]

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KEY TO THE GENERA OF STERCULIACEAE

General characters: *trees to herbs; hairs simple and/or stellate; leaves alternate, simple, petioled, stipulate; inflorescences cymose; flowers small, regular, hypogynous, bisexual or rarely unisexual; perianth 5-merous, sepals and petals distinct, the latter sometimes wanting; stamens 5 to many, monadelphous, the antisepalous 5 sterile or wanting, rarely fertile; gynoecium usually 5-carpellate, syncarpous, rarely apocarpous, or 1-carpellate, ovules 2 to many in a locule; fruit simple or rarely aggregate.*

A. Plants arborescent; leaves large, the blade commonly 15–20 cm. long and 20–30 cm. broad, usually deeply 3–5-lobed, long petioled; inflorescences ample thyrses 20–50 cm. long; flowers apetalous, unisexual; stamens (10–)15, on a conspicuous androgynophore; fruit of 5 stalked follicles 6–9 cm. long, leaflike after dehiscence, with 2 seeds on each margin. 1. *Firmiana.*

A. Plants herbaceous, suffruticose, or rarely fruticose; leaves not more than 8 cm. long usually unlobed; inflorescences small or flowers solitary; flowers petaliferous, bisexual; stamens 5; fruit simple, capsular.

   B. Flowers axillary, solitary or in fascicles of 2 or 3; petals long clawed, ± hooded, inflexed and attached by the tips to the apex of staminal tube, the corolla appearing parachute-like; androgynophore present; anthers 3-locular; capsule covered with short subcylindrical prickle-like protuberances; seeds coarsely reticulate. .... 2. *Ayenia.*

B. Flowers in dense headlike or umbel-like inflorescences; petals short clawed, adnate at base to the staminal tube, ± spreading; androgynophore wanting; anthers 2-locular; capsule and seed smooth.

  C. Corolla orange-yellow; gynoecium 1-carpellate, stigma brushlike, style 1, ovary 1-locular; capsule inclosed in persistent calyx, 1(2)-seeded, 2-valved. .... 4. *Waltheria.*

  C. Corolla pink to purple, or white, very rarely yellowish; gynoecium 5-carpellate, stigmata 5, subulate to subclavate, styles 5, connate at base to half their length, ovary 5-locular; capsule subtended by persistent calyx, 5–10-seeded, 5–10-valved. .... 3. *Melochia.*

Tribe STERCULIEAE

1. **Firmiana** Marsili, Saggi Sci. Lett. Accad. Padova 1: 106. 1786.

Deciduous trees [rarely shrubs], with minute stellate-tomentose pubescence. Leaves large, membranaceous, palmately 5–7-veined and -lobed, deeply cordate [or truncate to rounded] at base, long petioled; stipules caducous. Inflorescences large axillary and terminal thyrses; bracts caducous. Flowers regular, hypogynous, apetalous, unisexual by abortion (the plants monoecious), pedicels articulate in the upper half. Calyx with a short [rarely rather long], campanulate to urceolate tube with a dense transverse band of long hairs in the throat and a nectariferous disc around the androgynophore, the 5 lobes longer [or shorter] than the tube, somewhat fleshy, yellow-green [to yellow-orange, or white], reflexed. Stamens usually 15; anthers subsessile to sessile on margin of a ±campanulate to subcylindrical (in ♂) or saucer-like (in ♀ flowers) staminal tube at the apex of a conspicuous androgynophore, forming a globular clump concealing the pistillodium in ♂, and encircling the ovary base and indehiscent in ♀ flowers, 2-locular, the locules contiguous, often unequal; pollen medium sized, prolate-spheroid, 3-colpate, reticulate. Gynoecium nearly apocarpous, but appearing syncarpous, the densely pubescent, closely appressed carpels usually connate by the upper part of the styles; rudimentary in ♂ flowers; stigmata 5, subpeltate, spreading, closely appressed adaxially and appearing as a single 5-lobed stigma; styles 5, connate for a short distance near their apices; ovaries 5, each with 4 submarginal, sessile, anatropous, nearly horizontal ovules. Fruit of 5 stalked membranaceous follicles, each opening before maturity into a leaflike body exposing 2–4 seeds on its margins. Seeds subglobular; the outer seed coat brown, subcoriaceous, subreticulately wrinkled, the inner crustaceous; endosperm copious, firm, fleshy; embryo straight, axial; cotyledons thin, suborbicular, cordate at base; radicle short, stoutish, inferior. TYPE SPECIES: *Sterculia platanifolia* L. f. = *F. simplex* (L.) W. F. Wight. (Named in commemoration of Count K. J. von Firmian, 1716–1782, Austrian statesman, Governor of Lombardy under Maria Theresa.)

An Asiatic genus of about ten species, primarily tropical, ranging from the western Himalaya to eastern China, the Philippines, Malesia, and Papuasia. *Firmiana simplex* (*F. platanifolia* (L. f.) Schott & Endl.), Chinese parasol tree or phoenix tree, $2n = 40$, indigenous to subtropical and warm-temperate China (Yunnan to Kwantung, north to Shensi and Hopeh) is grown as an ornamental in our area and has become naturalized locally, mostly in the Coastal Plain, from northern Florida to North Carolina, southern Alabama, and Louisiana. It is a fast-growing tree with smooth gray-green bark, occurring on roadsides, in city lots, thickets, and mixed deciduous woods.

The inflorescences are either predominantly staminate or carpellate with a few flowers of the opposite type appearing by the end of blooming; both kinds of inflorescences occur on the same tree. Flowers intermediate between staminate and carpellate have also been observed occasionally. The staminate inflorescences seem to flower before the carpellate. Although insect-pollination may safely be assumed for the genus (presence of a nectariferous disc, petaloid sepals, etc.), no data on pollinators are available. Cross-pollination is favored by the unisexual flowers and the somewhat earlier expansion of the staminate ones, but some self-pollination is very probable. In both floral anatomy and embryology *Firmiana* seems to be very similar to *Sterculia* L. Chromosome counts for three species are $2n = 40$. The seeds, which remain firmly attached to the margins of the opened, leaflike, apparently deciduous follicles, are probably dispersed by wind.

The genus is closely related to *Scaphium* Schott & Endl. (follicles two-seeded), *Pterocymbium* R. Br. (follicles with a single basal seed), and *Sterculia* (follicles leathery to woody, seeds dropping off the carpels, radicle opposite the hilum).

The caffeine-containing seeds of *Firmiana simplex* are sometimes roasted and used to make a tea in China. The timber finds application in the paper industry, and the phloem fibers are utilized in making cordage.

REFERENCES:

Under family references see DUMONT (pp. 198–201, under *Sterculia*), GAZET DU CHATELIER (pp. 211–259), RADFORD *et al.* (p. 229), RAO (1954, as to *Sterculia colorata*), SAUNDERS (pp. 118, 119, under *Sterculia*), and SCHUMANN (1890, p. 97).

KOSTERMANS, A. J. G. H. A note on some African Sterculiaceae. Bull. Jard. Bot. Bruxelles **24**: 335–338. 1954. [*Erythropsis* Lindl. ex Schott & Endl. congeneric with *Firmiana*; some African spp. of *Sterculia* and *Firmiana* transferred to *Hildegardia* Schott & Endl.]

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YEN, T. K. Carpel dehiscence in *Firmiana simplex.* Bot. Gaz. **93**: 205–212. 1932.

Tribe BYTTNERIEAE DC.

2. **Ayenia** Linnaeus, Sv. Vet.-Akad. Handl. 17: *23. pl. 2.* 1756.

Usually decumbent [prostrate or erect] subshrubs [or deciduous shrubs, rarely small trees], ± pubescent with simple and/or stellate hairs [or glabrous]. Leaves small (to 1 × 0.7 cm.) [to rather large, 21 × 10 cm.], membranaceous [rarely coriaceous], 3–5-veined at base, toothed [or entire], petioled; stipules small, subulate, persistent at least in part [or caducous]. Flowers pediceled, axillary, solitary or in fascicles of 2 or 3 [to 12, or arranged in axillary or terminal, simple, peduncled, sometimes fascicled or panicled cymes], small 2–3[–7] mm. long, pink to red, bisexual [rarely unisexual, or sometimes cleistogamous]. Sepals 5, oblong-lanceolate, connate at base. Petals 5, slender clawed, ± rhombic (in ours), ± hooded in the upper part, cleft and 2-dentate [or entire] at apex, with [or without] a clavate [to linear] abaxial appendage below the cleft, inflexed toward center of flower and attached by means of teeth to apex of staminal tube, the whole corolla resembling a parachute with the style protruding through its center. Androgynophore usually conspicuous [rarely wanting]. Stamens 5, antipetalous, staminodia 5, antisepalous, all connate into a ± campanulate staminal tube; upper parts of filaments of fertile stamens distinct, reflexed; upper parts of staminodia distinct, ± triangular [sometimes hooded], recurved; anthers with 3 contiguous locules; pollen small to medium sized, oblate-spheroid, 3-aperturate, reticulate [rarely spinuliferous]. Gynoecium usually 5-carpellate, syncarpous; stigma subcapitate, 5-lobed; style single; ovary 5-locular, minutely tuberculate, with axile placentae; ovules 2, hemianatropous, somewhat curved toward the placenta, superposed in each locule, the lower one rudimentary (in ours). Fruit a small, subglobular, usually 5-locular capsule covered with short, subcylindrical [or wartlike to trigonous] protuberances, both septicidally and loculicidally dehiscent, 10-valved. Seed solitary in each locule, narrowly ovoid, slightly curved, abruptly narrowed into a subcylindric-conical beak at apex; seed coat crustaceous, dark brown, with a few broad longitudinal and transverse ribs forming a few-meshed reticulum [or corrugated to smooth], minutely black-verruculose; chalazal knot round, subbasal, close to hilum; endosperm wanting; embryo straight; cotyledons bisect [or bilobed?], plicate, spirally rolled around an elongated superior radicle. TYPE SPECIES: *A. pusilla* L. (Name commemorating Louis de Noailles, 1739–1777, Duc d'Ayen, later Maréchal de Noailles, promoter of sciences, amateur gardener, and owner of a famous garden in St. Germain; see Linnaeus, Schwed. Akad. Wiss. Abh. **18**: 25. 1757.)

A tropical American genus of about 70 species, extending north to California, Arizona, New Mexico, Texas, and Florida, and south to Argentina and Uruguay, centered in Mexico and northern Central America, with a secondary center in Bolivia, Paraguay, and central and eastern Brazil; one species of sect. AYENIA in our area.

Grisebach subdivided the genus into three sections differing mainly in the structure of the petals, the length of the distinct parts of filaments, the characters of the surface of fruits and seeds, and in the sculpture of the pollen. Cristóbal's species concept, although perhaps a little too narrow, is followed here.

The Cuban *Ayenia euphrasiifolia* Griseb. occurs in pinelands on the Florida Keys and in southernmost peninsular Florida (Dade and Monroe counties).[3] It is closely related to and perhaps not specifically distinct from the Cuban-Bahamian *A. tenuicaulis* Urb. Four Mexican species range into Texas, New Mexico, and Arizona, and one reaches California.

The pink to red, sometimes foetid flowers are pollinated by small insects. The petals perfectly separate the stigma from the anthers, preventing self-pollination. Unisexual flowers occur at least in the Brazilian *A. angustifolia* St. Hil. & Naud. Cleistogamous flowers with reduced petals and androgynophore and mostly introrse anthers have been recorded in four species (Cristóbal).

The comparative morphology and ontogeny of the cucullate petals in Byttnerieae (Schumann, Leinfellner) suggest that in *Ayenia* (§ *Ayenia*) the petal blade is reduced to a clavate [or linear] appendage, while the hooded rhombic portion of the petal ("face" or "mask") is homologous with the upper part of the claw.

Chromosome counts made for eleven species are $2n = 20$ and 40, the latter number occurring in three species. Fruits in *Ayenia*, which dehisce first septicidally and then loculicidally, as well as along the adaxial (ventral) suture, the valves detaching themselves from a persistent central column, may be regarded as a capsule type transitional to the schizocarp. There seem to be no special adaptations for seed dispersal, and seed dispersing agents are unknown.

The genus is closely related to the pantropical *Byttneria*, which differs mainly in petals with an evident apical portion (corresponding to the petal blade) not attached to the staminal tube.

REFERENCES:

Under family references see DUMONT (p. 217), GRISEBACH (pp. 91, 92), LAKELA & CRAIGHEAD (p. 61), LEINFELLNER (pp. 158–162), and SCHUMANN (1886a, pp. 101–108, *pls. 23, 24*; 1886b, pp. 294–297; 1890, pp. 83–85).

CRISTÓBAL, C. L. Revisión del género *Ayenia* L. (Sterculiaceae). (English summary.) Op. Lilloana 4: 1–230. 1960.

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[3] No other species seems to occur in Florida. Small's record of *A. pusilla* from that area (Man. SE. Fl. 863. 1933) apparently was based either on misidentifications or on a very broad interpretation of that species, which has been recorded only from Ecuador and northern Peru (Cristóbal, p. 191). All specimens from Florida labeled as *A. pusilla* were annotated by Cristóbal as *A. euphrasiifolia.*

———. Nueva contribución al estudio del género *Ayenia* L. (Sterculiaceae). Anales Instituto Biol. México **32:** 191–200. 1961. [One new Mexican sp. and several new records from Mexico, Central America, and Colombia; first record of cleistogamous flowers in *A. fruticosa* Brandegee.]

———. Notas sobre el género *Ayenia*. Lilloa **31:** 207–212. 1962. [A new sp. from Colombia described; 1 sp. from Cuba redescribed and illustrated.]

Tribe HERMANNIEAE Schott & Endl. emend. Benth.

3. **Melochia** Linnaeus, Sp. Pl. 2: 774. 1753; Gen. Pl. ed. 5. 304. 1754.

Herbs to shrubs [or rarely trees]; pubescence of simple and/or stellate hairs. Leaves narrow to broad, palmately 3–5-veined at base, serrate, petioled; stipules small, persistent at least in part. Inflorescences few-flowered umbel-like peduncled cymes or many-flowered dense headlike thyrses composed of 2- or 3-flowered dichasia or monochasia, or thyrses sometimes secondarily arranged into interrupted spikelike panicles, axillary and/or terminal (rarely opposite the leaves); bracts persistent or caducous. Flowers small, bisexual, heterostylous, often with an involucel of 3 or 4 distinct bract(let)s at base, pediceled or sessile. Calyx ± campanulate, 5-dentate to -cleft, persistent, nectariferous at base. Petals 5, pink to purple, usually yellow or white at base, or white, or rarely yellowish, spatulate to oblong, clawed, adnate at base or higher up to staminal tube, longer than the sepals, marcescent. Stamens 5, antipetalous, the staminal tube cylindrical, inflated after fertilization; free part of filaments elongated in short-styled, very short in long-styled flowers; 5 obsolete, toothlike staminodia sometimes present in short-styled flowers; anthers 2-locular, the locules contiguous before and ± divaricate after fertilization; pollen medium sized, spheroid to oblate-spheroid, 3-colpate, finely reticulate. Gynoecium 5-carpellate, syncarpous; stigmata 5, subulate or filiform to ± clavate, papillose, or shortly and racemosely branched; styles 5, distinct or connate to half their length; ovary sessile to short stipitate, 5-locular, the placentation axile; ovules 2 in each locule, superposed, ascendent, anatropous, apotropous. Fruit a 5-locular, loculicidal and/or septicidal capsule [rarely a schizocarp], the locules 1- or 2-seeded. Seed obovoid, nearly round in cross-section or ± angular on adaxial (ventral) surface, with a prominent humplike chalazal knot and thin threadlike raphe; outer seed coat thin, membranaceous, usually obliterated, the inner crustaceous; endosperm fleshy; embryo straight, spatulate, cotyledons large, foliaceous; radicle short, inferior. LECTOTYPE SPECIES: *M. corchorifolia* L.; see Medicus, Künstl. Geschl. Malven-Fam. 10. 1787, and Britton & Millspaugh, Bahama Fl. 277. 1920.[4] (Name from *melokhiya* or *melukhiye*, an Arabic

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[4] Hitchcock & Green (Int. Bot. Congr. Cambridge 1930. Nomencl. Propos. Brit. Bot. 172. 1929) proposed *Melochia pyramidata* L. as the lectotype species, reasoning that it was "the only one of the original species included in Section *Eu-Melochia* Griseb. by K. Schumann." They overlooked, however, a few earlier circumstances.

In his *Genera Plantarum* (ed. 5. 1754, p. 304) Linnaeus attributed *Melochia* to Dillenius, referring to *plate 176* of *Hortus Elthamensis* on which Dillenius's *Melochia corchori folio* (*M. corchorifolia* L.) was figured. Thus Linnaeus himself seems to name for *Corchorus olitorius* L., widely cultivated as a potherb in the eastern Mediterranean, particularly in Egypt, since ancient times.)

A pantropical, predominantly American genus of about 60 species, with one extending into warm-temperate regions; four species (one naturalized) in our area.

The three predominantly American sections of the genus established by Grisebach are delimitable by the shape and/or the kind of dehiscence of fruits and sometimes by the type of inflorescence and presence or absence of a floral involucel. The fourth, the Indo-Malayan-Pacific sect. VISENIA (Houtt.) Benth. & Hook. differs in the arborescent habit and usually apically winged seeds of its species.

Section MELOCHIA (§ *Riedlea* (Vent.) Griseb.; *Riedlea* Vent.). Capsules sessile, subglobular, slightly 5-lobed, the lobes rounded; inflorescences dense, many-flowered, peduncled to sessile headlike thyrses; flowers sessile, with an involucel. About 30 (or more) species, centered in tropical America, a few in the Old World, two endemic on Madagascar; *M. melissifolia* Benth. in America and Africa.

The paleotropical *Melochia corchorifolia*, chocolate weed, with pedunculate, usually terminal inflorescences and long-petioled leaves glabrous or with scattered hairs on the veins beneath, has become naturalized in old, especially sandy, fields, cultivated grounds, and waste places in the Coastal Plain, from southern peninsular Florida north to southeastern North Carolina and west to southeastern Texas. In the New World it is also recorded from Panama, suggesting that it may become a pantropical weed. *Melochia villosa* (Mill.) Fawc. & Rendle (*M. hirsuta* Cav., *Riedlea hirsuta* (Cav.) DC.), with sessile axillary and terminal inflorescences forming interrupted spikelike thyrses and short-petioled leaves silky-pubescent or glabrescent beneath, is widely distributed in tropical America. It reaches southern Florida, where it occurs on moist sands in marshy lands, flatwoods, and pinelands. In the Old World this species has become naturalized at least on Madagascar.

Section MOLUCHIA (Medic.) Brizicky (§ *Eumelochia* Griseb.; *Moluchia* Medic.). Capsules ± stipitate, pyramidal, deeply 5-lobed, the lobes wing-

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have indicated the type of this genus, and the generic description does not contradict this assumption. In 1787, Medicus, considering *M. corchorifolia* to be the typical species of *Melochia* established the segregate genus *Moluchia*, clearly based on *Melochia pyramidata*, and thus effectively typified *Melochia*. In choosing *M. corchorifolia* as the lectotype species, Britton and Millspaugh formally accomplished the typification of the genus, which had already been indicated by Linnaeus and effected by Medicus.

With this typification the following nomenclatural changes in two of three sections recognized by Grisebach are necessary:

Melochia sect. **Melochia** (*Melochia* sect. *Riedlea* (Vent.) Griseb. Fl. Brit. W. Indian Is. 93. 1859.) TYPE SPECIES: *M. corchorifolia* L.

Melochia sect. **Moluchia** (Medic.) Brizicky, stat. nov. (*Melochia* sect. *Eumelochia* Griseb. Fl. Brit. W. Indian Is. 93. 1859. *Moluchia* Medic. Künstl. Geschl. Malven-Fam. 10. 1787.) TYPE SPECIES: *M. pyramidata* L. (*Moluchia herbacea* Medic., nom. superfl.).

like; inflorescences 3–10-flowered umbel-like peduncled [sometimes panicled] cymes; flowers pediceled, without an involucel. About nine species, eight American, one endemic on Madagascar.

Melochia tomentosa L. (*Moluchia tomentosa* (L.) Britt.), with axillary cymes and tomentose leaves and capsules, occurs in pinelands in southernmost Florida (Dade County) and ranges widely in tropical America. *Melochia pyramidata* L., with inflorescences opposite the glabrous leaves and capsules with scattered minute stellate hairs, has also been reported from Dade County, Florida (Lakela & Craighead). Widely distributed in tropical America (north to Mexico and Texas), it has been introduced into the Old World, where it seems to have become a pantropical weed. In Texas the flowers of this species open at noon and close in late afternoon [from a collector's field note].

The nectaries and the bright-colored petals indicate insect-pollination, but pollinators have not been observed. Heterostyly seems to be common within the genus. Floral anatomy and embryology have been investigated only in *M. corchorifolia*. The single chromosome count recorded is $2n = 14$ (in *M. bracteosa* F. Hoffm. = *M. melissifolia* Benth. var. *bracteosa* (F. Hoffm.) K. Schum., from West Africa). Although fruits in *Melochia* mostly are septicidal and/or loculicidal capsules, types intermediate to schizocarps ("pentacoccous capsules") also occur (sect. MOUGEOTIA (HBK.) Griseb.). Seed-dispersal agents are unknown, except in the species of sect. VISENIA, the usually winged seeds of which are said to be dispersed both by wind and ocean currents. The very wide distribution of *M. pyramidata* and *M. corchorifolia* is due mainly to human agency.

Melochia is closely related to *Waltheria* L. The genus is in need of a modern revision.

REFERENCES:

Under family references see GERMAIN (pp. 255–258), GRAY (pp. 85, 86, *pl. 134*), GRISEBACH (pp. 93, 94), LAKELA & CRAIGHEAD (p. 61), RADFORD *et al.* (p. 230), RAO (1950a; 1951; 1952, p. 179), ROBYNS (pp. 77–85), and SCHUMANN (1886a, pp. 27–49, *pls. 7–10*; 1890, pp. 80, 81).

GARCKE, A. Über einige Arten von *Melochia*. Bot. Jahrb. **12**(Beibl. 27): 29–32. 1890.

JONES, S. B., JR. Additional Alabama weeds. Castanea **26**: 136–138. 1961. ["Currently it (*M. corchorifolia*) is one of the most troublesome weeds in cultivated fields in Mobile and Baldwin counties, but was not observed north of those counties."]

MEDICUS, F. K. Ueber einige künstliche Geschlechter aus der Malven-Familie, denn der Klasse der Monadelphien. 158 pp. Mannheim. 1787. [*Moluchia* Medic., 10–12.]

4. **Waltheria** Linnaeus, Sp. Pl. **2**: 673. 1753; Gen. Pl. ed. 5. 304. 1754.

Herbs or subshrubs [or shrubs], erect, single stemmed or much branched from the base, rarely diffuse and prostrate; pubescence mainly of stellate hairs. Leaves usually oblong to ovate, 3–5-veined at base, toothed, petioled; stipules small, lanceolate-subulate, caducous. Inflorescences axillary and terminal, peduncled to sessile, dense headlike compound cymes (or thyrses?) composed of 2- or 3-flowered sessile or subsessile dichasia or monochasia, sometimes forming short-branched or spikelike thyrses. Flowers small, bisexual, homostylous [or often heterostylous], sessile, with 1 or more bractlets at base. Calyx persistent, the tube campanulate-turbinate, slightly 5-angled, 10-veined, nectariferous at base, equaling or exceeding the 5 lanceolate-subulate lobes. Petals usually orange-yellow, spatulate, clawed, adnate at base to the staminal tube, longer than the sepals, marcescent. Stamens 5, connate into a tubular staminal tube equaling [or shorter than] the pistil; free upper parts of filaments very short [or elongated]; anthers 2-locular, the locules contiguous; pollen medium sized, usually oblate-spheroid, (3)4(–8)-colpate, reticulate. Gynoecium 1-carpellate; stigma brushlike [or clavate?]; style single, solid, excentric (sublateral); ovary sessile, 1-locular, subtruncate and hairy at apex; ovules 2, submarginal, superposed, ascendent, anatropous, apotropous. Capsule obliquely obovoid, hairy at apex, 1(2)-seeded, 2-valved. Seed obliquely obovoid, slightly compressed laterally, with a shallow adaxial raphe-bearing groove, dark brown to black except the rusty-colored round or elliptic chalazal knot; endosperm fleshy; embryo straight; cotyledons large, foliaceous; radicle short, inferior. LECTOTYPE SPECIES: *W. indica* L. (*W. americana* L.); see R. Brown in Tuckey, Narr. Exped. Congo 484. 1818.[5] (Name commemorating Augustin Friedrich Walther, 1688–1746, professor of botany in Leipzig; see Linnaeus, Crit. Bot. 95. 1735.)

An almost exclusively tropical American genus of about 30 (or fewer) species, one pantropical and two African (one endemic on Madagascar); one species in our area.

The polymorphic, pantropical *Waltheria indica* (*W. americana* of almost all American authors), a usually ± canescent herb or subshrub, occurs in hammocks, pinelands, and on sand dunes on the Florida Keys and in southern peninsular Florida, north to Highlands and Lee counties. It was recorded as adventive on the coast of Alabama (Small, Man. SE. Fl. 863. 1933) but does not seem to occur there at present.

Heterostyly is fairly frequent within the genus. Pollination by wasps and bees has been recorded for *W. indica* and *W. viscosissima* St. Hil. in Brazil. The floral anatomy and embryology of *W. indica* appear to be very similar to those of *Melochia corchorifolia*, but embryo development conforms to the Polygonum variation of the Asterad type (in contrast with the Urtica variation in *Melochia* and other genera of Sterculiaceae thus far investigated).[6] The single recorded chromosome count is $2n = 14$. Seed

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[5] "Robert Brown (in Tuckey, Narr. Exp. Congo 484. 1818) appears to have been the first to unite *Waltheria americana* L. (Sp. Pl. 673. 1753) and *W. indica* L. (Sp. Pl. 673. 1753). He adopted the name *Waltheria indica* for the combined species, and this name must accordingly be retained" (Art. 57, Int. Code Bot. Nomencl. 47. 1961).

[6] The following comment by Rao (1950b, p. 175) is enigmatic: "Embryological evidence supports the retention of the genus *Waltheria* in Sterculiaceae as indicated by Hutchinson and is against its transfer to Bombacaceae as suggested by Engler and Prantl." In the references to Rao's article "Engler, A. and Prantl, K. (1928). — Natürliche Pflanzenfamilien. 2. Auflage" is cited. This incomplete and apparently erroneous

dispersal by wild goats and perhaps by some granivorous birds (e.g., doves) has been recorded for *W. indica.*

The genus is closely related to *Melochia.* A modern revision is desirable.

REFERENCES:

Under family references see GERMAIN (pp. 258, 259), RAO (1950a & b; 1952, p. 179), ROBYNS (pp. 74–77), and SCHUMANN (1886a, pp. 50–68. *pls. 11–14*; 1890, p. 81).

DIERS, L. Der Anteil an Polyploiden in den Vegetationsgürteln der Westkordillere Perus. Zeitschr. Bot. **49**: 437–488. 1961. [$2n = 14$ in *W. ovata* Cav., 450.]

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reference provides no clue to Rao's statement. The order Malvales (or Columniferae) has not appeared in the second edition of the *Natürlichen Pflanzenfamilien*, and the only volumes of this series published in 1928 are Bd. 2 and Bd. 5, with treatments of Algae and Fungi respectively.

IDENTIFICATION OF THE SPECIES AND HYBRIDS IN THE LONICERA TATARICA COMPLEX

P. S. Green

The need to verify the identity of the numerous plants of *Lonicera* growing in the Arnold Arboretum became an urgent matter with the start of a karyological survey of the genus which is at present being undertaken by Mrs. Lily Rüdenberg. Alfred Rehder, whose revision of the genus, published in 1903 (Annual Rep. Missouri Bot. Gard. **14**: 27–232), is still the latest comprehensive account, identified the older plants in the collection but, as might be expected, there have been many new accessions. The determination of most species presents no difficulties, but under cultivation hybridization has become intensive in the group around *L. tatarica*. Keys already exist for the identification of species but not for these very confusing hybrids. Furthermore, some of the bush honeysuckles most highly prized in horticulture belong to this difficult group, so it was decided, after having studied them for some time, that an attempt should be made to construct a key and provide aids to their identification.

Spontaneous wild hybrids are not common in *Lonicera* but, under cultivation, whenever *L. tatarica, L. morrowii*, and *L. ruprechtiana* grow together it is probable that much of the seed set is of hybrid origin. Introgressive hybridization and the resultant hybrid swarms are well known in the wild but *Lonicera* provides a good example among cultivated plants. The first records of hybrids occur towards the end of the last century, when Zabel, in particular, was cultivating and studying the genus. Apparently the hybrids arose spontaneously and without artificial aid, and their hybrid nature was perceived through their intermediate characters. At first they were propagated vegetatively but later plants were grown from seed collected from these hybrids and, where either or both parental species were growing nearby, it is clear that back-crossing had often taken place. The result today is that collections of shrubby honeysuckles in cultivation invariably include some hybrid plants which to varying degrees resemble one parent more than the other. Furthermore, triple hybrids occur as well, for the hybrids themselves are interfertile with the other species in the group.

Figure 1 portrays, diagrammatically, the main complex with which *Lonicera tatarica* is involved. As will be seen, three other species are included and four interspecific hybrids. Of these latter, three have further crossed with other species and it is quite probable that if an attempt were made it might prove possible to create every conceivable cross involving these species.

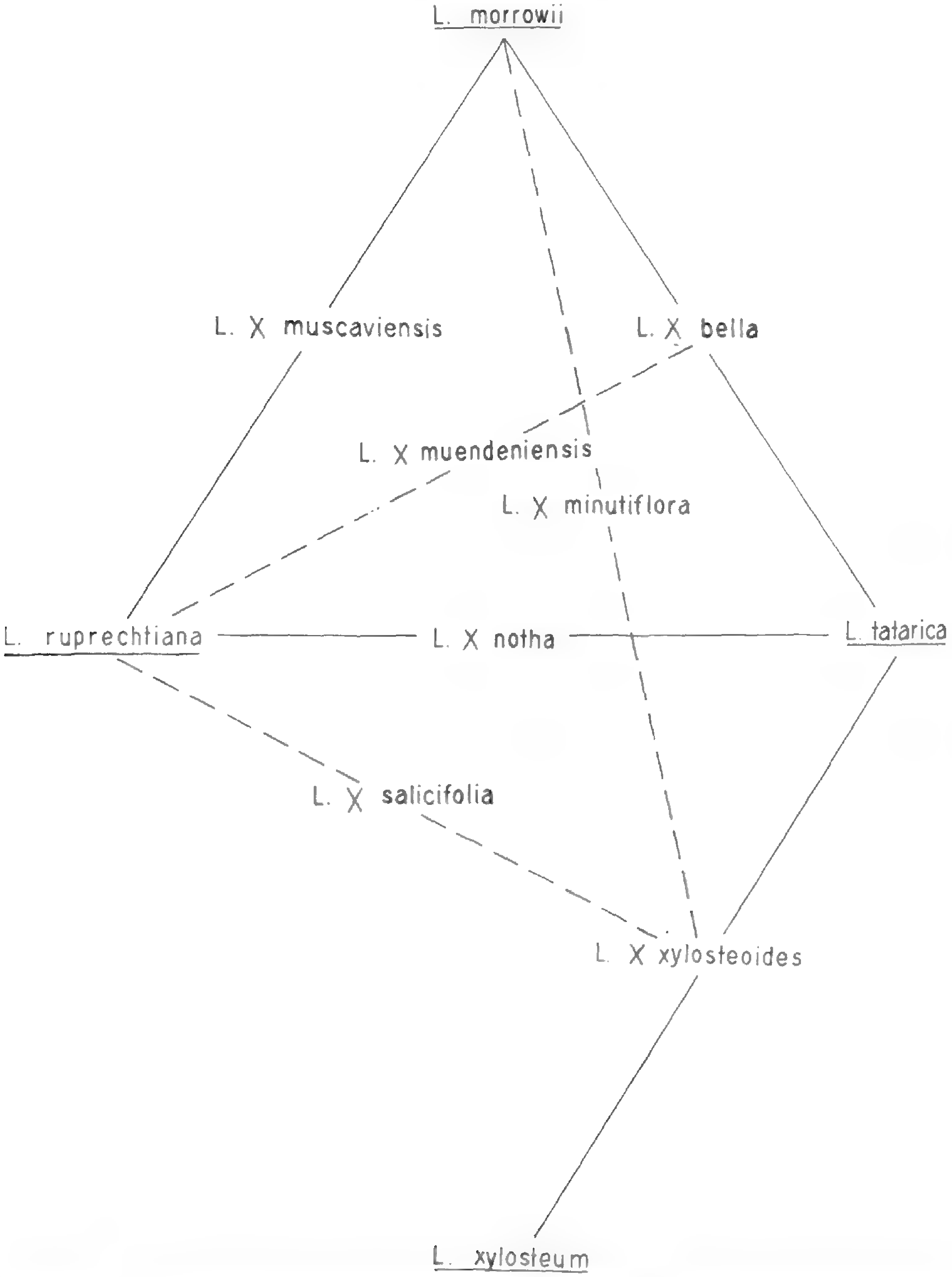

FIG. 1. Diagram representing the main complex of hybrids involved with *Lonicera tatarica.*

Lonicera tatarica also hybridizes with *L. korolkowii*, the resultant hybrid being called *L.* × *amoena.* In FIGURE 3 typical leaf outlines and ovary types for these two species and their hybrid are illustrated.

Hybridization has also been reported between *Lonicera tatarica* and *L. nigra.* Zabel (Gartenflora **38**: 524. 1889) incorrectly referred the plant to

L. micrantha, but no recent material of it has been seen in this investigation and it is doubtful whether it is still in cultivation. For these reasons it is not included either in the illustrations or the key.

In the identification of these plants the characters of the leaves, and of the ovary with its bracts and bracteoles have proved of particular help with both living and dried material. For this reason they are illustrated in FIGURES 2 and 4 respectively. The arrangement of FIGURE 2 is the same as that of FIGURE 1 in order to illustrate most readily the interrelationship of the hybrids and double hybrids. It proved impracticable, however, to arrange the drawings of ovary types in the same manner, instead, they are set out in simple alphabetical order. Other characters of value not portrayed in all the figures are the degree of hairiness or glaucousness of the leaf and, in fresh flowering material, where it may be easily observed, the extent to which the corolla lobes are reflexed or recurved and the position, in the fully open flower, in which they are displayed in relation one to another. For some of the species this is also shown in FIGURES 5, 6, and 7 by means of close-up photographs of living flowers.

Rehder, in his revision, classified *Lonicera tatarica* and *L. korolkowii* in a separate subsection from the other species involved in this complex of hybrids, but in view of the ease with which fertile hybrids are produced between the species separated by this classification it is very doubtful whether subsectional recognition is justified. The main distinction used was whether or not the flowers turned yellow on fading, and certainly those of *L. tatarica* and *L. korolkowii* do not appear to turn yellow or orange-yellow as is strongly characteristic of the other species and of their hybrids. Where fresh material is available for observation this yellowing of the corolla seems to be a useful character and appears in *L. tatarica* backcrosses, even when the hybrid nature of the plant is otherwise barely perceptible.

It is not always easy to tell just how much backcrossing has taken place, for the parental species are themselves very variable. *Lonicera tatarica*, for instance, has many variants, coming as it does from a wide geographical area. Nor have many of the cultivated plants of this species or its hybrids been considered distinct and distinguished enough to be named as cultivars, the same hybrid name is applied, therefore, to any plants which involve the same two parental species, whether or not backcrossing has taken place.

In the key that follows it is hoped that plants of hybrid origin will key out under the appropriate name without any difficulty. However, as many of the plants in cultivation arose from seed collected in botanic gardens, nurseries, etc., where more than one species are often grown together, it should be realized that a high proportion may be crosses or backcrosses. For this reason the key should be used in close association with the figures. Furthermore, it should be borne in mind that species like *Lonicera tatarica* exhibit considerable variation even without hybridization. Fortunately perhaps, the species show less variation in cultivation, due to their relatively few introductions, than they do throughout their total distributional range

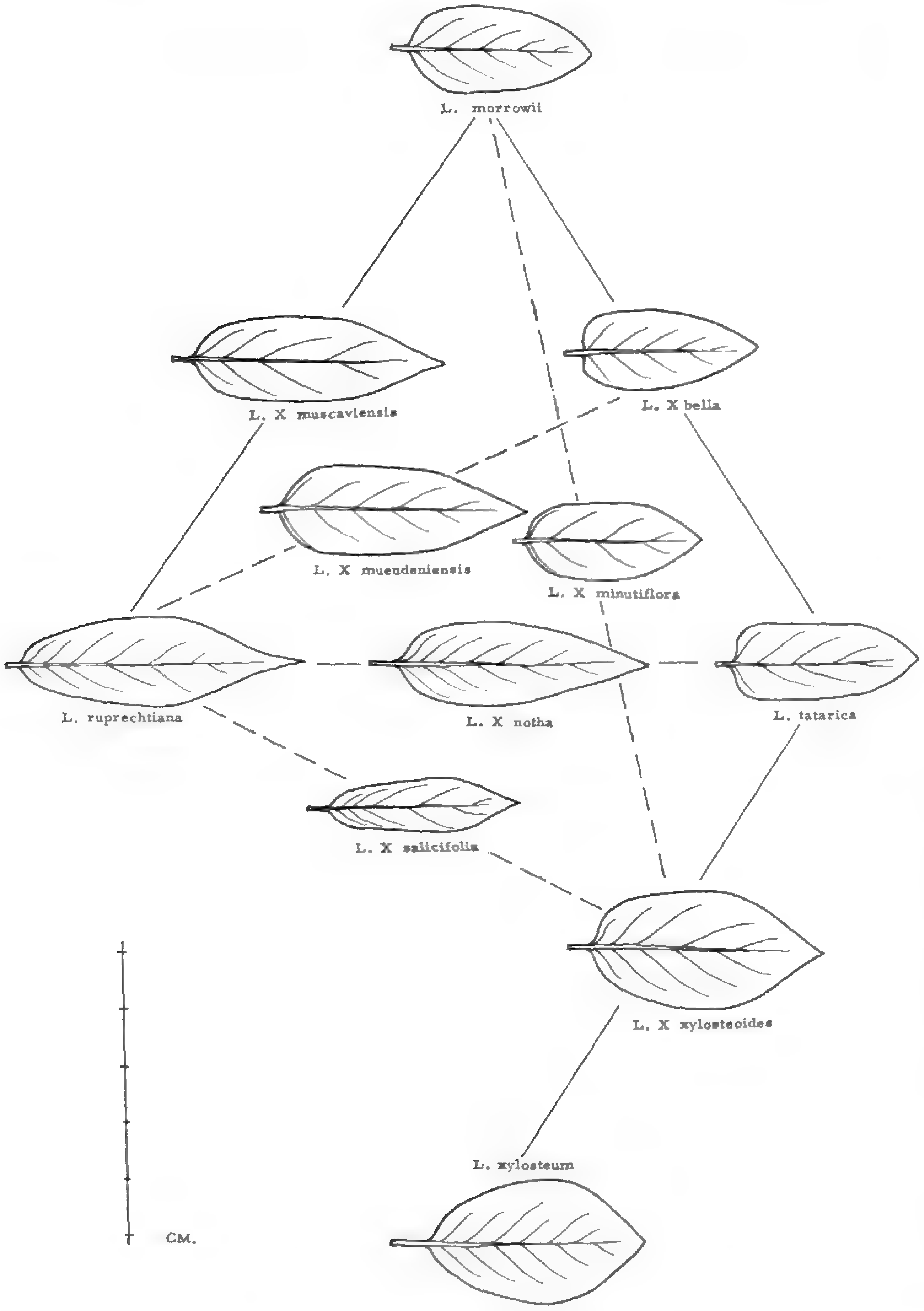

FIG. 2. Leaf-outlines of species and hybrids of *Lonicera* arranged to be comparable with FIGURE 1.

in the wild, but it is important to realize that the leaf shapes and ovary types portrayed in the figures were selected as being "average" for the species and, it is hoped, typical of the taxa as best known in cultivation or, in the case of hybrids, of plants of the first generation.

KEY TO LONICERA TATARICA, ITS ALLIES AND HYBRIDS IN CULTIVATION

1. Leaves usually broadest at or below the middle.

2. Plant glabrous throughout (rarely a few hairs on the petioles), occasionally a few glands on the calyx lobes and bractlets. . . . . *L. tatarica.*

2. Plant ± hairy, especially the leaves, pedicels, and bracts.

3. Bracts usually shorter than the ovary, occasional bracts slightly longer (in *L.* × *amoena* sometimes all longer); leaves elliptic or ovate; whole plant ± glaucous.

4. Back of bracts and calyx lobes hairy. . . . . *L. korolkowii.*

4. Back of bracts and calyx lobes glabrous (only ciliate). . . . . *L.* × *amoena.*

3. Bracts as long as, or longer than the ovary, rarely occasional ones shorter; leaves lanceolate, oblanceolate or obovate (or even ovate in *L.* × *bella* and occasionally in *L.* × *morrowii*).

5. Corolla (from base of tube to tip of upper lobe) usually not more than 11 mm. long, rarely up to 12 mm.

6. Length of corolla tube 2.5–4 mm.

7. Corolla from base of tube to tip of upper lobes 10–13 mm. long; ± floriferous. . . . . *L. ruprechtiana.*

7. Corolla from base of tube to tip of upper lip 7–9 mm. long; most flowers abortive. . . . . *L.* × *salicifolia.*

6. Length of corolla tube 4–5 mm.

8. Bractlets 3/4 to equal the length of the ovary (not including the calyx lobes). . . . . *L.* × *minutiflora.*

8. Bractlets up to 1/2 length of the ovary, rarely 2/3 as long. . . . . *L.* × *muendeniensis.*

5. Corolla (from base of tube to tip of upper lobe) 12 mm. long or more.

9. Bractlets between 3/4 and the full length of the ovary, rarely 1/2 its length (not including the calyx teeth).

10. Calyx, bractlets, and bracts glandular and hairy.

11. Bracts only sparsely hairy and glandular; margins of bractlets sparsely hairy and glandular. . . . . *L.* × *minutiflora.*

11. Bracts ± densely hairy (and glandular); margins of bractlets usually with numerous longish hairs (and glands). *L.* × *muscaviensis.*

10. Calyx, bractlets, and bracts hairy but without glands. . . . . *L. morrowii.*

9. Bractlets usually not more than 1/2 the length of ovary, occasionally up to 2/3 its length.

12. Corolla tube about 3 mm. long, not more than 4 mm., glabrous. . . . . *L.* × *notha.*

12. Corolla tube 4–6 mm. long, usually with at least a few scattered hairs.

13. Leaf apex somewhat acuminate or, at least, acute; corolla, from base of tube to tip of upper lobes, 9–12 mm. long. . . . . *L.* × *muendeniensis.*

13. Leaf apex usually somewhat obtuse, or sometimes

acute; corolla, from base of tube to tip of upper lobes, 14–18 mm. long. .... *L.* × *bella.*

1. Leaves usually broadest above the middle, tip often ± acuminate.
  14. Length of leaf not more than twice the breadth.
    15. Bractlets and calyx lobes usually hairy on the back (rarely only a very few hairs). .... *L. xylosteum.*
    15. Bractlets and calyx lobes ciliate and glandular. *L.* × *xylosteoides.*
  14. Length of leaf usually more than twice the breadth.
    16. Corolla tube up to 4 mm. long.
      17. Bracts with numerous short hairs (also glands); corolla tube 2–3 mm. long; leaf apex distinctly acuminate. *L. ruprechtiana.*
      17. Bracts without or with few scattered short hairs, only glandular; corolla tube 3–4 mm. long; leaf apex acute or subacuminate.
        18. Flowers very small, 7–9 mm. long, usually most flowers abortive. .... *L.* × *salicifolia.*
        18. Flowers larger, 12–16 mm. long, usually floriferous. .... *L.* × *notha.*
    16. Corolla tube 4–5 mm. long.
      19. Bractlets 3/4 the length of the ovary (not including the calyx lobes) or more; corolla 12–14 mm. long. *L.* × *muscaviensis.*
      19. Bractlets 1/3 to 1/2 the length of the ovary; corolla 9–12 mm. long. .... *L.* × *muendeniensis.*

NOTES ON THE SPECIES AND HYBRIDS

Lonicera × amoena Zabel, Mitt. Deutsch. Dendr. Ges. **1901**: 96. 1901 (*L. korolkowii* × *tatarica*).

This is a very graceful shrub up to eight feet or more high and noted for its slender growth, abundance of blossom, and the bluish-green or glaucous color of its foliage. Zabel (*l.c.*) divided the hybrid into two forms, f. *alba* and f. *rosea,* based mainly on the possession of white and rose-colored flowers respectively, but such a division is an over simplification for individual plants differ in the amount of color in their flowers.

Another plant, var. *arnoldiana* Rehd. (Mitt. Deutsch. Dendr. Ges. **1908**: 163. 1908), has a particularly delicate growth habit, with narrower leaves and somewhat larger flowers, which start as pale pink and fade until they are almost white. This plant arose from seed collected in 1899 from a plant of *Lonicera korolkowii* growing in the Arnold Arboretum.

Lonicera × bella Zabel, Gartenflora **38**: 525. 1889 (*L. morrowii* × *tatarica*).

Apparently first raised from seed collected from *Lonicera morrowii* and distributed by the botanic garden at Leningrad (when it was called St. Petersburg). This is one of the hybrids which can readily arise when the two parent species are grown together. Similar in many ways to *L. tatarica,* the flowers are not so attractive as those of some forms of that species. They are not quite as large and, in fading, turn quite rapidly to a dull

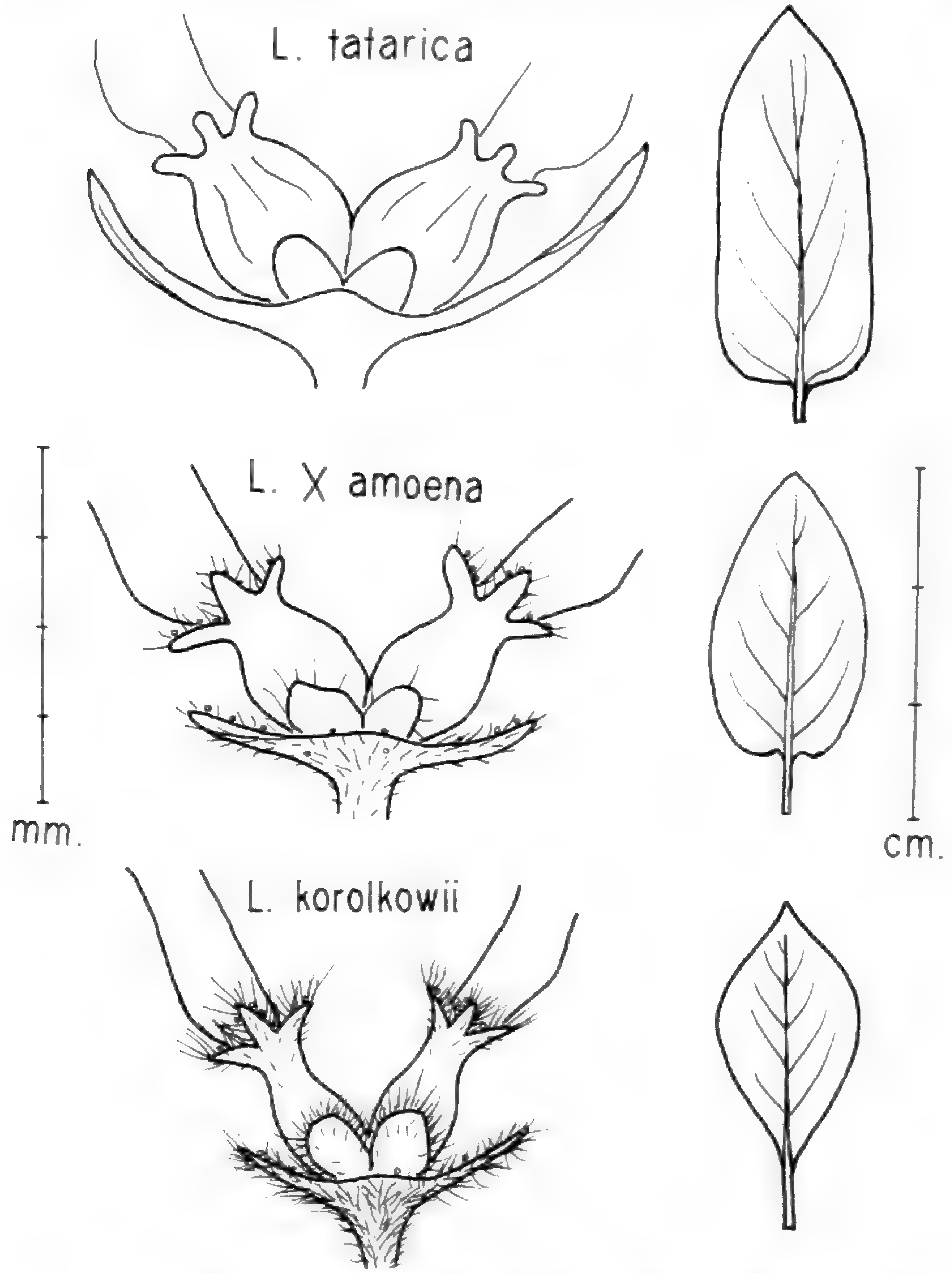

FIG. 3. Sketches of ovaries and leaf-outlines of *Lonicera tatarica*, *L. korolkowii*, and their hybrid, *L.* × *amoena*.

yellowish color, a character inherited from the other parent, *L. morrowii*, and one which tends to spoil the effect of the pink or white flowers still in bud or opening.

However, *Lonicera* × *bella* shows considerable hybrid vigor and, as might be expected, when one of the parents, *L. tatarica*, has so many color variants, the hybrid is variable too. Variants have been described, first as varieties by Zabel (Gartenflora **38**: 525. 1889) and then as forms by Rehder (Annual Rep. Missouri Bot. Gard. **14**: 206. 1903) with pure white flowers (f. *candida*), white with a tinge of pink in the bud (f. *albida*), light flesh-colored with a darker middle stripe (f. *incarnata*), rose-pink, usually clearly bordered (f. *rosea*) and dark rose, also distinctly margined (f. *atro-rosea*). The cultivar 'Dropmore' belongs to this hybrid. A very hardy plant, it was raised at the Skinner Nurseries at Dropmore, Manitoba, and on careful examination shows traces of a possible backcross to *L. tatarica*.

Lonicera korolkowii Stapf, Garden & Forest, 7: 34, *fig. 4.* 1894.

A handsome species, native to Turkestan, which was at first mistakenly named *Lonicera floribunda* by Zabel (Gartenflora **38**: 525. 1889) but despite the fact that the name was particularly appropriate for this plant because of its floriferous habit, it was a misidentification for another, unrelated honeysuckle from Persia, named almost thirty years previously. *L. korolkowii* is an attractive species, notable for its bluish-green foliage and graceful twiggy habit, two characters it has passed on to the hybrid *L.* × *amoena*.

Three varieties are known in cultivation: var. *aurora* Koehne (Repert. Sp. Nov. **8**: 31. 1910), var. *floribunda* Nicholson (Ill. Dict. Gard. Suppl. 503. 1901) and var. *zabelii* (Rehd.) Rehd. (Annual Rep. Missouri Bot. Gard. **14**: 131. 1903), varieties differing mainly in their leaf shapes and the intensity of the pink coloration in their flowers.

Lonicera × **minutiflora** Zabel, Gartenflora **38**: 523. 1889 (*L. morrowii* × *L.* × *xylosteoides*).

This shrub is grown for its botanical interest rather than its horticultural value, for, as its name suggests, the flowers are smaller than those of the parental species, all of which are superior to this triple hybrid. It apparently originated from seed collected on a plant of *Lonicera morrowii* in the botanic garden at Münden in Germany.

Lonicera morrowii A. Gray in Perry, Narr. Exp. Chin. Jap. **2**: 313. 1857.

A distinctive species, native of Japan, which may grow to about 7 or 8 feet but does not reach this height as quickly as the other species in the complex. It tends to have a more wide-spreading habit and, in a fully grown bush, presents a more or less rounded outline of dense twigs. Its leaves are distinctive too, being softly pubescent, especially below. The flowers, which have a deeply divided corolla (FIG. 5), are white when they first open but turn yellowish on fading. Like several of these species it is most attractive in fruit, producing large, deep red and juicy berries which are highly attractive to birds, who have been responsible for the fact that *Lonicera morrowii* is now dispersed and naturalized in numerous places throughout the eastern United States. In addition there is a f. *xantho-*

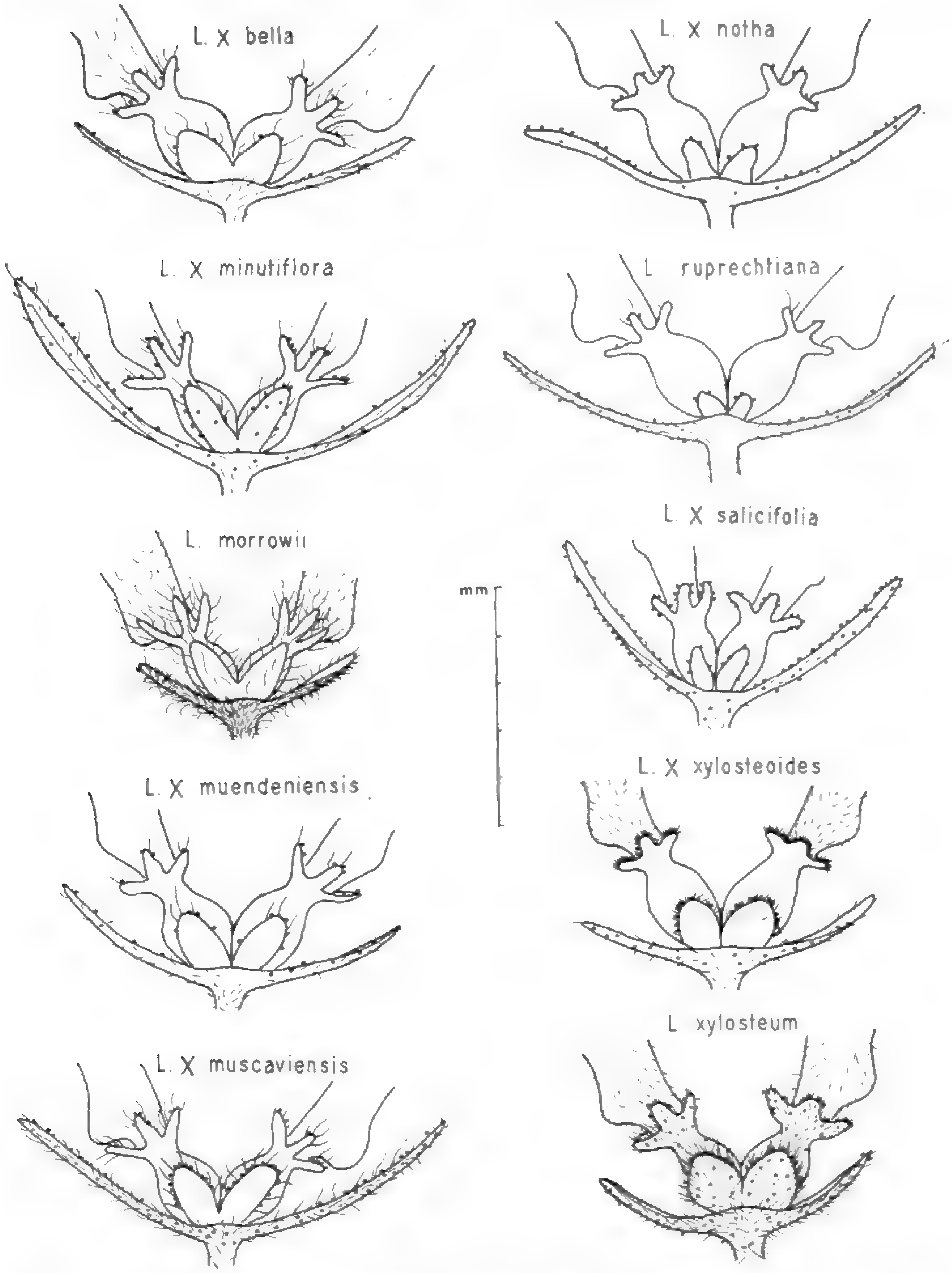

FIG. 4. Sketches of the ovaries, bracts, and bractlets of the species and hybrids in the main complex involved with *Lonicera tatarica.*

carpa Nash ex Teuscher (Addisonia **17**: 37, *t. 563.* 1932) with yellow fruits.

Lonicera × muendeniensis Rehd. Gartenflora **42**: 102. *fig. 18, 4–6.* 1893 (*L. × bella × ruprechtiana*).

Mainly of interest as a triple hybrid, this plant arose in the botanic

FIG. 5. Photograph of flowers of *Lonicera morrowii* from a plant growing in the Arnold Arboretum (accession number 1232.53), × 7.

garden at Münden from seed collected on *Lonicera* × *bella* sometime before 1883. It forms a handsome shrub with red, juicy fruits and, like the species from which it arose, also has a yellow-fruited form.

Lonicera × **muscaviensis** Rehd. Gartenflora **42**: 100, *fig. 18, 1–3.* 1893 (*L. morrowii* × *ruprechtiana*).

This hybrid apparently arose before 1888 from seed sent from the botanic garden at St. Petersburg, collected from a plant of *Lonicera morrowii.* Its name commemorates the fact that it was raised at the arboretum at Muskau, in what was then called Prussian Silesia. Interesting as a hybrid, floriferous, and of dense shrubby habit, it is nevertheless in no way superior, from the horticultural point of view, to either of its parental species.

Lonicera ×**notha** Zabel, Gartenflora **38**: 525. 1889 (*L. ruprechtiana* × *tatarica*).

This hybrid, also tracing its origin to seed distributed from the St.

Petersburg botanic garden under the name of one of the parent species, and presumably open pollinated, arose in 1878.

As might be expected, considering the variability of *Lonicera tatarica,* one of the parents, individual plants vary considerably in their flower color. In fact, five forms were described by Zabel (Gartenflora **38**: 525. 1889): *alba* with white flowers turning yellowish-white on fading; *gilva* with yellowish-white flowers bordered with yellow; *carneo-rosea* with light flesh-colored flowers margined with rose; *grandiflora* with large white to yellowish-rose flowers margined with light or dark rose; and *ochroleuca* with yellowish-white flowers fading to dark yellow, and followed by yellow fruit. In the same year Dippel (Handb. Laubh. **1**: 237. 1889) described three forms under the name *L. ruprechtiana* which, from their descriptions, clearly apply to this hybrid: f. *carnea* with light red flowers, f. *striata* with them striped white and rose, and f. *rosea* with flowers tinged pale rose. It is tempting to try and equate Dippel's forms with those of Zabel but considering the variability of the parental species, and therefore of the hybrids, this would be foolish. It is wiser to consider them as names given to some of the first segregates to be grown, for all intermediate shades of flower color may be expected from further hybridization.

As a hybrid, *Lonicera* × *notha* shows considerable vigor and floriferousness. It is attractive, especially in the forms with slightly larger flowers, but as the flowers turn yellow on fading it is a matter of taste whether, as an ornamental, it is preferable to the species, especially *L. tatarica.*

Lonicera ruprechtiana Regel, Gartenflora **19**: 68, *t. 645.* 1870.

This native of northeastern Asia is the hardiest member of the group. With its upright and then spreading branches, its habit is very similar to that of *Lonicera tatarica.* It is mainly distinguished by the shape of its leaves (see FIG. 2), which are pubescent below in the typical plant, in the color of the flowers, which are creamy-white turning to yellow, and in the manner in which the narrow petals are curled back at the margins (FIG. 6).

As in *Lonicera tatarica* and *L. morrowii* there is a yellow-fruited f. *xanthocarpa* (Zabel) Zabel (in Beissner et al., Handb. Laubh.-Benenn. 458. 1903) which, in this case, is also said to have somewhat smaller, more yellowish flowers. The species shows considerable variations in the wild and its glabrous extreme with leaves only sparingly hairy on the veins below, has been named var. *calvescens* Rehd. (Mitt. Deutsch. Dendr. Ges. **1912**: 194. 1913), a plant also notable in cultivation for bearing fruits which are a dull purplish-red, instead of the typical, light orange-red.

Lonicera × **salicifolia** Dieck ex Zabel, Gartenflora **38**: 524. 1889 (*L. ruprechtiana* × *L.* × *xylosteoides*).

This triple hybrid is included here only for completeness. With its very small, almost minute, flowers, a large proportion of which abort and

FIG. 6. Photograph of flowers of *Lonicera ruprechtiana* from a plant growing in the Arnold Arboretum (accession number 352.62), × 6.

never develop, it has very little merit to horticultural recognition. The leaves, too, are narrow and small and, although first raised before 1880, it is grown only as a botanical curiosity

Lonicera tatarica L. Sp. Pl. 173. 1753.

This is the most important and valuable species in the group, occurring in the wild from the Altai and Ural Mountains in central Asia to the area of the Volga River in southern Russia. It has been cultivated for over 200 years and has escaped and become naturalized in many places throughout the northern and eastern United States. The showiness and beauty of this species depends in part on the breadth of the corolla lobes and the way in which they are borne, not curling back as in related species (FIG. 7), and also because they tend to retain their color as they fade and shrivel, rather than become yellowish.

With a wide range in character, it is not surprising that many of the variants in cultivation have been given names. There are some twenty forms listed either in Rehder's revision of the genus (Annual Rep. Missouri Bot. Gard. **14**: 27–232. 1903) or his *Manual of Cultivated Trees and Shrubs* (ed. 2. 1940) which today would be assigned to the rank of cul-

FIG. 7. Photograph of flowers of *Lonicera tatarica* from a plant growing in the Arnold Arboretum (accession number 304.58), × 4.

tivar. Other names have been treated in synonymy by Rehder, although it is quite possible that, in modern terms, each represented a different clone. For the most part, differences rest upon variations in the size and color of the flowers, to a lesser degree on the size and breadth of the leaves, and even, in the case of the dwarf cultivar 'Nana', on the habit. There would be little point in listing all the names in this context but a few notes on one or two growing in the Arnold Arboretum may be of value.

Lonicera tatarica 'Arnold Red' is noteworthy as bearing the darkest red, and therefore showiest, flowers of all the cultivars. Also handsome in fruit, it is one of the most desirable clones in the whole group. Two other cultivars were selected in relatively recent times for their red flowers: 'Hack's Red' and 'Sheridan Red' but neither compares with 'Arnold Red' in richness and depth of color.

'Morden Orange' might at first be thought to have orange flowers but, in fact, it has been selected for the most attractive, light orange fruits. 'Lutea' has bright yellow berries (tinged almost orange) and has been in cultivation for well over a century. Throughout the species the berries are covered with an attractive, slight glaucous bloom and the clones, grown mainly for their flower colors, show considerable variation in the lightness or depth of color in their red fruit.

There is a dwarf form in cultivation today with pure white flowers and although grown under the name 'Nana' it is not this original form. If considered worthy of distinction it needs a new name. The original dwarf var. *nana* Hort. ex Alphand (Descr. Arb. Arbriss. 42. 1875), which transposed into modern terms becomes cv. Nana, was described as bearing rose-colored flowers.

Lonicera × xylosteoides Tausch, Flora 21: 736. 1838 (*L. tatarica × xylosteum*).

A botanically interesting hybrid of no particular distinction from the horticultural point of view, except that the blue-green glaucousness of the undersides of its leaves is somewhat unusual. It is, in fact, the reason why this hybrid was also, but later, given the name *Lonicera coerulescens* Dippel (Handb. Laubh. **1**: 233, *fig. 149.* 1889).

Lonicera xylosteum L. Sp. Pl. 174. 1753.

This species, of long cultivation, is native from Europe through Turkey and European USSR to the Altai Mountains, and has occasionally escaped from cultivation in eastern North America. It is worth growing for its soft, abundant, light green foliage and attractive deep red fruits, although its yellowish-white flowers are undistinguished.

As in any species with such a wide natural range and long history as a cultivated plant, many variants have been described and named, both from the wild and the garden. Perhaps the best known is f. *lutea* (Veillard) Rehd. (Annual Rep. Missouri Bot. Grad. **14**: 138. 1903), distinguished by its yellow fruits, but f. *glabrescens* Zabel (Mitt. Deutsch. Dendr. Ges. **1901**: 92. 1901) and f. *mollis* (Regel) Rehd. (Annual Rep. Missouri Bot. Gard. **14**: 139. 1903) are often met in the literature and represent the two extremes of variation in pubescence exhibited by the species: the former having leaves glabrous or almost so, above, and the latter having them densely pubescent on both surfaces.

A form with a dwarf compact habit which has attracted attention of late is *Lonicera xylosteum* 'Claveyi' (also referred to as 'Clavey's Dwarf'). Although a different clone, it is not certain just how it differs from f. *compacta* which Zabel described from a plant received from Dessau in Germany in 1899 (Mitt. Deutsch. Dendr. Ges. **1901**: 92. 1901) and which is possibly extinct now. Because of its habit 'Claveyi' is a valuable plant in a small garden or for forming low, dense hedges.

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ON THE IDENTITY OF DROSERA BREVIFOLIA

C. E. WOOD, JR.

THE PRINCIPLE OF TYPIFICATION of the names of plants or of groups of plants as now embodied in the International Code of Botanical Nomenclature offers one of the best pathways to nomenclatural stability, for only by typification can the application of names be fixed precisely. Once all plant names have been typified accurately, a major source of nomenclatural instability will have been eliminated, since many of the changes which still have to be made are the result of either lack of typification or inaccurate typification. Hasty or careless typification, however, can introduce confusion and provide justification for the accusation that taxonomists are continually changing the names of plants (presumably just for the joy of changing).

This paper is an outgrowth of both a long-standing interest in *Drosera* and work on a generic flora of the southeastern United States.[1] It seems to me to have grown to be very long for its limited title. However, a number of well-known names, of which *Drosera brevifolia* is one, have been upset recently on more or less capricious grounds. I have therefore gone in some detail into the background and typification of this name in the hope of settling its status finally. One can have no objections to changing a name if this is clearly necessary, but it is irresponsible and not in the interests of taxonomy to overthrow current usage of a name when the full evidence is not available.

For more than a hundred years, the name *Drosera brevifolia* Pursh was applied consistently to a distinctive American species characterized by its annual habit; cuneate, short-petiolate, exstipulate leaves; gland-tipped hairs on scapes, pedicels, and calyces; relatively large corollas (for sect. *Drosera*) mostly 1–1.6 cm. across; and generally obovoid seeds with 10–12 longitudinal rows of shallow pits (formed by the collapse of the outer wall of individual large cells of the outer seed coat). In the United States it occurs primarily in moist, acid, sandy soils on the Atlantic and Gulf

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[1] I am grateful to the directors and curators of the institutions which I have visited and to Caroline K. Allen, Mary T. Dillon, Frances M. Jarrett, Alicia Lourteig, C. E. B. Bonner, H. R. De Selm, Joseph Ewan, and W. R. Ernst for their help in various ways. The work on the generic flora has been supported through the generosity of George R. Cooley and grants from the National Science Foundation.

coastal plains from southeastern Virginia to southern Florida, westward through Alabama, Mississippi, and Louisiana, to Arkansas, southeastern Oklahoma, and eastern Texas. Disjunct stations occur in northern Alabama and Tennessee. In the eastern part of this range the petals are white; in at least Tennessee and Louisiana populations with both white-flowered and pinkish- to rose-purple-flowered plants are known; and in Texas, Arkansas, and Oklahoma white-flowered plants apparently are unknown. Many of the plants from this westernmost part have flowers of reduced size which may open only partly or hardly at all, strongly suggesting self-pollination, or even cleistogamy, linked with the less favorable rainfall conditions of this area. These western populations are thought by some to represent a distinct species, *D. annua* Reed (Torreya **15**: 246. 1915). *Drosera brevifolia* also occurs disjunctly in southern Brazil, Paraguay, Uruguay, and northeastern Argentina, where both the white and rose-purple forms occur (cf. G. Dawson, Revista Argent. Agron. **5**: 231–239. 1938, and notes on herbarium specimens). Originally described as *D. maritima* St. Hil. (Hist. Pl. Remarq. Brés. Parag. 264. 1825), these populations have long been recognized as being conspecific with the plant of the southeastern United States. White-flowered plants of this species are known from Oaxaca, Mexico (*Galeotti 7246* [G]), and, to judge from the description, *D. chiapasensis* Matuda (Anal. Inst. Biol. Méx. **27**: 362. 1957), described from the state of Chiapas, Mexico, most probably represents additional disjunct populations of the same plant. (Such wide disjunctions also occur in the ranges of *D. intermedia* Hayne [Europe, from the Caucasus, northward to Finland and Sweden, and westward to Portugal and Ireland; eastern North America; Cuba and Hispaniola; Suriname, British Guiana and Trinidad; and southern Brazil and Paraguay] and in *D. capillaris* Poir. [see below]. It is also notable that in various parts of the ranges of these species petal-color varies in the former from white to pink or purple, and in the latter from pink to white or *vice versa*, paralleling the situation in *D. brevifolia*.)

In 1962, in an unnecessarily ill-humored paper on *Drosera* in the southeastern United States (Sida **1**: 53–59), Lloyd Shinners argued that the plant described by Pursh is not the species which has been known for so long as *Drosera brevifolia* but is instead *D. capillaris* Poiret, another well-marked species described from the southeastern United States. Since Shinners recognized both *D. maritima* (of which he saw only five individuals, one sterile) and *D. annua* as distinct species, and there is no other name available (unless it be *D. chiapasensis*, of which he seemingly was unaware), he redescribed the plant of the Atlantic Coastal Plain of the southeastern United States as *D. leucantha* Shinners. The holotype was given as *Cronquist 5255* (SMU) (apparently an error for *4255*, the number on isotypes in GH and NY), from Glynn County, on the coast of Georgia. Unfortunately, his conclusion was too hastily arrived at and was based on inadequate evidence. It is quite unnecessary to abandon the well-established *D. brevifolia* Pursh.

Since *Drosera capillaris* Poir. is also involved, the account which follows deals first with the typification of that species to eliminate any question of its identity, and then with the selection of a lectotype for *D. brevifolia* Pursh.

Drosera capillaris Poiret in Lamarck, Encycl. Méth. Bot. **6**: 299. 1804.

Poiret's Latin diagnosis reads, "Drosera scapis radicatis, capillaribus, paucifloris, glabris; foliis spathulatis, petiolatis. (N.)." In the discussion he says that this species should be distinguished from *Drosera longifolia* L., which in his sense included both *D. longifolia* (*D. anglica* Huds.) and *D. intermedia* Hayne (1800). He notes the spatulate leaves, rather long petioles "enlargis insensiblement à leur partie supérieure," and the small, nearly sessile, very glabrous flowers. He further notes, "Cette plant croît à la Caroline; elle m'a été communiquée par M. Bosc, qui en a fait la découverte. (*V. s.*)." Nothing else in the description can be regarded as of diagnostic value. The slender, glabrous scape and small, glabrous flowers are characteristic features of this species as usually understood. Spatulate leaves in combination with glabrous scapes may also suggest *D. intermedia*, which occurs in the same area of the Coastal Plain of the southeastern United States. The leaf blades of *D. capillaris* are characteristically almost orbicular, tapering abruptly into the petiole, but some individuals, presumably in response to varying ecological conditions, have distinctly spatulate blades gradually tapering into the long petiole. Plants with leaves of the latter kind are sometimes misidentified as *D. intermedia*, although the quite different seeds and the distinctive inflorescences of *D. intermedia* (curving outward and often downward at the base before becoming erect, in contrast with the strictly erect inflorescences of *D. capillaris*) provide ready characteristics for distinguishing between the two. Fortunately, the spatulate leaves of the description need introduce no doubts as to the application of the name, for there is a type specimen.

In early July, 1964, through the courtesy of Prof. A. Aubréville, director of the Laboratoire de Phanérogamie, Muséum National d'Histoire Naturelle, Paris, and with the kind help of Mlle Alicia Lourteig, I was able to locate the holotype of *Drosera capillaris*. According to the labels on the sheet, the specimen passed in turn from Poiret to Moquin-Tandon, to Cosson, to [Ernest] Durand, and finally to its present location in the general phanerogamic herbarium of the Muséum. It is a single skimpy plant bearing seven leaves and a scape 15 cm. long with four mature or nearly mature fruits, the seeds from one of which have been removed by a previous worker and placed in a small packet on the sheet. The conspicuous stipules; the long, slender, straight, glabrous scape; the glabrous calyces; and the seeds with longitudinal rows of papilliform cells all testify that this name is being applied correctly.

The label reads:

Drosera capillaris. (n.)
dict.
an *Dr. longifolia?* Mich. non Lin.
bosc. *caroline*
herb. Poiret [in another hand]

This species is currently known to occur from southeastern Virginia, southward along the Atlantic Coastal Plain to southern Florida and westward along the Gulf Coastal Plain to eastern Texas; in the states of Veracruz and Tabasco, Mexico, and in British Honduras; in eastern and western Cuba and in Jamaica; and in Suriname, British Guiana, and Trinidad. Reaffirming the importance of seed characteristics as the most constant and reliable specific characters in this vegetatively plastic genus, C. H. Brummer-Dinger has shown that the later-described *Drosera tenella* Willd. is conspecific with *D. capillaris* (Acta Bot. Neerl. **4**: 136–138. 1955). The petal color of *D. capillaris* is rose-pink to almost white in the United States, and has been recorded as white or pink in British Honduras and in Cuba.

Drosera brevifolia Pursh, Fl. Am. Sept. **1**: 211. 1814.

Pursh's description reads:

> 3. D. pusilla; scapis radicatis simplicibus, foliis brevibus cuneatis vix petiolatis, petalis ovalibus. *brevifolia.*
> In sandy swamps of Georgia. Enslen. June. *v. s. in Herb. Enslen.* The smallest of all the species known; flowers rose-coloured.

All of the Latin diagnosis applies to the plant with which this name has long been associated. It can be argued that it can also apply to *Drosera capillaris* Poir., and, indeed, a part of it can. However, the short, cuneate, scarcely petiolate leaves described are not at all those of *D. capillaris*, in which the petiole is quite distinct and usually very much longer than the almost orbicular to obovate-spatulate blade. (Cf. *D. capillaris* above.) Of all the species of the southeastern United States, the leaves described by Pursh are most nearly those of the plant long known as *D. brevifolia.*

The petal color of this same plant, however, is generally white in populations from the Atlantic Coastal Plain, whereas that of *Drosera capillaris* is generally pale pink to rose. (A collection of *D. capillaris* from Louisiana, *Shinners 23514*, carries the comment "petals nearly white, with pink tinge," and both pink- and white-flowered plants occur elsewhere.) I have seen pink-tinged petals on the plant in question (*D. brevifolia*) in North Carolina (*Wood 8500, Channell & Rock* [GH]), an occasional collector notes "petals white, turning pink on drying" (cf. *Cooley & Eaton 5777* [GH]), and the petals of many herbarium specimens are pink, white with pink tips (cf. *Kral 6428* [GH]), or brown with suggestions of pink. If herbarium specimens were entirely without notes on flower color (and the majority are), one might conclude, depending upon the age of the specimen and conditions of drying, that the plant is pink, white, or yellow flowered. On these grounds, and especially since Pursh saw only dried specimens, one is justified in questioning whether the pink color noted in Pursh's description is necessarily associated with *D. capillaris*, rather than with the cuneate-leaved plant of the Latin description.

After considering these possibilities in the course of preparing an account of the Sarraceniaceae and Droseraceae for a generic flora of the southeastern United States (Jour. Arnold Arb. 41: 152–163. 1960), I had concluded that the entire description best fitted herbarium specimens of the cuneate-leaved, exstipulate, white-flowered, glandular-scaped plant. In the event that a mixture with *D. capillaris* was involved, it seemed that greater weight should be given to the Latin diagnosis than to the single comment on flower color, and that this procedure was consistent with the recommendations on typification in the International Code of Botanical Nomenclature. It seems particularly in the spirit of Recommendation 7B, then in Appendix IV (ICBN, ed. 1956, p. 294), but now included in both the "Guide for the determination of types" (ICBN, ed. 1961, p. 65) and the main body of the Code (p. 20): "Whenever the original material is heterogeneous, the lectotype should be so selected as to preserve current usage unless another element agrees better with the original description and (or) figure." Thus I continued to apply the name *Drosera brevifolia* in its usual sense and, because of the press of other work on the generic flora, did not attempt to typify it further.

Shinners (*loc. cit.* 55) came to quite a different conclusion: "Without seeing the type (location unknown; possibly not in existence; Diels cites another Enslen specimen bearing no locality beyond Southern U. S.) there may be a little doubt as to what Pursh had, since the description says nothing about pubescence on the scape (though failure to mention it suggests there was none) or presence of stipules. Pursh listed only four species, the other three being *D. rotundifolia*, *D. longifolia*, and *D. filiformis*; he makes no mention of *D. capillaris*. But his statements 'smallest of the species known; flowers rose-coloured' apply exactly to *D. capillaris* among the Southeastern species. The words cannot possibly refer to the plant with large, white flowers which Chapman and later authors mistakenly have called *D. brevifolia*. The phrase 'foliis brevibus cuneatis vix petiolatis' of course excludes *D. filiformis*, and makes both the very long-petioled *D. intermedia* and the round-leaved *D. rotundifolia* very unlikely candidates. Enslen collected in Lower Georgia, which I take to mean the Coastal Plain. The only species in this area to which Pursh's description reasonably applies is *D. capillaris*."

This conclusion does not seem to be very well founded. "Smallest of the species known" applies to plants, not flowers, as Shinners implies, and fits better the glandular-scaped plant than *Drosera capillaris*, although either may flower at small size. "Foliis brevibus cuneatis vix petiolatis" does not apply to *D. capillaris* with its well-developed petioles, but to the species which has been known for so long as *D. brevifolia*; furthermore, the argument based on flower color does not necessarily hold. The description can apply in its entirety to the white-flowered, cuneate-leaved, exstipulate, glandular-scaped plant, but not to *D. capillaris* or any other species of the southeastern United States. On the basis of the description alone there is little justification for assigning the name *D. brevifolia* to the synonymy of *D. capillaris*.

In the hope of resolving the question, I have sought to locate the Enslen collections on which Pursh based his description and to typify *Drosera brevifolia* by a specimen.

In the preface to his *Flora Americae Septentrionalis* Pursh discusses some of the sources of his specimens and information. On page xii he writes, "While I was thus engaged in describing and figuring those new acquisitions to the American Flora [the specimens from the Lewis and Clark Expedition], another opportunity offered to augment my resources. Mr. Aloysius Enslen, who had been sent to America by Prince Li[e]chtenstein of Austria, as a collector of new and interesting subjects of natural history, returned to Philadelphia from his extensive travels through the Western Territories and Southern States. This gentleman, with whom I had previously been on terms of intimate friendship, was now in possession of an extremely valuable collection of living and dried plants, to which I had unrestrained access. To his liberality I am indebted for many new and scarce specimens, which filled up a desideratum in my collection, particularly in the plants of Lower Louisiana and Georgia. Those species exclusively received from his collection I have distinguished by '*v. s. in Herb. Enslen.*' "

Little is recorded about Aloysius Enslen and his activities in the United States, but a few comments and clues are scattered through Pursh's *Flora*, in the correspondence or publications of Enslen's contemporaries, and in various other places. Professor Joseph Ewan, of Tulane University, whose scholarly and fascinating studies of the Pennsylvania botanists of this period have cleared up many botanical mysteries, has most generously shared all the bits of information about Enslen he has accumulated in the course of his extensive research.

The information in the next three paragraphs is entirely from his notes or published papers; most of the documentation is omitted here, for he will present this material later in another context. The data about Pursh, Barton, Lambert, and their collections are drawn from either Prof. Ewan's studies (Frederick Pursh, 1774–1820, and his botanical associates. Proc. Am. Philos. Soc. **96**: 599–628. 1952) or those of the late F. W. Pennell (The elder Barton — his plant-collection and the mystery of his floras. Bartonia **9**: 17–34. 1926; Benjamin Smith Barton as naturalist. Proc. Am. Phil. Soc. **86**: 108–122. 1942; Historic botanical collections of the American Philosophical Society and the Academy of Natural Sciences of Philadelphia. *Ibid.* **94**: 137–151. 1950).

Enslen apparently arrived in America at the expense of Prince Liechtenstein about 1800 (1799–1801). He set up a garden in Philadelphia to grow plants which would either be collected by himself or acquired from others (see especially John Lyon; cf. Ewan & Ewan, Trans. Am. Philos. Soc. **53**(2): 10. 1963). These plants would be for reshipment to Vienna, not for public sale. It is known that he was in Savannah in at least 1804 and that he collected between Savannah and Louisville, Georgia. He traveled to New Orleans, evidently following the Coweta Falls trail from Augusta, Georgia, *via* Mitchell, Macon, and Cowetatown (near Columbus).

He also met the entomologist and artist John Abbott in Georgia, and Alexander Wilson cites him in his *American Ornithology*. In 1806, he traveled to St. Louis *via* Pittsburgh, and he at least intended to travel beyond with the Osage Indians. In 1809, Henry Muhlenberg wrote to Stephen Elliott of his visit to Enslen's growing garden where he was cultivating a number of Georgia plants. On December 17 of the following year Muhlenberg wrote to Elliott: "Mr. Enslin [sic] is allmost gone & past recovery of a consumption" (quoted by Ewan & Ewan, *loc. cit.* 14).

"There is evidence that [John] Lyon and Enslen . . . traded nursery stocks during the years of their activities in Philadelphia. Lyon is credited with the introduction of the copper-colored *Iris fulva* into English gardens in 1812. This plant Enslen had discovered in the marshes near New Orleans. [See Pursh, Fl. Am. Sept. 1: 30, under *I. cuprea.*] Pursh acquired specimens from both Lyon and Enslen; and in at least one instance, *Sida hispida*, he credited to Lyon a collection almost certainly taken by Enslen" (Ewan & Ewan, *loc. cit.* 10).

There is nothing to show that Enslen ever returned to Vienna after coming to America, but a large number of living plants (ca. 1000 species) and herbarium specimens (representing ca. 670 species) reached there. The latter are incorporated in the herbarium of the Naturhistorisches Museum, Vienna. All are without data and bear labels wholly in the handwriting of Leopold Trattinick (1764–1849), who presumably discarded any original labels. Trattinick was curator of the herbarium in Vienna at the time Enslen's plants were being studied by Pursh.

In addition to these specimens, there are 69 Enslen collections, also without data, in the herbarium of Benjamin Smith Barton, which is now at the Academy of Natural Sciences of Philadelphia (Pennell, 1950, p. 141). This herbarium, built up almost entirely between 1797 and 1807, is directly connected with Pursh, who was employed by Barton about 1805 and who made two collecting trips (1806, 1807) for him. Pursh was largely responsible for Barton's herbarium of about 2000 sheets, and 1149 of the 1674 sheets now in it were collected by him. Little or nothing was added to the herbarium after Pursh left Philadelphia and went to New York in the late autumn or early winter of 1807 (Pennell, 1942).

In the winter of 1811–1812, Pursh went to England, where, under the patronage of Aylmer Bourke Lambert (1761–1842), he prepared his flora for publication. The specimens he took with him (including, among others, many of his own collections from the trip of 1807 and some of those of the Lewis and Clark Expedition which had come to Barton for study in November, 1805) went to Lambert before Pursh left England in 1816 for Canada, where he died in 1820.

There appear, then, to be three possible sources for Enslen collections which Pursh might have used in drawing up his description of *Drosera brevifolia*: Lambert's herbarium; the herbarium of the Naturhistorisches Museum, Vienna; and the Benjamin Smith Barton herbarium in Philadelphia.

Upon Lambert's death in 1842, his large collection was broken up, sold at auction, and widely dispersed. Most of the North American materials were bought by Edward Tuckerman (collections of Fraser, Bradbury, Nuttall, Lewis and Clark, etc.) and by Pamphlin (Pursh's own collections, largely from his trip of 1807). Tuckerman also bought a bundle of "Miscellaneous Plants, N. America, &c." which proved to include only Pursh collections (cf. Ewan, 1952). The specimens bought by Tuckerman are now at the Academy of Natural Sciences of Philadelphia, while those bought by Pamphlin are in the herbarium of the Royal Botanic Gardens, Kew (*fide* Ewan). Other parts of Lambert's collections, including the important Ruiz and Pavon specimens which went to the British Museum (Natural History), are preserved in various herbaria, but a large part seems to have disappeared.

There are no Enslen specimens among the materials from the Lambert herbarium now in Philadelphia, nor was I able to locate any at either Kew or the British Museum (Natural History) in the summer of 1964. I also checked hopefully, but without success, the collections of the Conservatoire Botanique, Geneva; those of the Botanical Museum and Herbarium, Copenhagen; and, insofar as possible, those of the Muséum d'Histoire Naturelle, Paris. Enslen collections apparently are known only in Vienna and Philadelphia. If, however, an Enslen specimen of *Drosera brevifolia* from Lambert's (hence Pursh's) herbarium should be found, it would take precedence over others in the typification of the name.

Professor K. H. Rechinger, director of the Naturhistorisches Museum, Vienna, has kindly sent on loan Enslen's specimens of *Drosera* preserved there. There are four large, gray sheets ca. 32 × 48 cm. which dwarf even more the small plants on them. The labels written by Trattinick bear only a name and "Amer. bor. Enslen." The first sheet, labeled "Drosera brevifolia," has six specimens of the cuneate-leaved, glandular-scaped plant which is usually known by this name. It was annotated by Diels as *D. brevifolia* during the preparation of his treatment of the Droseraceae for *Das Pflanzenreich* (IV. 122(Heft 26): 1–136. *map.* 1906) and is presumably the collection cited by him (p. 90) and mentioned by Shinners. The second sheet, with two specimens of this same species, is labeled "Drosera brevifolia α. flor[i]b[us] albis Tratt[inick]." The third, also bearing two specimens of this species, is labeled "Drosera brevifolia β. florib[us] roseis Tratt." The fourth, labeled "Drosera cuneifolia glabrata Tratt.," was annotated by Diels as *D. cuneifolia* Thunb., certainly a lapse on his part, since he undoubtedly knew better and later cited only South African specimens in *Das Pflanzenreich.* The two specimens on it are *D. capillaris*, neither with open flowers. Seven of the ten plants of the other species have open but badly pressed flowers. The petals of all are brown with age.

The Barton herbarium in Philadelphia also contains an Enslen collection of *Drosera* which was located for me by Dr. W. R. Ernst. The single sheet, which I have since seen in Philadelphia, bears two small specimens: to the left, a plant of *Drosera capillaris*, and to the right a flowering plant of *D. brevifolia*. On the label is written only "Drosera cuneifolia" (which one suspects may have been the name on the original labels of the Enslen specimens in Vienna) and "Mr Enslin" in two different handwritings which I have not identified. Again, the flower color is impossible to determine, but the size of the flower clearly shows that it was not one of the short-petaled forms from the western part of the range of the species.

From these specimens in Vienna and Philadelphia it seems that Enslen's material was a mixture of *Drosera capillaris* and the cuneate-leaved plant with glandular scapes, with a great predominance of the latter. To judge from the size of the three specimens of *D. capillaris* (scapes 15–20 cm. long), it is most likely that Pursh's "D. pusilla" and "smallest of all the species known" are derived from the other species, for the ten plants in Vienna are only three to five centimeters tall, while that in Philadelphia is seven.

Trattinick's sorting of Enslen's collections shows that he thought some plants to be white, others to be pink flowered. His third category without indication of color suggests that he was uncertain of the flower color of these specimens. Pursh's "flowers rose-coloured" may once again be explained as applying either to plants of *D. capillaris*, to white-flowered plants of the second species, the petals of which turned pink in drying, or to pink- to rose-purple-flowered plants of the same species from the western part of the range. Since Enslen is known to have collected in southeastern Georgia where both species occur and since Pursh attributed the specimens to "sandy swamps of Georgia," it would seem that the last possibility is the least likely of the three, especially when the flower size is also considered.

Of the two species involved, one, *Drosera capillaris*, had already been named when Pursh described *D. brevifolia*. Pursh's description best fits the new element, and the name has been applied in that sense for more than a hundred years. A specimen of that element, therefore, should be used in typifying the name, in accordance with Recommendation 7B of the International Code. There is no reason for interpreting *D. brevifolia* as a synonym of *D. capillaris*, and there is no obstacle to the continued use of the former name.

In the absence of a specimen from Pursh's herbarium, it seems best to select as lectotype the right-hand plant on the sheet in Barton's herbarium in the Academy of Natural Sciences of Philadelphia, for this is more clearly associated with Pursh than is any part of the material sorted by Trattinick in Vienna, although, as Pursh's comments suggest, he may well have seen much of that material. It is certain that Pursh saw all of the specimens that went into Barton's herbarium, for he was largely responsible for the care and development of it, and little or nothing was added to it after he left Philadelphia in 1807. The specimen in the Barton Herbarium is linked with Pursh and will serve adequately as a lectotype. Since it was said to have come from Georgia and since Enslen is known to have collected in southeastern Georgia, this plant should be taken as the white-flowered form which occurs there.

Since I have not yet seen material of *Drosera chiapasensis*, the detailed taxonomy of *D. brevifolia* (including *D. maritima* and *D. annua*) will be dealt with at another time, but it should be noted again that in what I regard as a single well-marked species Dr. Shinners sees three. To show the basis for his conclusion, his comparisons of *D. brevifolia* (*D. leucantha*) with *D. annua* and of *D. maritima* with *D. annua* are summarized in tabular form below. He did not give any comparison of *D. maritima* with *D. brevifolia*, with which it has long been considered conspecific.

D. BREVIFOLIA (*D. leucantha*)	D. ANNUA
Petals 5, pure white, 5–10 mm. long	Petals 1–5, light to deep lavender-pink, 2.5–8 mm. long
Sepals 3–4.5 mm. long	Sepals 2.5–4 mm. long

D. MARITIMA (based on 4 plants)	D. ANNUA
Naked portion of scape 1.5–2.5 (rarely –4) times as long as leaves	Naked portion of scape 2.5–7 times as long as leaves
Sepals obtuse or subacute	Sepals subacute or acute
Lowest pedicel 1–3.5 mm. long	Lowest pedicel 1–5 mm. long

Writing of *Drosera annua* and *D. maritima*, Shinners says (*loc. cit.* 56), "These differences may appear slight. But considering how closely herbarium specimens of *D. annua* and *D. leucantha* may resemble each other when well-opened flowers and color data are lacking, while live plants could not possibly be confused, I prefer to treat the North and South American plants as two species. Some rather robust specimens collected by Dr. B. C. Tharp on Padre Island, Texas, greatly resemble the South American species. At the other extreme, collections made by Dr. H. K. Svenson in Coffee and Franklin Counties, Tennessee [where both white- and purple-flowered plants occur in the same populations; cf. *Svenson 9974*], are exceptionally small."

These differences do indeed appear to be slight, and measurements based on larger numbers of specimens make them appear even slighter, particularly when the specific differences between the other American species of *Drosera* are considered. Petal color (essentially presence or absence of anthocyanin) as a primary specific difference is not very convincing, especially when populations with both white- and purple-flowered forms are known (Tennessee; Louisiana), when both white and rose-purple forms are known in South America, and when similar color shifts occur within such well-marked species as *Drosera intermedia* and *D. capillaris*. Neither is it very convincing when, in a genus notable for its morphological plasticity, minor and almost completely overlapping size-differences in calyces, petals, and pedicels are used to distinguish species. Most lamentable of all is the lack of mention anywhere in his paper of the most dependable specific characters in the genus: the shape and markings of the seeds. This seems inexplicable, since Dr. Shinners makes many references to Frances Wynne's paper on the North American species of *Drosera* (Bull. Torrey Bot. Club 71: 166–174. 1944) in which she stresses the usefulness of seed characters and illustrates the seeds of the North American species. Many botanists, beginning with Hayne (1800) and continuing to such recent workers as Wynne, C. H. Brummer-Dinger (Acta Bot. Neerl. **4**: 136–138. 1955), and Maguire and Wurdack (Mem. N. Y. Bot. Gard. **9**: 331–336. 1957) have realized that seed characteristics are among the most useful and stable in this genus. It is unfortunate that seeds were not studied, for those of the three supposed species match one another well. Altogether it would seem that species based on such trivial differences as those used by Dr. Shinners have very little to do with the concept of the species as a natural biological unit.

NOTES ON THE NOMENCLATURE OF CORNUS[1]

I. K. FERGUSON

DURING THE PREPARATION of an account of the Cornaceae for a generic flora of the southeastern United States it was found that the genus *Cornus* has been delimited in different ways by various workers, some accepting the genus in a broad sense and dividing it into subgenera and sections, others segregating these groups as distinct genera. As a result of these quite varied taxonomic treatments the nomenclature of the sections, subgenera, and segregate genera has become very confused. The purpose of this paper was to try to find the correct names at different ranks for the various categories that have been recognized and to bring these names together with some of their relevant synonymy.

The characters used by most workers for subdividing *Cornus* are mainly those of the inflorescence, and there appears to be little other supporting evidence. These characters do not seem to be sufficient for recognizing segregate genera, and in this work the subdivisions of *Cornus* are treated as subgenera. No taxonomic revision is proposed here, and the treatment of Wangerin (Pflanzenreich IV. 229(Heft 41). 1910), who recognized seven subgenera within *Cornus*, is closely followed. However, *C. alternifolia* L. and *C. controversa* Hemsl., with alternate leaves and pitted stones, are separated as an additional subgenus, *Mesomora* Raf.

The genus *Cornus* as established by Linnaeus comprised five species: *C. mas*, *C. suecica*, *C. canadensis*, *C. sanguinea*, and *C. florida*. Hill (Brit. Herbal 331. 1756) established the genus *Chamaepericlymenum*, and, though he did not describe any species, he refers to only one, *Cornus suecica* L. *Chamaepericylmenum* must be based on this species. Some recent workers, including Warburg (in Clapham, Tutin & Warburg, Fl. Brit. Isles, ed. 2. 493. 1962) and Pojarkova (in Komarov, Fl. URSS 17: 324. 1951), maintain this genus for the herbaceous species of *Cornus*.

Dumortier (Florula Belgica 83. 1827) recognized two sections in *Cornus*: *Thelycrania*, based on *C. alba* L. and *C. sanguinea* L., and *Cornotypus*, based on *Cornus* "nudiflora = Mas, L." This latter division may be considered as effectively typifying the genus.

In 1830, Lindley (Nat. Syst. Bot., ed. 1. 241) mentioned *Benthamia* incidentally and without a description as a genus in the Boraginaceae. Later (Bot. Reg. *tab. 1579*. 1833) he formally established *Benthamia*,

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[1] Continuing a series of miscellaneous notes and papers on the flora of the southeastern United States made possible through the support of George R. Cooley and a grant from the National Science Foundation. I am indebted to Dr. Carroll E. Wood, Jr., Dr. George K. Brizicky, and Dr. Rolla M. Tryon for aid and valuable advice; and to Dr. P. W. Ball, of Flora Europaea, for drawing my attention to the place of publication of *Swida* Opiz.

based on *Cornus capitata* Wall., as a genus in the Cornaceae. Unfortunately, this name had been validly published in 1828 by Richard as the name for a genus of orchids. *Benthamia* Lindl. is thus a later homonym.

Later, Rafinesque (Alsograph. Am. 58. 1838) recognized a number of categories within *Cornus*. The status of some of these has been discussed by various workers (O. A. Farwell, Rhodora **34**: 29, 30. 1932, and Torreya **42**: 130. 1942; H. W. Rickett, Torreya **42**: 11–14, 131. 1942), but without agreement. Rafinesque, on page 58 of his *Alsographia*, recognizes a genus *Cornus* with a typical element, *Cornus*, and two subgenera, *Mesomora*[2] and *Kraniopsis*. Under the typical element he includes "most of the American species," as well as *C. sanguinea* and *C. alba*. *Mesomora* includes only *C. alternifolia*, and in *Kraniopsis* Rafinesque places *C. paniculata* L'Hér. (= *C. racemosa* Lam.) and *C. comosa* Raf. On the following page he lists three further categories without clearly designating their rank: *Eukrania*, with *C. mas*, *C. canadensis*, and *C. suecica*; *Cynoxylon*, comprised of *C. florida*; and *Benthamia* Lindl. The names *Mesomora* and *Kraniopsis* must clearly be adopted for subgenera, while it appears that *Eukrania*, *Cynoxylon*, and *Benthamia* may be considered to be genera or subgenera.

The evidence available suggests that *Eukrania* should be regarded as a subgenus because, in the account of a new species following his description of *Eukrania*, Rafinesque makes no combinations under *Eukrania* but refers to "*Cornus* (*Eukrania*) *cyananthus* Raf.," commenting that it is "a very curious herbaceous *Cornus* very near to *C. canadensis*." Since he included *Cornus mas*, the type of Dumortier's section *Cornotypus*, in *Eukrania*, this name must be treated as a synonym of the typical subgenus.

On the other hand, *Benthamia* Lindl. would appear to have been intended to be a distinct genus, for Rafinesque cites his own earlier work, *Sylva Telluriana* (1836), under *Benthamia*, and in this work he clearly refers to *Benthamia* Lindl. as a genus and also to his "subgen. *Cynoxylon* of Med. Fl. of 1828." This latter statement illustrates the uncertainty surrounding the rank of *Cynoxylon*, since Rafinesque had clearly applied this name to a section of *Cornus* in the *Medical Flora* (1828). However, there does not seem to be any evidence to indicate that he intended *Cynoxylon* to be a distinct genus, and for this reason it is accepted as a subgeneric name here. Merrill (Index Rafinesquianus 184. 1949) has indicated that Rafinesque recognized *Cynoxylon* as a subgenus of *Cornus* and *Eukrania* as a separate genus, but the reasons for this treatment are quite obscure.

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[2] Rafinesque (Alsograph. Am. 58. 1838) in his formal description of subgenera uses the spelling "*Mesomera*," but later, in his discussion on page 62, he refers to "*Mesomora*" and "the Mesomoras." Rudbeck (Acta Lit. Suec. **1**: 98. 1720) proposed the name *Mesomora* for the plant that was later known as *Cornus suecica* L. *Mesomora* is derived from the Greek, *mesos*, middle, and *maurus*, dark, in allusion to the dark-colored flowers in the middle of the white involucre. Linnaeus (Fl. Lapponica 36. 1737, and Fl. Suecica 48. 1755) cites *Mesomora* in his synonymy of *Cornus suecica*, and he uses the epithet in *Philosophia Botanica* (201, 202. 1763) for an informal category in *Cornus*. It seems that Rafinesque's spelling "*Mesomera*" should be considered a typographical error.

Opiz (in Berchtold & Opiz, Oekon.-tech. Fl. Böhmens **2**: 174–180. 1838) segregated *Cornus alba* and *C. sanguinea* as a separate genus *Swida*.[3] Some later authors (e.g., Pojarkova, Not. Syst. Leningrad **12**: 170. 1950), overlooking this valid publication, have considered *Swida* Opiz as a nomen nudum, citing the place of publication as *Seznam Rostlin Kveteny Ceské* (1852), where the name is mentioned without description.

The next author to add to the confusion was Endlicher (Gen. Pl. 798. March, 1839), who recognized three categories of undesignated rank in *Cornus*: a. *Arctocrania*, b. *Tanycrania*, and c. *Thelycrania*. Since Endlicher makes no statement either in the preface or elsewhere as to what he intended these subdivisions to be, they cannot be taken into consideration. Later in the same year, Spach (Hist. Nat. Vég. 8. October, 1939) described three sections in *Cornus* (*Macrocarpium*, *Microcarpium*, and *Cornion*) and segregated *Cornus florida* as the genus *Benthamidia*. *Cornion* Spach is the earliest sectional name for the herbaceous species of *Cornus*. Two years later, Reichenbach (Repert. Herb. 143. 1841) validated Endlicher's *Tanycrania* and *Arctocrania* as subgenera, while still later, Ledebour (Fl. Rossica **2**: 377, 378. 1844) validated *Arctocrania* and *Tanycrania* as sections. *Thelycrania*, originally published by Dumortier as a section (1827), was raised to generic rank by Fourreau (Ann. Soc. Linn. Lyon II. **16**: 394. 1868), who cited only one species, *T. sanguinea*. He thus selected a lectotype for both the section and the genus. As a genus, however, *Thelycrania* is antedated by *Swida* Opiz. Schneider (Illus. Handb. Laubholz. **2**: 437. 1909) attributed subg. *Thelycrania* to Endlicher and subg. *Benthamidia* to K. Koch, but neither author treated these as formal categories. Instead, Schneider, himself, appears to be the first author to validate the names at the rank of subgenus.

Harms (Nat. Pflanzenfam. III. **8**: 266. 1898) described the African *Cornus Volkensii* and placed it in a separate section *Afrocrania*. At the same time, he also segregated the Mexican *C. disciflora* and *C. grandis* as sect. *Discocrania*. Wangerin (Pflanzenreich IV. **229**(Heft 41). 1910) later raised both to subgeneric rank, and Hutchinson (Ann. Bot. II. **6**: 89. 1942) treated *Afrocrania* as a genus.

In 1906, Rydberg (Bull. Torrey Bot. Club **33**: 147) proposed the generic name *Cornella* for the herbaceous species of *Cornus*, but this is a superfluous name for *Chamaepericlymenum* Hill. Nakai later (Bot. Mag. Tokyo **23**: 39. 1909) raised *Arctocrania* Endl. to generic rank, providing

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[3] Various spellings have been used for the generic name *Swida*. The author of the name, Opiz (in Berchtold & Opiz, Oekon.-tech. Fl. Böhmens **2**: 174–180. 1838), used *Swjda*, but later he changed the spelling to *Svjda* (Opiz, Seznam Rostlin Kveteny Ceské 94. 1852). Small (Fl. SE. U. S. 853. 1903) and other authors have used the form *Svida*. The name is derived from the Czech common name for *Cornus sanguinea*, and the differences in spelling are probably attributable to old and modern usage of that language. Following the International Code, the original spelling, *Swjda*, is the form which must be retained. However, Art. 73. Note 6 of the Code states, "The letters 'j' and 'v' must be changed to 'i' and 'u' respectively when they represent vowels." It is proposed that *Swjda* be changed to *Swida* which makes pronunciation easier.

yet another synonym for the same group of herbaceous species. He also raised sect. *Macrocarpium* Spach to generic rank, restricting *Cornus* to the species of Dumortier's section *Thelycrania*, in direct contradiction of Dumortier's typification of *Cornus*.

Adding still further to the already formidable nomenclatural problems, Nieuwland & Lunell (Am. Midl. Nat. **4**: 487. 1916) adopted two new names for segregate genera of *Cornus*, attributing both to pre-Linnaean authors without giving descriptions for either genus, a practice neither outlawed nor recommended by the International Code. These authors recognize the genus *Mesomora* [Rudbeck] Nieuwland & Lunell, which they apply to *Cornus canadensis* L., as still another synonym for *Chamaepericlymenum* Hill. Under *Ossea* Lonicer, both a pre-Linnaean and a post-Linnaean reference are given. The post-Linnaean reference (Adams Lonicers Völlstandiges Kräuter-Buch, B. Ehrhart, ed., with indices by P. Uffenbach. 1783) is an unaltered reprinting of earlier editions of Lonicer, but there is also an *Anhang* by Ehrhart, published in the same year, in which he comments (p. 23) under *Ossea*, "Dieses Gewächses rechter lateinischer Name is nur gar zu wohl bekannt, nemlich *Cornus foemina*, oder *Virga sanguinea*." Thus it seems that Ehrhart cannot be considered to have accepted *Ossea*. Since the International Code states "a name is not validly published when it is not accepted by the author who published it," Lonicer's work (1783) cannot be taken as a place of valid publication of the genus *Ossea*. It must be then attributed to Nieuwland and Lunell (1916). However, Lonicer's description and illustrations are inadequate and do not seem to refer clearly to any species of *Cornus*, no references are cited, and, as a result, the validity of the name seems doubtful. In the sense of Nieuwland & Lunell, *Ossea* is a synonym of the genus *Swida* Opiz.

Other historical items and nomenclatural combinations will be evident from the summary of the nomenclature of the eight subgenera given below. In order to fix the application of the names involved, the type or lectotype species is given for each name. When lectotype species are cited without an author these have been selected here.

Cornus Linnaeus, Sp. Pl. **1**: 117. 1753; Gen. Pl. ed. 5. 1754. (Lectotype species: *C. mas* L.; see Dumortier, Florula Belgica 83. 1827, and P. A. Rydberg, Bull. Torrey Bot. Club **33**: 147. 1906.)

Cornus subg. **Kraniopsis** Rafinesque, Alsograph. Am. 58. 1838. (Lectotype species: *C. paniculata* L'Héritier = *C. racemosa* Lamarck.)

Cornus subg. *Cornus* Rafinesque, *ibid.* (Lectotype species: *C. sanguinea* L.)
Cornus sect. *Thelycrania* Dumortier, Florula Belgica 83. 1827. (Lectotype species: *C. sanguinea* L.; see Fourreau, Ann. Soc. Linn. Lyon II. **16**: 394. 1868.)
Cornus c. *Thelycrania* Endlicher, Gen. Pl. 798. March, 1839.
Thelycrania (Dumortier) Fourreau, Ann. Soc. Linn. Lyon II. **16**: 394. 1868. (Lectotype species: *T. sanguinea* (L.) Fourreau.)
Cornus subg. *Thelycrania* (Dumortier) Endlicher ex Schneider, Illus. Handb. Laubholz. **2**: 437. 1909.

Cornus sect. *Microcarpium* Spach, Hist. Nat. Vég. **8:** 92. 1839. (Lectotype species: *C. sanguinea* L.)

Cornus subsect. *Amblycaryum* Koehne, Gartenflora **45:** 286. 1896. (Lectotype species: *C. corynostylis* Koehne.)

Cornus sect. *Amblycaryum* (Koehne) Nakai, Bot. Mag. Tokyo **23:** 37. 1909.

Swida Opiz in Berchtold & Opiz, Oekon.-tech. Fl. Böhmens **2:** 174–180. 1838, "*Swjda.*" (Lectotype species: *S. sanguinea* (L.) Opiz.)

Ossea [Lonicer] Nieuwland & Lunell in Lunell, Am. Midl. Nat. **4:** 487. 1916. (Type species: *O. instolonea* (A. Nelson) Nieuwland & Lunell in Lunell, Am. Midl. Nat. **4:** 487. 1916.)

Cornus subg. **Mesomora** Rafinesque, Alsograph. Am. 58. 1838. (Type species: *C. alternifolia* L.)

Cornus sect. *Mesomora* (Rafinesque) Nakai, Fl. Sylv. Koreana **16:** 81. 1927.

Cornus sect. *Microcarpium* subsect. *Bothrocaryum* Koehne, Gartenflora **45:** 285. 1896. (Lectotype species: *C. macrophylla* Wallich sensu Koehne = *C. controversa* Hemsley; see Pojarkova, Not. Syst. Leningrad **12:** 169. 1950.)

Cornus sect. *Bothrocaryum* (Koehne) Harms ex Nakai, Bot. Mag. Tokyo **23:** 36. 1909, "*Brothrocaryum.*"

Bothrocaryum (Koehne) Pojarkova, Not. Syst. Leningrad **12:** 169. 1950. (Type species: *B. controversum* (Hemsley) Pojarkova.)

Cornus subg. **Afrocrania** (Harms) Wangerin, Pflanzenreich IV. 229 (Heft 41): 76. 1910.

Cornus sect. *Afrocrania* Harms, Nat. Pflanzenfam. III. **8:** 266. 1898. (Type species: *C. Volkensii* Harms.)

Afrocrania (Harms) Hutchinson, Ann. Bot. II. **6:** 89. 1942. (Type species: *A. Volkensii* (Harms) Hutchinson.)

Cornus subg. **Cornus.**

Cornus sect. *Cornotypus* Dumortier, Florula Belgica 83. 1827. (Type species: *C. nudiflora* Dumortier, nomen superfluum = *C. mas* L.)

Cornus subg. *Eukrania* Rafinesque, Alsograph. Am. 59. 1838. (Lectotype species: *C. mas* L.)

Cornus b. *Tanycrania* Endlicher, Gen. Pl. 798. March, 1839.

Cornus subg. *Tanycrania* Endlicher ex Reichenbach, Repert. Herb. 143. 1841. (Type species: *C. mas* L.; see Endlicher.)

Cornus sect. *Tanycrania* (Endlicher ex Reichenbach) Ledebour, Fl. Rossica **2:** 378. 1844.

Cornus sect. *Macrocarpium* Spach, Hist. Nat. Vég. **8:** 101. October, 1839. (Type species: *C. mascula* L. = *C. mas* L.)

Cornus subg. *Macrocarpium* (Spach) Schneider, Illus. Handb. Laubholz. **2:** 450. 1909.

Macrocarpium (Spach) Nakai, Bot. Mag. Tokyo **23:** 38. 1909. (Type species: *M. mas* (L.) Nakai.)

Cornus subg. **Arctocrania** Endlicher ex Reichenbach, Repert. Herb. 143. 1841. (Lectotype species: *C. suecica* L.)

Cornus a. *Arctocrania* Endlicher, Gen. Pl. 798. March, 1839.

Cornus sect. *Arctocrania* (Endlicher ex Reichenbach) Ledebour, Fl. Rossica **2:** 377. 1844, "*Orctocrania*."

Arctocrania (Endlicher ex Reichenbach) Nakai, Bot. Mag. Tokyo **23:** 39. 1909. (Lectotype species: *A. suecica* (L.) Nakai.)

Chamaepericlymenum Hill, Brit. Herb. 331. 1756. (Type species: *Cornus suecica* L. = *Chamaepericlymenum suecicum* (L.) Graebner.)

Cornus sect. *Cornion* Spach, Hist. Nat. Vég. 8: 103. October, 1839. (Lectotype species: *C. suecica* L.)

Cornella Rydberg, Bull. Torrey Bot. Club 33: 147. 1906. (Lectotype species: *Cornella suecica* (L.) Rydberg.)

Mesomora [Rudbeck] Nieuwland & Lunell in Lunell, Am. Midl. Nat. **4:** 487. 1916. (Type species: *M. canadensis* (L.) Nieuwland ex Lunell.)

Cornus subg. **Discocrania** (Harms) Wangerin, Pflanzenreich IV. **229** (Heft 41): 84. 1910.

Cornus sect. *Discocrania* Harms, Nat. Pflanzenfam. III. **8:** 266. 1898. (Lectotype species: *C. disciflora* Mociño & Sessé ex De Candolle.)

Cornus subg. **Cynoxylon** (Rafinesque) Rafinesque, Alsograph. Am. 59. 1838.

Cornus sect. *Cynoxylon* Rafinesque, Med. Fl. 132. 1828. (Type species: *C. florida* L.)

Cynoxylon (Rafinesque) Small, Fl. SE. U. S. 854. 1903. (Type species: *Cynoxylon floridum* (L.) Small.)

Cornus b. *Tanycrania* Endlicher, Gen. Pl. 798. 1839.

Cornus subg. *Tanycrania* Endlicher ex Reichenbach, Repert. Herb. 143. 1841. (Type species: *C. florida* L.; see Endlicher.)

Benthamidia Spach, Hist. Nat. Vég. **8:** 92. 1839. (Type species: *B. florida* (L.) Spach.)

Cornus Gruppe *Benthamidia* (Spach) K. Koch, Dendrologie **1:** 694. 1869.

Cornus subg. *Benthamidia* (Spach) K. Koch ex Schneider, Illus. Handb. Laubholz. **2:** 453. 1909. (Type species: *C. florida* L.)

Cornus subg. **Benthamia** (C. B. Clarke) Schneider, Illus. Handb. Laubholz. **2:** 454. 1909.

Cornus sect. *Benthamia* C. B. Clarke in Hooker f. Fl. Brit. India **2:** 745. 1879. (Lectotype species: *C. capitata* Wallich in Roxburgh.)

Benthamia Lindley, Bot. Reg. **19:** *tab. 1579.* 1833, not *Benthamia* Richard, Mém. Soc. Hist. Nat. Paris **4:** 37. 1828. (Type species: *B. fragifera* Lindley = *Cornus capitata* Wallich in Roxburgh.)

Dendrobenthamia Hutchinson, Ann. Bot. II. **6:** 92. 1942. (Type species: *D. capitata* (Wallich) Hutchinson.)

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THE CORNACEAE IN THE SOUTHEASTERN UNITED STATES[1]

I. K. FERGUSON

CORNACEAE Dumortier, Anal. Fam. Pl. 33, 34. 1829, "Corneae," nom. cons.
(DOGWOOD FAMILY)

Trees or shrubs [rarely perennial herbs]. Flowers small, bisexual [unisexual in dioecious species], regular. Floral tube adnate to the ovary; calyx lobes small to obsolete. Petals 4 [5], [rarely absent], inserted on an epigynous disc. Stamens equal in number to the petals and alternate with them. Ovary inferior, 1–4-locular, with a single pendulous, anatropous ovule in each locule. Fruit a drupe [rarely a berry]. Embryo straight; endosperm copious. (Excluding Alangiaceae DC., Garryaceae Lindl., and Nyssaceae Dumort.) TYPE GENUS: *Cornus* L.

A rather heterogeneous family of seven to sixteen genera, depending upon the generic and familial concepts adopted, with about 100 species, mainly in north-temperate regions, a few in the Tropics, in Africa, Madagascar, South America, and also in New Zealand; only *Cornus* occurs in eastern North America.

The family has been placed in the Umbellales on the basis of its few-carpellate inferior ovary, reduced calyx, and tendency toward a many-flowered umbellate inflorescence. The anatomy of Cornaceae differs in many respects from that of the Umbelliferae and Araliaceae, but the secretory ducts and extrorse micropyle of *Mastixia* Blume are thought by some authors to link Cornaceae with Araliaceae. Biochemical studies have shown aucubin to be present in Cornaceae but absent from Umbelliferae and Araliaceae. Garryaceae, Alangiaceae, and Nyssaceae are very closely re-

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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 Carroll E. Wood, Jr., and Reed C. Rollins. The treatment follows the pattern established in the first paper in the series (Jour. Arnold Arb. **39**: 296–346. 1958) and continued to the present paper. The area covered includes North and South Carolina, Georgia, Florida, Tennessee, Alabama, Mississippi, Arkansas, and Louisiana. The descriptions apply primarily to the plants of this area, with supplementary information in brackets. References marked with an asterisk have not been seen by the author.

I am grateful to Dr. Wood for his generous suggestions and valuable criticisms and to Dr. George K. Brizicky for his patient guidance and discussion. I am also grateful to Dr. R. H. Eyde for his comments on the manuscript. The typescript was prepared by Mrs. Gordon W. Dillon, and the plate is the work of Arnold D. Clapman.

lated families more or less recently segregated from the Cornaceae. Although studies by Moseley and Beeks and by Eyde (1964) confirm the affinity of Garryaceae with Cornaceae, the highly specialized amentiferous structure of its inflorescence appears to justify treating the group as a separate family. Nyssaceae and Cornaceae have been grouped together as the Cornales, but on the basis of their valvate petals Hutchinson places Cornaceae and Araliaceae (one tribe of which has imbricate petals) in an order Araliales next to the Cunoniales and distinct from the Umbelliferae, which have imbricate petals. Serological studies on *Nyssa* L., *Davidia* Baill., and *Cornus* may be interpreted to support the separation of Nyssaceae from Cornaceae. In anatomy and morphology the Cornaceae resemble the Caprifoliaceae in many ways, and the pollen, in particular, is similar to that of *Viburnum* and *Sambucus.* Metcalfe and Chalk draw attention to a similarity between Cornaceae and Hydrangeaceae in wood anatomy.

Within the family, Harms separated the subfamilies Curtisioideae and Mastixioideae, both with seeds with an adaxial (ventral) raphe, from the Cornoideae, which have seeds with an abaxial (dorsal) raphe. Wangerin divided the Cornoideae into four tribes: Toricellieae, Helwingieae, Corneae, and Griselineae. The Toricellieae and Helwingieae are considered distinct families by some workers, and studies of pollen morphology (Chao) and wood anatomy (Li & Chao) support this treatment. On the basis of wood anatomy, Adams has proposed the removal of *Aucuba* Thunb. and *Kaliphora* Hook. f. to separate tribes. The position of *Corokia* A. Cunningh. is doubtful (cf. Eyde). Engler places it near *Argophyllum* J. R. & G. Forst. in the Saxifragaceae subfam. Escallonioideae. Eyde, on the basis of floral anatomy, rejects the assignment of *Corokia* to Cornaceae, but questions certain points in Engler's alternative taxonomic treatment.

Pollination is probably by insects; *Griselinia* Gmel. is believed to be wind pollinated, but at least one species produces nectar (Percival, New Phytol. **60**: 235. 1961). Some species of *Helwingia* Willd., *Corokia, Griselinia, Aucuba,* and many species of *Cornus* are cultivated for their ornamental value; and some also possess medicinal properties. *Curtisia dentata* (Burm. f.) C. A. Sm. (*C. faginea* Ait.) is a useful African hardwood tree.

Chromosome numbers of $2n = 16, 18, 20, 22, 27, 32, 36, 44$, ca. 72, 120, and 144 have been reported.

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1. **Cornus** Linnaeus, Sp. Pl. **1:** 117. 1753; Gen. Pl. ed. 5. 54. 1754.

Deciduous trees or shrubs [rarely perennial herbs]. Leaves opposite, rarely alternate, simple, usually petiolate, exstipulate; blade entire, or obscurely serrate, pinnately veined, often pubescent, the lower surface occasionally covered with a fine network of short hairs or papillae and sometimes with appressed, erect, or curling, simple or characteristic bifid hairs. Inflorescences terminal or axillary, dichotomously branched, ebracteate cymes or panicles, [or bracteate umbelliform cymes,] or heads (reduced cymes) surrounded by petal-like involucral bracts and an inner ring of small, obtuse, membranaceous bracteoles. Flowers bisexual [unisexual in dioecious species], epigynous, sessile or short pedicellate. Floral tube turbinate, urceolate or campanulate, adnate to the ovary; calyx lobes 4, distinct or obsolete. Petals 4, valvate in bud, inserted on the margin of a fleshy nectariferous disc, oblong or ovate, white, purple, or yellow.

Stamens 4, exserted; filaments filiform or subulate; anthers oblong, 2-locular, dorsifixed, versatile, introrse, longitudinally dehiscent; pollen small or medium, prolate, tricolporate, reticulate or granular [occasionally united in tetrads]. Gynoecium (1)2(3)-carpellate, syncarpous; style single, filiform or columnar, sometimes dilated below the stigma; stigma capitate or truncate; ovary inferior, adnate to the floral tube and to the disc, (1)2(3)-locular, 1 locule sometimes aborting; ovules solitary in each locule, pendulous, anatropous, with abaxial raphe, micropyle superior. Fruit a globose, ellipsoid, or ovoid drupe; stone 2(rarely 1)-seeded, furrowed, rarely with a distinct pit at the apex. Seeds oblong, compressed; endosperm copious; embryo as long as the endosperm, straight, the cotyledons foliaceous, radicle terete and near the micropyle. Embryo sac development of the Fritillaria type in some species, reported to be of the normal (Polygonum) type in others. (Including *Afrocrania* (Harms) Hutchins., *Benthamidia* Spach, *Bothrocaryum* (Koehne) Pojark., *Chamaepericlymenum* Hill, *Dendrobenthamia* Hutchins., *Swida* Opiz.[2]) LECTOTYPE SPECIES: *C. mas* L.; see B. C. Dumortier, Florula Belgica 83. 1827, and P. A. Rydberg, Bull. Torrey Bot. Club **33**: 147. 1906.[3] (Name from Latin, *cornu*, a horn, presumably because of the hardness of the wood.) — DOGWOOD.

A genus of about 60 species, mainly of temperate regions of the Northern Hemisphere, but extending to Central and South America, with one species in Africa; some 17 species in North America and about six in our area.

The treatment of the genus has varied widely, some authors recognizing a number of segregate genera, others treating these divisions as either subgenera or sections. Eight subgenera compose the genus as delimited here (cf. Ferguson, Jour. Arnold Arb. **47**: 100–105. 1966); four are represented in the United States, and three in our area. Only the correct sectional or generic names are given here as synonyms of the subgenera.

All but two of the species in the southeastern United States are members of subg. KRANIOPSIS Raf. (sect. *Thelycrania* Dumort.; *Swida* Opiz), characterized by ebracteate cymose or paniculate inflorescences appearing

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[2] Although usually given as *Svida* and originally published as *Swjda*, the orthography used here seems to be most in accord with the International Code (Art. 73, Note 6), which prescribes the change from "j" to "i," thus making the name pronounceable.

[3] Hutchinson (Ann. Bot. II. **6**: 83–93. 1942) proposed *Cornus sanguinea* L. as lectotype species because it is a more typical representative of the genus and because *C. mas* L. was removed to the genus *Macrocarpium* Nakai (Bot. Mag. Tokyo **23**: 38. 1909). He incorrectly cited Britton and Brown (Illus. Fl. No. U. S. **2**: 660. 1913) as the earliest authors to select *C. mas* as lectotype species. Rehder (Bibliogr. Cult. Trees Shrubs 496. 1949) also adopted *C. sanguinea* as lectotype. However, *Cornus* was effectively typified by Dumortier (Florula Belgica 83. 1827) when he established the section *Cornotypus* which included only *C. mas*. Rydberg selected *C. mas* as lectotype species in 1906, and, in 1908, Britton (N. Am. Trees 741), a year earlier than Nakai proposed his genus *Macrocarpium*, also selected the same species. Furthermore, *C. sanguinea* is a component of both *Swida* Opiz (Berchtold & Opiz, Oekon.-tech. Fl. Böhmens **2**: 174. 1838) and *Thelycrania* (Dumort.) Fourreau (Ann. Soc. Linn. Lyon II. **16**: 394. 1868).

FIG. 1. **Cornus.** a–e, *C. Amomum* subsp. *Amomum*: a, flowering branchlet, × 1/2; b, flower, × 6; c, flower (with petals and stamens removed) in semi-diagrammatic vertical section to show nectariferous disc and two-locular ovary with solitary, pendulous ovules, × 6; d, mature drupe, × 2; e, stone in lateral view and from above, × 4. f–h, *C. florida*: f, flowering branchlet seen from above, × 1/2; g, flower, × 4; h, stone from above and in lateral view, × 4. i, *C. alternifolia*: i, stone in lateral view and from above to show apical pit.

with or after the foliage. *Cornus Amomum* Mill. (*Swida Amomum* (Mill.) Small), distinguished by its usually blue fruit, smooth leaves, dilated style, brown pith, and long calyx lobes, is represented with us by two subspecies treated as distinct species by some authors. Subspecies *Amomum*, $2n = 22$, with leaves rounded at the base and green on the lower surface, extends from southern New England, west to southern Illinois and Kentucky, and south to Tennessee, the Carolinas, Georgia, Alabama, and northern Mississippi; subsp. *obliqua* (Raf.) J. S. Wilson, $2n = 22$, characterized by cuneate leaf bases and white papillae on the lower surfaces of the leaves, occurs from northwestern New England and adjacent Canada, westward to North Dakota, Kansas, and Nebraska, and south to Arkansas and western Tennessee.

Cornus asperifolia Michx. and *C. Drummondii* C. A. Meyer (*Swida asperifolia* sensu Small, *S. Priceae* Small) are distinguished from other species in the subgenus by their scabrid upper leaf surfaces. These two species are closely related, although Wilson has treated the former as a subspecies (*microcarpa* (Nash) J. S. Wilson) of *C. foemina. Cornus microcarpa* Nash (*Swida microcarpa* (Nash) Small) appears to be only a variant of *C. asperifolia. Cornus Drummondii*, occurring from Alabama and western Tennessee to Texas, Arkansas, Nebraska, and Ontario, is separated by its white drupes and white papillose indumentum on the lower surface of the leaves from *C. asperifolia*, a species of the southeastern Coastal Plain from Florida to Georgia, South Carolina, and Alabama with blue drupes and nonpapillose leaves.

The complex *Cornus foemina* Mill. is distinctive in its smooth twigs and the smooth upper surface of the leaves. Subspecies *foemina* (*Swida stricta* (Lam.) Small), characterized by blue fruits, usually flat-topped inflorescences, and red young branches, occurs throughout the southeastern United States and extends to Delaware, Indiana, and Texas. Some workers regard the closely allied *C. racemosa* Lam. (white fruit, usually convex inflorescences, and brown young branches) as occurring in the southeastern United States, but the treatment followed here is that of Wilson, who regards this taxon as *C. foemina* subsp. *racemosa* (Lam.) J. S. Wilson with a distribution to the north of our area.

The frequent hybridization between species of subg. KRANIOPSIS often makes identification difficult. The color of the pith and of the fruit, important taxonomic characters for distinguishing between some of the subspecies, should be recorded by collectors.

The similar subg. MESOMORA Raf. (sect. *Bothrocaryum* (Koehne) Harms ex Nakai; *Bothrocaryum* (Koehne) Pojark.) is distinctive in the alternate leaves, stones with a characteristic deep apical pit, and chromosome number. It includes only *Cornus controversa* Hemsl., $2n = 20$, of eastern Asia, and *C. alternifolia* L. (*Swida alternifolia* (L.) Small), $2n = 20$, widespread in the northeastern United States and adjacent Canada and extending southward through eastern Tennessee, the Carolinas, Georgia, and Alabama to northwestern Florida (Gadsden County), and westward to Minnesota and northern Arkansas.

Subgenus CYNOXYLON (Raf.) Raf. (sect. *Cynoxylon* Raf.; *Benthamidia* Spach; *Cynoxylon* (Raf.) Small), characterized by woody habit, flowers aggregated into sessile heads surrounded by large, white, petaloid involucral bracts, and free, thin-fleshed drupes, is represented by *Cornus florida* L. (*Cynoxylon floridum* (L.) Small), $2n = 22$, widespread in our area (but probably absent from southern Florida) and extending north to southern Maine and Ontario, and west to eastern Texas and Kansas, with the disjunct but doubtfully distinct var. *Urbiniana* (Rose) Wangerin in Mexico (Nuevo Léon and Veracruz). A calciphile, it is one of the most characteristic and conspicuous spring-flowering trees of the eastern United States.

The herbaceous subg. ARCTOCRANIA Endl. ex Reichenb. (sect. *Cornion* Spach; *Chamaepericlymenum* Hill) is represented in the eastern United States by *Cornus canadensis* L., bunchberry, $2n = 44$, of transcontinental distribution northward and sporadic occurrence southward to California and New Mexico, in the West, and to Pocahontas County, West Virginia, in the East. Wherry has suggested that the migration of *C. canadensis* southward "is restricted by its inability to establish itself in soils which are heated above 65° [F.] [18° C.] during the summer."

The morphological relationships between the subgenera appear to be reticulate. (See also Rickett, 1950.) A number of interspecific hybrids are known, but only a single hybrid between subgenera, *Cornus* × *acadiensis* Fern. (*C. alternifolia* × *C. stricta* [*C. stolonifera*]), has been recorded. Basic chromosome numbers of 9, 10, and 11 have been reported: $2n = 18$ in subg. CORNUS; 20 in MESOMORA; 22 in BENTHAMIA, CYNOXYLON, and KRANIOPSIS; and 22 or 44 in ARCTOCRANIA. (A triploid count of 27 has also been recorded for *C. mas*, $2n = 18$.) Serological studies support the distinctness of subg. ARCTOCRANIA, CYNOXYLON, and KRANIOPSIS but show a close relationship between subg. BENTHAMIA (*C. Kousa* Buerger ex Miq., $2n = 22$) and subg. CYNOXYLON (*C. florida* and *C. Nuttallii* Audubon).

Flowers are usually homogamous, but may be proterandrous in subg. ARCTOCRANIA (e.g., *Cornus suecica* L., $2n = 22$), with exposed nectar secreted by the epigynous disc surrounding the style. Pollination is probably accomplished by insects, including small creeping Coleoptera and some Diptera and Hymenoptera. Cross-pollination is favored by the differing lengths of style and stamens, but self-pollination may also occur by the spreading of the stamens to touch neighboring flowers.

Fossils of *Cornus* have been reported from late Cretaceous, Tertiary, and Pleistocene strata. The remains include leaf impressions, stones, wood, and pollen.

Many species, especially *Cornus florida*, are cultivated as ornamentals. *Cornus florida* contains a bitter principle, cornine, which has been used for its medicinal properties. The wood of some species is valuable for its hard, smooth, fine texture and is used for tool handles, cotton reels, meat skewers, and charcoal.

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THE NYSSACEAE IN THE SOUTHEASTERN UNITED STATES [1]

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NYSSACEAE Dumortier, Anal. Fam. Pl. 13. 1829 (A. L. de Jussieu, Dict. Sci. Nat. **35**: 267. 1825, "Nysées"), nom. cons.
(TUPELO FAMILY)

Trees, mostly [polygamous or] androdioecious, with alternate, exstipulate leaves. Flowers small, ± regular, subtended by 1–5 bracts. Floral tube adnate to the ovary in bisexual or ♀ flowers; calyx lobes small or obsolete. Petals usually 5–10 [or absent]; stamens in ♂ flowers usually 10 or more in 2 ± distinct whorls around a nectariferous disc. Ovary inferior 1(rarely 2)-locular [or often 2-locular, or 6–8-locular], with 1 pendulous, apotropous ovule in each locule. Fruit a drupe; each locule of stone opening at apical part by a ± triangular abaxial valve at germination. Embryo straight; endosperm copious. (Cornaceae, in part, of many authors; including Davidiaceae H. L. Li.) TYPE GENUS: *Nyssa* L.

Three genera and seven or eight species, distributed in eastern Asia and eastern North America, mostly in warm-temperate areas. *Camptotheca* Decaisne and *Davidia* Baillon are monotypic genera of China, while *Nyssa* is eastern American-eastern Asian in distribution.

Harms treated *Camptotheca* and *Nyssa* as subfam. Nyssoideae and *Davidia* alone as subfam. Davidioideae of the Cornaceae. Wangerin retained these as the two subfamilies of a separate family, Nyssaceae. A close relationship between Cornaceae and Nyssaceae, supported by evi-

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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 Carroll E. Wood, Jr., and Reed C. Rollins. The treatment follows the pattern established in the first paper in the series (Jour. Arnold Arb. **39**: 296–346. 1958) and continued to the present paper. The area covered includes North and South Carolina, Georgia, Florida, Tennessee, Alabama, Mississippi, Arkansas, and Louisiana. The descriptions apply primarily to the plants of this area, with supplementary information in brackets.

Preserved flowers and fruits were obtained with the aid of Mr. W. W. McNeil, Superintendent, Seashore Natural Area, Virginia Beach, Virginia; Mr. Gurdon L. Tarbox, Jr., Director, Brookgreen Gardens, Murrells Inlet, South Carolina; Prof. Elso S. Barghoorn, Harvard University; and Prof. R. B. Channell, Vanderbilt University. Dr. Wood gave generously of his time and experience to assist me in revising and condensing my earlier publications for this article. I thank Prof. Robert F. Thorne, Rancho Santa Ana Botanic Garden, for his thoughts on the infraspecific variants of *Nyssa sylvatica*. The drawings illustrating *Nyssa* were made by Arnold D. Clapman under the supervision of Dr. Wood.

dence from palynology, floral and wood anatomy, serology, and cytology, has not been challenged in recent years; however, the Nyssaceae are here tentatively treated as a separate family because of their greater number of petals and stamens and their unique triangular germination valves.

The chromosome number of *Davidia* has been reported as $2n = \pm 40$ and that of *Nyssa sylvatica* as $2n = 44$. The latter count may provide further evidence that Cornaceae and Nyssaceae are related, since $2n = 22$ for most species of *Cornus*.

Considering the present small size of the group and its rather limited modern distribution, the Nyssaceae have one of the most remarkable fossil records of all angiosperm families. Excellently preserved fruits have been found in England, continental Europe, Siberia, Japan, and the western United States; nyssaceous pollen is a frequently encountered microfossil in continental deposits of Tertiary age throughout the Northern Hemisphere; and leaf impressions resembling foliage of *Nyssa* are often found in association with the pollen and fruits. Moreover, silicified woods from Japan and from the state of Washington and a lignitized wood from the Netherlands have been assigned to the family. Fossil Nyssaceae are common in all major time zones from the Eocene through the Pliocene; the present restricted distribution of the family is clearly a relatively recent phenomenon connected with Pleistocene glaciation.

Comparative floral anatomy of modern Nyssaceae indicates that in ancestral members the floral parts were more numerous, and this is nicely confirmed by fossils. Many of the oldest fruits are three- or four-carpellate, and vestiges of major vascular bundles provide evidence for the greater number of petals and stamens in these extinct forms. Some of the ancient fruits are also much larger than their present-day counterparts. The affinities of certain fossils from North America are with modern Asiatic Nyssaceae.

Aside from *Nyssa*, only *Davidia involucrata* Baill., dove tree, cultivated to a limited extent for its showy, bracteate inflorescences, is of any economic importance.

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1. **Nyssa** Linnaeus, Sp. Pl. 2: 1058. 1753; Gen. Pl. ed. 5. 1028. 1754.

Deciduous trees, becoming shrubby under adverse conditions of growth; branching markedly excurrent; bark gray, divided into segments by deep fissures; base of trunk enlarged and roots sometimes forming arches when growing in water. Leaves alternate, often crowded near ends of branches, simple, petiolate, exstipulate; blade membranaceous or subcoriaceous, elliptic or ovate to narrowly or broadly obovate, entire (or irregularly dentate, especially on seedlings and on sprouts arising from roots). Inflorescences (or solitary flowers) axillary, pedunculate, produced with the leaves from mixed imbricate buds. Staminate flowers in short racemes or heads; calyx lobes minute; petals 5–10; stamens 8–15, much longer than petals, usually in 2 ± distinct whorls, the outer whorl antipetalous, the

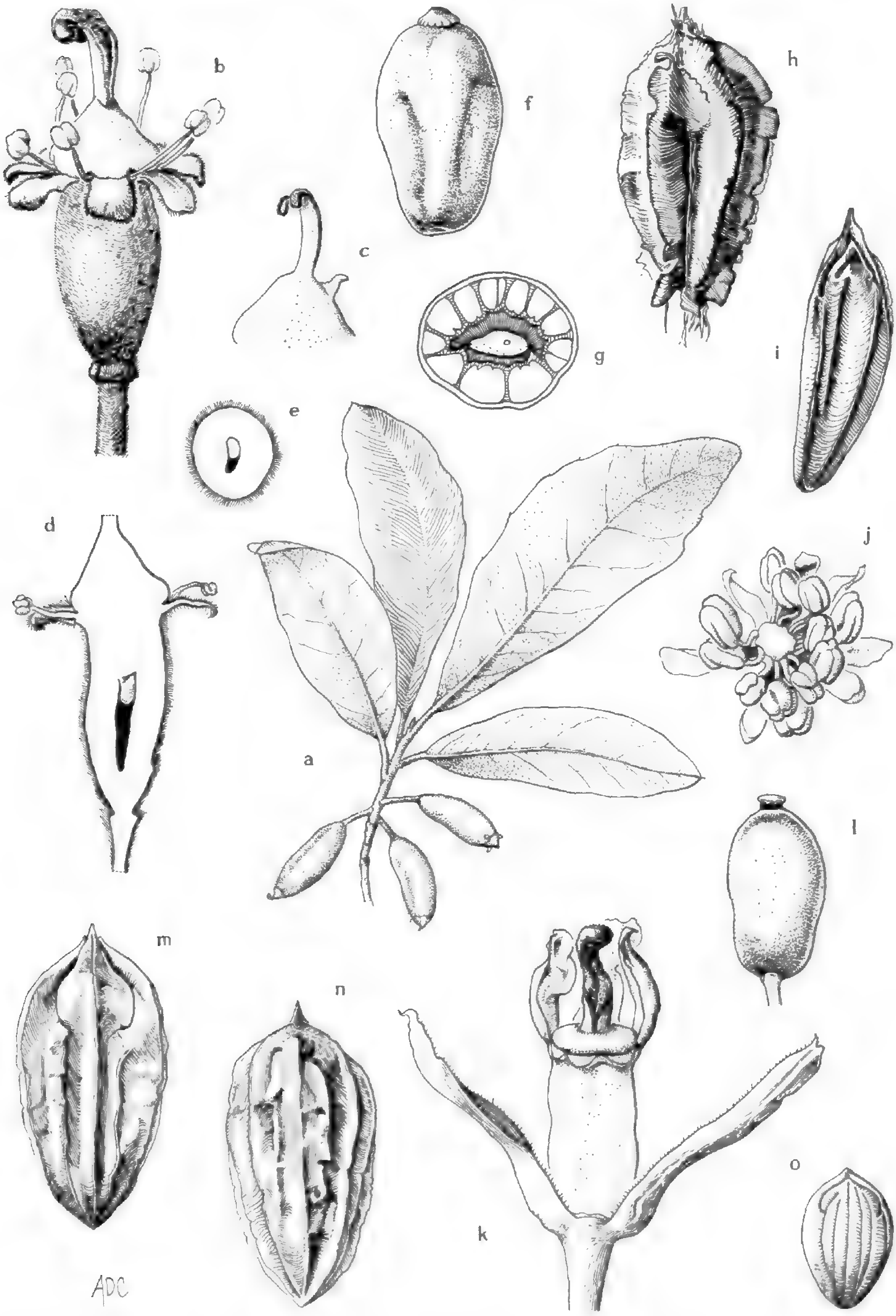

FIG. 1. **Nyssa.** a–i, *N. ogeche*: a, branchlet with immature fruit, × 1/2; b, functionally unisexual flower — note scars of fallen bracts at base of ovary, × 4; c, disc and style with rudimentary second style, × 4; d, flower in diagrammatic vertical section to show locule and ovule, × 4; e, diagrammatic cross section of ovary and ovule, × 4; f, mature fruit, abaxial surface, × 1; g, immature fruit from "a" in diagrammatic cross section to show radicle of embryo, endosperm

inner alternipetalous; anthers on short, green, filiform filaments, introrse, longitudinally dehiscent, basifixed; pollen tricolporate; gynoecium absent, except for occasional presence of stylar rudiment at center of pulvinate disc. Bisexual, ♂-sterile, or ♀ flowers solitary or in inflorescences of 2–4 [or more] and sessile (in ours) on slender peduncles; floral tube urceolate or campanulate, densely tomentose to glabrous, adnate to the ovary; calyx lobes, when present, usually 5; petals 5–8, tomentose or glabrous, ovate or oblong; stamens often visibly abortive, fewer than in ♂ flowers or lacking, about equal in length to petals; nectariferous disc pulvinate or conical; gynoecium syncarpous, 1 (rarely 2)-carpellate; style 1 (rarely 2, more often with only the rudiment of a second style); stigma reflexed or revolute, abaxially sulcate; ovary inferior, adnate to floral tube and disc, usually 1-locular (or 2-locular when 2 styles are present) and pseudomonomeric, with 1 apotropous, 1-integumented ovule pendent from the axile placenta near apex of (each) locule. Drupe ovoid or ellipsoid, blue-black, purple, or red, with corky epidermal spots, crowned by the persistent disc; outer tissues fleshy; woody endocarp ovate, obovate, or elliptic in outline, sometimes flattened abaxially, bearing broad longitudinal ridges, sharp ridges, or papery wings. Seed conforming to locule; seed coat membranaceous. TYPE SPECIES: *N. aquatica* L. emend. Du Roi; see Eyde, Taxon 13: 129. 1964. (*Nyssa* or *Nysa,* the name of a nymph, applied by Linnaeus in the belief that all members of the genus are aquatic; cf. *Hortus Cliffortianus* 462. 1738.) — TUPELO, GUM.

Three or four species in North America and two in southeastern Asia. *Nyssa sylvatica* Marsh. var. *sylvatica* (including vars. *dilatata* Fern. and *caroliniana* (Poir.) Fern.), black gum, sour gum, or pepperidge, $2n = 44$, is a common constituent of moist forests from Maine to southern Florida, west to Texas (Brazos River), Oklahoma, eastern Kansas, Illinois, and Michigan, with disjunct Mexican stations in Hidalgo, Puebla, and Chiapas. A tree frequently 20 m. tall (occasionally more than 25 m.), it is characterized by entire-margined obovate to elliptic leaves; pediceled staminate flowers; two, three, or four fertile flowers on each peduncle; blue-black ovoid (to globular) drupes 1–1.5 cm. long with five distinct calyx lobes; and stones with low, rounded ridges. The var. *biflora* (Walt.) Sarg. (including *N. ursina* Small), swamp black-gum, $2n =$ ca. 44, differs in its narrower leaves more gradually tapered at base, shorter fruiting peduncles, and a predominance of paired fertile flowers (although one or three may occur). It is largely confined to very wet soils or standing water in swamps

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(stippled), developing endocarp (note germination valve, cf. "i"), and papery wings in mesocarp, × 2; h, mature stone with papery wings — note vascular bundle between wings, × 2; i, same, wings removed, abaxial surface with germination valve, × 2. j–n, *N. aquatica*: j, staminate flower seen from above, showing petals, stamens, and disc, × 4; k, carpellate flower before anthesis, stigma and style not fully developed, three petals removed, × 4; l, mature fruit, × 1; m, stone, abaxial surface, showing germination valve, × 2; n, same, adaxial surface, × 2. o, *N. sylvatica*: stone, abaxial surface, showing germination valve, × 2.

of the Coastal Plain from eastern Texas to eastern Virginia. This variant is treated as a species, *N. biflora* Walt., by some authors, but the morphological differences that separate it from var. *sylvatica* are not as great as those that distinguish undisputed species of *Nyssa,* and plants are found that are intermediate in character between the two taxa. Since var. *biflora* can be roughly delimited ecologically, geographically, and morphologically, some authors may prefer to treat it as a subspecies.

The closest relative of *Nyssa sylvatica* is *N. sinensis* Oliver, of mesophytic forests in southern China and Burma. *Nyssa sinensis* is notable for having pediceled fertile flowers borne mostly four in a cluster and in commonly having two styles and a bilocular ovary. Of the two, *N. sinensis* is morphologically more primitive and somewhat less winter hardy. Fossil materials show that the subgeneric stock which gave rise to this pair of species has been in existence since early Tertiary times and that it was distributed around the Northern Hemisphere before the Pleistocene glaciation.

Although bearing no close relationship either to each other or to the *Nyssa sylvatica* alliance, *N. aquatica* L. and *N. ogeche* Bartr. ex Marsh. share in common capitate staminate inflorescences, solitary fertile flowers with obsolete calyx lobes, and drupes longer than 2 cm. *Nyssa aquatica* has leaves with coarse, irregularly distributed mucronate teeth; purple, oblong drupes with the floral tube constricted below the flat disc; and mucronate stones with eight to ten sharp longitudinal ridges. It is common in backwaters of the Mississippi Embayment and Gulf and Atlantic coastal plains, reaching its limits in southern Illinois, eastern Texas, northern Florida, and southeastern Virginia. In contrast, *N. ogeche* (including *N. acuminata* Small) has leaves with variable margins; hairy-peduncled red drupes without a constriction beneath the conical disc; and sharp-pointed stones with about 12 ridges, their crests extended as wide, papery wings. Reaching only about 10 m. (*vs.* 33 m. in *N. aquatica*), it grows only in swamps of southern Alabama, northern Florida, southern Georgia, and southernmost South Carolina. Anatomical features of the fruit suggest an affinity between *N. aquatica* and *N. javanica* (Blume) Wangerin, of southeastern Asia.

Locally, some nyssas develop a shrubby form when subjected to adverse growing conditions, such as periodic burning; the segregation of these forms as separate species (*Nyssa acuminata, N. ursina*) seems unsupportable.

The tolerance of *Nyssa* species for saturated soil and standing water is remarkable. Of our species, only *N. sylvatica* var. *sylvatica* is found in upland situations; the others are characteristic of deep fresh-water swamps, where they occur in dense stands, with *Taxodium* the most frequent associate. The genus contributes a substantial proportion to the pollen-rain in fresh-water swamps; it is not surprising, therefore, that *Nyssa* is an important entity in palynological studies of fresh-water peats and brown coals. It is clear that many extinct species of the genus occupied aquatic habitats like their modern counterparts. Some of the brown coals that have yielded nyssaceous pollen and fruits originated as long ago as the Eocene epoch. Although aquatic nyssas can grow in sites where water rises annually to depths of five feet or more and seeds can remain viable after months of submergence, periodic drought is required for germination and perpetuation of the species. Fruits float well, and water currents undoubtedly play a major role in distributing the aquatic species. The fruits of *N. sylvatica,* on the other hand, are relished by birds, which apparently aid in maintaining the wider distribution of this species.

Pollination is by insects, but Wodehouse reports the collection of airborne pollen about 150 m. from a tree of *Nyssa sylvatica* var. *sylvatica.*

The leaves of *Nyssa sylvatica* var. *biflora* have the capacity for accumulating unusually large amounts of cobalt, a phenomenon which has been used in evaluating the cobalt status of soils.

In the United States, *Nyssa* species annually provide more than 200 million board feet of lumber. Although a tendency to warp because of interlocking grain makes the wood unsuitable for many purposes, it is used extensively for boxes and crates, as well as for furniture, flooring, and paper pulp. The light wood from roots and stumps of *N. aquatica* was formerly used for floats and for a kind of surgical sponge called "tupelo tent." *Nyssa sylvatica* is cultivated for its colorful autumn foliage. Plantings of *N. ogeche* have been undertaken in western Florida in an effort to increase the production of the highly regarded tupelo honey; fruits of this species can be made into a preserve, "ogeechee limes."

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DIVISION OF PLANT ANATOMY
SMITHSONIAN INSTITUTION

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

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ARALIACEAE A. L. de Jussieu, Gen. Pl. 217. 1789, "Araliae," nom. cons. (GINSENG FAMILY)

Perennial herbs, vines, shrubs [or trees, rarely scandent epiphytes]. Leaves alternate on the stem or basal from the rhizome, petiolate, [simple,] palmately compound or pinnately or ternately compound or decompound, the stipules either adnate (in varying degrees) to the base of the slightly sheathing petiole or wanting. Inflorescence basically umbellate, the umbels many flowered, solitary or arranged in panicles, racemes [corymbs, or rarely in compound umbels], the peduncles and pedicels subtended by lanceolate, deciduous or persistent bracts. Flowers regular, bisexual and/or unisexual, the plants polygamomonoecious, polygamodioecious, or dioecious. Floral tube adnate to the ovary, cupuliform, obconic, or cylindrical, articulated or continuous with the pedicel; calyx lobes 5, small, deltoid [or the apex of the floral tube merely undulate], persistent. Petals 5[–10], valvate or imbricate in bud, broad [or narrow] at base, greenish white to pink, arising from the margin of a fleshy, epigynous, flattened or cupuliform nectariferous disc, free and separately deciduous or ± connate and falling as a unit. Stamens 5 [to many], generally as many as the petals and alternate with them, inserted epigynously; filaments filiform [or ligulate]; anthers oblong [to subglobose], dorsifixed, versatile, 2-locular, longitudinally dehiscent; pollen usually 30–40 μ long, oblate-spheroid [to prolate], 3-colporate, the pores often transversely elongated, the exine reticulate. Gynoecium 2–5(6)[–15]-carpellate, syncarpous; styles persistent, generally as many as the carpels, distinct or

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The author is indebted to Dr. Lily M. Perry for references to Chinese medicinal uses of *Panax* and to Dr. Wood for his generous assistance and suggestions. Harry E. Ahles and Wilbur H. Duncan have kindly contributed information on *Hedera* in the Carolinas and Georgia, respectively.

united for a short distance above the disc [or completely united into a cone or column, or rarely wanting and the stigmata sessile]; stigmatic surfaces terminal and/or along the adaxial surface of each style; ovary inferior, 2–5(6)[–15]-locular, the wall adnate to the floral tube, the apex fused to the disc; ovules 2–5(6)[–15], one in each locule, anatropous, epitropous, pendulous, the raphe ventral, the placentation axile. Fruit a subglobose [or ellipsoid], sulcate [or smooth] drupe, bearing the persistent styles and calyx lobes; exocarp thin, this and the fleshy mesocarp drying to a membranaceous covering holding together the 2–5(6)[–15] oblong, laterally flattened [or globose] stones (pyrenes) [in one genus the fruit dry and the carpels partly separating]. Seeds with thin seed coat; endosperm abundant, uniform [or ruminate]; embryo straight, in the micropylar end of seed, minute at maturity of seed, the radicle superior. TYPE GENUS: *Aralia* L.

A predominantly woody family of about 60 genera and 750 species, with the two major centers of speciation, tropical America and Indo-Malaya, sharing few genera; represented in the southeastern United States by *Aralia* and *Panax*, both of eastern American-eastern Asiatic distribution, and possibly by the introduced *Hedera Helix* L.[2]

The familial classification generally followed is that of Harms, who divided the group on the basis of somewhat unsatisfactory characters of aestivation and shape of petals into three tribes: Scheffleraeae (petals with a broad base, valvate in bud), Aralieae (petals with a broad base, ± imbricate in bud), and Mackinlayeae (petals narrowed at the base, valvate in bud). Viguier later recognized ten tribes (invalidly published) based mainly on anatomical characters. No modern treatment is available for the whole family, and few of the genera have been monographed, making it necessary to rely almost solely on regional treatments for determination of species and information regarding their biology.

The Araliaceae are closely allied to the Umbelliferae, but the latter differ in being chiefly herbaceous and in possessing consistently bicarpellate dry fruits, the carpels of which separate at maturity. Anatomically, the two families are very similar. The Araliaceae are notable for secretory canals in the pith, phloem, and cortex, the distribution of which is valuable in identifying the species and, to a more limited extent, in recognizing the genera. The pollen of Araliaceae is similar to that of the Umbelliferae and Cornaceae.

In a study of some woody Umbellales, Rodriguez (p. 276) has sum-

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[2] *Oplopanax horridus* (J. E. Sm.) Miq., which ranges from Alaska, south to California, and east to Montana, with disjunct stations in the Thunder Bay District, Ontario, and Isle Royale, Michigan, has recently been reported in an ecological study from the Coastal Plain of South Carolina (Bull. Torrey Bot. Club **92**: 357, 363. 1965). The South Carolina plant is undoubtedly *Aralia spinosa*, not *Oplopanax horridus*. *Aralia spinosa* is common in South Carolina, while the easternmost station for *Oplopanax* is more than a thousand miles away. It seems likely that a confusion in common names ("devil's club" vs. "devil's walking stick") led to the misidentification. — C. E. W.

marized what he believes is the relationship of the Araliaceae to related families: "Although the Umbelliferae form highly specialized expressions of characters already present in the Araliaceae, no linear phylogenetic sequence involving existing genera may be postulated. *Myodocarpus* [a small araliaceous genus endemic to the serpentine massifs of New Caledonia], whose fruit approximates most that of the Umbelliferae, resembles rather the Cornaceae in its wood anatomy. Both families, Umbelliferae and Araliaceae, apparently diverged from a single ancestral source. Of the tribes of Araliaceae, the Mackinlayineae [Mackinlayeae Harms] appear to be closest to the Umbelliferae on anatomical grounds. The information available on Cornaceae, Nyssaceae, and Garryaceae does not conflict with the assumption that they too may be divergent offshoots of the same source. Within the complex of families, the Umbelliferae are the most advanced in habit, fruit type, and secondary-xylem characteristics; the Garryaceae are the most advanced in flower morphology; the Araliaceae occupy a wide central position bridging the distance between those advanced families and the more primitive Cornaceae and Nyssaceae."

The fossil record of Araliaceae, represented by leaves and pollen of several genera, is extensive. Leaves of *Aralia* and *Hedera* are reported from the Upper Cretaceous and Palaeocene of Alaska, far north of their present ranges. *Panax* is reported from the Oligocene of Colorado, and the tropical American *Oreopanax* Dec. & Planch. has been recorded from the Eocene of Tennessee, Mississippi, Arkansas, and Texas, and the Miocene of Oregon. Another tropical genus, *Schefflera* J. F. & G. Forst., has been reported from the Eocene of Tennessee and Kentucky. The Cretaceous occurrence of members of the Araliaceae places it among the oldest known angiosperm families.

Chromosome numbers of $2n = 22$, 24, 44, 48, ca. 54, 96, ca. 127, and 192 have been reported, the most frequent numbers being $2n = 24$ and 28.

The family is of little economic importance. Rice paper, a soft, velvety material which finds limited use in the manufacture of artificial flowers, is the thinly sliced pith of *Tetrapanax papyriferus* (Hook.) K. Koch, a monotypic genus from Formosa and China. Roots of *Panax* are valued in China for medicinal use. About 28 genera are cultivated as ornamentals in the United States.

The European ivy, *Hedera Helix* L., widely cultivated in eastern North America, is known to reproduce vegetatively to some degree as a waif around dumping places in scattered parts of the southeastern United States. In some areas of southeastern Virginia it appears to be truly naturalized, but it is uncertain whether this is so elsewhere and whether it ever spreads by seeds. Both the vars. *Helix*, $2n = 48$, and *hibernica* (Kirchn.) Jaeger, $2n = 96$, are said to be "naturalized in wooded areas of Virginia and North Carolina" (Lawrence). *Hedera Helix* is easily distinguished from other species by its 4–10-rayed stellate hairs; in the four other species the hairs are scaly or scalelike. *Hedera* is of special morphological interest because of its distinctive juvenile and adult forms, the unbranched juvenile stems climbing by adventitious rootlets and bearing lobed leaves lying in a single plane, in contrast with the nonclimbing, branched and shrubby adult flowering stems with their unlobed leaves circling the stem. The leaves of juvenile stems are necessary for the determination of varieties, for within a given species of *Hedera* the leaves of adult stems do not show similar variation. The juvenile leaves of *H. Helix* var. *Helix* are rarely more than 6 cm. long, dark green with prominently whitish veins above; those of var. *hibernica* are glossier and larger (to 13 cm.) with green venation above. A number of references dealing with *Hedera* have been included with the family references.

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KEY TO THE GENERA OF ARALIACEAE

General characters: *perennial herbs, shrubs, trees, or vines with alternate, often compound or decompound leaves; inflorescence basically an umbel; flowers regular, generally 5-merous; ovary inferior, the ovules solitary and pendulous in each locule; fruit a drupe, with 2–5 or more oblong stones.*

A. Leaves simple, lobed or entire; vines climbing by adventitious roots. .... [*Hedera.*]

A. Leaves compound; perennial herbs or shrubs to small trees.

  B. Leaves ternately or pinnately compound or decompound, alternate or basal; inflorescence of 2 to many umbels; fruit purple or black. .... 1. *Aralia.*

  B. Leaves palmately compound, whorled at the summit of the stem; inflorescence a solitary umbel; fruit red or yellow. .... 2. *Panax.*

Tribe ARALIEAE

1. **Aralia** Linnaeus, Sp. Pl. 1: 273. 1753; Gen. Pl. ed. 5. 134. 1754.

Glabrous or spinescent perennial herbs, shrubs, or small trees, with stout, elongate rhizomes, our species generally inhabiting rich, moist woods. Leaves alternate on stem or (in acaulescent species) arising directly from rhizome; petiole broad at base and partially fused with stipules, glabrous or with prickles; blade pinnately or ternately compound or decompound, the leaflets composing each pinna 3 to many, ovate to lanceolate-elliptic [or orbicular], obliquely cordate to acute or rounded at base, acute to acuminate at tip, glabrous [to densely pubescent], the margin finely to coarsely serrate or biserrate. Inflorescence axillary, terminal, or basal, the umbels solitary or paniculate [rarely compound]. Flowers 5-merous, bisexual and/or unisexual, the plants reportedly polygamomonoecious or dioecious [or polygamodioecious]. Floral tube cupuliform, obconic, or cylindrical, articulated with pedicel; pedicel slightly swollen at apex beneath flower and bearing small involucral bracts. Petals greenish white, oblong, the apex inflexed, valvate to slightly imbricate in bud, arising from the margin of the flattened disc, separately deciduous. Stamens introrse in bud; filaments long in ♂ flowers, short in ♀ flowers. Gynoecium (2–)5(6)-carpellate; styles (2–)5 (6), completely free or connate for a short distance above the disc, much shorter than stamens in ♂ flowers, much longer in ♀ flowers; stigmatic surfaces terminal; ovary inferior, (2–)5(6)-locular, each locule with a single ovule. Fruit a subglobose purple to black drupe with (2–)5 (6) oblong, laterally flattened stones. LECTOTYPE SPECIES: *A. racemosa* L.; see N. L. Britton, N. Am. Trees 733. 1908. (Etymology of name obscure; adopted by Linnaeus from Tournefort, who first received seeds of a plant bearing this name from Holland [Elemens Bot. 1: 249. 1694]. According to Fr. Marie-Victorin [Fl. Laurent. 411. 1947], the name is of American Indian origin [perhaps Iroquoian, *fide* Webster's New Int. Dict. ed. 2. 1959] and was communicated to Tournefort by the Quebec physician Sarrazin.)

A genus of about 30 species in six sections, with eight species indigenous to North America, the remainder in Asia and Malesia. Three, perhaps four, species range into the Southeast, the most widespread being *Aralia spinosa* L. (sect. ARBORESCENTES Harms), $2n = 24$, a shrub or small tree with stout, often curved prickles, bipinnate leaves up to 75 cm. long, and a showy, compound terminal panicle of umbels. Popularly known as Hercules' club or devil's walking stick, it occurs locally throughout our area, except in southern Florida, in and along edges of damp woods. It is occasionally cultivated for the somewhat tropical appearance of its leaves and inflorescence. *Aralia racemosa* L. (sect. ARALIA, § *Genuinae* Harms), spikenard, widely distributed outside the southeastern United States, is known or reported from scattered counties in Tennessee, North and South Carolina, and northern Georgia, Alabama, and Mississippi. The plant is an unarmed perennial herb with bipinnate leaves, the lower pinnae having more leaflets than the upper ones, and a compound, paniculate, terminal inflorescence. The dried rhizomes have been used, without medical basis, as a home remedy in the treatment of rheumatic fever, syphilis, and dermatoses. *Aralia nudicaulis* L. (sect. NANAE Harms), wild sarsaparilla, $2n = 24$, of northern, almost transcontinental, distribution, but with a southern extension through the Blue Ridge physiographic province to northern Georgia, is easily recognized by its glabrous, acaulescent habit; ternately divided leaves, the pinnae of which are 3–5-foliolate; and scapose inflorescence. A fourth species, *A. hispida* Vent. (sect. HUMILES Harms), is reported in various floras as extending south in the mountains to North Carolina, but its presence there has not been confirmed. It is known with certainty as far south as Augusta County, Virginia, and Pocahontas County, West Virginia. A perennial herb, it is densely bristly, especially near the base, and produces several short, clustered stems from a stout horizontal rhizome.

Twenty-five fossil species of *Aralia* have been described from the Tertiary of North America, several from areas no longer within the range of the genus. Leaves have also been reported from the Upper Cretaceous (see family discussion).

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2. **Panax** Linnaeus, Sp. Pl. 2: 1058. 1753; Gen. Pl. ed. 5. 481. 1754.

Perennial herbs of moist, rich woods; stem unbranched, erect, arising from a short rhizome and an elongate, often branched, or globose, unbranched tuberous root; base of stem subtended by a few membranaceous [or fleshy], deciduous [or persistent] scales. Leaves 1–5, generally 3, in a single whorl at summit of stem, palmately compound, membranaceous, exstipulate, subtended by a narrow, lanceolate bract; leaflets 3–5, mostly 5, petiolulate or sessile, glabrous or with sparse [to dense] setae along the veins on the upper (adaxial) surface, narrowly elliptic to obovate, the base acute to rounded, the apex acute to long acuminate or obtuse, the margin coarsely to finely serrate or biserrate. Inflorescence a single long-peduncled, terminal umbel of many flowers [rarely 2–6 umbels arising at irregular intervals along the peduncle], the pedicels subtended by lanceolate bracts. Flowers bisexual and/or unisexual, the plants hermaphroditic or polygamodioecious (reportedly also polygamomonoecious). Floral tube obconical or cylindrical, articulated with the pedicel in bisexual and

♀ flowers, continuous in ♂ flowers; pedicel slightly swollen at the apex beneath the flower in all but the ♂ flowers; lobes of the calyx 5, broadly deltoid, small to minute. Petals greenish white to white or pink, oblong or broadly ovate, slightly imbricate in bud, arising from the margin of the cupuliform nectariferous disc, generally separately deciduous, occasionally coherent and falling together. Stamens wanting in ♀ flowers. Gynoecium 2- or 3-carpellate, reduced to a single column in ♂ flowers; styles 2 or 3 (in bisexual and ♀ flowers only), arising from the center of the disc, free to the base or slightly united, the apices and adaxial surfaces stigmatic; ovary 2- or 3-locular, generally wanting in ♂ flowers; ovules 2 or 3. Fruit a red or yellow, subglobose, 2- or 3-sulcate drupe with 2 or 3 oblong, laterally flattened [or globose] stones. LECTOTYPE SPECIES: *P. quinquefolius* L.; see Britton & Brown, Illus. Fl. No. U. S. ed. 2. **2**: 618. 1913. (Name Greek and Latin, *panax* [= panacea], an herb to which was ascribed the power to heal all diseases, from Greek, *panakes*, all-healing.[3])

An eastern American-eastern Asiatic genus of about seven species, the two American species occurring in our area. *Panax trifolius* L., dwarf ginseng, usually not over 20 cm. tall, with a globose root, sessile leaflets, often unisexual flowers, three styles, and yellow fruits, extends southward along the mountains from Quebec into Tennessee, North Carolina, and northern Georgia. *Panax quinquefolius*, ginseng, 20–60 cm. tall, with a fusiform root, petiolulate leaflets, mostly bisexual flowers, two styles, and red fruits, ranges from Quebec to Minnesota, south to Oklahoma and Georgia, but has become rare in the wild because of exportation of its tuberous roots to China, where they are esteemed for their reputed curative powers.

The closely related Asiatic *Panax Ginseng* C. A. Meyer (*P. Schin-seng* T. F. L. Nees),[4] $2n = 44$, has been used for centuries by the Chinese, who believe the resemblance of the roots to the human figure signifies their power to cure illnesses. The common name in China, "schin-seng," "jen-seng," or "ginseng," means "essence of the earth in the form of a man."

The first description of ginseng by a European was published in 1714 by Père Jartoux, a missionary in China. Soon afterward, Père Lafitau, a missionary among the Iroquois in Quebec, found a similar plant (*Panax quinquefolius*) growing at Montreal. Exports of the dried roots to China

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[3] A number of recent authors have treated *Panax* and its compounds (e.g., *Dendropanax*, *Oplopanax*, *Tetrapanax*) as neuter instead of masculine, contrary to Recommendation 75A of the International Code of Botanical Nomenclature (1961). The classical gender of *Panax* is masculine in both Greek and Latin; it is immaterial that Linnaeus treated it as neuter. See A. C. Smith's pertinent comments in N. Am. Fl. **28B**: 9. 1944.

[4] Although *Panax Schin-seng* T. F. L. Nees (Ic. Pl. Medicinal. fasc. 5, *pl. 16.* [conspectus *pl. 70.*] 1833) has been widely used for this species, this name was superfluous when published, for *P. Schin-seng* expressly included the earlier and legitimate *P. pseudoginseng* Wallich (Pl. Asiat. Rar. **2**: 30. *pl. 137.* 1831) *Panax Schin-seng* is thus illegitimate under Art. 63 of the International Code. The earliest legitimate name available is *P. Ginseng* C. A. Meyer (Bull. Phys.-Math. Acad. Sci. St.-Pétersb. II. **1**: 340. 1843).

soon began, probably at first by way of France or England, but later directly from northeastern American ports. In 1860, alone, 600,000 lbs. of dried roots of *P. quinquefolius* were exported to China; in 1886, the value of exported roots was $998,332 (Butz). The export of ginseng has greatly declined since World War II, but even in 1957 approximately 100,000 lbs. were shipped, mainly to Hong Kong, with collectors or growers receiving 20–24 dollars a pound for wild roots and some 40 per cent less for cultivated roots (Williams). Populations of wild ginseng have been greatly depleted in the eastern United States by "sang" (a contraction of ginseng) diggers who dig the roots in the spring and summer before the plant produces seeds. Cultivation of the species has been attempted, but *Alternaria* blight and other fungal diseases have discouraged many growers. Today there are relatively few growers; the largest is Fromm Bros., Inc., with about 100 acres under cultivation in Hamburg, Wisconsin.

Originally, the most valuable roots were those of *Panax Ginseng* grown in Chinese imperial gardens. Now the most valuable are those from Manchuria and Korea, the roots of the American *P. quinquefolius* and the Japanese *P. japonicus* (T. F. L. Nees) C. A. Meyer (*P. Ginseng* var. *japonicus* (T. F. L. Nees) Makino) being considered less effective. Now rare in the wild as a result of collecting, ginseng is currently being cultivated in both Korea and Manchuria. *Panax Ginseng* is grown from seeds which are collected in the fall when the embryo is not yet completely developed. Seeds must be stored for a year under moist conditions, with a three- to four-month cold period during which the embryo lengthens from 0.3 to 4.5 mm., and the surrounding endocarp splits along one suture. The stratified seeds are sown the following fall for germination in the spring. Five or six years' growth is required before flowering begins.

The germination and maturation of *Panax quinquefolius* is apparently similar to that of *P. Ginseng*. Characters used to distinguish the species pair are minor: the slope of the base of the leaflets and the degree of persistence of the fleshy or membranaceous scales at the base of the stem.

The root, generally ground to a powder and made into a tea, is said to have a stimulating effect, enhancing digestion, blood circulation, and sexual desires, and is believed by users to be valuable in treating fatigue, nervous disorders, and blood diseases. At present there is little sound evidence that the constituents of the roots (which seem to be approximately the same in the American and Asian species) act as more than a mild stimulant. The major components are a glucoside, panaquilon; a saponin, panaxine; and a volatile oil, panacen. In addition, the roots contain mucilage, resin, a hormone of the steroid group, and vitamins B_1 and B_2.

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NOTES ON SOME PLANTS OF PUERTO RICO

RICHARD A. HOWARD

AMONG SOME GENERAL BOTANICAL COLLECTIONS made during the initial stages of a research program on the mossy or elfin forests of eastern Puerto Rico (a forest type found at the summit of several peaks in the Luquillo Mountains) are several plants worthy of special mention or requiring new names to permit their proper use in other publications.

The research program on the mossy or elfin forest of higher elevations is supported by grant GB-3975 from the National Science Foundation. Special acknowledgement is also made of the hospitality and the physical assistance rendered in this program by Mr. Joseph B. Martinson. The illustrations were prepared by Miss Judy Appenzeller. Cytological information has been supplied by my colleague Dr. Lorin Nevling.

Cordia wagnerorum sp. nov. PL. I.

Frutex scandens, ad 4 m. altus; folia lanceolata, irregulariter obtuseque dentata, iridescentia, scabrida cum umbonibus parvis solitariis, umbonibus singulis apice uno pilo brevi rigidoque coronatis; inflorescentia sessilis, axillaris, 3–5-flora; calyx et corolla quadripartita; stamina 3–4; fructus ruber, drupaceus.

A weak shrub with trailing or scrambling branches reaching 4 m. in length. Young stems brown and densely covered with arching, ascending, stiff hairs. Petioles 8–12 mm. long, pubescent with conspicuous appressed ascending hairs and globular glandular hairs. Leaf blades lanceolate, 5.5 × 2.5, 8 × 3, to 10 × 3.5 cm. long and wide, apex short and acute, base acute to cuneate, margin undulate in the lower portion, bluntly irregularly dentate in the upper half or two-thirds; primary veins arcuate, ascending, 8–10 pairs, not conspicuously anastomosing; upper surface grayish green and iridescent when fresh, with distinct, isolated umbos each topped with a short, stout, curved and rigid trichome producing a scabrous condition. smaller curved trichomes scattered on the surface or marginal; lower surface lighter in color with abundant glandular exudates when dry. Inflorescence an axillary sessile cluster of 3 to 4 flowers. Calyx ovoid, tube 2.5 mm. long, the lobes 4, greenish white, broadly triangular, 2.5 mm. long, with simple elongate thin-walled hairs and globular resinous hairs; corolla white, the tube 5–7 mm. long, the lobes 4, narrowly triangular, 1–1.5 mm. long, glabrous outside; stamens 3 or rarely 4, attached above the middle of the tube in the few flowers examined, the free portion of the filament 1 mm. long, the attached portion bearing long white-pilose pubescence, anthers oblong, 1 mm. long; ovary ovoid, 2–3 mm. in diameter, glabrous, the style 2–2.5 mm. long, slightly flattened, glabrous, bifid, each portion divided nearly to the base, the stigmatic areas 1–2 mm. long. Fruit ovoid, 4–6 mm. in diameter, slightly fleshy, red, endocarp warty, style persistent, the persistent calyx surrounding basal portion of fruit; fertile seed unknown.

Puerto Rico. South side of Luquillo Mountains along the El Toro trail 0.5 km. from Route 191. Collected in flower October 4, 1964, *Richard J. Wagner 695* (holotype, A); collected in fruit in November, 1964, *R. A. Howard 15735* (A).

This species was found by Dr. and Mrs. Richard J. Wagner and is named in their honor. It is one of the many botanical collections made by the Wagners which have greatly increased our knowledge of the flora of eastern Puerto Rico.

The closest relative of *Cordia wagnerorum* is *C. bellonis* Urban, a species of the Maricao area of western Puerto Rico. *Cordia bellonis,* described by its recent collectors as a small compact shrub, is smaller in all its parts than *C. wagnerorum* and is distinguished from it by the color of its leaves and the uniform distribution of its dense indument.

In discussing *Cordia bellonis*, Britton noted that it is "a peculiar species, not closely related to the others, perhaps generically distinct" and transferred it to the genus *Varronia*. This species is distinguished partly by its glomerulate axillary inflorescence, a character shared by *Cordia wagnerorum* and not known in other species of Puerto Rico or the West Indies.

Although only a very few plants of *Cordia wagnerorum* have been found in the single location cited, the search continues for additional material. It is hoped that cytological data and additional information about the morphology of the fruit may also be obtained. All fruits examined up to the present contain only a single aborted seed in a single large locule, a condition similar to that noted by Urban in the original description of *Cordia bellonis*. Not one of the few fruits planted germinated; however, a small number of seedlings were found near the type locality of *Cordia wagnerorum*. It should be mentioned that one wall of the endocarp is abnormally thicker than the others which may result from the inclusion of a vascular canal or a reduced cavity representing locules. The characteristics of the fruit and the nature of the inflorescence seem to be significant characters to distinguish the two species discussed here from others assigned to the genus *Cordia*.

Solanum woodburyi sp. nov. PL. II.

Frutex virgatus, ad 3 m. altus; caules, axes inflorescentiarum, perianthium et folia abaxialiter copiose stellato-pubescentia; inflorescentia cymosa; corolla purpurea; stamina subsessilia, antherae elongatae.

Wand-like shrub to 3 m. tall, stems 1–2 cm. in diameter at breast height, the young stems, petioles, lower leaf surface, the midrib above, inflorescence, and outer surfaces of the perianth densely covered with golden multi-armed, spherical, stellate hair clusters. Petioles 1.5 cm. long, tapering to the base of the blade. Leaf blades oblong to elliptic, 5.5 × 2.5 to

10 × 4 cm. long and wide, apex obtuse and often short mucronate, base rounded, margin entire, slightly recurved, primary veins 7 pairs, arcuate and conspicuously anastomosing within the margin, upper surface dark green, glabrous except for the depressed midrib which is stellate-pubescent; prickles 8–10 mm. long at maturity, golden, few, mostly 2 at apex of petiole and occasionally 1 or 2 on the midrib near the base of the blade on the lower surface only. Inflorescence axillary, cymose, 2–4 cm. long, usually less than 10-flowered, axes densely stellate-pubescent. Calyx densely stellate, 6 mm. in diameter, shallowly lobed; corolla rich purple when fresh, drying bluish purple or blue, tube 1 mm. long or less, the lobes 5, ovate-lanceolate, to 8 mm. long and 3.5 mm. wide at the base, bluntly acute at the apex, stellate-pubescent outside, glabrous inside; stamens 5, subsessile or the free portion of the filament less than 0.5 mm. long, glabrous, anthers oblong-ovate, broadest at the base but only slightly tapering above, 4.5–5 mm. long, obliquely poricidal and slightly cleft towards the outside at the apex; ovary glabrous, ovoid, 2 mm. in diameter, style terminal, stout, glabrous, 5 mm. long, stigma capitate; fruiting inflorescence erect, stout, berry depressed-globose, green when immature, 2 cm. in diameter and 1.5 cm. long, glabrous.

Puerto Rico. South side of Luquillo Mountains along the El Toro trail 2 kms. from Route 191. Collected in flower and fruit, October 13, 1964, *R. A. Howard & George Taylor 15692* (holotype A).

This handsome plant is named for Mr. Roy Woodbury who has so generously shared his knowledge of the flora of Puerto Rico. Although Woodbury showed us the small and isolated population of this new species in 1964, an unidentified specimen of it is in the herbarium of the New York Botanical Garden, having been collected by W. R. Barbour along the El Toro trail on March 18, 1935.

This species is clearly distinct from any previously described *Solanum* of the West Indies in its virgate habit, woody structure, density of stellate pubescence, rich purple flowers, and golden prickles.

The type locality of *Solanum woodburyi* has been visited frequently by Woodbury and others yet only one fruit has been found. This fruit is associated with the holotype and, regrettably, it is immature. The lack of fruit suggests some type of developmental anomaly as yet undetermined. Pollen stainability, with cotton blue in lactophenol, was 88.5 per cent based on 614 grains. Meiotic cell division appears normal and Nevling has obtained a chromosome count of $n = 12$ from pollen mother cells of buds collected on April 1, 1965. The voucher specimen for this count is *Howard & Nevling 15747* (A).

Psychotria guadalupensis (DC.) comb. nov.

Loranthus guadalupensis DC. Prodr. **4**: 294. 1830.
Viscoides pendulum Jacq. Select. Amer. 73. *t. 51. f. 1.* 1763.
Psychotria parasitica Sw. Prodr. 44. 1788; Fl. Ind. Occ. **1**: 408. 1797, *nomen illegit.*

Loranthus portoricensis DC. Prodr. **4:** 293. 1830, not *Psychotria portoricensis* DC. Prodr. **4:** 515. 1830.
Uragoga grosourdieana Baill. Adansonia **12:** 227, 328. 1876–9; Urb. Engl. Bot. Jahrb. **24:** 72. 1898.
Mapouria parasitica K. Sch. in Engler, Pflanzenfam. **4:** 112. 1891.
Uragoga parasitica Maza, Anal. Soc. Esp. Nat. II. ser. **3:** 293. 1894.
Psychotria pendula Urb. Symb. Antill. **1:** 445. 1900, non Hooker, Fl. Brit. Ind. **3:** 164. 1880.
Psychotria pendula subsp. *tetrapyrena* Urb. Symb. Antill. **1:** 445. 1900.
Psychotria pendula subsp. *grosourdyana* Urb. *ibid.*
Psychotria pendula subsp. *genuina* Urb. *ibid.* 446.
Psychotria pendula subsp. *pachyphylla* Urb. *ibid.* 447.
Psychotria pendula subsp. *grenadensis* Urb. *ibid.*
Psychotria pendula subsp. *trinitensis* Urb. *ibid.*
Psychotria grosourdyana (Baill.) Urb. *op. cit.* **4:** 596. 1911.
Psychotria tetrapyrena (Urb.) Urb. *op. cit.* **8:** 677. 1921.

This epiphytic but weak shrubby plant assigned to the genus *Psychotria, sensu latu*, is common in the Greater Antilles and abundant in the Lesser Antilles. The earliest name applied to the plant is *Viscoides pendulum* Jacquin. In 1788 Olaf Swartz described *Psychotria parasitica* and cited in synonymy *Viscoides pendulum.* The Swartz name, although used in many floras, must be rejected as illegitimate. In 1900 Urban published the name *Psychotria pendula* presumably basing it on the earlier Jacquin epithet (see subsp. *genuina*) but he stated clearly "*non Hook. f. Fl. Brit. Ind. III p. 164*". The name *Psychotria pendula* (Jacq.) Urb. is also widely used in floras of tropical America but it is illegitimate, being a later homonym of the Hooker name *Psychotria pendula* which was applied to a plant from the Andaman Islands.

The earliest name available for this species is *Loranthus guadalupensis* DC. which is based on a Bertero specimen. The type is in the *Prodromus* herbarium in Geneva, Switzerland. The correct name is *Psychotria guadalupensis* (DC.) Howard.

In establishing *Psychotria pendula* Urban noted it was polymorphic and he described six subspecies including a subspecies called *genuina.* These minor taxa are based primarily on differences in leaf size and shape and on the number of pyrenes in each fruit. Three of the subspecies are found on single islands of the West Indies and three on groups of islands. Urban's subsp. *genuina* had a geographic range from Cuba to Grenada. In subsequent issues of his *Symbolae Antillanae* Urban elevated two of the subspecies to specific rank as *Psychotria tetrapyrena* and *P. grosourdyana* without explanation or comment.

I have seen this plant on every island of the West Indies from which Urban recorded it and on a few for which he had no records. There appear to be two growth forms represented by herbarium specimens which can be recognized in the field and which are often closely associated. The plants may have stout upright branches in their epiphytic habitat and leaves with thick blades and short petioles. Other plants have a few to all branches weak and drooping, tending to be thinner and more delicate and leaves thinner in texture with narrowed bases and more elongate petioles. It is difficult to conclude that two species would be growing in such close proximity often intermingled in the crotch of a single tree, yet it is impossible to be certain that only one plant is involved in many such collections. The variation in leaf thickness is great in fresh condition and is often accentuated in drying. The thicker leaves tend to dry more slowly and therefore turn dark brown or black in the process.

Variation in peduncle color is mentioned by Urban as an accessory characteristic. In living specimens seen in the field this color varies from deep red through bright red to pale green. A collection from the summit of Cerro de la Punta in the center of Puerto Rico (*Howard & Nevling 15417*) has peduncles clear white in color. This albino phase is the extreme variation.

Urban places undue emphasis on the number of pyrenes produced by these plants, culminating in the recognition of *Psychotria tetrapyrena,* having four pyrenes. An examination of herbarium specimens from throughout the range revealed quite unexpectedly that these plants are heterostylous, a fact not previously reported for the species. Further, the pollen proved to be of three types which will be described in a later paper. There was a correlation between the number of stigma lobes and the number of locules in the ovary; however, a variation was noted in the number of sepals. Recently it has been possible to examine a large number of plants in Puerto Rico, for the species is common in the Luquillo Mountains, occurring in wet but open forests and in the mossy or elfin forest zone. One flower was taken from each plant, and the number of sepals and stigmas recorded. In the following tabulation the first number is of calyx points (sepals); the second, the number of stigma lobes; and the third, the number of examples seen.

7–3–1
6–4–2
6–3–3
6–2–1
5–4–7
5–3–41
5–2–9
4–4–2
4–3–6
4–2–2

Britton and Wilson (Flora Puerto Rico and Virgin Islands 6: 244. 1925) use the name *Psychotria grosourdyana* for this plant saying it is "parasitic on forest trees" and describe it as having a fruit containing "3 pyrenes." In an actual check of the mature fruit the calyx of the soft black multistoned drupe was examined and then the drupe squashed between fingers to separate and count the number of fertile (the hard brown) pyrenes. White pyrenes were regarded as sterile since they did not contain seeds. Again, using one mature fruit from each plant the following count was obtained representing, respectively, number of calyx lobes, number of pyrenes, the number of mature and fertile pyrenes, and the number of examples seen.

6–4–4–1
6–4–3–3
6–3–3–1
6–3–1–1
5–4–3–2
5–4–2–2
5–3–3–14
5–3–2–19
5–3–1–15
5–3–0–2
5–2–1–1
4–4–2–1
4–3–3–2
4–3–2–1

It is clear from this tabulation of plants growing in eastern Puerto Rico that the variation in number of pyrenes removes any value the character might have for purposes of classification.

Representative recent collections of *Psychotria guadalupensis* (DC.) Howard from eastern Puerto Rico are *Wagner 81, Howard & Nevling 15749* and *15963,* all of which have been distributed widely to major herbaria.

Curculigo capitulata (Lour.) O. Ktze. Rev. Gen. Pl. **2**: 703. 1891.

Leucojum capitulatum Loureiro, Fl. Cochinchin. 199. 1790.
Curculigo recurvata [Dryander in] Aiton, Hort. Kew. ed. 2. **2**: 253. 1811.
Molineria recurvata Herbert, Amaryll. 84. 1837; Brackett, Rhodora **25**: 161. 1923.
Molineria hortensis Britton in Fl. Puerto Rico and Virgin Islands **5**: 161. 1924.

Britton described *Molineria hortensis* as a new species similar to *Molineria recurvata* and based it on a specimen cultivated in a garden near La Muda. The collection, *Britton 7892*, is preserved at the New York Botanical Garden. It was collected in flowering condition in March, 1923. Britton stated the species was cultivated in "Porto Rico gardens" and that its origin was unknown but it probably came from tropical India or Malaya. In the New York Botanical Garden herbarium there is also an older specimen collected by *J. A. Stevenson* (1891) at Rio Piedras (Agricultural Experiment Station) on April 30, 1914. A hand written annotation label by N. E. Brown is attached to this sheet and states "Curculigo sp. (not C. recurvata). I have looked through the whole of the Kew material twice and through the collection of drawings and cannot match this with anything." This annotation appears to be the sole basis for Britton's conclusion that the plant represented a new species. The published description in no way differs from one of "Curculigo recurvata."

Regrettably, the illustrations which have been published and were available at the time of Brown's search vary greatly in their accuracy and a comparison of Stevenson's specimen or that collected by Britton with certain illustrations could easily lead to the conclusion drawn. Today even the status of the genus *Molineria* is uncertain. It was recognized by Herbert and by Baker, early authorities on the Amaryllidaceae, and by Pax and Hoffman in their treatment of the family for *Die Pflanzenfamilien* (ed. *2*). More recently Brackett indicated *Molineria* as a distinct genus and so did Neal in her book, *In Hawaiian Gardens*, published in 1965. By contrast most recent floras, horticultural encyclopedias and taxonomic works place *Molineria* in the synonymy of *Curculigo*.

In describing the genus *Molineria* Colla (Hortus Ripulensis, Append. 2. 331. *t. 18.* 1825) noted that the anthers in the species he considered were fused. Later Herbert (Amaryll. 84. 1837) questioned the monadelphous character of the anthers and, surprisingly, this condition has not been further discussed in any recent study yet encountered. The several authors who have accepted *Molineria* as distinct from *Curculigo* all adopt different characteristics as generically significant and a further study of the broad-leaved and petioled species is needed.

If the fusion of the anthers is a character of generic value in the Amaryllidaceae, and it may be in related families, then the material Britton described is properly placed in *Molineria*. The collection, *Britton 7892*, does have the anthers fused. Collections made in the Luquillo Mountains by Dr. and Mrs. Wagner, e.g. *486*, *567*, also have fused anthers and the consistency of this character has been checked with an abundance of living materials from this population. No mention is made of the fusion of anthers in the description of *Curculigo recurvata* (by Dryander in Hortus Kewensis), although the character is clearly shown and is mentioned in Edwards *Botanical Register* (**9**: *pl. 770. 1823*) where the description is credited to Roxburgh "Mss." Merrill appears to be the first to accept the application of the Loureiro name to this complex and has repeated the synonymy given above. The syngenesious character is not mentioned by Loureiro in his description of the basionym *Leucojum capitulatum*, yet if *Molineria* is to be recognized as the proper genus a new combination is needed for the specific name. In any case *Molineria hortensis* Britton is not a new species but a synonym of *Curculigo capitulata* (Lour.) Ktze. as currently accepted.

Conostegia hotteana Urban & Ekman Ark. Bot. *22A.* **17**: *29.* 1928.

A single plant identified as this species and verified by Dr. John Wurdack was collected by Dr. and Mrs. Wagner, numbers *678* and *843*. It was growing at km. 21.3 on route 191 on the south side of the Luquillo Experimental Forest. The plant is a small tree, 5 meters tall with a trunk diameter of 15 cm. at breast height. The flowers are 2.5 cm. in diameter and the white petals are characteristically broadly cuneate.

As the specific name indicates, *Conostegia hotteana* was described from material collected July 12, 1928, by Erik Ekman, between Dame-Marie and Montagnac in the Massif de la Hotte in Haiti. The exact location is at the extreme western end of the southern peninsula of Hispaniola. The present collection is not only the first record of the species since the original collection but also the first record of the genus in Puerto Rico. These disjunct localities are not represented in any other genus or species occurring in either Puerto Rico or Haiti. Although the Puerto Rican plant is but a few yards from the roadside, on the steep slopes of a river bank and within an experimental forest it is not a planted specimen. There is neither a reason nor a record of the deliberate introduction of this non-economic plant to Puerto Rico. The location of the original collection in Haiti is not one commonly visited by tourists and so does not suggest a chance introduction. The occurrence of this species in Puerto Rico and in Haiti defies immediate explanation.

EXPLANATION OF PLATES

PLATE I

Cordia wagnerorum Howard. FIGS. a–e from *Wagner 695* (holotype); FIG. e from *Howard 15735*. a, habit, × 1/2; b, portion of upper leaf surface, showing umbo, × 50; c, seedling, × 1/4; d, external view of flower, × 4; e, longitudinal section of flower, × 4; f, fruit, × 5.

PLATE II

Solanum woodburyi Howard. All FIGS. from *Howard & Taylor 15692* (holotype). a, habit, × 1/2; b, trichome showing stellate character, × 20; c, external view of flower, × 2; d, portion of inflorescence showing buds and mature flower, × 2; e, anther, × 5; f, immature fruit, × 1; g, chromosomes at first meiotic division, $n = 12$.

PLATE I

Cordia Wagnerorum Howard

HOWARD, PLANTS OF PUERTO RICO

Solanum Woodburyi Howard

HOWARD, PLANTS OF PUERTO RICO

STUDIES IN DIOSCOREA, I: A COLLECTION FROM BRITISH HONDURAS

BERNICE G. SCHUBERT [1]

IN 1924, WHEN KNUTH PUBLISHED his monograph of the Dioscoreaceae, he maintained in the family nine genera and 654 species, of which 614 were members of the genus *Dioscorea*. It was not until about 20 years after the publication of Knuth's work that serious interest in *Dioscorea* extended beyond the purely botanical aspects or the cultivation of the few species used in tropical areas for food. However, with the discovery of the presence of steroidal sapogenins in the underground parts of many species of *Dioscorea*, there was a sudden realization of the great lack of adequate botanical collections and accurate biological data about the majority of species. Spurred on by the interests and requirements of chemists and pharmacologists, botanical collectors, under the auspices of both the federal government and private companies, concentrated great effort on the collection and study of native species of *Dioscorea* in many parts of the world. The botanical results of this sudden acquisition of both materials and data for study have been very rewarding and should, with sufficient time, provide a much better understanding of this interesting genus than has been possible previously.

The difficulties met in studying species of *Dioscorea* are to be expected in a genus composed almost entirely of dioecious twining plants with extensive, sometimes fragile, usually subterranean rhizomes or tubers. Collection of material is difficult because the stems are most often entangled with stems of other genera and are difficult to trace to the proper base; the stem may break off at the base or the rhizome itself may break while it is being dug. Plants of both sexes usually grow rather close together, but both sexes cannot always be found; as a result, species are often described from one sex only. Although it is possible to determine the relationship of a plant from flowers of only one sex (especially the staminate) there are at least several, if not many, examples of two species being described, one from staminate the other from pistillate material, which were, in fact, the same. In spite of these difficulties, however, many recent collections made with great skill and care (and including both

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[1] My taxonomic studies on the genus *Dioscorea* were begun while I was botanist with the New Crops Research Branch, Agricultural Research Service, U. S. Department of Agriculture, at Beltsville, Maryland, and have been continued since my leaving there at the Arnold Arboretum of Harvard University. I am glad to be able to continue this work and acknowledge with gratitude the helpfulness and interest of my former and present colleagues.

The illustrations were drawn with great skill and care by Mrs. Regina O. Hughes, Crops Research Division, U. S. Department of Agriculture.

photographs and detailed notes) have helped immeasurably in clarifying old problems and in increasing our knowledge of the genus.

Among the collections which I have had an opportunity to study is one made in British Honduras and presented to the herbarium of the Royal Botanic Gardens, Kew, by Dr. S. S. Bampton. Although small, this collection is of such interest that it seems appropriate to discuss some of the significant numbers, to provide more complete descriptions for two previously inadequately known species, and to describe one which is new. I shall conclude the paper with a list of determinations of all the identifiable Bampton numbers in the hope that this may provide the basis for an accurate account of the species of *Dioscorea* in British Honduras.

I appreciate the interest and consideration of the officers of many institutions who have made available collections in their care for my study, either on loan or when I visited their herbaria. Full representation of any one species may be so inadequate in one herbarium that only a combined collection in a genus such as *Dioscorea* can help to give a clear understanding of the material. The institutions concerned are cited in the paper by the symbols given in *Index Herbariorum* (Lanjouw and Stafleu, Reg. Veg. **31.** 1964).

B	Botanisches Museum, Berlin-Dahlem, Germany
F	Chicago Natural History Museum, Chicago, Illinois, U. S. A.
GH	Gray Herbarium of Harvard University, Cambridge, Massachusetts, U. S. A.
K	The Herbarium, Royal Botanic Gardens, Kew, Richmond, Surrey, Great Britain
LE	Herbarium of the Komarov Botanical Institute of the Academy of Sciences of the U. S. S. R.
LL	Lundell Herbarium, Texas Research Foundation, Renner, Texas, U. S. A.
MEXU	Herbario Nacional del Instituto de Biología, UNAM, Ciudad Universitaria, México, D. F., México
MICH	University Herbarium, University of Michigan, Ann Arbor, Michigan, U. S. A.
MO	Missouri Botanical Garden, St. Louis, Missouri, U. S. A.
NA	U. S. National Arboretum, Washington, D. C., U. S. A.
NY	New York Botanical Garden, Bronx Park, New York, U. S. A.
US	Department of Botany, U. S. National Museum, Smithsonian Institution, Washington, D. C., U. S. A.

Dioscorea hondurensis Knuth, Repert. Sp. Nov. **38:** 120. 1935. Holotype, *Peck 549* ♀ (B); isotypes (GH, K). FIGS. 1–3.

D. belizensis Lundell, Contr. Univ. Mich. Herb. **6:** 5. 1941. Holotype, *Gentle 2998* ♂ (MICH); isotypes (F, GH, US).

D. tabascana Matuda, Bol. Soc. Bot. Méx. **21:** 1. *2 figs.* 1957. Holotype, *Gilly, Hernández & Berlin 44a* ♂ (US); photo. and fragment (MEXU).

Dextrorse vine. Rhizome conical at apex, becoming horizontal about 3 dm. below surface, cylindrical, little branched, with creamy to yellow or almost orange flesh, 1–4 m. long, 1–5 cm. in diameter, 5.9–65.9 kg. in weight. Stem stout, reddish brown (in age becoming dark brown or gray at base, the bark sloughing off), cylindrical, striate, somewhat pilose or with only glandular trichome bases remaining, to 5 mm. in diameter. Leaves alternate, mostly coriaceous, cordate or ovate to ovate-suborbicular, abruptly acuminate into a short-attenuate tip, nearly truncate at base or more often with a rather deep inverted U-shaped to inverted V-shaped sinus, or sinus very narrow and the basal lobes overlapping; 9-nerved, the two outer nerves bifurcate, glabrous above with veins impressed, below with veins prominent and abundantly pilose with multicellular, branched or fasciculate trichomes (0.6–1 mm. long), gland-dotted throughout, to 26 cm. long, 23 cm. broad; petioles slightly winged above with decurrent leaf tissue, sulcate, somewhat angulate, striate, swollen at apex and base (in age becoming contorted at base), ⅓ to scarcely ½ length of leaf (3–10.5 cm.). Inflorescence of ♂ plant an axillary, solitary panicle of racemes up to 1.5 m. long, rachis essentially glabrous, angulate, minutely serrulate-alate on the angles, secondary rachises similar; flowers solitary, bibracteate, pedicellate, the outer bract ovate-acuminate, to 2 mm. long, 1.5 mm. wide, the inner ovate, abruptly attenuate, 1.5 mm. long, 1 mm. wide, pedicels 1.5 mm. long, scarcely differentiated from the 1.5–2 mm. long perianth tube; tepals fleshy to papyraceous (in age), ovate-obtuse, ca. 1.5 mm. long and wide, narrowed to a claw 0.8 mm. wide at base; stamens 6, introrse, inserted at base of tube and slightly exceeding it in length, becoming conspicuous as tepals become reflexed, 0.5–0.6 mm. long; stylar rudiment central, 3-parted, rather conspicuous, to 0.5 mm. high. Inflorescence of ♀ plant a solitary, axillary, densely flowered raceme to 4.5 dm. long, rachis gland dotted, angulate, striate, essentially glabrous; flowers bibracteate, bracts gland dotted, the outer ovate-attenuate, 3 mm. long, 1.5 mm. wide, inner ovate-acuminate, 2 mm. long, 1 mm. wide; tepals fleshy, somewhat gland dotted, ovate-obtuse, early reflexed, 2.5 mm. long, 1.5–2 mm. wide, tube to 0.6 mm. long; staminodia 6, inserted at base of tube, introrse and somewhat antheriferous; styles 3, fused below, becoming distinct and bifid above with the stigmatic surface extrorse; ovary (excluding neck) to 7 mm. long. Capsule broadest above the basal third, its wings obtusely oblong, surface glabrous and remotely gland dotted at maturity, 4.8–5.5 cm. wide, 3.6–4 cm. high, on a pedicel 6 mm. long; seeds suborbicular, alate throughout, to 2.2 cm. long, 1.8 cm. wide (including wing).

DISTRIBUTION: Southern Mexico (Tabasco), British Honduras, Guatemala [Costa Rica, where probably cultivated] to Panama.

Mexico. Tabasco: between the Escuela Agricola and Cuevas de Cocomá, Teapa, *Gilly, Hernández & Berlin 44a* ♂ (MEXU, US); between Escuela Agricola

FIG. 1. *Dioscorea hondurensis* Knuth. Photograph of type (B).

and Gruta de Cocomá, along trail to Gruta, *Gilly, Hernández & Berlin 7129* ♂ (NA). **British Honduras.** Stann Creek District, in acahual, Carib Reserve, *Gentle 2998* ♂ (F, GH, MICH, US). Toledo District, Monkey River, *Gentle 3728* ♀ (F, GH). Punta Gorda, five-year old *Pinus caribaea* plantation at Machaca Forest Station, alt. 100 ft., *Bampton 22* [sterile] (K). Upper Moho River, *Peck 549* ♀ (B, GH, K). **Guatemala.** Dept. Alta Verapaz: Panzas, alt. ± 400 ft., *Gentry 12468* [sterile] (NA); 4–6 miles west of Panzas, alt. ± 500 ft., *Gentry 12476, 12477* [sterile] (NA); 12 miles west of Estor, alt. ± 200 ft., *Gentry 12475* [sterile] (NA). Dept. Izabal: brushy slope, alt. 75–225 m., *Standley 24112* [sterile] (GH, NY, US). **Honduras.** Dept. Atlantida: wet forest, Lancetilla Valley, near Tela, alt. 20–600 m., *Standley 53857* ♀ (F, US); idem, *Standley 55218* ♂ (F, US); Lancetilla Field Station, alt. ± 100 ft., reddish porous clay soil, *Gentry 12493* [sterile] (NA); about 3 miles w. of Ceiba, in sandy loam, alt. 20 ft., *Gentry 12502* [sterile] (NA). **Costa Rica** [probably cultivated]. Prov. Alajuela: llanuras de San Carlos, alt. 500 ft. (received from Experimental Plantations Inc., Chicacao, Guatemala, where probably also cultivated), *Krukoff 2012* (F [sterile], US [1 coll. sterile, 2024529 ♀]). **Panama.** Canal Zone: Barro Colorado Island, *Silvestre Aviles 12* ♀ (F).

In 1935 Knuth described *Dioscorea hondurensis,* of British Honduras, from pistillate material only (FIG. 1), assigning it to a new section, TRIANGULARES. He did not indicate to which subgenus these new taxa might be referred. Morton, in 1936, suggested that the section might "belong to Eudioscorea," but material was not available to confirm this. Recent examination of the holotype from Berlin and the isotype from the Gray Herbarium confirms Morton's suggestion. From 1935 until now no staminate material has been associated with Knuth's species. However, the pistillate flowers bear six equal staminodia indicating that the staminate flowers probably have six equal stamens.

FIG. 2. *Dioscorea hondurensis* Knuth. Portions of rhizomes, the lowermost showing base of leafy stem emerging, from *Bampton 22*, × 3/8.

In 1941, Lundell described *Dioscorea belizensis*, of British Honduras, from staminate material, suggesting no relationship, but describing the

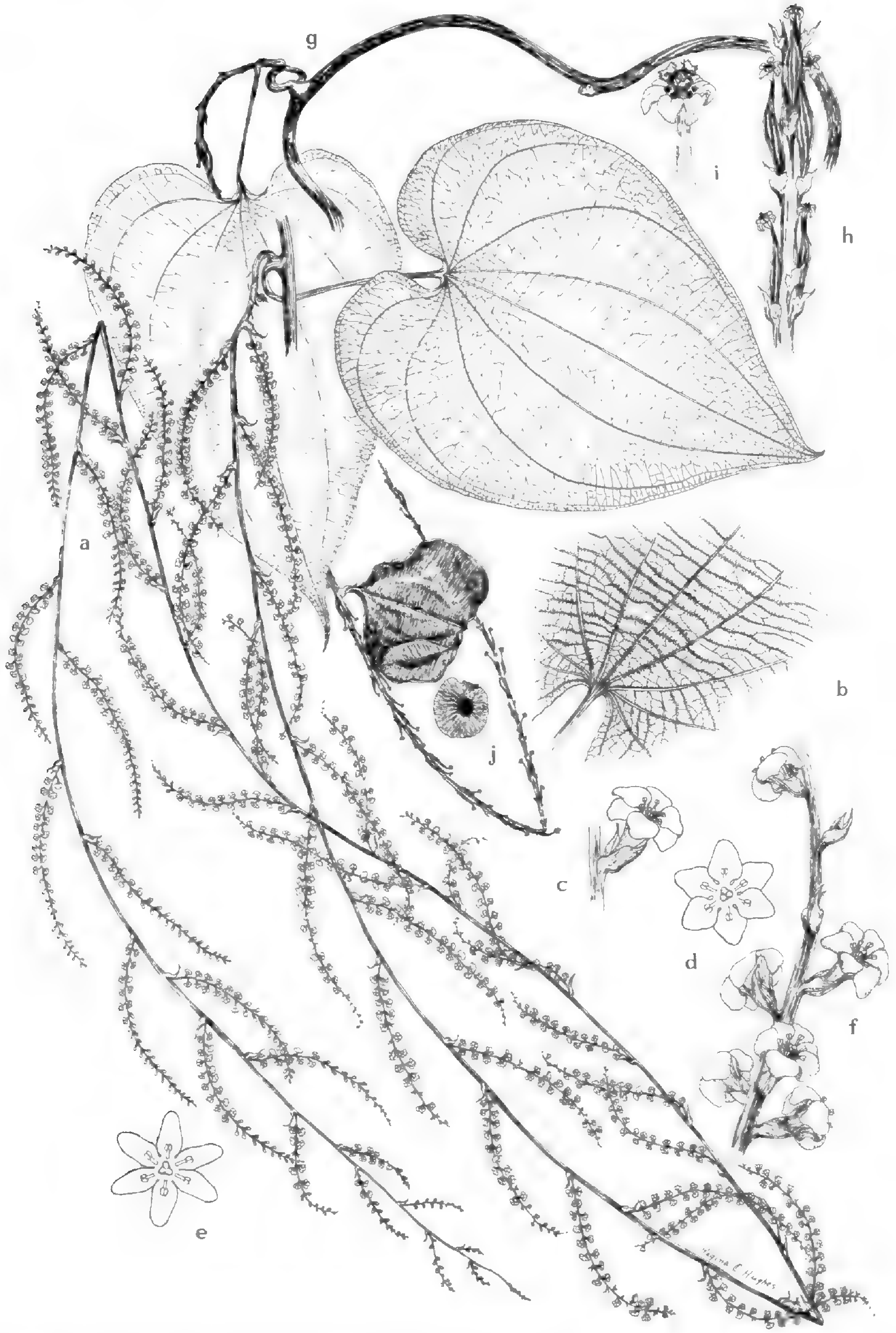

FIG. 3. a–j, *Dioscorea hondurensis* Knuth. a, portion of stem with leaf and elongate staminate inflorescence, from *Gentle 2998* (US 1807877), × 1/3; b, portion of lower leaf surface to show venation and pubescence, from *Gentle 2998* (US 1808657), × ca. 1/3; c, solitary staminate flower and subtending bracts, from same specimen, × 3; d, staminate flower opened to show the 6 introrse stamens and 3-parted rudimentary style, from same specimen, × 3; e,

material very fully. The species was characterized by its large leaves pubescent below, and by its extremely long (to 150 cm.), branched, staminate inflorescences. The staminate flowers are solitary, dark red, and with six stamens. In 1952, Morton identified *Krukoff 2012* from Costa Rica (where it was probably cultivated) as *D. belizensis*. This was the first material other than the type, and the first pistillate collection, assigned to the species.

In 1957, Matuda described *Dioscorea tabascana*, from the state of Tabasco, Mexico, from staminate material. This species was also characterized by its large leaves pubescent below, and its very long (60–90 cm.) staminate inflorescence. The staminate flowers were said to be castaneous and with six stamens (which were incorrectly observed to be extrorse rather than introrse). Matuda assigned his new species to subgenus EUDIOSCOREA, § MACROGYNODIUM, distinguishing it from the other members by its solitary flowers and extrorse stamens. The form of the inflorescence cannot be reconciled, however, in a section characterized by densely flowered scorpioid or cymosulous branchlets in a compound raceme (§ MACROGYNODIUM).

The chief difference between the staminate flowers in the type collection of *Dioscorea belizensis* and those of the type of *D. tabascana* is in the texture of the tepals. The tepals of *D. belizensis* are thick, fleshy, and with glands only remotely visible; those of *D. tabascana* are papyriferous and abundantly gland dotted. This variation seems to me to be a function of age rather than a morphological differentiation. With more collections the problem can be clarified.

From close and careful examination of the type material of *Dioscorea hondurensis* Knuth, *D. belizensis* Lundell, and *D. tabascana* Matuda, I have come to the conclusion that they are all one species (FIG. 3). There is not even sufficient variation in the collections to distinguish geographical varieties. The name to be maintained, therefore, is the oldest one, *Dioscorea hondurensis* Knuth. For the present it seems expedient to maintain also Knuth's § TRIANGULARES, but I think it will be possible to show, after examination of more material of other species, that *D. hondurensis* is a perfectly characteristic member of § SARCANTHA Uline, up to now thought to be limited to South America.

In the thirty years it has taken to associate staminate with pistillate elements of *Dioscorea hondurensis* a good representation of material from a rather wide geographical range has accumulated. It may be seen in the case of *D. hondurensis*, as will be shown for other species also, that with

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staminate flower opened to show the 6 introrse stamens and 3-parted rudimentary style, × 3, from *Gilly, Hernández & Berlin 44a* US), holotype of *D. tabascana*; f, portion of staminate inflorescence to show solitary, pedicellate character of flowers, × 3, from *Gentle 2998* (US 1808657); g, portion of leafy stem and pistillate inflorescence with 1 mature capsule, × 1/3, from *M. E. Peck 549* (B); h, portion of pistillate inflorescence, × 2, from same specimen; i, pistillate flower to show 3 stigmas and 6 staminodia, × 3, from same specimen; j, mature seed, × 3, from *Krukoff 2012* (US 2024529).

intensive collecting many species formerly considered very local are, in fact, rather widespread. Although some material of *D. hondurensis* is sterile, it can be placed with relatively little doubt because of the characteristic pubescence on the lower leaf surface (FIG. 3b). Such pubescence is not known to occur on plants of other species with leaves of similar size, texture, and outline.

When collectors have given notes on underground parts of *Dioscorea hondurensis* their information is remarkably uniform. For photographs (FIG. 2) indicating the general aspect of the rhizomes I am indebted to Dr. Bampton. Sketches sent to me by Dr. Gentry are similar.

Dioscorea (§ *Higinbothamia*) **gaumeri** Knuth. Notizbl. Bot. Gart. Berlin **7**: 199. 1917 [type cited from Colombia]; Pflanzenreich IV. **43**(heft 87): 122. 1924 [same type cited from Yucatan]. Holotype, *Gaumer*, Pl. Yucat., sub *Higinbothamia* ♀ ! (B). FIGS. 4, 5a–d.

Higinbothamia synandra Uline, Publ. Field Mus. Bot. **1**: 415. *pl. 22*. 1899. Lectotype, *Gaumer 794* p.p. ♂ (F 36597).

Dioscorea synandra (Uline) Standl. Publ. Field Mus. Bot. **3**: 231. 1930, non *Dioscorea synandra* Uline, Nat. Pflanzenfam. Nachträge zu II: 86. 1899, *nomen nudum*; Uline ex Knuth, Pflanzenreich IV. **43**(heft 87): 219. 1924. Lectotype to be chosen from among the syntypes, since Knuth cited both a ♂ and a ♀ type and neither collection has been examined.

Sinistrorse vine.[2] Rhizome more or less cylindrical ca. 3½ cm. long and 1 cm. in diameter, becoming subconical at apex [not branched in photograph of specimen seen], growing near surface, flesh whitish brown. Stem slender, not ridged when fresh, becoming finely ridged and grooved, to 10 feet or more long (or high) [fide Bampton], tawny to yellowish, glabrous, 1–1.5 mm. in diameter. Leaves alternate, thin, glabrous, cordate-ovate, narrowed to a long-attenuate apex, basal sinus broad, inverted V- or U-shaped, 5–11.5 cm. long, 3.5–11 cm. wide, 5-nerved, the two outer

FIG. 4. *Dioscorea gaumeri* Knuth. Portion of rhizome with base of emerging stem, from *Bampton 10*, × 1/2 (photo. Bampton).

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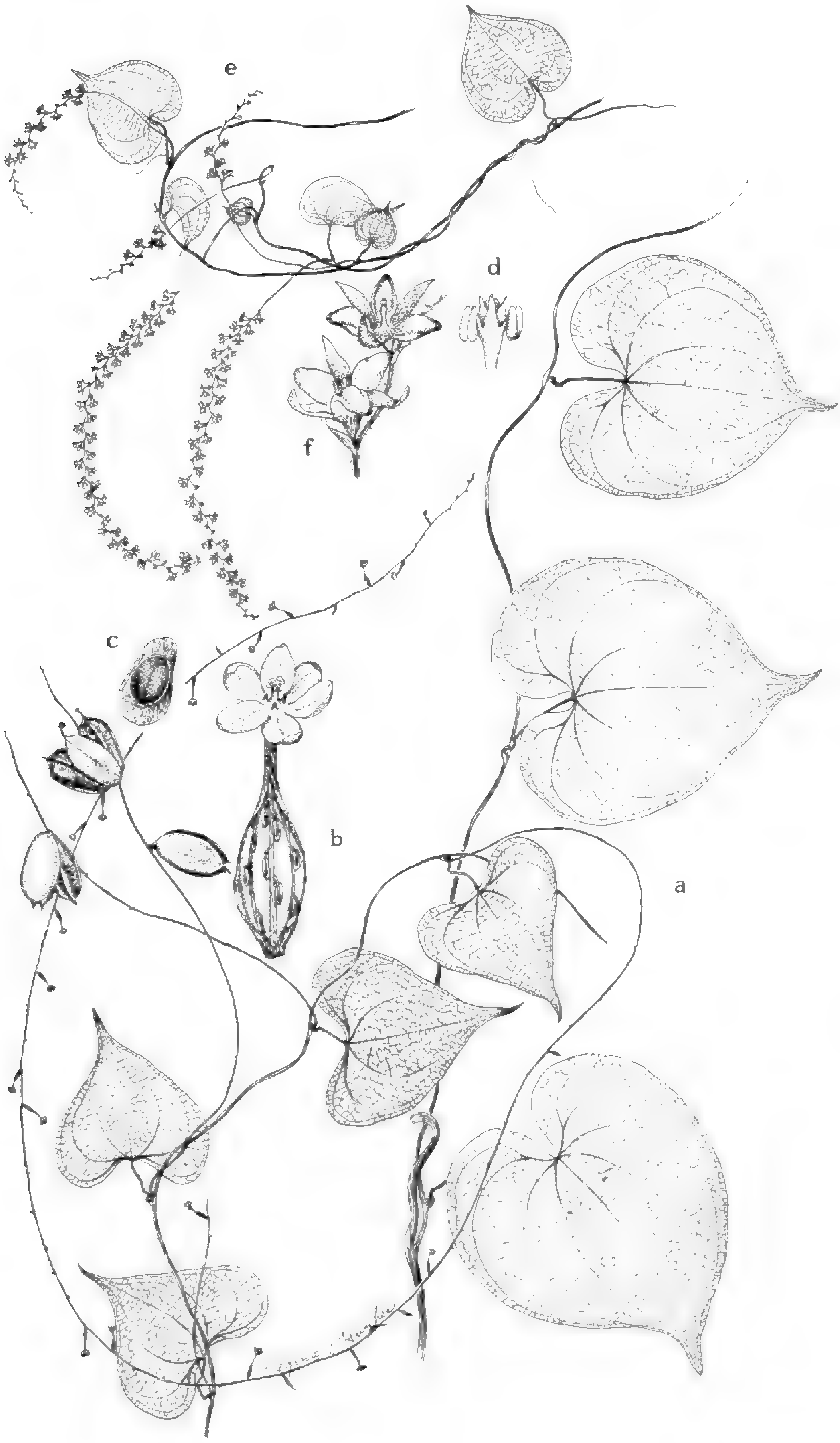
[2] *Dioscorea gaumeri* was described as dextrorse by Knuth, but observations on material at hand agree with those of Uline and Bampton that the plants are sinistrorse.

nerves bifurcate; petioles sulcate on adaxial surface, ridged and grooved otherwise, glabrous throughout, 1.5–3 cm. long, contorted at base. Inflorescence of ♂ plant composed of solitary axillary racemes or a basally branched panicle of racemes 10–20 cm. long, rachis minutely and often densely serrulate-alate on the fine ridges; flowers usually solitary (but sometimes two on a short peduncle (*Lundell & Lundell 7918*), bracteate, pedicellate, each (if flowers solitary) subtended by two lance- to oblong-attenuate bracts moderately to densely papillate and somewhat glandular on the adaxial surface, to about 1.5 mm. long and 0.5 mm. wide (if 2 flowers borne together then each unibracteate); pedicels also serrulate-papillate, glandular and ± angulate, to about 3 mm. long; the 6 tepals purple even when fresh [Bampton], free from slightly above base, in 2 series, elliptic-ovate, acutish to rounded at apex, the inner 3 mm. long, 1.5–2 mm. wide, the outer similar or slightly longer and narrower, but not sharply differentiated; stamens 3, filaments fused, anthers extrorse at the apex of the staminal column (to 1 mm. high), staminodia alternating with stamens in an inner whorl and usually at least slightly exceeding them. Inflorescence of ♀ plant lax, elongate, simple, axillary and usually solitary racemes, often becoming more than 7 dm. long; rachis ± angulate, serrulate-papillate to remotely alate; flowers solitary, bibracteate, bracts papillate-granular, the inner ca. 1.6 mm. long, the outer a little longer, lance-attenuate from a clasping base; tube very shallow, ca. 1 mm., tepals 6, the 3 inner ovate-subacuminate, the 3 outer ovate-obtuse, or all subacute, essentially equal, somewhat gland dotted on adaxial surface, papillate all over abaxial surface and somewhat puberulent, ca. 3 mm. long and 2 mm. wide; staminodia 3, borne at base of stylar column opposite the outer tepals; styles fused, column gland dotted, ca. 1 mm. long, stigmas 3, slightly bifid, outwardly curved; ovary, excluding neck ca. 6 mm. long. Capsule on a short stout pedicel, exalate, oblong to narrowly elliptical, tapering to acutish base and apex, 3-locular, each locule [3-]4-seeded; seeds 6 mm. long, 2.5 mm. wide (including wing), alate all around.

DISTRIBUTION: Yucatan and British Honduras.

Mexico. Yucatan: Kaua road, Chichen Itza, *Lundell & Lundell 7918* ♂ (US); Merida-Uxmal road, km. 40, *Lundell & Lundell 8092* ♂ (GH, LL, US). Without locality, *Gaumer & sons 1580* ♂ & ♀ (G, LE, MO, US). **British Honduras.** San Andres, *Gentle 1084* ♀ [3 seeds in each locule] (GH); Pembroke Hall near Corozal, alt. 100 ft., *Bampton 14* ♀ (K); 3 miles south of Maskall, *O'Neill 8385* ♂ (US); limestone outcrop on Mountain Pine Ridge near Augustine, *Bampton 10* ♂ (K).

It may be seen from both the nomenclatural and taxonomic history of *Dioscorea gaumeri* that much confusion has resulted from inadequate material, mixed collections, and some misjudgements. Inadequate material, as well as misjudgement, presumably led Knuth (1917, p. 199; 1924, pp. 120, 122) to place *D. gaumeri* in subgenus HELMIA, section MONADELPHA. Morton (1936, p. 244) was the first to recognize the confusion and correctly identify *Higinbothamia synandra* Uline (*Dioscorea*


e
d
f
c
b
a

synandra (Uline) Standl., not Knuth) with *D. gaumeri,* which he then reassigned to subgenus EUDIOSCOREA (now, according to the Code, to be known as subg. DIOSCOREA). At the same time Morton united the genus *Higinbothamia* with *Dioscorea* as a section, under the correct subgenus. This seems to be a proper disposition of *Higinbothamia,* although some few botanists still propose to maintain it as a distinct genus. The larger number of ovules in each locule of the ovary is scarcely a character of sufficient significance for generic distinction (particularly since the number varies from three to four) when all characters of flowers and fruit are so clearly those of *Dioscorea.*

After Uline's publication of *Higinbothamia synandra* in 1899, it was discovered that several Gaumer collections were mixed and some of the numbers cited as representing *Higinbothamia synandra* actually represented at least two other species. Knuth noted (1924, p. 327) that *Gaumer 794* the "staminate type" was a mixed collection and illustrated portions of both elements of the collection in his *fig. 63* (p. 326). Standley, in his *Flora of Yucatan* (1930, p. 158), discussed the Gaumer collections and some of the difficulty in organizing them. Surely the difficulties must have been greater with specimens of *Dioscorea* than with material of many other genera because *Dioscorea* species cannot be easily distinguished by superficial characters, and the dioecism of the plants leaves greater margin for error. Caution should be used in annotating any collection bearing the same number as that cited here.

Although Uline expressed some uncertainty about which were generic and which specific characters when he described the genus *Higinbothamia* and its one species, *H. synandra,* it now seems reasonably clear that possession of a staminal column is a sectional character, the position of stamens on it and their relation to the staminodia are specific, as are the shape and differentiation of the tepals. On the basis of these conclusions the material collected by Dr. Bampton as his number 25 seems to be a new species in section *Higinbothamia.* It may be distinguished from *Dioscorea gaumeri* by the characters noted in the key which follows.

Leaves with broad basal sinus, inflorescence a simple raceme, flowers pedicellate; tepals all alike, obtuse; stamens exceeded by staminodia. . . . . *Dioscorea gaumeri.*

Leaves with narrow basal sinus or the lobes overlapping; inflorescence a somewhat zigzag raceme, flowers almost sessile; tepals differentiated into outer

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FIG. 5. a–d, *Dioscorea gaumeri* Knuth. (a–c from *Bampton 14* (K); d from *Lundell & Lundell 8092* (GH).) a, portion of ♀ plant with both young flowers and mature capsules, × 1/3; b, pistillate flower and almost mature ovary opened to show loculi and seeds, × 3; c, mature seed, × 3; d, portion of androecium to show stamens and staminodia, × 3.

FIG. 5. e and f, *Dioscorea sandwithii* Schubert, from cultivated material grown from rhizome of *Bampton 25* (K); e, leafy stem and staminate inflorescences, × 1/3; f, portion of staminate inflorescence to show differentiation of 2 series of tepals and androecial structure, × 3.

and inner series, acuminate; stamens exceeding staminodia. .... *Dioscorea sandwithii.*

Dioscorea sandwithii Schubert, sp. nov. FIG. 5e and f.

Volubilis, sinistrorsum torta, caulibus angulatis subtiliter canaliculatis papillatis canis vel flaventibus; foliis basi sinu angusto vel lobis attingentibus, 9-nerviis, nervis extremis bifurcatis. Inflorescentiae ♂ axillares solitares racemosi, rachibus racemorum angulatim flexuosis papillato-serrulatis vix alatis; floribus solitariis bibracteatis pedicellatis, bracteis glabris sparsim glandularibus; pedicellis ca. 0.8 mm. longis, tubo perianthii similibus ± equilongis. Perianthium 6-partitum, carnosum atro-purpureum, segmentis exterioribus lanceo-obtusis vel -acutis, interioribus ovato-obtusis. Stamina 3, filamentis in columnam centralem fusis, antheris extrorsis apicalibus, staminodiis 3, cum antheris longioribus alternantibus. Planta ♀ incognita.

Sinistrorse vine, rhizome similar to that of *D. gaumeri*, stem angulate, finely grooved and papillate, grayish to yellowish, 1.5 mm. in diameter. Leaves alternate, almost orbicular, apex narrowly acuminate, basal sinus narrow or the lobes overlapping, 11 (or more) cm. long and 9 cm. wide, 9-nerved, the two outermost nerves bifurcate, surfaces essentially glabrous, somewhat papillate below; petioles swollen when fresh "becoming 3–4 times diameter of stem" to 4 mm. in diameter (when dry), 4–8 cm. long, sulcate, finely ridged and grooved and papillate-serrulate. Inflorescences of ♂ plant axillary, solitary, zigzag racemes to 1.5 dm. long, rachis angulate, papillate-serrulate, remotely alate; flowers solitary, bibracteate, pedicellate, bracts glabrous and sparsely gland dotted, outer bract lance-ovate, acute, 1.5 mm. long, 0.5 mm. wide, inner bract lanceolate, ca. 1 mm. long and 0.4 mm. wide; pedicels ca. 0.8 mm. long, not especially distinguished from the 1 mm. long perianth tube; corolla of 2 whorls of ± fleshy dark-purple tepals, the outer lance-obtuse to -acute, to 3.5 mm. long, 1.3 mm. wide, the inner ovate-obtuse, 3 mm. long and 1.5 mm. wide. Stamens 3, the filaments fused in a central column 1 mm. long, the extrorse anthers apical, staminodia 3, in a whorl within and between the stamens, usually a little shorter than the anthers but often folded over and seeming much exceeded by them. No ♀ plants known.

HOLOTYPE: rocky limestone hill, Gracie Rock near Belize, British Honduras, February 23, 1959, *Bampton 25* ♂ (K). CULTIVATED: Royal Bot. Gard., Kew, December 16, 1959, from *Bampton 25* ♂ (A).

It seems appropriate to name this new species of *Dioscorea* for the late NOEL YVRI SANDWITH (8 September 1901–7 May 1965), through whose interest the collection of Dr. Bampton came to me for study. Mr. Sandwith's interest in and knowledge of tropical American plants and his generous helpfulness to all American botanists was great indeed. His sudden death means the loss of a good friend to many of us and creates a great gap in the understanding of tropical American botany neither soon nor easily filled.

DIOSCOREAE BAMPTONIANAE

British Honduras — 1959

Collection number	Species
1.	Dioscorea bartlettii Morton
1 A.	Dioscorea bartlettii Morton
2.	Dioscorea cf. bernoulliana Prain & Burkill
4.	Dioscorea spiculiflora Hemsley
5.	Dioscorea alata L.
8.	Dioscorea convolvulacea Cham. & Schlecht.
9.	Dioscorea pilosiuscula Bertero ex Spreng. vel aff.
10.	Dioscorea gaumeri Knuth
11.	Dioscorea spiculiflora Hemsley
12.	Dioscorea densiflora Hemsley
12 A.	Dioscorea densiflora Hemsley
13.	Dioscorea floribunda Mart. & Gal.
14.	Dioscorea gaumeri Knuth
15.	Dioscorea spiculiflora Hemsley [very immature]
16.	Dioscorea spiculiflora Hemsley
17.	Dioscorea cf. cayenensis Lam. [sterile]
19.	not identifiable
20.	Dioscorea pilosiuscula Bertero ex Spreng.
21.	Dioscorea composita Hemsley
22.	Dioscorea hondurensis Knuth
23.	Dioscorea convolvulacea Cham. & Schlecht. var. glabra (Hemsl.) Uline
25.	Dioscorea sandwithii Schubert
26.	Dioscorea convolvulacea Cham. & Schlecht. var. glabra (Hemsl.) Uline
27.	Dioscorea floribunda Mart. & Gal.
30.	Dioscorea sp.
s.n.	Dioscorea sp.

ADDITAMENTA AD FLORAM JORDANICAE [1]

BAKI KASAPLIGIL

THE PLANTS DESCRIBED IN THIS PAPER were collected by the author during an assignment in the Hashemite Kingdom of Jordan, during the years 1954 to 1956, as a Forest Ecologist of the Food and Agriculture Organization of the United Nations. Specimens of the new taxa proposed were distributed among the following herbaria: Jubeicha Agricultural College, Jordan; Université Saint Joseph, Beiruth, Lebanon; Conservatoire et Jardin Botaniques, Geneva, Switzerland (G), the University of California, Berkeley, California (UC), and the Arnold Arboretum of Harvard University, Cambridge, Massachusetts (A).

Atriplex asphaltitis sp. nov. FIGS. 1 and 2.

A. halimus var. *argutidens* Bornm. Mitt. Thür. Bot. Ver. **30**: 82. 1913; Post & Dinsmore, Fl. Syr. Palest. & Sinai, ed. 2. **2**: 436. 1933; Aellen, Bot. Jahrb. **70**: 13. 1940; Eig, Palest. Jour. Bot. **3**(3): 124. 1945.

Frutex 1–1.5 m. altus, glaucus, dioicus; folia inferiora 1.5–2 cm. longa, 1–1.5 cm. lata, rhomboidea vel late trullata vel elliptica, apice acuta vel obtusa, basi cuneata vel truncata, margine integra vel sparse dentata, folia superiora triangularis mucronata, margine subintegra, basin versus sparse dentata; glomeruli laxe spiciformes, distincte interrupti, fasciculi diametro 6–8 mm.; bracteae fructiferae 4 mm. longae, 7 mm. latae, depresse ovales vel reniformes, basi auriculatae, margine distincte dentatae, basi solide coniunctae et fructus cingentes, nervi prominuli, sine appendicibus; stylus brevis, 0.25–0.5 mm. longus, stigmata dua 1–1.5 mm. longa, in statu fructifero e bractea cingente leviter exserta; semina diametro 2–2.5 mm., brunnea, radicula sursum curvata; grana pollinis sphaeroidea, multiforata, numerus foraminum 60 (50–72), foramina in superficie granae

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[1] The present study was carried on during a sabbatical leave from Mills College, Oakland, California, in the academic year 1962–63. I wish to thank Monsieur René Gombault, Attaché au Muséum National d'Histoire Naturelle, Paris, who gave generously of his time to compare my specimens with those of his collections from Syria. I am very grateful to Dr. Haino Heine of the Laboratoire de Phanérogamie of the same institution for the translations of the diagnoses into Latin and to Dr. Rimo Bacigalupi, Curator of the Jepson Herbarium, University of California, Berkeley, California, for reading the manuscript. I appreciate also the generosity of the officials in charge of the collections listed here for making available materials for my study: Laboratoire de Phanérogamie, Muséum National d'Histoire Naturelle, Paris (P); Conservatoire et Jardin Botaniques, Museés de Genève (G); the Herbarium, Royal Botanic Gardens, Kew, Great Britain (K), and Botanischer Garten und Institut für Systematische Botanik der Universität Zürich (Z).

FIG. 1. *Atriplex asphaltitis* Kasapligil. Fruiting branch, × 4/10.

pollinis regulariter dispersa, textura granularis, 24.7 (21.1–29.9) micra diametro.

HOLOTYPE: Kale (or Kallia), south of Jericho and at the north end of the

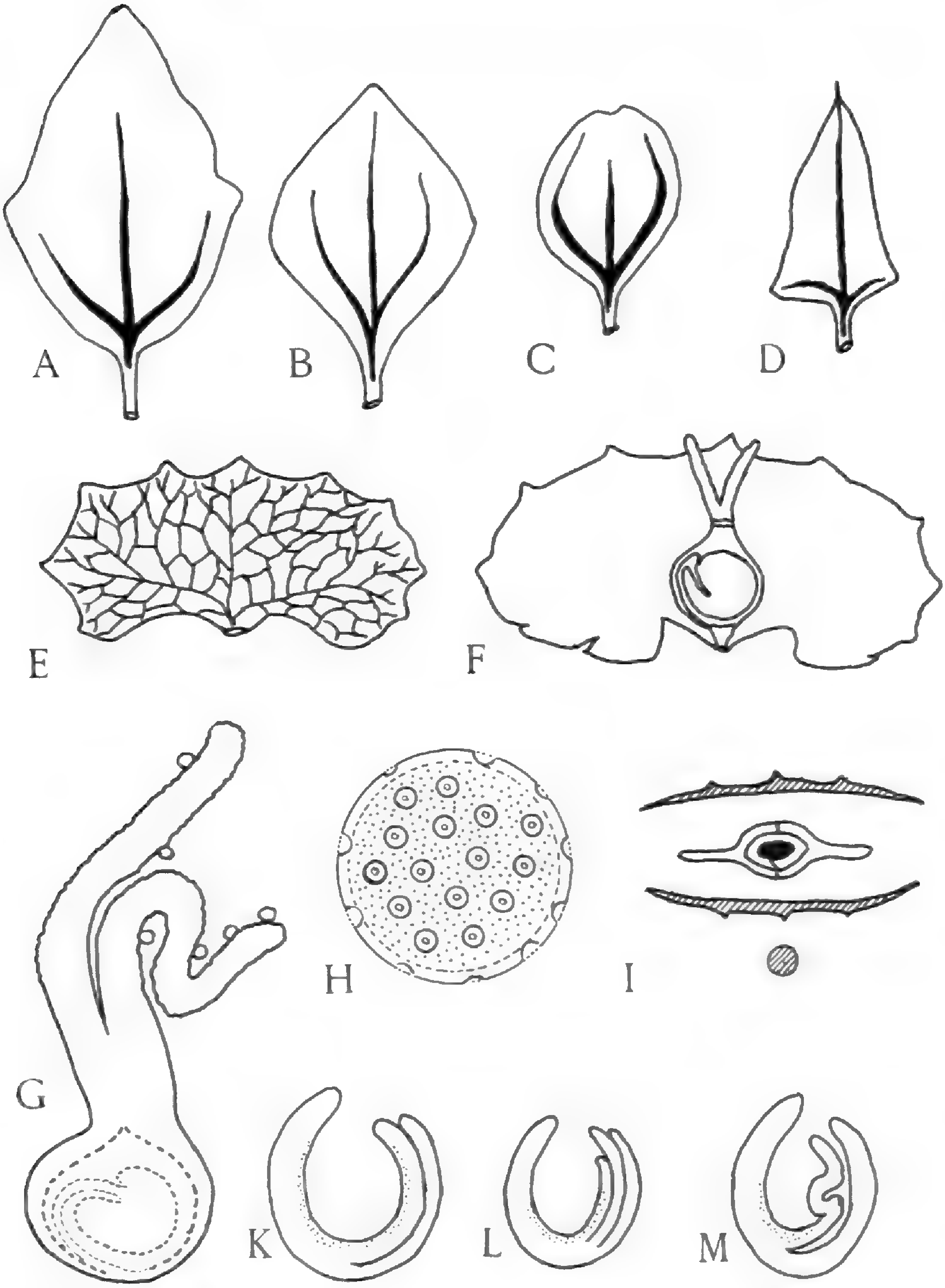

FIG. 2. *Atriplex asphaltitis* Kasapligil. A–C, variation in the lower leaves, × 3; D, triangular upper leaf, × 3; E, adaxial view of a prophyll (fruiting bract) showing the vascular reticulum, × 10; F, prophyll attached to mature fruit [note protruding stigmas and upwardly pointed radicle], × 10; G, pistil at time of pollination [dotted lines showing locule, campylotropous ovule and funiculus attached to ovary base], × 70; H, spheroidal, polyforate pollen grain resembling golf ball [note ± equally spaced pores and thick ectexine], × 1600; I, ground plan of pistillate flower showing both prophylls and bicarpellate ovary; K–M, dissected embryos showing structural and size variation [note the presence of three cotyledons in L, and folded inner cotyledon in M], × 15.

Dead Sea (= Lacus Asphaltites, hence the specific epithet), on dry calcareous salines, alt. ca. 390 m. below sea level, Dec. 8, 1954, *B. Kasapligil 1656* (UC 1,083,535; photo, A). Arabic names: Kataf, Rughat.

In its native habitat *Atriplex asphaltitis* is associated with the following species, *Anabasis haussknechtii* Bunge, *Arthrocnemum glaucum* (Del.) Ung.-Sternb., *Suaeda* sp., *Statice pruinosa* L., *Phragmites communis* Trin. var. *stenophylla* Boiss., *Nitraria retusa* (Forsk.) Aschers., *Tamarix pentandra* Pall., *T. amplexicaulis* Ehrenb., and *T. jordanis* Boiss.

The new species, *Atriplex asphaltitis*, is a member of section FRUTICULOSAE Aellen (1940) and is related to *A. griffithii* Moq., which is indigenous to regions from the Persian deserts to Afghanistan. The compari-

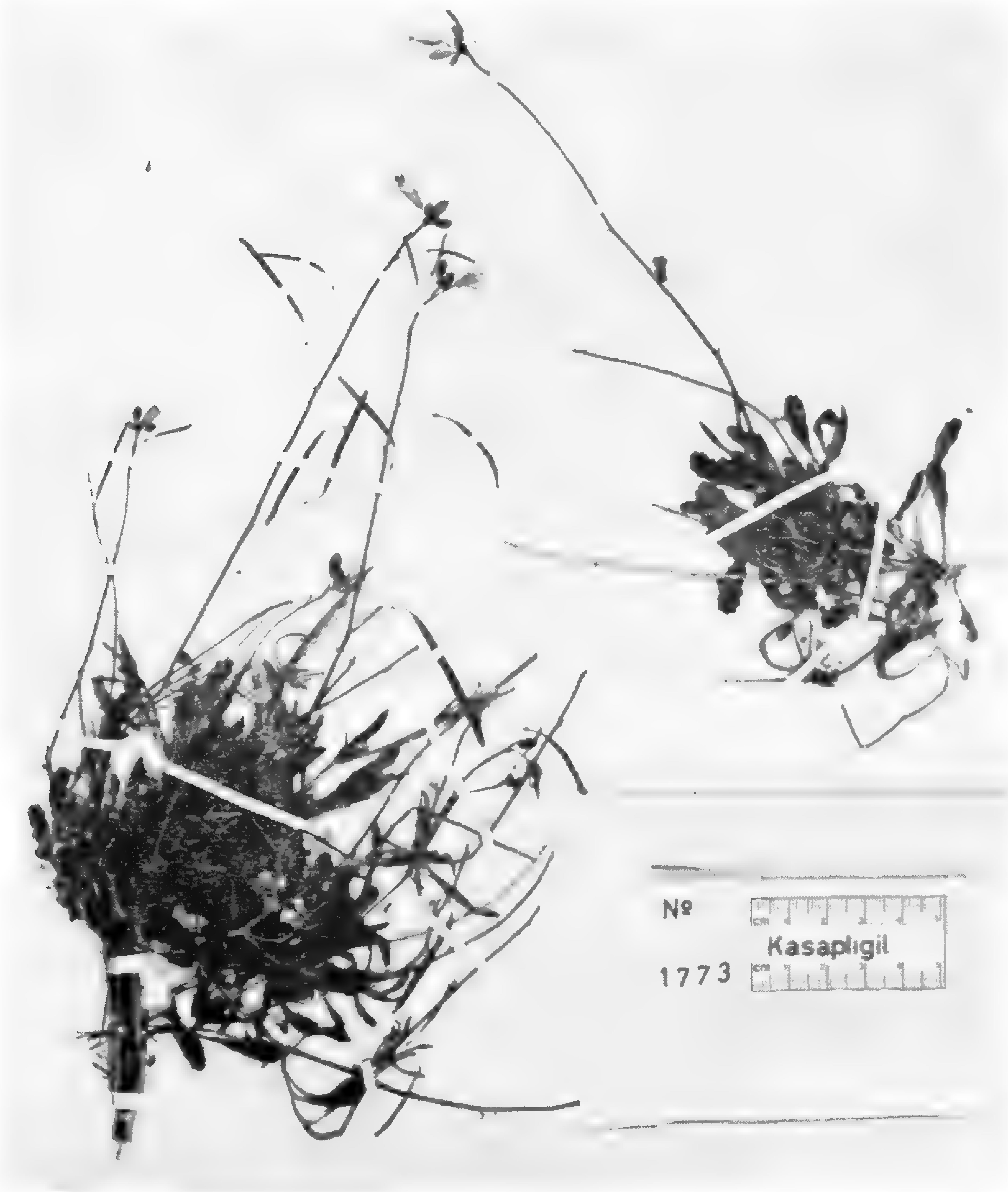

FIG. 3. *Diplotaxis kerakensis* Kasapligil. Habit of fruiting plants [note profuse branching of stems at base].

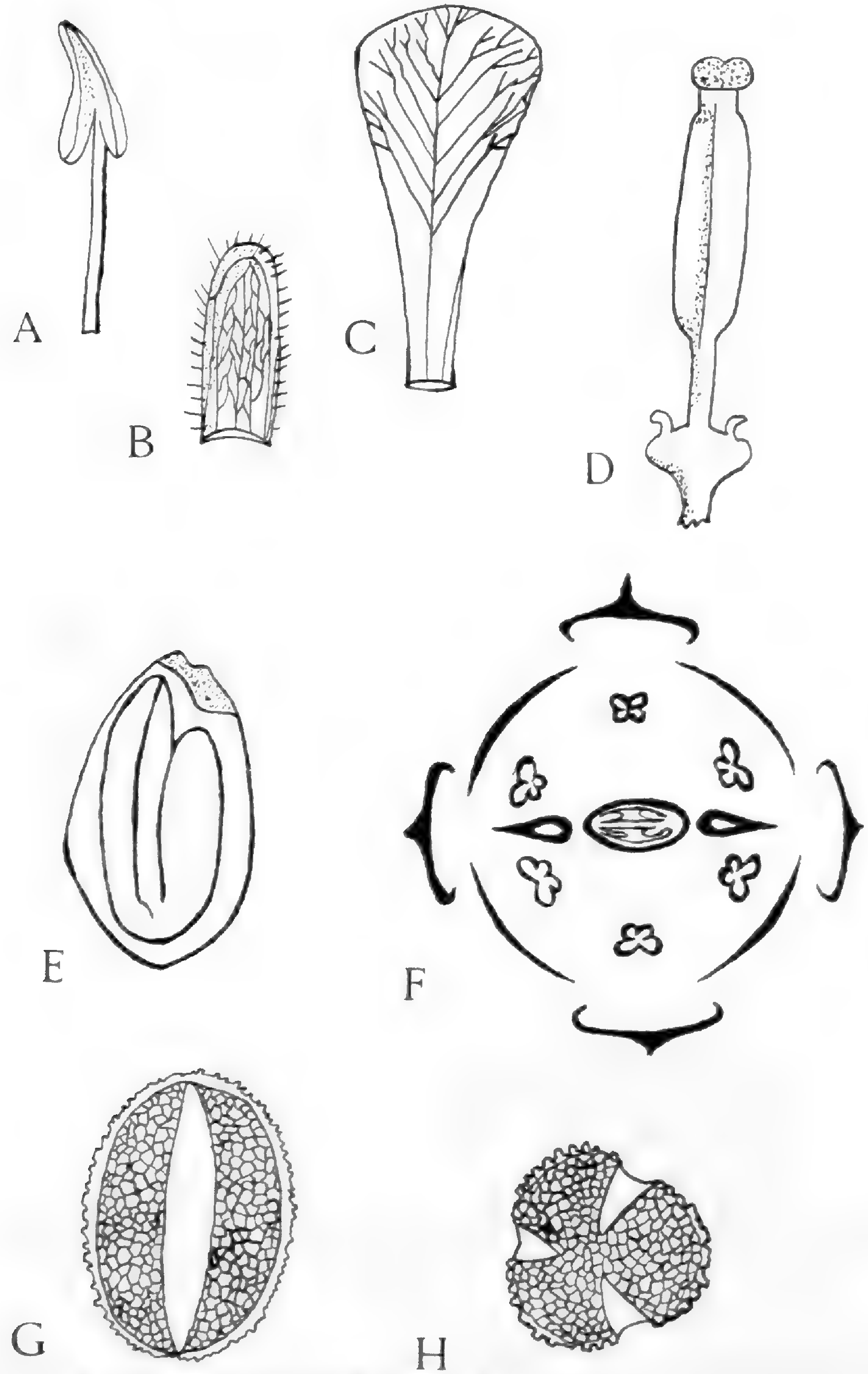

FIG. 4. *Diplotaxis kerakensis* Kasapligil. A, stamen, × 8; B, adaxial view of sepal with involute margins, × 5; C, petal with single trace, × 5; D, floral receptacle bearing pistil and horn-shaped nectaries, × 5; E, longitudinal section of

son of characters of *A. asphaltitis* and *A. griffithii* is summarized in the table which follows.

	Atriplex asphaltitis	**Atriplex griffithii**
HABIT	Shrub, 1–1.5 m. high, white-glaucous.	Shrub, to 1 m. high, white-glaucous.
LOWER LEAVES	Alternate, entire or sparsely dentate, rhombic to broadly trullate or elliptic; acute or retuse at apex; cuneate or truncate at base; 1.5–2 cm. long, 1–1.5 cm. wide.	Opposite or alternate, entire, narrowly ovate; acuminate at apex, cuneate at base; 2.5 cm. long, 2 cm. wide.
UPPER LEAVES	Triangular, mucronate, the margins entire, but dentate at base.	Narrowly ovate, margins entire or sparsely dentate.
SEXUALITY	Dioecious.	Monoecious.
INFLORESCENCE	Glomerules loosely spicate, prominently interrupted, clusters 6–8 mm. thick.	Glomerules densely spicate, unisexual, clusters 10–11 mm. thick.
STIGMA	2 stigmas from a short style, slightly protruding from bracts at maturity, 1–1.5 mm. long.	2–3 stigmas from a longer style, completely hidden within bracts at maturity, ca. 1.5 mm. long.
FRUITING BRACTS	Depressed-ovate to reniform, auriculate at base, margins conspicuously dentate, firmly united at base and around fruit, vasculature conspicuous, appendages none, 4 mm. long, 7 mm. wide.	Roundish oval or triangular-cordate, rounded at base, margins obsoletely denticulate, firmly united halfway, vasculature very prominent, appendages present, up to 11 mm. long, 9 mm. wide.
SEEDS	Light brown, 2–2.5 mm. in diameter.	Dark brown, 2–2.5 mm. in diameter.
EMBRYO	Cotyledons 2 or 3, radicle directed upwardly.	Cotyledons always 2, radicle directed laterally.
POLLEN	24.74 (21.12–29.92) microns in diameter, germ pores 60 (50–72).	22.31 (19.36–24.64) microns in diameter, germ pores 33 (24–44).

Unfortunately, staminate specimens of *Atriplex asphaltitis* were not available for study. The pollen grains described here were obtained from the stigmatic surfaces of the pistillate flowers. *A. asphaltitis* is remarkably distinct from *A. griffithii*. Its relationship to *A. halimus* L. which belongs to section CORIACEA Aellen is remote.

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seed showing folded embryo [note that cotyledons are longer than the radicle], × 45; F, ground plan of flower; G–H, equatorial and polar views of tricolpate pollen grains showing polygonally reticulate surface, × 1200.

FIG. 5. *Zilla spinosa* (Turra) Prantl var. *emarginata* Kasapligil. Portion of intricately branching stem.

Diplotaxis kerakensis sp. nov. FIGS. 3 and 4.

Planta basi lignescens, ramosa; pedicelli et flores aequilongi; petala intense lutea; antherae acumine cuspidatae; nectariae corniformes; cotyledones quam radiculae longiores; grana pollinis prolata vel subprolata.

tricolpata, exina 2.5 micra crassa, polygonali-reticulata, axis polaris 36.7 (33–40) micra longa, diameter aequatorialis 26.2 (24–28.5) micra longus.

Perennial herb 20–30 cm. high, branching only at the woody base, the lower parts of stems sparingly hairy, the upper parts glabrescent, rarely bearing leaves; leaves spatulate-oblanceolate, 2–4.5 cm. long, 0.5–1 cm. broad, glaucous, coarsely dentate, hispid; pedicels equaling flowers in length; sepals 6–7 mm. long, 1.5–2 mm. broad, ovate, the margins membranous, involute, the dorsal surface velutinous, with 3–5 vascular traces from base; petals spatulate, twice as long as sepals, bright yellow, with a single vascular trace from base; short stamens 7 mm. long, long stamens 9–9.5 mm. long, anthers 2–2.5 mm. long, pointed at tip, filaments without appendages, with a single trace from base; pistil 6–6.5 mm. long, 1 mm. broad on flat side, gynophore filiform, 2–2.5 mm. long, stigma obscurely bilobed, style very short; nectaries horn-shaped, 0.5 mm. long, persistent at fruiting stage; silique 3.5–4 cm. long, 2.5–3 mm. broad, erect-ascending when young, drooping at maturity; seeds 76–98 per silique, 1–1.5 mm. long, 0.75–1 mm. broad, oval, flat, the seed coat brownish yellow, the embryo folded, cotyledons longer than radicle; pollen grains prolate to subprolate, tricolpate, exine 2.5 microns thick, polygonal-reticulate, polar axis 36.7 (33–40.5) microns, equatorial diameter 26.2 (24–28.5) microns.

HOLOTYPE: Kerak district, Kerak, Castle of Crusaders, on walls, alt. ca. 1000 m. above sea level, Dec. 16, 1954, *B. Kasapligil 1773* (UC 1.083.543; isotype, A).

This new species of *Diplotaxis*, *D. kerakensis*, is a member of section CATOCARPUM DC. (Syst. **2**: 629. 1821; Prodr. **1**: 221. 1824), in which the silique is characterized by having a filiform gynophore and 50–150 ovules. *D. kerakensis* is allied to *D. harra* (Forsk.) Boiss. (cf. Schulz in Engler, Pflanzenfam. **17b**: 343. *fig. 188 A, B.* 1936), but it differs from that species as shown in the summary which follows.

	Diplotaxis kerakensis	**Diplotaxis harra**
HABIT	Stems branching at woody base.	Stems branching above.
FLOWER	Large, bright yellow.	Small, pale yellow.
PEDICEL	Equaling the flowers.	Longer than the flowers.
SEPALS	6–7 mm. long.	4–5 mm. long.
PETALS	12–13 mm. long.	7–9 mm. long.
ANTHERS	Pointed at tip.	Blunt at tip.
STIGMA	Capitate or slightly bilobed.	Distinctly bilobed.
NECTARIES	Horn shaped	Club shaped.
COTYLEDONS	Longer than radicle.	Shorter than radicle.

Zilla spinosa (Turra) Prantl var. **emarginata** var. nov.

FIGS. 5 and 6 A. B.

Folia 2–4.5 cm. longa, 3–14 mm. lata, lanceolata; spini graciles, usque

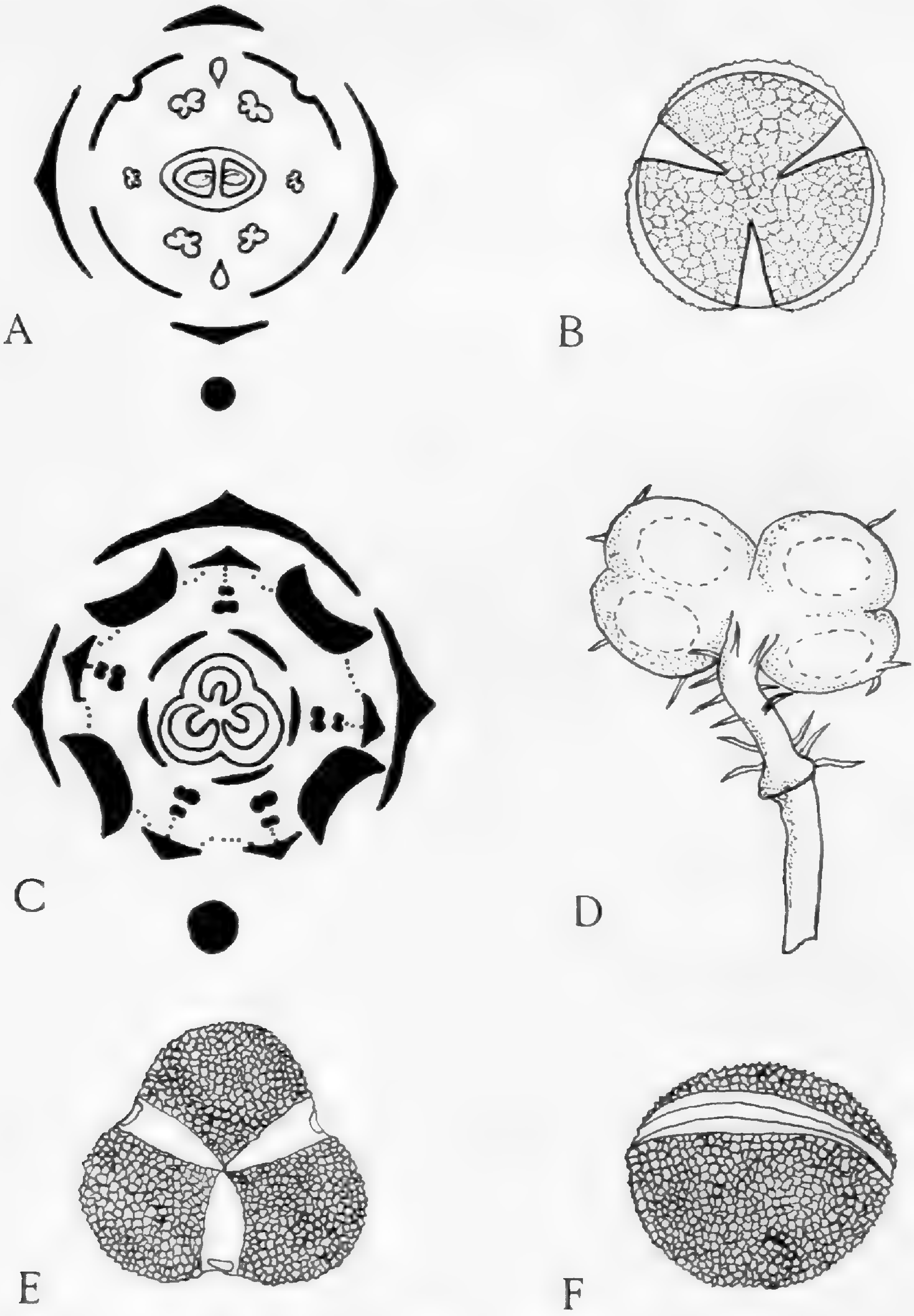

FIG. 6. A and B, *Zilla spinosa* (Turra) Prantl var. *emarginata* Kasapligil. Ground plan of flower showing positions of emarginate petals and polar view of a pollen grain, × 1800.

FIG. 6. C–F, *Euphorbia aleppica* L. var. *prostrata* Kasapligil. C, Ground plan of cyathium showing three subtending bracts (outermost whorl), four crescent-shaped glands forming an involucral tube with five alternating prophylls, ten staminate flowers adnate to involucral tube, five residual perianth segments

FIG. 7. *Euphorbia aleppica* L. var. *prostrata* Kasapligil. Branching habit of plant.

adjacent to tricarpellate ovary of pistillate flower in center; D, staminate flower with a single anther and four microsporangia, × 76; E, polar view of pollen grain showing three furrows and irregularly reticulate exine, × 1000; F, equatorial view of a pollen grain, × 1000.

ad 7 cm. longae; sepala interna 6–7 mm. longa, 1 mm. lata, lanceolata, sepala lateralia 7–8 mm. longa, 2–3 mm. lata, ovata; petala 16 mm. longa, lobi 3 mm. lati, petala dua externa apice emarginata; grana pollinis tricolpata, exina 3 micra crassa, superficies polygonali-reticulata, axis polaris 16.5–19.5 micra longa, diameter aequatorialis 22.5–24 micra longus.

HOLOTYPE: Amman district, eastern desert near Azraq, in Wadi Ratam (a branch of Wadi Sirhan) between Chechan and Druse (in Arabic "Duruz") villages, calcareous loam, alt. ca. 570 m. above sea level, Apr. 25, 1955, *B. Kasapligil 2605* (UC 1,083,534; isotype, A).

Zilla spinosa (Turra) Prantl is a variable species indeed. The specimens from Maan district of Jordan, Sinai peninsula, Egyptian deserts and Algeria which are deposited in the herbarium of the Royal Botanic Gardens, Kew, show considerable variation in the size of the floral appendages. However, all the specimens I examined from other localities had petals with rounded apices.

Euphorbia aleppica L. var. **prostrata** var. nov. FIGS. 6 C–F, 7.

Planta procumbens; folia inferiora 6–10 mm. longa, 0.5–1 mm. lata, linearia, mox decidua; folia superiora 2–8 mm. longa, 2–5 mm. lata, ovoideo-rhomboidea; grana pollinis tricolpata, exina irregulariter reticulata, axis polaris 42 (40–43) micra longa, diameter aequatorialis 37 (36–39) micra longus.

Plant procumbent; lower leaves 6–10 mm. long, 0.5–1 mm. broad, linear, readily deciduous; upper leaves 2–8 mm. long, 2–5 mm. broad, ovate-rhombic; pollen grains tricolpate, exine irregularly reticulate, polar axis 42 (40–43) microns long, equatorial diameter 37 (36–39) microns.

HOLOTYPE: Burak Suleiman, between Bethlehem and Hebron, common in terra rossa and limestone crevices, alt. ca. 800 m. above sea level, Dec. 10, 1954, *B. Kasapligil 1709* (UC 1,083,533; photo. A).

Other specimens examined: Syria, Hauran, Kneia, *E. Peyron 667* (G); Cyprus, Kyrenia, *E. W. Kennedy 612* (K).

Besides the procumbent habit, *Euphorbia aleppica* var. *prostrata* differs from *E. aleppica* var. *aleppica* with respect to the sizes of the lower as well as of the upper leaves on stems which are considerably larger in the latter. On the other hand, seed-coats are rugose in both varieties.

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A REVISION OF THE MALESIAN SPECIES OF ZANTHOXYLUM (RUTACEAE)

THOMAS G. HARTLEY

THIS STUDY OF THE GENUS *Zanthoxylum* L. is the first of a series of studies on the Rutaceae of Malesia, a family represented by about 30 genera in that area. The geographic delimitation of Malesia as interpreted here (see MAP 1) is the same as that outlined by van Steenis (1950) for *Flora Malesiana* except that the Solomon Islands are included as well.

A genus of about 200 species, *Zanthoxylum* is mainly pantropical in distribution. There are, in addition, several temperate-latitude species in eastern Asia and one in North America. To my knowledge, the range of individual species is restricted so that no single species has a completely pantropical distribution.

The genus is readily recognizable for it is the only Malesian genus of the Rutaceae with the following combination of characteristics: armed, leaves alternate and compound (generally pinnate), carpels entirely or partially distinct. *Geijera,* which occurs in New Guinea, also has alternate leaves and a somewhat similar gynoecium, but is unarmed and the leaves are simple. *Toddalia,* of western Malesia and the Philippines, is similarily armed and has alternate, trifoliolate leaves, but in it the gynoecium is syncarpous.

Since both are present in the area, a treatment of the Malesian species of *Zanthoxylum* involves the problem of whether or not to consider the segregate genus *Fagara* L. (with a biseriate, differentiated perianth) distinct from *Zanthoxylum* L. *sensu stricto* (with a uniseriate, undifferentiated perianth). In general, botanists who favor recognition of the two genera consider the perianth of *Zanthoxylum* to be primitive, with segments homologous to petals, while those who include *Fagara* with *Zanthoxylum* consider the *Zanthoxylum* perianth to be derived from that of *Fagara.* This problem has recently been reviewed and discussed by Brizicky (1962) who concludes 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." He further states that "The occurrence of species of *Zanthoxylum* which appear in their perianth structure to be transitional to *Fagara* not only supports this view [of reduction], but also is ample reason to regard *Fagara* as a subgenus of *Zanthoxylum*." I agree with these conclusions, except in the formal recognition of *Fagara* as a subgenus. To the supporting evidence cited by Brizicky I can add that selected specimens of *Zanthoxylum dimorphophyllum* Hemsl., of China, illustrate what appears to be rather complete transition between the *Fagara* and *Zanthoxylum* types of perianth. The following data, taken from three staminate collections of this species in the herbarium of the Arnold Arboretum, serve to demonstrate this:

1. *Fagara* (primitive) type of perianth (*Lau 1870*, Hainan Island). Perianth biseriate; sepals 4, triangular, 0.2–0.5 mm. long; petals 4, clawed, 1.5 mm. long. Stamens 4, opposite the sepals.
2. Intermediate type of perianth (*Wilson 113*, Hupeh Province). Perianth irregularly uniseriate; sepals 1–4, ligulate, about 1.2 mm. long; petals 4–6, slightly clawed, about 2 mm. long. Stamens 5, opposite sepals where sepals are present.
3. *Zanthoxylum* (derived) type of perianth (*Wilson 4770a*, Hupeh Province). Perianth segments irregularly uniseriate, all similar, 7–8, 2–2.5 mm. long. Stamens 5–6, generally opposite 2 or 3 of the segments.

As might be expected, there has been considerable disagreement among authors as to the proper genus for *Z. dimorphophyllum*. Hemsley, in the original description (Ann. Bot. **9**: 150. 1895), placed it in *Zanthoxylum*, stating, in regard to the carpellate flowers, ". . . apetali, vel sepala petalis simillima. . . ." Engler (1896) and Reeder and Cheo (1951) assigned it to *Fagara*, whereas Rehder and Wilson (1914) and Huang (1957) placed it in the genus *Zanthoxylum*, section *Euzanthoxylum* Endl. and subgenus *Thylax* (Raf.) Rehd., respectively.

The description of the genus and the synonymy, presented below, applies only to the Malesian species of *Zanthoxylum*. Each of the species is dealt with completely, however, including where applicable, data regarding extra-Malesian as well as Malesian collections and nomenclature.

I was able to study and collect three of the New Guinea species (*Zanthoxylum conspersipunctatum*, *Z. ovalifolium* and *Z. pluviatile*) while employed as a botanist for the Australian Commonwealth Scientific and Industrial Research Organization, Phytochemical Survey of New Guinea, 1961–1965. This study is otherwise based on herbarium specimens. The contributing herbaria are listed below, with abbreviations from Lanjouw and Stafleu's *Index Herbariorum*, Part I. Ed. 5 (Regnum Vegetabile, **31**. 1964).

A	Arnold Aboretum of Harvard University, Cambridge
BM	British Museum (Natural History), London
BRI	Botanic Museum and Herbarium, Brisbane
CANB	C.S.I.R.O. Division of Plant Industry, Canberra
GH	Gray Herbarium of Harvard University, Cambridge
G-DC	Herbier DeCandolle, Conservatoire et Jardin Botaniques, Geneva
K	Royal Botanic Gardens, Kew
L	Rijksherbarium, Leiden

M	Botanische Staatssammlung, Munich
MEL	National Herbarium of Victoria, Melbourne
MICH	University Herbarium, University of Michigan, Ann Arbor
NY	New York Botanical Garden, New York
P	Muséum National d'Histoire Naturelle, Paris
PR	Botanical Department of National Museum, Prague
SING	Herbarium of the Botanic Gardens, Singapore
TI	Botanical Institute, Faculty of Science, University of Tokyo
US	U.S. National Museum (Department of Botany), Smithsonian Institution, Washington

I wish to thank the directors and curators of these herbaria for making specimens in their care available to me. Sincere thanks are also extended to Drs. Lily M. Perry and Lorin I. Nevling, Jr., for their cordial assistance in various technical problems.

Zanthoxylum[1] L. Sp. Pl. 1: 270. 1753. Type species: *Xanthoxylum americanum* Mill. (see Fosberg, 1959, and Brizicky, 1962).

Fagara L. Syst. ed. 10. 897. 1759, nom. cons. Type species: *Fagara pterota* L.
Tipalia Dennst. Schlüss. Hort. Malab. 31. 1818. Type species: *Tipalia limonella* Dennst. [*Zanthoxylum limonella* (Dennst.) Alston].

Scandent or erect shrubs or trees; aromatic, dioecious or rarely monoecious, evergreen or deciduous, armed. Leaves alternate, (occasional leaves unifoliolate) trifoliolate, imparipinnate or paripinnate, to 175 cm. long; rachis terete or winged; leaflets to 15 pairs, opposite to alternate, often inequilateral, with or without scattered and/or marginal oil dots. Inflorescences racemose, paniculate or cymose, axillary and/or terminal. Flowers small, unisexual or rarely bisexual; perianth of 6–8 irregularly uniseriate, undifferentiated segments or differentiated and biseriate with 4–5 sepals and 4–5 petals; stamens 4–6, uniseriate, opposite the sepals, rudimentary or absent in carpellate flowers; disc flat to pulvinate; gynoecium 1–5-carpellate, rudimentary or absent in staminate flowers, ovaries distinct or connate to about the middle, 1-locular, each with 2 collateral, pendulous ovules, styles coherent to divergent, stigmas capitate, coherent to free. Fruits of 1–5 distinct or partially connate, 1-seeded, 2-valved follicles; outer pericarp glandular punctate or pustular, firm to rather fleshy, red to black; endocarp cartilaginous, straw-colored; seeds ovoid to globose, often hanging from the opened follicle by a funiculus at maturity, the testa black or reddish, shining and crustaceous, the endosperm fleshy.

The habit of plants in the genus is variable and five of the seven scandent species are also known as semi-erect or erect shrubs.

A variety of spines and prickles, ranging from broad, corky-based spines to 4 centimeters in diameter to small, scattered or pseudostipular, flattened or terete, recurved, straight or ascending prickles occur in the Malesian species. While all of the species are more or less armed, the presence of spines or prickles on a given part of a plant is quite variable. Thus an

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[1] *Xanthoxylum*, *Xanthoxylon* and *Zanthoxylon* are variant spellings.

unarmed herbarium specimen (perhaps chosen by the collector for easier handling!) may often be encountered in a heavily armed species.

Oil dots are found in the leaflets of most species but are seldom consistently present. These glands may be scattered and/or marginal, and, judging from the study of cleared leaflets of *Zanthoxylum conspersipunctatum* and *Z. pluviatile,* may consist of large, oil-filled cavities that are not traversed by the veins, or single cells or small groups of cells that do not interrupt the venation pattern. If these are the same as the "secretory cavities and secretory cells" described by Stern and Brizicky (1960) in a study of the genus *Diomma* (Rutaceae), they seem here to be less significant taxonomically. In *Zanthoxylum conspersipunctatum, Z. limonella* and *Z. nitidum,* for example, only occasional specimens have what appear to be the large cavity type of oil dot scattered in the mesophyll. To distinguish them taxonomically, on this basis, would be doing so in the absence of other correlating morphological differences and would necessitate description of several new taxa.

The larger marginal crenations of the leaflets of a number of species are also irregular in occurrence. In *Zanthoxylum limonella* and *Z. nitidum,* for instance, the leaflet margins range from entire to glandular crenate with as many as three or four crenations per centimeter.

The geographic affinities of the Malesian species of *Zanthoxylum* appear to be Asian and Malesian. Nine of the nineteen species occur in both continental Asia and Malesia and an equal number are endemic to single islands or otherwise limited areas in Malesia. *Zanthoxylum parviflorum,* a close relative of the widespread *Z. limonella,* is endemic to the Northern Territory of Australia and adjacent southwestern New Guinea.

The wide and often rather discontinuous distributions of a number of the species is possibly due, in part, to long-distance dispersal of the attractive seeds by birds.

In general the species grow in rain forests and thickets at low and medium altitudes. Three of them, *Zanthoxylum limonella, Z. ovalifolium* and *Z. parviflorum,* are most often found in monsoonal areas and one, *Z. conspersipunctatum,* appears to be restricted to montane forests and thickets.

The flowers are fragrant and pollination is apparently by insects.

The following comments concern the citation of collections:

1. The collections are cited in the following geographic sequence: Asia, Malesia and Australia. Within these major areas they are cited in an east to west sequence, following, for Malesia, the sequence outlined in *Flora Malesiana* (Ser. 1. 1: LXXVI – LXXVIII. 1950).

2. The sex of each collection is indicated by the appropriate symbol following the collection number, or, in instances where two or more specimens of a collection from two or more herbaria are of different sex, by the appropriate symbol in parentheses following each herbarium citation. Herbarium sheets with male and female specimens of one collection are indicated by "♂ & ♀." Specimens that are monoecious with unisexual flowers are indicated by "♂ ♀." Specimens with perfect flowers are desig-

nated " ☿ ". Specimens for which I do not give an indication of sex are either sterile or at a stage where the determination could not be made.

3. Following are the abbreviations used for collections numbered in series:

BS	Bureau of Sciences, Manila
BSIP	British Solomon Islands Plants
BW	Boswezan, Forestry Division, Netherlands New Guinea
CCC	Canton Christian College
CP	Ceylon Plants
FB	Forestry Bureau, Manila
HB	Herbarium Bogoriense
LU	Lingnan University
NIFS	Netherlands Indies Forest Service, Forest Research Institute, Buitenzorg. NIFS Ja: Java series. NIFS bb: series bossen buitengewesten — islands outside Java
NGF	New Guinea Forces (now New Guinea Forest Department)
NU	Nanking University
PNH	Philippine National Herbarium
Sar	Sarawak Forestry Service
SB	Species Blancoanae, Philippines
SF	Singapore Field Series
TNSM	Tokyo National Science Museum

KEY TO THE SPECIES

1\. Branchlets armed, the prickles mostly flattened and predominantly pseudostipular; leaf rachises usually with conspicuous wings extending to as much as 6 mm. on each side; perianth uniseriate or irregularly biseriate, of 6–8 similar segments . . . . 2.

  2\. Main veins of leaflets evident, 10–28 on each side of the midrib; inflorescences in the axils of lateral leaves, 0.5–2 cm. long; anthers reddish purple prior to anthesis; gynoecium 2–5-carpellate 18. *Z. acanthopodium.*

  2\. Main veins of leaflets generally faint, 7–15 on each side of the midrib; inflorescences terminal on short, lateral branchlets and occasionally in the axils of lateral leaves as well, 1–7 cm. long; anthers yellow prior to anthesis; gynoecium 1–3-carpellate . . . . 19. *Z. armatum.*

1\. Branchlets armed or unarmed, the prickles terete and usually scattered; leaf rachises terete or with narrow wings extending to not more than 1 mm. on each side; perianth biseriate, of 4–5 sepals and 4–5 petals . . . . 3.

  3\. Scandent or suberect shrubs; branchlets and/or leaf rachises armed with retrorse prickles; gynoecium 4- or 2-carpellate[2] . . . . 4.

    4\. Inflorescences mostly in the axils of lateral leaves; gynoecium 4-carpellate . . . . 5.

      5\. Lateral leaflets subopposite to alternate; terminal leaflet on an extension of the rachis generally less than one-half the width of the blade . . . . 1. *Z. scandens.*

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[2] The number of carpels in the Malesian species other than *Z. acanthopodium* and *Z. armatum* can be determined in fruiting as well as carpellate flowering material since carpels that do not develop into fruit are persistent.

        5. Lateral leaflets opposite; terminal leaflet on an extension of the rachis generally more than one-half the width of the blade . . . . 2. *Z. nitidum.*
    4. Inflorescences terminal and from upper leaf axils; gynoecium 2-carpellate . . . . 6.
        6. Inflorescences cymose, the primary branches generally whorled; perianth and androecium 5-merous; follicles 4.5 mm. in diameter . . . . 5. *Z. avicennae.*
        6. Inflorescences paniculate, the primary branches opposite or alternate; perianth and androecium 4-merous; follicles 6–10 mm. in diameter . . . . 7.
            7. Leaves ascending, spreading or arching; acuminate apices of leaflets about one-fourth the length of the blade; follicles about 10 mm. in diameter . . . . 8. *Z. backeri.*
            7. Leaves strongly reflexed at the pulvinate base of the rachis; acuminate apices of leaflets about one-seventh the length of the blade; follicles 6–7 mm. in diameter . . . . 9. *Z. retroflexum.*
3. Erect shrubs or trees; branchlets with straight or ascending prickles or unarmed; gynoecium 3-, 2- or 1-carpellate (*Zanthoxylum scandens* is occasionally, in Asia, an unarmed, erect shrub, but is always 4-carpellate) 8.
    8. Leaves trifoliolate . . . . 17. *Z. ovalifolium.*
    8. Leaves pinnate . . . . 9.
        9. Inflorescences cymose, the primary branches generally whorled; leaflets less than 8 cm. long; perianth and androecium 5-merous; gynoecium 2-carpellate . . . . 5. *Z. avicennae.*
        9. Inflorescences paniculate, the primary branches opposite or alternate; leaflets more than 8 cm. long *or* perianth and androecium 4-merous and gynoecium 1-carpellate . . . . 10.
            10. Perianth and androecium 5-merous; gynoecium 3-carpellate . . . . 11.
                11. Leaflets elliptic, broadest at about the middle . . . . 3. *Z. myriacanthum.*
                11. Leaflets elliptic-lanceolate to lanceolate, broadest near the base . . . . 4. *Z. ailanthoides.*
            10. Perianth and androecium 4-merous; gynoecium 1- or 2-carpellate . . . . 12.
                12. Leaves more than 40 cm. long; leaflets 3–5 pairs; gynoecium 2-carpellate . . . . 13.
                    13. Leaves more than 70 cm. long; leaflets 4–5 pairs, the petiolules obsolete to 5 mm. long . . . . 6. *Z. megistophyllum*
                    13. Leaves less than 70 cm. long; leaflets 3–4 pairs, the petiolules 7–10 mm. long . . . . 7. *Z. forbesii.*
                12. Leaves less than 40 cm. long *or* with more than 5 pairs of leaflets; gynoecium 1-carpellate . . . . 14.
                    14. Branchlets unarmed; leaflets usually obovate, broadest above the middle, the margins entire . . . . 16. *Z. integrifoliolum*
                    14. Branchlets armed or unarmed; leaflets ovate to oblong, broadest at about the middle or below, the margins entire or crenate . . . . 15.

15. Deciduous (the flowers appearing before or with the young leaves); acuminate apices of leaflets one-eighth to one-fourth the length of the blade; flowers 1.5–3 mm. long. . . . . 16.
    16. Leaves 30–40 cm. long; leaflets 7–13 cm. long, the petiolules 3–5 mm. long . . . . 10. *Z. limonella.*
    16. Leaves 22–28 cm. long; leaflets 5–8 cm. long, the petiolules 1.5–3 mm. long . . . . 11. *Z parviflorum.*
15. Evergreen; acuminate apices of leaflets one-sixteenth to one-ninth the length of the blade; flowers 3–9 mm. long . . . . 17.
    17. Leaves 10–30 cm. long; leaflets 2–8 pairs; sepal margins entire or subentire . . . . 15. *Z. conspersipunctatum.*
    17. Leaves 30–60 cm. long; leaflets 5–12 pairs; sepal margins ciliate . . . . 18.
        18. Inflorescence axes and branches puberulent . . . . 12. *Z. celebicum.*
        18. Inflorescence axes and branches glabrate . . . . 19.
            19. Leaflet bases subcordate . . . . 13. *Z. vinkii.*
            19. Leaflet bases oblique to rounded . . . . 14. *Z. pluviatile.*

1. **Zanthoxylum scandens** Bl. Bijdr. Natuurk. Wetens. 249. 1825. Type: *Blume 1603,* Java.

Xanthoxylum cuspidatum Champ. ex Benth. Jour. Bot. Kew Misc. **3:** 329. 1851. Type: *Champion 86,* Hong Kong.

Zanthoxylum khasianum Hook. f. Fl. Brit. Ind. **1:** 494. 1875. Type: *Hooker f. & Thomson 1517,* India, Assam.

Fagara scandens (Bl.) Engl. Nat. Pflanzenfam. III. **4:** 118. 1896.

Fagara cuspidata (Champ. ex Benth.) Engl. *Ibid.*

Fagara khasyana (Hook. f.) Engl. *Ibid.*

Fagara laxifoliolata Hay. Ic. Pl. Formosa **3:** 50. 1913. Type: *Kawakami & Shimada,* 1911, Taiwan.

Fagara cyrtorhachia Hay. *Ibid.* **6:** 8. 1916. Syntypes: *Ito & Hayata,* 1914 and *Hayata,* 1914, Taiwan.

Fagara leiorhachia Hay. *Loc. cit.* 10. Type: *Hayata,* 1913, Taiwan.

Fagara chinensis Merr. Philip. Jour. Sci. Bot. **13:** 141. 1918. Type: *Merrill 10660,* China, Kwangtung Province.

Zanthoxylum chinensis (Merr.) Chung, Mem. Sci. Soc. China **1:** 123. 1924 (*fide* Huang, Acta Phytotax. Sinica **6** (1): 72. 1957).

Fagara kwangsiensis Hand.-Mazz. Sinensia **3:** 186. 1933. Type: *Ching 5401,* China, Kwangsi Province.

Zanthoxylum yunnanense Huang, Acta Phytotax. Sinica **6** (1): 59. 1957. Type: *Tsai 55960,* China, Yunnan Province.

Zanthoxylum laxifoliolatum (Hay.) Huang, *Ibid.* 81.

Zanthoxylum leiorhachium (Hay.) Huang, *Ibid.*
Zanthoxylum cyrtorhachium (Hay.) Huang, *Ibid.*

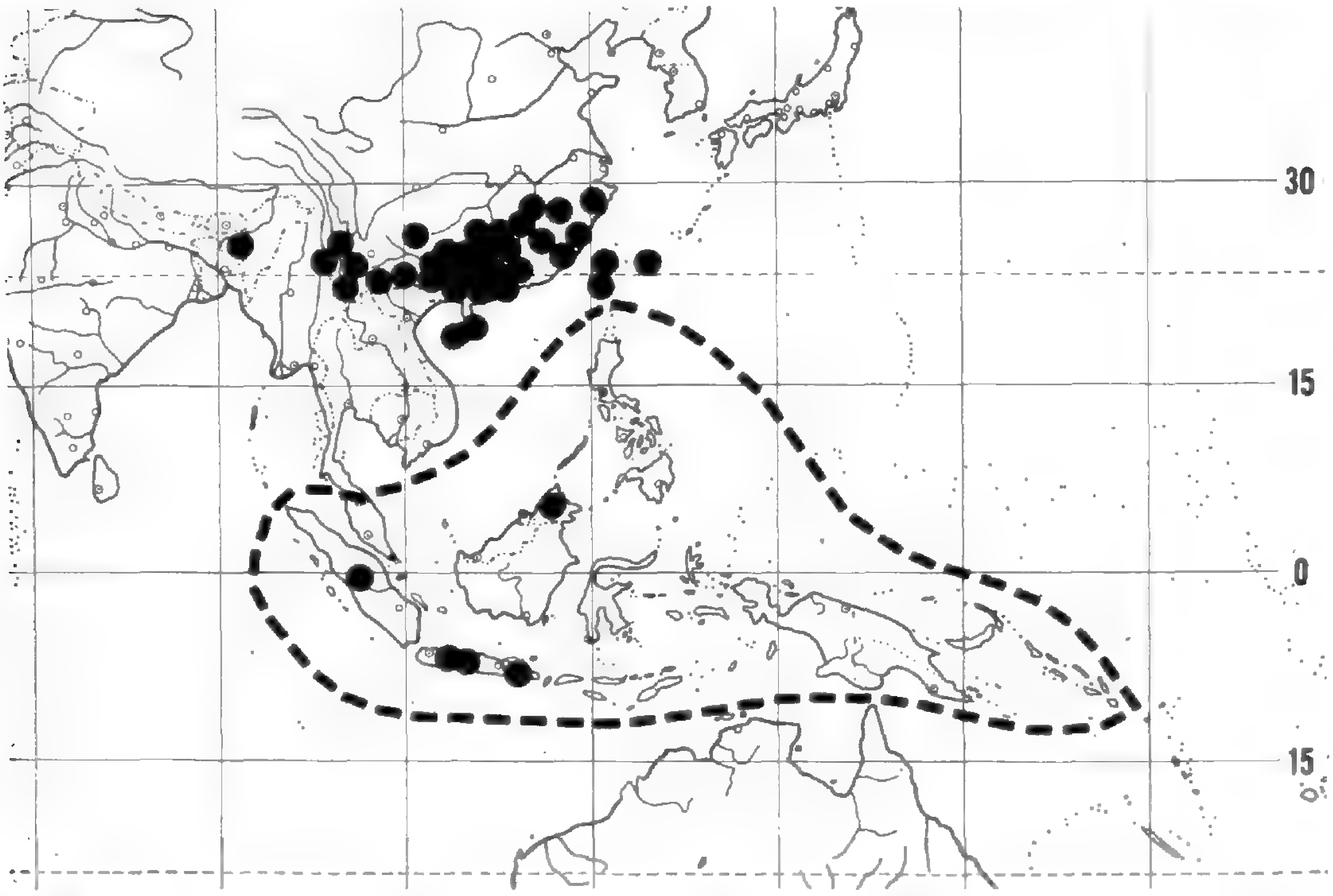
Scandent and generally climbing or occasionally suberect or erect shrubs; dioecious; evergreen; branchlets and leaf rachises generally armed, the prickles scattered and retrorse. Leaves imparipinnate, 8–37 cm. long; rachis glabrous to short pubescent; petiolules 1–5 mm. long; leaflets (1) 2–12 pairs, subopposite to alternate, chartaceous to subcoriaceous, dark green and glabrous above, paler and glabrous or sparsely pubescent below, generally blackening slightly with drying, ovate to elliptic-lanceolate, 3–9 cm. long, 1–4 cm. wide, base cuneate to obtuse, main veins 4–14 on each side of the midrib, margins, especially in the apical half of the blade, finely glandular crenate with as many as 20 crenations per cm., apex abruptly acuminate to attenuate. Inflorescences axillary or axillary and terminal, paniculate, to 12 cm. long and generally about one-half as wide, the axes and branches glabrous to short pubescent. Staminate flowers 3–6 mm. long; pedicels obsolete to 5 mm. long; sepals 4, triangular to rounded, about 1 mm. long; petals 4, white to pale yellow, occasionally with a purple margin, elliptic-ovate, about 3 mm. long; stamens 5–6 mm. long, anthers about 1 mm. long; disc flat, about 0.3 mm. high; rudimentary carpels 1–4, to 1.5 mm. high. Carpellate flowers about 3 mm. long; pedicels, sepals, petals and disc as in staminate flowers; rudimentary stamens obsolete to 1 mm. long; gynoecium 4-carpellate, 1–1.5 mm. high, styles divergent at anthesis, stigmas globose. Fruiting pedicels 1–6 mm. long; follicles subglobose, 4–5 mm. in diameter, in 4's, 3's, 2's or single with 0, 1, 2, or 3 undeveloped carpels, respectively.

India. Assam: Khasia Hills, *Chand 4908* ♀ (MICH), *Hooker f. & Thomson 1517* ♀ (K — holotype of *Zanthoxylum khasianum*; GH — isotype), *Ruse 62* (A), *62A* ♀ (A). **China.** Yunnan Province: Sungkwei Range, *Forrest 21554* ♀ (A, US); Mengtsz, *Henry 10421A* ♂ (A), *11163* ♀ (A), *Tsai 52369* ♀ (A); Wen-shan Hsien, *Tsai 51703* ♀ (A), *51764* ♀ (A); O-shan Hsien, *Tsai 53494* ♂ (A); Lan-ping Hsien, *Tsai 54018* ♀ (A); Ping-pien Hsien, *Tsai 55108* ♀ (A), *60072* ♀ (A) *60451* ♀ (A); Lung-ling Hsien, *Tsai 55610* ♂ (A), *55695* ♂ (A); A-tuntze, Huann-fu-ping, *Wang 69107* ♀ (A); Fo Hai, *Wang 74145* ♀ (A); Kiukiang Valley, *Yu 19463* ♀ (A), *20409* ♀ (A); without definite locality, *Forrest 11922* ♀ (A), *15715* ♂ (A) *17712* ♂ (A), *Tsai 55960* ♀ (A — isotype of *Zanthoxylum yunnanense*), *60269* ♀ (A). Kweichow Province: Fan Ching Shan, *Steward, Chiao & Cheo 757* ♀ (A); Tsingchen, Mou-po, *Teng 90156* ♂ (A), *90174* ♂ (A). Kwangsi Province: Luchen, Moo Shan, *Ching 5401* ♀ (A — isotype of *Fagara kwangsiensis*); Lau Ha Tung, *Ching 6584* ♀ (A, US); N. Hin Yen, Yeo Mar Shan, *Ching 7130* ♀ (A, US); Tzu Yuen District, *Chung 83584* ♀ (A); Waitsap District, Se Tze Shan, *Tsang 23310* ♀ (A); Shang-sze District, Shap Man Taai Shan, Na Wai Village, *Tsang 23924* ♀ (A); Yao Shan, *Wang 39369* ♀ (A), *40057* ♀ (A); without definite locality, *Wang 41125* ♀ (A). Kwangtung Province: Road to Mahang, *Chun 5952* ♀ (A); Lung Tau Shan, *Kang, W. T. Tsang & U. K. Tsang CCC 12266* ♀ (US), *CCC 12770* ♀ (US), *To & Tsang 12770* ♀ (A); Wung Yuen District, Tsing Wan Shan, *Lau 2463* ♀ (A); Loh Fau Mt., *Levine, McClure & To*, August 31–September 4, 1921 ♀ (A), *Merrill 10660* ♀ (US — isotype of *Fagara chinensis*; A, photo. of holotype from Manila, specimen destroyed); Canton Delta, Heung Shan, Tung Hang, *To CCC 2237* ♂ (A); Sin-fung District, Ngok Shing Shan, *Taam 426* ♂ (A); Tseungshing District, *Tsang 20149* (A); Tsung-fa District, Sam Kok Shan, *Tsang 25017* ♂ (A), *25193* ♀ (A); Hwei-yang District, Lin Fa Shan, *Tsang 25698* ♀ (A); Jen-hua District, Man Chi Shan, *Tsang 26248* ♂ (A); Ho-yuen District, Kwai Shan, *Tsang 28508* ♂ (A); Ying Tak, Tai Tsan, Chung Tung, *Tsang & Wong 3110* ♀ (A); Wai-yeung District, Pak-Wan Cheung, *Tsui 137* ♀ (A, US). Hainan Island: Po-ting, *How 73154* (A). Hong Kong: *Champion 86* ♂ (K — holotype of *Xanthoxylum cuspidatum*), *Hance 1145* ♂ (GH), *Taam 1111* ♂ (A, US), *1825* ♀ (A, US), *Wright 82* ♂ & ♀ (GH), *s.n.* ♂ (US). Hunan Province: Yun-schan prope Wukeng, *Handel-Mazzetti 2563* ♀ (A), *Hui Handel-Mazzetti Expedition 12321* ♂ (A); Yi Chang District, Ping Tou Shan, Pai Mu Village, *Tsang 23387* ♂ (A, US). Kiangsi Province: Kaling, *Chun 4278* ♀ (A); Swe-chuen Hsien, *Hu 840* ♀ (A); Chung Yih Hsien, *Hu 934* ♀ (A); circa carbonis minas Pinghsiang, *Hui 158* ♀ (A); Lungnan District, Oo Chi Shan, near Lam Uk Tung Village, *Lau 4529* ♀ (A, US). Fukien Province: Hinghwa District, *Chung 1030* ♂ (A); Kuliang, *Chung 6647* ♀ (A), *Norton 1393* ♀ (US). Chekiang Province: Kwanying Tung, Yen Tang Shan, *Chiao NU 14760* ♀ (A, US). **Taiwan.** Mt. Lee-shan, Taichung Hsien, *Feung & Kao 4583* ♀ (A); Mt. Arisan, between Heishana and Funkiko, *Hayata*, April 24, 1913 ♀ (TI — holotype of *Fagara leiorhachia*; A, photo.); Mt. Arisan, between Heishana and Nimandaira, *Hayata*, April 28, 1914 ♀ (TI — syntype of *Fagara cyrtorhachia*; A, photo.); South Cape, *Henry 343* ♀ (US), *1969* ♀ (US); between Funkiko and Taroyen, *Ito & Hayata*, March 29, 1914 ♂ (TI — syntype of *Fagara cyrtorhachia*; A, photo.); Mt. Shichiseitonzan, *Kawakami & Shimada*, April 2, 1911 ♀ (TI — holotype of *Fagara laxifoliata*; A, photo.); Tamsu, *Oldham 59* ♀ (GH); Batakan Tabito, *Tanaka*, October 22, 1930 (A); Nanto Province, Lake Candidius, *Wilson 9973* ♀ (A, US); Taihoki Province, near Hesinbi, *Wilson 10229* ♂ (A, US); without definite locality, *Faurie 8216* (A). **Ryukyu Islands.** Ishigaki Island, *Hatusima 18923* ♀ (US), *Masamune*, March 31, 1935 ♂ (US). **Sumatra.** Sumatra occidentale nel Pandangesche bovenlanden (alto Padang), *Beccari 132* ♀ (K, L, MEL); Westkust, G. Koerinajr, *Bunnemeyer 9574* ♂ (L); Bukit G. Sembilang, Mt. Sago, near Ladang Lawas, *Meijer 4043* ♀ (L). **Java.** West Java: ad montem Tjerimai Provinciae Cheribon, *Blume 1603* ♀ (L — holotype of *Zanthoxylum scandens*; A — isotype); Tjibodes, *Ooststroom 13255* ♂ (L). Central Java: Dieng (Dijeng Plateau), *Junghuhn* ♀ (L). Southeast Java: *Forbes 1001* ♀ (BM), *s.n.*, 1880–82 ♀ (BM). Without definite locality: *Horsfield 66* ♀ (MEL), *1093* ♀ (K), *s.n.* [GH (♀), K (♂)]. **British North Borneo (Sabah).** Mt. Kinabalu, Tenompok, *J. & M. S. Clemens 29213* [A (♂), K (♂), L (♀), NY (♂)], *29243* ♂ (A, K, L, NY).

Distribution. NE India east to Taiwan and Ryukyu Islands; south in Sumatra, Java and British North Borneo; on dry, rocky or sandy slopes and in thickets and mountain forests at altitudes from 1000 to 2000 meters in Malesia and from 300 to 3400 meters in continental Asia. See Map 1.

Illustrations. Huang, C. C., Acta Phytotax. Sinica **6**(1): *t. XI.* 1957, as *Zanthoxylum yunnanense.* Liu, T. S., Illustrations of native and introduced ligneous plants of Taiwan **2**: *t. 728.* 1962, as *Zanthoxylum cuspidatum.*

Acceptance of the extremely variable characters of pubescence, number



MAP 1. Distribution of *Zanthoxylum scandens* Bl. The broken line surrounding the southern stations indicates the geographic area of Malesia as delimited in this paper.

of leaflets, and presence or absence of prickles as being of taxonomic significance would necessitate recognition of an even larger number of taxa than has already been described in this complex. The more conservative delimitation presented here is based on floral characters, arrangement of leaflets, and the type of crenation of the leaflet margin, all of which are relatively constant and, I feel, serve best to show the natural relationship of the various morphological forms involved.

A number of species from continental Asia, including *Zanthoxylum dissitiodes* Huang, *Z. laetum* Drake, *Z. calcicolum* Huang, *Z. chaffanjoni* Levl. and *Z. oxyphyllum* Edgw., show a close relationship to *Z. scandens*.

The following have previously been listed as synonyms of *Zanthoxylum cuspidatum* or *Fagara cuspidata* (= *Zanthoxylum scandens*): *Zanthoxylum khasianum*, by Guillaumin in Flore générale de l'Indo-Chine 1: 640. 1911; *Fagara laxifoliolata, F. cyrtorhachia* and *F. leiorhachia*, by Li, Woody flora of Taiwan, 373. 1963; and *F. chinensis*, by Huang, Acta Phytotax. Sinica **6** (1): 72. 1957.

2. **Zanthoxylum nitidum** (Roxb.) DC. Prodr. 1: 727. 1824.

Fagara nitida Roxb. Fl. Ind. ed. Carey & Wall. 1: 439. 1820. Lectotype: *Roxburgh Icones 2430*, Cult. Bot. Gard. Calcutta.

Nugae sylvarum silvestris Rumph. Herb. Amb. **5**: 124. 1747.

Piper pinnatum Lour. Fl. Cochinch. 31. 1790 (nomen illegit.).

Zanthoxylum torvum F. Muell. Frag. Phyt. Austral. **7:** 140. 1871. Type: *Dallachy*, August 21, 1869, Queensland.

Zanthoxylum hamiltonianum Wall. ex Hook. f. Fl. Brit. Ind. **1:** 494. 1875. Type: *Hamilton*, February 12, 1809 (Wallich cat. n. 7117), India.

Fagara torva (F. Muell.) Engl. Nat. Pflanzenfam. III. **4:** 119. 1896.

Fagara warburgii Perk. Fragm. Fl. Philip. 160. 1905. Type: *Warburg 11784*, Philippines, not seen.

Zanthoxylum hirtellum Ridl. Jour. Fed. Malay States **10:** 131. 1920. Type: *Ridley 11291*, Malay Peninsula.

Zanthoxylum collinsae Craib, Kew Bull. **1926:** 165. 1926. Type: *Collins 705*, Thailand.

Fagara hamiltoniana (Wall. ex. Hook. f.) Engl. Nat. Pflanzenfam. ed. 2. **19a:** 221. 1931.

Fagara hirtella (Ridl.) Engl. *Ibid.*

Zanthoxylum scabrum Guill. Bull. Soc. Bot. Fr. **91:** 215. 1944. Type: *Poilane 28200*, North Vietnam.

Fagara oblongifolia Bakh. f. Blumea **6:** 366. 1950. Syntypes: *Blume 1814* and *s.n.*, Java.

Fagara pendjaluensis Bakh. f. *Ibid.* Type: *Koorders & Koorders-Schumacher 47963β*, Java.

Zanthoxylum asperum Huang, Acta Phytotax. Sinica **6** (1): 75. 1957. Type: *Wang 75548*, China, Yunnan Province.

Zanthoxylum asperum var. *glabrum* Huang, *Ibid.* 76. Type: *Wang 77912*, China, Yunnan Province.

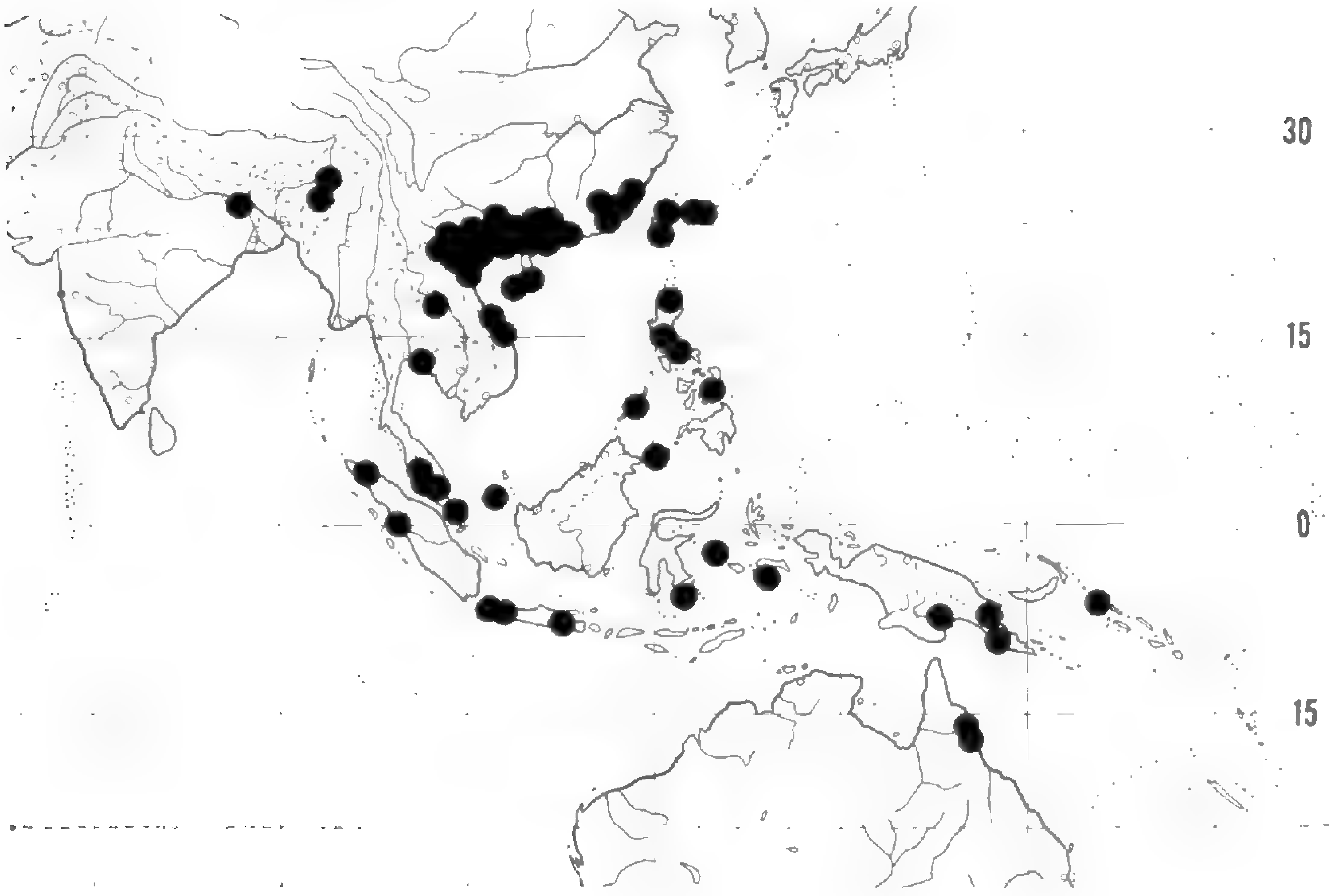
Scandent and generally climbing or occasionally suberect or erect shrubs; dioecious or rarely monoecious; evergreen; old stems occasionally with thick, corky spines to 2 cm. long; branchlets, leaf rachises and midribs of leaflets generally armed, the prickles scattered and retrorse. Leaves imparipinnate, 5–40 cm. long; rachis glabrous to short pubescent; petiolules 2–4 mm. long; leaflets (1) 2–4 pairs, opposite, chartaceous to coriaceous, with or without scattered and/or marginal pellucid dots, glabrous to slightly scabrous above, glabrous to short pubescent below, ovate to elliptic, (1.3) 5–12 (16) cm. long, (0.7) 2.5–6 (8.2) cm. wide, base cuneate to truncate, main veins 5–15 on each side of the midrib, margins entire to glandular crenate with as many as 4 crenations per cm., apex acuminate to obtuse. Inflorescences axillary or axillary and terminal, racemose to paniculate, to 15 cm. long and generally less than one-half as broad, the axes and branches glabrous to short pubescent. Staminate flowers 4–5 mm. long; pedicels 1–3 mm. long; sepals 4, broadly triangular, about 1 mm. long; petals 4, white to pale yellow or rarely reddish, elliptic-ovate, 2–3 mm. long; stamens 4, 4–5 mm. long, anthers about 1 mm. long; disc flat, about 0.3 mm. high; rudimentary carpels 2 or 4, about 1 mm. high. Carpellate flowers 2–3 mm. long; pedicels, sepals and petals as in staminate flowers; disc flat to pulvinate, 0.1–0.5 mm. high; gynoecium 4-carpellate, 1.5–2 mm. high, stigmas coherent at anthesis, the combined stigmatic structure peltate. Fruiting pedicels 1–7 mm. long; follicles subglobose, 5–7 mm. in diameter, in 4's, 3's, 2's or single with 0, 1, 2 or 3 undeveloped carpels, respectively.

India. BIHAR: Borybari (near Bhagalpur), *Hamilton*, February 12. 1809 (K — holotype of *Zanthoxylum hamiltonianum*, not seen; A, photo.). NORTHERN BENGAL: *Biswas 1707* (A). ASSAM: Naga Hills, *Prain's Collector* 758 (A), 883 ♀ (A), *987* ♀ (A); Mahkoti Dumur, Dullung, *Watt 10441* ♀ (US). Without definite locality: *Kamphovener 169H* ♂ (A). **Thailand.** Sriracha, Tapibut, Lapeboot-tong Kan Forest, *Collins 705* ♂ (K — holotype of *Zanthoxylum collinsae*); Ponpissay, *Kerr 8573* ♂ (SING). **North Vietnam.** Si Ninh Binh Province. *Petelot 875* ♂ (A, US); Lontoy Province, *Petelot 1309* (A); Bhai Nginfen Province, *Petelot 2691* ♀ (A); Than-hoa Province, La-han, *Poilane 1687* (A, photo.); inter Suyut et Cho Bo, *Poilane 28200* (P — holotype of *Zanthoxylum scabrum*, not seen; A, photo.). **South Vietnam.** Mt. Bana, ca. 25 km. W of Tourane (Da Nang), *J. & M. S. Clemens 3996* ♀ (A, US); Hue, *Squires 170* ♀ (A, SING, US). **China.** YUNNAN PROVINCE: Si-chour-hsien, Faa-doon, *Feng 11735* ♀ (A); Fohai, *Wang 74643* ♀ (A); Che-li Hsien, *Wang 75548* ♀ (A — isotype of *Zanthoxylum asperum*), *77546* ♀ (A), *77912* ♀ (A), *79173* ♀ (A). KWANGSI PROVINCE: Lar Pan, W of Hochih, *Ching 6510* ♀ (A); W. Poseh, Bako Shan, *Ching 7685* ♀ (A, US); Pin-lam, *Ko 55674* ♀ (A); Lungchow, *Morse 332* ♂ (US), *382* ♂ (US); Sui-luk, SW of Nanning, *Tsang 21919* ♂ (A); Sun-to District, Po Yam Shan, near Tai Chung Village, *Tsang 22973* ♀ (A). KWANGTUNG PROVINCE: Lofoushan, *Chun 40435* ♂ (A, SING), *Tsiang 1619* ♂ (A), *1651* ♀ (A, US); vicinity of Yeungkong, *Ferris 11934* ♀ (GH); Canton and vicinity, *Hai 33* ♂ (A), *Levine CCC 201* (A, US), *CCC 236* ♀ (A, US), *CCC 407* ♂ (A, US), *CCC 1130* ♀ (A), *CCC 1625* ♀ (A, US), *Merrill 9940* ♀ (A), *To CCC 407* ♂ (A), *CCC 1130* ♀ (A, US), *Tsiang 17* ♂ (A), *31* ♀ (A); Chung Shan District, Tong Ka Wa Village, *Hom 7–79* ♂ (A); SE of Shangsze, *Tsang 23924A* ♀ (A); Ho-yuen District. Nam Shan, Tsung-shue Village, *Tsang 28864* ♀ (A); Yingtak District, *Tsiang 1927* ♂ (A, SING); Sun-wui District, *Tso & Tsaing 2008* ♀ (A, SING); Yun Fou District, West River, Lou Lu Tsun, *Wang 382* ♂ (A); without definite locality, *Tsoong 1472* ♂ (A). HAINAN ISLAND: Dung Ka, *Chun & Tso 43581* ♀ (A); Fan Maan Tsuen & vicinity, Chim Shan, *Fung 20202* ♀ (A, US); Ta Hau, *Gressitt 965* ♀ (A); Yaichow, *How 70306* ♂ (A, US), *70675* ♀ (A), *Liang 62340* ♀ (US); vicinity of Manning, *How 71366* ♂ (A); Manyun, Tun Shan Ling, *Ko 52130* ♀ (A), *Liang 61515* ♀ (A); Ngai District, Yeung Ling Shan, *Lau 62* ♀ (A, US); Tan District, I Kap Shan & vicinity, *Lau 1079* (A); Kan-en District, Chim Fung Ling, *Lau 3605* ♀ (A), *5523* ♂ (A); Ching Mai District, *Lei 342* (A), *363* ♀ (SING), *800* ♀ (SING); Seven Finger Mt., *Liang 61631* ♀ (A); Taam-chau District, *Tsang 98* ♀ (A, US); *115* ♀ (A, US), *422* ♀ (A, US), *601* ♀ (A, US), *667* ♀ (A, US); without definite locality, *Liang 65076* ♂ (A), *65207* ♂ (US), *65216* ♀ (A), *65318* ♂ (A). HONG KONG: *Chun 4809* ♀ (A), *Taam 1159* ♂ (A, US), *2024* ♀ (US), *Tsang LU 16697* ♂ (A, US), *Wright 81* ♂ & ♀ (GH), *83* ♂ & ♀ (GH), *s.n.* ♀ (US). FUKIEN PROVINCE: Hinghwa District, *Chung 936* ♀ (A, SING); Inghok Hsien, Fang-quang-yen, *Chung 2652* ♀ (A), *7977* ♀ (A); Amoy & vicinity *Chung 4770* (A), *5607* ♀ (A), *5889* ♂ (A), *5892* ♀ (A), *5935* ♂ (A), *6014* ♀ (A), *6252* ♀ (A); Foochow vicinity, *Chung 8417* (A), *Ging 13051* (A), *13531* ♂ (A), *Norton 1394* (US); Kushan, *Dunn 72* ♀ (A); Hok Chiang vicinity, *Ging 15333* ♀ (A); without definite locality, *Chung 6951* ♀ (A), *Dunn's expedition*, April to June, 1905 ♀ (A). **Taiwan.** Tamnii, *Faurie 23* ♀ (A); Hokuto, *Faurie 1268* (A); Kuraru, *Gressitt 478* ♀ (A); South Cape, *Henry 205* two sheets, ♂ & ♀ and ♂ (A); Tchow, *Henry 205A* ♀ (US), *205G* ♀ (US), *1782* [A (♂), US (two sheets, ♂ and ♀)]; Taitung Mts., *Keng & Kao K2674* ♀ (A); Taihoku and vicinity, *Kou & Kae 4496* ♂ (A), *Odashima*, June 22, 1934 ♀ (A, GH, SING, US), *Suzuki*, June 18, 1933 ♀ (A), *Wilson 10161* [A (two sheets, ♂ and ♀), US (♀)]; Tamsuy, *Oldham 60* ♂ (US); Mt. Daiton and vicinity, *Tanaka 1784* ♂ (A, GH); without definite locality, *Faurie 23* ♀ (A), *Henry 464* ♂ (A), *Oldham*, 1864 ♀ (GH). **Ryukyu Islands.** SAKISHIMA GUNTO: Iriomote Island, *Hatusima 18833* ♀ (US); Ishigaki Island, *Smith 85* (US); Yonaguni Island, *Walker & Tawada 6801* (US). **Sumatra.** Middle Patani Valley, *Lorzing 15257* ♀ (L); Sibolangit, *Galoengi 231* ♀ (L). **Malay Peninsula.** PERAK: Padang Rengas, *Haniff SF 14978* (SING); Dindings, *Ridley 10281* ♀ (SING). PAHANG: Manchio, *Haniff SF 16778* (SING); Temerloh, *Ridley*, 1891 ♀ (SING). SINGAPORE: *Ridley 11291* ♀ (SING — holotype of *Zanthoxylum hirtellum*; K, fragments). **Java.** WEST JAVA: Batavia vicinity, *Backer 73* ♀ (L); Lengkong, *Backer 16980* ♂ (L); Res. Batavia, Omgeving Goea si Gadjah, *Backer 31164* ♀ (L); Preanger Regencies, Mt. Megamendoeng, *Blume 1814* ♀ (L — syntype of *Fagara oblongifolia*); Mt. Papandjan, *Blume* ♀ (L — syntype of *Fagara oblongifolia*); Depok, *Hallier*, August 11, 1896 (L); vicinity of Buitenzorg, *Hochreutiner 28* (L); Natuurmonument-eilandje Noesagede in het meer van Pendjaloe, *Koorders & Koorders-Schumacher 47963β* ♀ (L — holotype of *Fagara pendjaluensis*). EAST JAVA: Kediri, *Backer 11717* ♀ (L). **Anambas Islands.** Siantan Island, *Henderson SF 20132* ♀ (SING), *Steenis 748* ♀ (L, SING). **Philippines.** PALAWAN ISLAND: vicinity of Puerto Princesa, *Ebalo 448* (A), *Sulit PNH 12282* ♀ (A, L). LUZON ISLAND: Cagayan Province, Penablanca, *Ramos & Edano BS 46617* ♀ (NY, SING); Nueva Vizcaya Province, *Afalla FB 30213* ♀ (NY, US); Tayabas, *Ramos BS 13261* ♀ (BM). LEYTE ISLAND: Palo, *Elmer 7278* [A, K (♂), L]; without definite locality, *Wenzel 1232* ♀ (GH, NY). TAWITAWI ISLAND: *Ramos & Edano BS 44007* ♀ (A, BM, BRI, K, NY, SING, US). **Celebes.** Kabaena Island, *Elbert 3445* ♀ (A, L, SING). **Moluccas.** Soela Islands, Sanana Island, *Atje* ♀ (L); Amboina Island, *Robinson Plantae Rumph. Amb. 250* ♀ (BM, GH, K, L, NY, SING, US). **Papua.** Western District, Lower Fly River, east bank opposite Stuart Island, *Brass 7983* ♀ (A, BRI, L); Central District, Dieni, Ononge Road, *Brass 3833* ♀ (A, BM, BRI, NY). **Territory of New Guinea.** MOROBE DISTRICT: Wampit River ¾ mile from Lae-Wau Road, *Millar NGF 9997* ♀ (BRI, CANB, K); Bulolo Valley, *Floyd NGF 7471* ♀ (L). **Solomon Islands.** Bougainville Island, Karngu, Bbuin, *Kajewski 2304* ♀ (A). **Australia.** QUEENSLAND: Daintree River, *Brass & White 180* ♀ (A); Rockingham Bay, Herbert's River, *Dallachy*, October 4, 1866 ♀ (BRI, MEL), August 21, 1869 [MEL (two sheets, ♀ and ♂ ♀) — syntypes of *Zanthoxylum torvum*; GH (♂)]; Mossman, *Jones 2060* (CANB); Johnstone River, *Ludbrook 58* ♀ (BRI); Cairns, *Nugent* ♀ (BRI); Tully, Jarra Creek, *Webb 2352* (CANB). **Cultivated.** India: Calcutta, *Roxburgh Icones 2430*, drawn from a plant from Canton, China (K — lectotype of *Fagara nitida*, not seen; A, photo.).

DISTRIBUTION. NE India east to Taiwan and the Ryukyu Islands; south in South Vietnam, Thailand, Sumatra, Malay Peninsula, Java, Anambas Islands, Philippines, Celebes, Moluccas, E New Guinea, Solomon Islands and NE Queensland; in rain forests and thickets at altitudes up to 1100 meters in Malesia and up to 1400 meters in continental Asia. See MAP 2.

ILLUSTRATIONS. HUANG, C. C., Acta Phytotax. Sinica **6**(1): *t. XV* (as *Zanthoxylum nitidum*) and *t. XVI* (as *Zanthoxylum asperum*). 1957. LI, H. L., Woody flora of Taiwan 374. 1963. LIU, T. S., Illustrations of native and introduced ligneous plants of Taiwan **2**: *t. 729*. 1962. PIERRE, L., Flore forestière de la Cochinchine **4**: *t. 291*. 1893.

Occasionally cultivated as a hedge plant in China. In Taiwan the root



MAP 2. Distribution of *Zanthoxylum nitidum* (Roxb.) DC.

is used in making pipe stems. In both the Philippines and China (Hainan Island) collectors have noted that the plant was pounded and placed in pools to stupefy fish. In the Malay Peninsula the bark is used for treatment of toothache.

According to Merrill, Comm. Lour. Fl. Cochinch. 218. 1935, the cultivated material at Calcutta that provided the type for Roxburgh's *Fagara nitida* was originally from Canton, China.

Sealy, Kew Bull. **11**: 339. 1956, points out that another Roxburgh drawing at Kew, that of *Elaeagnus arborea* Roxb., bears the same number as *Fagara nitida* Roxb.

Merrill, Interp. Rumph. Herb. Amb. 288. 1917, lists *Nugae sylvarum silvestis* Rumph. as a synonym of *Fagara torva* (F. Muell.) Engl. (= *Zanthoxylum nitidum*).

The name *Piper pinnatum* Lour. is listed as a synonym of *Zanthoxylum nitidum* by Merrill, Comm. Lour. Fl. Cochinch. 218. 1935, who reasoned that Loureiro must have been misled by the peppery taste of the fruit. The epithet *pinnatum* was used earlier to describe a Norfolk Island species, *Blackburnia pinnata* J. R. & G. Forst. [*Zanthoxylum pinnatum* (J. R. & G. Forst.) Druce].

I have not seen the type of *Fagara warburgii* Perk. (*Warburg 11784*), which was apparently lost at Berlin. Merrill, Enum. Philip. Fl. Pl. 2: 327. 1923, cites this Warburg number (apparently from an isotype at Manila, also presumably lost) and lists the name as a synonym of *Zanthoxylum torvum* F. Muell. (= *Zanthoxylum nitidum*).

Vegetatively, *Zanthoxylum nitidum* exhibits a wide range of variation that appears to correspond with ecological differences within its range.

In general, the collections fall into two groups: large-leaved plants of rain forests and small-leaved plants of dryer situations, generally described as thickets. Plants of the first group are high climbing lianas with leaves over 25 cm. (up to 40 cm.) long, leaflets chartaceous or subcoriaceous, dull above and generally with some pubescence on the rachis and lower surface. This form predominates in the Malesian area and is otherwise scattered throughout most of the range of the species. Plants of the second, smaller-leaved group are climbing or semi-erect shrubs with leaves less than 25 cm. (down to 5 cm.) in length, leaflets tending to be coriaceous, shiny above, and glabrous. For the most part this form is restricted to the Asiatic mainland, though there are a few outliers at higher elevations in the islands of Malesia (*Ebalo 448*, from the Philippines; *Elbert 3445*, from the Celebes; and *Galoengi 231*, from Sumatra). There is a great deal of intermingling of the various vegetative features of these two groups, especially on the Asiatic mainland, and while this further complicates the problem by giving rise to several local races that at first appear distinct from either of the two main morphological groups, intergradation is so complete that I have found it impossible to recognize but a single species.

The closest relative of *Zanthoxylum nitidum* appears to be *Z. tetraspermum* Wight & Arn., of southern India and Ceylon, which differs from *Z. nitidum* in having primarily terminal inflorescences, rather fleshy petals, sepals connate basally and leaflets with 15–20 main veins on each side of the midrib. *Z. caudatum* Alston, of Ceylon, is also closely related and is otherwise interesting since it seems to combine some vegetative characters of *Z. scandens*. An isotype examined [*Silva 128* (K)] has leaflets resembling *Z. scandens* in size, shape and color, but with the arrangement and margins of *Z. nitidum*.

3. **Zanthoxylum myriacanthum** Wall. ex Hook. f. Fl. Brit. Ind. **1**: 496. 1875. Type: *Porter* (Wallich cat. n. 1214), Malay Peninsula.

Zanthoxylum rhetsoides Drake, Jour. Bot. Paris **6**: 275. 1892. Syntypes: *Balansa 4044* (not seen) and *4045*, North Vietnam.

Fagara myriacantha (Wall. ex Hook. f.) Engl. Nat. Pflanzenfam. III. **4**: 118. 1896.

Zanthoxylum diabolicum Elmer, Leafl. Philip. Bot. **2**: 477. 1908. Type: *Elmer 10217*, Philippines.

Evodia odorata Levl. Repert. Sp. Nov. **9**: 458. 1911. Type: *Cavalerie 2978*, China, Kweichow Province.

Zanthoxylum odoratum (Levl.) Levl. *Ibid.* **13**: 266. 1914.

Fagara gigantea Hand.-Mazz. Anzeig. Akad. Wiss. Wien. **58**: 64. 1921. Type: *Handel-Mazzetti 12327*, China, Hunan Province.

Zanthoxylum giganteum (Hand.-Mazz.) Rehd. Jour. Arnold Arb. **8**: 151. 1927.

Fagara diabolica (Elmer) Engl. Nat. Pflanzenfam. ed. 2. **19a**: 220. 1931.

Fagara odorata (Levl.) Hand.-Mazz. Symb. Sinica **7**: 623. 1933.

Fagara rhetsoides (Drake) Reeder & Cheo, Jour. Arnold Arb. **32**: 69. 1951.

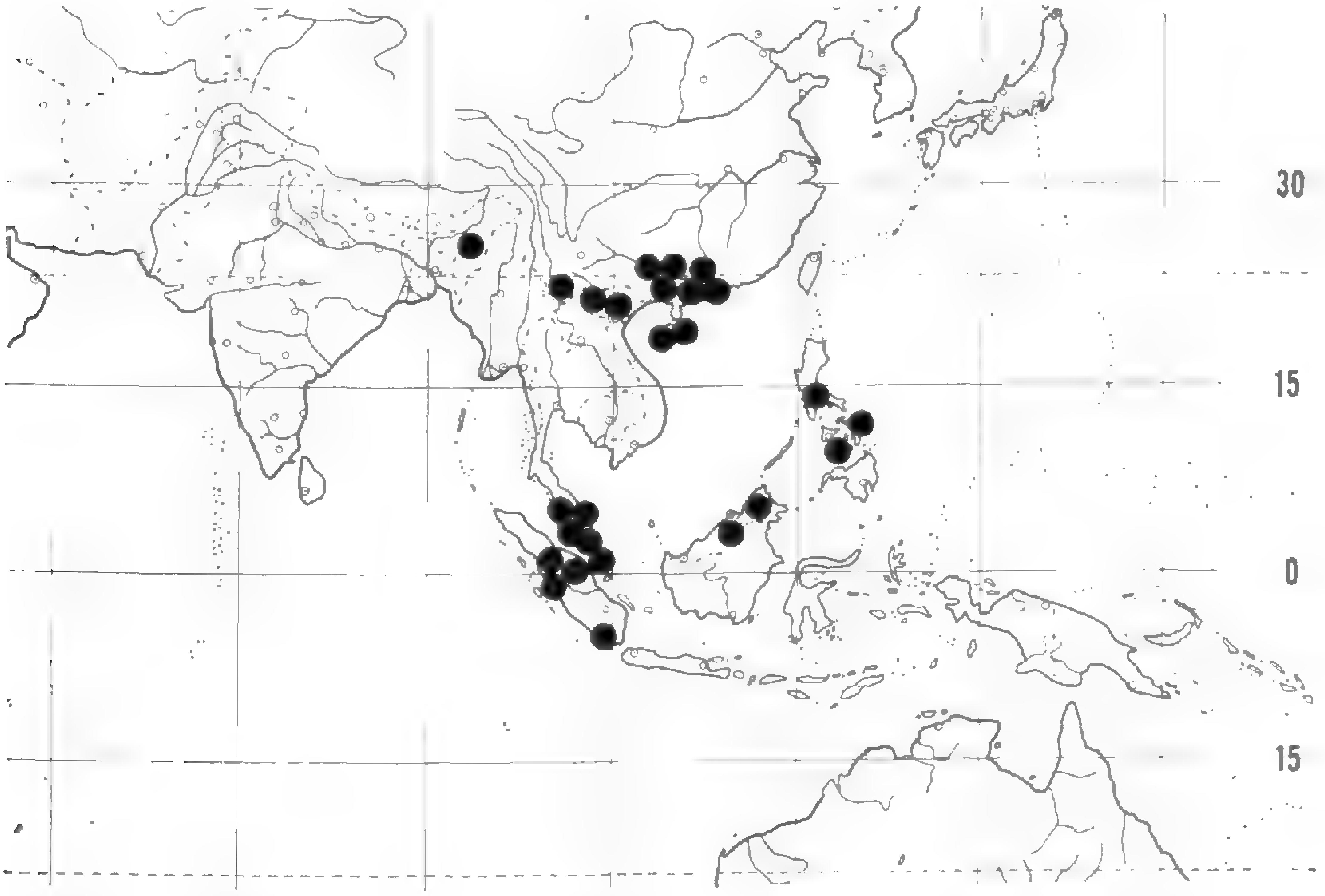
Zanthoxylum rhetsoides Drake var. *pubescens* Huang, Acta Phytotax. Sinica **6** (1): 48. 1957. Type: *Wang 77979*, China, Yunnan Province.

Small to large trees to 25 m.; dioecious; evergreen; main stems prickly or with thick, conical spines to 3 cm. long; branchlets with numerous straight prickles, generally swollen and hollow and apparently housing ants. Leaves imparipinnate, 25–45 (60) cm. long, glabrous or (rarely) short pubescent on the lower surface; petiolules obsolete to 5 mm. long; leaflets 4–9 (11) pairs, opposite or subopposite, chartaceous to coriaceous, dark green and lustrous above, pale green below, pellucid dotted, elliptic, 8–18 cm. long, 2.5–8 cm. wide, base obtuse to subcordate, slightly oblique, main veins 8–18 on each side of the midrib, margins finely (often indistinct) glandular crenate with 6–8 crenations per cm., apex acuminate. Inflorescences terminal and from the upper leaf axils, paniculate, 15–25 cm. long and generally about as wide, the axes and branches glabrous to (rarely) short pubescent. Staminate flowers 3–4 mm. long; pedicels obsolete to 2 mm. long; sepals 5, broadly triangular, about 0.75 mm. long; petals 5, white, pale yellow or occasionally violet, elliptic, 1.5–2.5 mm. long; stamens 5, 3–4 mm. long, anthers 0.5–1 mm. long; disc flat; rudimentary carpels 3, about 1 mm. high. Carpellate flowers 2–3 mm. long; pedicels, sepals, petals and disc as in staminate flowers; rudimentary stamens absent; gynoecium 3-carpellate (occasional flowers 4-carpellate), 1.5–2 mm. high, styles and stigmas coherent, the combined stigmatic structure peltate. Fruiting pedicels obsolete to 2.5 mm. long; follicles subglobose, 3–6 mm. in diameter, in 3's, 2's or single with 0, 1 or 2 undeveloped carpels, respectively.

India. Assam, Naga Hills, *Koelz 25762* ♀ (MICH). **North Vietnam.** Vallei de Lomkok, *Balansa 4045* ♀ (P — syntype of *Zanthoxylum rhetsoides*, not seen; A, photo.; L); Chapa, *Petelot 3569* ♂ (US), *7911* ♀ (A); Tien-yen, Kau Nga Shan, *Tsang 30511* ♀ (A). **China.** YUNNAN PROVINCE: Che-li Hsien, *Wang 77979* ♀ (A — isotype of *Zanthoxylum rhetsoides* var. *pubescens*), *78566* ♂ (A). KWEICHOW PROVINCE: Pin-fa, *Cavalerie 1771* ♂ (A, photo. and fragment); Ma-ho (Ma-jo), *Cavalerie 2978* ♀ (P — holotype of *Evodia odorata*, not seen; A, photo., and fragment); Feng Hsiang Ping, Fan Ching Shan, *Steward, Chiao & Cheo 708* ♀ (A, US). HUNAN PROVINCE: Wukang, Yun-shan, *Handel-Mazzetti 12327* ♂ (A — isotype of *Fagara gigantea*). KWANGSI PROVINCE: S Nanning, Seh-feng Dar Shan, *Ching 8128* ♀ (A); Tzu Yuen District, *Chung 83485* ♂ (A); Pin-lam, *Ko 55597* ♂ (A); San Chiang Hsien, *Steward & Cheo 969* ♀ (A, SING). KWANGTUNG PROVINCE: Wung Yuen District, Fan Shiu Shan, *Lau 2770* ♀ (A); Ying Tak, *Tsang & Wong 2453* ♂ (A). HAINAN ISLAND: Po-ting, *Lau 28166* ♀ (A); Taam-Chau District, Hoi Ta Shan, *Tsang 837* ♀ (A); without definite locality, *Liang 64222* ♀ (A). **Sumatra.** CENTRAL SUMATRA: Padang and Bedagei, *Lorzing 15199* ♀ (L); Gouv. O. kust. ond afd. Simeloengoen, *NIFS bb. 2910* ♀ (L); vicinity of Aek Moente (Aer Moette), Asahan (NE of Tomoean Dolok and W of Salabet, *Rahmat si Boeea 9383* (A, L, MICH). SOUTHERN SUMATRA: Res. Benkoelen ond. afd. Redjang, *Endert NIFS E 1078* ♂ (L). **Malay Peninsula.** PERAK: Goping District, Tohoflow Hills, *King's Collector 8157* ♀ (BM); without definite locality, *Scortechini 275* (L, SING). PAHANG: Fraser's Hill, *Corner SF 33166* ♂ (SING), *Nur SF 11310* ♂ (BM, K, SING); Bukit Suvin, *Henderson SF 21706* (SING); Cameron Highlands, Sg. Ikon, *Jaamat SF 27628* ♂ (SING); Telom, *Ridley 13541* ♀ (BM, K, SING). SELANGOR: Kepong, *Sou & Tachou SF 16893* ♂ (SING). MALACCA: Sg. Udang, *Alvins 36* ♀ (SING), *Derry*

1121 ♀ (SING); Bukit Bruang. *Holmberg 857* ♂ (SING); without definite locality. *Maingay 279* ♂ (A, K, L), *1098* ♀ (K). PENANG: Penang Hill. *Corner*. July 27. 1936 (SING): Govt. Hill. *Curtis 1076* ♂ (BM, SING, US). November, 1890 ♂ (SING): without definite locality. *Porter* ♀ (K — holotype of *Zanthoxylum myriacanthum*; BM — isotype). SINGAPORE: *Ridley* ♂ (BM). **Borneo.** Sarawak, Ulu Lawas. *Omar Sar 00107* ♂ (SING); British North Borneo (Sabah), Mt. Kinabalu. *J. & M. S. Clemens 26344* ♀ (A, BM, L, NY), *26344A* ♀ (L, NY). **Philippines.** Luzon Island, Laguna Province, Mt. Makiling, *Canicosa FB 31197* ♂ (NY); Samar Island, *Ramos BS 1680* ♂ (BM, BRI, GH, L, NY, SING, US), *Rosenbluth FB 12866* ♂ (US); Negros Island, Dumaguete, Cuernos Mts., *Elmer 10217* ♂ (isotypes of *Zanthoxylum diabolicum*: A, BM, K, L, NY, US).

DISTRIBUTION. Assam, North Vietnam, SW China, Sumatra, Malay Peninsula, Borneo and the Philippines; in forests and thickets at altitudes from 100 to 1230 meters in Malesia and from 200 to 2145 meters in continental Asia. See MAP 3.



MAP 3. Distribution of *Zanthoxylum myriacanthum* Wall. ex Hook. f.

The fruit is said to be used as a condiment in Assam.

This species is very closely related to *Zanthoxylum ailanthoides*, which has identical flowers and fruits. *Z. molle* Rehd., a species from Hupeh and Anhwei Provinces, China, is also closely related, differing mainly in having leaves that are white tomentose below.

Reeder & Cheo, Jour. Arnold Arb. 32: 69. 1951, cited *Evodia odorata* and *Fagara gigantea* as synonyms of *Fagara rhetsoides* (= *Zanthoxylum myriacanthum*). Handel-Mazzetti, Symb. Sinica 7: 623. 1933, listed *Fagara gigantea* as a synonym of *F. odorata* (= *Zanthoxylum myriacanthum*).

4. **Zanthoxylum ailanthoides** Sieb. & Zucc. Abh. Akad. München **4** (2): 138. 1846 ("*Zanthoxylon*"). Type: *Siebold*, Japan.

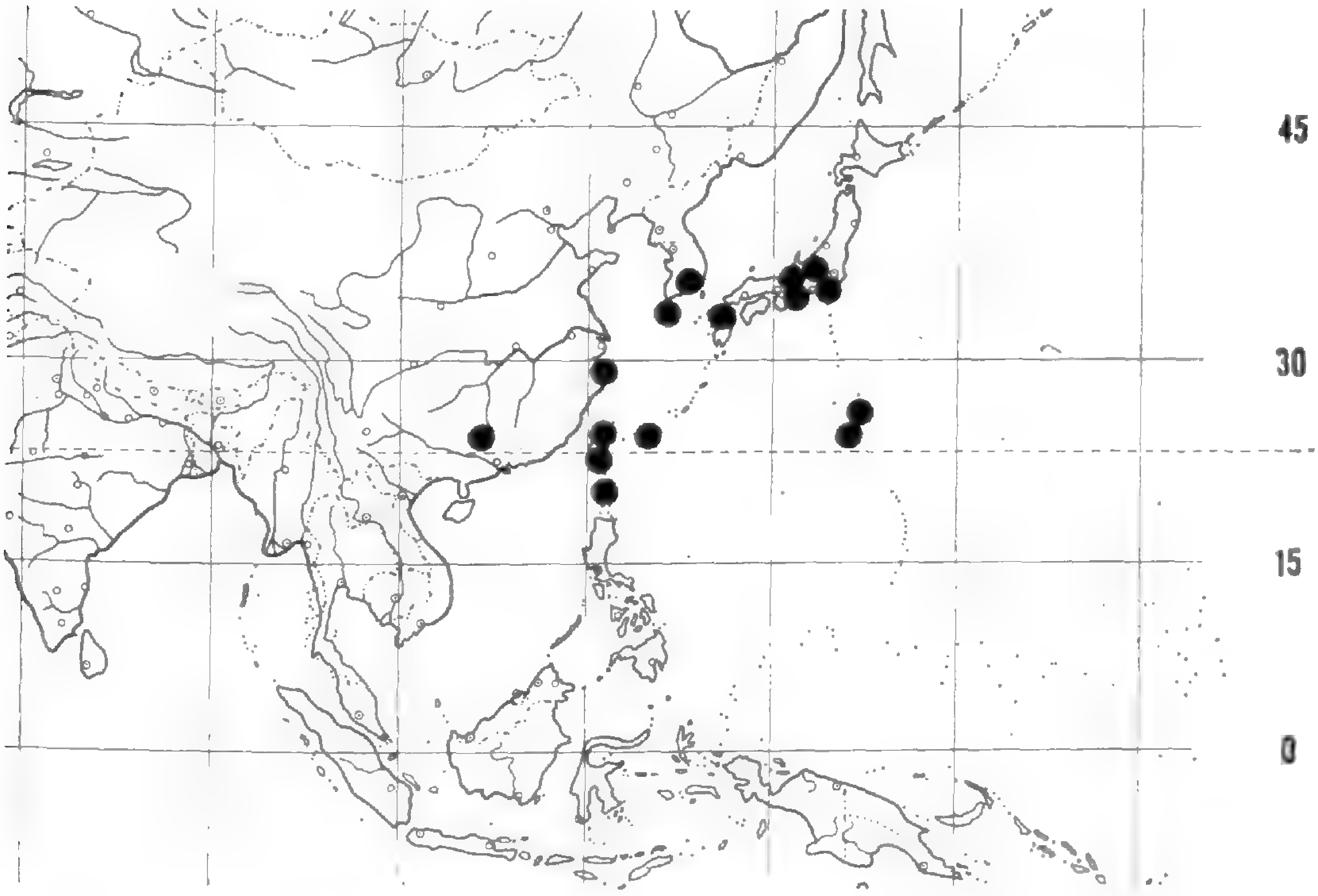
Zanthoxylum emarginellum Miq. Ann. Mus. Lugd.-Bat. **3:** 22. 1867. Type: *Siebold*, Japan.
Fagara ailanthoides (Sieb. & Zucc.) Engl. Nat. Pflanzenfam. III. **4:** 118. 1896.
Fagara emarginella (Miq.) Engl. *Ibid.*
Zanthoxylum hemsleyanum Makino, Bot. Mag. Tokyo **21:** 86. 1907 (*Zanthoxylum emarginellum sensu* Hemsley, Ann. Bot. **9:** 149. 1895). Syntypes: *Cunningham*, Chushan Archipelago (not seen); *Ford*, June, 1884, Taiwan.
Fagara hemsleyana (Makino) Makino, Bot. Mag. Tokyo **21:** 161. 1907.
Zanthoxylum ailanthoides Sieb. & Zucc. var. *inerme* Rehd. & Wils. Jour. Arnold Arb. **1:** 118. 1919. Type: *Wilson 8265*, Bonin Islands.
Zanthoxylon inerme (Rehd. & Wils.) Koidz. Bot. Mag. Tokyo **33:** 218. 1919 (nomen illegit.), *non* Sessé & Mociño.
Fagara boninshimae Koidz. ex Hara, Enum. Spermat. Jap. **3:** 25. 1954 (based on *Zanthoxylum ailanthoides* var. *inerme*).

Medium to large trees to 25 m.; dioecious; apparently evergreen; main stems prickly or with thick, conical spines or rarely unarmed; branchlets generally armed, the prickles straight and scattered. Leaves imparipinnate, 25–80 cm. long, glabrous; petiolules obsolete to 3 mm. long; leaflets 7–15 pairs, opposite, chartaceous to subcoriaceous, medium to dark green above, glaucous below, pellucid dotted, elliptic-lanceolate to lanceolate, broadest near the base, 9–14 cm. long, 2.3–4.7 cm. wide, base rounded to cordate, slightly oblique, main veins 12–20 on each side of the midrib, margins glandular crenate with 4–8 crenations per cm., apex long acuminate to attenuate. Inflorescences terminal and from the upper leaf axils, paniculate, 10–30 cm. long and generally about as wide, the axes and branches glabrous. Staminate flowers 3–4 mm. long; pedicels 1–2 mm. long; sepals 5, broadly triangular, about 0.75 mm. long; petals 5, white or pale yellow, elliptic, 1.5–2.5 mm. long; stamens 5, 3–4 mm. long, anthers 0.5–1 mm. long; disc flat; rudimentary carpels 3, about 1 mm. high. Carpellate flowers 2–3 mm. long; pedicels, sepals, petals and disc as in staminate flowers; rudimentary stamens absent; gynoecium 3-carpellate, 1.5–2 mm. high, styles and stigmas coherent, the combined stigmatic structure peltate. Fruiting pedicels 1–3 (4.5) mm. long; follicles subglobose, about 3.5 mm. in diameter, in 3's, 2's or single with 0, 1 or 2 undeveloped carpels, respectively.

China. KWANGSI PROVINCE: N Hin Yen, Yeo Mar Shan, *Ching 7102* ♂ (A, US). CHEKIANG PROVINCE: Shihpu, *Chiao NU 14130* (A); without definite locality, *Barchet 83* ♀ (US), *84* (US). **Korea.** Circa Hongnu, *Faurie 1632* ♂ (A); Ooryong-too (Dagelet Island), *Wilson 8514* (A); Quelpaert Island, *Faurie 467* ♀ (A), *Moran 5517* ♀ (GH, US), *Taquet 619* ♂ (A), *2713* ♀ (A), *2714* ♀ (A), *4142* ♂ (A), *Wilson 9440* ♀ (A). **Japan.** HONSHU ISLAND: Nakatsugawa, Nojiri, Shinano, *Jack*, September 6, 1905 ♀ (A, GH); Yokohama, *Maximowicz*, 1862 [GH (♂), US (♀)]; Shima, Toba, *Sakurai*, August 2, 1908 (A); Mino, *Shiota 4459* (A); Oshima Island, *Mizushima 573* ♀ (A). KYUSHU ISLAND: Nagasaki, *Maximowicz*, 1863 ♂ (US), *Wilson 6313* ♀ (A). Without definite locality: *Sargent*, August 26, 1892 ♂ (A), *Siebold* (K — sketch of holotype of *Zanthoxy-*

lum emarginellum), *Siebold* (M — isotype of *Zanthoxylum ailanthoides*, not seen; A, photo.). **Bonin Islands.** Chichi-jima, *Gonzales*, 1917 (A), *Otomo*, May 4, 1917 ♂ (A); Haha-jima, *Wilson 8265* ♀ (A — holotype of *Zanthoxylum ailanthoides* var. *inerme*; US — isotype); without definite locality, *Wright 41* ♀ (GH, US). **Ryukyu Islands.** Yaeyama Gunto, Iriomote Island, Funauki Bay, *Walker & Tawada 6762* (US). **Taiwan.** Kelung, *Ford*, June, 1884 (K — syntype of *Zanthoxylum hemsleyanum*, not seen; A, photo.), June 14, 1884 (A, photo.); South Cape, *Henry 1353* ♂ (A); Tamsuy, *Oldham 58* ♀ (GH); Taihoku vicinity, *Shimada 39* ♂ (A), *Wilson 11220* ♀ (A); without definite locality, *Henry 1630* ♀ (A, US). **Philippines.** BATAN ISLAND: Mt. Iraya, *Ramos BS 80273* ♂ (K, NY); Basco, *Ramos BS 80381* ♂ (NY). **Cultivated.** Japan, Tokyo, *Okamoto*, July 25, 1958 ♂ (US), *Terakawa*, June 23, 1946 (US).

DISTRIBUTION. China (Kwangsi and Chekiang Provinces), Korea, Japan, Bonin and the Ryukyu Islands, Taiwan and the Philippines (Batan Island); in lowland forests at altitudes up to 300 meters. See MAP 4.



MAP 4. Distribution of *Zanthoxylum ailanthoides* Sieb. & Zucc.

ILLUSTRATIONS. LIU, T. S., Illustrations of native and introduced ligneous plants of Taiwan 2: *t. 727.* 1962. MAKINO, T., Illustrated flora of Japan, ed. *2. t. 1173.* 1940, as *Fagara ailanthoides*; revised ed. *t. 1173.* 1949; New illustrated flora of Japan *t. 1328.* 1961.

The wood is used in the Bonin Islands to make canoes.

Zanthoxylum ailanthoides is closely related to both *Z. myriacanthum* and *Z. micranthum* Hemsl. The latter species, known from Hupeh, Hunan, and Szechuan Provinces, China, differs in having more slender branchlets and smaller leaves.

Li, *Woody flora of Taiwan* 372. 1963, has cited *Zanthoxylum emarginellum* and *Z. hemsleyanum*, both based on collections from immature plants, as synonyms of *Fagara ailanthoides*.

5. **Zanthoxylum avicennae** (Lam.) DC. Prodr. **1**: 726. 1824.

Fagara avicennae Lam. Encycl. **2**: 445. 1788. Type: *d'Incarville 179*, China (probably Kwangtung Province, *fide* Merrill, Comm. Lour. Fl. Cochinch. 218. 1935).

Xanthoxylum lentiscifolium Champ. ex Benth. Jour. Bot. Kew Misc. **3**: 329. 1851. Type: *Champion*, Hong Kong (not seen).

Zanthoxylum tidorense Miq. Ann. Mus. Lugd.-Bat. **3**: 246. 1867. Type: *Teysmann HB 5167*, Moluccas, Tidore Island.

Zanthoxylum diversifolium Warb. in Engl. Bot. Jahrb. **13**: 339. 1891. Type: *Warburg 20145*, Moluccas, Kai Island.

Fagara diversifolia (Warb.) Engl. Nat. Pflanzenfam. III. **4**: 118. 1896.

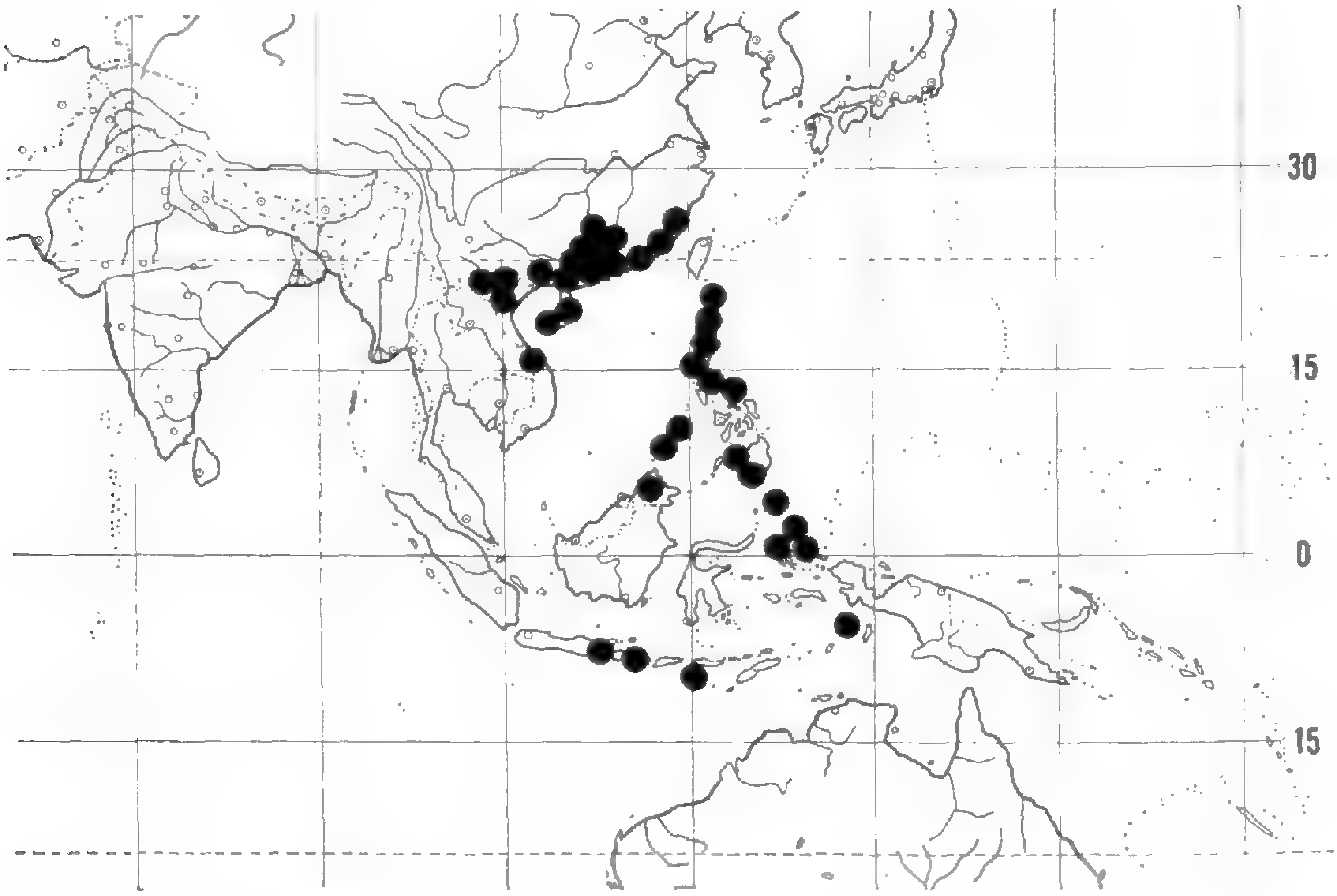
Zanthoxylum iwahigense Elmer, Leafl. Philip. Bot. **5**: 1833. 1913. Type: *Elmer 12751*, Philippines, Palawan Island.

Scandent (rarely) or erect shrubs or small trees to 13 m.; dioecious; evergreen; branchlets generally armed, the prickles straight and scattered or recurved and predominantly pseudostipular. Leaves imparipinnate, 5–30 cm. long, glabrous; rachis often with narrow wings extending to 1 mm. on either side; petiolules 2–5 mm. long; leaflets 2–11 pairs, subopposite, chartaceous to subcoriaceous, dark green above, pale below, generally blackening somewhat in drying, pellucid dotted, ovate to elliptic-lanceolate, 1–8 cm. long, 0.75–3 cm. wide, base obtuse to cuneate, main veins 4–11 on each side of the midrib, margins subentire to finely glandular crenate with as many as 8 crenations per cm., apex obtuse to acuminate. Inflorescences terminal and occasionally from the upper leaf axils, cymose, the primary branches generally whorled, 5–21 cm. long, flat-topped, glabrous. Staminate flowers 1.5–3 mm. long; pedicels 0.5–3 mm. long; sepals 5, broadly triangular or rounded, 0.5–0.8 mm. long; petals 5, white to greenish yellow, elliptic, 1–2.5 mm. long; stamens 5, about 2 mm. long, anthers about 0.75 mm. long; disc flat; rudimentary carpels 2, about 0.75 mm. high. Carpellate flowers 1.5–3 mm. long; pedicels, sepals and petals as in staminate flowers; rudimentary stamens about 0.5 mm. long; disc pulvinate, about 0.3 mm. high; gynoecium 2-carpellate, about 1 mm. high, styles and stigmas coherent, the combined stigmatic structure peltate. Fruiting pedicels 1–3 mm. long; follicles subglobose, about 4.5 mm. in diameter, in pairs or occasionally single and paired with an undeveloped carpel.

Thailand. Dauang-Quinom, *Smitinand & Abbe 24842* ♀ (L). **North Vietnam.** Ninh Binh Province, Cho Ganh, *Petelot 822* ♀ (A), *1676* ♀ (A); Lontoy Province, *Petelot 2591* ♂ (A); Ha-coi, Taai Wong Mo Shan, *Tsang 27016* ♀ (A), *29377* ♂ (A, SING), *29549* ♂ (A, SING); Tien-yen, Kau Nga Shan, *Tsang 27392* ♀ (A), *30494* ♂ (A, SING); Dam-ha, Sai Wong Mo Shan, *Tsang 30448* ♂ (A, SING). **South Vietnam.** Mt. Bana, 25 km. W of Tourane (Da Nang), *J. & M. S. Clemens 4067* ♂ (A, US), *4445* ♀ (A, US). **China.** Kwangsi Province: S Nanning, Seh-feng Dar Shan, *Ching 7827* ♀ (A, US); Sun-to District, Po Yam Shan, *Tsang 23022* ♀ (A); Waitsap District, Tou Ngok Shan, near Tung Chung Village, *Tsang 23291* ♀ (A); Shang-sze District, Shap Man Taai Shan, *Tsang 24326* ♀ (A). Kwangtung Province: Canton and vicinity, *Hai 43* ♀ (A), *Levine CCC 170* ♀ (A, GH, US), *CCC 563* ♀ (A, GH, US), *CCC 1298* ♂ (A, GH, US), *CCC 1814* ♀ (A, GH, US), *CCC 3134* ♂ (A, GH), *Merrill BS 10052* ♀ (A); Wung-yuen District, Yung-yun, *Lau 632* ♀ (A); Wong Chuk I, Tsing Wan Shan, *Lau 2495* ♀ (A); Kao-yao District, Ting Woo Shan, *Lau 20292* ♂ (SING); Wah Shau Toi, *Levine & McClure CCC 6913* ♂ (US); Pakhoi, *Playfair*, April, 1883 ♀ (GH); Hwei-yang District, Sam Hang Shek Tau, Lin Fa Shan, *Tsang 25872* ♀ (A); Fang Cheng District, Taan Faan, Kung Ping Shan, *Tsang 26868* ♂ (A); Lofoushan, *Tsiang 1645* ♀ (A, SING, US); Yan Fon District, West River, *Wang 322* ♀ (A). Hainan Island: Nodoa, *Chun NU 5825* ♀ (US); Dung Ka, *Chun & Tso 43401* ♀ (A); Tai Pin, *Gressitt 1117* ♂ (A); Yaichow, *How 70939* ♂ (A); Nagai District, Yeung Ling Shan, *Lau 133* ♀ (A, US); Chang-kiang District, Ka Chik Shan, *Lau 3085* ♀ (A); Kan-en District, Chim Fung Mt., *Lau 4932* ♀ (A); Loktung, *Lau 27140* ♂ (A); Pak Shik Ling vicinity, Ku Tung Village, *Lei 55* ♀ (SING, US), *876* ♀ (A, SING, US); San Hu, Tin Si, *McClure CCC 7731* ♀ (A); Lam Ko District, Lin Fa Shan, *Tsang 213* ♂ (A, US); Hung Mo Shan, *Tsang 787* ♂ (A); without definite locality, *Liang 62183* ♂ (US), *63604* ♀ (US). Macao: *Callery 248* ♂ (GH). Hong Kong: *Brigham* ♀ (GH), *Chun 3153* ♀ (A, SING), *6806* ♀ (A), *Ford* ♀ (A), *Sargent* ♀ (A), *Taam 1617* ♂ (US), *1718* ♂ (US), *Tsang 16529* ♀ (A, US), *Wright 84* ♀ (GH), *s.n.* ♀ (US). Fukien Province: Kushan, *Chung 7583* ♂ (A); Kuliang and vicinity, *Tang 6751* ♀ (A); Foochow, *Tang 13119* ♀ (A); Lien-gong and vicinity, *Tang 16040* ♂ (A); Hok-chang, Ling-soik Temple, *Tang 16055* ♂ (A). Without definite locality: *Father d'Incarville 179* ♀ (P — holotype of *Fagara avicennae*, not seen; A, photo.). **Java.** East Java, Madiun Province, Ngebel, *Koorders 23208β* (L). **Lesser Sunda Islands.** Lombok Island, Rindjani-vulkangebirge, *Elbert 1582* [A (♂), CANB (♀), L (♀)]; Soemba Island, *de Voogd 1991* ♀ (L). **British North Borneo (Sabah).** Mt. Kinabalu, Penibukan, *J. & M. S. Clemens 31036* ♂ (A, K, L, NY), *40530* ♀ (A, L); between Ranau and mile 3 on road to Hot Springs, *Darnton 119* ♂ (BM). **Philippines.** Palawan Island. Mt. Gantung, *Edano BS 77626* (NY); Mt. Manalsal, *Edano BS 77760* ♂ (NY, SING); Mt. Pulgar, *Elmer 12751* ♀ (isotypes of *Zanthoxylum iwahigense*: A, BM, GH, K, L, NY, US); Victoria Mts., Panacan, Aborlan, *Sulit PNH 12396* (A, L, SING); without definite locality, *Curran FB 3860* ♀ (NY), *Foxworthy BS 905* ♀ (GH, K, NY, US). Batan Island. Mt. Iraya, *Ramos BS 80214* ♀ (NY, SING). Babuyan Islands. Dalupiri Island, *Bartlett 15109* [A (♂ & ♀), MICH (♀)], *15133* ♂ (A, MICH), *15827* ♀ (A, MICH). Luzon Island. Benguet Subprovince: Pauai, *Santos BS 32025* ♂ (BRI, NY, SING). Nueva Ecija Province: Mt. Umingan, *Ramos & Edano BS 26303* ♀ (A, BM, US). Zambales Province: *Ramos BS 5090* ♀ (NY, US). Rizal Province: Antipolo, *Ramos BS 20988* ♀ (A, BM, GH, K, L, NY, SING, US); without definite locality, *Loher 14840* ♂ (A), *Merrill SB 1002* (A, BM, GH, L, NY, US), *SB 1060* ♀ (A, BM, GH, L, NY, US). Camarines Province: *Simeon FB 28756* ♀ (A, K, US). Without definite locality: *Loher 241* (K), *Vidal 1445* ♂ (K). Mindanao Island. Misamis Province: *Caster FB 29749* ♀ (NY), *Cuming 1622* ♂ & ♀ (BM, K), *Klemme FB 22464* ♀ (BM), *Quimpo FB 30149* ♂ (NY, US). Cotabato Province: *Ferraris FB 23044* ♀ (A, BM, US), *Ramos & Edano BS 84843* ♂ (A). **Moluccas.** Taulaud Island, Karakelong, *Lam 3254* ♀ (A, L); Morotai Island, *Kostermans 1481* ♂ (BRI, K, L, SING); Kahatola Island, off Halmaheira, *Fairchild 3484* ♂ (A); Tidore Island, *Teysmann HB 5167* ♂ (isotypes of *Zanthoxylum tidorense*: K, L, MEL), *de Vriese & Teysmann*, 1859–

1860 (L); Ternate Island, *de Vriese*, 1857–1861 ♂ (L), *de Vriese & Teysmann*, 1859–1860 [A (♂), CANB (♀)]; Kai Island, *Beccari*, August, 1873 [A (♂ & ♀), K (♀)], *Jaheri HB 430* ♀ (L), *Warburg 20145* (A — isotype of *Zanthoxylum diversifolium*).

DISTRIBUTION. Thailand east to Fukien Province, China; south in Java, Lesser Sunda Islands, British North Borneo, the Philippines and the Moluccas; in dry forests, thickets and on open slopes at altitudes up to 1630 meters. See MAP 5.



MAP 5. Distribution of *Zanthoxylum avicennae* (Lam.) DC.

ILLUSTRATIONS. PIERRE, L., Flore forestière de la Cochinchine 4: *t. 289.* 1893, as *Zanthoxylum avicennae* vars. *touranense* Pierre and *tonkinense* Pierre.

I have not seen the type of *Xanthoxylum lentiscifolium* which is listed as a synonym of *Xanthoxylum avicennae* by Bentham in *Flora Hongkongensis* 58. 1861.

Plants from dry, open situations and high mountain areas tend to become dwarfed or scandent with considerably reduced leaves and inflorescences, and more or less recurved, predominantly pseudostipular prickles. Some of the extremes of this type, such as *Smitinand & Abbe 24842*, from Thailand, *Koorders 23208β*, from Java, *J. & M. S. Clemens 40530*, from Sabah and *Elmer 12751*, from Palawan Island, look strikingly different from the arborescent form of this species. They are not geographically isolated, however, and there are numerous intergradations. The Elmer collection cited here is the type of *Zanthoxylum iwahigense*, which has already been reduced to synonymy of *Zanthoxylum avicennae* by Merrill, Enum. Philip. Fl. Pl. **2**: 326. 1923. *Fagara anisata* Back. ex Bakh. f., listed as a provisional name by Bakhuizen, Fl. Java **2**: 97. 1965, also seems to represent this scandent form. I have not seen the collection cited (*Backer 11431*), but the description fits reasonably well and the author does not include *Zanthoxylum avicennae*.

6. **Zanthoxylum megistophyllum** (Burtt) Hartley, comb. nov.

Fagara megistophylla Burtt, Kew Bull. **1935**: 301. 1935. Type: *Waterhouse B344*, Solomon Islands, Bougainville Island.

Small trees to 8 m.; dioecious. Leaves imparipinnate, 80–175 cm. long, glabrous; petiolules of lateral leaflets obsolete to 5 mm. long; leaflets 4–5 pairs, opposite, chartaceous, dark green above, pale below, pellucid dotted, elliptic, 20–35 cm. long, 9–16.5 cm. wide, base obtuse to rounded, main veins 13–16 on each side of the midrib, margins entire, apex short acuminate. Inflorescences terminal or terminal and from upper leaf axils, paniculate, to 25 cm. long, broadly spreading, the axes and branches glabrate. Staminate flowers 4–5 mm. long; pedicels 2–3 mm. long; sepals 4, connate in the lower half, triangular, about 1 mm. long; petals 4, white, elliptic, 3–4 mm. long; stamens 4, 4–5 mm. long, anthers 0.5 mm. long; disc flat; rudimentary carpel 1, globose, 0.5 mm. high. Carpellate flowers 3–4.5 mm. long; pedicels, sepals, petals, and disc as in staminate flowers; rudimentary stamens about 0.3 mm. long; gynoecium 2-carpellate, about 2 mm. high, styles and stigmas coherent, the combined stigmatic structure peltate. Fruiting pedicels 2–5 mm. long; follicles subglobose, 9–12 mm. in diameter, in pairs or occasionally single and paired with an undeveloped carpel.

Papua. CENTRAL DISTRICT: Kairuku Subdistrict, near Maipa Village, *Darbyshire 934* ♀ (CANB, L), *998* ♂ (CANB, L); Sogeri Region, central position, *Forbes 96* ♀ (BM). **Solomon Islands.** BOUGAINVILLE ISLAND: Kugumaru, Buin, *Kajewski 1835* ♀ (A); Siwai District, *Waterhouse Y167* ♀ (BRI, NY); without definite locality, *Waterhouse B344* ♀ (isotypes: A, BRI). CHOISEUL ISLAND: northern part, *Whitmore's Collectors BSIP 5661* ♀ (L).

DISTRIBUTION. Solomon Islands and Papua; in well drained, primary rain forests at altitudes up to 600 meters.

A very distinctive species with probably the largest leaves of any *Zanthoxylum* in the Australasian-Pacific region. Additional collections are desirable since at present we lack flowering material from the Solomons and fruiting material from Papua.

7. **Zanthoxylum forbesii** Hartley sp. nov.

Arbor magna; foliis paripinnatis, 40–50 cm. longis, glabris; foliolis in paribus 3–4, oppositis, chartaceis, ellipticis, 15–25 cm. longis, 5–9 cm. latis, basi obtusis, apice breviter acuminatis, margine integris, venis primariis utrinsecus 12–15, petiolulis 0.7–1 cm. longis; infructescentiis terminalibus et axillis superioribus orientibus, paniculatis, 8–14 cm. longis, patentibus, glabris; pedicellis 2–3 mm. longis; sepalis persistentibus 4, late triangularibus, ca. 1 mm. longis; folliculis subglobosis, ca. 1 cm. diametro, in paribus vel interdum folliculo singulo et cum carpello abortivo; floribus non visis. Holotypus: *Forbes 1707* (GH). FIG. 1.

FIG. 1. *Zanthoxylum forbesii* Hartley. Photograph of type (GH), × 3/8.

Sumatra. Penangoengan, Lampongs, altitude 138 m., *Forbes 1707* ♀ (GH — holotype; BM, SING — isotypes).

Apparently allied to *Zanthoxylum megistophyllum* from which it differs in having smaller leaves, fewer leaflets, and longer petiolules.

8. **Zanthoxylum backeri** (Bakh. f.) Hartley, comb. nov.

Fagara backeri Bakh. f. Blumea **6**: 366. 1950. Type: *Backer 17017*, Java.

Liana 15 m.; branchlets sparsely armed with scattered, retrorse prickles. Leaves imparipinnate, to 30 cm. long, glabrous; petiolules about 3 mm. long; leaflets 6–8 pairs, opposite or subopposite, subcoriaceous, elliptic-ovate, 6–8 cm. long, 2.6–3.2 cm. wide, base oblique, main veins 10–12 on each side of the midrib, margins essentially entire, apex acuminate, the acumen about one-fourth the length of the blade. Infructescences terminal and from upper leaf axils, paniculate with opposite branching, 10 cm. (to 30 cm., fide Bakhuizen f.) long and broadly spreading, the axes and branches glabrate. Fruiting pedicels about 1 mm. long; persistent sepals 4, triangular, about 1 mm. long; follicles subglobose, about 1 cm. in diameter, in pairs or single and paired with an undeveloped carpel. Flowers not known.

Java. West Java, Preanger Regencies, Lengkong, in forest at 700 m., *Backer 17017* ♀ (L — isotype).

Although known from only a single collection, this species seems to be closely related to *Zanthoxylum retroflexum* of Sumatra.

9. **Zanthoxylum retroflexum** Hartley sp. nov.

Frutex scandens; ramulis et foliorum rhachibus parce aculeatis, aculeis retrorsis; foliis imparipinnatis, 15–30 cm. longis, glabris, acute reflexis, ad basin rhachibus pulvinatis; foliolis in paribus 4–5, oppositis, subcoriaceis, pellucido-punctatis, elliptico-oblongis, 4–7.5 cm. longis, 1.7–2.5 cm. latis, basi acutis vel leviter obliquis, apice acuminatis, acumine 6–9 mm. longo, ad apicem plerumque leviter emarginato, margine integris vel parce glanduloso-crenatis, venis primariis utrinsecus 12–15, petiolulis 3–5 mm. longis; paniculis fructiferis terminalibus et axillis superioribus orientibus, 10–12 cm. longis, 5–6 cm. latis, ramulis oppositis, axi et ramulis glabratis; pedicellis ca. 1 mm. longis; sepalis persistentibus 4, triangularibus, ca. 1 mm. longis; folliculis subglobosis, 6–7 mm. diametro, in paribus vel interdum singulis cum carpello abortivo; floribus non visis. Holotypus: *Yates 1850* (MICH). FIG. 2.

Sumatra. Asahan, Bandar Poelo, in forest at 250 m., *Yates 1850* ♀ (MICH — holotype; BRI, K — isotypes).

The sharply reflexed leaves of this species are not found in the other

FIG. 2. *Zanthoxylum retroflexum* Hartley. Photograph of type (MICH), × 3/8.

Malesian species of *Zanthoxylum*. *Z. backeri*, of Java, appears to be closely related but also differs in having longer acuminate leaflets with fewer main veins on either side of the midrib and larger follicles.

10. **Zanthoxylum limonella** (Dennst.) Alston, in Trimen, Handb. Fl. Ceylon suppl. 6. 37. 1931.

Tipalia limonella Dennst. Schlüss. Hort. Malab. 31. 1818. Type: plate and description, Rheede, Hort. Malab. **5:** 67. *t. 34.* 1685.
Fagara budrunga Roxb. Fl. Ind. ed. Carey & Wall. **1:** 437. 1820. Lectotype: *Roxburgh Icones 2113*, cult. Bot. Gard. Calcutta.
Fagara rhetsa Roxb. Fl. Ind. ed. Carey & Wall. **1:** 438. 1820. Lectotype: *Roxburgh Icones 185*, cult. Bot. Gard. Calcutta.
Zanthoxylum budrunga (Roxb.) DC. Prodr. **1:** 728. 1824, sub "*species non satis notae.*"
Zanthoxylum rhetsa (Roxb.) DC. Prodr. **1:** 728. 1824.
Zanthoxylum rhetsa var. *budrunga* (Roxb.) Pierre, Fl. Forestière Cochinch. **4:** *t. 290.* 1893.
Zanthoxylum budrunga var. *paucijuga* Koords. & Val. Booms. Java **4:** 224. 1896; Exk. Fl. Java **2:** 418. 1912, pro syn. sub *Zanthoxylum rhetsa* (Roxb.) DC. Syntypes: *Koorders 6983β* & *15353β*, Java (not seen).
Zanthoxylum? minahassae Koords. Fl. N.O. Celebes 639. 1898; Koorders-Schumacher, Syst. Verzeich. **3:** 59. 1914. Syntypes: *Koorders 16258β* (not seen), *18773β*, *18774β* (not seen) and *18775β*, Celebes.

Trees to 35 m.; dioecious; deciduous; rather long bole and spreading crown; main stem generally with broad, conical spines 2–3 cm. long; branchlets usually sparsely armed with straight or ascending prickles, often swollen and hollow and apparently housing ants. Leaves paripinnate or imparipinnate, 30–40 cm. long, glabrous; petiolules of lateral leaflets 3–5 mm. long; leaflets 5–8 pairs, opposite or subopposite, chartaceous, occasionally with scattered pellucid dots, ovate to elliptic, 7–13 cm. long, 3–5 cm. wide, base oblique, main veins 10–15 on each side of the midrib, margins entire to glandular crenate with as many as 3 crenations per cm., apex acuminate, the slender acumen at least one-eighth the length of the blade. Inflorescences terminal and from upper leaf axils, paniculate, 8–14 cm. long and generally about as broad, the axes and branches glabrous or glabrate. Staminate flowers 1.5–2.5 mm. long; pedicels 1–2 mm. long; sepals 4, green, rounded to triangular, 0.5–1 mm. long, connate at about half their length or free to the base, valvate, margins subentire or fimbriate; petals 4, white or yellowish white, elliptic, 1–2 mm. long; stamens 4, about as long as the petals at anthesis, anthers about 1 mm. long; disc pulvinate, irregularly lobed, about 0.5 mm. high; rudimentary carpel about 0.5 mm. high. Carpellate flowers 1.5–2.5 mm. long; pedicels, sepals and petals as in staminate flowers; rudimentary stamens absent; disc pulvinate, about 0.25 mm. high; gynoecium 1-carpellate, about 1 mm. high, style excentric, stigma flattened. Fruiting pedicels 2–4 mm. long; follicles single, globose, 6–7 mm. in diameter.

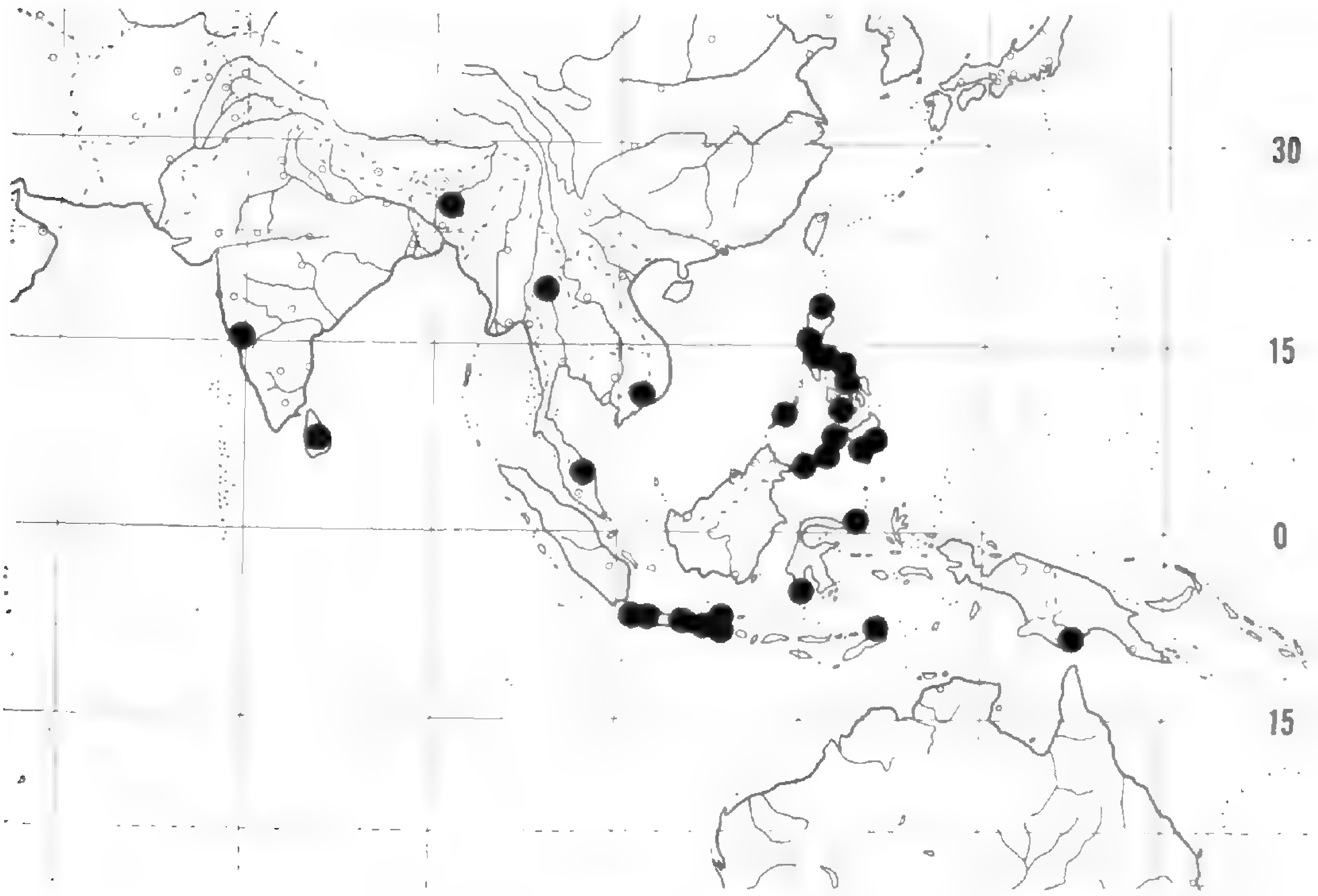
India. Bombay Presidency: region E of Goa boundary, *Fernandes 691* ♀ (A). Assam: Garo Hills, Phulbari, *Chand 3113* ♂ (MICH); Rani, *Koelz 29225* ♀ (MICH); without definite locality, *King's Collector 189* ♂ (A, US). Without definite locality: *Wight 353* ♀ (GH). **Ceylon.** *Thwaites CP 3490* ♀ (GH). **Thailand.** Hue Pang Huang, *Kerr 5473* ♂ (SING). **South Vietnam.** Bien Hoa

Province, Bao Chiang, *Bois 97* ♀ (A), *Pierre*, July, 1877 ♂ (A). **Malay Peninsula.** Kelantan, Kota Bharu, *Corner SF 33458* [A (♂), SING (2 sheets, ♂ and ♀)]. **Java.** West Java: Samarang Residency, *Koorders*, February 28, 1892 ♀ (L), *1161C* ♂ (L), March 20, 1892 ♀ (L); Cheribon Residency, Kromong Range, Mt. Djaja, *Steenis 12880* ♂ (L). Central Java: Tjilatjap, *NIFS Ja 2933* (A, L). Eastern Java: G. Baloeran, *Backer 24802* ♀ (K, L); Poeger, *Koorders 6995β* (L); Djalipapak, *Koorders 6997β* (L), *6998β* (L); Besoeki, *Koorders 11812β* (L); Banjoemas, *Koorders*, December 8, 1891 ♂ (L); Djember, *Ulbee*, March, 1921 (L); Bodjonegoro, *NIFS Ja 2229* (L). Peutjang Island: Udjung Kulon Reserve, *Kostermans*, December 3, 1960 ♂ (A, L). Kangean Island: Tjangkramaan, *Backer 27639* ♀ (L). **Philippines.** Palawan Island. *Curran FB 3822* ♀ (K, NY). Luzon Island. Ilocos Norte Province: *Addurn FB 22989* ♀ (A, US), *Ramos BS 32711* ♀ (US). Nueva Ecija Province: Bongabon, *Vidal 134* ♂ (A, K, L). Zambales Province: *Curran FB 6920* ♂ (US). Bataan Province: Mt. Mariveles, Lamao River, *Borden FB 1565* ♀ (BM, NY), *FB 3051* ♂ (NY, US); without definite locality, *Ahern's Collector FB 1455* ♀ (NY, US). Rizal Province: Morong, *Loher 5145* ♀ (K, US), *Ramos BS 1421* (NY, US), *Vidal 2269* ♀ (K); Antipolo, *Merrill SB 872* (A, BM, GH, K, L, NY, US), *SB 961* ♂ (A, GH, K, L, NY, US); Bosoboso, *Merrill 2706* ♂ (K, NY, US); San Mateo, *Vidal 1015* ♀ (K, L); without definite locality, *Ahern's Collector FB 3105* ♂ (NY, US). Laguna Province: Los Baños (Mt. Maquiling), *Elmer 18231* ♀ (A). Batangas Province: *Curran FB 7688* ♀ (NY), *Curran & Merritt FB 7715* ♀ (NY, US). Quezon Province: Tayabas, *Ware FB 16* ♀ (BM, K, NY, US). Camarines Province: *Curran FB 10695* ♂ (US), *FB 10726* ♂ & ♀ (US). Albay Province: *Cuming 1218* ♂ (BM, K, L), *1356* ♂ (BM, L). Masbate Island. *Clark FB 1710* ♀ (K, NY, US). Negros Island. *Curran FB 17437* ♀ (US). Tawitawi Island. *Ramos & Edano BS 44110* ♀ (A, BM, NY, US). Basilan Island. *Miranda FB 18971* ♀ (BM, K, US). Mindanao Island. Davao Province, Mt. Pagdaugan, *Ramos & Edano BS 49631* ♂ (A, NY, SING); Cotabato Province, Buayan, *Ramos & Edano BS 85175* ♂ (A); Zamboanga, *Whitford & Hutchinson FB 9067* ♀ (NY). **Celebes.** Minahasa Province, *Koorders 18773β* (L), *18775β* (L) — syntypes of *Zanthoxylum minahassae*; Paria van Longkang naar Giliraeng, *Noerkas 154* ♀ (L). **Moluccas.** Wetar Island, Tara, *NIFS bb 27284* ♀ (K, L, SING). **Papua.** Western District, Mabaduan, *Brass 6491* ♀ (A, BRI, L). **Cultivated.** India, Calcutta, *Roxburgh Icones 185*, drawn from a plant from Sikar, India (K — lectotype of *Fagara rhetsa*, not seen; A, photo.), *Roxburgh Icones 2113*, drawn from a plant from Silhet, India (K — lectotype of *Fagara budrunga*, not seen; A, photo.).

Distribution. India, Ceylon, Thailand, South Vietnam, Malay Peninsula, Java, Philippines, Celebes, Moluccas (Wetar Island) and southern Papua; in rather dry, often monsoonal, forests and thickets at altitudes up to 500 meters. See MAP 6.

Illustrations. Koorders, S. H., & Th. Valeton, Atlas der baumarten von Java **2**: *t. 352.* 1914, as *Fagara rhetsa.* Pierre, L., Flore forestière de la Cochinchine **4**: *t. 290 & 291.* 1893, as *Zanthoxylum rhetsa* var. *budrunga.*

As was pointed out in the discussion of the genus, the leaflets of this species are quite variable in the occurrence of oil dots and marginal crenations. This has been a source of confusion between *Zanthoxylum budrunga*



Map 6. Distribution of *Zanthoxylum limonella* (Dennst.) Alston.

and *Z. rhetsa* (see Hooker, f., Fl. Brit. Ind. 1: 495. 1875), although the main difference Roxburgh had in mind was the number of leaflets, also a variable character.

Koorders' *Zanthoxylum? minahassae*, based on sterile and apparently juvenile material with prickly leaf rachises and pellucid-dotted, crenate leaflets, is placed here with considerable uncertainty. It could easily be young material of the closely related *Z. celebicum*, which occurs in the same area in the northeast Celebes as *Z. limonella*.

11. **Zanthoxylum parviflorum** Benth. Fl. Austral. 1: 363. 1863. Lectotype: *Armstrong 569*, Australia, Northern Territory.

Fagara parviflora (Benth.) Engl. Nat. Pflanzenfam. III. 4: 119. 1896.

Trees to 20 m.; dioecious; deciduous; main stem with a few scattered prickles; branchlets unarmed or sparsely prickly. Leaves imparipinnate, 22–28 cm. long, glabrous; petiolules of lateral leaflets 1.5–3 mm. long; leaflets 5–8 pairs, opposite, chartaceous, with scattered pellucid dots, elliptic-oblong, 5–8 cm. long, 2–3.5 cm. wide, broadest below the middle, base rounded, main veins 8–11 on each side of the midrib, margins glandular crenate with 2–3 crenations per cm., apex acuminate, the acumen one-fourth to one-fifth the length of the blade. Inflorescences terminal and from upper leaf axils, paniculate, 6–8 cm. long and about as broad, the axes and branches glabrate. Staminate flowers 2–3 mm. long; pedicels 2–4 mm. long; sepals 4, green, rounded to triangular, about 1 mm. long, free to about the base, valvate, margins subentire; petals 4, white, elliptic, 2 mm.

long; stamens 2–3 mm. long, anthers about 1 mm. long; disc pulvinate, 0.5–1 mm. high; rudimentary carpel 0.25–0.5 mm. high, poorly differentiated. Fruiting pedicels 3–5 mm. long; follicles single, globose, about 7 mm. in diameter. Carpellate flowers not seen.

West New Guinea (West Irian). Merauke Area, *Versteeg 1910* ♂ (K, L). **Australia.** NORTHERN TERRITORY: Port Essington, *Armstrong 569* ♂ (MEL — lectotype); Darwin, *Bleeser 532* ♂ (MEL), *Holtze 160* ♂ (MEL); islands in the Gulf of Carpentaria, *Brown 5334* ♀ (BM, MEL); Golburn Island, *Cunningham 181* ♀ (BM, MEL); Arnhem Land, Liverpool River, *Gulliver*, October, 1867 ♂ (MEL); without definite locality, *Schomburgk* (US).

DISTRIBUTION. West New Guinea and Northern Territory of Australia; in monsoon forests at low elevations.

Bentham cited three collections in the original description — *Armstrong 569*, *Brown 5334*, and *Cunningham 181*. The most complete of these, *Armstrong 569*, is designated here as the lectotype.

This species is very similar to *Zanthoxylum limonella*, differing mainly in the smaller leaflets with rounded rather than oblique bases and smaller inflorescences. The New Guinea collection, *Versteeg 1910*, is somewhat intermediate between *Z. parviflorum* and *Z. limonella*.

12. **Zanthoxylum celebicum** Koords. Fl. N.O. Celebes 639. 1898; Koorders-Schumacher, Syst. Verzeich. 3: 59. 1914. Lectotype: *Koorders 18746β*, Celebes.

Trees to 35 m., dioecious; evergreen; branchlets with numerous straight or ascending prickles. Leaves paripinnate or imparipinnate, 40–50 cm. long, glabrous or puberulent on the rachises, petiolules and lower midribs; petiolules of lateral leaflets 3–5 mm. long; leaflets 6–10 pairs, opposite, subcoriaceous, elliptic-oblong, 10–20 cm. long, 4–6 cm. wide, base oblique, main veins 14–20 on each side of the midrib, margins entire or with a few glandular crenations near the apex, apex abruptly acuminate, the acumen about one-twelfth the length of the blade. Inflorescences terminal and from upper leaf axils, paniculate, 15–18 cm. long and about two-thirds as broad, the axes and branches densely puberulent. Staminate flowers (seen only in bud) about 2.5 mm. long; pedicels 1–2 mm. long; sepals 4, broadly rounded, about 1 mm. long, slightly imbricate basally, margins ciliate; petals 4, elliptic-ovate, about 2 mm. long; stamens 4, 1.5 mm. long, anthers about 1 mm. long; disc pulvinate, about 0.5 mm. high; rudimentary carpel about 0.3 mm. high. Fruiting pedicels 0.2–1.2 mm. long; follicles (premature) single, ovoid, about 7 mm. long and 4 mm. wide. Carpellate flowers not seen.

Celebes. Near Manado, Minahasa Province, *Koorders 18746β* (L — lectotype), *18747β* (L), *18772β* (L), *NIFS bb 19450* ♂ (A, L). **Moluccas.** MOROTAI ISLAND: Subdistrict Tobelo, N Tjao, *Tangkilisan NIFS bb 33848* (L, SING); Sangowo River, *Kostermans 1426* ♀ (L, SING).

DISTRIBUTION. NE Celebes and Morotai Island in the Moluccas; in primary rain forests at elevations from 60 to 500 meters.

Koorders' description of this species was based on sterile material and no collections were cited. Later, Koorders-Schumacher (Syst. Verzeich. 3: 59. 1914) cited four Koorders collections for this species, all made in 1895 from the same general locality in the Celebes. I have chosen the lectotype (*Koorders 18746β*) from the three duplicates of these collections at Leiden, each of which bears the name *Zanthoxylum celebicum* in Koorders' handwriting. It consists of a packet of leaflets, a section of a rachis with two leaflets attached and a vegetative stem apex.

The two collections from Morotai Island have a more pronounced pubescence of the inflorescences and more clearly ciliate sepals than the only fertile collection (*NIFS bb 19450*) I have seen from the Celebes. The leaves, however, are a reasonably good match for Koorders' type material of *Zanthoxylum celebicum* and I think there is little doubt that they belong here.

13. **Zanthoxylum vinkii** Hartley sp. nov.

Arbor dioica sempervirens; ramulis parce aculeatis, aculeis rectis, inflatis et cavis et, ut videtur, a formicis inhabitatis; foliis paripinnatis, ca. 60 cm. longis, glabris; foliolis in paribus 10, oppositis, subcoriaceis, elliptico-oblongis, 14–19 cm. longis, 4–6 cm. latis, basi subcordatis, apice abrupte et breviter acuminatis, acumine 6–15 mm. longo, margine integris vel ad apicem parce glanduloso-crenatis, petiolulis 2–3 mm. longis; inflorescentiis paniculatis, terminalibus vel in axillis superioribus orientibus, 15–30 cm. longis latisque, glabris; floribus ♀ 3.2 mm. longis, pedicellis 0–2 mm. longis; sepalis 4, virentibus, late rotundatis, 0.6 mm. longis, margine ciliatis; petalis 4, flavis, ellipticis, 2.7 mm. longis; staminibus rudimentariis 0.1 mm. longis; disco pulvinato, 0.5 mm. alto; gynoeceo 1-carpellato, 1.3 mm. alto, stylo excentrico, stigmate 0.75 mm. lato; floribus ♂ et fructibus non visis. Holotypus: *Vink BW 12065* (A). FIG. 3.

West New Guinea (West Irian). Schouten Islands. BIAK ISLAND: Siabes, primary forest on coral rock with thin clay covering, altitude 75 m., young tree 12 m., common, *Moll BW 7025* (L); Korim Road, old secondary growth forest on rocky soil, altitude 60 m., young tree 12 m., scarce, *Vink BW 12065* ♀ (A — holotype; CANB, L — isotypes).

The subcordate leaflet bases of this species distinguish it from the closely related *Zanthoxylum celebicum* (which also differs in having puberulent rather than glabrate inflorescences) and *Z. pluviatile*.

14. **Zanthoxylum pluviatile** Hartley sp. nov.

Arbor usque ad 35 m. alta, dioica, sempervirens; trunco spinoso vel exarmato, spinis magnis conicis, ramulis exarmatis vel parce aculeatis, aculeis saepe inflatis et cavis et, ut videtur, a formicis inhabitatis; foliis

FIG. 3. *Zanthoxylum vinkii* Hartley. Photograph of type (A), × 3/8.

impari- vel paripinnatis, 30–60 cm. longis, glabris; foliolis in paribus 5–12, oppositis, chartaceis, elliptico-oblongis vel anguste oblongis, 9–15 cm. longis, 2–4.5 cm. latis, basi obliquis vel rotundatis, margine integris vel glanduloso-crenatis, crenis 1 cm. distantibus, apice breviter acuminatis, acumine 5–

13 mm. longo, petiolulis 2–5 mm. longis; inflorescentiis terminalibus vel in axillis superioribus orientibus, paniculatis, usque 15 cm. longis, ramis patentibus, axi et ramulis glabratis; floribus ♂ 4–7 mm. longis, pedicellis usque 0.5 mm. longis vel nullis; sepalis 4, viridibus, late rotundatis, 1–2 mm. longis, ad basin leviter imbricatis, margine ciliatis; petalis 4, albis,

FIG. 4. *Zanthoxylum pluviatile* Hartley. Photograph of type [illegible]

ellipticis, 3–5 mm. longis, plerumque ad anthesin erectis; staminibus 4–6 mm. longis, antheris 1.5–2 mm. longis inclusis; disco pulvinato tenuiter 4-lobato, 0.75–1.5 mm. alto; carpello rudimentario ca. 0.5 mm. alto; pedicellis usque ad 1 mm. longis; folliculo singulo, globoso, 7–8 mm. diametro; floribus ♀ non visis. Holotypus: *Hartley 11349* (A), Territory of New Guinea. FIG. 4.

Papua. NORTHERN DISTRICT: Kakoda, *Carr 16422* ♀ (L). CENTRAL DISTRICT: Mt. Obree, *Lane-Poole 392* (BRI); Kanosia, *Carr 11582* ♂ (L); Boridi, *Carr 13256* ♀ (CANB, K, L). MILNE BAY DISTRICT: Milne Bay Area, *Smith NGF 1287* ♂ (L). **Territory of New Guinea.** MOROBE DISTRICT: 10 miles N of Lae, *Hartley 11349* ♂ (A — holotype; L — isotype); Lae Area, *Vickery NGF 1405* ♀ (L). **Solomon Islands.** SANTA ISABEL ISLAND: Sigana, *Brass 3449* ♂ (A, BRI, L, SING); Tatamba, *Whitmore BSIP 2719* (L). GUADALCANAL: near Point Cruz, *Walker & White BSIP 126* ♀ (A, BRI, CANB, L, US).

DISTRIBUTION. Eastern New Guinea and the Solomon Islands; in well-drained, primary rain forests at altitudes up to 2100 meters.

A flowering collection from the Solomon Islands (*Brass 3449*) seems to indicate a tendency of this species to grade into *Zanthoxylum limonella*. In this collection the flowers are smaller and have less exserted stamens and more spreading petals than the New Guinea material of *Z. pluviatile*. Collections from elevations of 1500 and 2100 meters in Papua (*Lane-Poole 392* and *Carr 13256*) differ from the lowland material in having smaller, more narrowly oblong leaflets and sparsely prickly branchlets. They may indicate a close relationship with *Zanthoxylum conspersipunctatum* of which there is a similar narrow-leaved form (*Brass 22553* and *22919* from Mt. Dayman, Milne Bay District, Papua).

15. **Zanthoxylum conspersipunctatum** Merr. & Perry, Jour. Arnold Arb. **22**: 33. 1941. Type: *Brass 11579*, West New Guinea.

Trees to 25 m.; dioecious; evergreen; rather long bole and spreading crown; main stem prickly, becoming smooth with age; outer bark gray-brown, longitudinally fissured; inner bark yellow or yellowish brown; wood yellow; branchlets with straight or ascending prickles, often swollen and hollow and apparently housing ants. Leaves paripinnate or imparipinnate, 10–30 cm. long, glabrous; petiolules 3–5 mm. long; leaflets 2–8 pairs, opposite, subcoriaceous to coriaceous, generally lustrous above, with scattered and/or marginal pellucid dots, ovate to elliptic, 5–13 cm. long, 2–5 cm. wide, base oblique to obtuse, main veins 12–18 on each side of the midrib, margins subentire to glandular crenate with as many as 2 crenations per cm., apex acuminate, the acumen about one-tenth the length of the blade. Inflorescences terminal and from upper leaf axils, paniculate, 6–10 cm. long and generally about as wide, the axes and branches glabrate. Staminate flowers 3.5–7 mm. long; pedicels obsolete to 1 mm. long; sepals 4, green to pink, broadly rounded, 1–1.3 mm. long, free to about the base, valvate or slightly imbricate basally, margins entire or slightly fimbriate;

petals 4, white to pink, elliptic, 3–5 mm. long; stamens 4, about as long as the petals at anthesis, anthers 1.3–2.5 mm. long; disc pulvinate, 4–lobed, 0.5–1 mm. high; rudimentary carpel 0.2–2 mm. high, well differentiated. Carpellate flowers 3.5–7 mm. long; pedicels, sepals and petals as in staminate flowers; rudimentary stamens 0.2–2 mm. long; disc pulvinate, slightly lobed, about 0.5 mm. high; gynoecium 1-carpellate, 1.5–2.5 mm. high, style excentric, stigma flattened, 0.5–1 mm. broad. Fruiting pedicels 1–2 mm. long; follicles single, globose to ovoid, 6–10 mm. in diameter.

West New Guinea (West Irian). Bele River, 18 km. NE of Lake Habbema, *Brass 11579* ♂ (A — holotype; L — isotype). **Papua.** Milne Bay District, Maneau Range, N slopes of Mt. Dayman, *Brass 22553* ♀ (A), *22919* ♂ (A). **Territory of New Guinea.** WESTERN HIGHLANDS DISTRICT: Mt. Hagen Range, Tomba Village, *Hoogland & Pullen 6116* ♀ (A, BRI, K, L, US); Mt. Kum, near Mt. Hagen, *Womersley NGF 9418* ♂ (A, BRI, K, L). EASTERN HIGHLANDS DISTRICT: Mt. Wilhelm, E slopes, *Brass 30345* ♀ (CANB, K, L, US), *30496* ♂ (A, K, L, US), *30614* ♂ (A, K, L, NY, US); about 1 mile S of Akuna, *Hartley 12027* ♀ (A, L); Marafunga, about 20 miles NW of Goroka, *Hartley 13270* ♀ (A), *Womersley & Sleumer NGF 14011* ♂ & ♀ (CANB); Asaro-Mairi Divide, near Daulo camp, *Hoogland & Pullen 5471* ♀ (CANB), *5475* ♂ (A, BRI, K, L, US), *Saunders 892* (CANB, L); ridge above Toromambuno Mission, *Pullen 309* ♂ (A, BRI, K, L, US); about 5 miles W of Keglsugl airstrip, *Saunders 770* (A, L); Wonatabe, 15 miles S of Okapa, *Womersley NGF 17629* ♂ (BRI, CANB). MOROBE DISTRICT: Yunzaing, *J. & M. S. Clemens 3574* ♀ (A), *4060* ♀ (A); Sambanga, *Clemens 6813* ♂ (A, L).

DISTRIBUTION. New Guinea; in mountain forests from 1500 to 2000 meters.

A highly variable species with four morphological extremes possibly representing incipient species. Apparently closely related to *Zanthoxylum pluviatile* and also to *Z. veneficum* F. M. Bailey and *Z. brachyacanthum* F. Muell. (distinct?) of eastern Australia.

The type collection of *Zanthoxylum conspersipunctatum, Brass 11579,* has much more conspicuous pellucid dots in the leaflets than any of the other collections cited for this species. Examination of cleared leaflets of this collection revealed that the dots are actually cavities in the mesophyll not traversed by the veins. The oil dots in the mesophyll of the other collections of this species examined proved to be small groups of cells not altering the venation pattern, though marginal dots in some of these were of the cavity type. As I have noted in the discussion of the genus, the presence and type of oil dots seem to be variable characters in the Malesian species of *Zanthoxylum*, and, without other morphological differences, I prefer not to make taxonomic distinctions.

Of the species of *Zanthoxylum* in New Guinea, *Z. conspersipunctatum* is by far the most frequent, being especially common in the mountain forests of the Eastern Highlands District.

16. **Zanthoxylum integrifoliolum** (Merr.) Merr. Enum. Philip. Fl. Pl. 2: 327. 1923.

Fagara integrifoliola Merr. Philip. Jour. Sci. Bot. 1(suppl.): 68. 1906. Lectotype: *Barnes FB 88*, Philippines.

Trees to 20 m.; dioecious; evergreen; older, apparently exposed roots sometimes (always?) covered with dense, soft, yellowish fibers that appear to be phelloderm tissue; main stems with short, scattered prickles when young, becoming smooth with age; branches relatively few, widely spaced, horizontal with ascending tips; branchlets unarmed. Leaves paripinnate or imparipinnate, 20–60 cm. long, glabrous, crowded toward tips of branchlets; petiolules of lateral leaflets 7–13 mm. long; leaflets 4–12 pairs, opposite, chartaceous to coriaceous, bright green above, much paler below, obovate to elliptic, generally broadest above the middle, 6–15 cm. long, 4–6 cm. wide, base obtuse to cuneate, often rather oblique, main veins 9–15 on each side of the midrib, margins entire, becoming cartilaginous with age, apex abruptly acuminate, the acumen usually about one-twelfth the length of the blade. Inflorescences terminal and from the upper leaf axils, paniculate, 12–46 cm. long and one-third to one-half as broad, the axes and branches glabrous or glabrate. Staminate flowers 4–5 mm. long; pedicels 2–4 mm. long; sepals 4, green, broadly triangular, about 1 mm. long, the margins entire; petals 4, white, elliptic-ovate, 2.5–3.5 mm. long; stamens 4, slightly exceeding the petals at anthesis, anthers about 1 mm. long; disc pulvinate, about 0.5 mm. high; rudimentary carpel conical, to 0.2 mm. high. Carpellate flowers 3–4 mm. long; pedicels, sepals, petals and disc as in staminate flowers; rudimentary stamens absent; gynoecium 1-carpellate, about 1 mm. high, style excentric, stigma flattened, about 0.5 mm. broad. Fruiting pedicels 3–5 mm. long; follicles single, subglobose, 6–9 mm. in diameter, with numerous, large oil glands.

Philippines. MINDORO ISLAND. Mt. Yagaw, S slope, *Conklin PNH 19019* (A, L); Bongabong River, *Merritt FB 3659* ♀ (NY), *Whitford 1464* ♀ (NY, US); Paluan, *Ramos BS 39551* ♀ (A, BM, GH). BATANES ISLANDS. Batan Island, Mt. Iraya, *Ramos BS 79957* ♀ (K, NY); without definite locality, *Fenix BS 3584* ♀ (NY). BABUYAN ISLANDS. Calayan Island, *Penas FB 26698* ♀ (US). LUZON ISLAND. Bataan Province: Mt. Mariveles, Lamao River, *Barnes FB 88* ♂ (US — lectotype of *Fagara integrifoliola*; BM, K, NY, SING), *Borden FB 2351* ♂ (NY, SING, US), *FB 2484* [NY, US (♀)], *FB 2740* ♀ (NY, SING, US), *Foxworthy BS 1567* (US), *Meyer FB 2307* ♂ (K, NY, SING, US), *Whitford 1044* ♀ (NY, US), *1295* ♀ (K, NY, US), *Williams 575* ♀ (GH, NY, US); Mamac River, *Barnes FB 336* ♀ (BM, K, NY, SING, US); without definite locality, *Curran FB 17578* ♂ (L). Rizal Province: Montalban, *Loher 6058* ♀ (K, US); without definite locality, *Ramos BS 22465* ♀ (A, BM, BRI, L, US). Camarines Norte Province: Paracale, *Ramos & Edano BS 33770* ♂ (A, K). Sorsogon Province: Irosin (Mt. Bulusan), *Elmer 15566* ♀ (A, BM, GH, NY, L, US); without definite locality, *Ramos BS 23421* ♂ (US). SAMAR ISLAND. Catubig River, *Ramos BS 24171* ♀ (A, K, US), *BS 24522* ♂ (L, US); Oquendo, Mt. Mahagna, *Sulit PNH 14512* ♀ (A, K, L); without definite locality, *Lasquety FB 23569* ♂ (A, US), *Ramos BS 1629* ♀ (BM, GH, L, SING). LEYTE ISLAND. Cabalian, *Ramos BS 41586* ♀ (A, L). PANAY ISLAND. Capiz Province: Magallanes (Mt. Giting-Giting), *Elmer 12063* ♀ (A, BM, GH, K, L, NY, US); without definite locality, *Edano BS 46165* ♂ (A, NY). MINDANAO ISLAND. Surigao Province, Mt. Cantugas, *Ramos & Convocar*

BS 83490 ♂ (NY); Davao Province, *de Mesa FB 27604* ♀ (SING); Zamboanga Province, *Quezon FB 30252* (BRI). DINAGAT ISLAND. *Ramos & Pascasio BS 35248* ♀ (BM, L), *Ramos & Convocar BS 83892* ♀ (NY).

DISTRIBUTION. Widespread in the Philippines in well-drained rain forests and thickets up to 640 meters elevation. Otherwise known from Lanyu Island (Botel Tobago) off the SE coast of Taiwan, *fide* Li, H. L., *Woody flora of Taiwan*, 373. 1963.

ILLUSTRATION. ITO, T., Illustrated flora of Formosa, *t. 13.* 1928.

Closely related to *Zanthoxylum limonella*, *Z. integrifoliolum* is distinguished by its obovate leaflets with entire, cartilaginous margins and unarmed branchlets.

The soft, fibrous material from the roots has reportedly been used by the natives of Lanyu Island to calk canoes.

17. **Zanthoxylum ovalifolium** Wight, Illus. Ind. Bot. 1: 169. 1839 ("*Zanthoxylon*"). Type: *Wight 356*, India, Madras.

Zanthoxylon sepearium Wight, Illus. Ind. Bot. **1**: 169. 1839. Type: *Wight 355*, India, Madras.

Zanthoxylum ovalifolium var. *sepearium* (Wight) Hook. f. Fl. Brit. Ind. **1**: 493. 1875.

Fagara ovalifolia (Wight) Engl. Nat. Pflanzenfam. III. **4**: 118. 1896.

Zanthoxylum inerme White & Francis Bot. Bull. (Dept. Agr. Brisbane) **22**: 6. 1920 (nomen illegit.) non Sessé & Mociño, nec Koidz. Type: *White*, January, 1918, Australia, Queensland.

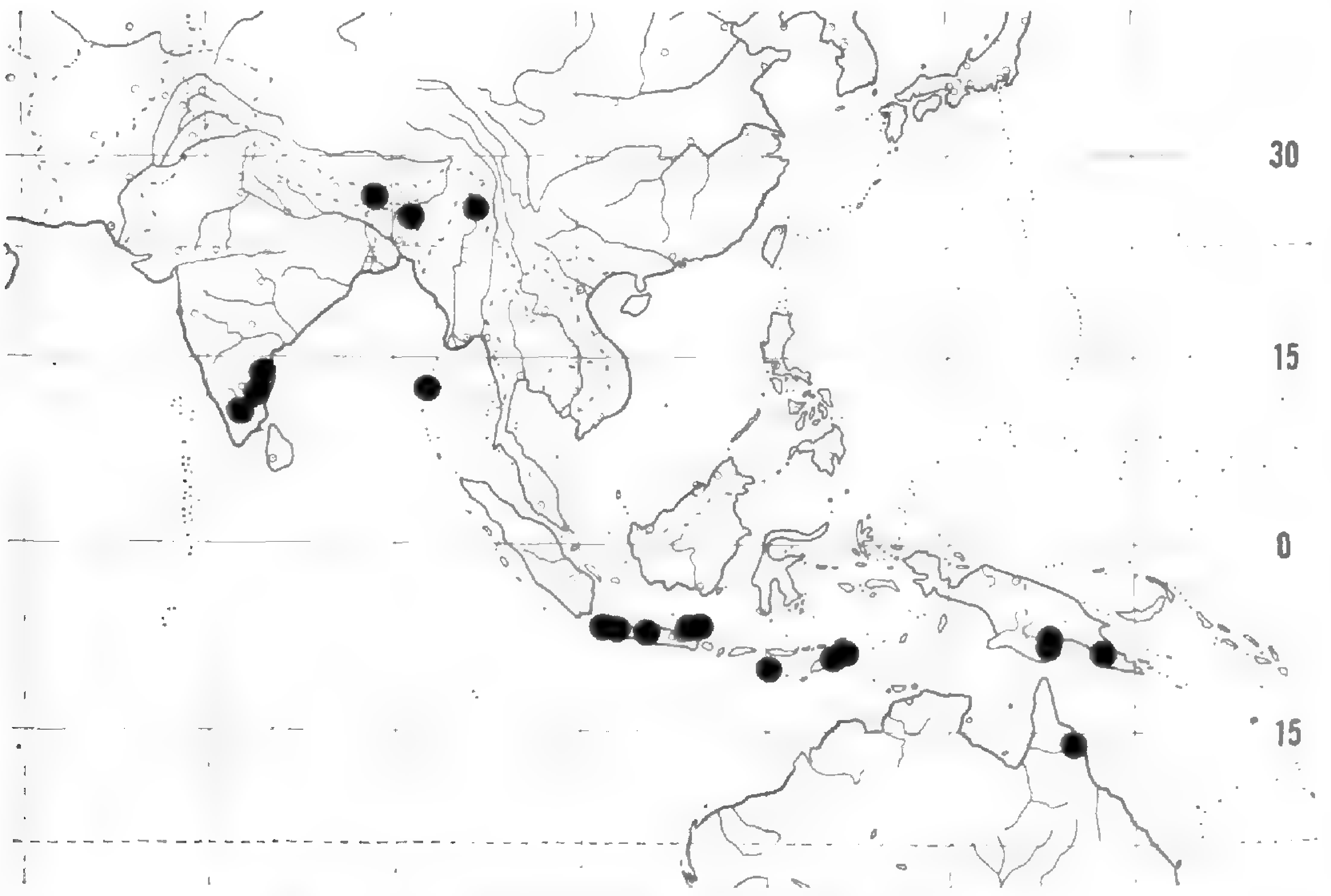
Fagara varians Domin Bibliot. Bot. **22** (894): 846. 1927 (nomen illegit.) non Benth. Type: *Domin 5657*, Australia, Queensland.

Zanthoxylum dominianum Merr. & Perry, Jour. Arnold Arb. **22**: 32. 1941 (based on *Fagara varians* Domin).

Zanthoxylum suberosum White, Proc. Roy. Soc. Queensland. **53**: 208. 1942 (based on *Z. inerme* White & Francis).

Erect shrubs or small trees to 8 m.; branchlets unarmed or rarely with a few straight, scattered prickles. Leaves trifoliolate (occasional leaves bi- or unifoliolate), 8–28 cm. long, glabrous; leaflets chartaceous to subcoriaceous, with scattered pellucid dots, ovate to elliptic, 3–19 cm. long, sessile or subsessile, base cuneate, main veins 7–20 on each side of the midrib, margins subentire to doubly crenate with about 5 crenations per cm., apex acute to short acuminate. Inflorescences axillary and terminal, paniculate, 3–12 cm. long and about half as broad, more or less flexuous, the axes and branches glabrate. Staminate flowers 2–3 mm. long; pedicels 1–3 mm. long; sepals 4, green, narrowly triangular, about 1 mm. long; petals 4, white, elliptic, about 2.5 mm. long; stamens 4 (in occasional pentamerous flowers, 5), 2–3 mm. long, anthers about 0.75 mm. long; disc pulvinate, about 0.75 mm. high; rudimentary carpel narrowly conical, about 0.5 mm. high. Carpellate flowers about 3 mm. long; pedicels, sepals and petals as in staminate flowers; rudimentary stamens 4, about 1 mm. long; disc pulvinate, about 0.5 mm. high; gynoecium 1-carpellate, about 1.5 mm. high, style excentric, stigma globose. Fruiting pedicels 2–4 mm. long; follicles single, subglobose, 6–7 mm. in diameter.

Sikkim. *Brandis 856* (A). **India.** ASSAM: Khasi Hills, *Chand 6328* ♀ (MICH), *Hooker f. & Thomson* ♀ (GH), *Koelz 30380* ♀ (MICH), *30809* ♀ (MICH), *31105* ♀ (MICH), *Ruse 122* ♂ (A). MADRAS: Nilghiri Mts., *Hooker f. & Thomson* ♂ & ♀ (GH); Pulicat Hills, *Wight 355* ♂ (K — holotype of *Zanthoxylon sepearium*; GH); Shevagherry Hills, *Wight 356* ♂ & ♀ (K — holotype of *Zanthoxylon ovalifolium*; GH). Without definite locality: *Blinkworth* (Wall Cat. n. 7469) ♀ (K), *Griffith* ♂ (GH). **Burma.** Kachin Hills, *Mokim*, 1897 ♂ (A), *s.n.*, 1898 ♀ (A). **Andaman Islands.** *Heinig*, December 12, 1900 ♀ (A), *King*, December 13, 1890 ♂ (SING), *King's Collector 102* ♀ (SING), October 1, 1892 ♀ (SING), *Prain's Collector*, October, 1900 ♀ (GH). **Java.** WESTERN JAVA: Goenoeng Poetjah Tjatjing, *Forbes 838* ♂ (BM, GH, SING); Bandoeng Tjigenteng, *Koorders 26284β* ♀ (A, L), *26333β* ♀ (L); Kjaja, *Lam 299* ♂ (L). CENTRAL JAVA: Semarang, Ambarawa Telomojo, *Koorders 27929β* ♀ (L), *27938β* ♀ (L). KANGEAN ISLANDS: Tambajangan, *Backer 27465* ♀ (L), *27590* ♀ (L), *27892* (L), *27921* ♀ (L), *27968* ♀ (L), *Beguin*, May 24, 1919 (L); Kajoe Waroe, *Backer 28122* ♀ (L). **Lesser Sunda Islands.** SOEMBAWA ISLAND: Batuduhang, Batu la nteh Mt., *Kostermans 18075* ♀ (CANB, L). TIMOR: Plateau of Fuiloro, Muapitine, *Steenis 18153* ♂ (L); Mt. Perdido, *Steenis 18317* ♂ (L). **Papua.** WESTERN DISTRICT: Lower Fly River, east bank opposite Sturt Island, *Brass 8060* ♂ (A, BRI, L); Wassi Kussi River, Tarara, *Brass 8507* ♂ (A, K, L). CENTRAL DISTRICT: Kanosia, *Carr 11183* ♀ (A); Koitaki, *Carr 11913* ♂ (A), *12594* ♀ (A); Boridi, *Carr 14925* ♀ (A); Sogeri, Mt. Sawada, *Forbes 875* ♀ (BM); tributary of Laloki River 2 miles E of Rouna, *Hartley 10704* ♂ (A). Without definite locality: *Chalmers*, 1885 ♀ (MEL). **Australia.** QUEENSLAND. Atherton Tableland: *Bailey*, June 27, 1899 ♀ (BRI); Forest Reserve 45, *Curry*, September 20, 1922 ♀ (A); in hygrodrymio apun lacum Lake Eacham, *Domin*



MAP 7. Distribution of *Zanthoxylum ovalifolium* Wight.

5657 ♀ (PR — holotype of *Fagara varians* Domin); Dunbella, *Forest Officer F71* (BRI); Herberton, *Kajewski 1358* ♀ (A, BRI); Tolga, *McKee 9296* ♀ (CANB); Ravenshoe, Millet Farm, *Samundsett 22* ♀ (BRI); near Atherton, *White*, January, 1918 ♀ (BRI — holotype of *Zanthoxylum inerme* White & Francis; MEL). Cairns: Trinity Bay, *Fitzalan*, 1882 ♀ (MEL).

DISTRIBUTION. Sikkim and India southeast to Queensland; in monsoon forests and thickets at elevations up to 1750 meters in Malesia and from 1000 to 2000 meters in continental Asia. See MAP 7.

ILLUSTRATION. WHITE, C. T., & W. D. FRANCIS (descr. of *Zanthoxylum inerme*), Bot. Bull. (Dept. Agr. Brisbane) 22: 6. 1920.

Zanthoxylum ovalifolium is markedly different from the other Malesian species and is apparently most closely related to two species of southwestern China, *Z. dimorphophyllum* Hemsl. and *Z. robiginosum* (Reeder & Cheo) Huang. The first of these, as I have pointed out in the introductory part of this paper, appears to be transitional between *Fagara* and *Zanthoxylum*, sensu stricto.

18. **Zanthoxylum acanthopodium** DC. Prodr. 1: 727. 1824. Type: *Wallich*, 1821, Nepal.

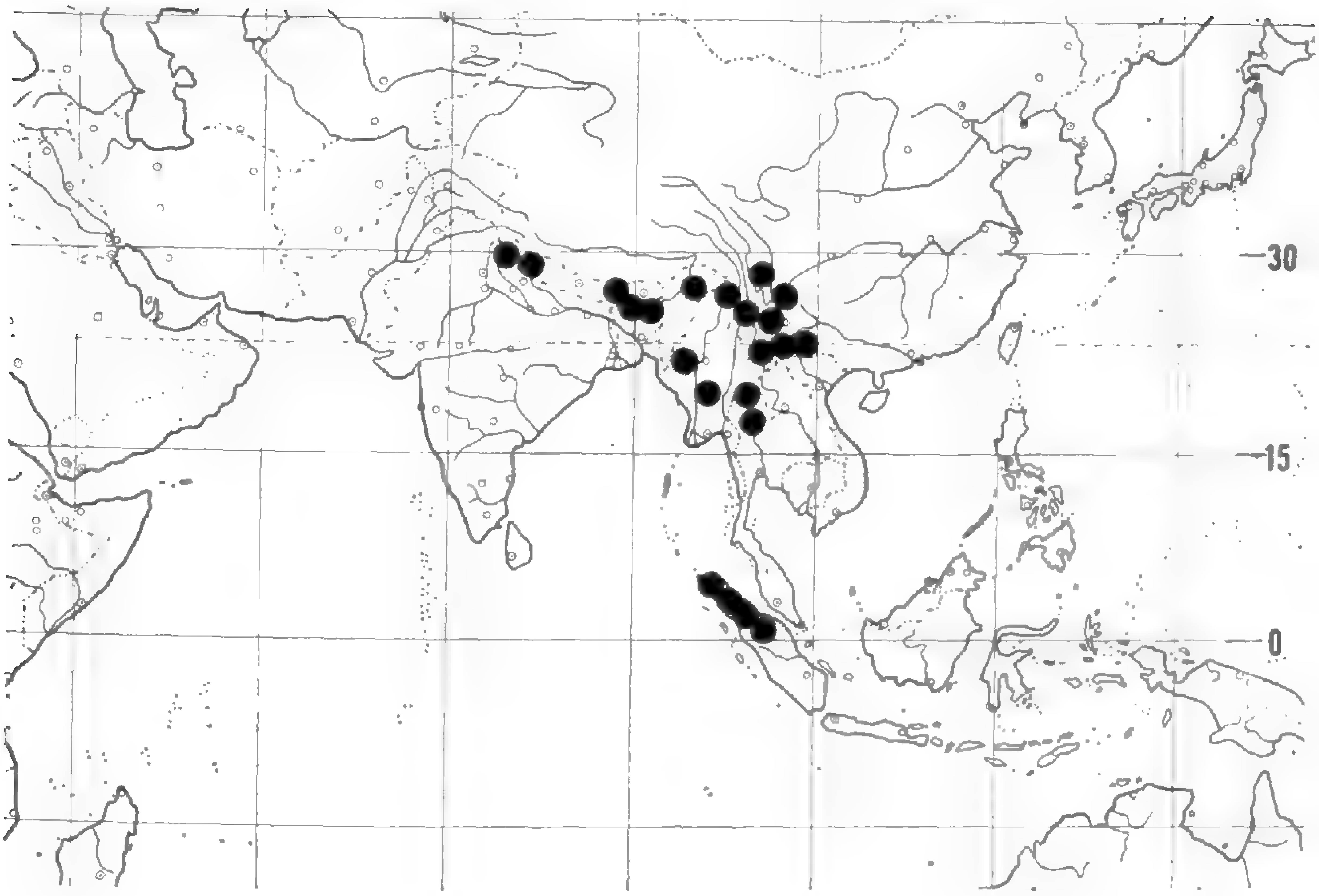
Scandent or erect shrubs or small trees to 6 m.; dioecious or (in Sumatra) with perfect flowers; apparently both deciduous and evergreen; branchlets villous with ferruginous hairs to glabrate, generally armed, the prickles flattened, predominantly pseudostipular, to 1.2 cm. long. Leaves trifoliolate or imparipinnate, 2–25 cm. long; rachis villous to glabrate, often with flattened prickles, narrowly to broadly (to 3 mm. on either side) winged; petiolules obsolete to 3 mm. long; leaflets 1–6 pairs, opposite, chartaceous, villous to sparsely hairy on the main veins below, with appressed hairs or glabrous above, often with flattened prickles along the midrib above and below, ovate to elliptic-lanceolate, 1–12 cm. long, 0.5–4.5 cm. wide, base obtuse, main veins generally conspicuous, 10–28 on each side of the midrib, margins subentire to glandular crenate with as many as 8 crenations per cm., apex acute to acuminate. Inflorescences axillary, paniculate to racemose, 0.5–2 cm. long and generally glomerate. Staminate flowers about 3 mm. long; pedicels obsolete to 2 mm. long; perianth segments 6–8, undifferentiated although occasionally slightly unequal in size, uniseriate to irregularly biseriate, green or yellowish green elliptic to ligulate, 1–2 mm. long, sparsely hairy to glabrous; stamens 6, about 2 mm. long, anthers about 1 mm. long and reddish purple prior to anthesis; disc pulvinate, about 0.75 mm. high; rudimentary carpels 2–5. Carpellate flowers about 2 mm. long; pedicels and perianth segments as in staminate flowers; rudimentary stamens none; disc pulvinate, 0.5–0.75 mm. high; gynoecium 2–5-carpellate, sparsely hirsute to glabrous, about 1.5 mm. high, styles about 0.75 mm. long, divergent, articulating about 0.3 mm. below the globose stigma. Perfect flowers (only in Sumatran specimens) about 3 mm. long; pedicels and perianth segments as in staminate flowers; stamens 3–6, about 3 mm. long, otherwise as in staminate flowers; gynoecium 2–4-carpellate, sparsely hirsute, otherwise as in carpellate flowers. Fruiting pedicels 0.5–1.5 mm. long; follicles generally reddish, subglobose, about 4 mm. in diameter, in 2's to 5's, the undeveloped carpels caducous.

India. Uttar Pradesh: Kumaun, Jagesar, *Strachey & Winterbottom 2* ♂ & ♀ (GH). West Bengal: Darjeeling District, *Smith*, April 20, 1908 ♀ (A). Assam: Naga Hills, *Chand 3376* ♀ (MICH); Khasia, *Hooker f. & Thomson* ♀ (GH, US); Mawphlang, *Koelz 31303* ♀ (MICH); without definite locality, *Simons 620* ♂ (L). **Nepal.** Doti District, *Ram*, May 15, 1929 ♀ (A); without definite locality, *Wallich*, 1821 (G-DC — holotype of *Zanthoxylum acanthopodium*, not seen; A, photo. and fragment). **Sikkim.** Sureil, *Smith 702* (A); without definite locality, *Hooker f. & Thomson* ♀ (GH). **East Pakistan (East Bengal).** *Griffith 1186/2* ♂ (GH). **Burma.** Thandaung, *Dickason 5273* ♂ (A), *6718* ♂ (A); Haka, *Dickason 7563* ♀ (A); North Triangle, *Kingdon-Ward 20736* ♀ (A). **Thailand.** Doi Sootep Mt. range, summit of Doi Chom Cheng, *Rock 1166* ♂ (US); Doi Chang Mt. near Hue San, *Rock 1726* ♀ (A, US). **China.** Yunnan Province: Likiang & vicinity, *Ching 21045* ♂ (A), *21882* ♀ (A), *Schneider 2877* ♂ (GH, US); S. Chungtien, Chiao-tou on Yangtze, *Feng 3067* ♀ (A); Si-Chour Hsien, Faa-doon, *Feng 11687* ♀ (A), *11807* ♂ (A); S of Red River from Manmei, *Henry 9758* ♂ (A); Mengtsz, *Henry 10150* [A (♂), US (2 sheets, ♂ & ♀ and ♂)], *10150B* ♀ (A, US), *11413* ♀ (A); Szemao, *Henry 12451* ♂ (A); Yunnanfu, *Schoch 268* ♂ (A, US); Peyen-tsien, *Ten 502* ♂ (A, US); Wen-shan Hsien, *Tsai 51691* ♀ (A); Kien-shuei Hsien, *Tsai 53113* ♀ (A); Pin-chuan Hsien, *Tsai 53686* ♂ (A); Lung-ling Hsien, *Tsai 55526* ♀ (A); Lan-ping Hsien, *Tsai 56103* ♀ (A); Lu-se, *Tsai 56423* ♀ (A); Che-tse-lo, *Tsai 58566* ♀ (A); Wei-si Hsien, *Tsai 59989* ♀ (A); Ping-pien Hsien, *Tsai 60761* ♀ (A), *61922* ♂ (A); W of Champutung, *Wang 67388* ♂ (A); Shunning, *Yu 16576* ♂ (A); Mienning, Poshang, *Yu 17849* ♂ (A); Kuikiang Valley, N of Mon-ting, *Yu 20391* ♀ (A); Muchietu, *Yu 21009* ♂ (A); without definite locality, *Forrest 7881* ♂ (A), *8846* ♂ (A), *11790* ♂ (A), *15914* ♂ (A), *Tsai 57118* ♀ (A), *57245* ♂ (A), *60092* ♀ (A). Szechwan Province: Yalung, *Handel-Mazzetti 482* ♀ (A); zwischen Ruapie und Takaioko, *Schneider 1353* ♀ (A), *1373* (A); Huei-li Hsien, *Yu 1607* ♀ (A). **Sumatra.** Gajo Loeas, Wenareh, *Pringgo Atmodjo* 55 ☿ (L); Karo Highlands, Berastagi, *Hamel & Rahmat Si Boeea 630* ☿ (A, MICH), *Lorzing 6100* ☿ (L), *Yates 1548* ☿ (A, BM, MICH); Karo Highlands, Kabandjahe, *Lorzing 13687* ☿ (L); Asahan, *Rahmat Si Boeea 10558* ☿ (A, L); Atjeh, Boer ni Telong, *Steenis 6342* ☿ (A, L).

Distribution. N India, Nepal, Sikkim, East Pakistan, Burma, Thailand, SW China and Sumatra; in mountain forests and thickets at elevations of 1200 to 1400 meters in Sumatra and up to 2900 meters in SW China. See MAP 8.

Illustration. Pierre, L., Flore Forestière de la Cochinchine **4**: *t. 290.* 1893.

Similar to *Zanthoxylum armatum* but with relatively constant differences in the size and position of the inflorescence, number of lateral veins in the leaflets and the color of the anthers prior to anthesis. These are maintained even though the two species apparently grow together in Kumaun, Nepal,



Map 8. Distribution of *Zanthoxylum acanthopodium* DC.

Assam, and Yunnan. Perfect flowers were noted only in material from Sumatra where the unisexual condition seems to be lacking entirely. This may indicate that the population of that island is a relict, particularly since there appears to be a considerable geographic discontinuity with the unisexual material of the Asiatic mainland. Aside from this, however, the Sumatran material matches the Asian very closely.

Two collections from Szechuan Province, China (*Schneider 1353* and *Handel-Mazzetti 2524*), with dwarf leaves 2–3 cm. long and very short, compact inflorescences have been designated in error as *Zanthoxylum acanthopodium* var. *diminutum* (Rehd.) Reeder & Cheo, Jour. Arnold Arb. 32: 71. 1951. I have seen the holotype of *Z. dimorphophyllum* Hemsl. var. *diminutum* Rehd. (Jour. Arnold Arb. 22: 577. 1941) which clearly is most closely allied to *Z. dimorphophyllum*, a distinctive species restricted to China. This misjudgement by Reeder and Cheo apparently occurred because Rehder cited *Schneider 1353* as a paratype of *Z. dimorphophyllum* var. *diminutum*.

19. **Zanthoxylum armatum** DC. Prodr. 1: 727. 1824. Lectotype: *Lambert*, 1816, India, non *Z. armatum* (Thunb.) Druce, 1917.

Zanthoxylum alatum Roxb. Hort. Beng. 72. 1814, nomen nudum; Roxb. Fl. Ind. 3: 768. 1832. Lectotype: *Roxburgh Icones 1916*, cult. Bot. Gard. Calcutta.

Zanthoxylon planispinum Sieb. & Zucc. Abh. Akad. München 4 (2): 138. 1846. Type: *Siebold*, Japan.

Zanthoxylum alatum Roxb. var. *planispinum* (Sieb. & Zucc.) Rehd. & Wils. Pl. Wils. 2: 125. 1914.

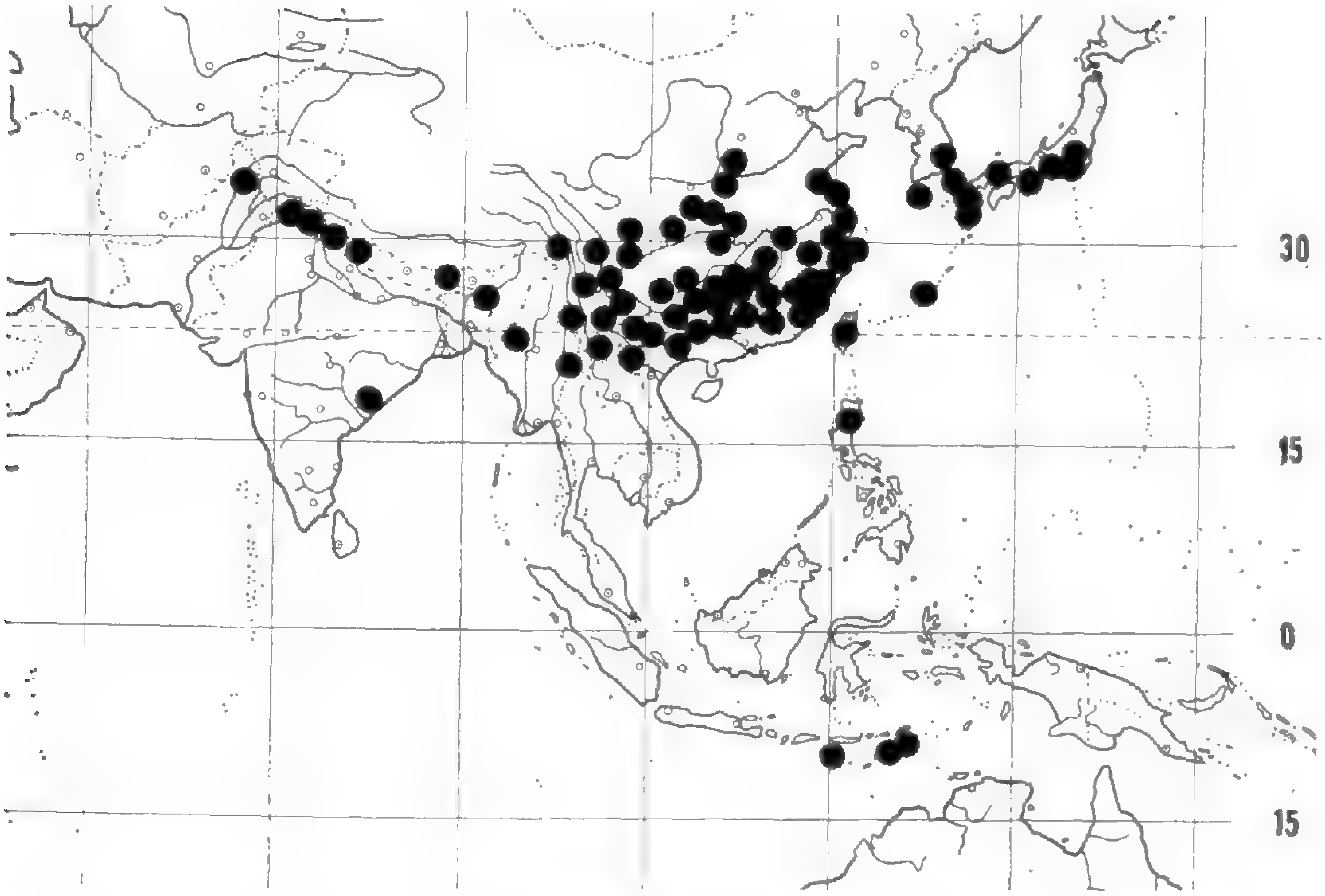
Scandent or erect shrubs or small trees to 6 m.; dioecious; apparently deciduous or evergreen; branchlets glabrous to short pubescent, generally armed, the prickles flattened, predominantly pseudostipular, to 2 cm. long. Leaves trifoliolate or imparipinnate, 5–23 cm. long; rachis glabrous, often with flattened prickles, narrowly to broadly winged (to 6 mm. on either side); petiolules obsolete to 3 mm. long; leaflets 1–5 pairs, opposite, chartaceous to subcoriaceous, glabrous or occasionally with a few hairs along the midrib below, often with flattened prickles along the midrib above and below, ovate to lanceolate, 1.5–13 cm. long, 0.5–4.7 cm. wide, base cuneate to acute, main veins generally faint, 7–15 on each side of the midrib, margins entire to glandular crenate with as many as 8 crenations per cm., apex acute to acuminate. Inflorescences terminal on short lateral branchlets and occasionally axillary, paniculate, 1–7 cm. long and generally about as wide. Staminate flowers about 2 mm. long; pedicels 0.2–1.5 mm. long; perianth segments 6–7, undifferentiated, uniseriate to irregularly biseriate, green to yellow, elliptic to ligulate, 0.3–1 mm. long, glabrous, stamens 4–6, 1–2 mm. long, anthers about 1 mm. long and yellow prior to anthesis; disc pulvinate, about 0.5 mm. high; rudimentary carpels none. Carpellate flowers about 2 mm. long; pedicels and perianth segments as in staminate flowers; rudimentary stamens none; disc pulvinate, 0.5–0.75 mm. high; gynoecium 1–3-carpellate, glabrous, about 1.5 mm. high, styles about 0.75 mm. long, divergent, articulating about 0.3 mm. below the globose stigma. Fruiting pedicels 1–2.5 mm. long; follicles generally reddish, subglobose, 4–5 mm. in diameter, single or in 2's or 3's, the undeveloped carpels caducous.

West Pakistan. Hazara (Abbottabad) District, Massar Reserve, Sirau Range, *Parker*, May, 1910 ♂ (A). **India.** PUNJAB: Kangra, Baijnath, *Koelz 4516* ♀ (US); Kulu Kulu, *Koelz 8315* ♀ (A), *10274* ♂ (A); Shahpur, Dharmsola Road, *Stewart 1823* ♀ (A). HIMACHAL PRADESH: Simla District, *Parker 3019* ♀ (A); Jaranda Range, between Sarahair & Gohoilhur, *Selhi*, July, 1953 ♀ (A). UTTAR PRADESH: near Mussoorie, *King*, 1869 ♀ (US); Dehra Dun, Siwalik & Jaunsar, *Singh 22* ♂ (US), May & June, 1912 ♂ & ♀ (A); Kumaun Division, *Strachey & Winterbottom 3* ♀ (GH), *4* ♀ (GH). ORISSA: Koraput District, near Pottangi, Sirimanda Parbat, *Mooney*, July 10, 1950 (A). ASSAM: Khasia & Jaintia Hills, *Bor 16083* ♂ (A), *Hooker f. & Thomson* ♀ (GH), *Koelz 22785* ♀ (MICH), *Ruse 73* ♂ (A). Without definite locality: *Lambert*, 1816 ♀ (G-DC — lectotype of *Zanthoxylum armatum*, not seen; A, photo.), *Thomson* ♀ (GH). **Nepal.** West Nepal, Doti District, Rikhar, *Ram 398* ♀ (A); without definite locality, *Ram 181* ♀ (A), *Wallich*, 1821 (A, photo.), *Wallich* ♀ (SING). **Sikkim.** *Hooker f.* ♀ (GH). **Burma.** Kalewa, *Dickason 6148* ♀ (A); Southern Shan State, *Khalil*, 1893 ♀ (A). **North Vietnam.** Chapa, *Petelot 5815* ♀ (A, SING). **Tibet.** Sikang Province, Dzer-nar, Tsa-wa-rung, *Wang 66378* ♀ (A). **China.** YUNNAN PROVINCE: Likiang City, *Ching 21062* ♀ (A); Tapintze, *Delavay 777* ♀ (A, photo. and fragment); NE. Likiang, between Min-ing and Hung-mun-kow, *Feng 2549* ♀ (A); W. Likiang, Kai-tze on Yangtze bank, *Feng 2647* ♀ (A); S. Chungtien, Chiao-tou on Yangtze bank, *Feng 3125* (A); Wen-shan-hsien, Maa-luh-tarng, *Feng 11245* ♀ (A); Mengtsz, *Henry 9366* ♀ (A, US), *9366A* [A (2 sheets, ♂ and ♀), US (♂)], *9366C* ♀ (A), *9366D* ♀ (A, US), *9366F* ♂ (A); Szemao, *Henry 11908* ♂ (A), *12249* ♀ (A, US); Kun-ming, Miao-kao-szu, Ta-pu-chi, *Ko 56310*

♀ (A); W of Mekong en route from Pingpo to Youngchang and Tengyueh, *Rock 6994* ♀ (A, US); Shweli River drainage basin & environs of Tengyueh, *Rock 8031* ♂ (A, US); zwischen Yunnanfu und Sah-ying-pan, *Schneider 281* (A); Talifu, *Schneider 2803* ♀ (A, GH, US); prope Yang Lin, *Schoch 351* ♀ (A, US); Kienshuei Hsien, *Tsai 53132* ♂ & ♀ (A); Shang-pa Hsien, *Tsai 54638* ♀ (A), *54984* ♀ (A); Ping-pien Hsien, *Tsai 55163* ♀ (A); Chenkang, near Feng-tai-szu, *Tsiang & Wang 16258* ♀ (A); Wei-si Hsien, Kang-pu, *Wang 64191* ♀ (A); Chen-kang Hsien, Wang *72187* ♀ (A); Fo-hai, *Wang 74490* ♀ (A); Che-li Hsien, Kuen-ger, *Wang 79257* ♀ (A); Saluen Valley, NW of Champutong, *Yu 19171* ♀ (A); without definite locality, *Forrest 7535* ♀ (A), *Schneider 3887* ♀ (A), *Tsai 57272* ♀ (A). Szechwan Province: Mt. Omei, *Chien 5565* ♂ (A), *Fang 3913* ♀ (A), *12666* ♀ (A), *Lee 2715* ♀ (US), *Liu 1032* ♀ (A), *1650* ♀ (A), *Wang 23192* ♀ (A), *Wilson 4769* ♂ (A), *Yu 254* ♀ (A), *325* ♂ (GH), *341* ♂ (A); Kuan Hsien, *Chien 5596* ♀ (A), *Fang 2026* ♀ (A), *Wang 20542* ♂ (A); Huili, *Handel-Mazzetti 248* ♀ (A); Mili Kingdom, Mili & Litang River Valley, near Mili Gomba, *Rock 16129* ♀ (A, US); Ningyuanfu, Lu-shan, *Smith 1790* ♀ (A); zwischen Mo-so-ying und Kung-mu-ying, *Schneider 645* ♀ (A); Yun-ching-hsien, *Sun 1287* ♀ (US); Mao Hsien, *Wang 21856* ♀ (A); Ping-shan Hsien, *Wang 22697* ♀ (A); Lo-shan Hsien, *Wang 23556C* ♀ (A); Wen Chuan Hsien, *Wilson 2693,* July, 1908 ♀ (A); He-chang Hsien, *Yu 1120* ♀ (A). Kweichow Province: Tsunyi Hsien, Liang Feng Yah, *Steward, Chiao & Cheo 34* ♀ (A, US); Ta Ho Yen, Fan Ching Shan, *Steward, Chiao & Cheo 696* ♀ (US); Tsingchen, Ju-long-san, *Teng 90201* ♂ (A). Kwangsi Province: Luchen, Tia Lian Shan, *Ching 5295* ♀ (A); E. Hin Yen, Bian Chen, *Ching 6710* ♀ (A, US); Hin Yen, Spring Cave, *Ching 6741* ♀ (A, US); Shuen-yuen, *Chung 81695* ♀ (A); Hing On District, Sai On Village, *Chung 83615* ♀ (A); Yang-so, Ching-o-ken, *Fung 21106* ♀ (A); Ling Yun District, *Lau 28557* ♀ (A); Ling Yun Hsien, Loh Hoh Tsuen, *Steward & Cheo 56* ♂ (A, SING); Yung Hsien, Ta Tseh Tsuen, *Steward & Cheo 795* ♀ (A, SING); Yung Hsien, Chang An, *Steward & Cheo 1188* ♀ (A); Mts. surrounding Pa Lau Village near Sui-luk, *Tsang 21871* ♂ (A); Ling-chuan District, Ling-chai-miao, Hai-yang Shan, *Tsang 27829* ♀ (A, US); Kwei-lin District, San-min Village, *Tsang 28021* ♀ (A, US); Nam Tanyuen, *Wang 40895* ♀ (A); without definite locality, *Wang 41127* ♀ (A). Kwangtung Province: Nan Shung, *Chun 5704* ♀ (A); Yim Na San, *Gressitt 1395* ♀ (A); Lung Tau Mt., *Kang, W. T. Tsang & U. K. Tsang CCC 12709* ♀ (US); North River Region, near Fung-wan, *Kang, W. T. Tsang & U. K. Tsang CCC 12857* ♀ (US); Sin-fung District, Hau Tong Shan, Fuk Lung Monastery, *Taam 757* ♀ (A); Jen-hua District, Man Chi Shan, Shek Pik Ha Village, *Tsang 26136* ♀ (A); Ying Tak District, Wan Tong Shan, *Tsui 302* ♀ (A, US); Yang Shan District, Yang Shan, *Tsui 458* ♀ (A, US), 665 ♀ (US). Hunan Province: Sinning Hsien, Ma-ling-tung, *Fan & Li 481* ♀ (A); Tschang-scha, *Handel-Mazzetti 2347* ♂ (A); Yi Chang District, Ping Tou Shan, Pai Mu Village, *Tsang 23406* ♂ (A, US); Wukang, Yun-shan, *Wang 15* ♂ (A). Hupeh Province: Yangtze-Hwaiho Divide on Hupeh-Honan border, Chikungshan, *Bailey,* June 29, 1917 (A); Ichang, *Chien NU 8034* ♀ (US), *Chun 3831* ♀ (US), *Tsung 3486* ♀ (A); Gran Gra Kon, *Ching 3560* ♀ (A); Patung Hsien, *Chow 349* ♀ (A); Enshih Hsien, *Chow,* June 14, 1934 ♀ (A); Kwan Ying Tong, *Chun 3686* ♀ (A), *NU 4028* ♀ (US); Liang-sun-yon, *Chun 3849* ♀ (A); Wuchang, Lokiashan, *Chung 9176* (A), *Sun 19* ♀ (A), *775* ♀ (A), *848* ♀ (A); U-tan Hsien, *Silvestri 4849* ♂ (A); Hoing-shan Hsien, *Wilson 138* [A (2 sheets, ♂ & ♀ and ♀), GH (♂ & ♀), US (♂ & ♀)]; Chang-to Hsien, *Wilson 2693,* April, 1907 [A (2 sheets, ♂ & ♀ and ♀), US (♀)]; without definite locality, *Henry 3584* ♀ (US), *7687* ♀ (A, GH), *Wilson 338* ♀ (US). Honan Province: Sung Hsien, Shih Tze Miao, *Hers 594* ♀ (A); Yungning, Tieh-lu-ping, *Hers 1001* ♀ (A). Kiangsi Province: Lu Shan, *Chiao NU 18767* ♀ (US); Nanchang, *Chung 10* ♀ (A); Kiennan District, Sai Hang Cheung, near Tung Lei, *Lau 4183* ♀ (US); Lungnan District, Oo Chi Shan, Lam Uk Tung Village, *Lau 4480* ♀ (A, US); Farr-yung, *Sing NU 7892* ♀ (A). Fukien Province: Foochow: Nantai Island, *Chang 4250* ♀ (A); Nanshan Monastery, *Chung 2802* ♀ (A, SING); Kushan, *Chung 8355* ♀ (A); Kuliang Hills, *Norton 1395* ♀ (US). Diong Loh Hsien, *Chung 1238* ♀ (A, SING); Diong Loh, Muoi Hua, on the seacoast, *Ging 13651* ♀ (A); Yeuping, Buong Kang, *Chung 3390* ♀ (A); N. Mountain, *Chung 8597* ♀ (A); Baekliang, *Ging 15596* ♀ (A), *15652* ♀ (A); without definite locality, *Dunn 845* ♀ (A). Chekiang Province: Shihpu, *Chiao NU 14139* ♀ (A, US), *NU 14152* ♀ (A, US); Sizchu, *Ching 1659* ♀ (A, GH, US); Tsing-tien, *Keng 56* ♀ (A); vicinity of Ningpo, *Macgregor, 1908* ♀ (A); Hangchow, *Tang & Hsia 79* ♀ (A); without definite locality, *Barchet 85* ♀ (US), *s.n.* ♀ (US). Anhwei Province: Tien Chu Shan, Chien Shan Hsien, *Fan & Li 115* ♀ (A); Chuchow, *Zee NU 1298* ♂ (US). Kiangsu Province: Nanking and vicinity, *Chen 8664* ♀ (A), *Merrill 11394* ♀ (A), *Steward NU 2169* ♀ (A), *Tso 1021* ♀ (A); Ih-shing, *Ching 4883* ♀ (A); Chiu-yong, *Ling NU 12192* ♀ (GH); Chankiang, Chin Shan, *Tso 254* ♀ (A); Ma An Shan, Quin Shan, *Tso 1633* ♀ (A). **Taiwan.** Maruyama, *Faurie 22* ♀ (A). **Korea.** Fusan, *Faurie 465* ♀ (A); Namtijoukak, *Taquet 820* ♀ (A); Hokeum, *Taquet 2707* ♀ (A); Nokan, *Taquet 2708* ♀ (A); Quelpart Island, *Faurie 1627* ♀ (A), *Wilson 9397* ♀ (A). **Japan.** Tsushima Island: *Wilford*, 1859 ♀ (GH). Honshu Island: Fuji san, *Faurie 2427* ♀ (A); Kasugayama, *Kume*, June 21, 1925 ♀ (A); Yokohama, *Maximowicz*, 1862 ♀ (GH, US); Musashi Province, Mt. Takao, *Mizushima TNSM 1080* ♀ (US), *11094* ♀ (A), *11437* (A); Mt. Setsuhiko, *Muroi 20* ♀ (A); Mt. Ruridera, *Muroi 914* ♀ (A); Owari Province, *Shiota 4462* ♀ (A); Kariyose-yama, *Suzuki 106* ♀ (US), *336–1* ♀ (A), *336–2* ♀ (A); Mt. Kogane, *Uno 2599* ♀ (A). Kyushu Island: Fukuoka, *Ichikawa 138* ♀ (A); Mt. Kirishima, *Tashiro*, September 23, 1917 ♀ (A); Kiushiu, Shiraishi, *Uno 2611* ♀ (A). Without definite locality: *Siebold* ♀ (M — isotype of *Zanthoxylum planispinum*, not seen; A, photo.). **Ryukyu Islands.** Kume-jima, *Amano 7074* (US). **Lesser Sunda Islands.** Soemba: Kanangar, *Iboet 559* ♀ (L). Timor: near Kapan, *Bloomborgon 3478* ♀ (A, L); en Ond. Z. midden Timor, *Steenis NIFS bb 17584* (A, L); Mt. Perdido, ascent of Ossu, *Steenis 18324* ♂ (L); Mt. Moetis, *DeVoogd 2283* ♀ (L); Kot Olim, *Walsh 252* ♀ (BM); without definite locality, *Forbes 3653* ♀ (BM, GH, L). **Philippines.** Luzon Island: Benguet Subprovince, *Loher 243* (K), *Merrill 774* ♀ (US), *Sinclair & Edano 9765* ♀ (SING). **Cultivated.** India: Calcutta, *Roxburgh Icones 1916*, drawn from a plant from northern India (K — lectotype of *Zanthoxylum alatum*, not seen; A, photo.). Japan: Fukuoka, *Ichikawa 247* ♀ (GH); Tokyo, *Mizushima TNSM 1398* ♀ (US), *Sargent*, August, 1892 ♀ (A).

Distribution. West Pakistan and northern India east to Japan and Taiwan; south only in the Philippines and Lesser Sunda Islands; in rain forests, thickets and, at higher elevations, often on open slopes and rock ledges; at elevations from 50–1750 meters in Malesia and up to 2400 meters in continental Asia. See MAP 9.

Illustrations. Huang, C. C., Acta Phytotax. Sinica **6** (1): *t. 3.* 1957, as *Zanthoxylum planispinum.* Liu, T. S., Illustrations of native and introduced plants of Taiwan **2**: *t. 730.* 1962, as *Z. planispinum.* Makino, T., Illustrated flora of Japan, 2nd. ed. *t. 1175.* 1940, as *Xanthoxylum*



MAP 9. Distribution of *Zanthoxylum armatum* DC.

planispinum; revised ed. *t. 1175.* 1949, as *Zanthoxylum alatum* var. *planispinum*; New illustrated flora of Japan *t. 1326.* 1961, as *Z. alatum* var. *planispinum*.

Occasionally cultivated as a hedge plant in China. The bark is pungent and several collectors noted that it is used to clean teeth. It also has been used, in China, to repel insects from furs. Indian collectors noted that the leaves, bark, and fruits were used in treatment of smallpox and cholera. Various parts of the plant are used to season food in China and India.

This is apparently the first use of the epithet *armatum* for this species since DeCandolle substituted it for Roxburgh's *alatum* in 1824. That *Zanthoxylum alatum* has so long been the accepted name may probably be accounted for by the fact that the DeCandolle name is listed as a misspelling in *Index Kewensis*. It is clear, however, that the spelling was intended since the Lambert collection (which is cited by DeCandolle) in the Prodromus Herbarium bears the annotation "*Zanthoxylum armatum* Roxb." in A. P. DeCandolle's handwriting. This collection is mounted on a sheet with a Wallich collection from Nepal and consists of two branchlets (both collected in 1816). I have chosen the larger of the two, in the lower right corner of the sheet, as the lectotype.

"*Zanthoxylum planispinum*" differs in having fewer leaflets — generally 3–5, compared to 5–11 in typical Indian material of *Zanthoxylum armatum*. The number of leaflets is extremely variable in this species, especially in specimens from China.

EXCLUDED SPECIES

The following species, described from Malesia, apparently belong to genera other than *Zanthoxylum.*

FAGARA DECANDRA Blanco, Fl. Filip. (ed. 1) 66. 1837 = **Buchanania arborescens** Bl. (Anacardiaceae) according to Merrill, Enum. Philip. Fl. Pl. **2:** 465. 1923.

FAGARA GLABRA Bl. Cat. Gew. Buitenz. 40. 1823 = **Evodia glabra** (Bl.) Bl. Bijdr. Natuurk. Wetens. 245. 1825.

FAGARA MONTANA (Bl.) Engl. Nat. Pflanzenfam. III **4:** 118. 1896 = **Turpinia montana** (Bl.) Kurz (Staphyleaceae), Jour. Asiat. Soc. Beng. **44:** 182. 1875.

?FAGARA PAPUANA Laut. Nova Guinea **8** (4): 823. 1912 = **Melicope papuana** (Laut.) Laut. in Engl. Bot. Jahrb. **55:** 241. 1918.

FAGARA SERRULATA (Bl.) Engl. Nat. Pflanzenfam. III. **4:** 118. 1896 = **Turpinia montana** (Bl.) Kurz (Staphyleaceae) according to Koorders, Exk. Fl. Java **2:** 528. 1912.

FAGARA TRIPHYLLA Lam. Encycl. **2:** 447. 1788 = **Melicope triphylla** (Lam.) Merr. Philip. Jour. Sci. Bot. **7:** 375. 1912.

ZANTHOXYLON ACCEDENS (Bl.) Miq. Fl. Ind. Bat. **1** (2): 671. 1859 (based on *Evodia accedens* Bl. Bijdr. Natuurk. Wetens. 246. 1825) = **Evodia accedens** Bl. according to Miquel, Ann. Mus. Lugd.-Bat. **3:** 242. 1867.

ZANTHOXYLON AROMATICUM (Bl.) Miq. Fl. Ind. Bat. **1** (2): 670. 1859 (based on *Evodia aromatica* Bl. Bijdr. Natuurk. Wetens. 246. 1825) = **Evodia glabra** (Bl.) Bl. according to Miquel, Ann. Mus. Lugd.-Bat. **3:** 243. 1867.

ZANTHOXYLON EUNEURON Miq. Fl. Ind. Bat. (suppl.) 532. 1860 = **Evodia euneura** (Miq.) Miq. Ann. Mus. Lugd.-Bat. **3:** 243. 1867.

ZANTHOXYLON MACROPHYLLUM (Bl.) Miq. Fl. Ind. Bat. **1** (2): 670. 1859 (based on *Evodia macrophylla* Bl. Bijdr. Natuurk. Wetens. 246. 1825) = **Evodia accedens** Bl. according to Miquel, Ann. Mus. Lugd.-Bat. **3:** 242. 1867.

ZANTHOXYLON MARAMBONG Miq. Fl. Ind. Bat. (suppl.) 533. 1860 = **Evodia marambong** (Miq.) Miq. Ann. Mus. Lugd.-Bat. **3:** 244. 1867.

ZANTHOXYLUM HORSFIELDII Turcz. Bull. Soc. Nat. Moscou **36** (2): 597. 1863. I have not seen type material but from the description — the leaves are described as opposite — it is clearly not a *Zanthoxylum.*

ZANTHOXYLUM JAVANICUM (Bl.) Walp. Repert. Bot. Syst. **1:** 519. 1842 = **Picrasma javanica** Bl. (Simaroubaceae) Bijdr. Natuurk. Wetens. 248. 1825.

ZANTHOXYLUM LAMARKIANUM Cham. Linnaea **5:** 58. 1830 = **Melicope triphylla** (Lam.) Merr. according to Merrill, Philip. Jour. Sci. Bot. **7:** 375. 1912.

ZANTHOXYLUM LATIFOLIUM (DC.) G. Don, Gen. Syst. **1:** 804. 1831 (based on *Ampacus latifolia* Rumph. Herb. Amb. **2:** 186. 1741) = **Evodia latifolia** DC. according to Merrill, Interpret. Rumph. Herb. Amb. 289. 1917.

ZANTHOXYLUM LUCIDUM Miq. Fl. Ind. Bat. (suppl.) 532. 1860 = **Evodia lucida** (Miq.) Miq. Ann. Mus. Lugd.-Bat. **3:** 244. 1867.

ZANTHOXYLUM MONTANUM Bl. Bijdr. Natuurk. Wetens. 248. 1825 = **Turpinia montana** (Bl.) Kurz (Staphyleaceae), Jour. Asiat. Soc. Beng. **44:** 182. 1875.

ZANTHOXYLUM RHIZINOIDES Bl. Bijdr. Natuurk. Wetens. 248. 1825. According to the description the leaves are simple and the calyx 3-parted, a combination not found in any of the known Malesian species of *Zanthoxylum.* Miquel (Fl. Ind. Bat. **1** (2): 669. 1859) and Koorders (Exk. Fl. Java **2:** 418. 1912) also express the opinion that the generic designation may be incorrect.

ZANTHOXYLUM ROXBURGHIANUM Cham. Linnaea **5:** 58. 1830 = **Evodia lunur-ankenda** (Gaertn.) Merr. according to Merrill, Philip. Jour. Sci. Bot. **7:** 378. 1912.

ZANTHOXYLUM RUMPHIANUM Cham. Linnaea **5:** 58. 1830 = **Evodia latifolia** DC. according to Merrill, Interpret. Rumph. Herb. Amb. 289. 1917.

ZANTHOXYLUM SERRULATUM Bl. Bijdr. Natuurk. Wetens. 249. 1825 = **Turpinia montana** (Bl.) Kurz (Staphyleaceae) according to Koorders, Exk. Fl. Java **2:** 528. 1912.

ZANTHOXYLUM TIMORIENSE Span. Linnaea **15:** 185. 1841. I have not seen type material of this but from the description it seems closer to *Toddalia* than *Zanthoxylum*.

ZANTHOXYLUM? TRIPLINERVE Turcz. Bull. Soc. Nat. Moscou **36:** 597. 1863. Reported from "Insula Lucon, in provincia North Hows." The leaves are described as simple, so this is probably not a *Zanthoxylum*. Perkins, Frag. Fl. Philip. 161. 1905, states that the type has not been accounted for and that the locality given is not clearly a Philippine one.

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A KARYOLOGICAL SURVEY OF LONICERA, I

LILY RÜDENBERG AND PETER S. GREEN *

RECORDS OF PLANT CHROMOSOME NUMBERS have been accumulating for about sixty years and counts now exist for a very great number of genera (Darlington & Wylie, 1955) of the families of temperate regions at least. For tropical, and for temperate plants from the southern hemisphere, the need for random investigations still exists, but for plants from the northern hemisphere the stage has been reached where the further counting of chromosomes will be most effective and useful when carried out either in conjunction with an intensive biosystematic investigation, or where an attempt is made to deal as comprehensively as possible with a whole genus or similar taxon. The present survey is just such an attempt.

The genus *Lonicera* was selected, not because of its particular cytological interest, but because the Arnold Arboretum possesses an unusually rich collection of its species, cultivars, and other taxa. Furthermore, and this was also significant in the selection of *Lonicera*, the late Alfred Rehder, whose revision of the genus (1903) is still the latest comprehensive account to be published, worked at the Arboretum and studied, handled, collected, and identified many of the accessions still in cultivation there.

CYTOLOGICAL MATERIALS AND METHODS

For chromosome counts at meiosis, and for the observation of chromosome pairing and possible abnormalities of division, buds containing microsporocytes undergoing meiosis were fixed in 3:1 parts of absolute alcohol: glacial acetic acid, and kept under refrigeration. The fixative was changed to 70 per cent alcohol for long storage in cases where material had to be preserved for some time before examination. The pollen mother cells were smeared on a slide in a drop of aceto-carmine, and after slight overstaining, a drop of Hoyer's medium (Alexopoulos & Beneke, 1952) was added, gently mixed with the stain, then covered by the cover slip. When carefully warmed and pressed, the slides were satisfactory for counting and have since kept well.

For mitotic counts, root-tip meristems and dividing cells in young leaves were generally used. This material was treated for one hour in a 0.002 Mol. aqueous solution of oxyquinoline (Tjio & Levan, 1950), and then fixed for ca. 12 hours in 3:1 alcohol; acetic acid. After hydrolysis in N HCl at 60°C for 25 or 15 minutes, for root-tips and leaves respectively, the material was washed in distilled water and sometimes hardened for 10

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* In this survey, the cytological investigations have been carried out by one of us (L.R.), and the complementary taxonomy by the other (P.S.G.).

minutes in 70 per cent alcohol. Best results were obtained by staining in leuco-basic fuchsin, followed by maceration on a slide in diluted aceto-carmine. After judicial warming and pressing the slides were made permanent, using the freezing technique of Conger and Fairchild (1953).

Because all counts have been documented, no meristematic cells from the roots of germinating seeds have been used in this investigation. Cuttings of the plants to be studied were rooted instead, and we wish to record our thanks to Alfred J. Fordham for carrying this out.

However, favorably squashed cells from anther walls sometimes permitted the counting of diploid cells while the PMC's were still in early prophase; tapetal cells were excluded because of the frequency of irregular or polyploid divisions that occur in them.

All observations were made with a Zeiss phase microscope.

DOCUMENTATION

Chromosome numbers without adequate documentation are almost without value, and in this investigation herbarium specimens have been preserved from each of the individual plants which has been examined cytologically. Either new material has been collected or the plants have been checked against specimens which already exist in the herbarium, i.e., specimens taken from the same plants on previous occasions. In the Arnold Arboretum each individual plant has its own accession number, and is recorded on a detailed map, so that even if labels are lost or transposed, the various plants can be accurately and positively related, each to its accession number and, through this number, to its identification. An attempt has also been made to ensure that the specimen growing under a particular number is the original plant and not, either the understock of a weak graft, or a bird-sown seedling, perhaps of hybrid origin and exhibiting heterosis, which has taken over and smothered the individual growing in that position in the first instance. This has happened, or was found to be taking place, in one or two cases, and *Lonicera tatarica* and its hybrid, *L.* × *bella*, are particular culprits.

Documentation of the counts recorded below has been achieved by the preservation of herbarium specimens in the herbarium of cultivated plants at Jamaica Plain (AAH) and by the recording of chromosome numbers on the Arboretum's master set of accession cards. The collectors who have been responsible for making specimens during the two years since this survey commenced are: Sandra Callaway, Madelon Dodd, Susan Kreps, Theodore R. Dudley, and Peter S. Green, whose invaluable help is gratefully acknowledged. Prior to this investigation, specimens of the honeysuckles growing in the Arboretum had been collected by Caroline K. Allen, C. E. Kobuski, F. P. Metcalfe, E. J. Palmer, A. Rehder, and C. S. Sargent and, where their collections coincide with plants which have been examined cytologically, their specimens are cited below. In a few cases the collector's name is not actually given on the herbarium sheet, but, from the handwriting or date, it is assumed that the collector was A. Rehder. The oldest specimen cited is one collected by C. S. Sargent in 1891 from the same clone of *Lonicera korolkowii* from which the actual type specimen was originally gathered. The clone is still living and its chromosomes have been counted.

In addition to the specimens incorporated in the herbarium at Jamaica Plain, duplicate collections have been made in a large number of cases. These are being distributed to other botanic gardens and arboreta, by way of exchange. In every case great care has been taken to check the identity of the plants reported upon, including a critical investigation of the complex of hybrids surrounding *Lonicera tatarica* and its allies (Green, 1966).

CYTOLOGY

The basic chromosome number of the genus *Lonicera* is nine and the majority of the species studied are diploid. Polyploidy seems to have played a minor role in speciation within the genus, for only a limited number of wild species are known to be tetraploids or hexaploids. However, some varieties and cultivars of diploid species have been found to be polyploid, but not among the many cultivars of Section LONICERA. No triploids have been reported for the genus, although *L. henryi* has been observed as being hexaploid, a condition also recorded for *L. periclymenum* by Gadella and Kliphuis (1963).

The chromosomes are small (from about 1.5μ), but preliminary karyogram studies of mitotic chromosomes show that the nine chromosomes have a definite morphology which enables the observer to distinguish some of them individually, while others are present in small groups of similar size and shape. Also, the overall size of the complement differs between some species, and investigations are in progress to determine whether or not these differences in size or morphology coincide with the infrageneric groupings proposed by Rehder. The results will be recorded in a subsequent paper but, as a preliminary observation, it may be said that in at least one group of related species a pair of chromosomes may be found which bear satellites consistently, while in others they are apparently absent. The satellites may be seen in FIGURE 1 which shows a root tip cell of *Lonicera morrowii* at metaphase and exemplifies the typical morphology of the complement found in *L. tatarica* and its related species.

As indicated below, hybridization between *Lonicera tatarica* and related species takes place very readily, yet, in these cases, no disturbance in the pairing relationships of the chromosomes was generally observed at meiosis, and the hybrids produced are abundantly fertile.

NOMENCLATURE

No attempt has been made to revise the genus *Lonicera*. The nomenclature and sequence of species is that of Rehder (1903), and as modified by him many years later (1949). If chromosome counts have already been recorded under names not recognized in these two publications, the names

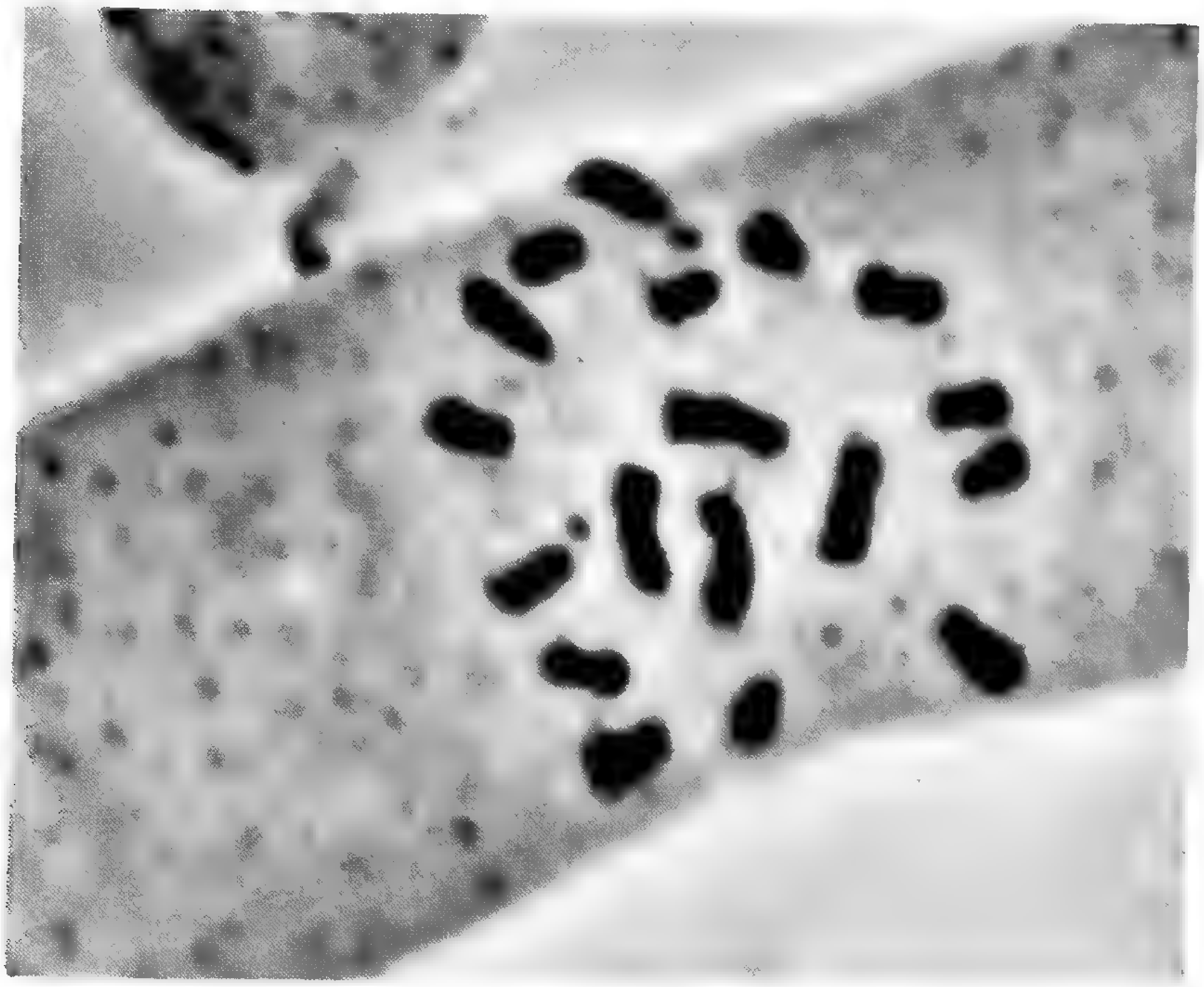

FIGURE 1. Mitotic metaphase in root-tip cell of *Lonicera morrowii* (AA 1283–65); note metacentric chromosomes and a pair with satellites.

are cited in parentheses, otherwise no attempt is made to provide synonymy.

Backcrossed hybrids are listed under their respective hybrid epithet, which is taken to cover all hybrids between the species involved, whether intermediate or backcrossed to either parent.

In accordance with the present International Code of Botanical Nomenclature the names of infrageneric divisions have been modified slightly from those of Rehder. The correct names at subgeneric and sectional level are discussed by Ferguson (1966) whose treatment is followed.

In the case of *Lonicera modesta* and its variety *lushanensis*, both described by Rehder, an examination of the material now available in the herbaria of wild (A) and cultivated (AAH) plants shows that some reassessment and differentiation is required. Rehder based the differences between the type variety and var. *lushanensis* upon pubescence and leaf-shape. Leaf-shape now appears to be valueless for distinguishing the two, and degree of pubescence is never a very reliable character alone. However, one of the two plants of this species whose chromosomes have been examined in this investigation (both raised from seed sent in 1936 from Lushan Botanic Garden in China) has proved to be diploid and the other tetraploid. The former has densely pubescent stems, and leaves with scattered hairs all over the lower leaf surface, and most nearly approaches the type variety, whereas, the latter has stems glabrous or with only a few hairs, and the leaves almost glabrous. The amount of flowering material available is still inadequate but it is suspected that more reliable morphological characters for separating these varieties will be found in the flower size (1 or 2 mm. larger in var. *modesta*) and flower color (a touch of anthocyanin in var. *lushanensis*). It is interesting to note that the sizes of mitotic chromosomes in the polyploid var. *lushanensis* were observed to be smaller than those in var. *modesta*.

HYBRIDS

Spontaneous hybridization in the wild is not common in *Lonicera*, even though it can take place very readily under cultivation when certain species which otherwise occupy separate geographical areas are brought together. Fertile progeny and frequent backcrossing may result, and it appears that in parts of the genus, at least, speciation has not been dependent upon the existence of genetical or cytological barriers.

Hybridization has been particularly prevalent in three groups: Section LONICERA and Subsections CYPHEOLAE (Raf.) Rehd. and EUCAPRIFOLIUM (Spach) Rehd. of Subgenus CAPRIFOLIUM. Hybridization between different subsections has frequently taken place, with the production of fertile offspring, and it would seem that they cannot be natural groups.

In order that the possible effects of hybridization on the behavior of the chromosomes could be borne in mind during this investigation, the following list of hybrids has been compiled from the literature. The parental species are arranged alphabetically, and the sequence is that of the first parental species in the classifications of Rehder (1903, 1949).

HYBRIDS OF WILD ORIGIN

LONICERA ALTAICA Pall. × L. PALLASII Ledeb. Recorded by Pojarkova (1958, p. 490); although these species are separated by her in separate series, Ser. *Stenanthae* Pojark. and Ser. *Pallasianae* Pojark. respectively, they are treated by Rehder (1903) as parts of the one variable species, *L. caerulea* L. Pojarkova reports that this hybrid, which is intermediate, occurs near either parent, and also in European USSR, beyond the range of *L. altaica*.

LONICERA HYPOLEUCA Decne. × L. QUINQUELOCULARIS Hardw. According to Wendelbo (1965, p. 15) one of the herbarium sheets of *Lace 4024* collected at Ziaret, West Pakistan, is a possible hybrid of these two species. If this is so, it is very interesting as representing a cross between species of different sections, Sect. ISIKA and Sect. LONICERA respectively.

LONICERA FLORIBUNDA Boiss. & Buhse × L. NUMMULARIIFOLIA Jaub. & Spach. Recorded by Pojarkova (1958, p. 552) from the western part of Kopet Dag in Turkmenistan; the second parent cited above is treated by Rehder (1903) as a synonym of the wide ranging *L. arborea* Boiss.

LONICERA NUMMULARIIFOLIA Jaub. & Spach × L. QUINQUELOCULARIS Hardw. Wendelbo (1965, p. 15) suggests that the mixture of characters in some plants, where the ranges of distribution of these two species overlap, indicates that introgressive hybridization may be taking place.

LONICERA NIGRA L. × L. XYLOSTEUM L., or L. × HELVETICA Brügger (Jahresber. Naturf. Ges. Graubündens II. **29**: 95. 1885 [Mitt. Neue & Krit. Formen der Bünder- & Nachbar-Floren, 50. 1886], Rehder 1903, p.

204). However, Rehder (1927, p. 832) suggests that this "supposed hybrid" is probably a form of *L. xylosteum.*

LONICERA CAPRIFOLIUM L. × L. ETRUSCA Santi, or L. × AMERICANA (Mill.) K. Koch, Wochenschr. Gärtnerei & Pflanzenkunde **10**: 279. 1867 (*L.* × *italica* (Schmidt) Tausch, Flora, **21**: 735. 1838).

LONICERA CAPRIFOLIUM L. × L. IMPLEXA Ait. (Rehder 1903, p. 211).

LONICERA CAPRIFOLIUM L. × L. PERICLYMENUM L. (Rehder 1903, p. 212).

LONICERA ETRUSCA Santi × L. IMPLEXA Ait. (Rehder 1903, p. 212).

HYBRIDS OF ORIGIN IN CULTIVATION

LONICERA FRAGRANTISSIMA Lindl. & Paxt. × L. STANDISHII Jacques, or L. × PURPUSII Rehder, Jour. Arnold Arb. **4**: 252. 1923.

LONICERA ALPIGENA L. × L. LEDEBOURII Eschsch., or L. × PROPINQUA Zabel, Gartenflora **38**: 580. 1889.

LONICERA TATARICA L. × L. XYLOSTEUM L., or L. × XYLOSTEOIDES Tausch, Flora **21**: 736. 1838 (*L.* × *coerulescens* Dippel, Handb. Laubh. **1**: 233. 1889; Zabel, Mitt. Deutsch. Dendr. Ges. **1901**: 94. 1901).

LONICERA KOROLKOWII Stapf × L. TATARICA L., or L. × AMOENA Zabel, Mitt. Deutsch. Dendr. Ges. **1901**: 96. 1901.

LONICERA RUPRECHTIANA Regel × L. TATARICA L., or L. × NOTHA Zabel, Gartenflora **38**: 525. 1889.

LONICERA MORROWII A. Gray × L. TATARICA L., or L. × BELLA Zabel, *loc. cit.*

LONICERA MORROWII A. Gray × L. RUPRECHTIANA Regel, or L. × MUSCAVIENSIS Rehder, Gartenflora **42**: 100. 1893.

LONICERA MORROWII A. Gray × L. × XYLOSTEOIDES Tausch, or L. × MINUTIFLORA Zabel, Gartenflora **38**: 523. 1889.

LONICERA × BELLA Zabel × L. RUPRECHTIANA Regel, or L. × MUENDENIENSIS Rehder, Gartenflora **42**: 102. 1893.

LONICERA RUPRECHTIANA Regel × L. × XYLOSTEOIDES Tausch, or L. × SALICIFOLIA Dieck ex Zabel, Gartenflora **38**: 524. 1889.

LONICERA CHRYSANTHA Turcz. × L. RUPRECHTIANA Regel, or L. × GIBBIFLORA Dippel, Handb. Laubh. **1**: 237. 1889, non Maximowicz.

LONICERA CHRYSANTHA Turcz. × L. XYLOSTEUM L., or L. × PSEUDOCHRYSANTHA Braun ex Rehder, Man. Cult. Trees & Shrubs 833. 1927.

LONICERA DEFLEXICALYX Batal. × L. QUINQUELOCULARIS Hardw., or L. × VILMORINII Rehder, Mitt. Deutsch. Dendr. Ges. **1912**: 194. 1913.

LONICERA FLAVA Sims × L. HIRSUTA Eaton (Rehder 1903, p. 211).

LONICERA FLAVA Sims × L. PROLIFERA (Kirchn.) Rehd. (Zabel in Beissner, Schelle & Zabel, Handb. Laubh.-Benenn. 450. 1903, as *L. flava* × *sullivantii*).

LONICERA HIRSUTA Eaton × L. PROLIFERA (Kirchn.) Rehd., or L. × SARGENTII Rehder, Jour. Arnold Arb. **7**: 37. 1926.

LONICERA HIRSUTA Eaton × L. SEMPERVIRENS L., or L. × BROWNII (Regel) Carr. Fl. des Serres, **11**: 123. 1856.

LONICERA ETRUSCA Santi × L. IMPLEXA Ait. (Rehder 1903, p. 212).

LONICERA ETRUSCA Santi × L. PERICLYMENUM L. (Mottet, Revue Hort. **1900**: 695. 1900).

LONICERA DIOICA L. × L. FLAVA Sims (Rehder 1903, p. 211).

LONICERA DIOICA L. × L. HIRSUTA Eaton (Zabel in Beissner, Schelle & Zabel, Handb. Laub.-Benenn. 450. 1903 as *L. glauca* Hill × *L. hirsuta* Eaton).

LONICERA DIOICA L. × L. PROLIFERA (Kirchn.) Rehd., or L. × EPSOMIENSIS Hort. ex K. Koch, Dendr. **2**(1): 12. 1872, *nomen.*

LONICERA SEMPERVIRENS L. × L. TRAGOPHYLLA Hemsl., or L. × TELLMANNIANA Magyar ex Späth, Hauptverz. no. 241. 1927–28 (not seen).

LONICERA CAPRIFOLIUM L. × L. ETRUSCA Santi, or L. × AMERICANA K. Koch, Wochenschr. Gärtnerei & Pflanzenkunde **10**: 279. 1867. (*L.* × *italica* Tausch, Flora **21**: 725. 1838).

LONICERA × AMERICANA K. KOCH × L. SEMPERVIRENS L., or L. × HECKROTTII Hort. ex Rehder, in Bailey, Cycl. Amer. Hort. **2**: 942. 1900.

In addition, it has been suggested that *Lonicera myrtilloides* Purpus (Mitt. Deutsch. Dendr. Ges. **1907**: 255. 1908) might be a hybrid of *L. angustifolium* Wall. × *L. myrtillus* Hook. f. & Thoms. (see Rehder, Man. Cult. Trees & Shrubs, 822. 1927) and that *L. micranthoides* Zabel (Mitt. Deutsch. Dendr. Ges. **1901**: 94. 1901) might be the hybrid *L. nigra* L. × *L. tatarica* L. (see Rehder, Annual Rep. Missouri Bot. Gard. **14**: 204. 1903), but *L. micranthoides* was later treated by Rehder (1927, p. 833) as a probable synonym of *L.* × *xylosteoides* Tausch. Likewise, and in the same works, Rehder treated *L. segreziensis* Lavallé ex Dippel (Handb. Laubh. 1: 221. 1889) first as a hybrid of *L. quinquelocularis* Hardw. and *L. xylosteum* L. and later as a probable synonym of *L. xylosteum* L. Rehder (1927, p. 832) also has a note that the supposed hybrid of *L. nigra* L. × *L. orientalis* Lam. is probably a form of *L.* × *xylosteoides.*

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Table. CHROMOSOME NUMBERS IN LONICERA

SPECIES	*n*	*2n*	AUTHORITY	DOCUMENTATION AND COLLECTOR	GENERAL DISTRIBUTION
Subgenus LONICERA (Subgen. *Chamaecerasus* (L.) Rehd.)					
Sect. ISOXYLOSTEUM Rehd.					
Subsect. MICROSTYLAE Rehd.					
L. myrtillus [a]		(18) [b]	7 [c]		Pakistan to Sikkim Himalaya
var. *depressa*		(36)	7		Himalaya
L. myrtilloides	(9)	(18)	6		? hybrid, *L. angustifolia* × *myrtillus*
L. tomentella		(18)	7		Sikkim
L. thibetica	(9, 18)		2		Western China
		(18, 36)	7		
L. rupicola		(18)	7		Himalaya
L. syringantha		(18)	7		Northwest China
Sect. ISIKA (Adans.) Rehd.					
Subsect. PURPURASCENTES Rehd.					
L. microphylla Willd. ex Roem. & Schult.	(18)		2		Central Asia
		(36)	7		
	18		12*	AA[d] 1008–52-B, *Dodd & Dudley*, 12 May 1965	
L. canadensis		(18)	7		Northeast America
L. tenuipes Nakai	(18)		2		Japan
		(18)	7		
	18	36	12*	AA 11147 (*Wilson 6713*, Japan, 1914), *Dudley & Dodd*, 10 May 1965	
Subsect. CAERULEAE Rehd.					
L. caerulea L.	(9, 18)		2		Eurasia
	(9)	(18)	6		
		(18, 36)	7		
	18	36	12*	AA 215–35, *Kreps*, 25 May 1964	
	18	36	12*	AA 126–37, *Kreps*, 25 May 1964	
	18	36	12*	AA 20–43, *Kreps*, 25 May 1964	
	18		12*	AA 808–51, *Kobuski & Metcalfe*, 9 May 1930 (as AA 5300)	
var. *edulis* Regel	18		12*	AA 6714, *Rehder*, 7 May 1924	Siberia and Tibet
f. *graciliflora* Dippel		18	12*	AA 15727, *Palmer*, 7 May 1921	Turkestan

[a] Species names cited without authority are those used in undocumented counts; the sequence of species is that of Rehder (1903, 1949).

[b] Numbers in parentheses are those given for undocumented counts.

[c] 1, Vilmorin & Simonet (1927); 2, Sax & Kribs (1930); 3, Matsuura & Suto (1935); 4, Sugiura (1936); 5, Hagerup (1941); 6, Poucques (1949); 7, Janaki Ammal & Saunders (1952); 8, Chuang et al. (1962); 9, Sorsa (1962); 10, Sorsa (1963); 11, Gadella & Kliphuis (1963); 12, Rüdenberg (1964); 12*, Rüdenberg, reported here for the first time.

[d] AA in the Documentation column indicates that the number which follows is an Arnold Arboretum accession number.

SPECIES	*n*	*2n*	AUTHORITY	DOCUMENTATION AND COLLECTOR	GENERAL DISTRIBUTION
Subsect. PILEATAE Rehd.					
L. gymnochlamydea Hemsl.	9		12*	AA 15032-A (*Wilson 266*, W. Hupeh, 1908), *Green*, 27 May 1965	Western China
L. pileata	(9)	(18)	6		Central and western China
L. nitida		(18)	7		Western China
	(9)		6		
		(18)	7		
Subsect. VESICARIAE (Komar.) Rehd.					
L. vesicaria		(18)	7		Korea
L. ferdinandii Franch.	(9)		2		Northern China
	(9)	(18)	6		
	9		12*	AA 18360, *Palmer*, 9 Sept. 1936	
var. *induta* Rehd.	9	18	12*	AA 18169-A (*Purdom 554*, Shensi, 1910), *Dodd & Callaway*, 28 May 1965	
var. *leycesterioides* (Graebn.) Rehd.		18	12*	AA 5902-A, *Kreps*, 25 May 1964	Northern China
Subsect. CHLAMYDOCARPI Jaub. & Spach					
L. iberica M. Bieb.	9		12*	AA 955–1, *Rehder* ?, 29 June 1916	Transcaucasia and Persia
Subsect. FRAGRANTISSIMAE Rehd.					
L. standishii Jacques	(9)	(18)	6		China
		(18)	7		
	9		12*	AA 15118–2, *Kobuski*, 30 Apr. 1932	
f. *lancifolia* Rehd.	9	18	12*	AA 6669–1–A, *Palmer*, 31 Mar. 1936 (as AA 6669–1)	
cv. Rosea	9		12*	AA 448–43, *Green*, 30 Apr. 1964	
L. fragrantissima Lindl. & Paxt.	(9)		2		Eastern China
	(9)	(18)	6		
		(18)	7		
	9	18	12, 12*	AA 2245–1, *Rehder*, 1 Dec. 1927	
L. × *purpusii* Rehd.	9	18	12*	AA 397–36–B, *Green*, 30 Apr. 1964	Cultivation
		18	12*	AA 486–43, *Green*, 30 Apr. 1964	
Subsect. BRACTEATAE (Hk. f. & Thoms.) Rehd.					
L. altmannii	(9)		2		Turkestan
		(18)	7		
L. praeflorens Batal.		18	12*	AA 10103-B (*Wilson 8441*, Japan, 1917), *Green*, 30 Apr. 1964	Manchuria, Korea and Japan
		18	12*	AA 657–26, *Palmer*, 25 Mar. 1938	
L. hispida	(9)	(18)	6		Turkestan
var. *bracteata*		(18)	7		Himalaya to western China

SPECIES	*n*	2*n*	AUTHORITY	DOCUMENTATION AND COLLECTOR	GENERAL DISTRIBUTION
L. chaetocarpa		(18)	7		Western China
Subsect. PYRENAICAE Rehd.					
L. pyrenaica		(18)	7		Pyrenees
Subsect. DISTEGIAE (Raf.) Rehd.					
L. involucrata (Richards.) Banks ex Spreng.		(18)	7		Northern America and south into Rocky Mts.
	9	18	12*	AA 16–44, *Palmer*, 16 July 1936 (as AA *221–33*)	
f. *humilis*		(18)	7		Colorado
f. *serotina* Koehne	9		12*	AA 817–61, *Green*, 21 June 1965	Colorado
L. ledebourii		(18)	7		California
Subsect. ALPIGENAE Rehd.					
L. alpigena	(9)	(18)	6		Central and southern European Mts.
		(36)	7		
f. *nana* (Carr.) Zabel		18	12*	AA 14994–1, *Allen*, 13 Aug. 1927	
L. glehnii	(9)		6		Japan
		(36)	7		
L. webbiana Wall. ex DC.	18	36	12*	AA 1735–4-B, *Green*, 20 May 1965	Afghanistan to the Himalaya
L. tatsiensis	(9)		6		Western China
Subsect. RHODANTHAE (Maxim.) Rehd.					
L. maximowiczii		(18)	7		Saghalin and Korea
L. subsessilis Rehd.		18	12	AA 11732 (*Wilson 9275*, Korea, 1917), *Rehder*, 29 May 1923	Korea
L. orientalis Lam.	(9)		2		Asia Minor to western China
		(18)	7		
		18	12*	AA 417–38-A, *Dudley*, 4 June 1965	
	9		12*	AA 798–41, *Dudley*, 4 June 1965	
var. *caucasica* (Pallas) Rehd.		(18)	7		Transcaucasia, Asia Minor and Persia
	9		12*	AA 15098–1, *Rehder* ?, 23 June 1916	
	9		12*	AA 364–29, *Palmer*, 6 June 1940	
var. *longifolia*		(18)	7		? Kamchatka
L. discolor		(18)	7		Afghanistan to Kashmir
L. modesta Rehd.	9	18	12*	AA 24–36, *Green*, 31 May 1965	Central China
var. *lushanensis* Rehd.	18	36	12*	AA 765–36, *Green*, 31 May 1965	Central China
L. nervosa		(18)	7		Northwest China
L. nigra L.	(9)	(18)	6		Central and southern European Mts.
		18	12*	AA 771–35, *Kreps*, 25 May 1964	

SPECIES	*n*	2*n*	AUTHORITY	DOCUMENTATION AND COLLECTOR	GENERAL DISTRIBUTION
Section LONICERA (Sect. *Coeloxylosteum* Rehd.)					
Subsect. TATARICAE Rehd.					
L. tatarica L.	(9)		2		Eastern Europe to Turkestan
	(9)	(18)	6		
		(18)	7		
		18	12*	AA 328–39-B, *Kreps*, 28 May 1964	
		18	12*	AA 287–41-A, *Kreps*, 25 May 1964	
	9		12*	AA 289–41-A, *Green*, 31 May 1965	
	9	18	12*	AA 112–42, *Green*, 20 May 1965	
	9	18	12*	AA 305–51, *Kreps*, 26 May 1964	
f. *angustifolia* (Kirchn.) Rehd.	9		12*	AA 4035, *Rehder* ?, 7 June 1916	
f. *elegans* Carr.	9		12*	AA 326–39, *Kreps*, 25 May 1964	
f. *fenzlii* Dippel	9		12*	AA 306–32, *Rehder* ?, 21 May & 12 July 1915 (as AA 7337)	
f. *grandiflora*		(18)	7		
f. *latifolia*		(18)	7		
f. *leroyana* (Zabel) Rehd.	9	18	12*	AA 566–57-A, *Kreps*, 25 May 1964	
f. *lutea* (Loud.) Rehd.	9		12*	AA 18293, *Kobuski & Metcalfe*, 9 May 1930	
f. *punicea*		(18)	7		
f. *rosea* Regel		(18)	7		
	9		12*	AA 7335, *Rehder*, 21 May & 12 July 1915	
f. *roseo-alba* Regel		18	12*	AA 15132, *Rehder*, 21 May & 12 July 1915	
f. *sibirica* (Pers.) Rehd.		(18)	7		
		18	12*	AA 3771–1-A, *Kobuski & Metcalfe*, 9 May 1930 (as AA 3771–1)	
	9		12*	AA 716–45-A, *Kreps*, 26 May 1964	
f. *virginalis* Jaeger	9		12*	AA 199–53, *Kreps*, 25 May 1964	
cv. Arnold Red	9		12*	AA 243–49 (Type clone), *Kreps*, 25 May 1964	
cv. Hack's Red		18	12*	AA 475–56, *Kreps*, 25 May 1964	
cv. Morden Orange	9		12*	AA 306–58, *Kreps*, 25 May 1964	
cv. Sheridan Red	9		12*	AA 476–56, *Kreps*, 25 May 1964	
var.	9		12*	AA 791–49, *Kreps*, 25 May 1964	
cv. (unnamed dwarf)		18	12*	AA 304–58, *Kreps*, 25 May 1964	
	9	18	12*	AA 302–59, *Green*, 20 May 1965	

SPECIES	*n*	2*n*	AUTHORITY	DOCUMENTATION AND COLLECTOR	GENERAL DISTRIBUTION
L. × *xylosteoides* Tausch	9		12*	AA 5406, *Palmer*, 7 July 1936	Cultivation
L. floribunda Boiss. & Buhse	18		12*	AA 341–44, *Kreps*, 1 June 1964	Northern Persia
L. korolkowii Stapf.	(9)		2		Turkestan, Afghanistan and Pakistan
		(18)	7		
	9	18	12*	AA 976–6-A (Type clone), *Sargent*, 31 May 1891 (as AA 976), and *Dudley*, 10 July 1965	
	9	18	12*	AA 10083-B, *Dudley*, 10 June 1965	
var. *aurora* Koehne		18	12	AA 20444, *Palmer*, 8 Sept. 1936	
var. *floribunda* Nicholson	9		12*	AA 10083–2-A, *Palmer*, 27 May 1936	
L. × *amoena* Zabel		(18)	7		Cultivation
(backcross to *L. tatarica*)	9		12*	AA 818–35, *Green*, 26 May 1965	
		18	12*	AA 181–44-B, *Kreps*, 25 May 1964	
var. *arnoldiana* Rehd.	9	18	12*	AA 180–44-A, *Kreps*, 25 May 1964	
f. *alba* Zabel	9		12*	AA 793–49-A & B, *Kreps*, 25 May 1964	
Subsect. OCHRANTHAE (Zabel) Rehd.					
L. ruprechtiana Regel	(9)	(18)	6		Manchuria to northern China
		(18)	7		
	9		12*	AA 15111, *Rehder*, 19 May 1910	
var. *calvescens* Rehd.		(18)	7		
	9		12*	AA 15112, *Kobuski & Metcalfe*, 16 May 1930	
f. *xanthocarpa* (Zabel) Zabel	9		12*	AA 15109–1-B, *Rehder*, 6 Aug. 1919 (as AA 15109–1)	
	9	18	12*	AA352–62, *Kreps*, 25 May 1964	
L. × *notha* Zabel	9		12*	AA 15134-A, *Green*, 24 May 1965	Cultivation
(backcross to *L. tatarica*)	9		12*	AA 572–1-A, *Palmer*, 15 May & 7 July 1936 (as AA 572)	
f. *alba* Zabel	9		12*	AA 969–4, *Palmer*, 7 July 1936	
	9		12*	AA 348–32, *Kobuski & Metcalfe*, 16 May 1930 (as AA 3744–1)	
f. *carnea* Dippel	9		12*	AA 5403, *Kobuski & Metcalfe*, 16 May 1930	
f. *carneo-rosea* Zabel	9		12*	AA 3743, *Palmer*, 7 July 1936	

SPECIES	*n*	2*n*	AUTHORITY	DOCUMENTATION AND COLLECTOR	GENERAL DISTRIBUTION
L. × *salicifolia* (Dippel) Zabel		18	12*	AA 898–49, *Green*, 25 May 1965	Cultivation
L. demissa	(9)		2		Japan
L. morrowii A. Gray	(9)		4		Japan
	(9)	(18)	6		
		(18)	7		
	9	18	12*	AA 1283–65, *Kobuski & Metcalfe*, 14 May 1930 (as AA 15086)	
f. *xanthocarpa* Nash ex Teuscher	9		12*	AA 18902-A, *Kreps*, 25 May 1964	
L. × *bella* Zabel	(9)	(18)	6		Cultivation
	9		12*	AA 10087-A, *Green*, 27 May 1965	
		18	12	AA 22206, *Palmer*, 17 May & 8 Aug. 1936	
(backcross to *L. morrowii*)	9		12*	AA 181–38-B, *Green*, 20 May 1965	
	9	18	12*	AA 48–42-A & B, *Kreps*, 25 May 1964	
(backcross to *L. morrowii*)		18	12*	AA 600–58, *Green*, 24 May 1965	
f. *atrorosea* (Zabel) Rehd.	9		12*	AA 346–32, *Kobuski & Metcalfe*, 16 May 1930 (as AA 6290)	

SPECIES	*n*	2*n*	AUTHORITY	DOCUMENTATION AND COLLECTOR	GENERAL DISTRIBUTION
f. *candida* (Zabel) Rehd.	9	18	12*	AA 3475, *Palmer*, 18 May 1938	
		18	12*	AA 3475–1, *Palmer*, 15 May & 7 July 1936	
f. *rosea* (Zabel) Rehd.	9		12*	AA 22843, *Green*, 31 May 1965	
cv. Dropmore	9		12*	AA 727–49, *Green*, 26 May 1965	
L. × *minutiflora* Zabel	(9)	(18)	6		Cultivation
	9		12*	AA 2–32-B, *Palmer*, 15 May 1936 (as AA 2–32)	
cv. Valencia		18	12*	AA 290–41-B, *Green*, 31 May 1965	
L. × *muendeniensis* Rehd.		(18)	7		Cultivation
	9		12*	AA 4996, *Rehder*, 27 May 1916	
(possible backcross to *L. morrowii*)	9		12*	AA 15110, *Green*, 20 May 1965	
	9		12*	AA 23152-A, *Green*, 21 July 1965	
	9	18	12*	AA 795–49-A & B, *Kreps*, 25 May 1964	
f. *xanthocarpa* Hort.	9		12*	AA 188–36-A, *Kreps*, 25 May 1964	
L. × *muscaviensis* Rehd.	9	18	12*	AA 11822, *Kobuski & Metcalfe*, 14 May 1930	Cultivation
		18	12*	AA 355–53, *Green*, 22 May 1965	

SPECIES	*n*	2*n*	AUTHORITY	DOCUMENTATION AND COLLECTOR	GENERAL DISTRIBUTION
L. xylosteum L.	(9)	(18)	6		Europe to Altai Mts.
	(9)		9		
		(18)	7, 10		
	9		12*	AA 15142-A, *Dodd & Callaway*, 25 June 1965	
	9		12*	AA 422–39, *Green*, 31 May 1965	
	9		12*	AA 57–42, *Kreps*, 26 May 1964	
		18	12*	AA 556–51, *Kreps*, 26 May 1964	
	9		12*	AA 281–53, *Green*, 31 May 1965	
f. *mollis*		(18)	7		
cv. Claveyi		18	12*	AA 349–55, *Kreps*, 25 May 1964	
L. chrysantha Turcz.	(9)		2		Northeast Asia and Japan
		(18)	7		
	9		12*	AA 61–29, *Kreps*, 25 May 1964	
var. *longipes* Maxim.		(18)	7		Northwest China
		18	12*	AA 21592 (*Rock*, S. W. Kansu, 1925), *Kreps*, 25 May 1964	
	9		12*	AA 558–51, *Kreps*, 26 May 1964	
f. *latifolia* Korshinsky	9		12*	AA 15008–2, *Kobuski & Allen*, 17 May 1933	
f. *regeliana* (Kirchn.) Rehd.		18	12*	AA 15015, *Palmer*, 7 May 1921	
f. *villosa* Hort. ex Rehd.	9		12*	AA 5297-B, *Green*, 21 July 1965	
L. × *pseudo-chrysantha*		(18)	7		Cultivation
L. koehneana Rehd.		(18)	7		Western China
	9		12*	AA 5976, *Palmer*, 10 July 1936	
	9	18	12*	AA 15043 (*Wilson 93a*, W. Hupeh, 1907) *Rehder* ?, 29 May 1913	
L. maackii (Rupr.) Maxim.	(9)		2		Manchuria and China
	(9)	(18)	6		
		(18)	7		
	9		12*	AA 15047, *Kobuski & Metcalfe*, 2 June 1930	
	9		12*	AA 1026–37-A, *Green*, 21 July 1965	
f. *erubescens*		(18)	7		
f. *podocarpa* Franch. ex Rehd.		18	12*	AA 10085-B, *Kreps*, 25 May 1964	China
L. deflexicalyx Batal.		(18)	7		Western China
		18	12*	AA 6674 (*Wilson 4179*, Szechuan, 1910), *Rehder*, 3 June 1918	
L. × *vilmorinii* Rehd.	9	18	12*	AA 4801-2-B, *Green*, 21 June 1965	Cultivation

Species	*n*	2*n*	Authority	Documentation and Collector	General Distribution
L. trichosantha		(18)	7		Western China
f. *acutiuscula* Rehd.		18	12	AA 15106–1, *Palmer*, 19 May & 18 Sept. 1936	
L. prostrata	(9)		2		Western China
L. quinquelocularis	(9)		2		Afghanistan to the Himalaya
	(9)	(18)	6		
f. *translucens* (Carr.) Zabel	9		12*	AA 5966–2, *Rehder*, 22 Sept. 1932	
	9		12*	AA 27–33, *Palmer*, 18 June 1940	
Sect. NINTOOA (Sweet) Maxim.					
Subsect. BREVIFLORAE Rehd.					
L. alseuosmoides	(18)		1, 2		Western China
		(36)	7		
var. "coriacea"[e]		(54)	7		
L. henryi Hemsl.	(27)		2		Western China
		(54)	7		
		54	12*	AA 5968-A (*Wilson 254*, W. Hupeh, 1907), *Green*, 3 Nov. 1965	
Subsect. LONGIFLORAE Rehd.					
L. biflora		(18)	7		Southern Europe and northeastern Africa
L. affinis var. *pubescens*	(8)		8	? *Chuang* & *Liu*, TIC 4945 [not seen]	China and Japan
L. japonica	(9)		2		Eastern Asia
		(18)	7		
L. hildebrandiana		(18)	7		Burma and southwestern China
Subgenus CAPRIFOLIUM (Adans.) Dippel (Subgen. *Periclymenum* (Mill.) Rehd.)					
Subsect. PHENIANTHI (Raf.) Rehd.					
L. sempervirens L.	(9)	(18)	6		Eastern and central North America
		(18)	3		
		36	12*	AA 771–57-B, *Dodd & Callaway*, 4 June 1965	
cv. Dreer's Everblooming	18		12*	AA 745–60, *Dudley*, 30 July 1964	
cv. Magnifica	18		12*	AA 543–61, *Dudley*, 30 July 1964	
L. × *tellmanniana* Magyar ex Späth		(ca. 45)	7		Cultivation
Subsect. CYPHEOLAE (Raf.) Rehd.					
L. yunnanensis		(18)	7		Southwestern China
L. dioica L.	(9)		2		Eastern North America
		18	12*	AA 130–49, *Kreps*, 1 June 1964	
L. prolifera	(9)		2		Central North America
		(18)	7		

[e] No such variety has been traced, it is suspected that this may have been an error for *L. henryi* Hemsl. var. *subcoriacea* Rehd.

SPECIES	*n*	2*n*	AUTHORITY	DOCUMENTATION AND COLLECTOR	GENERAL DISTRIBUTION
L. flava Sims	9		12*	*C. E. Wood, Jr. 8919,* Walker Co., Georgia (A); AA 557–59, a clonal propagation from this collection	Eastern North America
		18	12*	*C. E. Wood, Jr. 8963,* DeKalb Co., Alabama (A); AA 556–59, a clonal propagation from this collection, *Green,* 31 May 1965	
Subsect. EUCAPRIFOLIA (Spach) Rehd.					
L. implexa		(18)	7		Mediterranean
L. caprifolium	(9)	(18)	6		Europe and western Asia
		(18)	7		
L. × *americana* (Mill.) K. Koch		(18)	7		Cultivation
	9		12*	AA 18–43-B, *Dodd & Callaway,* 4 June 1965	
L. stabiana	(9)		1		Italy
L. splendida		(18)	7		Spain
L. etrusca Santi		(18)	7		Mediterranean
	9	18	12*	AA 231–46, *Dodd & Callaway,* 4 June 1965	
L. periclymenum L.	(18?)		5		Europe, western Asia and northern Africa
	(18)	(36)	6		
		(18, 36)	7		
		54	11	*Gadella & Kliphuis 534, 623, & 715* (U) [not seen]	
f. *belgica*		(36)	7		
cv. Wisleyensis		(36)	7		
		Unidentified			
Lonicera sp.	(36)		3		

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ANATOMY OF THE PALM RHAPIS EXCELSA
II. RHIZOME [1]

P. B. TOMLINSON AND MARTIN H. ZIMMERMANN

THE PALM *Rhapis excelsa* develops horizontal, subterranean rhizomes which bear only non-assimilating scales. This kind of axis may be contrasted with that of some other palms like *Nypa* or *Sabal minor* in which the foliage leaves are borne directly by the underground stem. Scale-leaf bearing rhizomes of the *Rhapis* type are relatively rare in the Palmae (Tomlinson, 1961) although common in other monocotyledonous orders (e.g., Scitamineae, Liliiflorae).

Anatomical comparison of the scale-leaf bearing rhizome with the aërial axis which bears the assimilating foliage is of considerable interest because the two types are morphologically equivalent but their development must be quite different from a nutritional point of view. The present paper is an account of the vascular structure of the mature rhizome. The development of the two types of axes will be described in a later paper in this series.

Palms show two major growth forms. In one kind the vegetative axis is unbranched, producing solitary columnar stems, as in the coconut, in the other it is caespitose by the production of axillary vegetative axes, as in the date. Branching of the second type is always restricted to the base of the parent axis for simple adaptive reasons which are well known (Tomlinson, 1964). Normally these basal suckers rapidly turn erect. The first leaves produced by lateral branches are reduced to scales, but there is a rapid transition to normal assimilating foliage leaves as the branch assumes a vertical position. Thus the construction of the parent axis is repeated and by further branching of all axes a tufted and congested sympodial system results. *Rhapis* represents a growth form in which mutual competition of successive segments of the sympodium is eliminated by long-continued horizontal growth of the branch before it turns erect (FIG. 1A). The rhizome in *Rhapis* is essentially the early stage of sucker development which has become much protracted. In some ways it is a "persistently juvenile" stage of axis development.

MORPHOLOGY OF THE RHAPIS RHIZOME

Axillary shoots which grow out as rhizomes appear in the seedling [2] of *Rhapis*. After a variable period of horizontal growth the rhizome apex turns

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[1] Research on the anatomy of palms by P. B. Tomlinson is supported by National Science Foundation Grant GB 2991.

[2] Seedling morphology and anatomy will be described in a subsequent paper.

erect and there is a rapid period of transitional growth leading to the establishment of an erect leafy shoot. Features of the construction and growth of rhizome segments are shown in FIGS. 1 and 2. In the transitional period of growth the axis is somewhat swollen (FIGS. 2B, C, D, 1B) and successive leaves are elaborated so that a transition between the scale leaves of the rhizome (FIG. 1C) and the foliage leaves of the aërial stem occurs (FIGS. 1D-F). Transitional leaves show a gradual development of the blade which may be initially either compound or simple depending on the vigor of the shoot. Only compound leaves are illustrated in FIG. 1D-F. This transitional sequence clearly illustrates that the scale leaf is morphologically equivalent to the base of the adult foliage leaf.

The sympodium is continued by new rhizomes originating as buds in the axils of scale or transitional leaves at the base of the newly-erect shoot

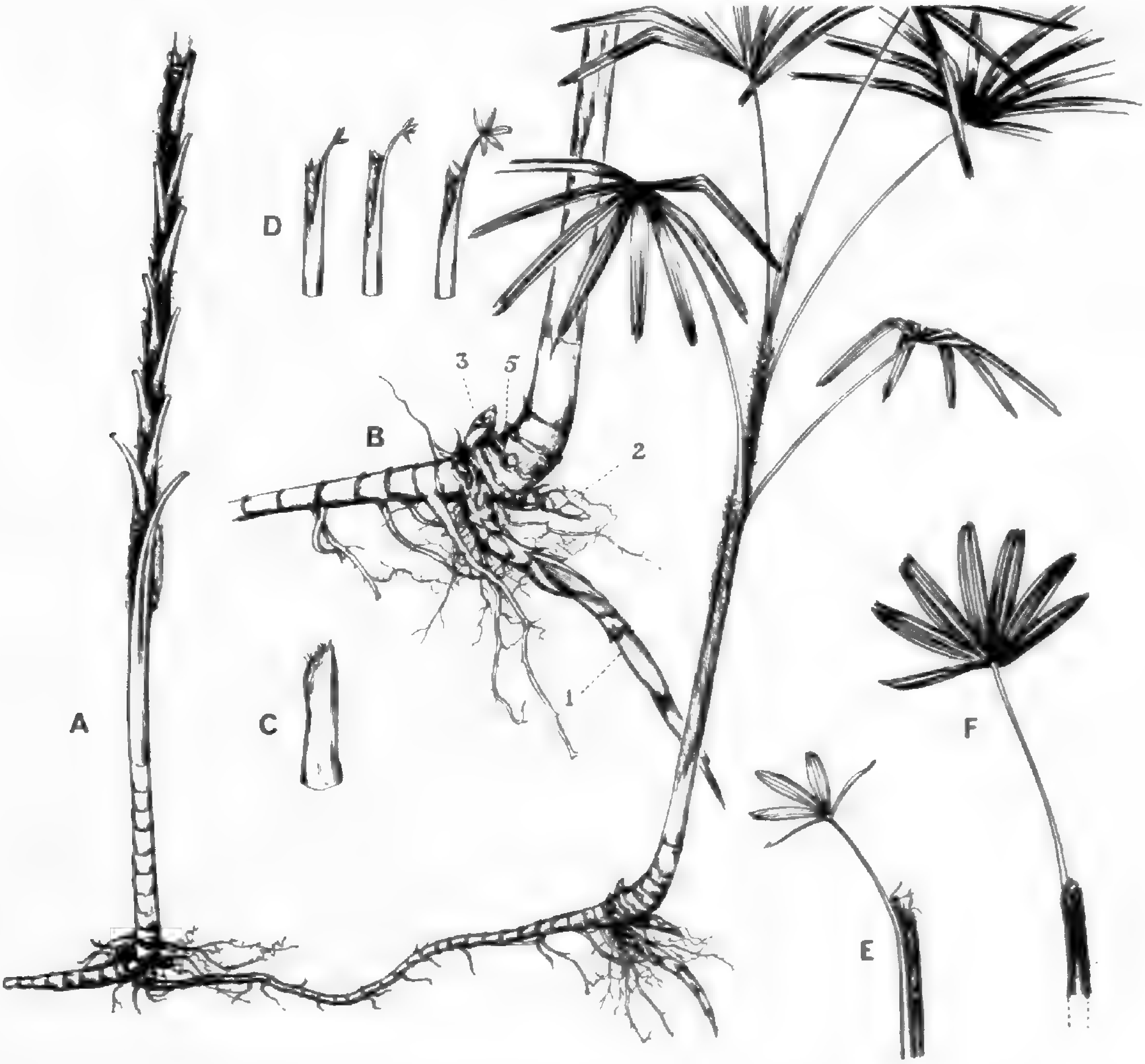

FIGURE 1. Relation of aërial to underground axes in *Rhapis excelsa*. A. One segment of sympodium, foliage leaves removed from aërial shoot at left. × 1/8. B. Base of right-hand aërial shoot of FIG. 1A, all but distal leaves removed. × 1/4. Numbers 1–5 refer to renewal shoots of successive age, youngest distal, oldest proximal, number 4 is on the remote side of the axis. C. Scale leaf from rhizome. × 1/2. D–F. Successive leaves from transitional sequence at base of erect shoot, × 1/4, showing gradual development of blade. Adult foliage leaves have blades 4–5 times wider than that of leaf illustrated in FIG. 1F.

(FIG. 2D). Several buds may grow out, in the order of their age (FIG. 1B) and in this way the sympodium multiplies. With frequent production of laterals sympodia may become very complex (FIG. 2E). Clonal spread of *Rhapis* under favorable conditions is therefore rapid. Erection of rhizome

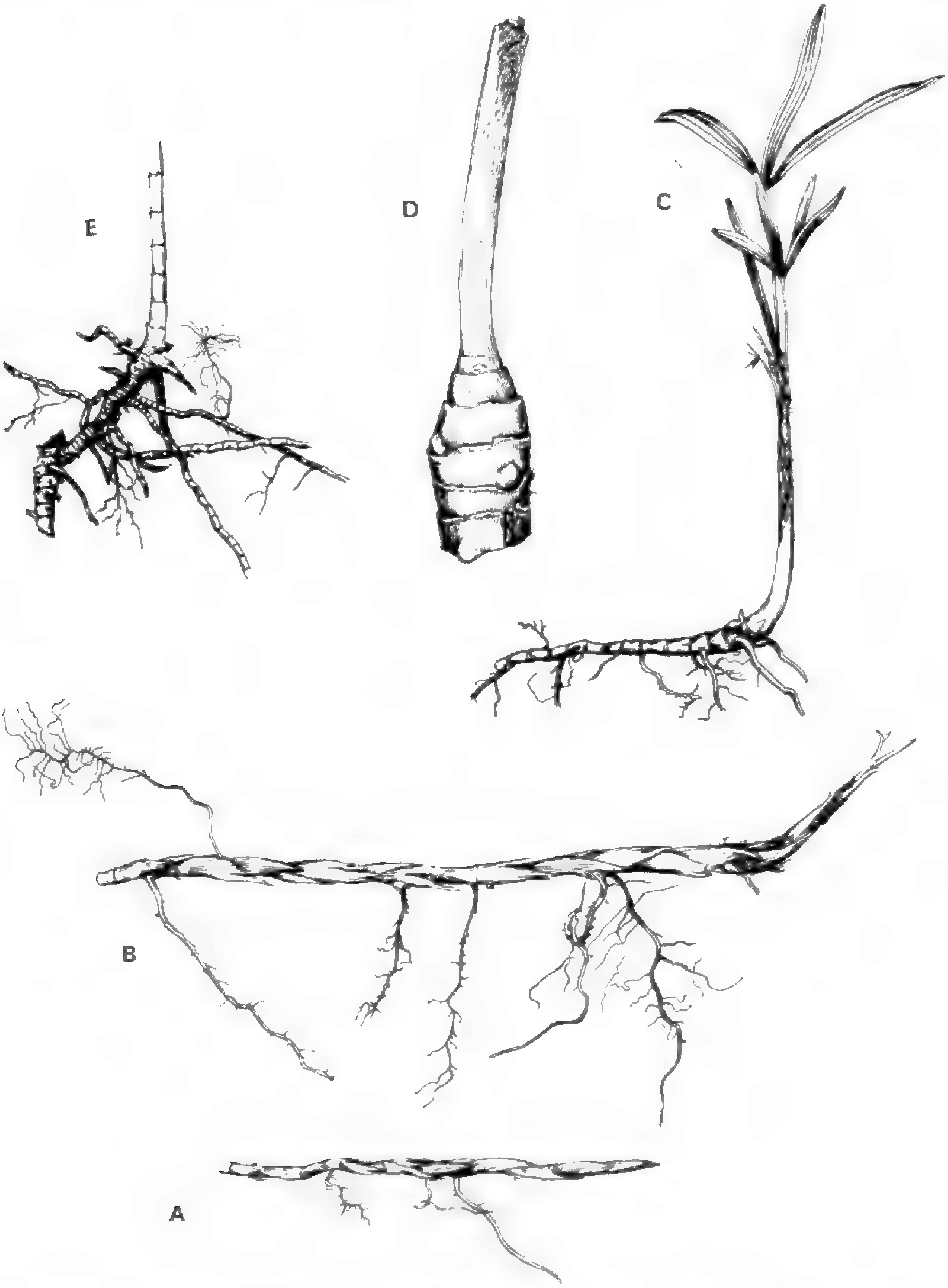

FIGURE 2. Development of rhizome system in *Rhapis excelsa*. A. Apex of underground creeping rhizome, × 1/4. B. Apex of rhizome becoming erect; transitional type of foliage initiated, × 1/4. C. Later stage, transitional leaves with well-developed blades, × 1/6. D. Base of erect shoot at a stage of development corresponding to FIG. 2C; leaves removed to show buds of renewal shoots, × 1/2. E. Old, much-branched rhizome complex, × 1/8.

apices and the morphological responses it induces seem independent of the season in South Florida since all stages of development can be found at any time of year.

Horizontal, underground parts of the rhizome, with which this article is concerned, may be up to 1 meter long and 1 to 1.5 cm. in diameter; the apex is protected by the rigid overlapping scales (FIG. 2A). Scales, like the foliage leaves of the aërial stem, are arranged in a 2/5 phyllotactic spiral. Each originates as a closed tube with a narrow distal opening which is widened by enlargement of enclosed organs (FIG. 1C). Internodes are 1.5 to 2 cm. long in older parts of the rhizome. The covering of scale leaves is retained for a long time (FIG. 2B). Very old rhizomes still bear the fibrous remains of decayed scales. Neither buds nor their vestiges are associated with scale leaves; they are restricted to the transition region where the rhizome turns erect (FIG. 2D). Roots are borne all around the rhizome at irregular intervals. We have not recorded this quantitatively but it seems to us that root insertions are associated (a) with each other and (b) less obviously, with the nodes. Root production is also vigorous on the swollen regions at the junction of successive sympodium segments. Rhizomes are always colorless and non-assimilating.

MATERIALS AND METHODS

Rhizome segments used in this investigation are all from specimens cultivated at Fairchild Tropical Garden. Sequential sections 30–50 μ thick were cut at 0.5 mm. intervals, stained and mounted by procedures previously described (Zimmermann & Tomlinson, 1965). In order to clarify the vascular system, starch was eliminated from the tissue by immersing sections for 5 to 10 minutes in 50 per cent hydrochloric acid prior to washing and bleaching. For details of nodal anatomy a continuous series of sections from a short length of rhizome was prepared.

Cinematographic analysis was carried out with the drawing method described before (Zimmermann & Tomlinson, 1965) as well as with the optical shuttle (Zimmermann & Tomlinson, 1966). The optical shuttle was also very useful in making quantitative plots of single vascular bundles of the types illustrated in FIG. 4.

In addition to microscopic analysis we have studied the rhizome structure extensively by macro-cinematography of cut surfaces on the microtome. A special clamp for the 'Reichert' sliding microtome was designed and constructed which allows continuous advance of long specimens. Such motion picture sequences give an excellent over-all view of the vascular system.

GENERAL RHIZOME ANATOMY OF RHAPIS

An over-all view of a transverse section of the rhizome is given in FIG. 3.

Rhizome 1–1.5 cm. in diameter, divided into cortex 1–1.5 mm., central

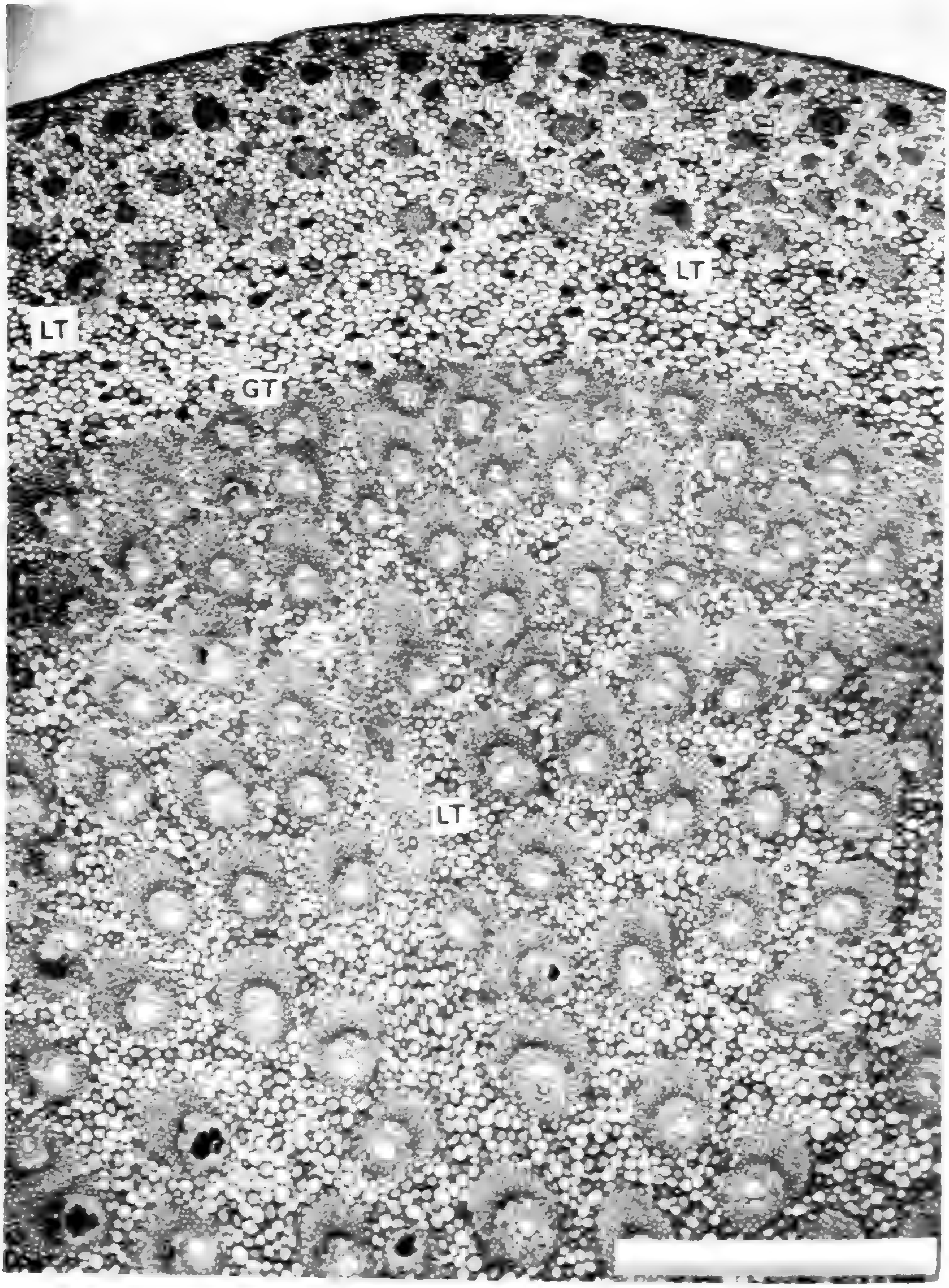

FIGURE 3. *Rhapis excelsa*, transverse section of rhizome. Major leaf trace (LT) to next node above level of section shown in center of figure; two minor leaf traces (LT) to same node shown in cortex. Peripheral girdling traces (GT) are ultimate endings of root traces. Black deposits in lower left-hand corner are tannins. Scale equals 1 mm.

cylinder 8–14 mm. wide. Epidermis uniform, cells elongated, rectangular in surface view with transverse end walls or frequently somewhat spindle-shaped with oblique end walls. Outer epidermal wall thickened, uniformly cutinized.

occasional cells with pronounced pitted thick secondary walls becoming lignified. Stomata not infrequent, resembling those of aërial stem but without chloroplasts and presumably non-functional. Periderm not developed except locally around wounds and leaf scars by ligno-suberisation of ground parenchyma accompanied by divisions of "etagen" type.

Cortex with 3–4 outermost layers of narrow cells with truncate end walls; walls thickened and becoming ligno-suberized to form a narrow hypodermal sclerotic layer interrupted below stomata by loose, wide unlignified cells continuous with middle cortex. Middle and inner cortical ground parenchyma with a well-developed intercellular space system, cells frequently becoming slightly thickened and prominently pitted with age. Cortex (FIG. 6), apart from inconspicuous transient leaf traces, including a series of purely fibrous strands, peripheral strands usually narrower than central; largest fibrous strands (up to 120 μ wide) including a narrow central strand of vascular tissue, often only phloem. Innermost cortical layers usually free of fibrous bundles.

Central cylinder not delimited from cortex by endodermis or other specialized layer, but by abrupt transition to narrow compact ground parenchyma with slightly thickened walls and zone of narrow, somewhat congested peripheral vascular bundles. Compact peripheral zone only interrupted by parenchyma at exit of leaf traces to form distinct "leaftrace gaps" (FIG. 6). Central vascular bundles wider, more diffuse. Central ground parenchyma very uniform, cells somewhat wider and looser than those at periphery. Individual vascular bundles of central cylinder more or less completely sheathed by fibrous tissue, but fibers least well developed around xylem. Fibers narrowest and most heavily lignified next to phloem. Peripheral vascular bundles somewhat more fibrous than central, but difference much less pronounced than in aërial stem. Vascular tissues including usually one wide metaxylem vessel and often protoxylem in varying amounts (see below). Phloem strand narrow, uniform, never with a distinct median sclerotic isthmus as is common in bundles of aërial stem. Metaxylem vessel elements average 60 μ wide, 1–1.5 mm. long with oblique or slightly oblique scalariformly perforated end walls with 6–10 thickening bars. Sieve-tubes average 15 μ wide with compound sieve-plates on slightly oblique end walls. Starch abundant in ground parenchyma except for narrow starch-free zone in outer cortex; grains either solitary, more or less spherical or more usually compound, angular. Tannin abundant as dark-brown deposits in otherwise unmodified parenchyma cells in all parts. Vascular tissues commonly occluded by tanniniferous deposits giving a strong positive lignin reaction with phloroglucinol and concentrated HCl; tannin occlusions not especially restricted to traces to old leaves. Stegmata (silica cells) only observed next to cortical fibrous bundles. Raphide sacs not observed.

In summary, the general anatomy of the rhizome, as seen in a single transverse section, differs from the aërial stem as follows: relatively greater development of cortex and cortical fibrous system; central and peripheral vascular bundles of central cylinder less conspicuously different; less obvious variation in the numbers of metaxylem elements.

COURSE OF VASCULAR BUNDLES IN THE RHIZOME

Central system. In spite of frequent root insertions the over-all course of vascular bundles in the *Rhapis* rhizome remains quite clear. It resembles

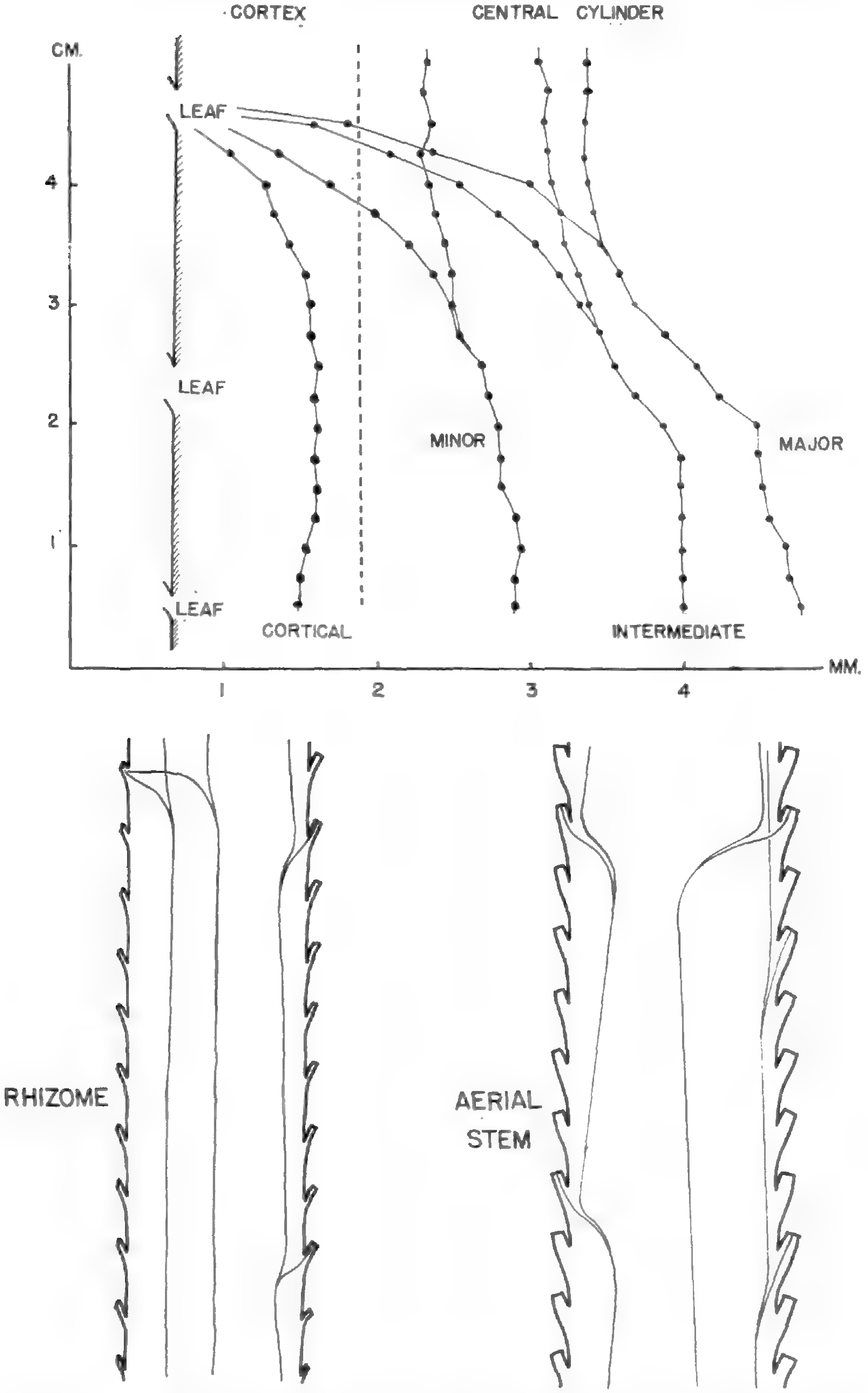

FIGURE 4. ABOVE: plots of vascular bundles supplying scale leaf of rhizome. Measurements taken from microtome sections. Course of major, intermediate, and minor bundles from central cylinder, with continuing vertical bundles, and a cortical bundle without a continuing vertical bundle. The figure is diagram-

the aërial stem and may be described in the same terms. Vascular bundles behave essentially alike, maintaining their individuality throughout the stem. At irregular intervals each of these *vertical bundles* [3] forks to give off a *leaf trace* which passes sharply outward into a scale leaf, the vertical bundle continuing distally, eventually to repeat the cycle. Each leaf receives a few branches from the central bundles (*major bundles*) which pass primarily to the dorsal side of the leaf, a larger number of branches from sub-peripheral bundles (*intermediate bundles*), and the largest number of branches from peripheral bundles (*minor bundles*) which pass to all parts of the leaf. There is a continuous series from major (dorsal) to minor (ventral) leaf traces around the stem circumference at each node. Major bundles pass into the leaf much more abruptly than minor bundles (Fig. 4); they may sometimes be horizontal or even pass below the horizontal and are commonly sinuous so that different parts of the same leaf trace occur in a single section. Part of this unevenness is due to the oblique insertion of most scale leaves.

The most significant way in which rhizome bundles differ from those of the aërial stem in over-all distribution is that rhizome bundles deviate from the vertical at points of leaf contact much less than in the aërial stem. Von Mohl's classic "double curve" which is so characteristic of the vascular bundles of aërial stems of palms is therefore not so obvious in the rhizome (Fig. 4 below). Likewise the central bundles of the rhizome do not describe a regular helical path as is common in the aërial stem.[4] A slight movement does, however, tend to occur in one direction, suggesting an incipient helix.

As in the aërial stem, departure of the leaf trace is complicated by the presence of *bridges* which link it with adjacent vertical bundles, always in an upward direction (Fig. 5D). One to four (usually two) bridges are developed by each leaf trace. Narrow bridges may contain only phloem; the narrowest are sometimes fibrous strands without vascular tissue. Most bridges are short, 2 to 6 millimeters long, but occasionally there are much longer ones resembling vertical bundles until they fuse distally. The significance of this is discussed below. Satellites, which in the aërial stem irrigate inflorescences (or their aborted vestiges), are absent from the rhizome which wholly lacks this lateral type of appendage.

Brief mention may be made of irregular *girdling traces* (Fig. 6 GT)

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[3] Vertical bundles of the rhizome run horizontally, of course, but the term is used because they are homologous with the vertical bundles of the aërial axis.

[4] More recent observation of the aërial stem of *Rhapis* has revealed that this internal helix is correlated with phyllotaxis; stems with a right-handed phyllotactic spiral have a right-handed internal helix and vice versa.

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matic in that the bundles are all represented in one plane, in fact they enter the leaf along different, widely divergent radii. Dotted vertical line represents limit between cortex and central cylinder, arbitrarily chosen as a base line in making measurements. Horizontal exaggeration 12.5 times.

Below: diagrammatic comparison of course of vascular bundles in rhizome and aërial stem (latter figure taken from Zimmermann & Tomlinson, 1965). For comparative purposes the horizontal rhizome is represented in an erect position.

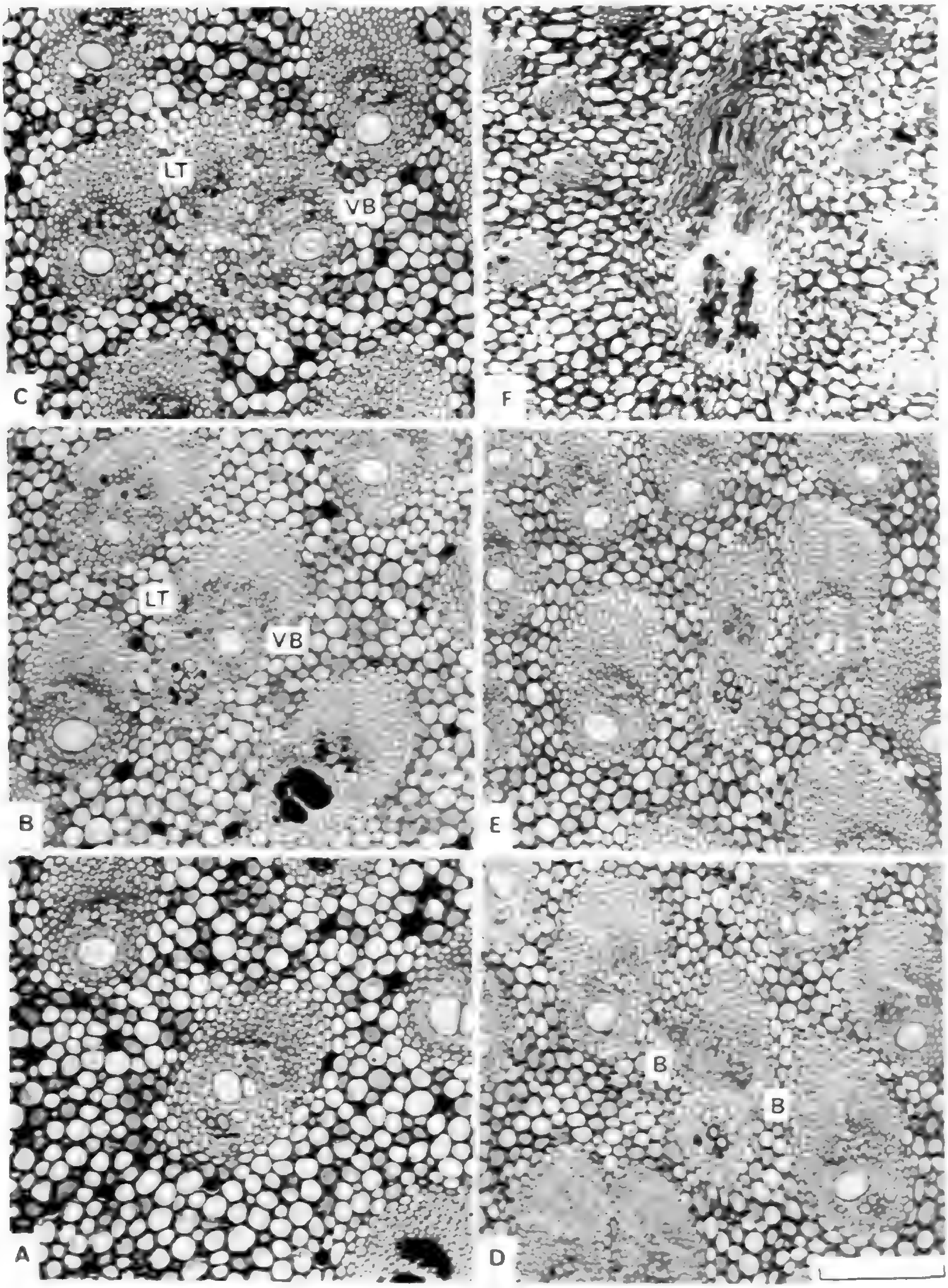

FIGURE 5. Successive transverse sections of the same leaf trace complex from rhizome of *Rhapis excelsa*. In all figures the cortex is towards the upper, the central cylinder towards the lower margin of the plate. Scale is 250μ. A. Vascular bundle in uncrowded central part of stem, below level of forking and with well-developed protoxylem. B. Vertical bundle (VB) to right splitting from leaf trace (LT) at left; 1.85 cm. above A. C. Vertical bundle (VB) at right including one wide metaxylem vessel, no protoxylem, free of leaf trace (LT) at left with no wide metaxylem elements; 2.25 cm. above A. D. Leaf trace further towards cortex splitting off bridges (B) to left and right; vertical bundle is now left behind and is no longer associated with leaf trace; 2.9 cm. above A.

among the peripheral bundles of the central cylinder. These appear to be the ultimate extensions of the root trace system which will be described in a subsequent article.

Cortical system. Fibrous (less commonly narrow vascular) bundles of the cortex are continuous with the same system in the leaf. Traced downwards from the leaf insertion they are seen to form an irregularly anastomosing system which remains quite independent of the central vascular system. Cortical bundles all ultimately seem to end blindly below; occasional cortical strands which end blindly in each direction have been observed. Endings are, however, always near other fibrous bundles and suggest branching during early stages of development. Larger bundles with distinct vascular tissue connect the leaf with the inner part of the cortex (e.g., Fig. 6 CBL and cortical bundle plotted in Fig. 4). Smaller bundles (Fig. 6 CBS), usually without vascular tissue, remain in the peripheral part of the cortex.

DETAILS OF VASCULAR BUNDLE ANATOMY

Variation in the anatomy of a single bundle throughout its length resembles that described for the aërial stem (Fig. 5). A vertical bundle at its point of divergence from a leaf trace includes one wide metaxylem vessel, no protoxylem (VB in Fig. 5C). At some higher level narrow protoxylem elements appear and increase to reach a maximum number of elements just below the next higher leaf contact (Fig. 5A). At the forking of the vascular bundle the leaf trace loses its metaxylem to the vertical bundle (Fig. 5B, C), so retaining only protoxylem. Scale leaves are thus irrigated solely by protoxylem (Fig. 5E, F). Unlike the aërial stem, however, there is little or no proliferation of metaxylem elements just below a leaf contact because there are fewer branches (no satellites). Proliferation of metaxylem represents vessel overlap. Overlapping vessels occur regularly where vascular bundles branch, for example in the leaf-trace complex and where bridges unite with vertical bundles (in the vertical bundle immediately to the right of the leaf trace in Fig. 5E), and at the periphery of the central cylinder under the influence of root insertions (GT in Figs. 5 and 6).

COMPARISON OF THE RHIZOME WITH THE AERIAL STEM

Described in qualitative terms, the vascular anatomy of the *Rhapis* rhizome seems to differ little from that of its aërial stem. Important differences become obvious, however, when quantitative aspects are considered. These show that the over-all plan is less regular than in the aërial stem. We are content at the moment merely to draw attention to this plasticity, an explanation of which must be deferred until development of the vascular

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E. Leaf trace passing through crowded periphery of central cylinder; 3.15 cm. above A. (Configuration of metaxylem of adjacent vertical bundle to right suggests a recent bridge linkage to another leaf trace.) F. Leaf trace in cortex passing almost horizontally into leaf; 3.65 cm. above A.

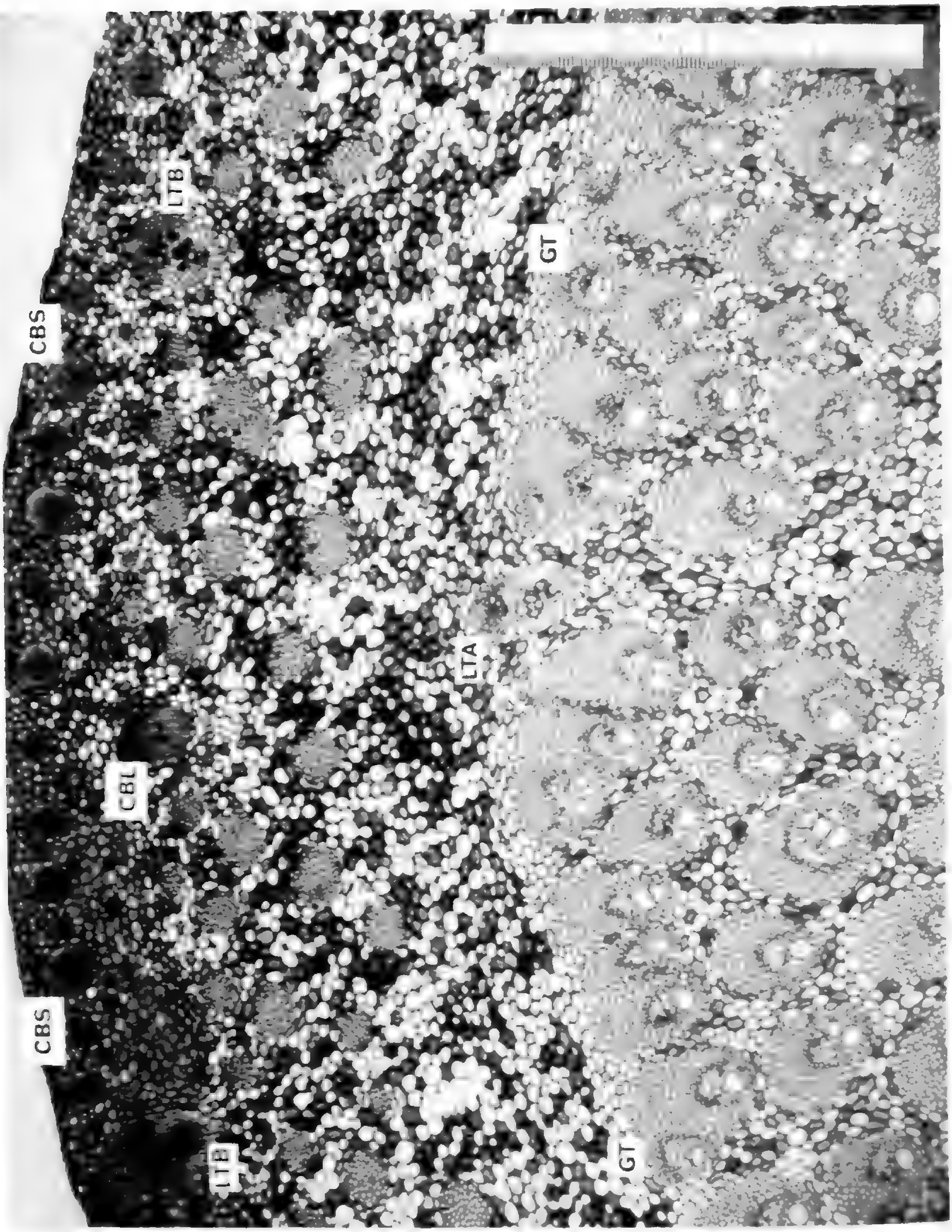

FIGURE 6. *Rhapis excelsa*, transverse section of rhizome including cortex and periphery of central cylinder immediately below a node. Sclerotic base of leaf, inserted obliquely on rhizome, included in upper left-hand part of figure. Trace system to this leaf includes a major leaf trace (LTA) at periphery of central cylinder, two minor leaf traces (LTB) close to their insertion in the leaf, a large cortical bundle (CBL) passing into the leaf from the inner cortex and the system of many small cortical bundles (CBS) diverging from the outer cortex. Girdling traces (GT) are ultimate ends of root traces. Scale equals 1 mm.

system in the rhizome apex is considered. Because relatively few leaf traces enter the scale leaves in proportion to the total number of central cylinder bundles, it is clear that on average any bundle must make a leaf contact

TABLE I. **Essential Differences Between Rhizomes and Aërial Stems**

RHIZOME	AËRIAL STEM
MORPHOLOGY	
Horizontal	Vertical
Subterranean	Aërial
Roots present	Roots absent
Scale leaves, protective, non-assimilating	Foliage leaves, assimilating
Axillary buds absent	Axillary buds developed distally as lateral inflorescences
Vegetative buds abundant in the transition region between rhizome and aërial stem.	
ANATOMY	
Cortex wide, with conspicuous system of fibrous bundles	Cortex narrow, with few fibrous bundles
Peripheral congested bundles of central cylinder mechanically insignificant	Peripheral congested bundles of central cylinder mechanically significant
Leaf contacts irregular, peripheral bundles often of "indefinite length"	Leaf contacts relatively uniform
Internal helix not obvious	Internal helix obvious
Vascular bundles deviate relatively little at leaf contact	Vascular bundles deviate considerably at leaf contact
Branching at leaf contact: Leaf trace Vertical bundle Bridges	Branching at leaf contact: Leaf trace Vertical bundle Bridges Satellites
Metaxylem vessel overlap not pronounced in leaf trace complex (few branches)	Metaxylem vessel overlap pronounced in leaf trace complex (many branches)

much less frequently than in the aërial stem. Measurements confirm this. Peripheral bundles without protoxylem have been traced up to distances of 20 cm. without change. This implies vascular bundles of "indefinite length." However, once protoxylem appears in such a bundle, the bundle will make a leaf contact by splitting off a leaf trace. Protoxylem-bearing lengths of vascular bundles from 3 to 14 cm. were measured in the rhizome. A measured leaf contact distance of 25 cm. (10 cm. bearing protoxylem, 15 cm. protoxylem-free) over 15 internodes compares favorably with central bundles in the aërial stem; values of 12 cm. (6 protoxylem-free, 6 protoxylem-bearing) over 6 internodes for a peripheral bundle may be cited to show that these may make frequent leaf contacts. However, we do not wish to emphasize these few isolated figures in the absence of developmental information.

Plasticity of the vascular system of the rhizome is also demonstrated by certain qualitative variations from the basic patterns which have been noted. Apart from the very long bridges already mentioned which resemble irregular anastomoses between vertical bundles, we have seen occasional vertical bundles split. As in the aërial axis, leaf traces occasionally give off either two or no vertical bundles. Once we recorded a single vertical bundle, originating as two separate strands one from each side of a leaf trace, which fused distally. Vertical bundles of the central cylinder never end blindly.

Essential differences between rhizomes and aërial stems are summarized in TABLE I. Structural differences between rhizome and aërial stem are based on the difference in the physiology of their respective development. In the aërial stem, leaf contacts are established in the apex; we assume therefore that mature leaves supply developing leaf primordia and young leaves. The rhizome, on the other hand, is never an assimilating organ; movement of nutrients must, therefore, be along the axis toward the apex. In this light, the presence of bundles of "indefinite length" seems explicable. However, differences between the aërial stem and the rhizome can only be fully understood when the anatomy and development of their respective apices are known. Such studies are under way; a report about them will be published in a later paper of this series.

SUMMARY

Analysis of the vascular system of the subterranean, scale-bearing rhizome of *Rhapis excelsa* by cinematographic methods demonstrates a system with the essential features of the aërial stem. Satellite bundles are absent since the rhizome bears no lateral inflorescences. The vascular system is less regular than that of the aërial stem and deviation of vertical bundles at points of leaf contact are less pronounced. Leaf contact intervals in peripheral bundles may be very long. These differences must be related to the non-assimilating nature of the rhizome.

ACKNOWLEDGMENTS

Miss Lesley Jackson carried out the routine serial sectioning on which this study is based. Her reliable help is very much appreciated. We are indebted to Miss Priscilla Fawcett, Botanical Illustrator at Fairchild Tropical Garden, for FIGURES 1 and 2.

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REDISCOVERY OF DAPHNOPSIS HELLERIANA

LORIN I. NEVLING, JR., AND ROY WOODBURY

AMOS ARTHUR HELLER (1867–1944) first discovered and collected plants of the Puerto Rican species *Daphnopsis helleriana* Urban. Several biographical sketches of Heller are to be found but they emphasize his botanical contributions to the study of plants of the United States. In 1898, "Through the kind liberality of Mr. Cornelius Vanderbilt, Mr. and Mrs. A. A. Heller have been sent to the island of Porto Rico to collect specimens illustrating the flora and natural vegetable resources of the new colony."[1] They returned to New York in June of 1899 ". . . with nearly 8,000 specimens, and copious notes referring to them."[2] This collecting excursion sometimes is mentioned in the biographical sketches but is not important in terms of the present note.

In 1900, however, Heller ". . . returned to Puerto Rico to extend his collections made in 1899. He will keep the field during January and February, with headquarters at Mayaguez in the western part of the island."[3] This trip may have been financed personally by Heller for the published herbarium accession record of the Garden shows "450 herbarium specimens given by Mr. A. A. Heller."[4] If financed by the Garden, or special funds through the Garden, the specimens would not have been accessioned under the gift category. Further, the following notice appeared in *Muhlenbergia* (1: fly leaf following page 30. August 9, 1900): "Several sets of my Porto Rican collection of 1900 may still be had at the rate of 10 cents per specimen, carriage prepaid. They contain about 100 species of flowering plants, among which are a number of species confined exclusively to Porto Rico, and one new species, *Daphnopsis Helleriana* Urban." In the same issue of *Muhlenbergia* (1: 10–17) an article by F. S. Earle included identifications of Heller's collection of fungi from this trip. The numbers and dates show that Heller did not restrict his collecting to the western part of the island but collected also in the vicinity of Santurce and Bayamon. It was while collecting on the "calcareous hills near Bayamon" on February 23 that he found (no. *4689*) *D. helleriana*. Thereafter, this plant was not recollected for nearly sixty years.

The lack of subsequent collections was particularly frustrating to Nevling in the preparation of a taxonomic revision of *Daphnopsis*. Al-

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[1] N. L. Britton. Report of the Secretary and Director-in-Chief. Bull. N. Y. Bot. Gard. **1**: 182. 1899.

[2] N. L. Britton. Report of the Secretary and Director-in-Chief. Bull. N. Y. Bot. Gard. **1**: 309. 1900.

[3] Anon. News, Notes and Comments. Jour. N. Y. Bot. Gard. **1**: 16. 1900.

[4] Anon. Accession. Jour. N. Y. Bot. Gard. **1**: 108. July, 1900.

though Heller's "type collection" had received relatively wide distribution it consisted of immature staminate specimens exclusively. An attempt to recollect the species, in January of 1963, by Nevling and Richard A. Howard was not successful.[5] Many of the limestone hills were (and are) in the process of being leveled to provide raw materials for the building industry. It was feared that the locality might have been destroyed.

Howard discussed the *Daphnopsis helleriana* mystery later in the same year with Woodbury who told of rediscovering it in 1958 during the course of a detailed examination of the flora of the chain of mogotes which parallel the north coast of Puerto Rico. The mogotes, in this instance, are low, steeply eroded, calcareous hills. The populations of *D. helleriana* are to be found at their summits except for the population at kilometer 21.2 which is found on the first ledge below the summit.

In the fall of 1963 Woodbury supplied a few seedlings for transport to Cambridge. Through an unfortunate accident these plants were lost. A second attempt, in 1964, was successful. Thymelaeaceous plants are, in general, difficult to propagate or transplant and it was necessary to keep the seedlings under mist propagation and polyethylene where they remain nearly two years later. Nevling was able to see living plants in the field in April of 1965, thanks to Woodbury's guidance.

Although this species has many of the typical thymelaeaceous features such as low stature, flexible branches, and a well-developed unlignified fiber structure within the bark, one feature was lacking. Missing was the nearly typical odor of stems or crushed leaves. This fragrance, from coumarin derivative compounds, or lack of it, may prove to be indicative of the presence or absence of certain compounds and may eventually serve as an accessory character of taxonomic value.

The scientific description published by Nevling (Ann. Missouri Bot. Gard. **46**: 287–289. 1959) has been recast to include additional information derived from more recent collections and from field observations.

Daphnopsis helleriana Urb. Symb. Antill. **2**: 453. Oct. 1901. [Type: *Heller 4689* (♂) !]

Dioecious shrubs or small trees to 4.5 m. tall, dichotomously branching, the bark thick, fibrous, the wood white, soft, the young branches with few leaves, flexible, golden-tomentose and glabrescent; tap root long. Leaves simple, alternate, the blade elliptic, oblong, or obovate, 3–16 cm. long, 2–7 cm. broad, mucronulate to obtuse at the apex, cuneate at the base, thin-coriaceous, glabrous, golden-tomentose to villous but soon glabrescent beneath; both surfaces light green but on drying the upper sometimes becoming reddish-brown, the lower glaucescent, developing reddish-brown pigment bordering the veinlets, the costa plane above, elevated beneath, primary lateral veins prominulous above, prominent beneath, somewhat

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[5] I am especially grateful to Mr. Robert B. Martinson for providing facilities and generous hospitality on numerous pleasant occasions in Puerto Rico. Acknowledgement also is made to the National Science Foundation for a grant to Richard A. Howard (GB-4975) which indirectly supported a portion of this study. L.I.N.

arcuate-ascending and extremely reticulate; petiole 2–6 mm. long, scarcely canaliculate. Inflorescences borne terminally on the very young stems, umbelliform, 3–5-flowered, golden-tomentose to villous throughout, the primary peduncle 5–10 mm. long, nodding, the rachis ca. 1 mm. long, secondary peduncles 1–3 mm. long. Staminate flowers: pedicel to 1 mm. long; calyx tube tubular, 5–11 mm. long, 2–3 mm. in diameter at the orifice, golden-tomentose without, glabrous and somewhat red-pigmented within; calyx lobes unequal, greenish white and indefinitely papillate within, the outer 2–3 mm. long, ca. 2.5 mm. broad, the inner 1.5 mm. long and broad, spreading; petals 4, squamelliform, as long as broad, inserted at the orifice, minute; antisepalous stamens inserted below the orifice, at most subexserted, the alternisepalous inserted about two anthers' lengths below the orifice, included, the anthers oblong, 1.25–1.5 mm. long, 0.25–0.5 mm. broad, sessile, the pollen yellow; disc of a few irregular lobes nearly as tall as the pistillode, free, glabrous; pistillode fusiform, ca. 11 mm. long, glabrous. Pistillate flowers: pedicel to 1 mm. long; calyx tube subcampanulate to urceolate, ca. 5 mm. long, ca. 2–3 mm. in diameter at the orifice, golden-tomentose without, glabrous within; calyx lobes unequal, spreading, indefinitely papillate and pale green within, ca. 2–3 mm. long and broad; petals 4, papilliform, inserted at the orifice, minute; staminodia 8 or sometimes absent, in two whorls below the orifice, minute, with brownish pigmentation; disc minute or absent (?); pistil conical, tapering to the stigma, ca. 5 mm. long, 1.5 mm. in diameter, glabrous, the stigma capitate, papillate, exserted. Fruit a white berry (pseudodrupe), elliptic-ovoid, 10–15 mm. long, 8–10 mm. in diameter.

Flowering irregularly from February through April. Found near the summit and at the summit of calcareous hills at an altitude of 75–300 feet.

Puerto Rico: San Juan, near Bayamon, *Heller 4689* (A, E, GH, L, MICH, NY, US); w. of Bayamon, Route 2, kilometer 23.7, *Woodbury 6711* (A, ARP[6]); w. of Bayamon, Route 2, kilometer 21.2, *Woodbury 6716* (A, ARP), *Howard, Nevling & Woodbury 15686* (A — chromosome voucher), seedlings under cultivation, *Nevling 118* (AAH); s. of Dorado, Higuillar *Bro. Alain Liogier 10680* (GH, NY); Guajataca Gorge, Quebradillas, *Woodbury 3196* (A, ARP).

The holotype of this species was destroyed in Berlin during World War II. Because of its relative completeness I am choosing the specimen of *Heller 4689* deposited in the Gray Herbarium as the lectotype.

Knowledge of the cytology and genetics of the Thymelaeaceae is limited severely except in isolated cases. Chromosome numbers have been reported for only a few genera and they, unfortunately, are all members of the same subfamily. Apomixis has been demonstrated in *Wikstroemia* and a polyploid series is known in *Pimelea*. The latter situation is of more than passing interest as all of the species of *Pimelea*, which have been examined in detail, have been found to be gynodioecious. All of the species of *Daphnopsis*, which are known in sufficient detail, are dioecious.

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[6] Agricultural Experiment Station, University of Puerto Rico, Rio Piedras.

To date, chromosome numbers of only two species have been reported: *D. americana* (Mill.) Johnst. ($n = 9$) and *D. philippiana* Krug & Urb. ($n = 9$). It was, therefore, somewhat of a surprise to find *D. helleriana* with a haploid number of 18. This count is based on observations of meiotic tissue, metaphase I through anaphase II, in developing pollen (Voucher: *Howard, Nevling & Woodbury 15785*). No configuration except bivalent formation was observed and all divisions appeared normal and orderly. Mature pollen is abnormal in that there are many collapsed grains and some size variation. Pollen stainability, with cotton blue in lactophenol, is not high but we are not reporting a percentage because of the small sample size. Fruit is set relatively frequently and seedlings are seen in nature. There appear to be no special modifications for vegetative reproduction and it is believed that the species reproduces solely by fruit. There is no evidence to support or reject apomixis in this case although the small size of the total population might be regarded as negative evidence. At present we do not wish to postulate the nature of this tetraploid species. Whether an allotetraploid or autotetraploid, it is of interest because it has arisen in a dioecious group.

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SCIAPHILA DOLICHOSTYLA (TRIURIDACEAE)

PETER S. GREEN AND OTTO T. SOLBRIG

ONE OF THE BEST WAYS to find small and insignificant plants is to look around as one sits down to eat lunch in the field. In just this way one of us (P.S.G.) noticed a small, red saprophyte, which was later identified as *Sciaphila dolichostyla* Schltr., growing in rich humus on the bank of a stream in New Caledonia.*

Unfortunately, full ecological notes were not made at the time, but bud material was fixed in acetic-alcohol and flown, by mail to Cambridge, Massachusetts, where one of us (O.T.S.) carried out the cytological examination reported upon below.

The Triuridaceae is a small family of saprophytic, monocotyledonous herbs, containing 7 genera and 70 or more species. It is confined to the tropics of both the New and Old Worlds, with the greatest concentration of species in southwest Asia, including the East Indies and New Guinea. The largest genus is *Sciaphila*, with about 50 species, while two of the genera are monotypic. The flowers are actinomorphic and apocarpous, with valvate perianth lobes usually in multiples of three. In some species the flowers are unisexual, in others hermaphrodite. As saprophytes, the plants contain no chlorophyll and are generally reported as being reddish, purplish or yellow in color. Endogenous mycorrhizae have been described by Larsen (1963), together with references to earlier reports.

The *Sciaphila* reported upon in this note (*P. S. Green 1329*), was growing on a fairly steep, earthy bank with patches rich in humus, and below a relatively light canopy of low to medium-sized trees fringing the Nekoroya, a rocky tributary stream of the Rivière Téné, near Bourail on the southern side of the central mountain chain and somewhat less than 150 km. northeast of Nouméa. Except for the woodland fringing the streams, the general area was one of "maquis," at an approximate altitude of 150 meters, where lateritic soils overlay the serpentines and peridotites so characteristic of much of New Caledonia.

The shoots of *Sciaphila*, approximately 5 to 12 centimeters high above the surface of the humus and leaf litter (FIG. 1, A & B), were red throughout with no sign of chlorophyll. The underground rhizome was very thin and brittle and appeared to branch and ramify throughout the humus, giving off numerous small, twisted roots which were presumed, from their appearance, to be mycotrophic. Examination showed the plant to be monoecious with actinomorphic, unisexual flowers, each with six strongly reflexed petals (FIG. 1, C & D), each tipped with a beard of abundant, mar-

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* This field work was supported by the National Science Foundation (Grant GB-1545) for which grateful acknowledgment is expressed.

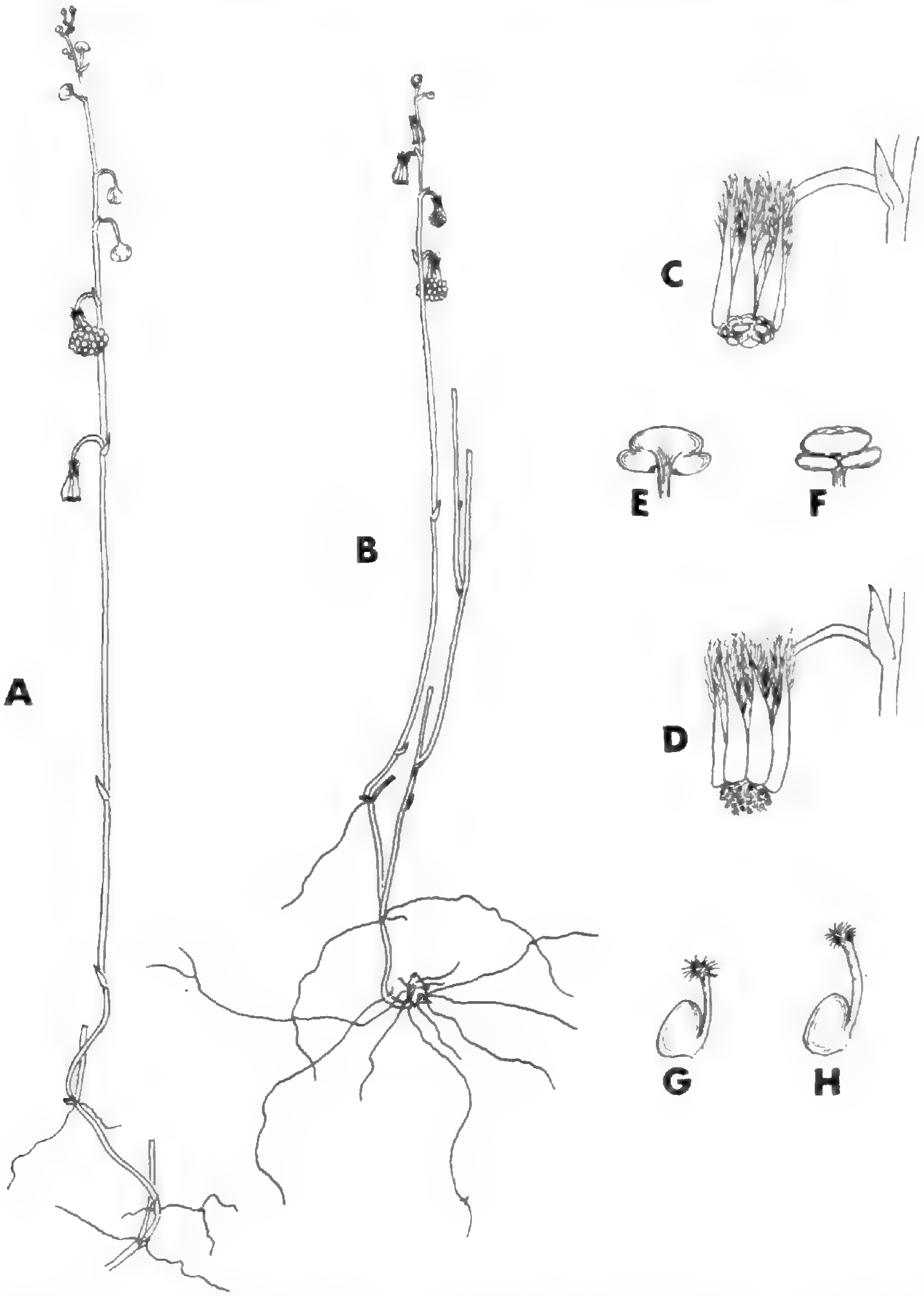


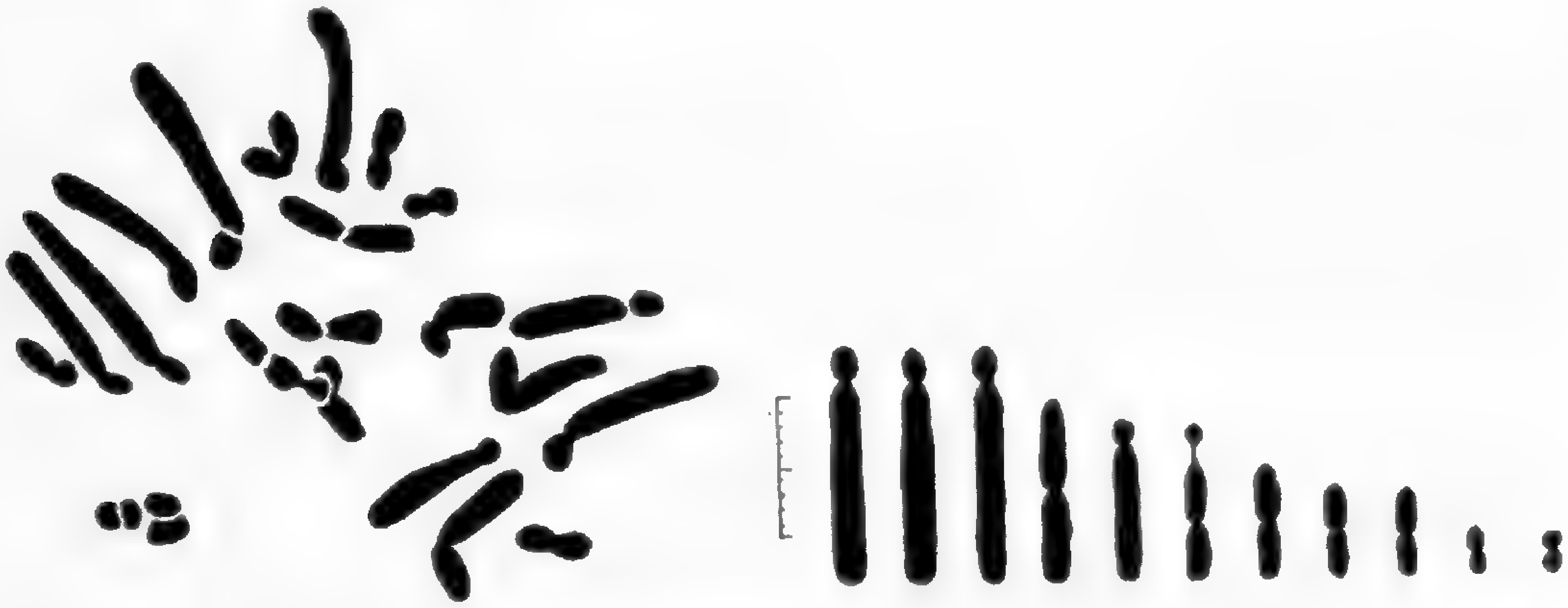
FIGURE 1. *Sciaphila dolichostyla.* A & B, habit, natural size; C, male flower, × 5; D, female flower, × 5; E & F, anterior and posterior view of stamen, × 20; G & H, single ovaries, × 25.

ginally borne, pale purplish hairs. The pedicels were arcuate and somewhat secund, as originally described by Schlechter (1907, p. 19).

The male flowers clearly possessed six stamens (FIG. 1, C) in contrast to the condition in the only other species of *Sciaphila* described from New Caledonia, *S. neo-caledonica* Schltr. which has three. The stamens each had three pollen sacs and were borne on distinct filaments about one-fourth millimeter long (FIG. 1, E & F).

In the female flowers (FIG. 1, D) the numerous ovaries, each capable of producing a single seed, were carried on a rounded receptacle and each possessed a simple basal style with stigmatic tuft (FIG. 1, G & H). The length of the style, to which allusion is made in the specific epithet, varied somewhat, perhaps depending upon the maturity of the flower, from about 0.3 to 0.5 millimeter in length.

The gametic complement was found to consist of 22 chromosomes, three of which were large, six medium and two small and which varied in length from approximately 17 to approximately 3 micra. All the large chromosomes were subterminal, while the smaller, and most of the intermediate sized ones, were median (FIGS. 2 & 3).



FIGURES 2 and 3. *Sciaphila dolichostyla.* LEFT, FIG. 2. Chromosomes at prometaphase, × approximately 1,000. RIGHT, FIG. 3. Idiogram of gametic complement of chromosomes in *Sciaphila dolichostyla.*

The first of two previous chromosome counts recorded for the family Triuridaceae was that of $2n = 48$ by Ohga and Sinoto (1924) for *Sciaphila japonica* Makino; but in his monograph of the family, this species was transferred by Giesen (1938) to the genus *Andruris.* Furthermore, and two years earlier, Nakai and Maekawa (1936) had proposed a somewhat doubtful segregate genus *Parexuris,* to contain this species and *Sciaphila tosaensis* Makino, a genus not accepted by Geisen. It would seem that *Andruris* may have 12 as its basic chromosome number, and Ohga and Sinoto suggest that *Andruris japonica* (as *Sciaphila japonica*) may be a tetraploid. They also record a karyotype of large and small chromosomes with two large, two intermediate in size and 20 small chromosomes in the gametic complement. The report of a count of $n =$ about 12, for a *Sciaphila* sp. by Wirz (1910) is also recorded by them, but while he deals at length with the developmental embryogeny of a plant from Java, said to be near *Sciaphila andajensis* (that is *Andruris andajensis*), there is no actual publication of a chromosome number.

More recently Larsen (1963) has investigated the karyotype of a new species of *Sciaphila* he described from Siam, *S. thaidanica* Larsen. Unlike *S. dolichostyla* and *Andruris japonica* the chromosomes were all found to be about the same size and, what is more, the haploid number was 14, a different base number than either of the other two species. However, with its three stamens and other distinguishing characters it belongs to Sect.

OLIGANTHERA Schltr. rather than Sect. HEXANTHERA Schltr., of which *S. dolichostyla* is a member.

Karyotypes of large and small chromosomes, such as those recorded here, and by Ohga and Sinoto, are also known in the Butomaceae and the Hydrocharitaceae, although in these families the differences between the large and small chromosomes appear more marked. Basic numbers of 11 (as in *Sciaphila dolichostyla*), 12 (as in *Andruris japonica*) and 14 (as in *Sciaphila thaidanica*) have all been recorded for the Hydrocharitaceae and Alismataceae, while 11 has also been recorded for the Scheuchzeriaceae (*Scheuchzeria*) and one genus of the Butomaceae (*Tenagocharis*). All of these are families with which the Triuridaceae has been associated in the classifications of Hutchinson, Engler, and Bentham and Hooker.

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POLYSCIAS VERTICILLATA (ARALIACEAE), A NEW SPECIES FROM THE SOLOMON ISLANDS[1]

BENJAMIN C. STONE

THE GENUS POLYSCIAS IS REPRESENTED on many Pacific Islands by local species, some of them narrow endemics. Some islands or archipelagoes possess two or more species, excluding the frequently cultivated forms (*Polyscias fruticosa, P. pinnata, P. scutellaria*, and *P. guilfoylei*), which are nearly ubiquitous. Thus in Micronesia, Kusaie is the sole habitat of *Polyscias subcapitata* Kanehira; in the Society Islands, *P. tahitensis* (Nad.) Harms is a local endemic; New Caledonia has a number of species exclusively, some of which, at least, are thought to form the separate genus *Tieghemopanax*; *P. corticata* Gibbs and *P. joskei* Gibbs are found only in Fiji; *P. neo-ebudara* (Guillaumin) B. C. Stone, *P. excelsa* (Guill.) Stone, and *P. nusedhul* (Guill.) Stone are strictly New Hebridean; and New Guinea also has several endemic species. Therefore, it is not surprising that in a study of specimens of *Polyscias* from the Solomon Islands an undescribed species was found among collections from that region, which still remains a virtual "terra incognita" from the botanical point of view.

Although the genus *Polyscias* has been involved in a number of taxonomic questions at the generic level, for example, the distinguishing of the genus *Tieghemopanax* R. Viguier, mentioned above, and the genus *Nothopanax* Miquel (now treated as a synonym), the species described in this paper corresponds in all pertinent generic features with *P. pinnata* J. R. & G. Forster, which is the type species of the genus, and therefore, presents no difficulties of generic placement. Furthermore, it is reasonably distinctive in its specific characters, though it seems to be of close affinity to *P. multijuga* (A. Gray) Harms, of Fiji, and somewhat less close but similar to *P. grandifolia* Volkens of Micronesia. From the Fijian *P. multijuga*, this new species differs in the structure of the inflorescence, having verticillate secondary branches bearing terminal and lateral umbellules, rather than having the secondary branches irregularly but mostly alternately arranged on the main rachis and bearing numerous lateral, short-pedunculate umbellules. Furthermore, the new species exhibits a marked, though short, columnar style, from which the two stylose stigmas diverge, rather than the disjunct styles characteristic of *P. multijuga*. From *P. grandifolia* this Solomon Islands species differs in its considerably taller habit (the Micronesian plants are rarely more than 4 m. tall), as well as in the

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[1] This is the fifth in a series of studies of plants of the Solomon Islands. The previous papers are listed in Proc. Biol. Soc. Wash. **76**: 1. 1963.

structure of the inflorescence, while the Micronesian plants share the more open, non-verticillate branching characteristic of *P. multijuga* and, indeed, of many other species of *Polyscias*. Furthermore, *P. grandifolia* shows

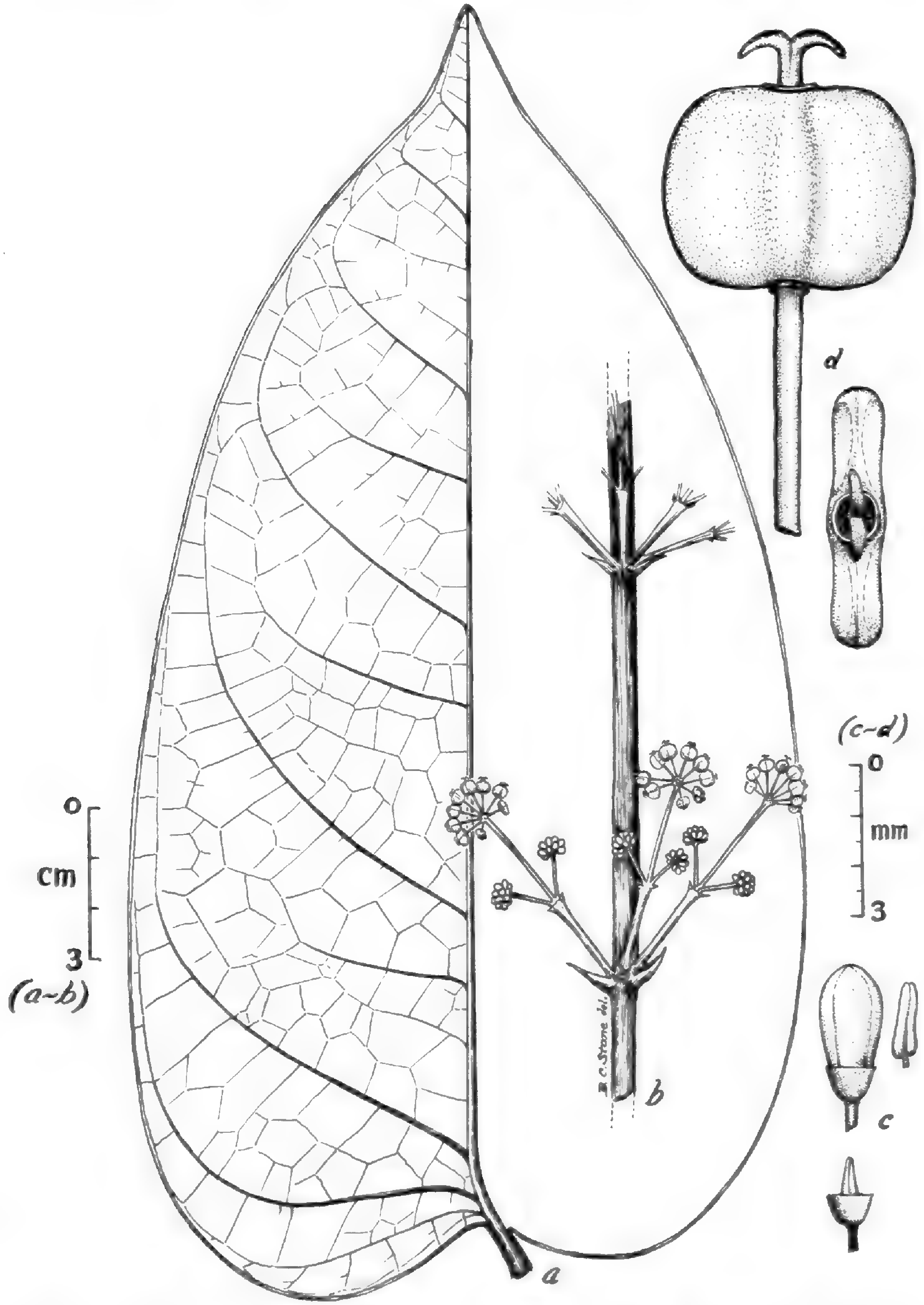

FIG. 1. *Polyscias verticillata* B. C. Stone. a, leaflet, showing venation; b, portion of an inflorescence; c, flower (in bud), a stamen, and (below) bud with corolla removed, showing calyx and styles; d, two views of a mature fruit.

little or no stylar process on the bilocular fruits, and its leaflets are borne on petiolules 1 cm. or more long, whereas in this new species, the petiolules are at most 6 mm. long. Finally, the leaflets of *P. grandifolia* are usually minutely and rather distantly serrulate-denticulate; those of the species described here are entire.

Polyscias verticillata B. C. Stone, sp. nov. FIG. 1.

Arbor parva ad 7 alta, foliis imparipinnatis ad 60 vel 90 vel ultra (?) cm. longis, 4 (in specimine typico, sed certe plus ultra)-jugatis, petiolo crasso stramineo ad 30 cm. longo basi ad 1 cm. diam. vaginante, marginibus vaginae angustis ca. 6–7 cm. longis; internodiis foliorum ca. 8–12 cm. longis; nodiis subtorulosis; foliolis oppositis breve petiolatis, petiolulis ca. 5–6 mm. longis, laminis oblongis apice acuminato-caudatis basi subcordatis, ca. 27 cm. longis, ca. 13 cm. latis, margine minute revolutis, costis subtus prominentibus supra subprominulentibus, nervis lateralibus patenti-arcuatis alternis subtus prominulentibus; inflorescentia verticillati-paniculata, rachibus majoribus ca. 8, ad 45 cm. longis, nodosis, nodiis bibracteatis bracteis deltoideo-lanceolatis 6–8 mm. longis caducis cum ramulis 3–5 in verticillo dispositis, ramulis ad 4 cm. longis ad medium nodosis bibracteatis (parte basi 1–2 cm. longa, apice 1–2 cm. vel ultra); umbellulis fere 10–14-floris pedunculatis, pedunculis umbellularum centralium 1–2.2 cm. longis, pedunculis umbellularum lateralium brevioribus ad 1 cm. longis, oppositis rare ternatis; floribus parvis pedicellatis, pedicellis gracilibus 1–4 mm. longis; calycis tubo obconico ca. 0.8 mm. longo ore truncato; corolla ca. 2 mm. longa; petalis 5, tenuiter deltoideo-ovatis; staminibus 5 filamentis brevibus antheris ca. 0.7–1.4 mm. longis; stylo unico ca. 0.6 mm. longo, stigmatibus 2, in fructu ca. 1 mm. longis; fructu valde compresso biloculari orbiculato basi cordato apice styli stigmatibus divaricatis coronato; fructu (subimmaturo ?) ca. 4–5 mm. lato, ca. 4 mm. longo, pallide luteo-virescenti.

HOLOTYPE: Solomon Islands (Australian Territory of Papua and New Guinea), Bougainville Island, Siwai, January 28, 1933, *J. H. L. Waterhouse 74* (US 1484858); isotypes (BISH, Y).

The specific epithet refers to the verticillately arranged branches of the inflorescence. Waterhouse records the species as a small tree about 20 feet high, with glossy leaves and large heads of small blossoms. The local name is "pupung."

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CIRCULATION

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COMPARATIVE ANATOMY OF THE LEAF-BEARING CACTACEAE, XVI.

THE DEVELOPMENT OF WATER-SOLUBLE CRYSTALS IN DEHYDRATED LEAVES OF PERESKIOPSIS

I. W. BAILEY [1]

WHEN FRESHLY COLLECTED LEAVES OF *Pereskiopsis* are preserved in ethyl alcohol of concentrations varying from 50 to 95 per cent, more or less numerous cells of the mesophyll tend to form colorless, hyaline, isotropic bodies that are soluble in water at ordinary room temperatures, as well as in distilled water chilled to 5 degrees centigrade. These isotropic bodies, which form in dehydrated cell sap, may exhibit internal structural details prior to the development of cold-water-soluble crystals within them.

STAINING IN RUTHENIUM RED

I now find that these bodies in *Pereskiopsis*, prior to the appearance of crystallization within them, stain in ruthenium red in 50 per cent alcohol, i.e., in a concentration of alcohol sufficient to prevent solution of the bodies, but not of a concentration, e.g. 75 to 95 per cent, in which the dye is insoluble. Similar coloration may be obtained by mixing aqueous ruthenium red in sufficient glycerin to inhibit solution of the bodies. This is advantageous in making mounts of sections of leaves for future study and photography. When the sections are mounted under a cover glass in such a mixture, and tightly sealed in place by application of "Tuf-on," the bodies retain their red coloration for many months, particularly when the slides are kept in the dark.

In more concentrated alcoholic solutions, above 70 per cent, small bodies of spherical or hemispherical form tend to occur in separated individual cells, FIG. 1, whereas in concentrations of alcohol closer to 50 per cent numerous additional larger bodies of multicellular composition

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[1] This investigation was supported by a grant from the National Science Foundation.

may be formed as illustrated in FIG. 2. Within the red stainable matrix of the bodies, crystallization may first appear internally, FIG. 3, peripherally, FIG. 11, progressing both internally and peripherally, FIG. 5, or at times to complete crystallization of unicellular and multicellular bodies, FIG. 6.

The crystals are slender, somewhat needle-like ones of varying length. The apparently larger anisotropic units mentioned in a previous paper (Bailey, 1965a), upon examination at high magnification can be resolved into compact aggregations of slender elementary units. The crystals themselves do not stain in ruthenium red as does the matrix in which they form.

The use of ruthenium red in histological techniques dates back to Mangin (1893) who obtained a sample of ammoniated sesquichloride of ruthenium from Joly (1892). Mangin emphasized the utility of the new dye in the study of pectic substances. He noted in his original paper that the dye in the form of dry powder is stable, but tends to deteriorate in aqueous solution when exposed to light at room temperatures and must, therefore, be kept in the dark in black bottles. My own experience with the dye is that commercial samples are variable in quality. I have relied lately upon a sample obtained in 1957 from Edward Gurr, Ltd. Aqueous solutions of this brand of the dye remain stable for many months when kept in the dark in a refrigerator. It is not essential to prepare fresh solutions of the dye prior to utilization as has been so generally assumed.

In the past ruthenium red has been considered by some to be a specific test for pectic and comparable substances, but such an assumption has been denied by others. In extensive investigations over a period of many years, and involving the behavior of the dye in buffers of widely varying pH, I have found that many pectic substances, gums, mucilages, and polyuronide hemicelluloses stain very rapidly and intensely in dilute solutions of the dye in distilled water. Such exceedingly rapid and intense staining in very dilute solutions of the dye is of considerable utility in preliminary investigations of plant tissues, e.g., for pollen, (see Bailey, 1960). It should be noted in this connection that the sugar acids, viz. pectic, glucuronic, and galacturonic, extractable from normally occurring complex substances, form salts which may stain with comparable rapidity and intensity. The salts vary in their solubilities in water, those of calcium and barium sometimes being less rapidly soluble in cold water.

Other substances occurring in or derived from plants, stain in dilute solutions of the dye, but usually much less rapidly and sometimes ultimately less intensely, e.g. nuclei, coagulated protoplasts, hydrocellulose, lignin residues, etc. Although a red coloration can no longer be considered a specific test for pectic and related substances, use of the dye in histological techniques should not be rashly abandoned. For when cogently utilized, striking differences in the behavior of substances in very dilute solutions of the dye can provide suggestive clues regarding chemical composition in various parts of intact sections of plant tissues. This is true in dealing with dehydrated leaves of *Pereskiopsis*.

The red staining of the cold-water-soluble bodies in this genus raises important questions regarding their chemical composition. For example, are the bodies composed largely of mucilage? Mucilage cells, which occur so abundantly throughout the Cactaceae, and are so physiologically and ecologically significant in the retention of moisture in xerophilous plants, are numerous in living foliar and other tissues of *Pereskiopsis* and *Pereskia*. At times, water-insoluble druses of calcium oxalate may be included within their red-stainable, concentrically layered contents, FIG. 4. In dehydrated leaves, the mucilage cells may retain their red-stainable contents in more or less modified form, but water-soluble crystals are not formed within them. Both the hyaline isotropic bodies and the contents of mucilage cells stain in ruthenium red, but the bodies of induced formation do not stain as rapidly and intensely in dilute solutions of the dye. The bodies are not composed of conspicuous, concentrically deposited layers of mucilage which expand rapidly in water forming copious, jelly-like modifications.

Furthermore, the bodies of induced formation, prior to complete crystallization, stain differently in other dyes. For example, in sections of leaves, preserved in 70 per cent alcohol and transferred to safranine-o or gentian violet in 70 per cent alcohol, the contents of mucilage cells stain very rapidly and intensely red or violet, whereas the bodies of induced formation do not, even after many hours. In addition, when such sections are transferred to a solution of toluidene blue-o in 50 per cent alcohol, the induced bodies may stain red in vivid contrast to the bluish coloration of mucilage cells, and also of primary cell walls, coagulated protoplasts, and "protein bodies" when present, (see Bailey, 1965b).

Upon the basis of superficial resemblances in certain induced forms of crystallization, it has been suggested by Lauterbach (1889) and others that the birefringent bodies in alcohol-dehydrated tissues of the Cactaceae are composed of inulin. If it is true that food reserves in the xerophilous Cactaceae are composed of inulin rather than of starch, it should yield data of much significance from phylogenetic, physiological, and ecological points of view. For example, as suggested by Parkin (1899), the presence of inulin rather than starch should aid in the retention of moisture. In any case such questions merit extensive and thoroughly reliable investigations.

During the resting season, the stems and roots of the primitive leaf-bearing genera *Pereskia* and *Pereskiopsis,* when growing in their native habitats, may be packed with starch. Excessive loss of moisture from the stems is inhibited, not only by a high content of mucilage, but also by structural features of their cuticle, stomata, epidermal, and sub-epidermal layers (Bailey, 1964). In the case of *Pereskiopsis,* the delayed intensity of staining in very dilute solutions of ruthenium red poses serious doubts that the bodies in desiccated leaves are composed of pectic substances, gums or polyuronide hemicelluloses. That the bodies of induced formation in leaves of this genus are not composed of inulin is indicated by a number of lines of evidence, the most significant of which are noted here:

(1) There appears to be no conclusive evidence that crystals of inulin develop in a red stainable, cold-water-soluble, isotropic matrix as the crystals of induced formation do in leaves of *Pereskiopsis*.

(2) In the case of tubers of *Dahlia* and *Helianthus*, preserved in strong concentrations of ethyl alcohol, the crystalline inulin remains insoluble in cold water after 500 hours, but dissolves very rapidly in water raised to a temperature between 50 and 60 degrees centigrade.

(3) The bodies of induced formation in *Pereskiopsis* contain much calcium as may be demonstrated by their behavior in sulphuric acid. When transferred to this acid, the crystallizing bodies quickly lose their anisotropy which is rapidly restored by the formation within them of abundant crystals of calcium sulphate. Not infrequently the transition to gypsum tends to occur more rapidly than in druses of calcium oxalate present in the same tissue. Inulin does not contain calcium in its crystalline forms.

(4) Inulin, as in the case of mucilage, gives convincing positive tests for carbohydrate composition with the classical "Molisch" reagents. The bodies of induced formations in *Pereskiopsis* do not. This appears to be true, not only of bodies ***in situ*** in sections of leaves, but also of their solutions in cold water.

THE BEHAVIOR OF NEUTRAL CALCIUM MALATE

In detailed investigations of the microchemical composition of water-soluble bodies induced by dehydration in cactus-like Euphorbiaceae, much emphasis was placed, particularly by Belzung (1893) and Mirande (1898), upon use of neutral calcium malate. Therefore, in the case of *Pereskiopsis*, it appeared essential to study the behavior of this form of calcium malate in greater detail.

Through the kind assistance of my colleague Professor Kenneth Thimann, I have studied aqueous solutions of calcium malate prepared as follows: Starting with a concentrated solution of L-(plus) malic acid, pure calcium oxide is added until no more will dissolve. After gentle warming and stirring, the excess calcium oxide is filtered off and the resulting solution slightly diluted to prevent precocious crystallization. It has a pH of 5.7.

This solution dissolves ruthenium red very rapidly and abundantly, yielding a solution which has and retains a normal dark red coloration. It should be noted however, that the uncolored solution, even if kept in a refrigerator, may in time become contaminated by micro-organisms and should be discarded.

When the uncolored solution, either nearly concentrated or considerably diluted, is dried on an ordinary slide or in the shallow concavities of a thicker one, two forms of residues persist. One of these consists of very fragile cracked films, FIG. 7, the other of more plastic uncracked material, FIGS. *22* and *23*. The cracked films tend to be more numerous when a solution is dried at 60 degrees centigrade than when it is dried at room temperatures. Both forms of residues are isotropic, stain red when ruthenium red is available, and commonly are devoid of numerous conspicuous crystals of calcium malate. It should be noted that when toluidine blue-o is dissolved in an aqueous solution of neutral calcium malate, the films formed on drying stain red rather than blue.

If the residues in the shallow concavities of a slide are dissolved by additional solution to calcium malate, large orthorhombic crystals tend to be formed, particularly in the outermost reforming cracked zone, during subsequent redrying, FIG. 9. These characteristic crystals of calcium malate appear colorless in ordinary light, but are vividly pleochroic in polarized light without the insertion of a mica plate or other optical devices. The crystals do not stain when ruthenium red is available, although they may appear to do so when jacketed by a residual coating of stainable isotropic material. However, similar crystallization may occur at times when the original residues are merely dissolved in distilled water prior to redying.

It should be emphasized that the phenomena involved in drying uncovered solutions on slides are complex and highly variable. Thus, in the case of solutions in circular concavities, evaporation occurs first and most rapidly in the peripheral parts and progresses toward the center where the depth of the solution is greater. In so doing, currents develop in the solution involving movements from the center toward the more rapidly evaporating periphery. The rapidity of such movements varies with different temperatures used in drying. As desiccation progresses, more or less widely separated zones of cracked and uncracked residues tend to be formed. In general, crystallization and the intensity of staining in ruthenium red tend to be greater in the first-formed, outermost, cracked zones. It appears likely, upon the basis of diversified observations, that the concentration of calcium malate and of ruthenium red in different parts of a solution may be modified by diffusion currents during drying.

When absolute ethyl alcohol is added to an uncolored solution of neutral calcium malate in proportions of three parts of alcohol to one part of calcium malate solution, a copious, finely granular, flocculent precipitate forms at once. This precipitate is white in reflected light and either isotropic or feebly opalescent in polarized light. If the reaction is induced in a solution colored by ruthenium red, the flocculent precipitate is similar but of red coloration, FIG. 13.

Upon leaving the precipitates in tightly stoppered residual alcohol, various forms of crystallization tend to develop within them in time. This frequently leads to the appearance of spherical bodies of varying sizes and intensities of anisotropy. The larger developing ones may be nearly isotropic and red-stainable throughout. Such spherical bodies frequently retain more or less isotropic, red-stainable material externally during the formation of slender, radially oriented crystals internally. The slender crystals are colorless, not conspicuously pleochroic in polarized light, and may exhibit four positions of extinction comparable to that illustrated in FIG. 15. At times, single large pleochroic crystals jacketed by isotropic, red-stainable material may occur in close association with the spheres, FIG. 14. However, numerous compact aggregations of relatively large pleochroic crystals may develop in other parts of the same flocculent precipitate. These aggregations commonly develop in circular cleared areas of the precipitate, and are not jacketed by red isotropic material as in the case of the crystals illustrated in FIGS. 14 & 23.

The variability in the forms of crystallization that ultimately develop in such precipitates may be influenced by a number of subtle variables, e.g., varying dilutions of the neutral calcium malate in which alcoholic precipitation is induced to form, variations in the volume of precipitate and its behavior during settling, redistribution of a precipitate in the residual alcohol and subsequent resettling during transfers from measuring cylinders to slender test tubes, and by differences at various levels of a compactly settled precipitate.

If the precipitates in some of the residual alcohol are dried in the concavity of a slide, the more rapid evaporation of alcohol than of water may lead to a dilution of alcohol in which a precipitate is soluble. Under such conditions the final stages of drying resemble those that occur when the precipitates are dissolved in water before drying. Under these conditions both cracked and uncracked, isotropic, red-stainable residues may persist during final stages of desiccation. Associated with them and frequently within them, FIG. 23, are crystals of extraordinarily diversified sizes, forms, and patterns of aggregation. At times, individual crystals varying from very tenuous ones to much larger, broader ones occur independently of each other, FIG. 17. In other cases, crystals of markedly different sizes, lengths, and forms are loosely associated in large clusters, FIG. 16. Not infrequently, compact circular aggregations of radially elongated, tenuous crystals are formed, FIG. 19. Such crystalline bodies may exhibit concentricities or have very extensive, more or less needle-like extensions externally, FIG. 18. It should be noted, in addition, that at times the cracked films formed during desiccation may be conspicuously anisotropic in polarized light, due to the presence of minute crystals that are hardly visible under ordinary magnifications.

Thus, it is evident from a summation of preceding data that crystals of pure neutral calcium malate are extraordinarily diversified and variable in size, form, and patterns of aggregation.

AQUEOUS SOLUTIONS FROM CRUSHED LIVING AND DEHYDRATED LEAVES OF PERESKIOPSIS.

Aqueous solutions can be obtained from crushed living leaves of *Pereskiopsis* and from dehydrated ones which contain cold-water-soluble isotropic and anisotropic bodies. The solutions from crushed living leaves are viscid and difficult to filter owing to the expansion of mucilage. Although all of the druses of calcium oxalate and most of the gelatinous constituent are removed during filtration, some of the more liquid mucilage is not. Thus, the finely granular, flocculent precipitate that forms in a filtered solution, upon addition of alcohol, contains elongated strands of coagulated mucilage within it. However, during subsequent treatments such strands do not appear to be concerned in the formation of water-soluble crystals.

In contrast to this, aqueous extracts from dehydrated leaves, particularly those fixed in F.A.A.[2] which contains water-soluble crystalline bodies filter readily and rapidly. Furthermore, the flocculent precipitates formed upon the addition of alcohol do not contain abundant strands of coagulated mucilage.

It is significant that the aqueous solutions obtainable from the leaves of *Pereskiopsis* behave much as do aqueous solutions of neutral calcium malate. They dissolve ruthenium red rapidly giving a characteristically red coloration. When dried in the concavity of a slide under comparable conditions, cracked (Fig. 8) and uncracked, isotropic, red-stainable residues remain. Small forms of crystals may occur within them under favorable conditions. However, the widely diffused crystals that develop in cracked films, Fig. 10, differ somewhat in size, form, and orientation from those that occur in the bodies of desiccated leaves. It is not unreasonable to believe that the forms of crystallization which occur within the confines of unruptured cells should differ more or less from those that may arise in aqueous solutions liberated from such confinements.

The aqueous solutions from leaves, whether uncolored or colored, form copious flocculent precipitates which closely resemble those formed by aqueous solutions of neutral calcium malate. In both cases, the precipitates, when allowed to remain in residual alcohol, not infrequently tend sooner or later, to form essentially similar spherical bodies. The larger of the spherical bodies in precipitates of *Pereskiopsis*, as in those of flocculent precipitates of neutral calcium malate, may be nearly isotropic and red stainable throughout, Fig. 20, more or less feebly anisotropic, Fig. 21, or composed of slender, radially oriented crystals that exhibit four positions of extinction, Fig. 15, in polarized light between crossed nicols.

In studying the cold-water-soluble bodies in dehydrated leaves of *Pereskiopsis,* there are complicating phenomena that must be taken into consideration and avoided if possible. One of these is the common tendency for the leaves of *Pereskiopsis,* as of *Pereskia,* to turn black during air-drying and at times in F.A.A., and in dilutions of ethyl alcohol. This culminates in changes of color in the water-soluble bodies of the mesophyll. Furthermore, aqueous extracts obtained from blackened leaves are dark colored as are flocculent precipitates formed by them. It is evident that the composition of the bodies is more or less seriously modified by absorption of diffusing extraneous substances. The blackening of the mesophyll of the thick leaves can be inhibited by removing thin periclinal

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[2] Forty per cent formaldehyde, five parts; glacial acetic acid, five parts; 50 per cent ethyl alcohol, ninety parts.

slices containing the epidermal and sub-epidermal tissue prior to the desiccation of the leaves. Furthermore, the blackening of entire leaves can be prevented by first immersing them in boiling water or by rapidly drying them at a temperature of 70 degrees centigrade. This at least suggests that the blackening may be due to the oxidation and subsequent diffusing of phenolic substances that are largely confined to the epidermal and subepidermal layers of living leaves. The blackening phenomena obviously merit detailed biochemical investigation. I have avoided this complication by obtaining, via airmail, freshly collected living leaves, from Professor Norman Boke, some of which do not blacken during transit or after dehydration in ethyl alcohol.

Another complicating factor occurs in making permanent mounts of foliar tissue by techniques which involve transfers from absolute alcohol to such non-polar solvents as xylol, diaphane solvent, etc. During such transfers, the water-soluble bodies tend to form more or less extensively blackened areas, FIG. 12, which conceal details of their internal composition, whether viewed in ordinary light or in polarized light. It is of interest in this connection that starch grains and druses of calcium oxalate, FIG. 4, behave similarly during such transfers, developing black interiors which conceal details of their internal crystallization. In all three cases, the darkening is due to the presence of minute black objects. To determine conclusively whether these are tiny inclusions of undissolved gas, small specks of some isotropic organic solid or merely optical artifacts will require detailed investigations in the future. I have avoided this complication by not basing significant observations upon tissue after transfers from alcohol to non-polar solvents.

SUMMARY AND CONCLUSIONS

When living leaves of *Pereskiopsis* are air-dried or preserved in ethyl alcohol of concentrations varying from 50 to 95 per cent, isotropic, cold-water-soluble bodies tend to form in desiccated cell sap. These bodies exhibit characteristic staining in ruthenium red, toluidine blue-o and other dyes, prior to the formation of cold-water-soluble crystals within them. In studying the bodies, it is essential to avoid complicating phenomena, particularly absorption of diffusing extraneous substances. This is particularly important in dealing with leaves which blacken during dehydration. Available evidence suggests that phenolic substances largely concentrated in the superficial layers of living leaves rapidly oxidize forming dark colored substances which subsequently diffuse throughout the thick mesophyll.

There is now much accumulated detailed evidence that the cold-water-soluble isotropic and anisotropic bodies are not composed of calcium oxalate, calcium phosphate, inulin, mucilage, or of substances of carbohydrate composition in general. On the contrary, aqueous extracts from dehydrated leaves during drying, crystallization, and precipitation in alcohol so closely parallel the behavior of aqueous solutions of pure neutral calcium malate under comparable treatments, as to indicate that the bodies probably are largely composed of calcium malate. Such a conclusion is in general agreement with results obtained, particularly by Belzung (1893) and Mirande (1898) in their detailed microchemical investigations of similar bodies that occur in alcohol-dehydrated tissues of cactus-like Euphorbiaceae and some highly specialized genera of other families.

However, there are some forms of crystallization in neutral calcium malate which differ from any of those that occur in extracts from leaves of *Pereskiopsis.* The reasons for this difference are at present obscure.

In the case of *Pereskiopsis,* the next step should be to determine with biochemical certainty whether the bodies of induced formation are composed of uncontaminated calcium malate.

Futhermore, it should be noted in conclusion, as was done in a previous paper (Bailey, 1965a), that the phenomena of desiccation in xerophilous representatives of the Euphorbiaceae and Cactaceae pose a fundamentally important biological question. Are there evolutionary changes in the metabolism of angiosperms (viz. those having excessive succulence) which lead to the formation of unusually large amounts of organic acids, as oxalic, malic, etc., and in turn to the extensive development of calcium salts of such acids? An adequate answer to this highly complex question will involve active and sustained cooperation between broadly informed botanists and chemists.

ACKNOWLEDGEMENTS

I am much indebted to Dr. Norman Boke for his continuing kindness in sending me living leaves from plants in his greenhouse. I am also indebted to Drs. C. B. Heiser, R. A. Howard, and C. E. Wood for assistance in obtaining tubers of *Helianthus* and *Dahlia.* I am particularly grateful to Dr. Ned Feder for reading the original manuscript of this paper and making a number of helpful suggestions.

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EXPLANATION OF PLATES

PLATE I

FIGS. 1–6. Parts of periclinal sections of leaves. FIGS. 1 and 2 ordinary light, FIGS. 3 and 4 polarized light with axes of nicols somewhat divergent from right angle, FIGS. 5 and 6 polarized light with nicols at right angles. 1. *Pereskiopsis* (*Boke B-18*), small isotropic bodies from leaf preserved in 75% alcohol, stained in ruthenium red, × 110. 2. *The same*, large multicellular, isotropic body from leaf preserved in 50% alcohol, stained in ruthenium red, × 110. 3. *Pereskiopsis* (*Boke B-20*) small body in single cell, isotropic matrix stained in ruthenium red, crystalline center with four positions of extinction in polarized light, × 420. 4. *Pereskia tampicana*, druse of calcium oxalate with blackened center in mucilage cell, × 510. 5. *Pereskiopsis* (*Boke B-22*) from leaf preserved in F.A.A., internal and peripheral crystallization in multicellular body, × 70. 6. *Pereskiopsis* (*Boke B-18*) from leaf preserved in F.A.A., multicellular body crystallized throughout, × 180.

PLATE II

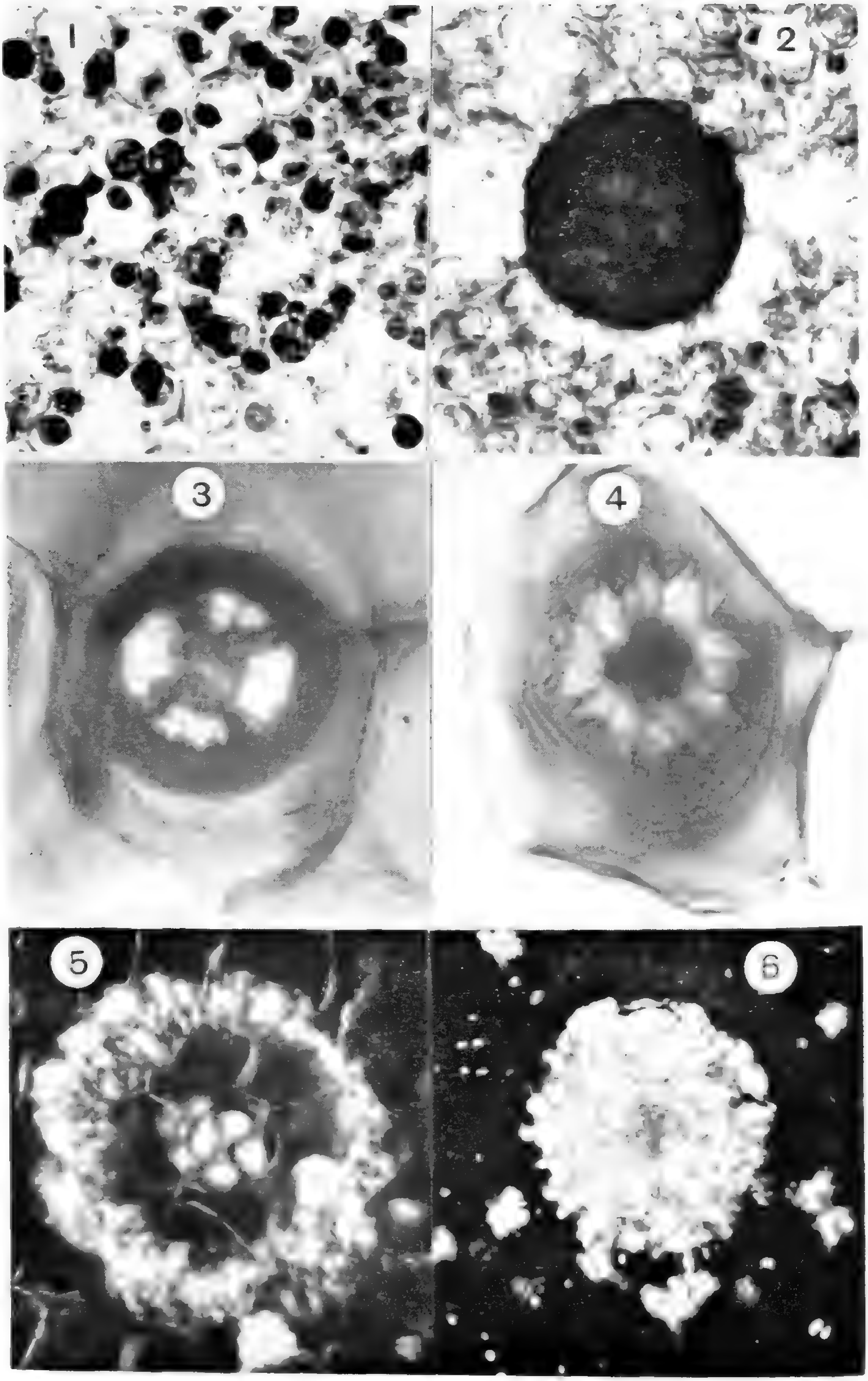
FIGS. 7–10. Cracked films formed during the drying of solutions of calcium malate and of aqueous extracts of *Pereskiopsis*. FIGS. 7, 8, and 10, ordinary light. FIG. 9, in polarized light with axes of nicols somewhat divergent from right angle. 7. Calcium malate, absence of crystallization, × 90. 8. *Pereskiopsis* (*Boke B-22*), aqueous extract from leaves preserved in F.A.A., film stained in ruthenium red, containing minute isotropic granules, × 110. 9. Calcium malate, stained in ruthenium red and containing large crystals (white), × 150. 10. *Pereskiopsis* (*Boke B-1*) aqueous extract from leaves preserved in F.A.A., film containing abundant minute, spherical crystals, × 150.

PLATE III

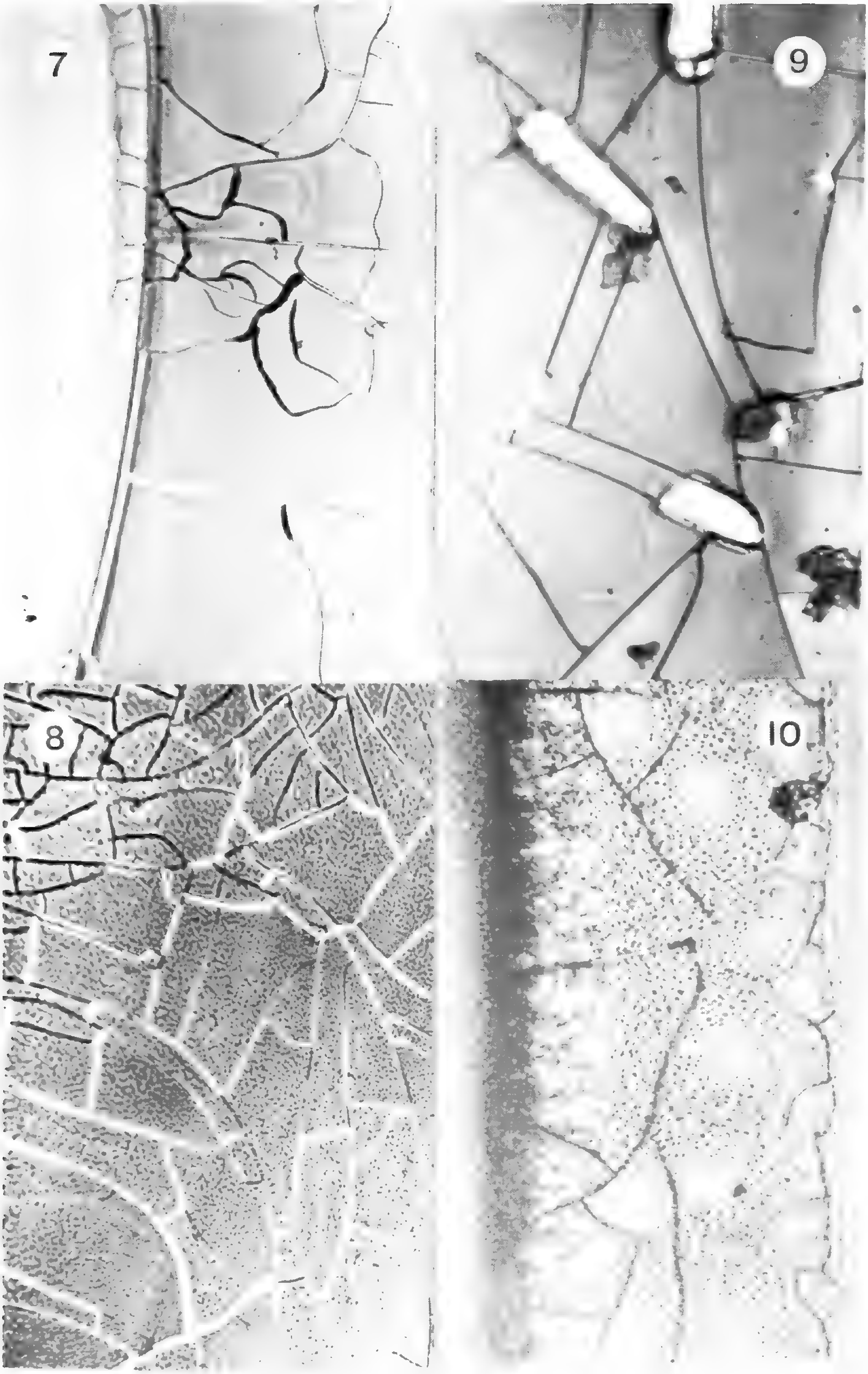
FIGS. 11–17. Forms of crystallization as seen in polarized light. 11. *Pereskiopsis* (*Boke B-20*) multicellular body from leaf preserved in F.A.A., showing peripheral crystallization in large multicellular body, and small druses of calcium oxalate internally, × 190. 12. *Pereskiopsis* (*Boke B-32*), blackening of multicellular body after mounting in diaphane, druses of calcium oxalate showing externally to body, × 114. 13. Calcium malate, formation of spheres in flocculent, isotropic red precipitate, × 260. 14. *The same*, red spheres (black) and crystals (white) formed in precipitate after longer standing in alcohol, × 60. 15. *Pereskiopsis* (*Boke B-6*), fully crystalline spheres with four positions of extinction developed in flocculent precipitate after long standing in alcohol, × 180. 16. Calcium malate, large loosely aggregated crystals of diversified sizes and forms, × 330. 17. *The same*, individual crystals of varied sizes and forms, × 330.

PLATE IV

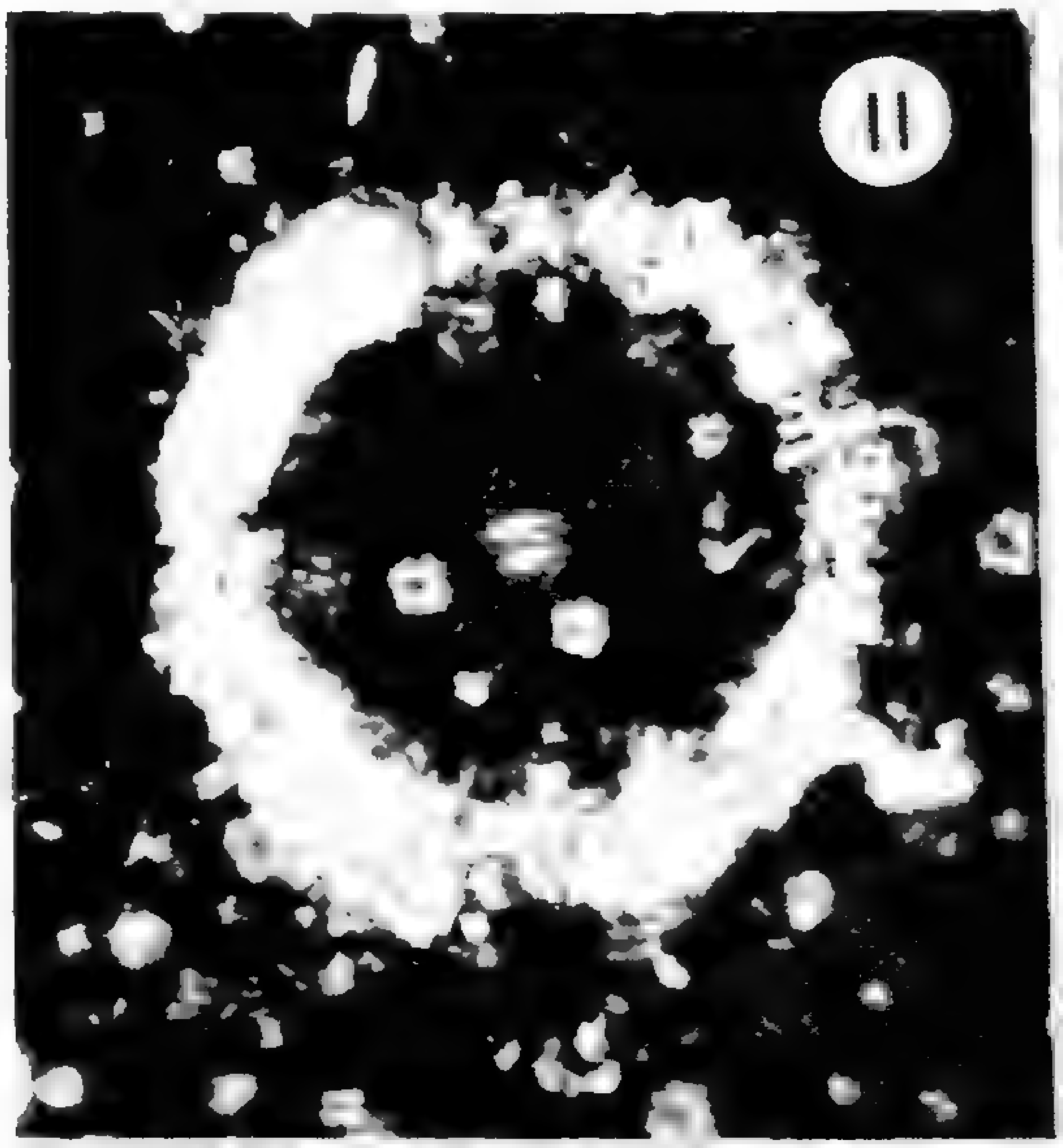
Figs. 18–23. Varied forms of crystallization. 18. Calcium malate, small compact crystalline body with elongated slender extensions, × 330. 19. *The same*, circular, very compact crystalline body, composed of slender, elongated, radially oriented units, × 330. 20. *Pereskiopsis* (*Boke B-18*), spheres stained in ruthenium red, × 180. 21. *The same*. Feeble anisotropy of spheres with two positions of extinction in polarized light, × 180. 22. Calcium malate, uncracked residue stained in ruthenium red, showing early stage in the formation of small spheres, × 110. 23. *The same*, stained uncracked residue, showing the formation of large crystals, × 110.

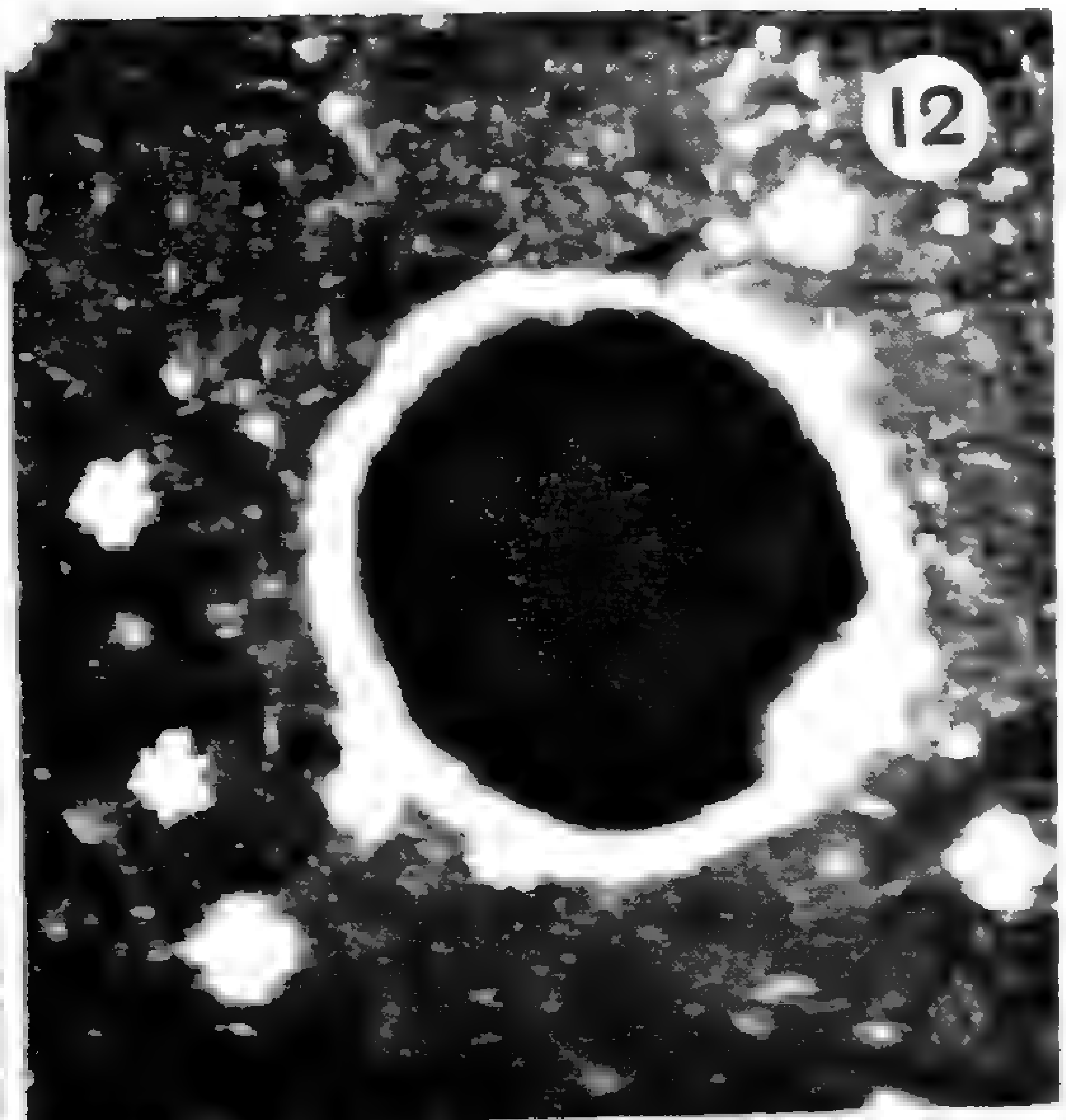


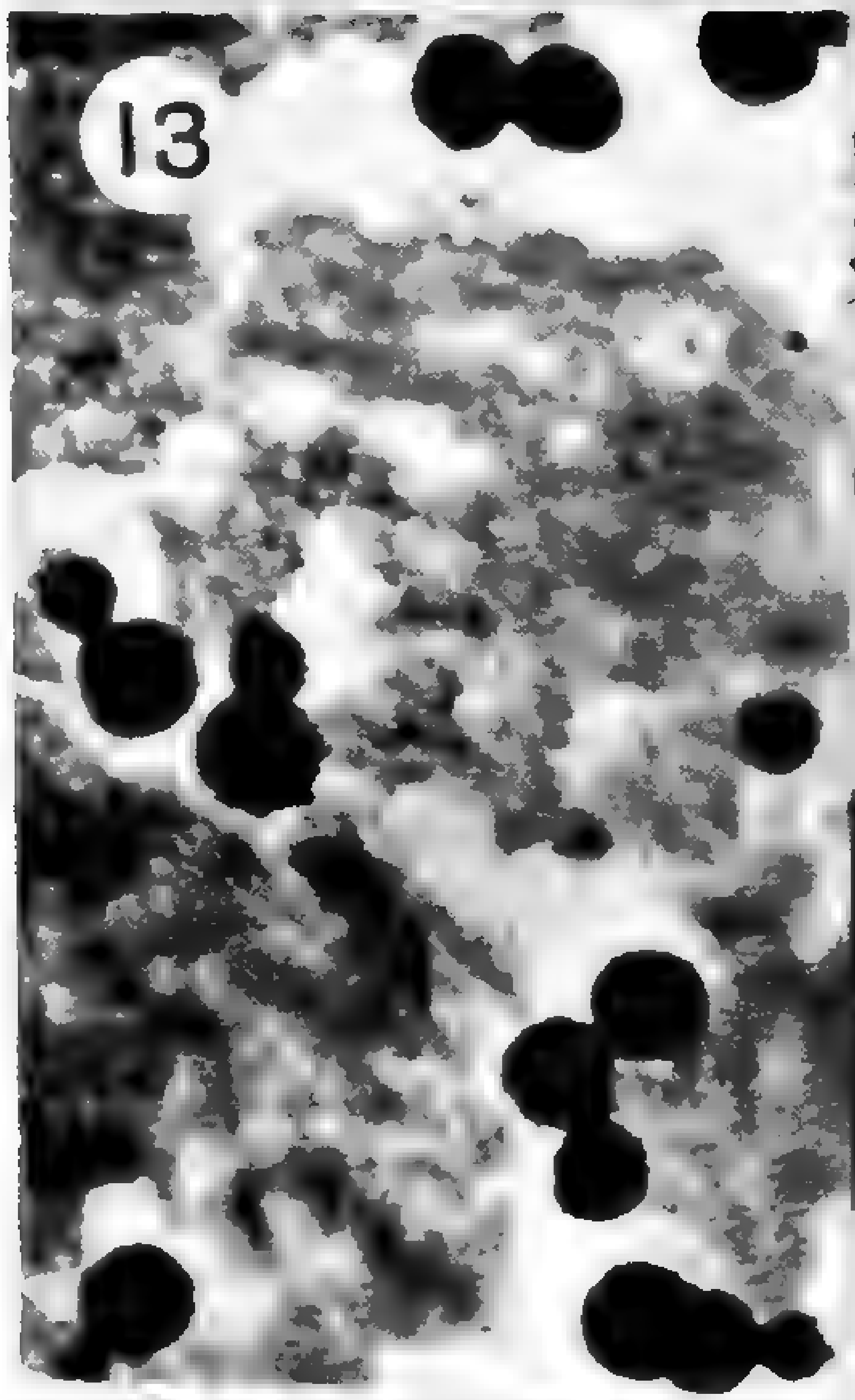
Bailey, Leaf-bearing Cactaceae. XVI

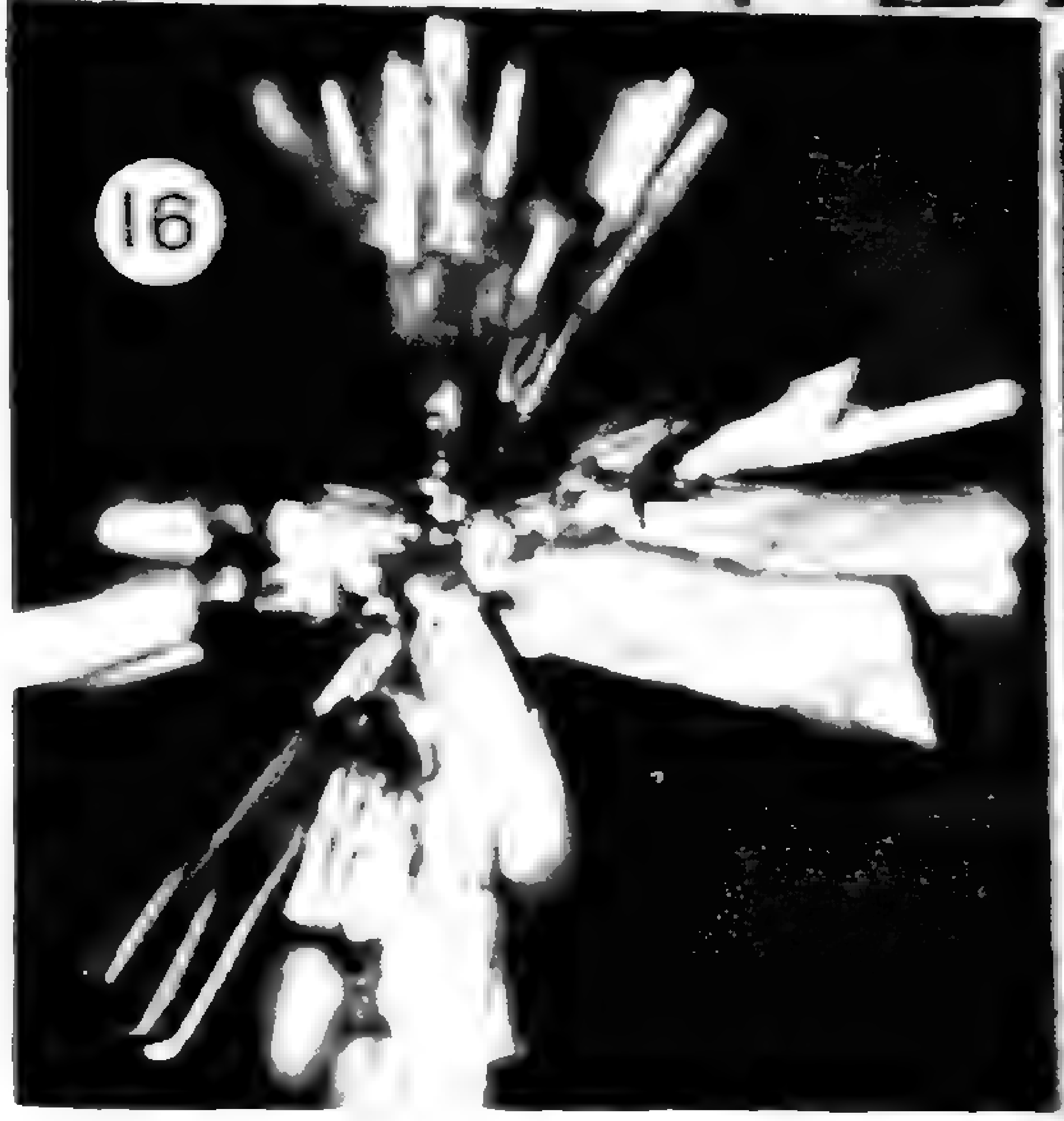


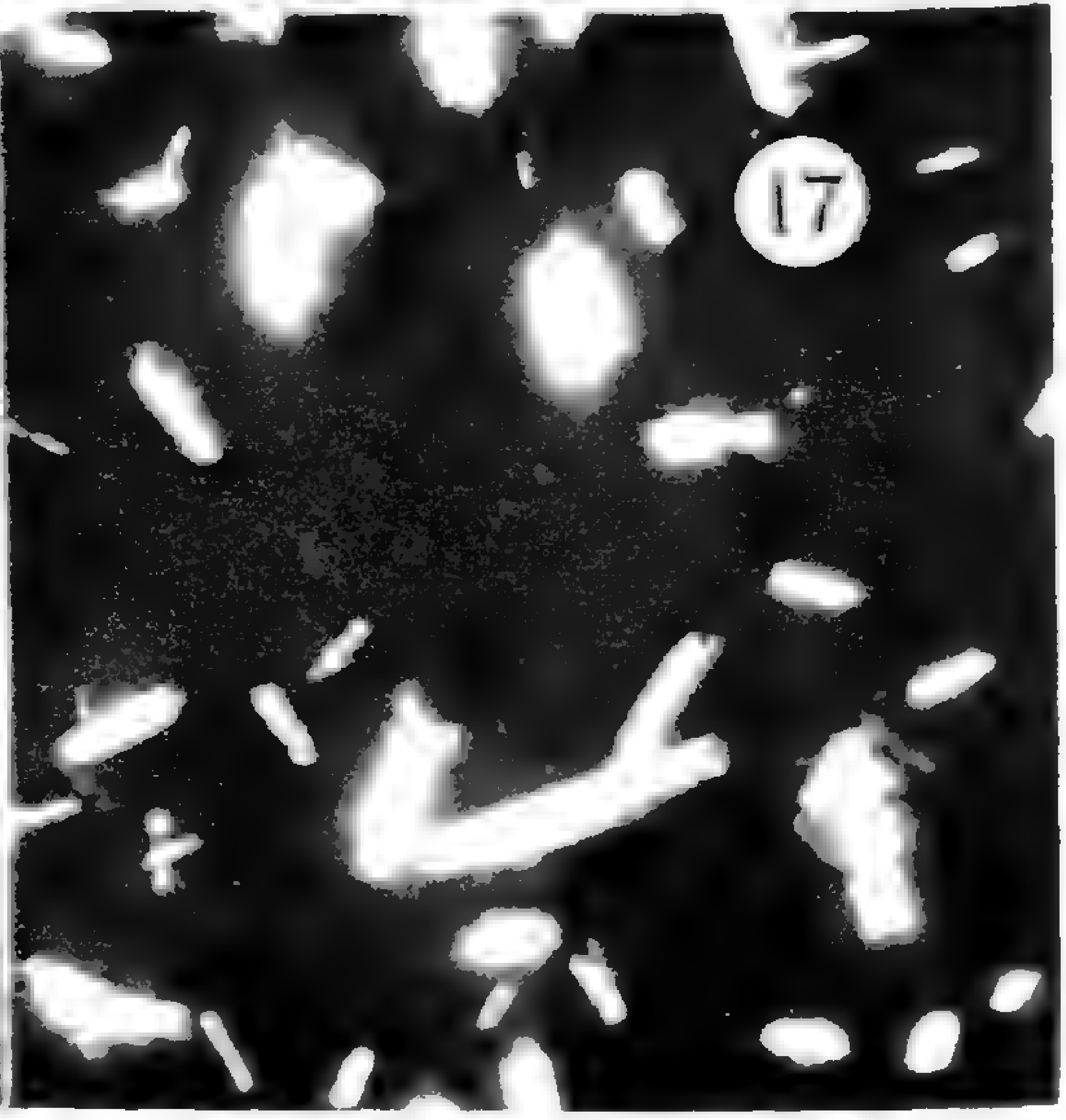
BAILEY, LEAF-BEARING CACTACEAE, XVI



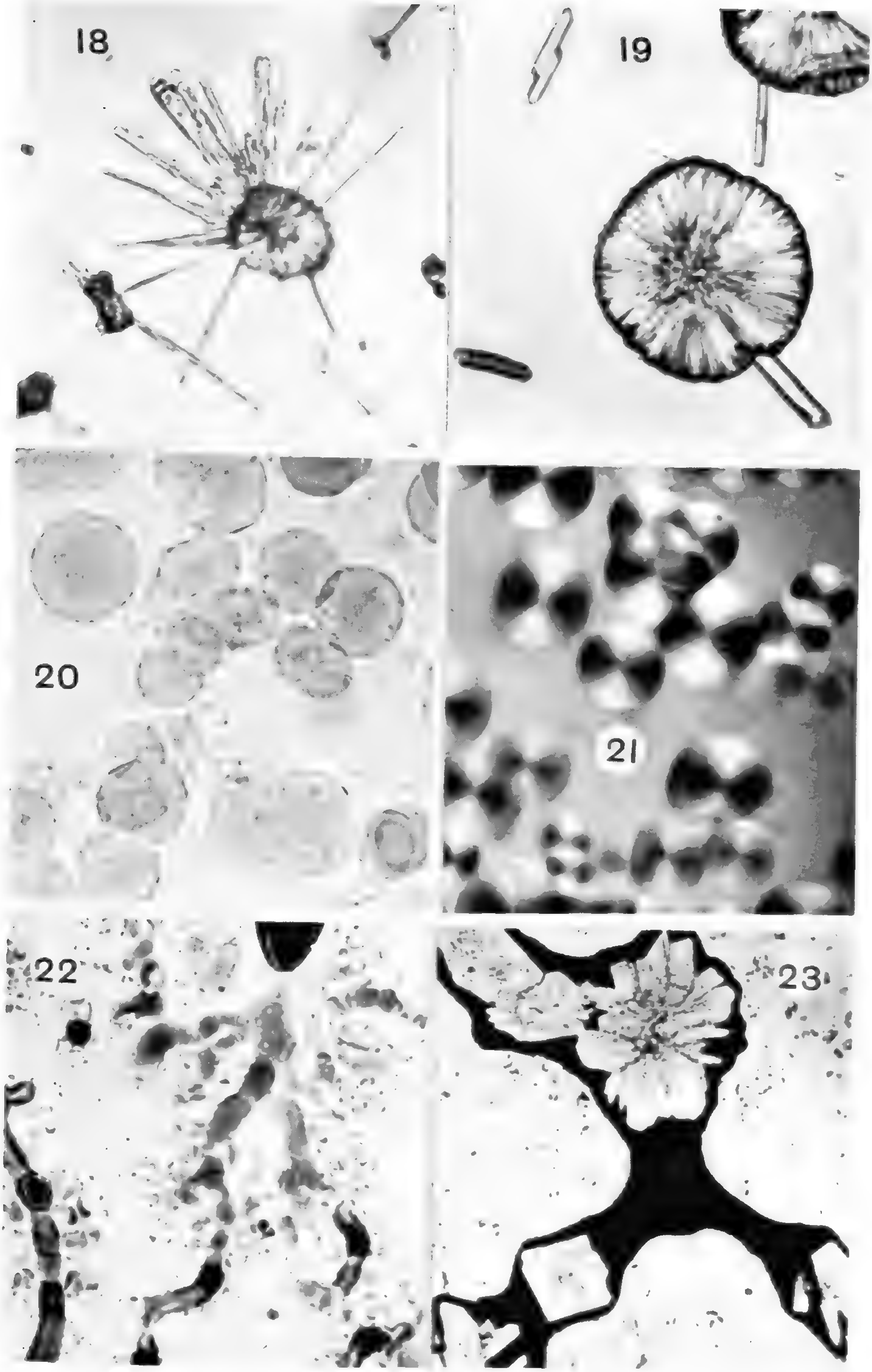








Bailey, Leaf-bearing Cactaceae, XVI



BAILEY, LEAF-BEARING CACTACEAE, XVI

THE SIGNIFICANCE OF THE REDUCTION OF VESSELS IN THE CACTACEAE

I. W. BAILEY [1]

SINCE THE EXTENSIVE SURVEY OF Bailey and Tupper (1918), broadly based summations of evidence from the vascular land plants, as a whole, demonstrate that vessels have developed in angiosperms by dissolution of membranes in scalariformly pitted tracheids, as they did in *Pteridium* among ferns. The major trends of specialization of such vessels in secondary xylem of numerous dicotyledonous families have been comprehensively investigated by various anatomists during the last 40 years, as they have in the primary xylem of monocotyledons by Cheadle (e.g. 1942, 1944). Thus, it is possible at present to arrange the vessels of both dicotyledons and monocotyledons in major trends of phylogenetic specialization. This can be done independently of the various systems of classifying angiosperms, thereby avoiding circular arguments based upon assumptions regarding the primitive or specialized character of plants in which the vessels occur. In other words, primitive vessels can be distinguished from specialized ones solely upon their own structural differences without dependence upon controversial taxonomic systems of classifying dicotyledons and monocotyledons.

In the secondary xylem of dicotyledons, the major trends of specialization in vessels are closely correlated with changes in the cytology of the cambium. The most significant modifications of the cambium and its tracheary derivatives appear to be largely unidirectional and are extensively irreversible. From a genetic point of view, it seems that, if mutations leading to prolonged reversals arise, they must in general be selectively disadvantageous since the adaptive specializations of vessels are concomitants of more or less profound changes in other cells and tissues and of physiological activities concerned in the survival of plants in which they occur.

It should be noted in this connection, however, that localized aberrations from the major trends of specialization in vessels do occur at times in vines, lianas, and other plants of divergent habits of growth. For example as shown by Carlquist (1962), the phenomenon of paedomorphosis leads to an extension during ontogenetic development of anatomical features of primary xylem into secondary xylem formed by the cambium. According to him, the phenomenon occurs in such anatomically highly specialized families as the Begoniaceae, Caricaceae, Compositae,

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[1] This investigation was supported in part by a grant from the National Science Foundation.

Crassulaceae, Goodeniaceae, Piperaceae, Portulacaceae, and Umbelliferae, particularly in certain herbs, stem succulents, and in "rosette shrubs" and "rosette trees." In the case of plants where the specialization of vessels in primary xylem lags behind that in secondary xylem, paedomorphosis may lead to the development of less specialized appearing vessels in the secondary xylem. But such divergent, superimposed aberrations do not result in extensive reversals to a primitive vesselless condition.

In discussions with botanists who are unfamiliar with the significance of anatomical evidence now available, one still meets individuals who argue that such primitively vesselless dicotyledons as the Winteraceae, *Tetracentron, Trochodendron, Amborella* and *Sarcandra* may once have possessed vessels and subsequently lost them. Similar arguments are advanced by taxonomists who wish to derive monocotyledons from herbaceous dicotyledons, the structure of the xylem in stems of arboreal Agavaceae being due, by implication, to evolutionary reversion to a primitive appearing vesselless condition. As a last resource in such arguments, the Cactaceae are cited as exhibiting a phylogenetic reversal to a vesselless condition.

Fortunately the Cactaceae provide unusually comprehensive and favorable evidence in the study of highly divergent trends of morphological specializations. These are so bizarre and so closely correlated, from ecological and physiological points of view, with adaptations for survival in excessively arid environments, as to leave few uncertainties regarding the directions in which phylogenetic changes are progressing. Furthermore, an unusually comprehensive and adequate record of the divergent trends of specializations is preserved in surviving representatives of the family. It is not essential to speculate, as one sometimes must in other families, regarding missing links in the major evolutionary sequences.

Morphological evidence indicates that the most primitive surviving representatives of the Cactaceae occur in the genus *Pereskia.* Such better known species as *P. sacharosa* Griseb., *P. bleo* DC., and *P. grandifolia* Haw., with their large thin leaves, have long been recognized by taxonomists as having a habit of growth and absence of succulence characteristic of many typically woody dicotyledonous trees and large shrubs. The internal structures of these species demonstrate that ancestral Cactaceae attained a high level of anatomical specialization in their cambium and vessels prior to the development of incipient succulence. Successive stages of accentuating succulence occur in other species of *Pereskia* and particularly in the leaf-bearing genera *Pereskiopsis* and *Quiabentia.*[2]

In the most primitive surviving Cactaceae, the fusiform initials of the cambium are much reduced in length and tend to be arranged in a stratified or "storied" condition such as occurs in dicotyledonous families that have attained a structurally advanced level of specialization. The vessel members formed by the fusiform cambial initials are correspondingly short and have simple porous perforations, whereas the libriform fibers

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[2] For detailed illustrations of the anatomy of these genera see fifteen papers by Bailey published in the Journal of the Arnold Arboretum, volumes **41** to **46**.

formed by the cambial initials elongate markedly during tissue differentiation and are of the highly specialized non-septate or septate, starch-storing modification.

In contrast to some families of the dicotyledons, vessels with highly specialized simple porous perforations have worked backward (phylogenetically) in the primitive Cactaceae throughout the primary xylem, occurring even in the first formed tracheary cells having annular and helical thickenings.

The tall, broader, more massively succulent representatives of the subfamilies Opuntioideae K. Sch. and Cereoideae K. Sch. commonly tend to retain more or less numerous vessels in their xylem. More conspicuous evidences of modification and reduction of vessels occur in the smaller more lowly forms of excessively xerophilous species, e.g. the mamillarias. In these plants, short, imperforate cells with annular and helical thickenings become increasingly abundant in the primary xylem and, by paedomorphosis, in the secondary xylem. Simultaneously fibers and vessels with bordered pits may be reduced in number or eliminated. Such structural aberrations were described and illustrated by Schleiden (1845) and Darbishire (1904) in their pioneering investigations.

Although more comprehensive and reliable investigations are needed to determine with accuracy whether vessels are ever completely eliminated throughout all parts of any of the Cactaceae, there is ample evidence available at present that the end-products of super-specialization in the xylem of the family in no way resemble the structure of such primitive vesselless dicotyledons as the Winteraceae, *Trochodendron, Tetracentron, Amborella*, and *Sarcandra*. The reduction of vessels in some representatives of the Cactaceae cannot be cited as evidence in favor of unsupported assumptions of an evolutionary reversal to a primitive vesselless condition.

It should be emphasized here, that in future investigations of anatomical differences in plants of divergent habits of growth more attention should be devoted to ecological and physiological influences in the habitats in which plants normally grow. This was recognized by Preston (1900, 1901) in his early investigation of certain cacti and has recently been stressed by Carlquist (1966) in connection with his extensive investigations of the xylem in Compositae.

Significant and reliable correlations between anatomy and physiological and ecological influences in specific habitats are more easily attainable in xerophilous plants where water-relations play a dominating role in survival. Cacti of the growth forms investigated by Preston have an extensive system of superficially located water-absorbing and -conducting roots and mechanically stronger, deeply penetrating anchoring roots. Reduction and elimination of fibers in the xylem tends to be conspicuous in the superficially located root system in contrast to the xylem of anchoring roots where vessels may be reduced in number. Thus from functional ecological points of view, in environments where temporary rains are of infrequent occurrence, the extensive superficial root system appears to be an adaptation for rapidly absorbing and transporting water for storage above ground in succulent stems. The structure of the xylem in other growth forms of excessively xerophilous cacti merits detailed future investigation, e.g. in those forming massive succulent anchoring roots with less extensive lateral roots. In addition, it remains to determine from a reliable physiological point of view whether the curious short cells with broadened annular and helical thickenings which attracted so much attention and discussion by earlier investigators of cacti, function primarily in storage of water, in strengthening excessively succulent tissues, or in both capacities, rather than fundamentally in translocation of sap.

Cheadle's numerous and comprehensive investigations (e.g. 1942, 1944) have demonstrated that in monocotyledons, in contrast to dicotyledons, vessels developed first in roots and subsequently became extended into their aërial parts. In the case of arboreal representatives of the Agavaceae, growing in arid environments, there is significant ecological evidence of why this should be. Their extensive superficial system of roots provides an essential adaptation, when rains occur, for absorption and rapid transportation of water for retention in their massive vesselless stems where concomitant adaptations for reduced evaporation can develop. The occurrence of primitive vesselless xylem in stems of such plants cannot be accounted for by assumptions of extensive anatomical reversals from highly specialized herbaceous dicotyledons.

In conclusion, it is advisable to comment upon the significance and utility of wood anatomy in the taxonomy and classification of angiosperms. As I emphasized in an earlier publication (1957), the major trends of specialization in xylem, when considered by themselves, are reliable in *negations*, owing to inherent difficulties in deriving a taxon with primitive xylem from one exhibiting a uniformly high level of anatomical specialization. Unfortunately, due to the frequent occurrence of parallel and convergent evolution, wood anatomy cannot be utilized by itself in reliable *positive* assertion without corroborative evidence from other parts of a taxon, e.g. the reproductive ones. In most families, morphological changes in different parts of the plants are not closely synchronized, some being precocious when others are markedly retarded. Assertions that anatomical characters are inherently more conservative than reproductive ones (some anatomists) and vice versa (many taxonomists), are no longer cogently reliable in view of extensive data now available. Since evidence from all organs and parts of plants must be harmonized if a natural classification of angiosperms is to be attained, data from wood anatomy should be given due consideration in taxonomy.

Anatomical evidence negates any possibility of deriving the primitive vesselless xylem of such relics as the Winteraceae, *Trochodendron*, *Tetracentron,* and *Amborella* from ancestors with vessels. However, wood anatomy, by itself, does not provide conclusive evidence that the Degeneriaceae, Magnoliaceae and other ranalian families were derived directly from the Winteraceae. Furthermore, although the anatomy of *Sarcandra* negates any possibility of deriving this genus from vessel-bearing genera of the Chloranthaceae, xylem anatomy alone does not provide reliable evidence for concluding that the latter genera were derived from *Sarcandra* rather from now extinct vesselless ancestors.

In the case of monocotyledons, xylem anatomy negates a derivation in the Agavaceae of primitive vesselless stems from vessel-containing ones, and particularly from those of herbaceous dicotyledons. But, it is not possible at present to determine which monocotyledonous families may have been derived from the Agavaceae. The retention of more primitive forms of vessels in the roots of some families, e.g. Amaryllidaceae, negates their derivation from existing Agavaceae. Of course, the possibility exists that such families may have diverged from ancestral Agavaceae, or plants of comparable form, prior to excessive specialization in their roots and reproductive organs.

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THE GOODENIACEAE IN THE SOUTHEASTERN UNITED STATES [1]

George K. Brizicky

Goodeniaceae R. Brown, Prodr. Fl. Nov. Holland. 1: 573. 1810, "Goodenoviae," nom. cons.

(Goodenia Family)

A very natural family of shrubs and herbs with usually alternate, exstipulate leaves; complete, bisexual, proterandrous, 5-merous flowers; irregular corollas; 5 free stamens; commonly 2-locular, usually inferior ovary; and a style bearing at the apex a pollen-collecting cup ("indusium") which subtends the stigma. Type genus: *Goodenia* J. E. Sm.

Eight of the fourteen genera are restricted to Australia. Of the six which also occur outside of Australia, *Selliera* and *Scaevola* are especially remarkable for their distributions, the former subantarctic (Australia, Tasmania, New Zealand, and Chile), the latter pantropical. Goodeniaceae are notable for their almost exclusive confinement to rather arid or periodically dry regions with open vegetation.

The chief peculiarity of the flowers is a pollen-collecting cup, which has attracted the attention of numerous botanists. This structure, comparable to, although not homologous with, the ring of stylar hairs in some genera of Campanulaceae, is perhaps a more specialized type of the same biological nature. The anthers closely surround the cup, and the pollen, which is released when the flowers are still in bud, is deposited in the cup (Fig. 1b). At this stage the stigma is very small and nonreceptive (Fig. 1d, e). During anthesis the pollen is shaken out by insect visitors or is forced out of the collecting cup by the growing stigma. After the pollen is removed from the collecting cup the stigma becomes receptive

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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 Carroll E. Wood, Jr., and Reed C. Rollins. This treatment follows the pattern established in the first paper in the series (Jour. Arnold Arb. **39**: 296–346. 1958) and continued to the present paper. The area covered includes North and South Carolina, Georgia, Florida, Tennessee, Alabama, Mississippi, Arkansas, and Louisiana. The descriptions are based primarily on the plants of this area, with any supplementary information in brackets. References which the author has not seen are marked by an asterisk.

The author is indebted to Dr. Wood for his many editorial suggestions and helpful criticism in the course of this work; to Dr. and Mrs. Richard J. Wagner for fresh fruits of *Scaevola*; and to Mrs. Gordon W. Dillon for her help in the preparation of the typescript. The illustrations were made by Arnold D. Clapman, primarily from flowering material collected by Dr. Wood (Fig. 1, a-i).

(FIG. 1f, g). Although self-fertilization has been reported, cross-fertilization seems to be the rule. Floral anatomical evidence suggests that the two- to one-locular ovary of Goodeniaceae is derived from four carpels (Carolin).

Development of the embryo seems to follow the Linum variation of the Solanad type. The embryological features of the family (ovules with one integument and thin nucellus, primary archesporium usually unicellular, monosporic 8-nucleate embryo sac, cellular endosperm, absence of haustoria, and the type of embryo development) suggest a relationship with Campanulaceae. Chromosome numbers of $2n = 14$, 16, and 18 appear to be typical for the genera of Goodeniaceae, with polyploids with $2n = 32$, 36, 48, 54, 64, 72, and 90 occurring at the specific and infraspecific levels.

Despite an abundant literature concerning the anatomy of the family, further comparative studies may be of taxonomic interest. The occurrence of three- to five-lacunar nodes and the presence of inulin as a storage carbohydrate in Goodeniaceae are notable.

Goodeniaceae are generally accepted as closely allied to the Campanulaceae-Lobelioideae (but cf. Carolin, 1960b) from which they differ chiefly in the lack of latex, in the presence of a pollen-collecting cup, and in the more complex anatomy of the cambial tissue. The monotypic Australian family Brunoniaceae (*Brunonia australis* J. E. Sm., $2n = 18$) is the closest relative of Goodeniaceae and has often been united with them. A relationship with Stylidiaceae is also presumed.

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1. **Scaevola** Linnaeus, Mant. Pl. Alt. 145. 1771, nom. cons.[2]

Shrubs [or herbs] with alternate [rarely opposite], simple, entire [or toothed], fleshy, isolateral [or bifacial], exstipulate leaves. Inflorescences axillary, simple to few-flowered compound dichasia sometimes reduced to a single flower, the terminal (central) flower sessile [or pedicellate] in the fork. Floral tube adnate to the ovary; calyx limb short, inconspicuously [or conspicuously], usually unequally, 5-lobed to subentire. Corolla white [yellow, purplish, or blue], 5-lobed, the long tube open to the base on the adaxial side, densely woolly inside, the lobes provided with very thin, membranaceous wings which are sharply folded inward in bud (induplicate-valvate). Stamens 5, alternate with the petals, free, with a conspicuous, cushion-like nectar gland[3] between the 2 abaxial ("anterior") stamens and a minute gland next to the odd adaxial ("posterior") stamen; filaments slender, ± equaling the corolla tube; anthers introrse, basifixed, 2-locular at anthesis, provided at tip with a small ± ovate appendage (prolongation of connective), longitudinally dehiscent; pollen usually medium, subprolate, 3-colporate, punctulate to subreticulate, 2-nucleate. Gynoecium 4-carpellate, appearing 2-carpellate, syncarpous; stigma slightly 2-lobed, subtended by a ciliate pollen-collecting cup ("indusium") hairy [or glabrous] without; style elongated, ±cylindrical, simple, hairy at base; ovary inferior, 2-locular [or 1-locular]; ovules usually solitary in each locule, anatropous and epitropous, ascending from base of partition, 1-integumented, with a thin nucellus. Fruit a juicy [or nutlike], blue-black [or white], 1- or (more rarely) 2-seeded drupe; endocarp bony [or with a corky outer layer], irregularly warty to subreticulate on the surface. Seed whitish, obovate in outline, planoconvex in cross section; seed coat thin, soft; endosperm fleshy; embryo straight; cotyledons flat [or ± semicircular in cross section], inequilaterally elliptic, divergent; radicle short, inferior. TYPE SPECIES: *Lobelia Plumieri* L. = *S. Plumieri* (L.) Vahl (*S. Lobelia* Murr., nom. illegit.).[2] (Name from Latin, *Scaevola*, a diminutive of the Roman surname *Scaeva*, the Left-handed, apparently after a legendary one-handed Roman hero,

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[2] Although the conservation of *Scaevola* L. is unnecessary (see Rickett & Stafleu, Taxon **9**: 122. 1960, and the International Code of Botanical Nomenclature 315. 1961), retention of this name in the list of *Nomina Generica Conservanda* of the Code was authorized by the International Botanical Congress in Montreal in 1959.

Conservation of the type of *Scaevola* also appears to be unnecessary. Having established the genus *Scaevola*, Linnaeus mentioned under *Lobelia* (Mant. Pl. Alt. 481. 1771) a single species, "Lobelia *plumieri*. *Scaevola* distincti generis," which, although not transferred by Linnaeus to *Scaevola*, became automatically the type of the genus. However, *L. Plumieri* L., of the *Species Plantarum* (as well as *Scaevola Lobelia* Murr., nom. illegit.), was a mixture of two species, the Indo-Pacific and Indo-Atlantic beach-berries. After Gaertner (Fruct. Sem. Pl. **1**: 119. 1788) segregated the Indo-Pacific species as *Lobelia Taccada* from *L. Plumieri*, the Indo-Atlantic species retaining the specific epithet *Plumieri* became the type of *Scaevola*, as *S. Plumieri* (L.) Vahl.

[3] This character, observed in *Scaevola Plumieri* and *S. Taccada*, apparently has not been reported previously for the genus.

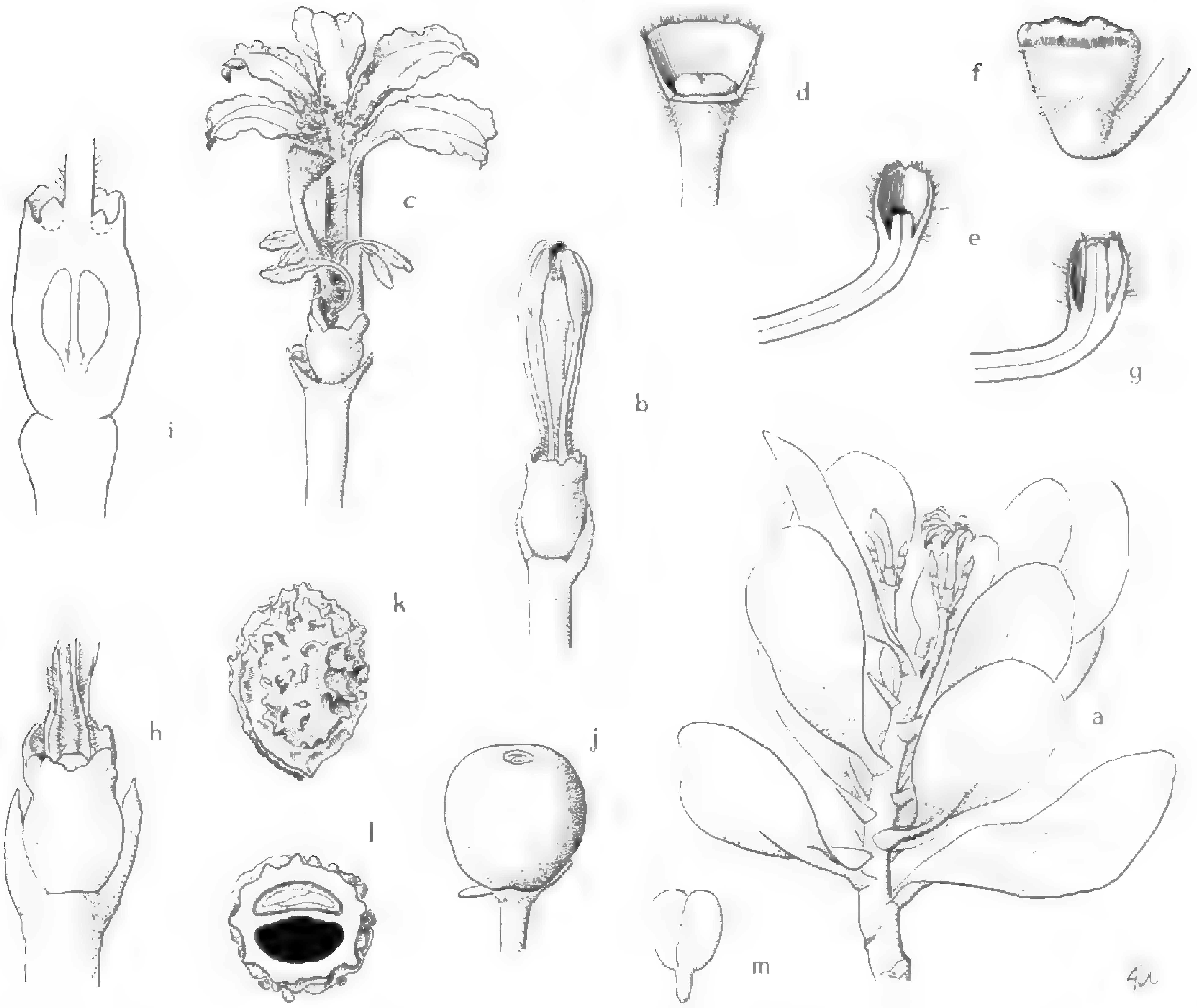

FIG. 1. **Scaevola.** a–m, *S. Plumieri*: a, flowering branch, × 1/2; b, flower bud, corolla removed to show pollen-collecting cup and introrse anthers at time of dehiscence, × 2; c, flower, from adaxial side, × 1 1/2; d, collecting cup at time of dehiscence of anthers, one side removed to show undeveloped stigma, × 4; e, cup, undeveloped stigma, and style (with stylar canal) at anthesis in semidiagrammatic vertical section (at right angles to "d"), × 4; f, mature stigma protruding from collecting cup, × 4; g, same, in semidiagrammatic vertical section, × 4; h, base of flower from abaxial side, corolla removed to show large nectar gland (protruding above calyx lobes), × 3; i, ovary in diagrammatic vertical section to show large abaxial nectar gland, small adaxial gland, and solitary epitropous ovules, × 4; j, mature fruit, × 1; k, stone, × 2; l, stone in semidiagrammatic cross section to show seed (endosperm stippled, cotyledons white) and empty locule (black), × 2; m, embryo, × 2.

Gaius Mucius Scaevola, because of the corolla somewhat resembles the shape of a man's hand.) — BEACH-BERRY.

The genus comprises about 80 species, 60 restricted to Australia. Most of the remaining species belong to the almost exclusively extra-Australian sect. SCAEVOLA (§ *Sarcocarpaea* G. Don), centered in the Pacific, but with two littoral species, *Scaevola Taccada* (Gaertn.) Roxb. (*S. frutescens* Krause, *S. sericea* Vahl), $2n = 16$, and *S. Plumieri*, $2n = 16$, of wide tropical distribution. The former species is confined to the Eastern Hemisphere, ranging from Madagascar and Mauritius to Ceylon and through southeastern Asia, Malesia, and tropical Australia to the central Pacific.

while the latter is distributed from Ceylon and India to Mauritius and Madagascar, and around tropical Africa to tropical America, the West Indies, southern Florida, and Bermuda. In southern Florida, *S. Plumieri* occurs from Key West northward to about Brevard County, on the east coast, and sporadically on the west coast, mostly on islands (with the exception of Pine Island, Lee County, and one or two others), to the mouth of Tampa Bay. Beyond our area the species has been recorded in the United States from Padre Island, Texas, and very sporadically on both coasts from southern Baja California and Yucatán to Ecuador and Brazil. A pioneer species on fresh calcareous sands of the upper beach and foredunes, *S. Plumieri* is usually associated with other dune-binding species, e.g., *Ipomoea stolonifera* (Cyrill.) J. F. Gmel. and/or *I. Pes-caprae* (L.) R. Br., *Uniola paniculata* L., *Croton punctatus* Jacq., *Tournefortia gnaphalodes* R. Br., and *Suriana maritima* L. It usually grows in dense clumps, sometimes forming large patches as it slowly spreads under the sand by stolons rooting at the nodes. The irregular distribution of *S. Plumieri* is probably due primarily to its rather low resistance to the destructive action of hurricanes and gales and locally to the action of cattle and goats which eat the entire plant.

Despite the existence of many inland species growing in rather diverse habitats, the genus seems, in general, to be adapted to a littoral life. The thick cuticle and epidermis, the massive development of palisade tissue, the development of water-storage parenchyma, and also, in some species, of water tracheids (*Scaevola Plumieri*, *S. crassifolia* Labill.) and/or mucilage cells (*S. Taccada*, *S. crassifolia*) in the leaves are regarded as xerophilous adaptations in littoral species. A resinous substance excreted by the peltate glandular hairs presumably protects young organs from desiccation. Stomata usually occur on both leaf surfaces. A number of primitive features (scalariform perforation plates, diffuse axial parenchyma, and a tendency toward transitional intervascular pitting) have been found in the wood of a few species of sect. SCAEVOLA (*S. Plumieri*, *S. Taccada*, and *S. Gaudichaudiana* Cham., $2n = 16$).

Large bees have been mentioned as very frequent visitors of the flowers of *Scaevola Taccada* and bees and butterflies of *S. Plumieri* (in South Africa and Madagascar). Chromosome numbers, known in about 30 species, are almost invariably $2n = 16$, but tetraploids and/or hexaploids ($2n = 32$ and 48) have also been found in three species.

The fleshy drupes of sect. SCAEVOLA are very probably dispersed locally by birds, but the stones of some species of this section (*Scaevola Plumieri*, *S. Taccada*, and *S. mollis* Hook. & Arn., $2n = 16$) and of sect. XEROCARPAEA G. Don (*S. porocarya* F. Muell., $2n = 16$, *S. crassifolia*, *S. globulifera* Labill., $2n = 16$, and *S. thesioides* Benth.) have been reported as water borne and liable to dispersal by sea currents. These stones usually owe their buoyancy to a corky outer layer (*S. Taccada*) sometimes in accompaniment with empty lacunae in the endocarp (*S. mollis*, *S. porocarya*). Stones of *S. Plumieri* lack a corky layer, but usually only one of the two locules holds a seed, and the empty locule is watertight, giving floating power to the stone. It is noteworthy that of all the species with buoyant stones only *S. Taccada* and *S. Plumieri* are widely distributed. Guppy showed that stones of the former can float in sea water for a year or more, while those of the latter can, on the average, endure in a sound condition for only four or five months.

Scaevola is closely related to *Goodenia* and *Verreauxia* Benth. The genus is in need of a taxonomic revision.

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ANATOMY OF THE PALM RHAPIS EXCELSA, III. JUVENILE PHASE

P. B. Tomlinson[1] and Martin H. Zimmermann

In the first paper of this series (Zimmermann & Tomlinson, 1965) we showed that in the adult aërial stem of *Rhapis excelsa* all vascular bundles maintain their individuality and proceed indefinitely through the stem. At intervals, each vertical bundle becomes a leaf trace, but gives off another vertical bundle prior to its departure into the leaf. The number of vertical bundles given off by a leaf trace can vary from zero to two or more, although it is normally one. This means that the number of bundles throughout the length of the stem does not necessarily have to remain constant. Indeed, such changes have been described by Strasburger (1906); they are, however, not great, the number remaining well within the same order of magnitude. In the seedling the situation is quite different. Before the palm can begin its growth in height it has to establish the stem diameter; and the number of vascular bundles has to increase several orders of magnitude. It is the purpose of this paper to account for the multiplication of vascular bundles in the aërial axis as it enlarges by primary growth, following the establishment of the seedling.

The phase of development which succeeds the establishment of the seedling is developmentally and morphologically quite distinct from the subsequent vegetative and reproductive phases; it has, therefore, been referred to as the "juvenile phase" (Tomlinson, 1964). In most palms morphological features of this phase include juvenile leaves (Tomlinson, 1960), leaves transitional to the adult type of foliage, numerous adventitious roots and, in multiple-stemmed palms, lateral vegetative branches. These are all borne on an obconical axis in which the internodes are usually much congested.

Literature on early stages of growth in palms is extensive, but deals almost exclusively with the germination of the seed, its early development, and with the anatomy and morphology of the seedling (e.g., Von Mohl, 1824; Gatin, 1906, 1912). Anatomical studies have been restricted to the vascular system of cotyledon, first plumular leaves, and the vascular transition between seedling, root, and stem (e.g., Gehrke, 1887; Micheels, 1889; Schlickum, 1896; and more recently Ginieis, 1952). The gross morphology of later stages has been considered by Karsten (1856). Unfortunately, our literature search has revealed no specific information about the seedling of *Rhapis excelsa*.

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[1] Research by P. B. T. on the anatomy of the palm stem is supported by National Science Foundation Grant GB 2991.

The significance of the post-seedling or juvenile phase of growth in the development of palms and other monocotyledons seems to have been little appreciated. An attempted analysis of the vascular system of the seedling of *Trachycarpus* by Suessenguth (1921, p. 50) is incorrect since it is based on theoretical principles which we now know are quite mistaken (Tomlinson & Zimmermann, 1966a). Helm (1937) discusses growth of palm seedlings in terms of the establishment of the primary thickening meristem which maintains the massive primary axis of the palm in the adult stage. The primary thickening meristem is essentially the end result of the juvenile phase of growth. That this phase of growth has been overlooked is indicated by the absence of any English term to describe it. It was not until 1936 that Troll first clearly distinguished the initial axial development of the juvenile phase as "Erstarkungswachstum" ("strengthening growth") from the continuing "Primärdickenwachstum" ("primary thickening growth") which maintains the diameter of the adult palm stem *after* the maximum diameter of the stem has been established in the juvenile phase (see also the discussion in Helm, 1937). Both German terms did exist prior to 1936 but they were used indiscriminately to describe primary thickening growth. Since the literal translation of the German word "Erstarkungswachstum" would be somewhat misleading, we suggest the term *establishment growth* for the type of growth in the juvenile phase which leads to the establishment of the primary thickening meristem. Since this type of growth involves the production of internodes with successively greater diameters, it produces an inverted conical structure.

This type of growth is exhibited by *Rhapis* which is suitably small for microscopic analysis. The only previous illustration of the vascular system in the juvenile axis of a palm is one of the coconut by Von Mohl (1824, *Fig. Q3*) which does not, however, throw light on the problem of vascular bundle multiplication. Our own study of the juvenile phase of *Rhapis* is concerned solely with this problem in structural terms.

MORPHOLOGY OF THE JUVENILE AXIS

Plants of the age investigated are illustrated in FIG. 1A. Earlier stages of seedling development are not shown. At the age illustrated the obconical outline of the axis is obscured by the development of numerous adventitious roots and vegetative branches. The latter arise from buds in the axils of basal leaves and grow out in order of their age (buds and suckers numbered in FIGS. 1B and C, 1 being youngest). Branches grow out as short rhizome segments (FIG. 1C) thereby initiating the sympodial rhizome system described in the second paper of this series (Tomlinson & Zimmermann, 1966b). In the aërial parent axis the transition to the adult vegetative phase is marked by elongation of the most distal internodes, once the maximum diameter has been reached (FIG. 1B). This transition is associated with suppression of axillary buds. No roots are borne on the distal part of the stem. Buds only recur distally in the reproductive phase as inflorescences which are often aborted.

MATERIALS AND METHODS

Propagation of *Rhapis excelsa* is normally by rhizome offsets because viable seeds are not readily available in South Florida. We are, therefore, indebted to Mr. Mulford B. Foster of Orlando, Florida, who generously supplied several 6-month-old seedlings on which this investigation is based. These were cultivated at the Fairchild Tropical Garden for an additional 6 to 18 months until they were fixed, at the age of 1 to 2 years, for anatomical study.

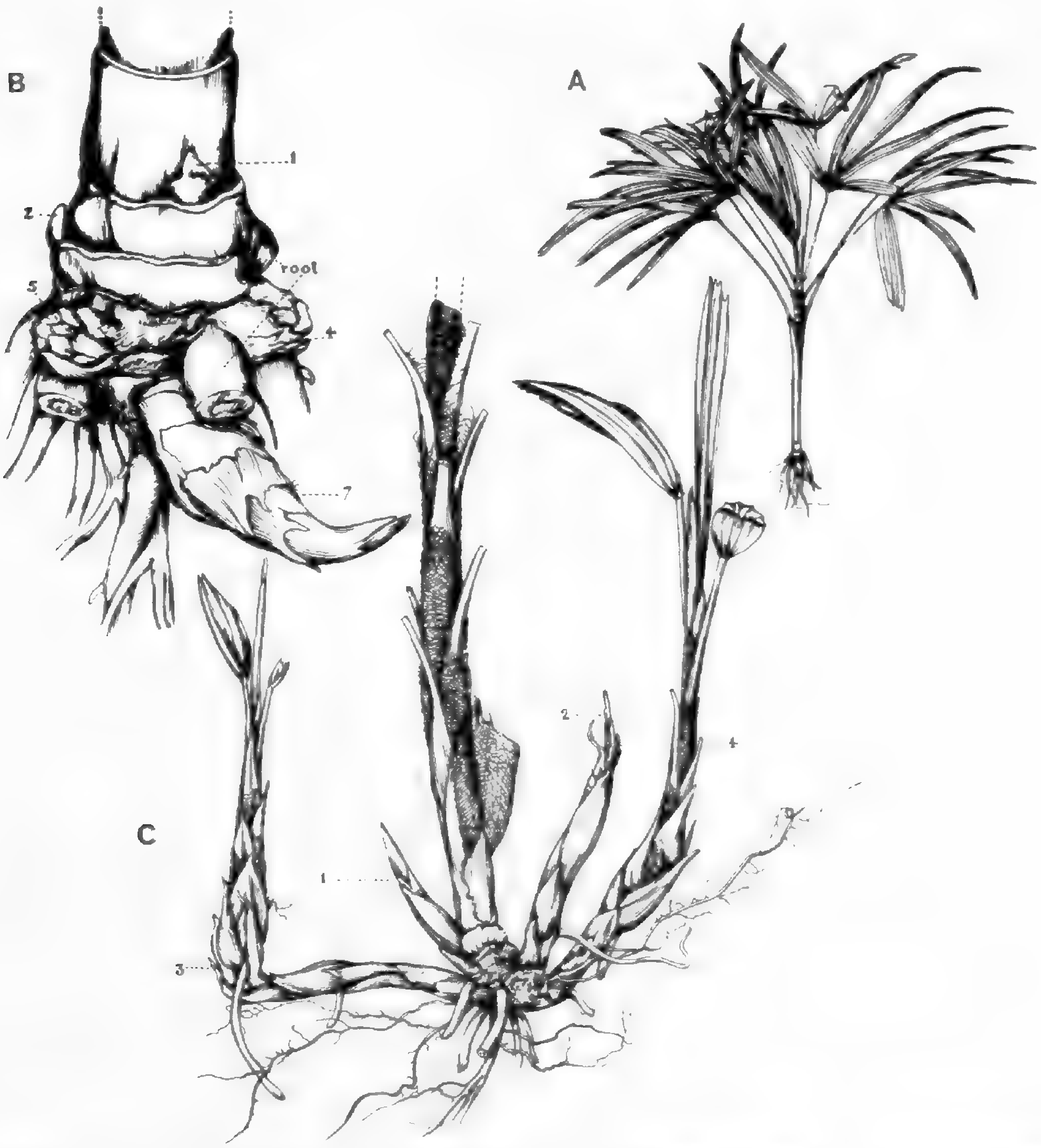

FIGURE 1. Morphology of juvenile phase in *Rhapis excelsa*. A. General habit of 1-year-old seedling, × 1/8. B. Base of same axis, leaves removed, × 2; early stages in development of axillary suckers. C. Older, more vigorous seedling, × 1/4; rhizomatous development of axillary suckers. In B and C, 1–7 indicate successive axillary suckers which develop in order of their age, 1 youngest, 7 oldest.

For microscopic analysis, continuous serial sections 30 μ thick of two seedling axes were cut on the sliding microtome and stained in safranin and Delafield's haematoxylin, as described previously. A complete series of sections was mounted, not every tenth as in previous studies, because the congested vascular system could only be understood by photographing each section. Each section was mounted on a separate slide, as is now our standard practice, in order that the optical shuttle method of aligning successive sections in the camera frame could be used (Zimmermann & Tomlinson, 1966). Photography of serial microtome sections was again supplemented by direct photography of successive surface cuts of seedlings clamped in the sliding microtome.

GENERAL ANATOMY OF THE JUVENILE AXIS

Over-all increase in diameter of the axis in the juvenile phase of growth of *Rhapis* is illustrated in FIGS. 2–4, representing sections at successively higher levels from one of the microtome series. Increase in certain dimensions in the same series is given in TABLE I.

TABLE I. **Increase of Certain Dimensions in the Seedling Axis of Rhapis excelsa**

Slide number	Level (mm.)	Average cortex diam. (mm.)	Central Cylinder			
			Av. diam. (mm.)	Approx. no. vascular bundles	Av. diam. vascular bundles	
					Periphery μ	Center μ
1 (FIG. 2A)	0	0.8	0.7	8	—	—
50 (FIG. 2B)	1.5	1.2	1.4	38	150	150
101 (FIG. 2C)	3.0	2.0	2.4	82	150	180
200 (FIG. 3)	6.0	1.6	5.5	160	300	240
349 (FIG. 4)	10.5	1.3	8.0	400	450	330

Axis outline irregular owing to distortion imposed by numerous root and branch insertions. Surface layers either resembling those of rhizome, or more usually with irregular divisions, but without a regular phellogen, cells lignosuberized, abundantly tanniniferous and forming an irregular periderm. Cortex very wide in lowest levels and exceeding central cylinder, but becoming proportionately narrower in higher levels (TABLE I). Cortical ground parenchyma irregular, outer layers compact, small-celled; inner layers less compact, often showing evidence of belated radial enlargement especially in association with branch insertions. Cortical fibrous strands well developed at all except very lowest levels, fibrous strands up to 120 μ wide, largest including narrow central vascular elements. Innermost cortical layers often free of fibrous strands. Central cylinder not delimited by endodermis or other specialized layer but by irregular region of somewhat congested vascular bundles. Central vascular bundles not congested. Vascular bundles irregular in transverse outline, leaf traces recognized by oblique, often more or less horizontal passage from central cylinder through cortex. Diameter of bundles increasing upwards (TABLE I), largely due to increase in amount of fibrous sheathing tissue, especially in peripheral bundles (cf. FIGS. 2–4). Metaxylem elements narrow, irregular, indistinct from protoxylem at lowest levels. Starch abundant in ground parenchyma except at periphery of cortex. Tannin cells mostly restricted to outer cortex. Stegmata (silica cells) common next to fibers of bundles in both cortex and central cylinder.

COURSE OF VASCULAR BUNDLES

Although complex, the distribution of vascular bundles can be interpreted readily in the light of our analysis of the vascular system in the aërial stem. The close interlinking of trace systems from roots and branches,[2] indicative of a close developmental relation, does not obscure the vascular system of the axis itself. Vascular systems of central cylinder and cortex remain distinct, although less so than in rhizome and aërial stem.

1. CENTRAL CYLINDER. Cinematographic analysis reveals frequent *leaf traces* passing more or less horizontally into leaves, and readily distinguished from the numerous *vertical bundles* cut more or less transversely in transverse sections. Vertical bundles are transformed into leaf traces by change from a vertical to a horizontal course. The constant relation between leaf traces and continuing vertical bundles which was found in the aërial stem does not exist in the seedling axis. This is discussed later. In addition to this main vascular system there is an interlinking network of usually narrow bundles which correspond to the bridges of the adult stem. They are sufficiently extensive to be referred to as an *anastomosing bridge system.*

Vertical bundles. Traced upwards, the distance of vertical bundles from the periphery of the central cylinder increases so that the bundles come to occupy the uncrowded center of the stem, prior to their conversion into leaf traces. This apparent displacement is largely the result of the widening of the central cylinder in the obconical axis. Vertical bundles may even diverge from the stem center, but at a shallower angle than the limit of the central cylinder. The helical pathway of the central bundles which is characteristic of the aërial stem is established early and again it corresponds in direction (but not in magnitude) to the phyllotactic spiral.

Leaf traces. Vertical bundles become leaf traces by an abrupt change to an approximately horizontal direction. Unlike the bundles of the adult axis, however, there is no fixed relation between leaf traces and continuing vertical bundles. In the lowest internodes where there are few bundles, the vertical part of each bundle is short and all bundles diverge from

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[2] Insertion of root and branch traces will be described in detail in a later paper in this series.

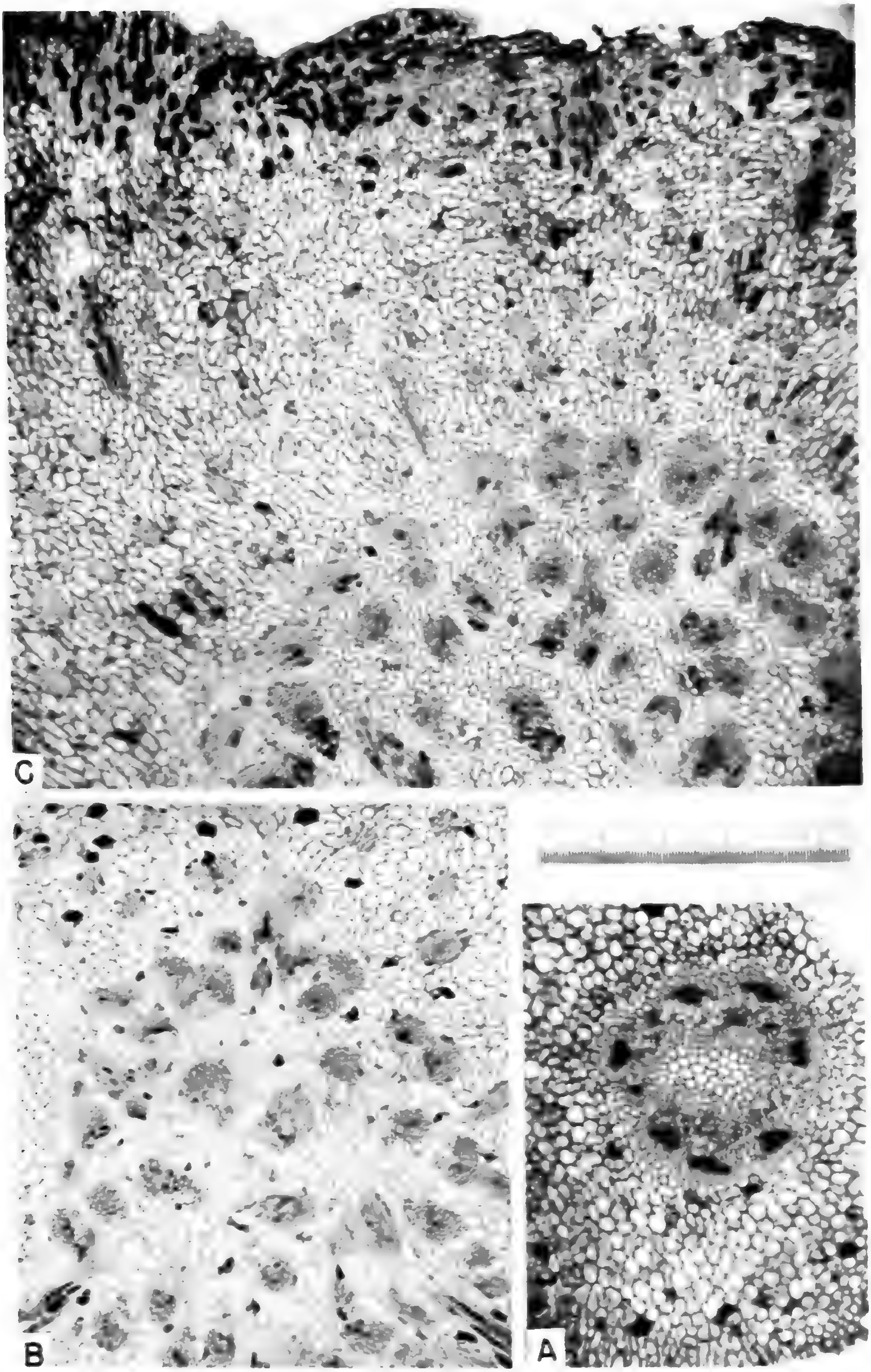

FIGURE 2. Transverse sections of a juvenile axis of *Rhapis excelsa* at successively higher levels. A. At approximate level of cotyledonary node. B. 1.5 mm. above A. C. 3 mm. above A. Scale equals 1 mm.

about the same depth in the stem center. Distally, as the total number of bundles increases, the length of the vertical part of the bundles' course rapidly increases and differences between major, intermediate, and minor leaf traces become evident as the trace complement to each leaf becomes larger.

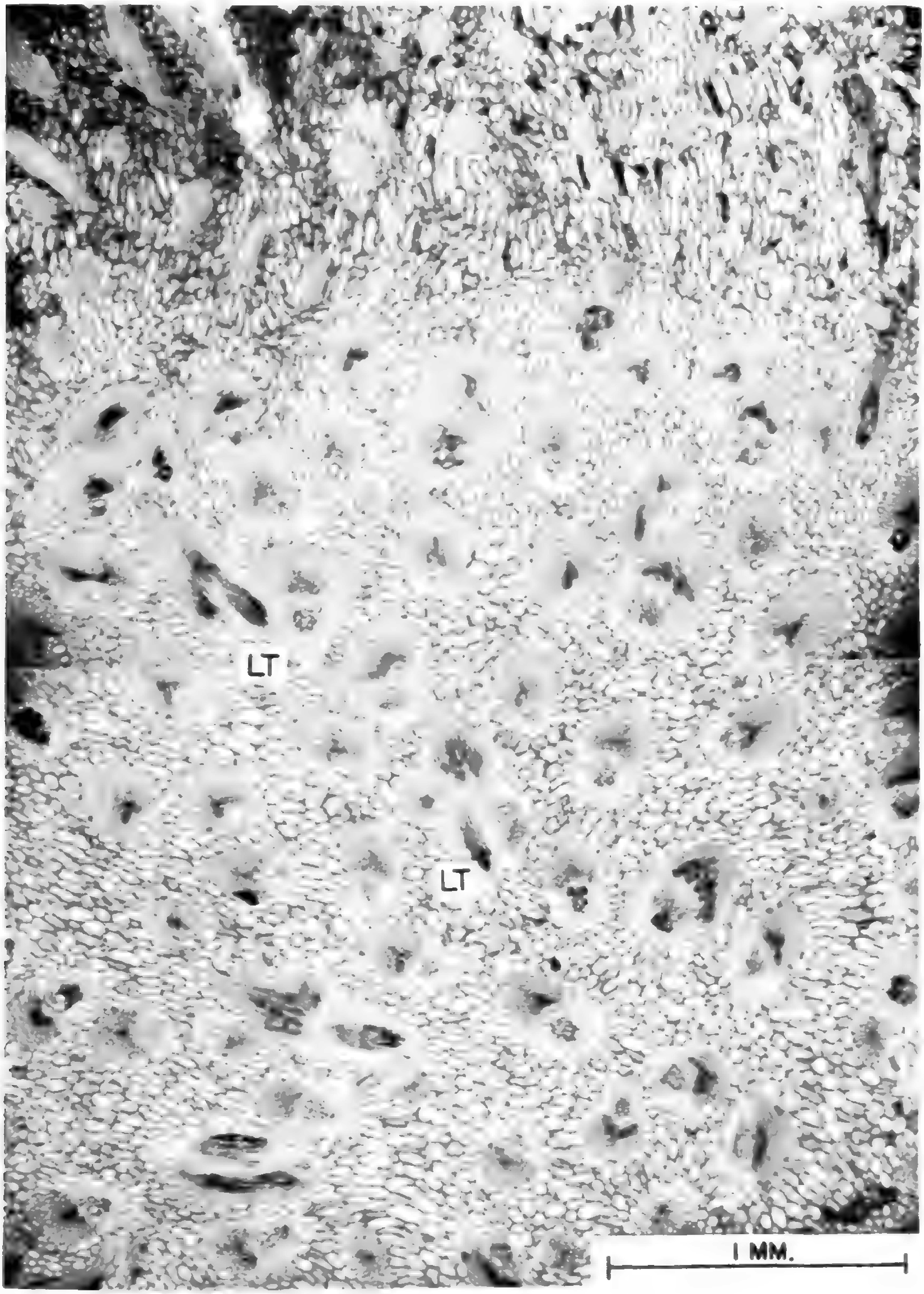

FIGURE 3. *Rhapis excelsa*, same axis as illustrated in FIG. 2, 6 mm. above 2A, same magnification. Two leaf traces (LT) indicated, the one in the center of the figure with two recently derived bridges.

Anastomosing bridge system. As in the adult axis departure of a leaf trace is associated with the development of bridges which are very pronounced in the juvenile phase. The first bridge originates as the vertical bundle turns outward as a recognizable leaf trace in the stem center. Subsequently more (up to 10) originate as the leaf trace passes through the crowded periphery. Bridges may even be given off by the leaf trace as it passes through the cortex, such bridges becoming incorporated into the cortical system. Bridges in the juvenile axis resemble those of the adult stem in diverging upwards from a leaf trace and often linking immediately with a nearby vertical bundle. Otherwise they may differ in three important respects: (a) they are often very long, extending irregularly without interruption through several internodes; (b) they commonly split; (c) they, or their branches, ultimately join vertical bundles or reach the periphery of the central cylinder where they become vertical bundles. Bridge bundles are narrow, with inconspicuous vascular elements although the largest resemble peripheral vertical bundles in the base of the stem. Small bridges may lack vascular tissue and appear as narrow fibrous strands. From the manner in which they diverge, upwards from leaf traces, these bridge bundles seem developmentally homologous with those of the aërial stem but their ramifications and extensive development justify referring to them as an anastomosing system. Root and branch traces connect extensively with these bridges or their branches.

2. CORTEX. The cortical system of fibrous bundles remains largely independent of the central system. Cortical bundles traced downwards from the leaves anastomose freely to form a reticulum but many bundles end blindly below. The reticulum is much distorted around branch and root insertions. Interconnection between vascular systems of cortex and central cylinder is somewhat more pronounced than in the rhizome and aërial stem, either because of direct interchange of vascular bundles between the innermost region of the cortex and the periphery of the central cylinder or because leaf traces, as they pass across the cortex, link with the cortical reticulum via bridges.

MULTIPLICATION OF VASCULAR BUNDLES

We come now to the most interesting anatomical aspect of the juvenile axis, namely the question of how the increase in number of vascular bundles is accomplished during establishment growth. In TABLE I it can be seen that during a height increase of 10.5 mm. the seedling axis had increased from 0.7 to 8 mm. in diameter (central cylinder) and from 8 to 400 vascular bundles. Thorough study of numerous motion picture sequences have revealed the following processes.

Ultimate branches of the anastomosing bridge system reach the periphery of the central cylinder, turn erect there and become vertical bundles. Each leaf trace thus contributes (via the anastomosing system) on the average more than one vertical bundle. In the higher levels of the seed-

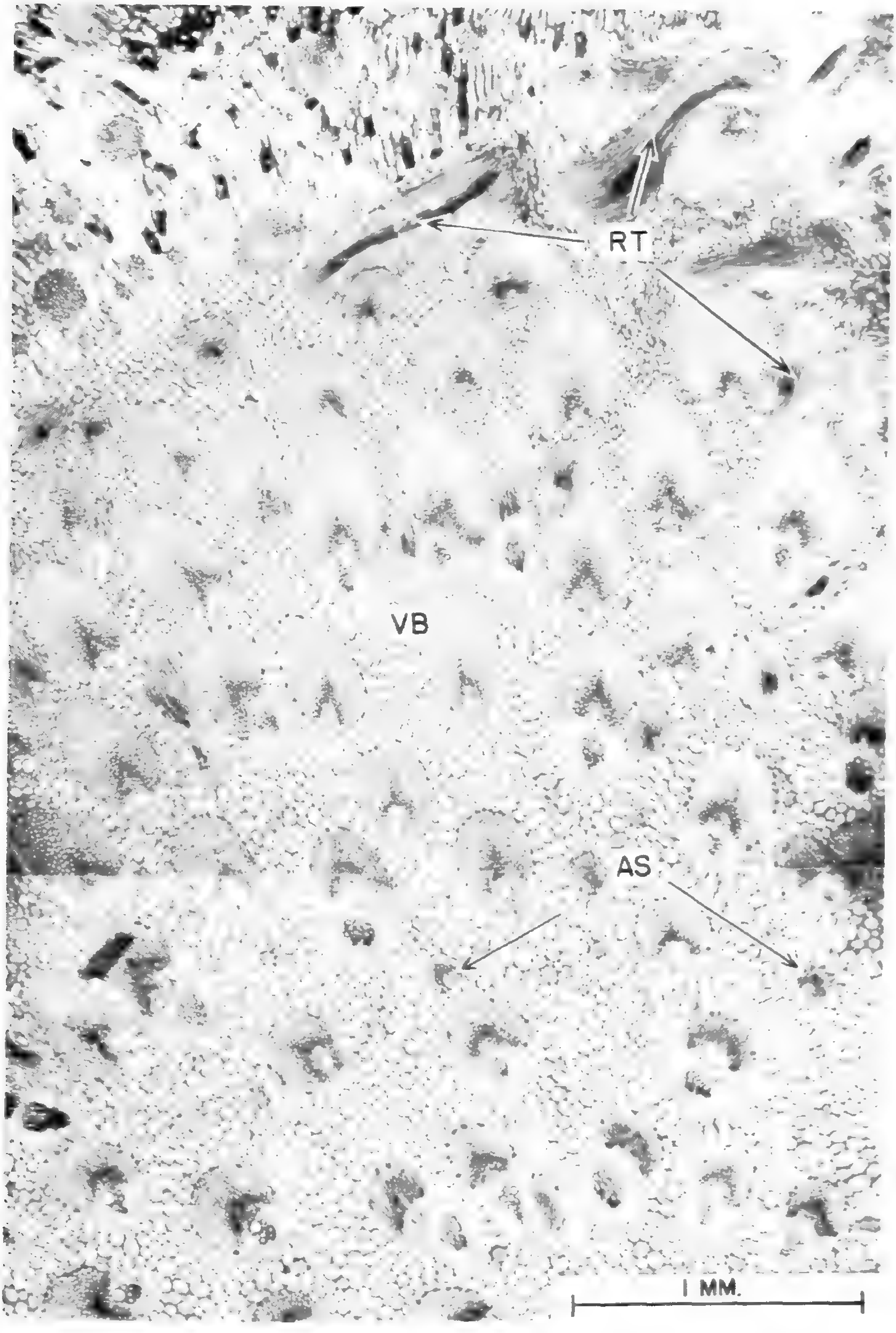

FIGURE 4. *Rhapis excelsa*, same axis as illustrated in FIG. 2, 10.5 mm. above 2A, same magnification. This now closely resembles adult stem, peripheral vertical bundles (VB) with well-developed fibrous sheaths. Bundles of the anastomosing bridge system (AS), root traces (RT).

ling axis the anatomy resembles more and more the mature vegetative stem (FIG. 4), leaf traces giving off several bridges and vertical bundles. In principle then, the increase in number of vascular bundles in the post-seedling stage is accomplished by the same mechanism by which the number of vascular bundles in the mature stem can be varied, i.e., by the variable number of vertical bundles which is given off by each leaf trace.

It must be emphasized that production of additional vertical bundles is a property of the periphery of the central cylinder. No vertical bundles are developed in the stem center. We have also seen occasional vertical bundles split in the peripheral region. It is quite clear that the system of vertical bundles becomes "directed" and "stabilized' in the peripheral region. This must be based upon the way in which the vascular system is produced in the developing apex, a problem which we shall have to take up in a later paper.

DISCUSSION

The most important finding of the present study is the fact that the vascular anatomy of the post-seedling stage is not fundamentally different from the anatomy of the mature vegetative axis. Leaf traces give off numerous bridges ("the anastomosing bridge system") which turn into vertical bundles at the periphery of the central cylinder. The structure of the post-seedling stage is quite confusing at first and it is very doubtful if conventional anatomical methods could have demonstrated it correctly. Only innumerable projections with the data analyzer during which a great number of bundles were followed in both directions finally led to an understanding of the anatomical principles.

The anatomy of the seedling axis of *Rhapis* may shed light on a botanical misconception to which we have drawn attention. Elsewhere (Tomlinson & Zimmermann, 1966a) we have shown that modern ideas about the distribution of vascular bundles in palm stems are erroneous. Diagrams by early investigators implied either a blind ending of vascular bundles at the periphery of the central cylinder when traced downwards, or possibly basal fusion between peripheral bundles. These early workers made it clear that they were undecided on this point. Later writers, often without first-hand familiarity with palm stems, produced diagrams which have become "standard" in modern textbooks in which peripheral fusion of bundles is regarded as a normal feature. But we have shown for *Rhapis* in the first paper of this series, and have much unpublished information about many larger palms, that in the adult aërial axis the continuing vertical bundle is derived from the leaf trace at its point of departure into the leaf. Splitting of vertical bundles in an upward direction (or their fusion if traced downwards) is not a normal property of the adult palm stem although it may occur as a rare abnormality in the center of the rhizome axis.

We have now shown that the inverted cone of the juvenile axis may contain splitting vertical bundles in the periphery of the central cylinder.

This may possibly be a rational explanation for previous botanical misconception of the vascular anatomy of the palm stem. Early workers who studied the juvenile axes might have seen these rare cases in the seedling without appreciating that this is not a property of the adult axis. Among these early workers Falkenberg (1876) and Nägeli (1858) both seem to have studied young plants of *Chamaedorea.* We have reason to believe that Nägeli in particular, who described downward fusion, may have influenced subsequent writers who constructed increasingly hypothetical diagrams of palm stems (Tomlinson & Zimmermann, 1966a).

SUMMARY

In the post-seedling establishment of the adult axis of *Rhapis excelsa* the obconical development at the basal internodes may result in multiplication (in a structural sense) of eight vascular bundles at the cotyledonary node to 400 vascular bundles 10.5 mm. higher. The leaf trace system corresponds closely to that of the aërial stem. Leaf traces give off numerous bridges (the "anastomosing bridge system") which are often quite long, branch, and join neighboring vertical bundles. Branches of the anastomosing system that reach the periphery of the central cylinder become vertical bundles. Since the number of vertical bundles thus produced by each leaf trace is greater than one, the number of vascular bundles in the stem increases. At higher levels the complicated anastomosing system is more and more reduced and the structure approaches that of the mature axis.

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PHENOLOGICAL NOTES ON LATIN AMERICAN PINUS AND ABIES

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Very little information has been reported on the time of pollen shedding of the many pines and firs native to Mexico and northern Central America. This kind of information is necessary for any breeding operation, and is often of considerable taxonomic and evolutionary interest as well. An example is the difference in pollination time of a month to six weeks between *Pinus radiata* D. Don and *P. attenuata* Lemmon, two closely related closed-cone pines native to California. This difference is a reliable means of distinguishing the two species, and is also the principal mechanism that limits natural hybridization between them.

The reproductive phenology of many conifers, especially the pines, is well documented (summarized by Bingham & Squillace 1957), but I have encountered only a few references to the time of pollen shedding and pollination in Latin American pines and firs growing in their native habitats. Shaw (1909) reported that *Pinus pringlei* Shaw flowers in November or early December, before the associated *P. oocarpa* Schiede. Martínez (1948) noted that *P. durangensis* Martínez, native to northwestern Mexico, flowers in April. Little (1962) reported that occasional trees of a few Mexican pines shed pollen in September and October, and noted pollen and receptive female strobili of *P. ayacahuite* Ehrenb. in October. Mirov (1962) observed in mid-February that *P. oocarpa* had recently completed pollination in the mountains of Nicaragua. Meiosis occurs in the pollen cones of *P. pinceana* Gord. in the middle of March in northeastern Mexico, according to Díaz Luna (1962). Since meiosis in pines generally precedes pollen shedding by about 3 weeks, pollination probably takes place in early April in this pinyon pine. The only mention of the time of pollen shedding in the Latin American firs is Martínez' report (1963) that the pollen cones of *Abies religiosa* (H.B.K.) Schlecht. & Cham. mature between March and May in central Mexico (Hidalgo and the Distrito Federal).

The phenological observations summarized in Table 1 were made by three people: John W. Andresen, in southern Mexico and Guatemala during December, 1962; Elbert L. Little, Jr., in northern and central Mexico during March, 1963; and the author on an assignment in Honduras with the Food and Agriculture Organization of the United Nations during January, 1965, and in Guatemala and southern Mexico the following month. Many of these observations are the dates on which pollen collections were made. They often pertain to single trees, and are not always representative of the prevalent stage in the surrounding stand.

Because of the dearth of information on the reproductive phenology of these species, I have also included observations of species that either had not yet begun to shed pollen or had completed shedding when they were observed.

The places listed in TABLE 1 are accurately located by latitude and longitude in most instances, but the elevations are much less reliable, especially in Mexico. The elevations of Mexican localities are in most cases either altimeter readings or estimates from the topographic maps published by the Mexican government, at a scale of 1:500,000. Specimens corresponding to most of the tabulated observations are deposited in the conifer herbarium of the Institute of Forest Genetics at Placerville, California. Some of them are duplicated in the U.S. National Herbarium and in the herbaria of Michigan State University and the Instituto Nacional de Investigaciones Forestales in Mexico City.

The pines shed their pollen earlier in the season in Latin America than in the southern and western United States. The earliest of the southern pines, *Pinus clausa* (Chapm.) Vasey, begins shedding pollen in late December (Dorman & Barber 1956). *P. radiata*, the earliest of the western pines, sometimes begins shedding as early as late January (Duffield 1953). *P. caribaea*, probably the earliest of the Central American pines, was shedding pollen in late October and early November, 1964, in eastern Nicaragua, near the southern end of its range.[1] Farther north, in British Honduras, neither *P. caribaea* nor *P. oocarpa* had begun to shed on November 2–7, 1960.[2] In Honduras *P. caribaea* had completed pollen shedding by late January, 1965, except for a few possibly aberrant trees in one locality (TABLE 1: Agalteca). The condition of the pollen cones in Honduran stands suggested that this species had shed its pollen earlier than the associated *P. oocarpa*. Central American *P. caribaea* is much earlier in time of pollen shedding than the closely related *P. elliottii* Engelm. This pine of the southeastern United States starts shedding at the end of January and continues for about a month (Dorman & Barber, 1956).

Other Latin American pines also begin to shed pollen much earlier than their U. S. relatives. Pollen shedding of *P. lawsonii* Roezl was at its peak on December 13, 1962, near Lake Patzcuaro in Michoacán, Mexico (elev. 2,000 m.).[3] E. L. Little, Jr., observed a few trees of *P. oocarpa* shedding pollen on October 17, 1960, in western Chiapas, Mexico (N. lat. 16°45′, W. long. 99°30′, elev. 1,100 m.).[4] In Guatemala and Oaxaca, *P. oocarpa* and *P. teocote* Schiede & Deppe had begun to shed in mid-December, 1962, when J. W. Andresen collected their pollen (TABLE 1). In Honduras *P. oocarpa* had completed shedding nearly everywhere that I saw it during the last half of January, 1965 (TABLE 1).

[1] Personal communication from L. C. Saylor.

[2] Personal communication from E. L. Little, Jr.

[3] Personal communication from L. C. Saylor. Branches bearing mature pollen cones and ovulate strobili are illustrated in North Carolina State College 1963 (*Fig. 9*).

[4] Personal communication.

Another widespread Honduran pine, *Pinus tenuifolia* Benth. (often identified as the closely related but more northern *P. pseudostrobus* Lindl.), exhibited, in 1965, an unexpected inversion of the usual relationship between greater elevation and later pollen shedding (see Duffield, 1953, for examples). On El Picacho, a peak of about 1,300 meters (4,360 ft.) elevation in the suburbs of Tegucigalpa, the pollen cones of this species had not yet begun to emerge from the bud by February 3, but two days earlier pollen shedding was general in a stand only a few miles distant but 440 meters (1,440 ft.) higher (TABLE 1: Jutiapa). I observed the same unexplainable phenomenon two weeks later in the Sierra Madre del Sur, south of the city of Oaxaca, Mexico. In the foothills south of this range at an elevation of 760 meters, *P. tenuifolia* had not yet begun to shed, but at the crest of the mountains, 1,200 meters (3,900 ft.) or more higher, shedding was nearly complete (TABLE 1: San Gabriel Mixtepec).

Although the date of pollination in conifers is very much affected by the weather, the sequence among associated species is usually undisturbed by seasonal fluctuations — at least in the U. S. The data presented in TABLE 1 suggest that the Latin American conifers may not all exhibit this degree of constancy in relative pollination time. In the following list of pollen-shedding sequences taken from TABLE 1, simultaneous shedding is indicated by = , successive shedding by /.

PLACE	CHRONOLOGICAL ORDER OF POLLEN SHEDDING
Uruapan, Michoacán	*P. douglasiana*/*P. pseudostrobus*
" "	*P. oocarpa*/*P. pseudostrobus*
Ciudad Hidalgo, Michoacán	*P. montezumae* − *P. teocote*
Paso de Cortés, México	*A. religiosa*/*P. montezumae*/*P. hartwegii*
Zacatepec, Puebla	*P. pseudostrobus* = *P. teocote*
Perote, Puebla	*A. religiosa* = *P. hartwegii*
Ixtlán, Oaxaca	*P. lawsonii*/*P. pseudostrobus* var. *oaxacana*/*P. patula* var. *longipedunculata*
San Gabriel Mixtepec, Oaxaca	*P. oocarpa*/*P. tenuifolia*
Honduras (general)	" "

One notable inconsistency appears in these sequences. *Abies religiosa* was just beginning to shed pollen in mid-February, 1965, at 3,400 meters (about 11,000 ft.) in the State of México, long before its associate, *Pinus hartwegii* Lindl. I estimated that this pine would not begin to flower for another month or six weeks. E. L. Little, Jr., collected pollen of the same species in this vicinity near the end of March, 1963 (TABLE 1: Paso de Cortés). But pollen of *A. religiosa* and *P. hartwegii* was collected on the same date near Perote, Puebla, in 1963 (TABLE 1: Cofre de Perote).

Two of the observations listed in TABLE 1 do not agree with earlier reports. I collected pollen of *Abies religiosa* in the State of México (TABLE 1: Paso de Cortés) a month and a half before the April-May date reported

TABLE 1. — **Observations on the time of pollen shedding in Latin American pines and firs**

SPECIES	DATE	STATE AND/OR COUNTRY	NEARBY PLACE NAME	N. LAT. ° ′	W. LONG. ° ′	ELEVATION METERS	POLLEN STAGE [1]
ABIES							
religiosa (H.B.K.) Schlecht. & Cham.	March 24, 1963	México, Mex.	Bosencheve	19 26	100 11	2950	[Sh]
”	March 28, 1963	Puebla, Mex.	Cofre de Perote	19 30	97 11	3250	[Sh]
”	Feb. 16, 1965	México, Mex.	Paso de Cortés	19 06	98 41	3400	St
vejari Martínez	March 30, 1963	Nuevo León, Mex.	Cerro Potosí	24 51	100 13	2950	Sh
PINUS							
caribaea Morelet	Jan. 20, 1965	Honduras	Agalteca	14 28	87 12	770	MS
”	Jan. 25, 1965	”	San Esteban	15 10	85 55	800	SO
”	Jan. 27, 1965	”	Miravalles	14 40	87 14	750	SO
montezumae Lamb.	March 25, 1963	Michoacán, Mex.	Ciudad Hidalgo	19 41	100 40	2700	[Sh]
”	”	México, Mex.	Bosencheve	19 24	100 04	3150	[Sh]
”	March 26, 1963	”	Mexico City	19 19	98 50	3100	[Sh]
”	March 29, 1963	Hidalgo, Mex.	Jacala	20 51	99 14	2250	[Sh]
”	Feb. 5, 1965	Guatemala	Chimaltenango	14 38	90 54	2100	NS [2]
”	Feb. 16, 1965	México, Mex.	Paso de Cortés	19 06	98 41	3400	NS [2]
hartwegii Lindl.	March 26, 1963	”	”	19 05	98 39	3250	[Sh]
”	March 28, 1963	Puebla, Mex.	Cofre de Perote	19 30	97 11	3250	[Sh]
”	Feb. 16, 1965	México, Mex.	Paso de Cortés	19 06	98 41	3400	NS [3]
michoacana Martínez	Feb. 11, 1965	Oaxaca, Mex.	Sola de Vega	16 31	96 58	1400	NS [3]
pseudostrobus Lindl.	March 24, 1963	Michoacán, Mex.	Mil Cumbres	19 39	100 46	2400	MS
”	March 25, 1963	”	Zitácuaro	19 27	100 19	2650	[Sh]
”	March 28, 1963	Puebla, Mex.	Zacatepec	19 19	97 33	2650	[Sh]
”	March 29, 1963	Hidalgo, Mex.	Jacala	20 48	99 16	1860	[Sh]
”	March 30, 1963	Nuevo León, Mex.	Iturbide	24 45	99 57	1600	MS
”	Feb. 5, 1965	Guatemala	Solalá	14 49	91 12	2300	Sh
”	Feb. 18, 1965	Michoacán, Mex.	Uruapan	19 26	102 04	1700	NS [2]
pseudostrobus var. *oaxacana* Martínez	Feb. 10, 1965	Oaxaca, Mex.	Ixtlán de Juárez	17 21	96 27	2800	Sh
tenuifolia Benth.	Jan. 15 to Feb. 1, 1965	Honduras	Los Limones	14 10	87 08	1440	NS to SO
”	Jan. 26, 1965	”	Mateo	14 02	87 21	1570	NS
”	Feb. 1, 1965	”	Jutiapa	14 12	87 07	1750	Sh
”	Feb. 3, 1965	”	Tegucigalpa	14 08	87 11	1310	NS [3]
”	Feb. 12, 1965	Oaxaca, Mex.	San Gabriel Mixtepec	16 03	97 06	760	NS
”	”	”	”	16 11	97 06	1950	MS
douglasiana Martínez	Feb. 18, 1965	Michoacán, Mex.	Uruapan	19 26	102 04	1700	SO
teocote Schlecht. & Cham.	March 25, 1963	”	Ciudad Hidalgo	19 41	100 40	2700	[Sh]
”	March 28, 1963	Puebla, Mex.	Zacatepec	19 19	97 33	2650	St
”	March 29, 1963	”	Cofre de Perote	19 32	97 12	2650	[Sh]
”	Dec. 13, 1962	Oaxaca, Mex.	Oaxaca de Juárez	17 10	96 40	1930	St
”	”	”	”	17 11	96 39	2400	St
”	Feb. 10, 1965	Oaxaca, Mex.	Ixtlán de Juárez	17 21	96 27	2800	SO
patula Schlecht. & Cham.	March 29, 1963	Veracruz, Mex.	Jalapa	19 35	96 58	2100	[Sh]
”	Feb. 9, 1965	Hidalgo, Mex.	Lake Tejocotal	20 09	98 10	2200	NS [3]
patula var. *longipedunculata* Loock	Feb. 10, 1965	Oaxaca, Mex.	Ixtlán de Juárez	17 21	96 27	2800	NS
oocarpa Schiede	Dec. 18, 1962	Guatemala	Quezaltenango	15 08	91 36	2360	St
”	Jan. 26, 1965	Honduras	Mateo	14 02	87 21	1570	MS
”	Jan. 16, 1965	”	Tegucigalpa	14 08	87 11	1310	SO
”	Feb. 5, 1965	Guatemala	Guatemala City	14 44	90 22	1000	SO
”	Feb. 12, 1965	Oaxaca, Mex.	San Gabriel Mixtepec	16 03	97 06	760	SO
”	Feb. 18, 1965	Michoacán, Mex.	Uruapan	19 26	102 04	1700	MS
pringlei Shaw	Feb. 11, 1965	Oaxaca, Mex.	Sola de Vega	16 29	97 01	2050	Sh

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[1] NS = not yet shedding; St = starting to shed; Sh = shedding; MS = mostly shed; SO = shed out; [Sh] = pollen collected but stage not noted.

[2] Pollen cones emerging from bud; estimated 2 to 3 weeks until shedding begins.

[3] Pollen cones still covered by bud scales; at least a month until shedding begins.

by Martínez (1963) in the nearby Distrito Federal. And pollen shedding was general in a stand of *Pinus pringlei* in the Sierra Madre del Sur (TABLE 1: Sola de Vega) in mid-February, two to three months after the flowering time reported by Shaw (1909) for this species. These discrepancies and some of the other observations reported here suggest that conifer pollen shedding may be under less rigid enviromental control in Mexico and Central America than in more northern regions.

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THE GENUS LINOCIERA (OLEACEAE) IN NEW CALEDONIA *

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THE POSSIBILITY THAT THE GENUS *Linociera,* might occur in New Caledonia, first became apparent when type material of *Notelaea brachystachys* Schltr. was examined. This suspicion was later brought to certainty in the field, on the lower slopes of Mt. Ignambi, toward the northern end of New Caledonia, when two small oleaceous trees were found with the flowers and fruit of a *Linociera.* That the phytogeographic distribution of this genus should include New Caledonia is not unexpected, for, with many species in the East Indies and New Guinea, others are known from Australia, Lord Howe Island, Fiji and Niue Island.

Furthermore, there have been reasons for doubting the distinctness of the genus *Sarlina,* described from New Caledonia in 1951, and examination of the type material shows that it, too, is a *Linociera,* as are other species previously treated as *Notelaea* or *Osmanthus* and not accounted for in the relatively recent revision of *Osmanthus* from New Caledonia (Green, Jour. Arnold Arb. 43: 268–283. 1963). Type material for all the Oleaceae described from New Caledonia has now been examined and I should like to express my gratitude to the directors and curators of the herbaria cited below, either for facilities to study their material or for its loan. All the material cited has been examined unless otherwise stated, and the respective herbaria are indicated by the abbreviations published in the *Index Herbariorum,* supplemented by those in Kent (*British Herbaria,* 1957).

Linociera brachystachys (Schltr.) P. S. Green, comb. nov.

Notelaea brachystachys Schlechter, Bot. Jahrb. **39:** 228. 1906; Guillaumin, Ann. Mus. Col. Marseille II. **9:** 191. 1911; Bull. Mus. Hist. Nat. Paris **28:** 199. 1922; Bull. Soc. Bot. France **89:** 232, 233. 1942, et Fl. Nouv.-Caléd. 283. 1948.

Notelaea francii Guillaumin, Bull. Mus. Hist. Nat. Paris **28:** 198. 1922; *ibid.* II. **10:** 520. 1938; *ibid.* **14:** 456. 1942; Bull. Soc. Bot. France **89:** 232, 233. 1942, et. Fl. Nouv.-Caléd. 283. 1948.

Osmanthus brachystachys (Schltr.) Knoblauch, Repert. Sp. Nov. **41:** 152. 1936.

Osmanthus francii (Guillaum.) Knoblauch, *loc. cit.*

Sarlina cylindrocarpa Guillaumin, Bull. Mus. Hist. Nat. Paris II. **23:** 539. 1951.

Evergreen *tree* 4–15 m. tall; branches glabrous. *Leaves* glabrous; petiole 10–25(–30) mm. long, glabrous; lamina thickish, slightly coriaceous,

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oblanceolate to broadly obovate, or more or less elliptic, (4.5–)7–14(–19) cm. long by (2.5–)3–5.5(–7) cm. broad; margin entire, scarcely thickened, more or less flat; apex obtuse (or acute) often almost rounded, sometimes very slightly and very shortly acuminate, tip blunt; base obtuse to acute, attenuate into the petiole; venation more or less obscure, except for slightly raised primary veins above and below, 6–8 per side. *Inflorescence* axillary, with or below the leaves, decussate, 1–3 cm. long, 7–13-flowered with a single terminal flower, pubescent, with somewhat flattened hairs; bracts broadly triangular, 1–1.5 mm. long, pubescent, deciduous. Flowers hermaphrodite, pale yellow, inodorous (?); pedicels 0.5–2 mm. long. *Calyx* 1–1.5 mm. long, pubescent, with somewhat flattened hairs, lobes 4, bluntly triangular, 0.5–0.75 mm. long, pubescent, especially toward the apex. *Corolla* thickish, lobes 4, joined in pairs by the filaments, 2–2.5 mm. long, strongly valvate, cucullate, enclosing the stamens in bud. *Stamens* 2, 1.5–2 mm. long; filament broad, 0.5 mm. long. *Ovary* 1.5 mm. long, more or less conical, tapering to style and stigma 0.5 mm. long, shallowly bifid; bilocular with four axile ovules. *Drupe* club-shaped, 4.2 cm. long, 2 cm. broad, obscurely ridged, mesocarp thick, fleshy, "rosé" (*Guillaumin & Baumann-Bodenheim 10424*), endocarp very hard, 1.5–2 mm. thick.

Bois des montagnes, Balade, 1861, *Vieillard 97* (P); humid forest, about 700 m. alt., Mt. Ignambi (about 10 km. south of Pouébo), 7 Dec. 1963, *Green 1764* (A); margin of humid montane forest, about 600 m. alt., Mt. Ignambi, 7 Dec. 1963, *Green 1798* (A); in den Wäldern der Berge bei Ou-Hinna, ca. 800 m. alt., 2 Jan. 1903, *Schlechter 15600* (isotypes: BM, E, K, LE, P, Z); forêt hygrophile sur schistes, 500 m. alt., Mé Aoui, 7 Feb. 1951, *Guillaumin & Baumann-Bodenheim 10270* (P); *ibid.*, *Guillaumin & Baumann-Bodenheim 10271* (P, not seen); *ibid.*, 8 Feb. 1951, *Guillaumin & Baumann-Bodenheim 10424* (A, P); Ourai, 31 Oct. 1876, 500 m. alt., *Lécard s.n.* (P); vallée de la Thi, 1951, *Sarlin 76* (holotype of *Sarlina cylindrocarpa*: P); forêt rocheuse, Prony, 15 Sept. 1914, *Franc 1867* (holotype of *Notelaea francii*: P; isotypes: A, BRI, K, P); *ibid.*, Dec. 1914, *Franc 1867a* (A, Z).

The divided corolla clearly distinguishes *Linociera* from *Osmanthus*, and its relatively massive fruit from both *Osmanthus* and *Notelaea*. The decussate inflorescence is common to all three genera, although in one or two places on the type material of *L. brachystachys* the inflorescence is slightly compound with three flowers borne where a single one is normally found (see the discussion under *L. paniculata* below).

Bud material was fixed in the field and flown to Dr. Barbara Briggs of the Royal Botanic Garden at Sydney, Australia, who examined it cytologically. I would like to take this opportunity to express my sincere gratitude to Dr. Briggs for her interest and willing help. Unfortunately, the material was not in proper condition for an accurate count but it was found that there were about 46 chromosomes in the somatic cells. This is close to a count of $2n = 46$ obtained by Dr. Briggs on material of *Linociera quadristaminea* (F. Muell.) Knobl. which I fixed on Lord Howe Island, and agrees with the number almost uniform throughout the whole subfamily *Oleoideae* (see Taylor, Brittonia **5**: 363. 1945).

Linociera paniculata (Guillaum.) P. S. Green, comb. nov.

Notelaea ? paniculata Guillaumin, Bull. Soc. Bot. France **89:** 233. 1943, et Fl. Nouv.-Caléd. 283. 1948.

Evergreen *tree* 10 m. high, branches glabrous. *Leaves* glabrous; petioles 8–12 mm. long, glabrous; lamina thickish, elliptic-oblanceolate, (4.2–) 6–9 cm. long by (2–)2.5–3 cm. broad; margin entire, scarcely thickened, flat; apex acute, tip blunt; base acute, long attenuate into the petiole; venation obscure above, only primary veins visible, slightly raised below, 7–8 per side. *Inflorescence* axillary, paniculate-decussate (? abnormal), 3.5–4.5 cm. long with up to 50 flowers, glabrous; bracts triangular, acute, very small, early deciduous or absent, 0.2–0.5 mm. long. Flowers hermaphrodite, pedicels 1–2 mm. long. *Calyx* glabrous, 0.75–1 mm. long, with 4 very shallowly triangular, more or less rounded lobes 0.25–0.5 mm. long. *Corolla* thickish, lobes 4, joined in pairs by the filaments, 2.25–2.5 mm. long strongly valvate, cucullate, more or less enclosing the stamens. *Stamens* 2, 2–2.25 mm. long; filaments flat, broad, 0.5 mm. long and 0.5 mm. wide. *Ovary* 1.5 mm. long, broadly conical with barely discernable style and two small stigmatic lobes 0.2–0.3 mm. long. Fruit unknown.

Sommet du Nékou, au-dessus de Bourail, vers 600 m. alt., 3 Apr. 1862, *Balansa 1224* (holotype and isotype, P).

It is strongly suspected that the paniculate condition of the inflorescences on these specimens is abnormal. The tree from which the branches were taken was obviously stunted in growth and a pair of leaves on the isotype are fasciated at the base. Knoblauch, has determined the specimens as *Notelaea brachystachys* and it is interesting to note that a careful examination of the type of this latter species (*Schlechter 15600*) shows slight subsidiary branching of the inflorescence in one or two places, where three flowers are borne in the place of a normal single one. When more collecting has been done, and more material is available for study, this may possibly prove to be the correct disposition, and, were it not for the specimens mentioned immediately below, I would be inclined to agree with Knoblauch.

In 1950 three specimens were collected on Mt. Koniambo in central New Caledonia, which bear immature fruit and appear to belong to *Linociera* (sur serpentine, Mt. Koniambo, 21 Dec. 1950), *Guillaumin & Baumann-Bodenheim 9458, 9479, 9487* (A, Z). They appear to represent a different species from *L. brachystachys*, for the fruits, which are probably slightly immature, are shorter and broader in proportion (12–20 mm. long, 7–13 mm. broad), and the leaves are somewhat different (elliptic to slightly oblanceolate, (3.5–)5–8(–9) cm. long and (1–)2–2.5(–3) cm. broad, with the veins more obscure).

Another gathering which is difficult to place, with the limited material at present available, is one collected in the Loyalty Islands by Däniker (vereinzelt im Walde am Weg von Donkin nach Nathalo beobachtet, Lifou, 2 Nov. 1923) *Däniker 2366* (Z). Judging by the size and narrowness of the leaves this may prove to be conspecific with the Guillaumin and Baumann-Bodenheim material from Mt. Koniambo but it may also be a small-leaved expression of *Linociera brachystachys*.

Linociera sp.

Tree 12 m.; branches glabrous. *Leaves* glabrous; petioles 4–5.5 cm. long, glabrous; lamina thickish, oblanceolate, 15– ca. 23 cm. long and 5–9 cm. broad; margin entire, scarcely thickened, more or less flat; apex ? acute; base acute, long attenuate into the petiole; venation raised and more or less reticulate towards the margins above and below, 10–11 primary veins per side. *Inflorescence* ? decussate, ? ca. 5 cm. long. Flowers unknown. *Drupe* asymmetrically ellipsoid, obscurely ridged, 4.7 cm. long and 2 cm. broad (? immature), with blunt apex.

Col d' Ignambi, above Oubatche, 900 m. alt., 1 Oct. 1956, *McKee 5379* (HLU).

This specimen, with its large leaves, bears a very close similarity to some of the species of *Linociera* from the East Indies and New Guinea. However, until at least the Asiatic members of this genus are revised, it is impossible to say whether it is different from all the previously described species. The material is inadequate for description as a new species. The opposite, exstipulate leaves, covered on both surfaces by small, sunken, peltate scales, and the type of fruit, all place the specimen in the Oleaceae. The type of fruit indicates *Linociera* and the size of the leaves and petioles distinguish it from *L. brachystachys*.

It is apparent that much collecting needs to be done in the more remote areas of New Caledonia. The flora in the northern part of the island and the mountainous hinterland is still inadequately known. It is to be hoped that future collectors will endeavor to obtain material from these relatively inaccessible areas at times of the year when they have not, as yet, been visited.

ARNOLD ARBORETUM
HARVARD UNIVERSITY

Present address:
ROYAL BOTANIC GARDENS
KEW, RICHMOND, SURREY
GREAT BRITAIN

THE DIRECTOR'S REPORT

The Arnold Arboretum During the Fiscal Year Ended June 30, 1966

The event which dominated the past year at the Arnold Arboretum was the decision rendered by the Supreme Judicial Court of Massachusetts in the case of the "Attorney General *vs.* President and Fellows of Harvard College." The Attorney General, alleging a breach of trust, had sought to compel the University to reverse its approval of a close association between the Arboretum and other departments of biological study at Harvard and of the location of certain activities and resources of the Arnold Arboretum in Cambridge, thereby forcing their return to Jamaica Plain. In a long opinion submitted by a majority of the Court (three justices) with two justices dissenting, the Court allowed for the continued close coöperation between the Arboretum and the University. The Court also found that "the effects of the move do not show that inadequate consideration was given to probable results or that bad judgment was exercised." The Court noted that "What we have said disposes of the contention that the move itself, so far as carried out as voted, was a breach of trust. We disagree with the view of our dissenting colleagues that it is implicit in the Indenture that the place of such implied related activities as the library and herbarium, if established, be the place specified for the growing of the trees, shrubs and plants. The dominant consideration is that those things and only those things be done that will, in the good judgment of the Corporation, promote the express purposes of the Indenture."

The Court did question whether "the implementation of the resolution of January 19, 1953, does not, or may not, conform to its terms." That resolution (cf. The Director's Report on the Arnold Arboretum, Jour. Arnold Arb. **35**: 367–381. 1954) "calls for the retention at Jamaica Plain of 'such books and specimens as may be required to provide there a working library and herbarium'." The "resolution required that the books and specimens to be housed at Cambridge be appropriately identified." The Court found that an "implication from the master's observation . . . may be that the intention of the Corporation's vote has not been met." The Court also ordered that "The rescript shall provide that the county court retain jurisdiction of the cause and that the defendant shall file with the clerk within six months of rescript (a) a report to it by the Arnold Professor or other appropriate person that in the Corporation's judgment shows either that an adequate working library and herbarium exist at Jamaica Plain or recommends the steps to cause them to exist; (b) a report of its proposals or action to amplify the catalogue and general listing references; and (c) a report of its proposal or action in respect of a general designation on or within the Harvard University Herbarium."

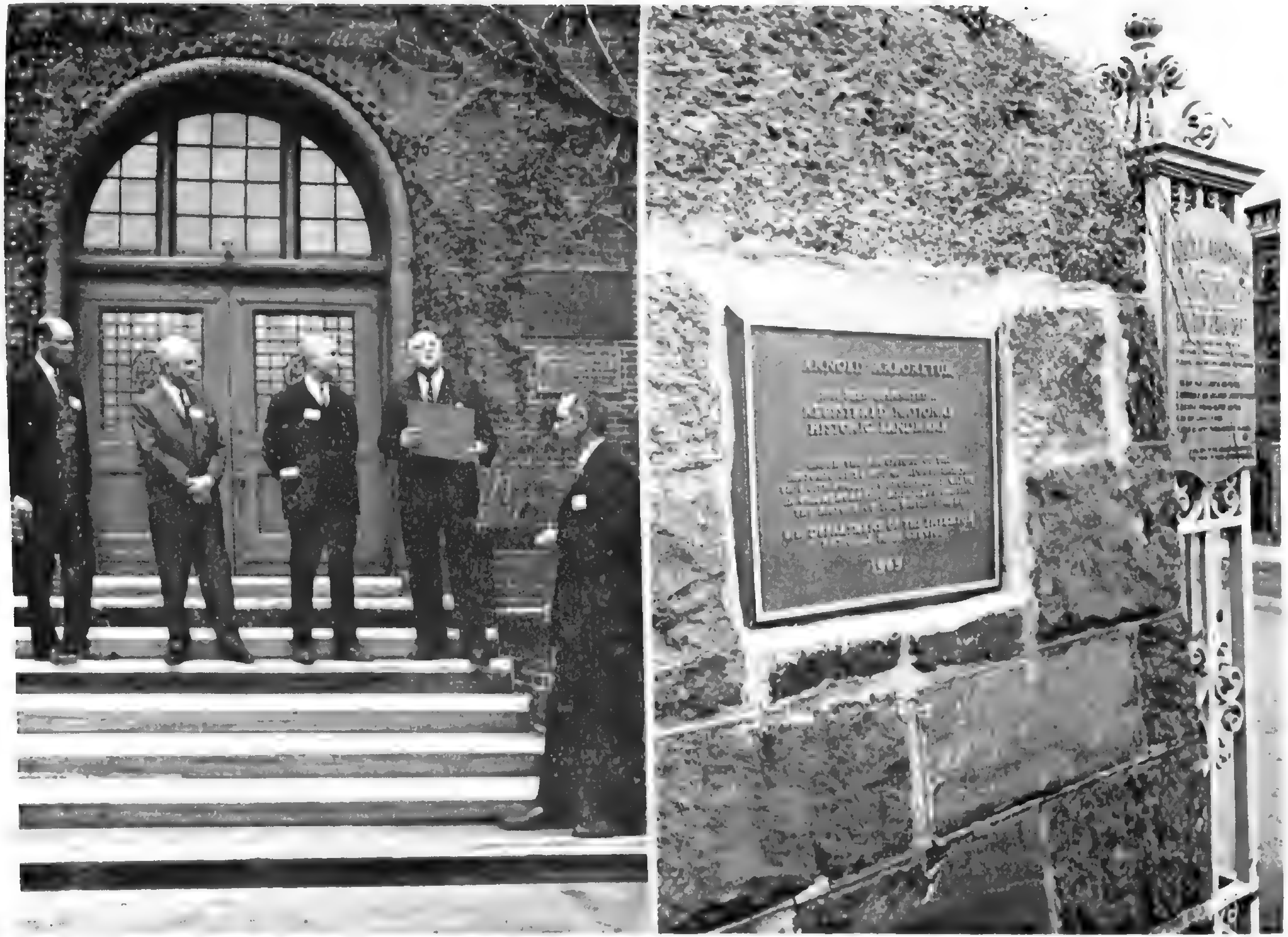
The required report showing the nature of the herbarium and library for horticultural research which are maintained in Jamaica Plain has been approved by votes of the President and Fellows and transmitted to the single justice for the entry of the final decree.

Since the decision of the Court in this litigation did not require the removal from Cambridge and the return to Jamaica Plain of all the books and specimens transferred in 1954, it is now possible for the staff to plan for permanent changes and improvements in the existing facilities in Jamaica Plain. Consequently, contracts were placed in the spring for (1) an additional unit at the Dana Greenhouses, constituting a one-third expansion; (2) air-conditioning of the laboratory for cytology and plant morphology; (3) new lighting in the library of the Administration Building; (4) changes in office arrangement.

In the Harvard University Herbaria in Cambridge equally important consideration must be given because of growth of collections and increase in personnel and visitors for whom facilities are now limited by the physical plant. The decision of the Supreme Judicial Court of Massachusetts was necessary before any new programs could be proposed. The staff believes that the present organization and locations will permit the goals of the Arnold Arboretum to be extended and is hopeful that the hesitation and uncertainty of the past are, indeed, over.

Two small sections of land have been officially incorporated into the Arnold Arboretum during the year. One piece of approximately five acres, including a house at 383 South Street, was in the title of the Bussey Institution. With the taking of the major part of the Bussey Institution property by the Commonwealth of Massachusetts in 1963, this area, adjacent to the collections of the Arboretum, remained. It has been used by the Arboretum staff and the house has been occupied by a staff member as an essential guard post for one corner of the grounds. The Corporation in a vote of June 6th approved that "the land shall be held and used for the general purposes of the Arnold Arboretum" and "in consideration the fair market value of $71,000.00 be transferred from the Martha Dana Mercer Trust gift held for the purposes of the Arnold Arboretum to the Bussey Institution Endowment."

A second piece of land in the northwest corner of the Arboretum was isolated from the main collections and could not be developed because of the use and retention of ownership of an old roadway by the Department of Public Works. After many years of effort the title to this isolated right-of-way was transferred to the owners of the abutting property, Harvard University and the City of Boston Department of Parks and Recreation, respectively, and its use given to the Arnold Arboretum. We deeply appreciate the efforts of the Commissioner, Mr. William J. Devine, and of his associates, Mr. Arthur J. O'Keefe and Mr. Daniel Byrnes,



LEFT. Mr. Edwin Small of the National Park Service presenting certificate designating the Arnold Arboretum a National Historic Landmark. Left to right, Mr. Henry Scagnoli, Mr. L. Gard Wiggins, Mr. A. H. Parker, Jr., Mr. Small and (far right) Dr. R. A. Howard.

RIGHT. The bronze plaque at the main entrance to the Arnold Arboretum.

in making this land available. The expansion of the conifer collection and the development of additional plantings of ornamental apple trees in this area, along United States Route 1, will greatly enhance the site for visitors approaching Boston.

Much time was devoted by the staff to securing aid to defeat a bill submitted to the Massachusetts legislature ordering the construction of a ski tow within the Arnold Arboretum, on Peters Hill. Although the bill was filed by a representative living in Jamaica Plain, the legislature properly realized that passage and implementation of it would destroy a major collection of apples and crab apples, and defeated the bill by voice vote. The staff is grateful to the many Friends of the Arboretum whose aid in contacting their representatives and expressing their disapproval was essential in defeating the bill.

A pleasant occasion to record occurred on May 17 during the meeting of the Committee to Visit the Arnold Arboretum. At that time Mr. Edwin Small, of the National Park Service, representing Stewart L. Udall, Secretary of the Interior, presented the certificate officially recognizing the Arnold Arboretum as a National Historic Landmark. Mr. A. H. Parker, Jr., Chairman of the Committee, accepted the certificate for the Arnold Arboretum. Also present were Mr. Henry Scagnoli, representing John F. Collins, Mayor of the City of Boston; Mr. L. Gard Wiggins, representing Mr. Pusey and the Harvard Corporation; and Mr. Daniel Byrnes, representing Mr. Devine and the Department of Parks and Recreation. Earlier in the year a bronze plaque was placed on a gate post at the main entrance to the Arboretum.

Staff:

The retirement of one staff member and the resignation of four others took place during the past year. Mrs. Lilian Burian, who had mounted herbarium specimens for ten years, retired on January 30th. Dr. Theodore Dudley, Assistant Horticultural Taxonomist, resigned to accept a position at the U. S. National Arboretum. Mr. Peter Green, Horticultural Taxonomist, resigned to join the staff of the Royal Botanic Gardens at Kew, and Dr. Keith Ferguson resigned to work as a Fellow on the Staff of the Flora Europaea Research Project. Dr. Mary Sanders accepted an appointment at the Mount Alto Campus of the Pennsylvania State University, and resigned her appointment as Research Associate.

The appointment of Dr. Harrison Leigh Flint as Associate Horticulturist was approved by the Corporation to become effective near the end of the present fiscal year. Dr. Flint, whose research interests include problems of winter hardiness of woody plants, joins us from the staff of the University of Vermont. Miss Dulcie Alicia Powell, formerly of the staff of the Institute of Jamaica, Kingston, Jamaica, was appointed Research Fellow, and will continue her work on the cultivated ornamental plants of tropical areas. Miss Stephanne Barry Sutton was also appointed

Results of damage caused by severe snow storm of January 23, 1966. LEFT: Trees in the *Quercus* collection with broken branches. RIGHT: Damage to branches of this 40-year-old *Cercidiphyllum* necessitated complete removal of the tree.

a Research Fellow and continues her work toward a biography of Charles Sprague Sargent and a history of the Arnold Arboretum.

The promotion of Dr. Thomas G. Hartley to be Associate Curator of Pacific Botany was approved by the Corporation, to become effective during the next academic year.

Five Mercer Research Fellows were appointed during the year for varying lengths of time. Dr. Charles Tseng, of Windham College, Putney, Vermont, is carrying on morphological studies in the Araliaceae. Mr. Pablo Legname, of the Instituto Lillo, Tucuman, Argentina, has undertaken studies on the unworked collections from Argentina in the herbarium of the Arnold Arboretum. Appointments as Mercer Fellows in the area of horticulture, for work with the living and herbarium collections, were made to Miss Sandra Shannon, of the University of Massachusetts; Mr. Frank Wolfe, of the University of Vermont; and Mr. William Gensel, of the University of Rhode Island.

Among honors to staff members was the award of the Jackson Dawson Medal of the Massachusetts Horticultural Society to Mr. Alfred Fordham. It was accompanied by the citation, "To Alfred James Fordham, who following in the footsteps of famous propagators at the Arnold Arboretum, is doing much to maintain the high standards set by them years ago in this often difficult and sometimes most perplexing art."

Dr. Wyman was presented the "Silver Alder Leaf" by the Scandinavian Horticultural Congress, at Aulanko, Finland, in July, 1965.

Horticulture:

The drought which has plagued New England and which has been mentioned in several recent reports continued during the fall and winter of this past fiscal year. The records show that the calendar year 1963 ended with the total rainfall 7.93 inches below average, 1964 was 6.30 inches below normal, while 1965 had a deficiency of 16.76 inches from the 44 inches normally expected at the Arnold Arboretum. The first four months of 1966 were 3.26 inches below normal, but the drought appeared to be broken, at least temporarily, by occasional heavy showers during the early part of June. The effects of a long continuing drought, however, are very evident in the resultant loss of plants. The few ponds in the Arboretum remained dry again during the summer of 1965, indicating how low the water table had dropped.

In addition to the dry spell, the grounds were also affected by surface fires caused by carelessness and vandalism. Twenty-one separate fires were recorded during the past year. Fires beginning at the base of Bussey Hill have severely damaged plantings of azaleas so that many large plants have had to be pruned to the base in an attempt to save them.

Adding to the damage caused by the continued drought was a major storm on January 23rd with a heavy wet snow which remained on the branches of shrubs and trees. Colder weather following the storm caused the weighted branches to break. Bushes bent by the accumulation of snow remained frozen in abnormal positions. The damage is now particularly obvious in the collections of *Thuja* and *Chamaecyparis*, in many of the azalea plantings, and in the shrub collection and nursery area.

The planting program, drastically limited in the last two years, had to be resumed during the past spring because of the accumulation of plants in the nurseries. Over 1000 plants were added to the living collections. New azalea plantings numbered 265. About 50 new *Cytisus* plants were added to the collection on Bussey Hill.

One purpose of Dr. Wyman's travels through Europe during the spring and summer of 1965 was to select from many sources, including botanic gardens, private gardens, nurseries, and the wild, plants worthy of introduction into the United States. During the current fiscal year material of 930 species and varieties of 119 genera was received, recorded, and propagated at the Arboretum. Of several thousand individual plants now growing in the greenhouse area, some will be ready for hardiness testing during the next year. These are included among the 167 shipments received during the year from 11 countries, comprising 1012 species and varieties. In addition, shipments of seeds received numbered 130 from 35 different countries, comprising 364 species and varieties. Many of the seeds were of specifically requested herbaceous species to be grown for anatomical studies, or of unusual species to be grown as vouchers and for representation in the herbarium of cultivated plants. In response to specific requests, the staff of the greenhouses distributed 109 shipments of seeds, representing 306 species and varieties, to 15 different countries. Plants and vegetative propagating material formed 173 shipments of 1009 taxa to ten countries. Included in these figures are twelve taxa of *Cornus, Ilex, Ligustrum, Magnolia, Malus, Pieris, Potentilla, Syringa,* and *Viburnum* which were offered to coöperating nurserymen as plants introduced or selected by the Arnold Arboretum and worthy of greater horticultural use.

A total of 389 taxa was propagated for replacements or additions to the collections on the grounds. One hundred and fifty-one taxa were propagated for taxonomic or analytical studies by staff members.

Continued experimental work in the greenhouse area concerned methods of plant propagation and the accumulation of data on seed germination. Through the year 112 taxa were processed for such investigations.

Work on the registration of cultivars continued, the publications including a check list for the genus *Weigela* and one issue of *Arnoldia* devoted to newly registered names in various genera. Inquiries for information and for the proper registration forms still far exceed actual returns. A full discussion of the registration procedure is planned for the International Horticultural Congress scheduled for the summer of 1966, when the future of cultivar registration may become more evident. Compilation of a listing of cultivars for the genus *Lantana* nears completion.

Dr. Dudley gave special attention to the material of *Viburnum* in our herbarium of cultivated plants and to that obtained on loan from other institutions, as well as to the living collections. Mr. Green and Mrs. Rüdenberg continued their study of *Lonicera,* annotating many of the specimens in the Arboretum herbarium collections and making additional chromosome counts.

The horticultural herbarium received sizable and welcome additions from the collections made by Dr. Dudley on the Burpee Fordhook Farm and at other locations and by the gift of the herbarium of the American Herb Society.

A new edition of Dr. Wyman's book, *Trees for American Gardens,* was published by Macmillan at the end of December.

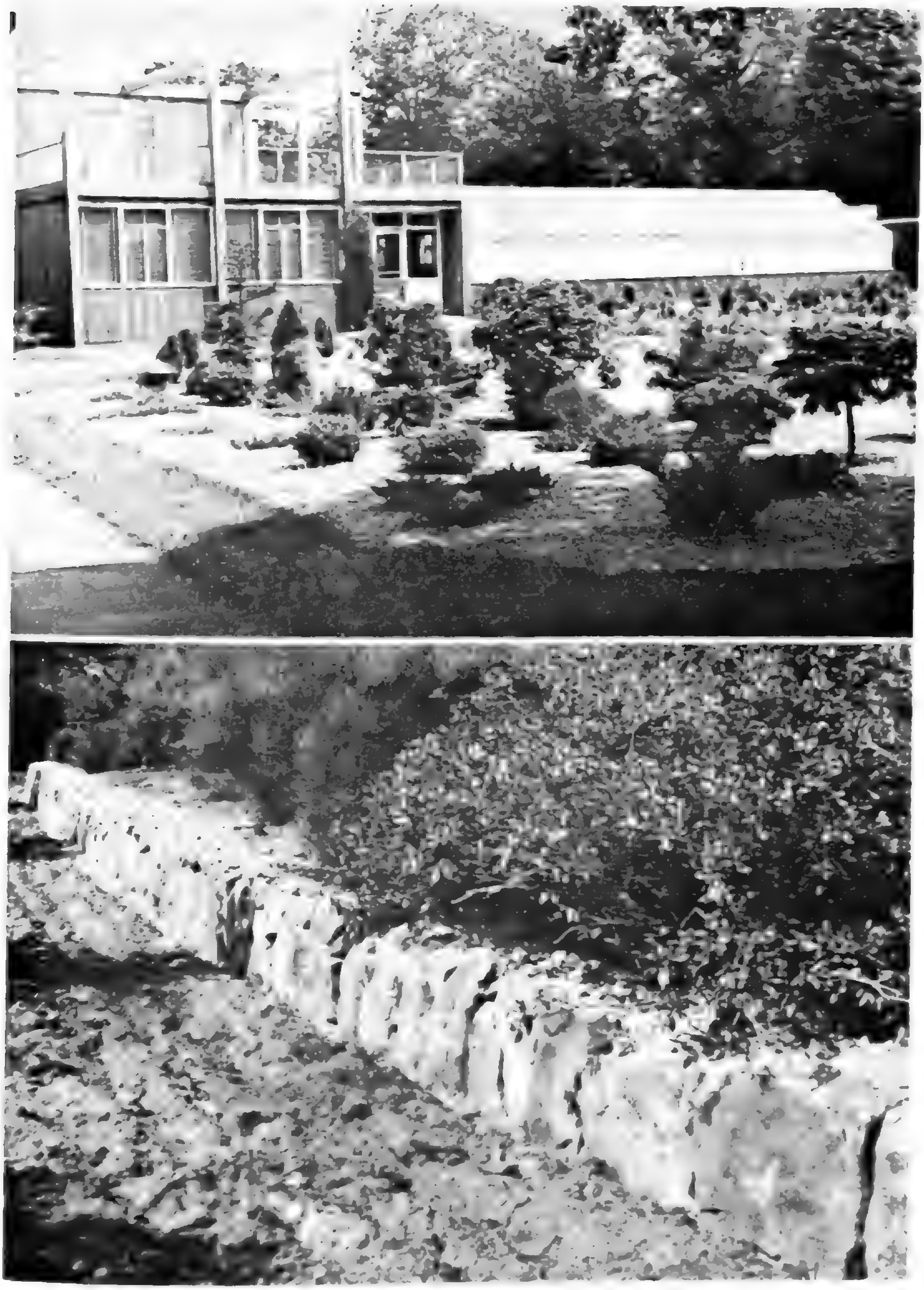
Changes of various sorts have been made at Jamaica Plain, some on the grounds which will become apparent in better landscaped plantings, more convenient paths for visitors, or healthier specimens; others will result in more efficient use of the facilities in the buildings, both for research and maintenance. On Bussey Hill a new retaining wall of natural boulders was constructed so that a level path could be established. Heavy mulching and the laying of a plastic pipe from South Street to the top of the hill, making water available for the first time, will improve the condition of both old and new plantings and enhance the general appearance of the collections. Adjacent to the oak collection on Bussey Hill a beginning has been made on the establishment of a collection of *Viburnum* species. At the base of Hemlock Hill many evergreen rhododendrons have been planted in mass.

Work has commenced on the establishment of terraces and walks on the slopes below the *bonsai* house in the greenhouse area, using rocks obtained from the Case Estates in Weston. When completed this will become the location for the smaller plants of the genetic dwarf conifer study collection. Larger plants will continue to be placed in the area of the chestnut collection.

Much effort is being expended on the rehabilitation of the old Centre Street roadbed, obtained from the Department of Public Works by the Department of Parks and Recreation. The city has removed the work house and the Arboretum has contracted for the excavation of the road to a depth of about 3 feet, using this excavated material for filling in a swampy area and a dangerous pond on the South Street tract. Much fill will be needed in the roadbed, but localized plantings will be used in the meantime. In coöperation with the Department of Parks and Recreation a six-foot chain link fence is being erected around the new property.

The chain link fence bordering the Arborway was painted during the summer by boys in the Job Corps, a project directed by the City of Boston.

Also with the coöperation of the Department of Parks and Recreation, the gates to the Arboretum were closed to driving on week-ends during the months of May and June. With very few exceptions this practice has



ABOVE. Collection of genetic dwarf conifers in a temporary location near the Dana greenhouses. Mulch of gray stone is being used for these plants.

BELOW: Dry wall of natural boulders bordering the rebuilt beds of *Cytisus* on Bussey Hill.

met with the approval of those commenting, since it permits individuals and families to walk without concern for automobiles.

The problem of parking space on the periphery of the Arboretum remains unsolved. An even more serious problem is the continued vandalism within the Arboretum, with malicious cutting and felling of trees. Since the City was unable to supply additional police protection, special police were hired for the summer months to patrol the grounds during the evening hours.

With the coöperation of the planning office of the University and the Medical School branch of the Department of Buildings and Grounds, plans are being completed for a new garage facility to remove the mechanical equipment from its cramped and crowded quarters in the basement of the Administration Building.

Case Estates:

It is pleasant to record again a marked increase in the use of the Case Estates, both by individual visitors and by groups requesting special tours. In both spring and fall, classes were held as afternoon walks around the grounds, and in May an Open House was held on what, unfortunately, was a cold, rainy Sunday. Parking for visitors remains a problem both on Wellesley Street and near the barn.

Display area at the Case Estates, Weston, for authentically named clones of *Hosta* sent from special collections in Sweden, England, and the United States.

One new planting has been established, and additions have been made to others. A display of mulching materials prepared for exhibit at the Spring Flower Show of the Massachusetts Horticultural Society, in 1964, aroused such interest that the plan was developed for use in Weston. Two long beds, 6 by 100 feet, were prepared in the fall and planted in the spring. Each bed is divided into units ten feet long, permitting the use of 20 different kinds of mulching materials. Instead of using the same plant materials in each bed an alphabetical arrangement of perennials by their generic names has been used, omitting only such "exotics" as genera beginning with "Q" and "X".

Additions have been made to the collection of *Hemerocallis*. New taxa of *Allium* have been acquired by gift and purchase in the hope of establishing a new bed for next year.

An experimental nursery planting of 132 trees was set out in the large field along Newton Street, and 89 trees of 37 species and varieties were added as display specimens in the same field.

The town of Weston was given 193 trees and shrubs in the fall of 1965 for planting in the town. All had been placed by spring, and a letter of appreciation for the gift was received from the members of the Weston Park and Cemetery Commission.

Herbarium:

The decision of the Supreme Court granting permission to keep collections of the herbarium and library in Cambridge has made feasible a reëxamination of the herbarium building and its facilities. In 1954, when the collections were moved, the capacity of the building for the combined collections of the Arnold Arboretum and the Gray Herbarium was considered adequate for ten years' growth. It is now twelve years since the move occurred and the increase in the herbarium collections has exceeded what was expected, partly from the study and incorporation of previously unworked collections and partly from expanded and increased interest in plant groups and geographical areas not formerly studied by the Arboretum staff. A developing interest in the herbaceous plants of all floras has resulted in such material being studied, mounted, and inserted as a part of the Arboretum herbarium, rather than as formerly, being donated to, or exchanged with, other institutions, or even discarded. An increasing awareness of the importance of the floras of Africa and Australia, and the deficiency of our collections in these areas, have led to active efforts to increase our collections by gift or exchange with institutions working seriously on these floras. The collections so expanded will make available for research and teaching interesting representatives of the plant families characteristic of these parts of the world. As a result, the collections are increasing in a normal way for an active herbarium.

The number of staff, students, and visitors also increased since 1954 and should continue to do so. This, however, is straining the existing working facilities beyond capacity. A small table and simple microscope are inadequate to cope with the newer and more sophisticated taxonomic techniques which require laboratory space and, often, photographic equipment. The building has become inadequate both for the staff needs and for housing the collections. In fact, it has become necessary to store certain groups of specimens in cardboard boxes on top of the steel cases.

In the horticultural herbarium in Jamaica Plain the situation for growth is more favorable. Case space is adequate for a decade of expansion, and space for more cases and for special laboratory facilities in the Administration Building is available.

During the year 18,647 specimens were mounted and added to the herbarium collections in Jamaica Plain and Cambridge, bringing the total number of sheets to 824,920. Also during the year 14,483 specimens were received, the greater portion by exchange. Special attention was given to the organization and distribution of plants from Brazil and Colombia collected about 1940 by Richard Evans Schultes, making available some extremely interesting representatives of that flora. A very important addition to the horticultural herbarium was the gift of the herbarium of the Herb Society of America which is now being appropriately marked to indicate its origin, and inserted into the herbarium. Access to this collection will, of course, be available to members of the Herb Society when needed, but the specimens will also be available on loan to monographers for research studies, and to the staff for reference.

During the past year staff members and students requested or received for identification 2,496 herbarium sheets representing 51 loans from 36 institutions. The staff filled requests for 120 loans to 65 institutions, including 16,491 specimens.

Arrangements were made during the year to collaborate with the Universidad Nacional Autónoma de México on the production of an ecologically oriented Flora of the State of Veracruz, México. The study will be under the direction of Dr. Arturo Gómez Pompa, a former Mercer Research Fellow, now Director of the National Herbarium of México. The staff of the Arnold Arboretum will collaborate in the study of the cultivated plants and by supplying assistance in herbarium, library, and research facilities. Dr. Lorin Nevling is expected to serve as coördinator for the rest of the staff.

Mr. Baranov prepared for publication taxonomic studies in the genus *Prinsepia* of the Rosaceae, and has completed a study of the morphological variation in *Sorbaria sorbifolia.* It is hoped that additional species and forms of these genera may be procured from the wild sources in Asia for cultivation in the Arboretum.

Dr. Brizicky devoted much attention to recent publications on cultivated plants and native floras from Russia. Since discussions at the 1966 International Horticultural Congress will consider the registration of cultivar names, problems of the code of nomenclature regarding translation and transliteration were the basis of a joint publication with Dr. Howard. He completed his studies of the Sterculiaceae and Goodeniaceae for the generic flora of the southeastern United States and has turned to a study of the Malvaceae represented in the area.

Dr. Dudley continued his studies of *Alyssum* and its relatives, including the evaluation of hardiness trials of many species introduced to the United States for the first time and grown at the Case Estates. He completed a review of Asian species of *Viburnum*. He also compiled bibliographic information on taxa of *Sambucus* under cultivation, preliminary to the publication of a cultivar registration list for the genus.

Dr. Ferguson completed the revision of the Cornaceae, Caprifoliaceae, and Chenopodiaceae for the generic flora of the southeastern United States.

Mr. Green was fortunate to be able to establish collaboration with botanists in Australia interested in the floras of Lord Howe and Norfolk Islands, since he has turned his attention to a review of the flora of these islands with special emphasis on the origin and distribution of the plants and the nature of the plant communities involved. He completed a study of the cultivated taxa of *Jasminum* which was published in *Baileya*. A review of the species and hybrids in the *Lonicera tatarica* complex was also completed and has been published.

Dr. Hartley's monographic study of the genus *Zanthoxylum* in Malesia is being prepared for publication. He is continuing studies of his own collections from New Guinea and those of some other expeditions sponsored by the Arboretum or received as exchange.

Dr. Howard received several collections of plants representing native and cultivated floras of the West Indies, among which special collections from the Bahamas, Bermuda, Tortola, and small adjacent and poorly known islands, and from Puerto Rico represented valuable additions to the herbarium. The study of the mossy summit forest on Pico del Oeste in the Luquillo Mountains of Puerto Rico is well under way. Coöperative environmental studies done with the National Center for Atmospheric Research have permitted the establishment of accurate weather instruments in a small building on the summit and within the elfin forest. Both automatic and manual recording instruments are being used to make various kinds of measurements related to environmental factors. Vegetational studies include measurement of growth of parts, persistence of leaves, time of flowering and fruiting, observations on pollination methods or pollinators, and on seed and fruit dispersal. Dr. Nevling and Mrs. Rüdenberg are collaborating on the cytological study of species within this forest. This complete and detailed biological-environmental study is made possible by a grant from the National Science Foundation and with the coöperation of many people and institutions in Puerto Rico and the continental United States. The permission of the Forestry Service of the Commonwealth of Puerto Rico for the use of this land is gratefully acknowledged. The contribution by Mr. Joseph B. Martinson of facilities for housing the field staff is most important in the development and continuation of this work.

Dr. Hu continued her work on the Compositae of China. The first three parts of this study, representing approximately one-third of the total, have been published. Dr. Hu is also writing special treatments of the genus *Hemerocallis* for a Daylily Handbook being prepared by a committee of the American Horticultural Society and the American Hemerocallis Society.

Dr. Nevling, as Supervisor of the Herbarium of the Arnold Arboretum and Supervisor of the Gray Herbarium, has directed various projects involving the two collections. He has continued his studies of the Thymeleaceae, devoting special attention to South American genera and species in preparation for field work in Brazil, Venezuela, and Trinidad. He has also worked with Dr. Howard in the field study of the mossy forest noted earlier.

Dr. Perry has made much progress in handling the Cape York, Australia, collections of the Archbold Expedition of 1948. With the collaboration of Dr. Hartley these collections have been labelled, at least partly named, and divided into sets for distribution.

Dr. Schubert has completed a treatment of the genus *Desmodium* for the *Flora of Panama* and is working on treatments of the genus for the *Flora of East Tropical Africa* and the *Flora Zambesiaca.* Together with Dr. Lyman Smith of the Smithsonian Institution she is continuing a review of the genus *Begonia* in Colombia, to bring up-to-date a study published by the same authors in 1946. The first of a series of investigations of the genus *Dioscorea* was published during the year and further work on the genus is in progress. Dr. Schubert visited Belém, Pará, Brazil, in December and spent time there collecting in the Area de Pesquisos Ecologicas do Guama, an ecological study area maintained cooperatively by the Smithsonian Institution, The Instituto Agronómico do Norte, and the Belém Virus Laboratory of the Rockefeller Foundation. With the aid of representatives of these institutions she was able to obtain specimens of considerable interest.

Dr. Wood continued his direction of the project concerned with the generic flora of the southeastern United States. He has supervised the preparation of illustrations and edited and contributed to the manuscripts published during the past year. He did field work in Florida during the spring, collecting material for critical studies and for illustration. He continued to serve actively on the Subcommittee for Family Names of the Committee for Spermatophyta, which is now concentrating its efforts on the names of families of living gymnosperms. During the spring Dr. Wood served on a committee of the American Society of Plant Taxonomists which met at the Smithsonian Institution to consider the feasibility of a Flora of North America.

We are pleased to have had many visitors who worked on special groups in our collections. In addition to the Mercer Research Fellows, Dr. Charles C. Tseng and Mr. Pablo Legname, Mr. Lindsay Smith of Brisbane, Australia, visited the Herbarium to study species of *Lantana* which have become noxious weeds in Australia. Mrs. S. G. M. Carr devoted her attention to the extensive collections of *Eucalyptus.* Mr. Ramón Riba, a Guggenheim Fellow, has come from the University of

Mexico to study tree-ferns. Mr. Lucio Quimbo from the College of Forestry, University of the Philippines, was particularly interested in the large wood collection with herbarium specimen vouchers.

Library:

The status of the library of the Arnold Arboretum was also affected by the decision of the Supreme Court permitting the retention of books in Cambridge. Since a complete reorganization of the whole library is not now necessary, it has been possible to initiate a rearrangement of the horticultural library in Jamaica Plain to make it more easily usable. The work of cataloguing the material in the new arrangement will, of necessity, continue through the summer, but an important start has already been made this year. The new arrangement will permit greater use of the library in association with the horticultural herbarium and make it easier to use the library in the reference room as an open-stack-library.

In the catalogue of the combined libraries of the Arnold Arboretum and the Gray Herbarium in Cambridge the librarian, Mrs. Schwarten, is indicating the ownership of the book on each catalogue card, and for the Arboretum books, specially marking each one housed in Jamaica Plain. This work has been completed for about one-half of the catalogue and the whole task should be finished within this calendar year.

During the year 431 bound volumes were added to the library of the Arnold Arboretum. The total count of bound volumes is 53,295. Reprints numbering 320 were catalogued bringing the total of the reprint collection to 20,594. The annual increment of 3000 cards was added to the *Card Index of American Plants* published by the Gray Herbarium and 2650 cards were added to the *Index to American Botanical Literature* published by the Torrey Botanical Club. Series 21 to 23 of the *Index Nominum Genericorum* were received and incorporated into that file. Approximately 900 reference cards were prepared and added to the Rehder index of cultivated plants.

Miss Stephanne Sutton continues her work on the history of the Arnold Arboretum, on the biography of Charles Sargent, and on the organization of the historical correspondence of the Arboretum. During the year Miss Sutton made a study trip to England to consult letters of Charles Sargent in the files of the Royal Botanical Gardens, Kew, the British Museum (Nat. Hist.), and at the library of the Royal Horticultural Society. The assistance rendered Miss Sutton in this search is gratefully acknowledged, as are the many photocopies of letters to and from Sargent which have been sent from many institutions and individuals in the United States. It is hoped that still other letters representing different periods or other facets of Sargent's life will be found.

The Arboretum received several large collections of reprints and personal files and also collections of books. The work on the reorganization of the reprints of Professor Joseph Faull, described in earlier reports, is now nearly complete, and the collection is in usable condition. The complete files of Harlan P. Kelsey have proven to be extremely valuable for their material pertaining to the Arnold Arboretum, to the introduction of native species into cultivation, to the development of standardized plant names, and to the development of natural areas and national parks. Materials from this gift concerned with city planning have been transferred to the Harvard University Library of the Graduate School of Design. The numerous letters are being classified and will be available for research purposes.

During the year Mrs. George Hamor presented to the Arboretum many books from the library of her late husband which increase our source material on agriculture and botany in the American tropics, especially in the West Indies.

The library also had many visitors during the year. Among the very special projects in which our collection was of great usefulness we note that of the Rachel McMasters Miller Hunt Botanical Library to photograph the title pages of books of botanical and horticultural interest. Since much of the material is most conveniently available here, we are glad to allow it to be photographed and reproduced.

Comparative Morphology:

Professor Bailey has continued his research on the primitive leaf-bearing Cactaceae under an extension of his grant from the National Science Foundation. A paper considering the significance of the reduction of vessels in the Cactaceae is being prepared. Investigations also have been made of the biochemical nature of materials within the tissues of these plants.

Professor van der Schijff, Mercer Research Fellow from the University of Pretoria, continued his studies of the peculiar growth characteristics and enlarged subterranean stem development of species of the Leguminosae. Some of the new techniques being developed for work associated with electron microscope studies were modified for application to special problems of fixation and sectioning of this difficult material.

Dr. Charles Tseng continued his studies of the pollen and floral morphology of the Araliaceae and Umbelliferae.

Dr. Howard concentrated his studies of nodal and petiolar anatomy on plants from the mossy forest study area in Puerto Rico, and to variations in the secondary body developed in leaves of more than one year's duration.

Cytology and Genetics:

Mrs. Lily Rüdenberg developed her studies of the taxa of *Lonicera* under cultivation in the Arnold Arboretum in conjunction with the systematic investigations of Mr. Green. Chromosome counts have now been obtained for all but a few of the most recent introductions and a publication recording the counts and the documenting herbarium specimens is soon to be published.

Dr. Nevling and Mrs. Rüdenberg are both participating in the cytological study of the component species of the mossy forest in Puerto Rico. The 84 genera of flowering plants in the area present a variety of difficulties in the search for division figures in which the chromosomes can be counted. Accurate chromosome counts have been obtained in certain plants only from buds collected in the early morning hours, while in other taxa the most active stages of microspore division figures seem to occur at different hours or in different sequences. The length of stages in which divisions can be obtained also seems to vary considerably among the species comprising the elfin forest.

Education:

No formal courses were given by members of the Arboretum staff, but several of them were special lecturers in a course in Plant Geography, or supervised the work of students. Informal field classes were offered at Jamaica Plain under the direction of Dr. Wyman and on the Case Estates in Weston by Dr. Hartley. A course in Plant Propagation was offered throughout the year by Mr. Fordham. The staff took part in the regular series of weekly seminars held in the Herbaria in Cambridge.

The Arboretum staff served as host to various visiting groups for conducted tours, special seminars, and general discussions or provided space and facilities for meetings. The horticultural judging and identification competition sponsored jointly by the University of Massachusetts, the Massachusetts Department of Agriculture, and the Boston Public Schools was held in the auditorium of the Administration Building. The midwinter meeting of the Northeast section of the American Society for Horticultural Sciences was held in the lecture rooms of the Biological Laboratories and in the Harvard University Herbaria in Cambridge. A special open house in Jamaica Plain and an invitation to visit all of the Arboretum facilities was extended to members of the Department of Biology of Harvard.

The Arboretum was represented at many national and international meetings and several staff members presented papers. Mr. Fordham attended the annual meeting of the International Plant Propagators' Society, the meetings of the American Society for Horticultural Science and the Horticultural Day program at the University of New Hampshire and spoke on all these programs.

Dr. Hartley attended the public symposium "Scientific Aspects of Pest Control," arranged by the National Academy of Sciences, National Research Council, held in Washington, D.C.

Dr. Howard, as lecturer for the American Institute of Biological Sciences visited the campus of Ohio University in Athens, Ohio. He spoke about the Spice Trade of Colonial New England at the Gardeners' Workshop at Sturbridge Village; to the Connecticut Nurserymen's Association short course at the University of Connecticut, and on the lecture series of the New York Botanical Garden. He attended the meetings of the

American Association of Botanic Gardens and Arboretums where he led a discussion of cultivar registration procedures; the annual meeting of the American Horticultural Society, at Callaway Gardens in Georgia; the meeting of the Directors of Systematic Collections at the Bishop Museum in Honolulu, and of the scientific advisory board of the Fairchild Tropical Garden in Miami; and represented the Arboretum at the celebration of the centennial of the Smithsonian Institution. At the request of the Department of Global Medicine of the U.S. Naval Medical School in Bethesda, Maryland, Dr. Howard presented a program on the medical significance of the vegetation of southeast Asia, considering the edible, poisonous, and dangerous plants of the area. The program was later taped in color for television use and as an educational film.

Dr. Nevling presented a paper during the symposium on the Biota of the Amazon Basin, on the need for further material and knowledge of tropical American taxa of uncertain systematic position, particularly in relation to activity in the proposed International Biological Programs.

Dr. Wood was invited to lecture at Kent State University on his work with carnivorous plants and on the generic flora of the southeastern United States.

Dr. Wyman addressed the Scandinavian Horticultural Congress in Aulanka, Finland. He attended the American Horticultural Society annual meeting in Georgia, and spoke on the program of the Clara B. Ford Garden Forum in Dearborn, Michigan, the Williamsburg Garden Symposium, the Farm and Home Week of the University of Maine, and at the Western Association of Nursery Men in Kansas City. He also presented a special workshop on "Trees, shrubs and vines for small gardens" for the Brooklyn Botanic Garden.

Travel and Exploration:

The convenience and speed of air travel and the availability of federal and foundation grants to support field work and attendance at scientific meetings have made it possible in recent years for botanists and horticulturists to travel widely.

Dr. Dudley visited several gardens in New York, New Jersey, and Pennsylvania to collect specimens for the horticultural herbarium. Mr. Fordham continued his field studies of naturally occurring witches' broom in conifers in several New England states and visited six botanical gardens and arboreta in Ohio. Dr. Howard and Dr. Nevling made two study trips to eastern Puerto Rico during the year. Dr. Nevling attended a symposium in Belém, Pará, Brazil, and en route was able to do field work on plants of his speciality near Rio de Janeiro, in Venezuela, and in Trinidad. Dr. Schubert attended a council meeting of the Association for Tropical Biology, also in Belém, and spent a week collecting near there. Miss Sutton made a trip to England to carry on her biographical and historical investigations. Dr. Wood took part in one of the study trips to Puerto Rico and was able to have several weeks in the field in Florida where he collected from Tampa to the Florida Keys and northward to Jacksonville. Dr. Wyman completed his European trip during the present fiscal year.

Members of the staff are most grateful to all those individuals who helped in various ways to make their trips both successful and interesting.

Gifts and Grants:

Three grants were received by staff members from the National Science Foundation. Dr. Howard was awarded a grant for two years to study the biology and environment of the mossy or elfin forest in Puerto Rico. A one-year grant to Dr. Wood is a terminal grant for the project on the generic flora of the southeastern United States. The National Science Foundation has supported this work generously for the past ten years. Dr. Bailey received a grant to continue his investigations of the leaf-bearing Cactaceae.

In addition, a travel grant from the Association for Tropical Biology supported the work and travel of Dr. Nevling in Brazil. Special anonymous gifts were used to aid the travel of Dr. Wyman in Europe and of Miss Sutton in England.

An appeal to the Friends of the Arnold Arboretum brought renewed contributions from many loyal supporters. This assistance is used entirely for work in horticulture and on the grounds of the Arnold Arboretum unless otherwise designated. Certain groups of plants and certain of the plantings in the Arboretum have their own special friends who designate the purposes of their gifts. It is a pleasure to carry out such wishes.

Every year special gifts of books, herbarium specimens, botanical prints, plants, Kodachrome slides, and photographs are received from many sources. Special acknowledgment is sent directly to these donors for their interest in and generosity to the Arboretum.

Publications:

The regular publications of the Arnold Arboretum are the *Journal of the Arnold Arboretum* and *Arnoldia*.

The Journal was edited by Dr. Schubert and the four issues published during the year comprised 430 pages and 25 articles. Publication of the letters from Charles Sprague Sargent to Reginald Somers Cocks, edited by Dr. Joseph Ewan of Tulane University, was completed in this period. A detailed bibliographic study of Grisebach's *Flora of the British West Indian Islands* was contributed by the British botanist William T. Stearn. A group of related papers on a new genus of palms by Dr. Harold E. Moore, Jr., and Dr. Natalie Uhl of the Bailey Hortorium and Dr. P. B. Tomlinson of the Fairchild Tropical Garden represent another of the interesting contributions published during the year.

During Dr. Wyman's absence *Arnoldia* was edited by Mr. Green. The twelve issues during the year contained a variety of articles on horticultural topics ranging from a check list of cultivars in *Weigela* to new and additional pictorial studies of tree barks. One issue devoted to plants which could be used to screen junk yards and dumps has been reprinted twice and, by request, rewritten slightly for other magazines.

A new section "Arnoldia Reviews" will appear from time to time to call attention to publications of interest in horticulture, botany, and forestry.

A cumulative index to the nine volumes of the *Symbolae Antillanae* of I. Urban was issued as a special publication. The Index was prepared by Miss Carroll and Miss Sutton, under the direction of Dr. Howard, who prepared a biographical sketch of Dr. Urban.

A set of 18 postcards was printed to supplement and replace those already issued. In response to special requests cards of the *bonsai*, fall foliage colors, and winter scenes were included. Two new brochures with new maps of the Arnold Arboretum and the Case Estates were prepared by Miss Jeanne Taylor.

The bibliography which follows includes 56 articles and books by members of the staff, published during the past fiscal year.

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RICHARD A. HOWARD, *Director*

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during at least part of fiscal year 1965–1966

William Gensel, University of Rhode Island, Providence, Rhode Island.
Pablo Raul Legname, Instituto Lillo, Tucuman, Argentina.
Sandra Shannon, University of Massachusetts, Amherst, Massachusetts.
Charles C. Tseng, Windham College, Putney, Vermont.
Hermanus Philippus van der Schijff, University of Pretoria, South Africa.
Francis H. Wolfe, University of New Hampshire, Dover, New Hampshire.

Staff of the Arnold Arboretum

1965–1966

RICHARD ALDEN HOWARD, Ph.D., Arnold Professor of Botany, Professor of Dendrology, and Director.

IRVING WIDMER BAILEY, S.D., Professor of Plant Anatomy, *Emeritus*.
KARL SAX, S.D., Professor of Botany, *Emeritus*.

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MICHAEL ANTHONY CANOSO, M.S., Senior Curatorial Assistant.*
HENRY DRAPER, Superintendent, Case Estates.
THEODORE ROBERT DUDLEY, Ph.D., Assistant Horticultural Taxonomist.**
IAN KEITH FERGUSON, Ph.D., Botanist, Southeastern Flora Project.*†
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HEMAN ARTHUR HOWARD, Assistant Horticulturist.
SHIU-YING HU, Ph.D., Botanist.
MARGARET CATHERINE LEFAVOUR, Herbarium Secretary.
LORIN IVES NEVLING, JR., Ph.D., Associate Curator and Supervisor of the Herbaria.*
DULCIE ALICIA POWELL, M.A., Research Fellow.
MARY ELIZABETH SANDERS, Ph.D., Research Associate.†††
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ROBERT GEROW WILLIAMS, B.S., Superintendent.
CARROLL EMORY WOOD, JR., Ph.D., Associate Curator.
DONALD WYMAN, Ph.D., Horticulturist.

* Appointed jointly with the Gray Herbarium.
** Resigned January 31, 1966.
† Resigned February 28, 1966.
†† Resigned May 13, 1966.
††† Resigned October 1, 1965.

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