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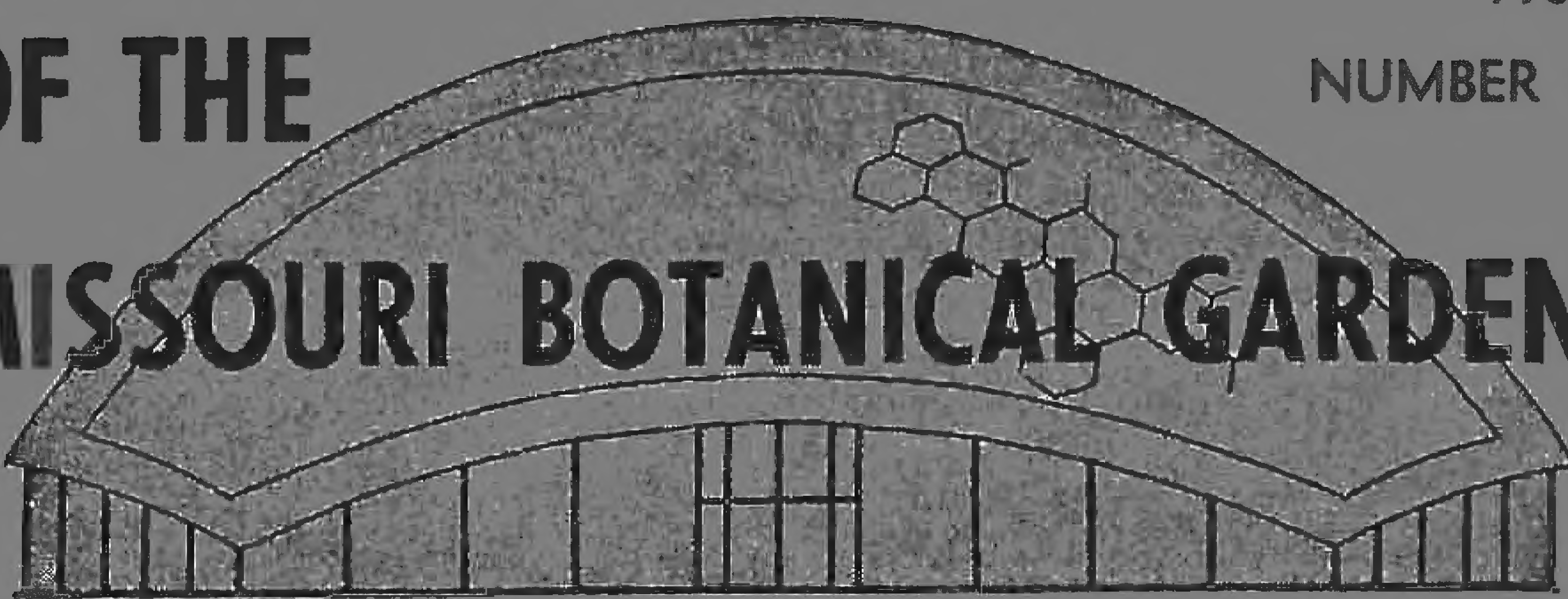

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REVISION OF BOUVARDIA (RUBIACEAE)[1]

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ABSTRACT

The study of specimens, including many types, from 24 major North American and European herbaria has led to the recognition and description of 31 species of *Bouvardia,* including the novelty *B. standleyana.* The three subgenera proposed by Schlechtendal are retained as the foundation of taxonomic order in the genus, although their retention is admittedly partially fostered by convenience. Keys to the subgenera and species are presented and synonymy, typification and information on distribution and habitat are given for each species in so far as possible.

INTRODUCTION

Bouvardia, a rubiaceous genus of primarily small shrubs, is a notable but poorly understood component of the Mexican (with extensions into the southwestern United States) and northern Central American flora. The habitat differs but is often a rocky outcrop of steep hillsides or barrancas at elevations above 500 meters, the ambient conditions varying from xeric to very mesic.

No economic significance is attributed to the genus. However, the attractive flowers of a number of species have led to their adoption as ornamentals, and artificial hybrids between some of them have been obtained. The nomenclature of these horticultural subjects is considered outside the scope of this study.

The taxonomy of *Bouvardia* has received little attention since Standley's treatment in the North American Flora (1921b), in which 30 species were recognized, a number being newly described. Since Standley's revision, descriptions of 19 additional species have appeared, scattered throughout the literature. The immediate needs in the genus were to evaluate the status of the species described since

[1] Based on a dissertation submitted to the Graduate School of The University of Texas at Austin in partial fulfillment of the requirements for the degree of Doctor of Philosophy. Assisted by a grant-in-aid, The Society of the Sigma Xi and by National Science Foundation Grant No. GB-4128 (Principal Investigator, W. Frank Blair). Dr. Marshall C. Johnston is gratefully acknowledged for supervision of this research.

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Standley's revision and re-evaluate those recognized by Standley. The recent aquisition of material by herbaria throughout the world has emphasized the pertinence of such a study.

The grouping of species within the genus has also been a matter of concern. Standley did not formally recognize the three subgenera introduced by Schlechtendal (1854), although his organization of species in the key corresponds closely to them. I have found Schlechtendal's subgenera to be at least a useful contrivance and consider their retention worthwhile for the sake of convenience alone. However, as nature is not systematically perfect, it is to be understood that some intermediacy exists between them, and that their delimitation is perhaps more pragmatic than phylogenetic.

The position of *Bouvardia* within the *Rubiaceae* has undergone drastic, and probably justified, alteration. *Bouvardia, Heterophyllaea, Hindsia, Manettia, Danais, Coursiana* and *Hymenopogon* were traditionally treated as members of the *Cinchoneae* (Hooker, 1873; Schumann, 1891). However, Bremekamp (1952) considered winged seeds (the only character uniting the tribe *Cinchoneae*) to be of little morphological significance and transfered these genera to the subfamily *Rubioideae* and tribe *Hedyotideae* (having transfered the tribe *Hedyotideae* from the subfamily *Cinchonoideae*) based on the presence of raphides, the absence of large pits in the basal wall of the testa cells, and the peltate placentas. Bremekamp reaffirms this transfer in a later paper (1966) in which he outlines his revisionary subdivision of the *Rubiaceae*.

Of the above genera, *Bouvardia* appears most closely related to *Heterophyllaea* and *Hindsia* from which it is distinguished by characters of the fruit and by flowers with four rather than five stamens and to *Manettia* from which it differs in its shrubby (not scandent) habit, terminal inflorescences and loculicidal capsules. It is doubtful that the position of placental attachment may be employed as a character delimiting *Bouvardia* and *Mannetia*, as attempted by Standley (1921a, see key). In specimens of both genera examined, the placenta is attached to the base of the septum. *Bouvardia* is distinguished from *Hedyotis* (sensu Lewis, 1961) by characters of the placenta, seed, endosperm and stipules.

Systematic Treatment[3]

Bouvardia Salisbury, Parad. Lond. **pl. 88,** 1807.

Aeginetia Cav., Anal. Ci. Nat. **3:** 129, 1801; Ic. **6:** 51, 1801, not *Aeginetia* L. (Sp. Pl. 632, 1753).

Shrubs, suffrutices or perennial herbs; raphides present. *Leaves* opposite or 3 to 4(-6)-nate, petiolate or infrequently sessile; stipules interpetiolar, consisting of a basal sheath and a usually trullate, green (not hyaline or scarious) mucro or free-portion; blades simple, entire, usually membranous. *Inflorescences* terminal, cymose (occasionally reduced to solitary flowers). *Flowers* actinomorphic, often showy; calyx-lobes 4, most often lanceolate, typically erect or ascending, persisting

[3] A list of exsiccatae may be obtained by writing the author. Address as of September 1, 1968: Department of Botany, Miami University, Oxford, Ohio 45056.

in fruit; corolla tubular or salverform, the tube usually well exceeding the lobes, the lobes 4 (very rarely 5 on the same plant), valvate; stamens 4, epipetalous, the anthers linear, dehiscing by longitudinal slits, usually included and subsessile in pin flowers (but typically positioned well above the middle of the corolla-tube), included or exserted (the filaments becoming free from the corolla-tube at the throat and extending beyond) in thrum flowers; ovary ± subglobose, inferior to ⅓ superior, the style single, slender (to ca 1 mm broad), compressed, elongate, exserted in pin flowers, included in thrum flowers, terminating in 2 rather short, linear, often minutely papillose style-branches. *Capsules* subglobose or slightly oblate, often somewhat compressed loculicidally, 2-celled (the septum complete), dehiscing loculicidally then septicidally, with a single ascending, fleshy, peltate placenta in each cell affixed to the based of the septum; seeds ∞, brown, vertically imbricate on the placenta, uniformly and ± evenly winged, the wing neither dissected nor fringed, the nucleus disciform, flattened or slightly pulvinate in cross-section, the testa cells thin-walled, lacking large pits in the basal wall, the endosperm fleshly.

Type: *Bouvardia triphylla* Salisbury [=*B. ternifolia* (Cav.) Schlecht.].

Key to the Subgenera

a. Leaves opposite.
  b. Inflorescences 3 to many-flowered, each partial inflorescence (flower or group of flowers, and their pedicels and peduncle, arising from each leaf-axil of the terminal 1-4 leaf-pairs of a floriferous stem tip) often composed of 3 or more flowers (sometimes of only 1); corolla tubular to salverform, white or variously colored, the tube 0.4-3.5(-4.4) cm long, the lobes 1-7(-8.5) mm long, flared 10-90°; anthers in thrum flowers variously included or exserted. If the corolla is white (often greenish- or yellowish-white rather than pure white) and salverform and the partial inflorescences are solitary flowers, then the floriferous branchlets are often very short and terminate in nodding, 3 to 7-flowered inflorescences (cf. *B. multiflora*) .... I. *Bouvardiastrum* (p. 3)
  bb. Flowers solitary or if the inflorescences several-flowered, then each partial inflorescence composed of only a solitary flower; corolla salverform, white, the tube (1.5-)3.5-8.5 cm long, the lobes (4-)7-28 mm long, flared at 90°; anthers included in thrum flowers or only the tips protruding .... II. *Bouvardioides* (p. 16)
aa. Leaves 3 to 4(-6)-nate at most nodes .... III. *Bouvardia* (p. 22)

I. Subg. Bouvardiastrum Schlecht., Linnaea **26:** 58, 1854.

Shrubs, suffrutices or rarely perennial herbs, the seasonal branches opposite, elongate or very short, pubescent or glabrous. *Leaves* opposite, typically petiolate; blades glabrous to conspicuously pubescent, the secondaries pinnate, less frequently subpalmate or plinerved, arcuate, rarely obscure, the reticulation obscure to prominent. *Inflorescences* few to many-flowered; partial inflorescences often composed of 3 or more flowers (occasionally 1-flowered). *Flowers* pedicellate or rarely sessile; calyx-lobes free to the floral cup or joined basally by a calyx-tube; corolla tubular to salverform, red, orange, yellow, violet, lavender, white, yellowish-white or greenish-white, externally glabrous or puberulent or more elongate-pubescent, the tube internally with a villous ring toward the base or more often generally pilose or villous in the lower half, rarely entirely glabrous within; anthers included in pin flowers (rarely exserted), in thrum flowers included or often exserted; style glabrate or rarely pubescent, the branches 0.5-2.5(-4) mm long.

Lectotype: *Bouvardia triflora* H.B.K. [=*B. multiflora* (Cav.) Schultes & Schultes f.].

a. Leaf-blades typically pinnately nerved, less frequently subpalmately nerved (the majority of the secondaries arising ± together near the base of the mid-vein but at least 2 arising near the middle).
  b. Corolla-tube with an internal villous ring toward the base.
    c. Stipular processes lanceolate, eglandular; inflorescences 7 to 12-flowered; corolla externally minutely puberulent with trichomes to 0.05 mm long (sometimes sparsely so), the lobes to 1.3 mm broad ....6. *B. conzattii*
    cc. Stipular processes often filiform and terminally glandular; inflorescences 7 to 60-flowered; corolla externally glabrous, the lobes 2-4 mm broad .... 10. *B. dictyoneura*
  bb. Corolla-tube often pubescent in the lower half but the pubescence not organized into an isolated villous ring.
    d. Calyx-lobes joined basally by a calyx-tube 0.5-2.5 mm long.
      e. Flowers short-pedicellate, not subtended by stipule-sheaths, the corolla externally minutely puberulent or glabrous.
        f. Seasonal branches glabrate; petioles 2.5-11.5 mm long; leaf-blades cuneate to rounded at the base; corolla white to greenish- or yellowish-white, the lobes spreading to 90°; anthers exserted by 2-5 mm in thrum flowers ....3. *B. loeseneriana*
        ff. Seasonal branches distally sparsely to densely pubescent (the trichomes variously 0.05-1 mm long); petioles 0.5-2(-7) mm long; leaf-blades rounded or cordate basally; corolla red-orange or apricot, the lobes yellow, spreading to 45°; anthers included in thrum flowers or only the tips protruding ....5. *B. cordifolia*
      ee. Flowers sessile, each with its base surrounded by the stipule-sheath of a bract-pair, the corolla externally glabrous ....4. *B. capitata*
    dd. Calyx-lobes free to the floral cup.
      g. Leaf-blades slightly crassulate, the secondaries partially or totally obscure; corolla red-orange, the lobes yellow ....7. *B. chrysantha*
      gg. Leaf-blades membranous, the secondaries readily evident their whole length; corolla variously colored.
        h. Corolla externally puberulent or pubescent.
          i. Inflorescences obviously terminal on usually well-developed, leafy branches; corolla externally sparsely or densely pubescent with trichomes 0.3-1.3 mm long.
            j. Seasonal branches distally glabrous or sparsely pilose; lower leaf-blade surface and distal portion of corolla-tube sparsely pilose; secondary veins subpalmate ....8. *B. subcordata*
            jj. Distal portion of seasonal branches, lower leaf-blade-surface and distal portion of corolla-tube densely villous; secondaries pinnate ....9. *B. xylosteoides*
          ii. Inflorescences pseudoaxillary on greatly reduced, slender, leafless branchlets; corolla externally minutely papillose-puberulent (trichomes to 0.05 mm long) ....12. *B. gracilipes*
        hh. Corolla externally glabrous.
          k. Seasonal branchlets distally glabrous or papillose-puberulent with trichomes to 0.2 mm long; leaf-blades with the secondary veins not brochidodrome, the reticulation obscure or inconspicuous; inflorescences with fewer than 15 flowers; corolla at least sparsely pilose in the lower half.
            l. Floriferous branchlets often suppressed (the vegetative portion as short as 2 mm); leaf-blades sparsely to

moderately papillose-puberulent above and below; floral cup minutely hirtellous with trichomes 0.05-0.3 mm long; calyx-lobes typically lanceolate, usually somewhat hirtellous; corolla white to greenish- or yellowish-white, less frequently yellow or red, tubular to salverform; anthers often exserted in thrum flowers ....1. *B. multiflora*

ll. Floriferous branchlets often well-developed; leaf-blades glabrate but often ciliate marginally; floral cup glabrous or obscurely puberulent with trichomes to 0.1 mm long; calyx-lobes linear or linear-lanceolate, often glabrate; corolla red or occasionally yellow, tubular; anthers included in thrum flowers or only the tips protruding ....2. *B. laevis*

kk. Seasonal branchlets distally rather sparsely pilose to densely arachnose-pubescent with trichomes 0.2-1 mm long; leaf-blades with the secondary veins often brochidodrome, the reticulation prominent below; inflorescences usually more than 15-flowered; corolla entirely glabrous within ....11. *B. standleyana*

aa. Leaf-blades (3-)5-plinerved.

m. Inflorescences with fewer than 25 flowers; pedicels 6-13 mm long; calyx-lobes deltoid-acuminate, ca 1 mm long; corolla-tube with an internal villous ring toward the base ....13. *B. rekoi*

mm. Inflorescences more than 25-flowered; pedicels 0.5-6 mm long; calyx-lobes lanceolate to linear or subulate, 2-9 mm long; corolla-tube often villous in the lower half but the pubescence not organized into a villous ring.

n. Reticulation of leaf-blades obscure above, inconspicuous below; calyx-lobes lanceolate or elliptic-lanceolate, 1-2 mm broad; corolla tubular, red, the tube 10-17 mm long; style glabrate ....14. *B. oaxacana*

nn. Reticulation of leaf-blades visible above, prominent below; calyx-lobes linear-subulate, 0.3-1 mm broad; corolla tubular to salverform, violet or lavender, the tube 4.5-8.5 mm long; lower half of the style often pubescent ....15. *B. quinquenervata*

1. Bouvardia multiflora (Cav.) Schultes & Schultes f., Mant. Syst. Veg. **3:** 118, 1827.

Aeginetia multiflora Cav., Anal. Ci. Nat. **3:** 131, *t. 28, fig. 2,* 1801; Ic. **6:** 52, *t. 572, fig. 2,* 1801.

Bouvardia versicolor Ker, Bot. Reg. **3:** *pl. 245,* 1817. (Based on a greenhouse-grown plant, the illustration is taken as the type)

B. triflora H.B.K., Nov. Gen. Sp. Pl. **3:** 386, 1820. (Type *Humboldt & Bonpland s.n.* P, not seen; fragment P)

B. cavanillesii DC., Prodr. **4:** 366, 1830. (Based on *Aeginetia multiflora*)

Anotis longiflora Bentham, Pl. Hartw. 23, 1839. (Type *Hartweg 206* GH, K; photo MICH)

Bouvardia triflora var. hirsuta Martens & Galeotti, Bull. Acad. Bruxelles **11**(1): 236, 1844. (Type *Galeotti 2658* BR)

B. bicolor Kunze, Linnaea **20:** 24, 1847. (Based on garden plants grown from Mexican seed, the description is taken as the type)

B. mutabilis Walpers, Ann. Bot. Syst. Lipsiae **5:** 127, 1849, as synonym of *B. versicolor.*

B. schiedeana Schlecht., Linnaea **26:** 123, 1854. (Type *Schiede s.n.* B†)

Houstonia triflora (H.B.K.) A. Gray, Proc. Amer. Acad. Arts Sci. **4:** 314, 1860.

Bouvardia gracilis A. Gray, loc. cit. **22:** 306, 1887. (Type probably *Pringle 1255* G, GH)

B. versicolor var. *graciliflora* A. Gray in S. Watson, loc. cit. 416. (Syntypes *Palmer 154, 369* & *708,* all GH)

B. heterophylla Standley, N. Amer. Fl. **32:** 107, 1921. (Holotype *Heyde & Lux 3137* US 398167; isotype GH)

B. macrantha Standley, loc. cit. (Holotype *Purpus 3981* US 841341; isotypes BM, F, GH, MO, UC)

B. latifolia Standley, loc. cit. 111. (Holotype *Langlassé 246* US 385804; isotypes F fragment, GH, P)

B. salvadorensis Steyermark, Ceiba **4**: 302, 1955. (Holotype *Tucker 1368* F 1492726; isotypes MICH, UC, US)

Shrubs to 2 m; seasonal branchlets very short (2 mm) or to 10 cm or more in length, papillose-puberulent with trichomes to 0.2 mm long. *Leaves* with petioles to 5 mm long; blades most often ovate-lanceolate (varying from broadly ovate to narrowly lanceolate or elliptic-lanceolate), 0.7-6.7 cm long, 0.2-3.2 cm broad, membranous, sparsely or moderately hirtellous with papillose trichomes to 0.3 mm long, the secondaries 4-8, usually pinnate, the reticulation often obscure. *Inflorescences* terminal but often seemingly axillary by virtue of the very short branchlets, 3 to 7(-11)-flowered, often nodding; partial inflorescences 1 to 3-flowered; *Flowers* with pedicels 0.5-6(-16) mm long which are papillose-puberulent; floral cup hirtellous with papillose trichomes to 0.3 mm long; calyx-lobes typically lanceolate (varying from deltoid-acuminate to subulate), 1-8 mm long, usually somewhat hirtellous; corolla tubular to virtually salverform, white to greenish- or yellowish-white, less frequently yellow or red, glabrous, the tube 6-36(-44) mm long, internally sparsely pilosulous toward the base, the lobes 1-7(-8.5) mm long, spreading 10-90; anthers 1.5-2.5 mm long, in thrum flowers either exserted by 1-5 mm or included (tips sometimes protruding), included by 1-6 mm in pin flowers; style glabrous, the branches 1-4 mm long. *Capsules* 3-7 mm long, 3.5-9 mm broad; seeds 2-3.5 mm broad.

Holotype: MA, not seen. Cavanilles gives no information about the locality or collector in the original description.

Chihuahua to Nicaragua; no specimens known from Vera Cruz, Chiapas or the Yucatan Peninsula; moist slopes or ravines to dry, rocky hills or buffs; with pine-oak or thorn-scrub-cactus association; 1000-3000 m; flowering May through September.

Bouvardia versicolor, B. heterophylla, B. latifolia, B. macrantha and *B. salvadorensis* are reduced to synonymy for the first time. I consider *B. multiflora* to be a polymorphic species, the description given encompassing the variability of specimens referred to all the above segregates.

The types of *B. heterophylla* (Guatemala) and of *B. salvadorensis* and certain collections from Temascaltepec, Mexico and Zitacuaro, Michoacan (*Hinton 7899, 7911, 7925, 7933, 11996,* all US) possess elongate pedicels (often 5-16 mm), short calyx-lobes (2 mm or less) and seasonal branches often more elongate than those of the average specimen of *B. multiflora.* Type specimens of *B. latifolia* and other Guerreran specimens such as *Crisman & Willis 193* (MICH, TAES) and *Cooper & Rowell 2511* (MICH) possess elongate (to 44 mm), subsalverform (lobes spreading at ca 60°), white corollas which closely approach the type of corolla found in the subg. *Bouvardioides.* The type of *B. macrantha* (Tlacuilotepec, Puebla) and collections from the vicinity of San Luis Tultitlanapa, Puebla (*Purpus 3324, 3328, 3330, 3331, 3332,* all MO) are characterized by rather elongate (to 36 mm), tubular corollas in which the anthers are included (or only the tips protruding) in thrum flowers. All these specimens are assignable to *B. multiflora* based on their total morphology and when all specimens of B. *multiflora* are considered, complete intergradation is seen to exist. Attempting to formalize components of this reticulum of variation by the application of different Latin names would lead to confusion.

2. BOUVARDIA LAEVIS Martens & Galeotti, Bull. Acad. Bruxelles **11**(1): 236, 1844.

B. flava Decaisne, Fl. Serres **1**: 215, *pl.* 38, 1845. (Based on a greenhouse-grown plant, the illustration is the type)
B. mollis Linden ex Schlecht., Linnaea **26**: 85, 1854. (Type LZ†)
B. nubigena Standley & Steyermark, Publ. Field Mus. Nat. Hist., Bot. Ser. **22**: 382, 1940. (Holotype *Steyermark 31901* F 1043221; photos F, TEX)

Shrubs to 1.5 m; seasonal branches usually well-developed, glabrous or distally sparsely papillose-puberulent with trichomes to 0.2 mm long. *Leaves* with petioles 1-7.5 mm long; blades ovate-lanceolate, subattenuate or subacuminate at the apex, 1.5-10.5 cm long, 0.7-5 cm broad, membranous, glabrate but often ciliate marginally with trichomes 0.05-0.8 mm long, less frequently sparsely puberulent above and below (often primarily along the veins), the secondaries 4-10, pinnate, the reticulation apparent or obscure. *Inflorescences* 3 to 11-flowered; partial inflorescences 1 to 5-flowered. *Flowers* with pedicels (1-)3-27 mm long which are glabrous to moderately papillose-puberulent; floral cup glabrous or sparsely puberulent with trichomes to 0.1 mm long; calyx-lobes linear-lanceolate or linear, glabrate or sparsely ciliate, 4-12 mm long; corolla tubular, red or occasionally yellow, glabrous externally, the tube 16-39 mm long, pilosulous in the lower half, the lobes 2.5-5.5 mm long, flared up to 40°; anthers 2-4 mm long, included or only the tips protruding; style glabrate, the branches 1-2.5 mm long. *Capsules* 4-9 mm long, 5-10 mm broad; seeds 2-3 mm broad.

Type: Mexico. Vera Cruz: ravines around Zacuapan, 3000 ft, April 1840, *Galeotti 2600* (BR, F fragment ex G-Deless., P not seen; photo of P specimen at F, TEX, US).

Southwestern Tamaulipas to northwestern Oaxaca, Michoacan and southern Jalisco; centered in Hidalgo and western Vera Cruz; also found in Guatemala and extreme southern Chiapas; slopes of barrancas or rocky outcrops of mountainsides; oak-pine woodlands in mesic to semi-arid conditions; 1000-3300 m; flowering April to August.

Bouvardia laevis and *B. multiflora* are closely related species and intermediates are sometimes encountered. Keying out a "problematical" specimen often requires consideration of a number of characters in combination (see key, p. 5), some of which are not statable in quantitative or absolute terms, and none of which will alone serve to identify the plant with certainty. Although it would be easy to build a case for combining these two species, the majority of specimens are easily identifiable and the extremes quite divergent. At present it seems unwise to combine them, increasing still further the complexity of the variation coming under the name *B. multiflora*.

3. BOUVARDIA LOESENERIANA Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. **11**: 186, 1936.

B. hintoni Bullock, Kew Bull. **1937**: 307, 1937. (Type *Hinton 8107* BM, F, G, GH, K, MO, US)

Shrubs, seasonal branches short or well-developed, glabrate. *Leaves* with petioles 2.5-11.5 mm long; blades ovate to ovate- or elliptic-lanceolate, basally cuneate to rounded, 2.5-9.8 cm long, 1.3-6.7 cm broad, sparsely pilosulous below and at the margins with white trichomes 0.2-1 mm long, glabrate above, the secondaries 4-12, pinnate, the reticulation apparent or obscure. *Inflorescences* (3-)7 to 20-flowered. *Flowers* with pedicels 0.5-5 mm lcng; floral cup glabrous to pruinose-puberulent (trichomes to 0.05 mm long) or hirtellous (trichomes to 0.5 mm long); calyx-lobes deltoid to broadly or narrowly lanceolate, 1-3(-4) mm long, marginally ciliate with trichomes to 0.2(-0.4) mm long, joined basally by a calyx-tube 0.5-2 mm long; corolla typically salverform, white to greenish- or yellowish-white, externally densely pruinose- or papillose-puberulent with white trichomes to 0.05 mm long or glabrous, the tube 24-32 mm long, internally sparsely or moderately pilosulous with trichomes 0.4-1 mm long, the lobes oblong-elliptic or oblong-lanceolate, 3.5-7 mm long, spreading at ca 90°, often arcuate; anthers 2-2.5 mm lcng, exserted in thrum flowers by 2-5 mm; style glabrate, the branches 0.5-2 mm long.

Holotype: Mexico. Guerrero: Texquitzín nr Chilapa, 28 Oct 1829, *Schultes 89* (B†); isotype F (fragment).

Guerrero and the southern portion of the State of Mexico to Nayarit; precipitous mountainsides, wooded slopes and barrancas, steep ravines; typically in moist habitats but occasionally occurring in more arid barancas; 300-2400 m; flowering July through December.

In typical specimens of *B. loeseneriana* the corolla-tubes are minutely but densely pruinose- or papillose-puberulent externally, the floral cups glabrous or obscurely puberulent with trichomes to 0.05 mm long, the calyx-lobes deltoid or broadly lanceolate and not exceeding 3 mm, a calyx-tube to 2 mm long is present and the seasonal branches are well-developed (see types of *B. loeseneriana* and *B. hintoni* and such collections as *Hinton 10521,* US; *15003,* US; *15979,* US; *McVaugh & Koelz 1046,* MICH). However, in Colima, southwestern Jalisco and Nayarit, variable specimens are encountered with glabrous corolla-tubes, glabrous or pruinose-puberulent (trichomes to 0.05 mm long) or conspicuously hirtellous (trichomes to 0.5 mm long) floral cups, often slender-lanceolate calyx-lobes to 4 mm long and short or elongate seasonal branchlets (see *McVaugh 15260, 18060, 18964, 19832; Wilbur & Wilbur 2335, 2439, 2440, 2464, 2465;* all MICH). Specimens with glabrous corollas, hirtellous floral cups, slender-lanceolate calyx-lobes and short branchlets are difficult to distinguish from *B. multiflora* and are doubtless closely allied to the latter. They differ from *B. multiflora* in the presence of a calyx-tube and usually in the more numerous flowers (more than 7) of the inflorescence.

4. Bouvardia capitata Bullock, Hook. Ic. Pl. *t. 3296,* 1935.

Shrubs to 1.5 m; seasonal branchlets rather elongate, to 2 mm broad, woody or suffrutescent, glabrous or sparsely pilose distally with trichomes to 0.7 mm long. *Leaves* with petioles 1-14 mm long; blades ovate to suborbicular or broadly elliptic, 2-10.3 cm long, 1.3-6.3 cm broad, usually sparsely pilose with white trichomes to 1 mm long (occasionally restricted to the margins), the secondaries 4-10, pinnate or the lower 4-6 arising subpalmately near the base of the midvein, the reticulation obscure. *Inflorescences* capitate, 6 to 36-flowered. *Flowers* sessile, each subtended by the stipule-sheath of a bract-pair; floral cup typically glabrous; calyx-lobes linear-lanceolate, 3-8 mm long, pilosulous toward the margins with trichomes 0.3-0.8 mm long, joined basally by a calyx-tube 1-2.5 mm long; corolla ± salverform, probably white, glabrous externally, the tube 15-23 mm long, pilosulous in the lower half; the lobes 3-7 mm long, oblong, spreading to 90°, often arcuate; anthers 1-2 mm long, exserted by 2-4 mm in thrum flowers; style glabrous. *Capsules* 4.5-8 mm long, 4.5-11 mm broad; seeds 2.5-4 mm broad.

Type: Mexico. Mexico: Distr Temascaltepec, Palmar, in a barranca, 7 July 1934, *Hinton 6319* (BM, F, K).

Known only from the District of Temascaltepec in the State of Mexico; barrancas and open woodlands at 1000-1500 m; flowering in July and August.

As pointed out by Bullock (loc. cit.) the congested inflorescence of *B. capitata* is distinctive, probably representing a reduction from a compound dichasium. The base of each sessile flower is surrounded by the often membranous and pluriaristate stipule-sheath of a bract-pair, the lamina being suppressed. The flowers are grouped in threes and then in multiples of three, each flower-group or partial inflorescence being in turn subtended by a stipule-sheath showing an increasing development of the bract lamina.

Bouvardia capitata is closely related to *B. loeseneriana,* but in addition to the sessile flowers subtended by stipule-sheaths, specimens of *B. capitata* may often be distinguished by the glabrous corollas with the tube usually less than 23 mm long, linear-lanceolate calyx-lobes typically exceeding 3 mm in length and possessing a more elongate marginal pubescence, and the always glabrous floral cups.

5. Bouvardia cordifolia DC., Prodr. **4:** 366, 1830.

? *Hedyotis lutea* Sessé & Mociño, Fl. Mex. 22, 1891. (Type *Sessé & Mociño s.n.* MA, not seen).

Shrubs, slender or suffrutices to 1 m; seasonal branches ascending, distally sparsely to densely papillose-puberulent or villosulous with white trichomes 0.05-1 mm long. *Leaves* with pubescent petioles 0.5-2(-7) mm long; blades broadly ovate to ovate-lanceolate, cordate or rounded at the base, 1.5-6.6 cm long, 0.7-5.2 cm broad, sparsely puberulent with papillose to villous trichomes 0.05-1 mm long, the secondaries 4-12, pinnate, the reticulation often conspicuous below. *Inflorescences* 7 to 50-flowered, subcapitate. *Flowers* with pedicels 0.5-2.5(-8) mm long which are sparsely to densely pubescent; floral cup glabrate to densely white-pubescent with trichomes 0.05-0.8 mm long; calyx-lobes lanceolate to subulate, 1.5-7.5 mm long, joined basally by a calyx-tube 0.5-2 mm long; corolla tubular, red-orange or apricot (the lobes and extreme distal part of the tube yellow) minutely white-papillose-puberulent externally with trichomes to 0.05 mm long, less frequently glabrous, the tube 12-30 mm long, pilose in the lower half but lacking a villous ring, the lobes ovate or deltoid to oblong or elliptic-lanceolate, flaring up to 45°, 1.2-5 mm long; anthers ca 2 mm long, brown, included by 1-6 mm or the tips protruding; style papillose-puberulent to glabrate, white, the branches 1-1.5 mm long. *Capsules* 3.5-6 mm long, 4-7 mm broad; seeds 1.5-3.5 mm broad.

Type: Mexico: *Sessé & Mociño s.n.* (MA, not seen); *pl. 487* of the *Calques des dessins* . . . is a drawing of the type.

Mexico, Michoacan, Oaxaca, Guerrero, Colima and Jalisco; steep moist slopes, shady arroyas or dry rocky cliffs or barrancas; often in oak or pine-oak woodlands; 200-2850 m; flowering June through November.

The majority of specimens of *B. cordifolia* deposited in herbaria are from the vicinity of Morelia, Michoacan and Temascaltepec, Mexico and are characterized by the minute but often dense external puberulence of their corollas (see *Blackwell 26 & 27,* TEX; *Hinton 7950,* F; *Hitchcock & Stanford 7146,* US; *Kenoyer A263,* F; *Rzedowski 20775,* ENCB). A few scattered collections of *B. cordifolia* have been made in Colima, southern Jalisco, Guerrero and Oaxaca, but these are all distinguished by glabrous corollas (see *Iltis et al. 570, McVaugh 15010 & 15813, Ryan & Floyed 37,* all MICH). As I have found no other character correlated with the difference in pubescence of the corolla which might serve to delimit these two "groups" of *B. cordifolia,* and since their apparent geographic separation may result from insufficient collecting rather than natural disjunction, I have not recognized them by formal infraspecific categories. It is perhaps worth mentioning that an analogous situation involving pubescent and glabrous forms exists in *B. loeseneriana* and that the geographic area of interest and pattern of distribution are roughly similar.

6. BOUVARDIA CONZATTII Greenman, Proc. Amer. Acad. Arts Sci. **39:** 92, 1903.

Shrubs; seasonal branchlets often distally white-papillose-puberulent with trichomes 0.05-0.1 mm long. *Leaves* with petioles 1-3 mm long; stipular processes lanceolate; blades ovate to lanceolate, 1.5-5 cm long, 0.4-2.8 cm broad, basally cuneate to broadly rounded, minutely papillose-hispidulous marginally and often sparsely so above and below (primarily along the main veins below) with trichomes 0.05-0.25 mm long, the secondaries 6-10, pinnate or occasionally the lower 4-6 arising subpalmately near the base of the midvein, the reticulation usually obscure. *Inflorescences* 7 to 12-flowered. *Flowers* with pedicels 0.5-5.5 mm long; floral cup glabrate; calyx-lobes linear or linear-lanceolate, 2.5-5.5 mm long, 0.3-0.8 mm broad, free to the floral cup; corolla tubular, red or yellowish-red, very minutely papillose-puberulent externally with trichomes less than 0.05 mm long (sometimes only sparsely so), the tube 8-17 mm long, 1.5-2 mm broad at the neck, internally with a villous ring toward the base, the lobes ovate to deltoid, 1-2 mm long, to 1.3 mm broad; anthers 2-3 mm long, included by 1-4.5 mm; style glabrate. *Capsules* 2.5-4.5 mm long, 3-5.5 mm broad; seeds 1.3-2 mm broad.

Holotype: Mexico. Oaxaca: 1750 m, July-Aug 1901, *Conzatti & Gonzáles 1067* (GH). (sphalm. *Conzatti & Gonzáles 1076* by Greenman)

Known only from Oaxaca; 1600-2000 m; known to be in flower May through August.

7. BOUVARDIA CHRYSANTHA Martius, Del. Hort. Monac. Sem. **1848:** 4, 1848 (not seen); Ann. Sci. Nat., Bot., sér. 3, **11:** 247, 1849.

B. myrtifolia Schlecht., Linnaea **26**: 121, 1854. (Type *Schiede s.n.* B†)
B. macilenta Blake, Contr. Gray Herb. **53**: 65, 1918. (Holotype *Conzatti & Reko 3288* GH)
B. cataphyllaris Bullock, Hook. Ic. Pl. *t.* 3297, 1935. (Type *Hinton 1131* BM, F, G, GH, K, MICH, MO, US)

Shrubs or suffrutices to 1 m; seasonal branchlets well-developed or very short, glabrous or distally papillose-puberulent (trichomes to 0.1 mm long) or pilosulous (trichomes to 1 mm). *Leaves* with petioles 0.5-3 mm long; blades ovate to elliptic or lanceolate, 1-7.8 cm long, 0.4-3 cm broad, often somewhat conduplicate, slightly crassulate, pale-satiny-green below, glabrous or sparsely puberulent with white trichomes 0.1-1 mm long (sometimes limited to the margins and midvein), rarely more densely pubescent, the secondaries usually totally or partially obscure, the reticulation not visible. *Inflorescences* 5 to 25-flowered, usually subcapitate. *Flowers* with pedicels 0.5-4 mm long; floral cup green, glabrous or occasionally pubescent; calyx-lobes linear-lanceolate to slender-subulate, 2.5-11 mm long, free to the floral cup; corolla tubular, red-orange (the lobes and extreme distal part of the tube yellow), externally glabrous or rarely sparsely pilosulous with white trichomes to 1 mm long, the tube 15-34 mm long, 2-4 mm broad at the neck, sparsely pilosulous in the lower half (trichomes ca 0.5 mm long), the lobes ovate to oblong, 1.5-4 mm long, 1-3 mm broad, flared up to 40°; anthers white or yellow-white, 1.5-3 mm long, included by 1-6 mm or the tips protruding; style glabrate, white or yellow-white. *Capsules* 3.5-8.5 mm long, 4.5-10 mm broad; seeds 2.5-3.5 mm broad.

Type: "Mexico": nr Sanjaguillo, *Karwinsky s.n.*, not seen.

Oaxaca and extreme southern Peubla to Jalisco; dark loamy soil of volcanic slopes or rocky bluffs of barrancas; oak zone; 1300-2900 m; flowering mostly from June through October.

Except for the small size of all structures, the type specimen of *B. macilenta* falls within the limits of variation under the name *B. chrysantha*.

Certain specimens of *B. chrysantha* such as *Hinton 10471* (MO, US) *& 10541* (MO, US) and the type of *B. cataphyllaris* resemble *B. multiflora* in their short floriferous branchlets, hirtellous floral cups and often partially evident secondary veins. It is thus probable that *B. chrysantha* intergrades to a limited extent with *B. multiflora*. However, *B. chrysantha* is retained as a separate species since all but a few specimens are clearly distinct from *B. multiflora*. As already indicated, combining closely related species with *B. multiflora* would only lead to the creation of one hopelessly polymorphic species.

8. Bouvardia subcordata Standley, N. Amer. Fl. **32**: 105, 1921.

Shrubs, the seasonal branches glabrous or pilose distally and at the nodes. *Leaves* with petioles 1-5 mm long; blades ovate to suborbicular, basally broadly rounded or cordate, 1.8-4.3 cm long, 1.2-3.4 cm broad, membranous, moderately or rather sparsely (but evenly) pilose with white trichomes 0.2-1 mm long, the secondaries 6-8, the lower 4-6 often arising subpalmately near the base of the midvein, the reticulation obscure. *Inflorescences* 3 to 7-flowered. *Flowers* with pedicels 1-5 mm long which are puberulent with white trichomes ca 0.5 mm long; floral cup tomentose; calyx-lobes lanceolate or elliptic-lanceolate, 2-7.5 mm long, sparsely pilose, free to the floral cup; corolla tubular, red (?), externally rather sparsely white-pilose distally with trichomes 0.3-1 mm long, the tube 15-31 mm long, 2.5-4.5 mm broad at the neck, pilose in the lower half, the lobes ovate to ovate-orbicular or rhombic, 2-4 mm long; anthers 2-2.5 mm long, included or the tips protruding; style glabrate.

Holotype: Mexico. Sinaloa: betw Rosario & Colomas, 13 July 1897, *Rose 1628* (US 300476); isotype F.

Known only from the type collection.

9. Bouvardia xylosteoides Hooker & Arnott, Bot. Beechey Voy. 428, 1840.

B. villosa Standley, N. Amer. Fl. **32**: 107, 1921. (Holotype *Conzatti 1486* US 764094; isotype GH)

Shrubs, the seasonal branchlets densely white-villous at least distally with trichomes to 1 mm long. *Leaves* with villous petioles 1-6 mm long; blades ovate to elliptic, basally cuneate to rounded, 1.3-3.3 cm long, 0.8-2 cm broad, villous with trichomes to 1 mm long (densely villous-tomentose below), the secondaries 4-8, pinnate, the reticulation obscure. *Inflorescences* 3 to 7-flowered. *Flowers* with villosulous pedicels 0.5-2 mm long; floral cup tomentose; calyx-lobes lanceolate or linear-lanceolate, 2-8 mm long, rather densely pubescent; corolla tubular, densely white-villous on the upper two-thirds with trichomes 0.4-1.3 mm long (sparsely pubescent toward the base), the tube 13-26 mm long, sparsely pilose within near the base, the lobes ovate, 1.5-3.5 mm long; anthers 2-4 mm long; style glabrous.

Type: Mexico. Oaxaca: low mountains around Mitla (sphalm. Mitlam by Hooker & Arnott), *Andrieux* 333 (F fragment ex G-Deless., G, K).

Bouvardia xylosteoides has been collected at 1800 m and is known to be in flower from May through July; all collections known (three, including the type collection) are from central Oaxaca.

10. Bouvardia dictoneura Standley, N. Amer. Fl. **32**: 109, 1921.

B. matudai Lundell, Lloydia **2**: 105, 1939. (Holotype *Matuda 2667* MICH; isotypes F, MO, US; photos F, TEX)

B. venosissima Lundell, Bull. Torrey Bot. Club **66**: 602, 1939. (Holotype *Matuda 2748* MICH)

B. pachecoana Standley & Steyermark, Publ. Field Mus. Nat. Hist., Bot. Ser. **23**: 22, 1943. (Holotype *Standley 86226* F 1093896; isotypes A, US; photo US)

Shrubs, slender, to 2.5 m; seasonal branches often elongate, slender, suffrutescent, bisulcate, sometimes sparsely pilose along the margins of the sulcae with trichomes 0.1-0.8 mm long, otherwise glabrous. *Leaves* with petioles 0.5-10 mm long; stipular processes 1.5-10.5 mm long, often filiform, glandular at the tip; blades ovate to lanceolate, basally rounded or cordate, 2-10.6 cm long, 1-5.8 cm broad, usually glabrous but often ciliate marginally with trichomes 0.1-1 mm long, occasionally sparsely pilose above and below with trichomes to 1 mm, the secondaries 4-12, pinnate or rarely subpalmate, the reticulation obscure to prominent. *Inflorescences* 7 to 60-flowered. *Flowers* with pedicels (1-)3-10 mm long; floral cup glabrous; calyx-lobes linear-lanceolate or linear-subulate, 1.5-6 mm long; corolla red or orange-red, externally glabrous, the tube 4-13.5(-20) mm long, 2-4.5 mm broad at the neck, a villous ring within toward the base, the lobes broadly ovate or rhombic to somewhat oblong, 1.5-6 mm long, 2-4 mm broad, flared up to

60°; anthers 2-3 mm long, included by 1-7 mm or the tips protruding; style glabrate. *Capsules* 3-5 mm long, 3.5-6 mm broad; seeds 1-2 mm broad.

Holotype: Mexico. Chiapas: Chicharras (sphalm. Chichorras by Standley), 3000-6000 ft, 6 Febr 1896, *Nelson* 3757 (US 256554); isotype GH.

Southwestern Guatemala and southern Chiapas; volcanic slopes, often in pine forests; 1000-3800 m; apparently flowering the year round.

A collection from Guerrero (Pilas-Pasion, Distr Montes de Oca), *Hinton 10759* (UC, W), has 3-nate leaves (a characteristic of the subg. *Bouvardia*) but is otherwise indistinguishable from many specimens of *B. dictyoneura*. Field work is needed in the attempt to find additional specimens with ternate leaves and to assess the reality of the apparent geographic separation from typical opposite-leaved forms.

11. Bouvardia **standleyana** Blackwell, sp. nov.

Frutex B. gracilipedi affinis, sed foliorum laminis supra saltem sparse pubescentibus, inflorescentiis terminalibus in ramis foliosis elongatis dispositis, corollaque omnino glabro differt.

Shrubs; seasonal branches 7-30 cm long, suffrutescent, distally sparsely pilose (often irregularly so) to densely arachnose-pubescent with white trichomes 0.2-1 mm long. *Leaves* with petioles 1-7.5 mm long; blades ovate to trullate, 1.5-7.5 cm long, 0.8-4.3 cm broad, membranous, at least sparsely pubescent on both surfaces with white trichomes 0.2-1 mm long (below primarily concentrated along the main veins, the trichomes often spreading or curling), occasionally densely arachnose-puberulent below, the secondaries 6-12, pinnate, often brochidodrome, the reticulation apparent above, prominent below. *Inflorescences* (10-)15 to 50-flowered, terminal on leafy branches more than 7 cm long (including flowers) and more than 1 mm broad. *Flowers* with pedicels 3-14 mm long (at least a few pedicels 8 mm or more) and less than 0.5 mm broad; floral cup sparsely pilosulous to conspicuously hirsute with trichomes 0.2-0.7 mm long or glabrous; calyx-lobes lanceolate or elliptic-lanceolate to subulate, 1-3 mm long; corolla tubular, yellow or light orange, externally and internally glabrous, the tube 7-24 mm long, the lobes ovate or deltoid to oblong, 2-4 mm long, flared up to 45°; anthers 1-2 mm long, exserted by 1-3.5 mm in thrum flowers, included by 1-2 mm in pin flowers; ovary subglobose, ca 1 mm long, the style glabrous, with branches 1-2.5 mm long.

Holotype: Mexico. Michoacan: Distr Coalcoman, S of Naranjillo, 1360 m, 26 Nov 1938, *Hinton 12677* (US 2020693); isotypes K, MICH, UC.

Western Jalisco, Michoacan and Guerrero; mountain summits, steep mountainsides or rocky slopes; often found in the oak zone but occasionally in sandy soil in association with more tropical vegetation; 800-1700 m; flowering September through February.

Bouvardia standleyana is distinguished from its nearest relative, *B. gracilipes,* by the glabrous corollas (externally and internally), the well-developed and leafy floriferous branches, the presence of pubescence on the upper blade surface (though often sparse) and the more elongate pubescence on the distal portion of the seasonal branches.

Two collections, *Hinton 14901* (US) & *15408* (F), from Mina, Guerrero are interesting in their apparent intermediacy between *B. standleyana* and *B. bouvardioides* (subg. *Bouvardia*). Although the majority of floral and inflorescence characters, as well as the pilose to arachnose pubescence of the branchlets and leaves resemble *B. standleyana,* the leaf size, form, verticillation and the red corollas strongly suggest specimens of *B. bouvardioides* from the Western Sierra of Mexico. However, *B. bouvardioides* is not known from Guerrero and definitely solving the problem of the ancestry of such putative hybrids will require intensive field work followed by experimental studies.

12. BOUVARDIA GRACILIPES B. L. Robinson, Proc. Amer. Acad. Arts Sci. **45**: 404, 1910.

Shrubs to 1.5 m; seasonal branches glabrous or distally white-papillose-puberulent with trichomes to 0.05 mm long. *Leaves* with petioles 0.5-3.5 mm long; blades ovate to ovate-lanceolate, 2-9 cm long, 1-4.4 cm broad, membranous, glabrous above, often puberulent or pilosulous below on the main veins (and marginally) with trichomes 0.05-0.5 mm long, otherwise glabrous, the secondaries 6-10, pinnate, often brochidodrome, the reticulation most conspicuous below, imparting a minutely varicose appearance to the blade above. *Inflorescences* 5 to 50-flowered, pseudo-axillary, the floriferous branchlets less than 7 cm long (including flowers), less than 1 mm broad, leafless (only a stipule-sheath present at the nodes), with only 1 or 2 very short internodes below the peduncle. *Flowers* with pedicels 5-22 mm long (at least a few pedicels 8 mm or more) and less than 0.5 mm broad; floral cup minutely papillose-puberulent with trichomes to 0.05 mm long or glabrate; calyx-lobes deltoid to lanceolate, 0.5-2 mm long; corolla tubular, yellow or orange-yellow, externally minutely papillose-puberulent with trichomes to 0.05 mm long, the tube 10-19 mm long, often somewhat pilosulous within just below the middle (but not with a dense, villous ring), the lobes broadly ovate to oblong, 2-4.5 mm long; anthers 1.5-3 mm long, exserted in thrum flowers by 1-2 mm; style glabrate, the branches 0.5-1 mm long. *Capsules* 3.5-5.5 mm long, 4-7 mm broad; seeds 1.5-2.5 mm broad.

Holotype: Mexico. Nayarit: Tepic, 5 Jan to 6 Feb 1892, *Palmer 1971* (GH); isotypes F, US.

Nayarit and northwestern Jalisco; steep, heavily forested stream valleys in the oak zone; growing in cracks and among rocks in stream beds; known to be in flower in November and December.

13. BOUVARDIA REKOI Standley, N. Amer. Fl. **32**: 108, 1921.

Shrubs; seasonal branches glabrous or distally minutely puberulent with trichomes to 0.05 mm long. *Leaves* with petioles 1-3 mm long; blades ovate-lanceolate, rounded at the base, 3-6.5 cm long, 0.9-2.7 cm broad, glabrous, 3 to 5-plinerved, the reticulation often prominent below. *Inflorescences* few-flowered. *Flowers* with pedicels 6-13 mm long and 0.2-0.3 mm broad; floral cup sparsely pruinose-puberulent or hispidulous with trichomes to 0.05 mm long; calyx-lobes deltoid-acuminate, ca 1 mm long; corolla tubular, externally glabrate, the tube 10-19 mm long, a villous ring within near the base, the lobes oblong or oblong-lanceolate, 2.5-4 mm long; anthers 1.5-3 mm long, exserted in thrum flowers by 1-4 mm; style glabrate, the branches 1-1.5 mm long.

Holotype: Mexico. Oaxaca: Cafetal Montecristo (Cerro Espino), 1000 m, 7 Dec 1917, *Reko 3650* (US 867149).

Known only from the type collection.

14. Bouvardia oaxacana Standley, Jour. Wash. Acad. Sci. **13**: 7, 1923.

Herbs, perennial or suffrutices; stems simple or sparsely branched, slender, distally puberulent with white trichomes 0.05-0.3 mm long. Leaves with petioles 0-2.5 mm long; blades broadly ovate to ovate-lanceolate, basally rounded, 3.4-6.7 cm long, 1.3-3.8 cm broad, glabrate or sparsely white-puberulent with trichomes 0.1-0.5 mm long (often primarily along the margin), 5-plinerved, the reticulation obscure above, visible but inconspicuous below. Inflorescences often more than 30-flowered, subcapitate. *Flowers* with pedicels 0.5-4 mm long and 0.5 broad; floral cup usually densely hirtellous; calyx-lobes lanceolate to elliptic- or linear-lanceolate, 2-9 mm long, 1-2 mm broad; corolla tubular, red, externally glabrous or sparsely hirtellous, the tube 10-17 mm long, villous toward the base within but lacking a villous ring, the lobes mostly oblong-lanceolate, 3-6 mm long; anthers 2-3 mm long, exserted by 2-6 mm in thrum flowers; style glabrate, the branches 1-2 mm long.

Holotype: Mexico. Oaxaca: Distr Juquila, betw Santa Cruz & El Aguacate, 500 m, 24 Dec 1921, *Conzatti 4513* (US 1110842); isotype GH.

Known only from the type collection.

15. Bouvardia quinquenervata Standley, N. Amer. Fl. **32**: 108, 1921.

Shrubs; seasonal branches rather elongate, distally hirtellous with trichomes 0.05-0.3 mm long. *Leaves* with petioles 1-5 mm long; blades broadly ovate to ovate- or elliptic-lanceolate, basally obtuse to rounded or cordate, 2.6-5.9 cm long, 1.3-3.7 cm broad, glabrate above, obscurely puberulent below on the main veins with trichomes to 0.1 mm long, 5-plinerved, the reticulation visible above, prominent below. *Inflorescences* usually more than 50-flowered. Flowers with pedicels 1.5-6 mm long, to 0.5 mm broad; floral cup rather densely hirtellous; calyx-lobes linear-subulate, 2-6 mm long, 0.3-1 mm broad; corolla tubular to virtually salverform, violet or lavender, externally sparsely hirtellous (mainly toward the base) with trichomes 0.1-0.2 mm long, the tube 4.5-8.5 mm long, rather densely villous in the lower half (the pubescence not organized into a villous ring), the lobes oblong to oblong-lanceolate, 2.5-4 mm long; anthers 2-3.5 mm long, exserted in both pin and thrum flowers by 1-5.5 mm; style somewhat hirtellous or villosulous on the lower half. *Capsules* 3-4.5 mm long, 2.4-4 mm broad.

Holotype: Mexico. Chiapas: San Bartolomé, 22 March 1904, *Goldman 769* (US 470574).

Southern Chiapas; pine forests on volcanic slopes; ca 1400 m; known to flower December through March.

Based on the many-flowered inflorescences, the short lavender corollas and stamens exserted in both pin and thrum flowers, *B. quinquenervata* appears more closely related to specimens of *B. bouvardioides* from Chiapas and Guatemala than to any member of the subg. *Bouvardiastrum*.

II. SUBG. BOUVARDIOIDES Schlecht., Linnaea **26:** 58, 1854.

Shrubs or suffrutices; seasonal branches opposite, glabrous or pubescent. *Leaves* opposite, usually petiolate; blades glabrous or pubescent, the secondaries pinnate, obscure or rarely subpalmate, the reticulation obscure or inconspicuous. *Inflorescences* 1- or several (to 15)-flowered (when several-flowered, each partial inflorescence composed of only 1 flower). *Flowers* pedicellate or sessile, ± erect; calyx-lobes free to the floral cup or rarely connected basally by a calyx-tube; corolla salverform (lobes spreading at an angle of 90°), white, externally glabrous or pubescent, the tube internally sparsely pilose throughout or the pubescence limited to the upper half (never limited to the lower half), less often glabrate internally; anthers in both pin and thrum flowers included or only the tips protruding; style glabrate or more often minutely papillose-pubescent (at least on the distal half), the branches 1-7.5 mm long.

Type: *Bouvardia longiflora* (Cav.) H.B.K.

a. Flowers sessile or subsessile on a branch terminus (rarely with pedicels to 1 mm long), usually solitary (if inflorescences several-flowered then the leaf-blades conspicuously villous beneath toward the base with trichomes to 1 mm long and the floral cup villous-tomentose or else the flowers with a calyx-tube ca 2 mm long extending beyond the floral cup).
  b. Flowers solitary (if inflorescences 3 or more-flowered then the floral cup villous-tomentose with trichomes to 1.5 mm long and the leaf-blades conspicuously villous below toward the base); calyx-lobes free to the floral cup.
    c. Stipular processes lanceolate or slender-subulate, 2.5-10 mm long; blades glabrate or infrequently puberulent with trichomes to 0.3 mm long (not concentrated below toward the base); floral cup glabrate or rarely densely puberulent with trichomes to 0.3 mm long; corolla-tube glabrous externally or rarely sparsely puberulent with trichomes to 0.3 mm long; flowers always solitary .... 16. *B. longiflora*
    cc. Stipular processes often pluriaristate, 1-3.5 mm long; blades conspicuously villous below toward the base with trichomes to 1 mm; floral cup densely villous with trichomes 0.5-1.5 mm long; corolla-tube externally sparsely villous distally with trichomes 0.3-1.5 mm long (if glabrous then the inflorescences with 3-11 flowers) .... 17. *B. langlassei*
  bb. Inflorescences 3 to 5(-7)-flowered (floral cup pruinose-puberulent with trichomes to 0.05 mm long and the leaf-blades glabrate); calyx-lobes connected basally by a calyx-tube ca 2 mm long .... 19. *B. rosei*

aa. Flowers typically at least short-pedicellate; inflorescences often 3- or more-flowered (if flowers solitary, the leaf-blades less than 9 mm broad and the plants often low, dense shrubs of xerophytic habit).
  d. Petioles (0.5-)3-12 mm long; leaf-blades usually broader than 9 mm, the secondaries evident; inflorescences 3 to 15-flowered.
    e. Plants glabrate; pedicels (0.5-)2.5-19 mm long; calyx-lobes (0.5-)1.5-5 mm broad, often rather broadly linear-elliptic; corolla-tube 1.5-4.5(-5.6) cm long .... 20. *B. glabra*
    ee. Plants glabrate or conspicuously pubescent; pedicels 0.5-2.5(-6) mm long; calyx-lobes 0.5-1(-2) mm broad, ± linear; corolla-tube (3.5-)4.5-8.5 cm long .... 21. *B. induta*

dd. Petioles 0-3(-4.5) mm long; leaf-blades usually less than 9 mm broad, the secondaries usually obscure; inflorescences 1 to 9-flowered.
f. Xerophytic, low, dense shrubs, the branchlets often becoming pseudo-spinescent; leaf-blades to 12(-18) mm long, often papillose-puberulent with trichomes to 0.2 mm long (sometimes very sparsely so); flowers solitary (inflorescences rarely 3-flowered); calyx-lobes 1.5-5(-6.5) mm long ....18. *B. erecta*
ff. Typically not xerophytes, the branches not at all spinescent; leaf-blades 0.9-7 cm long, glabrate or rarely papillose-puberulent with trichomes to 0.3 mm long; inflorescences often 3 to 9-flowered, the flowers occasionally solitary; calyx-lobes 2-32 mm long.
g. Leaf-blades having a length/width ratio of 2.4/1 to 18/1; floral cup typically pruinose- or papillose-puberulent with trichomes to to 0.05(-0.3) mm long (sometimes sparsely so); calyx-lobes 2-11 mm long; ovary ± subglobose, 1-2 mm long ....22. *B. dolichantha*
gg. Leaf-blades having a length/width ratio of 10/1 to 42/1; floral cup glabrous; calyx-lobes 12-32 mm long; ovary turbinate or sub-cylindrical, 2-3.5 mm long ....23. *B. karwinskyi*

16. Bouvardia longiflora (Cav.) H.B.K., Nov. Gen. Sp. Pl. **3**: 386, 1820.

Aeginetia longiflora Cav., Anal. Ci. Nat. **3**: 130, *t. 28, fig. 1,* 1801; Ic. **6**: 51, *t. 572, fig. 1,* 1801.

Bouvardia longiflora var. *latifolia* Martens & Galeotti, Bull. Acad. Bruxelles **11**(1): 236, 1844. (Holotype *Galeotti 2659* BR)

Houstonia longiflora (Cav.) A. Gray, Proc. Amer. Acad. Arts Sci. **4**: 314, 1860.

Shrubs to 1.6 m; seasonal branches ascending, glabrous or distally white-papillose-hirtellous with trichomes to 0.2 mm long, often short and slender and herbaceous. *Leaves* with petioles to 10 mm long; stipular processes lanceolate or slender-subulate, 2.5-10 mm long; blades lanceolate or occasionally ovate- or elliptic-lanceolate, 1.5-5.7 cm long, 0.5-2.2 cm broad, glabrous or infrequently white-puberulent with trichomes 0.05-0.3 mm long, the secondaries 4-12, pinnate. *Flowers* solitary, sessile or subsessile (pedicels to 1 mm long); floral cup glabrate or rarely densely puberulent with white trichomes 0.1-0.3 mm long; calyx-lobes linear to linear-lanceolate or linear-oblanceolate, rarely more broadly oblanceolate or ± elliptic, (2.5-)6-26 mm long; corolla glabrous externally or rarely sparsely puberulent with trichomes to 0.3 mm long, the tube 3.5-8.5 cm long, internally sparsely pilose throughout, the lobes 8-28 mm long; anthers 3-5 mm long; ovary 2-5 mm long, the style glabrate or pruinose-puberulent, the branches 2-6 mm long. *Capsules* 8-12.5 mm long, 7-12 mm broad; seeds 1.5-4 mm broad.

Holotype: Mexico: betw Queretaro & Guanajuato, Oct (MA, not seen). The description is based on a specimen in the herbarium of L. Née without reference to the collector.

Aguascalientes, Jalisco and San Luis Potosi to Puebla and Oaxaca; occasional on rhyolitic or basaltic hillsides or steep roadcuts at elevations of 2000-4000 m; sometimes associated with xerophytic plants in arid or semiarid habitats but more frequently occurring in mesic woodlands of oak and pine; flowering most commonly from May through August.

Two collections of *B. longiflora* from Puebla, *Purpus 1249* (GH, MO) from Tehuacan and *Purpus 3327* (MO, UC) from the vicinity of San Luis Tultitlanapa, are distinguished by their puberulent leaves, densely puberulent floral cups and shorter calyx-lobes (2.5-6 mm long). At first I thought these formed a distinct subspecies. However, other collections of "typical" *B. longiflora, Purpus* 3323 (F) & 3326 (GH, MO), from the vicinity of San Luis Tultitlanapa were subsequently seen and cast doubt on the geographical separation of the puberulent forms. Additional collecting is needed to elucidate their status.

17. Bouvardia langlassei Standley, N. Amer. Fl. **32:** 110, 1921.

Shrubs to 1.5 m; seasonal branches distally villous with trichomes 0.2-1 mm long, often short and herbaceous. *Leaves* with villous petioles to 7 mm long; stipular processes 1-3.5 mm long, often pluriaristate; blades obovate or oblanceolate to ovate or ovate-lanceolate, 1.2-5.2 cm long, 0.5-2.8 cm broad, villous (particularly beneath toward the base) with white trichomes 0.3-1 mm long, the secondaries 4-10, pinnate or infrequently ± plinerved. *Flowers* solitary or 3-11 on a seasonal branch, sessile or subsessile (pedicels to 1 mm); floral cup densely white-villous with trichomes 0.5-1.5 mm long; calyx-lobes linear or slender-lanceolate, 2.5-9 mm long; corolla distally sparsely villous externally with slender trichomes 0.3-1.5 mm long or glabrous (when glabrous, the inflorescence typically several-flowered), the tube 3.5-6.6 cm long, internally glabrate or sparsely pilose throughout, the lobes 6-14 mm long; anthers 3-4 mm long; ovary 1-3 mm long, the style glabrate, the branches 1.5-3.5 mm long.

Holotype: Mexico. Guerrero: Testla (Yextla), 45 km W of Chilpancingo, 1500 m, 8 June 1899, *Langlassé 1049* (US); isotypes F (fragment), G, GH, P; photo US.

Guerrero and northwestern Michoacan; infrequent; mountain slopes in rocky soil, often under semiarid conditions; 1000-2000 m; known to be in flower in June.

18. Bouvardia erecta (DC.) Standley, N. Amer. Fl. **32:** 110, 1921.

Catesbaea erecta DC., Prodr. **4:** 401, 1830.
Hedyotis spinescens Sessé & Mociño, Fl. Mex. **22,** 1891. (Type *Sessé & Mociño s.n.* MA, not seen)
Bouvardia flos-joannis Schumann in Loesener, Bull. Herb. Boiss. **3:** 621, 1895. (Type *Seler 846* GH)
B. flos-joannis var. *latifolia* Loesener, Repert. Sp. Nov. **18:** 358, 1922. (Type *Endlicher 1966* W, not seen)

Shrubs to 1.2 m; seasonal branches glabrous or papillose-hispidulous with white trichomes to 0.2 mm long, ± herbaceous, becoming woody and pseudospinescent. *Leaves* often pseudofasiculate by virtue of crowding and the development of axillary buds which produce leaves but fail to elongate; petioles to 2.5 mm long; stipular processes slender-deltoid, 0.5-2 mm long; blades lanceolate or linear to elliptic-lanceolate or oblanceolate, 3.5-12(-18) mm long, 1-4.5 mm broad, chartaceous, glabrous or white-papillose-puberulent with trichomes to 0.2 mm long, the secondaries obscure. *Flowers* solitary (rarely 3 terminating a branchlet); pedicels (0-)1-8 mm long; floral cup glabrous or puberulent with trichomes to 0.2 mm long; calyx-lobes linear to lanceolate or slightly oblanceolate, 1.5-5(-6.5) mm long; corolla white but often lightly suffused with rose, inconspicuously puberulent externally with trichomes to 0.05 mm long or glabrate, the tube 2.5-5.5 cm long, sparsely pilose in the upper half (sometimes densely so at the throat), the lobes

5-12 mm long; anthers 2-4 mm long; ovary 1-2.5 mm long, the style often minutely papillose-puberulent, the branches 1.5-5 mm long. *Capsules* 4-9 mm long, 4-8.5 mm broad; seeds 2-3 mm broad.

Type: Mexico: *Sessé & Mociño s.n.* (MA, not seen); *pl. 460* of the *Calques des dessin* . . . is a drawing of the type.

Puebla; limestone slopes with gray or whitish soil and frequent rock outcrops; often in association with thorn-scrub, cactus and hat palms under arid conditions; 1300-2500 m; flowering from June through early October.

Bouvardia erecta is unique in the subg. *Bouvardioides* in its adaptation to xeric conditions. The habit is that of a dense, low shrub of scrubby appearance. The branchlets are often pseudospinescent and the leaves small and rather densely crowded.

19. Bouvardia rosei Standley, N. Amer. Fl. **32:** 109, 1921.

Shrubs, the branches minutely puberulent when young. *Leaves* with petioles ca 1 mm long; stipular processes narrowly lanceolate, 3-5 mm long; blades ovate to elliptic, 2-3.8 cm long, 0.7-2 cm broad, glabrate, the secondaries 4-8, subpalmate (two arising from the midvein slightly below the midpoint of the leaf and the remainder originating together near the base or occasionally all originating near the base). *Inflorescences* 3 to 5(-7)-flowered. *Flowers* typically sessile (occasionally with pedicels to ca 1 mm); floral cup pruinose-puberulent; calyx-lobes linear-lanceolate, 4-9 mm long, connected basally by a calyx-tube extending ca 2 mm above the floral cup; corolla glabrate externally, the tube 4-7 cm long, internally sparsely pilose throughout, the lobes 11-15 mm long; anthers 3-4 mm long; ovary ca 1.5 mm long; style moderately papillose-hispid distally, the branches 4-6 mm long. *Capsules* 6-8 mm long and broad; seeds 2-3 mm broad.

Holotype: Mexico. Durango: Sierra Madre, 16 Aug 1897, *Rose 3516* (US); isotype F; photo US.

Sierra Madre of Durango and Sinaloa; infrequent; known to be in flower in August (probably also in September).

20. Bouvardia glabra Polakowsky, Linnaea **41:** 565, 1877.

B. glabra var. *gracilis* Polakowsky, loc. cit. 566. (Type *Polakowsky 172* B†, BM, W; photos F, G, TEX)

B. glabra var. *obtusa* Loesener, Verh. Bot. Ver. Brandenburg **65:** 106, 1923. (Type *Seler 2920* B†)

Shrubs to 1.5 m; branches glabrous. *Leaves* with petioles (2-)3-12 mm long; stipular processes lanceolate or linear-lanceolate, 1.5-6 mm long; blades ovate- or elliptic-lanceolate, 2.5-10.5 cm long, 0.9-4.3 cm broad, glabrous or glabrate, the secondaries 6-12, pinnate. *Inflorescences* 3 to 7-flowered. *Flowers* with pedicels (0.5-)2.5-19 mm long; calyx-lobes elliptic to oblanceolate or ± linear, 3.5-17 mm long, (0.5-)1.5-5 mm broad; corolla externally glabrous or rarely minutely puberulent with trichomes to 0.05 mm long, the tube 1.5-4.5(-5.6) cm long, glabrate within, the lobes 5-16 mm long; anthers 2.5-4 mm long; ovary 1.5-3 mm long; style pruinose-puberulent, the branches 1.5-7.5 mm long. *Capsules* 4-10 mm long, 5-10 mm broad; seeds 2-4.5 mm broad.

Type: Costa Rica: San José, Aug 1875 *Polakowsky* 337 (B†, F fragment; photos F, G, TEX, US); possibly from cultivated material.

Guatemala, southern Chiapas and Costa Rica; wooded or shrubby slopes or barrancas of volcanic mountains in arid to very mesic (cloud forest) conditions; 1300-3500 m; flowering the year round.

I have seen collections from Honduras perhaps assignable to *B. glabra* but intermediate between *B. glabra* and *B. dolichantha.* Examples of these possibly hybrid specimens are *Hawkes et al. 2095* (C, G, K), *Molina 6501* (F) and *Rodriguez 3124* (F). Additional collecting is needed to ascertain more accurately the distribution of *B. glabra, B. dolichantha* and *B. induta* and to look for intermediate forms. These three taxa are a closely related complex in northern Central America and I view the specific status of *B. dolichantha* and *B. induta* as tentative at present.

21. Bouvardia induta (Robinson) Standley, N. Amer. Fl. **32**: 109, 1921.

B. longiflora var. *induta* B. L. Robinson, Proc. Amer. Acad. Arts Sci. **45**: 404, 1910.
B. purpusii Brandegee, Univ. Calif. Publ. Bot. **10**: 415, 1924. (Holotype *Purpus 9251* UC 223423 †?; isotypes F, GH, MO, US)

Shrubs to 1 m; branches distally rather densely white-hirsute with trichomes to 0.8 mm long or glabrous. *Leaves* with petioles (0.5-)3-9 mm long; stipular processes subulate, 1-3.5 mm long; blades lanceolate to ovate- or elliptic-lanceolate, (1.5-)2-7.3 cm long, (0.5-)1-2.5 cm broad, conspicuously white-hirsute with trichomes to 1 mm long or glabrous, the secondaries 4-10, pinnate. *Inflorescences* 3 to 15-flowered. *Flowers* with pedicels 0.5-2.5(-6) mm long which are densely hirsute to glabrate; floral cup white-hirsute-tomentellous with trichomes to 1 mm long or minutely puberulent (trichomes to 0.05 mm long) or glabrate; calyx-lobes linear to linear-lanceolate or linear-elliptic or slightly oblanceolate, 2.5-16 mm long, 0.5-1(-2) mm broad; corolla externally villosulous or hirsute with trichomes 0.1-0.7 mm long or pruinose- or papillose-puberulent with trichomes to 0.05 mm long, rarely glabrate externally, the tube (3.5-)4.5-8.5 cm long, pilose in the distal half with trichomes to 1 mm long, the lobes 7-22 mm long; anthers 3-5 mm long; ovary 1-2.5 mm long, the style distally minutely puberulent and proximally glabrous, with branches 1-5 mm long.

Holotype: Mexico. Chiapas: June-July 1864-70, *Ghiesbreght s.n.* (GH). The holotype is one of three collections of *B. induta* on one herbarium sheet, viz. the one in the middle. The specimens on the left and right are *Ghiesbreght 108* and *692* respectively.

Chiapas and adjacent Guatemala; rocky, dry limestone areas in pine forests; 1000-2200 m; flowering March through September.

Some specimens of *B. purpusii* differ from *B. induta* in the glabrescence of all parts (see *Purpus 9252* MO, UC, US). However, the holotype is a pubescent plant similar to the majority of specimens of *B. induta.* An isotype (F) is a mixed collection, the specimen on the left side of the herbarium sheet being glabrate and the one on the right conspicuously pubescent. The specimens on the right is probably a duplicate of the holotype.

22. Bouvardia dolichantha Loesener, Verh. Bot. Ver. Brandenburg **65:** 106, 1923.

B. steyermarkii Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. **22:** 383, 1940. (Holotype *Steyermark 29671* F 1043386; photos F, TEX)

Shrubs or low suffrutices; branches glabrous or sparsely papillose- or pruinose-puberulent distally with trichomes to 0.05(-0.3) mm long. *Leaves* opposite but occasionally crowded and pseudoverticillate; petioles 0.5-3(-4.5) mm long; stipular processes deltoid to lanceolate, 0.5-3 mm long; blades linear or lanceolate to elliptic- or narrowly ovate-lanceolate, 0.9-7 cm long, 1.5-9 mm broad, glabrate or rarely papillose-puberulent with trichomes to 0.3 mm long, the secondaries obscure or 4-6 and pinnate. *Inflorescences* (1-)3 to 9-flowered. *Flowers* with pedicels 0.5-5.5 mm long which are glabrous or minutely puberulent; floral cup typically pruinose- or papillose-puberulent with trichomes to 0.05(-0.3) mm long; calyx-lobes linear or lanceolate to narrowly elliptic or oblanceolate, 2-11 mm long, 0.5-1.3(-2) mm broad; corolla externally glabrous or sparsely papillose-puberulent with trichomes to 0.05(-0.2) mm long, the tube 1.7-8 cm long, internally glabrate or papillose-puberulent to pilose (trichomes 0.1-1 mm long) in the upper half, the lobes 4-19 mm long; anthers 2-4 mm long; ovary usually subglobose, 1-2 mm long, the style minutely puberulent on the distal two-thirds, with branches 1-5 mm long. *Capsules* 3.5-8.5 mm long and broad; seeds 2-3.5 mm broad.

Loesener cites *Seler 2795* and *2883* without selecting one or the other as the type. I designate *Seler 2883* (US 1205579) as lectotype (Guatemala: Dept of Huehuetenango, Distr of Nenton, nr Uaxackanal & toward Quen Santo, 1100 m, 9 July 1896); isolectotypes GH, F (fragment); photos F, G, US from B†.

Guatemala and Honduras; occasional on mountainsides along humid banks in mixed woodlands of oak and pine; 1000-3400 m; flowering May through October.

23. Bouvardia karwinskyi Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. **8:** 155, 1930.

Shrubs to 1.5 m; seasonal branches glabrate or obscurely hirtellous with trichomes to 0.1 mm long. *Leaves* opposite but often crowded, sometimes pseudofasciculate by the production of leaves by axillary buds which fail to develop into branches; petioles 0-2 mm long; stipular processes lanceolate, 1.5-5.5 mm long; blades linear to linear-lanceolate or narrowly linear-elliptic, 1.6-5.3 cm long, 0.7-3 mm broad, glabrous, the secondaries obscure. *Inflorescences* 1 to 5-flowered. *Flowers* with pedicels 0.5-6 mm long which are glabrous; floral cup glabrous, calyx lobes linear, 12-32 mm long, 0.5-1.5 mm broad; corolla glabrous externally, the tube 3.5-6.2 cm long, sparsely pilose in the upper half, the lobes 7-13.5 mm long; anthers 3-3.5 mm long; ovary turbinate or subcylindrical, 2-3.5 mm long, the style papillose-puberulent (particularly distally) with trichomes to 0.05 mm long, with branches 1-2 mm long.

Holotype: Mexico: betw Victoria & Río Blanco, 1842, *Karwinsky 312* (LE); isotype F (fragment).

I have been unable to learn the state(s) in which the type and other specimens of *B. karwinskyi* were collected; flowering July through October.

III. Subg. Bouvardia Schlecht., Linnaea **26:** 58, 1854.

Shrubs, suffrutices or perennial herbs; seasonal branches opposite or verticillate, pubescent to glabrous. *Leaves* 3 to 4(-6)-nate at some or all of the nodes, petiolate or sessile; blades conspicuously pubescent (mostly below) to glabrous, the secondaries pinnate, arcuate, less frequently obscure, the reticulation obscure to prominent. *Inflorescences* few to many-flowered; partial inflorescences 3- or more-flowered. *Flowers* pedicellate or virtually sessile; calyx-lobes free to the floral cup; corolla tubular to salverform (lobes spreading 10-90°), red, less frequently lavender, rose, violet-blue or pink, externally pubescent or glabrous, the tube internally pilose or villous in the lower half (rarely glabrate) or the pubescence organized into a villous ring near the base; anthers included (rarely exserted) in pin flowers; included or often exserted in thrum flowers; style usually glabrate, the branches 0.5-3 mm long.

a. Corolla externally pubescent, rarely obscurely pruinose-puberulent or glabrate but then the leaves obovate and 5 to 6-nate at some of the nodes.
  b. Leaves not more than 4-nate, the blades typically neither obovate nor mucronulate; corolla-tube puberulent externally with trichomes usually 0.1-0.4 mm long, internally with a villous ring toward the base.
    c. Well-branched shrubs or low suffrutices (occasionally the stems simple and herbaceous but broader than 1.5 mm at the midpoint); leaves at least short-petiolate, the blades having a length/width ratio of 1.5/1 to 19/1 and most often not linear, the secondaries usually apparent .... 24. *B. ternifolia*
    cc. Herbaceous or suffrutescent perennials, the stems 1-1.5 mm broad at the midpoint, simple or sparsely branched distally; leaves often sessile or subsessile (occasionally short-petiolate), the blades linear, with a length/width ratio of 12/1 to 50/1, the secondaries obscure .... 25. *B. tenuifolia*
  bb. Leaves 5- or 6-nate at one or more nodes, the blades often obovate and mucronulate; corolla-tube puberulent externally with trichomes to 0.05 mm long or rarely glabrate, lacking an internal villous ring toward the base (though occasionally somewhat villosulous) .... 26. *B. obovata*

aa. Corolla externally glabrous.
  d. Seasonal branches distally villosulous or hirsute with trichomes 0.2-2 mm long; leaves short-petiolate or subsessile (petioles 0.5-3 mm long), the blades often conspicuously pubescent (particularly below) with trichomes 0.2-1.1 mm long (the pubescence either coarse and yellowish or villous and white); corolla red, the tube 10-27 mm long; inflorescences with fewer than 60 flowers and often subcapitate.
    e. Slender shrubs or suffrutices, the branches angular or terete in cross-section and less than 3 mm broad at the midpoint; leaf-blades various (often ovate-lanceolate), white-villous-pubescent below, the secondaries 4-14 (often fewer than 12); calyx-lobes usually less than 5.5 mm long; anthers exserted 1-3 mm in thrum flowers, included in pin flowers.
      f. Corolla tubular, the tube typically with a villous ring internally toward the base, the lobes usually less than 2.2 mm broad, spreading up to 45° .... 27. *B. leiantha*
      ff. Corolla salverform, the tube villous internally toward the base but lacking a definite villous ring, the lobes frequently 2.2 mm broad or more, spreading at 90° .... 28. *B. viminalis*
    ee. Coarse perennial herbs, often with distinctly tetragonal stems 3-4 mm broad at the midpoint; leaf-blades usually rhombic-ovate or ovate, yellowish, with a coarse yellow pubescence beneath concentrated primarily on the main veins, the secondaries (8-)12-22; calyx-lobes subulate (or approaching filiform), (3-)5.5-12 mm long; anthers included in pin and thrum flowers .... 29. *B. scabra*

dd. Seasonal branches distally glabrous or puberulent with trichomes to 0.1 mm long; leaves entirely sessile or conspicuously petiolate (at least some of the petioles exceeding 4 mm), the blades glabrous or sparsely hirtellous with trichomes to 0.3 mm long; corolla deep-rose, lavender, violet-blue, pink or red (when red the inflorescences more than 60-flowered and not subcapitate), the tube 2-19 mm long.
g. Leaves sessile, the blades linear, having a length/width ratio of 4/1 to 20/1, the secondaries obscure; inflorescences 3 to 20-flowered ....30. *B. rosea*
gg. Leaves distinctly petiolate, the blades ovate- or elliptic-lanceolate, having a length/width ratio of 2.2/1 to 4.9/1, the secondaries conspicuous; inflorescences usually more than 60-flowered ....31. *B. bouvardioides*

24. Bouvardia ternifolia (Cav.) Schlecht., Linnaea **26:** 98, 1854.

Ixora ternifolia Cav., Ic. **4:** 3, *t. 305,* 1797.
I. americana Jacquin, Hort. Schönbr. **3:** 4, 1798. (Based on *I. ternifolia*)
Houstonia coccinea Andrews, Bot. Repos., *pl. 106,* 1800. (Illustration is taken as the type)
Bouvardia triphylla Salisbury, Parad. Lond., *pl. 88,* 1807. (Based on *I. ternifolia*)
B. linearis H.B.K., Nov. Gen. Sp. Pl. **3:** 383, 1819. (Type *Humboldt & Bonpland s.n.* P, not seen; photos F, P, TEX, US).
B. angustifolia H.B.K., loc. cit. 384. (Type *Humboldt & Bonpland s.n.* F, P not seen, US; photos F, P, TEX, US)
B. hirtella H.B.K., loc. cit. (Type *Humboldt & Bonpland s.n. P,* not seen; photos F, P, TEX, US)
B. jacquinii H.B.K., loc. cit. 385, 1820. (Based on *I. americana*)
B. coccinea (Andrews) Link, Enum. Hort. Berol. **1:** 139, 1821.
B. quaternifolia DC., Prodr. **4:** 365, 1830. (Type *Alaman s.n.* G-DC, not seen; photo IDC)
Carphalea pubiflora Sessé & Mociño ex DC., loc. cit. (As synonym of *B. quaternifolia*)
Bouvardia jacquinii var. *β exogyna* DC., loc. cit. (Based on a plant grown in Salm-Dyck's garden; type G-DC, not seen; photo IDC)
B. jacquinii var. *γ ovata* DC., loc. cit. (Based on "*Bouvardia triphylla* var. *β* Salisb.," the supposedly broader-leafed form, the type of which is Salisbury's *pl.* 88)
B. splendens Graham, Bot. Mag., *pl. 3781,* 1840. (Based on greenhouse-grown plants; K)
B. triphylla var. *splendens* (Graham) Lindley, Bot. Reg. **26:** *t.* 37, 1840.
B. tolucana Hooker & Arnott, Bot. Beechey Voy. 427, 1840. (Type *Andrieux* 332 K, W)
B. quaterniflora Steudel, Nomen. Bot. ed. 2, part 1, 300, 1841, as synonym of *Carphalea pubiflora;* probably a mistake for *B. quaternifolia* DC.
B. scabrida Martens & Galeotti, Bull. Acad. Bruxelles **11**(1): 237, 1844. (Holotype *Galeotti 2624* BR)
B. hypoleuca Bentham, Pl. Hartw. 288, 1848. (Type *Hartweg 1605* K; photo MICH)
B. glaberrima Engelmann in Wislizenus, Tour N. Mex. 106, 1848. (Type *Wislizenus 161* GH, MO)
B. ovata A. Gray, Pl. Wright. **5:** 67, 1853. (Type *Wright 1117* GH, MO, US)
Aeginetia hyssopifolia Willd. ex Schlecht., Linnaea **26:** 60, 1854. (As synonym of *Bouvardia angustifolia*)
Bouvardia tenuiflora Schlecht., loc. cit. 97. (Type B†)
B. houtteana Schlecht. ex Planchon, Fl. Serres **10:** 149, *t.* 55, 1855. (Illustration is taken as the type)
B. hirtella var. *quaternifolia* (DC.) Rothrock in Wheeler, Rept. U.S. Geogr. Surv. **6:** 137, 1879.
B. triphylla var. *angustifolia* (H.B.K.) A. Gray, Syn. Fl. N. Amer. **1**(2): 24, 1884.
B. ternifolia var. *angustifolia* (H.B.K.) B. L. Robinson, Proc. Amer. Acad. Arts Sci. **45:** 405, 1910.
B. endlichii Loesener, Repert. Sp. Nov. **18:** 357, 1922. (Type *Endlicher 176a* B†; photos F, G, TEX, US).
B. orizabensis Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. **8:** 334, 1931. (Holotype *Botteri 604* P; isotypes F fragment, G)

Shrubs or suffrutices or perennial herbs to 1.5 m, the branches sparsely to rather densely papillose-hispidulous when young with white trichomes 0.1-0.3 mm long. *Leaves* with petioles 0.5-12 mm long; blades extremely variable (linear, lanceolate, elliptic, ovate, obovate) though most often elliptic-lanceolate, 1-11 cm long, 0.1-3.1 cm broad, glabrate to densely papillose-hispidulous or villosulous with white trichomes variously 0.05-1 mm long, the secondaries 4-12 (often obscure in narrow, linear leaves), the reticulation apparent or obscure. *Cymes* 3 to 40-flowered, sometimes subcapitate. *Flowers* with pedicels 1-15 mm long; floral cup sparsely to densely papillose-hispidulous; calyx-lobes lanceolate to linear, 2-10 mm long; corolla tubular, salmon-red or orange-red or scarlet, externally pubescent with papillose, white, red-tipped trichomes 0.1-0.4 mm long (rarely obscurely puberulent with trichomes 0.05 mm long or less or villosulous with trichomes to 0.8 mm long), the tube 9-35 mm long, typically with a villous ring internally toward the base, the lobes ovate to oblong, 1.5-3.5(-5) mm long, spreading up to 60°, internally white-pruinose-puberulent; anthers 2-4 mm long, white or red, included by 1-4 mm or the tips protruding; ovary 1-2.5 mm long, the style-branches red, 1-2.5 mm long. *Capsules* 4.5-9 mm long, 5-10.5 mm broad, glabrous or sparsely papillose-hispid; seeds 2-3.5 mm broad.

The original description of *Ixora ternifolia* was based on a plant growing in the Royal Botanical Garden of Madrid, the seed having been sent from Mexico. The illustration is taken as the type.

Southwestern Texas and New Mexico and southeastern Arizona to Oaxaca and southern Vera Cruz; the most common species of *Bouvardia;* frequent in desert and mesic, montane habitats; 800-3000 m; flowering mostly from late February through October.

In examining type material of *B. scabrida, Galeotti 2624,* specimens at P and W (and photos A, F, MICH, TEX) were found to be *B. viminalis.* However, the specimen at BR is *B. ternifolia* and *Galeotti 2624* is thus a mixed collection. As the original publication clearly describes the BR specimen, it is regarded as the type of *B. scabrida.* The "isotypes" and "phototypes" discussed are merely additional specimens of *B. viminalis.*

Standley (Publ. Field Mus. Nat. Hist., Bot. Ser. **8:** 334, 1931) considered *B. orizabensis* to be a "well marked" species "related clearly to *B. bouvardioides.*" Examination of type material, however, showed *B. orizabensis* to be synonymous with *B. ternifolia.* Confusion may have arisen because of the obscurity of the pubescence, particularly of the corolla, on the F and P type specimens of *B. orizabensis.* It is worthy of mention, however, that the external pubescence of the G specimen is similar to that of typical specimens of *B. ternifolia* and may be from another plant. Even if *Botteri 604* represents a mixed collection, all the specimens involved are still referable to *B. ternifolia.*

25. Bouvardia tenuifolia Standley, N. Amer. Fl. **32:** 104, 1921.

Herbs, often suffrutescent toward the base; stems simple or sparsely branched distally, 1-1.5 mm broad at the midpoint, glabrous or distally minutely puberulent to villosulous (white trichomes 0.05-0.7 mm long). *Leaves* with petioles 0-3 mm long; blades linear, 2-9.5 cm long, 0.7-4.5 mm broad, glabrous or pubescent with trichomes similar to those of the distal portion of the stem, the secondaries and reticulation obscure. *Cymes* 3 to 25-flowered, often subcapitate. *Flowers* with pedicels 0.5-6 mm long; calyx-lobes narrowly deltoid to subulate or linear, 1-3 mm long; corolla tubular, red, externally pubescent with papillose, white, red-tipped trichomes 0.1-0.4 mm long, the tube 7-26 mm long, a villous ring within near the base, the lobes ovate or elliptic, 1.5-5 mm long; anthers 2-4 mm long, included by 1-6 mm or the tips protruding; ovary 1-1.5 mm long, the style-branches 0.5-2 mm long.

Holotype: Mexico. Jalisco: grassy hillsides nr Guadalajara, Oct 1899, *Pringle 2292* (US); isotypes A, BM, BR, F, G, LE, M, MICH, MO, MSC, P, UC, W.

Sinaloa and western Durango to northern Jalisco; found in various habitats: precipitous slopes with pine and oak, open slopes in palm-oak country, grassy hillsides, gravelly banks of ravines, dry hills; 150-2700 m; flowering July through December.

Intergradation occurs between *B. tenuifolia* and *B. ternifolia* where their ranges overlap, viz. the Western Sierra Madre from extreme western Durango and eastern Sinaloa to Nayarit and northwestern Jalisco. The shaky separation of the two species by a combination of leaf and habit characters may prove untenable in the light of future collecting.

26. BOUVARDIA OBOVATA H.B.K., Nov. Gen. Sp. Pl. **3:** 385, 1820.

Hedyotis fruticosa Sessé & Mociño ex DC., Prodr. **4:** 365, 1830. (Type *Sessé & Mociño s.n.* BM, F)

Herbs or suffrutices to 1.3 m; stems glabrous or sparsely papillose-puberulent (most noticeably at the nodes and on the extreme distal portion) with white trichomes to 0.1 mm long. *Leaves* 3 to 6-nate (at least one or two nodes 5- or 6-nate); petioles 0-7 mm long; blades obovate to elliptic, 3.5-13 cm long, 0.9-3.8 cm broad, often mucronulate, glabrate, the secondaries 6-12, the reticulation apparent below, often subobscure above. *Cymes* 10 to 60-flowered. *Flowers* with pedicels 0.5-12 mm long; calyx-lobes lanceolate, 2-4 mm long; corolla tubular, red, externally minutely papillose-puberulent with white, red-tipped trichomes to 0.05 mm long, the tube 10-32 mm long, internally glabrate or somewhat villosulous toward the base (not with a villous ring), the lobes ovate to elliptic or oblong, 2-5 mm long, flared up to 30°; anthers 2.5-3.5 mm long, included by 1-8 mm or the tips protruding; ovary 1-2 mm long, the style-branches 1-3 mm long. *Capsules* 5.5-9 mm long, 6-10 mm broad, glabrous; seeds 2-3.5 mm broad.

Type: Mexico. Distrito Federal: betw Chapultepec & Tezcoco, "1200 hex.?", June 1803-04, *Bonpland s.n.* (P).

Occuring sporadically in Nayarit, Mexico State, the Federal District, Morelos and Oaxaca; wooded slopes and barrancas of volcanic mountains; rolling grassy hills in oak forests with a few pines; 1000-2150 m; flowering June through September.

27. BOUVARDIA LEIANTHA Bentham, Pl. Hartw. 85, 1841.

B. corymbosa Örsted, Vid. Medd. Nat. For. Kjöbenh. **1852:** 46, 1852. (Type probably *Örsted 11039* C)

Shrubs to 1.5 m, the branches hirtellous or villosulous with white trichomes 0.2-1 mm long when young. *Leaves* with petioles to 3 mm long; blades ovate to ovate- or elliptic-lanceolate, 1.5-7.5 cm long, 0.7-3.5 cm broad, sparsely to densely villosulous (particularly below) with white trichomes 0.3-1 mm long, the secondaries 6-14, the reticulation often prominulous below. *Cymes* 6 to 45-flowered, often subcapitate. *Flowers* with pedicels 1-6 mm long; calyx-lobes lanceolate or elliptic-lanceolate to linear or subulate, 2-5.5 mm long; corolla tubular, deep red, glabrous externally, the tube 10-19 mm long, often with an internal villous ring toward the base, the lobes ovate to elliptic or elliptic-lanceolate, 1.5-3.5 mm long, 0.8-2.2 mm broad, spreading up to 45°; anthers 1.5-2 mm long, exserted 1-3 mm in thrum flowers; ovary 1-1.5 mm long, the style-branches 1-2 mm long. *Capsules* 2.5-5.5 mm long, 3.5-6 mm broad, glabrous; seeds 1.5-2 mm broad.

Type: Guatemala: in fields nr Tejar & Chimaltenango, July-Aug 1841, *Hartweg* 583 (GH, K, P, W, photo US from B†).

Chiapas to Nicaragua; rocky, open or bushy, moist or dry hillsides in oak-pine forests; sometimes growing in dense tropical forests at lower elevations; 400-4000 m; apparently flowering the year round.

28. Bouvardia viminalis Schlecht., Linnaea **26:** 120, 1854.

Shrubs or suffrutices to 1 m; branches villosulous when young with slender white trichomes 0.2-1 mm long. *Leaves* spreading, often arcuate and ± conduplicate; petioles to 3 mm long; blades ovate-lanceolate, 1.5-5.7 cm long, 0.3-2.6 cm broad, villosulous (particularly below) with white trichomes 0.2-1 mm long, the secondaries 4-13, the reticulation prominulous to obscure. *Cymes* 7 to 35-flowered, often subcapitate. *Flowers* with pedicels 0-4 mm long; calyx-lobes lanceolate or elliptic-lanceolate or linear, 1.5-5.5 mm long, somewhat villosulous or hirtellous; corolla salverform, externally pinkish-red and glabrous, the tube 10-20 mm long, internally villosulous toward the base but lacking a villous ring, the lobes typically 4 but occasionally 5 on the same plant, ovate to elliptic or oblong, 2-6.5 mm long, 1-5 mm broad, internally scarlet, flared at ca 90°; anthers 1.5-2.5 mm long, yellowish-white, exserted 1-2 mm in thrum flowers; ovary 1-2.5 mm long, the style-branches 1-2.5 mm long, pink or white. *Capsules* 3-6.5 mm long and broad, sparsely hirtellous; seeds 1.5-2 mm broad.

Type: *Schiede s.n.* (B†). I designate *Pringle 4888* (MO) as neotype (Oaxaca: Monte Alban, 6000 ft, 4 Sept 1894); isoneotypes BM, BR, F, GH, M, MSC, P, UC, US, W.

Oaxaca and southern Peubla; rocky, open hillsides in sandy soil; sometimes in association with *Agave, Karwinskia, Croton* and cactus; flowering June through March.

29. Bouvardia scabra Hooker & Arnott, Bot. Beechey Voy. 427, 1840.

Herbs to 1 m, often woody toward the base; stems often simple and tetragonal, 3-4 mm broad at the midpoint, hirsute with yellow trichomes 0.3-2 mm long for virtually the entire length. *Leaves* with petioles to 3 mm long; blades ovate or rhombic-ovate to elliptic-lanceolate, 2.5-9.8 cm long, 0.7-4.7 cm broad, chartaceous or subcoriaceous, yellowish-hirsute with trichomes 0.2-1.1 mm long (often concentrated below along the main veins), the secondaries (8-)12-22, raised below, the reticulation often prominent below. *Cymes* 15 to 60-flowered, often subcapitate. *Flowers* with pedicels 0.5-7 mm long; calyx-lobes subulate, suffused with red, hispidulous, (3-)5.5-12 mm long, often spreading; corolla salverform, red, glabrous externally, the tube 10-27 mm long, rather densely villous internally toward the base but rarely with a villous ring, the lobes ovate, 2.5-8 mm long, spreading to 90°; anthers 1-2.5 mm long, included by 2-8 mm; ovary 1-2.5 mm long, the style-branches 1-2 mm long.

Type: Mexico. Nayarit: betw San Blas & Tepic, *Sinclair s.n.* (K).

Nayarit and Jalisco; rocky mountainsides, wooded ravines, slopes of barrancas; in oak zone or sometimes in tropical deciduous forests; 900-1700 m; flowering August through January.

30. Bouvardia rosea Schlecht., Linnaea **26**: 116, 1854.

B. violacea Rzedowski, Ciencia (Méx.) **19**: 82, 1959. (Holotype *Rzedowski 7680* MEXU, not seen; isotype ENCB)

Herbs to 0.5 m; stems often simple, green, distally compressed, 1-1.5 mm broad at the midpoint, glabrate or pruinose- or papillose-puberulent with white trichomes to 0.1 mm long. *Leaves* ascending, sessile; blades linear, 2-10 mm long at the lower nodes, to 40 mm long at the upper nodes (except immediately subtending the inflorescence), 0.5-3 mm broad, chartaceous, glabrous or hirtellous with white trichomes to 0.3 mm long, the secondaries and reticulation obscure. *Cymes* 3 to 20-flowered. *Flowers* with pedicels 0.5-5 mm long; floral cup glabrous; calyx-lobes lanceolate or elliptic-lanceolate, 1-4 mm long; corolla salverform, rose or violet-blue or clear pink, glabrous externally, the tube 5-19 mm long, internally often villous toward the base but lacking a villous ring, the lobes ovate or elliptic-lanceolate or oblong, 2.5-6 mm long, spreading at 90°; anthers 1-2 mm long, exserted 1-2 mm in thrum flowers; ovary turbinate, 1-1.5 mm long, the style-branches 0.5-2 mm long.

Type: Mexico. Hidalgo (?): nr San José del Oro, *Schiede s.n.* (B†). I designate *McVaugh 14819* (MICH) as neotype (Guanajuanto: 22 mi W of Xichu, rd from Xichu to San Luis de la Paz, 2300 m, 14 June 1957).

San Luis Potosi, Guanajuato, Queretaro and Hidalgo; rhyolitic and andesitic hillsides in pine-oak forests; sometimes in dry habitats; 1800-2800 m; flowering April through June.

31. Bouvardia bouvardioides (Seemann) Standley, N. Amer. Fl. **32**: 102, 1921.

Hedyotis bouvardioides Seemann, Bot. Voy. Herald 296, 1856.

Houstonia bouvardioides (Seemann) Bentham & Hooker, Gen. Pl. **2**: 60, 1873.

Bouvardia pallida Standley, Jour. Wash. Acad. Sci. **14**: 245, 1924. (Holotype *Standley 22977* US; isotype GH)

Shrubs to 5 m, often slender and clambering, the branches pruinose-puberulent or hirtellous when young with white trichomes to 0.1 mm long. *Leaves* with petioles (2)4-15 mm long; blades ovate- or elliptic-lanceolate, 2.5-11.5 cm long, 0.7-4.5 cm broad, thinly membranous, glabrate or sparsely appressed-hirtellous with white trichomes to 0.3 mm long (often confined to the main veins below), the secondaries 8-14, the reticulation prominulous below. *Cymes* typically more than

60-flowered. *Flowers* with pedicels 1-7 mm long; calyx-lobes linear to lanceolate, 1.5-6 mm long; corolla tubular to somewhat salverform, red or lavender, glabrous externally, the tube 2-18 mm long, internally somewhat villous toward the base (but lacking a definite villous ring), the lobes rather narrowly oblong or elliptic-lanceolate, 2.5-6 mm long, 1-3 mm broad; anthers 1.5-2.5 mm long, exserted by 1-8 mm in pin and thrum flowers; ovary 1-1.5 mm long, the style branches 1-2 mm long. *Capsules* 2-3 mm long, 2.5-3.5 mm broad, hirtellous with white trichomes to 0.2 mm long; seeds 0.4-0.8 mm broad.

Type: Mexico. Durango (?): Sierra Madre, *Seemann s.n.* (GH).

A disjunct pattern of distribution is evident: one center of dispersal being in the Western Sierra Madre of Mexico at lower elevations from Durango and Sinaloa to northwestern Jalisco, the other from southern Chiapas to El Salvador. This species occupies diverse habitats at elevations of 300-2000 m and flowers from October to April.

Standley (Jour. Wash. Acad. Sci. **14**: 245, 1924) treated the Central American component of this species as a separate species, *B. pallida*, reserving the name *bouvarioides* for plants of the Western Sierra Madre of Mexico. Although the two groups are apparently widely disjunct geographically, the characters reputedly distinguishing them (corolla size and color) completely break down on careful scrutiny.

EXCLUDED AND DOUBTFUL SPECIES

1. *Bouvardia alexanderae* A. Carter, Madroño **13**: 142, *fig. 1 & 2*, 1955 (Holotype *Carter 2577* UC 985926, not seen; isotype F). Carter (loc. cit. 144) recognized that *B. alexanderae* has wingless, angular seeds but still felt it to be best placed in *Bouvardia* in the section "having large, white, salverform corollas with long tubes" (subg. *Bouvarioides* ?). However, based on total morphology, choromosome number (n = 13) and geographical location, I believe *B. alexanderae* to have closest affinity with Baja California species of *Hedyotis* subg. *Edrisia* such as *H. saxatalis* Lewis and H. *brevipes* (Rose) Lewis. = *Hedyotis alexanderae* (A. Carter) W. H. Lewis.
2. *B. chlorantha* Bertoloni ex Schultes & Schultes f., Mant. Syst. Veg. **3**: 116, 1827, apparently based on a specimen in Bertoloni's herbarium (not seen); the description is not adequate for determination.
3. *B. coccinea* (Aublet) A. Richard, Mém Soc. Hist. Nat. Paris **5**: 272, 1834, not *B. coccinea* (Andrews) Link (Enum. Hort. Berol. **1**: 139, 1821). = *Nacibea coccinea* Aublet = *Manettia coccinea* (Aublet) Willd., fide Standley, N. Amer. Fl. **32**: 97, 1921.
4. *B. deamii* Donn. Sm., Bot. Gaz **49**: 445, 1910 (Holotype *Deam 6190* US; isotype MO). = *Rondeletia deamii* (Donn. Sm.) Standley, N. Amer. Fl. **32**: 60, 1918.
5. *"Bouvardia?" discolor* Hooker & Arnott, Bot. Beechey Voy. 428, 1840 (Type *Andrieux 334* K). = *Rondeletia leucophylla* H.B.K., fide Standley, N. Amer. Fl. **32**: 54, 1918.
6. *B. ferruginea* A. Richard, Mém. Soc. Hist. Nat. Paris **5**: 272, 1834, nomen nudum.
7. *B. havanensis* (H.B.K.) A. Richard, loc cit. = *Manettia coccinea* (Aublet) Willd., fide Standley, N. Amer. Fl. **32**: 97, 1921.
8. *B. hirsuta* (Swartz) A. Richard, loc. cit. = *Rondeletia hirsuta* Swartz, fide Standley, N. Amer. Fl. **32**: 75, 1918.
9. *B. microphylla* Schlecht., Linnaea **26**: 112, 1854 (Type *Schiede s.n.* B†), the description is not sufficient for determination.
10. *B. quinqueflora* Dehnhardt, Rivista Napolitana 1, **3**: 167. Standley questionably placed *B. quinqueflora* in the synonymy of *B. chrysantha*. However, I have been unable to trace Dehnhardt's original publication or the specimen(s) on which it

was based. A description of *B. quinqueflora* by Walpers (Repert. **2:** 507, 1843) is not sufficiently detailed to permit certainty of disposition.

11. *B. racemosa* (Ruiz & Pavon) A. Richard, Mém. Soc. Hist. Nat. Paris **5:** 272, 1834. = ? *Mannetia racemosa* Ruiz & Pavon.
12. *B. scandens* A. Richard, loc. cit., nomen nudum.
13. *B. strigillosa* Baxter, Loudon's Hort. Brit. Suppl. **3:** 502, 1850, the description is too scanty for determination.
14. *B. strigosa* Bentham, Pl. Hartw. 75, 1841 (Type *Hartweg* 503 K). = *Rondeletia strigosa* (Bentham) Hemsley, fide Standley, N. Amer. Fl. **32:** 50, 1918.
15. *B. uniflora* (H.B.K.) A. Richard, Mém. Soc. Hist. Nat. Paris **5:** 272, 1834. = *Manettia coccinea* (Aublet) Willd., fide Standley, N. Amer, Fl. **32:** 97, 1921.
16. *B. viperalis* Schlecht., Linnaea **26:** 114, 1854 (Type *Schiede s.n.* B†), the description does not suffice for determination.
17. *Cestrum spermacocifolium* Willd. ex Roemer & Schultes in L., Syst. Veg. **4:** 808, 1819 (Type *Humboldt & Bonpland s.n.,* not seen), provisionally excluded from the synonymy of *Bouvardia multiflora.* Standley incorrectly says that Willdenow's name was published in synonymy.
18. *Hedyotis mexicana* Standley, N. Amer. Fl. **32:** 104, 1921, as synonym of *Bouvardia ternifolia;* possibly an error for *Hedyotis fruticosa* Sessé & Mociño ex DC. (= *Bouvardia obovata* H.B.K.).
19. *Houstonia ochroleuca* Raf., Ann. Gen. Sci. Phys. **5:** 226, 1820, based on *H. coccinea* var. *alba* Dum. which I have been unable to trace. Merrill (Index Rafinesquianus 226, 1949) states that *Houstonia "ochroleuca"* Raf. = *Bouvardia triphylla* Salisb. = *B. coccinea* (Andrews) Link. The basis of this synonymy is not known.

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————. 1921b. *Bouvardia.* N. Amer. Fl. **32:** 100-111.

INDEX OF LATIN NAMES

New taxa are in **boldface** type, all other taxa are in roman type; numbers in **boldface** type refer to descriptions, numbers in roman type refer to synonyms, numbers with dagger (†) refer to names incidentally mentioned.

NOTES ON HEDYOTIS (RUBIACEAE) IN NORTH AMERICA[1]

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ABSTRACT

The following rubiaceous taxa are proposed: *Hedyotis acerosa* var. *polypremoides* (Gray) W. H. Lewis, *H. alexanderae* (A. Carter) W. H. Lewis, *H. crassifolia* f. *albiflora* (Standley) W. H. Lewis, and *H. nigricans* var. *parviflora* (Gray) W. H. Lewis. Range extensions are also given for *H. australis* Lewis & Moore and *H. rosea* Raf.

1. *Hedyotis acerosa* Gray var. **polypremoides** (Gray) W. H. Lewis, stat. nov.

≡ *Houstonia polypremoides* Gray, Proc. Amer. Acad. **21**: 379, 1886. Lectotype selected *Pringle 356* (GH) (isolectotype MO), Santa Eulalia Mts, nr Chihuahua, Mexico, Sept 1885 in fruit; several plants are mounted on the same sheet, some of which tend toward the typical variety . . . therefore the fruiting specimen in the lower right hand corner is chosen lectotype of the var. *polypremoides*. Also on the same sheet is the syntype *Pringle 16* (GH) with plants varying as for *Pringle 356;* they were collected at the same locality, but in flower May 1885.

≡*H. polypremoides* var. *bigelovii* Greenman, Proc. Amer. Acad. **32**: 291, 1897. Type *Bigelow 437* (GH).

≡ *Hedyotis polypremoides* (Gray) Shinners, Field & Lab. **17**: 168, 1949.

Occasional throughout the range of the typical variety, the var. *polypremoides* has stems suffruticose below, opposite leaves, and flowers mostly pedunculate. Stems of the var. *acerosa* are usually suffruticose throughout, leaves are commonly 3- or 4-verticillate, and flowers may be sessile or pedunculate. The new variety is diploid and tetraploid where $x = 11$ (Lewis, Amer. Jour. Bot. **49**: 855-865, 1962).

CHIHUAHUA: Santa Eulalia Mts, *Pringle 1066* (MO). NEW MEXICO: Lincoln Co, Gray, *Earle & Earle 429* (MO), nr Gray, *Skehan 36* (GH, MO), W of Ruidosa, *Harrison & Hicks s.n.* (GH), White Mts, *Wooton 179* (GH, MO); Otero Co, 1.7 mi W of High Rolls, *Lewis 5525* (MO, SMU), 2.5 mi W of Mescalero, *Lewis 5535* (SMU); San Miguel Co, Las Lagunitas, 15 mi S of Las Vegas, *Brandegee 11795* (MO). TEXAS: Brewster Co, Chisos Mts, *Mueller 8170* (GH); Culberson Co, Apache Mts, ca 28 mi NW of Kent, *Correll 31667* (LL), E of El Capitan, *Waterfall 4492* (GH, MO), nr Frijole, *Shreve 10245* (GH), below McKittrick Canyon, *Correll & Johnston 19133* (LL), N McKittrick Canyon, *Lewis 5538* (MO), 3 mi E of Nickel Creek, *Muller 8254* (LL); Hudspeth Co, Black Mt, Cornudas Range, *Correll & Johnston 24310* (LL), Victoria Canyon, *Muller 8220* (LL), id., *Waterfall 4787* (GH, MO).

2. *Hedyotis* **alexanderae** (A. Carter) W. H. Lewis, comb. nov.

≡ *Bouvardia alexanderae* A. Carter, Madroño **13**: 142, *fig. 2,* 1955. Holotype *Carter 2577* (UC).

Endemic to the Cape region of Baja California, Mexico and known only from granitic bluffs along the east coast.

BAJA CALIFORNIA SUR: Arroyo de Leon (ca 22 mi SE of La Paz), *Wiggins et al. 471* (MO), growing on steep granite walls; Arroyo del Salto, E of La Paz, *Carter 2577* (UC), on steep, granite, walls of arroyo; Saltito (ca 30 km E of La Paz), *Lewis 5349* (MO, SMU), occasional in cracks of granite slopes above beach.

By its long corolla tubes and large capsules *H. alexanderae* superficially resembles many but not all species of *Bouvardia;* yet because of a number of well marked characters shared with *Hedyotis,* the species clearly belongs to this genus.

[1] Supported by National Science Foundation Grant No. 5042.

ANN. MISSOURI BOT. GARD. **55**(1): 31-33, 1968.

(1) Stipules: scarious in *Hedyotis* and *H. alexanderae*, greenish in *Bouvardia;* (2) Inflorescences: central flower of cyme shortly pedunculate in many species of *Hedyotis* and *H. alexanderae,* never shorter but peduncles always as long as or longer than that of adjacent flowers in *Bouvardia;* (3) Placentae: fused ± medially to septum in *Hedyotis* and *H. alexanderae,* fused basally to septum in *Bouvardia;* (4) Seeds: wingless in *Hedyotis* and *H. alexanderae,* winged in *Bouvardia;* (5) Chromosome number of $2n = 26$: known for six species of *Hedyotis* from Baja California and *H. alexanderae,* unknown for *Bouvardia;* (6) Pollen morphology: os uniquely flared into crescent shaped extensions on both sides of each colpus (cf. Lewis, Amer. Jour. Bot. **52:** 259, *fig.* 2, 1965) in all species of *Hedyotis* from Baja California and *H. alexanderae,* unknown for *Bouvardia;* (7) Distribution: *Hedyotis* and *H. alexanderae* native to Baja California, *Bouvardia* unknown to the peninsula. Thus by gross morphology, cytology, pollen morphology and distribution *H. alexanderae* differs from *Bouvardia,* yet is strikingly similar to *Hedyotis,* especially *H. brevipes* (Rose) W. H. Lewis, *H. saxatilis* W. H. Lewis and other species also endemic to Baja California.

3. *Hedyotis crassifolia* Raf. f. **albiflora** (Standley) W. H. Lewis, comb. nov.

≡ *Houstonia pusilla* Schoepf f. *albiflora* Standley, Rhodora **34:** 177, 1932. Holotype *Benke 5191* (F), New Iberia [Iberia Par], Louisiana.

≡ *Hedyotis caerulea* (L.) Hooker var. *minor* (Michx.) Torrey & Gray f. *benkei* Fosberg, Castanea **19:** 31, 1954.

The white flowered form is usually found in the same population as the more common blue flowered form; the f. *albiflora* is known from Louisiana, Missouri (Steyermark, Fl. Missouri 1400, 1963), and Texas (Brazoria Co, 5 mi N of Angleton, *Lewis 6929,* MO, SMU).

4. *Hedyotis nigricans* (Lam.) Fosberg var. **parviflora** (Gray) W. H. Lewis, comb. nov.

≡ *Houstonia stenophylla* Torrey & Gray var. *parviflora* Gray, Pl. Wright. **1** [Smithsonian Contr. Knowledge **3**(5)]: 81, 1852. Type *Wright* 238 (GH), San Pedro River, Texas.

≡ *H. rupicola* Greenman, Proc. Amer. Acad. **32:** 286, 1897.

≡ *Hedyotis angulata* Fosberg in Shinners, Field & Lab. **17:** 166, 1949.

≡ *H. nigricans* var. *angulata* (Fosberg) W. H. Lewis, Amer. Jour. Bot. **49:** 865, 1962.

A variety close to the var. *rigidiuscula* (Gray) Shinners but differing by having capsules about as long as broad, globose, ± ½ inferior and when mature with calyx-lobes equalling their length. Infrequent in rocky crevices and hillsides in western Texas.

5. *Hedyotis australis* Lewis & Moore.

An extension of this rarely collected though rather common early white flowering species of *Hedyotis* is reported to include Mississippi and Oklahoma. It is also known from Arkansas, Georgia (Chambers, Rhodora **65:** 271-273, 1963), Louisiana, and Texas and should be found in Alabama and Tennessee.

MISSISSIPPI: Madison Co, Natchez Trace Pkwy, *McDougall 1217* (US); Warren Co, 6.3 mi SE of Vicksburg, *Lewis 5118* (SMU). OKLAHOMA: McCurtain Co, Tom, *Lewis 6952* (DUKE, MO, NY, OKLA).

6. *Hedyotis rosea* Raf.

≡ *Houstonia patens* Elliot var, *pusilla* Gray, Syn. Fl. **1**(2): 25, 1886. Lectotype selected *Hale s.n.* (GH), Alexandria [Rapides Par], Louisiana.

≡ *H. pygmaea* Mueller & Mueller, Bull. Torrey Bot. Club **63**: 33, 1936. Syntypes *Mueller* 3 (NY), *4* (NY), DeWitt Co, Texas.

≡ *Hedyotis taylorae* Fosberg in Shinners, Field & Lab. **17**: 169, 1949.

≡ *H. minima* (Beck) Torrey & Gray f. *albiflora* Lathrop, Rhodora **59**: 95, 1957. Holotype *Lathrop & McGregor* 35 (KANU), Sec. 32, T25S, R15E, Woodson Co, Kansas.

A very small spring (Febr-early April) annual with large light rose corollas paling white with age; infrequently collected in the south-central U.S. The species is known from Arkansas (Moore, Rhodora **58**: 331, 1956), Louisiana, Oklahoma (Waterfall, Rhodora **55**: 201, 1953), Texas, and now Mississippi [Simpson Co, 1.4 mi SE of Pinola, *Lewis 5124* (SMU, US); Warren Co, 6.3 mi SE of Vicksburg, *Lewis 5117* (SMU)], and, on the basis of the holotype of *H. minima* f. *albiflora*, Kansas. Material in herbaria is often determined as *Hedyotis* (or *Houstonia*) *minima* (Beck) Torrey & Gray which in fact is *H. crassifolia* Raf.

NEW AND NOTEWORTHY WOODY RUBIACEAE OF PANAMA

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ABSTRACT

Three genera, previously unreported for Panama, *Bathysa, Duroia,* and *Exostema* are discussed with *B. panamensis* and *D. panamensis* described as new. Four new species of *Cephaelis,* one new species of *Faramea,* and four new species and one subspecies of *Psychotria* are also described. Complete diagnoses of *Ronabea latifolia* Aublet and *Uragoga emetica* (L.f.) Baillon are included. Additional notes on *Coussarea* and *Schradera* are presented.

1. *Bathysa* **panamensis** Dwyer, sp. nov.

Arbores parvae, ramulis laevibus minute lenticellatis, in sicco opaco-griseis. *Folia* subsessilia aut pedicellis ad 0.5 cm longis; lamina obovato-elliptica aut obovato-elliptico-subtrapeziformis, ad apicem lato-cuneata, ultime gradatim acuminata, acumine ad 1.5 cm longo, versus basim lato-cuneata, basi truncata aut plerumque brevi-auriculata, rigido-papyracea, laevis, supra glabra, infra in costa venisque albido-appresso-pilosis, concolor, in sicco brunnea, costa supra plana, infra prominenti, convexa, venis lateralibus ca 15, arcuatis, 1.5-2 cm distantibus, venis tertiariis leviter pinnatiformibus; stipulae non visae, caducae. *Inflorescentiae* terminales, pyramidali-paniculatae, ad 10 cm longae, pedunculo compresso tortoque, basi ca 0.5 cm lato, ramis oppositis, divergentibus, usque ad 8 cm longis, jugis ramorum ca 4, bene distantibus, ca 3 cm longis, cymis terminalibus, patulis, paucifloribundis, bracteis plerumque persistentibus, patulis, angusto-lanceolatis, maioribus ad 1.5 cm longis. *Flores* sessiles aut subsessiles; calyx cupula elliptica, ca 3.5 mm longa, carnosa, puberula, lobis 4, subtriangularibus, ultime obtusis, irregularibus inaequilateralibusque, ciliolatis, ca 0.8 mm longis, marginibus erosulis; corolla tubo subcampanulato, basim contracto, tunc dilatato, 3-5 mm longo, carnoso, extus minute villosuloso, lobis 3-4, ellipticis, 3-4 mm longis, usque ad 3 mm latis, plerumque quam tubo longioribus, reflexis sed apice involutis; stamina 3-4, antheris sagittatis, ca 3-4 mm longis, glabris, exsertis, dorsifixis, filamentis ca 3 mm longis, dense barbatis praeter basim; ovarium disco quattuor lobis rotundis coronato, uniloculare ovulis ∞ in duabus brevibus placentis intrusis, stylo basi gracili, supra medium dilatato, usque ad 6.5 mm longo, stigmatibus 2, erectis, ca 1.5 mm longis. *Fructus* non visi.

PANAMA: Río Ucurganti, *Bristan 1187* (holotype MO).

This is the first report of the genus *Bathysa* north of South America. It is readily distinguished by its leaf-blades being truncate or briefly auriculate at the base.

2. *Cephaelis* **bristanii** Dwyer & Hayden, sp. nov.

Suffrutices ad 30 cm lati, caulibus in sicco nigris, laevibus, glabris vix nodosis, plerumque prostratis et radices longos angustos ferentibus. *Folia* petiolis ad 4 cm longis, ad 1.5 mm latis; lamina oblonga, apice cuneata, ultime obtusa, basi contracto-cuneata, 9-16 cm longa, 3.5-6 cm lata, rigido-papyracea, concolor, glaber, costa supra gracili, subtus prominula aut plano-convexa, venis lateralibus 15-30, 0.5-0.8 cm distantibus, arcuatis, venis intermediis evanescentibus; stipulae connatae, depresso-annulares, 1-2 mm longae, utraque minute obtuso-apiculata. *Inflorescentiae* axillares, pedunculo solitario, ad 2 cm longo, in sicco nigro, laevi, floribus crebris in 1-2 capitula rotunda ad 1 cm aggregatis; bracteae multae aggregataeque, bracteis interioribus gradatim angustioribus, oblongis, acutis, puberulis. *Flores* calyce infundibuliformi, vix 2 mm longo, corona cupiformi petaloidea instructo, lobis indistinctis, fortasse 4, brevibus, truncatis vel obtusis aut saepe redactis tunc marginibus irregulari-erosis, saepe paucis ciliis rectis ornatis, tubo marginibusque omnino ca 0.8-1 mm longis; corolla tubo angusto-cylindrico, ad 7 mm longo, in medio ca 1 mm lato, petaloideo, extus glabro, intus supra medium tubi dense albido-piloso, lobis 4, usque ad 2 mm longis, obtusis; antherae 5, exsertae, oblongae, ca 0.8 mm longae, filamentis linearibus, usque ad 2 mm longis, supra medium tubi affixis; ovarium disco prominenti, coronuliformi, obtuso, 0.5-0.8 mm longo, in sicco fusco, 2-loculare, stylo lineari, ca 3 mm longo, stigmatibus 2, rectis, ca 1 mm longis, ovulis 2, basaliter affixis, septo crasso. *Fructus* rubri (fide Bristan).

COSTA RICA: rain forest nr Río Toro Amarillo, vic Guapiles, ca al ca 350 m, *Godfrey 66248* (MO). PANAMA: BOCAS DEL TORO: premontane rain forest, Quebrada Lugron & Cerro Bonyik nr Río Teribe, alt 300-900 ft, *Kirkbride & Duke 641* (MO). DARIEN: cloud forest, Cana-Cuasi Trial, Cerro Campaniento nr Tres Bocas, Río Cuasi headwaters, *Kirkbride & Duke 1243* (MO); Cerro *Pirre, Bristan 575* (holotype MO).

The new species, named in honor of the native Panamanian collector, Narcisco Bristan, is readily distinguished by its leaf-blades being very obtuse or rounded at the apex and having lateral veins which are numerous, strict, and parallel; these in general give a corrugated effect to the blade. The flower heads are reduced and compact; the flowers have delicately petaloid floral tubes with the anthers exserted and borne on relatively elongate filaments. The Cuna name (Prov. Darien) for the species is "hinupichica" (fide Duke).

3. *Cephaelis* **camponutans** Dwyer & Hayden, sp. nov.

Suffrutices ad 0.75 m lati, ramulis laevibus, glabris, subnodosis, radicibus gracilibus, lignosis. *Folia* valde ascendentia, petiolis gracilibus, ad 3 cm longis; lamina angusto-elliptica, apice attenuato-acuminata, acumine ad 3 cm longo, basi vix inaequilaterali, acuta, ad 18 cm longa, ad 5 cm lata, subcoriacea, laevis, glabra, in vivo subtus purpureo-fusca, costa subtus vix prominula ad plana, proximaliter ca 2 mm lata, venis lateralibus 15-20, in sicco evanescentibus, fortiter ascendentibus, marginibus leviter crassis; stipulate obovato-rotundae, apice obtusae (vix bifidae?), ad 1.5 cm longae, ± 1 cm latae, tenues, raphidibus minutis ornatae, marginibus erosulosis. *Inflorescentiae* axillares, 1-3 per axillam, terminaliter in pedunculo dispositae, cernuae capitulataeque, pedunculo ad 1 cm longo, capitulis compresso-rotundis, ad 2 cm latis, in sicco nigris, bracteis exterioribus solitariis, subovatis, ad 1.5 cm longis, coriaceis, in dorso mediano-carinatis, bracteis interioribus minoribus angustioribusque, jugo florem solitarium includente, apice eroso-marginatis. *Flores* ex parte vidimus; calyx tubularis, lobis 5-6, erectis, inaequilateralibus, subulatis quam tubo longioribus, marginibus scariosis; corolla purpurea; ovarium biloculare, septo integro mediano, ovulo 1 per loculum, basaliter affixo, stigmatibus 2, erectis, digitiformibus, ca 1 mm longis, stylo fortasse nullo. *Fructus* hic immaturi, calyce persistenti coronati, pyrenis 2, ellipticis, seminibus superficie adaxiale plano, leviter mediporcato, superficie abaxiale convexo, endospermio laevi, testa modice pigmentifera, fortasse bilamellosa, cellulis macroscopicis parenchymatis subisodiametricis, 23-55μ diam.

BOCAS DEL TORO: Punta Peña, vic Chiriquicito, ca 2700 ft elev, *Lewis et al. 2171* (MO). PANAMA: Cerro Jefe, alt 2700 ft, *Dwyer & Gauger 7346* (holotype MO).

As the axillary inflorescences are cernuous and bell-shaped the name *camponutans* (L. *nutans* = bent) was chosen for the specific name. Its narrowly lanceolate and subcoriaceous leaves with the blades purple beneath in the fresh state and the lateral veins of the blade evanescent are unique among the Central American species of *Cephaelis.* No styles were observed in several flowers dissected, although the stigmas were evident.

4. *Cephaelis* **correae** Dwyer & Hayden, sp. nov.—Fig. 1.

Arbores parvae, ad 5 m altae, ramulis teretibus, laevibus. *Folia* petiolis 0.5-8 cm longis, gracilibus, ad 0.25 cm latis, laevibus, glabris; lamina oblonga, apice obtusa, basi cuneata, ad 17 cm longa, ad 8.5 cm lata, membranacea, laevis, glabra, costa supra vix prominula, ad 2.5 mm lata, subtus prominula, venis lateralibus, ca 20, 1-1.5 cm distantibus, strictis non nisi prope marginem arcuatis, venis intermediis leviter pinnatinervis; stipulatae connatae, corporibus brevibus interpetiolaribus, truncatis, ad 5 mm longis, lobis intrapetiolaribus connatis, ad 1 cm longis, subscutiformibus, apice bifidis. *Inflorescentiae* ultime cernuae, solitariae, ad 25 cm longae, pedunculo ad 20 cm longo, in medio ca 3 mm lato, distaliter ca 4.5 mm lato, glabro, in sicco porcato, bracteis exterioribus 2, ad 4.8 cm longis, conspicue nitido-rubris aut purpurascentibus, capitulis interioribus ad 1.5 cm longis rubris ad purpurascentibus. *Flores* albi, ca 1.5 cm longi, calyce subquadrato, ad 3 mm longo, dentibus 5, utroque dente irregulari-marginato; corolla tubo cylindrico, ad 10 mm longo, intus prope basin filamentorum staminum puberulo, lobis 5, triangularibus, ca 3 mm longis; antherae 5, filamentis infra medium tubi affixis. *Fructus* nitido-azurei, obovato-oblongi, ca 1.5 cm longi, calyce persistenti, fusco, pericarpio carnoso, in sicco atro-fusco, seminibus funiculo basi loculo conspicue affixis, subtriangularibus, superficie ventrale plana et in medio breviter sulcata, testa fuscata.

COCLE: El Valle de Antón, foot of Cerro Pilón, alt ca 2000 m, Duke *1247* (MO); id., *Lewis et al. 1759* (MO).

The new species is readily distinguished by its large pendent inflorescences and conspicuous subscutiform stipules. It is named in honor of Panama's first woman systematic botanist, Miss Mireya Correa.

5. *Cephaelis* **rigidifolia** Dwyer & Hayden, sp. nov.

Suffutices parvi, ramulis nodosis, teretibus sed in sicco internodiis contractis sic angularibus, glabrescentibus. *Folia* petiolis 1-2 cm longis, ca 0.2 cm latis, lignosis; lamina oblonga, apice acuta, ultime acuminata, acumine ad 1.3 cm longo, basi acuta, ad 13 cm longa, ca 6.5 cm lata, rigido-coriacea, discolor, supra in sicco fusca, subtus opaco-luteo-viridis, subtus aureo-strigiloso-puberula, costa supra

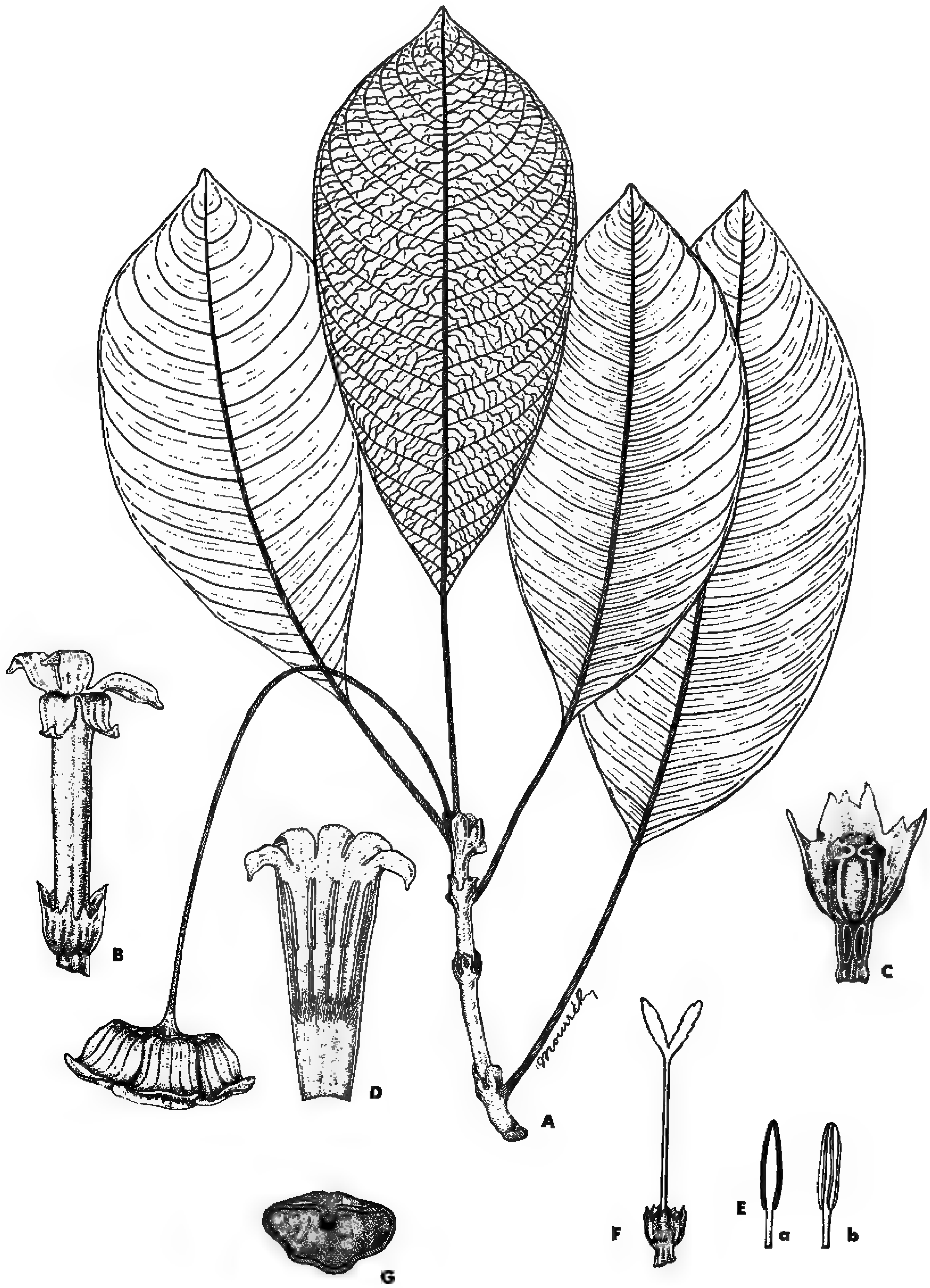

Fig. 1. *Cephaelis correae* Dwyer & Hayden: A, habit (×½); B, flower showing calyx and corolla (×2); C, longitudinal section of calyx, large ovarian disc and ovary with two ovules (×4); D, longitudinal section of corolla tube showing five stamens and pubescence of tube (×2); E, two stamens: a, axial view (×3); b, abaxial view (×6); F, calyx cup, style and two stigmas (×2); G, cross-section of seed showing median sulcus on ventral face (×3). After *Lewis et al. 1759* (MO).

prominula, subtus prominenti, venis lateralibus ca 15, arcuatis, prominentibus, venulis minoribus intermediis ornatis, venis tertiariis pinnatiformbus; stipulae 2, connatae, compresso-cupiformes, ca 5 mm longae, coriaceae, utraque stipula dentibus 2 erectis rigidis ciliolatis, ca 3 mm longis, instructa. *Inflorescentiae* (hic in fructu) ad 10 cm longae, ad 2.5 cm latae, spiciformes, pedunculo compresso-torto, lignoso, puberulo, ramis paucis, basalibus, distantibus, ad 1.5-2 cm longis, simplicibus vel ramulis paucis brevibus lignosis terminatis, fructibus terminali-aggregatis, plerumque 1-2 in utroque capitulo persistentibus. *Fructus* sessiles, compresso-rotundi, didymi, apice cicatrice parvo plerumque excentrico notati, ad 0.8 cm diam quam longi latiores, puberuli, in sicco virides, pericarpio crasso, seminibus in $\times$-sect. rotundis, septo crasso.

PANAMA: Cerro Jefe, alt ca 2700 ft, *Dwyer 8075A* (holotype MO).

C. rigidifolia has markedly stiff-coriaceous leaves with a golden puberulence beneath. This vegetative character coupled with the large didynamous fruits borne on a spike-like inflorescence readily distinguishes the species.

6. *Coussarea enneantha* Standley, Jour. Wash. Acad. Sci. **18:** 282, 1928.

DARIEN: La Boca de Pirre, *Bristan 1272* (MO); s. loc., *Duke 13781* (MO).

These are the third and fourth collections of this species, all of which are from the province of Darien, Panama; the other collections are *Terry 1476* (MO) from the Cana-Cuasi Trail (Camp 2) and *William 841* (F, photo of type) from Cana.

The mature fruits of *Duke 13781* are noteworthy as the fruits of *C. enneantha* have not been described. Thus: fruits stipitate for 3 mm, the stipe rufo-pubescent, the pericarp oblong or ovate-oblong, cuneate at the apex, obtuse at the base, 2-2.5 cm long, 0.9-1.1 cm wide, pilose, capped by a cylindrical calycine tube, 5-10 mm long, ca 2 mm diam, the lobes 4, unequal, ca 3 mm long, truncate or rounded, the seeds solitary, vertical, the testa membranaceous, the endocarp smooth, fibrous, the endosperm horny, turning blue-black on drying.

While the membranous seed coat has the cell pattern characteristic of *Coussarea,* the usual wall thickenings are not apparent throughout. One side of the seed coat is much more vascular and thicker than the other; the raphides are abundant.

7. *Duroia* **panamensis** Dwyer, sp. nov.

Arbores ad 8 m altae, ramulis subteretibus, in sicco leviter longitudinali-rimosis, junioribus dense pilosis, nodosis. *Folia* petiolis 1-2.5 cm longis, lignosis, pilosis; lamina obovato-elliptica, apice late cuneata, acuminata, acumine ad 1.5 cm longo, usque ad 26 cm longa, ad 15 cm lata, rigido-papyracea, subconcolor, in sicco fusca, supra appresso-albido-ciliata, ciliis ca 1-2 mm distantibus, ad tactum scabridiuscula, infra pilosa, ciliis aliquibus uncinatis rigidioribusque, costa supra prominula, infra prominenti convexaque, venis lateralibus ca 12, primo a costa divergentibus, tunc ad marginem leviter arcuatis, in foliis maioribus 2-2.5 cm distantibus, infra prominentibus, venis tertiariis irregulari-pinnatiformibus, marginibus ciliolatis; stipulae ovato-ellipticae, deciduae, hic junioribus ad 1.5 cm longis, dense pilosis.

Flores solitarii, terminales vel axillares sessiles; calyx cupula campanulata, ca 0.8 cm longa, ca 0.5 cm lata, dense barbata, ciliis albido-luteis, adscendentibus, fortasse 4-5 mm longis, lobis ad 3 mm longis, extus dense pilosis, in fructu persistentibus; corolla tubo tubaeformi, ad 4.5 cm longo, ca 0.6 cm in medio lato, extus dense albido-piloso, lobis hic 5, ellipticis erectis obtusis, ca 1 cm longis, dense albido-pilosis, intus glabris. *Fructus* elliptici, nuciformes, calyce persistenti coronati, usque ad 3 cm longi, usque ad 1.5 cm lati, 5-7-costati, dense albido-luteo-pilosi, pariete pericarpii crasso, ad 2 mm lato, placentis 2, intrusis, T-formibus, seminibus multis, elliptico-oblongis, ca 2 mm longis, trigonis, sub lente minute favosis.

BOCAS DEL TORO: Duwebdulup Peak, N of Río Teribe at Quebrada Huron, behind chief's house, alt 300-900 ft, *Kirkbride* & *Duke 571* (holotype MO).

This is the first report of the genus in Panama. Only one other species of *Duroia* is known from Central America, *D. costaricensis* Standley, endemic to Sierpe, Costa Rica (*Pittier 6903*, type); this has smaller leaves and presumably much smaller calycine lobes. Noteworthy is the fact that *Duroia* is dioecious; Standley's type description is based on material with ♂ flowers. With only one flower available for dissection I am electing to describe only its external morphology. The flower is ♀ and all the material deposited at MO is fructiferous. Vegetative and reproductive features point to *Duroia*, although the fruits, which seem mature, are devoid of any gelatinous covering. Superficially the ♀ flower in the pressed condition looks like a large-flowered *Clitoria*. In their field-notes Duke & Kirkbride describe the corolla tube as green-white, the anthers yellow, and the stigmas green. Obviously ♂ flowers were observed in the field and perhaps were collected. The collection site of the new species is the home of the few remaining survivors of the Teribe Indians of Bocas del Toro.

8. *Exostema mexicanum* A. Gray, Proc. Amer. Acad. **5:** 180, 1861.

CANAL ZONE: Madden Dam, Boy Scout Camp Rd, *Dwyer & Elias 7510* (MO); id., *Dwyer 8391* (MO).

This is the first report of the genus in Panama. It is well known in Mexico where it is native. *Exostema caribaeum* (Jacq.) Roem. & Schult. occurs in Costa Rica and ranges from Florida to the West Indies and to Mexico.

9. *Faramea* **caput-anguis** Dwyer & Hayden, sp. nov.—Fig. 2.

Arbores ad 8 m altae, ramulis in sicco glabris, laevibus. *Folia* petiolis 2-4 cm longis, laevibus; lamina oblonga, apice acuta vel acuminata, acumine ad 1.5 cm longo, basi acuta, ad 20 cm longa, ad 10 cm lata, tenui-coriacea, plerumque subtus luteo-viridis, minute luteo-puberula, costa supra subplana, infra prominenti, venis lateralibus ca 20, arcuatis, prominentibus, 1-2 cm distantibus, venulis intermediis pinnatiformibus; stipulae persistentes, triangulari-subulatae, acutissimae, ad 3 cm longae, ad 0.8 cm latae, lignosae, glabrae. *Inflorescentiae* per axillam plures, hic ad 4, pedunculis divergentibus, laevibus, glabris, ad 9 cm longis, capitulis terminalibus solitariis condenso-cymosis, primo gemminoideis, oblongo-fusiformibus, ad 2 cm longis, ca 1 cm latis, bracteis exterioribus fortasse 5, late oblongo-fusiformibus, glabris, foliosis, floribus 7-9 per capitulum, jugo utroque bracteolis duabus vel pluribus (?) instructo. *Flores* glabri, calyce angusto-campanulato, ad 8 mm longo,

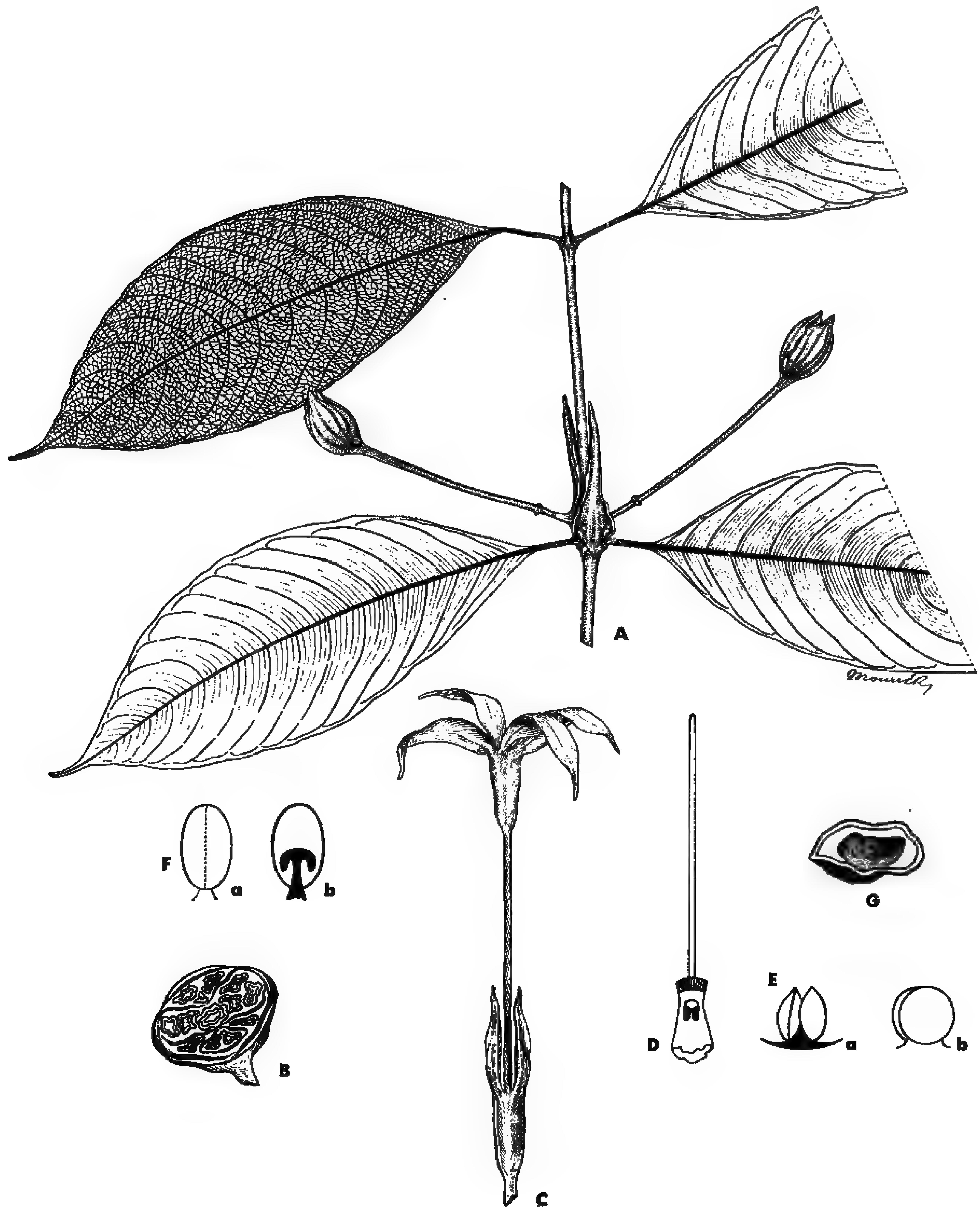

Fig. 2. *Faramea caput-anguis* Dwyer & Hayden: A, habit, showing leaves, axillary inflorescences, and erect stipules (ca $\times 1/3$); B, inflorescence showing diagrammatically in cross section ($\times 1\frac{1}{2}$); c, flower, showing calyx and corolla ($\times 2$); D, pistil with style, the ovary and its two ovules in longitudinal section ($\times 7$); E, two ovules with basal septum: a, longitudinal section ($\times 7$); b, face view ($\times 7$); F, seed: a, face view ($\times 1$); b, endosperm with T-shaped septum, adaxial view ($\times 1$); G, fruit in cross-section ($\times 1\frac{1}{2}$). A-E, after *Dwyer 7248* (MO); F-G after *Dwyer et al. 8236* (MO).

lobis 4, inaequilateralibus, subulatis, brevioribus, ca 4 mm longis, longioribus ca 8 mm longis; corolla tubo ca 25 mm longo, angusto ad medium, tunc supra diliatato lobis 4, lanceolatis, acutis, ad 7 mm longis; antherae 4, oblongo-lineares, ca 5.5 mm longae, filamentis proxime medium tubi affixis; ovarium ca 1 mm longum, uniloculare, ovulis 2, orbicularibus, geminatis, ca 0.5 mm longis, jugo ovulorum septo incompleto basali affixo. *Fructus* glabri, longitudinaliter elongati, oblongi, ca 1.4 cm longi, ca 1 cm lati, calyce persistenti, cylindrico, ca 5 mm longo, pericarpio carnoso, endocarpio fibroso tenui-friabili, azureo-purpureo, endospermio corneo, sulco ad aream junctionis seminum duorum ornato, seminibus solitariis magnis, testa cellulis exterioribus sclerenchymatis bene distantibus, polymorphis, plerumque oblongis aut triangularibus, 34.5-69 longis $\times$ ca 46μ latis, eis stratum unum cellulorum parenchymatorum tegentibus.

PANAMA: Cerro Jefe, alt ca 2700, *Dwyer 7248* (MO); id., *Dwyer & Gauger 7375* (holotype MO); id., *Dwyer et al. 8236* (MO).

The new species is named *caput-anguis* because of the fancied resemblance of the floral heads to that of a snake. The pattern of the inflorescence is unmatched by any *Faramea* seen. The field notes for *Dwyer & Gauger 7375* describe the external bracts as persistent and black-purple. The pulp of the seed is soft-cartilaginous. The sclerenchyma elements of the testa are typical of *Faramea* seeds; the testa was prepared for microscopic examination by soaking the same for 15 minutes in warm 5% NaOH solution.

10. *Psychotria* **carnosocarpa** Dwyer & Hayden, sp. nov.

Frutices, ramulis rigidis, divergentibus, cinereo-fuscis, glabrescentibus praeter ad apicem dense hirsutis, ciliis pellucidis, subulatis. *Folia* petiolis ad 1.5 cm longis, dense villosulis; lamina oblonga, apice cuneata, acumine ca 1 mm longo, basi cuneata, ad 13 cm longa, ad 5.5 cm lata, rigido-papyracea, discolor, costa prominula, infra conspicue villosa, ciliis crebris appresso-ascendentibus, venis lateralibus ca 12, primo stricto-ascendentibus, tunc proxime marginem arcuatis, 0.5-1.2 cm distantibus; stipulae biaristatae, corpore hic indistincto, aristis subulatis, ad 0.9 cm longis, dense hirsutis. *Inflorescentiae* terminales, paniculatae, dense puberulae, breves, ad 6 cm longae, ca 4 cm latae, pedunculo ad 2.2 cm longo, ramis paucis, inferioribus fortasse quattuor, radiate dispositis, ad 4 cm longis; *Flores* non vidimus. *Fructus* didymi, lobis calycinis brevibus plerumque puberulis coronati, subrotundi vel compresso-rotundi, $\pm$5 mm longi, 4.5-7 mm lati, in vivo manifeste carnosi, in sicco nigri, glabrescentes, pyrenis 2, hemisphericis, testa rubro-fusca, cellulis fortasse uno strato dispositis, subisodiametricis, pigmentis luteis ad aurantiacis coloratis, endocarpio superficie ventrale plana sed dorsaliter ecostata et sulco alto mediano instructa, etiam minutum basalem porum gerente, albumine non ruminato, ca 3.5 mm longo, 2.5 mm lato.

BOCAS DEL TORO: Changuinola to 5 mi S at jct Ríos Changuinola & Terebe, alt 100-200 ft, *Lewis, Dwyer, Elias & Robertson 964* (holotype MO).

The new species is readily distinguished from the vast majority of *Psychotria* of the New World by its biaristate stipules, radiately branched panicle, and didynamous fruits. The structure of the fruit and the conspicuously acuminate leaf-blades suggest *P. cuspidata* Bredem and *P. patens* Sw. These three species differ widely in the patterns of the inflorescence. *Psychotria carnosocarpa* can be easily distinguished from the pair by its leaf-blades being densely hairy beneath.

11. *Psychotria* **grandicarpa** Dwyer & Hayden, sp. nov.

Suffrutices, ramulis teretibus glabris, laevibus. *Folia* petiolis 1-4 cm longis, subteretibus lignosis glabris; lamina late elliptica, apice cuneata vel rotunda, basi acuta inaequilateralique, 10-19 cm longa, 5-10 cm lata, tenui-coriacea, in sicco hic griseo-viridis, costa supra prominula, infra prominenti et proximaliter ad 2.5 mm lata, venis lateralibus 10-12, supra planis, late arcuatis, subtus prominulis, ultime in venam tenuem submarginalem undulatam conjunctis; stipulae semicirculares, ad 1.5 mm longae, brunneae, deciduae. *Inflorescentiae* fortasse pseudo-terminales (hic in fructu), pedunculis 3-6, umbellate dispositis, 4-6 cm longis, lignosis, glabris, simplicibus aut ramulis terminalibus brevibus paucis instructis, floribus in capitula terminalia, ad 0.8 cm longa, aggregatis. *Fructus* subsessiles aut pedicellati, pedicellis ad 2 mm longis, in sicco nigri, magni, oblongi aut subfalcato-oblongi (plerumque semine uno abortivo), apice basique obtusi, apice calyce opaco-luteo persistenti coronato, lobis calycinis obtusis, omnino ca 5 mm longis, pubescentibus, ad 1.5 cm longi, distincte 10-costati, pyrenis 2, utraque pyrena utrinque plana, seminibus 2 aut 1 abortu.

PANAMA: Cerro Jefe, alt ca 2700 ft, *Dwyer 7244* (holotype MO); Cerro Jefe nr Río Indio, *Duke 15228* (MO).

The new species is readily recognized by its coriaceous leaf-blades, its inflorescence with several peduncles radiately disposed, and its very large ribbed fruit. The pyrenes which appear ruminate in cross-section suggest the sect. *Mapouria.*

12. *Psychotria horizontalis* Sw. subsp. **basicordata** Dwyer, subsp. nov.

Suffrutices. *Folia* superiora sessilia, aliquibus infimis vix petiolatis, lamina basi plerumque cordata, marginibus in sicco crispis. *Fructus* puberuli.

CANAL ZONE: Fort Sherman, *Dwyer 5160* (MO). VERAGUAS: Isla de Coiba (Penal Colony), *Dwyer 2348A* (holotype MO).

Superficially the two collections appear to be quite different from the numerous Panamanian collections of *P. horizontalis.* On closer examination the fruits of the material cited above exhibit the typically persistent calycine lobes, although admittedly the pyrenes are pubescent. The fact that the leaf-blades are often subcordate at the base distinguishes them from all other Panamanian *Psychotria,* except *P. insignis* Standley, widely separated phylogentically from *P. horizontalis.* The leaves of the new subspecies resemble those of typical *P. horizontalis* in having minute domatia on the undersurface of the lamina. The domatia often have ostioles from which project minute tufts of hairs.

13. *Psychotria* **olgae** Dwyer & Hayden, sp. nov.—Fig. 3.

Frutices ad 7 m alti, ramulis primo teretibus tunc saepe ultime subplano-compressis laevibus vix nodosis. *Folia* valde ascendentia sub-sessilia aut vix petiolata, petiolis ad 5 cm longis, lignosis; lamina obovato-elliptica aut elliptica, saepe angusto-elliptica, apice late cuneata, rotunda aut obtusa, basi cuneata, 4.5-11 cm longa, 1.5-4 cm lata, crasso-coriacea, glabra, marginibus conspicue revolutis, costa supra prominula, subtus versus basim prominula, proximaliter ad 1.5 mm lata, venis lateralibus ca 6, arcuatis, 0.8-1.5 cm distantibus, supra evanescentibus, subtus vix prominulis, gracilibus; stipulae deciduae (unam juvenilem vidimus) integrae, triangulares. *Inflorescentiae* ad 11 cm longae, gemmis oblongo-rotundis, hic ca 3 mm longis; calyx ca 1.5 mm longus, cupula calycina intus jugum glandularum minutarum nigrarum ferente, utroque jugo lobis calycinis alternanti, lobis 5, triangularibus, ca 0.5 mm longis; corolla tubo brevi, intus basi puberulo, lobis 5, apice galeatis; antherae hic immaturae quadratae, ca 1 mm longae, in dorso raphidibus ornatae; ovarium septo crasso integro instructum, ovulis 2 basaliter affixis. *Fructus* in vivo vivido-rubri, obovato-oblongi, ca 2 cm longi, ca 1 cm lati, apice obtusi, basi acuti, in sicco carnosi, sulcis 12 longitudinalibus ornati, utroque putamine superficie interiore plana superficie exteriore ruminata seminibus 2, endocarpio fibroso infra corpus endospermii, ad 3 mm caudate disposito, ultime acuto, basi porum minutum ferente, testa opaco-rubra, cellulis epidermidis parenchymatis, endospermio albo-ruminato.

Fig. 3. *Psychotria olgae* Dwyer & Hayden: A, habit (×½); B, floral bud: a, lateral view showing calyx and corolla lobes (×3); b, top view with five valvate corolla lobes (×3); C, fruit, external view showing costae and apical calycine ring (×1½); D, cross-section of fruit, ruminate endosperm shown (×1½). A-B after *Dwyer 7288* (MO); C-D after *Dwyer et al. 8193* (MO).

PANAMA: Cerro Jefe, alt ca 2700 ft, *Dwyer 7288* (MO), *8193* (MO); betw Cerro Jefe & Eneida, alt 2100-2900 ft, *Dwyer, Duke* & *Dressler 8193* (holotype MO).

A combination of characters readily segregates the new species from all New World *Psychotria*: the thick coriaceous leaves with the secondary veins evanescent, the large red fleshy fruits, and the calyx cup with internal glands. Miss Olga Herrera, in whose honor the species is named, discovered calycine glands in several species of *Psychotria* found in Panama: *P. horizontalis* Sw; *P. chagrensis* Standley; *P. psychotriaefolia* (Seem.) Standley, *P. carthaginensis* Jacq., *P. undata* Jacq., *P. fruticetorum* Standley, and *P. graciliflora* Benth. The ruminate endosperm of *P. olgae* suggests the sect. *Mapouria.*

14. *Psychotria* **umbelliformis** Dwyer & Hayden, sp. nov.

Frutices, ramulis valde ascendentibus, saepe strictis, teretibus, opaco-cinereis. *Folia* petiolis ad 0.7 cm longis, dense aureo-villosulis; lamina ovato-elliptica, apice acuta ad distincte acuminata, basi obtusa, 6-10 cm longa, 3-4.5 cm lata, rigido-papyracea, subtus dense villosula, costa gracili, supra prominula, subtus prominenti, venis lateralibus principalibus 6-10, arcuatis, in sicco luteis, infra prominentibus, 0.7-2 cm distantibus, venis minoribus intermediisque valde irregularibus, aliquibus a costa stricte orientibus vel aliquibus a costa reflexis, omnibus mox evanescentibus, venis tertiariis irregulari-pinnatiformibus, patulis; stipulae connatae, puberulae, corporibus brevibus, truncatis, 1-2 mm longis, utroque duo cornua vix divergentia lateralia, ad 5 mm longa, ferente. *Inflorescentiae* terminales, puberulae, pedunculo 3-4 cm longo, rigido, ramis 3, radiate dispositis, ca 2 cm longis, plerumque ad apicem dilatatis, uno medio strictiore, bracteis inferioribus 2, divergentibus vel vix reflexis, lineari-lanceolatis, ad 0.4 cm longis, capitulo solitario in utroque ramo et terminaliter disposito, pauciflora (fortasse ±10 floribus), ad 1 cm longo, quam longo latiore, bracteis exterioribus paucis, uniseriatim in involucrum aggregatis, late triangularibus, ad 4 mm latis, ca 3 mm longis, leviter pubescentibus, sub-anthesi divergentibus, bracteis interioribus angustioribus, paucis ovatis, in gemmis fortasse jugo bractearum florem solitudinum includente. *Flores* calycis tubo camp-anulato, ca 2.5 mm longo, modice crasso, puberulo, lobis 5, ovatis vel triangulari-bus, apice obtusis vel acutis, ca 0.8 mm longis; corolla in gemmis subfusiformis sed apice obtusa, albido-puberula sub anthesi ad 20 mm longa, subcarnosa, puberula, intus infra medium tubum pilosa, lobis 5, sublinearibus, ca 8 mm longis, ±0.8 mm latis, extus puberulis, patulis; antherae 5, lineari-oblongae, ca 3 mm longae, ca 0.35 mm latae, dorsifixae, filamentis gracilibus, ca 0.8 mm longis, glabris, a basi tubi ca 8 mm affixis; ovarium vix 1 mm longum, biloculare, septo integro, ovulis 2, modice magnis, basaliter affixis, disco in sicco nigro, ca 0.6 mm alto, stylo ca 16 mm longo, ca 0.35 mm lato, stigmatibus 2, rectis, ca 2 mm longis, subcrassis. *Fructus* non visi.

COCLE: E slope Cerro Pilón, nr El Valle de Antón, cloud forest, alt 700-900 m, *Duke 12154* (MO). PANAMA: degraded cloud forest, peaks of Cerro Trinidad, *Duke & Kirkbride 1641* (holotype MO).

Several characters serve to distinguish the new species: the umbelliform inflorescences which often assume the form of a Neptunian trident, the densely villulose undersurface of the leaf-blades with the veins drying yellow, and the few-flowered capitate inflorescences subtended by an involucral-like series of bracts. The flowers are described by *Duke & Kirkbride* as white and presumably the shrubs are common.

15. *Ronabea latifolia* Aublet, Hist. Pl. Gui. Fr. 154, 1775.
R. erecta Aublet, loc. cit. 156.
Psychotria axillaris Willd. in L., Sp. Pl., ed. 4 [i.e. 5] **1:** 962, 1798.

Shrub 0.5-8 m high, the branchlets quadrangular, ridged, often nigrescent, sericeous or glabrescent. *Leaves* short-petiolate, the petioles 6-16 mm long, often stout, sericeous or glabrescent; blade elliptic to oblong, acuminate at the apex, sometimes abruptly short-acuminate, attenuate or obtuse at the base, 9-15 cm long, 3-12 cm wide, subcoriaceous, olive-black when dry, glabrous above, sparsely sericeous beneath, sometimes abundantly so along the veins, the midvein prominent beneath, the lateral veins 6-12, arcuate, clearly anastomosing close to the margin, the veinlets conspicuous; stipules subpersistent, free, entire, lanceolate or subulate, acuminate or obtuse at the apex, sericeous. *Inflorescences* axillary, geminate or solitary, bearing a few sessile flowers, up to 8 mm long, larger in fruit, the peduncle and bracts densely sericeous; peduncle rather thick, up to 7 mm long, equalling the petals or smaller; bracts minute, up to 1 mm long, triangular-ovate, acute or obtuse at the apex. *Flowers* ca 5 mm long, white or yellow; calyx cupuliform, the tube ca 2 mm long, subtruncate or minutely and irregularly toothed, glabrous; corolla with the tube ca 3 mm long, glabrous on the outside, sericeous in the throat, the lobes suboblong, strongly cucullate, ca 2.5 mm long, glabrous on the outside, papillose within; stamens attached to the throat of the tube; anthers oblong, short-acuminate at the apex, ca 1.2 mm long; disc cylindraceous, 0.8-1 mm long; ovary ca 2 mm long, the style rather thick, ca 2.8 mm long, dilated above, the stigmas obtuse, ca 0.6 mm long. *Fruits* (here immature), elliptic, 5.5-7.5 mm long, 2.5-6 mm wide, black, glabrous; pyrenes 2, the ventral face of the seed plane, the dorsal face ecostate but perhaps muricate.

Known from Panama and Costa Rica, both in lowlands and highlands.

BOCAS DEL TORO: Fish Creek Mts, *von Wedel 2358* (MO); Punta Peña, vic Chiriquicito, alt ca 1000 ft, *Lewis et al. 2187* (GH, MO, US). CANAL ZONE: W of Pine Base Camp, *Johnston 1593* (MO). DARIEN: El Real on Río Pirre, *Duke 5425* (MO); s. loc., *Duke 8351* (MO); Loma Cuasi behind Manene, *Duke 13613;* Tumaganti, *Duke 14242* (MO). PANAMA: Cerro Azul, alt ca 2000 ft, *Dwyer 2796;* Cerro Jefe, alt 2700-3000 ft, *Dwyer & Hayden 4363* (MO); id., *Dwyer & Gauger 7344* (MO). SAN BLAS: rd betw Mandinga & Cangandi, *Duke 14742* (MO); betw Río Diabolo & Río Acuati, nr Nargana, *Duke 14894* (MO); Río Diabolo & Río Acuati, nr Nargana, *Duke 14898* (MO).

In view of the wealth of collections from Panama of this little known species it is deemed appropriate to present a detailed description. The species obviously does not belong in *Psychotria* as is evidenced by the muricate surface of the mature pyrenes. A less important but obvious character is the few-flowered, axillary inflorescence, although a few species of *Psychotria* admittedly have axillary inflorescences.

16. *Schradera blumii* Dwyer & Hayden, Phytologia **15:** 59, 1967.

COCLÉ: Cerro Pilón, El Valle, alt ca 3000 ft, *Duke 14996* (MO). PANAMA: Cerro Jefe, alt 2900 ft, *Tyson et al. 3218* (holotype MO).

In studying *Duke 14996* we encountered the first collection with complete flowers. In describing the species Dwyer & Hayden had only fruit with the persistent calyx. It seems appropriate, therefore, to describe the flowers: calyx ca 1 mm long, irregularly dentate at the apex, glabrous; corolla-tube cylindrical, surrounded for 1.7 cm of its length by the calyx, the tube and the valvate lobes up to 2.5 cm long, the upper portion of the tube with white silky hairs within, the lobes thick, leathery, acute; anthers rectangular, ca 6 mm long, subsessile or on filaments ca 1 mm long, dorsifixed; ovary 2-celled, the septum thick, entire, the axile placentae bearing numerous ovules, the style ca 7 mm long, the stigmas 2, erect, subulate, ca 2.5 mm long, papillate on the inner surface.

17. *Uragoga emetica* (L.f.) Baillon, Hist. Pl. **7**: 371, 1880.

Psychotria emetica L.f., Suppl. Pl. 144, 1781.
Cephaelis emetica Pers., Syn. Pl. **1**: 203, 1805.
C. plagiantha Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. **11**: 190, 1936.

Shrubs up to 1 m tall, the roots rather thick and gnarled; stems simple, terete, strigose. *Leaves* short-petiolate, the petioles 5-16 mm long, flattened, puberulent; blade elliptic-oblong to oblanceolate, acute to attenuate at the base, acute or short-acuminate at the apex, sometimes abruptly acuminate, the acumen often pungent, 8-15 cm long, 3-6 cm wide, membranaceous, glabrous above, strigose beneath, more densely so along the veins, otherwise glabrous, the costa prominent beneath, the lateral veins 7-11, arcuate, clearly anastomosing close to the margins, elevated beneath; stipules subpersistent, free, entire, triangular-lanceolate, sometimes subulate, acuminate or obtuse, puberulent. *Inflorescences* axillary, solitary or geminate, subcapitate, up to 8 mm long, larger in the fruit, strigose; peduncle rather slender, up to 7 mm long, ca equalling the petioles or shorter; bracts ovate, acuminate or subulate, up to 2 mm long. *Flowers* 5-merous, white, subsessile; calyx cupuliform, the tube 0.8-1.5 mm long, glabrous, often irregularly lobed, the lobes ovate to oblong, acuminate or obtuse, 0.9-2 mm long; corolla ca 5 mm long, the tube glabrous, the 5 obtuse lobes slightly shorter than the tube, elongate pilose within; anthers narrowly oblong, ca 1.5 mm long, elongate-pilose, attached in the middle of the tube; ovary 2-loculate, with a single basally attached ovule per locule. *Fruit* bright-blue, drying black, capped by the persistent calyx, elliptic, 0.5-1 cm long, 0.2-0.25 mm wide, glabrous; pyrenes 2, twisted, each pyrene hemispherical in cross-sect, the ventral face of the seed plane and with a median ridge, with a small pore at the base, the dorsal face ecostate, the albumen entire.

Ranging from Guatemala to Bolivia.

BOCAS DEL TORO: Changuinola Valley, *Dunlap 436* (F); vic of Chiriqui Lagoon, *von Wedel 1258* (MO). CANAL ZONE: Barro Colorado I, *Aviles 10* (F); id., *Bailey & Bailey 510* (F); id., *Hayden 122A* (MO), *1038* (MO); id., *Ebinger 549* (MO). DARIEN: vic of El Real, alt ca 15 m, *Allen 955* (MO); La Boca de Pirre, *Bristan 1276* (MO); S of El Real, *Duke 5047* (MO); El Real on Río Pirre, ca 10 mi S, *Duke 5445* (MO); s. loc., *Duke 8345* (MO); cuipo forest nr Sante Fe, *Duke 12264* (MO); forested ridge parallel to Río Sancanti, ca 2 mi upstream from Piria, alt ca 120 m, *Duke 14386* (MO); Puerto St Dorotea, *Dwyer 2298* (MO); vic of Campamento Buena Vista, Río Chucunaque & Río Tuquesa, *Stern et al. 931* (MO). PANAMA: Río Bayano above confluence with Río Chepo, *Duke 3991* (MO). SAN BLAS: headwaters of Río Mulatupo, *Elias 1773* (MO).

The numerous collections cited above permit us to describe this important species. The twisted pyrenes and pilose anthers immediately segregate this species from *Psychotria* and *Cephaelis.* The axillary inflorescences are striking and are suggestive of those of *Hoffmannia.* The roots have a strong and somewhat nauseous odor and are the source of the drug ipecacuanha, but it is said to be inferior to *Cephaelis ipecacuanha.* According to Duke's field notes the plant is known as "raicillo macho" in Spanish and as "macua" or "moncoa" among the Choco Indians (Darien, Panama & Colombia).

We are placing this species in *Uragoga* with some reluctance as the limits of *Uragoga* are not well-defined.

NOTES ON ASCLEPIADACEAE OF PANAMA

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ABSTRACT

Three new species of *Asclepiadaceae* are described: *Cynanchum infimicola, Gonolobus inaequalis* and *G. lewisii.*

The center of diversity of the *Asclepiadaceae* in North America is in Mexico with the greatest concentration of species in Chiapas and in adjacent Guatemala. The number of asclepiads diminishes rapidly as one proceeds southward from this center. There are a fair number of species known in Costa Rica and Panama. Certainly there are more to be expected as botanical exploration continues, especially in Panama. It would not be surprising if the number now known, 29 native species and one introduced, were doubled in the course of time.

The *Asclepiadaceae* are considered a difficult family and often, I suspect, avoided in the field as well as in the herbarium. It is a fascinating group of plants very much in need of a friend.

Cynanchum **infimicola** L. Wms., sp. nov.

Lianae parvae, herbaceae. *Folia* lanceolata vel angusti-ovata, acuminata, glabra. *Inflorescentia* umbelliformis, pauci- ad multiflora. *Flores* pedunculis gracilibus; lobi calycis elliptici vel lanceolati, acuti; corolla campanulata, lobis lanceolatis acutis intus barbellato-puberulentibus; lobi coronae filiformes; gynostegium stipitatum. *Folliculi* ignoti.

Small herbaceous *vines*, the stems twining, sparsely crisped-pubescent in lines, mostly less than 1 mm in diam, with 1 or more dactyliform glands on the interpetiolar scar. *Leaves* lanceolate to narrowly ovate, acuminate, with ca 7 pairs of lateral nerves, glabrous or nearly so; mature blades 1.5-4.5 cm long and 0.8-2 cm broad; petioles slender, crisped-pubescent, 3-9 mm long. *Inflorescences* umbelliform, few to many-flowered, axillary or nearly so, the peduncles slender, crisped-pubescent, mostly 6-10 mm long, the pedicels 2 mm or less long. *Flowers* white, ca 2-5 mm long; calyx lobed to the base, lobes elliptic to lanceolate, acute, sparsely puberulent to glabrous, ca 0.7 mm long; corolla campanulate, ca 2.5 mm long; lobes twice as long as the tube, lanceolate, acute, slightly spreading at anthesis, barbellate-puberulent along the margins within; corona ca as long as the gynostegium, the lobes filiform, as long as and attached near the base of gynostegium; gynostegium stipitate, ca 2.5 mm long. *Follicles* unknown.

CANAL ZONE: K-2 rd, *Dwyer & Hayden 7540* (holotype F; isotype MO). COCLÉ: rd to El Cope ca 7 mi from Interamerican Hwy, *Correa 403* (MO). PANAMA: Río Mar, along rd to beach, *Blum & Dwyer 2485* (MO); nr beach at Nueva Gorgona, 8 Oct 1961, *Duke 4491* (F, MO); Isla Taboga, alt 0-186 m, 23-24 July 1938, *Woodson et al. 1499* (MO).

This is unusual among the species of sect. *Metastelma* in that it is a lowland species, occurring not far from the Pacific Ocean; most other species grow in the mountains. The specific name is derived from this fact. The species is allied to

ANN. MISSOURI BOT. GARD. **55**(1): 48-50, 1968.

Cynanchum sepicola (Pittier) L. Wms. from which it is easily distinguished by the filiform corona lobes attached near the base of the gynostegium instead of lobes nearly as broad as long attached near the apex of the gynostegium.

Gonolobus **inaequalis** L. Wms., sp. nov.

Liana herbacea, sparse hirsuta vel glabra. *Folia* ovata vel oblongo-ovata, cordata, acuminata, sparse hirsuta vel glabrescentia, petiolis gracilibus. *Inflorescentia* axillaris vel extra-axillaris, subracemosa. *Flores* calyce usque ad basim diviso, lobis lineari-oblongis vel lanceolatis acutis vel obtusis; corolla rotata, profunde lobata, tubo perbrevi, lobis inaequalibus, 3 lobis lineari-oblongis, 2 lobis lanceolate-ovatis, annulo subnullo; corona carnosa, 5-lobata et undulata; appendices antherarum lobo suborbiculari munitae.

Herbaceous *vines,* sparsely hirsute or glabrous, internodes 6-12 cm long. *Leaves* ovate or oblong-ovate, cordate, acuminate, glabrous or very sparsely hirsute and glabrescent, the blade 5-11 cm long and 2-5 cm broad, the petioles slender, obscurely hirsute, shorter than the blade, 3-6 cm long. *Inflorescence* axillary or extra-axillary, subracemose, 1-4-flowered, the peduncles hirsute, 1-2 cm long, the pedicels slender, to 4 cm long. *Flowers* with the calyx divided to near the base, glabrous, lobes linear-oblong to lanceolate, acute or obtuse, ca 5 mm long and 2 mm broad; corolla rotate, the tube short and inconspicuous, deeply lobate, ca 3.5 cm across, the lobes inequal, 2 smaller than other 3, 3 lobes linear-oblong, acute or acuminate, 15-17 mm long and ca 5 mm broad, 2 lobes lance-ovate, acute, ca 11-13 mm long and 5 mm broad; annulus of corolla very obscure; gynostegium ca 3 mm high, corona fleshly, 5-lobate and undulate, ca 1 mm high; dorsal appendage of the anther with a central suborbicular lobe ca 1 mm long. *Follicles* unknown.

The specimens have all been determined as *G. dubius* Pittier but R. E. Woodson, Jr. had indicated some of the differences on the type sheet. The specimens available show the unusual inequality in size of the corolla lobes which would seem to be a tendency toward zygomorphy.

CANAL ZONE: vic of Madden Dam, alt 90 m, 8 Oct 1939, *Allen 2012* (MO); Palo Seco, 17 Nov 1940, *Allen 2249* (MO). PANAMA: vic of Pacora, alt ca 35 m, 5 Nov 1939, *Allen 2031* (holotype MO, isotype F).

Gonolobus **lewisii** L. Wms., sp. nov.

Lianae herbaceae vel suffruticosae. *Folia* ovata vel oblongo-ovata, acuminata, cordata, utrinque strigosa. *Inflorescentia* subumbellata vel subracemosa, pauciflora. *Flores* calyce sparse strigoso, lobis lanceolatis acutis vel acuminatis; corolla rotata, praeter annulum ciliatum glabra, lobis ovato-lanceolatis acutis; corona erecta, carnosa; stigma stellatum; appendices antherarum rotundatae cum utrinque processo auriculiformi vel lunato.

Herbaceous or possibly suffrutescent *vines,* the stems slender and sparsely crisped-pubescent. *Leaves* ovate to oblong-ovate, acuminate, cordate to the base, strigose-pubescent on both surfaces, with 4-6 pairs of secondary veins; blade 4.5-7.5 cm long and 2.5-4 cm broad; petiole slender, sparsely strigose, 1.5-3.5 cm long. *Inflorescence* subumbellate or subracemose, few-flowered, shorter than the leaves, the peduncles extra-axillary ⅓ as large as the stem, 2-3 cm long, the pedicels to ca 2 cm long. *Flowers* with the calyx sparsely strigose, divided to near the base, the lobes lanceolate, acute or acuminate, ca 5 mm long and 2 mm broad; corolla green, rotate, glabrous (except annulus), 2.5-3 cm across, lobed to near the center, the lobes ovate-lanceolate, acute, ca 10 mm long and 5 mm broad, the annulus (outer corona) inconspicuous, barbellate-ciliate; corona erect, fleshy, "scalloped," ca 0.5 mm high; anther appendages rounded with a lateral auriculiform or lunate process on either side; gynostegium ca 2 mm high and 5 mm broad, the stigma stelliform. *Fruits unknown.*

Species of the subg. *Gonolobus* are an interesting lot often quite easily distinguished by characters in the gynostegium. This is the only one I know with lateral processes on the dorsal appendages of the anthers. Vegetatively it is like a dozen others but the umbelliform inflorescence is less compact than in other Panamanian species.

LOS SANTOS: cloud forest & disturbed margins, Loma Prieta, Cerro Grande, alt 2400-2800 ft, 8 June 1967, *Lewis, Baker, MacBryde & Oliver 2248* (holotype F; isotype MO).

BOMBACACEAE NEOTROPICAE NOVAE II. NEW SPECIES OF ERIOTHECA, HAMPEA AND QUARARIBEA

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ABSTRACT

Seven species from the neotropics are described as new to the *Bombacaceae*: *Eriotheca peruviana* (Peru), *Hampea dukei* (Panama), *H. micrantha* (Panama), *Quararibea bilobata* (Peru), *Q. longitubulosa* (Peru), *Q. sanblasensis* (Panama), and *Q. wurdackii* (Peru). In addition, a key to the Panamanian species of the genus *Hampea* is given.

Eriotheca **peruviana** A. Robyns, sp. nov. [subg. *Millea* (Standley) A. Robyns]; a *E. discolori* (H.B.K.) A. Robyns (Bull. Jard. Bot. État Brux **33**: 159, 1963) et *E. ruizii* (K. Schum.) A. Robyns (loc. cit. 162) floribus longioribus et 3.2-4 cm longis, staminibus numerosioribus et 75-80 primo visu sat distincta; etiam *E. vargasii* (Cuatr.) A. Robyns (loc. cit. 165) affinis, sed floribus leviter longioribus pedicello dense minuteque stellato-puberulo, receptaculo calyceque extus minute stellato-tomentello, staminibus tantum 75-80 valde differt.—Fig. 1.

Arbor (?), decidua, ramulis teretibus minute puberulis sed glabrescentibus. *Folia* alterna, digitata, 5-foliolata; petiolus teres, basi leviter dilatato-complanatus apiceque leviter dilatato-subglobosus, usque ad 13 cm longus, sparsissime pilosus pilisque simplicibus, foliola articulata, sessilia; lamina elliptica ad subobovata, basi cuneiformis, apice acuta ad breviter acuminata inconspicueque mucronata, usque ad 10.7 cm longa et 4.5 cm lata, membranaceo-chartacea, marginibus serrulatis, leviter discolor, supra glabra laevisque (ad scabridula et stellato-puberula?), subtus pallidiora et dense scabridulo-stellato-arachnoidea, nervo mediano infra prominenti, nervis lateralibus infra vix prominulis. *Inflorescentiae* praecoces, cymoso-paniculiformes, laxiflorae, axibus pedicellisque dense minuteque stellato-puberulis. *Flores* usque ad 4 cm longi; pedicellus usque ad 8 mm longus, 3-bracteolatus bracteolisque caducis; receptaculum 1.5-2 mm longum, minute stellato-tomentellum, pauciglandulosum; calyx cupuliformis, apice truncatus vel vix sublobatus, 3.5-5 mm longus et apice ca 5 mm diam, extus minute stellato-tomentellus, intus basi longe sericeo-villosus apiceque breviter adpresseque sericeus, persistens; petala oblongo-linearia, basi tubi staminei adnata, 3.2-4 cm longa et 4-5 mm lata, utrinque praeter basin glabram velutina; stamina 75-80, glabra; tubus stamineus cylindricus, 6.5-7 mm longus, in medio 2-2.3 mm diam, basi leviter dilatatus, apice disciformi-dilatatus discoque 3.5 mm diam 5-undulato et sulcato; filamenta in disci sulco inserta, erecta, filiformia, inaequalia, 1.5-2.3 cm longa, apice dilatata; antherae oblongae, horizontales, extrorsae, ca 0.8-1.5 mm longae, uniloculares, longitudinaliter dehiscentes; ovarium sessile, plus minusve piriforme, ca 2.5 mm longum et basi 2 mm latum, tomentellum, 5-loculare, ovulis ∞ in columella centrali affixis, stylo filiformi usque ad 2.5 cm longo praeter basin stellato-puberulam glabro, stigmate truncato (vel inconspicue 5-undulato?). *Capsula* ut videtur

ANN. MISSOURI BOT. GARD. **55**(1): 51-59, 1968.

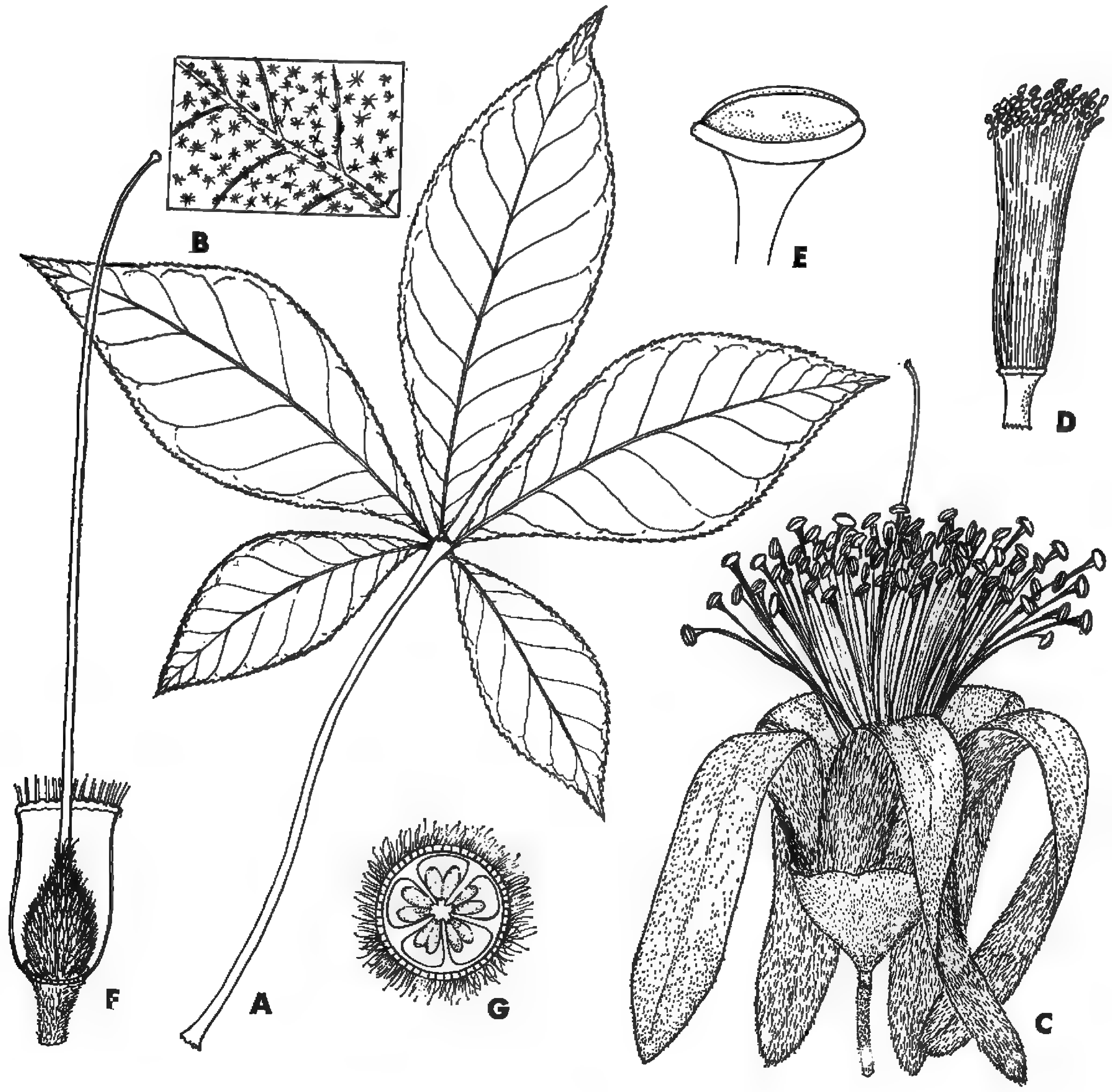

Fig. 1. *Eriotheca peruviana* A. Robyns: A, leaf (×½); B, indumentum of lower leaf-surface (much enlarged); C, flower (×2); D, androecium (×1½); E, anther (×15); F, gynoecium (×3); G, ovary, cross-section (×13). After *Hutchinson et al. 6228.*

obovoidea, apice breviter apiculata, valvis ochraceis induratis extus stellato-puberulis pilisque hyalinis; semina late ovoidea, ca 4 mm longa et 3.5 mm lata, testa fusca minuteque punctata; lana copiosa ferrugineaque.

Peru. la libertad: Prov Pataz, Canyon of the Río Marañon, E side of river on rd to Buldibuyo, 5 km above Chagual, alt 1300 m, 9 Aug 1964, *Hutchinson, Wright & Straw* 6228 (holotype UC, isotype US).

As the type collection is leafless, the description of the leaves was made from cultivated plants originating from the seeds of the type collection (Honolulu Botanical Garden, cultivation number 65.1166, pressed by Hutchinson in July 1967 and deposited at UC under the type collection number).

Hampea **dukei** A. Robyns, sp. nov.; *H. punctulatae* Cuatr. (Phytologia **4**: 472, 1954) affinis, sed floribus hermaphroditis multo minoribus et usque ad 14 mm longis valde distincta.

Arbor trunco 15 cm diam, ramulis novellis dense et minute granuloso-tomentellis pilisque ochraceis et stellatis sed glabrescentibus. *Folia* alterna, simplicia, longe petiolata petioloque tereti usque ad 14 cm longo stellato-tomentello ad stellato-puberulo; lamina latissime ovata, basi aperte cordata ad late rotundata, apice breviter acuminata, usque ad 15 cm longa et lata, tenuiter chartacea, marginibus integris, discolor, atro-punctulata, supra praecipue secus nervos minute stellato-puberula glabrescensque, infra pallidiora et stellato-tomentella, e basi distincte 5-7-nervia, nervis principalibus supra prominulis infraque valde prominentibus. *Flores* axillares, paucifasciculati fasciculisque usque ad 4-floris, hermaphroditi, pedicellis longitudinaliter striatis usque ad 15 mm longis dense et minute granuloso-tomentellis pilisque ochraceis et stellatis; bracteolae non visae; calyx campanulato-cupuliformis, usque ad 6 mm longus, apice 5-lobatus lobisque transverse anguste triangularibus et vix 1 mm longis, extus minute denseque ochraceo-stellato-tomentellus, intus glaber et atro-punctatus; petala 5, usque ad 14 mm longa, tubo ventricoso ca 6 mm longo glabroque, lobis albis contortis inaequilateralibus obovatis leviter cucullatis extus dense minuteque stellato-tomentellis intusque glabris et atro-punctatis; tubus stamineus usque ad 3 mm longus, dense barbatus, filamentis usque ad 2.5 mm longis glabrisque, antheris hippocrepiformibus; ovarium late oblongum, usque ad 3 mm longum, breviter villosum, 3-loculare loculisque pauci-ovulatis, stylo filiformi apicem versus sensim dilatato usque ad 12 mm longo apice declinato parte inferiore glabro parteque superiore papillato. *Fructus* nondum visus.

PANAMA. SAN BLAS: Río Chucunaque, 2-10 mi above the Cuna-Darien boundary, 21 Aug 1966, *Duke 8554* (holotype MO).

Hampea **micrantha** A. Robyns sp. nov.; ab ominibus speciebus generis *Hampeae* Schlecht. floribus masculinis brevissime pedicellatis parvibusque facile distincta.

Frutex vel arbuscula 2-4 m altus, ramulis conspicue fusco-punctatis, novellis stellato-puberulis sed glabrescentibus. *Folia* alterna, simplicia, longe petiolata petioloque tereti 3.5-12.5 cm longo conspicue fusco-punctato stellato-puberulo glabrescentique, stipulis subulatis usque ad 7 mm longis stellato-puberulis caducisque; lamina aequilateralis ad interdum inaequilateralis, ovata, basi rotundata ad late obtusa, apice acuminata acumineque obtuso, 10-25 cm longa et 4.5-12 cm lata, tenuiter ad rigide chartacea, conspicue fusco- ad atro-punctata, marginibus integris ad leviter sinuatis, supra glabra, infra praecipue secus nervos stellato-puberula glabrescensque, e basi distincte 3(-5)-nervia, costa supra elevata et infra valde elevata basique glandulo elongato ornata, nervis secundariis supra prominulis infraque prominentibus ad prominulis. *Flores* axillares, paucifasciculati fasciculisque usque ad 4-floris, unisexuales. *Flores masculini* ca 10 mm longi, breviter pedicellati pedicelloque crasso usque ad 3 mm longo minute stellato-tomentello; braeteolae 3, calycis basi insertae, anguste oblongo-ovatae, usque ad 2.5 mm longae, minute stellato-tomentellae; calyx cupuliformis, apice truncatus et breviter 5-denticulatus, ca 4.5 mm longus et apice 4 mm diam, fusco-punctatus, extus minute stellato-tomentellus, intus glaber; petala 5, tubo obconico farcto ca 2.5 mm longo glabroque, lobis contortis inaequilateralibus obovatis 7.5 mm longis et 4 mm latis conspicue fusco-punctatis extus praeter partem glabram petalum vicinum tegentem minute stellato-tomentellis intusque glabris; tubus stamineus anguste conicus, farctus, apice breviter 5-lobulatus, usque ad 4 mm longus, glaber, parte dimidia superiore filamenta ferens filamentisque brevissimis et vix 1 mm longis glabrisque, antheris ca 45 1-2 in quoque filamento hippocrepiformibus; pistillum nullum. *Flores foeminei* non visi. *Capsula* calyce persistenti circumcincta, distincte stipitata, late obovoidea, apice emarginata et minute mucronulata, usque ad 1.5 cm longa, coriacea, extus minute fusco-tomentella, in valvis 3 intus glabris loculicida; semina 1-2 in quoque loculo, usque ad 8 mm longa, testa nigro-fusca cum venulis pallidioribus, arillata.

PANAMA. PANAMA: betw Cerro Jefe & "School House," NE of Cerro Azul, forest, thicket at edge of road, *Dressler* 3227 (staminate flowers, holotype MO); betw Cerro Jefe & La Eneida, by rd, 16 Febr 1968, *Dressler* 3383 (capsules, MO).

Only one species of *Hampea* [*H. appendiculata* (J. D. Sm.) Standley] was reported in my revision of the *Bombacaceae* for the Flora of Panama (Ann. Missouri Bot. Gard. **51**: 62, 1964). A key which permits separation of the three species now reported from Panama follows:

a. Leaf blades auriculate-appendaged at the base; flowers 16-18 mm long .... *H. appendiculata*
aa. Leaf blades without auriculate appendages at the base; flowers up to 14 mm long.
  b. Leaf blades very broadly ovate, shallowly cordate to broadly rounded at the base, short-acuminate at the apex, stellate-tomentellous beneath; flowers to 14 mm long; pedicel to 15 mm long; staminal tube densely barbate, indument ochraceous .... *H. dukei*
  bb. Leaf blades ovate, rounded to broadly obtuse at the base, acuminate at the apex, stellate-puberulous especially along the veins to glabrescent beneath; flowers to 10 mm long; pedicel to 3 mm long; staminal tube glabrous; indument not ochraceous .... *H. micrantha*

Quararibea **bilobata** A. Robyns, sp. nov.—Fig. 2

Arbor 10 m alta, ramulis novellis breviter stellato-ferrugineo-tomentellis sed glabrescentibus. *Folia* alterna, simplicia, breviter petiolata petioloque crasso 0.8-1 cm longo breviter stellato-ferrugineo-tomentello sed glabrescenti, stipulis deltoideis ca 0.3-0.6 mm longis persistentibusque; lamina leviter asymmetrica, elliptica ad subobovata, basi subrotundata vel obtusa acutave, apice obtusa, 12-25 cm longa et 5.5-11 cm lata, tenuiter chartacea, utrinque sordida, supra sparse stellato-puberula glabrescensque, infra stellato-pubescens, basi conspicue triplinervia, nervatura supra manifesta sed non prominula, costa nervisque secundariis subtus prominentibus, nervulis venulisque subtus reticulum prominulum formantibus. *Flores* solitarii, oppositifolii (?) vel ramis brevibus inserti; pedicellus brevis, usque ad 1 cm longus sed vulgo brevior, breviter stellato-ferrugineo-tomentellus, bracteolis deltoideis ca 1.5 mm longis nigricantibus persistentibusque; alabastra claviformia; calyx campanulatus, longitudinaliter et conspicue nervatus nervisque prominentibus, usque ad 2 cm longus, extus scaber et dense breviterque stellato-ferrugineo-tomentellus, intus dense sericeus, apice 3-lobatus lobisque inaequalibus obtusis usque ad 6 mm longis; petala 5, alba, anguste obovata, apice rotundata, usque ad 4.5-5 cm longa et 1.5 cm lata, membranacea, utrinque praeter basin stellato-tomentella ad stellato-

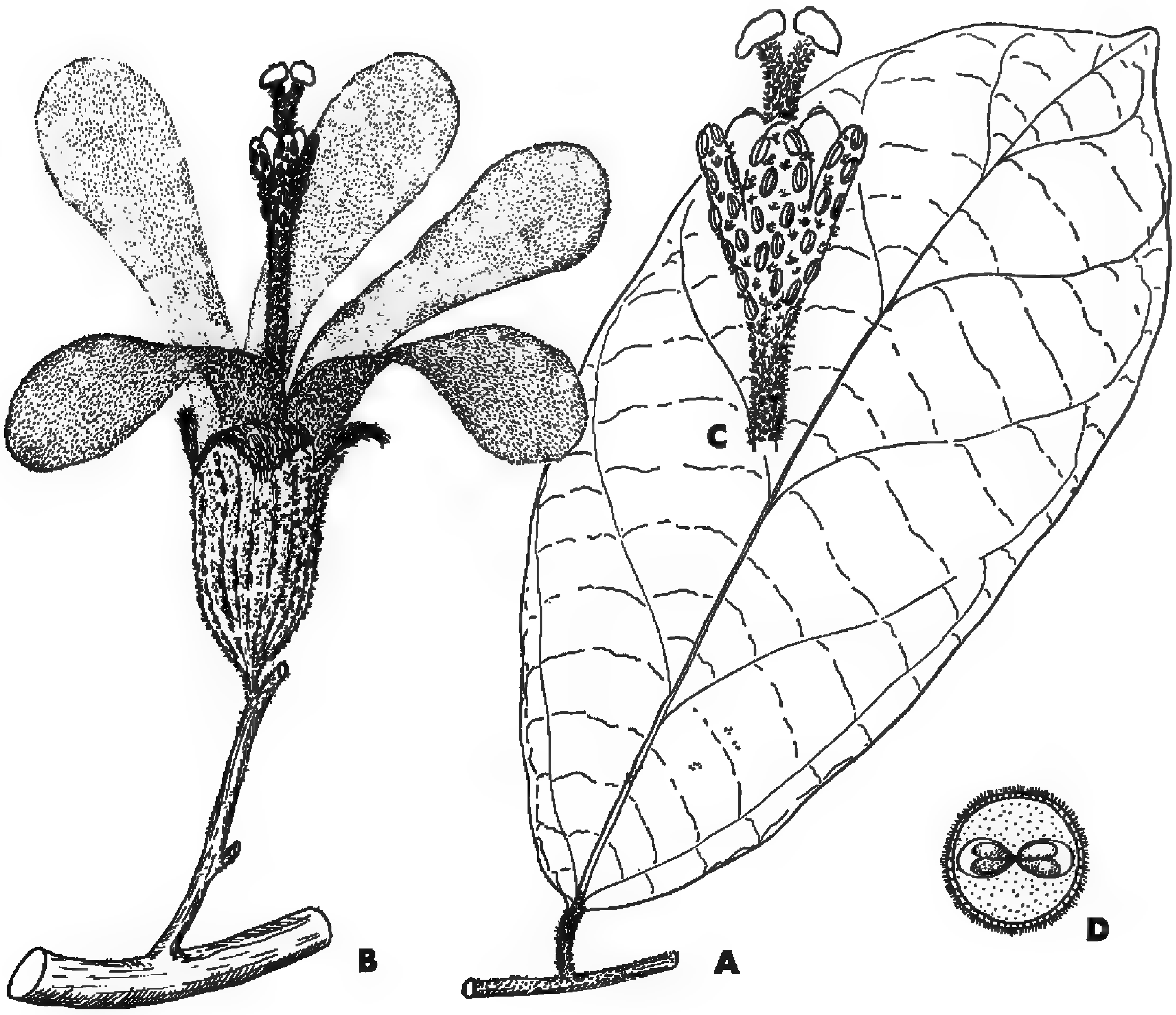

Fig. 2. *Quararibea bilobata* A. Robyns: A, leaf (×½); B, flower (×1); C, upper part of staminal tube with anthers, and upper part of style with stigmas (×2); ovary, cross-section (×6). After *Wurdack 2450.*

puberula; androecium inclusum, 3-3.7 cm longum, tubo cylindrico apice breviter 5-lobato lobisque rotundatis 2-4 mm longis praeter basin stellato-albido-arachnoideo, antheris sessilibus tubi apice et lobis insertis ca 1.5-2 mm longis; ovarium conicum, adpresse stellato-tomentellum, 2-loculare loculisque 2-ovulatis, stylo androecio longiore 3.5-4.5 cm longo stellato-arachnoideo-tomentello apicem versus dilatato et manifeste bilobato, stigmatibus flabelliformibus usque ad 4.5-5 mm latis. *Fructus* ignotus.

PERU. LORETO: Prov Alto Amazonas, rainforest at upper end of Pongo de Manseriche, Río Marañón, alt 250 m, 26-28 Oct 1962, *Wurdack 2450* (holotype UC, isotype US).

Quararibea bilobata is close to *Q. amazonica* Ulbr. (Verh. Bot. Ver. Prov. Brandenburg **50:** 91, 1909) from the State of Amazonas in Brazil (type *Ule 37b,* probably destroyed in Berlin; photo Field Museum of Natural History 9552 at MO). These species can be separated as follows:

a. Young branchlets and petioles shortly stellate-ferruginous-tomentellous; leaf blades sparsely stellate-puberulous to glabrescent above, stellate pubescent beneath; flowers 4.5-5 cm long; bracteoles deltoid, ca 1.5 mm long; calyx densely and shortly stellate-ferruginous-tomentellous outside; staminal column 5-lobate, the lobes 2-4 mm long .... *Q. bilobata* aa. Young branchlets reddish and glabrous; leaves glabrous except for a few stellate hairs along the veins on the lower surface; flowers 3.5-3.7 cm long; bracteoles subulate to lanceolate-subulate; calyx lepidote outside; staminal column dentate at the apex, the teeth 0.75-1 mm long ....*Q. amazonica*

Quararibea **longitubulosa** A. Robyns, sp. nov.—Fig. 3.

Arbor 25-35 m alta, ramulis teretibus dense minuteque stellato-puberulis sed glabrescentibus. *Folia* alterna ad subopposita, simplicia, petiolata petioloque tereti 2.5-13 cm longo basi apiceque parum dilatato et dense minuteque stellato-puberulo, stipulis lineari-ovatis acutis obtusisve usque ad 19 mm longis et 4 mm latis stellato-tomentellis mox deciduis; lamina parum asymmetrica, elliptica ad late elliptica, interdum leviter obovata, basi cordata, apice obtusa ad breviter obtuseque acuminata, 10-30 cm longa et 5.5-19 cm lata, chartacea, leviter discolor, praecipue supra subnitida, utrinque sed praecipue secus venas sparse minuteque stellato-puberula, basi 7-9-nervia, nervatura supra prominula, costa nervisque secundariis subtus prominentibus, nervulis venulisque subtus reticulum prominulum formantibus. *Flores* ramiflori et cauliflori, paucifasciculati, pedicello apicem versus

Fig. 3. *Quararibea longitubulosa* A. Robyns: A, leaf (×½); B, inflorescence and flower (×1); C, detail of a lobe of the staminal column with 2 anthers (×6); D, ovary, cross-section (×7). After *Wurdack 2102*.

sensim dilatato usque ad 2.5 cm longo minute stellato-tomentello, bracteolis prope pedicelli basin insertis caducisque; alabastra claviformia; calyx infundibuliformis, ca 2 cm longus, apice 3-lobatus lobisque inaequalibus rotundatis usque ad 8 mm longis, extus minute stellato-tomentellus, intus dense sericeus; petala 5, alba, anguste obovata, apice asymmetrica, ca 3.5 cm longa et 9 mm lata, membranacea, extus dense stellato-tomentella, intus villosa; androecium longe exsertum, tubo stamineo cylindrico saltem in sicco obtusiuscule 5-subangulato basi leviter dilatato usque ad 5.5 cm longo (lobis exclusis) stellato-tomentello indumentoque interdum apicem versus paucis pilis glandulosis longioribusque intersperso apice in 5 lobos antheriferos producto, lobis linearibus carnosis usque ad 2 cm longis stellato-puberulis et sparse glanduloso-pilosis, antheris ca 12-18 in quoque lobo sessilibus oblongis et ca 2-3 mm longis; ovarium conicum, 5-obtuso-angulatum, stellato-tomentellum, 5-loculare loculisque 2-ovulatis, stylo androecio parum breviore dense stellato-tomentello apice parum dilatato curvato et breviter 5-lobato. *Fructus* ignotus.

PERU. LORETO: Prov Alto Amazonas, high rainforest along Río Marañón nr Teniente Pinglo, just above Pongo de Manseriche, alt 250-300 m, occasional, 4-7 Oct 1962, *Wurdack 2102* (holotype US, isotypes F, UC).

Quararibea **sanblasensis** A. Robyns, sp. nov.; ab affini *Q. leptandra* Cuatr. (Lloydia **11:** 185, 1948) foliorum lamina angustiore basi obtusa ad subrotunda et membranaceo-chartacea, pedicello 6-8 cm longo, bracteolis longe persistentibus primo visu sat recedit.—Fig. 4.

Arbor mediocris et 10-20 m alta, ramulis novellis stellato-puberulis. *Folia* alterna, petiolo robusto tereti usque ad 2.4 cm longo et stellato-puberulo; lamina plus minusve inaequilateralis, anguste oblongo-elliptica ad anguste elliptica subobovatave, basi obtusa ad subrotundata, apice plus minusve longe acuminata acumineque minute mucronulato, 12-40 cm longa et 4-11.5 cm lata, membranaceo-chartacea, marginibus integris ad leviter sinuatis, utrinque minute puberula, e basi manifeste 3-5 nervia, costa nervisque secundariis subtus prominulis infraque valde prominentibus, nervis tertiis plus minusve transversis cum venulis in reticulum prominulum anastomosantibus. *Flores* oppositifolii, solitarii, longe pedicellati pedicelloque tereti 6-8 cm longo stellato-puberulo, bracteolis 3 pedicelli apicem versus insertis plus minusve distantibus inaequilateralibus subulato-deltoideis ad anguste deltoideis usque ad 15 mm longis et basi 3.5 mm latis utrinque minute puberulis longe persistentibusque; calyx tubulosus, usque ad 18 mm longus et 8 mm diam, apice 3(-5)-lobatus lobisque inaequalibus usque ad 4 mm longis, in vivo viridis, extus dense minuteque puberulus, intus dense sericeus, accrescens; petala ut androecium nondum visa; ovarium 5-loculare loculisque biovulatis. *Capsula* calyce accrescenti late campanulato et usque ad 2 cm diam circumcincta, drupacea, ovoidea, apice truncato-mamillato et minute apiculato, usque ad 3 cm longa et 1.5 cm diam, in vivo viridis, in sicco fulva, lepidato-stellato-tomentella, fibroso-lignosa, 5-locularis loculisque ut videtur uniseminalibus.

PANAMA. SAN BLAS: headwaters of Río Cuadí, Camp Diablo (Drill Site 22, N 82.2, E 87.8, alt 273.4 ft, seasonal evergreen forest along river, 18 Dec 1967, *Duke, Robyns & Verhoek 3634* (holotype MO); plain of Sperdi, nr Puerto Obaldía, nr sea level, *Pittier 4353* (US).

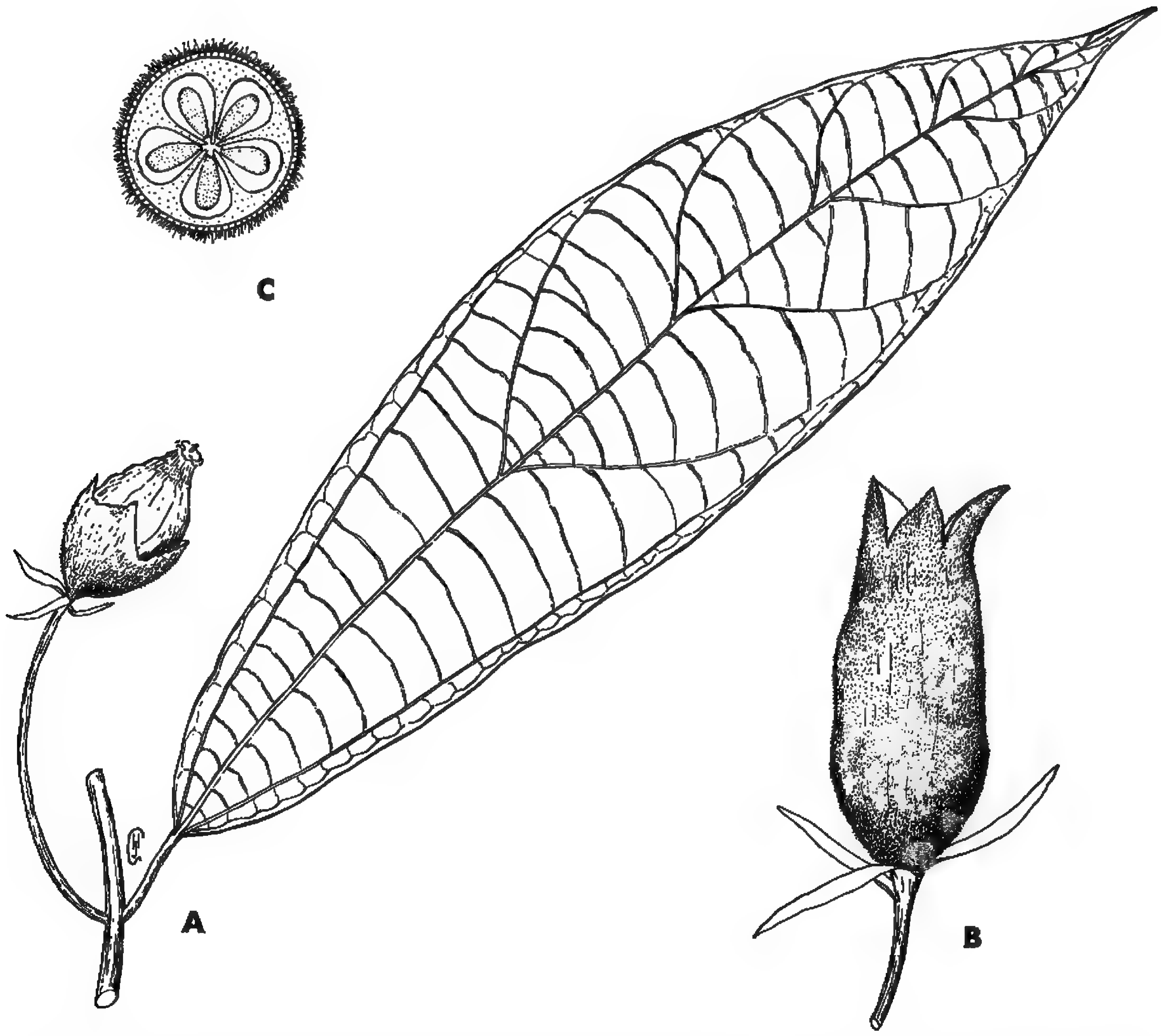

Fig. 4. *Quararibea sanblasensis* A. Robyns: A, leaf and capsule (×½); B. bracteoles and calyx (×2); C, capsule, cross-section (×1). After *Duke et al.* 3634.

Quararibea sanblasensis can readily be distinguished from the other seven species of *Quararibea* occuring in Panama (cf. A. Robyns, Ann. Missouri Bot. Gard. **51**: 54-62, 1964 & **54**: 185-186, 1967) by a combination of the following characters: leaf blades ± inequilateral, distinctly 3-5-nerved from the base; flowers oppositifolious; pedicels elongated, 6-8 cm long; bracteoles 3, inserted towards the apex of the pedicel, ± distant, to 15 mm long, persistent; calyx tubular, to 18 mm long and 8 mm in diam, wingless, broadly campanulate and up to 2 cm in diam when surrounding the fruit; ovary 5-locular, each locule 2-ovulate; capsule ovoid, truncate-mamillate and minutely apiculate at the apex, to 3 cm long and 1.5 cm in diam.

Quararibea **wurdackii** A. Robyns, sp. nov.

Arbor 6-8 m alta, ramulis novellis fusco-stellato-tomentellis sed mox glabrescentibus. *Folia* alterna, simplicia, petiolo tereti apice leviter pulvinato 2.7-5 cm longo praecipue apicem versus fusco-stellato-tomentello, stipulis caducis; lamina anguste elliptica ad elliptica vel subobovata, interdum asymmetrica, basi obtusa ad rotundata, apice acuminata, 17-35 cm longa et 6-14 cm lata, tenuiter chartacea, subtus glabra, infra secus costae partem inferiorem stellato-puberula, basi conspicue 3(-5)-nervia, costa nervisque secundariis subtus prominentibus, nervulis venulisque subtus reticulum prominulum formantibus. *Flores* axillares, ramis brevibus inserti, longe pedicellati pedicelloque tereti gracili usque ad 7 cm longo minute stellato-puberulo ad stellato-tomentello, bracteolis 3 pedicelli parte superiore insertis lineari-subulatis usque ad 16 mm longis et ca 1 mm latis stellato-tomentellis caducisque; calyx tubuliformi-campanulatus, apice 3-4-lobatus, usque ad 2.3 cm longus, extus minute fusco-stellato-tomentellus, intus sericeus, lobis inaequalibus acutis et usque ad 5 mm longis; petala eburnea, asymmetrica, anguste obovata, apice rotundata, usque ad 3.5 cm longa et 7-8.5 mm lata, membranacea, extus praeter basin stellato-puberula indumentoque parte superiore pilis glandulosis intermixto, intus fere glabra, marginibus glanduloso-ciliolatis; androecium longe exsertum, tubo cylindrico saltem in sicco leviter sigmoideo usque ad 6 mm longo, antheris in quoque lobo 6 biseriatis sessilibus oblongis inaequalibus usque ad 3 mm longis; ovarium depresse conicum minute stellato-tomentellum 5-loculare loculisque 2-ovulatis, stylo androecium aequanti vel androecio leviter breviore apice ut videtur obscure 5-lobulato. *Fructus* ignotus.

PERU: LORETO: Prov Alto Amazonas, high rainforest along Río Marañón nr Teniente Pinglo, just above Pongo de Manseriche, alt 250-300 m, 4-7 Oct 1962, *Wurdack 2129* (holotype US, isotype F).

NEW SPECIES OF LISIANTHUS (GENTIANACEAE) FROM PANAMA

BY ANDRÉ ROBYNS AND THOMAS S. ELIAS

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ABSTRACT

Two species of *Lisianthus* L. from Panama are described as new: *L. jefensis* and *L. scopulinus.*

Study of collections of *Lisianthus* L. from hitherto uncollected areas in Panama, viz. Cerro Jefe in the Province of Panama and the mouth of Río Concepción in the Province of Veraguas, yielded the following two new species: *L. jefensis* and *L. scopulinus.* During the December 1967 Missouri Botanical Garden's expedition to Panama under the direction of Walter H. Lewis (in which the senior author took part), collecting along the mouth of Río Concepción and in other inaccessible areas was made possible through a grant from the U.S. Air Force Office of Scientific Research (Grant No. F44620-67-C-0055). This included transportation by helicopter from Albrook Air Force Base in the Canal Zone to sites in the Provinces of Colón, Darien, Los Santos, Panama, Veraguas, and in the Comarca de San Blas.

Lisianthus **jefensis** A. Robyns & Elias, sp. nov.; a *L. seemannii* (Griseb.) O. Ktze. foliorum lamina subcoriacea, inflorescentiis laxis paucíflorisque, pedicellis 1-2.5 cm longis, floribus leviter minoribus, calycis tubo longiore, corolla tubulosa lobisque valde minoribus et tantum 4-5.5 mm longis, antheris ca duplo longioribus valde distinctus; a *L. scopulino* A. Robyns et Elias foliorum lamina subcoriacea, dichasiis simplicibus vel interdum compositis sed paucifloris, floribus minoribus, calycis tubo longiore, corollae lobis multo longioribus et 4-5.5 cm longis, antheris majoribus et ca 3.5-4 mm longis primo visu sat differt.—Fig. 1.

Herba vel frutex 1.2-2.4 m altus, omnino glaber, caulibus viridibus teretibus sed apicem versus subangulatis. *Folia* opposita, decussata, petiolata petiolisque amplexicaulibus; lamina anguste obovata ad ovata, basi in petiolum longe attenuata decurrensque, apice acuminata, usque ad 12 cm longa et 4 cm lata, subcoriacea, costa subtus prominenti, nervis lateralibus utroque latere 2-3 arcuatis subtus vix conspicuis ad inconspicuis. *Inflorescentiae* terminales et axillares, laxae, dichasiales, dichasiis simplicibus vel interdum compositis sed paucifloris, pedunculis usque ad 4.5 cm longis, pedicellis 1-2.5 cm longis, bracteis oppositis et 2-5 mm longis. *Flores* 2.8-3.2 cm longi, 5-meri; calyx tubulosus, 7-9.5 mm longus, lobis anguste ovatis dorsaliter leviter carinatis apice longe acuminatis 4-6.5 mm longis et ca 2-2.5 mm latis secus margines plus minusve scariosis; corolla vivide flava cum lobis viridi-flavis, 2.8-3.2 cm longa, tubulosa, parte $\frac{1}{3}$ inferiore constricta, lobis erectis triangularibus apice acuminatis 4-5.5 mm longis et ca 3 mm latis; stamina plus minusve corollam aequantia vel manifeste exserta, filamentis tubo corollae ca $\frac{1}{3}$ supra basin insertis filiformibus et 19-24 mm longis, anthersis introrsis versatilibus

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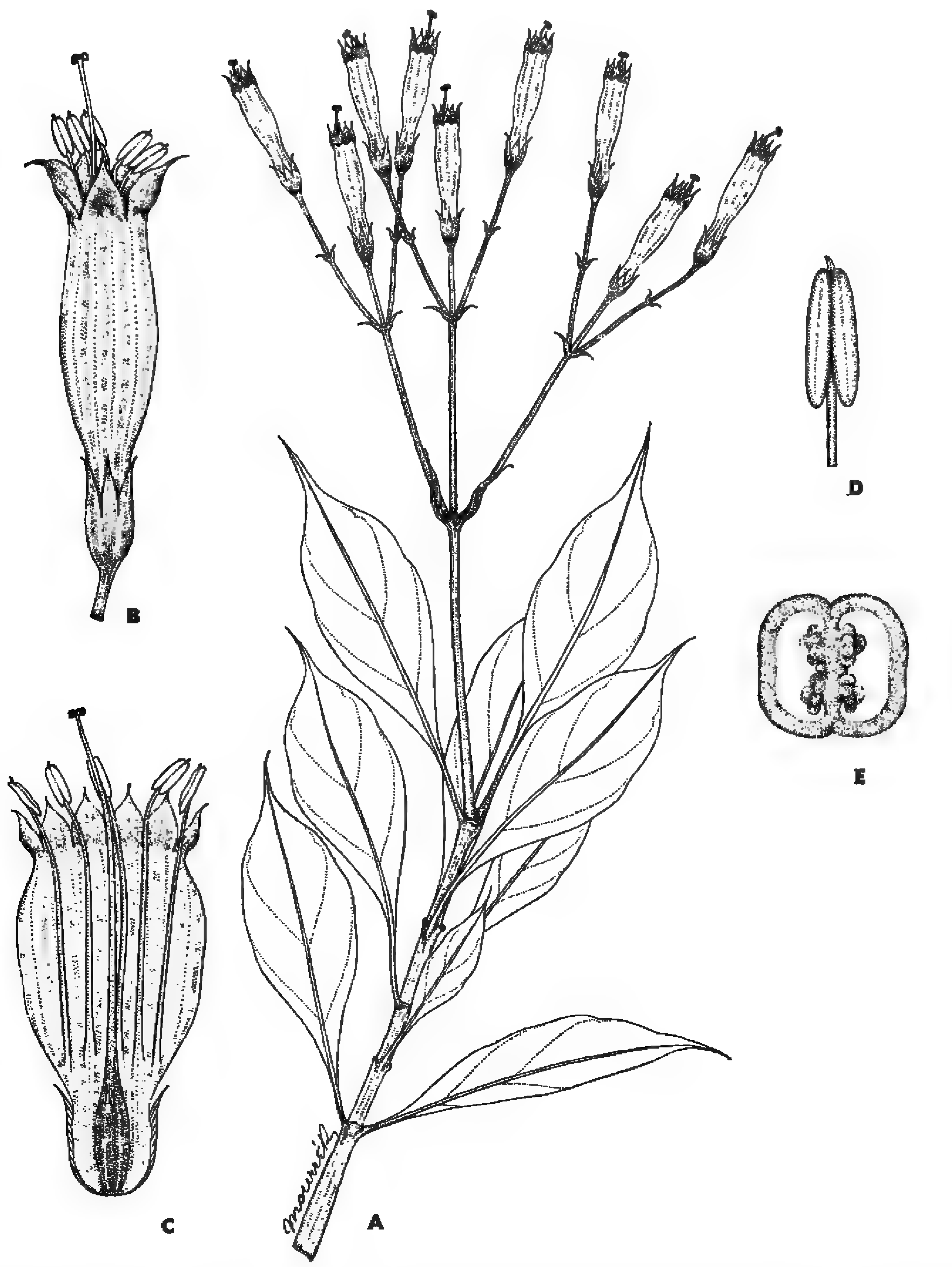

Fig. 1. *Lisianthus jefensis* A. Robyns & Elias: A, habit (×½); B, flower (ca ×1 ½); C, id., longitudinal section (ca ×1 ½); D, anther (ca ×4); E, ovary, cross-section (much enlarged). A, after *Elias & Hayden 1798* (MO); B-E, after *Tyson et al. 3203* (MO).

oblongis ca 3.5-4 mm longis basi bilobatis apice mucronatis mucroneque curvato et ca 0.3-0.4 mm longo; ovarium anguste ovatum, basi leviter obtuseque 4-angulatum, 6-7 mm longum et ca 1.5-2 mm diam, 2-loculare, stylo filiformi plus minusve tubum corollae aequanti ad longe exserto, stigmate capitato et ca 1 mm diam. *Capsula* calyce persistenti corollaque marcescenti circumcincta, fusiformis, usque ad 12 mm longa, apice rostrata, 2-septicidali-valvata; semina irregularia, ca 0.5 mm longa, processibus parvis acutisque tecta.

PANAMA: Cerro Jefe, *Duke 9413* (MO); id., 10-13 mi S of Goofy Lake, Febr 1966, *Duke 8010* (MO); id., alt ca 2900 ft, roadside thicket, Aug 1967, *Dwyer & Hayden 8087* (MO, UC); id., cloud forest, Aug 1967, *Elias & Hayden 1798* (holotype MO, isotype UC);

id., summit & forests along rd beyond summit, Aug 1967, *Hayden 1008* (COL, DUKE, MO, UC); id., in *Clusia* forest, alt 2700-3000 ft, Jan 1966, *Tyson et al. 3203* (MO); id., top, very common, July 1966, *Tyson et al. 4438* (MO).

This new species can readily be distinguished from *L. seemannii* by the subcoriaceous leaf blades, the loose few-flowered inflorescences, the much longer pedicels (1-2.5 cm long in *L. jefensis* versus 2-5 mm long in *L. seemannii*), the somewhat shorter flowers, the longer calyx tube, the tubular corolla with lobes only 4-5.5 mm long, and the anthers about twice as long; from *L. scopulinus* it can be separated by the subcoriaceous leaves, the simple or sometimes compound but few-flowered dichasia, the shorter flowers, the longer calyx tube, the much longer corolla lobes and the longer anthers. *Lisianthus jefensis* is closely related to *L. peduncularis* L. Williams (Fieldiana: Bot. **31:** 408, *fig. 1,* 1968), but differs mainly in the more coriaceous texture of the leaves and the much smaller flowers (2.8-3.2 cm long in *L. jefensis* versus 4.2-6 cm in *L. peduncularis*).

Lisianthus **scopulinus** A. Robyns & Elias, sp. nov.; *L. skinneri* (Hemsl.) O. Ktze. proximus, sed calycis lobis anguste ovatis apice longe acuminatis longioribus et 5-5.5 mm longis primo visu sat differt; etiam *L. jefensi* A. Robyns et Elias affinis, sed dichasiis compositis amplis multiflorisque, floribus majoribus, calycis tubo ca dimidio breviore, corollae lobis ut antheris etiam brevioribus praecipue recedit.—Fig. 2.

Frutex 1.5 m altus, omnino glaber, caulibus teretibus sed apicem versus angulatis canaliculatisque. *Folia* opposita, decussata, petiolata petiolisque amplexicaulibus; lamina obovata ad obovato-elliptica, basi in petiolum longe attenuata, apice longe acuminata, 6.5-18.5 cm longa et 2.8-6.6 cm lata, chartacea, costa et nervis lateralibus subtus conspicuis, nervis lateralibus utroque latere 2-3 arcuatis. *Inflorescentiae* axillares, dichasiales, dichasiis compositis amplis multifloris laxis

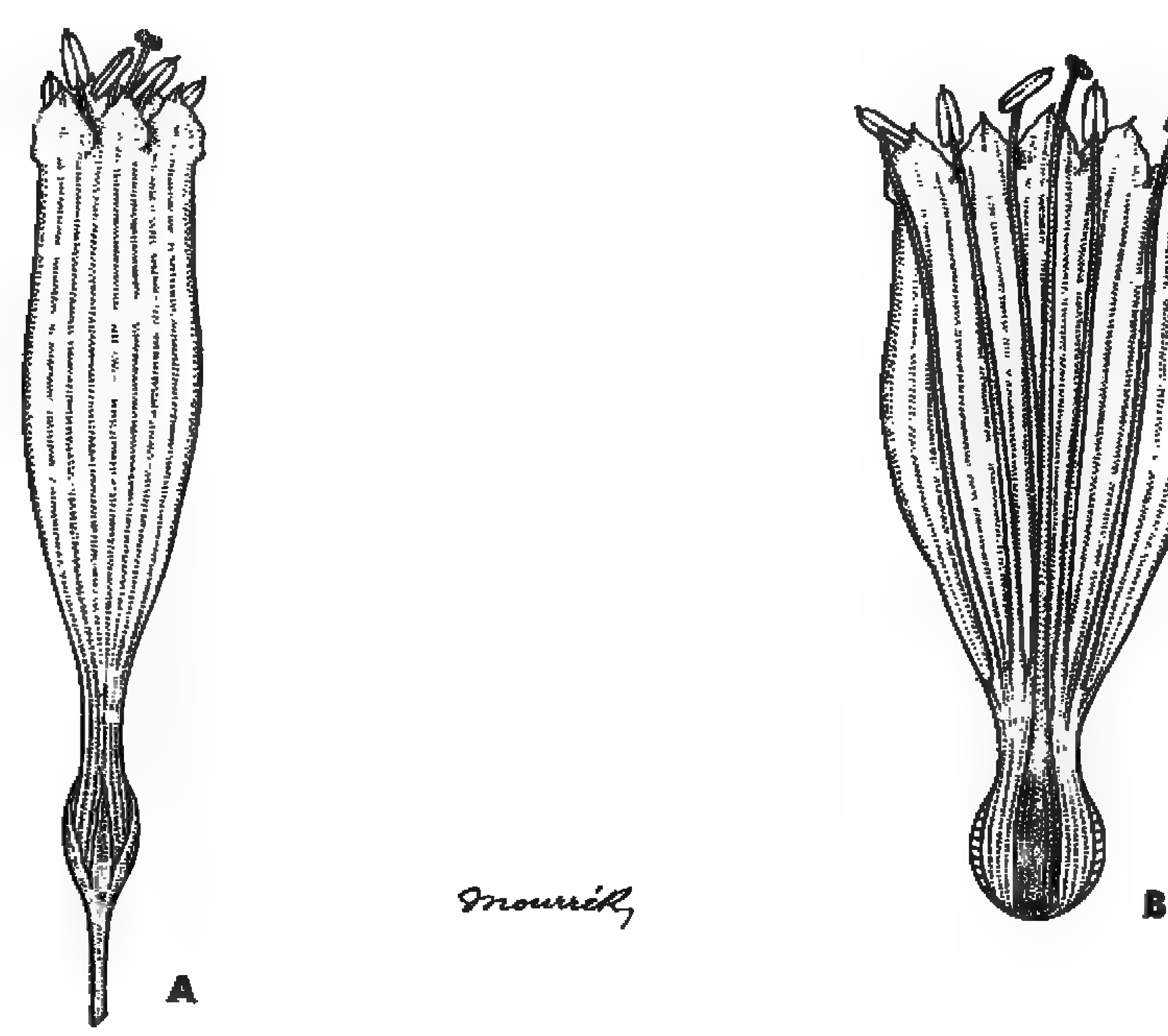

Fig. 2. *Lisianthus scopulinus* A. Robyns & Elias: A, flower (ca ×1 ¼); B, id., longitudinal section (ca ×1 ¼). After *Lewis et al. 2799* (MO).

saepeque irregularibus, pedunculis teretibus ad angulatis 1.5-3.5 cm longis, pedicellis 0.8-2.2 cm longis, bracteis oppositis ovatis ca 1.5 mm longis. *Flores* 3.8-4.6 cm longi, 5-meri; calyx tubulosus, 6.5-7 mm longus, lobis anguste ovatis dorsaliter carinatis apice longe acuminatis 5-5.5 mm longis et basi ca 2 mm latis secus margines membranaceis; corolla flavo-viridis, 3.8-4.6 cm longa, tubulosa, parte ⅓ inferiore constricta, lobis erectis ovatis apice acutis 2-3 mm longis et basi latis; stamina breviter exserta, filamentis tubo corollae ca ⅓ supra basin insertis filiformibus et 2.6-3.5 mm longis, antheris introrsis versatilibus oblongis 2-3 mm longis basi bilobatis apice mucronatis mucroneque ca 0.5 mm longo; ovarium anguste ovatum, basi leviter 4-angulatum, 6-11 mm longum, 2-3 mm latum, 2-loculare, stylo exserto filiformique, stigmate capitato et ca 1.5 mm diam. *Capsula* calyce persistenti corollaque marcescenti circumcincta, fusiformis, 11-14 mm longa et ca 4 mm diam, longitudinaliter carinata, apice rostrata rostroque usque ad 5 mm longo, 2-septicidali-valvata; semina irregularia, ca 0.5 mm longa, processibus parvis acutisque tecta.

VERAGUAS: mouth of Río Concepción, cliffs, Dec 1967, *Lewis, Croat & Hawker 2799* (holotype MO; isotypes DUKE, F, K).

The new species is related to *L. skinneri* but differs strongly in having narrowly ovate calyx lobes which are long-acuminate at the apex and are longer (5-5.5 mm long, in contrast with 2-3 mm in *L. skinneri*); it is also close to *L. jefensis* from which it can easily be separated by the large, compound, many-flowered dichasia, by the larger flowers, by the calyx tube about half as long, and by the shorter corolla lobes and anthers; from *L. peduncularis* it can be distinguished by the large, compound, many-flowered dichasia, the shorter calyx tube, the shorter corolla lobes (2-3 mm long in *L. scopulinus* versus 6-8 mm long in *L. peduncularis*), and the smaller anthers.

KARYOTYPES IN RELATION TO CLASSIFICATION AND PHYLOGENY IN CLAYTONIA

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ABSTRACT

Chromosomal morphology in *Claytonia* involving symmetry, large size and few satellites is correlated with the gross morphologically less specialized species and their classification into sections, while karyotypes with asymmetrical and medium- or small-sized chromosomes having the most satellites typify the advanced perennials and one annual species studied. These data further suggest that there are at least two lines of evolution in the genus, viz. from sect. *Caudicosae* to sect. *Rhizomatosae* to sect. *Claytonia*, and from a taxon similar to *C. sibirica* to sect. *Limnia*.

In the classification of the genus *Claytonia* L. (*Portulacaceae*) proposed by Gray (1887) and as recently modified (Swanson, 1966; Nilsson, 1966), one annual and three perennial sections are recognized. Those species in the sect. *Caudicosae* with heavy taproots are considered primitive, those with rhizomes or runners in the sect. *Rhizomatosae* intermediate between the caudicose perennials and the specialized geophytic species of the sect. *Claytonia*, while the annual species of the sect. *Limnia* are also thought to be advanced. This subgeneric classification and proposed phylogeny are based only on morphological characters to which we now add data from chromosomal morphology.

Species of each section were studied: (1) *C. sibirica* L., sect. *Caudicosae*, $2n = 24$ (British Columbia: N of Squamish, Black Tusk recreational area, *Lewis 6810*, nr Sechelt, Sechelt Peninsula, *Lewis 6827;* Vancouver I, Cougar Creek at Hwy 19, *Lewis 6822*); (2) *C. cordifolia* S. Watson, sect. *Rhizomatosae*, $2n = 10$ (Washington: Kittitas Co, Table Mt Rd, *Lewis 6736*); (3) *C. sarmentosa* C. A. Meyer, sect. *Rhizomatosae*, $2n = 10$ and 15 from one population (Alaska: Hatcher Pass, Talkeetna Mts, *Mitchell 927D1*); (4) *C. virginica* L., sect. *Claytonia*, $2n = 12$ (North Carolina: Buncombe Co, 0.2 mi W of Swannanoa, *Lewis 6582*) and $2n = 14$ (Texas: Bowie Co, Texarkana, *Suda 6*); (5) *C. perfoliata* Donn ex Willd., sect. *Limnia*, $2n = 12$ (Washington: Kittitas Co, 10 mi W of Cle Elum, *Lewis 6728*).

Plants were grown in an underground room with 12 hr of light (500 ft candles) at 24°C and 12 hr of darkness at 18°C. Root tips excised from pot-bound plants were pretreated with low temperatures (0-2°C) for 16 hr and fixed by modified Carnoy's solution (4:3:1, chloroform-absolute ethanol-glacial acetic acid) for 30 min. After maceration in N HCl for 45 min, roots were immersed in 2% aceticorcein for 24 hr. Temporary slides were made by the squash method; the best slides were then made permanent (McClintock, 1929) and are deposited in the Missouri

[1] We wish to thank Dr. Wm. W. Mitchell, Alaska Agricultural Experiment Station, Palmer, for sending material of *Claytonia sarmentosa*, and U. S. Public Health Grant No. 1 P10 ES 00139 ERT for financial assistance.

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Botanical Garden Herbarium (MO). Chromosomal measurements were made from photomicrographs enlarged 5600×; idiograms (Fig. 1-5) are based on arm ratios of chromosomes from 3-4 metaphase plates each from different root tips.

Chromosomal symmetry, length, number and satellite frequency for seven races of five species are summarized in Table 1. Certain trends are striking. For example, symmetry, expressed by pairs of V (± median and symmetrical) and I (subterminal and asymmetrical) chromosomes and by percentages of subterminal chromosomes, is of three kinds. More or less symmetrical karyotypes are characteristic of *C. cordifolia* (Fig. 2) and *C. sarmentosa* (Fig. 3), those of *C. virginica* (Fig. 4-5) are strongly asymmetrical, while the karyotypes of *C. perfoliata* (Fig. 1) and *C. sibirica* are intermediate between these extremes. This grouping correlates at least in large part with the subgeneric classification, viz. species in the sect. *Rhizomatosae* differ markedly in chromosomal symmetry from *C. virginica* (sect. *Claytonia*), both of which differ from *C. perfoliata* of the sect. *Limnia*. The latter is similar to C. *sibirica* which is, however, an atypical member of the sect. *Caudicosae* forming a connecting link with the sect. *Limnia* (Swanson, 1966) a conclusion entirely confirmed by the degree of chromosomal symmetry.

On the basis of chromosomal lengths the five species separate into four groups corresponding exactly to their sectional classification (Table 1). Shortest chromosomes averaging 2.2μ are found for the annual *C. perfoliata* (sect. *Limnia*), those of *C. sibirica* (sect. *Caudicosae*) are short to medium, those of *C. virginica* (sect. *Claytonia*) are still longer, while the longest chromosomes averaging 8μ and 8.6μ are found for *C. cordifolia* and *C. sarmentosa* (sect. *Rhizomatosae*), respectively. Since phylogeny and chromosomal size may be correlated with plants having larger chromosomes lacking evolutionary specialization (Davis & Heywood, 1963), the more primitive *C. cordifolia* and *C. sarmentosa* should possess large chromosomes. They do and, in fact, are the longest in the genus. The annual *C. perfoliata* with many specialized features (Swanson, 1966) has in contrast the smallest chromosomes; hence small chromosomes and evolutionary advancement are seemingly correlated as found for example in *Crepis* (Babcock et al., 1942). Chromosomes of the annual or perennial *C. sibirica* are also small and thus parallel *C. perfoliata* in this character as well as in symmetry and number. But only the tetraploid race

Table 1. Chromosome number, length, symmetry, and number of satellites per plate for *Claytonia* species.

	2n=	Length (μ) range	Length (μ) average	Symmetry pairs of V : I	Symmetry per cent I	Number of satellites
C. sibirica	24	2.5–3.7	3.2	5:7	58	2
C. cordifolia	10	6.4–9.8	8.0	4:1	20	1
C. sarmentosa	10	7.5–9.8	8.6	5:0*	0*	1
C. sarmentosa	15	—	—	7.5:0*	0*	1
C. virginica	12	4.0–7.3	4.9	1:5	83	4
C. virginica	14	3.9–5.4	4.8	0:7	100	2
C. perfoliata	12	1.6–2.5	2.2	2:4	67	4

* one pair tending toward subterminal (I).

of *C. sibirica* was examined and as polyploids within a ploidy series generally have smaller chromosomes than diploids a direct comparison between this tetraploid and the other species studied (only diploid races) is not really possible. As noted the chromosomes of *C. virginica* are intermediate in size, yet a relationship with those of *C. cordifolia* and *C. sarmentosa* is indicated, i.e. structural alterations and loss in one arm of each chromosome of *C. cordifolia* (Fig. 2) or *C. sarmentosa* (Fig. 3) would give rise to smaller, asymmetrical chromosomes typical of *C. virginica* (Fig. 4-5).

We noted also that the number of satellites per karyotype varied by species and section (Table 1): maximum satellite frequency of species in the morphologically evolved sect. *Claytonia* and *Limnia* is 3.3 per mitotic plate, whereas those species in the more primitive sect. *Rhizomatosae* and the tetraploid *C. sibirica* average only 1.3 per plate. It appears that a multiplication of satellites is related to evolutionary advancement of chromosomes and of species *per se* quite apart from their level of ploidy.

Finally brief mention should be made of two infraspecific chromosomal differences illustrated by our results. *Claytonia sarmentosa* has been examined from only two localities in Alaska and already plants with $2n = 10, 14, 15, 16, 28$ and 32 are known. Further sampling will undoubtedly expand this impressive infraspecific aneuploidy and polyploidy and hopefully lead to an understanding of such divergence. These numerical differences, however, are not unique: *C. virginica* is known with no fewer than 45 races at many levels of ploidy and including extensive aneuploidy even at the diploid level (Lewis, 1967; Lewis et al., 1967a; Lewis et al., 1967b). A hint as to the origin of a diploid race is suggested by the $2n = 12$ cytotype (Fig. 4) which has a large median pair of chromosomes with secondary constrictions, a pair clearly absent from the $2n = 14$ race (Fig. 5). It would not be difficult to imagine breakage of the median pair at the centromere to form two $\pm$ similar pairs, such as those observed in the $2n = 14$ race, in which the (now) subterminally positioned secondary constrictions function as centromeres. Such an occurrence would give rise to a $2n = 14$ race from a presumed base of $x = 6$ for the species.

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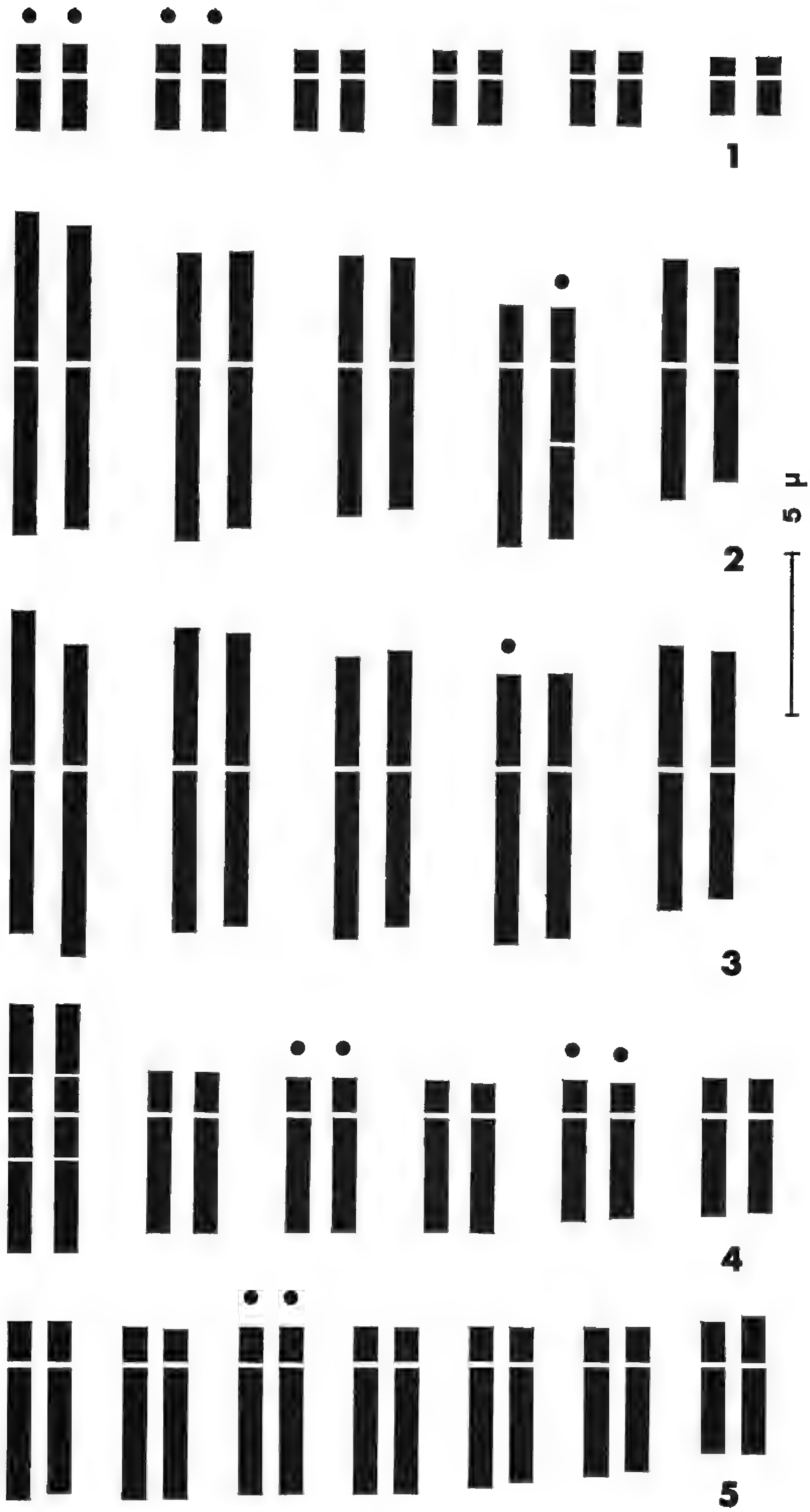

Fig. 1-5. Chromosomal idiograms of *Claytonia* species. Fig. 1. *C. perfoliata*, 2n = 12 (*Lewis* 5728). Fig. 2. *C. cordifolia*, 2n = 10 (*Lewis* 6736). Fig. 3. *C. sarmentosa*, 2n = 10 (*Mitchell 927D1*). Fig. 4-5. *C. virginica*, 2n = 12 (*Lewis* 6582), 2n = 14 (*Suda* 6).

NOTES

A NEW SPECIES OF STELIS (ORCHIDACEAE) FROM PANAMA

Stelis **fimbriata** R. K. Baker, sp. nov.—Fig. 1.

Herba caespitosa, epiphytica, glabra, usque ad 15 cm alta, caulibus secundariis brevibus gracilibus ad 5 mm longis, vaginis tubularibus deciduis usque ad 10 mm longis. *Folia* lamina coriacea elliptica ad ovata marginata 4-5 cm longa et 2-3 cm lata apice obtusa minuteque tridentata basi in petiolum 5-8 mm longum breviter angustata. *Inflorescentia* usque ad 13 cm longa, folio subtento multo longior, parte ⅔ distali florifer, bracteis infundibuliformibus roseis 1 mm longis pedicellos persistentes 1.5 mm longos includentibus. *Flores* rosei et albi; sepala 3-nervia, late ovata, 3 mm longa, 2.5 mm lata, rosea, basibus marginibusque albis, apicibus obtusis aut rotundatis, marginibus undulatis dense fimbriatis candidisque; petala claro-lutea, depresse obovata, undulata, 0.6 mm longa, 0.8 mm lata, secus costam

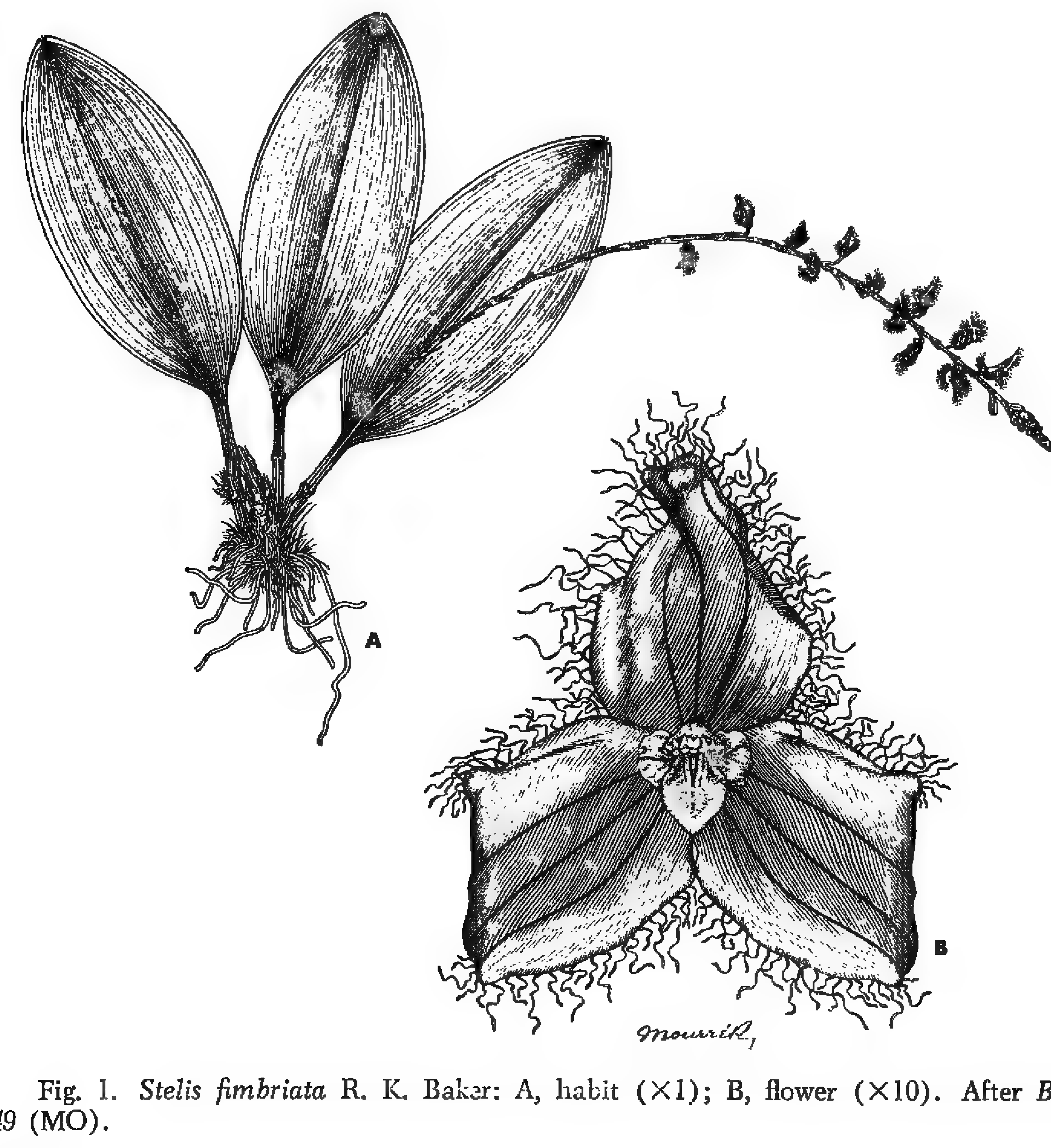

Fig. 1. *Stelis fimbriata* R. K. Baker: A, habit (×1); B, flower (×10). After *Baker 249* (MO).

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solitariam aliquantum incrassata, aliter ecarnosa; labellum luteum, ovatum, undulatum, 1 mm longum, 0.8 mm latum, in unguem brevem attenuatum, costae dimidio basali in callum angustum longitudinalem unguem breviter acuteque bifurcatum incrassato, venis lateralibus parallelis etiam incrassatis sed leviter brevioribus; columna lutea, 0.6 mm longa, valde alata, basin versus angustata, alis labelli margines basales subinvolutos amplectentibus; ovarium gracile, pedicellatum, 1.4 mm longum.

Herb, caespitose, epiphytic, glabrous, up to 15 cm tall; secondary stems short, slender, up to 5 mm long; sheaths tubular, deciduous, up to 10 mm long. *Leaves* 4-5 cm long, 2-3 cm wide, coriaceous, elliptic to ovate, marginate, obtuse, the apex minutely tridentate, the base attenuated into a short petiole up to 5 mm long. *Inflorescence* up to 13 cm long, much longer than subtending leaf, upper ⅔ floriferous; bracts pink, 1 mm long, infundibuliform, enclosing a persistent 1.5 mm pedicel. *Flowers* pink and white, showy; sepals 3-nerved, broadly ovate, 3 mm long, 2.5 mm wide, pink, with clear white bases and margins, the apex obtuse to rounded, the margin densely white-fimbriate, undulate; petals bright yellow, depressed obovate, undulate, 0.6 mm long, 0.8 mm wide, somewhat thickened along a solitary mid-vein, otherwise not fleshy; lip yellow, ovate, undulate, 1 mm long, 0.8 mm wide, attenuated into a short claw, the basal half of the mid-vein thickened into a narrow longitudinal callus which is shortly and acutely bifurcate at the claw, the parallel side-veins also thickened, but somewhat shorter; column yellow, 0.6 mm long, strongly winged above, tapering toward the base, the wings clasping the upturned basal margins of the lip; ovary slender, pedicellate, 1.4 mm long.

PANAMA: Cerro Jefe, in mossy forest nr summit, alt 2900 ft, 11 Febr 1967, *Baker 249* (holotype MO; living specimen MBG 67-73-137).

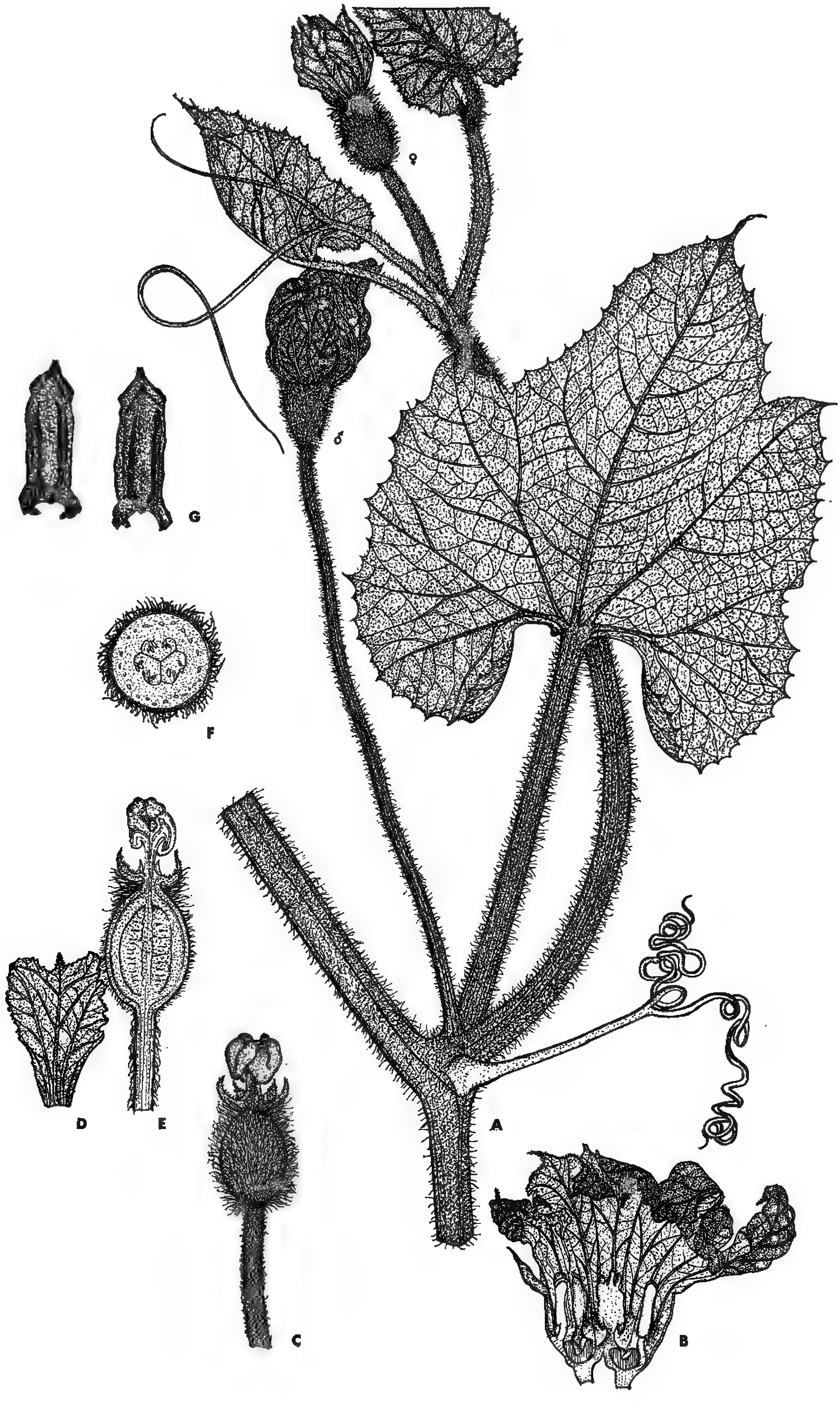
This attractive species (subg. *Stelis,* sect. *Concavae* Garay) is reminiscent of *S. eublapharis* Reichb. f., but is distinctive in the relative simplicity of the lip, and in the absence of pronounced marginal thickenings of the petals.—*R. Kendall Baker, Department of Botany, Washington University & Missouri Botanical Garden, St. Louis.*

A NEW SPECIES OF AFRICAN LAGENARIA (CUCURBITACEAE)

While on a botanical expedition to the northern regions of Ghana during the latter part of December, 1966, I came across a curious *Lagenaria* at Gambaga near Wali Wali. The plant is cultivated for shells which are used for manufacturing musical drums and vessels. The fruits are large with bitter pulp and two-horned (bicornate) seeds. The description and illustrations are based on plants raised in the college nursery from seeds gathered during the expedition.

Lagenaria **bicornuta** Chakravarty, sp. nov.; *L. siceraria* (Molina) Standley affinis a quo semine majore et bicorni, fructu giganteo et fere rotundo differt.—Fig. 1-2.

Monoecious *vines* with thick, 5-ridged, hairy stems which harden at maturity. *Leaves* with petiole erect, thick, biglandular (glands turbinate 2-3 mm in diam at the base) at apex, merged with narrow marginal basal veins of the blade; lamina



♀
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G
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Fig. 2. Some massive fruits of *Lagenaria bicornuta* growing in a field at Gambaga, Northern Ghana; photo taken by the author on 1 Jan 1968.

softly hairy, cordate-orbicular, shortly 7-angled or lobed, apex filiform-mucronate, 10-25 cm long and 15-35 cm broad, the margin glandularly serrate except mucronate midrib-end, the basal sinus deep-semilunar, 3-costate, 2 lateral costa divided at the base and outer lateral vein again redivided near the base; veins reticulate prominently raised on the lower surface, almost at the same level with the blade on the upper. *Flowers* axillary, solitary, male and female usually occurring on different branches, the female branches few and arising laterally from the longer and more vigorous male branches. *Male flowers* with peduncle 5-ridged, longer than the petiole (10-25 cm long); perianth tube deeply cupular ca 1 cm in diam, the lobes triangular remote softly hairy; corolla lobes white later brownish-white, 5-6 cm in diam, ± spathulate, the incurved margin somewhat lobed, the midrib with a bearded apex, mucronate, the veins whiter than brownish-white blade and distinctly raised on the lower surface, ca 3 cm long, and 2 cm broad at upper part, the lower part ± cuneate, unlobed and thicker, thickly 5-nerved; stamens 3, attached at base of throat of tube, 2 bithecial, 1 monothecial, the filaments of two thicker than the third, 5-6 mm long, with a glandular cup-shaped disc (metamorphosed

Fig. 1. *Lagenaria bicornuta* Chakravarty: A, part of one flowering branch showing male and female flowers (×½); B, male flower split open to show back portion of bithecous and monothecous stamens, center, and part of bithecous stamen, left & right side (×⅓); C, petal of female flower showing bearded mucronate apex (×½); D, female flower without petals showing hairy ovary and thickened stigma (×½); E, longitudinal section of female flower (×½); F, cross section of ovary (×½); G, seeds (×¾).

pistillodium) forming honey chamber, the anther not glossy, ca 1 cm long, 0.7-0.8 cm broad, loculi long convoluted in an ornamental pattern, the lower surface of anther (connective) smooth and creamy white, shortly ovate-acuminate, glandular hairs present between the folds of loculi. *Female flowers* with peduncle much shorter than the petiole (2-5 cm long); perianth tube very short or almost absent; corolla lobes much smaller than in the male; ovary oblong, conspicuously softly hairy, triplacentiferous, the style short, the stigma trilobed each lobe again deeply bilobed i.e. stigma apparently 6-lobed, the lobes glabrous on upper surface, the lower hairy. *Fruit* very large, almost perfectly round, 35-40 cm in diam, almost white when fully mature; seeds bicornate, ca 3 cm long (including horns), ca 1.1 cm broad, the horns somewhat incurved, ca 4 mm thick, 2-3 mm high, the surface ornamentally margined, the margin lines having pyramidal apex and open base.

GHANA. CAPE COAST: Univ Farm Akotokyir, 20 Febr 1967, *Chakravarty C1001:* K, K1 holotype, K2 (UCCC); *C1002* (UCCC); *C1003* (K, UCCC).

The species differs from *Lagenaria siceraria* (Molina) Standley by the presence of conspicuous two-horned seeds (almost double the size of the seeds of *L. siceraria*) and in having gigantic (35-40 cm in diam) and almost perfectly rounded fruits.—*H. L. Chakravarty, Department of Botany, University College, Cape Coast, Ghana.*

NOTES ON THE GENUS INGA. II

Two poorly known species of *Inga* can now be adequately described as to flowering and fruiting material and one of the species, *I. brenesii*, placed in its proper section. Distributional records from recent field work for Darien and San Blas areas of Panama are also given for several members of the genus.

Inga brenesii Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. **18:** 495, 1937.

This species previously known only from two collections from the forest of the central highlands of Costa Rica was placed by León (Ann. Missouri Bot. Gard. **53:** 330, 1966) in sect. *Inga* without having seen the fruit. Series *Inga* is distinguished from all other series and sections of *Inga* by having a rounded, sulcate legume. Recently, however, a specimen was collected from Costa Rica (*Jimenez 2620* F, 2 sheets & 1 bag fruit) with both flowering and fruiting material thus making possible the accurate placement of this species. The fruit is flattened, 20 cm long, 3-3.4 cm broad, 1.1 cm thick, densely ferrugineous-hirsute, slightly curved with elevated margins.

Although varying in two minor series characters, gland shape and stipule duration, this species as supported by other vegetative, floral and especially fruiting characters should now be placed with sect. *Inga* ser. *Vulpinae* sensu León. Series *Vulpinae* is restricted to South America excepting this species and the closely related *I. tonduzii* J. D. Sm. both of which are found in Costa Rica but are not known from Panama.

Inga saffordiana Pittier, Contr. U.S. Nat. Herb. **18:** 176, 1916.

This species previously known only from an incomplete specimen collected in the forest of Cerro de Garagará in Darien, Panama was believed to be intragenerically unique in exhibiting a cauliflorous condition. The type specimen, *Pittier 5676* (US) is without flowers and has only immature legumes. One of the distinguishing characters used by Pittier was that the inflorescences seem to come from the old wood of the trunk. León (Ann. Missouri Bot. Gard. **53:** 354, 1966) described the flowers apparently from a Colombian collection (*Fernandez 267*) which he regarded as matching the type closely. The Colombian specimen differs, however, by having only 2-3 pairs of leaflets and a long pedunculate inflorescence which is ramiflorous instead of being cauliflorous. In August, 1967 James Duke and I discovered on the slopes of Cerro Pirre in Darien, Panama a specimen of *I. saffordiana* (*Duke & Elias 13865* GH, MO). The tree was small, forming a part of the understory and its flowers were cauliflorous with some of the inflorescences issuing from older branchlets. The flowers are long-pedicellate, the calyx conical, 10-12 mm long, with small, acute teeth, the corolla tubular, 14-17 mm long, expanding slightly toward the apex, the lobes 3-4 mm long, ovate, acute at the apex. Both the calyx and the corolla are covered with spreading hairs. Since the flowering material of the Duke & Elias collection matched the description of the Colombian specimen, I feel that this species can now be adequately described as to flowering and fruiting material and is probably restricted to the mountain slopes in Darien, Panama and the neighboring Chocó region in Colombia.

Recent collections in Panama in the province of Darien and the Comarca de San Blas have yielded species which were previously unknown from those areas and the eastern one-third of the country.

DARIEN:

I. thibaudiana DC.: nr Río Canglon, *Duke & Bristan 356* (MO).

I. multijuga Benth.: Puerto St. Dorotea, *Dwyer 2226* (MO).

I. pauciflora Walp. & Duchass.: Río Tuira betw Río Punusa & Río Mangle, *Duke 14609* (MO); Río Pucro, below village of Pucro, *Duke 13127* (MO); along Río Tuira below El Real, *Stern et al. 968* (MO).

I. hayesii Benth.: 3 mi E of Santa Fe, *Tyson et al. 4669* (MO); vic of Campamento Buena Vista, nr Quebrada Felix, *Stern et al. 964* (MO).

I. spectabilis (Vahl) Willd.: vic of El Real, *Stern et al. 762* (MO).

I. portobellensis Beurl.: main stream of Río Cuasi, 0-2.5 m S of Tres Bocas, *Kirkbride & Duke 1132* (MO, NY).

SAN BLAS:

I. multijuga Benth.: opposite Ailigandi, *Lewis et al. 149* (GH, K, MO, UC, US), *194* (GH, MO, UC, US); along headwaters of Río Mulatupo, *Elias 1728* (GH, MO, US).

I. spectabilis (Vahl) Willd.: opposite Ailigandi, *Lewis et al. 139* (GH, K, MO, NY, UC); Río Ailigandi, *Duke 10838* (MO).

I. goldmanii Pittier: opposite Ailigandi, *Lewis et al. 190* (GH, MO, UC, US).

I. mucuna Walp. & Duchass.: Ailigandi, *Dwyer 6847* (MO).

I. quaternata Poeppig: Ailigandi, *Dwyer 6844* (MO).

—Thomas S. Elias, St. Louis University, St. Louis.

A NEW ANNUAL ERIOGONUM FROM UTAH[1]

Soon after the manuscript for the *Eriogonum deflexum* complex (Brittonia **20**: 13-33, 1968) was accepted, a population of dried stems was found which did not seem to belong to any of the species recognized in that paper. On returning to this site near Westwater, Grand Co, Utah in September, 1967, the dried stems were found to represent an undescribed species which may now be known as:

Eriogonum **scabrellum** Reveal, sp. nov.

A *Eriogono deflexo* Torrey (subg. *Ganysma*) differt involucris horizontalibus sessilibus, perianthiis 1-1.5 mm longis pustulosis basi obtusis, ramis omnibus scabrellis.

Annual herbs, 1-3(-5) dm high, with one or rarely two or more stems arising from thin tan caudices. *Stems* erect, slender, 5-15 cm long, sparsely tomentose with tangled white hairs covering the green, scabrellous surface. *Leaves* subbasal and sheathing up the stems 2 cm, the leaf-blades 1-3 cm long and wide, cordate, the apices rounded, the bases cordate, with crispate margins, densely tomentose below, lightly floccose and green above; petioles as long as or longer than the leaf-blades, prominently winged. *Inflorescences* sparsely branched, tending to become flat-topped, the crowns up to 4 dm long and 15 dm across. *Branches* dichotomous, rarely trichotomous, lightly to sparsely floccose with white hairs over the green scabrellous branches; main branches with 1-4 secondary branches each with a series of alternating short tertiary branchlets mostly less than 10 cm long at right angles to it. *Bracts* scalelike, ternate, 1 mm long, the acute apices widening to the connate base. *Peduncles* lacking. *Involucres* solitary, horizontal, arising from the bracts at each node, 1.5-2.5 mm long, 1.5-2 mm wide, the 5 acute lobes less than 0.5 mm long, scabrellous. *Bractlets* linear, 1.5-2.5 mm long, hirtellous. *Pedicels* up to 3 mm long, glabrous. *Perianth* 1-1.5 mm long, white with green midribs at anthesis, becoming 1.5 mm long and pink to rose or red in fruit, minutely pustulose over the entire abaxial surface. *Tepals* dissimilar, the outer whorl of segments 0.6-0.8 mm wide, obovate, the apices rounded, the bases obtuse, the inner whorl of segments 0.2-0.5 mm wide, ovate, the apices acute. *Stamens* excluded, up to 1.5 mm long, the filaments glabrous except for a few microscopic projections near the point of attachment, the anthers 0.3 mm long, red, oblong, the pollen grains pale-yellow, elliptic. *Achenes* light brown, 2 mm long, the globose base tapering to a long, sharp, minutely roughened beak. *Chromosome number* $n=20$.

Type: 3 mi S of U.S. Hwys 50 & 6 on the dirt road to Westwater, jct 6.8 mi W of Utah-Colorado state line & ca 17 mi NE of Cisco, along banks of an arroyo on heavy dark Cretaceous clay soil where it is locally common, Grand Co, Utah, 8 Sept 1967, *Reveal & Davidse 949* (UTC holotype; 34 isotypes will be distributed from UTC).

Additional collection: 3.5 mi S of U. S. Hwys 50 and 6 along the Westwater Rd, 12 Oct 1967, *Reveal 958* (BRY, DAOM, NY, UTC).

Eriogonum scabrellum is a member of the sect. *Pedunculata* Benth. in DC. of the subg. *Ganysma* (S. Wats.) Greene and is most closely related to the mem-

[1] The field work was supported by the Texas Research Foundation. This paper was submitted to the Department of Botany, Brigham Young University as partial fulfillment of three hours of Doctoral Research.

bers of the *E. deflexum* complex. The species in this complex have involucres that are either erect or deflexed. However, *E. scabrellum* has involucres that are in a horizontal, or intermediate, position. Other species, such as *E. deflexum* and *E. hookeri* S. Wats., which have sessile involucres, have their scalelike bracts arranged so that the involucres are positioned below the branches. In *E. scabrellum* the bracts are arranged so that the involucres are positioned to the side of the branches and project outwardly although in fruit, the involucres tend to tip downwardly slightly. The disposition of the involucres for this new species is unique to the genus. Unlike any other annual species in the genus, stems and branches of E. *scabrellum* are scabrellous, a characteristic known only in *E. heermannii* Dur. & Hilg. and its related taxa, a perennial shrub.—*James L. Reveal, Department of Botany, Brigham Young University, Provo, Utah.*

A SECOND SPECIES OF COCHLOSPERMUM (COCHLOSPERMACEAE) FROM PANAMA

Since the publication of the *Cochlospermaceae* for the Flora of Panama (Ann. Missouri Bot. Gard. **54:** 61-64, 1967) four fruiting collections of *Cochlospermum williamsii* Macbr. collected in the Canal Zone, in the Province of Darien, and in the Comarca de San Blas were received at the Herbarium. This species, originally described from Amazonian Peru, belongs to the sect. *Diporanda* and can be readily distinguished from *C. vitifolium* (Willd.) Spreng. by the compound-digitate leaves and by the mature seeds with only a tuft of long, wooly hairs.

Cochlospermum williamsii Macbr., Candollea **5:** 388, 1934.—Fig. 1.

Tree 12-23 m tall, the trunk to 15 cm in diam, the wood soft, the branchlets densely brownish-puberulous, becoming glabrous. *Leaves* compound-digitate, usually 5-7 foliolate, the petiole to 25 cm long, longitudinally sulcate, angulate-dilated at the apex, puberulous when young, glabrescent, the stipules small, deltoid, to 3 mm long, caducous; leaflets inarticulate, subsessile, the petiolule canaliculate above, the blade narrowly elliptic, sometimes subobovate, attenuate and decurrent at the base, short-to long-acuminate at the apex, entire-margined, up to 20 cm long and 6.5-9 cm wide, thin-chartaceous, very brittle when dry, the upper surface ± lustrous and glabrous, the lower surface dull and puberulous especially along the very prominent costa and prominulous lateral veins, glabrescent. *Inflorescences* apparently both terminal and axillary, paniculate, few-flowered, the axes thick, divaricate, brownish-puberulous. *Flowers* bright yellow, to 6 cm long, the pedicels ca 1 cm long, elongated and to 3 cm long in fruit, ± densely brownish-puberulous; calyx imbricate, the 2 outer sepals smaller than the 3 inner ones, subcoriaceous, brownish-tomentellous outside, very minutely so inside, caducous; outer sepals elliptic, obtuse to subacute at the apex, to 1.7 cm long and 1.1 cm wide; inner sepals elliptic to subobovate, rounded at the apex, thinner towards the margins, to 2.5 cm long and 1.7 cm wide; petals obovate to broadly obovate, apically deeply 2-lobed, to 6 cm long and 5.8 cm wide, thin-membranous, the lobes rounded, to 2

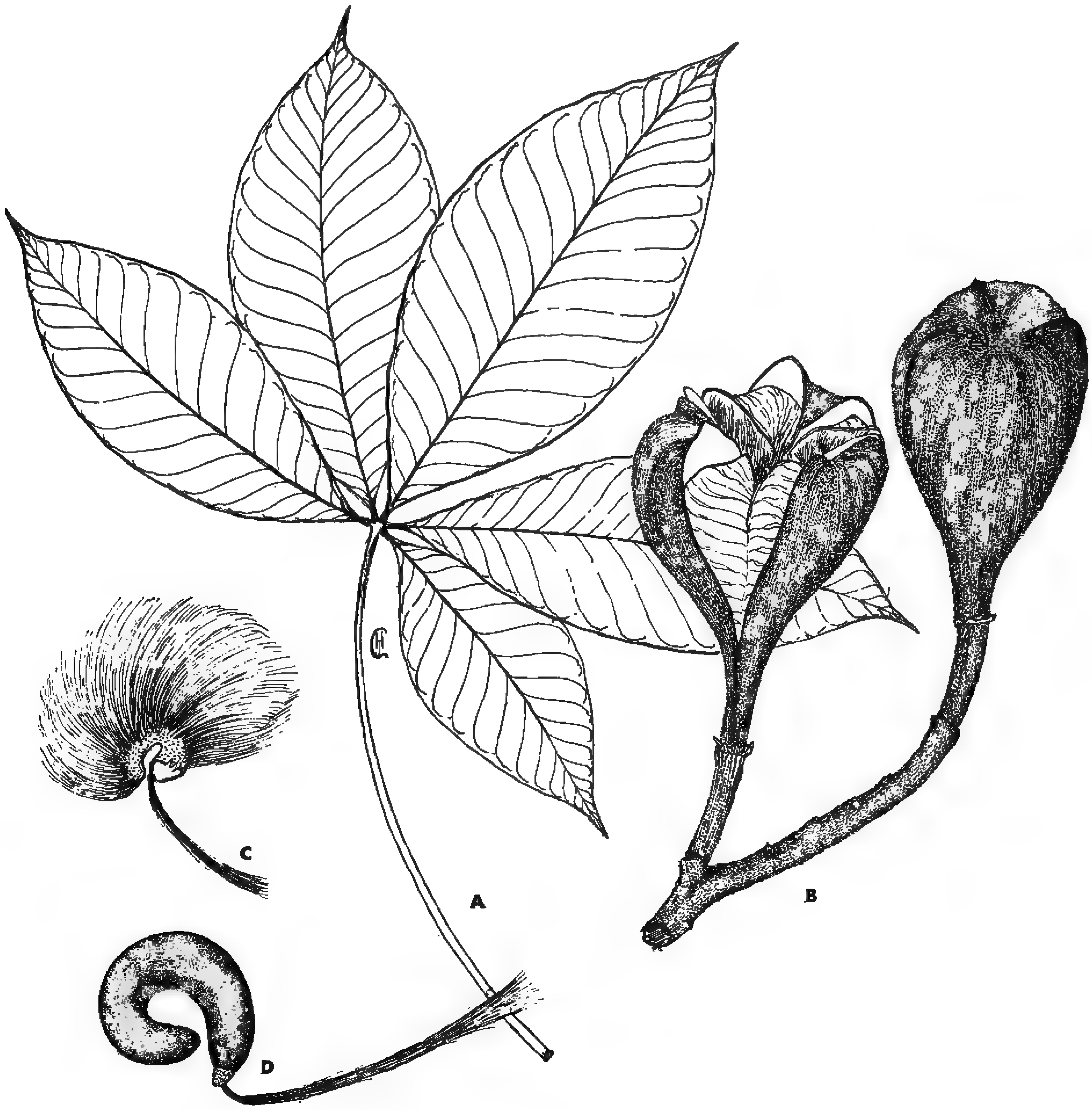

Fig. 1. *Cochlospermum williamsii* Macbr.: A, leaf (×½); B, capsules (×½); C, seed (×2); D, id., later stage of development (×4). A & D, after *Duke 11818* (MO); B & C, after *Dressler 3487* (MO).

cm long; filaments ∞, unequal, 5-18 mm long, glabrous, the anthers narrowly oblong, somewhat arcuate, to 4 mm long, glabrous or sparsely and minutely pilose, apically 2-porate; ovary subsessile, broadly obovoid, obtusely triquetrous, ca 5 mm long and 4.5 mm in diam, minutely fulvous-tomentellous; style filiform, to 13 mm long, densely short-villous at the base, otherwise glabrous, the apex recurved (?). *Capsule* obovoid, triquetrous, long-attenuate at the base, emarginate at the apex, to 7 cm long and 4 cm wide, dark brown, longitudinally striate, and minutely velvety tomentellous outside, 3-valvate, the exocarp separating from the endocarp the latter cream-colored to reddish-brown; seeds coiled into a ring, densely lanate, the hairs tan-colored and 5-10 mm long, the outer seed coat (to which the hairs are attached) thin and easily detachable at maturity leaving only a small tuft of hairs at the hilum, the inner seed coat dark brown to nearly black and ± lustrous.

Reported for the first time in Panama as well as North America; Colombia, Amazonian Peru, and Amazonian Brazil.

PANAMA. CANAL ZONE: Piña rd, 21 Apr 1968 (fr), *Dressler 3487* (MO). DARIEN: Río Uruti (fol, fr), *Duke & Bristan 231* (MO); woods nr El Real, 4 June 1967 (fol, fr), (Bristan for) *Duke 11818* (MO). SAN BLAS: along the headwaters of the Río Malatuppu, seasonal evergreen forest, 17 Aug 1967 (fol, fr) *Elias 1757* (MO).

COLOMBIA. AMAZONAS: Trapecio amazónico, Río Loretoyacu, alt ca 100 m, Sept-Nov 1944 (fol, fl, fr juv), *Schultes 6025* (US), 20-30 Oct 1945 (fol, fr), *6616* (US); Río Amazonas, nr mouth of Río Loretoyacu & Puerto Nariño, 13-15 Sept 1966 (fol, fl, fr), *Schultes et al. 24115* (ECON).

PERU. LORETO: Pebas on the Amazon River, forest, July 1929 (fol, fl, fr juv) *Williams 1778* (F, US), *1964* (holotype F); Cabollo-Cocha on the Amazon River, forest, Aug 1929 (fol, fl), *Williams 2090* (F); Alto Río Itaya, alt 145 m, Sept-Oct 1929 (fol, fr), *Williams 3485* (US).

BRAZIL. AMAZONAS: Basin of Río Solimoes, Municipality São Paulo de Olivença, nr Palmares, terra firma, high land, Sept-Oct 1936 (fol, fr), *Krukoff 8313* (F, MO).

Cochlopsermum williamsii is very closely related to and perhaps conspecific with *C. wentii* Pulle (Enum. Vasc. Pl. Surinam 310, *pl. 13,* 1906) from Surinam, from which it seems to differ only by the sepals being minutely tomentellous inside, those of *C. wentii* being glabrous inside. Study of the type of *C. wentii* is needed, however, in order to establish the synonomy.—*André Robyns, Missouri Botanical Garden, St. Louis, Missouri & National Foundation for Scientific Research, Belgium.*

HASSELTIA RIGIDA WOODSON EX A. ROBYNS, A NEW SPECIES OF FLACOURTIACEAE FROM PANAMA

Hasseltia ***rigida*** Woodson ex A. Robyns, sp. nov.; affinis *H. monagensi* Steyermark (Fieldiana: Bot. **28:** 407, 1952), sed arboris magnitudine, foliorum lamina coriacea marginibusque integerrimis et leviter recurvatis, floribus minoribus et usque ad 3 mm longis primo visu sat differt.—Fig. 1.

Arbor usque ad 30 m alta, ramulis glabris vel fere glabris. *Folia* alterna, petiolo robusto usque ad 2 cm longo supra canaliculato adpresso-puberulo sed glabrescenti; lamina elliptica ad anguste elliptica vel subcordata, basi cuneata, apice obtuse acuminata, usque ad 10 cm longa et 4 cm lata, coriacea, marginibus integerrimis leviterque recurvatis, utrinque sordida, e basi manifeste 3-nervia, supra glabra basique 2-glandulifera, infra praecipue secus nervos 3 principales prominentes adpresso-puberula ad glabrescens, nervis secundariis infra prominulis. *Inflorescentiae* ut videtur terminales, composito-umbellatae umbellisque iterum atque interum 3-4-radiatis, axibus adpresso-puberulis ad adpresso-tomentellis, bracteis parvis deltoideisque. *Flores* flavido-fusci, hermaphroditi, pedicellis usque ad 5 mm longis et adpresso-tomentellis; sepala 4, in aestivatione valvata, leviter inaequalia, ovata, apice acuta, usque ad 3 mm longa et 1.8 mm lata, extus tomentella, intus puberula, persistentia; petala 4, in aestivatione valvata, ovata, apice acuta, sepalis paululo breviora, extus tomentella, intus puberula, persistentia; stamina ∞, filamentis filiformibus usque ad 2.5 mm longis sparseque puberulis,

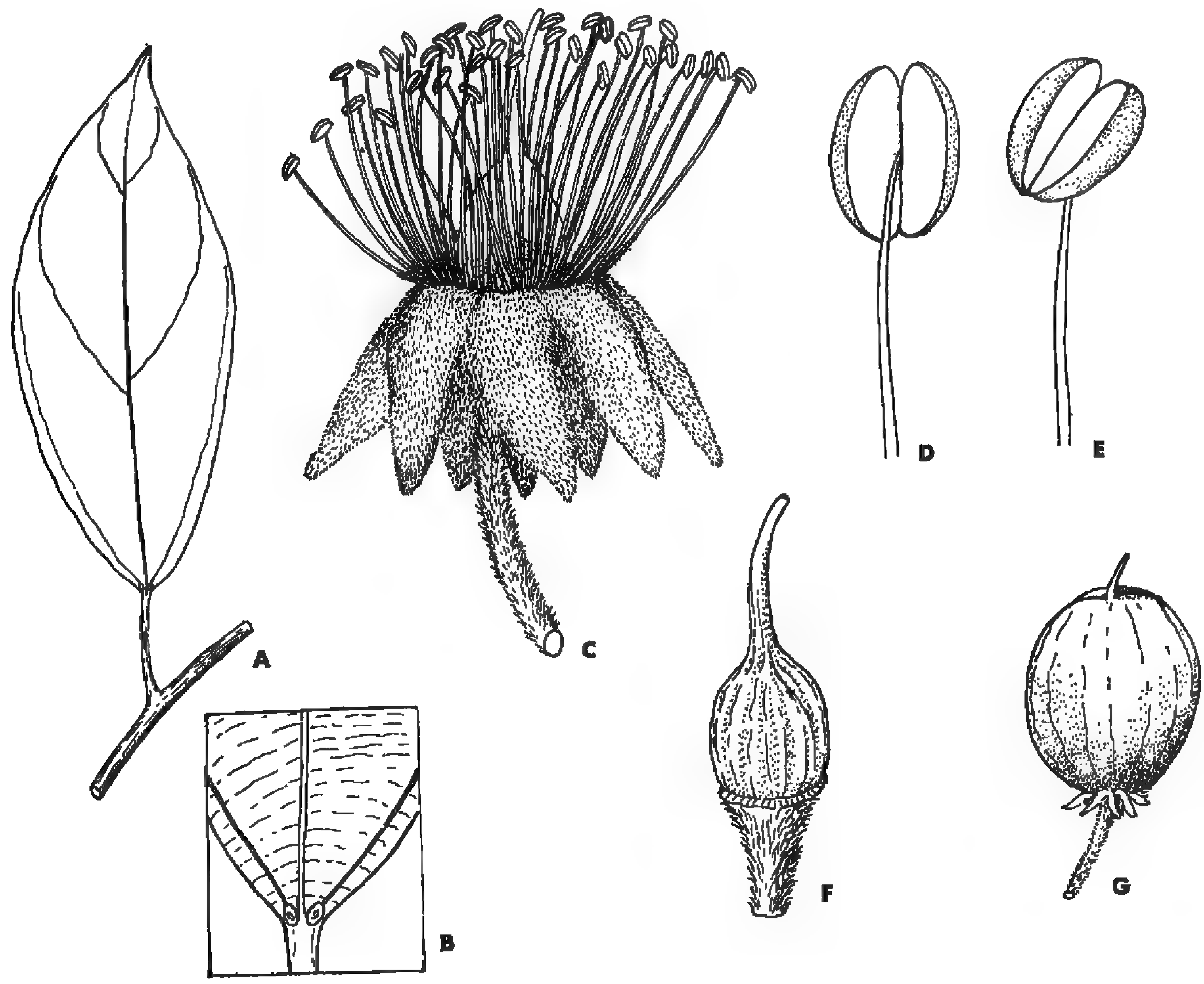

Fig. 1. *Hasseltia rigida* Woodson ex A. Robyns: A, leaf, upper surface (×½); B, base of leaf blade upper surface with 2 glands (×2); C, flower (×8); D & E, upper part of filament and anther (×30); F, gynoecium (×8); G, bacca (×2). After *Allen* 3733.

antheris minutis subglobosisque; ovarium globosum, glabrum, biloculare, placentis multiovulatis, stylo simplici usque ad 2.2 mm longo glabroque. *Bacca* rubra, subglobosa, usque 7-8 mm longa, glabra, seminibus 2-4 glabris.

COCLÉ: region N of El Valle de Antón, alt 1000 m, Sept 27, 1946, *Allen* 3733 (holotype MO).

—*André Robyns, Missouri Botanical Garden, St. Louis, Missouri & National Foundation for Scientific Research, Belgium.*

MAYNA ZULIANA (PITTIER) A. ROBYNS, COMB. NOV. (FLACOURTIACEAE)

The revision of the genus *Mayna* Aublet for the Flora of Panama has turned up two species for that country, i.e. *M. longicuspis* (Standley) Standley and another species, represented by several collections from the provinces of Darien and Panama, which I was unable to name until I examined the holotype of *Carpotroche zuliana* Pittier in the U. S. National Herbarium (*Pittier 10513*, San Martin on Río Palmar, Zulia, Venezuela). As the baccate fruits are bristly (in *Carpotroche* the capsular fruits are longitudinally alate) transfer to the genus *Mayna* is needed: *Mayna* **zuliana** (Pittier) A. Robyns, comb. nov., based on *Carpotroche zuliana*

Pittier, Bol. Com. Ind. (Venezuela) **4**(34): 38, 1923 (Arboles y Arbustos Nuevos de Venezuela, secunda y tercera decadas). —*André Robyns, Missouri Botanical Garden, St. Louis, Missouri & National Foundation for Scientific Research, Belgium.*

A NEW ORMOSIA (LEGUMINOSAE) FROM PERU

Ormosia **peruviana** Rudd, sp. nov.

Arbor usque ad 18 m alta; ramuli novelli fulvo- vel ferrugineo-subsericei; stipulae deltoideae, tomentulosae, circiter 1-2 mm longae, basi 1 mm latae, caducae; folia 7-9-foliolata, axe subtiliter sericeo, glabrata, 6-12 cm longo, petiolo 2-4 cm longo, jugis inter sese plerumque 2-2.5 cm distanotibus, petiolulis circiter 5 mm longis, 2 mm diametro, laminis coriaceis vel subcoriaeceis, ovatis, 5-10 cm longis, 3-5 cm latis, apice obtusis, nonnunquam retusis, basi obtusis vel subcordatis, supra glabris, subtus plus minusve glabris praeter venis maioribus saepe sericeis, venis secundariis mediocriter elevatis, utrinsecus circiter 10, fere parallelis, inter sese 4-10 mm distantibus, angulis venarum costaeque circiter 45°-50°, inflorescentiae cum axibus fulvido-subsericeis, nec bracteis bracteolisque nec floribus completis visis, calyce (effracto) fortasse circiter 10 mm longo; fructus dehiscens coriaceus vel sublignosus, rugulosus, brunneus et fulvo-sericeus, glabrescens, 1-spermus (fortasse 2- vel 3-spermus), 5-6 cm longus, circiter 3 cm latus, 1-1.2 cm crassus, valvulis 0.5-1 mm crassis; semina cinnabarina, circiter 17 mm longa, 16 mm lata, 9 mm crassa, hilo elliptico apicali, 3 mm longo et 1.5 mm lato.

CAJAMARCA: open place, mountain slope, alt 2100 m, Colasay, *Woytkowski 6964* (holotype MO, isotype US).

Vernacular name: *huayruru.*

This species is readily referable to my *Ormosia* series *Isthmenses* (Contr. U. S. Nat. Herb. **32**: 317, 1965). The pods most resemble those of *O. colombiana* Rudd but the large seeds are only matched in *O. venezolana* Rudd.—*Velva E. Rudd, Smithsonian Institution, Washington, D. C.*

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ANNALS of the MISSOURI BOTANICAL GARDEN

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ANNALS of the MISSOURI BOTANICAL GARDEN

VOLUME 55
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FLORA OF PANAMA

BY ROBERT E. WOODSON, JR. AND ROBERT W. SCHERY
AND COLLABORATORS

Part VI

FAMILY 112. VITACEAE[1]

BY THOMAS S. ELIAS
St. Louis University, St. Louis, Missouri

Climbing *shrubs*, vines or rarely erect shrubs or small trees, unarmed or rarely armed, stems usually sympodially branched, often with watery juice, bearing tendrils which may end in discoid suckers; nodes often swollen or jointed, the stem occasionally winged. *Leaves* alternate or the lower sometimes opposite, usually 2-ranked, simple, digitately or bipinnately compound, often pellucid-punctate, usually stipulate. *Inflorescences* cymose, racemose, spicate or paniculate, usually well developed and opposite a leaf; axis occasionally flattened and expanded; peduncles[2] often cirrhose; bracteoles present. *Flowers* minute, bisexual or unisexual (the plants then usually monoecious), actinomorphic, numerous; calyx entire or toothed, the sepals (3-) 4-5 (-7), distinct or basally connate, the petals as many as the sepals, valvate in bud, minute or obsolete, flat, distinct (connate in *Leea*) or as in *Vitis* apically connate, separating from each other at the base and falling away as an early deciduous cap; disc evident, annular or lobed; stamens as many as the petals and opposite them, somewhat perigynous, arising from the base of the disc, the anthers distinct, rarely connate, introrse, rarely extrorse, 2-thecate, dehiscing longitudinally; pistil 1, the ovary superior, 2-(3-8)-loculed and carpelled, the placentation axile, the ovules 1-2 on each placenta, anatropous, the style 1 and usually short, the stigma discoid, capitate, or shallowly 2-4-lobed. *Fruit* a berry,

[1]Assisted by National Science Foundation Grant No. GB-5674 (Principal Investigator, Walter H. Lewis).

[2]Due to the existing confusion concerning the terminology of inflorescences, the term "peduncle" is used in this paper to refer only to the main supporting branch of the inflorescence.

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1-4 (-6)-seeded, the seeds with a small, straight embryo and copious to sometimes ruminate endosperm.

The family contains 11 or 12 genera with 600-700 species occurring mainly in subtropical and tropical areas of the world. The Old World genus *Leea* has been placed by some workers in a subfamily of the *Vitaceae* (Gilg in Engler & Prantl, Nat. Pflanzenfam. **3**(5): 427-456, 1896) or in a family of its own (Suessenguth in Engler & Prantl, loc. cit. ed. 2., **20d**: 372-390, 1953; Cronquist, The Evolution & Classification of Flowering Plants, p. 261, 1968). Two genera, *Cissus* and *Vitis*, are to be found in Panama.

Useful reference:

Planchon, J. E., Monographie des Ampélidées Vraies. *In* DC., Monogr. Phaner. **5**(2): 305-648, 1887.

a. Inflorescence a well developed panicle; flowers 5-merous; petals fused at the apex, dropping off as an early deciduous cap; leaves simple; pith brown ....1. *Vitis*
aa. Inflorescence cymose; flowers 4-merous; petals free, expanding, dropping singly; leaves simple or 3-foliolate; pith white ....2. *Cissus*

1. VITIS

Vitis L., Sp. Pl. 202, 1753.

Woody *vines*, deciduous, rarely evergreen, scandent or climbing by tendrils borne opposite the leaves or arising from the peduncles, the bark often shredding and falling away, the pith usually interrupted by nodal diaphragms, brown; tendrils usually branched, rarely simple. *Leaves* simple or palmately compound, often lobed, usually rounded and cordate, dentate. *Inflorescence* a panicle. *Flowers* pedicellate, usually umbellate clustered, polygamodioecious, some plants with perfect flowers, others staminate with a rudimentary ovary, 5-merous; calyx cupular, fused with an entire or shallowly lobed margin; petals fused at the apex to form a deciduous cap; stamens 5, the hypogynous disk of 5 ± free or connate glands alternate with the stamens and adnate to the base of the ovary, lobed; ovary bicarpellate, the style short, conical, the stigma usually shallowly bilobed, the carpels 2-celled. *Fruit* baccate, usually edible, pulpy, 2-4-seeded, the seeds usually pyriform and narrowly rostrate basally.

A genus of 60-70 species, mostly of the temperate regions of the northern hemisphere. Two species are found in Panama, *V. vinifera*, the common cultivated grape which has been occasionally planted and the native *V. tiliifolia* which occurs throughout Middle America.

1. **Vitis tiliifolia** Humb. & Bonpl. ex Roem. & Schult. in L., Syst. Veg. ed. 15, **5**: 320, 1819.—Fig. 1.

V. caribaea DC., Prodr. **1**: 634, 1824.

Vine becoming woody, often climbing, with thick angulate to terete, striate stems, the pith interrupted by nodal diaphragms, the young branches densely floccose-tomentose, becoming glabrate, the nodes slightly swollen. *Leaves* chartaceous, rounded-ovate to orbicular, frequently with 3 shallow lobes, finely to coarsely dentate, rarely subentire except at the apex, lateral veins conspicuous

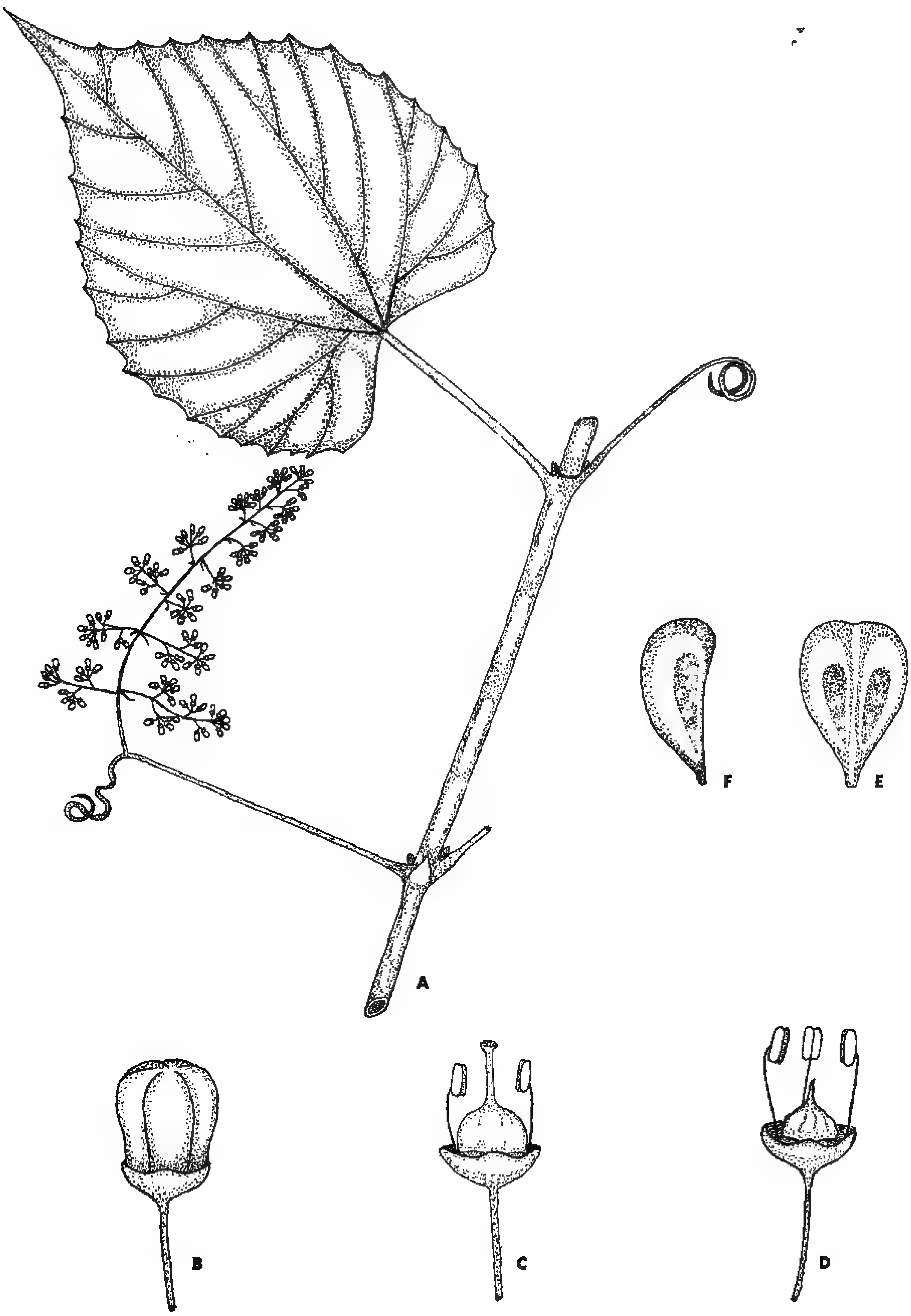

Fig. 1. *Vitis tiliifolia* Humb. & Bonpl. ex Roem. & Schult.: A, habit (×½); B, mature bud showing apically connate petals (×10); C, perfect flower (×10); D, staminate flower with abortive pistil (×10); E, seed, ventral surface (×5); F, seed, side view. A-C after *von Wedel 1539* (MO), D after *Davidson 567* (MO), E & F after *Blum & Tyson 531* (MO).

beneath, ending at the apex of the marginal teeth, acute to short acuminate at the apex, shallowly to deeply cordate at the apex, 5-15 cm long, 4.5-12.5 cm broad, floccose-tomentose above when young becoming sparsely floccose-tomentose to glabrate with age, densely floccose-tomentose beneath, the tan to light ferrugineous tomentum close to lax, usually persistent. *Inflorescences* of well developed panicles, the peduncles 4-15 cm long, sparsely to densely floccose-tomentose. *Flowers* pale yellow to greenish-yellow, unisexual or bisexual, the calyx undulate, scarcely toothed, the pedicel 1.5-3 mm long, the corolla 1-1.5 mm long, the lobes oblong to oblong-obovate, the unisexual flowers with well developed stamens and an abortive pistil, the perfect flowers with short stamens, the hypogynous glands ± united, the pistil 1-1.5 mm long, the ovary orbicular, the style short, ending with a shallowly bilobed stigma. *Berries* green becoming purplish-black with maturity, 4-6 mm in diam, orbicular, usually 2-seeded; seeds 3-4 mm long, pyriform, slightly curved, ± stipitate.

Mexico, Central America, the West Indies and northern South America.

BOCAS DEL TORO: vic of Chiriquí Lagoon, Water Valley, *von Wedel 829* (GH, MO), *954* (MO), *1539* (GH, MO, US). CANAL ZONE: W slope of Ancon Hill, *Woodson et al. 717* (A, MO); s. loc., *Blum 555* (MO); Barro Colorado I, *Frost 152* (F); *Shattuck 736* (F), *1060* (F, US); *Woodworth & Vestal 624* (F); Cocolí, *Riley 135* (MO). CHIRIQUÍ: Boquete, *Davidson 567* (F, MO); forest nr Boquete, *Pittier 3141* (GH, US). COCLÉ: hills N of El Valle de Antón, vic of La Mesa, *Allen 2486* (GH, MO, US). COLÓN: vic of San Juan nr Cement Plant Lake, *Blum & Tyson 531* (MO). DARIEN: road from El Real to Pinogana, *Duke 5131* (GH, MO); Río Balsa, betw Manene & Tusijuanda, *Duke 13548* (MO); vic of Campamento Buena Vista, nr Quebrada Felix, *Stern et al. 952* (GH, MO); El Punteadero at bridge crossing over Río Chucunaque, *Stern et al. 162* (GH, MO); Río Uroganti, *Bristian 1152* (MO). PANAMA: nr Río Tapía, *Maxon & Harvey 6619* (GH); San José I, *Johnston 591* (GH, MO, US). SAN BLAS: Mulatuppu, *Duke 8550* (MO).

The original spelling was *tiliaefolia,* a name widely adopted. Other spellings like *tilifolia* and *tiliifolia* have also been used. According to note 2 of Article 73 and recommendation 73G of the Code (Regnum Veget. **46**: 73, 1966) the use of a wrong connecting vowel or vowels in a name or epithet is considered an orthographic error. Recommendation 73G states that before a consonant the final vowel in Latin is reduced to *i.* Thus in place of *tiliaefolia* the corrected epithet should read *tiliifolia.*

Commonly referred to as "uva" in Panama, the grapes of this species are reported by Duke (personal communication) to be more often used for making wine and vinegar than for eating. In addition the larger vines contain quantities of potable water. The tough stems are occasionally used for cordage by the indians.

2. CISSUS

Cissus L., Sp. Pl. 117, 1753.

Climbing *vines,* herbs or small shrubs, often woody, occasionally fleshy and succulent; roots often tuberous; stems terete or angulate, glabrous to densely pubescent, often ramifying, tendrils always present and opposite the leaves, simple or bifurcate; stipules paired, always present, generally caducous. *Leaves* usually simple or 3-5-foliolate, often lobed, petiolate, the shape, pubescence and texture highly variable, the venation pinnate or palmate, the margins entire or frequently toothed. *Inflorescences* always opposite the leaves, cymes regular or corymbiform or umbelliform, pedunculate, with bracts and bracteoles. *Flowers* 4-merous, perfect, pedicellate, the calyx cupular, entire or with 4 valvate lobes; corolla generally ovoid or campanulate at the base, the petals valvate, inwardly cucullate, opening at anthesis and falling away separately; stamens opposite the petals, inserted on the receptacle at the base of the disc, the filaments erect, the anthers introrse, the disc surrounding the ovary, the margin 4-lobed; ovary bilocular with 2 anatropous ovules, the style cylindrical and often persisting after anthesis, the stigma small, discoid. *Fruit* a 1(-2)-seeded berry, the seeds obovoid, attenuate at the base, often trigonous.

A pantropical genus of ca 400 species of which six are reported from Panama. This genus exhibits great variation. In *C. sicyoides*, for example, the amount of variation expressed within the species is greater than the differences between the trifoliolate species. The neotropical members of this genus are in need of serious monographic study. The name *Cissus* was derived from the Greek *kissos* meaning ivy.

a. Leaves 3-foliolate.
  b. Terminal leaflets rhombic; plants densely pubescent with glandular &/or eglandular hairs; stipules on the younger branches linear-lanceolate to lanceolate, 3-6 mm long .... 1. *C. rhombifolia*
  bb. Terminal leaflets elliptic to obovate; plants usually glabrous or with sparse eglandular hairs; stipules on the younger branches broadly ovate to subrotund, 2-4 mm long.
    c. Mature peduncles (6-) 7-12 cm long; stems 4-gonous, often winged; fruits 4-6 mm in diam .... 2. *C. erosa*
    cc. Mature peduncles 1-1.8 cm long; stems terete to subangulate, unwinged; fruits 6-10 mm in diam.
      d. Terminal leaflets with a petiole 0.5-2 cm long; leaves mucronate-serrate, mature leaves 4-10 long; flowers red or reddish-orange; fruits 6-8 mm in diam .... 3. *C. microcarpa*
      dd. Terminal leaflets sessile; leaves sparsely denticulate, mature leaves 2-4 cm long; flowers pale green; fruits ca 1 cm in diam ...... 4. *C. martiniana*
aa. Leaves simple.
  e. Berries 10-12 mm in diam; buds 3-4 mm long, dark red; leaves strongly dimorphic, mature leaves coriaceous, glabrous .... 5. *C. biformifolia*
  ee. Berries 4-6 mm in diam buds 1-1.5 mm long, greenish-white, white to yellow, rarely red; leaves not strongly dimorphic, mature leaves chartaceous, glabrous to densely villous .... 6. *C. sicyoides*

1. **Cissus rhombifolia** Vahl, Eclog. Amer. **1:** 11, 1796.—Fig. 2A, B.

Vine becoming woody, often climbing, the stems subangulate to terete, striate, frequently canaliculate, unwinged, slightly swollen at the nodes, densely pubescent with glandular and/or eglandular hairs, the eglandular hairs to 2 mm long, septate and transparent except for the darkened junctions of the cells, the glandular hairs to 0.5 mm long, usually more abundant than the eglandular hairs; stipules on the younger branches linear-lanceolate to lanceolate, 3-6 mm long, becoming ovate to broadly ovate on the older stems, 6-12 mm long, subpersistent, usually densely pubescent. *Leaves* 3-foliolate, densely villous, especially beneath, the petiole 1.5-8 cm long, striate, densely pubescent, the leaflets chartaceous to subcoriaceous, ser-

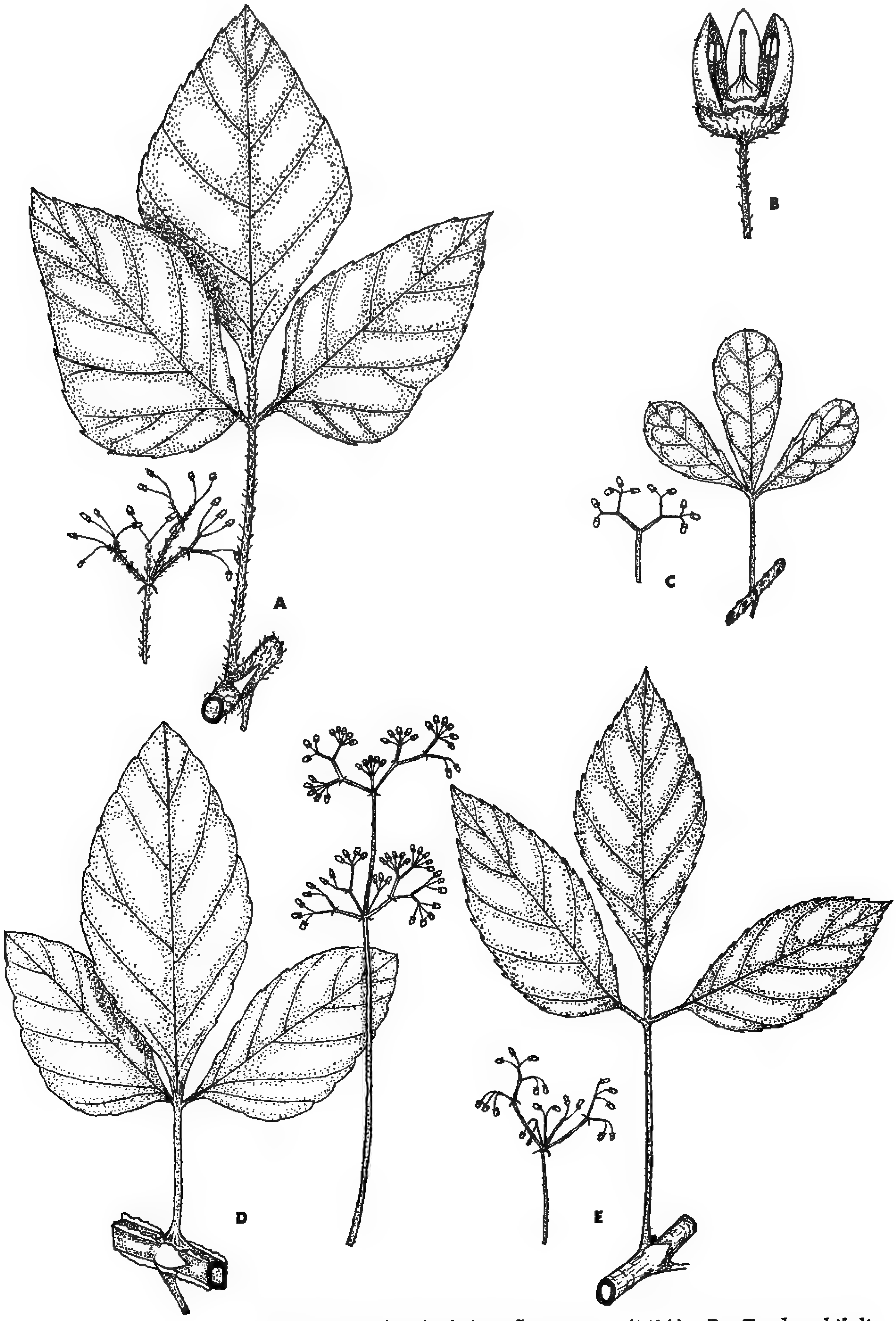

Fig. 2. A, *Cissus rhombifolia* Vahl, leaf & inflorescence (×½); B, *C. rhombifolia* Vahl, flower (×10); C, *C. martiniana* Woodson & Seibert, leaf & inflorescence (×½); D, *C. erosa* L. Rich., leaf & inflorescence (×½); E, *C. microcarpa* Vahl, leaf & inflorescence (×½). A-B after *Lewis et al. 1544* (MO), C after *Seibert 241* (MO holotype); D after *Stern et al.* 305 (MO).

rate, the lateral veins 5-7 pairs, ascending and terminating at the apex of the serrations; tendrils borne opposite the leaves; terminal leaflet 4.8-13 cm long, 2.2-6.5 cm broad, rhombic, the young leaves commonly narrowly ovate, cuneate at the base, sessile or petiolulate to 5 mm long, acute to short acuminate at the apex; lateral leaflets 3.6-10 cm long, 1.8-7 cm broad, rhombic to broadly ovate, strongly oblique at the base, acute to short acuminate at the apex. *Inflorescences* cymose, often appearing corymbose with the flowers congested in pseudoumbels, the peduncles 1-3 cm long, often bright red with exposure to the sun, pubescence of densely spreading hairs. *Flowers* pale yellow to greenish-yellow, the pedicel 3-8 mm long, the calyx cupular with four scarsely discernible teeth, densely pubescent, the corolla of four free petals, oblong to oblong-ovate, acute at the apex, ca 1 mm long; pistil 1.5-2 mm long, the ovary 2-locular. *Berries* green becoming black with maturity, 6-8 mm in diam, orbicular, 1-seeded; seeds broadly pyriform, 5-7 mm long, 4-5 mm broad.

Mexico, Central America, the West Indies and South America.

CANAL ZONE: Barro Colorado I, *Shattuck 252* (A), *Wetmore & Woodworth 873* (A), *Wetmore & Abbe 139* (A, MO), *Bailey & Bailey 337* (GH); vic of Miraflores Lake, *White 242* (MO); K-9 road at bridge, *Stern et al. 975* (GH, MO); Fort Clayton; Cardenas Creek area, *Tyson 1293* (MO); Farfan beach road, *Kirkbride & Elias 58* (MO); U. S. Army Tropic Test Center, Albrook, *Dwyer 6717* (MO); Fort Kobbe, *Duke 3944* (GH, MO); Curundu, nr Survival School, *Tyson 1068* (MO). CHIRIQUÍ: Cerro Chorcha, *Allen 5062* (MO); trail from San Felix to Cerro Flor, *Allen 1936* (GH, MO); 12.4 mi N of David, *Lewis et al. 701* (GH, MO, UC, US). COCLÉ: betw Las Margaritas & El Valle de Antón, *Woodson et al. 1762* (A, MO); betw Aguadulce & El Valle de Antón, *Woodson et al. 1210* (A, MO); El Valle de Antón, *Lewis et al. 2597* (DUKE, K, MO, NY, UC). DARIEN: vic of El Real, Río Tuira, *Stern et al. 788* (GH, MO, US); betw El Real & Río Canalones, *Duke 4982* (GH, MO); Boca Grande I, *Duke 8841* (MO). HERRERA: Pesé, ca 50 mi, *Allen 793* (GH, MO, US). LOS SANTOS: Río Tonosi, vic of Tonosí, *Lewis et al. 1544* (MO); 1-2 mi W of Candelaria, *Duke 12451* (MO). PANAMA: vic of El Llano, *Duke 5521* (GH, MO); Gorgona beach, *Woodson et al. 1691* (A, MO); thickets & forest nr Arraiján, *Woodson et al. 1354* (A, MO); betw Pacora & Chepo, *Woodson et al. 1653* (A, MO); San José I, *Johnston 973* (GH); Río Tartaré, *Woodson & Schery 1005* (MO); Piria, *Duke 14447* (MO). VERAGUAS: vic of Sona, along highway, *Woodson et al. 512* (MO); ca 5 mi NE of La Mesa, *Blum & Tyson 659* (MO), *665* (MO); 12 mi from Santiago toward Divisa, *Dwyer & Kirkbride 7436* (MO); 2-4 mi E of Santiago, roadside savanna, *Duke 12359* (MO).

This species is easily recognized by the rhombic-shaped leaves and dense pubescence. The glandular hairs characterizing most of the Panamanian material were not observed on collections from southern Mexico or Guatemala. Although this condition may warrent subspecific status, I am hesitant about creating another taxon in this genus until this species has been adequately studied through its range.

2. **Cissus erosa** L. Rich., Act. Soc. Hist. Nat. Paris **1:** 106, 1792.—Fig. 2D.

C. salutaris Kunth in H.B.K., Nov. Gen. Sp. Pl. **5:** 225, 1821.

Vitis salutaris Baker in Mart., Fl. Bras. **14**(2): 211, *pl.* 52, 1871.

Vine becoming woody, often climbing, the stems angulate, tetragonal, frequently winged on the margins, slightly nodose, glabrous or with a few scattered, appressed, pilose hairs; stipules broadly ovate to subrotund, subpersistent, 3-4 mm long, the apex obtuse, glabrous. *Leaves* 3-foliolate, the petiole 1.8-6.5 cm long, 4-gonal especially at the base, glabrescent, occasionally winged, the wing up to

1.5 mm broad; leaflets chartaceous to subcoriaceous, sharply serrate to sparsely dentate, occasionally shallowly so, glabrous to sparsely pilose beneath, especially on the costa, the lateral veins 4-6 pairs, ascending and terminating between the teeth; terminal leaflet 4.5-15.5 cm long, 1.5-8 cm broad, elliptic to elliptic-ovate to ovate, cuneate at the base, acute to subobtuse at the apex, sessile to short-petiolate, rarely to 1.5 cm long; lateral leaflets 3.5-12 cm long, 2-6 cm broad, inequilateral, ovate to ovate-elliptic, oblique and rounded to subcuneate at the base, acute to obtuse at the apex. *Inflorescences* cymose, appearing corymbose with the flowers congested in pseudoumbels, the mature peduncles (6-)7-12 cm long, glabrous or with a few scattered, appressed, pilose hairs. *Flowers* bright red to reddish-orange, the pedicel 2-5 mm long, pilose often sparsely so, the calyx with four short lobes, often indiscernible, the corolla of four free petals, oblong, acute at the apex, ca 1 mm long; pistil 1-1.5 mm long. *Berries* green becoming black with maturity, 4-6 mm in diam, orbicular to subpyriform, 1-seeded; seeds pyriform, 4-5 mm long.

Southern Mexico, Central America, the West Indies and South America.

CANAL ZONE: Ancon Hill, *Duke 4587* (MO); Barro Colorado I, *Brown 33* (F), *Woodworth & Vestal 530* (A, F); Gamboa, *Tyson et al. 4588* (MO); vic of Miraflores, *White 135* (GH, MO); vic of Río Cocolí, K-9 road, *Stern et al. 36* (GH, MO), *305* (GH, MO); Frijoles, nr boat dock, *Ebinger 70* (MO); Howard Air Force Base, SE of Kobbe Beach, *Oliver & MacBryde 1890* (MO). COCLÉ: vic of El Valle de Antón, *Allen 750* (GH, MO, US); betw Las Margaritas & El Valle de Antón, *Woodson et al. 1763* (GH, MO). COLÓN: vic of Río Piedras, along road to Puerto Bello, *Blum et al. 2536* (MO); vic of Sardinilla ca 7-8 mi E of Cement Plant, *Blum & Tyson 504* (MO); betw Río Piedras & Puerto Pilon, *Lewis et al. 3215* (DUKE, MO, UC). HERRERA: 12.5 mi S of Ocú, *Lewis et al. 1624* (GH, MO, US). PANAMA: Cerro Azul, *Tyson 2151* (MO); Cerro Campana, trail from Campana to Chica, *Allen 2649* (MO); San José I, *Erlanson 68* (GH), *Johnston 429* (GH), *885* (GH), *973* (MO), *976* (GH, MO). SAN BLAS: along the headwaters of the Río Mulatupo, *Elias 1727* (MO). VERAGUAS: hills W of Soná, *Allen 1035* (GH, MO, US).

Cissus erosa occurs frequently throughout Middle and South America and shows considerable variation in leaf margins and the occasional presence of indumentum on the lower leaf surfaces. Despite Planchon's (in D.C., Monogr. Phan. **5**(2): 548-9, 1887) reduction of *C. salutaris* to a synonym of *C. erosa*, some workers (Publ. Field Mus. Nat. Hist., Bot. Ser. **24**: 302, 1949) have maintained the two as distinct based mainly on the degree of pubescence of the leaves. As specimens assigned to the two species show an intergradation of characters, the reduction by Planchon is apparently justifiable.

3. **Cissus microcarpa** Vahl, Eclog. Amer. **1**: 16, 1796.—Fig. 2E.

Vine, usually woody, the stems terete, sulcate, unwinged, lenticels sparse and inconspicuous, glabrous except for occasional appressed pilose hairs on the younger stems, the nodes swollen; stipules broadly ovate to subrotund, subpersistent, 3-4 mm long, the apex acute to obtuse, glabrescent. *Leaves* 3-foliolate, the petiole 1.5-6 cm long, striate, glabrous or occasionally appressed-pilose on the juvenile forms, the lateral veins conspicuous beneath, chartaceous to subcoriaceous, mucronate-serrate; terminal leaflet 3-10 cm long, 1.4-6 cm broad, broadly elliptic, elliptic, ovate-elliptic, cuneate at the base, petiolule 0.5-2 cm long, acuminate at the apex, mucronate, the lateral veins 5-6 pairs; lateral leaflets 3-8 cm long, 0.6-5 cm broad, obliquely elliptic or ovate to rhombic, obliquely rounded at the base, acute to shortly acuminate at the apex, mucronate, the lateral veins 3-5 pairs. *Inflorescences* cymose-umbellate and appearing corymbiform, the peduncles 0.6-1.8 cm long, glabrous or with a few scattered hairs. *Flowers* appearing red or reddish-orange, the pedicel 1-4 mm long, glabrous to sparsely pilose; calyx cupular, the lobes indiscernible; corolla ca 1 mm long, the lobes ovate to ovate-triangular, acute at the apex, pistil 1-1.5 mm long. *Berries* green, turbinate to spherical (?), ca 6-8 mm in diam, usually 1-seeded, the seeds pyriform, 4-6 mm long.

Mexico, the West Indies, Central and South America.

BOCAS DEL TORO: vic of Chiriquí Lagoon, *von Wedel 1040* (GH, MO, US), *1334* (GH, MO), *1517* (GH, MO); Almirante, on rd to Bomba, *Blum 1335* (MO); Changuinola Valley, Potrero I, *Dunlap 77* (F); Río Cricamola, betw Finca St. Louis & Konkintoe, *Woodson et al. 1916* (MO). CANAL ZONE: Barro Colorado I, *Ebinger 277* (MO); vic of Salamanca Hydrographic Station, Río Pequerí, *Woodson et al. 1626* (MO); Coco Solo, U. S. Army Tropic Test Center, Mine Emplacement Center, *Dwyer & Duke 7920* (GH, MO, US). COCLÉ: foothills of Cerro Pilon, nr El Valle de Antón, *Duke & Correa 14714* (MO); betw Cerro Pilón & El Valle de Antón, *Duke & Dwyer 13951* (MO). PANAMA: along Pan-Am Highway, nr Jenine, *Duke 3820* (MO); gallery along Río Terable, nr Pan-Am highway & El Llano, *Duke 5657* (MO); tributary of Río Chagres, 5 mi SW of Cerro Brewster, *Lewis et al. 3372* (DUKE, K, MO, NY, UC), *3458* (DUKE, K, MO, UC); Cerro Jefe, 10-13 mi beyond Goofy Lake, *Duke 8027* (MO).

In Panama this species has been consistently confused with *C. rhombifolia. Cissus microcarpa* can be readily identified by long petiolate leaves which are mucronate-serrate and the generally glabrous condition. Like several other species of *Cissus* the upright inflorescences are often showy due to the bright red peduncles.

4. **Cissus martiniana** Woodson & Seibert, Ann. Missouri Bot. Gard. **24**; 191, 1937.—Fig. 2C.

Woody *vine* or small prostrate shrub, the stems subangulate to terete, unwinged, conspicuously lenticellate on the older stems, glabrous except for occasional appressed pilose hairs on the younger stems, the nodes slightly swollen; stipules broadly ovate to subrotund, persistent, 2-3 mm long, the apex obtuse to subacute, glabrescent. *Leaves* 3-foliolate, the petiole 1.5-2.5 cm long, striate, glabrous or rarely with a scattered, ferrugineous-pilose indumentum, sessile, obtuse at the apex, minutely mucronate, the lateral veins 4-5 pairs, inconspicuous, subcoriaceous, sparsely denticulate; terminal leaflet 2-4 cm long, 1-2.2 cm broad, obovate to elliptic, cuneate at the base; lateral leaflets 1.5-4 cm long, 0.8-2 cm broad, obliquely obovate to obovate-elliptic, unequally cuneate at the base. *Inflorescences* cymose, appearing corymbiform, the peduncles 1-3 cm long with a few scattered tomentose hairs. *Flowers* pale green, the pedicel 2-4 mm long, glabrous; calyx with 4 subreniform to broadly ovate lobes, the lobes rounded at the apex; corolla 1-1.5 mm long, the lobes oblong to ovate-triangular, acute at the apex; pistil 1-2 mm long. *Berries* green, spherical, ca 1 cm in diam, usually 1-seeded, the seeds pyriform, 6-8 mm long.

Guatemala southward to Panama and (?)northern South America.

CHIRIQUÍ: valley of the upper Río Chiriquí Viejo, vic of Monte Lirio, *Seibert 241* (MO holotype, GH isotype); vic of Bajo Chorro, *Woodson & Schery 676* (MO), *Davidson 248* (A, F, MO, US); valley of the upper Río Chiriquí Viejo, *White 72* (GH, MO, US).

This species is closely related to *C. erosa* but can be distinguished by its much smaller leaves, flowers and berries.

5. **Cissus biformifolia** Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. **4:** 225, 1929.

C. cardiophylla Standley, loc. cit. 226.

Vine, often climbing and hanging; stems terete to 4-gonal, sulcate to canaliculate, glabrous except for the appressed pilose hairs on the young stems, swollen at the nodes, with sparse minutely elevated lenticels. *Leaves* dimorphic, the younger ones narrowly elliptic to narrowly obovate, 4-10 cm long, 1.5-4 cm broad, long cuneate at the base, short acuminate at the apex, glabrous, chartaceous, the petiole 1.5-4.5 cm long, the older leaves ovate to broadly ovate, 10-18 cm long, 5-13 cm broad, rounded, cordate or deeply cordate at the base, short acuminate to acute at the apex, glabrous, coriaceous, the petiole 3.5-7 cm long, often sulcate and canaliculate; all leaves with 5-7 pairs of ascending lateral veins and entire at the base becoming sparsely and shallowly serrate toward the apex; stipules broadly obovate, 3-4 mm long, early caducous, subrotund at the apex. *Inflorescences* of small compacted cymes appearing as pseudoumbels, the peduncles up to 2 cm long, younger ones appressed pilose; buds 3-4 mm long. *Flowers* dark red, the pedicel 1-2 mm long, with scattered appressed pilose hairs; bracts and bracteoles 2-3 mm long, ovate, acute at the apex; calyx cupular with four rotund teeth which persist in fruiting; corolla of four free petals, the petals ovate-oblong, 3-4 mm long, obtuse at the apex; pistil 2-3 mm long, 2-locular. *Berries* green becoming purple at maturity, 10-12 mm long, 8-10 mm broad, suborbicular to obovoid, apex rounded and usually with a small persistent beak, 1-seeded, the seed 8-10 mm in diam, obovoid.

Reportedly from British Honduras and ranging southward to Panama. The dimorphic leaves, larger flowers and fruits and the glabrous condition distinguish this species from the common *C. sicyoides.*

BOCAS DEL TORO: Changuinola valley, *Dunlap 323* (US holotype, F isotype); 10-15 mi inland from mouth of Changuinola River, *Lewis et al. 861* (GH, K, MO, UC, US); vic of Chiriquí Lagoon, *von Wedel 2983* (GH, MO); Duwebdulup Peak, N of Río Teribe across from Quebrada Huron, *Kirkbride & Duke 576* (MO, NY); Santa Catalina, river bank & beach. *Blackwell et al. 2692* (MO).

6. **Cissus sicyoides** L., Syst. Nat. ed. 10, **2:** 897, 1759.

C. obtusata Bentham, Bot. Voy. Sulphur, 77, 1844.
Vitis sicyoides (L.) Morales in Poey, Repert. Fis-Nat. Isla Cuba, **1:** 206, 1866.
Cissus brevipes Morton & Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. **18:** 653, 1937.

Vine, occasionally shrubby, climbing or sprawling; stems terete, striate, ± canaliculate, glabrous, tomentose to villous, lenticels usually sparse, inconspicuous, ± swollen at the nodes, the older stems often woody with the epidermis becoming loose to form a sheath around the stem and peeling off. *Leaves* variable, broadly ovate to ovate-elliptic to oblong to subrotund, 2.5-15 cm long, 1.7-12.5 cm broad, truncate to rounded to cordate at the base, acute to short acuminate at the apex, the margins shallowly serrate, the teeth short tipped, the lateral veins 4-6 pairs, ascending, the costa and veins ± conspicuous beneath, chartaceous; petiole

1-6.5(-8.5) cm long, terete, ± swollen at the base, glabrous to densely villous; stipules narrowly ovate to ovate-oblong, acute to obtuse at the apex, 2-4 mm long, caducous. *Inflorescences* of small congested cymes, often appearing as pseudo-umbels, the peduncles 1-5 cm long, terete to angulate, ± sulcate, densely villous to glabrous; buds ca 1 mm long, ovoid. *Flowers* greenish-white, white or yellow, becoming red when growing in bright, exposed areas, the pedicel 2-3 mm long, densely villous to glabrous, the calyx cupular with 4 shallow rotund lobes, the lobes often persisting in fruit, the corolla of 4 free, oblong petals, 1.8-3 mm long, pistil 2-3 cm long, bilocular; the 4-lobed disc conspicuous, persisting in fruit. *Berries* 4-6 mm in diam, obovoid, 1-seeded, often with the style persisting as a beak, green turning dark red to black at maturity; seeds 3.5-5 mm in diam, obovoid.

Southern United States, the West Indies, Central and northern South America.

BOCAS DEL TORO: vic of Chiriquí Lagoon, *von Wedel 1367* (GH, MO); id., Old Bank I, *von Wedel 1891* (MO), *1958* (MO), *2070* (MO); id., Water Valley, *von Wedel 838* (GH, MO), *1811* (MO); id., Isla Colon, *von Wedel 2470* (GH, MO), *2952* (GH, MO); region of Almirante, *Cooper 183* (F), *Blum 1334* (MO); Chiriquicito to 5 mi S along Río Guarumo, *Lewis et al. 2015* (GH, MO); vic of Nievecito, *Woodson et al. 1854* (MO); 10-15 mi inland, S from mouth of Changuinola River, *Lewis et al. 981* (GH, MO, US); s. loc., *von Wedel 309* (MO); Santa Catalina, *Blackwell et al. 2751* (COL, MO, UC). CANAL ZONE: Ancon Hill, *Duke 4588* (GH, MO); Barro Colorado I, *Shattuck 268* (MO), *588* (F), *589* (F), *810* (F), *Woodworth & Vestal 38* (F), *154* (F, GH), *553* (F), *Wilson 3* (F); Fort Amador on causeway & I, *Tyson 2009* (MO), *2010* (MO), *2020* (MO), Chagres, *Fendler 52* (MO); 5 mi N of Cocolí *Tyson 3874* (MO); Farfan beach, from Thatcher Hwy to Palso Seco, *Lewis et al. 54* (GH, K, MO, UC, US); Farfan Beach road, *Kirkbride & Elias 59* (MO); 5 mi N of Gamboa on pipeline rd, *Blum & Loftin 2305* (MO); in government forest along Las Cruces Trail, *Hunter & Allen 693* (MO), *700* (MO); vic of Río Chilibre bridge, *Blum & Dwyer 2133* (MO); Fort San Lorenzo, *Tyson & Blum 3674* (MO); Trans Isthmian Highway ca 19 mi from Colón, *Burch et al. 1001* (DUKE, F, GH, K, MO, NY. UC, US). CHIRIQUÍ: vic of San Bartolomé, Peninsula de Burica, *Woodson & Schery 913* (MO); vic of Puerto Armuelles, *Woodson & Schery 832* (MO); Boquete, *Davidson 675* (F, MO). COCLÉ: N rim of El Valle de Antón, nr Cerro Turega, *Woodson & Schery 182* (MO), COLÓN: vic of San Juan at Cement Plant Lake, *Blum & Tyson 526* (MO). DARIEN: Cana, Río San Jose below former goldmine headquarters, *Stern et al. 635* (GH, MO); forest nr Sante Fe, *Duke 8431* (MO); 3 mi E of Santa Fe, *Tyson et al. 4659* (MO); 0-4 mi up Río Sabana from Santa Fe, *Duke 4138* (GH, MO); Río Chico, vic of Yavisa, *Allen 5093* (MO); Río Lara, *Duke 8853* (MO); vic of El Real, along trail to Río Pirre, *Stern et al. 291* (GH, MO), *295* (GH, MO); Tucutí, *Terry & Terry 1400* (F. GH, MO); Río Balsa, betw Manene & Tusijuandra, *Duke 13575* (MO); Patiño, *Duke 10507* (MO); Río Piñas, *Duke 10559* (MO). HERRERA: rd from La Avena to outskirts of Pesé, *Burch et al. 1310* (GH, K, MO, UC, US); Pesé, ca 50 mi, *Allen 792* (F, GH, MO). LOS SANTOS: 1-2 mi W of Candelaria, *Duke 12448* (MO); 5-9 mi from Chitré on rd to Las Tablas, *Burch et al. 1221* (GH, MO); Monagre beach rd, 0.3-1.5 mi from beach, ca 5 mi SE of Los Santos, *Lewis et al. 1681* (COL, MO, UC); Tonosi, on river bank, *Tyson et al. 2996* (MO). PANAMA: Río Cañasas, gravel bar, *Duke 14514* (MO); 1 mi N of Río Chagres along Roosevelt Boyd Hwy, *Blum & Tyson 1985* (MO), *1986* (MO); Chimán, *Lewis et al. 3324* (MO), *3336* (MO); ca 6 mi E of Chepo on Pan-Am Highway, *Duke 4031* (MO), *4041* (MO), *4062* (GH, MO); Gorgona Beach, *Woodson et al. 1697* (GH, MO); Las Sabanas, E of Panama City, *Maurice 811* (MO); Las Sabanas, nr Chepo, *Hunter & Allen 96* (MO); savanna nr Playa Río Mar, *Duke 11763* (MO); vic of Pacora, *Allen 1007* (MO); Pedro Gonzales I, *Dwyer 680A* (MO), *Allen 2584* (MO); San José I, *Johnston 875* (GH, MO), *Duke 12518* (MO); Taboguilla I, *Duke 5876* (MO); Tocumen, *Dwyer 1848* (MO). SAN BLAS: Soskatupu, *Elias 1687* (MO).

Cissus sicyoides, a highly polymorphic species, is one of the more common vines in the neotropics. Readily adapting to disturbed areas, it is one of the few plants to invade successfully the very rocky beaches along lakes and the seacoasts. In this habitat, the leaves are usually small, subrotund and are glabrous. An alternate form is encountered in more protected, less exposed habitats where the leaves are usually ovate, truncate at the base and usually quite pubescent. I hesitate to attempt assigning varietal names since Planchon (loc. cit. 521-531) listed 16 varieties in 1887 and since then no adequate work exists on the neotropical species of *Cissus*. Although some Panamanian collections of *C. sicyoides* can be assigned to a variety, e.g. *C. sicyoides* var. *ovata* Planchon, the majority of the material seems to defy placement.

The tough stems are often used for cordage. In addition, the leaves when macerated in water yield a soapy solution which may be utilized for washing clothes. Practically every specimen I examined from Panama showed varying degrees of infection by the smut, *Mycosyrinx cissi* (DC.) Beck. The internodes of severely infected plants are reduced, the leaves fail to develop properly and the plant has the appearance of "witches broom." The diseased plant is so strange that Presley (Rel. Haenk. **2:** 35, *t.* 53, 1834) described a new genus (*Spondylantha*) of flowering plants from such a specimen.

INDEX OF LATIN NAMES

Numbers in **boldface** type refer to descriptions; numbers in roman type refer to synonyms; numbers with dagger (†) refer to names incidentally mentioned.

FLORA OF PANAMA

BY ROBERT E. WOODSON, JR. AND ROBERT W. SCHERY
AND COLLABORATORS

FAMILY 128. FLACOURTIACEAE[1]

BY ANDRÉ ROBYNS[2]

Missouri Botanical Garden and Department of Botany, Washington University, St. Louis, Missouri

Trees or shrubs, the branchlets sometimes spine-tipped or axillary spinose. *Leaves* usually alternate and/or distichous, rarely opposite or verticillate, persistent, the petiole short to long, sometimes 2-glandular at the apex, the stipules usually small and caducous, sometimes large, foliaceous and persisent, rarely absent; blade simple, entire or not, sometimes 2-glandular at or near the base, penninerved or 3-5-nerved from the base, sometimes with pellucid dots or lines. *Inflorescences* axillary or terminal, fasciculate, racemose, spicate, corymbose or paniculate, sometimes flowers axillary and solitary, the peduncles or pedicels sometimes adnate to the petioles of the subtending leaves, the bracts and bracteoles minute. *Flowers* actinomorphic, ☿ or ♂ ♀, sometimes dioecious or polygamous; sepals 2-several, contorted or imbricate, rarely valvate, sometimes undifferentiated from the petals, usually distinct, sometimes more or less united into a tube, sometimes persistent or even accrescent; petals, when present, hypogynous or $\pm$ perigynous, rarely epigynous, equal in number to the sepals and alternating with them, or sometimes more numerous than the sepals, contorted or imbricate, sometimes with a scale within the base; torus often glandular or sometimes expanded into a glandular disk (between androecium and gynoecium); stamens usually more numerous than the petals, often ∞, 1- or many-seriate, or isomerous with the petals and opposite to them; filaments free or in fascicles alternating with glands, rarely united into a tube; anthers 2-thecate, sometimes appendaged, usually longitudinally dehiscent, rarely opening by terminal pores; pollen grains usually 3-colporate; ovary superior, semi-inferior to rarely inferior, 1-locular with several (2-10) parietal placentas, the later sometimes $\pm$ deeply protruding into the middle of the ovary, infrequently 3-5-locular; ovules usually ∞ on each placenta, anatropous or amphitropous; styles isomerous with the placentas, free to completely united, rarely absent. *Fruit* a valvately dehicent capsule, or fleshy or dry and indehiscent, the pericarp sometimes alate or prickly; seeds few to numerous, sometimes conspicuously arillate, the endosperm usually copious and fleshy, the embryo straight or curved; cotyledons usually broad, often cordate. —x = 10, 11, 12.

A family of about 85 genera and 1300 species, nearly all woody, chiefly of tropical distribution, with some extensions into the temperate zone; 15 genera, at

[1] Assisted by National Science Foundation Grant No. GB-5674 (Principal Investigator, Walter H. Lewis).

[2] Visiting Curator of the Flora of Panama, Missouri Botanical Garden; *Chargé de Recherches* of the National Foundation for Scientific Research, Belgium.

ANN. MISSOURI BOT. GARD. **55**(2): 93-144, 1968.

present, reported from Panama, several additional genera occurring in Central America, namely: *Bartholomaea* Standley & Steyermark, *Macrohasseltia* L. Wms. (Honduras, Costa Rica), *Olmediella* Baillon, and *Pleuranthodendron* L. Wms. (from Mexico, through Central America, to northern South America).

Economically the family is of little importance; *Oncoba spinosa* Forsk. from Africa, cultivated at the Plant Introduction Garden at Summit, Canal Zone (*Steyermark s.n.*, MO, in 1935) has edible fruits.

The *Flacourtiaceae* are characterized by a combination of several characters: numerous stamens, receptacle often glandular or often expanded into a glandular disc, ovary superior and 1-locular with parietal placentation, copious endosperm, and often undifferentiated perianth. In some genera the placentas are deeply protruding into the middle of the ovary and the ovary is sometimes even plurilocular, e.g. in *Prockia* with a 3-5-locular ovary and *Hasseltia* with a 2(-3)-locular ovary; these genera are perhaps better placed in the *Tiliaceae* (see Hutchinson, The Genera of Flowering Plants **2:** 476, 478, 1967). The family is somewhat indeterminate and, as noted by Sleumer (in Van Steenis, Fl. Males., ser. I, **5:** 2, 1954), "no single character exists wherewith to distinguish *Flacourtiaceae* from other families or to recognize them in the field."

The following key to the genera is based only on Panamanian collections.

a. Petals present.
  b. Petals more numerous than the sepals.
    c. Fruits echinate.
      d. Styles simple; stigma shortly 3-lobulate; flowers ☿ or ♂ by abortion ....1. *Lindackeria*
      dd. Styles 3, each one 2-lobed, the lobes laciniate; flowers dioecious ....2. *Mayna*
    cc. Fruits with broad, vertical wings ....3. *Carpotroche*
  bb. Petals isomerous with the sepals.
    e. Leaves 3-nerved from the base.
      f. Flowers small, in large, compound, repeatedly 3- to 4-radiate umbels; anthers small, subglobose; ovary 2(-3)-celled ....4. *Hasseltia*
      ff. Flowers large, in few-flowered racemes; anthers elongated-linear; ovary incompletely 5-9-locular by the intrusion of the placentas ....5. *Neosprucea*
    ee. Leaves penninerved.
      g. Sepals 3(-4); stamens pluriseriate, inserted on a densely villosulous disc; ovary superior, with 5-8 intruding, lamelliform placentas ....6. *Banara*
      gg. Sepals (5-)6-7; stamens in fascicles of 3, rarely 2, the fascicles alternating with minutely tomentellous glands; ovary half inferior, with 2-6(-8) parietal placentas ....7. *Homalium*
aa. Petals absent.
  h. Flowers ☿, branchlets unarmed (except in *Casearia stjohnii*).
    i. Stipules large, foliaceous, and persistent or not.
      j. Stipules inequilateral, glandular-crenate along the margins, persistent; leaves slender and rather long-petiolate; flowers pedicellate, in racemes; calyx 5.5 to 6.5 mm long; stamens ∞; ovary 3-5 locular ....8. *Prockia*
      jj. Stipules somewhat falcate, entire-margined, caducous; leaves short-petiolate; flowers sessile, paniculate-spicate, densely crowded or not along the secondary rachises; calyx to 3.5 mm long; stamens 4; ovary 1-locular ....9. *Tetrathylacium*
    ii. Stipules small to usually very small, caducous, or absent; ovary 1-locular.

k. Inflorescences mostly fasciculate, sometimes cymose or flowers solitary; leaves stipulate, penninerved; sepals 4-6(-9).
l. Staminodes alternating with the stamens.
m. Style present, simple or divided at the apex into 3 branches, the stigmas 1-3, capitate ....10. *Casearia*
mm. Style absent or obsolete, the stigma thick and peltate ....11. *Zuelania*
ll. Staminodes absent.
n. Indumentum of simple hairs; leaf blades pellucid-punctate; sepals to 9 mm long; anthers not appendaged ....12. *Laetia*
nn. Indumentum mostly stellate; leaf blades epunctate; sepals 1.3-5 cm long; anthers mucronate ....13. *Ryania*
kk. Inflorescences racemose; leaves estipulate, 3-(5-)nerved from the base; calyx, at length, split into 2-3 lobes ....14. *Lunania*
hh. Flowers ♂ ♀ (or polygamous); branchlets often with axillary spines; leaves estipulate ....15. *Xylosma*

1. LINDACKERIA

Lindackeria C. Presl, Reliq. Haenk. **2:** 89, *pl.* 65, 1835.

Shrubs or trees, unarmed. *Leaves* alternate, petiolate, the petiole often elongate and pulvinate at the apex, the stipules none or early caducous, the blade rather large, entire-margined or the margins dentate, glabrous or pilose below, the hairs simple or stellate, penninerved. *Inflorescences* axillary or terminal, short to elongate, racemose or paniculate, usually many-flowered, infrequently flowers solitary. *Flowers* rather small, ☿ or ♂ by abortion, pedicellate, the bracts early caducous; sepals 3, imbricate; petals 6-12, imbricate, equalling ± the sepals; stamens ∞, the filaments filiform, free or rarely united into a tube, the anthers basifixed, linear, longitudinally dehiscent; ovary shortly stipitate, smooth, muricate, or echinulate, usually hairy, 1-locular, with 3 parietal placentas, the placentas pauci- or multi-ovulate, the style simple, the stigma simple or obscurely 3-lobulate. *Fruits* capsular, globose, coriaceous to ligneous, tuberculate or echinate, tardily 3-valvate; seeds few, ovoid, the endosperm copious, the embryo large, the cotyledons large, cordate, foliaceous.

About 12 species in the tropics of Africa and America; only the following species reported from Panama and Central America.

1. **Lindackeria laurina** C. Presl, Reliq. Haenk. **2:** 89, *pl.* 65, 1835.—Fig. 1.
Mayna laurina (C. Presl) Bentham, Jour. Proc. Linn. Soc., Bot. **5** (Suppl. 2): 87, 1861.
Oncoba laurina (C. Presl) Warb. in Engler & Prantl, Nat. Pflanzenfam. **3**(6a): 18, 1893.

Tree 3-8 m high, sometimes to 15(-35) m high, the trunk 5-35 cm in diam, the branchlets angulate, striate, glabrous, often grayish. *Leaves* glabrous, the petioles 2.5-11 cm long, slightly pulvinate at the apex; blade narrowly elliptic, elliptic or ± ovate, obtuse to rounded at the base, long-acuminate at the apex, the margins entire to usually undulate, 10-31 cm long and 5-11 cm wide, papyraceous, ± shiny above, paler beneath, the costa prominent beneath, the secondary veins slightly prominent beneath. *Inflorescences* axillary and terminal, paniculate, to 22 cm long, the rachis glabrous. *Flowers* white, the pedicels angulate, to 1.5 cm long, glabrous, ± shining; sepals ± obovate or largely obovate, cucullate, reflexed at anthesis, 6-9 mm long and 4.5-5.5 mm wide, glabrous or inconspicuously

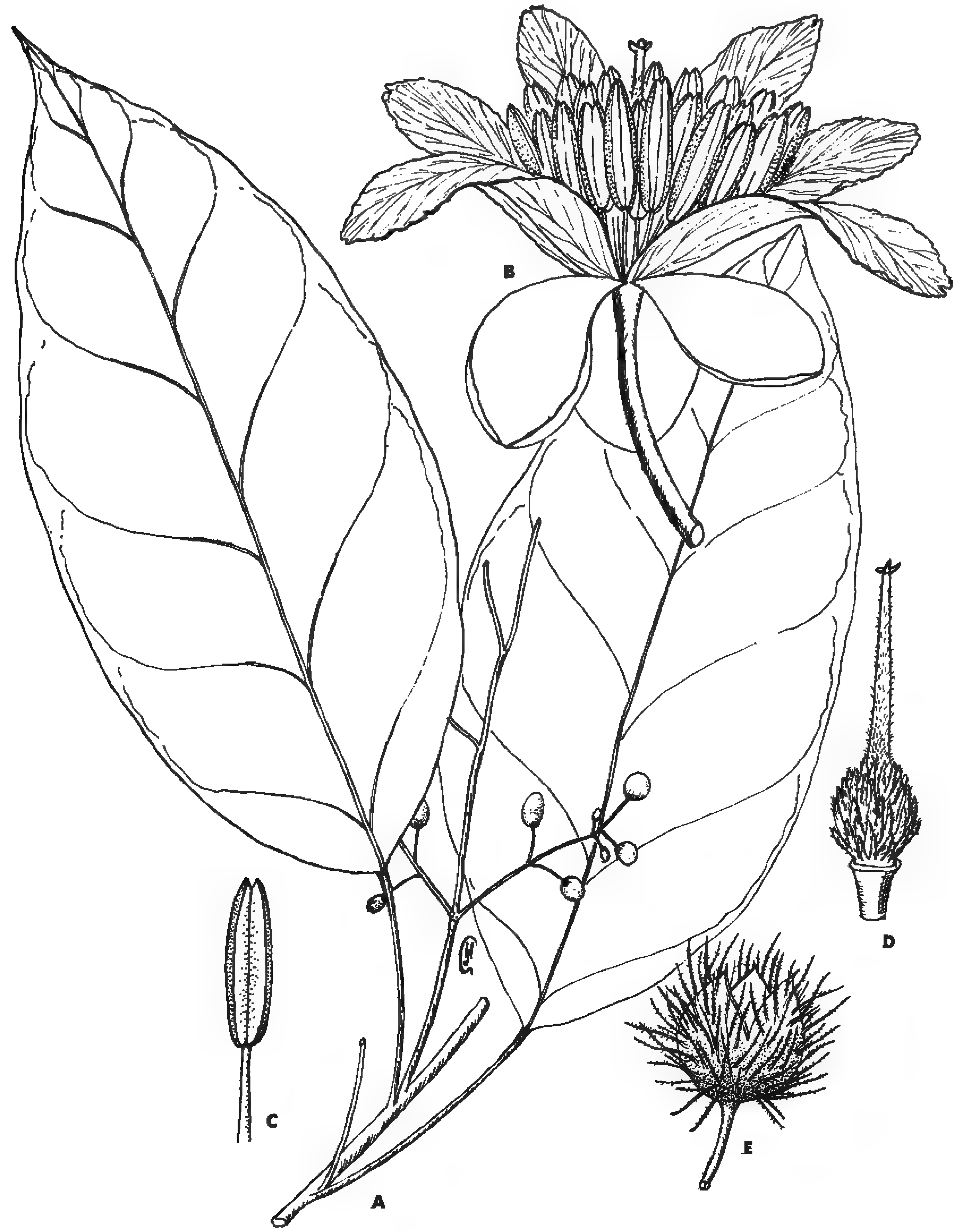

Fig. 1. *Lindackeria laurina* C. Presl: A, habit (×½); B, flower (×4); C, stamen (×5); D, gynoecium (×5); E. dehiscent capsule (×1). A-D after *Blum 1271* (MO); E after *Stern et al. 516* (MO).

puberulous and shining outside, caducous; petals elliptic to narrowly elliptic, obtuse to ± rounded at the apex, ± undulated along the margins, 9-12 mm long and 2.5-5 mm wide, glabrous, shining outside; stamens 26-40, the filaments scarcely connate at the base, unequal, 2-4.5 mm long, glabrous or sparsely and inconspicuously puberulous, the anthers ± oblong, emarginate at the base, slightly bifid at the apex, ca 3.5-4.2 mm long, glabrous or sparsely and inconspicuously puberulous at both ends; ovary very shortly stipitate, the stipe ca 0.5 mm long or less, ovoid, densely appressed-soft-echinate, the bristles minutely puberulous; style 5-6 mm long, minutely puberulous especially on the lower half, the stigma shorty 3-lobulate. *Capsule* long surmounted by the persistent style, echinate, to 1.5 cm in diam (without bristles), the pericarp rugose, shiny, and inconspicuously puberulous, the bristles to 8 mm long and inconspicuously puberulous; seeds few - 1, ± angulate, to 7 mm long.

Southern Mexico, Guatemala, British Honduras, Costa Rica, Panama, and perhaps Colombia and Venezuela; known colloquially in Panama as *uvre* (cf. *Cooper & Slater 167*) and *chopo cucullo* (cf. *Duke & Bristan 394*).

This species is generally known in Panama under the name *Oncoba laurina.* According to Duke & Bristan the fruits have a bad flavor and the leaves are used in the Province of Darien to cure snakebites.

CANAL ZONE: Mojinga swamp nr mouth of Río Chagres, alt below 1 m, *Allen 907* (F, MO, NY, US); Barro Colorado I, *Aviles 110* (F), *Bangham 406* (F, US), *Frost 137* (F), *Shattuck 687* (F, MO), *1088* (F, MO, US), *Starry 296* (F); vic of Cerro Viejo on K 16 C, *Blum 1271* (MO); drowned forest of Río Puente nr jct with Río Chagres, alt 66 m, *Dodge et al. 16828* (MO); Thatcher Ferry Rd, *Duke 5755* (MO); Madden Dam, Boy Scout Camp Rd, roadside woods, *Dwyer & Elias 7472* (MO); Gatun Station, *Hayes 15* (MO, US), 92 (NY); s. loc., *Hayes 18* (US); rd W of Pina Base Camp, *Johnston 1589* (MO), *1770* (MO); vic of Frijoles, *Piper 5794* (NY, US); Agua Clara, on the Trinidad River, alt 10-40 m, *Pittier 3991* (NY, US); betw Corozal & Ancon, alt 10-30 m, *Pittier 6727* (NY, US); 5 mi NW of Cocoli, alt 500 ft, *Tyson 1616* (MO). CHIRIQUÍ: vic of Remedios, alt 0-150 m, on edge of mangrove swamp, *Allen 3665* (F, MO, NY, US); Progreso, *Cooper & Slater 167* (F, NY, US); Tolé, vic of Santa Ana Well, alt ca 1000 ft, thicket on hillside paralleling brook, *Dwyer & Kirkbride 7464* (MO); vic of San Felix, alt 0-120 m, *Pittier 5228* (F, NY, US). COLÓN: vic of Camp Pina, alt 25 m, *Allen 3675* (MO, NY, US). DARIEN: Río Tuira, betw Río Punusa & Río Mangle, *Duke 14581* (MO); San José River, *Duke & Bristan 394* (MO); vic of Cana, summit of Cerro Cana, alt 2500 ft, *Stern et al. 516* (MO, US). PANAMA: vic of La Chorrera, alt 30 m, *Allen 2751* (MO, US); Río Tocumen down road from La Siesta, *Dwyer 4338* (MO); Chimán, rain forest, *Lewis et al. 3236* (MO); La Chorrera, *Bro. Paul 501* (MO, US).

2. MAYNA

Mayna Aublet, Hist. Pl. Gui. Fr. 921, *pl.* 352, 1775.
Dendrostylis Karsten & Triana, Linnaea **28:** 431, 1856[3].

Shrubs or small to medium-sized trees. *Leaves* alternate, petiolate, the petiole pulvinate at the apex, the stipules early caducous, the blade entire-margined or the margins dentate. *Flowers* dioecious; staminate flowers axillary, in small fascicles or sometimes solitary; pistillate flowers axillary and usually solitary; sepals 3, imbricate; petals 6-9, imbricate, longer than the sepals; staminate flowers with ∞ stamens, the filaments inserted on a scarcely thickened torus, free or almost so, pilose, the anthers linear, longitudinally dehiscent; pistillate flowers with the ovary echinulate, 1-locular, with 3 parietal placentas, the placentas multi-ovulate, the styles 3 or 4, each one 2-lobed, the lobes laciniate. *Fruits* baccate, globose,

[3] According to a note by A. Dugand in the U. S. National Herbarium the correct citation for *Dendrostylis* should read: *Dendrostylis* Karsten & Triana in Triana, Nuevos Generos i Especies di Plantas para la Flora Neo-Granadina 27, 1854 (Bogota).

bristly, indehiscent; seeds ∞, the testa red or orange, fleshy; endosperm copious; embryo straight; cotyledons cordate.

A small genus much in need of revision; about 15 species in tropical America, mainly in northern South America; two species reported from Panama.

In the absence of fruits it is very difficult, if not impossible, to distinguish this genus from *Carpotroche* Endl.

a. Leaf blades glabrous; staminate flowers with the sepals 5-7 mm long and with the petals 10-11.5 mm long; fruit to 2.5 cm in diam ....1. *M. longicuspis*
aa. Leaf blades with the upper surface sparsely hirtellous especially along the veins and with the lower surface softly hirsute; staminate flowers with the sepals to 8 mm long and with the petals 12-14.5 mm long; fruit to 1.5-2 mm in diam ....2. *M. zuliana*

1. **Mayna longicuspis** (Standley) Standley, Trop. Woods **52:** 27, 1937.
Sloanea longicuspis Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. **4:** 229, 1929.
Carpotroche subintegra Standley, loc. cit. 236.

Shrub or small tree 2-5 m high, the trunk 2.5-5 cm in diam, the branchlets terete, ochraceous, glabrous or almost so. *Leaves* clustered towards the tip of the branchlets, the petiole 1-4 cm long, thickened at the apex, canaliculate above, sparsely puberulous to glabrous; blade elliptic to obovate, usually narrowly so, attenuate and acute to obtuse at the base, acuminate to long-acuminate at the apex, the margins entire to remotely and obscurely serrulate, sometimes coarsely serrate towards the apex, the serrations often mucronulate, 15-23 cm long and 4-8.5 cm wide, chartaceous, glabrous, the costa prominent beneath, the lateral veins prominulous beneath. *Staminate flowers* white, in few-flowered fascicles, the pedicels 1-3 mm long, shortly appressed-puberulous, the bracteoles triangular-filiform; sepals ± rotund, conchiform, 5-7 mm long and 6-6.5 mm wide, shortly appressed-puberulous; petals 7, obovate, rounded at the apex, 10-11.5 mm long and 5.5-6 mm wide, glabrous; stamens ∞, the filaments ca 0.5-0.6 mm long, strigillose, the anthers oblong-linear, ca 1.8 mm long, strigillose along the margins. *Pistillate flowers* not seen. *Fruit* yellow or green, globose, to 2.5 cm in diam (without bristles), surmounted by the 3 persistent styles, densely bristly, the bristles to 7 mm long and hirtellous as the pericarp; seeds orange, to 1 cm long, the testa striate, shining.

Only reported from Panama. This species is close to and perhaps conspecific with the Colombian *M. suaveolens* (Karsten & Triana) Warburg (in Engler & Prantl, Nat. Pflanzenfam. **3**(6a): 19, 1893).

CANAL ZONE: Quebrada Lopez, alt 30 m, *Allen 2127* (F, MO, US). CHIRIQUÍ: Progreso, *Cooper & Slater 234* (type US); vic of San Bartolomé, Peninsula de Burica, alt 0-50 m, *Woodson & Schery 870* (F, MO). COCLÉ: N rim of El Valle de Antón, alt 600-1000 m, *Allen 1646* (F, MO). DARIEN: Quebrada Bidoto (Peccary Creek) off Río Areti, *Duke 13591* (MO). PANAMA: Cerro Trinidad, alt 800-1000 m, *Allen 3771* (F, MO). SAN BLAS: Permé, *Cooper 638* (type *Carpotroche subintegra* F, NY); along headwaters of Río Malatupu, seasonal evergreen forest, *Elias 1763* (MO); forest around Puerto Obaldía, alt 0-50 m, *Pittier 4296* (F, US).

2. **Mayna zuliana** (Pittier) A. Robyns, Ann. Missouri Bot. Gard. **55:** 78, 1968.—Fig. 2.
Carpotroche zuliana Pittier, Bol. Com. Ind. (Venezuela) **4**(34): 38, 1923 (Arboles y Arbustos Nuevos de Venezuela, secunda y tercera decadas).

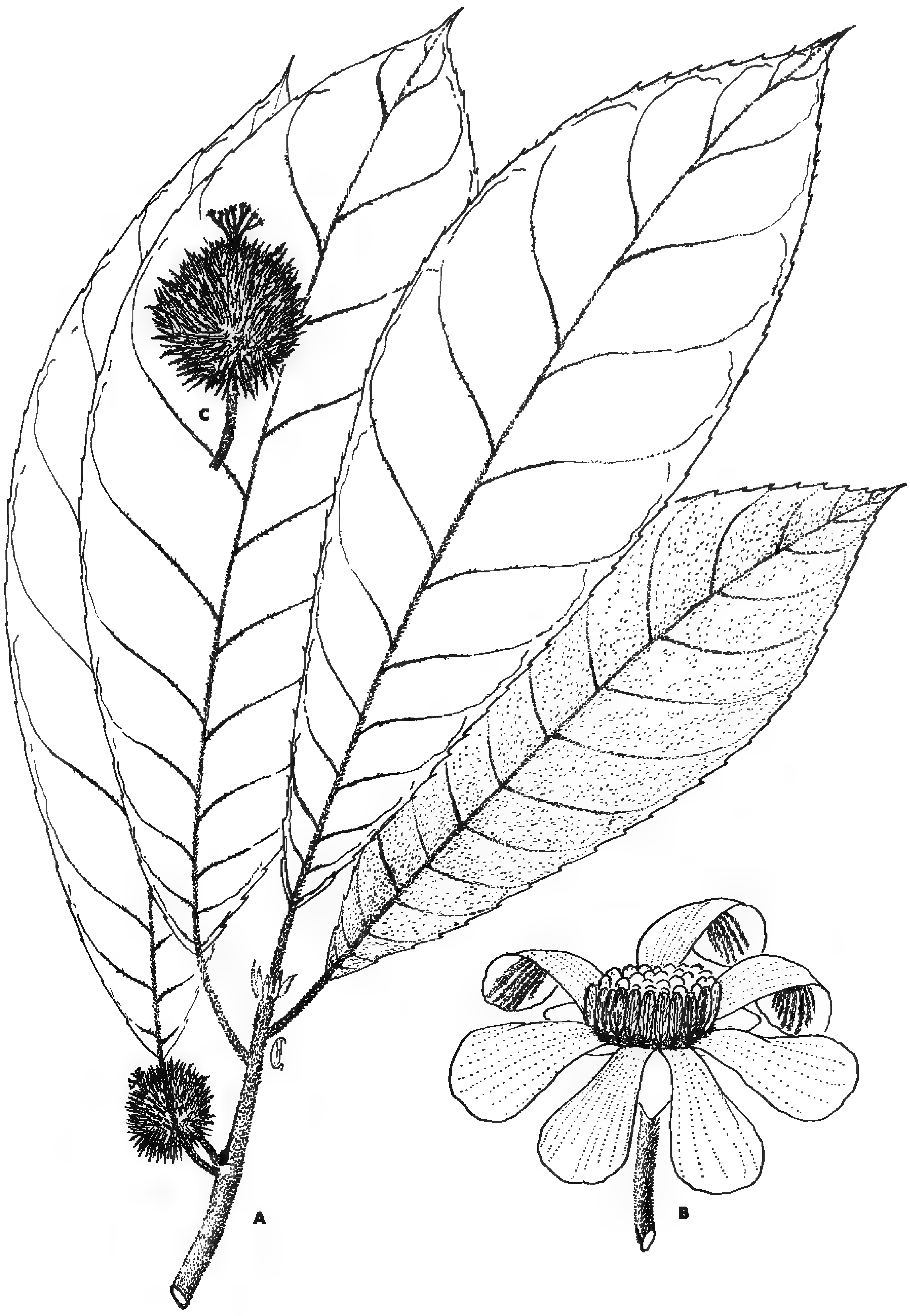

Fig. 2. *Mayna zuliana* (Pittier) A. Robyns: A, habit (×½); B, staminate flower (ca ×2); C, fruit (×1). A & C after *Duke 4994* (MO); B after *Allen 4630* (MO).

Shrub or small tree, 4.5-7.5 m tall, the trunk 7.5-15 cm in diam, the branchlets hirsute when young. *Leaves* with the petioles slender, 0.8-3 cm long, canaliculate above, hirsute, the stipules subulate, 7.5-10 mm long, hirsute; blade narrowly obovate to elliptic-obovate, long-attenuate towards the base, ± obtuse at the base, acuminate at the apex, remotely serrulate-ciliate along the margins, 11-30 cm long and 4-11.5 cm wide, chartaceous, the upper surface ± shiny and sparsely hirtellous especially along the veins, the lower surface dull and softly hirsute, the costa prominent beneath, the secondary veins prominulous. *Staminate flowers* solitary or in small fascicles towards the end of the branchlets, the pedicels to 10 mm long, densely short-sericeous, the bracts subulate, 4-6 mm long, densely short-sericeous; calyx valvate, the sepals rotund-conchiform, to 8 mm long and wide, densely short-sericeous outside except on the margin covered in prefloration, glabrous inside; petals 7-8, white, obovate, rounded, 12-14.5 mm long and 5-7 mm wide, appressed-silvery-sericeous in the middle outside, glabrous inside and marginally outside; stamens ca 50, the filaments almost free, ca as long as the anthers, silvery-pilose, the anthers oblong, ca 2 mm long, very sparsely pilose, longitudinally dehiscent; rudimentary ovary lacking. *Pistillate flowers* not seen. *Fruit* with the pedicel to 8 mm long, articulate below the middle (?), densely short-sericeous, the bracts and sepals as in the staminate flowers, long-persistent; bacca globose, surmounted by the persistent styles, 1.5-2 cm in diam (without bristles), densely bristly, the bristles ca 3-5 mm long, hirtellous, the styles 3 or 4, hirtellous below, each style deeply bifid, the lobes laciniate; seeds few, broadly ovate-angulate, to 7.5 mm long, striate, glabrous.

Panama and Venezuela (Dept Zulia).

DARIEN: headwaters of Río Chico, alt 500-750 ft, fairly frequent in heavy forest, *Allen 4630* (MO); betw Quebrada Venado & Peje swamp on the headwaters of Río Tuqueza, *Bristan 1060* (MO); km 16 from Yaviza along Quebrada Uvital off Río Chucunaque, *Duke 4994* (MO); Río Balsa, betw Manene & Tusijuanda, *Duke 13570* (MO); InterAmer Hwy, ca 1 mi SE of Río Tuira, *Duke 14561* (MO); betw Río Punusa & Río Pucro, *Duke 14648* (MO); in pasture belonging to Mr. Pablo Othon, *Duke & Bristan 290* (MO); Patiño, on cliffs along the beach, *Pittier 6673* (US); vic of Campamento Buena Vista, Río Chucunaque above confluence with Río Tuquesa, growing on muddy bank, *Stern et al. 908* (MO, US). PANAMA: woods along PanAmer Hwy ca halfway betw El Llano & Río Mamoni, *Duke 5629* (MO); Tocumen, *Dwyer 1179* (MO).

3. CARPOTROCHE

Carpotroche Endl., Gen. Pl. 918, 1839.

Shrubs or trees. *Leaves* alternate, short- to long-petiolate, the stipules early caducous, the blade entire-margined or the margins mostly serrate. *Flowers* odoriferous, rather large, monoecious, dioecious or rarely polygamo-dioecious, the staminate flowers axillary, in short racemes or almost fasciculate, the pistillate ones axillary and solitary or few-fasciculate; sepals 2-3, imbricate, persistent; petals 4-12, ± biseriate, imbricate; stamens ∞ (pistillate flowers lacking any rudiments of stamens), the filaments short, inserted on a slightly thickened torus, pubescent, the anthers linear, basifixed, longitudinally dehiscent; ovary superior (no rudimentary ovary in staminate flowers), longitudinally costate, 1-locular, the placentas 4-8, many-ovulate; styles isomerous with the placentas, short, persistent, the stigmas scarcely capitellate. *Fruits* capsular, rather large, coriaceous to ligneous, longitudinally alate, the wings up to 16, large and undulated, crowned by the persistent styles, indehiscent; seeds numerous, smooth, immersed in a fleshy pulp; albumen copious; embryo straight; cotyledons foliaceous.

A neotropical genus of about 20 species; one species reported from Panama.

1. **Carpotroche platyptera** Pittier, Contr. U. S. Nat. Herb. **12:** 178, *pl. 19, figs. 15, 16,* 1909.—Fig. 3.

Shrub 1.50-2.40 m high, or small tree up to 6 m high, the trunk to ca 7.5 cm in diam, the young branchlets inconspicuously puberulous. *Leaves* on petioles to 5 cm long, thick, and inconspicuously puberulous; blade obovate to narrowly obovate, long-attenuate towards the base, obtuse at the base, acuminate at the apex, coarsely serrate to serrulate along the margins, to 50 cm long and 18 cm wide, chartaceous, inconspicuously puberulous mainly along the costa and lateral veins beneath, the costa very prominent and the lateral veins prominent below. *Staminate flowers* fasciculate in the leaf-axils (or on the trunk?), the pedicels short, puberulous; sepals 2, concave, to 6.5 mm long, puberulous outside, glabrous inside; petals 4 or more (5 or 6 in Panamanian material), oblong-elliptic to narrowly oblong-elliptic, the apex involute at least in bud, to 6.5 mm long and 1.7-2.7 mm wide, sparsely appressed-pilose in the middle especially outside; stamens ∞ (21-26 counted in Panamanian material), the filaments ca 0.5 mm long, densely barbate, the anthers to 3.5 mm long, appressed-pilose. *Pistillate flowers* (not seen; description acc. to Pittier, loc. cit. 179), solitary, to 30 mm in diam; sepals as in staminate flowers but larger; petals 8, elliptic-obovate, $\pm$ obtuse; ovary ovoid, longitudinally 8(-10)-ribbed, pilose, with 4(-5) placentas, the styles 4(-5), distinct, very short. *Capsule* $\pm$ globose, reddish or purplish, 2.5-4.5 cm long (wings included), ligneous, with 8-10 broad, vertical, undulate-margined wings, these 0.8-2 cm broad in the middle, rigid-chartaceous, inconspicuously puberulous; seeds ovoid, angulate, to 0.8 cm long.

Guatemala to Panama, along the Atlantic coast, in forest.

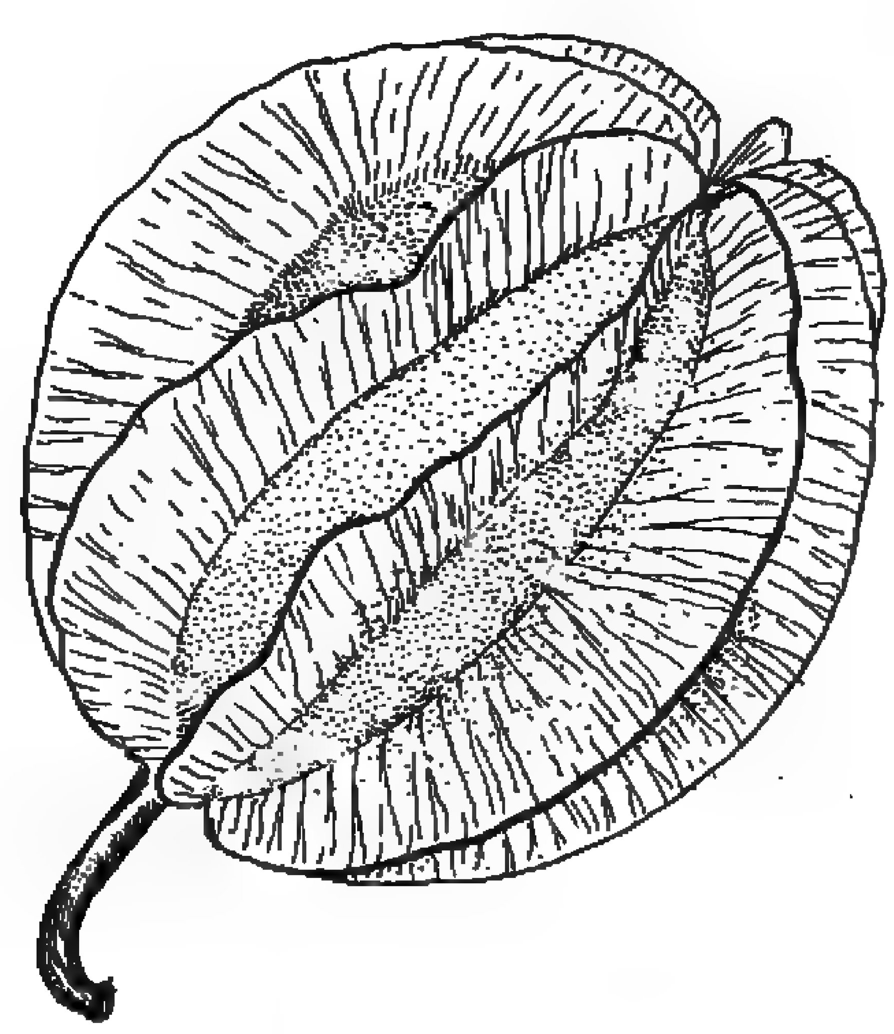

Fig. 3. *Carpotroche platyptera* Pittier: Capsule (×1), after *von Wedel 1453* (MO).

It is difficult to say whether the plants are monoecious or dioecious. On several herbarium sheets, however, staminate flower buds and capsules are present (although the latter are never attached to the specimens) and this suggests that the flowers are monoecious. I did not see pistillate flowers!

Carpotroche crassiramea Pittier (loc. cit. 180) from Costa Rica is probably synonymous with our species, the only significant difference being the number of wings on the capsule: 10 wings in *C. crassiramea* and 8 wings in *C. platyptera.*

This species is called colloquially *rabo de gallo* in Panama (cf. *von Wedel 2186*). According to Seibert (*1571*) the bark and wood smell much like potassium cyanide.

BOCAS DEL TORO: region of Almirante, Daytonia Farm, *Cooper 367* (F, US), *377* (F, NY, US); Changuinola Valley, *Dunlap 129* (F); 10-15 mi S from mouth of Changuinola River, *Lewis et al. 879* (MO); Nievecito, United Fruit Co., *Seibert 1571* (US); lower Changuinola River, *Stork 129* (US); vic of Chiriquí Lagoon, *von Wedel 1029* (MO, US); Water Valley, vic of Chiriquí Lagoon, *von Wedel 1453* (MO), *1471* (MO), *1650* (MO); Fish Creek, vic of Chiriquí Lagoon, *von Wedel 2186* (MO, US).

4. HASSELTIA

Hasseltia H.B.K., Nov. Gen. Sp. Pl. **7:** 231, *pl. 651,* 1825.

Shrubs or trees. *Leaves* alternate, petiolate, the stipules soon caducous; blade entire or serrate along the margins, 3-nerved from the base, with 2 glands on the upper side at the base. *Inflorescences* terminal or axillary, in large, compound, repeatedly 3- to 4-radiate umbels. *Flowers* small, ☿, pedicellate; sepals (3)4, valvate, persistent; petals (3)4, valvate, persistent; stamens ∞, free, inserted on a glandular or eglandular disc, the filaments filiform, the anthers small, subglobose, 2-thecate, basifixed, longitudinally dehiscent; ovary free, superior, 2-(3-)celled by complete union of the 2(3) opposite parietal placentas, the ovules ∞, the style simple, entire. *Fruits* baccate, each cell usually 1-seeded; seeds pendulous, the testa coriaceous, the endosperm present; embryo straight; cotyledons foliaceous.

A neotropical genus of about five to eight species; three species reported from Panama.

a. Leaf blades chartaceous, coarsely and irregularly serrate along the margins .... 1. *H. floribunda*
aa. Leaf blades subentire- to entire-margined.
  b. Leaf blades charteaceous, the margins subentire; sepals ca 4 mm long; ovary puberulous .... 2. *H.* cf. *guatemalensis*
  bb. Leaf blades coriaceous, the margins entire and slightly recurved; sepals to 3 mm long; ovary glabrous .... 3. *H. rigida*

1. **Hasseltia floribunda** H.B.K., Nov. Gen. Sp. Pl. **1:** 232, *pl. 651,* 1825.—Fig. 4.

Shrub or small tree 3-10 m high, the trunk to 30 cm in diam, the branchlets glabrous or appressed-puberulous. *Leaves* dark green, with the petioles to 4 cm long, canaliculate above, glabrous or appressed-puberulous; blade from narrowly to broadly-elliptic, sometimes oblong-elliptic, acute at the base, obtusely acuminate at the apex, coarsely and irregularly serrate along the margins, to 22.5 cm long and 11 cm wide, chartaceous, glabrous above, glabrous or appressed-puberulous especially along the veins below, the main veins and secondary veins prominent

Fig. 4. *Hasseltia floribunda* H.B.K.: A, habit (×½); B, flower (×9); C & D, stamen (×30); E, gynoecium (×8); F, bacca surmounted by the persistent style (×5). A-E after *Erlanson 380* (US); F after *Shattuck 855a* (MO).

beneath, the network of the veins prominulous below. *Inflorescences* usually large and many-flowered, the axes puberulous. *Flowers* greenish, yellowish-white or white, the pedicels slender, to 1 cm long, puberulous to tomentellous; sepals 4, reflexed, ovate, acute, to 2.8 mm long and 1.3-1.7 mm wide, puberulous to tomentellous; petals 4, reflexed, obovate, acute, to 2.7 mm long and 1.2-1.4 mm wide, puberulous to tomentellous; stamens 30-40, inserted on a glandular disc (apparently 8 separate glands), the filaments 3-4 mm long, puberulous to sparsely puberulous, the anthers ca 0.25-0.3 mm long; ovary substipitate, globose-ellipsoid, ca 1.5-1.8 mm long and 1.3-1.5 mm wide, puberulous to subglabrous, the style ca 1.5-2 mm long. *Bacca* subglobose, surmounted by the persistent style, 4-6 mm long, the pericarp succulent, red to black, puberulous, becoming glabrous; seeds 1 or 2, 3.5-4.5 mm long, the testa glabrous.

From Honduras to Panama, and in northern South America.

BOCAS DEL TORO: nr Bocas del Toro, *Carleton 198* (F, US); Changuinola Valley, *Dunlap 550* (F). CANAL ZONE: Barro Colorado I, *Bailey & Bailey 534* (F), *Bangham 539* (F), *Brown 39* (F), *57* (F), *Dwyer 1450* (F), *Shattuck 674* (MO), *855a* (MO, US), *855b* (MO), *Standley 31441* (US), *40929* (US), *Wetmore & Abbe 196* (F), *Wilson 58* (F), *103* (F), *Woodworth & Vestal 448* (F), *646* (F), *Zetek 5071* (F); on Las Cruces Trail, vic Trans-Isthmian Hwy, *Blum & Miller 2283* (MO); 12 m S of Colón, vic Río Providencia, *Blum & Tyson 2318* (MO); nr Quebracho on Panama Railroad, *Christopherson 122* (US); Monte Lirio, *Christopherson 129* (US); vic of Hill C-6, Ft. Sherman, shaded areas, *Duke 4389* (MO); Madden Dam, *Dwyer 2183* (MO); Empire Station, *Hayes 36* (MO); Bojio Station, *Hayes 946* (NY); common in many places along Panama Railroad, *Hayes 1016* (NY); vic of Gatuncillo, *Piper 5604* (NY, US), *5655* (US); hills N of Frijoles, *Standley 27428* (US); Darien Station, moist thicket, *Standley 31614* (US); Obispo, *Standley 31686* (US); rd from Ft. Sherman to Gatun Locks, *Tyson & Blum 3805* (MO). COLÓN: Portobello, La Cruzio Trail, *Ebinger 100* (MO); betw France Field, Canal Zone, and Catival, wooded swamp, *Standley 30266* (US), *30297* (US). DARIEN: trail betw Pinogana and Yavisa, alt ca 15 m, *Allen 246* (F), *289* (F, MO, NY); headwaters Río Chico, alt 500-750 ft, *Allen 4604* (F, MO); Río Pirre, 2-5 mi above El Real, *Duke 5089* (MO); hills nr Pidiaque, *Duke 8039* (MO); Río Pirre, *Duke & Bristan 8272* (MO), *8278* (MO); Río Sabana, *King Leopold III 104* (MO); forest around Pinogana, *Pittier 6528* (US); El Real de Sta. Maria, *Pittier 6967* (NY, US); vic of Paya, Río Paya, *Stern et al. 186* (MO, US); Río Tuira, S of El Real, Don Pablo Othon's pasture, foothills of Cerro Pirre, *Stern et al. 748* (MO, US); Cana & vic, alt 2000-6500 ft, *Williams 984* (NY, US). PANAMA: along Río Juan Díaz above Juan Díaz, alt ca 30 m, *Allen 940* (F, MO, NY, US); Bohio Soldado, *Cowell 243* (NY, US); nr confluence of Río Pacora & Río Corso, alt ca 450 m, *Duke 11968;* San José I, *Erlanson 380* (NY, US), *Johnston 372* (MO, US); nr Chepo, *Kluge 32* (F), *s.n.* (US); Río Tapía, *Standley 26139* (US), *28231* (US); Río Tocumen, moist forest, *Standley 29330* (US), *29360* (US); Juan Díaz, *Standley 31597* (US). PROVINCE UNKNOWN: s. loc., *Seemann s.n.* (NY).

2. **Hasseltia** cf. **guatemalensis** Warb. in Engler & Prantl, Nat. Pflanzenfam. **3**(6a): 32, *fig. 12, D-E,* 1893 .

Tree to 30 m tall, the trunk to 55 cm in diam, the branchlets puberulous when young. *Leaves* with the petioles to 2 cm long, canaliculate above, appressed-puberulous when young; blade elliptic, obtuse to acute at the base, obtuse to obtusely short-acuminate at the apex, subentire-margined, to 12.5 cm long and 5.5 cm wide, chartaceous, somewhat shiny and glabrous above, dull and sparsely appressed-puberulous when young especially along the veins beneath, the main veins and secondary veins prominulous beneath. *Inflorescences* large and many-flowered, the axes puberulous to tomentellous. *Flowers* with the pedicels slender, to 1 cm long, tomentellous; sepals (3-)4, ovate, acute, ca 4 mm long and 3 mm wide, tomentellous; petals (3-)4, ovate, acute, ca as long as the sepals but somewhat narrower, tomentellous; stamens inserted on a glandular disc, with glabrous filaments to 3 mm long; ovary puberulous, 2- or 3-celled, the style ca 1.5 mm long. *Bacca* (immature) subglobose, sparsely puberulous.

CHIRIQUÍ: nr sawmill on Río Chiriquí Viejo, 3 km N of Camp El Volcán, alt 4300 ft, evergreen rain forest, *Little 6063* (F, MO, NY).

The above described collection is very close to *H. guatemalensis* (see Standley & L. Williams, Flora of Guatemala, Fieldiana: Bot. **24**(7): 94, 1961) (Mexico to Nicaragua), but differs by the tomentellous pedicels and sepals, and by the sparsely puberulous young fruits. Furthermore, some flowers are 3-merous (3 sepals and 3 petals), and the dissection of one ovary showed clearly a 3-celled condition. More material is needed, however, to evaluate these characters.

3. **Hasseltia rigida** Woodson ex A. Robyns, Ann. Missouri Bot. Gard. **55**: 77, 1968.

Tree to 30 m tall, the branchlets glabrous or nearly so. *Leaves* with the petioles robust, to 2 cm long, canaliculate above, appressed-puberulous, becoming glabrous; blade elliptic to narrowly elliptic, or subobovate, cuneate at the base, obtusely acuminate at the apex, the margins entire and slightly recurved, to 10 cm long and 4 cm wide, coriaceous, dull on both sides, glabrous and with the venation inconspicuous above, appressed-puberulous especially along the 3 prominent main veins to glabrescent beneath, the secondary veins prominulous and the network of the venation inconspicuous below. *Inflorescences* apparently terminal, large, many-flowered, the axes appressed-puberulous to appressed-tomentellous, the bracts small, deltoid. *Flowers* tan-colored, the pedicels to 5 mm long, appressed-tomentellous; sepals 4, slightly unequal, ovate, acute, to 3 mm long and 1.8 mm wide, tomentellous outside, puberulous inside; petals 4, ovate, acute, slightly shorter than the sepals, tomentellous outside, puberulous inside; stamens with the filaments to 2.5 mm long, sparsely puberulous, the anthers minute; ovary globose, glabrous, the style to 2.2 mm long and glabrous. *Bacca* red, subglobose, to 7-8 mm long, glabrous; seeds 2-4, glabrous.

Known only from Panama.

COCLÉ: region N of El Valle de Antón, alt 1000 m, *Allen* 3733 (holotype MO).

5. NEOSPRUCEA

Neosprucea Sleumer, Notizbl. Bot. Gart. Mus. Berlin **14**: 47, 1938.

Spruceanthus Sleumer, loc. cit. **13**: 362, 1936, non Verdoorn (Ann. Bryol. Suppl. **4**: 151, 1934).

Small *trees*. *Leaves* alternate, petiolate, the stipules minute and caducous; blade 3-5-nerved from the base, distinctly 2-glandular at the base on the upper surface or eglandular, the margins remotely and obtusely glandular-serrate. *Inflorescences* axillary or terminal, few-flowered, racemose. *Flowers* large, ☿, the pedicels articulated; sepals (3)4, valvate, persistent; petals (3)4, similar to the sepals, valvate, persistent; stamens ∞, subperigynous, multiseriate, the filaments filiform, distinct, short, the anthers elongated-linear, basifixed, 2-thecate, dehiscing by an oblique introrse slit at the apex; receptacle (or disc?) densely pilose between the filaments; ovary free, superior, incompletely 5-9-locular by the intrusion of the placentas, the ovules ∞; style simple. *Fruits* baccate, dry, indehiscent, surrounded by the persistent perianth and surmounted by the persistent style; seeds numerous, small, angulate, the testa smooth.

A genus of six species occuring in tropical South America, but with one species extending northwards into Panama.

1. **Neosprucea** aff. **sararensis** Cuatr., Trop. Woods **101**: 21, 1955.

Small *tree* (?), the branches glabrous. *Leaves* with the petioles to 15 mm long, canaliculate above, rounded beneath, short-strigose; blade narrowly elliptic to narrowly oblong-elliptic, ± rounded to attenuate (and somewhat oblique?) at the base, long-acuminate at the apex, remotely crenate along the margins, the crenations distinctly glandular below, 14-20.5 cm long and 4.5-7.5 cm wide, chartaceous, distinctly 3-nerved from the base, sparsely short-strigose beneath especially along the prominent main nerves, the secondary nerves transversely subparallel and prominulous. *Flowers* light green, in short, axillary racemes, the (fruiting) pedicels to 12 mm long, terete, rather thick, articulated close to the base, densely and rather stiff-puberulous; sepals (surrounding the fruit) unequal, broadly ovate, apparently shortly united at the base, obtuse at the apex, 11-13 mm long and 9-13 mm wide, rather fleshy, tomentellous outside, glabrous inside in the middle but tomentellous towards the margins; petals (surrounding the fruit) ovate, obtuse, 11 mm long and 5-6 mm wide, rather fleshy, tomentellous outside, puberulous inside; stamens not seen; receptacle densely short-hirsute (the hairs ca 1 mm long). *Fruit* globose, longitudinally several-lobed, ca 1 cm in diam, apiculate (base of persistent style), the pericarp thin, brittle, blackish, glabrous, ± shiny, incompletely several-locular; seeds to 4.5 mm long, the testa brown, shiny, thin.

Panama and Colombia.

COCLÉ: El Valle de Antón at the foot of Cerro Pilón, cloud forest, alt ca 2000 ft, *Dwyer & Correa 7997* (GH, MO, US); El Valle de Antón & vic, alt 500-700 m, *Seibert 465* (F, MO).

In absence of flowering material, especially of stamens, it is impossible to name the above collection with certainty. In the key to the genus published by Cuatrecasas in 1955 (Trop. Woods **101**: 24-25) it is closest to *N. sararensis* described from the Dept Norte de Santander, Colombia. This collection was determined: *N. grandiflora* (Spruce) Sleumer by Williams in 1962 (Fieldiana: Bot. **29**: 376). According to Cuatrecasas (loc. cit.), in *N. grandiflora* the leaves are glabrous, the flowers are sessile or subsessile, the calyx is ca 7 mm long, the filaments 2 mm long, and the anthers 5 mm long, while in *N. sararensis* the leaves are subglabrous beneath, the pedicels 12-14 mm long, the calyx 9-10 mm long, the filaments 3-4 mm long, and the anthers 2 mm long.

6. BANARA

Banara Aublet, Hist. Pl. Gui. Fr. 547, *pl. 217*, 1775.

Trees or shrubs. *Leaves* alternate, distichous, short-petiolate, the petiole sometimes 1- or 2-glandular at the apex, the stipules small and fugacious; blade simple,

± inequilateral and oblique at the base, the margins glandular-serrate (the glands on the lower side of the serrations), penninerved. *Inflorescences* usually terminal, infrequently oppositifolious, paniculate or racemose, rarely corymbose. *Flowers* small, ☿, rarely polygamous or dioecious, the pedicels articulated above the base, the bracts and bracteoles deltoid, minute; sepals 3(-4), valvate, shortly united at the base, persistent; petals isomerous with the sepals and similar to them, ± imbricate in bud, persistent; stamens ∞, hypogynous or the outer ones slightly epigynous, pluriseriate, inserted on a glabrous or villosulous disc, distinct; filaments filiform; anthers small, introrse, didymous-subglobose, basifixed, 2-thecate, longitudinally dehiscent; ovary sessile, 1-locular or incompletely pseudo-3-8-locular, the placentas 3-8, parietal, filiform or lamelliform and intruding into the ovary, the ovules ∞, small and pluriseriate; style simple, the stigma minutely capitate. *Fruits* baccate, fleshy or coriaceous, surmounted by the persistent style, indehiscent; seeds numerous, embedded in a fleshy pulp, the testa crustaceous; endosperm copious, carnose; embryo small; cotyledons thick.

A neotropical genus of about 30 species; one species reported from Panama.

1. **Banara guianensis** Aublet, Hist. Pl. Gui. Fr. 548, *pl. 217,* 1775.—Fig. 5.

Shrub or small tree 3-15 m high, the trunk up to 20 cm in diam, loosely branched, the branchlets whitish-gray-appressed-tomentellous. *Leaves* with the petioles (3-)6-12 mm long, canaliculate above, whitish-gray-appressed-tomentellous, the apex (junction of blade and petiole) often provided with 1 or 2 somewhat stalked cupulate glands; stipules narrowly triangular, to 4 mm long, whitish-gray-appressed-tomentellous; blade ovate or oblong, sometimes narrowly oblong, rarely oblong-obovate, equilateral to markedly inequilateral, rounded or truncate or subcordate at the base, bluntly caudate-acuminate and usually inconspicuously mucronate at the apex, coarsely serrate along the margins, 7-16 cm long and 3-7 cm wide, chartaceous, discolor, the upper surface dark grayish-green when fresh, ± shiny and usually dark brown when dry, and sparsely appressed-pubescent, the lower surface dull, pale, densely to sparsely appressed-puberulous, the costa very prominent and the secondary veins prominent beneath. *Inflorescences* terminal or rarely oppositifolious towards the end of the branchlets, paniculate, sometimes ± racemose, the axes whitish-gray-appressed-tomentellous. *Flowers* with the pedicels 3-5 mm long, whitish-gray-appressed-tomentellous; sepals 3, rarely 4, oblong-ovate, obtuse to acute at the apex, ca 4.5 mm long and 3 mm wide, appressed-tomentellous on both sides; petals ± obovate, rounded at the apex, ± crispate along the margins, slightly longer than the sepals; stamens inserted on a densely villosulous disc; ovary ovoid, glabrous, with 5-8 lamelliform placentas, the stigma minutely capitate and obsoletely 5-8-lobulate. *Bacca* subglobose, 6-10 mm in diam, the pericarp thin-coriaceous, green when fresh, blackish when dry; seeds ovate, ca 1-1.5 mm long, the testa black, shining, longitudinally sulcate.

A rather variable species (especially regarding leaf shape) distributed in Costa Rica, Panama, and northern South America. According to field notes, the flowers are said to be white, yellow-green, cream tinged with pale green, or pale purple.

CANAL ZONE: Barro Colorado I, *Aviles 894* (F), *Bailey 225* (F), *308* (F), *618* (F), *Bangham 379* (F), *402* (F), *Kenoyer 449* (US), *663* (US), *Shattuck 894* (US), *Starry 226*

(F); Albrook, U. S. Army Tropic Test Center, *Dwyer 6712* (MO); betw Chagres Batteries & Fort San Lorenzo, Fort Sherman Military Reservation, *Maxon & Valentine 6981* (US); Cerro Gordo, nr Culebra, alt 50-290 m, *Pittier 3738* (F, US); Chiva Chiva Trail nr Miraflores Lake, *Tyson 1361* (MO); Curundu Survival School Area, *Tyson & Dwyer 4453* (MO). CHIRIQUÍ: Tolé, vic of Santa Ana Well, alt ca 1000 ft, *Dwyer & Kirkbride 7464* (MO). COCLÉ: Río Hato Airstrip, *Blum & Dwyer 2472* (MO); El Valle de Antón, on slopes of Cerro Pilón, alt 600-1000 m, cloud forest, *Duke 12077* (MO), *12128* (MO), *13201* (MO), *Dwyer & Correa 7969* (MO), *7981* (MO); betw Las Margaritas & El Valle, *Woodson et al. 1242* (F, MO, NY). COLÓN: vic of Sardinilla, ca 7-8 mi E of cement plant, *Blum & Tyson 484* (MO). PANAMA: Cerro Campana, elfin forest beyond Motel Su-Lin, alt 2700-3000 ft, *Duke 8652* (MO); San José I, along rd betw Bodega Bay & Río Mata Puerco, common even in abandoned road bed, *Duke 12564* (MO), vic of Naval Station, *Erlanson 498* (NY, US); Chilibre, *Dwyer 1030* (MO), *1130* (MO); thickets & forests nr Arraijan, alt ca 15 m, *Woodson et al. 1351* (F, MO, NY). VERAGUAS: ca 5 mi N of Santiago by the Santa Maria River, *Blum & Tyson 609* (MO); Isla de Coiba, Penal Colony, *Dwyer 2349* (MO); Cerro de Tute, *Dwyer 4319* (MO).

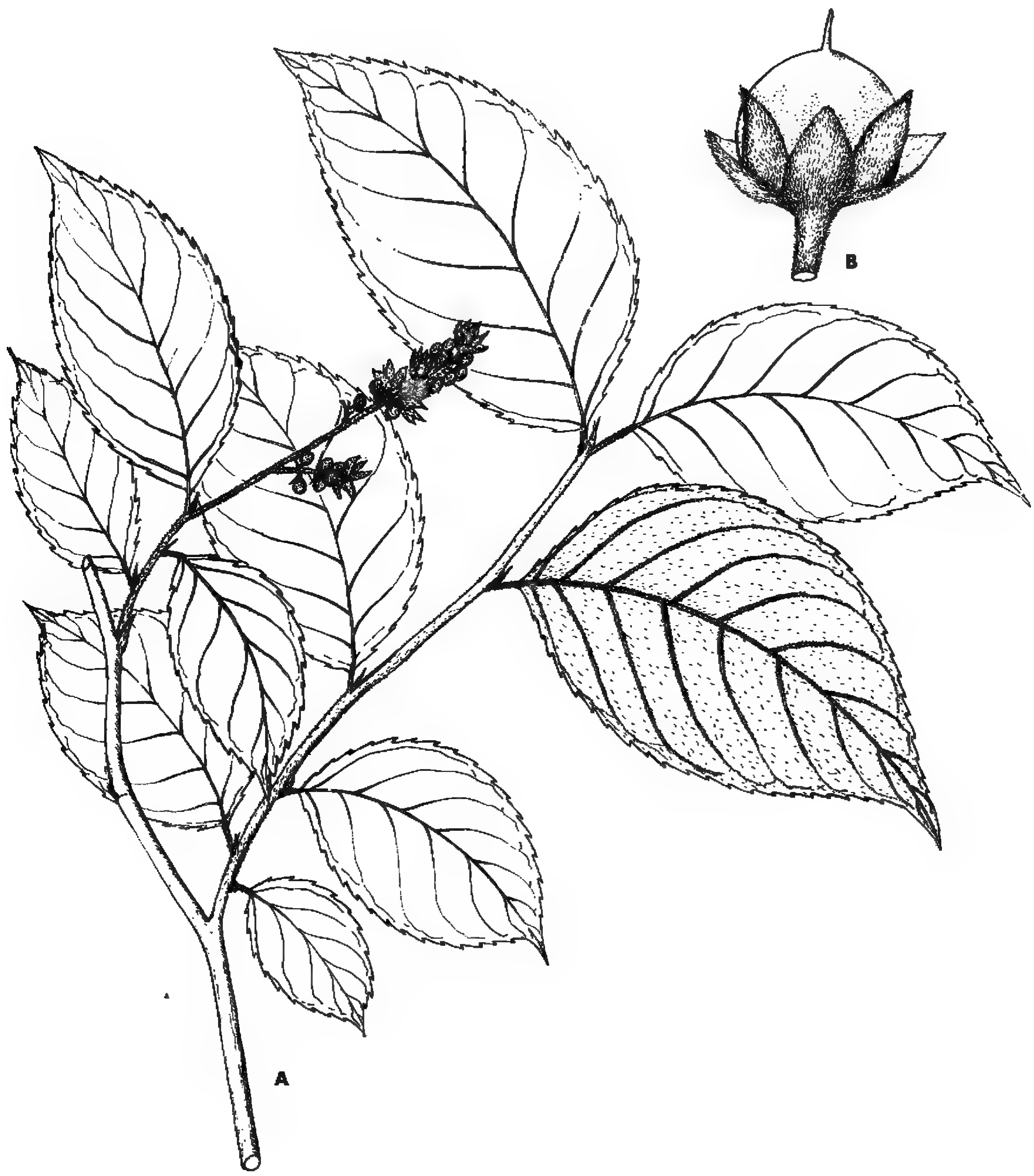

Fig. 5. *Banara guianensis* Aublet: A, habit (×½); B, bacca surrounded by the persistent calyx and corolla (×2). A after *Woodson et al. 1242* (MO); B, after *Dwyer 4319* (MO).

7. HOMALIUM

Homalium Jacquin, Enum. Syst. Pl. Ins. Carib. 5, 24, 1760.

Trees or shrubs. *Leaves* usually alternate, petiolate, the stipules minute and caducous, rarely absent, the blade entire to usually serrate-crenate, the teeth glandular beneath, penninerved, without pellucid glands. *Inflorescences* axillary, racemose or paniculate. *Flowers* ☿, sessile or pedicellate, the pedicels articulated, the bracts usually minute, caducous or ± persistent; calyx tube (or receptacle?) turbinate, adnate to the base of the ovary; calyx lobes 5-8(-12), usually narrow, persistent or accrescent; petals isomerous with the calyx lobes, inserted in the throat of the calyx, alternating with the calyx lobes, persistent or accrescent; stamens epipetalous, isomerous with the petals or in fascicles of 2-8(or more), the filaments filiform, the anthers small, extrorse, dorsifixed, longitudinally dehiscent; disk represented by a gland opposite each sepal and alternating with the filaments or fascicles of filaments; ovary with the lower half adnate to the calyx tube (or half inferior?), 1-locular, the placentas parietal, 2-6(-8), each with (1-)2-7 ovules near the apex, the styles isomerous with the placentas, the stigmas simple or capitellate. *Fruits* capsular, half inferior, ± coriaceous, indehiscent or incompletely 2-8-valvate from the apex; seeds few or solitary, small, angulate, the testa crustaceous; endosperm copious.

A large pantropical genus of over 200 species (cf. Hutchinson, The Genera of Flowering Plants **2:** 216, 1967).

All the neotropical species of *Homalium* belong to the subg. *Myriantheia* Warb. (stamens in fascicles) sect. *Racoubea* Aublet; at present, only one species is reported from Panama.

Useful references:

Blake, S. F., The genus *Homalium* in America. Contr. U. S. Nat. Herb. **20:** 221-235, 1919.

Williams, L. O., *Homalium* Jacq., *In* Tropical American plants, II. Fieldiana: Bot. **29:** 262-263, 1961.

1. **Homalium racemosum** Jacquin, Enum. Syst. Pl. Ins. Carib. 24, 1760.—Fig. 6.
H. stenosepalum Blake, Contr. U. S. Nat. Herb. **20:** 234, 1919.

Tree to 30 m tall, the trunk to 90 cm in diam, the bark grayish, the branchlets glabrous to finely puberulous, lenticellate. *Leaves* with the petioles 3-13 mm long, glabrous or finely puberulous; blade elliptic to oblong-elliptic, sometimes narrowly so, acute to obtuse at the base, acuminate at the apex, the acumen often blunt, the margins undulate-crenulate to crenate, 8-15 cm long and 3-6 cm wide, thin-chartaceous to chartaceous, ± shiny on both sides, glabrous or almost so, the costa prominent below, the lateral veins slightly prominent below. *Inflorescences* usually racemose, sometimes paniculate, to 12 cm long, the rachis minutely puberulous. *Flowers* white, the pedicels to 10 mm long, articulated above, near or below the middle, puberulous, the bracteoles narrowly triangular, to 1.5 mm long, minutely puberulous, caducous or ± long persistent; calyx tube turbinate, minutely puberulous; calyx lobes (5)6-7, ovate to narrowly oblong-ovate, subobtuse to acute at the

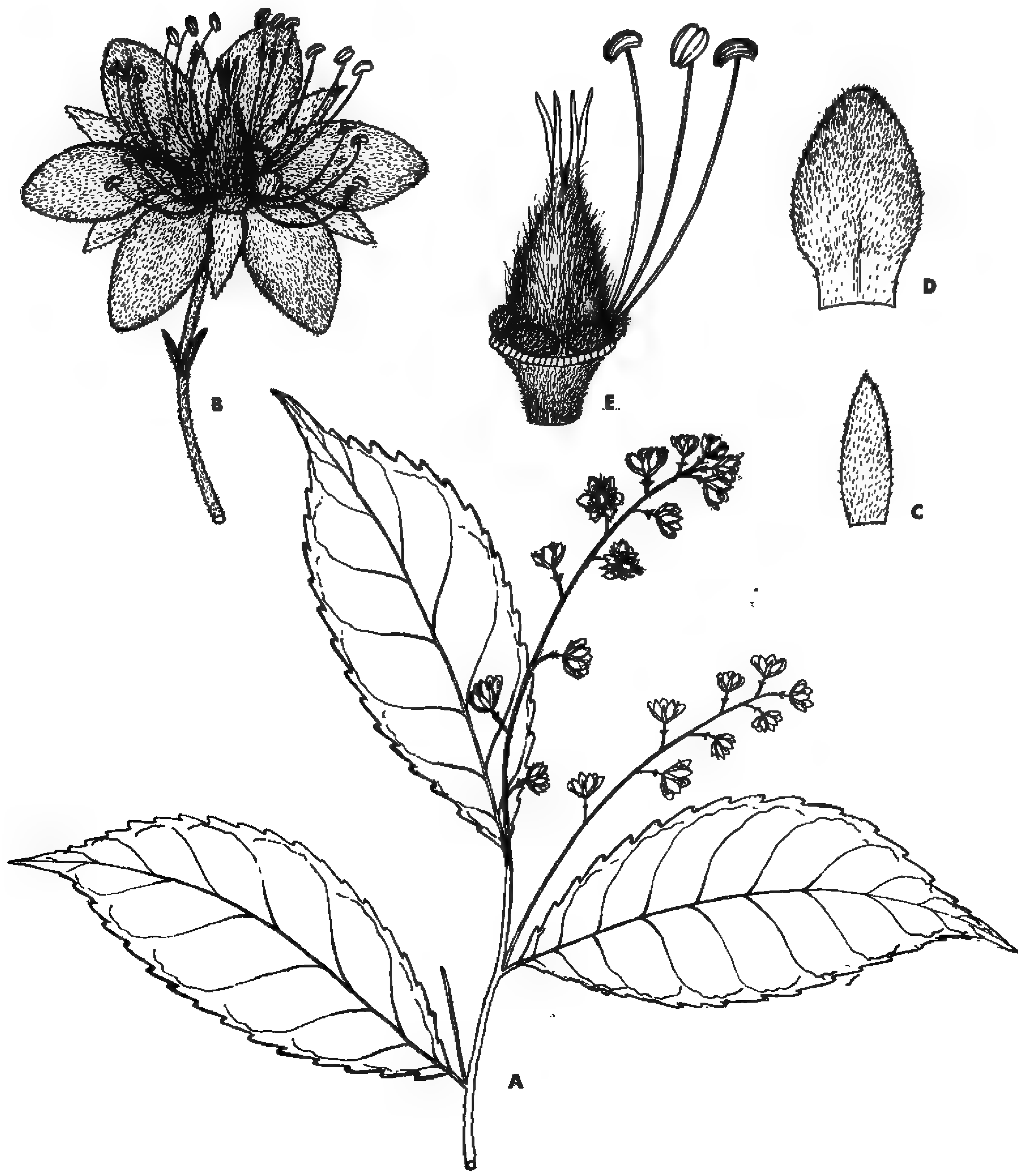

Fig. 6. *Homalium racemosum* Jacquin: A, habit (×½); B, flower (×4); C, sepal (×5); D, petal (×5); E, gynoecium, glandular disc, and one fascicle of stamens (×8). After *Stern et al. 917* (MO).

apex, 2.5-5 mm long and 1-1.5 mm wide, minutely puberulous, persistent; petals ovate to broadly ovate, subobtuse at the apex, to 5-6 mm long and 3.5 mm wide, minutely puberulous, persistent; stamens in fascicles of 3, rarely 2, the filaments to 4 mm long, glabrous, the anthers ca 0.5 mm long; glands ± transversely elliptic, to 1.3 mm × 0.8-1 mm, minutely tomentellous; ovary conical, tomentellous, the styles 3 or 4, distinct from the base, to 1.2 mm long, glabrous or puberulous beneath, the stigmas simple. Mature *fruit* not seen.

Mexico, Central America, northern South America, and the West Indies; called colloquially *guayabillo* in Panama (cf. *Duke & Bristan 234*).

CANAL ZONE: s. loc., *Christopherson 139* (US); around Frijoles, alt 10-30 m, on river bank, *Pittier 2693* (NY, US); along Río Chagres, below Gatun, nr sea level, *Pittier 2804* (holotype *H. stenosepalum* US; isotypes F, MO, NY). DARIEN: Río Ucurganti, *Bristan 1180* (MO); Río Chucunaque betw Río Membrillo & Río Subcuti, *Duke 8586* (MO); Uruti, frequently found nr rivers, *Duke & Bristan 234* (MO); Río Tuira betw Río Paya & Río Pucro, *Duke & Kirkbride 14059* (MO); vic of Campamento Buena Vista, Río Chucunaque above confluence with Río Tuquesa, *Stern et al. 917* (MO, US).

Analysis of immature fruits (*Christopherson 139 & Pittier 2804*) shows that the capsules are only 1-seeded at maturity. The inner walls of the pericarp are hairy.

8. PROCKIA

Prockia P. Br. ex L., Syst. Nat. ed. 10, 1074, 1759.

Shrubs or small trees. *Leaves* alternate, slender-petiolate, the stipules usually large, foliaceous, persistent; blade membranous, 5-7-nerved from the base, glandular-serrate along the margins (the glands on the lower side of the serrations), 2-glandular above at the base. *Inflorescences* terminal, racemose or fasciculate, rarely flowers solitary. *Flowers* ☿, the pedicels articulated above the base, the bracteoles 2, narrowly triangular; sepals 3, rarely 4, valvate, persistent; petals isomerous with and smaller than the sepals, persistent, or none; stamens ∞, pluriseriate, free, inserted on the slightly elevated receptacle, the filaments filiform, the anthers small, didymous-subglobose, basifixed, 2-thecate, longitudinally dehiscent; ovary free, 3-5-locular, the ovules ∞; style simple, the stigma scarcely enlarged. *Fruits* baccate, dry, surmounted by the persistent style, indehiscent, 3-5-locular; seeds numerous, small, imbedded in a white pulp, the testa brittle; endosperm copious; embryo straight; cotyledons thick.

A neotropical genus of about 10 species; one species known, at present, from Panama.

1. **Prockia crucis** P. Br. ex L., Syst. Nat. ed. 10, 1074, 1759.—Fig. 7.

Shrub or small tree 1.2-10 m high, the trunk to 10 cm in diam, the branchlets grayish-puberulous or glabrous. *Leaves* with the petioles to 20 mm long, glabrous or softly hirtellous, the stipules conspicuous, sessile or nearly so, extremely inequilateral, oblique at the base, acuminate at the apex, glandular-crenate along the margins, up to 17 mm long, usually ca 5-8 mm long, glabrous or softly hirtellous; blade broadly to narrowly ovate, usually rounded or sometimes subcordate at the base, acuminate at the apex, glandular-crenate or -serrate along the margins, 4-11 cm long and 2-7 cm wide, thin-chartaceous, slightly discolor, glabrous or shortly puberulous above, glabrous or softly hirsute below, 5-7-nerved from the base, the main nerves slightly prominent. *Inflorescences* racemose. *Flowers* with the pedicels terete, slender, 7-17 mm long, glabrous or softly hirtellous, the bracteoles narrowly triangular, 3-5 mm long; sepals ovate, attenuate and obtuse to acute at the apex, 5.5-6.5 mm long and 3.5-4 mm wide, green, short-hirsute outside, glabrous below to tomentellous towards the apex inside; petals none; filaments unequal, 4-6 mm long, yellow, glabrous, the anthers ca 0.3 mm long; ovary subglobose, ca 2-2.5 mm long and 2.5-3 mm in diam, shortly appressed-hirsute, the style to 4 mm long, short-hirsute below to glabrous above, the stigma slightly thickened. *Bacca* $\pm$ globose, 6-7 mm in diam, the pericarp thin, green when young, becoming light red

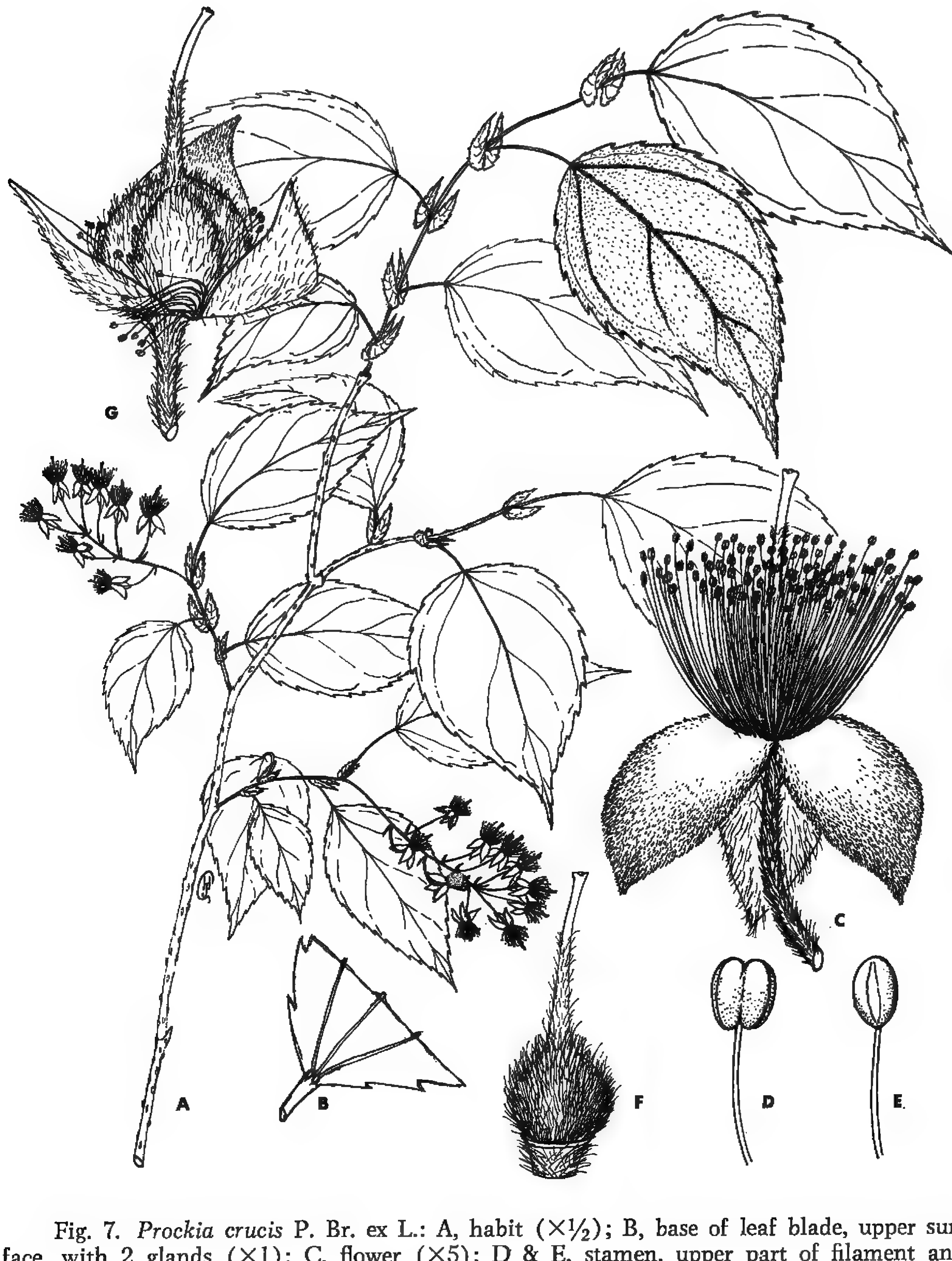

Fig. 7. *Prockia crucis* P. Br. ex L.: A, habit (×½); B, base of leaf blade, upper surface, with 2 glands (×1); C, flower (×5); D & E, stamen, upper part of filament and anther (ca ×20); F, gynoecium (×5); G, fruit surrounded by the persistent calyx and topped by the persistent style (×5). A-F after *Stern & Chambers* 35 (MO); G after *Tyson & Blum 4104* (MO).

to very deep red, almost black when completely ripe, shortly pilose; seeds ± ellipsoid, ca 1.5 mm long and 1 mm in diam, the testa black, longitudinally striate.

A polymorphic species, especially regarding the indument, ranging from southern Mexico, through Central America, to South America; also in the West Indies.

CANAL ZONE: vic Tropic Test Center Albrook tower, out C-15, *Blum 2174* (MO); Rd K-10, 1-2 mi from Kobbe-Arraijan Hwy, *Duke 11709* (MO); Madden Dam, Boy Scout Camp Road, roadside woods, *Dwyer & Elias 7493* (MO); s. loc., *Johansen 20* (US); Naval Ammunition Depot, Group 300 Rd, *Stern & Chambers 35* (MO, NY, US); Madden Dam area nr road, Transisthmian Hwy, edge of woods, *Stern et al. 44* (MO, US); Fort Clayton nr old hospital building #519, *Tyson & Blum 3913* (MO); old town site of Red Tank, *Tyson & Blum 4015* (MO); several mi off main road S of the island (Barro Colorado I?), damp shady habit, *White 111* (F, MO). PANAMA: along Chiva-Chiva trail to Search Light Station beyond Chiva-Chiva, alt 10-100 m, *Allen 952* (F, MO, US); nr Río Tapía, Juan Díaz region, edge of forest, *Maxon & Harvey 6633* (US); area just NE of Madden Dam, *Stimson 5179* (MO); 1 mi W of Tocumen, in frequently burned areas, *Tyson & Blum 4104* (MO); boggy grasslands and marginal thickets, betw Pacora & Chepo, alt ca 25 m, *Woodson et al. 1666* (F, MO, NY).

9. TETRATHYLACIUM

Tetrathylacium Poeppig in Poeppig & Endl., Nov. Gen Sp. Pl. **3:** *pl. 240*, 1841[4], p. 34, 1843[4].

Edmonstonia Seemann, Bot. Voy. Herald *pl. 18*, 1852[4], p. 98, 1853[4].

Trees, infrequently shrubs, unarmed. *Leaves* alternate, short-petiolate, the stipules large, foliaceous, caducous, the blade rather large, rounded to cordate at the base, the margins entire to remotely repand-serrate, epunctate, penninerved. *Inflorescences* axillary, paniculate-spicate, the flowers sessile and densely crowded or not along the secondary rachises (spikes), elongated in fruit. *Flowers* small, ☿, each one subtended by a bract and 2 bracteoles, these small and closely appressed along the rachis; calyx urceolate, thickened, 4-gibbous or 4(-5)-angulate (compressed by the crowding of the flowers along the rachis), 4-lobed, persistent, the lobes small, rounded, membranous, biseriately imbricate; petals none; stamens 4, inserted within the calyx tube, the filaments alternate with the calyx lobes, the anthers introrse, longitudinally dehiscent, exserted or not; ovary sessile, 1-locular, with 4 parietal, many-ovulate placentas; style very short, the stigma obscurely 4-lobed. *Fruits* baccate, coriaceous, the seeds numerous, exarillate, each seed surrounded by a thin membrane (small compartment, of placentary origin?), the testa foveolate-alveolate.

A genus of three species, ranging from Costa Rica to Peru; two species reported from Panama.

a. Flowers very densely crowded along the secondary rachises (spikes) of the inflorescences, calyx 4(-5) angled by the crowding of the flowers ....1. *T. johansenii*
aa. Flowers not crowded along the secondary rachises (spikes) of the inflorescences; calyx 4-gibbous ....2. *T. macrophyllum*

[4] For dates of publication see Stafleu, Regnum Veget. **52:** 362, 441, 1967.

1. **Tetrathylacium johansenii** Standley, Jour. Wash. Acad. Sci. **15:** 479, 1925.—Fig. 8.

Tree to 30 m high, the trunk sometimes buttressed, infrequently shrub, the branchlets inconspicuously puberulous to glabrous. *Leaves* with petioles to 7 mm long, the foliaceous stipules narrowly oblong-ovate, somewhat falcate, to 17 mm long and 3 mm wide, minutely puberulous; blade oblong, often narrowly so, or obovate-oblong, or elliptic-oblong, slightly unequal and rounded to subcordate at the base, long-caudate-acuminate at the apex, remotely repand-serrate to subentire along the margins, to 25 cm long and 9 cm wide, subcoriaceous, lustrous and glabrous above, dull and glabrous to minutely puberulous especially along the prominent costa beneath, the secondary veins prominulous below. *Inflorescences* to 8 cm long, the spikes to 2.5 cm long, much enlarged in fruit, the flowers very densely crowded along the secondary rachises (spikes), the primary and secondary rachises densely and minutely puberulous, the bracts and bracteoles minute, deciduous. *Flowers* white, the calyx 4(-5)-angled (by crowding of the flowers along the rachis), not gibbous, to 2 mm long, glabrous outside, pubescent inside, the lobes ca 0.5 mm long; stamens with the filaments ca 0.5 mm long, the anthers 0.5 mm long; ovary apparently glabrous. *Bacca* globose to obovoid, to 2.5 cm long, glabrous, the seeds ovoid, to 2 mm long.

Costa Rica(?), Panama, and probably Colombia.

The crowding of the flowers along the axes of the spikes makes them look like a tiny mosaic and gives the inflorescences a very distinctive look. The fruits are (acc. to *Duke 13115*) in clusters to 30 cm in diam and are loaded with ants.

CANAL ZONE: Mojinga swamp nr mouth of Río Chagres, alt below 1 m, *Allen 904* (F, NY, US); Barro Colorado I, *Carpenter 76* (F); nr Gatun, *Goldman 1863* [holotype US, isotype NY (fragment of inflorescence)]; forest along the Río Indío de Gatun, nr sea level, *Pittier 2772* (US); Naval Ammunition Depot, Group 300 Rd, *Stern & Chambers 34* (F, MO, NY, US). DARIEN: vic of El Real, alt ca 15 m, *Allen 959* (F, MO, NY, US); Río Pucro, below village of Pucro, *Duke 13115* (MO); trail betw El Real & Pinogana, *Stern et al. 280* (MO, US). SAN BLAS: forests around Puerto Obaldía, alt 0-50 m, *Pittier 4300* (US).

The following sterile collections belong probably to this species: CANAL ZONE: s. loc., *Johansen 4* (US); Mount Hope Cemetery, *Standley 28767* (US). PANAMA: Río Tocumen, moist thicket, *Standley 29408* (US).

2. **Tetrathylacium macrophyllum** Poeppig in Poeppig & Endl., Nov. Gen. Sp. Pl. **3:** *pl. 240*, 1841, p. 34, 1843.

Edmonstonia pacifica Seemann, Bot. Voy. Herald *pl. 18*, 1852, p. 98, 1853.
Tetrathylacium macrophyllum var. *pacificum* (Seemann) Tr. & Pl., Ann. Sci. Nat., Bot., sér. 4, **17:** 106, 1862.
T. pacificum (Seemann) Standley, Jour. Wash. Acad. Sci. **15:** 479, 1925.
T. costaricense Standley, loc. cit. 480.

Tree to 15 m tall, the branchlets inconspicously puberulous to glabrous. *Leaves* with robust petioles 0.5-1.5 cm long, the stipules not seen; blade from narrowly to broadly (in Panamanian collection) oblong, somewhat asymmetrical and deeply cordate to ± truncate at the base, long-acuminate to caudate-acuminate at the apex (shortly caudate-acuminate in Panamanian collection), entire to remotely and rather inconspicuously serrate along the margins, to 26 cm long and 14 cm wide (in Panamanian collection, usually narrower in extra-Panamanian collec-

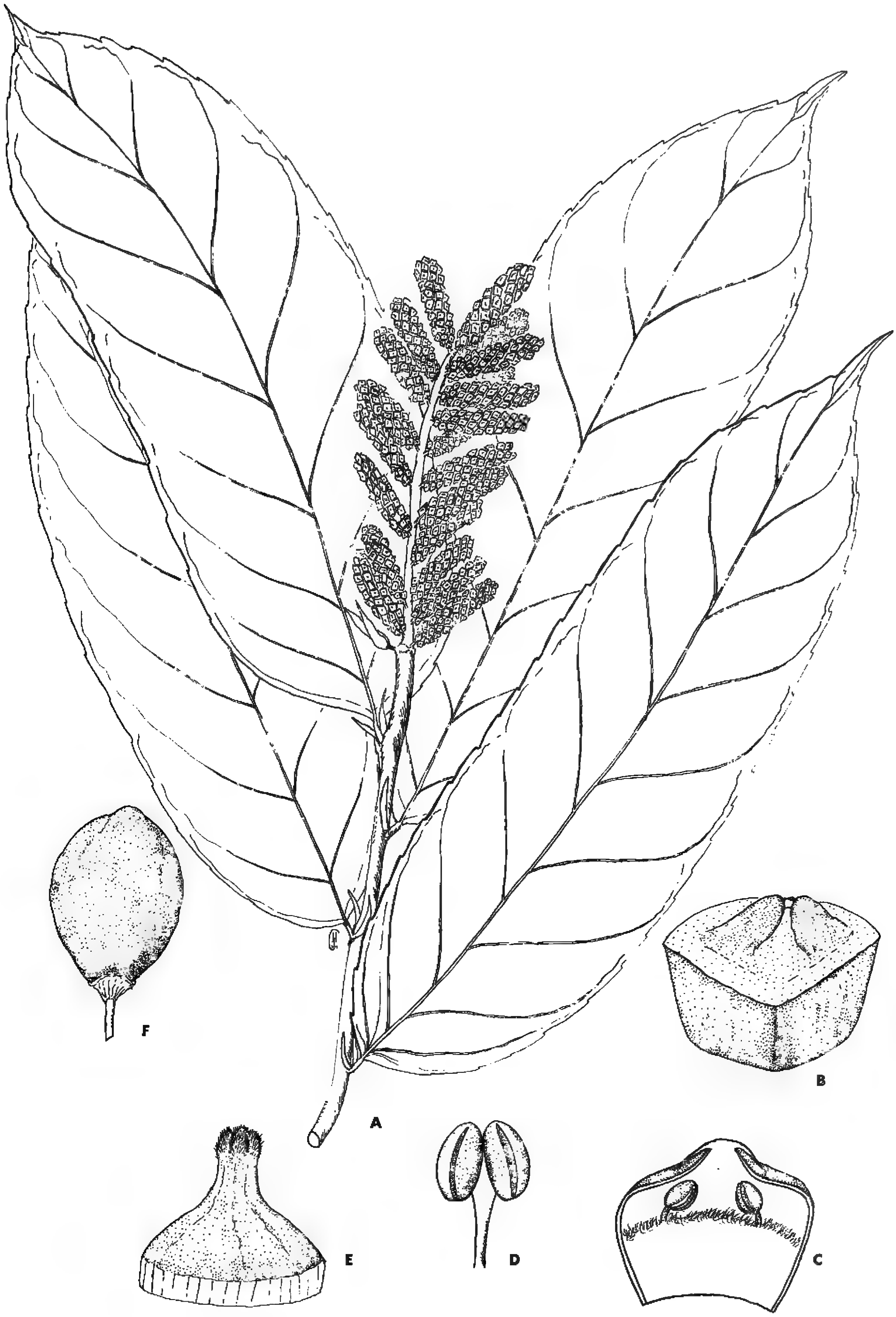

Fig. 8. *Tetrathylacium johansenii* Standley: A, habit (×½); B, flower (×10); C, id., longitudinal section, the gynoecium removed (×10); D, stamen (×20); E, gynoecium (×20); F, bacca (×1). A-E after *Allen 959* (MO); F after *Stern et al. 280* (MO).

tions), coriaceous, glabrous above, glabrous or puberulous beneath, the costa and secondary veins prominent below. *Inflorescences* up to 16 cm long, much elongated in fruit, flowers not crowded along the secondary rachises (spikes), the primary and secondary rachises densely and minutely puberulous, each flower subtended by a bract and 2 connate bracteoles, the bract and bracteoles less than 1 mm long, ciliolate and persistent. *Flowers* reddish or maroon; calyx 4-gibbous, to 3.5 mm long, glabrous outside, pubescent inside, the lobes to 1.5 mm long; stamens with the filaments to 2.2 mm long, glabrous, the anthers exserted, sagittate, to 1.5 mm long; ovary minutely puberulous, the style thick, less than 1 mm long. *Bacca* red, subglobose, to 15 mm long, minutely puberulous; seeds ± ovoid, to 1.5 mm long.

Costa Rica to Peru.

COCLÉ: hills N of El Valle de Antón, alt 1000 m, *Allen 2147* (F).

10. CASEARIA

Casearia Jacquin, Enum. Syst. Pl. Ins. Carib. 4, 21, 1760; Select. Stirp. Amer. Hist. 132, 1763.

Trees or shrubs. *Leaves* alternate, distichous, petiolate, the stipules usually very small and early caducous, rarely ± persistent, the blade entire-margined or the margins crenate or serrate, often pellucid-punctate and/or striate. *Flowers* axillary, mostly in fascicles or glomerules, rarely solitary, sometimes in corymbose or paniculate inflorescences, ☿, small, usually greenish or yellowish; pedicels articulated, bracteate at the base, the bracts usually numerous, scale-like and often forming a cushion in the leaf axils; sepals 4-6(-9), imbricate, ± united at the base into a short or rather elongated calyx tube, persistent or sometimes slightly accrescent; petals absent; stamens (5-)6-15(-22), 1-seriate, inserted on the tube of the calyx or at its base, alternating with as many staminodes, these inter- or intrastaminal, clavate or flattended and often pilose especially at the apex; filaments equal or alternately unequal, free or united among themselves and with the staminodes at the base into a ± perigynous tube; anthers small, elliptic or subglobose, sometimes apically and dorsally glandulose; ovary free, 1-locular, the ovules usually numerous on 3-4 parietal placentas; style simple or divided at the apex into 3 branches, the stigmas 1 or 3, capitate. *Fruit* a dry or succulent capsule, 3-4-valved (3-angled when fresh, often 6-ribbed when dry); seeds few to numerous, with a fleshy aril, the testa coriaceous or crustaceous; endosperm fleshy, embryo straight, cotyledons flat.

About 250 species in the tropics and subtropics of both hemispheres.

The genus is badly in need of a comprehensive revision, "for some of the common species have been repeated by various authors under several different names" (cf. Bentham, Jour. Proc. Linn. Soc., Bot. **5** (Suppl. 2): 88, 1861). Eight species are reported here from Panama, while a few other species occur in Central America, north of Panama.

a. Stigma 1; staminodes interstaminal (sect. *Pitumba*).
  b. Inflorescences fasciculate; seeds without resinous glands.
    c. Fascicles distinctly pedunculate, the peduncles to 4 mm long ....1. *C. arborea*
    cc. Fascicles sessile or nearly so.

d. Branchlets densely tawny-tomentellous; leaves conspicuously discolorous .... 2. *C. grandiflora*

dd. Branchlets minutely pubescent to inconspicuously puberulous; leaves not conspicuously discolorous.

e. Sepals 5-7 mm long, united at the base into a tube 1-1.5 mm long; leaf blades with the margins sharply serrate .... 3. *C. arguta*

ee. Sepals 4.5-5.5 mm long, scarcely united at the base.

f. Pedicels ca 2-3 mm long, articulated below the apex; branches often with stout, spreading spinescent twigs; stipules deltoid, ca 1.5 mm long; leaf blades ± distinctly crenate .... 4. *C. stjohnii*

ff. Pedicels to 6 mm long, articulated ca 2-2.5 mm above the base; twigs without spines; stipules subulate, 2-5 mm long; leaf blades serrulate-denticulate .... 5. *C. guianensis*

bb. Inflorescences cymose-corymbiform; seeds with the testa covered with numerous, dark, resinous glands .... 6. *C. nitida*

aa. Stigmas 3; staminodes ± intrastaminal or intrastaminal.

g. Style simple; leaves copiously pellucid-punctate; sepals 2-3 mm long; anthers didymous, subglobose, with a dorsal, apical gland; staminodes ± intrastaminal (sect. *Crateria*) .... 7. *C. sylvestris*

gg. Style divided at the apex into 3 branches; leaves without pellucid dots; didymous, subglobose, with a dorsal, apical gland; staminodes ± intrastaminal (sect. *Piparea*) .... 8. *C. commersoniana*

1. **Casearia arborea** (L. Rich.) Urban, Symb. Ant. **4:** 421, 1910 & **8:** 447, 1920.
Samyda arborea L. Rich., Act. Soc. Hist. Nat. Paris **1:** 109, 1792.

Shrub to 5 m high, the branchlets puberulous when young, soon glabrous. *Leaves* shortly petiolate, the petiole up to 4-5 mm long, the stipules narrowly ovate, to 1 cm long, puberulous, early caducous; blade narrowly oblong, somewhat inequilateral, slightly oblique and acute to rounded at the base, long-caudate-acuminate at the apex, closely crenulate-serrulate at the margins, to 12 cm long and 4.3 cm wide, chartaceous, pellucid-punctate or -lineate, the upper surface shining, glabrous or with the slightly prominent costa puberulous, the lower surface somewhat paler, dull, puberulous along the venation, the costa and lateral veins prominent. *Inflorescences* fasciculate, the fascicles up to 25-flowered, distinctly pedunculate, the peduncles to 4 mm long, minutely puberulous, the bracts minute. *Flowers* yellow, the pedicels up to 4 mm long, articulated at or slightly below the middle, minutely puberulous especially below the articulation; calyx ca 4-4.5 mm long, the lobes 5, oblong, united at the base into a short, 5-angulate tube less than 1 mm long, rounded and slightly cucullate at the apex, ca 2-2.5 mm wide, minutely puberulous to nearly glabrous on both sides; stamens 10, inserted near the apex of the calyx tube, slightly united at the base among themselves and with the staminodes, the filaments unequal, ca 2-2.3 mm long, glabrous, the anthers didymous, subglobose, ca 0.5 mm long, with a dorsal, apical gland, the latter slightly pilose or not; staminodes 10, interstaminal, to 1.5 mm long, barbate at the apex; gynoecium ca 3.7 mm long, the ovary 3-angular, ca 1-1.2 mm in diam, glabrous but pilose at the apex, gradually attenuate into the style, the latter pilose at the base, otherwise glabrous, the stigma capitate. *Capsule* ellipsoid-subglobose, angulate, apiculate, ca 4-5 mm long, pilose at the apex, splitting into 3 valves at maturity; seeds up to 6 per capsule, ellipsoid, ca 2 mm long, the testa minutely alveolate, the aril fimbriate-lacerate.

West Indies, British Honduras to Panama, Guianas, and Brazil.

CANAL ZONE: Barro Colorado I, clearing, *Shattuck 670* (F); PANAMA: top of Cerro Jefe, alt 2700-3000 ft, *Tyson et al. 4398* (MO).

2. **Casearia grandiflora** Camb. in St.-Hil., Juss. & Camb., Fl. Bras. Merid. **2:** 239, *pl. 126*, 1830.

Small *tree* (?), the branchlets densely tawny-tomentellous. *Leaves* shortly petiolate, the petiole to 4 mm long, densely tawny-tomentellous, the stipules linear, fugaceous; blade oblong, obtuse or ± acute and sometimes slightly inequilateral at the base, rather long-acuminate at the apex, crenulate-serrulate at the margins, up to 10 cm long and 3 cm wide, chartaceous, obscurely pellucid-punctate, markedly discolorous, the upper surface dark green when fresh, dark brown when dry, ± shining and glabrous or with the costa puberulous, the lower surface dull, densely tawny-tomentellous and with the costa and lateral veins prominent. *Inflorescences* sessile or nearly so, fasciculate, 10-20-flowered, the bracts rather large, subcircular, tawny-tomentellous outside, glabrous inside. *Flowers* shortly pedicellate, the pedicel articulated close to the base, tawny-tomentellous; calyx ca 7 mm long, the tube ± 5-costate and ca 2-2.5 mm long, the lobes 5, rather broadly elliptic, rounded at the apex, ca 3.5 mm wide, tawny-tomentellous without, puberulous within; stamens 10, inserted near the apex of the calyx tube, scarsely united at the base among themselves and with the staminodes, the filaments unequal, up to 2.5 mm long and glabrous, the anthers didymous, subglobose, ca 0.5 mm long, with a dorsal, apical, barbate gland; staminodes 10, interstaminal, ca 1.8-2 mm long, tomentose-barbate; gynoecium 5.5-6 mm long, the ovary ca 1.5-1.8 mm in diam, glabrous at the base, densely whitish-pilose at the apex, gradually attenuate into the style, the latter densely whitish-pilose below to glabrous apically, the stigma capitate and densely papillate. *Capsule* (acc. to Eichler in Mart., Fl. Bras. **13**(1): 479, 1871) turbinate-ellipsoid, 6-angulate, apiculate, 7-8 mm long, glabrous; seeds 3-4, oblong, ca 2.5 mm long, the testa glabrous, minutely reticulate-foveolate, the aril small, fimbriate-lacerate.

Southern Darien in Panama, Colombia, Venezuela, the Guianas and Brazil (Pará, Ceará, Maranhão).

DARIEN: vic of La Palma, alt 0-50 m, *Pittier 5709* (F, US).

3. **Casearia arguta** H.B.K., Nov. Gen. Sp. Pl. **5:** 364, 1823.

Shrub or small tree 1.5-12 m tall, the trunk to 12 cm in diam, unarmed, the branchlets minutely pubescent. *Leaves* short-petiolate, the petiole up to 1 cm long, canaliculate above, minutely pubescent; blade narrowly oblong or narrowly ovate-oblong, obtuse to acute at the base, long-acuminate at the apex, to 17 cm long and 6 cm wide, chartaceous to rigid-chartaceous, pellucid-punctate or not, slightly discolor, the margins sharply serrate, more or less shining and minutely pubescent to glabrous above, somewhat paler, dull and minutely pubescent below, the costa and lateral veins prominent beneath. *Inflorescences* sessile, fasciculate, the fascicles dense, the bracts numerous and forming a cushion in the leaf axils. *Flowers* greenish-white or white, the pedicels up to 8 mm long, usually shorter and to 4-5 mm long, articulated close to the base, minutely pubescent; calyx 5-7 mm long, the lobes rarely 6, narrowly ovate-oblong, united at the base into a tube 1-1.5 mm long, acute to obtuse at the apex, 3-nerved, minutely puberulous without, minutely puberulous to nearly glabrous within; stamens (9) 10(11), the filaments filiform, slightly unequal, 1.5-3.5 mm long, glabrous, united at the base among themselves and with the staminodes into a very short tube less than 0.5 mm long, the anthers ca 0.5-0.7 mm long, usually inconspicuously mucronate and often with 1 or few whitish setae at the apex; staminodes (9) 10(11), interstaminal, narrowly obovate, 1-2 mm long, densely whitish-pilose; gynoecium 3.5-5.5 mm long, the ovary narrowly ovoid, ca 0.8-1.2 mm in diam at the base, densely whitish-pilose, gradually attenuate into the style, the latter pilose at base to glabrous at apex, the stigma capitate and densely papillate. *Capsule* ± globose, mucronate (base of style), 1-2 cm in diam, yellow at maturity, blackish when dry, glabrous except the slightly pubescent apex; seeds conglutinate, to 5 mm long, the aril reddish or pinkish.

Southern Mexico, Central America, and tropical South America; known in Panama as *pica lengua* (fide *Pittier 5142*) and *raspa lengua* (fide *Standley 28149*).

BOCAS DEL TORO: vic of Chiriquí Lagoon, *von Wedel 1052* (MO, US), *1322* (MO, US); Changuinola Valley, *Dunlap 216* (F, US); banks of Changuinola River, *Dunlap 518* (F, US). CANAL ZONE: vic W end Gatun Lake dam, *Blum & Tyson 1992* (MO); along drowned Río Axote Caballo, alt 6-70 m, in clumps in savanna, *Dodge et al. 16847* (MO); Cruces, *Hayes 1019* (NY); Gamboa, moist thicket, *Standley 28483* (US); vic of Miraflores, in shaded swamps, *White & White 47* (F, MO); nr mouth of Río Cocolí, *White 96* (F, MO); Balboa Heights, *Greenman & Greenman 5023* (MO). CHIRIQUÍ: vic of San Felix, alt 0-120 m, *Pittier 5142* (F, NY, US). COCLÉ: Aguadulce, nr sea level, in savannas, *Pittier 4939* (US); 4 mi W of Antón on Río Chico, *Tyson & Blum 2594* (MO); El Valle, valley floor & lower slopes along highway, *Miller 1836* (US); vic of El Valle, alt 600-1000 m, *Allen 1178* (F, MO, US). DARIEN: Río Tuira, betw Río Punusa & Río Mangle, *Duke 14596* (MO). HERRERA: rd from La Avena to outskirts of Pesé, alt ca 200 ft, *Burch et al. 1319* (MO); vic of Ocú, hill above the cantera of Sr. Joaquin Carrizo, limestone area, much cut over & browsed by animals, *Stern et al. 1714* (MO). PANAMA: Punta Paitilla, *Piper 5422* (US); nr Punta Paitilla, moist thicket, common, *Standley 26244* (US); vic of Bella Vista, *Piper 5381* (NY, US); vic of Juan Franco Race Track, nr Panama City, moist thicket, common, *Standley 27768* (US); Sabanas, N of Panama City, *Bro. Paul 579* (US); nr Old Panama, *Bro. Heriberto 290* (F, NY, US); Nuevo San Francisco, in thicket, *Standley 30727* (US); Río Tapía, moist thicket, *Standley 26201* (US), *28149* (US), *30681* (US); nr the big swamp E of the Río Tocumen, wet forest, common, *Standley 26556* (US); along rd betw Panama City & Chepo, *Dodge et al. 16649* (MO); Laguna de Portala, nr Chepo, alt 50 m, *Pittier 4770* (NY, US). VERAGUAS: Cañazas, *Tyson 3645* (MO); 2 mi S of Cañazas, *Tyson 3730* (MO); hills W of Soná, alt ca 500 m, *Allen 1039* (MO). PROVINCE UNKNOWN: s. loc., *Hayes 350* (NY), *603* (NY).

4. **Casearia stjohnii** Johnston, Sargentia **8:** 213, 1949.

Tree or large shrub 3-12 m tall; branches often with stout, spreading, spinescent twigs 1-3.5 cm long; branchlets minutely pubescent. *Leaves* with the petioles slender, 5-15 mm long; blade obovate, obovate-elliptic or ± elliptic, acute at the base, rounded-obtuse and acuminate at the apex, 6-12 cm long and 3-6.5 cm wide, the acumen 4-7 mm long, chartaceous, the margins ± distinctly crenate, conspicuously pellucid-punctate, the upper surface lustrous and glabrous, the lower surface dull and inconspicuously appressed-pubescent mainly along the prominulous costa and the 5-7 pairs of lateral veins. *Inflorescences* axillary, densely fasciculate, the fascicles sessile, 8-15-flowered. *Flowers* greenish, the pedicels articulated below the apex, 1-2 mm long, the bracts numerous, crowded, often longer than the pedicels, ca 2-3 mm long, pallid-strigulose towards the apex, persistent; buds subglobose; calyx 4.5-5.5 mm long, the lobes ovate-oblong, obtuse, 1.8-2.3 mm wide, scarcely united at the base into a tube 0.5 mm long or less, minutely appressed-pubescent without, glabrous or sparsely strigulose within; stamens 8(9), the filaments filiform, 1.5-2.5 mm long, glabrous, united at the base among themselves and with the staminodes into a very short tube, the anthers oblong, ca 0.5-0.7 mm long; staminodes 8(9), elongated-oblong, ca 1-2 mm long and 0.4-0.5 mm wide, conspicuously white-pilose; gynoecium 3-3.5 mm long, pilose, the ovary ovoid, 1 mm in diam at the base, gradually attenuate into a short style, the stigma conical-capitate. *Fruit* unknown.

Known only from San José Island.

PANAMA: San José I, northern end of island, *Erlanson 369* (holotype US, isotype NY), *274* (US).

5. **Casearia guianensis** (Aublet) Urban, Symb. Ant. **3:** 322, 1902.

Iroucana guianensis Aublet, Hist. Pl. Gui. Fr. 329, *pl. 127,* 1775.
Casearia ramiflora Vahl, Symb. Bot. **2:** 50, 1791.

Shrub or small tree 1.5-6 m high, deciduous, without spines, the branches few, elongate, the branchlets inconspicuously puberulous, soon glabrous. *Leaves* with the petioles to 10 mm long, the stipules subulate, 2-5 mm long, minutely ferruginous-puberulous, soon caducous; blade obovate, acute at the base, acuminate at the apex, the acumen rather blunt, serrulate-denticulate at the margins, to 18 cm long and 7 cm broad, chartaceous, with numerous pellucid dots and lines, minutely puberulous on both sides when young, the costa prominent and the lateral veins prominulous below. *Inflorescences* sessile, densely fasciculate, axillary (but usually on defoliated branchlets). *Flowers* white, the pedicels to 6 mm long, articulated ca 2-2.5 mm above the base, minutely ferruginous-puberulous especially below the articulation; calyx ca 5 mm long, the lobes ± oblong, scarcely united at the base, obtuse and subcucullate at the apex, 1.5-1.8 mm broad, minutely puberulous; stamens (7)8, united at the base with the staminodes into a very short tube, the filaments subequal, ca 2.5 mm long, glabrous, the anthers oblong, ca 0.7-0.8 mm long (sometimes inconspicuously apiculate?); staminodes (7)8, linear-spathulate, ca ½ as long as the filaments, villous; gynoecium ca 4-4.5 mm long, the ovary pyriform, ca 1 mm in diam at the base, villous, gradually attenuate into the glabrous style, the stigma conical-capitate. *Capsule* subglobose, with 6 longitudinal, blunt ridges, 8-13 mm long, white or green outside when fresh, glabrous or nearly so, the pericarp ± reticulated, splitting into 3 valves at maturity, these reddish inside; seeds up to 13 per capsule, subovoid, 3-3.5 mm long, very minutely foveolate, the aril orange-colored.

West Indies, Costa Rica, Panama, and northern South America; known colloquially in Panama as *palo de la cruz* (cf. *Pittier 6551*).

CANAL ZONE: Chagres, *Fendler 192* (US); Barro Colorado I, forest along shore of Gatun Lake, E of Laboratories, *Killip 40020* (US); Balboa, thicket, *Standley 32105* (US). DARIEN: forests around Pinogana, *Pittier 6551* (US). HERRERA: 12.5 mi S of Ocú, alt 1200 ft, secondary woods on hillside, *Lewis et al. 1665* (MO). PANAMA: Bella Vista, *Bro. Heriberto*

224 (US); id., in thicket, *Standley 25305* (US); low woods E of Bella Vista, along beach, *Maxon & Valentine 6929* (US); Sabanas, N of Panama City, *Bro. Paul 606* (US); nr Tapía River, Juan Díaz region, thicket at edge of forest, *Maxon & Harvey 6717* (US); San José I, *Erlanson 94* (NY, US), *261* (NY, US), *Johnston 1139* (MO, US).

This species is very closely related and perhaps even conspecific with *C. aculeata* Jacq.

6. **Casearia nitida** (L.) Jacquin, Enum. Syst. Pl. Ins. Carib. 21, 1760; L. Wms., Fieldiana: Bot. **29**: 359, 1961.

Samyda nitida L., Syst. Nat. ed. 10, 1025, 1759.
Casearia corymbosa H.B.K., Nov. Gen. Sp. Pl. **5**: 366, 1823.
C. banquitana Krause, Beih. Bot. Centralbl. **32**, Abt. 2: 345, 1914.
C. laevis Standley, Contr. U. S. Nat. Herb. **23**: 845, 1923.
C. banquitana var. *laevis* (Standley) Johnston, Sargentia **8**: 211, 1949.

Shrub or small tree 1.5-7.5 m tall, the branchlets inconspicuously puberulous to glabrous. *Leaves* short-petiolate, the petiole to 5(6) mm long, canaliculate above, inconspicuously puberulous to glabrous; blade oblong-elliptic to oblong-obovate, often narrowly so, the base oblique or not, ± rounded to subcordate or sometimes obtuse, the apex usually bluntly short-acuminate, rarely long-acuminate or obtuse or rounded (and subemarginate?), the margins minutely serrulate to crenulate-serrulate, to 16 cm long and 5.5 cm wide, membranous to chartaceous, copiously provided with pellucid dots or lines, glabrous above, glabrous or inconspicuously puberulous beneath, the costa and lateral veins prominent beneath. *Inflorescences* axillary, cymose-corymbiform, the axes glabrous to inconspicuously puberulous. *Flowers* white, the pedicels to 6 mm long, articulated below the middle, the bracteoles small and deltoid; calyx to 5 mm long, the lobes 5, united at the very base, elliptic, rounded, erect-patent at anthesis, inconspicuously puberulous; stamens 8, inserted at the apex of the calyx tube (or even above?), the filaments subequal, 2.5-3 mm long, glabrous, slightly united at the base among themselves and with the staminodes, the anthers oblong-ellipsoid, ca 0.7 mm long; staminodes 8, interstaminal, linear-spathulate, to 1.5 mm long, pilose; gynoecium ca 4 mm long, the ovary ovoid, ca 1 mm in diam at the base, rather sparsely pilose as the style, attenuate into the style, the stigma capitate. *Capsule* globose to ellipsoid, with 3, rarely 4, prominent longitudinal ridges, to 15 mm long and 11 mm in diam, the pericarp glabrous, yellowish-orange or reddish when mature and fresh, blackish when dry; seeds 1-3, ovoid to angulate-ovoid, to 7(8) mm long, the testa glabrous but covered with numerous dark resinous glands, the aril incomplete.

Widely distributed in tropical America; known in Panama as *comida de loro* (fide *Cooper & Slater 14*), *mamar* and *mako* (fide *Duke 14461*).

BOCAS DEL TORO: Almirante region, *Cooper & Slater 14* (US). CANAL ZONE: edge of forest at roadside just beyond Fort Sherman Research Forest Site, *Stimson 5224* (MO); rd to Devils Beach, *Johnston 1573* (MO); S of island (Barro Colorado I?), *White 113* (F, MO); Madden Dam, *Dwyer & Hayden 3* (MO); vic of Miraflores Lake, *White 143* (F, MO); nr junction of Miraflores & Cocoli roads, *White 87* (F, MO); Sosa Hill, Balboa, brushy slope, *Standley 25257* (US); Farfan Beach area, *Tyson 1828* (MO). CHIRIQUÍ: Progreso, *Cooper & Slater 199* (F, NY, US). COLÓN: Fató (Nombre de Dios), at sea level, *Pittier 3836* (US). DARIEN: Río Ucurganti, *Bristan 1186* (MO); Río Chucunaque, betw Río Membrillo & Río Subuti, *Duke 8585* (MO); Río Chucunaque, betw Río Membrillo & Río

Yaviza, *Duke 8617* (MO). LOS SANTOS: 1-2 mi W of Candelaria, *Duke 12444* (MO); nr Santo Domingo, *Dwyer 2499* (MO); Monagre Beach thicket, *Dwyer 4137* (MO); several km SE of Pedasi, beside dirt rd just S of Río Caldera nr Punta Mala, *Stimson 5289* (MO). PANAMA: Alhajuela, *Dwyer 1141* (MO); around Alhajuela, Chagres Valley, forest on dry limestone, alt 30-100 m, *Pittier 3497* (US); nr Matías Hernández, moist thicket, *Standley 28922* (US); Agricultural Experiment Station at Matías Hernández, *Pittier 6724* (US); betw Las Sabanas and Matías Hernández, moist thicket, *Standley 31908* (US); nr Tapía River, Juan Díaz region, edge of forest, *Maxon & Harvey 6625* (US); vic of Pacora, alt 0-20 m, *Allen 3448* (F, MO, NY, US); betw Cañazas & Sabalo, alt ca 100 m, *Duke 14461* (MO); Taboga I, alt 0-250 m, *Pittier 3540* (US), *Woodson et al. 1522* (F, MO, NY); San José I, in shade of forest, *Erlanson 151* (US), rocky bluffs, *Erlanson 159* (NY, US), *255* (US), *448* (US), *588* (NY, US). SAN BLAS: Mulatuppu, *Duke 8531* (MO). VERAGUAS: Santiago, 12 mi from Santiago towards Divisa on Transisthmian Hwy, roadside thicket, *Dwyer & Kirkbride 7408* (MO).

7. **Casearia sylvestris** Sw., Fl. Ind. Occ. 752, 1798.

Samyda sylvestris (Sw.) Poiret in Lamarck, Encycl. Méth., Bot. **6:** 492, 1805.

Shrub or small tree 2-10 m high, the trunk to 12 cm in diam, the branchlets puberulous but soon glabrous. *Leaves* with the petioles to 10 mm long, slender, canaliculate above, minutely puberulous when young but soon glabrous, the stipules minute, 1-1.5 mm long, caducous; blade narrowly oblong-ovate or narrowly oblong-elliptic, sometimes narrowly ovate or elliptic, the base symmetrical or often somewhat asymmetrical and usually acute, the apex long-acuminate, the acumen slender and up to 2.5 cm long, the margins entire or nearly so, to 14 cm long and 5 cm wide, membranous to thin-coriaceous, dark green, lustrous especially above, pellucid-punctate, glabrous, the costa prominulous below. *Inflorescences* axillary, sessile, densely fasciculate, the fascicules many-flowered, the bracts minute and forming a cushion in the leaf axils. *Flowers* pale yellow or white, the pedicels slender, to 5 mm long, articulated near or below the middle, puberulous to densely puberulous below the articulation; calyx 2-3 mm long, the lobes 5, broadly ovate, united at the base into an obtusely angulate tube 0.5-0.8 mm long, rounded, 1-1.5 mm wide, erect-patent at anthesis, minutely ciliolate, glabrous or sparsely puberulous outside, sparsely puberulous to puberulous inside; stamens 10, inserted at the apex of the calyx tube, the filaments slightly unequal, to 1.5 mm long, almost glabrous to sparsely puberulous, slightly united at the base among themselves and with the staminodes, the anthers didymous, subglobose, ca 0.3 mm long, with a dorsal, apical gland; staminodes 10, ± intrastaminal and alternating with the stamens, to 1-1.2 mm long, whitish-puberulous; gynoecium 2-2.2 mm long, the ovary obtusely angulate, ca 0.7-1 mm in diam, glabrous or sparsely pilose at the apex, attenuate into the style, the stigmas 3, capitellate, papillate. *Capsule* surrounded by the persistent, patent calyx, ovoid-globose, 3-4 mm long, obtusely angulate, apiculate, glabrous or nearly so, reddish or purple at maturity, splitting into 3 valves; seeds 2-6, ± ovoid, to 2 mm long, the testa light brown, glabrous, foveolate, the aril incomplete, reddish.

Throughout tropical America; known locally as *corta lengua* (*Cooper & Slater 213*).

BOCAS DEL TORO: vic of Chiriquí Lagoon, Water Valley, *von Wedel 1747* (MO, US); Isla Colón, *von Wedel 64* (MO), *2970* (MO, NY, US); region of Almirante, Buena Vista Camp on Chiriquí Trail, alt 1250 ft, *Cooper 587* (F, US). CANAL ZONE: Río Chagres, *Fendler 186* (MO, US); forest along banks of Quebrada La Palma & Cañon of Río Chagres, alt 70-80 m, *Dodge & Allen 17359* (MO); nr Fort Randolph, brushy slope, *Standley 28701* (US); nr Coco Solo Weather Station, *Duke 4286* (MO); Barro Colorado I, *Bangham 408* pro parte (F), *436* (F), *Shattuck 293* (F, MO), *749* (MO), *1097* (F, MO), *Woodworth & Vestal 429* (F); Cerro Gordo, nr Culebra, alt 50-290 m, *Pittier 2315* (US); Ancon Hill, woods, *Killip 39951* (US), *Standley 25155* (US), *26391* (US). CHIRIQUÍ: Progreso, *Cooper & Slater 213* (F, NY, US). COCLÉ: Bismark above Penenomé, *Williams 557* (NY, US). COLÓN: 1 mi from Puerto Pilon on side of dirt rd to Maria Chiquita Beach, *Correa 137* (MO); betw France Field, Canal Zone, & Catival, wooded swamp, common, *Standley 30169* (US); along trail to triangulation station on top of Tumba Vieja, alt 90-400 m, *Dodge 16759* (MO). DARIEN: El Real Quebrada Trapiche, *Duke & Bristan 323* (MO). PANAMA: La Chorrera, *Bro. Paul 498* (US); Juan Díaz, moist woods, common, *Standley 30589* (US); Río Tapía, moist woods, *Standley 30679* (US); Río Tocumen, wet forest, *Standley 26733* (US); San José I, in forest or edge of forest, *Johnston 232* (MO, US), *345* (MO, US), *1334* (MO, US). SAN BLAS: along the headwaters of the Río Mulatupo, seasonal evergreen forest, *Elias 1744* (MO). VERAGUAS: Isla de Coiba (Colonia Penal), *Dwyer 2316* (MO).

8. **Casearia commersoniana** Camb. in St.-Hil., Juss. & Camb., Fl. Bras. Merid. **2**: 235, 1830.—Fig. 9.

C. myriantha Turcz., Bull. Soc. Imp. Nat. Moscou **36**(1, fasc. 2): 609, 1863; Johnston, Sargentia **8**: 212, 1949.

C. javitensis Auct. non H.B.K.; Standley, Contr. U. S. Nat. Herb. **27**: 274, 1928.

Shrub or small tree 3-10(-15) m tall, the trunk to 10-20 cm in diam, the bark smooth, the branchlets glabrous or almost so. *Leaves* glabrous, short-petiolate, the petiole to 5-8 mm long, the stipules linear-subulate, early caducous; blade narrowly elliptic to narrowly ovate-elliptic to narrowly oblong, sometimes elliptic, acute at the base, acuminate at the apex, the acumen usually long and rather blunt, remotely crenulate-serrulate to almost entire along the margins, to 25 cm long and 9 cm wide, rigid-chartaceous, lustrous especially above, dark green, without pellucid dots, the costa and 5-8(-10) pairs of lateral veins prominent beneath. *Inflorescences* sessile, fasciculate, the fascicles few- to many-flowered, the bracts small and forming a cushion in the leaf axils. *Flowers* white or greenish, the pedicels 3-10 mm long, articulated below the middle, puberulous; sepals 4-5, scarcely united at the base, ovate, acute, unequal, ca 3-4 mm long, reflexed to erect-patent at anthesis, puberulous especially outside, persistent or slightly accrescent; stamens 9-15, slightly longer than the sepals, the filaments to 4.5 mm long, slightly unequal, glabrous, the anthers ellipsoid, ca 0.5-0.7 mm long, eglandular; staminodes intrastaminal, usually isomerous with the stamens, linear, ca 1.5-2 mm long, puberulous, especially towards the apex; gynoecium ca 3.5-4.2 mm long, the ovary subglobose, ca 1-1.5 mm in diam, sparsely to ± densely hirsute, the style glabrous or nearly so, divided at the apex into 3 branches to 0.8 mm long, the stigmas 3, capitate. *Capsule* subglobose, 3-angulate, apiculate, 5-10(-15) mm long, red or brownish outside when fresh, blackish outside and yellowish brown inside when dry, sparsely appressed-pilose, thin-walled, splitting into 3 valves at maturity; seeds 1-2, subglobose, 4-5 mm long, the testa brown, whitish-pilose, the aril pale, incomplete, subentire, carnose.

Southern Mexico, Central America, and northern South America.

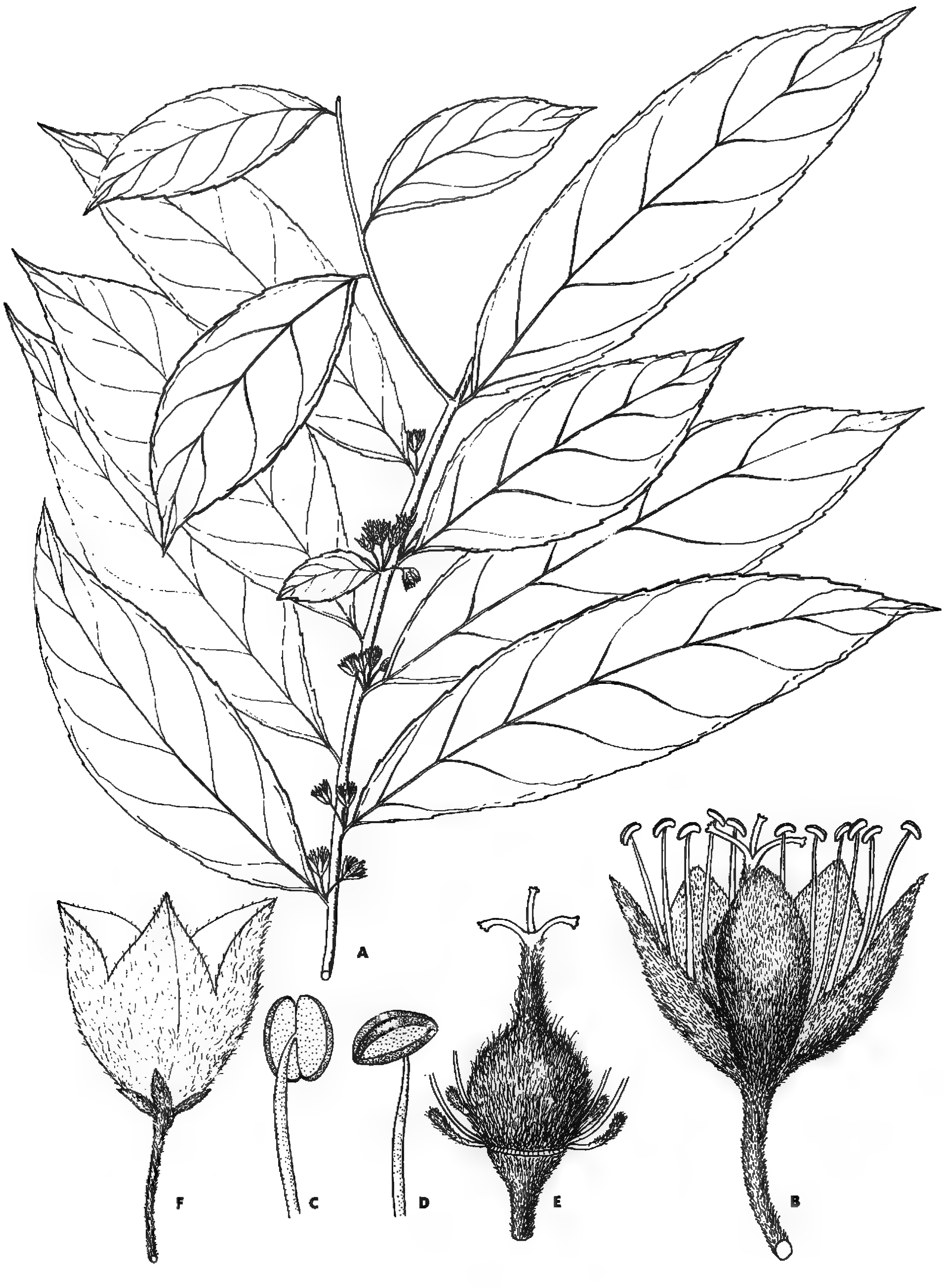

Fig.9. *Casearia commersoniana* Camb.: A, habit (×½); B, flower (×8); C & D, stamen, upper part of filament & anther (×20); E, gynoecium (×8); F, dehiscing capsule (×3). A-E after *Tyson & Blum 3911* (MO); F after *Dwyer 6837* (MO).

BOCAS DEL TORO: Almirante, just N of Dos Milla, hillside, *McDaniel 5123* (MO). CANAL ZONE: Chagres, Isthmus of Panama, *Fendler 185* (type *C. myriantha*, MO, US); headwaters Río Arenal, *Johnston 1501* (MO); Camp Pina, vic of Hill C-6, Ft. Sherman, *Duke 4406* (MO); Mount Hope Cemetery, moist thicket, *Standley 28834* (US); Gatun, *Hayes 98* (NY), *606* (NY), *613* (NY); Barro Colorado I, *Bangham 443* (F), *587* (F, US), *Shattuck 1151* (F, MO), *Starry 289* (F); Gamboa, *Stevens 1058* (US); Obispo, moist woods, *Standley 31759* (US); Ft. Clayton nr old hospital building #519, *Tyson & Blum 3911* (MO); Cerro Galero, Rd K6, alt 1000 ft, *Stern & Chambers 29* (F, MO, NY, US); s. loc.; *Epplesheimer s.n.* (F). CHIRIQUÍ: vic of David, alt 30-80 m, along streamlet, *Pittier 2831* (US); vic of San Felix, alt 0-120 m, *Pittier 5256* (F, NY, US). COLÓN: betw France Field, Canal Zone, & Catival, brushy slope, *Standley 30322* (US); Loma de la Gloria, nr Fató (Nombre de Dios), in forests, alt 10-104 m, *Pittier 3854* (F, NY, US). DARIEN: Río Pirre, *Duke & Bristan 8295* (MO); Camp Esloganti, helipad in premontane rain forest, alt 656 ft, *Duke 15502* (MO). PANAMA: hills above Campana, alt 600-800 m, *Allen & Alston 1863* (F, MO); Río Tapía, moist forest, *Standley 28259* (US); San José I, *Andersson s.n.* (MO, US), *1347* (MO, US). SAN BLAS: Ailigandi, *Duke 9318* (MO), *Dwyer 6837* (MO).

Because of insufficient material, a few collections of *Casearia* remain unnamed: (1) *Hayes* 3 (MO, US) = *899* (NY) (Canal Zone: nr Gatun): tree 10 m high, the branchlets rusty-tomentose; leaves short-petiolate, the blade ovate to obovate, discolorous, shiny and glabrous above, rusty-pubescent below; capsule ± globose, apiculate, with 3 longitudinal, prominulous ridges, to 2.5 cm long, tawny-tomentellous; this collection can perhaps be referred to the West Indian species *Casearia hirsuta* Sw.
(2) *Woodson et al. 987* (MO) (Chiriquí: vic of Casita Alto, Volcán de Chiriquí, alt ca 1500-2000 m); tree 6 m high; leaves like in *C. arguta;* capsule to 3 cm long, glabrous, the seeds conglutinate, to 12 mm long; this collection is related to *C. arguta*, but the capsule and seeds are unusually large.
(3) *Williams 646* (NY, US) (Darien: nr Marraganti): according to the field notes, this is a plant 5 m high, with the stem ca 6.5 cm in diam, with thorns 2.5 cm long; it is perhaps related to *C. aculeata* Jacquin, but the absence of stipules and flowers makes positive determination difficult.

11. ZUELANIA

Zuelania A. Richard in Sagra, Hist. Fis. Pol. Nat. Isla Cuba **10:** 33, 1841.

Trees or shrubs. *Leaves* alternate, petiolate, the stipules fugacious, the blade entire to serrulate, penninerved, pellucid-punctate. *Inflorescences* axillary, fasciculate towards the apex of the branchlets. *Flowers* often precocious, ☿, the pedicels bracteate at the base and articulated; sepals 4-5, imbricate, shortly united at the base, persistent; petals wanting; stamens ∞ (20-40), subperigynous, the filaments filiform, alternating and united basally with many clavate staminodes, the anthers subbasifixed, introrse, longitudinally dehiscent; ovary free, 1-locular, the ovules ∞ on 3 parietal placentas, the stigma sessile or subsessile, thick, peltate. *Fruit* a fleshy capsule, globose, opening at length by 3-valves; seeds numerous, arillate; endosperm carnose.

A genus of three species in the West Indies, with one species extending into Central America and Panama.

1. **Zuelania guidonia** (Sw.) Britton & Millsp., Bahama Fl. 295, 1920.—Fig. 10.
Laetia guidonia Sw., Nov. Gen. Sp. Pl. Prodr. 83, 1788.
Zuelania roussoviae Pittier, Contr. U. S. Nat. Herb. **18:** 163, *pl. 79*, 1916.

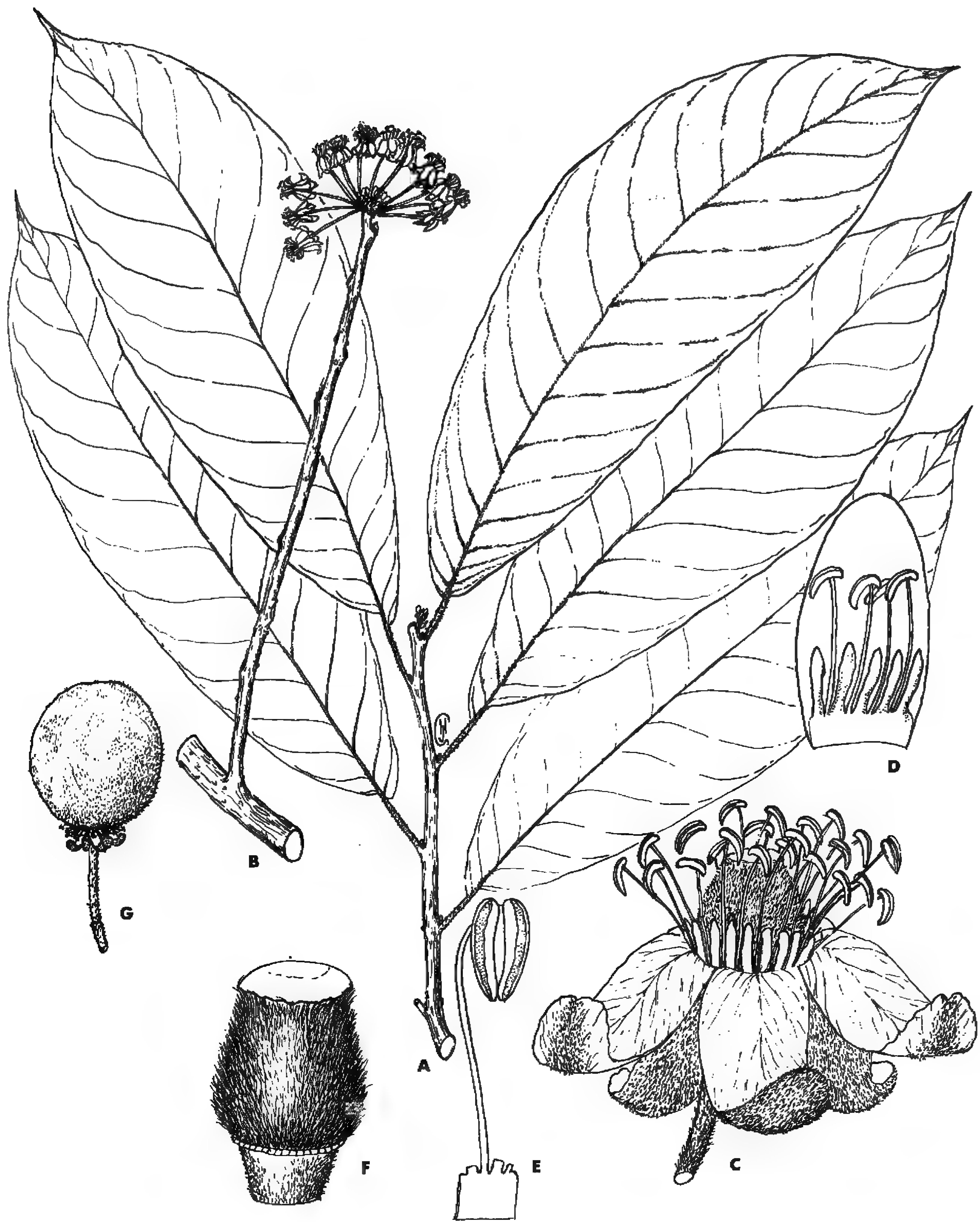

Fig. 10. *Zuelania guidonia* (Sw.) Britton & Millsp.: A, habit (×½); B, inflorescence (×½); C, flower (×5); D, sepal, 4 stamens, and 5 staminodes (×5); E, stamen (×10); F, gynoecium (×6); G, fruit (×1). A-F after *Johnston 613* (MO); G after *Pittier 2710* (MO).

Tree, deciduous, 10-25 m high, the trunk 30-50 cm in diam at the base, the crown rounded, the bark grayish, the branches sparsely verruculose, the branchlets brownish-hirsute. *Leaves* often fasciculate towards the apex of the branchlets, the petiole to 2 cm long, brownish-hirsute, the stipules narrowly ovate, 3-6 mm long, appressed-pubescent; blade narrowly oblong to oblong to oblong-elliptical, oblique and rounded or obtuse at the base, obtuse to acute to shortly obtusely acuminate, serrulate to subentire along the margins, 6-25 cm long and 3-9 cm wide, chartaceous, discolorous, green above and grayish or slightly brownish beneath when fresh, pellucid-punctate, pubescent on both sides but the indumentum denser beneath, the costa and lateral veins prominent beneath. *Inflorescences* in globose fascicles in generally defoliate axils at the apex of the branchlets, the fascicles to 15-flowered. *Flowers* yellowish, the pedicels to 18 mm long, shortly fulvous-hirsute, articulated below the middle, the bracts thin-scarious, to 4 mm long, short-hirsute without; calyx to 6-7 mm long, the sepals ovate, rounded at the apex, deflexed at anthesis, tomentose without except on the covered margins; stamens with the filaments to 4 mm long, glabrous or sparsely pilosulose, the anthers $\pm$ ovate-oblong, subemarginate at the base, obtuse at the apex, to 1.8 mm long; staminodes about $\frac{1}{2}$ as long as the filaments, glabrous or sparsely pilosulose; gynoecium to 4 mm long, the ovary ovoid, ca 2.5-3 mm broad, densely tomentellous, the stigma subsessile. *Capsule* baccate, $\pm$ globose to depressed-globose, shallowly 5-sulcate, up to 5 cm broad (5-10 cm broad acc. to *Zetek Z-3343*) and 3 cm high, yellowish-green to dark green when fresh, pilose; seeds numerous, obovoid, angular, ca 4 mm long, the aril orange.

Southern Mexico, Central America, and the West Indies; known colloquially in Panama as *cagajón* (fide *Aviles* X-11 & *Zetek* Z-3343) or *carañon* (fide *Pittier 6605*).

CANAL ZONE: Chagres, *Fendler 318* (MO); nr Fort Randolph, swampy woods, *Standley 28665* (US); Barro Colorado I, *Aviles X-11* (F), *Shattuck 796* (F), *Wilson 91* (F), *Woodworth & Vestal 719* (F), *Zetek Z-3343* (F), *3463* (F), *Z-5089* (F); hills betw Río Grande & Pedro Vidal, on rd to Arraiján, alt 50-150 m, *Pittier 2710* (holotype US, isotypes F, MO, NY); rd K9D, alt 260 ft, *Stern & Chambers 44* (F, MO, NY, US). COCLÉ: Penonomé & vic, alt 50-1000 ft, *Williams 235* (US). DARIEN: vic of La Palma, alt 0-50 m, *Pittier 6605* (NY, US). PANAMA: Río Tocumen, moist forest, *Standley 26750* (US); San José I, *Johnston 611* (MO, US), *613* (MO, US).

On San José Island, Johnston (Sargentia **8**: 215, 1949) describes this tree as follows: "The tall pallid trunk and the shallow wide crown give it a distinctive appearance, especially so during the dry season, when it is leafless . . . When freshly cut the thick bark is tan and marked with dark streaks, but it soon changes to mustard color and begins oozing a clear, yellowish exudation. The twigs are slightly reddish and roughened with somewhat protruding transverse lenticels . . . The foliage is shed early in February and generally not renewed until late in the dry season . . . It [the fruit] is firm but somewhat juicy in texture, produces honey-like exudations when bruised, and eventually splits into three broad diverging parts to expose the seeds and the conspicuous orange placentas."

12. LAETIA

Laetia Loefl. ex L., Syst. Nat. ed. 10, 1074, 1373, 1759.

Shrubs or trees. *Leaves* alternate, distichous, petiolate, the stipules early caducous, the blade crenate or serrate, rarely entire-margined or nearly so, usually pellucid-punctate, sometimes coriaceous and epunctate. *Inflorescences* axillary or terminal, fasciculate or cymose. *Flowers* rather small, ☿, the pedicels articulated above the base, the bracteoles small, the bracts and bracteoles sometimes united into a cupule; sepals 4-5, imbricate, free or scarcely united at the base, somewhat petaloïd, reflexed or not at anthesis, deciduous; petals absent; stamens 10-20 or ∞, inserted on an obsolete disc, the filaments free, equal or not, the anthers small, elliptic or linear, not appendaged, introrse, attached at or above the base, longitudinally dehiscent; staminodes none; ovary free, 1-locular, with 3 parietal placentas, the placentas few- to many-ovulate; style short, simple or shortly but distinctly 3-lobed, the stigmas capitate or lobed. *Fruit* a berry-like capsule, tardily valvately dehiscent, sometimes resinous within; seeds few to numerous, arillate, the testa coriaceous; endosperm copious; embryo straight; cotyledons broad and foliaceous.

A neotropical genus of about 20 species; three species, at present, reported from Panama and North America.

a. Inflorescences fasciculate, many-flowered; sepals 5.
  b. Pedicels to 4 mm long, minutely puberulous; sepals ca 1.8-2 mm long, erect at anthesis, minutely puberulous outside; stamens 10, the anthers ca 0.3 mm long; style shortly but distinctly 3-fid at the apex; leaf blades with the margins serrulate .... 1. *L. micrantha*
  bb. Pedicels to 12 mm long, glabrous; sepals to 4 mm long, reflexed at anthesis, glabrous; stamens 12-20, the anthers to 1.5 mm long; styel undivided; leaf blades with the margins minutely appressed-serrulate to almost entire ....2. *L. procera*
aa. Inflorescences dichasial, few-flowered; sepals 4, 8-9 mm long; stamens ∞; style undivided; leaf blades with the margins entire to indistinctly crenulate ....3. *L. thamnia*

1. **Laetia micrantha** A. Robyns, Ann. Missouri Bot. Gard. **54**: 190, 1967.—Fig. 11.

Tree 18-20 m tall, the trunk 12.5-25 cm in diam, the wood hard, the branchlets puberulous. *Leaves* pendent on branches, the petioles 5 mm long, puberulous-villous, the stipules narrowly triangular, ca 4 mm long and 1 mm wide at the base, fugacious; blade narrowly ovate-oblong to narrowly oblong, the base suboblique to markedly oblique, obtuse to rounded on one side and acute to obtuse on the other side, the apex long-acuminate, the acumen slender, the margins serrulate, 6-13 cm long and 1.5-4.5 cm wide, membranous to thin-chartaceous, densely pellucid-punctate, ± shining especially above, minutely puberulous on both sides, the costa prominent and the lateral veins prominulous beneath. *Inflorescences* axillary, densely fasciculate, the bracts numerous, small, ca 1 mm long, persistent, forming cushions in the axils of the leaves. *Flowers* white, the pedicels filiform, to 4 mm long, articulated ca 1 mm above the base, minutely puberulous; sepals 5, free or nearly so, ± obovate, slightly cucullate, rounded at the apex, ca 1.8-2 mm long and 1-1.3 mm wide, membranous, erect at anthesis, minutely puberulous outside; stamens 10, exserted, uniseriate, the filaments filiform, ± equal, 2-2.5 mm long, glabrous, the anthers ca 0.3 mm long; ovary subglobose, ca 0.7-0.8 mm in diam, glabrous, each placenta 2-ovulate, the style ca 1.3 mm long, shortly but distinctly 3-fid at the apex, the branches each 0.2 mm long, the stigmas 3, slightly enlarged. *Capsule* unknown.

Endemic in the Province of Darien; known colloquially as *raspa lengua* (fide *Duke & Bristan* 238).

DARIEN: Perrecenico River, *Duke & Bristan 238* (MO); trail betw Paya & Palo de las Letras, *Stern et al. 206* (US); vic of Caná, alt 1750 ft, hillside, in dense wood, *Stern et al. 513* (holotype MO, isotype US).

Duke & Bristan (238) report that the fruit is edible and that the wood may be used for firewood when dry.

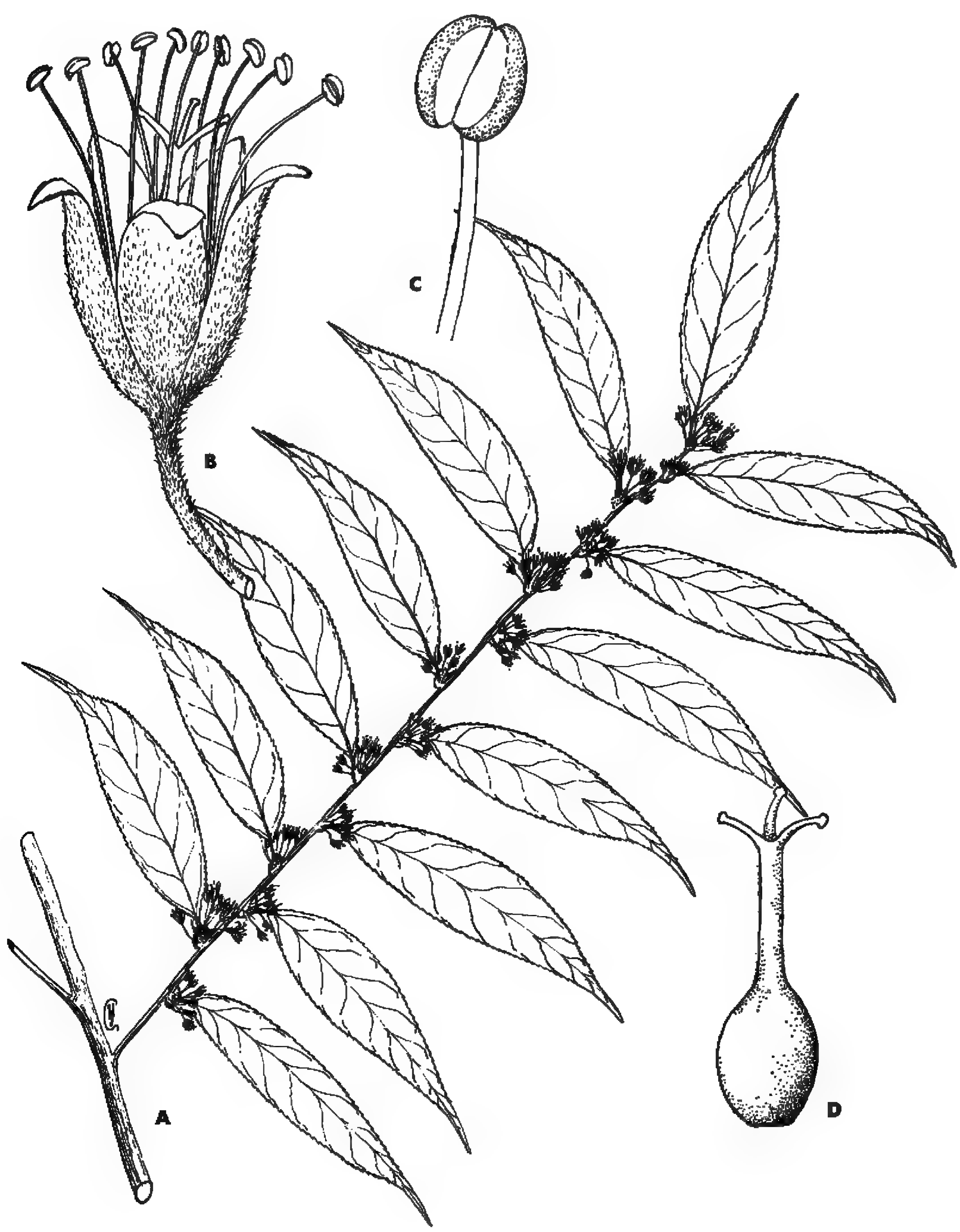

Fig. 11. *Laetia micrantha* A. Robyns: A, habit (×½); B, flower (×15); C, stamen, upper part of filament and anther (ca ×40); D, gynoecium (×15). After *Stern et al. 513* (MO).

2. **Laetia procera** (Poeppig) Eich. in Mart., Fl. Bras. **13** (1): 453, 1871.
Samyda procera Poeppig in Poeppig & Endl., Nov. Gen. Sp. Pl. **3**: 67, 1845.
Guidona procera (Poeppig) O. Ktze., Rev. Gen. Pl. **1**: 44, 1891.

Slender *tree* to 12 m tall or more, the trunk terete, the branchlets glabrous, sometimes pruinose. *Leaves* with the petioles to 1 cm long, canaliculate above, glabrous and sometimes pruinose, the stipules deltoid, 0.5-0.8 mm long, caducous; blade narrowly oblong, sometimes slightly inequilateral, rounded to subcordate at the base, long-acuminate at the apex, the acumen mostly blunt and to 12 mm long, minutely appressed-serrulate to almost entire along the margins, to 16 cm long and 4.5 cm wide, chartaceous, densely pellucid-punctate, ± lustrous on both sides, slightly paler beneath, glabrous, the costa and lateral veins prominent beneath. *Inflorescences* supra-axillary, in sessile 15-30-flowered fascicles, the bracts numerous, small, forming a cushion. *Flowers* white, glabrous, the pedicels slender, to 12 mm long, articulated close to the base; sepals 5, obovate, rounded at the apex, to 4 mm long and 2.5 mm wide, reflexed at anthesis, persistent; stamens 12-20, scarcely perigynous, the filaments filiform, ± crispate, to 3 mm long, the anthers oblong, to 1.5 mm long; ovary ovoid, attenuate at the apex into a short, undivided style, the stigma capitate. *Capsule* globose-ellipsoid, 1.5-2 cm long, splitting into 3 valves stellate-coherent at the base, the pericarp often wrinkled; seeds numerous, ovoid, to 3.5 mm long, reticulate-foveolate, the aril white and fleshy.

Reported for the first time from Panama and North America; Guyanas; northern Brazil.

CANAL ZONE: River rd nr Congo bridge, *Johnston 1527* (MO); rd W of Pina Base Camp, *Johnston 1791* (MO).

3. **Laetia thamnia** L., Amoen. Acad. **5**: 379, 1760.

Tree to 10 m high, the branchlets glabrous. *Leaves* with the petioles to 1 cm long, caniliculate above, glabrous, the stipules broadly triangular, ca 1 mm long, caducous; blade narrowly elliptic to elliptic, slightly inequilateral, the base oblique, acute to obtuse on one side, ± rounded on the other side, the apex obtuse to acuminate, the margins entire to indistinctly crenulate, to 12.5 cm long and 4 cm wide, membranous to chartaceous, pellucid-punctate, glabrous or inconspicuously puberulous when young, the costa prominent beneath. *Inflorescences* axillary, dichasial, few-flowered, the peduncles inconspicuously puberulous to glabrous, the bracts broadly triangular, ca 1 mm long; buds globose, minutely to inconspicuously puberulous. *Flowers* white, the pedicels slender, 9-13 mm long, articulated 2-3 mm above the base, inconspicuously puberulous especially below the articulation to glabrous; sepals 4, broadly elliptic or obovate, rounded at the apex, 8-9 mm long and 5-7 mm wide, reflexed at anthesis, minutely puberulous to glabrescent, caducous; stamens ∞, the filaments filiform, unequal, 2.5-4.5 mm long, finely and softly puberulous, the anthers broadly elliptic, ca 0.5-0.7 mm long; gynoecium ca 4-5 mm long, the ovary broadly ovoid, to 3 mm in diam, tomentellous, attenuate at the apex into a short, undivided style, the stigma capitate. *Capsule* globose or nearly so, to 3 cm in diam, densely and minutely ferruginous-tomentellous, the pericarp to 5 mm thick and fleshy, many-scaled.

Southern Mexico, Central America, Colombia, and the West Indies; known locally as *conejo* (fide *Pittier 3514*).

CANAL ZONE: Chagres, *Fendler 106* (MO, US); betw Chagres Batteries & Fort San Lorenzo, Fort Sherman Military Reservation, *Maxon & Valentine 6969* (F, NY); around Alhajuela, Chagres Valley, alt 30-100 m, forests on dry limestone, *Pittier 3514* (F, NY); Barro Colorado I, *Bailey & Bailey 504* (F), *Shattuck 1096* (F, MO, US). PANAMA: along Río Juan Díaz, alt ca 30 m, *Allen 932* (MO).

The following sterile collections probably belong to this species: *Zetek 3687* (F, MO), *3906* (F, MO), *4999* (F), all from Barro Colorado I, Canal Zone.

13. RYANIA

Ryania Vahl, Eclog. Amer. **1:** 51, *pl.* 9, 1796, nom. gen. conserv.
Patrisia L. C. Richard, Act. Soc. Hist. Nat. Paris **1:** 110, 1792.

Trees or shrubs, the wood hard, the indumentum mostly stellate. *Leaves* alternate, distichous, shortly petiolate, the stipules 2, glandular near the base within, deciduous; blade equilateral or subasymmetrical, the margins entire to irregularly denticulate-serrate, membranous to coriaceous, epunctate. *Flowers* often showy, axillary, solitary to 4-fasciculate, ☿, heterostylous, pedicellate, the pedicels articulated and bracteolate at the base; sepals 5, quincuncial, nearly free, petaloid, spreading at maturity, erect after anthesis, deciduous or persistent; petals none; stamens 30-70, inserted in 2-3 series at the apex of the very short calyx tube, free or nearly so, subequal, the anthers attached above the base, oblong to linear, to 9 mm long, often conspicuously mucronate at the apex, introrse, longitudinally dehiscent; pollen smooth, with a single longitudinal colpus; disc coroniform, urceolate; ovary superior, sessile or manifestly stipitate, 1-locular, with 3-9 parietal placentas; ovules ∞, many-seriate, anatropous; style short to long, entire or 3-9-fid at apex, the stigmas capitellate. *Fruits* capsular, ultimately valvately dehiscent, 1-locular, many-seeded; seeds small, arillate, hispidulous with scattered stellate hairs; endosperm copious; embryo straight; cotyledons flat and thin.

A neotropical genus of 9 species distributed in Panama, Trinidad and South America; one variety of the polymorphic *R. speciosa* reported from Panama.

Useful reference:

Monachino, J., A revision of *Ryania* (*Flacourtiaceae*). Lloydia **12:** 1-29, 1949.

Probably all the species of *Ryania* are poisonous. All parts of the plant are to a greater or lesser extent deadly, the concentrated alkaloid acting as a violent stomach poison on both warm and cold blooded animals. According to Monachino (loc. cit. p. 5) the Indians of the Amazon have used *R. angustifolia* to poison alligators. Derivatives of *Ryania* (e.g. *R. speciosa*) are used as insecticides and "it is said to be as good and possibly better than DDT against the European Corn Borer, promising against the sugar cane borer and the Oriental fruit moth, and effective control of the soybean caterpillar." (Monachino, loc. cit.).

1. **Ryania speciosa** Vahl var. **panamensis** Monachino, Lloydia **12:** 18, 1949.—Fig. 12.

Shrub or tree 1-12 m tall, the branches elongated, the branchlets minutely stellate-tomentose. *Leaves* with the petioles to 0.5(1) cm long, canaliculate above, densely and minutely stellate-tomentose, the stipules small, subulate, ca 3-7 mm

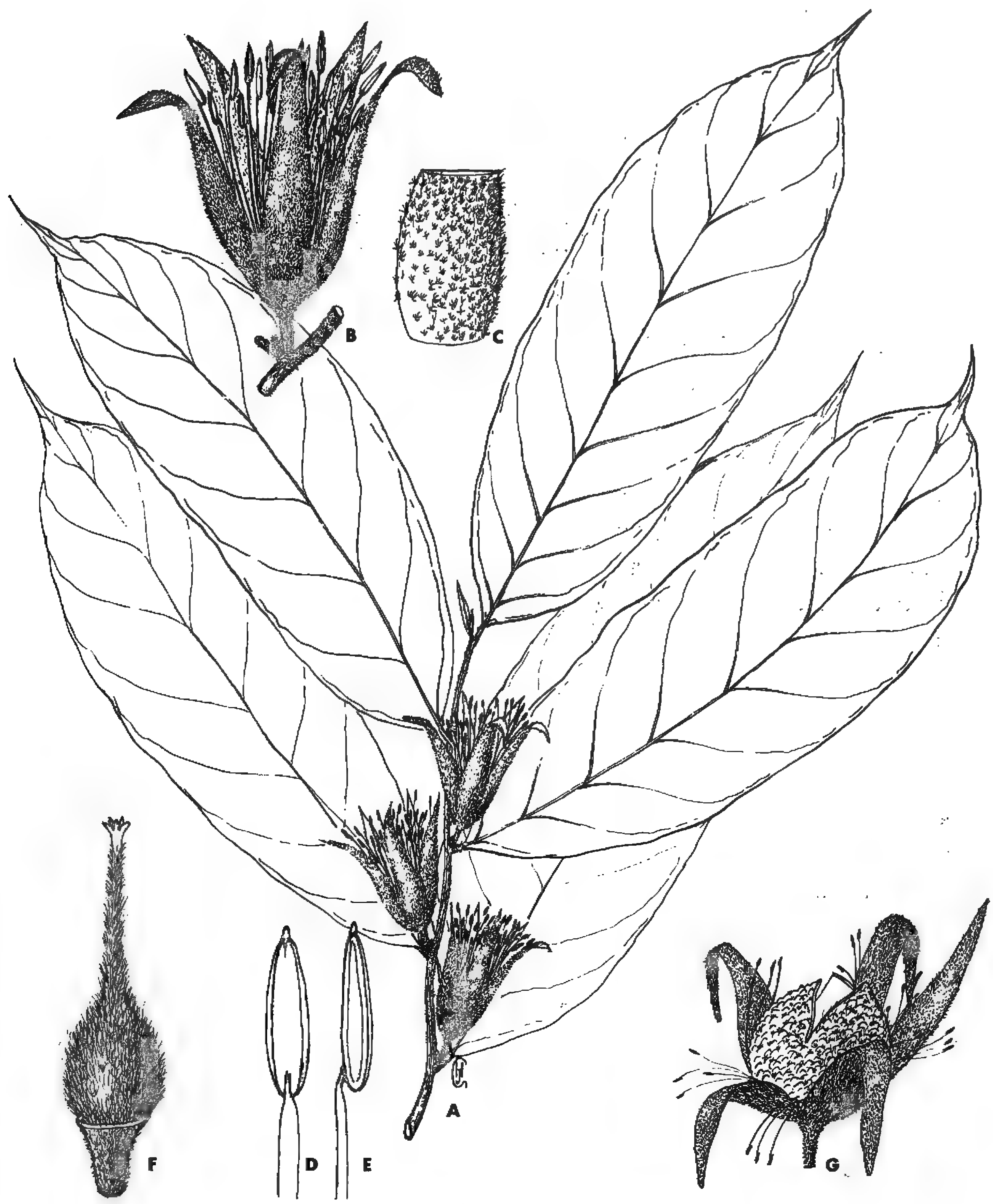

Fig. 12. *Ryania speciosa* Vahl var. *panamensis* Monachino: A, habit (×½); B, flower (×1); C, section of sepal showing the stellate indument (×2); D, stamen, upper part of filament and anther (×5); E, id., lateral view (×5); F, gynoecium (×2); G, dehiscent capsule surrounded by the persistent calyx (×1). A-F after *Stevens 1251* (US); G, after *von Wedel 1947* (MO).

long, deciduous; blade narrowly elliptic to slightly obovate, slightly oblique or not and mostly rounded to sometimes obtuse at the base, caudate to long-caudate-acuminate at the apex, to 21 cm long and 7 cm wide, chartaceous, the acumen to 2.5 cm long, the margins entire, the upper surface ± shining and glabrous or nearly so (midvein often stellate-puberulous near the base), the lower surface sparsely and minutely stellate-puberulous to glabrous except for the stellate-tomentellous to stellate-puberulous prominent costa and lateral nerves. *Flowers* white or light green, solitary to 2(-3)-fasciculate, the pedicels to 8 mm long, disarticulating at the base, minutely stellate-tomentose, the bracteoles 3.5-5 mm long, subulate, caducous; buds angulate-ovate; sepals narrowly ovate, acute, scarcely united at the base, 1.3-5 cm long and 0.4-0.8 cm wide, minutely stellate-tomentose to stellate-puberulous outside, minutely and softly stellate-tomentellous inside, persistent; stamens 2-seriate, the filaments filiform, free, subequal, to 2.5 cm long, glabrous or the lowermost part pilose, the anthers 2.5-4 mm long, mucronate; disc ca 2 mm high (teeth included), the teeth up to 1 mm long, barbate-villose; ovary sessile or nearly so, ovoid to ellipsoid, densely appressed-fulvous-sericeous, the style up to 1.7 cm long, appressed-sericeous at the base to glabrescent or glabrate at the apex. *Capsule* baccate, surrounded by the persistent calyx, ± globose, apiculate (persistent base of style), to 2.5 cm or more in diam, the exocarp thick, suberose, scabridulous and ferrugineous-stellate-tomentellous outside, the endocarp crustaceous; seeds ovoid, ± bluntly angulate, ca 5 mm long, the testa with scattered stellate hairs, the aril unilateral, membranous.

Known at present only from the Province of Bocas del Toro, the Comarca de San Blas, and from the Canal Zone.

BOCAS DEL TORO: vic of Chiriquí Lagoon, Big Bight, *von Wedel 2886* (holotype NY; isotypes MO, US); id., Old Bank I, *von Wedel 1928* (MO, US), *1947* (MO), *2119 A* (MO, US); Laguna de Chiriquí & vic, *Hart 312* (US); s. loc., *von Wedel 306* (MO). CANAL ZONE: Fort Lorenzo Trail, *Stevens 1251* (US); along Pavon Road, forest understory, *Johnston 1537* (MO); Santa Rita hills, cut-over secondary forest, *Smith & Smith 3438* (F). COLÓN: E Santa Rita Ridge, *Correa & Dressler 647* (MO). SAN BLAS: 2-5 mi S of Mandinga airport, trail E of Cangandi-Mandinga airport road, *Duke 14766* (MO).

The only significant distinction between the above variety and the var. *speciosa* resides in the length of the anthers. In var. *speciosa* they are 5-7 mm long, while in var. *panamensis* they are only 2.5-4 mm long. Study of additional material is needed in order to evaluate this characteristic properly.

14. LUNANIA

Lunania W. J. Hooker, Lond. Jour. Bot. **3:** 317, 1844, nom. gen. conserv.

Shrubs or trees. *Leaves* alternate, petiolate, estipulate, the blade entire-margined or nearly so, 3-(5-)nerved from the base, with or without scattered pellucid dots. *Inflorescences* axillary or terminal, in simple or branched racemes, the pedicels short and articulated at the base, the bracts and bracteoles minute. *Flowers* ☿, small; calyx subglobose, at length valvately split to the base into 2-3(-5) spreading or reflexed membranous lobes; petals none; stamens 6-12, inserted around a cupular hypogynous disk and alternating with its lobes, the filaments shorter to longer than the anthers, the anthers basifixed, 2-thecate, longitudinally and extrorsely dehiscent; ovary free, 1-locular, the ovules ∞, multiseriate on 3 broad, parietal placentas; styles 3, free to the base or not, short to elongate, the stigmas terminal. *Capsules* coriaceous, 3-valvate, few- to many-seeded; seeds small, the testa usually punctate, arillate; endosperm present.

A neotropical genus of probably less than 20 species; two species, represented by only four collections, reported at present from Panama.

a. Calyx splitting into 2-3 lobes, these reflexed and curled after anthesis; filaments very short and ca 0.2-0.3 mm long; anthers to 1.5 mm long; disc and ovary tomentellous .... 1. *L. parviflora*
aa. Calyx splitting into 2 spreading, cucullate lobes; filaments to 1.5(-3) mm long; anthers ca 0.5 mm long; disc and ovary glabrous .... 2. *L. piperoides*

1. **Lunania parviflora** Spruce ex Bentham, Jour. Proc. Linn. Soc., Bot. **5** (Suppl. 2): 90, 1861.—Fig. 13.

L. cuspidata Warburg in Engler & Prantl, Nat. Pflanzenfam. **3**(6a): 47, 1893.
L. pittieri Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. **18**: 722, 1937.

Tree to 20 m tall, the branchlets glabrous or inconspicuously puberulous. *Leaves* with the petioles to 2.2 cm long; blade inequilateral, ovate to elliptic, or ovate-oblong, sometimes narrowly so, oblique and acute to rounded at the base, long-caudate-acuminate at the apex, the acumen to 3 cm long and blunt, the margins entire or nearly so, to 19 cm long and 7.5 cm wide, thin-chartaceous to chartaceous, somewhat lustrous above, dull beneath, 3- to 4- to 5-nerved from the base, glabrous above, inconspicuously puberulous and hirtellous along the main veins to glabrous below, the main veins somewhat impressed above and prominent below, the veinlets scarcely prominulous and loosely reticulate on both sides. *Racemes* pendulous, to 40 cm long, the rachis inconspicuously puberulous. *Flowers* yellowish-green to cream-colored, the pedicels 1.5-2 mm long; buds subglobose, inconspicuously puberulous; calyx splitting into 2-3 lobes, these 1.5-2 mm long, reflexed and curled after anthesis, long persistent; stamens 10-12, the filaments very short and ca 0.2-0.3 mm long, glabrous, the anthers narrowly deltoid, to 1.5 mm long, apiculate; disc ca 0.5 mm high, tomentellous; ovary ca 1 mm long, tomentellous, the styles 3, to 1 mm long, at first close together, later on spreading, glabrous, the stigmas papillate. *Capsule* when young puberulous, mature one not seen.

Costa Rica, Panama, Colombia, Ecuador, Peru, Bolivia, and Amazonian Brazil.

SAN BLAS: Ailigandi River, *Duke & Bristan* 353 (MO); headwaters of Río Cuadí, Camp Diablo (Drill Site 22), N. 82.2, E. 87.8, alt 273.4 ft, seasonal evergreen forest along river, *Duke et al. 3609* (MO).

2. **Lunania piperoides** Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. **4**: 317, 1929.

Shrub to medium-sized tree to 20 m tall, the branchlets minutely puberulous and hirtellous, glabrescent; blade somewhat inequilateral, ovate to oblong-ovate, sometimes narrowly so, rounded to ± cuneate at the base, long-caudate-acuminate at the apex, the acumen to 2.5 cm long and blunt, the margins entire to somewhat undulate, to 13.5 cm long and 5.5 cm wide, thin-chartaceous to chartaceous, 3-nerved from the base, somewhat shining on both sides, glabrous above, minutely puberulous and hirtellous along the main veins to glabrous beneath, the main veins slightly impressed above and prominent beneath, the veinlets slightly prominulous and loosely reticulate on both sides. *Inflorescences* of branched racemes, the racemes to 10 cm long, the rachis densely and minutely puberulous. *Flowers* greenish, the pedicels to 1.5 mm long, the bracts ca 0.8 mm long, the bracteoles ca 0.5 mm long,

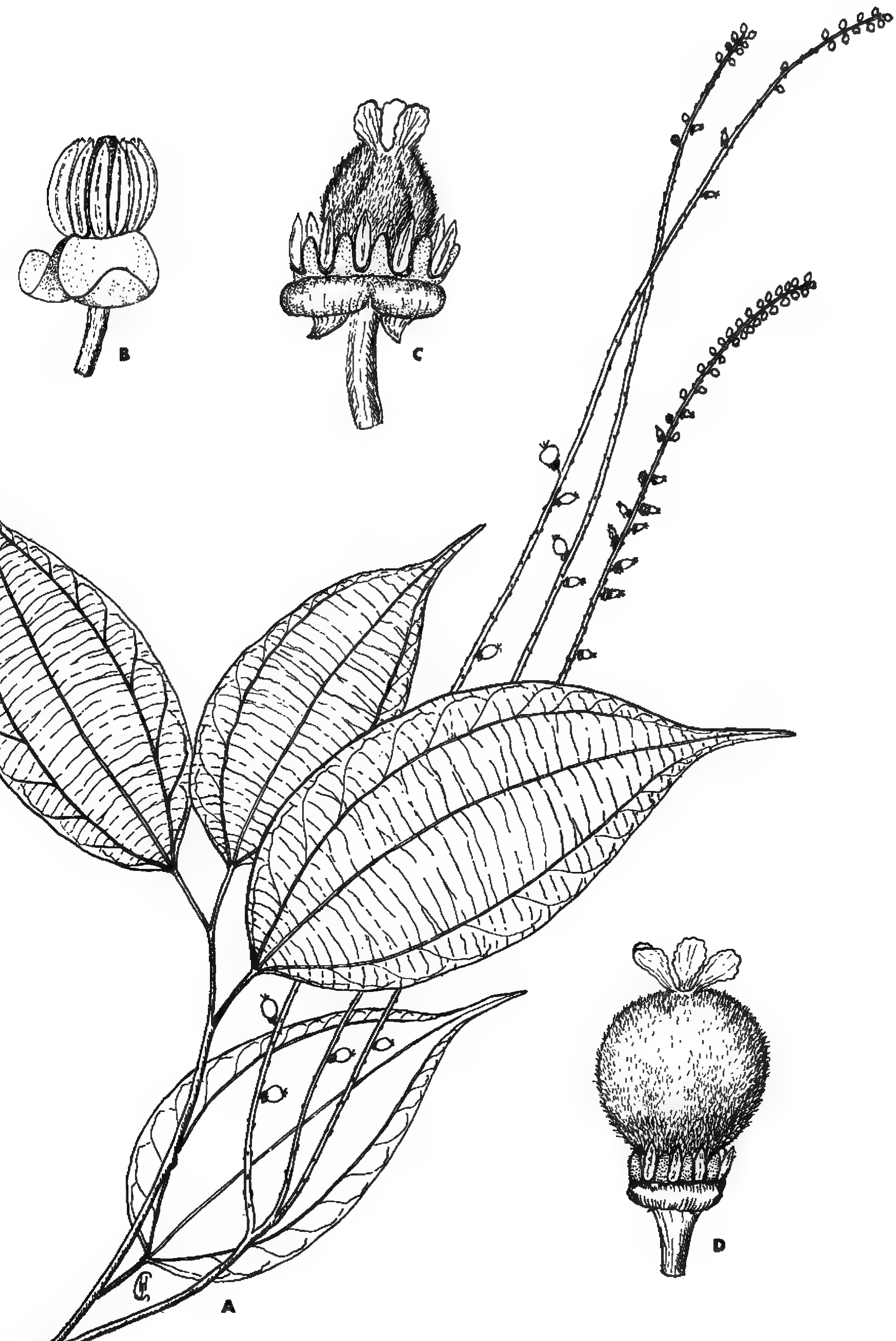

Fig. 13. *Lunania parviflora* Spruce ex Bentham: A, habit (×½); B, flower (ca ×10); C, id., later stage of development, the anthers fallen off (ca ×10); D, young capsule (×6). After *Duke et al. 3609* (MO).

persistent; calyx splitting into 2 spreading, cucullate, glabrous lobes to 2 mm long; stamens 10, the filaments to 1.5(-3) mm long, the anthers subglobose, ca 0.5 mm long, the disc ca 0.5 mm high, glabrous; ovary glabrous, the styles 3, somewhat flabellate towards the apex, glabrous. *Fruit* (not seen, acc. to original description) subglobose, 5 mm long, the pericarp smooth, pale red, and glabrous; seeds numerous, embedded in pulp, ovoid, 1 mm long.

Honduras and Panama.

BOCAS DEL TORO: vic of Chiriquí Lagoon, Fish Creek, mountains, *von Wedel 2396* (MO, US). COCLÉ: El Valle de Antón, forest behind Club Campestre, alt ca 700 m, *Duke 13248* (MO).

15. XYLOSMA

Xylosma G. Foster, Fl. Ins. Austr. Prodr. 72, 1786, nom. gen. conserv.

Myroxylon J. R. & G. Foster, Char. Gen. Pl. 125, 1776, non L. f. (Suppl. 34, 233, 1781).

Shrubs or small trees, often with axillary spines, the branchlets commonly lenticellate. *Leaves* alternate, sometimes borne in fascicles, usually short-petiolate, estipulate, the blade often ± coriaceous, usually glandular-dentate, penninerved, rarely entire-margined, without pellucid-glands. *Inflorescences* axillary, fasciculate or contracted-racemose, rarely racemose. *Flowers* small, dioecious or rarely polygamous; pedicels articulated above the base, the bracts minute; sepals 4-5(-6), imbricate, usually scale-like, slightly connate at the base, often ciliolate along the margins, usually persistent; petals none; stamens ∞ (8-35 in Panamanian spp.), usually surrounded by an annular or glandular, fleshy disc, the filaments free, filiform, short- to usually long-exserted, the anthers minute, basifixed, extrose, longitudinally dehiscent; ovary sessile, inserted on an annular disc, 1-locular, with 2-3, rarely 4-6, parietal placentas, each placenta with 2, sometimes 4-6, ovules, the style entire or ± divided, sometimes very short, the stigmas scarcely dilated to dilated; rudimentary ovary wanting in ♂ flowers. *Fruits* baccate, rather dry, indehiscent, surmounted by the persistent style, the pericarp rather thin-coriaceous, the seeds 2-8, ± angular by mutual pressure, the testa thin; endosperm copious; embryo large, the coyledons broad.

About 100 species throughout the tropics, but absent in Africa.

In the absence of a comprehensive revision of the genus as a whole, it is impossible to give a satisfactory treatment of the genus in a regional flora. The specific delimitations within the genus are extremely difficult and neither the flowers nor the fruits yield good distinctive characters. All the keys in the regional tropical American floras are based mainly on vegetative characters, and I have been forced, alas, to do the same in this flora. It is consequently obvious that my treatment of *Xylosma* is only provisional.

Nine species are listed in the following keys, four species without specific name. In view of the existing confusion within the genus I am reluctant to describe any new taxon and I leave the evaluation of the given characters of the unnamed species to the monographer-to-be of the genus!

The bark contains tannin and the fruit is sometimes the source of dyestuff; the wood is moderately hard and rather heavy.

a. Inflorescences fasciculate or contracted-racemose.
  b. Leaves, at least most of them, borne in fascicles at the end of very short pseudo-branches ....1. *X. anisophylla*
  bb. Leaves not fasciculate.
    c. Leaves glabrous.
      d. Flowers dioecious.
        e. Stamens 16 or more (up to 35).
          f. Leaves usually broadly rounded at the apex, the margins with small, sometimes even inconspicuous, closely appressed, rounded serrations, their tips slightly overlapping the margin of the blade, the network of the venation inconspicuous on the upper surface; stamens ca 20-25; along the Atlantic Coast ....2. *X. panamensis*
          ff. Leaves obtuse to acute or long-acuminate, the margins distinctly crenate or serrate.
            g. Leaves commonly obtuse to acute at the apex, the network of the veins clearly noticeable on the upper surface when dry; stamens 16-20; style 2-3 lobed; Prov of Chiriquí, at 900-2250 m alt ....3. *X flexuosa*
            gg. Leaves long-acuminate at the apex, the network of the venation prominulous on both sides; stamens ca 35; style 4-5 lobed; Prov of Panama, lowlands ....6. *Xylosma* sp. 1
        ee. Stamens 8-12; Prov of Coclé, at ca 500 m alt ....7. *Xylosma* sp. 2
      dd. Flowers polygamous; Prov of Coclé, at sea level ....8. *Xylosma* sp. 3
    cc. Leaves hispidulous or minutely hirtellous below.
      h. Branchlets and petioles densely short-hispid; leaf blades hispidulous below; petioles 2-4 mm long; Prov of Bocas del Toro, at sea level ....4. *X. hispidula*
      hh. Branchlets and petioles inconspicuously puberulous; leaf blades minutely hirtellous below; petioles to 1 cm long or slightly longer; at 1800-2100 m alt ....9. *Xylosma* sp. 4
aa. Inflorescences racemose ....5. *X. intermedia*

1. **Xylosma anisophylla** Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. **11:** 135, 1932.

Shrub or small tree 2-7 m tall, glabrous, the branchlets often armed with spines, these to 4.5 cm long. *Leaves,* at least most of them, borne in fascicles at the end of very short pseudo-branches, subsessile to very shortly petiolate, the petiole to 4 mm long; blade usually narrowly obovate to obovate, infrequently elliptic, cuneate-attenuate at the base, obtuse to rounded at the apex, remotely and obtusely glandular-serrulate along the margins, the serrations inflexed towards the margin and with their tips covering slightly the margin, to 6 cm long and 3.5 cm wide, chartaceous to rigid-chartaceous, slightly lustrous above, dull beneath, the costa prominulous beneath, the venation reticulate and inconspicuous on both sides. *Flowers* fasciculate, dioecious, yellow, with slender, glabrous pedicels to 8 mm long; sepals 4, triangular-ovate, acute, to 1.5 mm long, ciliolate along the margins, glabrous; stamens ca 20, the filaments slender, to 2.5 mm long before dehiscence, to 4 mm long after dehiscence. *Bacca* subglobose, 5-6 mm long, glabrous, surmounted by the persistent, 2-3-lobed style, the stigmatic lobes spreading; seeds (acc. to Standley, loc. cit. 136) 5, ferrugineous.

Mexico, British Honduras, and Panama.

PANAMA: nr Río Mar, savanna, alt 5-20 m, *Duke 12417* (MO); Taboguilla I, *Miller 2017* (US); Sabana de Juan Corso, nr Chepo, alt 60-80 m, *Pittier 4682* (US); Río Tapía, moist forest, *Standley 28256* (US); nr Matías Hernández, moist thicket, *Standley 28873* (US); Nuevo San Francisco, in thicket, *Standley 30739* (US); betw Pacora & Chepo, boggy grasslands & marginal thickets, alt ca 25 m, *Woodson et al. 1667* (F, MO).

2. **Xylosma panamensis** Turcz., Bull. Soc. Imp. Nat. Moscou **36** (1, fasc. 2): 554, 1863.

Myroxylon panamense (Turcz.) O. Ktze., Rev. Gen. Pl. **1**: 44, 1891.
M. ellipticum (Clos) O. Ktze. *var. panamense* O. Ktze., loc. cit.

Shrub or small tree 2-10 m high, the trunk up to 20 cm in diam, often spiny, the axillary spines on twigs sharp and up to 4 cm long, the branchlets inconspicuously puberulous to glabrous. *Leaves* subsessile to short-petiolate, the petiole to 6 mm long; blade polymorphous, typically elliptic to broadly elliptic (sometimes ± subrotund) and rounded on both ends, sometimes ovate or even narrowly ovate and obtuse to acute at the apex, the margins remotely appressed-glandular-serrulate, the serrations rounded, inflexed towards the margin and with their tips slightly overlapping the margin, to 12 cm long and 8 cm wide, rigid-chartaceous to subcoriaceous, ± lustrous above and dull beneath, the costa prominent beneath, the reticulated venation inconspicuous on either side, glabrous. *Flowers* in fascicles, dioecious, yellowish, the pedicels slender, to 6 mm long, minutely puberulous, bracteate at the base; sepals 4-5, subrotund to ovate, ca 1.2-2 mm long, ciliolate along the margins, minutely puberulous externally; stamens ca 20-25, the filaments short- to long-exserted and to 2-3 mm long. *Bacca* subglobose, to 6 mm long, at first green, turning red, and finally black at maturity, glabrous, surmounted by the persistent, 2-3-lobed style, the stigmatic lobes spreading; seeds 2-5, angulate-ovoid, the testa reddish-brown, glabrous.

Collected only along the Atlantic Coast in Panama; called colloquially *canirico* (cf. *Duke 8480*) and *jobo de lagarto* (cf. *Pittier 4111*).

The species is allied to the X. *flexuosa* complex, but can be distinguished by the leaves usually broadly rounded at the apex, by the small, sometimes even inconspicuous, closely appressed, rounded serrations (small auricles) with their tips slightly overlapping the blade, and with the network of the venation inconspicuous on the upper surface.

BOCAS DEL TORO: region of Almirante, Flat Rock, along beach & in second growth, *Cooper 548* (F, NY, US); Changuinola Valley, Bar Mouth, *Dunlap 512* (F, US), *532* (F, US); Isla Colón, alt 0-120 m, *von Wedel 499* (MO), *2479* (MO, NY, US), *2823* (MO, NY, US), *2850* (MO, NY, US); vic of Chiriquí Lagoon, *von Wedel 1361* (MO); id., Water Valley, *von Wedel 1516* (MO, US). CANAL ZONE: Fort Sherman, front of army barracks, on beach, *Dwyer & Robyns 153* (MO); Chagres, *Fendler 194* (type F, MO, US); rd S of Fort Sherman, edge of mangrove swamp, *Johnston 1650* (MO); vic of Fort Sherman, thicket along beach, *Standley 31142* (US); Fort Sherman on main post, *Tyson 2238* (MO), *Tyson & Blum 3771*. COLÓN: Aspinwall, *Hayes 885* (NY); Colón, *Kuntze 1884* (F, NY); mouth of Río Piedras, beach & adjacent area, *Lewis et al. 3175* (MO); vic of Viento Frio, along beach & nr sea level, *Pittier 4111* (MO); betw France Field, Canal Zone, & Catival, brushy slope, *Standley 30430* (US). SAN BLAS: Mulatuppu, *Duke 8480* (MO), *8546* (MO); Isla Soskatupo, *Duke 8512* (MO); Nargana I, nr Airport, *Tyson & Dwyer 1172* (MO). VERAGUAS: mouth of Río Concepcíon, beach, cliffs & adjacent swamp, *Lewis et al. 2823* (MO), *2828* (MO). PROVINCE UNKNOWN (Canal Zone or Colón): s. loc., *Hayes 644* (NY).

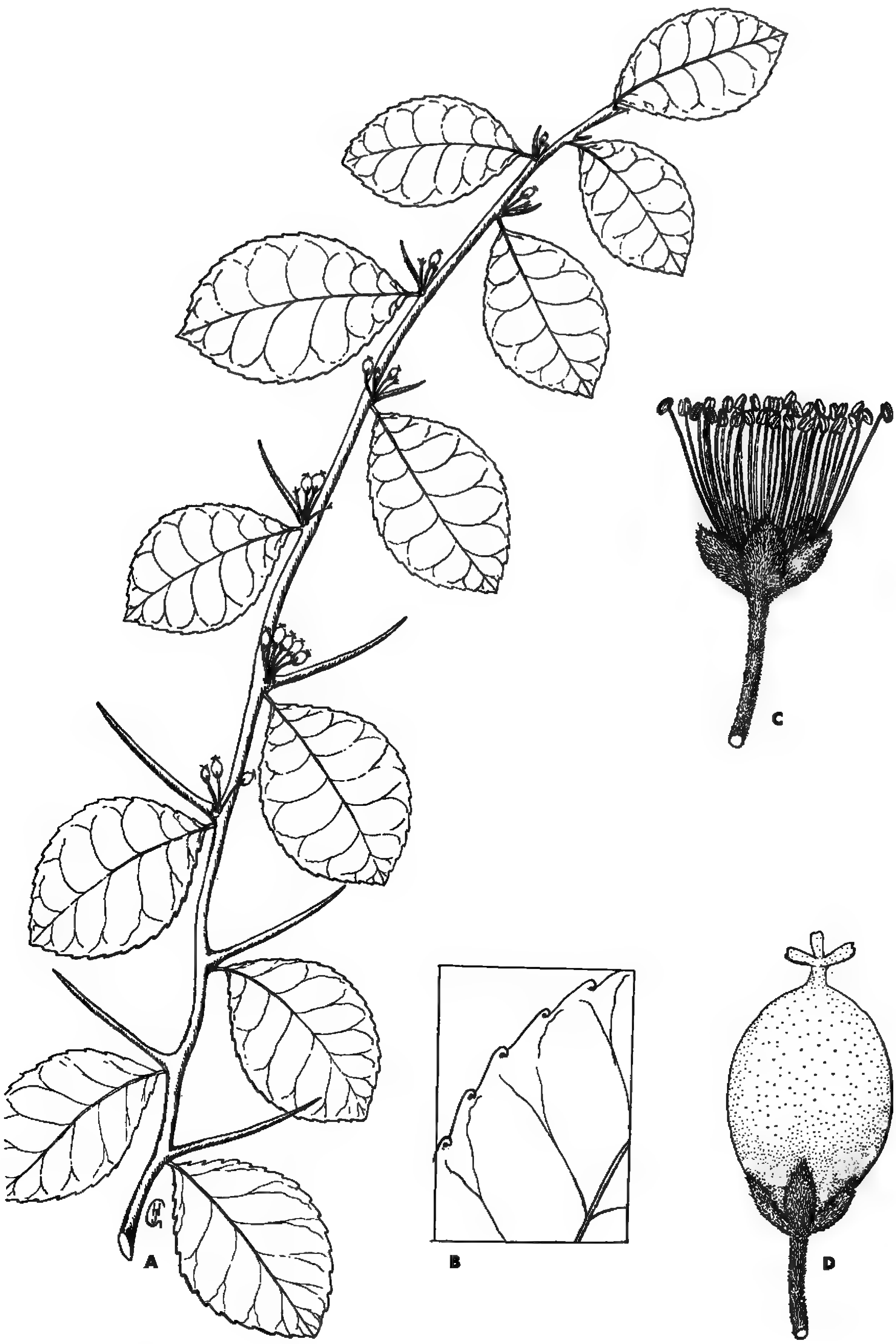

Fig. 14. *Xylosma panamensis* Turcz.: A, habit (×½); B, leaf margin, upper surface (much enlarged); C, flower (×8); D, bacca surmounted by the persistent style (×6). A, B & D after *Tyson & Dwyer 1172* (MO); C after *von Wedel 2479* (MO).

3. **Xylosma flexuosa** (H.B.K.) Hemsley, Biol. Centr.-Amer. **1:** 57, 1879, sensu lato.

Flacourtia flexuosa H.B.K., Nov. Gen. Sp. Pl. **7:** 239, 1825.
Hisingera nitida sensu Seemann, Bot. Voy. Herald 249, 1854.
H. elliptica Clos, Ann. Sci. Nat., Bot., sér. 4, **8:** 226, 1857.
Myroxylon ellipticum (Clos) O. Ktze., Rev. Gen. Pl. **1:** 44, 1891.
Xylosma hemsleyana Standley, Jour. Wash. Acad. Sci. **17:** 169, 1927.

Shrub or small tree, 2-12 m high, the trunk to 10-12.5 cm in diam, armed or not, the spines on the trunk often branched, the spines on the branches simple, the branchlets inconspicuously puberulous to glabrous. *Leaves* short-petiolate, the petiole to 5(-7) mm long; blade polymorphic, glabrous, commonly elliptic to broadly elliptic, infrequently ovate (or even narrowly ovate), acute at the base, obtuse to acute at the apex, seldom obtusely acuminate, distinctly glandular-crenate-serrate along the margins, to 6(-8) cm long and 4.5 cm wide, rigid-chartaceous, ± lustrous and with the network of the veins conspicuous on the upper surface, rather dull and with the costa prominent below, the network of the veins less conspicuous on the lower surface. *Flowers* in fascicles or contracted racemes, dioecious, greenish to yellowish, the pedicels to 5 mm long, minutely puberulous or glabrous, bracteate at the base; sepals 4 or usually 5, broadly ovate or deltoid, acute, ca 1.5-2 mm long, spreading in ♂ flowers, ciliolate along the margins, usually minutely puberulous on both sides; stamens ca 16-20, the filaments to 2.5 mm long, glabrous; ovary oblong-ovoid, glabrous, the placentas 2-3, each one 2-ovulate. *Bacca* subglobose, 5-6 mm in diam, at first green, turning bright red at maturity, surmounted by the persistent, 2-3-lobed style, the fruiting pedicel elongated and to 8 mm long, usually distinctly articulate ca 2 mm above the base; seeds 4-6, angulate-ovoid, to 4 mm long, the testa reddish-brown, glabrous.

Mexico, Central America, and northern South America; in Panama, this species is found only in the Province of Chiriquí at 900-2250 m altitude; known in Panama as *cachito* (cf. *Stern et al. 2029*) and *roseto* (cf. *Pittier* 3330).

Xylosma flexuosa, treated here in a rather broad sense, can be easily distinguished from X. *panamensis* by the leaf blades distinctly crenate-serrate and by the network of the veins clearly noticeable when dry on the upper surface. Furthermore, the mature berries are said to be bright red in X. *flexuosa,* while they are black in X. *panamensis*. Finally, the habitat of the two species is quite different.

CHIRIQUÍ: llanos on slopes of Volcan de Chiriquí Viejo & along Río Chiriquí Viejo, alt 1200 m, *Allen 969* (F, MO); Boquete, Boquete Distr, alt 3800-5500 ft, *Davidson 615* (F, MO, US), *736* (F, MO, US), *779* (F, MO, US), savanna, *787* (F); vic of Boquete, from Boquete to 3 mi N, alt 3300-4200 ft, second growth, cultivated areas & roadsides, *Lewis et al. 577* (MO); Bajo Boquete, alt 900-1300 m, *Bro. Maurice 736* (MO), *Pittier 3330* (US); vic of El Boquete, *Maxon 5141* (US); vic of Boquete, Finca Collins, alt 5800-6700 ft, *Stern et al. 2029* (MO); Camiseta, Volcan de Chiriquí, alt 7500 ft, *Terry 1360* (MO); Río Chiriquí Viejo Valley, on llanos, *White 56* (MO), *109* (MO); Finca Lérida to Boquete, alt ca 1300-1700 m, *Woodson et al. 1104* (F, MO), *1168* (F, MO).

4. **Xylosma hispidula** Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. **18:** 724, 1937.

Shrub or small tree, the trunk provided with numerous, long, slender, compound spines, the branchlets slender, densely short-hispid, the hairs brownish, the axillary spines to 2.5 cm long. *Leaves* very short-petiolate, the petiole 2-4 mm long, densely short-hispid; blade narrowly elliptic to elliptic, obtuse at the base, acuminate to caudate-acuminate at the apex, the acumen from acute to obtuse, the margins obtusely serrulate, the serrations glandular on the lower side, to 9 cm long and 3.5 cm wide, rigid-chartaceous, glabrous or nearly so above, hispidulous below especially along the slightly prominent costa and prominulous lateral veins. *Inflorescences* axillary, fasciculate, up to 10-flowered, bracteate at the base. *Flowers* dioecious (or polygamous?). *Male flowers* not seen. *Female flowers* (young fruits) (or hermaphrodite flowers?) with slender hispidulous pedicels to 5 mm long; sepals 4, subcircular, rounded apically, 1-1.5 mm long, the margins densely ciliolate, glabrous or nearly so dorsally, pilose inside. *Bacca* (juvenile) globose-ovoid, ca 4 mm long, glabrous, surmounted by the 2 persistent, subsessile, spreading stigmas.

Known only from one collection from Panama.

BOCAS DEL TORO: Changuinola Valley, Spur 2, *Dunlap 561* (holotype, F, isotype US).

There is some doubt whether the flowers are dioecious since one occasionally observes what appears to be a filament of a stamen around juvenile berries and within the glandular disc.

5. **Xylosma intermedia** (Seemann) Tr. & Pl., Ann. Sci. Nat., Bot. sér. 4, **17:** 100, 1862.

Hisingera intermedia Seemann, Bot. Voy Herald 249, 1854.
Myroxylon intermedium (Seemann) O. Ktze., Rev. Gen. Pl. **1:** 44, 1891.

Shrub ca 3 m high, unarmed, the branchlets lenticellate. *Leaves* short-petiolate; blade oblong-elliptic, narrowed towards the base, acuminate at the apex, obtusely serrate along the margins, 10-12.5 cm long and 3.5-5 cm wide, coriaceous, lustrous and glabrous on both surfaces. *Inflorescences* racemose, 8-10-flowered, ca 3.5 cm long, the peduncles and pedicels pubescent. *Flowers* polygamous (originally described as hermaphrodite), the calyx 4-merous, the sepals oblong, obtuse; stamens 25-30 or more, the filaments slender, somewhat longer than the sepals, glabrous, the anthers globose; ovary ovoid, attenuate at the apex into a short, 3-lobed style, the stigmatic lobes cuneate, the ovules 6. *Bacca* with 1-2 oblong seeds.

Known only from Panama.

CHIRIQUÍ: nr village of San Lorenzo, *Seemann 1623* (type K, not seen; photo NY).

As I have not seen the type, which is the only known collection of this species, the description given here has been taken from the original publication by Seemann and from the description given by Triana & Planchon. The species is remarkable on account of the racemose inflorescences and the polygamous flowers.

6. **Xylosma** sp. 1

Shrub or small tree to 5 m tall, the trunk unarmed or with branched spines, the branchlets unarmed or with small, axillary spines, glabrous. *Leaves* glabrous, the petiole to 5 mm long; blade narrowly ovate, obtuse to acute at the base, long-acuminate at the apex, obtusely glandular-crenate to -serrate along the margins, to 11.5 cm long and 4 cm wide, chartaceous to rigid-chartaceous, ± shiny on both surfaces, the costa slightly prominent below, the network of the venation prominulous on both sides. *Flowers* yellow, dioecious, in axillary fascicles, the pedicels to 7 mm long, articulated in the lower ⅓ (in ♂ flowers) or ± in the middle or slightly above the middle (fruiting pedicels), inconspicuously puberulous; sepals (in ♂ flowers) usually 4, very broadly ovate, obtuse, ca 2-2.5 mm long and 2 mm wide, inconspicuously ciliolate or not along the margins, puberulous especially at the apex externally; stamens ca 35, the filaments slender, long-exserted, to 6 mm long, glabrous. *Bacca* ellipsoid to subglobose, ca 6 mm long, not surrounded by the calyx (calyx apparently caducous), orange-pink, glabrous, surmounted by the short, persistent, 4-5 lobed style, the lobes short and spreading; seeds angulate-ovoid, to 4.5 mm long, the testa reddish-brown, glabrous.

Costa Rica and Panama.

CANAL ZONE: Barro Colorado I, *Bailey & Bailey 484* (F), *Woodworth & Vestal 419* (F); on rd from Chepo to El Llano, *Tyson & Smith 4125* (MO).

This species has been erroneously determined as X. *intermedia* (Seemann) Tr. & Pl. (cf. Standley, Contr. U. S. Nat. Herb. **27**: 273, 1928). In the latter species the inflorescences are racemose and the flowers are polygamous while in our species the inflorescences are fasciculate and the flowers are dioecious.

The above species is close to X. *excelsa* Standley & L. Williams (Ceiba **1**: 245, 1951) from Costa Rica. The leaves of both species are very similar, but X. *excelsa* differs from the above by the large size of the tree (to 25 m) and by the polygamous flowers (own observation of type collection: *Allen 5650* in F, MO, US).

7. **Xylosma** sp. 2

Small *tree* to 4 m tall, the branchlets unarmed, glabrous or inconspicuously puberulous. *Leaves* glabrous, short-petiolate, the petiole to 2-3 mm long; blade elliptic to broadly elliptic, acute at the base, short-acuminate at the apex, glandular-serrulate along the margins, the serrations sometimes very small and ± obtuse, to 6 cm long and 4 cm wide, chartaceous, the costa slightly prominent beneath, the network of the venations slightly prominulous above. *Flowers* fasciculate, dioecious. *Male flowers* yellowish, the pedicel to 3.5 mm long, inconspicuously puberulous; sepals 4, ovate to oblong-ovate, acute or rounded apically, 1.5-2 mm long and ca 1 mm wide, finely ciliolate along the margins, glabrous outside, puberulous inside; glandular disc ca 0.5 mm high; stamens 8-12, the filaments to 2 mm long, glabrous. *Female flowers* and *fruit* not seen.

COCLÉ: N rim of El Vallé, *Allen & Alston 1856* (F, MO, US).

8. **Xylosma** sp. 3

Shrub or tree (?), the branchlets glabrous, armed, the axillary spines 1-4 cm long. *Leaves* glabrous, subsessile or the petiole to 2 mm long; blade elliptic, obtuse to acute at the base, obtuse to rounded-obtuse at the apex, appressed-glandular-serrulate along the margins, the serrations obtuse, inflexed towards and slightly overlapping the margin, to 4 cm long and 2.5 cm wide, rigid-chartaceous, somewhat shiny especially above, the costa prominulous beneath, the network of the venation slightly prominulous on both sides. *Flowers* fasciculate, polygamous. *Male flowers* not seen. *Bacca* subglobose, 5-6 mm in diam, glabrous, surmounted by the persistent, deeply 2-lobed style, the fruiting pedicel to 8 mm long, glabrous, the persistent sepals 4, deltoid, to 2 mm long, ca 1 mm wide, glabrous, the persistent filaments of the stamens to 3.5 cm long; seeds 1 or 2, orbicular or semi-orbicular, 3.5-4 mm long, the testa reddish-brown, glabrous.

COCLÉ: Aguadulce, along outskirts of tidal belt, *Pittier 4991* (US).

9. **Xylosma** sp. 4

Shrub 2.4 m tall, the branchlets with stout, axillary spines to 7 mm long, inconspicuously puberulous. *Leaves* with the petiole to 1 cm long or slightly longer, ± canaliculate above, inconspicuously puberulous; blade elliptic to ovate-elliptic, acute and somewhat decurrent at the base, long-acuminate at the apex, rather coarsely and obtusely glandular-serrate along the margins, to 13.5 cm long and 6.5 cm wide, rigid-chartaceous to subcoriaceous, dull on both sides, inconspicuously puberulous along the veins to glabrescent above, minutely hirtellous below, the network of the venation inconspicuous above, the costa prominent and the secondary veins and veinlets prominulous beneath. *Inflorescences* contracted-racemose. *Flowers* dioecious. *Male flowers* pale yellow, the pedicels to 6 mm long, minutely puberulous, bracteolate at the base; calyx 4- or 5-merous, the sepals ± subrotund, somewhat acute at the apex, to 2.8 mm long and 2.3 mm wide, eciliolate, glabrous outside, short-pilose inside; glandular disc around the stamens ca 1 mm long; stamens 16-17, the filaments slender, to 3-3.5 mm long, glabrous. *Female flowers* and *fruit* not seen.

BOCAS DEL TORO: N slopes of Cerro Horqueta, Robalo Trail, alt 6000-7000 ft, *Allen 4941* (F, MO).

INDEX OF LATIN NAMES

Numbers in **boldface** type refer to descriptions; numbers in roman type refer to synonyms; numbers with dagger (†) refer to names incidentally mentioned.

FLORA OF PANAMA

BY ROBERT E. WOODSON, JR. AND ROBERT W. SCHERY
AND COLLABORATORS

Part VIII

FAMILY 154. SAPOTACEAE[1, 2]

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Trees or shrubs with milky latex (lactiferous sacs present in the pith and cortex and the leaves and fruit), glabrous or pubescent (the trichomes unicellular and 2-armed). *Leaves* alternate or rarely opposite, petiolate, estipulate; blades simple, entire, often leathery, penninerved. *Flowers* usually ☿, regular, axillary to leaves and/or leaf-scars, fasciculate or occasionally solitary, the pedicels sessile; sepals 4-12, imbricate or spiralled, in one or two whorls, free or united only at the base; corolla gamopetalous, the lobes 4-8, shorter or longer than the tube, as many as or fewer than (rarely more than) the sepals, with or without basal petaloid appendages; stamens epipetalous, usually equal in number to and opposite the corolla-lobes, an outer antisepalous whorl of staminodes often present (typically equal in number to and appearing to be in the same whorl with the stamens); ovary superior, (1-)4 to 14-carpelled and -loculed, completely septate, with 1 ascending, lateral or basal, anatropous, bitegmic ovule in each locule, the style single, entire or lobed at the summit. *Fruit* a berry, often fleshy, the exocarp frequently becoming corky or sclerotic; seeds 1-several, large, with or without endosperm, the testa hard and shiny, the scar lateral to basal, large or small.

A family of about 40 genera and 600 species, widespread in the tropics of the New and Old World; six genera occur in Panama. Several representatives are economically important.

KEY TO GENERA[3]

a. Each corolla-lobe with a pair of petaloid appendages arising from the base (the appendages dorsal or lateral), if these lacking then the sepals in two distinct whorls of three each; staminodes present and petaloid.
  b. Sepals biseriate (3 + 3); corolla-lobe appendages dorsal or absent; ovules attached laterally; seed-scar lateral or essentially so, equalling or extending beyond the middle of the seed .... 1. *Manilkara*

[1] Assisted by National Science Foundation Grant No. GB-5674 (Principal Investigator, Walter H. Lewis).

[2] Synonyms presented in this paper included, in addition to names used in a previous flora dealing with a portion of Panama (e.g. Standley, Flora of the Panama Canal Zone, Contr. U. S. Nat. Herb. **27**: 299-301, 1928), only those based on Panamanian types or those relegated to synonymy for the first time. For additional information on nomeclature and synonymy, reference should be made to Cronquist's excellent publications (enumerated after the generic descriptions) and to Moore & Stearn (The identity of *Achras zapota* L. and the names for the sapodilla and the sapote. Taxon **16**: 382-395, 1967).

[3] The key to genera is intended for identification of Panamanian representatives only. Broader application may lead to misidentification.

ANN. MISSOURI BOT. GARD. **55**(2): 145-169, 1968.

bb. Sepals not in two distinct whorls though sometimes quincuncial; corolla-lobe appendages lateral; ovules attached basilaterally; seed-scar basal or basilateral, not reaching the middle of the seed.
  c. Plants unarmed; flowers borne at defoliated nodes only; ovary glabrous, the style 1.5-2 mm long; apex of fruit abruptly tapering to the persistent style; seeds with endosperm .... 2. *Dipholis*
  cc. Plants often with spines; flowers axillary to leaves and occasionally also leaf-scars; ovary pubescent, the style 3-7 mm long; apex of fruit rounded or subtruncate, not tapering to the style; seeds lacking endosperm .... 3. *Bumelia*

aa. Corolla-lobes lacking appendages; sepals usually uniseriate (though often strongly imbricate or spiralled), if distinctly biseriate then 2 + 2; staminodes present (often not petaloid) or absent.
  d. Secondary lateral veins ± paralleling the primary laterals; staminodes absent .... 4. *Chrysophyllum*
  dd. Secondary laterals not paralleling (often essentially perpendicular to) the primary laterals; staminodes present (frequently scale-like or linear-lanceolate or filiform, occasionally petaloid).
    e. Leaf-blades usually canaliculate above the midvein, the channel terminating in a small pouch at the base of the blade; petiole usually ½ the length of the blade or more; ovary glabrate; seed-scar often elongate but not reaching the middle of the seed; endosperm present .... 5. *Mastichodendron*
    ee. Leaf-blades not as above; petiole less than ½ the blade length; ovary conspicuously pubescent; seed-scar exceeding the middle of the seed; endosperm lacking .... 6. *Pouteria*

1. MANILKARA

Manilkara Adanson, Fam. **2**: 166, 1763.

Trees, unarmed. *Leaves* alternate; blades coriaceous, the primary laterals numerous, fine, rather closely spaced, often subobscure, straight (not arcuate near the margin). *Flowers* fasciculate in the axils of leaves or leaf-scars or solitary; sepals usually 6, infrequently 4 or 8, in 2 whorls of (2)3(4); corolla-lobes as many as the sepals, each with a pair of dorsal ± petaloid appendages arising from the base, occasionally these fused to the lobes or lacking; staminodes usually petaloid, rarely minute or replaced by functional stamens; stamens as many as corolla-lobes or rarely twice as many (morphologically 2 whorls), typically attached to the corolla at the juncture of the tube and lobes; ovary often pubescent, 6 to 14-celled, the ovules affixed laterally. *Fruit* 1 to several-seeded, fleshy; seed compressed, the scar rather elongate, lateral or basilateral (but equalling or surpassing the middle of the seed), ± linear, the endosperm copious.

Thirteen species are known in North America, four occurring in Panama.

Useful reference:

Cronquist, A. Studies in the *Sapotaceae,* IV. The North American species of *Manilkara.* Bull. Torrey Bot. Club **72**: 550-562, 1945.

a. Flowers 2-12 per axillary fascicle; corolla-tube usually shorter than the corolla-lobes; ovary glabrate or pubescent only on the upper portion.
  b. Pedicels glabrous; outer sepals glabrate by anthesis; corolla-lobes equalled in length by dorsal appendages arising from their base (each appendage deeply bifid or trifid); ovary glabrate; fruit smooth or but slightly roughened .... 1. *M. bidentata*

bb. Pedicels and outer sepals sericeous-strigulose; corolla-lobes lacking dorsal appendages; ovary pubescent on the upper portion; fruit mealy roughened .... 2. *M. chicle*

aa. Flowers solitary in the leaf-axils; corolla-tube usually exceeding the corolla-lobes; ovary densely pubescent over the entire surface.

c. Corolla-lobes narrowly oblanceolate or spatulate, 0.5-1 mm broad, equalled in length by simple dorsal appendages .... 3. *M. meridionalis*

cc. Corolla-lobes oblong to ovate, 1.5-3 mm broad, lacking dorsal appendages .... 4. *M. zapota*

1. **Manilkara bidentata** (DC.) Chevalier, Revue Bot. Appl. & Arg. Trop. **12**: 270, 1932.

Mimusops darienensis Pittier, Contr. U. S. Nat. Herb. **18**: 249, 1917.
Manilkara darienensis (Pittier) Standley, Trop. Woods **31**: 45, 1932.

Tree to 35 m. *Leaves* with petioles 1.3-4.2 cm long; blades narrowly obovate or sometimes elliptic, obtuse or rounded to shallowly emarginate or short-acuminate, 6-30 cm long, 3-12 cm broad, glabrous, the primary laterals fine and rather closely spaced, occasionally subobscure. *Flowers* 3-12 per fascicle, the fascicles axillary to both leaves and leaf-scars; pedicels glabrous, 1.2-3 cm long; sepals ovate or ovate-oblong, 4-6 mm long, the inner minutely appressed-sericeous, the outer soon glabrate; corolla 5-7 mm long, subrotate, the tube ca 1/5 the total length, the lobes narrowly elliptic-lanceolate, the dorsal appendages as broad as and usually slightly longer than the lobes, free from the lobes to the tube, distally divided for ca 2/3 of their length into 2 or 3 slender lanceolate segments; staminodes 1.2-3 mm long, ovate-lanceolate, erose; staminal filaments equalling or slightly exceeding the staminodes; ovary glabrate, the style glabrous, 4-5 mm long. *Fruit* smooth or slightly roughened, globose or ellipsoid-globose, 2-3.5 cm long.

Hispaniola, Puerto Rico, Lesser Antilles, northern South America and Panama.

BOCAS DEL TORO: s. loc., *Cox s.n.* (US). CANAL ZONE: hills aroud Gatún, *Pittier 2699* (US). PANAMA: nr Chepo, *Kluge 55* (US). SAN BLAS: hills nr Puerto Obaldía, *Pittier 4318* (holotype of *Mimusops darienensis* US), *4384* (US).

Manilkara bidentata is important as a source of balata, a nonelastic rubber obtained from the latex which is a nonconductor, resistant to water. Balata and a similar product, gutta-percha (obtained from another member of the *Sapotaceae*), are used in the construction of marine cable, machine belting, telephone receivers, golf balls, waterproofing, adhesives and a number of other items.

2. **Manilkara chicle** (Pittier) Gilly, Trop. Woods **73**: 14, 1943.—Fig. 1.

Achras calcicola Pittier, Jour. Wash. Acad. Sci. **9**: 438, 1919.
Manilkara calcicola (Pittier) Gilly, Trop. Woods **73**: 15, 1943.

Tree to 40 m. *Leaves* with petioles 1-3.5 cm long; blades 8-24(-29) cm long, 3-7(-10) cm broad, oblanceolate or narrowly obovate to elliptic or elliptic-oblong, obtuse or rounded to acute or acuminate, paler and more yellowish beneath, appressed-sericeous-strigulose below when young but eventually glabrate. *Flowers* yellowish- or grenish-white, 2-5 per fascicle; pedicels strigulose, 0.5-3 cm long; sepals 5-9 mm long, ovate to ovate-lanceolate or ovate-oblong, the inner and outer sericous-tomentulose; corolla 5.5-9 mm long, the tube 1/4-1/2 the total length, the lobes ovate, often erose or erose-dentate at the apex, lacking dorsal appendages; sta-

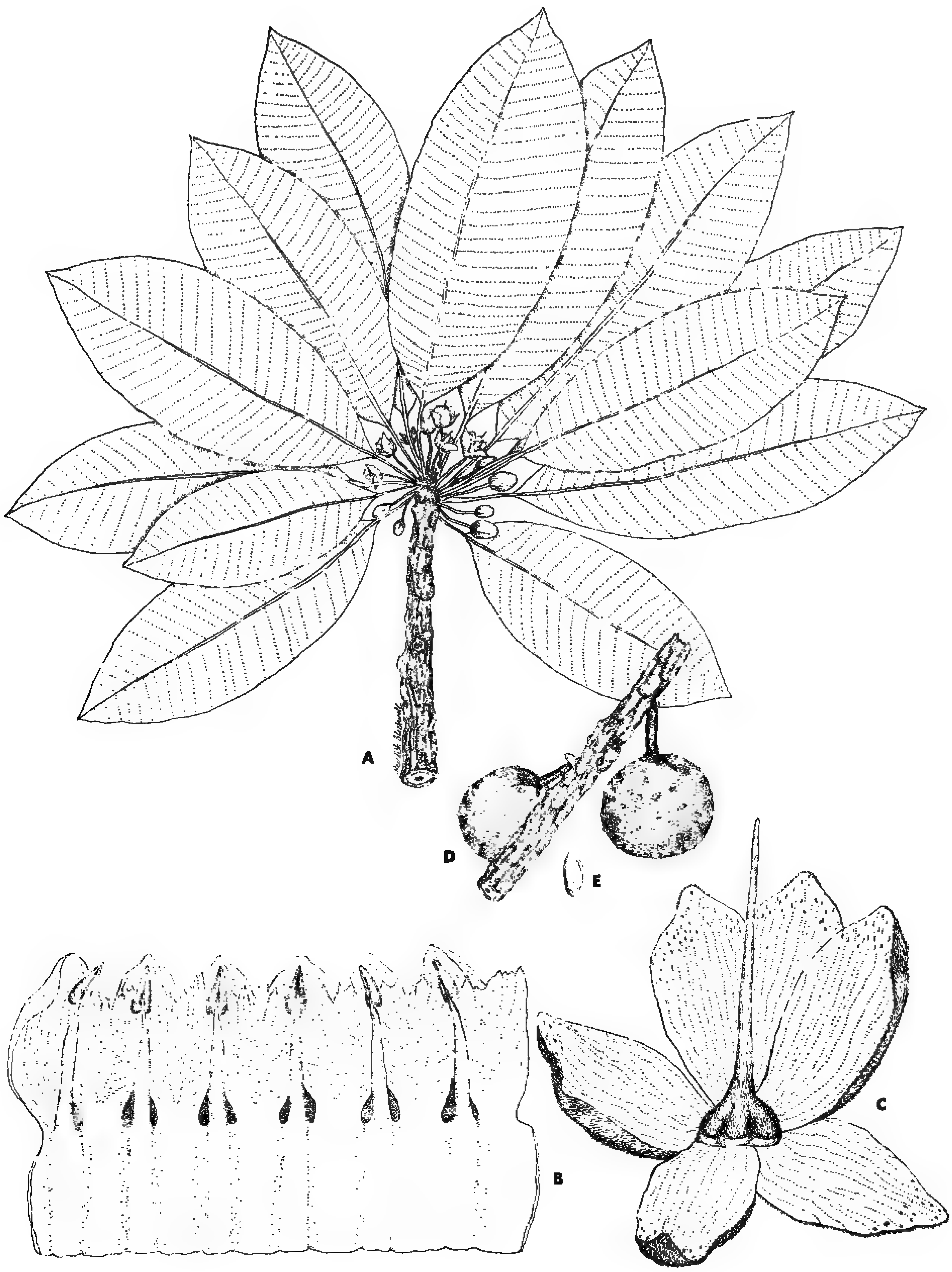

Fig. 1. *Manilkara chicle* (Pittier) Gilly: A, habit (×½); B, corolla opened to show attachment of stamens and staminodes (×5); C, flower with corolla removed (×5½); D, fruit (×⅖); E, seed (×⅖). A-C after *Stimson 5294* (MO); D-E after *Johnston 753* (GH).

minodes 2.5-4.5 mm long, distally erose-laciniate, often shallowly bifid; stamens equalling the staminodes; ovary minutely sericeous on top, glabrous elsewhere, the style 6-9 mm long, glabrous except at the base. *Fruit* mealy-roughened, 2-4 cm in diam, subglobose or obovoid, several-seeded; seeds 14-19 mm long, flattened, the basilateral scar barely reaching the middle.

Oaxaca, Mexico through Central America to Colombia.

CANAL ZONE: area W of Limon Bay, Gatún Locks & Gatún Lake *Johnston 1535* (A); Ancon Hill, *Standley 26384* (US). DARIEN: vic of Piñas, *Duke 10653* (MO); Patiño, *Pittier 5698* (GH, US). LOS SANTOS: pastures ca ½ mi S of Pedasí, *Stimson 5294* (MO). PANAMA: San José I, *Johnston 336* (GH), *342* (MO, GH), *646* (GH), *753* (GH, MO, US); around Alhajuela, Chagres Valley, *Pittier 3457* (holotype of *Archras calcicola* US).

Although bearing the specific epithet *chicle*, this species is not the principal source of chicle gum. The latex is difficult to coagulate and inferior to that of *M. zapota.*

3. **Manilkara meridionalis** Gilly, Trop. Woods **73:** 12, 1943.
M. tabogaensis Gilly, loc. cit. 10.

Tree to 30 m. *Leaves* clustered toward the branch tips; petioles 1-2.7 cm long; blades elliptic or oblong-elliptic to narrowly obovate, 5.5-13 cm long, 1.7-4.5 cm broad, glabrous or sparsely rufescent along the midrib beneath. *Flowers* solitary in the leaf-axils; pedicels 1-2.3 cm long, tomentulose or eventually glabrate; sepals ovate, 6-9 mm long, minutely tomentulose externally; corolla cylindric, glabrous or pubescent, ca 9 mm long, the tube usually comprising ½-⅔ of the length, the lobes narrowly oblanceolate or spatulate, 0.5-1 mm broad, the dorsal appendages ovate-lanceolate to elliptic or obovate, broader than but ca equal in length to the lobes, simple (not divided into elongate segments distally), basally united with the lobes for ca ⅓ of their length; staminodes ± ovate, erose-fimbriate, 2.5-5 mm long, exceeding the staminal filaments; ovary tomentose, the style 5.5-8.5 mm long, glabrous except at the base. *Fruit* brown, mealy-roughened, to 3.5 cm long; seed strongly compressed, ca 2 cm long, the linear scar extending from near the base to well beyond the middle of the seed.

Guerrero, Mexico to Colombia and Venezuela; introduced in the West Indies.

PANAMA: Taboga I, *Standley 27099* (US), *Woodson et al. 1455* (holotype of *M. tabogaensis* NY, not seen; isotypes A, MO).

4. **Manilkara zapota** (L.) van Royan, Blumea **7:** 410, 1953[4].
Achras zapota L., Sp. Pl. 1190, 1753.

Tree to 40 m. *Leaves* clustered toward the branch tips; petioles 0.8-3 cm long; blades elliptic or oblong-elliptic to somewhat obovate or oblanceolate, 4-15 cm long, 1.5-6 cm broad, subconcolorous, glabrate at maturity, the reticulation usually evident below. *Flowers* solitary in the leaf-axils; pedicels 1.2-2.5 cm long, rufous-tomentulose (some of the pubescence deciduous with age); sepals 6-10 mm long, ovate or occasionally oblong, tomentulose, the outer often losing some

[4] For a discussion of nomenclature and complete list of synonyms of *M. zapota* see Moore & Stearn, Taxon **16:** 382-395, 1967.

(rarely all) their pubescence with age; corolla 6-11 mm long, the tube usually comprising $\frac{1}{2}$-$\frac{2}{3}$ the total length, the lobes oblong to ovate, 1.5-3 mm broad, entire or erose or dentate at the apex, lacking dorsal appendages; staminodes petaloid, rather narrowly ovate-lanceolate, 3-4.5 mm long, erose; stamens $\frac{2}{3}$-$\frac{3}{4}$ as long as the staminodes; ovary densely sericeous, the style 4.5-8 mm long, glabrous except at the base, the apex often irregularly toothed or lobed. *Fruit* brown, mealy-roughened, ellipsoid or ovoid or subglobose, to 10 cm in diam; seeds brown, compressed, 16-24 mm long, the linear scar extending from near the base to beyond the middle.

Mexico (as far north as San Luis Potosi and Nayarit) to northern South America and from southern Florida through the West Indies; probably native only from Mexico to Costa Rica.

CANAL ZONE: *Balboa, Standley 27121* (US), *30860* (US).

The latex of the sapodilla or chicle-tree is the commercial source of the gum base of the chewing gum industry. It contains 20-25% of the gutta-percha-like gum and is obtained by tapping the trunk by a series of connected, half-encircling, zig-zag gashes. To prevent death of the trees, they are tapped only once every two or three years. The United States is the leading consumer of chicle, the bulk being imported from British Honduras. The pear-shaped fruit is esteemed by people of tropical America and is eaten uncooked.

2. DIPHOLIS

Dipholis DC., Prodr. **8:** 188, 1844.

Trees or shrubs, lacking spines or thorns. *Leaves* alternate, the blades coriaceous or subcoriaceous. *Flowers* small, white or green, numerous or few per axillary fascicle, occasionally solitary, the clusters axillary to leaves, leaf-scars or both; sepals (4)5(-9), uniseriate; corolla rotate or funnelform, 5(6)-lobed, each lobe with a pair of lateral appendages arising from the base; staminodes petaloid, these and the appendages of the corolla-lobes often erose, fimbriate or laciniate; anthers often exserted; ovary glabrous or rarely appressed-puberulent, 5-celled, the ovules attached basilaterally. *Fruit* fleshly, usually 1-seeded at maturity, abruptly tapering to the short, persistent style; seed with a small, virtually basal scar and copious endosperm, the cotyledons thin.

Approximately 15 species; heavily centered in the West Indies (principally the Greater Antilles) but also occurring in Central America, Mexico and southern Florida; one species is known from Panama.

Although Stearn (Jour. Arnold Arb. **49:** 282-283, 1968) argues impressively against the recognition of *Dipholis* as an entity generically distinct from *Bumelia*, I favor its retention at present. I have found the delimiting characters listed by Cronquist (Jour. Arnold Arb. **26:** 445, 1945) to hold up rather well in the species I have examined personally and there can be no doubt of their validity with regard to Panamanian representatives.

Useful reference:

Cronquist, A. Studies in the *Sapotaceae*, III. *Dipholis* and *Bumelia*. Jour. Arnold Arb. **26:** 435-471, 1945 (*Dipholis* p. 435-445).

1. **Dipholis minutiflora** Pittier, Contr. U. S. Nat. Herb. **13**: 464, 1912.—Fig. 2.
Tree to 35 m. *Leaves* with petioles 0.5-1.8 cm long; blades elliptic-oblanceolate or narrowly elliptic-obovate, rounded to acute or subacuminate, 5-20 cm long, 2-10 cm broad, glabrous or finely white-strigulose (particularly below). *Flowers*

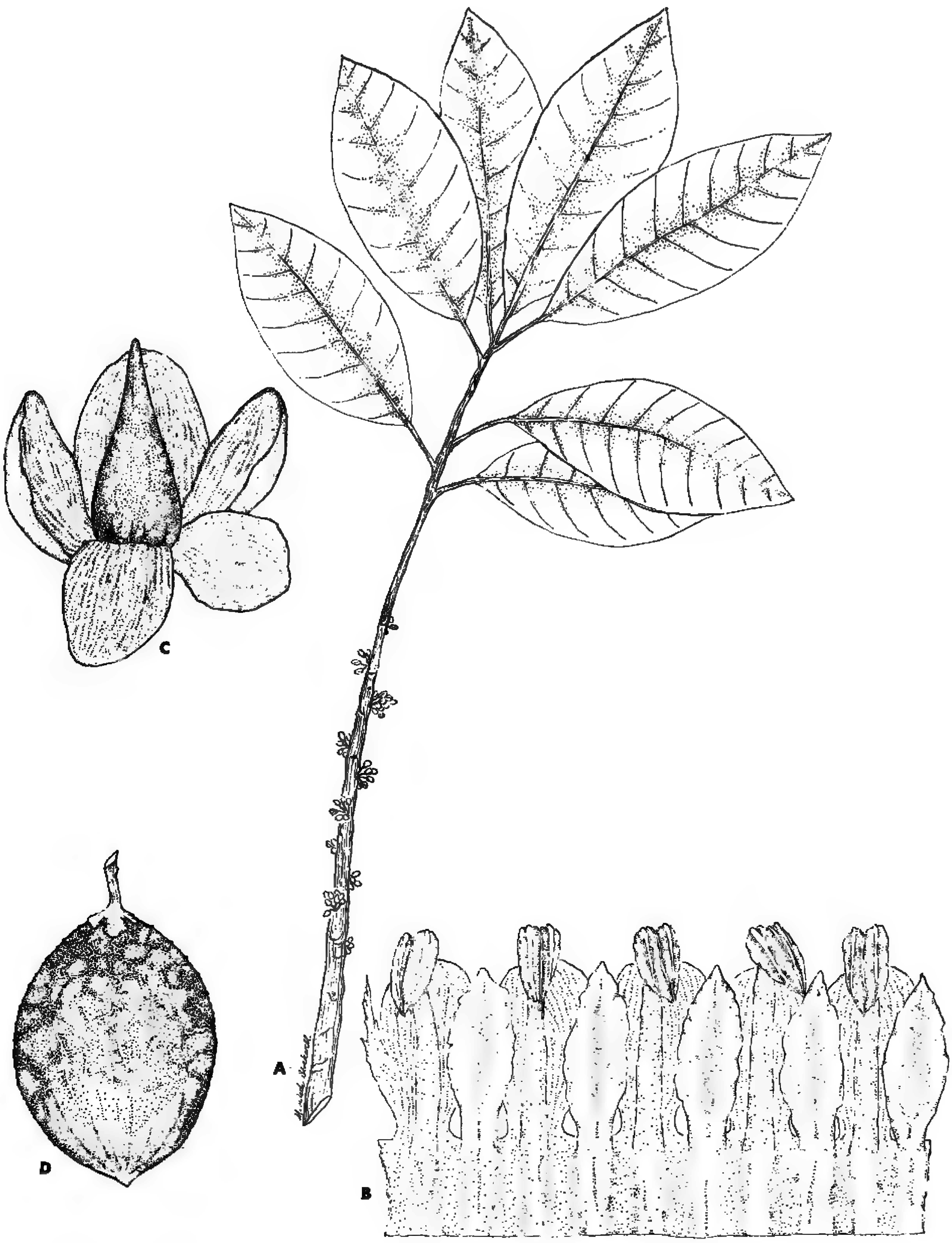

Fig. 2. *Dipholis minutiflora* Pittier: A, habit (×½); B, corolla opened to show attachment of stamens and staminodes (×8); C, flower with corolla removed (×10); D, fruit (×1½). A after *Woodson et al. 995* (MO); B-C after *Allen 1564* (MO); D after *Hinton 7600* (MO), Mexico.

often numerous per fascicle, the fascicles occurring only at defoliated nodes, each borne on a small woody cushion; pedicels 3-10 mm long, very sparsely to moderately appressed-sericeous; sepals 5(-8), closely imbricate, sometimes unequal, suborbicular or broadly ovate, glabrate, carnosulous, ca 2 mm long; corolla 4-4.5 mm long, the 5 lobes erose, ca 3 mm long, ± ovate, narrowed toward the base, the appendages lance-ovate, laciniate, ½-¾ the length of the lobes; staminodes 2-3 mm long; narrowly ovate, erose; staminal filaments ca 2 mm long; ovary glabrous, 1 mm long, the style 1.5-2 mm long, glabrous, conical, evenly tapered from the ovary, virtually as broad as the ovary at the base. *Fruit* broadly ovoid, 1.5-2.5 cm long, 1-2 cm broad, conical-apiculate, the flesh scant; seed ellipsoid, slightly compressed, 14-18 mm long, the scar 3-5 mm long.

State of Mexico to Panama.

CHIRIQUÍ: vic of Cerro Punta, *Allen 1564* (F, MO); Quebrada Velo, vic of Finca Lerida, *Allen 4676* (MO); valley of the upper Río Chiriquí Viejo, *White 109b* (F, MO), *White & White 1* (MO); Bajo Mona, mouth of Quebrada Chiquero, along Río Caldera, *Woodson et al. 995* (F, MO). PANAMA: hills above Campana, *Allen 1314* (F, MO).

3. BUMELIA

Bumelia Swartz, Nov. Gen. Sp. Pl. Prodr. 49, 1788.

Shrubs or trees, usually spiny or thorny. *Leaves* alternate or casually opposite, the blades firm. *Flowers* few to numerous per axillary fascicle, rarely solitary, green or white, (4)5(6)-merous; sepals uniseriate; corolla-lobes well exceeding the tube, each with a pair of lateral appendages arising from the base or these rarely lacking; staminodes petaloid, entire to erose or laciniate; anthers often exserted; ovary pubescent or less frequently glabrous, usually 5-locular, the ovules affixed basilaterally, the style slender to virtually filiform. *Fruit* fleshy, 1-seeded, broadly rounded or subtruncate or retuse at the apex (not tapering to the persistent style); seed with a small subbasal scar, lacking endosperm, the cotyledons fleshy.

A New World genus of about 23 species, the majority in the United States, Mexico and the West Indies but several extending into Central and South America; one species occurs in Panama.

Useful reference:

Cronquist, A. Studies in the *Sapotaceae,* III. *Dipholis* and *Bumelia.* Jour. Arnold Arb. **26:** 435-471, 1945 (*Bumelia* p. 445-471).

1. **Bumelia persimilis** Hemsley subsp. **persimilis,** Biol. Centr.-Amer., Bot. **2:** 298, 1882.—Fig. 3.

B. panamensis Standley, Trop. Woods **4:** 9, 1925.

Shrub or tree to 18 m, possessing spines. *Leaves* with petioles 2-10(-12) mm long; blades elliptic- or somewhat ovate-lanceolate to elliptic or elliptic-oblanceolate, acute or acuminate to obtuse, 3.5-12.5 cm long, 1.3-5 cm broad, glabrous and lustrous above, at first sparsely appressed-rufous- or cinereous-sericeous below, soon glabrate, with 10-30 pairs of primary lateral veins, these brochidodrome. *Flowers* white, several to numerous per fascicle, the fascicles axillary to leaves and occasionally also leaf-scars; pedicels 3-6 mm long; sepals ovate, 1.8-3.7 mm long, unequal, quincuncial, glabrate to moderately appressed-sericeous; corolla rotate-

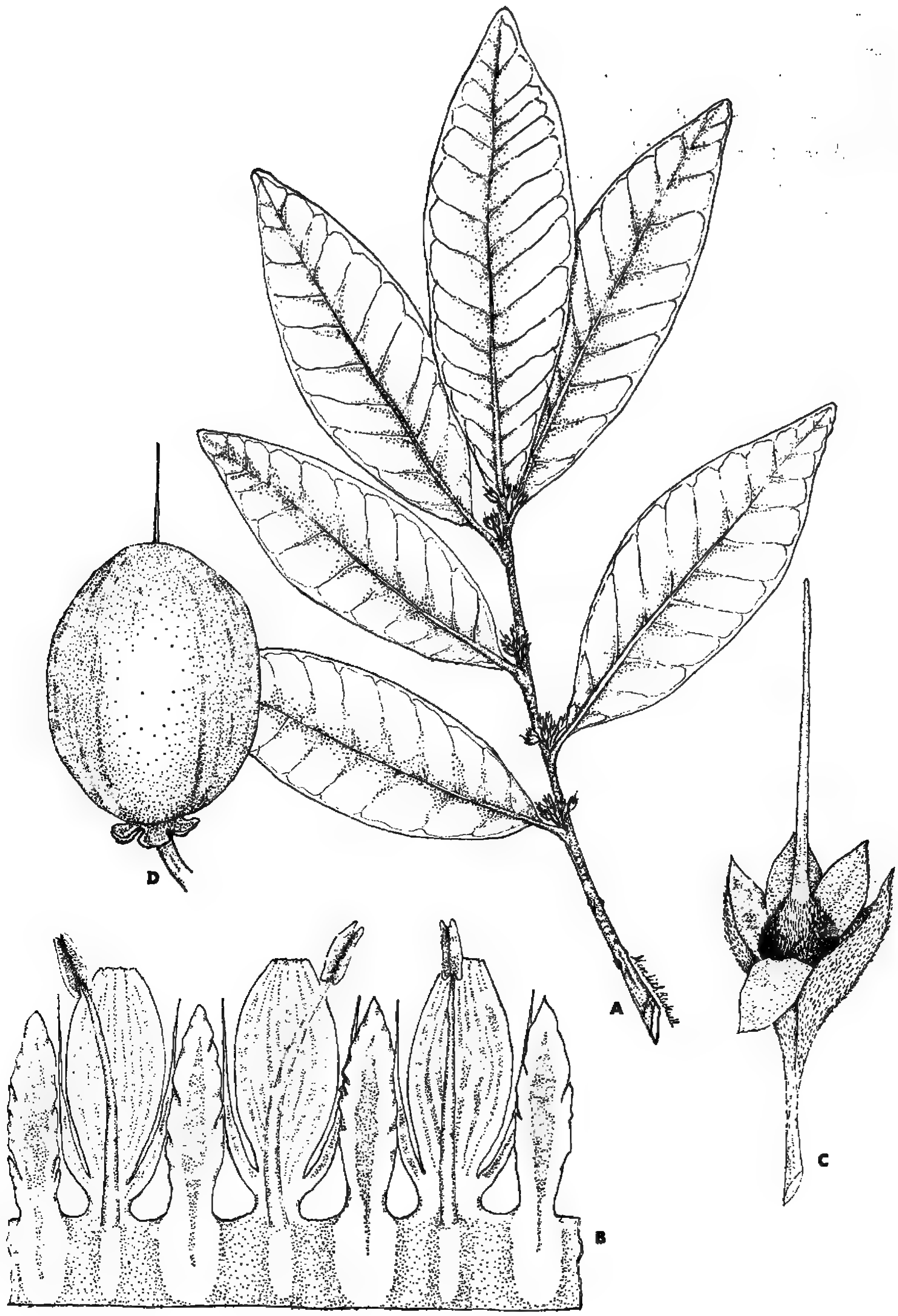

Fig. 3. *Bumelia persimilis* Hemsley subsp. *persimilis*: A, habit (×½); B, portion of corolla showing attachment of stamens and staminodes (×7½); C, flower with corolla removed (×7½); D, fruit (×2). A after *Williams 16585* (MO), Costa Rica; B-C after *Schipp 1077* (MO), British Honduras; D after *Hunter & Allen 298* (F).

funnelform, the tube ca 1.5 mm long, the lobes 3-4.5 mm long, oblong-ovate, subtruncate and erose at the apex, narrowed at the base, the appendages lance-filiform, ca 3/4 the length of the lobes; staminodes 2.5-3 mm long, lanceolate to obovate, ± laciniate; staminal filaments 3-3.5 mm long, the anthers 0.7-2 mm long; ovary appressed-sericeous, the style 3-7 mm long, a stigma not apparent. *Fruit* spheroid or ellipsoid, smooth, 1.2-2.5 cm long, the apex rounded.

Vera Cruz and Oaxaca, Mexico through Central America to Venezuela.

COCLÉ: El Valle de Antón, along Río Indio trail, *Hunter & Allen 298* (F). PANAMA: nr Chepo, *Kluge 12* (holotype of *B. panamensis* US, not seen).

The other subspecies of *B. persimilis*, subsp. *subsessiliflora* (Hemsley) Cronquist, is exclusively Mexican (Chihuahua and Durango to Michoacán and Oaxaca) and is characterized, among other features, by a dense, rufous, spreading pubescence of the young twigs and lower leaf-blade surface.

4. CHRYSOPHYLLUM

Chrysophyllum L., Sp. Pl. 192, 1753.

Shrubs to medium-sized trees. *Leaves* alternate; blades with the secondary laterals and areoles ± paralleling the primary laterals. *Flowers* several to numerous in each axillary cluster, occasionally solitary; sepals (4)5(6), uniseriate, often quincuncial when 5, united at the base; corolla not exceeding 6 mm in length, the lobes (4)5(6), lacking appendages; staminodes absent; staminal filaments attached to the top of the corolla-tube or base of the corolla-lobes; ovary appressed-pubescent, 4 to 12-celled, the ovules affixed laterally or basilaterally, the style short (less than 1.75 mm in Panama taxa), columnar, the stigma discoid, marginal lobes often evident. *Fruit* fleshy; seeds 1-several, the scar large, broadly elliptic to subcordate, at least 5 mm long, lateral or basilateral, the endosperm copious.

Approximately 40 species occur in the New World and a number of Old World species are known; two species are found in Panama.

Useful references:

Cronquist, A. Studies in the *Sapotaceae*, I. The North American species of *Chrysophyllum*. Bull. Torrey Bot. Club **72**: 191-204, 1945.

———. Studies in the *Sapotaceae*, V. The South American species of *Chrysophyllum*. loc. cit. **73**: 286-311, 1946.

a. Blades sparsely white-strigulose below or glabrate; corolla-lobes less than 1/2 as long as the tube; stigma 5-lobed; fruit to 2 cm broad .... 1. *C. panamense*
aa. Blades densely rufous-sericeous below (with a coppery sheen, even on dried specimens); corolla-lobes equalling or slightly exceeding the tube; stigma 7 to 12-lobed; fruit 3 cm broad or more .... 2. *C. cainito*

1. **Chrysophyllum panamense** Pittier, Contr. U.S. Nat. Herb. **18**: 165, 1916.—Fig. 4.

C. panamense var. *macrophyllum* Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. **22**: 366, 1940.

Tree to 15 m. *Leaves* with petioles 0.8-2.5 cm long; blades elliptic or broadly oblong to elliptic-obovate, acuminate, to 25(-33) cm long and 11(-14) cm broad,

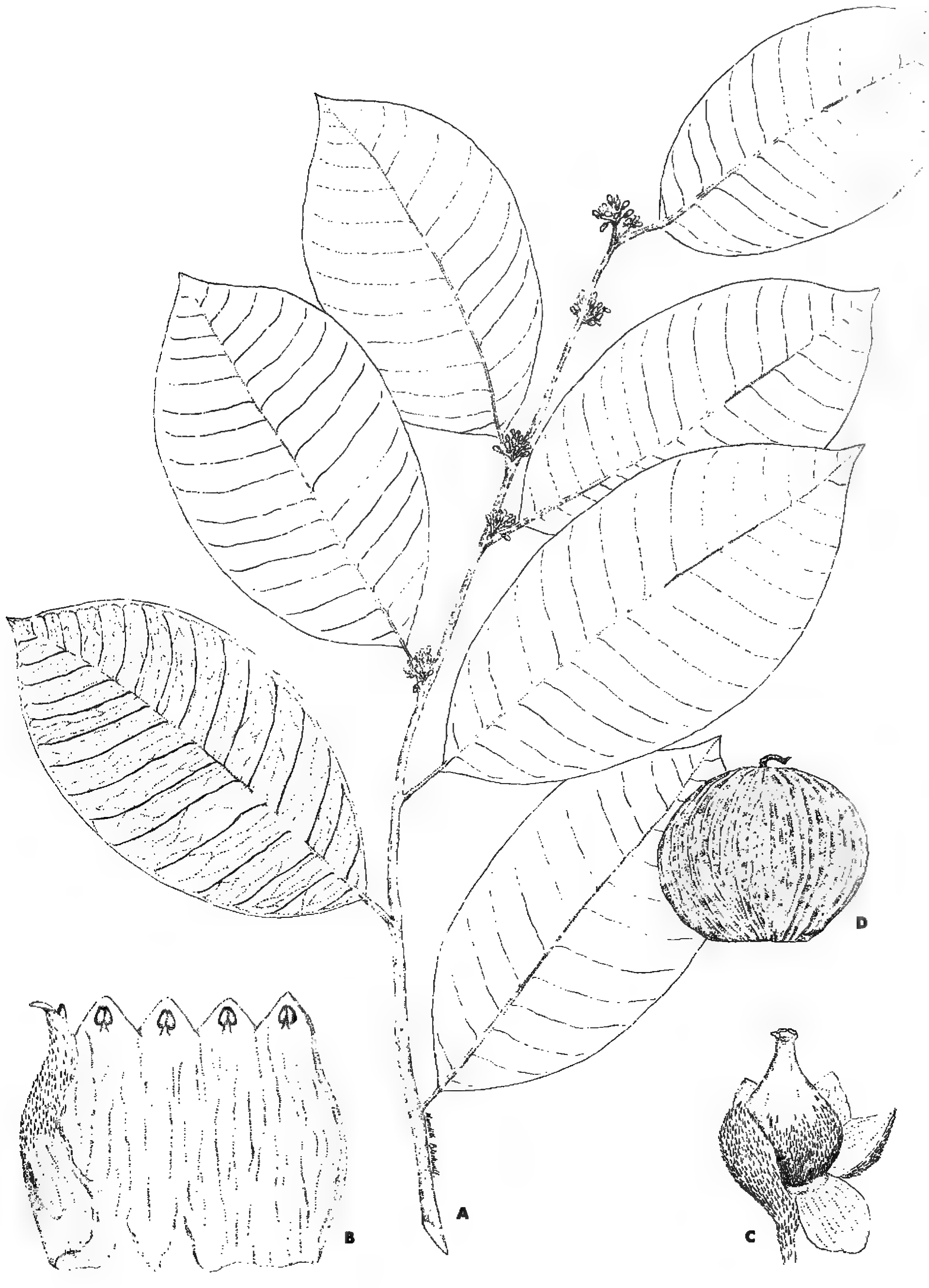

Fig. 4. *Chrysophyllum panamense* Pittier: A, habit (×2/5); B, corolla opened to show attachment of stamens (×7); C, flower with corolla removed (×7); D, fruit (×1¾). A after *Starry 82* (F) and *Shattuck 1024* (F); B-C after *Zetek 3810* (F); D after *Zetek Z4327* (F).

glabrous above, glabrate below or sparsely and finely white-strigulose. *Flowers* several-numerous in each axillary cluster, the pedicels 3-7 mm long, appressed-gray-pubescent; sepals to 2 mm long, ovate or suborbicular, strigulose externally (occasionally losing some of the pubescence); corolla subcylindric, pale green to yellow or white, 3.5-5.5 mm long, externally often appressed-rufous-sericeous on the lobes and adjacent portions of the tube, the lobes deltoid-ovate, ± erect, less than ½ the length of the tube; anthers 0.4-0.6 mm long, the filaments attached at the juncture of the corolla-tube and lobes; style 1-1.5 mm long, the stigma with 5 small marginal lobes. *Fruit* several-seeded, to 2 cm broad, oblate-spheroid to ovoid, often lightly ribbed; seeds pale brown, ca 1 cm long, with the basilateral scar extending to the middle or beyond.

Panama and Costa Rica, chiefly on the Atlantic slope.

BOCAS DEL TORO: region of Almirante, *Cooper 353* (F); s. loc., *von Wedel 230* (F, MO). CANAL ZONE: Barro Colorado I, *Aviles 969* (F), *Bailey & Bailey 397* (F), *Bangham 591* (F), *Ebinger 210* (MO), *Shattuck 778* (F), *969* (MO), *1024* (F, MO), *Starry 82* (F), *118* (F). *Wetmore & Abbe 169* (F), *Zetek 3810* (holotype of var. *macrophyllum* F, isotype MO), *Z-4327* (F). *Z-4330* (F); s. loc., *Hayes s.n.* (F, MO); along the Trinidad River, *Pittier 4005* (holotype US).

2. **Chrysophyllum cainito** L., Sp. Pl. 192, 1753.

Tree to 30 m. *Leaves* with petioles 0.8-2.3 cm long; blades elliptic or oblong, occasionally ovate or somewhat obovate, short-acuminate, to 15(-19) cm long and 8.3 cm broad, shiny-glabrous above, appressed-rufous-tomentulose below. *Flowers* often numerous per axillary cluster, the pedicels 5-16 mm long, appressed-rufous-sericeous; sepals ca 1 mm long, suborbicular or broadly ovate, closely rufescent; corolla green, yellow or purplish-white, 3-5 mm long, rotate-funnelform, the tube glabrous, the lobes appressed-sericeous externally except at the margins, ovate or lance-ovate, equalling or slightly exceeding the tube; anthers 0.6-0.9 mm long, the short filaments attached to the corolla-lobes near the base; style 0.5 mm long or less, the stigma with 7-12 small marginal lobes. *Fruit* 3-10 cm broad, subglobose, several-seeded; seeds oblique-obovate, flattened, 1-2.5 cm long, the scar lateral, extending nearly the length of the seed.

Probably native to the West Indies; cultivated and often naturalized in Central America and Mexico and occasionally in northern South America and southern Florida.

BOCAS DEL TORO: Changuinola Valley, *Dunlap 24* (F); vic of Chiriquí Lagoon, *von Wedel 2523* (MO). CANAL ZONE: nr Madden Dam & along Azote Caballo Rd nr Alajuela, *Dodge 16573* (MO); upper Chilibre River, ½-1 mi below Chilibre, *Seibert 1505* (MO). CHIRIQUÍ: pastures & forested river banks E of Gaulaca, *Allen 5033* (MO); Progreso, *Cooper & Slater 247* (F), *264* (F). COCLÉ: floor of El Valle de Antón, *Allen 2747* (F). DARIEN: Río Sabana above Sante Fé, *Duke 14104* (MO); vic of Campamento Buena Vista, Río Chucunaque above confluence with Río Tuquesa, *Stern et al. 853* (MO). HERRERA: vic of Ocú, *Allen 3647* (MO). LOS SANTOS: from 1 mi S to 10 mi N of Tonosí, *Duke 12488* (MO). PANAMA: woods along Pan-Am Hwy ca halfway betw El Llaon & Río Momoni, *Duke 5527* (MO); Chepo, *Kluge 49* (F); Taboga I, *Woodson et al. 1537* (MO). VERAGUAS: dry slopes of Cerro Tute, region W of Santa Fé, *Allen 4441* (MO); Coiba I, *Dwyer 2331* (MO).

Chrysophyllum cainito is the best known species of the genus and is widely planted as a shade tree and for its succulent, edible fruit which resembles a small apple. When the fruit is cut in cross-section, the several compressed, brown seeds are seen to radiate in a star-like fashion around the central axis—hence the common name "star apple." The foliage is bright blue-green above and coppery or golden beneath and offers a striking contrast when stirred by the wind.

5. MASTICHODENDRON

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

Trees, unarmed. *Leaves* alternate or subopposite; blades typically exceeding 6 cm, ± canaliculate above the midrib, the channel often terminating in a small pouch at the base of the blade. *Flowers* in clusters at defoliated nodes; sepals 5, uniseriate; corolla subrotate to ± cylindric, the lobes 5, exceeding the tube, lacking appendages; staminodes not petaloid; staminal filaments attached to the corolla near the level of the sinuses; ovary glabrate, usually 5-locular, the ovules attached basilaterally. *Fruit* fleshy, 1-seeded at maturity; seed 1-2.7 cm long, the scar basilateral, as much as 9 mm long but not extending to the middle of the seed, the endosperm copious.

Five species are known in North America, one reaching Panama; the status of several Chinese species is open to question (Cronquist, Lloydia **9:** 245, 1946).

Useful reference:

Cronquist, A. Studies in the *Sapotaceae*, II. Survey of the North American genera. Lloydia **9:** 241-292, 1946 (*Mastichodendron* p. 244-252).

1. **Mastichodendron capiri** (DC.) Cronquist var. **tempisque** (Pittier) Cronquist, Lloydia **9:** 250, 1946.—Fig. 5.

Tree to 25 m. *Leaves* often clustered toward the branch tips; petioles 3-9 cm long, 1-1.5 mm broad, usually ½-⅔ the blade length; blades elliptic or elliptic-ovate to elliptic-obovate, acuminate or acute to rounded or emarginate, 6.5-15 cm long, 3-7 cm broad, glabrate, the secondary laterals angled at ca 45° with respect to the primary laterals or irregularly anastomosing, the reticulation prominulous and rather coarse. *Flowers* several-numerous per cluster, the clusters occasionally closely spaced (seemingly one large cluster below the leaves of the season); pedicels 3-8 mm long, glabrate or pubescent; sepals 1.5-3.2 mm long, rounded or broadly ovate; corolla yellow or greenish-yellow, 5-8.5 mm long, the lobes broadly oblong to obovate, slightly cucullate, imbricate; staminodes squamiform, ovate or ovate-lanceolate, erose, 0.75-1.5 mm long, not more than ½ the length of the staminal filaments; anthers 2.3-3.8 mm long, sagittate at the base; style 2-3 mm long, thickening gradually toward a vitually imperceptible juncture with the ovary, with several longitudinal creases, the stigma inconspicuous, the lobing scarcely evident. *Fruit* ovoid or ellipsoid, yellowish, apiculate, to 4 cm long and 2.5 cm thick, the flesh scant; seed ellipsoid, 1.5-2.5 cm long, only slightly compressed, the scar ovate-ellipsoid, 6-9 mm long.

Panama to Oaxaca, Mexico and perhaps occasionally north-westward.

COCLÉ: Penonomé & vic, *Williams* 421 (F, US).

Mastichodendron capiri var. *capiri*, characterized by pubescent leaves, occurs primarily from Oaxaca to Nayarit, Mexico.

Fig. 5. *Mastichodendron capiri* (DC.) Cronquist var. *tempisque* (Pittier) Cronquist: A, habit ($\times\frac{1}{2}$); B, corolla opened to show attachment of stamens and staminodes ($\times 5$); C, flower with corolla removed ($\times 6$); D, fruit ($\times\frac{3}{4}$). A-C after *Godfrey 67075* (MO), Costa Rica; D after *Smith 2508* (MO), Guatemala.

6. POUTERIA[5]

Pouteria Aublet, Hist. Pl. Gui. Fr. 85, *pl.* 33, 1775.

Trees or occasionally shrubs, lacking spines. *Leaves* alternate or sometimes subopposite; blades membranous or coriaceous, the primary lateral veins strongly arcuate near the margin, not crowded, the secondary laterals often ± perpendicular to the primary laterals (at least toward the margin), occasionally irregular. *Flowers* white to yellow or green, pedicellate or sessile, the fascicles axillary to leaves or leaf-scars; sepals 4-12, uniseriate or biseriate (always 2 + 2); corolla cylindric to subrotate, the lobes 4-6(-7), lacking appendages; staminodes petaloid or more often not petaloid (lance-filiform, linear or small and inconspicuous); staminal filaments attached at or near the top of the corolla-tube, less frequently at the middle or near the base (virtually free); ovary pubescent, (1-)4 to 10-loculed, the ovules attached laterally. *Fruit* fleshy or woody or gall-like; seeds 1-several, lacking endosperm, the scar lateral, exceeding the middle of the seed, often broad.

About 40 species occur in North America; 15 species, as recognized in this treatment, are found in Panama.

Useful reference:

Cronquist, A. Studies in the Sapotaceae, II. Survey of the North American genera. Lloydia **9:** 241-292, 1946 (*Pouteria* p. 257-292).

a. Sepals 4-7 [unknown in *P. lucentifolia* but presumably so].
  b. Flowers obviously pedicellate (the majority of the pedicels more than 2 mm long).
    c. Leaf-blades sericeous beneath.
      d. Pubescence pale; corolla-lobes fringed-ciliolate; staminal filaments attached at the middle of the corolla-tube .... 1. *P. euryphylla*
      dd. Pubescence rufous; corolla-lobes not ciliolate; staminal filaments attached at the level of the sinuses .... 2. *P. calistophylla*
    cc. Leaf-blades glabrous or pubescent only on the main veins beneath.
      e. Sepals 2-3 mm long.
        f. Reticulation of leaf-blades coarse; fruit 5-seeded, 4-5 cm broad; seed scar 1.5-2 mm broad .... 3. *P. lucentifolia*
        ff. Reticulation of leaf-blades fine; fruit 1-seeded, less than 2 cm broad; seed scar 8-10 mm broad .... 4. *P. stipitata*
      ee. Sepals 4-12 mm long.
        g. Secondary lateral veins without specific orientation (irregularly anastomosing); sepals 4; corola glabrous externally ...... 5. *P. dominigensis*
        gg. Secondary laterals ± perpendicular to the primary laterals and parallel to each other; sepals (4)5-6; corolla sparsely sericeous-strigose externally .... 6. *P. campechiana*
  bb. Flowers sessile or subsessile (the majority of the pedicels less than 2 mm long).

[5]Although Cronquist's study of *Pouteria* is a careful and invaluable revision, the limited amount of herbarium material available precludes, even now, the possibility of attaining a really satisfactory classification. A number of species are known only from the type collection and the complete morphology of the flower and/or fruit remains unknown for several, e.g. *P. cooperi*, *P. sambuensis*, *P. lucentifolia*. The key to species should be regarded as only a tentative guide.

h. Sepals 5; corolla-tube shorter than the corolla-lobes.
  i. Petioles 6-17 mm long; secondary lateral veins irregularly anastomosing, rather coarse; outer sepals ovate, the inner oblong-spatulate; corolla tubular or campanulate; ovary 4-locular ......7. *P. chiricana*
  ii. Petioles 15-33 mm long; secondary laterals fine, close, regularly disposed (though sinuous); all sepals ovate; corolla subrotate; ovary 5-locular ....8. *P. subrotata*
hh. Sepals 4, 6 or 7; corolla-tube exceeding the corolla-lobes [unknown in *P. sambuensis*].
  j. Sepals 6-7; corolla-lobes 5; staminal filaments attached at the top of the corolla-tube; fruit pyriform or obovoid ....9. *P. sclerocarpa*
  jj. Sepals and corolla-lobes 4; staminal filaments attached at the middle or base of the corolla-tube; fruit oblate-spheroid to ellipsoid [only sepal characters known for *P. sambuensis*].
    k. Fruit conspicuously hairy ....10. *P. sambuensis*
    kk. Fruit glabrous.
      l. Leaf-blades finely appressed-sericeous below (sometimes glabrate in age); outer sepals ovate and finely rufescent, the inner rather narrowly oblong-spatulate; corolla 2.5-3 mm long; staminal filaments attached at the base of the corolla-tube ....11. *P. stylosa*
      ll. Leaf-blades glabrate; sepals all ± ovate, the outer soon glabrate; corolla 4.5-8 mm long; staminal filaments attached at the middle of the corolla-tube or slightly below ....12. *P. caimito*
aa. Sepals 8-12 or more.
  m. Secondary lateral veins mostly perpendicular to the primary laterals, decidedly more prominent than the fine reticulum; sepals conspicuously appressed-pubescent on the back; fruit fleshy.
    n. Primary lateral veins 20-50 pair; sepals (at least some) emarginate or more deeply bilobed at the apex; fruit ellipsoid to ovoid or subglobose, brown, mealy-roughened ....13. *P. sapota*
    nn. Primary laterals 12-20 pair; sepals entire or scarcely emarginate; fruit obovoid, yellowish-green, the surface irregularly wrinkled (at least in herbarium specimens) and also mealy roughened ....14. *P. fossicola*
  mm. Secondary laterals rather irregularly disposed, scarcely more prominent than the coarse reticulum; sepals glabrous; fruit woody ....15. *P. cooperi*

1. **Pouteria euryphylla** (Standley) Baehni, Candollea **9:** 249, 1942.[6]

"Tree about 15 m high; leaves elliptic or elliptic-obovate, rather abruptly and narrowly acuminate, about 10-22 cm long, 4-12 cm wide, glabrous above, very closely and finely sericeous-strigose with pale hairs beneath; primary lateral veins about 9-13 pair, not becoming crowded and obscure near the base of the blade, as they do in many species; secondary lateral veins, except those near the midrib, nearly perpendicular to the primary ones, but also somewhat sinuous and often branched; petioles about 1.5-6 cm long; flowers few in the axils, the closely sericeous-strigose pedicels about 4-5 mm long; sepals 4, about 3.5 mm long, broadly elliptic-ovate, the outer closely hairy on the back, the inner glabrous except for a strip down the middle of the back; corolla about 3.7-4.5 mm long, the lobes a little shorter than the tube, evidently fringed-ciliolate; filaments attached about

[6]Quotation marks are used for descriptions when material was extremely poor or not available for study and the text is a direct quote from Cronquist's descriptions (Lloydia **9:** 257-292, 1946).

at the middle of the corolla-tube, and trace raised and conspicuous to the base; anthers about 1 mm long, short-cuspidate; staminodes about 1 mm long, triangular-lanceolate, ciliolate like the corolla-lobes, and alternating with them, nearly or quite in the same series; ovary densely hairy, 4-loculate, the style a little over 2 mm long; fruit unknown."

Known only from the type collection.

BOCAS DEL TORO: Buena Vista Camp on Chiriquí Trail at 1250 ft, Almirante region, *Cooper 611* (holotype F, isotype NY; not seen).

2. **Pouteria calistophylla** (Standley) Baehni, Candollea **9:** 419, 1942.

Tree ca 20 m high. *Leaves* with petioles 1-3 cm long; blades obovate or elliptic-obovate, acuminate, 10-22 cm long, 4.5-10 cm broad, glabrous above, rufous-sericeous-tomentulose beneath (the pubescence mostly appressed), the primary laterals 12-22 pair, prominently raised below, the secondary laterals (except the 2-3 most medial ones) subperpendicular to the primary laterals (although somewhat sinuous), sometimes obscured beneath by pubescence, the reticulation subobscure. "Well-developed flowers unknown, but a very young flower has a stout pedicel 5 mm long, with 5 sepals and a 5-lobed corolla, the filaments attached at the level of the sinuses, the staminodes narrow, approximately triangular-lanceolate; an overmature flower has 5 deltoid-ovate very firm sepals about 2 mm long, the ovary parasitized, probably originally 2-loculate; fruit unknown."

Known only from the type collection.

BOCAS DEL TORO: region of Almirante, Cricamola Valley, *Cooper 481* (holotype F, not seen; isotype US).

3. **Pouteria lucentifolia** (Standley) Baehni, Candollea **9:** 424, 1942.
Lucuma pentasperma Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. **4:** 251, 1929.
Pouteria pentasperma (Standley) Baehni, Candollea **9:** 353, 1942.

Tree ca 11 m high. *Leaves* with petioles 8-24 mm long; blades elliptic-obovate, acuminate or occasionally obtuse or acute, 7-25 cm long, 3.3-10 cm broad, lustrous, glabrous or occasionally sparsely hirsutulous on the midrib beneath, the primary lateral veins 8-15 pair, the secondary laterals prominent below and often slightly raised, becoming ± perpendicular to the primary laterals toward the margin although somewhat irregularly anastomosing, the reticulation coarse, often prominent below. "Flowers unknown, but a young developing fruit has a thick pedicel 5 mm long and nearly glabrous ovate sepals 3 mm long; pedicels evidently not elongating in fruit." *Fruit* golden-brown, mealy-roughened, globose, 4-5 cm in diam, the fruiting pedicel 5-6 mm broad; seeds 5, ellipsoidal, strongly flattened, 2.5-3.5 cm long, 1.3-1.6 cm broad, lustrous-brown, the seed-coat 0.4-0.6 mm thick, the scar linear, 1.5-2 mm broad. extending the length of the seed.

Honduras, Costa Rica and Panama.

BOCAS DEL TORO: region of Almirante, *Cooper 369* (holotype of *Lucuma pentasperma* F, not seen; isotype A); Changuinola Valley, *Dunlap 591* (F).

4. **Pouteria stipitata** Cronquist, Lloydia **9:** 265, 1946.

Tree to 10 m. *Leaves* with petioles 4-17 mm long; blades narrowly obovate to elliptic, acuminate, 5.5-13 cm long, 2-4.5 cm broad, glabrate or appressed-pubescent along the main veins beneath, the primary laterals 7-11 pair, the secondary laterals conspicuous but often irregularly anastomosing, sometimes becoming ± perpendicular to the primary laterals toward the margin, the reticulation fine. *Flowers* fasciculate at defoliated nodes; pedicels 2-5 mm long; sepals 4-5, suborbicular or broadly ovate, 2-2.5 mm long, finely strigulose to glabrate; corolla thin, 2.4-3.2 mm long, the lobes 4, subrectangular, 0.7-1.2 mm long, fringed-hairy on the margin; staminodes oblong-spatulate, 0.3 mm long, marginally fringed-hairy (especially near the tip); staminal filaments attached at the middle of the corolla-tube; ovary 4-locular, densely ascending-hirsute externally with pale trichomes, the style glabrous, 1-1.5 mm long. *Fruit* yellow, finely warty-roughened, the body ellipsoid or obliquely-ellipsoid, 2-2.5 cm long, ca 1.6 cm broad, constricted basally to a stipe ca 7 mm long and 3 mm broad; seed 1, ellipsoid, ca 1.5 cm long, not compressed, the scar elliptic-obovate, 8-10 mm broad, extending the length of the seed.

Panama; known only from Barro Colorado Island and the Perlas Archipelago.

CANAL ZONE: Barro Colorado I, *Shattuck 1125* (F), *Zetek 4693* (holotype F). PANAMA: San José I, *Erlanson 324* (GH, US), *Johnston 634* (GH, MO, US), *1291* (GH).

5. **Pouteria dominigensis** (Gaertner f.) Baehni var. **dominigensis,** Lloydia **9:** 278, 1946.

Lucuma serpentaria H.B.K., Nov. Gen. Sp. Pl. **3:** 242, 1819.

Tree to 10 m. *Leaves* with petioles 0.5-2 cm long; blades obovate-oblanceolate, rounded to subacute, 4-13 cm long, 1.8-6 cm broad, glabrate except when very young, lustrous, usually conspicuously reticulate-veiny on both sides, the primary laterals less than 1 cm apart, the secondary laterals without specific orientation, sometimes subequalling the primary laterals. *Flowers* 1-several per axil; pedicels 3-8 mm long; sepals 4 (2 + 2), 4-9 mm long, subequal, ovate, the outer finely appressed-rufous-sericeous, the inner similarly pubescent down the middle, otherwise glabrous; corolla cylindric, yellow or white, minutely papillose but glabrous, 8-16 mm long, the tube comprising ca ⅔ of the total length, the lobes (5)6, ± oblong; staminodes linear-subulate, ca 3 mm long; staminal filaments 1-2 mm long, attached at the top of the tube, the anthers 1.3-2 mm long; ovary densely rufous-pubescent, (5)6(-8)-loculed, the style 6-11 mm long, glabrous except at the base. *Fruit* yellow, fleshy, oblate, 2-5 cm long, 3-6 cm broad, the base of the persistent style surrounded by a conspicuous light-colored areola 1-2 cm broad; seeds 1-several, 1-3 cm long, the scar 3-10 mm broad.

West Indies and southern Florida; cultivated in the Canal Zone.

CANAL ZONE: s. loc., *Johansen 36* (F); Ancon, *Mell s.n.* (F); Balboa, *Standley 26894* (F), *30859* (F).

The other variety of *P. dominigensis,* var. *cuprea* (Urban & Ekman) Cronquist, is apparently limited to Haiti and the Dominican Republic and is distinguished by the leaves which are strongly rufous-strigose beneath or only tardily glabrate.

6. **Pouteria campechiana** (H.B.K) Baehni, Candollea **9:** 398, 1942.—Fig. 6.

Lucuma salicifolia H.B.K., Nov. Gen. Sp. Pl. **3:** 241, 1819.

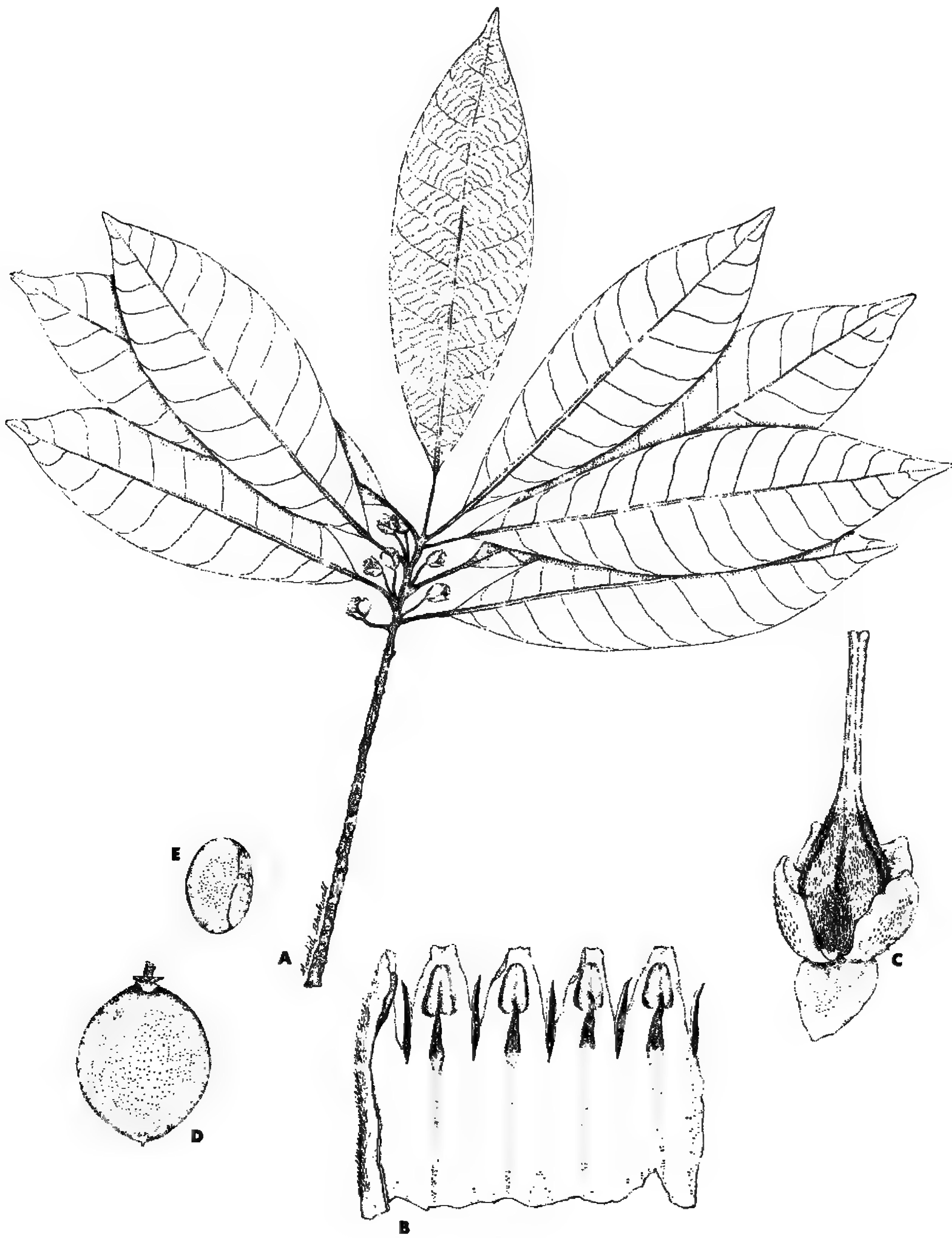

Fig. 6. *Pouteria campechiana* (H.B.K.) Baehni: A, habit (×½); B, corolla opened to show attachment of stamens and staminodes (×4); C, flower with corolla removed (×3½); D, fruit (×¾); E, seed (×½). A after *Piper 6027* (F); B-C after *Palmer 386* (MO), Mexico; D after *Hinton 9185* (MO), Mexico; E after *Allen 2609* (F).

L. glabrifolia Pittier, Contr. U. S. Nat. Herb. **20**: 481, 1922.
Pouteria glabrifolia (Pittier) Cronquist, Lloydia **9**: 282, 1946.

Tree to 25 m. *Leaves* with petioles 6-33 mm long; blades oblanceolate or narrowly obovate to elliptic, often acuminate but sometimes acute or broadly obtuse or virtually rounded, 6.5-30 cm long, 2-8.5 cm broad, glabrous, the secondary laterals subparallel, ± perpendicular to the primary laterals (the 3-4 most medial secondary laterals rather strongly arcuate and joining the midvein), the reticulation fine, prominent to subobscure. *Flowers* 1-9 per leaf-axil; pedicels 5-17 mm long; sepals (4)5-6, ovate (sometimes very broadly so), appressed-puberulent externally, 4-12 mm long, the innermost the longest; corolla cylindric, 7-16 mm long, sparsely to moderately sericeous-strigose externally (glabrous toward the lobe-margins and on the lower portion of the tube), the tube comprising ½-⅔ of the total length, the lobes (4)5(-7), oblong; staminodes narrowly linear-lanceolate, often minutely papillose, 2.5-5 mm long; staminal filaments attached slightly below the top of the tube, ca 1.5 mm long, the anthers ca 2 mm long; ovary densely rufous-pubescent, usually 5-locular, the style 5-12 mm long, glabrous except at the base but minutely papillose, the stigma subcapitate, usually 5-lobed. *Fruit* edible, subglobose or pyriform, apiculate, brown to orange or yellow at maturity, to 7 cm long and broad, the pulp orange or yellow; seeds 1-4, brown, polished, 2-4 cm long, the scar 1-2 cm broad, extending the entire length.

Mexico (as far north as Colima and San Luis Potosi) to Panama; also in Cuba and the Florida Keys but probably introduced.

CANAL ZONE: vic of Ancon, *Piper 6027* (F, US). COCLÉ: Penonomé & vic, *Williams 56* (US). COLON: vic of Donoso, *Holdridge 6202* (MO). DARIEN: Casaya I, *Duke 10374* (MO); vic of Piñas, *Duke 10589* (MO); forests around Pinogana, *Pittier 6542* (holotype of *P. glabrifolia* US; isotypes F, GH); 2 mi E of Santa Fé, *Tyson et al. 4839* (MO). PANAMA: Trapiche I, *Allen 2609* (F), *2627* (F); Chepillo I, *Duke 10320* (MO); Saboga I, *Duke 10343* (MO); San José I, *Erlanson 201* (US), *235* (US), *396* (US), *Johnston 526* (MO, US), *733* (MO, US), *1171* (MO, US).

Though pointing to a close relationship, Cronquist (Lloydia **9**: 282, 1946) considered *P. glabrifolia* distinct from *P. campechiana* by virtue of its larger flowers with corollas more loosely hairy on the back. However, I find nothing distinctive in the corolla pubescence of the type of *P. glabrifolia* and, save for the slightly larger flowers, it would seem to be a typical specimen of *P. campechiana*.

7. **Pouteria chiricana** (Standley) Baehni, Candollea **9**: 421, 1942.

Tree to 30 m. *Leaves* with petioles 6-17 mm long; blades elliptic or oblong-elliptic to somewhat obovate, acuminate, 8-16 cm long, 2.5-6.2 cm broad, glabrous or sparsely sericeous below along the midrib, usually conspicuously reticulate-veiny beneath, the secondary laterals irregularly anastomosing, often slightly raised below. *Flowers* subsessile in small axillary clusters; sepals 5, 2.2-2.6 mm long, closely pubescent, the outer ovate, the inner oblong-spatulate; corolla tubular or campanulate, 3-3.2 mm long, the lobes 5, ca 2 mm long, rounded; staminodes small and inconspicuous; ovary 4-locular. *Fruit* ca 3.5 cm long, broadly ellipsoid, smooth, 1-seeded, narrowed to a ± definite, short and broad, stipitate base; seed ellipsoid, ca 2.4 cm long and 1.8 cm broad, the seed-coat dull, with a fine raised honeycomb pattern on the external surface, 0.5-0.7 mm thick, the scar oblanceolate, ca 8 mm broad, extending the length of the seed.

Panama.

BOCAS DEL TORO: region of Almirante, *Cooper 457* (F). CHIRIQUÍ: Progreso, *Cooper & Slater 230* (A, US), *254* (holotype F, isotype Y; not seen).

8. **Pouteria subrotata** Cronquist, Lloydia **9:** 277, 1946.

Tree 10-15 m high, the limbs and branchlets erect. *Leaves* with petioles 1.5-3.3 cm long; blades obovate to elliptic-obovate, acuminate, 10-23 cm long, 5-11.5 cm broad, glabrous above, glabrous or sparsely strigulose below (the trichomes scattered and not concentrated along the main veins), not conspicuously reticulate-veiny, the primary lateral veins prominent, 8-11 pair, the secondary laterals numerous, fine, close, sinuous but regularly disposed and subperpendicular to the primary laterals except near the midrib (there strongly curved). *Flowers* subsessile (pedicels to 2 mm), clustered in leaf-axils and at defoliated nodes; sepals 5, ovate, 1.7-2 mm long, densely appressed-puberulent externally (the margins of the inner sepals glabrous), more sparsely pubescent within; corolla white, subrotate, 3.5-3.8 mm long, the lobes 5, 2.5-3.1 mm long, ovate-oblong, sparsely to moderately appressed-sericeous externally except near the margins; staminodes linear-filiform, ca 2 mm long; staminal filaments 1.7-1.9 mm long, attached at the base of the corolla-lobes, the anthers ca 1 mm long; ovary densely appressed-white-sericeous, 5-locular, the style stout, 1.5-2.5 mm long, glabrous except at the base. *Fruit* green or yellow-green, turning red, oblong-ellipsoid, 2-2.5 cm long, ca 1.2 cm broad, 1-seeded, the flesh scant; seed ellipsoid, ca 2 cm long, filling the fruit, the scar 8-9 mm broad, extending the length of the seed.

Panama (Darien).

DARIEN: Río Paya, *Duke & Kirkbride 14073* (MO); forests around Pinogana, *Pittier 6548* (holotype US).

9. **Pouteria sclerocarpa** (Pittier) Cronquist, Lloydia **9:** 287, 1946.

Tree to 25 m. *Leaves* with petioles 1-2.2 cm long; blades rather narrowly elliptic-obovate, acuminate, 10-25 cm long, 4-8 cm broad, glabrous, the primary laterals 13-20 pair, the more marginal secondary laterals ± perpendicular to the primary laterals, the reticulum slightly raised beneath. *Flowers* subsessile (pedicels to 2 mm long), several per fascicle, the fascicles occurring at defoliated nodes; sepals 6-7, ovate, the 2 outermost sepals appressed-pubescent externally, 3-4 mm long, the inner sepals glabrate externally and 5-6.5 mm long, all sepals pubescent within; corolla 6-8 mm long, the tube comprising ca ⅔ of the total length, the lobes 5, ovate; staminodes ca 2 mm long, petaloid, narrowly ovate, subtruncate; staminal filaments attached at the top of the corolla-tube, the anthers ca 1 mm long; ovary 5-locular, densely ascending-sericeous externally, the style glabrous, 5-7 mm long, the stigma 5-lobed. *Fruit* yellow, sclerous, pyriform to obovoid, somewhat narrowed toward the base, 5-7.5 cm long, 3-4.5 cm broad; seed solitary, to 4 cm long and 2.5 cm broad, the large scar extending its full length.

Known only from the type collection.

SAN BLAS: plain of Sperdi, nr Puerto Obaldía, *Pittier 4357* (holotype US, isotype MO).

10. **Pouteria sambuensis** (Pittier) Baehni, Candollea **9:** 250, 1942.

Labatia sambuensis (Pittier) Pittier, Contr. U. S. Nat. Herb. **20:** 481, 1922.

"Tree 10 m high; leaves glabrous, oblanceolate to obovate, acute at the base, acuminate at the tip, mostly 20-25 cm long and 5-9 cm wide; primary lateral veins about 13-15 pair; secondary lateral veins prominent, anastomosing, somewhat irregular; petioles short, about 1-1.5 cm long; sepals 4, presumably large; other flower parts unknown; fruit sessile or subsessile, fleshy, densely hairy, ovoid, about 5.5 cm long, 4 cm thick, obscurely sulcate from base to top."

Known only from the type collection.

DARIEN: foothills of the Garagará Mts, Sambú Valley, *Pittier 5621* (holotype US, isotype F; not seen).

11. **Pouteria stylosa** (Pierre) Dubard, Not. Syst. **1:** 381, 1909.

Lucuma standleyana Pittier, Contr. U. S. Nat. Herb. **18:** 166, 1916.
Labatia standleyana (Pittier) Pittier, loc. cit. **20:** 481, 1922.
Pouteria standleyana (Pittier) Baehni, Candollea **9:** 255, 1942.

Tree to 7 m. *Leaves* with petioles 3-10 mm long; blades elliptic to narrowly obovate, acuminate, 7-20 cm long, 2.5-7 cm broad, glabrous above, finely and closely appressed-sericeous below (the trichomes white to slightly fulvous) or sometimes glabrate in age, the primary laterals 10-20 pair, the more marginal secondary laterals perpendicular to the primary laterals, the more medial skewed at about 45°, the reticulation more apparent above. *Flowers* axillary to leaves and leaf-scars, 1-several per axil, sessile (often several borne on a low, woody cushion); sepals 4 (2 + 2), 2.5-3.6 mm long, the outer broadly ovate and finely rufescent, the inner rather narrowly oblong-spatulate and glabrous except down the middle; corolla cylindric, glabrous, 2.5-3 mm long, the tube ⅔ of the total length or more, the lobes 4, broad, subtruncate or slightly emarginate; staminodes lanceolate, 0.7-0.8 mm long; staminal filaments attached at the base of the corolla-tube; ovary densely ascending-rufescent, 4 to 6-locular, the style usually glabrous, 1-2 mm long, the stigma 4 to 6-lobed, the lobes readily evident. *Fruit* woody, glabrous, ca 3 cm long and 3.5 cm broad; seeds 2, to 2 cm long and 1.6 cm broad, somewhat compressed, the seed-coat 1-2 mm thick, firmly grown to the pericarp.

Panama; perhaps also Honduras, Costa Rica and Colombia.

BOCAS DEL TORO: region of Almirante, Konkintoe 10 mi above Holstein, *Cooper 509* (F). CANAL ZONE: area W of Limon Bay, Gatún Locks & Gatún Lake, *Johnston 1820* (A, MO); Mamei Hill, *Pittier 3807* (holotype of *Lucuma standelyana* US, not seen; isotype F). PANAMA: vic of El Cermeño, *Allen 2572* (F), *Zetek 4804* (F); Vista Alegre, Río Aguacate, 2 mi beyond Arraiján, *Zetek 5511* (F, US). PROVINCE UNKNOWN: s. loc., *Hayes 67* (type, not seen).

Cronquist (Lloydia **9:** 273, 1946) states that several sterile specimens from Costa Rica and Honduras (*Standley 40129, 54634, 55606 & 55816,* all F) resemble this species but have much larger (to 50 cm long and 20 cm broad) and less markedly acuminate leaves possesing 20-40 pairs of primary lateral veins and petioles 2-7 cm long. He indicates that these plants may prove to represent a distinct species when better known. I have seen a similar specimen from Colombia (*Killip et al. 38307* US).

12. **Pouteria caimito** (Ruiz & Pavon) Radlkofer, Stizungsb. Akad. Wissens. München **12:** 333, 1882.

Tree to 30 m. *Leaves* with petioles 5-17 mm long; blades obovate-oblanceolate to elliptic, acute or acuminate, 5-24 cm long, 2-11 cm broad, glabrate, the secondary laterals without particular orientation, the reticulation close. *Flowers* 1-several per axil, sessile or subsessile (pedicels to 1.5 mm); sepals 4 (2 + 2), 3-4.5 mm long, ovate to oblong-ovate, the inner appressed-sericeous down the middle, otherwise glabrous, the outer soon glabrate; corolla cylindric-urceolate, glabrous, 4.5-8 mm long, the tube ⅔ of the total length, the lobes 4; staminodes linear, flattened, ca 1.5 mm long; staminal filaments ca 2 mm long, attached at the middle of the corolla-tube or slightly below, the anthers ca 1 mm long; ovary 4-locular, densely ascending-sericeous externally (the trichomes 1-2 mm long), the style glabrous, 2-4.5 mm long. *Fruit* yellow, fleshy, globose to ellipsoid, 5-10 cm long, 4-8 cm broad; seeds 1-4, the scar extending the entire length.

Brazil and Peru to Trinidad and southern Panama.

DARIEN: Sambú River, *Pittier 5555* (F, US).

13. **Pouteria sapota** (Jacquin) Moore & Stearn, Taxon **16:** 383, 1967[7].

Calocarpum mammosum (L.) Pierre in Urban, Symb. Antill. **5:** 97, 1904, auct. quoad descript.

Tree to 30 m. *Leaves* clustered toward the branch ends, the branch ends often fulvous-tomentose; petioles 1-4.5 cm long; blades oblanceolate or obovate, often acuminate, 10-40 cm long, 4-14 cm broad, glabrate or tawny-sericeous below along the midvein and primary laterals, the primary laterals 20-50 pair, the secondary laterals essentially perpendicular to and connecting the primary laterals, more prominent than the close reticulum. *Flowers* subsessile (pedicels to 2 mm long), clustered at defoliated nodes, each cluster often borne on a small woody cushion; sepals 8-12, spirally imbricate, ± orbicular, densely appressed-sericeous externally except at the margins (there entirely glabrous), often emarginate or more deeply bilobed at the apex, 2-6 mm long, the innermost the longest; corolla ± cylindric, 6-10 mm long, the tube comprising ⅖-½ of the length, the lobes 4-5, oblong-obovate, appressed-sericeous except at the margins; staminodes linear-lanceolate, 2-3 mm long; staminal filaments attached at the top of the tube, 2-3.5 mm long, the anthers ca 2 mm long; ovary densely ascending-sericeous, 5-locular, the style 3.5-7 mm long, often pubescent on the basal ⅓-½, the stigma 5-lobed. *Fruit* fleshy, ellipsoid or ovoid or subglobose, mealy-roughened, 8-20 cm long, brown, the pulp yellow to red or pink, often milky; seed 1, ellipsoid, not compressed, often 5-6 cm long, lustrous brown, the elliptic or obovate scar extending the entire length, ca 2-2.5 cm broad.

Southern Mexico to northern South America and the West Indies; widely cultivated; original natural range uncertain.

CANAL ZONE: ½-1 mi below Chilibre, *Seibert 1517* (MO, US); Balboa, *Standley 26080* (US). CHIRIQUÍ: banks of Río Tabasará, on hwy, *Woodson et al. 441* (MO). COCLÉ:

[7]For a discussion of nomenclature and complete list of synonyms of *P. sapota* see Moore & Stearn, Taxon **16:** 382-395, 1967.

vic of Olá, *Pittier 5089* (US). HERRERA: rd betw Las Minas & Pesé, *Duke 12307* (MO). PANAMA: Laguna de Portala, nr Chepo, *Pittier 4628* (US); Taboga I, *Standley 27916* (US). SAN BLAS: Ailigandi, *Dwyer 6849* (MO); mainland opposite Ailigandi, from mouth of Ailigandi River to 2.5 mi inland, *Lewis et al. 163* (MO). PROVINCE UNKNOWN: s. loc., *Duchassaing s.n.* (F-fragment).

Pouteria sapota, like several other members of the *Sapotaceae* valued for their edible fruits or other uses, has numerous common names, the most frequent probably being "sapote." The fruit is a favorite among natives throughout tropical America and is eaten raw or used to make sherbets, preserves and beverages.

14. **Pouteria fossicola** Cronquist, Lloydia **9:** 289, 1946.

Tree 10 m high. *Leaves* ± clustered toward the branch tips; petioles 1.2-4 cm long; blades obovate, often acuminate, 8-30 cm long, 4-13 cm broad, finely white-strigulose on the main veins beneath, sometimes also with a few similar hairs scattered over the lower and occasionally the upper surface, the primary laterals 12-20 pair, the secondary laterals regularly disposed, mostly perpendicular to the primary laterals, decidedly more conspicuous than the fine reticulum. *Flowers* clustered at defoliated nodes; pedicels ca 5 mm long; sepals ca 8, broad, densely appressed-grayish-sericeous dorsally except for thin glabrous margins, rounded or scarcely emarginate, spirally arranged, increasing the size centripetally, the largest ca 6 mm long; other flower parts unknown. *Fruit* obovoid, fleshy, 8.5 cm long, 4.5 cm broad, yellow-green, the surface irregularly wrinkled (at least in herbarium specimens) and also mealy-roughened; seed 1, obovoid, not compressed, 7 cm long, 3.5 cm broad, the scar obovate, basally acuminate, 3 cm broad, extending the length of the seed, the seed-coat firm, shiny, yellowish-tan.

Known only from the type locality.

CANAL ZONE: Barro Colorado I, *Bangham 583* (A, F), *Salvoza 999* (holotype A), *Zetek 3870* (F).

15. **Pouteria cooperi** Cronquist, Lloydia **9:** 291, 1946.

Tree ca 15 m high. *Leaves* with petioles 0.7-3.1 cm long; blades elliptic or narrowly obovate, acuminate, 8-17 cm long, 3-7 cm broad, loosely hirsutulous on the main veins beneath, in addition with a few scattered hairs on the lower surface, the primary laterals 8-13 pair, the secondary laterals irregularly anastomosing or occasionally ± perpendicular to the primary laterals, scarcely more prominent than the coarse reticulum. "Flowers (separately preserved) apparently sessile or nearly so; calyx of about 12 or perhaps more thick and fleshy broad sepals, increasing in size centripetally, the inner about 4-5 mm long when dry, all finely warty-wrinkled when dry, otherwise apparently glabrous, with narrow thin margins; other flower-parts unknown; fruit reputedly woody."

Known only from the type collection.

BOCAS DEL TORO: region of Almirante, Cricamola Valley, Holstein farm, *Cooper 499* (holotype NY, not seen; isotypes F, US).

Index of Latin Names

Numbers in **boldface** type refer to descriptions; numbers in roman type refer to synonyms; numbers with dagger (†) refer to names incidentally mentioned.

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A journal containing scientific contributions from the Missouri Botanical Garden and the Department of Botany of Washington University in affiliation with the Missouri Botanical Garden. Outside contributions in systematic botany and allied fields will also be considered. These papers are subject to a charge of $25 per printed page.

Information

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THE FLORA OF PANAMA[1]

BY WALTER H. LEWIS
Missouri Botanical Garden, St. Louis

A pleasurable function Dr. Hugh Cutler gave me today is to introduce to you our first speaker this afternoon, Dr. Duncan M. Porter, our new staff member in the herbarium. But before we hear from him on the Galápagos Island project I want to give you a little propaganda on our own floral project, the *Flora of Panama.* In general style and approach the two Floras have much in common so I won't spend time on an aspect Dr. Porter will cover, but what I did want to do is to give you a brief history of the Panamanian project, its good and bad points and what value it has been in stimulating related systematic programs.

Panama is an exceedingly rich floristic area with large elements of both the Colombian and northern cordilleran floras represented. In its 47,000 square miles we estimate no fewer than 8,000 species. How did the Garden become interested in this piece of the tropics and what are some of the factors relating to the *Flora of Panama* today?

The Garden founded a tropical station in the Canal Zone in 1926, and began a series of expeditions from here in 1934. The first "Contributions toward a Flora . . ." appeared in 1937 with Dr. Robert E. Woodson, Jr. as editor and assisted first by Dr. Russell Seibert and later by Dr. Robert W. Schery. Seven Contributions were published through 1943, chiefly from collections made from 1934 till 1941 by members of the Garden staff (cf. Dwyer, Ann. Missouri Bot. Gard. **51**: 109-117, 1964). Earlier, collectors had concentrated their work in the Canal Zone or on off shore islands so what we had in fact was the initiation of the *Flora of Panama* in 1943, largely based on collections from the Canal Zone plus those from seven years of general collecting, some of it continuous, such as that by Paul H. Allen, but mostly by just periodic visits to Panama. Except for western Chiriquí and the El Valle region, no mountainous area north and west of the Zone was then conveniently accessible so of course little material was collected. The whole area

[1] The first of four papers and informal remarks on floristics given at the Missouri Botanical Garden's 15th annual symposium on systematics during the afternoon session of October 19, 1968. The symposium on "The Practical Values of Systematics" was chaired by Dr. Donovan S. Correll, Texas Research Foundation, Renner, and organized by Dr. Hugh C. Cutler of the Missouri Botanical Garden.

ANN. MISSOURI BOT. GARD. **55**(3): 171-178, 1969.

south and east of the Zone to the Colombian border had hardly been visited excepting by Pittier. My intention here is not to go into a long discourse on collecting or the lack of it, but rather to give an illustration of when *not* to start a flora; in this case with well over half of the country not yet visited by a botanist and when the richest area, the mountains, remained virtually untouched. But the *Flora* was started, ill-conceived in my opinion as a project for 1943, yet what is really worse is that by virtue of its beginning, collecting essentially stopped and was not reactivated until this decade, a lapse of nearly 20 years. It has become quite clear to us what a tragic mistake this was as we now uncover dozens of new species and dozens of generic extensions into Panama, particularly from South America. I think the lesson was learned, albeit the hard way, for apart from the quality of the *Flora,* which obviously suffered, we ignored the great stimulants to all aspects of an herbarium's operation, namely collecting and exploration. Yet on the basis of our collections since 1959 material has been almost doubled for families still to be treated in the *Flora.* With them we obviously have a better understanding of distribution and ecology of taxa, and a better opportunity for making correct taxonomic judgments.

One very positive effect of the *Flora* both during the non-collecting and current phase has been its role in graduate education. Too few floras, particularly those involving the tropics, have been a part of the academic world where stimulus to graduate training and graduate exposure to floristics is maximumly possible. Fortunately, because of our close association with Washington University, we are currently managing direct graduate participation by insisting that students join one collecting expedition to the tropics, and in our advanced course in taxonomy, that students choose to study a small family as it occurs in Panama. Such exposure may not be very great but we think it sufficient for a student to develop an appreciation for what is involved in writing a flora, often his only direct experience with floristics during a graduate career.

Apart from collecting and training as significant activities interwoven with our floral project, we have several others I want to mention only briefly. One has been our small help to the University of Panama in establishing their new herbarium (PAN). Miss Mireya Correa, its first curator who was trained at Duke University, arrived in St. Louis yesterday for about two months of study and determination of her collections. This perhaps best illustrates our desire to stimulate taxonomic resarch within Panama and to have a long-ranged program based at the University of Panama, now a reality of just a few months.

We have for several years discussed the feasibility of including all green terrestial plants in the *Flora* and thereby include the bryophytes. Our new Curator of Cryptogams, Dr. Marshall Crosby, will assume this responsibility as soon as our bryophytes are recurated and reorganized. Dr. Crosby comes to us from Duke University where he worked under Dr. Louis Anderson.

The last example I shall mention is the project of Dr. Thomas Croat who, in collaboration with the Smithsonian Tropical Research Institute in the Canal Zone, is doing a new concise manual of Barro Colorado Island. Dr. Croat has spent about five months on the Island during the past year collecting and making valuable notes on this typical rainforest community (he returned just two days ago brandishing a major leg wound inflicted by a charging peccary!). The manual he hopes to produce will include much needed biological data such as times of flowering and fruiting backed by complete herbarium specimens. I think it is a sad commentary of our manuals from the area that often one cannot associate fruiting material with the flowering specimens; flowers of course are needed for most keys and all too often fruiting specimens just remain undetermined. Dr. Croat plans to make a series of keys for the dominant taxa: to mature fruits, to vegetative parts alone and so forth. These ought to be very helpful for anyone working in the area including, for example, the mammologist who wants to know what his animals are eating . . . and as a matter of record, to help him find an answer provided the initial incentive for this manual. What the program is doing for the *Flora of Panama* is obvious, but what it will do as a practical guide to the rainforest plants of Central Panama is even more important.

Here then are our activities associated with the *Flora of Panama,* but the hard work of putting many of the familial treatments together rests with our new Curator of the Project, Dr. Duncan M. Porter. Dr. Porter comes to us from the Galápagos Islands project under Dr. Ira L. Wiggins, he taught at the University of San Francisco and has his doctorate from Harvard University. It is my distinct pleasure to introduce to you our new Curator of the Flora of Panama and Assistant Professor of Botany at Washington University, Dr. Porter.

THE FLORA OF THE GALÁPAGOS ISLANDS[1]

BY DUNCAN M. PORTER
Missouri Botanical Garden, St. Louis

The Galápagos Islands lie astride the equator in the eastern Pacific Ocean, about 500 miles west of Ecuador. This archipelago consists of some 15 larger islands and numerous islets and rocks, covering a land area of approximately 3,000 square miles. The largest island is 75 miles long and 45 miles wide at its broadest. Several of the mountains of the group reach to a height of over 5,000 feet, although most of the land is relatively low.

The islands in reality are immense piles of lava projecting out of the ocean, covered with craters, fumaroles, vents, and other volcanic phenomena. Great lava flows extend from the crater rims to the sea, and the area is one of the most volcanically active in the world.

About 1,200 people inhabit the Galápagos. They are concentrated in the few spots where there is either permanent water, or there is sufficient and constant enough rainfall to collect and store in barrels. Water is the great limiting factor

[1] I should like to acknowledge the many fruitful discussions on this topic with Dr. Ira L. Wiggins, Stanford University. Dr. Wiggins also kindly read the manuscript.

on the islands for all forms of life. Permanent water holes are few and far between. The plants depend mainly upon the sporadic rain that usually falls from January to April or May, although plants at higher elevations are bathed in fog almost daily. Most animals obtain their water by eating the plants. Both this scanty rainfall and the relatively cool climate (the thermometer rarely rises above 85°F) are due to the Humboldt Current, sweeping up from the south along the western edge of South America and bathing the Galápagos shores with the cool waters of the Antarctic Ocean.

Scanty and sporadic rainfall, a relatively cool climate, and drying winds have here combined to produce literature's classic desert islands. Their vegetation is much sparser than one would guess from their geographical position, and the number of species, subspecies, and varieties of vascular plants known to occur here is roughly 700.

Two so-called "floras" have been published for the Galápagos Islands in this century: that of B. L. Robinson (Flora of the Galápagos Islands, Proc. Amer. Acad. **38**: 77-270, 1902) and that of Alban Stewart (A botanical survey of the Galápagos Islands, Proc. Calif. Acad., ser. 4, **1**: 7-288, 1911). In reality both of these works are merely annotated checklists, giving only some synonymy, locality data, and in only a few cases any plant descriptions, and these minimal. At present there is no single publication to which one with an interest in the plants of the Galápagos Islands may refer in order to key out specimens from the archipelago or to determine the currently accepted names to be applied to the plants growing there.

In 1924 William Beebe wrote several sentences in his book *Galápagos: World's End* (Putnam, N. Y.) that still apply to the situation in 1968: "A very thorough list of plants has been published, giving exact distribution, elevation, ecological summary and relative abundance, but, except for the technical names, no hint as to the growths themselves. Professor Wheeler and I were very anxious to identify certain plants because of their relationships to animal organisms, but found it impossible from published works on the Galápagos. . . . If explorers would give just a thought to others who might come after, and take the time to write out the simplest kind of a key, it would be a kindness beyond gratitude."

Beebe is about to have his wish. Since July 1966 I have been privileged to be associated with Professor Ira L. Wiggins of Stanford University in the writing of a complete flora for the vascular plants of the Galápagos Islands.

The Flora of the Galápagos Islands project was instigated by the late Dr. E. Yale Dawson, who was very much interested in the cacti of the archipelago. Upon Dawson's leaving the San Diego Natural History Museum in late 1964, and the consequent loss of institutional backing for his proposed governmental grant, Wiggins took charge of the *Flora.* Research on the bulk of the project was carried out after Wiggins had taken it over. The project was funded by the National Science Foundation and administered by the California Academy of Sciences in San Francisco. I was employed by the project for 13 months as a Postdoctoral Assistant.

The primary function of a flora is to enable a person unfamiliar with the plants of an area to identify them and to determine the names to be applied to them. This we have attempted to do. However, this should not be taken to imply that *The Flora of the Galápagos Islands* is only a handbook or manual. It is a comprehensive study of the vascular plants occurring in the archipelago. Not only does the *Flora* include a detailed description of each taxon of vascular plant known to occur on the islands, it also includes an illustration of at least one representative of each genus, keys to all taxa, complete synonymy (or a reference to where it may be found), citations of herbarium specimens examined, geographical distributions, notes on variation and relationships, and ecological data for every species, subspecies, and variety treated.

Our chief concern has been with the plants as they occur in the archipelago. In the main, descriptions are based only upon specimens actually collected in the Galápagos Islands. The overwhelming majority of Galápagos collections are in the herbaria of the California Academy of Sciences, Harvard University, and Stanford University. Specimens in these herbaria and several others have been utilized in the preparation of the *Flora.* Field studies in the archipelago in 1964 and 1967 have added materially to previous collections and have helped us to gain a first-hand knowledge of the plants.

Plants known to occur in the Galápagos Islands are not the only ones included in the *Flora.* Notes are provided on species reported from the islands, but which are not represented by any known collections. However, such species are not included in the keys.

A number of cultivated plants also are included in the *Flora.* Some of these, such as *Psidium guajava* (the cultivated guava), have escaped from cultivation and become established in the native plant communities; others, like *Tropaeolum majus* (the garden nasturtium), have the capacity to do so; and still others, like *Mangifera indica* (the mango), may persist after cultivation has ceased and the native vegetation has moved back into the previously disturbed area. Such information is not usually to be found in a flora, unless an escape is able to reproduce itself in the wild. However, the non-taxonomist in particular is invariably interested in every plant that catches his eye, and the spectacular flowers to be found on many cultivated plants make them the first noticed by many.

Thus, *The Flora of the Galápagos Islands* is written not only for the specialist. A conscious effort has been made to provide a useful guide, not merely for the professional taxonomist, but for anyone interested in the Galápagos flora, whether he be an ecologist, a geologist, a herpetologist, an ornithologist, or a plant taxonomist; whether he be in the laboratory or in the field.

THE ILLUSTRATED FLORA OF ILLINOIS

BY ROBERT H. MOHLENBROCK
Southern Illinois University, Carbondale

A multi-volumed work on the complete flora of Illinois is under preparation at Southern Illinois University; I am editor and chief contributor to the series. The work will provide an account of every kind of plant known to occur in Illinois, except bacteria and certain groups of fungi. Keys for identification will be provided, along with the descriptions, synonymy, discussions of ecology and economic uses, chromosome numbers, and distribution maps for each species. In addition, line illustrations of each species, showing diagnostic features, are being prepared by a staff of illustrators. Publication will be by the Southern Illinois University Press. Financing for the project, thus far, has been by the University Press and the Graduate School of Southern Illinois University. A board of advisers has been created to screen the manuscripts and serve as consultants for the project. The board is composed of Dr. Gerald W. Prescott, Michigan State University; Dr. C. J. Alexopoulos, University of Texas; Dr. A. J. Sharp, University of Tennessee; Dr. Rolla M. Tryon, Jr., The Gray Herbarium; and Dr. Robert F. Thorne, Rancho Santa Ana Botanic Garden. The first volume dealing with the ferns of Illinois appeared in April, 1967. Two volumes on monocots (excluding grasses and sedges) are scheduled for release around August 1, 1969. The storage of the entire flora on magnetic tape is being investigated; computing techniques are already being employed in the recording of distributional data.

FLORA NORTH AMERICA PROJECT

BY STANWYN G. SHETLER
Smithsonian Institution, Washington, D.C.

Plant taxonomy serves an eminently practical function through floristics. Without the synoptical guides and floras that are the products of floristic research, neither the biologist nor the layman would be able to identify the plants of the earth and to know where each grows. Such diagnostic information is basic on the one hand to further scientific research and on the other hand to wise exploitation of our plant resources to meet human needs.

North American taxonomists have just undertaken an immense, new, cooperative effort to compile and integrate our knowledge of the plants of this continent. This effort, estimated to take about 15 years, is called the *Flora North America Project.* Taxonomists hope that it will become their "Project Synthesis" of the 20th century, providing the organizing theme and the intellectual rationale for the broader, more cooperative approach to floristic-taxonomic research that is necessary to meet the challenges of our ecological age, when society is becoming increasingly more conscious of its natural environment and of the need to control the quality of this environment. Public officials and laymen alike are depending on the biologists more than ever for instant facts and correlations concerning our plant and animal resources. *Flora North America* should fill a great void by providing for the first time in history a concise encyclopedia of *all* vascular plants in the *whole* of North America north of Mexico. The preparation of this flora will be accomplished through the cooperative labors of many taxonomists, organized and guided by several committees.

Apart from the preparation of the flora itself, a second, supporting objective is to place floristic-taxonomic research on a modern, computerized, information-system basis. *FNA* must be a computer-age treatise—a taxonomically-structured data bank with an associated package of computer programs ("flora software") to serve as a "kit of tools" for use in accessing and manipulating the data.

The third, intangible goal is to stimulate new interest in taxonomy and the study of the higher levels of biological integration—organisms, species, populations, communities, floras—especially among the coming generations of students who should find in the *FNA Project* the philosophical rationale, unifying and organizing genius, and advanced technical resources to conceive and carry out taxonomic researches on a scale hitherto impossible.

The time is overdue for plant taxonomists, who in a sense have always been the keepers of the botanical data bank, to develop a modern storage and retrieval system using the latest methods of electronic data processing and communication, so that they can regain their historic control of the data bank. Publication has exploded such that it no longer is possible to integrate new information rapidly and concisely by conventional methods and media.

Floras and systematic monographs are time-honored, if non-automated, storage and retrieval systems, which through the years the taxonomist has produced as both the means and the ends of his research. In the *FNA Project* we propose to computerize such systems and thereby to update and extend the concept of the flora or monograph to cover not only the traditional printed book but also today's dynamic electronic data bank. Output from a data bank can take many forms and present many different kinds of data. *FNA* output, in addition to the basic identification manual, may include distribution maps, illustrations, glossaries, indices, gazeteers, descriptions, ecological summaries, statistical calculations, phenetic diagrams, and research reports. Thus, *FNA* will not be a single publication, embalming the state of knowledge. Instant update, revision, and cumulation will be cardinal attributes of the automated FNA information system.

It is expected that the *FNA* data will be organized into a series of matrices which lend themselves to easy manipulation by computer. Computer programs are being developed to be used as a package or "black box" by taxonomists for performing automatically many of the purely mechanical chores of compiling, correlating, and editing floristic-taxonomic data. Some of the programs will enable the initiated user to construct by machine his own, up-to-the-minute identification keys, descriptions, maps, etc., from the data matrices. Time-share use of the computer will be exploited for on-line identification of plants from remote terminals. Data matrices and flora software will be constructed to serve not only the scientific research purposes of the taxonomists but also the practical needs of other scientists and laymen. *FNA* should help greatly to bridge the gap between scientist and layman. The electronic methods also should eliminate or simplify many of the routine labors which dilute the basic intellectual content of taxonomy. Then the taxonomist can be more scholar and less curator than in the past.

EXPERIMENTAL STUDIES OF THE SPECIES CONCEPT

BY EDGAR ANDERSON
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This review is dedicated to Dr. J. M. Greenman, former Curator of the Missouri Botanical Garden Herbarium and my colleague during much of the time these studies got underway. In answering my naive questions about the species problem, he frequently quoted to me the statement "Species are but judgments." It was due to him that I became fascinated with the problem of finding factual evidence as to the ways in which such judgments are formed.

Figure 1 illustrates two extreme uses of the word SPECIES in discussions of the species problem. Such discussions are often at cross purposes because those participating are unaware of these differences.

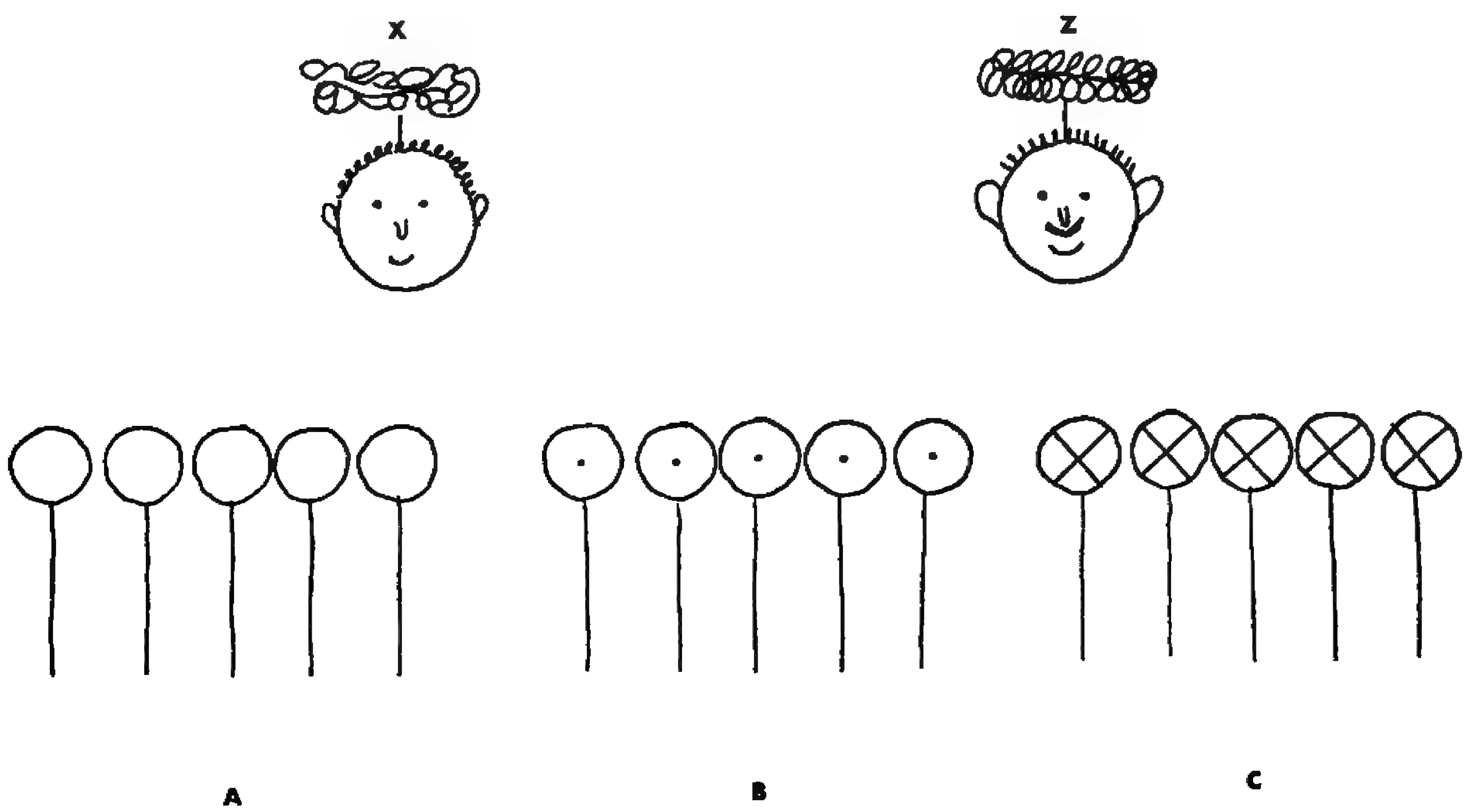

Fig. 1. Diagram of two extreme uses of the word Species.

The diagram shows three taxa of one genus, they may be species, subspecies, or formae but each of the three is represented by individual plants or animals which have certain features in common. This is symbolized in the diagram by 5 individuals of taxon A with no markings, 5 of taxon B with dots and 5 of taxon C with crosses. At the top of the figure are symbolic representations of two gentlemen, Mr. X and Mr. Z, each of whom has been studying the 15 specimens. Above Mr. X's head is symbolized his concept of the taxonomic relationship of A, B, and C. Mr. Z's concept is diagrammed in a similar manner. The diagram would be exactly the same if the two men were in perfect agreement as to the classification of the 15 specimens or if they disagreed in part, or completely. Mr. X, for example, might feel that A with no markings should be species A, and that B and C were

ANN. MISSOURI BOT. GARD. **55**(3): 179-192, 1969.

differing forms of that species. Mr. Z might think that all the differences among the 15 specimens were too minor for taxonomic recognition. In any such example, however, in discussions between Mr. X and Mr. Z, the word "species" might (1) be referring to groupings of the individual specimens of A, B, and C which merited recognition as species or (2) the word "species" might be equated to the concepts X and Z which had matured in the minds of the two men and in which examinations of A, B and C might or might not have played a part.

These matters are well known to most authorities on the species problem. Few of them have made experimental analyses of the species as a concept, but these prejudices are now breaking down rapidly.

Eight such papers were published between 1954 and 1966. They are reviewed below in the order in which they were published. In quoting from those papers of which I was one of the authors, the original text has been shortened but in no case has the sense been changed, though slight differences in shades of meaning are unavoidable in radical condensations.

(1) Speciation in *Uvularia*, by Edgar Anderson & T. W. Whitaker (1934). This paper was (pp. 30-31) "an attempt to present objectively in a codified form the essential facts as to resemblances and differences within and between two similar but distinct species; to reproduce in a concise manner for non-taxonomists the kind of data which are consciously or unconsciously used by taxonomists in the delimitation of species. If a species cannot as yet be defined in terms that are meaningful to workers in other fields, one can present the range of variation within and between two closely-related species in a summarized form for non-taxonomists.

"*It is not a taxonomic thesis.* The two species were chosen for study because there was general agreement that they were specifically distinct from one another and were closely related species of one genus." By diagrams to scale, objective evidence was presented that *Uvularia perfoliata* and *U. grandiflora* had four measurable differences in the leaves, five in the nodes of the stem and inflorescence and four in the flowers. Of all these, only three were discontinuous; the acknowledged discontinuity between the two species is "a discontinuity of combinations reinforced by a few truly discontinuous differences."

It does not seem to be generally realized that species may be, and customarily are, thought of in different ways by different groups of biologists. Biologists engaged in taxonomic work will think of species in terms of the precise differences that permit their ready classification; that make it possible to arrange species in an herbarium or to construct a key to a genus. To them the essential differences between these two species of *Uvularia* will be those few discontinuous ones that are ordinarily used in identifying the species.

"With this attitude we have no quarrel, recognizing systematics as a difficult and necessary business and that those who have it in hand must be allowed to develop their own methods. Yet there *are* those who are interested in the biological makeup of the units which are being classified. This group will include some taxonomists; the separation of the two kinds of thought is not absolute. To us the difference between two species is the difference between one kind of germplasm and another. As geneticists we have gained an impression of two different life-stuffs, each of which reacts variously with the environment. Individual plants produced cooperatively by the germplasm and the environment will show only one facet of that germplasm. For the full expression of a particular species there will be required a series of individuals produced under various environments."

In presenting evidence for differences between the two species of *Uvularia* in their branching patterns and leaf shapes and in the internode patterns of their stems, a combination of measurements and standardized glyphs was used (p. 32). These were developed into a series of charts for graduate classes and lectures at symposia and for the general public. They are discussed below in reviewing the fifth paper.

The first paper in the field of this review presents little objective evidence about the concepts in the minds of systematists, but the diagrams (Fig. 1) do analyze the kinds of evidence that are before ones eyes when working in an herbarium, a museum, or an experimental plot. Taxonomists certainly differ greatly in their ability to form useful "judgments" from such subtle data as trends in shape. Greater skill in that direction is probably responsible for the "taxonomic intuition" of such taxonomists as George Engelmann. His judgments about the classification of western American plants were derived mostly from tiny scraps of material, but they have stood the test of time.

(2) An experimental study of hybridization in the genus *Apocynum*, by Edgar Anderson (1936).

In his Doctor's thesis my colleague Dr. Robert E. Woodson published an interpretation of the phylogeny of the genus *Apocynum* which was decades ahead of its time. He envisaged it as a genus in which inter-specific hybridization has been so important that its evolutionary pattern is more like an anastomosing network than a branching tree. To me his ideas "though stimulating and interesting, seemed rather in need of experimental confirmation by other than purely morphological criteria. After much friendly argument an experiment was planned," a simple progeny test of two common American species, *Apocynum cannabinum* and *A. androsaemifolium,* strikingly different plants, and their putative hybrid, *Apocynum medium.* Woodson gathered seed from several different plants at a site in Indiana where all three species grew near one another, and I made supplemental collections in New England. I supervised raising the seedlings to flowering age, scoring pollen fertility, photographing the flowers and making herbarium specimens of each mature flowering plant (Fig. 2).

Since I was then working in Boston and Woodson in St. Louis, it was easy to get precise, objective data on his concepts of speciation in *Apocynum* from his labels on the 40 reticulately-related *Apocynum* specimens I sent him. They had all been collected the same day and were tagged with a randomized set of numbers, the only key to which was in my record book. Woodson had no way of knowing how the specimens fitted together to make 8 progeny tests until I sent him a

Table 1. Progeny tests of one plant of *A. cannabinum* (can), one of *A. androsaemifolium* (and) and five of *A. medium* (med).

Parent Plant	Seedling Number	Identification	Remarks
can-447	1	*A. cannabinum* var. *cannabinum*	
	2	*A. cannabinum* var. *cannabinum*	
	3	*A. cannabinum* var. *glaberrimum*	
	4	*A. cannabinum* var. *glaberrimum*	
	5	*A. cannabinum* var. *glaberrimum*	
	6	*A. cannabinum* var. *cannabinum*	
	7	*A. cannabinum* var. *cannabinum*	
and-503	2	*A. androsaemifolium*	very typical
	3	*A. androsaemifolium*	
	4	*A. androsaemifolium*	fairly typical
	5	*A. androsaemifolium*	
	6	*A. androsaemifolium*	essentially typical
	7	*A. androsaemifolium*	very typical
	8		
	10	*A. androsaemifolium*	
	Nos. 1 and 9 were lost before their determinations were recorded		
med-446	1	*A. medium*	glabrous leaves
	2	*A. medium?*	like a small *androsaemifolium*
	3	*A. medium*	glabrous
	4	*A. medium*	close to var. *leuco-neuron*
	5	*A. medium*	sparsely pubescent
	8	*A. medium*	glabrous
	9	*A. medium*	glabrous
	10	*A. medium*	unusually small flowers
	11	*A. cannabinum* var. *glaberrimum*	
med-448	1	Probably a glabrous *A. medium*	
	2	*A. medium*	
med-449	1	*A. medium*	but very small flowers
	2	*A. medium*	quite typical
	3	*A. medium*	but nearly glabrous
	4	*A. androsaemifolium*	
	5	*A. medium*	
med-502	1	*A. cannabinum var. glaberimum?*	
	2	*A. androsaemifolium?*	but small flowers
med-504	1	*A. medium?*	
	2	*A. androsaemifolium?*	possibly a hybrid
	3	*A. medium*	
	4	*A. androsaemifolium*	
	5	*A. androsaemifolium?*	corolla rather small

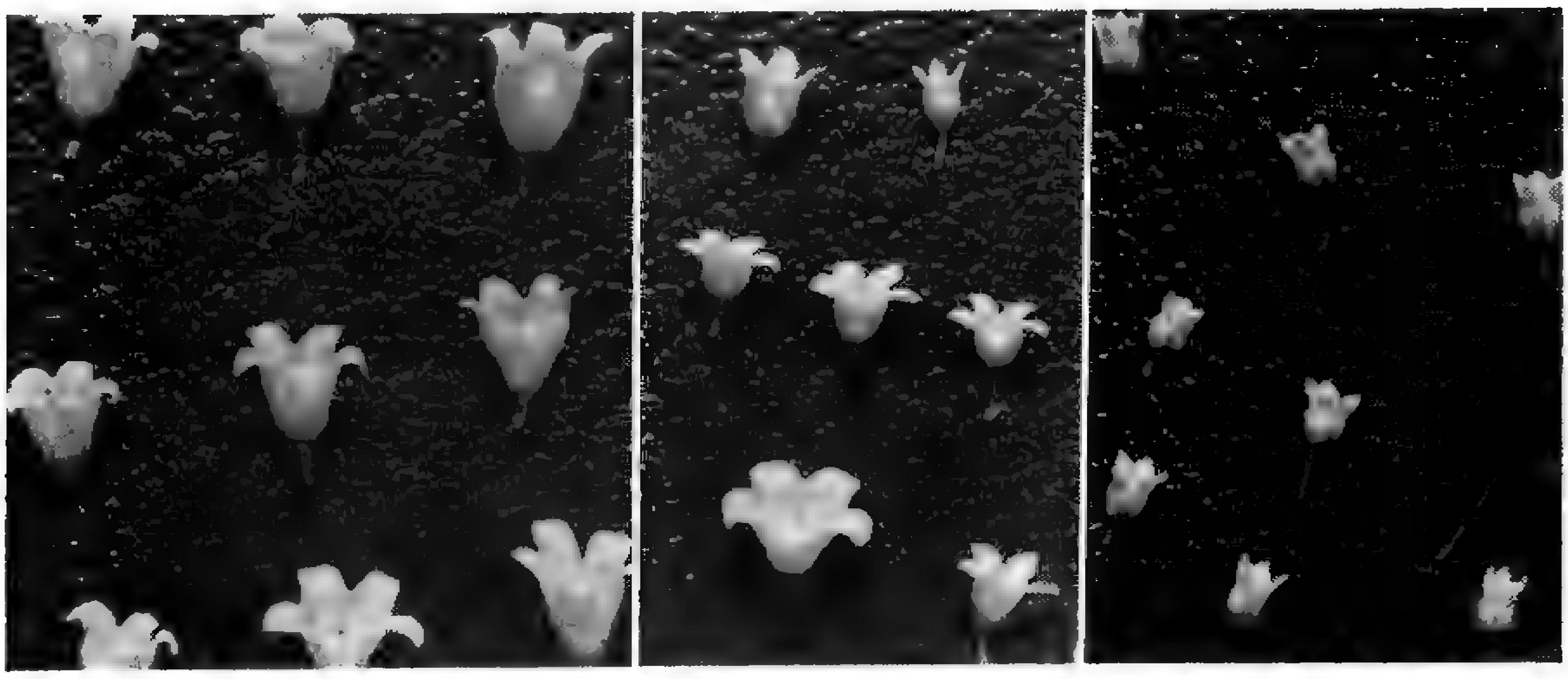

Fig. 2. Progeny tests of three species of *Apocynum*. Each flower was chosen as representative for one plant, all × ½. Left, *A. androsaemifolium;* Center, *A. medium;* Right, *A. cannabinum.*

rough copy of the information in Table 1. It confirmed all his hypotheses, including some I had been skeptical about.

Table 1 demonstrates that all the 6 aberrant specimens that he labelled with questions marks, as well as all the 13 which were so variant that he added informal comments to the label, were seedlings of *A. medium,* the supposed hybrid, thus indicating it to be of hybrid ancestry. Table 1 also presents evidence for a phenomenon that I do not remember having talked, read or thought about up to that time, the various restrictions to free recombination of multiple-factor characters which operate in hybrid germ plasms. The total effect of these restrictions in *Apocynum* is so strong that two *A. medium* seedlings, 449-4 and 504-4 were labelled by Woodson as unquestioned *A. androsaemifolium* and one, 446-11 as unquestioned *A. cannabinum* var. *glaberrimum!* The paper concluded by suggesting that "the chief effect of hybridization in this genus in eastern North America at the present time is to increase variability in the parental species."

It was these experiments with *Apocynum* which lead me to examine the general restrictions to recombination in multiple factor characters and eventually to describe, define and diagram introgressive hybridization.

(3) The Concept of the genus II. A survey of modern opinion, by Edgar Anderson (1940).

From discussions with my colleague Jesse M. Greenman and our students, I became increasingly interested in species as a concept. I sensed that there might be a "Genus Problem" as well as a species problem. Accordingly, when a national symposium on Genera was organized in 1938, I sent out a questionnaire asking in two different ways a basic question about genera and species. The questionnaire was set up to allow any one of five different answers to the first question and four to the second one and was mailed to 43 taxonomists.

Question 1	*No. of replies*
Genus the more natural unit	26
Species the more natural unit	8
Sometimes one, sometimes the other	11
No opinion	1
Question meaningless	2
Question 2	
Genera originate in the same way as species	31
Genera may originate in a different way	4
Genera may originate in same or in a different way	9
No opinion	4

Forty-two taxonomists responded, so many of them with additional comments that a negative correlation between age of respondent and interest in the symposium could be demonstrated in tabular form (see below).

The replies were more uniform than some of the respondents had expected. Twenty-one of them were identical. This orthodox opinion was that genera, on the average, are more natural groups than species, that they originate in the same way, and that generic differences could be compounded from specific differences.

By dividing the respondent into two groups: one, taxonomists whose experience had been mostly in monographic work, and group two, taxonomists who were not monographers or who had extensive experience in other biological disciplines, this correlation could also be tabulated. Of the monographers, two-thirds were "orthodox"; of the non-monographers less than one-third. However, though I was still under 40 when the questionnaires were mailed out, I felt that the "genus problem" required extensive experience with more than one group of organisms, to answer such questions intelligently. I agreed with Liberty Hyde Bailey when he answered "A fair agreement has been reached as to the limits of genera and the limits of species, without much reference to philosophical considerations. Discussion is likely to be made by persons who have no taxonomic training and the conclusions would be of little practical value." C. W. Weatherby, then the assistant curator of the Gray Herbarium, appended to his answer a short distillation out of his own experiences that has important overtones:

	AGE OF RESPONDENT			
INTEREST OF RESPONDENT	Under 40	40-55	Over 55	Total
Not in sympathy	0	0	2	2
Replied without comment	2	7	7	16
Replied with discussion	6	6	5	17
Replied and expressed interest	12	1	1	14
Total	20	14	15	49

"Taxonomy is only a glorified guess—an attempt to construct a cross-section of the lines of descent in a form intelligible to the human mind. It always contains two variable quantities—the plasticity of organic nature and the differing points of view of the people who work at it. You can generalize successfully, if at all, only by keeping these facts constantly in mind. The only general rule is that there is no general rule. Therein lines the fascination of taxonomy for those who like it. *Each group one tackles presents a fresh and original problem: for each, one has to work out anew the method by which he may best achieve that transforming of confusion into order which is the great satisfaction of pure taxonomy."**

When the replies to the questionnaire arrived they were of such interest to taxonomists and other biologists that they were bound and filed in the Missouri Botanical Garden Library. Unfortunately this volume was not put in the locked cases which house the Pre-Linnaean Library and other treasures. It was read so frequently that it became dog-eared. Twenty years later it disappeared from the shelf.

(4) Concordant vs. discordant. Variation in relation to introgressive hybridization, by Edgar Anderson (1951).

The above title is misleading for the purposes of this review. The extensive experimental studies of species concepts reported in the preceding review demonstrated great variation between able biologists in perceiving leaf shape and internode-pattern differences. This paper first presents evidence for the taxonomic validity of these characters. With mathematical precision it then constructs a demonstration of the differences in appearance to be expected between populations of plants in which extensive introgression has or has not taken place. The paper belongs in this review because it presents evidence about the importance of the complex differences it refers to as "trends", as measures of species differences in plants and animals.

All taxonomists tested were aware of leaf-shape differences, though most non-taxonomists were more conscious of size than of shape differences. Correlated changes in size and shape, however, had proved so difficult for them to grasp* that a large half of this paper is a demonstration of that relationship with tracings, diagrams, and discussions.

The first evidence presented is leaf shapes of two common wild cherries of the eastern United States, the choke cherry, *Prunus virginiana* and the rum cherry, *P. serotina*. "The outstanding difference is in the *trend* in proportion. As the leaves of *Prunus virginiana* get longer, they get correspondingly broader. As the leaves of *P. serotina* get longer they get only slightly wider. In *P. serotina*, therefore, the largest leaves are the narrowest, the smallest the broadest; in *P. virginiana* the largest are the broadest, the smallest the narrowest. Such differences in trend of related parts seem to be generally characteristic of specific differences. I found such differences in trend in all the species (of several genera) for which I had made pressed population samples."

Trends in internode patterns became easy to demonstrate and to record precisely by a method originated by a botany major, Dorothy Schregardus. She used it to analyze the growth and development of the common sunflower and it

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* Italics added by the reviewer.

* Though many of them apprehended them, apparently instinctively.

was published as Anderson & Schregardus (c), a method for recording and analyzing variations of internode pattern. The internodes of the stem were diagrammed along the horizontal axis at regular intervals from left to right, 1, 2, 3, 4, etc. as in a scatter diagram of correlation. The length of each internode was then diagrammed vertically in centimeters to an appropriate scale, with a dot. The successive dots were connected with straight lines whose slope was a precise record of the rate of increase or decrease from one internode to the next for the internodes of the entire stem. This simple device has been effective in various studies of plant development and in making exact measures of plant-to-plant differences when interpreting the variation of introgressing populations.

Its most extensive use has been in classifying *Zea mays*. Additional symbols were added to these maize-internode diagrams. A solid black circle marked the position of the last internode below the male inflorescence (the "tassel") and a solid black triangle the position of the corn ear, or of each ear in multiple ear varieties and races. Such diagrams, with minor variations, have been used in more graphs on the races of maize in Brazil, Cuba, Colombia, Central America, the West Indies, Chile, Peru, and Bolivia* sponsored by the National Academy of Sciences and the National Research Council. They are proving useful in developing hybrid corn for Latin America and in the tropics and sub-tropics generally. They demonstrate how a concern for understanding the concepts by which taxonomists evaluate differences between species grew into the use of basic physiological differences in classifying economic plants.

(5) Efficient and inefficient methods of measuring specific differences, by Edgar Anderson, (1954).

This reprint from Kempthorne, Bancroft, Gowen and Lush is included because, though it was prepared for an audience of statisticians and mathematicians, it contains the only published evidence of my most extensive experimental investigations of the species as a concept. As in the first paper reviewed, *Uvularia* furnished the research material. "To get at the fundamentals of the species problem, one needs to choose the simplest possible species. *Uvularia grandiflora* and *U. perfoliata* were chosen for demonstration because there has been universal agreement among those who have dealt with them that they are both good species, that they belong to the same genus, and that they present no special problems of classification, distribution or ecology. Both are known to be diploids; there are no indications of other complicating factors. These two species differ in the presence or absence of hairs on the underside of the leaves and by curious glandular outgrowths on the inner face of the perianth in *U. perfoliata* that have no counterpart in *U. grandiflora*." They also differ by many minor, more-or-less-correlated differences in the size, proportion, texture, number, and arrangement of the various internodes, leaves, and scales that make up the vegetative parts of the plant that

* See for example, Races of maize in Bolivia, Ramírez et al., in collaboration with G. Edward Nicholson Calle, Edgar Anderson, William L. Brown. 1960. Publication 747: Nat. Acad. Sci.—Nat. Res. Council, vii + 159 pp.

are above ground. To analyze the nature of these differences it was necessary to choose a few from among the hundreds of sense impressions coming to us from each plant. The length of every leaf and the length of every internode was recorded, as well as the position of every flower and every scale-leaf (cataphyll). From these measurements and scores, an "ideograph", a sort of diagrammatic skeleton of each specimen, was reconstructed (Fig. 3). The width of the leaf, the angle of branching, the sizes of the flowers, and of the cataphylls at the base of the stem, were all conventionalized. Flowers are represented as black disks, leaves as wide lines but to scale, cataphylls as short narrow lines. The length and number of internodes is indicated by the positions of the leaves and cataphylls. The variation of all these variables was analyzed mathematically. *Uvularia grandiflora* was shown to be "represented by a coherent group of individuals." *Uvularia perfoliata* was not so coherent. Some of the specimens vary in the direction of *U. grandiflora,* suggesting that introgression from that species, previously unsuspected, may be responsible for these variants. These conclusions were confirmed and extended by Dietz (1952).

Experimental studies of the perception of these species-differences were made with reproductions of the 20 ideographs on plain white cards, a little larger than playing cards, or with poster-size enlargements for public lectures. People being tested were usually not told how many species were represented. It was found that biologists differ greatly in ability to separate the two species correctly from these cards and in the speed with which they can do it. At one extreme was a graduate student in comparative anatomy. With no previous experience, he sorted all twenty

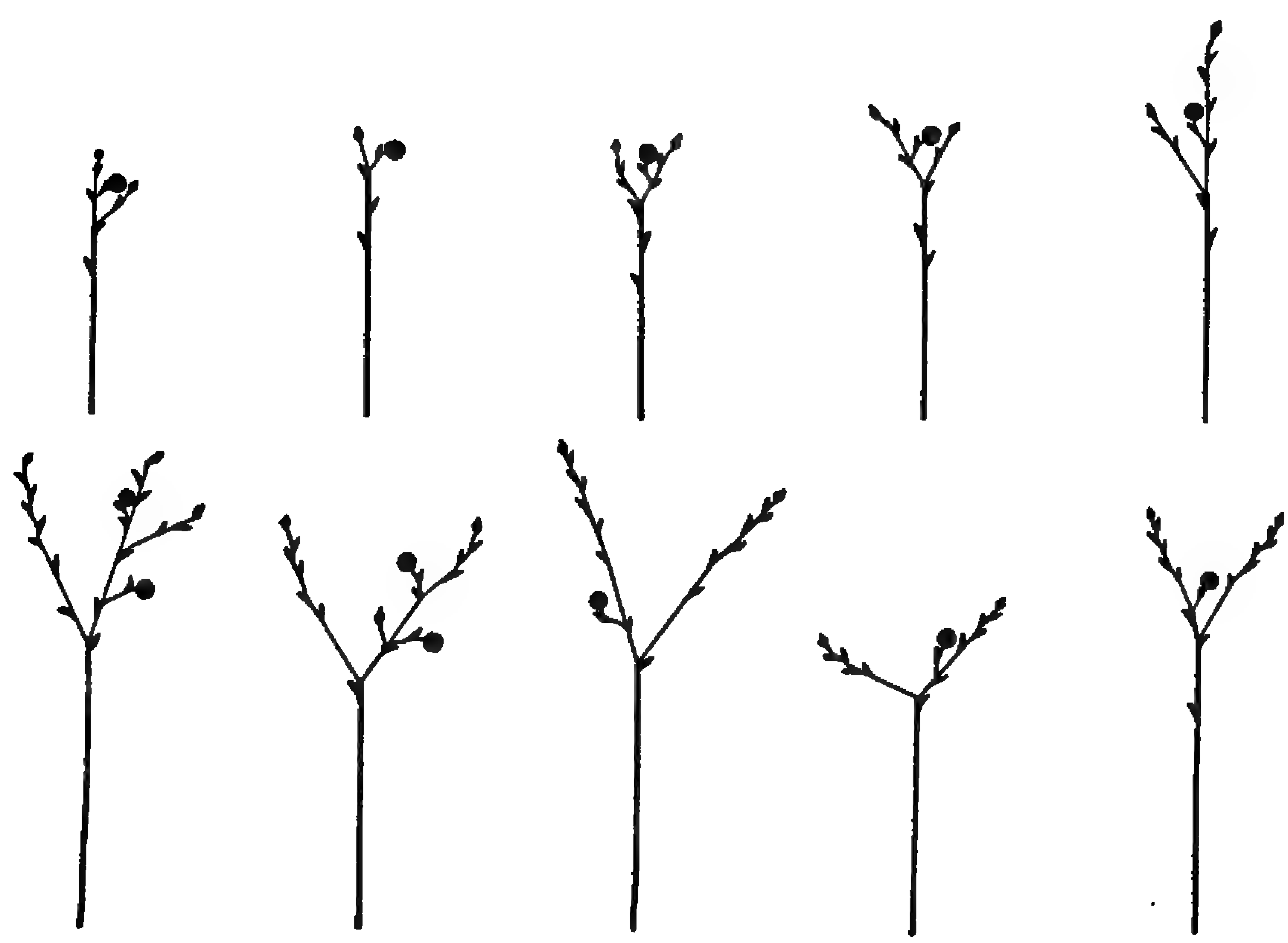

Fig. 3. Ideographs (to scale) of 5 plants each of two species of *Uvularia,* above *U. perfoliata,* below *U. grandiflora.*

out correctly in less than ten minutes. At the other extreme was an able monographer and museum curator. He studied the cards carefully and laid them out in little groups of almost identical ideographs. One or two of these he was able to unite, but most of his units he placed halfway between two others until the whole table-top was covered with a complex web-like arrangement of little groups of cards. He was intrigued by the challenge and kept at the problem intermittently for hours with no success. I suspect that he had more of the basic facts about each specimen in his mind than anyone else I ever tested, but that he had no instinctive way of ignoring maturity differences when looking for specific differences. I suspect also that he was not facile in apprehending differences in internode patterns. When the method of diagramming internode patterns described in the following review was adapted to the *Uvularia* ideographs, it produced diagrams which were easier for students to classify correctly.

From testing students with these ideographs, and from observing taxonomists at work, I believe that there are innate differences between people in their ability to apprehend significant clusters of variables as indicators for malnutrition, maturity, specific differences, etc. Some of those most highly endowed are unaware that they have exceptional gifts in that direction. Able scientists with little of this ability can be helped by a good teacher. Some able taxonomists with little of it, and that little not well-developed, are prejudiced in appraising the work of those who are highly endowed.

(6) An analysis of variation in a variable population of *Cladonia*, by Edgar Anderson and E. D. Rudolph (1956).

This analysis of introgression between species of two lichens is included in these reviews because the same specimens studied by the authors were sent to an authority on *Cladonia*, identified only by numbers, for precise identification. His groupings of the specimens and the authors' are in close agreement. The authors' groupings confirm the generalization of the second review that one of the important results of hybridization is enrichment of variation in the parental species. The contrast between his concept of speciation and their approach to the problem is shown in detail in Figs. 7 and 8. They demonstrate his concepts as well adapted to cataloguing such a hybrid swarm, and the authors' as adapted to analyzing its evolutionary dynamics. This also justifies the paper's introductory remark "that populations which suggest hybridization to the experienced eye have much the same variation pattern as back-crosses of experimentally produced hybrids."

More than any other study of introgression this paper shows step by step how precise measures were worked out for analyzing the variation. The methods adapted for measuring potential variation, demonstrated in figures one to four, could probably be adapted to various kinds of non-vascular plants.

(7) An experimental investigation of judgments concerning genera and species, by Edgar Anderson (1957).

Having learned (No. 3 above) that taxonomists agree in their judgments of species and genera more than they realize, I gathered objective evidence about concepts of species and genera by a simple method. I compared the assignments to species and genera made in two rival floras dealing with the vegetation of the eastern United States. From Fernald's last revision of Gray's Manual and Gleason's New Britton and Brown Illustrated Flora, I made extensive spot checks of their agreement or disagreement in various families and genera. For areas which they both cover they agree at least eight or nine times out of ten. "This is of course a rather limiting case. The flora of eastern North America is relatively stable and it has been well and intensively studied for over a century. In California speciation is much more intricate for all kinds of organisms. Microclimates are much more highly developed. Tertiary and Pleistocene sea-level, rainfall-pattern, and mountain-height changes have been extreme and have led to complicated speciation patterns. The flora furthermore has not been intensively studied for so long a time, yet when one takes two of the standard floras of the state and deals with comparable areas he finds complete agreement 4 to 6 times out of 10 and differences only in detail 2 to 3 times out of 10." Acrimonious disputes between taxonomists have mostly been over the small percentages of instances in which they did not agree.

These concurrences of opinion convinced me that there is a GENUS PROBLEM worth studying as well as a SPECIES PROBLEM. Through the kind offices of Dr. Robert Cooper, 16 specimens of *Uvularia perfoliata* and *U. grandiflora* were studied in turn by three New Zealand systematists who were unacquainted with the North American Flora. None of them had specialized on the *Liliaceae*. All three placed all 16 in the same genus, proving that there is a Genus Problem worthy of extensive study in its own right.

"The central core of the instructions accompanying the sheets was as follows: What I should like is your judgment after examining the specimens as to how many species, varieties, and genera are involved and (by the numbers) how these 16 plants are to be classified. I am not at all interested in having you identify them as to family or genus. Quite the opposite; I hope you will not refer to the literature until after you have dealt with the specimens (if then). This much I can assure you. They were chosen because their classification presents no problems and has never been under dispute. If, for instance, they belong to five species in two genera, then the species are all clear cut and the genera are universally recognized as coherent, distinct genera. If there are any varieties or sub-species present in the material then they too are well-marked variants but not so distinct as to merit specific recognition in the opinion of anyone who has dealt with them."

Note that the recipients were given no clue as to the number of genera, species and varieties included in the sample; they were, if anything, encouraged to believe that more than one genus was involved. They were assured that no problem genera, nor hybrid swarms, nor apomictic groups of doubtful relationship had been included in the sample.

Of the three systematists, one was a distinguished monographer of another family of plants, and he worked independently of the other two. They discussed the specimens with each other but made their final judgments independently. One had carried on extensive field work in biosystematics, the third was an algologist.

The latter separated *U. grandiflora* from *U. perfoliata* but divided each of them into two separate species. It was concluded that there is close agreement among taxonomists on the relation of species to genera even for specialists of different backgrounds and different kinds of training. Their judgments are apparently intuitive and inarticulate. The species-genus relationship deserves coordinated research with biological and psychological techniques.

(8) Folk taxonomies and biological classification, by Brent Berlin, Dennis E. Breedlove and Peter H. Raven (1966).

This short report summarizes the advancing understandings emerging from a remarkable project. It is Science's first accurate, comprehensive attempt to analyze differing concepts of classification in studying the flora of an entire community.

It begins with a refreshingly realistic appraisal of all recent work in this field, and the authors make an exception only for Harold Conklin's Yale dissertation on the Hanuoo culture. "Unfortunately most of the data contributing to our understanding of folk taxonomies are casually collected, non systematic, incomplete and anecdotal."

They concentrated on an area of about 160 square kilometers, the municipio of Tenejapa in Chiapas, Mexico. It ranges from 2700 feet above sea level with legume-evergreen forest in more moist areas, such as along rivers, to mixed pine-oak-sweet-gum forest in the more temperate, middle regions, rising to cloud forest at 9000 feet. "More than 1500 species of vascular plants probably occur in the municipio." From repeated interviews with native informants they believe their sample of more than 1100 plant names in Tzeltal, the native tongue, "is nearing completion."

All their analysis of Tzeltal plant names is based on the "Tzeltal specific" as a unit. They define it as "any taxon which includes no other taxa" and continue "For the purposes of this report we have taken a sample of about 20 percent of our data by including the first 200 Tzeltal-specific names in our alphabetical files. We have no reason to believe that such a procedure biases the results in any significant manner."

For exact comparisons between the taxonomies of Botanical Scientists and the Tzeltal specific names, they divided the latter into three categories, 1) *under-differentiation*, Tzeltal specifics which include two or more botanical species, 2) a one-to-one correspondence and 3) over-differentiation, when more than one Tzeltal specific corresponds to a botanical species. Approximately 41% of the 200 were under-differentiated, 25% were the same and 35% were over-differentiated.

The cultural significance of these Tzeltal specifics to the Tzeltal was graded high, moderate, and low for (1) plants of little or no utility for them, (2) plants of moderate cultural significance, as plants used for fuel or firewood but not cultivated, (3) plants intensively cultivated such as maize, beans, chili peppers and squash, primarily food or cash crops. From these scorings, a strong positive correlation between cultural significance and degree of differentiation was revealed. Forty of the 50 over-differentiated species were judged to be highly significant.

One unexpected result of the analysis was that 40 out of 68 of the plants with a one-to-one correspondence were introduced to Tenejapa after the Spanish conquest. They are invariably used today for the same purposes and in many instances retain their Spanish names.

The authors conclude on a philosophical note, telling us that when we put together such entities as species with the highest proportion of shared attributes, we cannot logically insist that these entities share any one particular attribute. This may tell us little about the structure of nature itself but a great deal about our own view of it!

Conclusions

During the period that I published the first seven papers of this review, I was increasingly impressed with the importance of joint taxonomic-psychological investigations of the two aspects of the species problem discussed and diagrammed in (1). For none of that time, however, did I have a colleague well-grounded in the fields of psychology pertinent to these studies. The 8th review demonstrates the ways in which such problems could have opened up fruitful new fields of investigation had such collaboration been possible.

Within the last decade I have become aware that experimental investigations of taxonomists' conceptions of taxa *above* the species might produce more effective collaboration of taxonomists with physiologists and biochemists.

When a taxonomic monograph of a group of plants has achieved its goal and put like ones close together that tend to share many common features, it can be widely useful. Taxonomists of the higher plants could be as helpful to biochemistry as were those medical school pharmacologists whose discoveries led to such useful concepts as "psychedelic drugs", in grouping whole sets of compounds together. A very little has already been done. The association of dangerous cyanogens with the *Rosaceae* had long been recognized. See Kingsbury (F) for discussion of this and many other examples.

Various taxonomists are already using biochemical information in classifying plants. The relationship between biochemists and plant taxonomists could become genuine collaboration, profitable to both sciences. Sorbitol, for instance, is common to closely related Asiatic and American species of *Larix* (larch) but is not produced in less closely-related species (reviewer's unpublished information). Such facts are useful not only to monographers of the genus *Larix* but also to chemical manufacturers looking for cheap sources of sorbitol.

Before such a two-way association could become facile, there would have to be a wider understanding among taxonomists as to which sub-genera, genera, sub families and families of higher plants are based on a wide variety of characteristics, each of which is shared by most of the group, in other words is a "natural" group and not an "artificial" one. Various genera, families and higher categories in plant taxonomy are widely recognized as "natural" or "artificial". Taxonomists frequently discuss these matters informally among themselves, but I know of no exposition of the problem except the elementary one cited in (5).

It is becoming widely understood, for instance, that the rose family is a natural group and less widely that one of its sub-divisions, the *Pomoideae,* (the pome fruits—apples, pears, quinces, hawthorns, etc., fruits with a core) are an introgressive, polyploid, apomictic complex whose genera, species and sub-species are artificial. They form such a complex, interwoven network of relationships that there have been wide disagreements between experts in cataloguing them.

No one or two taxonomists could yet compile a working list of outstanding natural and artificial taxa, complete enough to be generally useful. On the other hand, a modern taxonomist, familiar with computer techniques, could organize a survey of present day concepts that could be mechanically sorted. It would, at the very least, be a beginning that would call attention to the problem. It might grow into a catalogue that would be widely helpful.

The closing three paragraphs of the paper by Berlin et al. (8) with a discussion of "general" versus "special" classification, indicate the advances of understanding and of utility to be expected from expert conceptual classifications.

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INTERSPECIFIC RELATIONSHIPS IN THE POLYPODIUM PECTINATUM-PLUMULA COMPLEX[1]

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ABSTRACT

Studies of the life cycle, anatomy, morphology, cytology, ecology, distribution patterns and an analysis of the probable evolutionary relationships of taxa in the *Polypodium pectinatum-plumala* complex, compose the basis of a systematic study of this complex. Field studies in Florida, Jamaica, and Costa Rica, plus use of greenhouse grown plants sent from South America, have aided in the understanding of the biological interrelationships of the taxa. Specimens, including types, from 20 major American and European herbaria have been utilized in this study, which has led to the recognition of 35 taxa, including five new species, three new varieties and six new combinations. Keys, descriptions, typification, synonomy and specimen citations are included for each taxon.

INTRODUCTION

In attempting to understand the interrelationships of the very closely related species of the *Polypodium pectinatum-plumula* complex, studies of the ecology, variation in certain populations, and the natural history of the several species, as well as traditional morphological and anatomical studies, were of considerable help. Because the group has a wide tropical distribution, extensive field studies were not possible, but field studies were made in Florida, Jamaica and Costa Rica, and I obtained living rhizomes of several species for culture from collectors in South America. Although it was necessary to rely heavily on data obtained from the species in Florida and in greenhouse culture, several aspects of the life cycles of these species were examined, and this information was useful in interpreting the remaining species.

Historically, the major preoccupation of taxonomists has been in reducing the enormous and polyphyletic genus *Polypodium* to its present restricted sense. No systematic coverage of this whole group as a unit has ever been attempted, and the taxonomy has consisted mainly of the addition of new taxa one by one. Lindman (1903) treated eight of them in an overall study of tropical American

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species. De la Sota (1960), in his research on the *Polypodiaceae* of Argentina, grouped *Polypodium* into several complexes and treated the eight species of the present group from that country.

Morphology and Ecology

Microscopic morphological observations were facilitated by several techniques. The living material was first killed in FAA (formalin, acetic acid, alcohol) or dried material was relaxed in 5% NaOH for 2-3 days before sectioning. Rhizomes, roots, stipes, and blade segments were sectioned at 25μ on a freezing microtome and mounted unstained in diaphane; or they were imbedded in paraffin, sectioned on a rotary microtome, stained in safranin and fast green, and mounted in diaphane. For studies of venation and epidermal patterns, leaf segments were cleared in 5% NaOH, bleached in 10% Clorox, stained by the tannic acid-ferric chloride method (Foster, 1934) and mounted in diaphane or piccolite. Spore preparations were made either by the acetolysis technique (Erdtman, 1943) and mounted in silicone oil (20,000 viscosity grade), or teased from the frond in 95% EtOH and mounted directly in diaphane.

Gametophytes were grown on a variety of growth media. For young stages, spores were sown on either distilled water or liquid Biejerinck's Solution (Brown, 1920). For later stages and mature gametophytes, spores were sown on agar fortified with Knop's Solution (Brown, loc. cit.) in petri dishes, or sown in 3″ porous clay pots with either pulverized sphagnum or hardwood humus. The spores were sterilized by treating them with varying concentrations of Clorox, 10% for 10 minutes being optimal. However, good results were usually obtained in nonsterile conditions. The pots containing soil media were autoclaved, but the petri dishes with agar were not, because it was found that fungi were inhibited when the agar was not autoclaved. Spores, treated either by sterilization or from washed fronds which had been dried in sterilized envelopes, were sown in a sterile transfer chamber.

Gametophytes were observed microscopically either in water mounts, mounted in Hoyer's Solution without being killed, or were killed in 70% EtOH and cleared and stained as the leaf segments above. The small gametophytes were handled in quantity by transferring them in short upright sections of wide glass tubing with the bottom covered with cheese cloth.

Voucher specimens of all experimental collections are deposited in the University of Michigan Herbarium.

Rhizome

The stem (Fig. 17-19) is a long-creeping to short-creeping or sub-erect rhizome, with the fronds short-spaced (never more than 1.5 cm apart) or approximate to fasciculate and articulate on short pseudopodia 1 to 2 mm long. The plants may be epiphytic, terrestrial, or epipetric, but the rhizomes are always exposed. They vary in diameter from 1 to 3 mm in small species such as *P. truncorum* to 10 to 13 mm in the larger species such as *P. ptilodon* or *P. recurvatum*. The internal anatomy is quite uniform. The vascular system is dictyostelic with 3 (in *P. trun-*

corum) to 17 small exarch bundles in a single ring (Fig. 1, A-C). The endodermis is thin-walled, but the inner wall of the ground parenchyma cells adjacent to the endodermis is always strongly thickened. *Polypodium singeri* and *P. truncorum*, two small epiphytic ferns, show a good deal of dark staining, thick-walled collenchyma tissue in all but the outer portion of the rhizome (Fig. 1, C). No true sclerenchyma tissue is present.

The rhizomes are clothed with paleae throughout, which fall basically into two groups of scales—(a) the most common type, associated with the *P. pectinatum* allies, and (b) those found in the groups of *P. cupreolepis* and *P. truncorum*.

The former group (a) has narrow- to linear-triangular, dark red-brown lustrous paleae, basifixed and with an acuminate or filiform apex. The paleae are either broadly expanded at the basal attachment or have a narrow base at the apex of the rhizome. They are dark colored along their margins, usually with a paler area at the base. The cells are narrow, except at the base of the scale, where they usually become shorter and nearly isodiametric. They are non-clathrate. This is in contrast to several groups in *Polypodium* (such as the *P. vulgare* or the *P. squamatum* groups) in which the paleae are usually basally peltate, at least sub-clathrate, and are usually darker in the center rather than along the margin.

These paleae all have a dorsal cluster of unicellular hairs (and are therefore termed "comose") toward the base of the paleae, which are usually visible under low magnification (Fig. 1, G, J-L). In certain species, such as *P. pectinatiforme*, *P. atrum*, or *P. dispersum*, the hairs are uniformly present, although they may not be conspicuous. In *P. plumula*, on the other hand, the comose hairs are sometimes absent. In *P. bolivianum* the hairs of the paleae are long and dense, and they mostly obscure the scales themselves except at the rhizome apex (Fig. 1, K, L), and in *P. consimile* var. *pastazense* they totally obscure the paleae.

In the second group (b) the paleae are cordate or ovate, basifixed at a single point, not so polished or lustrous as in the previous group, and vary in color from golden to dark red-brown. They are non-comose and either concolorous or sometimes paler toward the base (Fig. 1, I).

Roots

The roots are approximately 0.5 mm in diameter with an outer thin-walled cortex of 3-9 layers of parenchyma cells, and a sclerified darkly colored inner cortex usually 4-6 layers deep occupying one-fourth to one-half of the diameter of the root. The endodermis is a thin-walled and inconspicuous layer lining the inner cortex. The bundle is diarch with few (4-8) large tracheids and clusters of small tracheids at the two protoxylem points.

Root Proliferations

Although root proliferation leading to sporophytic reproduction is known in pteridophytes, it is infrequent. Root proliferations are known in *Platycerium*, *Amphoradenium* (syn. *Adenophorus*), and *Asplenium*, and in the present study they have been found to occur in *Polypodium dispersum*, *P. ferrugineum*, *P. filicula*, *P. pectinatum*, *P. plumula*, *P. siccum*, and *P. singeri* (Fig. 7).

Although root proliferations have occasionally been thought to be new plants arising from slender elongated stems or rhizomes (similar to the stolons of *Nephrolepis*), this is not the case in the present complex. As seen in cross-section, a single vascular trace of the root type crosses the cortex of the parent root. The new rhizome is usually first noticed as a small scaly bump approximately 1 mm in diameter on the side of the root. New roots and leaves develop in typical fashion from this small rhizome.

JUVENILE LEAVES

Within the *Polypodium pectinatum-plumula* complex, sporophyte leaves of a "juvenile type" can develop from any of three sources—from root proliferations in various species (as discussed above), from apogamous outgrowths in *P. dispersum* and from sexual embryos.

Leaves produced from root proliferations and from gametophytes have the same morphological stages. Figure 2, D-F, shows the developmental leaf series of *P. dispersum, P. plumula,* and *P. ptilodon* var. *caespitosum.* The first leaves are invariably simple and elliptic with a single midvein of spirally thickened tracheids. The first leaves of *P. ptilodon* var. *caespitosum* are larger and more broadly elliptic than those of either *P. dispersum* or *P. plumula.* The three hair types, discussed below, appear on the first leaves of all the species listed (Fig. 15, C, D, F, G), except that ctenoid hairs are lacking on *P. plumula.* After the second or third leaf, the veins become forked and the blade becomes lobed. The leaves which follow are alternately lobed. Subsequent to these are leaves which are sub-oppositely lobed as in the mature leaf. The venation then develops the mature condition of being 2 or 3 times forked (Fig. 2). No young stages of any of the species with anastomosing venation were available for study, but presumably they follow the same pattern modified only by vein fusions.

MATURE LEAVES

The fronds may be upright, curved or pendent. Most of the species have upright and rather stiff fronds, but certain of the epiphytic ones with upright rhizomes attached to vertical substrates tend to have more flexuous or pendent fronds, such as *P. plumula* (Fig. 3, F), *P. curvans* (Fig. 3, C), *P. choquetangense, P. siccum,* or *P. truncorum.*

The frond outline is narrow-elliptic, -ovate, or -deltoid (Fig. 3). In those species that have narrowly elliptic fronds (e.g. *P. plumula, P. alfredii,* or *P. cupreolepis*) and those with narrow-ovate fronds (e.g., *P. ptilodon, P. dispersum, P. atrum,* or *P. camptophyllarium*) the stipe may be long or short. Several of the species have the lower segments contracted quite abruptly, as in *P. plumula* (Fig. 3, F), and a long stipe; in others, such as *P. consimile* or *P. filicula,* the stipe is reduced or almost absent, and the basal segments are very gradually reduced to lobes. The deltoid or subdeltoid fronds, such as those of *P. recurvatum* (Fig. 3, G) and *P. bolivianum,* have an abrupt demarcation between stipe and rachis at the base of the blade.

The fronds are articulate, abscissing from a short pseudopodium. The tip of the frond and the segments curl tightly adaxially in response to drought, either from atmospheric dryness or water loss after collection. The whole group possesses the ability to respond in this manner, but it is most strongly expressed in such species as *P. plumula, P. dispersum, P. filicula,* and *P. cupreolepis.* Both this curling ability and the articulation of the fronds reduce the exposed leaf surface, and appear to be adaptations to the epiphytic or epipetric mode of life and to periods or seasons of little atmospheric humidity.

Stipe and Rachis

The stipe and rachis are distinctive. In the mature leaf the main axes are either black or of various shades of red-brown; they always have a highly polished appearance. In juvenile fronds the main axis may be lighter or even stramineous, but it turns dark and lustrous as the blade matures. The only exception is that certain of the northern plants of *P. hygrometricum* have a light axis even at maturity, although the majority of specimens of this species have dark axes. The color may also vary between living and dried plants. The axes of *P. dispersum* and *P. plumula* are black in both states. In *P. recurvatum, P. truncorum,* and *P. ptilodon* var. *ptilodon* they are red-brown in both the living and dried state. *Polypodium ptilodon* var. *caespitosum* has a consistently red-brown axis and costa when dry, but the axis is quite blackish in living material. A wide sclerified layer in the outer cortex gives the axis its hard and lustrous external appearance. This layer also gives the rachis the characteristic springiness or elasticity readily recognizable even on herbarium sheets, particularly in the strongly pendent epiphytes, such as *P. plumula.* In *P. curvans* and *P. choquetangense* the main axis is usually sinuous or contorted, and the apex of mature fronds often remains circinate.

The stipe and rachis are terete, and the stipe has either narrow wings or narrow lateral green stripes along its entire length.

Trichomes

Three types of hairs are present on the fronds of these ferns, as illustrated in Fig. 4. (1) The first is a small, simple, clavate hair composed usually of only two or three cells, the terminal one being somewhat larger and blunt-tipped (Fig. 4, I_3). These hairs are usually no longer than 150μ. (2) The second type is apparently derived from the first. In its most characteristic form, this hair consists of an arched axis of approximately four cells, with lateral branches usually of only one, sometimes two, cells. There are usually three or four of these lateral branches all arising from one side producing a "ctenoid" hair. However, modifications of this type of hair are frequent in which the number of branches is reduced, sometimes to one, thus suggesting intergradation with the simple clavate hair (Fig. 4, I). (3) The third hair type is a long, simple, acicular, multicellular hair (Fig. 4, J_3, K_4). These hairs are usually pale on the young frond and turn a golden color at maturity. The acicular hairs vary considerably in length, from 0.2 to 2.0 mm. They are of diagnostic importance in several species, as indicated below.

The three hair types are found on the stipe, rachis, costa, and lamina. The ctenoid hair is apparently present on all juvenile fronds, but is not present on the mature fronds of *P. plumula, P. cupreolepis, P. truncorum* and their immediate allies. The small, clavate hairs are universally present, primarily on the lamina. They are usually so short as to be overlooked, except in *P. sursumcurrens,* in which they are long, blackish, and visible to the naked eye. The acicular hairs have not only considerable variation in size, but vary also in density and distribution. They are absent in a few species, such as *P. bolivianum,* and are only scattered on the lamina in most species, but are quite abundant and dense in *P. pectinatum,* and *P. camptophyllarium.* In all four varieties of *P. ptilodon* the acicular hairs have a curious pattern of distribution such that the lamina is essentially glabrous except for an oval area of dense pilosity around the sorus, often visible to the naked eye or with a hand lens (Fig. 1, E). These are not to be confused with the receptacular paraphyses discussed below.

PALEAE

The most frequent type of rachis scales or paleae are those of the *P. pectinatum* allies (Fig. 5, H, K) which are long, filiform, inconspicuous, and few in number. They are uniformly dark red-brown and of long, thin cells, except that they have more lightly colored and small isodiametric cells at the base. They occur on both the upper and lower surfaces of the main axis, although usually only on the stipe and lower portion of the rachis. At the base of the stipe they tend to have broader bases and approach the shape of the rhizome paleae, which, in the *P. pectinatum* assemblage, are invariably linear-triangular. The margins are entire except in *P. bolivianum,* where they have simple or forked fimbriae on the margin, and in *P. eurybasis,* which occasionally shows slightly fimbriate margins. In both of the latter species this is an amplified condition as regards stipe paleae, and approaches the more fimbriate condition of the rhizome paleae of those species. Several other species, such as *P. pectinatum* or *P. camptophyllarium,* have inconspicuously fimbriate rhizome paleae, but have entire rachis paleae. This is thus apparently a relative change: those species with quite heavily fimbriate rhizome paleae show some indication of this on the rachis paleae, but those species with few or no fimbriae on the rhizome paleae lack any at all on the paleae of the rachis.

The second group of species (*P. atrum, P. dispersum, P. bermudianum, P. plumula, P. filicula, P. ferrugineum, P. cupreolepis, P. alfredii* and *P. sursumcurrens*) have rachis paleae which are non-filiform (Fig. 5). They may be narrow-elliptic (*P. alfredii, P. sursumcurrens* and *P. ferrugineum*) (Fig. 5, F), narrow-triangular with irregular hastate bases (*P. dispersum, P. atrum, P. bermudianum,* and, in part, *P. plumula*) (Fig. 5, A_{4-7}, B, C, D, J) or they may be essentially cordate, as in *P. plumula, P. filicula,* and *P. cupreolepis* (Fig. 5, A_{1-3}, G, I, L). In all but the narrow-elliptic paleae, the margins may be inconspicuously and irregularly fimbriate (Fig. 5). *Polypodium filicula* is the only species with cordate or triangular paleae in which most paleae have an entire margin. Except for overall shape, all of the paleae of this group of species are similar to those of the rhizome in coloration and cell structure. Those species with hard, lustrous, red-brown rhizome paleae have similar rachis paleae. Species such as *P. cupreolepis* (Fig. 1, I and Fig. 5, G) and *P. ferrugineum,* with pale and dull rhizone paleae, have similar rachis paleae.

The narrow-elliptic paleae on the rachis are sparse like the filiform paleae in the previous group. However, those species with hastate-triangular or cordate paleae possess them on the rachis in greater quantity, so that they are readily visible to the unaided eye.

In all taxa except *P. plumula* and *P. filicula* the paleae are flat at the base. In the two exceptions the scales appear inflated or "bullate" at the base. This character appears occasionally also in the paleae of *P. curpreolepis*.

The species with conspicuous and numerous rachis paleae (*P. atrum*, *P. bermudianum*, *P. dispersum*, *P. plumula*, *P. filicula*, and *P. cupreolepis*) also have paleae on the costae. In all cases, these are reduced paleae similar to those of the rachis. In some, as shown in *P. plumula* (Fig. 4, H), the homologies between paleae and hairs are apparent. Although there are basically only three hair types, as described above, in those taxa with costal paleae an additional large, many celled, clavate, simple hair is also present. It is evident that this is the ultimate reduction of the paleae.

Segments

Figure 6 illustrates outlines and venation patterns of the segments of representative species. Figure 3 shows the orientation of the segments in selected species. All the species have simple and entire segments except *P. eurybasis*, *P. curvans* and *P. paradiseae*, which have crenate or crenulate segments, and *P. choquetangense*, which has pinnatifid segments. All species have inconspicuously ciliate segment margins.

Whereas the segments are typically perpendicular to the rachis and straight or slightly falcate, several of the species (*P. absidatum*, *P. curvans*, *P. truncorum*, and *P. choquetangense*) have noticeably ascending segments (Fig. 3, C, D). In most species the segments have a symmetrical base in which both the lower and upper edges are dilated. However, in those species with ascending segments the upper edge meets the rachis abruptly at a nearly right angle. Also, several species, such as *P. atrum*, *P. paradiseae*, *P. pectinatiforme*, and *P. filicula*, have segments of the lower portion of the frond deflexed, and the lower edge of the segment correspondingly meets the rachis at a right angle or less (Fig. 3, B & Fig. 18). In *P. alfredii*, several plants from the northern part of its range have basal segments deflexed so that the lowermost segments are nearly or quite parallel to the stipe. There are several species, however, with all segments essentially at right angles to the rachis, but in which the lower edge of the segment meets the rachis at a right angle, or in which it may even be slightly incised to form a small sinus between rachis and basal margin (Fig. 3, A).

Figure 4 shows variations in the shape of the abaxial epidermal cells and the arrangement of the stomates. The cells over the lateral veins are characteristically narrower and more attenuated than those away from the veins. The stomates occur only on the abaxial surface. The guard cells are slightly elevated above the epidermal cells and are without modified subsidiary cells. Guard cell sizes, as they relate to the ploidal level, are discussed below.

The internal tissue of the segments is compact and quite uniform from one species to another. They average approximately four layers of cells in the mesophyll (two to three in *P. truncorum* and five or six in *P. pectinatiforme*), two layers in a somewhat irregular palisade above and two (three, four) slightly less compact and more irregular layers in the spongy mesophyll (Fig. 1, D).

Figure 6 shows the representative range of venation patterns in the segments. Although the group typically has free-forked venation, three species (*P. filicula, P. siccum,* and *P. truncorum*) have simple veins. Entirely simple veins are not common in the *Polypodiaceae,* although the condition is frequent in the *Grammitidaceae,* a reason why *P. trucorum* has been considered as a ctenopteroid fern by Copeland (1956). However, on the basis of the spores, sporangia, trichomes, and the characters of the rachis, all three of these simple-veined species are properly members of the *Polypodium pectinatum-plumula* complex (de la Sota, 1963). Anastomosing venation, while not the rule in the present complex, occurs all through the *Polypodiaceae.* In the group under consideration here, anastomosing occurs in varying degrees from casual, irregular junctures in each segment, as in *P. pectinatum,* to very regular and complete patterns in *P. camptophyllarium* var. *macedoi. Polypodium camptophyllarium* var. *camptophyllarium* has considerable variation, although it usually has at least a sporadic distribution of areoles. In some plants in southern South America the anastomosing in the latter variety becomes extensive and may even exceed that which is expected in var. *macedoi* (Fig. 6, Q. S). When anastomoses occur in this complex, they are always with a free included veinlet. This is opposed to the areolate condition in the *Grammitidaceae,* in which there are no included veinlets.

The costa, in all cases, is sclerified, sometimes only in the abaxial portion of the bundle sheath (e.g. *P. dispersum* and *P. pectinatiforme*), and sometimes throughout the bundle sheath, but then usually more so on the abaxial side, as in *P. truncorum* and *P. ptilodon* (Fig. 1, D). In several of the species with large fronds, the bases of the secondary veins are also sclerified. Except in *P. ferrugineum,* in which the costae are black and the rachis brown, the costae and rachis are the same color.

SORI

The sorus is terminal on the first acropetal veinlet in all species (Fig. 6). In those with anastomosing venation this veinlet becomes the free included veinlet. Whereas the sorus is typically medially or extra-medially placed on the segment, it may vary all the way from infra-medial (in *P. consimile*) to submarginal (in *P. sursumcurrens, P. alfredii,* and *P paradiseae*).

Wilson (1959 a, b) has described in detail the sporangia of *P. plumula* and *P. ptilodon* var. *caespitosum* (as "*P. pectinatum*"). I have found these structures to be similar and with little deviation throughout the group. Although the annulus usually has 13 or 14 bow cells, *P. camptophyllarium* var. *lachniferum* has only 12, and *P. sursumcurrens* and *P. curvans* have 16.

Wagner (1964) discusses and summarizes the known types of paraphyses in the ferns. Figure 4 illustrates the types found in this complex. Sori of all species produce receptacular paraphyses, and in all but two these are simple or occasionally forked, multicellular, clavate hairs. In all but one species they are similar to the clavate laminar hairs, although they are often longer, and vary from 150-250μ long. In *P. camptophyllarium* var. *macedoi* the receptacular paraphyses are a curious mixture of the clavate and the acicular hair types (Fig. 4, M), being forked hairs with one clavate and one acicular branch. However, the same type of hair is also characteristic of the lamina. In *P. sursumcurrens* the paraphyses are unusual in differing considerably from the laminar trichomes (Fig. 4, P). They range up to 400μ long. Their outline is contorted, and a multicellular, expanded portion is developed near the apex. In most species the receptacular paraphyses are few and hard to observe except by dissection and microscopic examination, but in *P. sursumcurrens* they are numerous and visible even with low magnification. Unlike the elaborate "sporangiasters" of *P. virginianum*, apparently derived from modified sporangia (Martens & Pirard, 1943), the paraphyses of *P. sursumcurrens* are evidently related to the simple, clavate, laminar hairs, as in the remainder of the complex.

Capsular paraphyses (Fig. 4) also occur in approximately half of the species of the complex. They are always short, simple, 1- to 3-celled hairs arising near the top of the capsule near the annulus. They vary in length from 45μ in *P. pectinatum* to 100μ in *P. hygrometricum*. They may be of quite regular number and occurrence—one per capsule in *P. pectinatum*; two in *P. hygrometricum* and *P. ferrugineum;* or of quite variable number, as in *P. dispersum* or *P. plumula,* in which they range from one to five per capsule. In several species they are present on young capsules but may be shed as the capsule matures.

Spores

With two exceptions, spores in this complex are essentially alike. One exception, *Polypodium dispersum,* has only 32 mitotically produced, globose spores per sporangium. The other, *Polypodium camptophyllarium* var. *camptophyllarium,* has, for the most part, normal, reniform, tuberculate spores, but a few collections from Jamaica have quite irregular spores, which suggests that apogamous reproduction may be present in scattered populations of this species (see the taxonomic description of this variety).

The remaining taxa all have 64 spores per sporangium and are therefore presumed to have a normal sexual life cycle. The spores are uniformly reniform and monolete (Fig. 12, H), although they vary in shape from narrowly reniform and curved to globose-reniform. They are all without perispore and the surface is tuberculate, although the sculpturing varies from almost smooth to strongly tuberculate. The spore sizes, as they relate to the ploidal level, are discussed in the section on cytology and evolution.

Gametophytes

The gametophytes of *Polypodium dispersum* are so unusual that a separate section has been devoted to them in the section on sporogenesis. The gametophytes of the *Polypodiaceae* and *Grammitidaceae* have been treated by Stokey & Atkinson (1958), and the gametophytes of *P. plumula* and *P. ptilodon* var. *caespitosum* (as "*P. pectinatum*") were reported by Stokey (1959). All my observations agree with those previously described.

The sex organs are typical of the *Polypodiaceae*, as described by Stokey. After fertilization the sporophyte plant is first seen as a tiny elliptic leaf (Fig. 2) and a root that appears either at the same time or slightly before the leaf. The leaves then develop as described above in the section on juvenile leaves.

Ecology and Geography

These ferns extend from Bermuda, peninsular Florida, northern Mexico and the Galápagos Islands south to northern Argentina and southern Brazil (Fig. 8, B). I consider them to occupy five distributional zones (Fig. 8, D): (1) Central America, (2) western South America, (3) southern Brazil, (4) northern and northwestern South America, and (5) the West Indies, considered a sub-zone of the last. As the distribution maps show (Fig. 8-11), several species occur in more than one zone, although a particularly large number of species are confined to the Central American and southern Brazilian zones. I have included the West Indies as a sub-zone of the northern South American zone because, out of the nine species present in the West Indies, six are known also in northern South America and do not occur in Central America. The remaining three species (*P. dispersum, P. plumula,* and *P. pectinatum*) are wide-ranging and cross several zones (Fig. 9, 10).

Although as a whole the genus *Polypodium* is primarily epiphytic, some species are terrestrial or epipetric. The same is true of the *P. pectinatum-plumula* complex. No species is strictly terrestrial, although *P. ptilodon* (including all its varieties) and *P. consimile* var. *consimile* are primarily terrestrial or occur on the bases of trees (Fig. 7, E). *Polypodium bermudianum, P. dispersum* (Fig. 7, A, G) and *P. ferrugineum* are primarily epipetric, although the two latter are recorded as occurring also epiphytically or terrestrially. *Polypodium choquetangense, P. curvans,* and *P. cupreolepis* are either epipetric or epiphytic. *Polypodium sursumcurrens, P. siccum, P. singeri,* and *P. truncorum* are evidently strictly epiphytic. *Polypodium singeri* is curious in that it apparently grows with its roots reaching the ground, so that it perhaps is only hemi-epiphytic. *Polypodium truncorum* has a particularly narrowly defined substrate, and is found only among the old stipe bases of tree ferns, especially *Alsophila* and *Hemitelia*. The remaining species are primarily epiphytic, but also occur occasionally as epipetric or terrestrial plants.

On the whole, this is primarily a group of tropical and sub-tropical montane plants. Elevation data indicates that they grow from 1500-3500 m in altitude, but a few species are found at low altitudes. *Polypodium dispersum, P. plumula,* and *P. ptilodon* var. *caespitosum* occur in peninsular Florida at nowhere over 100 m in elevation, although they are known elsewhere at much higher elevations. *Polypodium hygrometricum* and *P. recurvatum* are known only from sea level to 1800 m and *P. bermudianum* is confined to the low lying Bermuda Islands.

Certain of the epipetric species are recorded from exposed rocky areas or cliffs. No species grow in the lowland rain forests of the Amazon basin. Judging from the generally montane distribution, the response to drying (desiccation and curling of the frond without the death of the plant) and the articulate stipes, this group is not adapted to areas of constant high humidity, such as in the Amazon basin.

Ecology of Root Proliferations

Several species in this complex reproduce partially by root proliferations; this appears to be related to their distribution and ecological requirements. Proliferations in *P. ferrugineum*, *P. filicula*, *P. siccum*, and *P. singeri* were found only on herbarium specimens, so it is difficult to note more than their mere presence. However, *P. singeri* normally grows as an epiphyte on small woody twigs. Several herbarium sheets show that the individual rhizomes are often short (ca 2 to 3 cm long) and grow in a series along the twigs (Fig. 7, D). The rhizomes and roots are exposed and the rhizomes arise as root proliferations.

Polypodium plumula and *P. pectinatum* grow either on the trunks or horizontal branches of trees, and are true epiphytes (Fig. 7, B). Root proliferations occur infrequently as small plantlets formed from the roots of larger plants. I have also observed small plantlets arising from the superficial roots of a greenhouse culture of the former species.

Although *P. dispersum* is capable of reproducing by spores (as discussed below in the treatment of sporogenesis), its primary mode of local dispersal is evidently by root proliferations. In Florida, for example, this species is usually seen as dense mats of juvenile plants completely covering limestone rocks (Fig. 7, G). Often none of these plants bear sporangia. I saw only three soriferous colonies of this species in the course of field trips in Florida, although I studied numerous populations.

The root proliferations in nature usually occur only a few centimeters apart when the plants are growing on rock surfaces. However, at "Blechnum Ravine" in Annutalaga Hammock, Florida, *P. dispersum* was growing in sand and the plants were widely spaced. In one case proliferations were spaced approximately 0.5 m apart on a very long root.

The rhizomes of these proliferations are always short and superficial on the substrate with no intermediate structure between parent root and rhizome, so that proliferations occur only on those roots that are close to the surface. As these seven species in which proliferations are known are all either epipetric or epiphytic, they normally grow where the substrate is thin and many of the roots are exposed or near the surface. These proliferations may be produced in response to reduced moisture or greater aeration around exposed roots. Increased light also might be a factor. However, the occurrence of proliferations in the dark at the bottom of the pot in greenhouse culture suggests that this is not so, unless a minimal exposure to light is sufficient.

Sporogenesis and the Life Cycle of Polypodium dispersum

I have carried out life cycle studies primarily on *P. dispersum* and *P. ptilodon* var. *caespitosum*. Experimental collections of *P. dispersum* have included a plant from Jamaica (*Proctor 22896*) and collections from Florida (Citrus Co, *Wagner 62061*, *Evans 2008*). Collections of *P. ptilodon* var. *caespitosum* have been from

Florida (Highlands Co, *Evans 1157*; Citrus Co, *Evans 2005*; Sumter Co, *Evans 2004*).

Sporogenesis studies were carried out using a modified acetocarmine squash technique. Segments with sporangia of a suitable age for meiotic figures were killed and fixed in Newcomer's Solution (Newcomer, 1953) and stored in a deep freeze until used. To prepare microscope slides, sporangia from a single sorus were placed in a drop of acetocarmine on a slide. No iron mordant was added, thereby avoiding overstaining of the cells. The sporangia were spread apart to avoid clumping, and a cover slip was added. The slide was heated slightly, but tapped only lightly with a dissecting needle in order not to spread the individual cells too far from the mother sporangium. Firm pressure was then applied with the thumb. The combination of few and wide-spaced sporangia, light tapping, and firm pressure with the thumb, resulted in preparations in which the cells were well squashed, but the individual cells of a particular sporangium were still in close proximity to each other. In this way numerous sporangia could be easily and quickly prepared and observed. The slides were made permanent by inverting them in 2:8 acetic acid: alcohol solution until the cover slips dropped off. After rinsing with the acetic acid-alcohol solution, the cover slips were replaced with a drop of diaphane.

In the *P. pectinatum-plumula* complex, the sexual life cycle (as determined by the number of spores per sporangium) is present throughout except in *P. dispersum*. In this common and widespread species, a pattern of apogamous reproduction thus far unique among pteridophytes has been found.

SEXUAL LIFE CYCLE

The sexual life cycle of the higher ferns is well known. In comparing this with apogamous reproduction, it is only necessary to summarize the process of sporogenesis in a sexual species, as exemplified by *P. ptilodon* var. *caespitosum* (Fig. 12). In the developing sporangium, the archesporial cell divides mitotically four times to form 16 2× spore mother cells (Fig. 12, B). The spore mother cells are readily recognized by their size and form, and also by the large, darkly staining nuclei. They undergo one meiotic division (Fig. 12, C, D) to form a tetrad of young spores (Fig. 12, E-G), resulting in 64 monolete spores per sporangium (Fig. 12, H). Upon spore germination and maturation of the bisexual gametophyte, fertilization may occur; the sporophyte plant develops from the fertilized egg, thus completing the cycle.

OBLIGATE APOGAMOUS (MEIOTIC APOGAMOUS) LIFE CYCLE

Although not so widely known as the sexual life cycle, this process is well documented, as in several papers by Döpp (c.f. 1939) and later by Manton (1950) and others.

Using herbarium specimens, apogamy can usually be detected by making preparations of mature but unopened sporangia. Some of the sporangia, if the plant is apogamous, will have 64 aborted spores, whereas others will show 32 normal-appearing spores.

Apogamous reproduction is normally a process in which sporogenesis is modified and sexual fusion is by-passed. It always involves plants with an unbalanced genotype that could not, in the usual sexual cycle, form viable spores. The process is known in many species of ferns and is considered to be quite widespread. Wagner (1963) estimates that approximately 7% of the 72 pteriodphytes of Giles Co, Virginia, U. S. A., reproduce apogamously. Mehra (1961) found 30 apogamous ferns among 350 cytologically known ferns from the Himalayan region, or about 8.6%. The highest frequency of obligate apogamy is among triploids, although apogamy is known at other ploidal levels, including the diploid (Mehra *loc. cit.*).

In order to compare the apogamous situation in *P. dispersum* with the more usual apogamous sporogenesis, the following brief outline of the latter will provide a comparison. In obligate apogamy the 2× archesporial cell in certain developing sporangia divides mitotically three times forming 8 cells. There is then a further chromosomal division without cytokinesis, and a reorganization of the genetic material into single nuclei ("restitution nuclei"). This results in eight 4× spore mother cells from the initial 2× archesporial cell. Meiosis in these doubled cells is then normal, but produces only 32 viable 2× spores per sporangium.

It should be added that these meiotic apogamous ferns usually also undergo spore formation in another way. In some sporangia, the spores develop without the formation of restitution nuclei. This is essentially the process of sporogenesis in sexual species. However, because of the hybrid-like behavior of the chromosomes in apogamous ferns, in which the genomes do not pair normally except in the restitution nuclei, this process results in irregular and aborted spores.

According to Manton (1950) these two processes can occur in different sporangia on the same apogamous plant, in the same or different sori, and in quite varying proportions, from only a few 32-spored sporangia per sorus to many sporangia of this type per sorus.

The spores produced from 32-spored sporangia develop into gametophytes which usually form sex organs. The archegonia are aborted, or may be absent; but the antheridia and sperms may be functional. The new sporophyte develops not from the sexual apparatus but directly from thallus tissue.

Ameiotic Alternation of Generations in Polypodium disperum

Obligate meiotic apogamy has been considered the only successful or functional apogamous life cycle in ferns, and Manton (1950) termed the process as "monotonously uniform." However, in the *P. pectinatum-plumula* complex, *P. dispersum* displays a unique alternative in apogamous reproduction in ferns (Evans, 1964).

A study of sporogenesis in *P. dispersum* (Fig. 13) shows four complete mitotic divisions of the archesporial cells to form 16 spore mother cells in *all* sporangia, without restitution nuclei. The 16 spore mother cells are readily visible, for they separate, enlarge, and stain more darkly than other cells in the sporangium (Fig. 13, C). All sporangia observed contained only 32 spores. This involved the observation of several hundred sporangia both in sporogenesis studies and on herbarium specimens. In metaphase figures *Polypodium dispersum* has 111 unpaired chromosomes (Fig. 13, E). Squashes of metaphase figures in the eight-celled stage of the archesporium and in the 16 spore mother cells show that the chromosome configuration is essentially identical, both stages showing 111 unpaired chromosomes (Fig. 13, A, D). The mode of cytokinesis of the 16 spore mother cells (Fig. 13, F, H) indicates that each mother cell produces only 2 spores.

The spores are thus formed by one additional mitotic division of the spore mother cells, and meiosis, characteristic of all other known apogamous ferns, is absent (hence my distinction of the two types of apogamy as "meiotic" and "ameiotic"). This is an example of diplospory. Mehra (1961) reports that "diplospory which is so widespread in apomictic angiosperms has so far not been observed as a functional mechanism in apomictic ferns, although there are stray records of its occurrence." Reports of *Trichomanes proliferum* forma β (Bell, 1960; Mehra & Singh, 1957) and in *Ophioglossum* and *Isoëtes* (Verma, 1956, 1960) suggest that this process may also occur in pteridophytes other than *P. dispersum.* However, none of the latter reports contain information pertaining to the gametophyte generation or whether or not these plants are capable of completing their life cycle. Braithwaite (1964) indicates a similar situation in *Asplenium aethiopicum* to that observed here. He describes the formation of 32 spores from 16 spore mother cells as being due to a partial meiotic division and a restitution nucleus. These would appear to be very similar processes in these two different genera.

The irregularities in this process are few. There are occasional sporangia which contain a lower number than 32 spores and some spore fragments. Occasionally, mature spores are contracted medially or submedially as though the cell had begun to divide again. I do not yet know whether these "pinched" spores are viable. In the examination of several hundred divisions only one cell was found that may have doubled its chromosomes. As I obtained over 60% germination of spores, I am quite sure that these few irregularities contribute little or nothing to this germination percentage, and that the viable spores are formed as outlined above.

The morphology of the *Polypodium dispersum* spore is a further departure from the norm. All other species in this complex have the usual reniform, monolete, polypodioid spores, which are formed in tetrads.

The *P. dispersum* spores, in contrast, are distinctly globose, and the scar is exceedingly variable, being either incomplete or suggesting a monolete or trilete pattern (Fig. 14). Occasionally the scar is absent. Spores of apogamous ferns normally resemble the spores of closely related species. In the surface tuberculation, spores of *P. dispersum* are like those of related species, but in the spore and scar shape they are readily distinguishable microscopically.

In agar plates fortified with Knop's Solution, and grown under constant light at 20°C, spores germinated in about 10 days, and development was rapid; young apogamous sporophytes forming in about two and a half months.

The first rhizoid appears with, or even before, the first prothallial cell (Fig. 2, A), and subsequent rhizoids develop with each additional cell, often more than one rhizoid per cell. After one to three filamentous cells develop, an elliptical plate is formed, and rhizoid initiation is reduced.

The cell plate of *P. dispersum* is not cordate, as are most polypodioid gametophytes. At the time of sporophyte proliferation the prothallus is either small and elliptical (Fig. 15, G), or it may be strap-shaped and several times branched (Fig. 2, D). The latter is typical of artificial cultures. In nature, both small elliptical thalli, not much larger than the bases of the sporophytic proliferations, as well as longer, branched thalli are found. Rhizoids are either marginal or near the margin. If the thallus is branched, rhizoids are usually more dense at the confluence of the branches. They are never wholly basal and ventral, as is normal in other sexual species of *Polypodium.* The shape of the thallus and the position of the rhizoids suggest that *P. dispersum* has gametophytes like those of the *Grammitidaceae.* However, the early development of both the rhizoids and the cell plate are characteristically polypodioid. Also, the rhizoids of *P. dispersum* are a light brown, not dark brown and stiff, as is typical of the *Grammitidaceae* (Stokey & Atkinson, 1958).

Two features of *Polypodium dispersum* gametophytes are unique: the absence of gametangia and the ability to produce stomata on a thallus one cell thick. Previously known apogamous ferns produce sex organs even though they are not functional in self-reproduction. No sex organs were observed in either wild or cultured collections of *P. dispersum* gametophytes.

Stomates were observed on several of the gametophytes that had already proliferated sporophytes. As the thallus is everywhere only one cell thick, the stomatal apparatus merely consists of two typical guard cells over an opening between thallus cells (Fig. 2, B & Fig. 15, D, E). Its function, if any, is unknown.

Stomates have previously been observed on apogamous gametophytes (Steil, 1919), but always at the base of the sporophyte and associated with cells already modified in morphology toward sporophytic epidermal cells (elongate and with undulate lateral walls). However, in *P. dispersum,* these stomates occur on lobes without sporophytes (although always on gametophytes containing proliferations) and in tissue with cells still strictly of gametophytic structure.

The sporophytic proliferation in *Polypodium dispersum* is first noticeable as a small swelling on the dorsal surface, usually near the margin of the thallus (Fig. 2, 15). In the very small, elliptic gametophytes it arises from the center and quickly occupies all but a small fringe of gametophyte tissue around the base of the small sporophyte plant. This swelling very early produces both the simple and ctenoid, clavate hairs of the juvenile sporophyte (Fig. 15, D, F, G). The swelling may be only a few cells high or it may become 1 or 2 mm long before differentiation takes place at the apex. A fine strand of two or three partially over-lapping, spirally thickened tracheids appears in a central core of narrow cells in the swelling. One or two tiny strap-shaped leaves with a delicate midrib, marginal acicular hairs and simple and ctenoid laminar hairs arise, followed by a series of leaves like those of sexually produced and root proliferated sporophytes. The first leaf (and sometimes the second) appears before the roots. This is in contrast to the sexually produced sporophyte, in which the first root appears with or usually before the first leaf.

As in any obligate apogamous fern, the ameiotic apogamous cycle of *P. dispersum* allows dispersion and colonization without the necessity of fertilization. It is unique, however, in that the cycle has entirely the character of sexual reproduction with neither meiosis nor syngamy and the usual associated opportunities for genetic assortment and recombination. At the same time that meiosis and syngamy of the sexual cycle are missing, syndiploidy and meiosis of the meiotic apogamous cycle are also missing. The only way to inject changes into the genome of *P. dispersum* would be by random mutation and selection for or against this mutation. But any mutations selected would then be carried by all spores of the plant. Consequently, one might expect that this species would have a limited ecological and geographical potential. Yet this species is frequently collected and is widespread in the New World tropics (Fig. 9). Morphological variation from one individual to another is about as great as in most of its relatives. There is even one distinctive collection of numerous specimens (*Wright 1051*) with incised segments from Cuba, where the typical form is common. In spite of its seemingly limited genetic potential, its somatic life cycle has evidently been quite successful in adapting this species to its environment.

CYTOLOGY AND EVOLUTION

One of the major efforts in recent systematic studies of the *Filicineae* has been to subdivide the classical all-encompassing and undoubtedly polyphyletic family *Polypodiaceae*. Serious attempts at a more natural arrangement have led to such revisions as those of Bower (1923), Christensen (1938), Ching (1940), Dickason (1946), Copeland (1947), Holttum (1947, 1949), Alston (1956) and Pichi-Sermolli (1959). Within the *Polypodiaceae sensu stricto* there has been, at the same time, a subdivision of the classical genus *Polypodium* into presumably more natural genera. Today there is a general agreement as to the extent of the genus *Polypodium,* although Copeland (1947) segregated out *Goniophlebium* Presl, a step I do not think warranted on present evidence.

The *Polypodium pectinatum-plumula* group is more similar in certain gross appearances to *Ctenopteris* in the *Grammitidaceae* than to the rest of the genus *Polypodium* as a whole—so close, indeed, that Copeland (1956) placed *P. truncorum* in *Ctenopteris* and suggested that *P. pectinatum* and *P. plumula* might also belong there. Copeland's paper inspired critical studies of the sporangia (Wilson, 1959 a, b) and gametophytes (Stokey, 1959) of the latter two species. Table 1 lists character differences between this complex and the *Grammitidaceae.*

I believe that these families, based primarily on the differences in spores, sporangia, paleae, and gametophytes, should be maintained, although there still remain vexing problems as to their origin. There are, basically, two lines of thought—one that the *Grammitidaceae* arose from the *Polypodiaceae* (Pichi-Sermolli, 1959; Christensen, 1938), and the other that the *Grammitidaceae* arose independently from gleichenioid stock (Holttum, 1947, 1949; Stokey, 1951; Copeland, 1947). There are also dual propositions as to the origin of the *Polypodiaceae,*

Table 1. Comparison of the *Polypodium pectinatum-plumula* complex with the *Grammitidaceae*.[1]

P. pectinatum-plumula complex	*Grammitidaceae*
SPOROPHYTE:	
Rhizome	
Creeping, short-creeping, or erect	Short, ascending
Paleae non-clathrate (rarely sub-clathrate), entire or partially and inconspicuously papillate or fimbriate	Paleae clathrate or not, often conspicuously setose
Frond	
Stipe usually articulate	Stipe rarely articulate
Rachis always paleate (often inconspicuously)	Rachis never paleate
Short-spaced or approximate to fasciculate	Mostly fasciculate
Lamina usually with flexuous or stiff multicellular acicular hairs	Lamina usually with long, stiff, unicellular or multicellular setose hairs
Venation forked (rarely simple), free, or if anastomosing, then with free included veinlet	Venation simple (sometimes forked), free, or rarely anastomosing without included veinlet
Sporangial stalk with 2-3 columns of cells	Sporangial stalk with 1 column of cells
Spores bilateral, monolete, golden (without chlorophyll)	Spores tetrahedral, trilete, green (with chlorophyll)
GAMETOPHYTE:	
Cordate, with ventral rhizoids (rarely strap-shaped with marginal rhizoids)	Strap-shaped, with marginal rhizoids
Rhizoids appearing with first prothallial cell, or later	Rhizoids appearing after 10-15 prothallial cells have appeared
Plate early forming (after 1-2 months)	Plate late forming (after 2 months- 1 year)
Simple papillate hairs common	Simple papillate hairs uncommon
Branched hairs uncommon	Branched hairs common

[1]Compiled from personal observations and those of Copeland (1947, 1956), Stokey (1951, 1959), Stokey & Atkinson (1958), Wilson (1959 a, b),and de la Sota (1960).

one that they arose from dipteroid stock (Holttum, 1947, 1949; Pichi-Sermolli, 1959), the other that the *Polypodiaceae* also arose from gleichenioid stock (Copeland, 1947; Stokey, 1951). The origin of the *Grammitidaceae* from gleichenioid ancestors appears to have much support in actual resemblances, i.e. the trilete spores, free forked or simple venation, and the rather stiff pectinate blades. It has been argued that the *Polypodiaceae* arose from dipteroid stock through forms like

Dipteris, *Matonia*, and *Cheiropleuria*, which have complicated stelar anatomy and anastomosing venation. However, one can also read the opposite sequence from gleichenioid stock to the free-veined polypodia, perhaps much like the present members of the *P. pectinatum-plumula* complex. One of several difficulties in tracing evolutionary patterns in *Polypodium* is that of the free vs. anastomosing venation. Christensen (1928) builds a case for the origin of free venation in the

Table 2. Chromosome observations.

Taxa, with collection & location	Number
P. alfredii Rosenst.—Mexico, Oaxaca, Zacatepec, *Mickel 1613*; Costa Rica, Guanacaste Prov, *Evans 2890*.	$n=37$
P. bolivianum Rosenst.—Costa Rica, Alajuela Prov, *Evans 2921*, Puntarenas Prov, *Evans 3155, 3057-1*.	$n=37$
P. camptophyllarium Fée var. *camptophyllarium*—Jamaica, Portland Parish, *Evans 2404, 2405, 2406, 2407, 2408, 2409, 2410, 2413*, St. Andrew Parish, *Evans 2378*.	$n=74$
P. camptophyllarium Fée var. *lachniferum* (Heiron.) Evans—Jamaica, St. Andrew Parish, *Evans 2440*, St. Thomas Parish, *Evans 2637-13*.	$n=74$
P. dispersum Evans—Florida, Citrus Co, *Evans 2007, 2008, Wagner 62061*, Hillsborough Co, *Evans 1189, 2019;* Jamaica, Portland Parish, *Evans 2400, 2402, 2403, Proctor 22896*.	"$2n$"$=111$
P. ferrugineum Mart. & Gal.—Mexico, Nayarit, Ceboruco volcano, *Mickel 1374*.	$n=37$
P. hygrometricum Splitg.—Costa Rica, Puntarenas Prov, *Evans 2733*.	$n=37$
P. paradiseae Langsd. & Fisch.—Brazil, Rio Grande do Sul, São Leopoldo, *Sehnen s.n.*	$n=37$
P. pectinatum L. s.s.—Jamaica, Portland Parish, *Evans 2534-1*, Trelawny Parish, *Evans 2588;* Costa Rica, Alajuela Prov, *Evans 2984-1*.	$n=37$
P. plumula Humb. & Bonpl. ex Willd.—Florida, Hernando Co, *Wood, s.n.*, Hillsborough Co, *Evans 1186*, Sumter Co, *Evans 1190, 1192, 1193;* Jamaica, Portland Parish, *Evans 2398*.	$n=74$
P. ptilodon Kunze var. *caespitosum* (Jenm.) Evans—Florida, Dade Co, *Delchamps 6/14/60*, Hernando Co, *Evans 2015*, Highlands Co, *Evans 1158*, Hillsborough Co, *Evans 2018*, Sumter Co, *Evans 2002, 2003;* Jamaica, Portland Parish, *Evans 2411, 2412, 2414;* Mexico, San Luis Potosi, Xilitla, *Mickel 602*.	$n=74$
P. ptilodon Kunze var. *ptilodon*—Peru, Prov Bagua, Dept Amazonas, *Hutchison 1470*.	$n=37$
P. recurvatum Kaulf.—Brazil, Rio Grande do Sul, São Leopoldo, *Sehnen s.n.*	$n=37$
P. siccum Lindm.—Brazil, Rio Grande do Sul, São Leopoldo, *Sehnen s.n.*	$n=37$

P. vulgare group from the goniophlebioid venation. In the group under present study there are several species with partial to almost complete reticulation, species which are also pubescent, as are most of the truly goniophlebioid species. These reticulate venation patterns could be considered as either generalized or specialized character states, but are here treated as examples of a condition derived from free venation. The interpretation of this character is involved with the interpretation of the origin of the family, either from free-veined gleichenioid stock or anastomosing dipteroid stock. The answer is not immediately self-evident.

Cytology

Fourteen taxa were available for chromosome counts (Table 2). These are too few to be of application in interpreting the whole picture of speciation in the complex; however, all counts are useful. It was initially assumed that *Polypodium dispersum* was a hybrid between *P. plumula* and *P. ptilodon* var. *caespitosum*, but chromosome counts indicate that this is not likely. In the case of *P. ptilodon* var. *ptilodon* and var. *caespitosum*, a difference in their chromosome counts helps in interpreting them as at least separate varieties. *Polypodium ferrugineum* is quite similar to *P. cupreolepis*, except that the former has larger spores. It might have been considered a tetraploid derivative of *P. cupreolepis*, were it not known to be a diploid.

Table 3 indicates mean spore and guard cell lengths (based on 10 measurements per specimen and 3-10 specimens of each species or variety). Those cytologically known taxa have their ploidal level also indicated. On the assumption that spore and guard cell length are usually affected by polyploidy, this can give some indication of possible ploidal levels in certain of the species. Unfortunately, there are not enough cytologically known taxa to give real indications of such levels, but certain suggestions can be made. The taxa are here arranged in descending order of length of spores.

In this table there is some indication that those taxa with guard cell lengths of ca 45μ or greater, correlated with a spore length of 50μ or greater, may be polyploids. Conversely, those taxa with guard cells less than 40μ long, correlated with spore lengths of less than 47μ could be expected to be diploids. On this basis it is predicted that those taxa marked with an (*) are probable polyploids, and those marked with an (o) are expected diploids.

Divergence Index and Common Ground Plan

The relationships of the *P. pectinatum-plumula* complex are diagrammed in Fig. 16. This is a method for expressing evolutionary relationships developed by Wagner (1961, 1962), at the University of Michigan and used by such previous authors as Hardin (1957), Mickel (1962), and Scora (1964).

A list of as many characters as possible that show contrasting character states within the complex is first compiled. The generalized and the specialized state of each character is indicated. This is ascertained by noting the frequency and distribution of a certain character state. The assumption is that the more common the character state the more likely it is to be the generalized state. It is necessary

Table 3. Comparison of spore and guard cell size and chromosome number.

Taxon	Spore length in μ	Chromosome number	Guard cell length in μ
**P. absidatum*	59		66
**P. ptilodon* var. *robustum*	56		52
var. *caespitosum*	56	$n=74$	50
**P. camptophyllarium* var. *lachniferum*	54	$n=74$	57
var. *camptophyllarium*	54	$n=74$	52
P. pectinatiforme	52		39
**P. venturii*	50		65
P. filicula	50		41
°*P. ferrugineum*	50	$n=37$	40
°*P. alfredii*	50	$n=37$	37
**P. plumula*	50	$n=74$	34
P. sursumcurrens	49		38
P. ptilodon var. *pilosum*	47		44
°*P. hygrometricum*	47	$n=37$	39
°*P. pectinatum*	45	$n=37$	47
P. truncorum	45		41
°*P. siccum*	45	$n=37$	37
P. eurybasis var. *glabrescens*	44		44
var. *villosum*	44		43
P. curvans	44		43
P. camptophyllarium var. *macedoi*	44		43
P. bermudianum	43		43
°*P. bolivianum*	43	$n=37$	43
°*P. recurvatum*	43	$n=37$	39
P. dispersum	43	"$2n$"$=111$	38
P. camptophyllarium var. *abbreviatum*	43		43
°*P. paradiseae*	42	$n=37$	43
P. choquetangense	42		50
°*P. ptilodon* var. *ptilodon*	41	$n=37$	40
P. eurybasis var. *eurybasis*	40		50
P. consimile var. *consimile*	40		43
var. *pastazense*	40		40
°*P. cupreolepis*	36		31
°*P. atrum*	34		35
P. singeri	32		45

to test this assumption by taking into account related taxa or groups of taxa outside the one in question. In the analysis of a genus one must thus examine other closely related genera. In the present case, members of the genus *Polypodium* outside the complex were considered. In this way, it is possible to evaluate with strong probability a character state which appears frequently in a given group, but which may actually be a derived character state when taking the overall group into consideration.[2]

[2] The polished aspect of the rachis of the *P. pectinatum-plumula* complex is present throughout the group and might therefore be considered as generalized. However, this is

An initial list of characters, each showing paired character states, was selected. However, certain of these characters did not appear to have direct evolutionary significance; they had no obvious correlations. To simplify the diagram and reduce the information to the most definite characters and trends, these fluctuating characters were eliminated from the ground plan.

Each of the remaining 23 characters was then evaluated as to whether it is a generalized or specialized character state, the generalized state being given the value (0), and the derived state (1). This is based on the principle that, as we do not really know any actual quantitative value for a specific character, it is best to give them all equal values. In two characters—pinnatifid vs. crenate or entire segments, and comose hairs obscuring the rhizome paleae vs. comose hairs few or absent—however, I have given a value of 1.5 to these isolated and exaggerated expressions of an already specialized character state. Also, in evaluating the character of basal segments perpendicular to the rachis (0) or deflexed (1), I have added an intermediate level (0.5) for those cases which have a sporadic expression of the specialized state. Such situations could be avoided by establishing additional characters for these conditions, e.g. segments pinnatifid (1) versus segments crenate (0). But considering that the "ultra" specialized character state 1.5 in each case occurred in species obviously related to other species exhibiting the specialized character state 1, this seemed to be the clearest path to take. The same is true of the intermediate 0.5 state.

The total values of the character states for each entity are totaled, giving each a quantitative index showing its approximate divergence from the hypothetical ancestor, which had all the characters in the generalized state. This value then indicates at which level, i.e. on which semicircle on the divergence figure, the species will be placed. The position depends on the correlation of as many derived character states as possible from one species to another. Where it is necessary to cause a line to fork and there is no extant plant which "fits" this position, a "hypothetical ancestor," or "prototype" to those following it on the lines (indicated by open dots in Fig. 16) is inserted. This brings out an interesting point regarding the use of these "hypothetical ancestors" within a very closely related group of plants. Mickel (1962), in constructing a ground plan for the species of the genus *Anemia,* subgenus *Coptophyllum,* had to use 19 "hypothetical ancestors" in evaluating 41 taxa. Scora (1964) had to use 13 "hypothetical ancestors" in placing 22 taxa in the genus *Monarda.* Yet in the present study, in placing 35 species, only 8 were necessary. This may be due to the wider spread of morphological diversity that usually occurs in the species of a whole genus or subgenus, as compared to a single species complex within a genus. In the present study the species are

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not so elsewhere in *Polypodium* and is therefore considered a derived character state. In the same way, the *black* polished rachis is considered a derived character state, as it occurs with less frequency than the red-brown polished rachis. In the case of the polished versus non-polished rachis, this character is not used at all in the ground plan analysis because this character state is present throughout the group and therefore has no evolutionary significance within the complex, though it might well have significance in an evaluation of the whole genus or family.

recognized to be closely related, and therefore the divergence pattern reflects this closeness in that many species appear to be directly related in a linear or diverging series.

The following are the evaluations of the characters used in formulating the common ground plan:

A. *Rhizome:* Throughout most of the genus, as well as the family, the rhizome is long-creeping. In this complex several of the species of smaller stature, particularly those allied with *P. plumula,* have a more specialized, short-creeping, suberect or erect rhizome.

B.-C. *Rhizome Paleae:* The generalized shape of the paleae is narrow- or linear-triangular. However, in several of the species, e.g. *P. cupreolepis, P. alfredii, P. ferrugineum, P. sursumcurrens,* and *P. filicula,* the paleae are ovate or cordate (B). One of the specialized features of practically the whole complex is the comose rhizome paleae (C) (Fig. 1). Inconspicuously comose paleae also occur in several species not closely allied to this complex as judged by other characters, which have been excluded from the present treatment. There are a few of the included taxa allied with *P. plumula* which characteristically lack this comose condition. Since palear comosity is probably specialized, those species which have not developed it are considered generalized in this respect.

D. *Rachis Color:* The rachis is lustrous or polished, and though this is undoubtedly a specialized condition, it is a null character as far as divergence within the complex is concerned. However, there are essentially two color phases: red-brown in the *P. pectinatum* allies and either red-brown or black in the *P. plumula* allies. As stated above, the black condition is considered specialized.

E.-F. *Rachis Firmness:* Though most of the group have a stiff and erect rachis, as do most species of *Polypodium* in general, several members have specialized springy elastic rachises, readily recognizable on herbarium sheets (E). There are also two species, *P. curvans* and *P. choquetangense,* that show an additional specialization in the twisting or curling of the rachis under normal growth conditions (F). (This is not to be confused with the curling of the rachis and costa causing the frond to curl up under dry conditions.)

G. *Rachis Pubescense:* Although the whole group is characterized by a variety of types of rachis trichomes, and the rachises vary from nearly glabrous to pilose, *P. eurybasis* var. *villosum* has a striking densely-villose rachis distinguishing it from all other species.

H. *Ctenoid Hairs of the Rachis:* Although inconspicuous ctenoid hairs can probably be found on any species of *Polypodium,* at least on juvenile fronds, the species of the *P. pectinatum* group are noteworthy because of the numerous, large, conspicuous ctenoid hairs developed also on the mature rachis (Fig. 1, F). This is considered a specialized condition.

I. *Rachis Paleae* (Fig. 5): Though the rachis paleae vary considerably throughout *Polypodium,* in this complex and in those polypods most similar to those of this complex, the inconspicuous, long, thin, filiform type of palea is most frequent and therefore considered primitive. However, a number of species allied with *P. plumula* exhibit numerous hastate-triangular or cordate, conspicuous paleae on the rachis, which are probably specialized. They are either concolorous or have a dark margin and paler base (Fig. 1, H) and are thus different from the clathrate paleae with pale margins in the *P. squamatum* and *P. vulgare* groups.

J. *Frond Size:* Though there is considerable size variation in *Polypodium* (Fig. 3), there are a few species which are significantly reduced in size. These are represented here by *P. ferrugineum, P. filicula,* and *P. camptophyllarium* var. *abbreviatum,* which have fronds generally less than 25 cm long.

K. *Length of the Stipe:* Whereas the majority of the species of *Polypodium* have a well-defined stipe that is readily disguishable from the rachis, several species have the specialized condition of sessile or nearly sessile blades, as represented in the *P. pectinatum-plumula* group by *P. consimile, P. filicula,* and *P. ptilodon* var. *pilosum.*

L. *Blade Base:* The most general blade outline in *Polypodium* is elliptic-ovate, or linear with a cuneate or subtruncate base. However, several species, here represented by *P. bolivianum* and *P. recurvatum,* have a specialized, very abruptly truncate blade base (Fig. 3, G).

M. *Basal Segments:* Most polypodioid ferns have segments that are all essentially perpendicular to the rachis, and this is considered a generalized character. Certain species, however, show a distinctly different orientation at the base of the blade, with the basal segments becoming increasingly deflexed (Fig. 3). This usually creates an asymmetry at the segment base in which the upper edge meets the rachis at a broadly confluent angle, whereas the lower edge meets the rachis at a much sharper angle (see character 0). Species with basal segments irregularly deflexed are given an intermediate value of 0.5.

N. *Segment Orientation:* Pinnatifid polypodioid ferns commonly have either straight or slightly falcate segments which are essentially perpendicular to the rachis or slightly ascending (usually not more than 20° above the horizontal). The group of *P. absidatum, P. curvans,* and *P. choquetangense* have distinctly ascending segments exceeding ca 30° above the horizontal (Fig. 3, C).

O. *Segment Base Symmetry:* The segments of pinnatifid polypodioid ferns usually have an essentially symmetrical base, expanded and confluent on the rachis. In several species of this complex the lower edge of the segment meets the rachis at a right angle or may even be partially incised on the lower side, creating a semi-pinnate condition. This character has only been considered as specialized, however, when the segments are at right angles to the rachis (Fig. 3, A). When the segments are either ascending or deflexed this is automatically reflected in an asymmetry at the base.

P. *Segment Margin:* Whereas the majority of these species have the generalized condition of segments with entire margins, the species allied to *P. eurybasis* and the *P. curvans—P. choquetangense* line have crenate margins, as do *P. paradiseae* and *P. sursumcurrens* (Fig. 3, Fig. 6). In *P. choquetangense* (Fig. 6, T) the segments are deeply pinnatifid, and I have assigned this character state the "ultra" value of 1.5.

Q.-R. *Laminar Pubescense:* This refers only to the relatively conspicuous acicular, non-appressed hairs, since all members of this group have inconspicuous clavate hairs. The presence of a conspicuous pubescence is considered derived from the essentially glabrous condition (Q), and the presence of definite patterns of distribution of these hairs, as in the *P. ptilodon* group (Fig. 1, E), is considered an additional derived character state (R).

S. *Lateral Veinlets:* The great majority of polypodioid ferns have either anastomosing or free forked venation patterns. However, the specialized state of simple venation is present in this group in *P. truncorum, P. siccum,* and *P. filicula* (Fig. 6).

T. *Sorus Position:* In the free veined species of *Polypodium* the sorus is always terminal on the first acropetal veinlet and is usually medial between the costa and the laminar margin (Fig. 6). However, in several instances, the fertile veinlet typically extends almost to the margin, thus reflecting the condition of comparable veinlets in a sterile segment. In these instances the sori are then marginal or submarginal, and this is considered a derived character state.

U. *Receptacular Paraphyses:* In almost all taxa the receptacular paraphyses are composed of uniform cells and are similar to the clavate hairs of the lamina, though they are occasionally branched. They are universally present in this complex, and in most of the species examined in the rest of the genus and the family *Polypodiaceae,* and so it is believed that this simple paraphysis type is generalized. However, *P. sursumcurrens* exhibits an unusual paraphysis with an irregular subterminal multicellular clavate head (Fig. 4, P). As the head is composed of undifferentiated, though contorted, cells, it is considered to be derived not from reduced sporangia ("sporangiasters" as in *P. virginianum*), but from coalesced cells of a strongly twisted simple type of paraphysis. *Polypodium camptophyllarium* var. *macedoi* exhibits another distinctive paraphysis type; this is regularly forked, but one fork is tipped by a clavate cell, the other by a sharply setose cell (Fig. 4, M). The small appressed hairs of the lamina of this species are similar to the paraphyses.

V. *Spore Length:* While great length may be a simple morphological specialization by itself or reflect polyploidy, in either case it represents a divergence from the ground plan and is thus considered specialized.

W. *Number of Spores Per Sporangium:* In the higher ferns, 64 spores per sporanguim is a regular occurrence and has become a standard for indicating the normal sexual life cycle. Similarly, 32 spores per sporangium indicates an apogamous asexual reproduction, as is the case in *P. dispersum.* Apogamy is considered a specialized type of life cycle.

TAXONOMIC REVISION OF THE POLYPODIUM PECTINATUM-PLUMULA COMPLEX[3]

In treating this group of closely related species of *Polypodium,* there are no clear-cut limits in inclusion and exclusion. The species here included are circumscribed by the characters of blades with pectinate segments, essentially free veins, approximate to fasciculate fronds, rigid or elastic, lustrous, red-brown or black stipe and rachis, triangular and comose or cordate and non-comose, non-clathrate

[3] Until a broad and thorough examination of all the species-complexes in *Polypodium* are made, it seems wisest to withhold a formal subgeneric or sectional designation for this complex.

rhizome scales, 2-3 rowed sporangial stalks, and reniform spores. The species of closest superficial resemblance in *Grammitidaceae* are excluded on the basis of the sporangial stalk, spores, and other characters (see Table 1 above). Certain species of *Polypodium* have been excluded that might, in a wider treatment of the whole genus, be included here in the future. *Polypodium hartwegianum, P. chnoophorum, P. moritzianum,* and others have inconspicuously comose rhizome scales but have been excluded on the basis of the lack of the lustrous rachis, the different texture of the lamina, or the more crisped silvery laminar trichomes. I have, on the contrary, included *P. hygrometricum* and *P. recurvatum,* which perhaps are more properly placed with these excluded species. However, the latter two have been particularly confused with the included species both as to taxonomy and nomenclature. Future work should be directed at delimiting the different groups (possibly as subgenera) within *Polypodium sensu stricto* so that all the species can eventually be grouped and treated systematically.

The measurements of rhizomes, fronds, blades, and segments include a mean size bracketed by an expected maximum and minimum limit. These were compiled by measuring ten random specimens of each recognized entity. "Ctenoid hairs" refer to small, appressed, multiple-branched hairs with all the branches arising from one side of the main axis (Fig. 1, F & Fig. 4, I). "Comose" rhizome paleae refer to those with tufts of unicellular hairs arising from the dorsal surface (Fig. 1). The costa is "decurrent on the rachis" when it joins the rachis in a downward arc to form a short wing along the rachis and a visible curvature of the costa. When the costa meets the rachis at a right angle, there is also a slight expansion on the rachis but no visible curvature of the costa. In defining plane shapes (e.g. fronds, segments, scales), I have attempted to follow the Systematics Association, Descriptive Terminology, Chart 1 (Taxon **11:** 145-156, 1962), with the addition of the term "cordate," as it so usefully applies to the overall shape of many paleae (Fig. 5). All observations have been made from mature fertile fronds, and all characters of rachis, costa and lamina, unless otherwise noted, refer to the abaxial surface only.

The colors of the paleae, rachis, and costa are treated as black or one of the following three shades of red-brown. Because there is no satisfactory equivalent for the intermediate color, I have used the terms "light red-brown" (ferrugineous), "red-brown", and "dark red-brown" (castaneous).

As a result of the close morphological similarity of many of these species, it has been necessary to rely heavily on what may appear to be quite minute and technical characters. In evaluating the shape or comosity of paleae, or the size, shape, and distribution of hairs, it has often been necessary to use optical magnifications beyond the hand lens and up to 20 to 30× or more.

The laminar trichomes consist basically of two types. One is the appressed, clavate, simple, forked, or ctenoid hair. These are rarely over 250μ long and would be generally overlooked in routine identifications, except when they are conspicuous on the stipe base in the larger members of the *P. pectinatum* group. The second are conspicuous, acicular, simple hairs from 0.25 mm to 2.0 mm long. These constitute the generally visible pubescence of the frond. However, in the descriptions both the conspicuous acicular hairs and the inconspicuous clavate hairs are referred to. Because the clavate hairs would often be overlooked, certain species may appear superficially glabrous, when in fact small clavate hairs are undoubtedly present. In these cases, the description may refer to the lamina as "essentially glabrous."

Where the soral size is important, it is indicated by the approximate portion of the width of the segment that two sori occupy, e.g. "occupying half the width of the segment." Only the mature sori are referred to in this measurement.

KEY TO THE SPECIES OF THE POLYPODIUM PECTINATUM-PLUMULA COMPLEX

1. Rachis paleae relatively conspicuous, persistent, other than filiform; rachis brown or black.
    2. Rhizome paleae cordate with acute apex, non-comose; rachis red-brown or black with lateral brown stripes; rachis paleae narrow-elliptic or cordate with acute apex, entire; sporangia with or without setae.
        3. Rachis paleae narrow-elliptic, few and sometimes inconspicuous, flat; basal segments of the blade strongly reflexed; sporangia without setae; rachis red-brown or black with lateral brown stripes ....5. *P. alfredii*
        3. Rachis paleae cordate, numerous and conspicuous, bullate or flat; all segments perpendicular to the rachis, with symmetrical bases; sporangia with or without setae; rachis red-brown.
            4. Rhizome paleae light golden color; rachis red-brown but costa black or darker brown than the rachis; sporangia with 2 long setae ....6. *P. ferrugineum*
            4. Rhizome paleae red-brown; rachis and costa both red-brown; sporangia naked ....4. *P. cupreolepis*
    2. Rhizome paleae narrow-triangular with acuminate apex, comose; rachis red-brown or black without lateral stripes; rachis paleae cordate, or narrow-triangular with acuminate apex and hastate base, inconspicuously toothed or fimbriate; sporangia always setose, sometimes inconspicuously so.
        5. Fronds 10 (6-17) cm long; rachis paleae cordate, dark brown with dark base, inconspicuously toothed; veins unforked ....10. *P. filicula*
        5. Fronds 15-65 cm long; rachis paleae cordate or narrow-triangular and hastate, dark red-brown, lighter at the base, fimbriate; veins 1-2-forked.
            6. Fronds narrow-ovate or linear; segments linear, the basal segments shorter, not deflexed, reduced to mere auricles; veins 1-forked ....9. *P. plumula*
            6. Fronds narrow-ovate; segments narrow-ovate, the basal segments shorter, deflexed, sometimes reduced to auricles; veins 2-forked.
                7. Rachis and costa brown; Bermuda ....8. *P. bermudianum*
                7. Rachis and costa black; not from Bermuda.
                    8. Rachis paleae subulate with hastate base; lower segments only slightly shortened, strongly deflexed; 64 reniform spores per sporangium; Central America ....12. *P. atrum*
                    8. Rachis paleae narrow- to linear-triangular with hastate base; lower segments sometimes reduced to auricles, slightly deflexed; 32 globose spores per sporangium; wide-ranging ....11. *P. dispersum*
1. Rachis paleae absent, or if present then filiform and inconspicuous; rachis brown.
    9. Basal segments one half as long as the longest segments or more.
        10. Fronds mostly less than 40 cm long; veins 1-forked ....26. *P. hygrometricum*
        10. Fronds mostly more than 40 cm long; veins 2- or 3-forked.
            11. Segments acuminate, gray-green, puberulent with short silvery hairs ....25. *P. recurvatum*
            11. Segments acute to obtuse, green, glabrous ....16. *P. bolivianum*

9. Basal segments less than half as long as the longest segments, often reduced to wings, lobes or auricles.
    12. Veins simple; rhizome paleae glabrous.
        13. Segments ascending 15°-25° above the horizontal; segments 3.5 (2.5-4.5) mm wide; rhizome paleae brown to dark brown ....1. *P. truncorum*
        13. Segments perpendicular to the rachis or only slightly ascending; segments 1-2 mm wide; rhizome paleae light red-brown ....2. *P. siccum*
    12. Veins 1-4-forked; rhizome paleae comose (except in *P. sursumcurrens*).
        14. Segments strongly ascending 25°-50° above the horizontal, crenulate to pinnatifid.
            15. Segments pinnatifid almost to the costa ....15. *P. choquetangense*
            15. Segments merely crenulate or crenate.
                16. Blades herbaceous; segments 2(1.5-3) mm wide; hairs of the rachis ca 1 mm long; apex of the blade usually circinate even at maturity ....14. *P. curvans*
                16. Blades coriaceous to herbaceous; segments 3.5(2-4.5) mm wide; hairs of the rachis ca 0.5 mm long; apex of the blade usually straight at maturity ....13. *P. absidatum*
        14. Segments perpendicular to the rachis or only slightly ascending, entire to crenulate.
            17. Lamina pilose only in an oblong patch around the sorus, otherwise glabrous or with only scattered acicular hairs (then these much denser around the sorus); basal segments gradually reduced to mere wings or lobes ....23. *P. ptilodon*
            17. Lamina glabrous or with an even distribution of pubescence; segments at the blade base various.
                18. Lamina essentially glabrous beneath (acicular hairs absent or only scattered, inconspicuous clavate hairs present); veins free throughout.
                    19. Lower edge of the segments perpendicular to the rachis, at least in the lower half of the blade; veins 1-forked.
                        20. Spaces between segments 2-3 times the width of the segments; clavate hairs on the lamina numerous, short, blackish; sori submarginal to nearly marginal; receptacular paraphyses twisted and with a subterminal clavate multicellular head; eastern Mexico ....7. *P. sursumcurrens*
                        20. Spaces between segments equal to or narrower than the segments; clavate hairs on the lamina few, golden and inconspicuous; sori medial to submarginal; receptacular paraphyses simple and straight.
                            21. Rachis 2-3.5 times as long as the stipe; fronds 28-130 cm long; blade 4-26 cm wide ....17. *P. eurybasis*
                            21. Rachis 4-14 times as long as the stipe; fronds 19-55 cm long; blade 3-7 cm wide.
                                22. Rachis paleae linear; sori medial; rhizome paleae narrow-triangular, red-brown; northern Argentina and southern Brazil ....3. *P. singeri*
                                22. Rachis paleae narrow-elliptic; sori medial to submarginal; rhizome paleae ovate to cordate, brown; Mexico and Central America ......5. *P. alfredii*
                    19. Upper and lower edge of the segments similar, equally expanded and adnate on the rachis; veins 2-forked.
                        23. Rachis 13 (6-20) times as long as the stipe; segments reduced at blade base to obtuse or rounded lobes, entire ....24. *P. consimile*
                        23. Rachis 2-5 times as long as the stipe; segments reduced at the blade base but not to mere lobes, narrow-triangular, acute at the apex, crenulate or crenate ....17. *P. eurybasis*

18. Lamina pilose with acicular hairs (inconspicuous clavate hairs also present); veins free or partially anastomosing.
    24. Lamina thinly pilose with long, conspicuous, blackish, clavate hairs; acicular hairs absent; sori submarginal or nearly marginal; veins 1-forked, free; rhizome paleae ovate, red-brown with dark brown base ....7. *P. sursumcurrens*
    24. Lamina pilose with pale or golden and acicular hairs; sori medial to nearly marginal; veins 1- or 2-forked, free or partially anastomosing; rhizome paleae narrow- or linear-triangular, red-brown, lighter at the base.
        25. Costa meeting the rachis at a perpendicular angle; veins free throughout; basal segments strongly deflexed; plants of Paraguay, Argentina, and southern Brazil.
            26. Fronds less than 65 cm long; veins 1(2)-forked; sori supramedial; segments entire or occasionally crenulate ....20. *P. pectinatiforme*
            26. Fronds over 70 cm long; veins 2- or 3-forked; sori submarginal; segments crenate ....21. *P. paradiseae*
        25. Costa curved downward and decurrent on the rachis; veins free or partially anastomosing; basal segments various; wide-ranging.
            27. Fronds less than 30 cm long; veins 1-forked, free throughout ....22d. *P. camptophyllarium* var. *abbreviatum*
            27. Fronds more than 30 cm long; veins 2(1)-forked, free or partially anastomosing.
                28. Lamina chartaceous-herbaceous, soft; veins rarely anastomosing; sporangia without setae; Peru and northern Argentina ....19. *P. venturii*
                28. Lamina herbaceous-coriaceous, firm; veins always at least partially anastomosing; sporangia setose; wide-ranging.
                    29. Lamina puberulent with hairs usually much shorter than 0.2 mm long; sporangial setae ca 65μ long; segments usually abruptly reduced to 2 or 3 pairs of lobes at the blade base, perpendicular to the rachis throughout, the basal lobes expanded and symmetrical at the base ....18. *P. pectinatum*
                    29. Lamina pubescent with hairs 0.35 to 0.5 mm long; sporangial setae more than 100μ long; segments reduced to lobes, or reduced, deflexed and abruptly terminated, the basal segments subsymmetrical at the base or with the lower edge perpendicular to the rachis ....22. *P. camptophyllarium*

1. *Polypodium truncorum* Lindm., Hedwigia **43:** 309, 1904.

P. elasticum Rich. var. *glaziovii* Baker in Mart., Fl. Bras. **1**(2):517, *t. 64, fig.* 2., 1870. (Syntypes: Brazil: Santa Catarina, *Muller s.n.* not seen; Rio de Janeiro, *Glaziou 1723, 2461* not seen; Minas Gerais, Caldas, *Regnell II 319** MO)

P. bakeri Lindm., Ark. Bot. **1:** 240, *t. 11, fig. 9,* 1903, non Luerss., 1882. (Lectotype: Brazil, Minas Gerais, Caldas, Pedra Branca, *Regnell II 319**a S; isolectotype S-PA)

Ctenopteris glaziovii sensu Copel., Phil. Jour. Sci. **84:** 416, 1956, p.p., not as to type.

C. truncorum (Lindm.) Copel., loc. cit. 450.

Rhizomes very short-creeping or erect, 1.5 (1-2) mm in diam; rhizome paleae narrow-triangular, brown to dark brown, lustrous, basifixed, non-comose, non-clathrate, the margins entire; *fronds* 25 (8-42) cm long, caespitose on the rhizome; rachis 9 (6-20) times as long as the stipe; stipe and rachis red-brown, with scattered whitish or golden acicular hairs, ctenoid hairs absent; rachis paleae inconspicuous or absent, if present then linear to short-filiform, entire; *blades* narrow- to linear-ovate or -obovate, 23 (7-38) cm long, 3.5 (2.5-4.5) cm wide, subtruncate to cuneate at the base; segments 19 (13-23) mm long, 3.5 (2.5-4.5) mm wide, narrow-triangular, acute, expanded and symmetrical at the base, chartaceous to membranaceous, slightly toothed, ascending ca 65°-75° from the rachis, slightly reduced but not deflexed at the blade base, the basal pair usually reduced to auricles, or occasionally blades gradually reduced to a cuneate base; lamina essentially glabrous except for a few long, clavate hairs; costae perpendicular to or slightly ascending on the rachis, with few long acicular hairs; veins simple, free; guard cells ca 41μ long; sori medial to extramedial, round, with long simple clavate paraphyses; *sporangia* without setae; spores globose-reniform, smooth, ca 45μ long.

Type: Based on *P. bakeri* Lindm., 1903, not Luerss., 1882. Regnell's numbering system was complex; *II 319a, II 319*, II 319*c* and *II 319*d* have been examined and they represent other species, the two last named numbers being *P. singeri.*

Habitat: epiphytic, mostly on tree-fern trunks, occasionally terrestrial, in wet forests, 500-1800 m alt.

Distribution: southern Brazil and northern Argentina.—Fig. 11.

BRAZIL: MINAS GERAIS: Canjerana, *Regnell II 319** p.p. (MO, non US); Caldas, *Regnell II 319*b* (S-PA); Carangola, N of Serra da Grama, *Mexia 4272* (GH); Viçosa, Fazenda de Aguada, *Mexia 5105* (GH). RIO DE JANEIRO: Tijuca, *Dusén 5022* (MO); nr Rio de Janeiro & Bahia, *Webb s.n.*, in 1867-1868 (MICH). SAO PAULO: Alto da Serra, Estação Biologica, *Smith 1844* (MICH); Campos do Jordão, *Leite 3562* (GH, MO); Serra da Bocaina, *Brade 20799* (MO), *20801* (MO); Serra da Cantareira, *Eiten & de la Sota 2170* (US). PARANA: Serra do Mar, Ypiranga, *Dusén 3651* (GH, MO); Desiro Ypiranga, *Dusén 6776* (MO). SANTA CATARINA: Ararangua, Serra da Pedra, *Reitz C271* (US); Azambuja, Brusque, *Reitz 1795* (US), *Smith & Reitz 6136* (GH, MO); Brusque, Mata Hoffmann, *Reitz 3071* (US); Ibirama, Horto Florestal, *Smith & Klein 7554* (US); Itacorobi, Santa Catarina I, *Rohr 320* (US); Luis Alves, Itajai, *Reitz 159* (US). RIO GRANDE DO SUL: São Leopoldo, *Reitz 1314* (US).

ARGENTINA: MISIONES: Yerbal Viejo, *Burkart 1584* (GH); Cainguás, Qae Mayo, *Montes 27.218* (US).

I have not seen the type of *P. glaziovii* Bak. (*Glaziou 9062*, presumably at BM or P), which I believe to be a *Ctenopteris*. Copeland (1956) transferred *P. glaziovii* Bak. to *Ctenopteris*, using Baker's original description and citing the type specimen, but in a way indicating that he had not seen it. He then stated, "I find the veins simple; the spores tetrahedral, the stipes glabrescent," and cited eight collections. I have examined five of these collections. The spores of these are not tetrahedral. The veins are simple, as Copeland stated, but this alone is insufficient for separation of *Ctenopteris* and *Polypodium* in all cases. The stipes are glabrescent, but with polypodioid articulate hairs and not ctenopteroid unicellular setiform hairs. These five sheets are all *P. truncorum*. It is evident thus that Copeland had a confused concept of his *Ctenopteris glaziovii* (Baker) Copel.; the type may be a true

Ctenopteris, but at least five of the collections cited by Copeland belong to *Polypodium*.

This species is very similar to *P. siccum*, from which it can be distinguished by the very small rhizome with crowded stipes, the dark chestnut rhizome scales, membranous frond texture, and the narrow ascending segments with the basal pair reduced to mere auricles and the next pair only slightly reduced. That it is a true *Polypodium* and not a *Ctenopteris* was shown by de la Sota (1963).

2. *Polypodium siccum* Lindm., Ark. Bot. **1**: 234, *t. 11, fig. 4,* 1903.

P. heteroclitum Fée, Crypt. Vasc. Bras. **1**: 93, *t. 26, fig. 4,* 1869, non Desv., 1811 (Type: Brazil, Rio de Janeiro, *Glaziou 2410* BR, C, P)

Rhizomes short-creeping to erect, 2 (1-3) mm in diam; rhizome paleae narrow-triangular, light red-brown, basifixed, non-comose, non-clathrate, entire; *fronds* 27 (10-50) cm long, caespitose on the rhizome; rachis 8 (4.5-11) times as long as the stipe; stipe and rachis red-brown, pilose with long acicular simple hairs, and also with long clavate hairs, ctenoid hairs absent; rachis paleae inconspicuous or absent, if present then linear to filiform, light red-brown, entire; *blades* linear to narrow-ovate, 23 (8-36) cm long, 3 (2-5) cm wide, cuneate to narrow-cuneate, occasionally subtruncate at the base; segments 15 (9-22) mm long, 1.5 (1-2) mm wide, perpendicular to the rachis, reduced to a narrow wing at the blade base, linear-triangular, chartaceous to herbaceous, acute, slightly toothed, expanded and symmetrical at the base, or with the lower edge perpendicular to the rachis in the lower part of the blade, the sinuses approximately equal to the width of the segment; lamina with numerous long golden clavate hairs; costa decurrent on the rachis, with scattered long acicular hairs; veins simple, free; guard cells ca 37μ long; sori submarginal, round, with simple clavate paraphyses, ca 0.3 mm long; *sporangia* without paraphyses; spores globose-reniform, smooth, ca 45μ long; $n=37$.

Lectotype: Brazil, Rio de Janeiro, *Glaziou* 3339 S; isolectotypes BR, C, S-PA. Syntypes: Brazil, Cañoas, Rio Grande do Sul, *Regnell I A391* G, GH, NY, S, S-PA, US; Brazil, Hamberger Berg, Rio Grande do Sul, *Regnell I A501* S, S-PA; Paraguay, Cordillera of Villa Rica, *Balansa* 667 B, BR, G, S-PA.

Habitat: epiphytic, often on tree ferns, in forests, 450-1200 m alt.

Distribution: southeastern Brazil, Paraguay and northern Argentina.—Fig. 10.

BRAZIL: RIO DE JANEIRO: Novo Friburgo, *Dusén 1899* (US), *Leite 4104* (MO); Rio de Janeiro & Teresópolis, *Clarke s.n.* (US); Santo Antonio, Serro dos Orgãos, *Brade 16317* (MO). SAO PAULO: Iguape, Rio Peronpaua, *Brade 7737* (US); Morro das Pedras, *Brade s.n.*, in 1918 (US). PARANÁ: Lapa, *Braga 1041* (US); Serra do Mar, Ypiranga, *Dusén 14433* (GH, MO); Villa Velha, *Dusén 14813* (US); Volta Grande, *Dusén 14141* (US). SANTA CATARINA: Mun. Curitibanos & Campos Novos, *Smith & Klein 8287* (US); Joinville, *Schmalz 59VIII* (MO); Lages, *Spannagel 67* (US); Mun. Pôrto União, *Smith & Reitz 8672* (US). RIO GRANDE DO SUL: Cañoas, *Regnell IA391* (G, GH, NY, S, S-PA, US); Neu-Wurstemberg, *Bornmüller 120* (GH); São Leopoldo, *Anchieta 2664* (US), Chacara Meyer, *Reitz 161* (US); *Regnell IA501* (S, S-PA).

PARAGUAY: E of the Vilarica Mts, *Balansa 667* (B, BR, G, S-PA).

ARGENTINA: CORRIENTES: General Paz, Paraje Angostura, *Ibarrola 3819* (MO); Mburucuyá, Santa Teresa, *Petersen 1758* (MO, US). MISIONES: Loreto, *Burkart 1551* (GH); Posadas, Bonpland, *Ekman 66* (MO).

This species is best recognized by its long, linear, delicate blades, submarginal sori, and bright ferruginous rhizome paleae. Within its range, the only similar species is *P. truncorum,* which has, however, much wider segments and darker paleae. *Polypodium siccum* (like *P. truncorum*) strongly resembles the ctenopteroid ferns, but in the critical characters of spores, sporangial stalks, and paleae, it is properly placed in *Polypodium.*

One specimen indicates that this species reproduces in part by root proliferations, though apparently not so commonly as in *P. dispersum* or *P. filicula.*

3. *Polypodium singeri* de la Sota, Opera Lilloana **5**: 181, 1960.

P. pectinatum L. var. *aurita* Rosenst., Hedwigia **46**: 138, 1906, non *P. auritum* Lowe, 1858. (Holotype: Brazil, Lages, *Spannagel 116a* S-PA)

P. pectinatiforme Lindm., loc. cit. **43**: 309, 1904, p.p., not as to lectotype.

Rhizomes short-creeping, 3 (2-4) mm in diam; rhizome paleae narrow-triangular, red-brown, lustrous, basifixed, acuminate, non-comose, non-clathrate, entire; *fronds* 25 (19-30) cm long, caespitose; rachis 6 (3-8) times as long as the stipe; stipe and rachis red-brown, with scattered golden, acicular hairs, ctenoid hairs absent; rachis paleae inconspicuous, red-brown, linear, entire; *blades* narrow-ovate, 22 (15-27) cm long, 4.3 (3-6) cm wide, cuneate at the base; segments 22 (15-25) mm long, 3 (2.5-3.5) mm wide, perpendicular to the rachis, strongly deflexed at the blade base or reduced to auricles, linear-ovate, obtuse at the apex, asymmetrical at the base with the upper edge widely adnate on the rachis and the lower edge perpendicular to the rachis or incised, occasionally auriculate, chartaceous, entire, the sinuses equal to or narrower than the segments; lamina essentially glabrous except for scattered clavate, simple hairs; costa perpendicular to the rachis, with scattered, golden, acicular hairs; veins simple or once-forked, free; sori medial, round, with simple clavate paraphyses; *sporangia* without setae or with one capsular seta ca 115μ long; spores reniform, slightly tuberculate, ca 32μ long.

Holotype: Argentina, Misiones, San Ignacio, Loreto, 2 Febr 1958, *Cristóbal, Ahumada,* & *de la Sota* 53 LIL, not seen; isotypes BR, S, US.

Habitat: epiphytic on very small tree stems and tree-fern trunks, occasionally terrestrial, in humid forest, 700-1200 m alt.

Distribution: southeastern Brazil to northern Argentina.—Fig. 8.

BRAZIL: MINAS GERAIS: Caldas, *Regnell II 319** p.p. (US, non MO), *II 319*c* (S), *II 319*d* (S); Passa-quatro, *Brade 19006* (MO). SAO PAULO: Campinas, *Heiner 504* (S), *616* (S-PA). PARANA: Jaguariahyva, *Dusén 14880* (GH, MO); Rio Negro, *Annies* (Rosenstock 113) (US); Villa Nova, *Annies* (Rosenstock 113) (S, S-PA, US); *Vierdel 1** (S-PA). SANTA CATARINA: São Carlos, Chapeco, *Reitz 3769* (US). RIO GRANDE DO SUL: Silveira Martins, Santa Maria, *Pivetta 158* (US); Serra Leitão, *Jürgens 105* (S); Santa Cruz, *Jürgens s.n.* (Rosenstock 113) (US), (Rosenstock 113a) (S-PA); *Regnell 750* (S).

ARGENTINA: MISIONES: Candelaria, La Pastora, *Montes 2340* (MO); Loreto, *Moreau s.n.,* 27 July 1931 (GH); San Ignacio, *Montes 2249* (GH); Posados, Bonpland, *Lilliesköld s.n.* (S), *Ekman 67* (S, S-PA), *81* (S).

This species has a curious habit due to its vegetative reproduction by root proliferation. It is usually found growing on small upright twigs as a series of short interconnected rhizomes. The whole appears as a layer of roots surrounding small stems with a series of short rhizomes imbedded in the root mass. The species is well characterized by this curious serial arrangement of rhizome, the conspicuously asymmetrical and glabrous segments, the small size of the frond, and the non-comose rhizome scales. It is apparently closely related to *P. alfredii* of Central America, although well separated by the broader blade, more asymmetrical segments, and the longer rachis paleae.

Within this species there appear to be two variations. One form has the segments with smooth entire margins and the sporangia generally without setae, while the other tends to have slightly undulate margins and one seta on most of the capsules. The plants are alike in all other respects, however, so that unless careful population studies in the future indicate otherwise, I believe them to be taxonomically inconsequential. Rosenstock based his *P. pectinatum* var. *aurita* on a leaf form with narrow excurrent auricles on the lower edge of the segment.

4. *Polypodium* **cupreolepis** A. M. Evans, sp. nov.—Fig. 17.

Rhizoma breviter repens, paleis ovatis vel cordatis, pallide vel fusco-brunneis, non comosis, integris, basi affixis, apice acutis, cellulis non clathratis; frondes approximatae articulatae, ca 30 cm longae; stipites et rhachides rigidae nitentes brunneae, pilose dissitos ferentes; paleae rhachidis numerosae consipcuae cordatae, aureae vel ferrugineae, integrae, apice acutae; lamina pectinata anguste ovata, ca 22 cm longa et 4 cm lata, basi abrupte cuneata vel subtruncata; segmenta linearia integra, rhachide perpendicularia vel interdum basalia paullo deflexa; lamina solum cum pilis inconspicuis clavatis; venae liberae, 1-furcatae; sporangia sine setis; sporae late reniformes laeves, ca 36μ longae.

Rhizomes short-creeping 4.5 (3-7) mm in diam; rhizome paleae ovate to cordate, pale to dark brown, non-lustrous, basifixed or basally cordate, acute, non-comose or rarely inconspicuously comose, entire; *fronds* 30 (10-60) cm long, approximate on the rhizome; rachis 3 (1.5-5) times as long as the stipe; stipe and rachis brown, with long, scattered, acicular hairs; rachis paleae numerous, conspicuous; broadly cordate, bullate, acute, basifixed, golden to light red-brown, non-lustrous, entire; *blades* narrow-ovate, 22 (9-47) cm long, 4 (2.5-6.5) cm wide, abruptly cuneate to subtruncate at the base; segments 20 (12-32) mm long, 2.5 (1.5-3) mm wide, perpendicular to the rachis, or occasionally slightly ascending in the upper part of the blade, strongly reduced and sometimes deflexed at the blade base, herbaceous, obtuse to acute at the apex, subsymmetrical at the base or the lower edge perpendicular to the rachis, entire; lamina essentially glabrous, but with inconspicuous clavate hairs; costa decurrent on the rachis, with scattered acicular hairs; veins once-forked, free; guard cells ca 31μ long; sori medial, round, with numerous, long, clavate paraphyses; *sporangia* without setae; spores broadly reniform, smooth, ca 36μ long.

Holotype: Mexico, Michoacán, hills of Patzcuaro, 8 Nov 1890, *Pringle* 3353 US; isotypes, B, GH, MICH, MO, US.

Habitat: epiphytic or epipetric, occasionally terrestrial, in montane forests, 1100-2900 m alt.

Distribution: western and southern Mexico to Costa Rica.—Fig. 10.

MEXICO: SINALOA: betw Durango & Villa Unión, *Ownbey 1939* (US); Ocurahui, Sierra Surutato, *Gentry 6337* (GH, MO). DURANGO: 22 mi E of Santa Lucía, rd from Villa Unión to Durango, *Reeder 2487* (US). JALISCO: 15 mi SSE of Autlán, *Wilbur 1927* (US); below Canoa de Leoncito, *McVaugh 13486* (US); Santa Mónica, *McVaugh 14042* (US); 7 mi SSW of Tecalitlán, *McVaugh 16254* (US). HIDALGO: Trinidad, *Pringle 13475* (US). PUEBLA: Ixtaccihuatl, *Purpus 1828* (GH, MO, US). MORELOS: Valle del Tepeite, *Lyonnet 779* (MO). DISTRITO FEDERAL: Eslava, *Lyonnet 3315* (US), *3316* (US). MICHOACÁN: Morelia, Campanario, *Arsène 8464* (GH, MO, US); Cerro Azul, nr Morelia, *Arsène*, 3 May 1910 (GH); Tancitaro, Uruapán, *Hinton et al. 15478* (GH, MO, US); Tancitaro, *Leavenworth 336* (GH), *516a* (GH), Mt San Miguel, *Leavenworth & Hoogstraal 1097* (MO); Zitácuaro, Zitácuaro-Cacique, *Hinton 13178* (GH, MO, US). COLIMA: Volcán Colima, *Goldsmith 40* (GH); Revillagigedo Islands, Socorro I, *Mason 1633* (GH). GUERRERO: Omilteme, *Rowell 3049A* (US); 2 mi W of Omilteme, *Hamilton & Rowell 3245* (US). OAXACA: Totontepec, *Nelson 796* (US). CHIAPAS: Pico de Loro, nr Escuintla, *Matuda 4268* (GH).

GUATEMALA: ALTA VERAPAZ: Cobán, von *Tuerckheim 645* (US). QUEZALTENANGO: Cerro Quemado, *Kellerman 5940* (US). CHIMALTENANGO: Las Calderas, *Standley 60040* (US). ESCUINTLA: Volcán de Fuego, *Salvin s.n.* (GH).

EL SALVADOR: SANTA ANA: NE of Cerro del Aguila, *Tucker 1249* (US). SAN VICENTE: Volcán de San Vicente, *Standley 21609* (US).

NICARAGUA: JINOTEGA: Jinotega, *Howard 79* (US).

COSTA RICA: SAN JOSÉ: Las Nubes, *Scamman 7228* (GH).

This species has generally been identified as "*P. pulchrum*," the type of which has, however, a black rachis and costa, triangular, lustrous, red-brown rhizome scales, setose sporangia, and somewhat different rachis scales. I consider *P. pulchrum* a synonym of *P. plumula* Humb. & Bonpl. *Polypodium ferrugineum* Mart. & Gal., a smaller plant with two setae per sporangium, a black costa, a brown rachis, and much paler golden-tan rhizome scales, appears to be its nearest relative.

The isotype at Berlin has been annotated by Hieronymus as "*P. patzcuarense*," which seems to be an unpublished name.

5. *Polypodium alfredii* Rosenst., Repert. Sp. Nov. **22**: 15, 1925.

P. alfredii var. *curtii* Rosenst., loc. cit. (Holotype: Costa Rica, region of Río Chris, nr Juan Vinas, 1200 m, *Brade 695* S-PA; isotype US)

P. tablazianum Rosenst., loc. cit. 14. (Lectotype: Costa Rica, Tablazo, 1800 m, 4 Mar. 1908, *Brade & Brade 14* S-PA. Syntypes: Costa Rica, Tablazo, 1900 m, 20 July 1909, *Brade & Brade* 696 NY; Costa Rica, Carpintera, 1500 m, 14 Dec 1909, *Brade & Brade 149* NY, S-PA, US)

P. cyathicola Copel., Univ. Calif. Publ. Bot. **19**: 292, *t. 43*, 1941. (Holotype: Mexico, Veracruz, Cuantlancillo (Orizaba) alt 1600 m, on *Cyathea* in wet ravine, 1 Mar 1938, *Copeland, Mex. Ferns 127* MICH; isotype US)

Rhizomes short-creeping, 4 (3-5) mm in diam; rhizome paleae brown, non-lustrous, ovate to cordate, acute to rounded, basifixed, entire or rarely irregularly fimbriate toward the apex; *fronds* 36 (20-55) cm long, fasciculate on the rhizome; rachis 7.5 (4-14) times as long as the stipe; stipe and rachis red-brown, or black with lateral brown stripes, with scattered, long, acicular hairs, ctenoid hairs absent or few and inconspicuous; rachis paleae brown, non-lustrous, acute, basifixed, entire; bullate-cordate to narrow-ovate and conspicuous, or narrow-ovate to narrow-obovate, inconspicuous and scattered, *blades* 31 (20-50) cm long, 4.8 (3.3-7) cm wide, narrowly oblong, cuneate at the base or subtruncate with the lower segments strongly deflexed, sometimes parallel to the stipe; segments linear-triangular to linear, acute, 25 (15-35) mm long, 3 (2-3.5) mm wide, symmetrical at the base in the upper half of the frond, the lower edge perpendicular to the rachis or deflexed in the lower half of the frond, ciliate, entire; lamina chartaceous, with scattered, short, clavate hairs; costa brown, occasionally darker than the rachis, with scattered, long, acicular hairs, slightly decurrent on, or perpendicular to, the rachis; veins once-forked, free; guard cells ca 35μ long; sori submarginal to extramedial, round, with numerous long, clavate paraphyses; *sporangia* without setae; spores reniform, smooth, ca 49μ long; $n = 37$.

Holotype: Costa Rica, Turrialba, 650 m, 5 Aug 1909, *Brade & Brade 697* S-PA; isotype US.

Habitat: epipetric or epiphytic on tree trunks, 1220-2500 m alt in ravines and mountain forests.

Distribution: southeastern Mexico to Costa Rica.—Fig. 10.

MEXICO: HIDALGO: Chapulhuacán, *Sharp 441768* (TENN, US); nr Jacala, *Knobloch 718* (US). VERACRUZ: Cuantlancillo, *Copeland 127* (GH); summit of El Cerro de Ejecatepetl, *Santos 2990* (MICH, US); nr El Puerto, above Acultzingo, *Sharp 44822* (US); Jalapa, *Orcutt 2819* (MO, US), *Smith 2219* (GH, MO); Orizaba, *Mohr s.n.*, in 1857 (US), *Mohr & Botteri s.n.*, in Sept, 1857 (US); Orizaba to Tzhuatlanchilla, *Bourgeau 2609* (GH, US). PUEBLA: summit of El Cerro de Cuhuatepetl Tehuacán, *Santos 3678* (MICH, US). MORELOS: Valle del Tepeite, *Lyonnet 779* (GH). OAXACA: Cuicatlán, Cuyamecalco, *Conzatti & Gómer 3499* (US). CHIAPAS: Los Lagos, SE of Comitán, *Carlson 1777* (US); Pico de Loro, *Matuda 4268* (MO); San Felipe, nr Ciudad las Casas, *Carlson 1615* (US); San Pablo, *Münch 121* (US); *Ghiesbreght 262* (GH).

GUATEMALA: ALTA VERAPAZ: Santa Cruz, *Johnson 980* (US). CHIMALTENANGO: Tecpán, *Skutch 572* (US).

HONDURAS: COMAYAGUA: El Achote, above Siguatepeque, *Yuncker et al. 6191* (US); nr El Rincón, *Yuncker et al. 6076* (GH, MO, US); Barranco El Socorro, *Williams & Williams 18377* (US). FRANCISCO MOROZÁN: Cerro de Uyuca, *Morton 6914* (US), *6975* (US); betw La Branza & Las Flores, *Molina R. 1107* (US), *1298* (US); betw Peña Blanca & Lo de Ponce, *Williams & Molina R. 17128* (US).

COSTA RICA: GUANACASTE: nr Tilarán, *Standley & Valerio 44666, 44713, 44757* (US). ALAJUELA: Alajuela, *Alfaro 6056* (GH, US). SAN JOSÉ: Tablazo, *Brade & Brade 696* (NY), *14a* (S-PA). CARTAGO: Cervantes & Padayas, *Biolley 95* (US); El Muñeco, *Stork 4708* (US); Juan Viñas, Reventazón Valley, *Cook & Doyle 204* (US), *242* (US); Orosi, *Scamman 6117* (GH); Pejivalle, *Skutch 4625* (GH, MO); Peralta, *Rowlee & Rowlee 60* (US); Tuis, *Tonduz 11309* (US); Turrialba, *Scamman 6116* (GH), *6121* (GH, US), *7230* (GH, US), *7765* (GH); Río Turrialba, *Smith 5091* (US).

There are two extreme types. Typical northern material (represented by Copeland's *P. cyathicola*) has either a long-cuneate frond base and a short stipe, or subtruncate and strongly deflexed segments at the blade base, a black rachis with lateral brown stripes, and inconspicuous narrow-ovate rachis scales. The typical southern material represented by *P. tablazianum* and *P. alfredii* has a brown rachis and conspicuous, cordate rachis scales. However, these characters are less consistent than the entire, dark brown rhizome scales, the linear-triangular chartaceous segments, and the extra-medial sorus position. The rachis scales throughout the *P. pectinatum-plumula* complex show patterns of consistency in some and inconsistency in other species. *Polypodium plumula* (see Fig. 5) has a clinal variation of rachis scales. The rachis scales of *P. dispersum* and *P. atrum* are very similar (more similar than the range of variation in *P. plumula*) but because of other over-riding characters, these species warrant recognition. In *P. alfredii* (as here construed) both the cordate and lanceolate scales can be found on any one frond except on those plants from Mexico where the broader scales are completely lost.

6. *Polypodium ferrugineum* Mart. & Gal., Mém. Acad. Bruxelles **15**: 36, *t. 6, fig. 2,* 1842.

Rhizomes short-creeping, 3.5 (2-5) mm in diam; rhizome paleae broad-ovate to cordate, golden-tan, basifixed, acute, non-clathrate, non-comose, the margins entire; *fronds* 20 (8-40) cm long, approximate to fasciculate on the rhizome; rachis light red-brown, thinly pilose with long, harsh, acicular hairs, and also with clavate hairs, ctenoid hairs absent; rachis paleae scattered, inconspicuous, linear-ovate to -obovate, light red-brown, obtuse to acute, entire; *blades* narrow-ovate, 17 (9-35) cm long, 4 (2-6.5) cm wide, cuneate to subtruncate at the base; segments 20 (10-32) mm long, 2.5 (1.5-3) mm wide, linear to narrow-ovate, perpendicular to the rachis except the strongly deflexed ones at the blade base, herbaceous, acute, the base expanded and symmetrical in the top half of the frond, subsymmetrical or with the lower edge perpendicular to the rachis in the lower half of the blade, entire; lamina with scattered clavate hairs, and occasional acicular hairs; costa decurrent on the rachis, dark red-brown or blackish, with scattered, long, acicular hairs, without paleae; veins once-forked, free; guard cells ca 40μ long; sori medial, round, with simple, clavate paraphyses; *sporangia* with 3 (2-4) capsular setae, 70-120μ long; spores globose reniform, smooth, ca 50μ long; $n = 37$.

Holotype: Mexico, Oaxaca, forests of Zacatepèque and Juquila, *Galeotti 6354* BR not seen, fragment US.

Habitat: epipetric, rarely epiphytic, from canyons, cliffs and river banks, 500-2100 m alt.

Distribution: western Mexico.—Fig. 8.

MEXICO: SINALOA: Colomas, *Rose 3201* (US); Panuco, *Pennell 20010* (US); Paraje del Zapote, *Salazar 393* (US); Sierra Monterey, *Gentry 5883* (GH, MO, US). NAYARIT: Ceboruco volcano, *Mickel 1374* (EVANS); La Atarjea, N of Yxtlán, *Mexia 880* (GH, MO, US); Santa María del Oro, *Pennell 19868* (US); Cerro de San Juán, *Mexia 690* (GH); E of Jalcocotán, rd to Tepic, *McVaugh 13342* (US). JALISCO: E of Mamantlán, S-SE of Autlán, *Wilbur 1969* (US); Pihuamo, *Jones 511* (MO, US). HIDALGO: Hidalgo, km 330, *Herb. Copeland 16056* (MICH). MORELOS: Cuernavaca, *Kenoyer 40* (US), *Rose & Painter 6870* (GH, US); Teposteco, *Lyonnet 2583* (US); Ramanoa Teatzalán, nr Tepoztlán, *Seler 4516* (GH); Tepoztlzán, *Herb. Copeland 125* (GH, MICH, US); Valle del Tepeite, *Lyonnet 779* (US). MEXICO: Temascaltepec, Ypericones, *Hinton 4161* (GH). COLIMA: Revillagigedo I, Socorro I, *Barkelew 236* p.p. (US). GUERRERO: Mina, Manchon, *Hinton 9607* (MICH); Mazatlán, *Correll 14391* (US). OAXACA: Cerro de San Felipe, *Conzatti & González 334* (GH). CHIAPAS: Ixtape, *Münch 12* (US).

This central and southern Mexican species is distinctive in its small size, light brown rachis and darker costa, long-setose sporangia, light brown rachis scales, and golden, ovate rhizome scales. Although this species has usually been identified as *P. plumula*, its nearest relatives are *P. cupreolepis* and *P. alfredii*, and it combines certain of the characters of each. It has normal appearing spores and is a diploid, so it is probably not of hybrid origin.

7. *Polypodium sursumcurrens* Copel., Univ. Calif. Publ. Bot. **19:** 291, *t. 42,* 1941.

Rhizomes short-creeping, 4 (3-5) mm in diam; rhizome paleae ovate to broad-ovate, red-brown at the margins with dark brown center, lustrous, basifixed or cordate, acute to obtuse, occasionally inconspicuously comose, non-clathrate, entire; *fronds* 30 (12-65) cm long, fasciculate on the rhizome; rachis 4 (2.5-6) times as long as the stipe; stipe and rachis red-brown, thinly pilose with blackish hairs up to 1 mm long, without ctenoid hairs; rachis paleae absent; *blades* narrow-ovate, 25 (10-56) cm long, 5.5 (3.5-8.5) cm wide, cuneate at the base; segments 28 (18-44) mm long, 3 (2-4) mm wide, perpendicular to the rachis, reduced and slightly deflexed at the blade base with the lowest 2 or 3 pairs reduced to auricles, linear-triangular, acute, asymmetrical at the base with the lower edge perpendicular to the rachis throughout the blade, herbaceous, entire to crenulate, the spaces between the segments 2 to 3 times the width of the segments; lamina with numerous blackish, simple, clavate hairs up to 175μ long; costa perpendicular to, or slightly decurrent on, the rachis, with scattered, long, acicular hairs; veins once-forked, free, guard cells ca 38μ long; sori marginal to submarginal, round, with numerous twisted paraphyses with a multicellular irregular clavate head, ca 375μ long; *sporangia* without setae; spores globose-reniform, smooth, thick-walled, ca 49μ long.

Holotype: Mexico, Veracruz, mountain tops at head of Orizaba Valley, 2400 m, epiphyte in mossy woods, *Copeland, Mexican Ferns 128* MICH; isotypes GH, US.

Habitat: epiphyte in montane forests, 2400-2600 m alt.

Distribution (Fig. 9): MEXICO: VERACRUZ: El Puerto, *Sharp 44822* (US). PUEBLA: Honey Station, *Pringle 13475* (MICH).—Fig. 9.

This species is a narrow endemic in eastern Mexico. I have seen only two collections in addition to the type. Copeland mentions the distinctive feature of the blackish hairs of the lamina. However, they are the usual golden color but are uniformly attacked by a pyrenomycete fungus, which gives them this characteristic blackish appearance.

The relationships of this species are not obvious, though it is clearly in the *P. plumula* group. It is probably closest to *P. alfredii, P. ferrugineum,* and *P. cupreolepis,* from which it differs in the larger size, more widely spaced segments, especially in the larger fronds, the gray-green color, long rachis hairs, dark brown, ovate rhizome paleae, the lack of rachis paleae, and especially the unique paraphyses.

8. *Polypodium* **bermudianum** A. M. Evans, sp. nov.—Fig. 17.

P. pectinatum var. *squamosum* Lindm., Ark. Bot. **1:** 238, 1903, p.p., as to Bermuda, *Herb. Farlow* (GH), not as to lectotype. (See *P. dispersum*).

Rhizoma breviter repens, paleis anguste ovatis, castaneis, non comosis, inconspicue dentatis, basi affixis, apice acuminatis; frondes approximatae articulatae, ca 35 cm longae; stipites et rhachides rigidae nitentes castaneae, sparse pilosae; paleae rhachidis numerosae parvae, anguste triangulares, castaneae, basi hastatae, apice acuminatae; lamina pectinata, anguste ovata, ca 25 cm longa et 7 cm lata, basi abrupte cuneata; segmenta anguste ovata, ca 35 mm longa et 4-5 mm lata, rhachide perpendicularia, apice obtusa, basi symmetrica; lamina solum cum pilos brevibus clavatis; venae liberae 1-furcatae; sporangia cum saepe 2-capsularibus setis; sporae globoso-reniformes, paullo tuberculatae, ca 43μ longae, 64 per sporangium.

Rhizome short-creeping, 5 (4-7) mm in diam; rhizome paleae narrow-ovate, red-brown, acuminate, non-comose, basifixed, non-clathrate, inconspicuously toothed; *fronds* 35 (15-55) cm long, approximate on the rhizome; rachis 3 (2.5-4) times as long as the stipe; stipe and rachis red-brown, pilose with long, simple, acicular hairs, ctenoid hairs absent; rachis paleae conspicuous, red-brown, paler at the base, narrowly triangular, hastate at the base, acuminate, occasionally toothed; *blades* narrow-ovate, 25 (14-33) cm long, 6.8 (5.7-8.5) cm wide, abruptly cuneate at the base; segments 35 (28-44) mm long, 4-5 mm wide, perpendicular to the rachis, slightly reduced or auriculate at the base of the blade, herbaceous, obtuse, symmetrical at the base, entire, the spaces between the segments equaling the width of the segments; lamina essentially glabrous, with short, clavate hairs; costa decurrent on the rachis, pilose with acicular hairs, with reduced paleae similar to those of the rachis; veins once-forked, free; guard cells ca 43μ long; sori medial, round, with simple clavate paraphyses; *sporangia* mostly with 2 two-celled capsular setae, 130-175μ long; spores globose-reniform, slightly tuberculate, ca 43μ long.

Holotype: Bermuda, Tuckers Town, on rocks, 10 Febr-9 Mar 1908, *Brown 464* US 848332; isotype GH.

Habitat: on limestone rocks in lime-sink areas.

Distribution: BERMUDA: *Goode s.n.*, Mar, 1877 (MO), Apr, 1877 (US); *Goode s.n.* (US); *Reinwardt s.n.* (GH). HAMILTON ISLAND: Walsingham, *Harshberger s.n.*, June 1905 (GH, US); Walsingham Caves, *Moore 3118a* (GH), *Taylor 49-1163* (MICH); Paynter Vale, *Farlow s.n.*, June 1881 (GH), *Britton & Brown 267* (US).

This species can be distinguished from *P. plumula* by the brown rachis and the broad segments, and from *P. ptilodon* var. *caespitosum* by the once-forked veins and the rachis scales. It is distinguished from *P. dispersum* by the number of spores per sporangium and the brown rachis. Of the sexual species, it is probably closest to *P. atrum*, from which it can be distinguished by its brown rachis, once-forked veins, basal segments not deflexed, and the costa being decurrent on the rachis. Its close similarity to *P. atrum* and *P. dispersum* indicates its affinities to these two species. The problem of specific and varietal rank in these three species is complicated by the unique life cycle of *P. dispersum*, which demands its separation. I have, therefore, accorded specific rank to this narrowly confined endemic.

9. *Polypodium plumula* Humb. & Bonpl. ex Willd. in L., Sp. Pl., ed. 4, **5:** 178, 1810.

P. schkuhrii Raddi, Opusc. Sci. Bol. **3:** 287, 1819. (as "*Schkuhri*"). Pl. Bras. **1:** 19, *t.* 27, *fig.* 2, 1825. (Holotype: Brazil, Corcovado, *Raddi* FI not seen; isotype B)

P. elasticum L. C. Rich. ex Desv., Mém. Soc. Linn. Paris **6:** 233, 1827, non *P. elasticum* Bory ex Willd., 1810. (Type: *P. elasticum* L. C. Richard, 1792, nom nud., was validated by Desvaux by accepting this name and citing *P. elegans* Poir. and *P. plumula* Humb. & Bonpl. ex Willd. as synonyms; the name is thus to be considered an illegitimate renaming. The name *P. elasticum* was subsequently accepted by Baker in Hooker & Baker, Syn. Fil., ed. 2, 332, 1874, who cited *P. plumula* as a synonym but not *P. elegans*, thus effectively fixing *P. plumula* as lectotype. Thus, *P. elasticum* is to be considered a superfluous renaming of *P. plumula* Humb. & Bonpl.)

P. pulchrum Mart. & Gal., Mém. Acad. Bruxelles **15**: 41, 1842. (Holotype: Mexico, Veracruz, Jalapa, ad quercos, 4000', *Galeotti* 6332 BR)
P. pectinatum var. *schkuhrii* (Raddi) Baker in Hooker & Baker, Syn. Fil., 333, 1867.
P. pulchrum Mart. & Gal. var. *minus* Fourn., Mex. Pl. **1**: 76, 1872 (nomen nudum).
Ctenopteris plumula (Humb. & Bonpl. ex Willd.) J. Smith, Hist. Fil., 185, 1875.

Rhizome short- to long-creeping, 5 (3-7) mm in diam; rhizome paleae narrow-triangular, red-brown, lustrous, basifixed, acuminate, non-comose or occasionally comose, non-clathrate, the margins regularly papillose; *fronds* 35 (20-60) cm long, approximate on the rhizome; rachis 4.5 (2-7.5) times as long as the stipe; stipe and rachis black, with scattered, long, acicular hairs, ctenoid hairs absent; rachis paleae broadly cordate with short-acuminate apex (in Central America), cordate- or hastate-acuminate (in Central America and the West Indies), or hastate and narrowly triangular (South America), basifixed or cordate, bullate or not, golden to red-brown, the margins toothed or papillate and occasionally fimbriate; *blades* narrow- to linear-elliptic, 28 (15-52) cm long, 4.7 (3-7.5) cm wide, cuneate or occasionally subtruncate at the base; segments 24 (16-40) mm long, 2.5 (2-3) mm wide, perpendicular to the rachis or slightly ascending, abruptly reduced to lobes at the blade base, linear, straight, obtuse, symmetrical and expanded at the base, herbaceous, entire, the spaces between the segments ½ to 1 times the width of the segments; lamina with scattered acicular and clavate hairs; costa decurrent on the rachis, black, occasionally brownish near the rachis in Central America, with scattered, long, acicular hairs; costal paleae similar to those of the rachis but reduced; veins once (or twice)-forked, free; guard cells 34μ long; sori medial, round, with long, simple, clavate paraphyses; *sporangia* mostly with 3 or 4 two-celled capsular setae; spores reniform, slightly tuberculate, ca 50μ long; $n=74$.

Lectotype: Venezuela, Caracas, *Bredemeyer* Herb. Willd. no. 19655-1, photograph B, fragm. NY. Syntype: Venezuela, Caripe, Cumana, *Humboldt & Bonpland 429* Herb. Willd. no. 19655-2, photograph B. The choice of lectotype is discussed below.

Habitat: epiphytic on tree trunks and branches, occasionally terrestrial or epipetric on wet swampy or montane forests, from sea level to 2600 m alt.

Distribution: Florida, West Indies, eastern Mexico, south to southern Brazil.—Fig. 9.

U. S. A.: FLORIDA: BREVARD CO: Indian River, *Whitney 1875* (GH). CITRUS CO: Pineola *Noble s.n.* (FLAS); Pineola grottoes, *Evans 2006* (MICH). DADE CO: Whiskey Creek, Everglades Ntl Pk, *Craighead s.n.*, Jan 1960 (FLAS); SW of Royal Palm Pk, *Cuthbert & Small s.n.*, 14 May 1919 (FLAS). HERNANDO CO: Brooksville, *Jones 24* (US). HILLSBOROUGH CO: Hillsborough River St Pk, R21E, T27S, Sect 8, *Evans 1186* (MICH); 10 mi NE of Tampa, *Correll 5868* (GH, US). MARION CO: Ocala, *Smith s.n.*, Apr 1879 (GH). MONROE CO: Aiken, Key Largo, *Pollard et al. 203* (US). POLK CO: 12 mi E of Lake Marion, vic of Winter Haven, *McFarlin 4112* (MICH). SEMINOLE CO: Oviedo, *Eaton 1023* (GH); Sanford, *Rapp s.n.*, Mar 1911 (FLAS). ST. JOHN'S CO: 14 mi W of St. Augustine, *Reynolds s.n., in* 1877 (US). SUMTER CO: Drake Point, Lake Astachula, *Smith s.n.*, 29 Mar 1879 (US); Indian Field Ledges, *Evans 1143* (MICH); Rutland Creek, *St. John s.n.*, 22 Dec 1934 (FLAS); Wonders Hammock, *Smith s.n.*, 21 Mar 1883 (GH, MICH, US). VOLUSIA CO: Enterprise, Faxon s.n., Apr 1873 (GH); Ormond Beach, *Freeman 59323* (US).

MEXICO: TAMAULIPAS: NW of El Progreso, *Stanford et al. 985* (GH, MO, US); Gómez Farías, *Palmer 300* (GH, MICH, MO, US); S of Huisachal, *Stanford et al. 2055* (US). SAN LUIS POTOSÍ: Los Canos, *Palmer 263* (GH, MO, US); 4 mi W of Pendencia, *Graber 233* (US); Tamasopo Canyon, *Pennell 17983* (US), *Pringle 3392* (GH, MO); Tamazunchale, *Lundell 7104* (MICH), *Copeland s.n.*, 27 Dec 1938 (MICH, US); E of Xilitla, *Mickel 590* (TENN); NE of Xilitla, *King 4354* (US); Xilitla Road 9 mi, *Kenoyer & Crum 3993* (GH, MICH). VERACRUZ: E of Chavarillo, *Weatherwax 181* (MO); Coatepec, *Sánchez S. 245* (US); El Mirador, *Purpus 16642* (US); Jalapa, *Johnson s.n.*, Oct 1906 (US); Orizaba, *Seaton s.n.*, 29 Aug 1891 (GH); Orizaba, Ojo de Agua, *Copeland s.n.*, 4 Febr 1938 (MICH, US); Potrero Viejo, *Copeland 126* (GH, MICH); Teocello Falls, *Rhoads s.n.*, Mar 1899 (US). HIDALGO: Jacala, *Chase 7426* (MICH, MO), *7458* (MICH), *Kenoyer*, 15 Nov 1937 (MO), *Lyonnet 1299* (US); 41 mi N of Jacala, *Barkley 17MO16* (MICH); Molango, *Moore 1970* (GH). OAXACA: Santiago de Jocotepec, *Santos 3378* (MICH, US). CHIAPAS: Munic. Pichucalco, *Gilly & Hernandez X. 175* (MICH). CAMPECHE: Hacienda San Pablo, nr Champotón, *Collins 50* (US).

GUATEMALA: EL PETÉN: San Clemente to Dos Arroyos, *Bartlett 12820* (MICH, US); Tikal National Pk, *Lundell 16748* (US); Uaxactum, *Bartlett 12754* (MICH); Uaxactum to San Clemente, *Bartlett 12810* (MICH). QUEZALTENANGO: Colahuaché, *Rojas 549* (US); San Felipe, *Kellerman 5575* (US). SUCHITÉPEQUEZ: Cuyotenango, *Rojas 151* (US); Las Animas, *Shannon 276* (US). RETALHULEU: San Felipe, *Kellerman 5584* (US). SANTA ROSA: Ojo de Agua, *Heyde & Lux 4083* (US).

BRITISH HONDURAS: COROZAL: Honey Camp, *Lundell 537* (GH, MICH, MO, US), *Meyer s.n.*, 22 July 1930 (US). BELIZE: Maskall, *Gentle 1240* (US). EL CAYO: Cohune Ridge, *Lundell 6460* (MICH); Mountain Pine Ridge, San Agustin, *Lundell 6748* (MICH); Valentin, *Lundell 6276* (MICH, US).

HONDURAS: COMAYAGUA: Agua Salada, *Williams & Molina R. 11451* (GH); Siguatepeque, *Standley & Chacón P. 6684* (GH). ATLÁNTIDA: La Fragua, vic of Tela, *Ames 7* (US).

EL SALVADOR: AHUACHAPAN: Sierra de Apaneca, Finca Colima, *Standley 20182* (US). SONSONATE: Izalco, *Standley 22189* (US). SAN SALVADOR: *Calderón 1274* (US). CUSCATLÁN: Colina de Santa Tecla, *Calderón 1786* (US). SAN VICENTE: Volcán de San Vicente, *Standley 21609* (GH, US).

COSTA RICA: ALAJUELA: Alajuela, *Scamman 6122* (GH), *Alfaro 6056* (US). SAN JOSÉ: Tablazo, La Uruca, *Beyer 1* (US); *Hitchcock s.n.*, 22-24 Oct 1911 (US); *Pittier 1231* (US).

PANAMA: VERAGUAS: Bahía Honda, *Taylor 1390* (MICH, US).

CUBA: ORIENTE: Finca Playucla, *Ekman 4451* (US); Baracoa, *Shafer 3927* (US); Gran Piedra, *Clément 7156* (US); Loma Mensura, *Shafer 3822* (US); Monte Verde, *Shafer 8696* (US); El Cobre, *Pollard & Palmer 394* (US); Loma del Gato, *Hioram & Clément 6486* (US), León, *Clément & Roca 9960* (US), *Clément 400* (US).

DOMINICAN REPUBLIC: SANTIAGO: Vallecito, San José de las Matas, *Valeur 465* (GH).

JAMAICA: Abbey Green, *Maxon 10096* (GH, US), Arntully, *Orcutt 3105* (MICH, MO); Chester Vale, *Philipson 758* (US); Mt Horeb, *Taylor s.n.*, 27 April 1956; Guys Hill P. O., *Proctor 5119* (MO); nr Kingston, *Lehmann 972* (US); Lucea, *Hitchcock s.n.*, 5 Jan 1891; Marshalls Pen, *Proctor 22898* (MICH); Silver Hill Gap, *Maxon & Killip 1234* (GH, US).

PUERTO RICO: Las Mesas, nr Mayagüez, *Holm 253* (GH, US).

GUADELOUPE: Camp Jacob, *Duss 4093* (GH); St. Lelande (Grand-Val), *Questel 1163* (US).

SURINAM: Avanavero Falls, *Stahel 4600* (MO); Augustus Falls, Tafelberg, *Maguire 24754* (US); Grassi Falls, Saramacca River headwaters, *Maguire 24945* (GH, MO, US), *24005* (GH, MO, US).

BRITISH GUIANA: Kanuku Mts, Takutu River, *Smith 3289* (GH, MO, US).

VENEZUELA: DELTA AMACURO: Lower Orinoco, Santa Catalina, *Rusby & Squires 367* (US). MIRANDA: Guatopo Ntl Pk, *Steyermark 90029* (US). CARABOBO: Maracai, *Vogl s.n.*, (GH).

COLOMBIA: MAGDALENA: Santa Marta, Campo Alegre, *Smith 1026* (GH); La Vuelta del Tigre, Minca Rd, *Bennett 36* (US). SANTANDER: Río Suratá valley, betw E Jaboncillo & Suratá, *Killip & Smith 16404* (GH, US). ANTIOQUIA: Frontino, West Andes of Antioquia, *Lehmann 7408* (US). VALLE DEL CAUCO: Cauca Valley, E of Zarzal, *Pennell et al. 8407* (GH, US). META: Los Llanos, Villavicencio, *Cuatrecasas 4690* (US); nr Río Guatiquía, *Pennell 1559* (US); Puerto López, *Little 8358* (US); mouth of Río Atacuarí, *Schultes & Black 46-226* (GH).

PERU: SAN MARTÍN: Río Negro, *Woytkowski 6198* (US); Tarapoto, *Woytkowski 35134* (MO); Tingo María, *Allard 20470* (US). LORETO: Maynas, Lupuna Cocha, *Tryon 5186* (US); Mishuyacu, nr Iquitos, *Klug 1382* (US); Santa Rosa, Urubamba Valley, *Cook &*

Gilbert 1727 (US). HUÁNUCO: Chinchao to Puerte Durend, *Coronado 90* (GH, US); Yanayacu, *Bües 2000* (US). JUNÍN: Colonia Perene, *Killip & Smith 25047* (US), along Río Perene, nr "Hacienda 3," *Killip & Smith 25169* (US); La Merced, *Killip & Smith 23941* (US); Río Paucartambo Valley nr Perene Bridge, *Killip & Smith 25382* (US); Schunke Hacienda, above San Ramón, *Schunke A158* (US); nr San Ramón, *Coronado 261* (GH); Manto, nr Yaupi, *Woytkowski 6522* (US), *6393* (US), *6413* (US), *6479* (US); Yunguy, *Woytkowski 6598* (US). CUSCO: Convención, *Herrera 147* (US); Convención, Sahuayaco, *Vargas C. 1825* (GH); Convención, Mission nr Quillabamba, *Mexía 8090* (GH, MICH, MO, US), *Coronado 112* (GH, US), *Soukup 162* (GH); Potrero, *Tryon 5390* (US); Playa Rosalina Río Alta Urubamba, *Bües 1720* (US).

BOLIVIA: LA PAZ: Apolo, *Williams 1120* (GH, MO, US); La Floride, South Yungas, *Buchtien 483* (US); Mapiri, *Williams 1118* (GH, US); Milluguaya, North Yungas, *Buchtien 5004* (US); Polo-Polo, nr Coroico, North Yungas, *Buchtien 3507* (GH, MO, US), *3507a* (US); San Antonio de Mapiri, *Buchtien 1074* (US); San Bartolomé (near Calisaya), South Yungas, *Krukoff 10073a* (MO); Tumupasa, *Williams 1121* (US). SANTA CRUZ: Buena Vista, Prov Sara, *Steinbach 5410* (GH); Espina, *Rusby 136* (US); Motacucito, Sara, *Steinbach 2506* (GH).

BRAZIL: AMAZONAS: Rosariulio, *Kuhlmann 218* (MO). CEARÁ: Sitio Uruguaniana, 4 km W of Guaramiranga, *Cutler 8318* (US). BAHIA: Monte Cruzeiro, *Rose 20041* (GH, US); Rio Grongogy Basin, *Curran 282* (GH, US); Toca de Onca, *Rose 20076* (US). MINAS GERAIS: Ilhen, Fazenda da Tabunha, *Mexía 4969-a* (GH); Mariana, *Vanthier 591* (GH). RIO DE JANEIRO: betw Alto da Serra & Meio da Serra, *Smith 1553* (GH, US); Corcovado Mt, *MacGillivray 149* (GH); Estrada Velha de Petropolis, *Smith 6466* (US); Ilha Grande, *Rose 20363* (US); Itaguai, Rio Mazomba, *Brade 20163e* (MO); Organ Mts, *Wagner s.n.*, in 1901-1902 (MICH); Petrópolis, *Smith 6466* (GH, MO); Rio de Janeiro, *Lindman A159* (US), *Regnell 250* (US), *Gaudichaud s.n.*, (GH).

This species has historically been broadly interpreted and frequently misconstrued. I have segregated out those entities which are clearly distinct, i.e. *P. bermudianum, P. dispersum, P. cupreolepis, P. ferrugineum* and *P. alfredii,* thus leaving a fairly uniform species but with some variation still to be more thoroughly explored. Figure 5 shows outline drawings of representative rachis paleae of specimens from different geographical areas. The broad cordate type from Central America appears to be the basic type and from that the narrower paleae of the West Indian plants and the extremely narrow paleae with large median marginal fimbriae of the South American plants have arisen as clinal modifications. The Central American plants with extremely cordate and golden rachis paleae also needs further study. These plants exhibit costae with brown bases and some brown streaking on the sides of the rachis. Although they are otherwise like the typical material, in these characters they show tendencies toward *P. alfredii* and *P. cupreolepis.* Their spores appear normal but no cytological information is known other than that *P. plumula* has been counted as a tetraploid in Florida and Jamaica.

A further question concerns a few collections from Brazil with only 32 spores in each sporangium. These spores are identical to the spores of the West Indian *P. dispersum;* and I have, therefore, included the specimens in that species. However, their morphology is closer to that of *P. plumula* than that of the typical West Indian *P. dispersum.* As I believe that *P. plumula* is probably one of the original parents of *P. dispersum,* it may be that the Brazilian *P. dispersum* is of different origin—possibly a hybrid between the southern *P. plumula* and *P. filicula.* There is, however, little evidence on which to base such an hypothesis and none of this material is known cytologically.

Polypodium elegans Poir. (1804), (non Cav. ex Swartz, 1806) has been referred to *P. plumula* (e.g. by C. Chr., 1906; de la Sota, 1960). However, the type (St. Dominique, *Nectoux s.n.,* Herb. Webbianum, ex Herb. Desfontaines (FI) can be referred to *P. otites* L. (*P. tenuifolium* Humb. & Bonpl. ex Willd.). I have included *P. schkuhrii* Raddi in synonymy. Though no type was designated, I have seen an illustration by Raddi (1825) and a Raddi collection (B) which fit his description (1819) and which I believe to represent an isotype. The type is probably at Firenze.

The choice of lectotype for *P. plumula* may be explained as follows. In the original description in 1810 of *P. plumula,* Willdenow attributed the name to Humboldt & Bonpland and cited the localities Cumana and Caracas, both in Venezuela. I have seen photos of the two syntypes in the Willdenow Herbarium in Berlin: Sheet 19655-2, collected in Cumana, Caripe, *Humboldt 429,* and Sheet 19655-1, collected in Caracas by Bredemeyer of which there is also a type fragment in NY. These two specimens represent different species in my opinion. In 1816, Humboldt, Bonpland, & Kunth described *P. plumula* again and a second species that they called *P. molle,* which are both represented in Paris by authentic specimens in the Humboldt & Bonpland Herbarium. The specimen called *P. plumula* and which agrees with their description corresponds with the Bredemeyer specimen in Berlin and the one called *P. molle* agrees with the *Humboldt 429* collection in Berlin. Thus, Humboldt & Bonpland did collect two species both of which are represented in Paris but only one in Berlin. Since the original *P. plumula* was based on a mixture, one element has to be selected as lectotype. It should be considered that Humboldt, Bonpland, & Kunth did this in 1816 by keeping one element under the epithet *plumula* and describing the other as a different species, *P. molle.* Thus the *Humboldt 429* specimen in Berlin was removed as *P. molle* from the concept of *P. plumula,* and inferentially the latter was left based on the Bredemeyer specimen, which is thus the lectotype. This specimen is conspecific with the Humboldt & Bonpland specimen in Paris which very likely originally provided the name. However, the Paris specimen can hardly be taken as lectotype since it may never have been seen by Willdenow at the time he drew up the original description. This Bredemeyer specimen represents a widespread species that has commonly been identified as *P. plumula.* The specimen *Humboldt 429* at Berlin, the isotype of *P. molle* H.B.K. (which is a later homonym thrice over), represents a species that has also not usually been separated from *P. plumula* but which is different, as noted elsewhere, and which I am calling *P. dispersum.*

10. *Polypodium filicula* Kaulf., Enum. Fil., 275, 1824.

P. elasticum L. C. Rich. var. *filicula* (Kaulf.) Baker in Mart., Fl. Bras. **1**(2): 517, 1870.

Rhizome short-creeping, 1-2 mm in diam; rhizome paleae narrow-ovate to narrow-triangular, brown, non-lustrous, basifixed, acute, non-comose, non-clathrate, finely serrate; *fronds* 10 (6-17) cm long, fasciculate on the rhizome; rachis 5.4 (3.5-11) times as long as the stipe; stipe and rachis red-brown, with scattered acicular hairs ca 0.3 mm long; rachis paleae numerous, conspicuous, cordate, bullate, acute, dark brown, finely serrate; *blades* narrow-ovate to narrow-obovate, 9 (5.5-15.5) cm long, 2.5 (1.5-3) cm wide, cuneate at the base; segments 15 (10-20) mm long, 1.5 (1-2) mm wide, perpendicular to the rachis or slightly ascending, not deflexed but reduced to lobes at the blade base, linear, herbaceous, obtuse or rounded, symmetrical and expanded at the base, entire or undulate, the spaces between the segments ca ½ to 1 times the width of the segment; lamina glabrous or with scattered, short, clavate hairs; costa decurrent on the rachis, with scattered acicular hairs ca 0.25 mm long, without paleae; veins simple, free; guard cells ca 41μ long; sorus supra-medial, round, with short, simple, clavate paraphyses; *sporangia* without setae; spores globose-reniform, smooth, ca 50μ long.

Type: Brazil, *Chamisso s.n.* not seen, B(?) or LE(?).

Habitat: epiphytic, occasionally epipetric, in humid forests at 500-2200 m alt.

Distribution: western and central South America from Colombia to southern Brazil and northern Argentina.—Fig. 9.

COLOMBIA: NORTE DE SANTANDER: Culagá Valley, nr Tapatá, *Killip & Smith 20162* (GH, US).

ECUADOR: CARCHI: km no 78, Río Blanco, Ibana to San Lorenzo, *Dodson & Thien 1563* (US).

PERU: AMAZONAS: Bagua, Río Utcubamba, 40 km S of Bagua Grande, *Hutchison 1472* (US). SAN MARTÍN: Tarapoto, *Woytkowski 35236* (MO). CUSCO: *Bües 1589* (US); Cusco to Santa Ana, *Herrera 874* (US); Convención, Potrero, 8 km W of Quillabamba, *Tryon 5373* (GH, US); Urubamba Machupicchu, *Vargas C. 3346* (US); Urubamba Valley, *Herrera 3297a* (US); nr Urubamba River, *Heller 2203* (US).

BOLIVIA: LA PAZ: Guanai to Tipuani, *Britton & Rusby 1448* (MICH); Tigre Pata, *Williams 1125* (GH, US). COCHABAMBA: Cañamina, *Rusby 82* (US). SANTA CRUZ: El Fuerte, Jamaipata, *Steinbach 8272* (GH); Tres Cruces, *Herzog 1538* (GH, US).

BRAZIL: MINAS GERAIS: Serra da Mutuca, nr Vargem de Ouro Podre, *Williams & Vicente 6196* (GH, US); São Sebastio do Paraiso, *Brade 17968* (MO). GOIÁS: Jatai, Queixada, Rio Corrente, *Macedo 21554* (MO, US). RIO DE JANEIRO: Estrada Velha de Petropolis, *Smith 6468* (US); Rio de Janeiro & Bahia, *Webb s.n.*, in 1868 (US). PARANÁ: Jaguariaiva, *Dusén 15925* (GH, MO, US). RIO GRANDE DO SUL: Pareci Novo, nr Monte Negro, *Beetle 1753* (US); São Luis, Latto Pirabó, *Jurgens & Stier* (Rosenstock 256) (US).

PARAGUAY: Guarapi, *Balansa 2874* (US); Cerros de Tobaty, *Hassler 6172* (GH).

ARGENTINA: JUJUY: Ledesma, *Dinelli 16726* (GH). MISIONES: Loreto, *Moreau s.n.*, 26 July 1931 (GH); San Ignacio, *Hunziker 764* (MO), *Vattuone & Bianchi 169* (US); Gobernador Roca, *Schwarz 6297* (GH); San Ignacio, Cristóbal, *Ahumada & de la Sota 51* (US); Yabebiry, *Moreau 48162* (US).

Although I have not seen the type, there can be little doubt about the application of *filicula* to this very distinctive species. It is easily recognized by its small size, cuneate blade base, dark cordate rachis scales, unforked veins, and its geographical isolation from any other closely similar species except *P. plumula.* It probably arose initially from the stock of the latter species, but it is presently quite distinct from it in a number of characters.

This species, like *P. dispersum* and *P. plumula,* reproduces readily by root proliferations. Several herbarium sheets show this character well, and a few sheets show dense mats of juvenile plants similar to the dense populations of small sterile plants of *P. dispersum.* It is presumed that this habit is correlated with dryness and exposure of the roots through a thin substrate.

11. *Polypodium dispersum* A. M. Evans, Amer. Fern Jour. **58:** 173, *pl. 27*, 1968.

P. molle H.B.K., Nov. Gen. Sp. Pl. **1:** 8, 1816, non Schreb., 1771. (Type: Venezuela, Cumaná, *Humboldt & Bonpland s.n.* P not seen, fragment B)

P. pectinatum var. *squamosum* Lindm. Ark. Bot. **1:** 238, 1903. (Lectotype: Brazil, Mato Grosso, Fazenda Sao José, *Regnell A2671* S. Syntypes: Jamaica, Herb. Alstroemer S-PA, and Herb. Casstroem S-PA; Bermuda, Herb. Farlow GH; Brazil, Rio de Janeiro, *Mosen 113* B, S, S-PA)

P. microsorum Lindm., Ark. Bot. **1:** 239, 1903, p.p. as to Cuba, *Wright 1051*, not as to lectotype. (See *P. pectinatiforme*, which is *P. microsorum* Lindm., not Mett.)

Rhizome short-creeping, 5 (4-8) mm in diam; rhizome paleae narrow-triangular, red-brown, lustrous, basifixed, acuminate, slightly comose, non-clathrate, inconspicuously toothed; *fronds* 43 (27-63) cm long, approximate on the rhizome; rachis 3 (2.5-4) times as long as the stipe; stipe and rachis black, thinly pilose with acicular hairs, occasionally with ctenoid hairs; rachis paleae conspicuous, narrow-triangular, hastate, non-bullate, basifixed, dark red-brown with pale base, lustrous, acuminate, inconspicuously toothed, fimbriate at the base; *blades* narrow-triangular, 32 (17-48) cm long, 6.8 (4.5-9) cm wide, subtruncate to abruptly cuneate at the base; segments 35 (23-47) mm long, 4 (3-6) mm wide, perpendicular to the rachis, occasionally deflexed at the blade base, reduced (sometimes to mere lobes) at the blade base, herbaceous, obtuse, symmetrical at the base, entire, the spaces between the segments approximately equal to the width of the segments; lamina with few, long, acicular and clavate hairs; costa decurrent on the rachis, thinly pilose with acicular hairs, with reduced paleae similar to those of the rachis; veins twice-forked, free; guard cells ca 38μ long; sori medial, round or occasionally oblong, with a few, simple, clavate, paraphyses; *sporangia* mostly with 2 (1-4) two-celled capsular setae; spores globose to ovoid, slightly tuberculate, ca 43μ long, with irregular, incomplete or interrupted variable scar, 32 per sporangium; $n=111$ (apogamous); gametophyte strap-shaped, branched, with marginal rhizoids, often with stomates, but without sex organs, proliferating 1-3 apogamous sporophyte proliferations.

Holotype: Florida, Citrus Co, R20E, T21S, Sect 1, Pineola Grottoes, 21 Sept 1963, *Evans 2008* MICH; isotypes TENN, US.

Habitat: epipetric (mainly limestone), occasionally terrestrial or epiphytic, on walls, in rocky hillsides, open woods, relatively dry areas, 100-2000 m alt.

Distribution: Florida, West Indies, eastern Mexico, through western South America to southern Brazil.—Fig. 9.

U. S. A.: FLORDIA: ALACHUA CO: Buzzard's Roost, Gainesville, *Weber & West s.n.*, 18 Nov 1927 (FLAS), *Knoppen s.n.*, 19 Mar 1928 (US); Devil's Mill Hopper, Gainesville, *West s.n.*, 11 Apr 1926 (FLAS). BREVARD CO: Indian River, *Palmer s.n.*, in 1899 (MO). CITRUS CO: Pineola, *West & Arnold s.n.*, 13 Nov 1932 (FLAS); Lecanto, *St. John 325* (FLAS). HERNANDO CO: Annutalaga Hammock, R19E, T21S, Sect 20 & 29, *Evans 2012* (MICH); on left bank of Withlacoochee River, 13 mi NE from Brooksville, *Smith s.n.*, 22 Mar 1883 (US); Brooksville, *Garrett s.n.*, 10 Oct 1953 (FLAS); Istachatta, *Underwood 287* (GH); nr Nobleton, *Knoppen s.n.*, Mar 1928 (US). HILLSBOROUGH CO: Hillsborough River St Pk, R21E, T27S, Sect 8, *Evans 1189* (MICH). MARION CO: Anthony, Sect 1, T14S, R21E, *Ward 1871* (FLAS), *Blake et al. s.n.*, 2 Apr 1950 (FLAS); Ocala, *Smith s.n.*, Apr 1879 (GH), *Shockley s.n.*, Mar 1878 (GH). MARTIN CO: Sewell's Point, *Curtis 5861* (GH, FLAS, MO, US). MONROE CO: Key Largo, *Small 7294* (US); Pumpkin Key, *Small s.n.*, 9 Mar 1915 (FLAS), R40E, T59S, Sect 12, *Evans 1165* (MICH). PASCO CO: Blandton, *Underwood s.n.*, (GH). SUMTER CO: Drake's Point, Lake Astachula, *Smith s.n.*, 29 Mar 1879 (GH); Indian Field Ledges, R21E, T20S, Sect 34, *Evans 1142* (MICH).

MEXICO: TAMAULIPAS: Gómez Farías, *Palmer 562* (GH, US). SAN LUIS POTOSI: Tamasopo, *Pringle 3999* (GH, US). HIDALGO: km 350, coll. unknown, 28 Mar 1938 (MICH). VERACRUZ: Río Seco, nr Córdoba, *Woronow 3002* (US). OAXACA: Cerro Concordia, *Conzatti 3043* (US).

GUATEMALA: ALTA VERAPAZ: Chilaseo, *Salvin* (GH); Cobán, *von Tuerckheim s.n.*, July 1885 (GH, US).

BRITISH HONDURAS: EL CAYO: Camp Six-Vaca Road, *Lundell 6545* (GH), Mt Pine Ridge, Río On, *Lundell 6798* (MICH). TOLEDO: Toledo, *Peck 820* (GH).

HONDURAS: COMAYAGUA: Agua Salada, *Williams & Molina R. 11451* (US); Siguatepeque, *Yuncker et al 5729* (GH, MICH, MO, US). FRANCISCO MORAZÁN: Las Mesea, *Standley 28656a* (US), *Williams & Molina R. 10096* (US). COLÓN: Cuyamel, *Carleton 476* (US). EL PARAISO: 5 km from Yuscarán, *Molina R. 10053* (US).

CUBA: *Wright 1051* (B, BR, G, GH, MO, L, NY, S-PA, US). PINAR DEL RIO: Arroyo del Sumidero, *Shafer & León 13699* (US); Bahía Honda to El Rosario, *Shafer 12009* (US); El Guama, *Palmer & Riley 161* (US); Taco-Taco, *Baker 3803* (US). LAS VILLAS: Cienfuegos, *Combs 349* (GH, MO); Hanabanilla Falls, Trinidad Mts, *Britton et al. 4856* (US); Las Vegas de Mataquá, Buenos Aires, *Jack 6524* (MO); Mina Carlota, SE of Cumanayagua, Sierra de San Júan, *Howard 5656* (GH); Sierra Gavilán, above San Blas, *Morton 3992* (US), *4142* (US); Trinidad Mts, power plant at San Blas, *Howard 5388* (GH, MO). CAMAGUAY: La Gloria, *Shafer 102* (US). ORIENTE: El Cobre, *Pollard & Palmer 412* (US); Arroyo Jiménez, Pico Turquino, Sierra Maestra, *Ekman 14794* (US).

HAITI: Bayeus, *Loomis s.n.*, May 1927 (US); Diquini, *Miller s.n.*, Mar 1925 (US); Furcy, *Leonard 4757* (GH, US); Hinche, Massif des Cahos, M. Vaillecife, *Ekman 6121* (US), Hinche, Massif du Nord, M. Pinquois, *Ekman 6160* (US); Jean Rabel, *Leonard 13048* (US); La Vallee, Tortue I, *Leonard 11681* (GH, US), *11580* (US); Mission, Fonds Varettes, *Leonard 3646* (US); Petionville, *Leonard 4928* (GH, US), Petionville, Massif de la Selle, Momence River, *Ekman 1514* (US); Riviere Soleilhet, *Holdridge 2047* (MICH); St. Michel de l'Atalaye, Mt la Cidre, *Leonard 7610* (US), La Lomas, *Leonard 7499* (US).

DOMINICAN REPUBLIC: AZUA: Sierra de Ocoa, San José de Ocoa, Bejucal, *Ekman 11887* (US). BARAHONA: Aceitillar, Sierra de Bahoruco, *Jiménez* (Marcano 3120) (US). LA VEGA: Cotuy, *Abbott 761* (US); Gajo de Constanza, *Jiménez 2111* (US). MONTE CRISTO: Arroyo Asiento Frío, Dist Monción, *Valeur 214* (MO). SANTIAGO: San José de las Matas, *Jiménez 926* (US), *861* (US). SANTO DOMINGO: Barrabas, *Raunkiaer* 72 (US); San Pedro de Macorís, *Rose 4189* (US).

JAMAICA: *Herb. Alstroemer* (S-PA); *Herb. Casstroem* (S-PA). Castleton, *Maxon 824* (US), *758* (US); Flamstead, Port Royal Mts, *Maxon 8647* (US); Greenwood, 5 mi ESE of Little River P. O., *Proctor 3931* (US); Kingston, Long Mt, *Wilson & Webster 436* (US); Lydford P. O.; mine area, *Howard & Proctor 13501* (GH); Mandeville, *Maxon 2556* (US), *Orcutt 5021* (MO); Montego Bay, nr Salt Spring, *Maxon & Killip 1658* (GH); Río Bueno, *Proctor 16619* (MO); 1 mi S of Rudds Corner, *Proctor 22896* (MICH); Schwallenburgh, Mt Diablo, *Wilson & Webster 489* (US); Silver Hill Gap, *Maxon 1144* (US); St. Andrews, Mt James, *Maxon 8602* (US).

PUERTO RICO: 10 mi SW of Carolina, *Wagner s.n.*, in 1944 (US); Maricao, *Hess 243* (US).

VENEZUELA: MONARAS: betw Caripe & San Agustín, *Steyermark 61778* (US). DISTRITO FEDERAL: Caracas, *Bailey 464* (US); Chacaíto Gorge, *Pittier 9479* (US); betw Caracas & La Guaira, *Rose 21727* (US); betw Cotiza & Los Venados, *Allart s.n.*, Oct 1924 (US), *Vogl s.n.*, (GH).

COLOMBIA: MAGDALENA: Santa Marta, *Smith 1026* (MO, US). META: Puerto López, *Little 8290* (US). NORTE DE SANTANDER: Región del Sarare, La Cabuya, Cuatrecasas, *Schultes & Smith 12135* (GH, US).

ECUADOR: MANABAI: hills S of Olmedo, *Haught 3492* (GH, US).

GALÁPAGOS ISLANDS: ALBEMARLE ISLAND: Iguana Cove, *Snodgrass & Heller 133* (GH, US), *14* (GH). CHARLES ISLAND: *Stewart 967* (US), *968* (US). CHATHAM ISLAND: SW End, Middle region, *Baur 358* (GH); *Stewart 966* (US); NW Ansel region, *Schimpff 155* (GH, MO, US). INDEFATIGABLE ISLAND: Academy Bay, *Stewart 962* (GH, US), *Svenson 74* (US); SE side, *Stewart 964* (GH, US); Fortuna, *Howell 9278* (GH).

BOLIVIA: Porango, *Herzog 1496* (S). LA PAZ: Guanai to Tipuani, *Bang 1448* (GH, US). BRAZIL: CEARÁ: Sitio Urguaniana, 4 km W of Guaramiranga, *Cutler 8318* (GH, MO). MINAS GERAIS: Ouro Preto, *Macedo 3074* (MO, US). MATE GROSSE: Buriti, nr Santa Anna da Chapada, *Malme* (*Regnell I 1716*) (S), *Regnell II 2482* (S). RIO DE JANEIRO: *Mosén 113* p.p (S-PA, not S).

This species was noted as distinct by Maxon, and numerous herbarium sheets at US from the West Indies and Florida are annotated with the epithet "*dispersum*" in his handwriting. Although Maxon never published it, I have adopted his epithet.

This species has a type of apogamous life cycle thus far unique among ferns, in which the spores number only 32 per sporangium and are formed by mitosis rather than meiosis (Evans, 1964). It reproduces commonly by root proliferations, often forming dense populations of sterile plants in this manner. A further discussion of the life cycle and reproduction of this species may be found above.

The similarity of this species to *P. atrum* is striking. They differ in that *P. dispersum* has broader rachis scales and the basal segments are only slightly or not at all deflexed. Of more fundamental importance, however, is that these two species reproduce very differently. *Polypodium atrum* has 64 spores per sporangium and therefore can be assumed to reproduce by the normal sexual process. *Polypodium dispersum* reproduces apogamously and has no sex organs on the gametophyte. This means that there is no possibility for interaction between these two species. *Polypodium dispersum* is a triploid and, on morphological grounds, I suspect it arose as a hybrid between *P. atrum* and *P. plumula*. *Polypodium plumula* is a tetraploid, so I predict that *P. atrum* is a diploid. As *P. atrum* occurs only in Mexico and northern Central America, *P. dispersum* perhaps arose there and then migrated to the other parts of its range.

The relationships between *P. dispersum* and *P. bermudianum* are discussed under the latter species. See also the discussion of *P. plumula* for comments on the typification of *P. molle* H.B.K.

12. *Polypodium* **atrum** A. M. Evans, sp. nov.—Fig. 18.

Rhizoma breviter repens, paleis lineari-triangularibus, basi affixis, castaneis, comosis, integris; frondes approximatae articulatae, ca 40 cm longae; stipites et rhachides rigidae nitentes nigrae, pilos dissitos aciculares gerentes; paleae rhachidis numerosae parvae anguste triangulares vel lineari-triangulares, castaneae integrae, basi saepe hastatae; lamina pectinata, anguste oblonga, ca 33 cm longa et 8 cm lata, basi subtruncata vel interdum abrupte cuneata; segmenta anguste ovata, ca 40 mm longa et 4 mm lata, apice obtusa, basalia paullo reducta et valde deflexa; lamina pilos dissitos aciculares ferens; venae liberae 2-furcatae; sporangia saepe cum 2-4 capsularibus paraphysibus; sporae globoso-reniformes, tuberculatae, ca 34μ longae, 64 per sporangium. *P. disperso* simile, segmentis basalibus deflexis, paleis rhachidis angustioribus, et numero sporae differt.

Rhizome short-creeping, 4-6 mm in diam; rhizome paleae linear-triangular, expanded at the base, red-brown with lighter base, basifixed, lustrous, comose, entire; *fronds* 42 (30-65) cm long, approximate on the rhizome; rachis 3.5 (2.5-5) times as long as the stipe; stipe and rachis black, with scattered, long, simple, acicular hairs; rachis paleae small, narrow- to linear-triangular, often hastate at the base, red-brown, entire; *blades* narrow-oblong, 33 (21-50) cm long, 8 (6-11.5) cm wide, herbaceous, subtruncate or occasionally abruptly cuneate at the base; segments 42 (32-60) mm long, 4 (3-7) mm wide, obtuse, symmetrical at the base in the upper half of the frond, with the lower edge perpendicular to the rachis in the lower half of the frond, entire, the basal segments slightly reduced and strongly deflexed, or occasionally abruptly reduced to auricles, the spaces between the segments equaling or exceeding the width of the segments; lamina with scattered acicular hairs and short, simple or occasionally forked clavate hairs; costa perpendicular to the rachis, black throughout or dark red-brown at the base, with scattered, long, acicular hairs; veins twice-forked, all free; guard cells ca 35μ long; sori medial, round, with long, simple, clavate paraphyses; *sporangia* mostly with 3 or 4 two-celled capsular setae 35-95μ long; spores globose-reniform, tuberculate, ca 34μ long.

Holotype: British Honduras, El Cayo District, Mountain Pine Ridge, San Augustín, on boulders on bank of Río Frio, July-Aug 1936, *Lundell 6639* US 1638286; isotypes GH, MICH.

Habitat: terrestrial or epipetric, woods, cliffs, river banks, 60-900 m alt.

Distribution: southeastern Mexico to British Honduras.—Fig. 9.

MEXICO: VERACRUZ: Atayác River, *Copeland 16058* (MICH); Córdoba, La Luz, *Kerber 97* (US); Córdoba, Metlac River, *Copeland 124* (MICH, US); Córdoba, Mt Orizaba, *Seaton 424* (GH, US); Córdoba, San Alejo Mts, *Couch M26* (US); Córdoba, Monte de San Pablo, *Woronow 2996* (US); Valle de Córdoba, *Bourgeau 1432* (GH); Playa Azul, nr Catemaco, *Stoutamire 3563* (TENN); Potrero Viejo, *Copeland 123, 126* (MICH); San Andrés Tuxtla, Laguna Encantada, *Dressler & Jones 77* (GH, MO, US); Zacualpán, *Purpus 2165* (GH, MO, US). OAXACA: Tuxtepec, Chiltepec, *Martinez-Calderón 693* (MICH, US); Mogoñe, *Orcutt 5211* (MO). TABASCO: Balancán, San Isidro, *Matuda 3372* (MICH, US). CHIAPAS: San Fernando de Tuxtla, *Collins & Doyle 167* (US).

GUATEMALA: EL PETÉN: Chicbul, La Libertad, *Lundell 3378* (US), *3378-A* (MICH), La Libertad, *Lundell 2980* (MICH), *4707* (US); Tikal Ntl Pk, Dos Aguadas, *Lundell 15588* (US), Remate rd S of Tikal, *Lundell 15878* (US). IZABEL: Cacão, betw Panzós & Senahú, *Barber 197* (US).

BRITISH HONDURAS: EL CAYO: Camp Six-Vaca Rd, *Lundell 6545* (MICH, US); Cohune Ridge, *Lundell 6494* (MICH, US); San Antonio, *Bartlett 13062* (MICH, US).

HONDURAS: SANTA BÁRBARA: San Pedro Sula, *Thieme 5692* (GH, US). COMAYAGUA: Tiquitapa River, Los Dragos, Seguatépequi area, *Steeves & Ray 435* (GH, US); Jutiapa, Seguatépequi area, *Steeves & Ray 414* (GH). YORO: Aguan River valley, Coyoles, Los Flores, *Yuncker et al. 8150* (MO, MICH); Río Pelo, Cordillera de Mico Quemada, *Ames 25* (US). ATLÁNTIDA: La Ceiba, nr Cangrajal River, *Yuncker et al. 8792* (MO, MICH, US).

The relationships of this species are discussed under *P. dispersum* and *P. bermudianum*.

13. *Polypodium* **absidatum** A. M. Evans, sp. nov.—Fig. 20.

Rhizoma longe repens, paleis anguste triangularibus, basi dilatatis, atro rubro-brunneis basi pallidoribus, acuminatis, comosis, integris vel inconspicue fimbriatis; frondes approximatae, stipitibus et rhachibus atro rubro-brunneis pilos aureis acicularibus praeditis; paleae rhachis inconspicuae filiformes integrae; laminae anguste ovatae, basi anguste cuneatae; segmentis ascendentibus acutis integris vel crenulatis, basi asymmetricis, infimis ad auriculas reductis; laminae subtus pilis dissitis acicularibus et pilis numerosis longis clavatis praeditae; costae valde decurrentes; venae unifurcatae; sori mediales, paraphysibus simplicibus clavatis praediti; sporangia plerumque setifera.

Rhizome long-creeping, 5 (3-7) mm in diam; rhizome paleae narrow-triangular, expanded at the base, dark red-brown, lighter at the base, lustrous, basifixed, acuminate, comose, non-clathrate, entire or inconspicuously fimbriate; *fronds* 38 (15-57) cm long, approximate on the rhizome; rachis 3.5 (2-5) times as long as the stipe; stipe and rachis dark red-brown, with golden, acicular hairs ca 0.5 mm long, ctenoid hairs present; rachis paleae inconspicuous, filiform, entire; *blades* narrow-ovate, 30 (12-46) cm long, 6.5 (3.5-9) cm wide, narrow-cuneate at the base; segments 33 (20-50) mm long, 3.5 (2-4.5) mm wide, ascending ca 20°-30° from the horizontal, reduced to auricles at the blade base, linear-triangular, coriaceous to herbaceous, acute, asymmetrical at the base, entire to crenulate; lamina with scattered acicular hairs ca 0.3 mm long, and with numerous, long, clavate hairs; costa strongly decurrent, with scattered acicular hairs ca 0.5 mm long; veins once-forked, free; guard cells ca 66μ long; sori medial, round, with simple, clavate paraphyses ca 0.25 mm long; *sporangia* mostly with 2 capsular setae up to 0.25 mm long; spores reniform, tuberculate, ca 59μ long.

Holotype: Colombia, Santander, Páramo de Romeral, *Killip & Smith 18518* US 1353919; isotype GH.

Habitat: montane forest, epiphytic, occasionally epipetric or terrestrial, 2800-4100 m alt.

Distribution: greater Antilles and western South America south to Bolivia.—Fig. 11.

CUBA: ORIENTE: Gran Piedra, *Clément 7155* (US).

DOMINICAN REPUBLIC: AZUA: top of La Pelona, *Ekman 13643* (US). LA VEGA: Sabana Alta, *Ekman 13794* (US).

JAMAICA: *Hart 45* (US), *771* (MO).

VENEZUELA: MÉRIDA: Laguna Negra, *Gines 1748* (US).

COLOMBIA: MAGDALENA: Páramos, Sierra Nevada de Santa Marta, *Seifriz 463* (US). SANTANDER: Páramo de Romeral, *Killip & Smith 18518* (GH, US); Páramo de Santurbán, Vetas, *Killip & Smith 17925* (GH). BOYACA: Valle de las Playas, *Grubb & Guymer P40* (US); Valle del Corallitos, *Grubb & Guymer P103* (US). VALLE: Páramo de Bavaya, Rio Bugalagrande, Corrales, *Cuatrecasas 20551* (US).

ECUADOR: CARCHI: Tufino, SE slopes of Volcán de Chile, *Wiggins 10605* (US). CUSCO: Quito, *Holdridge 1579* (US). PINCHINCHA: Mt Pichincha, *Holmgren 289* (GH, US), *Mille 15* (US), *Mille s.n.* (MO); *Sodiro s.n.*, in 1905 (US). NAPO-PASTAZA: Antisanilla, *Anthony & Tate 318, 319* (US); Mt Atazco, *Mille s.n.* (GH); Pifo, *Mille s.n.*, in 1899 (US).

PERU: LA LIBERTAD: Otuzco, Agallpampa, *López M. 1024* (US).

BOLIVIA: TARIJA: Padcaya, *Fiebrig 2875* (GH).

Although often identified as "*P. curvans*" or "*P. curvatum*" by various authors, the types of these taxa do not agree with this species. The affinities of *P. absidatum* are discussed below under *P. curvans* Mett.

14. *Polypodium curvans* Mett., Ann. Sci. Nat. (Paris) V, **2**: 253, 1864.

P. curvatum sensu Mett., Abhandl. Senckenb. Naturf. Ges. Frankfort **2**(1): 58, 1856, non Swartz, 1801.

P. circinatum Sodiro, Crypt. Vasc. Quit. 333, 1893. (Type: Ecuador, Azuay, nr Cuenca, *Rimbach* 35 Q?)

Rhizome short-creeping, 3 (2-5) mm in diam; rhizome paleae narrow-triangular, dark red-brown with a lighter base, lustrous, basifixed, acute to acuminate, comose, non-clathrate, entire or inconspicuously fimbriate; *fronds* 43 (18-90) cm long, approximate to fasciculate on the rhizome; rachis 8 (3-14) times as long as the stipe; stipe and rachis dark red-brown, with scattered, golden acicular hairs up to 1 mm long, and with scattered, short, clavate hairs, ctenoid hairs inconspicuous or absent; rachis paleae inconspicuous, filiform, dark red-brown, entire; *blades* linear, 38 (15-80) cm long, 4.5 (2.5-10) cm wide, linear-cuneate at the base, often circinate at the apex at maturity; segments linear, 30 (13-53) mm long, 2 (1.5-3) mm wide, strongly ascending ca 45° above the horizontal, herbaceous, acute, asymmetrical at the base, confluent, widely-spaced and gradually reduced to mere auricles at the blade base, crenulate to crenate; lamina with numerous, long, clavate hairs up to 200μ long, without acicular hairs; costa decurrent on the rachis, with scattered, acicular, golden hairs ca 0.75 mm long; veins once-forked, free; guard cells ca 43μ long; sori medial, round, occupying most of the lamina, with simple, clavate paraphyses ca 200μ long; *sporangia* with 1 or 2 capsular setae up to 200μ long, the sporangial stalk with 2 columns of cells; spores reniform, tuberculate, ca 44μ long.

Type: based on *P. curvatum* sensu Mett. Mettenius' description was based on a Lechler specimen from Peru. The locality and number are given in Mett. Fil. Lechl. **1:** 7, 1856, as Agapata, Peru, *Lechler 2006,* which is thus the holotype (B?; isotype L, Morton photo 1859).

Habitat: in montane forests, epiphytic or epipetric, 1600-4000 m alt.

Distribution: Ecuador to western Bolivia.—Fig. 11.

ECUADOR: Quitensian Andes, *Couthouy s.n.* in 1855 (GH). PICHINCHA: Quito, *Jameson s.n.*, in 1848 (GH). CHIMBORAZO: W slope of E Cordillera of Ríobamba, *Rimbach 27* (GH, US). NAPO-PASTAZA: Antisanilla, *Anthony & Tate 322* (US); Cubillán, W slope, *Rimbach 12* (US).

PERU: Agapata, *Hohenacker 2006* (GH); Chasqui, *MacBride & Featherstone* 27 July-13 Aug, 1922 (US); Mayuyoc, *Bües 1027* (US). JUNIN: Huancayo, *Killip & Smith 22129* (GH, US), *23364* (US); Quebrado de Occopilla, *Soukup 3642* (GH, US). APURIMAC: Prov Abancay, Ampay, *Stork et al. 10626* (MO); Bosques de Ampay, *Vargas 364* (GH, MO, US); Soccllaccasa Pass, Abancay-Cuzco trail, *West 3820* (GH, MICH, MO). CUSCO: Camino al Ampay (Apurimac), *Santander & Vargas,* Aug 1937 (GH); Prov Convención, Santa Ana, Hacienda Potrero, *Herrera 877* (US); Prov Paucartambo, Valle del Paucartambo, Hacienda Churu, *Herrera 271* (GH, US), *1107, 1605, 1655* (US); Prov Urubamba, Chupani, *Vargas C. 11130* (GH). PUNO: Carabaya, Ollachea to Puente Ackopampa, *Vargas C. 3346* (MO).

BOLIVIA: LA PAZ: Pelechuco, *Williams 2583* (GH, US).

Polypodium curvans is similar to *P. absidatum,* from which the former differs by having much smaller and more delicate fronds, strongly circinate at maturity, and longer hairs on the rachis and sporangia. The spore and guard cell sizes of *P. curvans* suggest that it may be a diploid, whereas the spores and guard cells of *P. absidatum* (see Table 3) are considerably larger and in the polyploid range. *Polypodium curvans, P. absidatum,* and *P. choquetangense* appear to be closely related species.

In superficial appearance, *P. curvans* strongly suggests ctenopteroid affinities. However, this is not confirmed in any of the critical criteria of sporangial stalks or spore shape, and it is probably placed in the *P. pectinatum* complex.

15. *Polypodium choquetangense* Rosenst., Meded. Rijks Herb. Leiden **19:** 18, 1913.

Rhizome long-creeping, 4-5 mm in diam; rhizome scales narrow-triangular, red-brown, lustrous, basifixed, acuminate, comose, non-clathrate, entire; *fronds* 55 (36-90) cm long, approximate on the rhizome; rachis 7 (3-10) times as long as the stipe; stipe and rachis dark red-brown, with very long, scattered, simple acicular hairs, and with long, irregular, ctenoid, clavate hairs, without paleae; *blades* narrow-ovate, cuneate at the base; segments linear, strongly ascending ca 25°-50° above the horizontal, reduced to auricles at the blade base, herbaceous, acute, with constricted attachments to the rachis, pinnatifid to a narrow wing along the costa; lamina essentially glabrous, with scattered clavate hairs; costa decurrent on the rachis, with scattered, long, acicular hairs; veins once-forked, free; guard cells ca 50μ long; sori inframedial, round, with simple clavate paraphyses; *sporangia* without setae; spores reniform, tuberculate, ca 42μ long.

Type: Bolivia, Hab. Choquetanga grande in silvis montanis ad arborum truncos, 3300 m alt, Oct 1911, *Herzog 2387* L, S.

Habitat: wet rocks and tree trunks, montane forest, 2700-3500 m alt.

Distribution: known only from the province of Cochabamba, Bolivia (Fig. 11).

BOLIVIA: COCHABAMBA: Ayopaya, Sailapata, *Cárdenas 3085a* (US), *3167* (US); Choro, *Brooke 6090* (G, S); Jatun Pino to Carrasco, *Cárdenas 5939* (US).

This species is unique because of its deeply pinnate-pinnatifid blades. It is the only pinnate member of the *pectinatum* complex. The base of the frond matures and sheds spores while the apical portion is still juvenile and unfurling, showing an almost indeterminate growth unknown elsewhere in the group. The very sinuous, almost circinate rachis, the strongly ascending segments, and the very long hairs of the stipe and rachis are found only in this species and *P. curvans,* which is clearly its nearest relative.

16. *Polypodium bolivianum* Rosenst., Repert. Sp. Nov. **5:** 236, 1908.

P. carpinterae Rosenst., Repert. Sp. Nov. **22:** 16, 1925. (Holotype: Costa Rica, La Carpintera, 1850 m 10 Apr 1908, *Brade & Brade* 14, p.p., S-PA)

Rhizome long-creeping, 8 (6-10) mm in diam; rhizome paleae narrow- to linear-triangular, expanded at the base, dark red-brown with pale base, lustrous, basifixed, acuminate, comose, with hairs obscuring most of the paleae, densely and conspicuously fimbriate; *fronds* 75 (35-135) cm long, spaced ca 1 cm apart to approximate on the rhizome; rachis 3 (2-5) times as long as the stipe; stipe and rachis dark red-brown, with numerous, conspicuous, ctenoid hairs, occasionally with short, acicular hairs; rachis paleae inconspicuous, small, filiform, with fimbriate margins; *blades* narrowly triangular, 55 (28-107) cm long, 15 (10-27) cm wide, truncate or rarely the lower segments slightly shortened; segments 80 (45-145) mm long, 6 (4-9) mm wide, perpendicular to the rachis or the lower segments occasionally deflexed, coriaceous, obtuse to acute, entire, symmetrical at the base, often slightly constricted near the base; lamina with few, short clavate hairs ca 125μ long; costae perpendicular to the rachis, with a few clavate and ctenoid hairs below, without paleae; veins 2 or 3 forked, free or occasionally partially anastomosing, obscure; guard cells ca 43μ long; sori supramedial, round, with a few clavate paraphyses ca 150μ long, and with a cluster of setiform hairs around the receptacle, these obscured in the mature sorus; *sporangia* without setae; spores reniform, tuberculate, ca 43μ long; $n = 37$.

Holotype: Bolivia, South Yungas, Sirupaya, nr Yanacachi, ca 16° lat, 2300 m, humid forests, 29 Nov 1906, *Buchtien 481* S-PA; isotype US.

Habitat: in montane forests, epiphytic on tree bases and trunks, occasionally terrestrial or epipetric on mossy rocks, (200) 1000-2700 m alt.

Distribution: southern Mexico, through western South America to western Bolivia.—Fig. 8.

MEXICO: CHIAPAS: *Ghiesbreght 394* (GH).

GUATEMALA: ALTA VERAPAZ: Finca Sepacuité, *Cook & Griggs 462, 555* (US); Pansamalá, *von Tuerckheim 644* (US).

HONDURAS: COMAYAGUA: Siguatepeque, *Standley 56350* (US); El Achote, hills above Siguatepeque, *Yuncker et al. 5973* (US); Barranco de Trincheras, nr Siguatepeque, *Morton 7582* (US).

COSTA RICA: ALAJUELA: Palmira, Zarcero region, *Smith 4332* (MO). HEREDIA: Vara Blanca, betw Poás & Barba volcanoes, *Maxon 8329* (US). SAN JOSÉ: Río del Convento, valle de Díquis, *Pittier 12112* (US); San Ramón, *Tonduz 17604* (US), *Brenes 14221* (US). CARTAGO: Pejivalle, *Standley & Valerio 47053* (US); Santa Clara de Cartago, *Maxon 8208* (US).

PANAMA: CHIRIQUI: Casita Alta, Volcán de Chiriquí, *Woodson et al. 887* (MO, US); Cerro de la Horqueta, *Maxon 5405, 5409, 5423* (US); Cerro de Lino, above El Boquete, *Maxon 5216, 5216a* (US); El Boquete, *Cornman 839, 1276, 1327* (US), *Maxon 5248, 5249* (US). DARIEN: Cana, *Williams 847* (US).

VENEZUELA: ARAGUA: Colonia Tovar, *Pittier 9358* (GH, US).

COLOMBIA: MAGDELENA: Santa Marta, Sierra de Onaco, *Smith 1027* (GH, MO, US); Mt San Lorenzo, Santa Marta, *Seifriz 36* (GH, US). SANTANDER: Cerro Armas, *Haught 1958* (US); Las Vegas, *Killip & Smith 21153* (US); Mt Peña Blanca, Charta, *Killip & Smith 19284* (GH); Río Suratá valley, above Suratá, *Killip & Smith 16569, 19284* (US). CUNDINAMARCA: Macizo de Bogotá, Quebrada Chica, *Schultes 18579* (US), *Cuatrecasas 5242* (US), *Black 46-424* (GH); W of Salto de Tequendama, nr Ermitaño, *Uribe 3352, 3354* (US). ANTIOQUIA: Boquerón, betw Medellín & Palmitas, *Hodge 6600* (GH). CALDAS: Río Boquia, Salento, *Killip & Hazen 8843* (GH, US); Río Santa Rita, Salento, *Killip & Hazen 8995* (US). VALLE DEL CAUCA: Pavas, *Killip 11660* (US); Río Cali, Pichindé, Alto de las Brisas, *Cuatrecasas 18280* (US).

ECUADOR: IMBABURA: Río Chaluayaco, below Magnolia, lower Intag Valley, *Drew E-604* (US). LEÓN: Hacienda Solento, nr Santa Rosa, Cantón, Pajii, *Mexia 6684, 6684a* (US). PICHINCHA: Mt Pichincha, *Mille 16* (MO, US). GALÁPAGOS ISLANDS: Albemarle I, *Stewart 963* (GH, US).

PERU: JUNÍN: Chanchosmayo valley, *Schunke 118* (US); Huacapistana, *Killip & Smith 24146* (US), *Coronado 272* (GH); Oxapampa, *Soukup 2347* (GH); E of Quimirí Bridge, nr La Merced, *Killip & Smith 23958* (US); Vitoc, *Soukup 4432* (US). CUSCO: San Miguel, Urubamba Valley, *Cook & Gilbert 1752, 1762* (US).

BOLIVIA: *Bang 2228* (US); *Bang s.n.* (MO). LA PAZ: Mapiri, *Rusby 356* (US); Polo-Polo, Coroico, N Yungas, *Buchtien 3510* (GH, US); Hacienda Simaco at Tipuani, *Buchtien 5269* (GH, US); Yungas, *Rusby 357* (US). SANTA CRUZ: Yungas de San Mateo, Comarapa, *Steinbach 8430* (GH).

This very large fern with coriaceous, almost waxy, fronds, strongly truncate blade bases, and densely fimbriate rhizome scales is one of the most distinctive members of the *P. pectinatum* group. Its affinities are not clear, although the generally glabrous lamina and the obscure tuft of setose hairs around the sorus suggest a relationship to *P. ptilodon*. In northern South America the rhizome scales are less densely fimbriate, and it becomes more difficult to separate the species from

P. eurybasis, which generally has a more pubescent lamina, subtruncate blade with more acute and crenulate segments, and not so harsh a texture.

I have included here two collections from the Galápagos Islands that are subtruncate and have a few ctenoid hairs and a few long hairs on the brown rachis. These may represent an endemic species, but because the specimens are juvenile, I am tentatively placing them here where they fit most closely.

17. *Polypodium eurybasis* C. Chr., Svensk. Vet. Akad. Handl. III, **16**(2): 71, *t. 16, fig. 12, 13,* 1937.

Rhizome long-creeping, 5-9 mm in diam; rhizome paleae narrow-triangular, light to dark red-brown, lustrous, basifixed, acute to acuminate, comose, nonclathrate, entire to inconspicuously fimbriate; *fronds* 28-130 cm long, approximate on the rhizome; rachis 3 (2-5) times as long as the stipe; stipe and rachis red-brown to dark red-brown, subglabrous to densely villose with acicular hairs, ctenoid hairs also present; rachis paleae inconspicuous, filiform or linear, entire; *blades* narrow-triangular to narrow-ovate, 20-88 cm long, 4-26 cm wide, subtruncate to abruptly cuneate at the base; segments 22-135 mm long, 3-9 mm wide, linear-triangular, narrow-triangular at the blade base, perpendicular to the rachis, straight or slightly falcate, herbaceous to subcoriaceous, acute, symmetrical at the base or with the lower edge approaching a right angle with the rachis, crenulate to crenate; lamina essentially glabrous, with simple and forked clavate hairs up to 200μ long, and occasionally with scattered acicular hairs; costa perpendicular to, or slightly decurrent on, the rachis, with a few reduced ctenoid hairs and with scattered acicular hairs up to 0.5 mm long; veins once- or twice-forked, free; guard cells 44-50μ long; sori medial, round, with simple or branched, clavate paraphyses; *sporangia* without setae; spores reniform, tuberculate, 40-44μ long.

This is a widespread and variable species distinguished primarily by its subtruncate blades, sharply acute and crenate segments, prominent veins, and glabrous lamina. It is probably most closely related to *P. bolivianum,* from which some of the northern South American material is difficult to distinguish. It can be subdivided into three varieties.

1. Rachis densely villose; rhizome paleae entire. ....17c. *P. eurybasis var. villosum*
1. Rachis subglabrous to thinly pilose; rhizome paleae entire to inconspicuously fimbriate.
   2. Veins once (twice)-forked; segments straight, crenate or crenulate; rhizome paleae red-brown, inconspicuously fimbriate ....17b. *P. eurybasis* var. *glabrescens*
   2. Veins twice-forked, segments straight or drooping at the apex, crenulate; rhizome paleae dark red-brown, entire to inconspicuously fimbriate. ....17a. *P. eurybasis* var. *eurybasis*

17a. *Polypodium eurybasis* var. *eurybasis.*

Rhizome paleae dark red-brown, attenuate, *fronds* 74 (30-114) cm long; stipe and rachis dark red-brown, with scattered acicular hairs 0.5 to 0.75 mm long, and also with conspicuous ctenoid hairs; *blades* narrow-ovate, 55 (21-87) cm long, 11 (4.5-18) cm wide; segments 58 (22-95) mm long, 6 (3-8) mm wide, straight or slightly drooping near the apex, herbaceous, symmetrical and expanded at the base, crenulate; veins twice-forked; guard cells ca 50μ long; spores ca 40μ long.

Holotype: Haiti, Massif de la Selle, Marigot, Jardins Bois-Pin, ca 1900 m, 9 June 1928, *Ekman H10062* S; isotypes B, US.

Habitat: terrestrial, epipetric or epiphytic on trunks or branches, in montane forests, 1000-2600 m alt.

Distribution: Cuba, Haiti, Venezuela.—Fig. 11.

Cuba: oriente: Pico Turquino, *Ekman 5455* (US), Loma Regino, *Ekman 14605* (US).

Haiti: Massif de la Selle, Croix-des-Bouquets, *Ekman 3088* (US); Mission, Fonds Varettes, *Leonard 3990* (GH, US).

Venezuela: monagas: Cerro de Turumiquire, *Tate 120* (US); Cerro Negro, above La Sabana de Las Piedras, NW of Caripe, *Steyermark 62080* (MO, US). distrito federal: El Junquito, *Killip & Rohl 37168, 37190* (US). aragua: Colonia Tovar, *Fendler 221B* (GH, MO). Bolivar: Ptari-tepuí, *Steyermark 59595* (US); Mt Roraima, *im Thurn 104* (US), *Steyermark 58741* (US).

See *P. eurybasis* var. *glabrescens* for discussion.

17b. *Polypodium eurybasis* var. **glabrescens** (Rosenst.) A. M. Evans, comb. nov.

P. lachniferum var. *glabrescens* Rosenst., Repert. Sp. Nov. **11**: 57, 1912. (Holotype. Bolivia, N Yungas, Unduavi, 3400 m, *Buchtien 2770* S-PA; isotype US)

P. lachniferum var. *glabrescens* f. *incurvatum* Rosenst., loc. cit. (as "*incurvata*"). (Holotype: Bolivia, N Yungas, Unduavi, 3400 m, *Buchtien 2769* S-PA; isotype US)

Rhizome paleae usually not expanded at the base, light red-brown, basifixed, inconspicuously fimbriate; *fronds* 80 (28-120) cm long, rachis 2.5 (2-3.5) times as long as the stipe; stipe and rachis red-brown, thinly pilose to subglabrous with short acicular hairs, ctenoid hairs present; *blades* narrow-triangular to narrow-ovate, 56 (20-88) cm long, 12 (4-26) cm wide, subtruncate; segments 65 (22-135) mm long, 6 (3-9) mm wide; lamina essentially glabrous, with scattered, simple, clavate hairs ca 0.25 mm long; costae perpendicular to the rachis, with scattered acicular hairs up to 0.35 mm long; veins once (twice)-forked, prominent; guard cells ca 44μ long; sori large, covering one-third to one-fourth of the width of the lamina, with simple, clavate paraphyses; spores ca 44μ long.

Habitat: pendent epiphyte in wet, shady, montane forests, 1500-3600 m alt.

Distribution: Costa Rica to western Bolivia.—Fig. 11.

Costa Rica: alajuela: Zarcero, *Smith H 127* (MO). Heredia: Cerros de Zurquí, NE of San Isidro, *Standley & Valerio 50346* (US). san josé: Laguna de la Chonta, NE of Santa María de Dota, *Standley 42128* (US); Las Nubes, *Standley 38846* (US).

Venezuela: aragua: Colonia Tovar, *Fendler 221* (US). mérida: La Venta, *Jahn 851* (GH, US). monagas: Cerro de Turumiquire, *Tate 148* (US).

Colombia: *Mutis 3236, 3237* (US). santander: California, *Killip & Smith 16902* (GH, US); La Baja, *Killip & Smith 18135* (GH, US). cundinamarca: Bogotá, *Ariste-Joseph s.n.* (US); Guadalupe, Bogotá, *Haught 5040* (US); Macizo de Bogotá, Quebrada de las Delicias, *Cuatrecasas 5463, 5608, 5675* (US); Bogotá, Río San Francisco Valley, Montserrate, *Hawkes & García-Barriga 94* (US), *Ewan 16901* (US); Bogotá Plateau, San Cristóbal, *Niemeyer 175* (US); Bogotá, old San Cristóbal to Ubaque rd, *Schiefer 322* (GH); Sabana de Bogotá, *Pring 133* (MO); Mun Chipaque, *Gutierrez V. 50* (GH). caldas: Magana, Old Quindio Trail, *Killip & Hazen 9431* (US); Páramo de Buena Vista, *Pittier 1147* (US); Cabeceras del Río Palo, Quebrada de Santo Domingo, *Cuatrecasas 19265* (GH, US). nariño: Córdoba, *Ewan 16235* (US); headwaters of Río Guapuscal, *Ewan 16553* (US); San José, below La Victoria, *Ewan 16218* (US); Soledad, *Ewan 16510* (US).

Ecuador: pichincha: Mt Pichincha, *Mille s.n.* (GH). napo-pastaza: Pifo, *Mille s.n.*, in 1898 (US).

Bolivia: la paz: Unduavi, N Yungas, *Buchtien 2771, 2772* (US); Sirupayo, nr

Yanacachi, S Yungas, *Buchtien 485* (US). COCHABAMBA: Prov Chapare, Incachaca-Chusi, *Steinbach 9235* (GH, MO); Río Tocorani, *Herzog 2275* (US); Prov Sacaba, *Steinbach 5868* (MO).

Of the three varieties of *P. eurybasis*, this one appears to be the most generalized element. It is distinguished from var. *eurybasis* by a more glabrous lamina, lighter green foliage, paler and broader rhizome scales, usually more crenate segments, and usually only once-forked veins. It is closer to var. *villosum*, as discussed below.

17c. *Polypodium eurybasis* var. **villosum** A. M. Evans, var. nov.—Fig. 19.

P. eurybasi var. *glabrescente* simile, paleis rhizomatis semper integris et rhachidibus dense villosis differt.

Similar to var. *glabrescens* except rhizome scales with entire margins; stipe and rachis densely villose with acicular hairs ca 0.5 mm long; range of dimensions not so great; *fronds* 75 (40-130) cm long; *blades* 56 (30-84) cm long, 12 (8.5-21) cm wide; segments 62 (45-104) mm long, 5.5 (4-7) mm wide.

Holotype: Colombia, Cundinamarca, collected on rocky ridge in brush on foothills above Bogotá, just N of mouth of Quebrada El Obispo, 830 m alt, 10 Jan 1943, *Fosberg 19688* US 2290492; isotype US.

Habitat: epiphyte, occasionally epipetric or terrestrial in rich humus, in montane forest, 220-330 (830) m alt.

Distribution: Panama to western Bolivia.—Fig. 11.

PANAMA: CHIRIQUÍ: Camp Aguacatal, *Maxon 5300* (US).

VENEZUELA: DISTRITO FEDERAL: Avila de Caracas, *Vareschi s.n.*, Feb 1963 (TENN).

COLOMBIA: *Mutis 3235* (US); *Ariste-Joseph s.n.* (US). MAGDALENA: Santa Marta, *Carriker 16* (US); Sierra de Perijá, Casacará Valley, 23 km E of Codazzi, *Grant 10982* (US). CUNDINAMARCA: Boca de Monte, W margin, Sabana de Bogotá, *Cuatrecasas, Jaramillo M. & Huertas 25809* (US); Bogotá, *Ariste-Joseph 1919, 1920* (GH, US); Montserrate, above Bogotá, *Ewan 16920* (US); Páramo de Cruz Verde, *Apollinaire & Arthur 4* (US), *Cuatrescasas 419* (US); Sibaté, *Pennell 2494* (US). CALDAS: Pinares, above Salento, *Pennell 9258a* (US). CAUCA: Canaan, Mt Puracé, *Pennell & Killip 6691* (GH, US).

ECUADOR: PICHINCHA: Corazón Peak & Corazón Pass, *Ewan 16421* (US); Mt Pichincha, *Mille 16* (US). CAÑAR: San Marcos, 5-8 km NE of Azogues, *Camp E-2614* (US). AZUAY: N of Sevilla de Oro, *Camp E-5209* (GH, MO, US). LOJA: Zamora-Huaico, *Espinosa 2271* (US).

PERU: HUÁNUCO: Mito, *MacBride & Featherstone 1621, 1731* (US); Muna, trail to Tambo de Vaca, *MacBride 4280* (US).

BOLIVIA: LA PAZ: Soratá, *Williams 2575* (GH, US). COCHABAMBA: Incachaca-San Antonio, Prov Chapare, *Steinbach 8988* (GH, MO); Prov Sacabá, Cochabamba, *Steinbach 5868* (GH, MO).

This variety is differentiated from var. *glabrescens* primarily on the basis of the more densely villose rachis and the entire rhizome scales. As they both cover essentially the same range, these apparently are not clinal variations, and appear sufficiently distinct to warrant formal recognition. The peculiar distribution and relationships of this variety to the other two suggest that, if this is truly a distinct variety, there may be an ecological isolation not evident from the data available.

18. *Polypodium pectinatum* L., Sp. Pl. 1085, 1753.—Fig. 20.

P. otites sensu Willd. in L., Sp. Pl. ed. 4, **5**: 177, 1810, non L., 1753 (Based on *Vahl s.n.*, Herb. Willd. no. *19653*, "Habitat in America," B-photo)

Goniophlebium pectinatum (L.) J. Smith, Lond. Jour. Bot. **4**: 57, 1842.

P. pectinatum L. var. *majus* Kuhn ex Krug, Bot. Jahrb. Engler **24**: 128, 1897, nomen nudum. (Based on: Santo Domingo, *Eggers 2595b, c, d* B; Dominica, *Eggers 12* B?; Martinique, *Hahn 55* P)

P. pectinatum L. var. *wagneri* sensu Jenm., Bull. Bot. Dept. Jamaica **4**: 125, 1897. (Not as to basionym *Polypodium wagneri* Mett., a species of sect. *Goniophlebium*. Based on: Jamaica, *Jenman s.n.* NY)

Rhizome long-creeping, 6.5 (5.9) mm in diam; rhizome paleae linear-triangular, dark red-brown with pale base, basifixed, filiform at the apex, inconspicuously comose, non-clathrate, inconspicuously and sparsely fimbriate; *fronds* 60 (30-126) cm long, approximate on the rhizome; rachis 6 (3.5-9) times as long as the stipe; stipe and rachis light red-brown, thinly pilose with acicular hairs up to 0.5 mm long, usually much shorter, ctenoid hairs inconspicuous to very conspicuous; rachis paleae usually absent, when present inconspicuous, filiform and entire; *blades* linear-elliptic, 50 (24-113) cm long, 7.5 (4.5-10.5) cm wide, abruptly cuneate at the base; segments 37 (23-53) mm long, 4.5 (3-7) mm wide, perpendicular to the rachis, abruptly reduced to a few pairs of lobes at the blade base, straight or slightly falcate, obtuse, the base expanded on the rachis and symmetrical, herbaceous, entire; lamina puberulous with small fine acicular hairs up to 0.25 mm long, usually shorter, also with inconspicuous, clavate hairs up to 100μ long; costa slightly decurrent on the rachis, the trichomes as on the lamina and with reduced ctenoid hairs; veins twice (once)-forked, partially to almost completely anastomosing except at the apex of the segments; guard cells ca 47μ long; sori medial, round, small, with a few simple, clavate paraphyses; *sporangia* ca 180μ in diam, usually with one inconspicuous clavate capsular seta ca 65μ long; spores reniform, tuberculate, ca 45μ long; $n=37$.

Type: There is no specimen labeled *P. pectinatum* in the Linnaean Herbarium, nor any specimen agreeing with the diagnosis; therefore, the species was evidently based only on the references cited. There were two of these: *Polypodium lonchitidis folio, Pet. fil. 31. t.7.f. 14* and *Polypodium nigrum tenerius sectum. Plum. amer. 26. t. 37* (The "*tenerius*" is an error of Linnaeus for "*tenuius*.") The Petiver figure is copied from Plumier, and therefore there is essentially only the Plumier citation left, automatically making the Plumier plate the lectotype. This question was put to Mr. J. E. Dandy of the British Museum (Natural History) and this is his conclusion also. The Plumier citation refers to his "Description des plantes de l'Amerique," 1693. The text indicates that his species came from "nos Antilles," i.e. from the French Antilles. In a later work, "Tractatus de filicibus Americanis," (p. 64, *t.* 83, 1705) Plumier repeated the same description and figure; he amplified the text by replacing "nos Antilles" by Martinique and by adding the locality Jamaica, on the basis of a publication by Sloane on Jamaica. Plumier's original description was thus based on one of his own collections from Martinique which is thus the type locality. In publishing *P. pectinatum*, Linnaeus picked up only the locality Jamaica in error. The only species of this group occurring in

Martinique is the species as I have delimited it here, which also does occur in Jamaica. Linnaeus' description of the rhizome as "nudo" was evidently taken from Plumier's illustration, in which the artist has omitted showing the rhizome scales, probably in order to show more clearly the leaf-scars (which are drawn in a very exaggerated way); no species of this alliance has or could be expected to have a naked (i.e. scaleless) rhizome.

Habitat: on limestone rocks or epiphytic on tree trunks and horizontal branches, occasionally terrestrial, in lowland or montane humid forest, from sea level to 1100 m alt.

Distribution: West Indies and Costa Rica to northwestern South America.—Fig. 10.

COSTA RICA: LIMÓN: Hamburg Finca, on the Río Reventazón, below Cairo, *Standley & Valerio 48712* (MO, US). SAN JOSÉ: El General, *Skutch 2153* (MO, US). CARTAGO: Tuis, *Tonduz 11309* (US).

PANAMA: San Pablo, *Blake s.n.*, 8 July 1872 (GH). BOCAS DEL TORO: Chiriquí Lagoon, *von Wedel 2611* (MO). COCLÉ: El Valle, *Allen 228* (US); Penonomé, *Williams 495* (US). CANAL ZONE: Frijoles, *Standley 27571* (MO, US); Barro Colorado I, *Standley 31410, 40973* (US); Río Indio de Gatún, *Maxon 4855* (US); Río Medio, *Miller 1729* (US).

CUBA: PINAR DEL RÍO: source of Río Taco-Taco, Sierra de Los Organos, *Morton 4295, 4300, 4315, 4485* (US). ORIENTE: El Yunque, nr Baracoa, *Underwood & Earle 1292* (US), *Pollard & Palmer 183* (US); Las Ninfas, Guantánamo, *Hioram 1458* (US); W of Santiago, *Graves 1482* (US); 20 km SW of Compañía de Moa Mill, Sierra de Moa, *Howard 5973* (MO); N spur of Sierra Maestra W of Río Yao, *Morton & Acuna 3352* (US); Sierra Nipe, Loma Mensura, *Ekman 3149* (US), *Woodfred & Shafer 3119, 3210* (US), Río Piloto, *Ekman 2100* (US); Yateras, Josephina, N of Jagüey, *Maxon 4103* (GH, US); Yateras, S of Jagüey, *Maxon 4219* (GH); Yateras, Monte Verde, *Maxon 4325* (GH, US), *Shafer 8701* (US), *Wright 1017* (GH).

HAITI: Marmelade, *Leonard 7289a* (US); Pilbury Hill, *Miller 188* (US).

DOMINICAN REPUBLIC: BARAHONA: *Fuertes 1013* (GH); Paradis, *Abbott 1580a* (US). DUARTE: San Francisco de Macorís, La Bracito, *Abbott 2033* (US). LA VEGA: Piedra Blanca, *Allard 13814, 13990, 13974, 13988* (US). SAMANÁ: Laguna, *Abbott 367, 369* (US); Rojo Cabo, *Abbott 164, 1164* (US); Samaná, *Abbott 490* (US); Sánchez, *Abbott 112, 113* (US). SANTO DOMINGO: La Cumbra, *Raunkiaer s.n.*, 4 Aug 1906 (US); Mt Isabel de la Torre, *Eggers 2595c, 2595d* (B). SEIBO: Samaná Bay, *Miller 1032* (US); 3-4 mi W of San Lorenzo Bay, *Abbott 1273* (US).

JAMAICA: *Roper s.n.*, in 1895 (MO). Cinchona, *Clute s.n.*, 21 Febr 1900 (GH); Hartford, Priestman's River, *Maxon 2525, 2538* (US); Hollymount, Mt Diablo, *Maxon 2319* (US); John Crow Mts, E of Seamen's Valley, Portland, *Maxon & Killip 239* (GH, US); Port Antonio, *Millspaugh*, 28 Jan-6 Feb 1899 (GH).

PUERTO RICO: Aibonito, *Hioram 269* (US); betw Arecibo & Utado, *Britton & Cowell 2048* (US); 8 mi SW of Carolina (US); El Yunque, *Scamman 6560* (GH); *Wagner s.n.*, 16 Apr 1944 (US); El Yunque, Río Piedras, *Johnston 750* (US); Loma Icaco, Sierra de Naguabo, *Shafer 3393* (US); Mariaco, *Kuhn 426* (US); Mayagüez, *Heller 4492* (GH, MO, US); rd from Ponce to Adjuntas, *Underwood & Griggs 765* (US); Adjuntas Rd, 7 mi from Ponce, *Heller s.n.*, 2 Dec 1902 (US); Sierra de Luquillo, *Dale s.n.*, Febr 1926 (MICH); Utuado, *Underwood & Griggs 21* (US); Vega Alta, *Wagner s.n.*, 30 Jan 1944 (US).

LESSER ANTILLES: ST. KITT'S: Nine Turn Gut, *Box 267* (US); Phillips Level, *Proctor 19556* (GH). MONTSERRAT: *Turner s.n.* (US); *Shafer 748* (US); Centre Hills, Salem, *Proctor 18837* (GH, US). GUADELOUPE: Camp Jacob, *Duss 4094* (US); Bains Jaunes, *Questel 3165* (US); Matouba, *Scamman 8168* (GH). DOMINICA: Roseau Valley, *Hodge 56* (GH); Morne Brule, Portsmouth, *Hodge 57* (MO, US); Sylvania, *Hodge 1151* (US); Morne Diablotin, *Hodge 2703* (GH, US). MARTINIQUE: Fontaines Didier, *Duss 1676* (GH, MO, US), *Hahn 55* (P). ST. LUCIA: 2.5 mi SSE of Soufrière, *Proctor 17869* (GH, US). ST. VINCENT: *Smith 249* (GH). GRENADA: St George Parish, Grenville Vale, *Hunnewell 19435* (GH), *Sherring 42* (US); Grand Etang, *Beard 1260* (MO, US); Mt Pleasant, *Milton*, 19 Mar 1924 (US). ST. EUSTATIUS: *Fairchild s.n.*, 22 Jan 1932 (US).

VENEZUELA: BOLÍVAR: Cerro Pijiguao, N end of Serranía Suapure, above Pijiguao, *Wurdack & Monachino 41300* (US).

COLOMBIA: SANTANDER: Río Suratá valley, above Suratá, *Killip & Smith 16569* (GH). META: Sierra de la Macarena, Caño, Entrada, *Philipson & Idrobo 1755* (US). VAUPÉS: Río Guaviare, San José del Guaviare, *Cuatrecasas 7468* (US). CHOCO: Negría, Río San Juán, *Killip 35027* (GH, US), Primavera, *Scolnik 1653* (US). CAUCA: Gorgona I, *Taylor 1227* (US). NARIÑO: Río Oretopungo, nr Río Putumayo, above Puerto Asís, *Ewan 16764* (US).

ECUADOR: MANABI: Salango, *Haught 3372* (US); Quininde, *Holdridge 1678* (US).

PERU: SAN MARTÍN: Tingo María, *Allard 21442* (US); Boquerón Pass, *Allard 21734* (US). LORETO: Pongo de Manseriche, Río Santiago, *Mexia 6212* (GH, MICH, MO, US), *6368a* (GH, US).

Polypodium pectinatum, as interpreted here on the basis of the type illustration mentioned above, agrees with the usual concept of the species as it occurs in the West Indies. This interpretation goes back at least to Swartz, who correctly understood the Plumier description and illustration. I have seen three specimens from the Swartz Herbarium in Stockholm which are labeled *pectinatum* by Swartz and which agree with my concept of the species. A number of specimens from the West Indies and elsewhere have been wrongly identified as *P. pectinatum;* these are now referred to *P. dispersum, P. ptilodon,* and other species.

This species is best characterized by the very short hairs of the lamina, the short sporangial setae, and the abrupt reduction in the segments to several pairs of mere lobes at the base of the blade. Morphologically, it is most similar to *P. camptophyllarium* var. *camptophyllarium,* which has much longer and more dense hairs and is a larger and coarser plant. Specimens of *P. pectinatum* from the Lesser Antilles tend to have somewhat longer, though sparse, hairs and have the basal segments more gradually reduced than is typical. However, these plants are clearly related to the other West Indian material of *P. pectinatum* and not to *P. camptophyllarium* var. *camptophyllarium.*

19. *Polypodium venturii* de la Sota, Opera Lilloana **5:** 186, *fig. 31,* 1960.

Rhizome long-creeping, 5 (4-6) mm in diam; rhizome paleae narrow-triangular, dark red-brown, lustrous, basifixed, acute, conspicuously comose, subclathrate with lighter non-clathrate base, entire; *fronds* 55 (45-60) cm long, approximate on the rhizome; rachis 3 (2-5) times as long as the stipe; stipe and rachis red-brown, pilose with acicular, golden hairs, ctenoid hairs conspicuous; rachis paleae inconspicuous, filiform, entire; *blades* narrow-ovate, 40 (28-47) cm long, 8 (6.5-9) cm wide, cuneate to subtruncate at the base; segments 40 (33-45) mm long, 5 (4.5-5) mm wide, perpendicular to the rachis or slightly deflexed at the blade base, linear-triangular, straight, obtuse, subsymmetrical at the base, chartaceous-herbaceous, entire, spaces between the segments ¾ to 1 times the width of the segments; lamina thinly pilose with clear, acicular hairs ca 0.35 mm long and with scattered clavate hairs ca 150μ long; costa decurrent on the rachis, the trichomes as on the lamina; veins once- or twice-forked, free or occasionally partially anastomosing; guard cells ca 56μ long; sori inframedial to medial, round, with simple clavate paraphyses ca 0.2 mm long; *sporangia* without setae; spores reniform, tuberculate, ca 50μ long.

Holotype: Argentina, Tucumán, Tafí, Yerba Buena, 800 m, 17 Apr 1921, *Venturi 1232* LIL. Not seen, but de la Sota has verified my material.

Habitat: epiphytic or on fallen logs, in forests, 600-2700 m alt.

PERU: CAJAMARCA: Colasay, *Woytkowski 7013* (US). LORETO: Pampayacu, *Kanehira 183* (US).

ARGENTINA: TUCUMAN: Chichigasta, Las Pavas, *Venturi 2974* (GH, US).

This species is similar to *P. camptophyllarium*, from which it can be distinguished by the usually completely free venation, smaller sori, non-setose sporangia, and the softer, more delicate foliage.

Although the two collections from Peru are less pilose and the hairs longer, in other characters they agree well with the Argentinian plants.

20. *Polypodium pectinatiforme* Lindm., Hedwigia **43**: 309, 1904.

P. microsorum Lindm., Ark. Bot. **1**: 239, *t. 11, fig.* 2, 1903, non Mett., 1855. (Lectotype: Brazil, Rio Grande do Sul, Porto Alegra, *Regnell I A381* S. Syntypes: Brazil, Rio de Janeiro, *Mosén 114* S, S-PA; Minas Gerais, Caldas, *Mosén 2195* C, M, S, S-PA; Rio Grande do Sul, Hamberger Berg & Colon, Silveira Martins, *Regnell I A493* S, S-PA, US, *493½* S; Cuba, *Wright 1051* B, BR, G, L, NY, S-PA).

P. pectinatum L. var. *truncatum* Rosenst., Hedwigia **43**: 228, 1904. (Holotype: Brazil, Santa Catarina, Joinville, *Schmalz 87* S-PA)

P. pectinatiforme Lindm. var. *hirsutum* Rosenst., Hedwigia **48**: 139, 1906 (as "*hirsuta*"). (Holotype: Brazil, Rio Grande do Sul, Lagoa, *Stier 255* S-PA)

Rhizome long- to short-creeping, 5 (2-10) mm in diam; rhizome paleae linear-triangular, dark red-brown with pale base, lustrous, basifixed, acute, inconspicuously comose, non-clathrate, entire; *fronds* 40 (12-65) cm long, approximate on the rhizome; rachis 7 (5-11) times as long as the stipe; stipe and rachis red-brown, thinly pilose with golden, acicular hairs up to 1 mm long, sometimes also villose with short acicular hairs, ctenoid hairs conspicuous; rachis paleae inconspicuous, filiform, entire; *blades* narrow-ovate, 35 (10-60) cm long, 9 (3.5-14) cm wide, cuneate at the base; segments linear to linear-triangular, straight, 40 (15-65) mm long, 3 (2-6) mm wide, perpendicular to the rachis, the basal segments strongly deflexed and shortened or reduced to auricles at the blade base, asymmetrical at the base, the lower edge perpendicular to the rachis, acute, herbaceous, entire to crenulate; lamina with numerous acicular hairs up to 0.3 mm long, also with occasional clavate hairs; costa perpendicular to the rachis, thinly pilose with long, acicular hairs up to 0.5 mm long, sometimes with ctenoid hairs; veins once (twice)-forked, free; guard cells ca 39μ long; sori supramedial to sub-marginal, round, with very long, simple, clavate paraphyses overtopping the young sorus, these obscure in the mature sori; *sporangia* without setae; spores reniform, tuberculate, ca 47μ long.

Type: based on *P. microsorum* Lindm., non Mett. The syntypes do not constitute a homogenous sample of the species, in that as presently construed *Wright 1051* is *P. dispersum*, *Mosén 2195* is *P. singeri*, and *Mosén 114* in S is *P. ptilodon* var. *robustum*, but in S-PA is *P. pectinatiforme*.

Habitat: epiphytic, occasionally epipetric or terrestrial, in forests, 1400-1700 m alt.

Distribution: southern Brazil, northern Argentina and Paraguay.—Fig. 10.

BRAZIL: MINAS GERAIS: Caldas, *Regnell 319* (MO, US); Serra de Caldas, *Mosén 2198* (C, S, S-PA); Serra de Mutuca, beyond Barreiro, *Williams 6642* (GH, US), *6644* (GH), Vargem de Ouro Podre, *Williams 6196a, 6197* (GH). RIO DE JANEIRO: Rio de Janeiro, *Glaziou 396* p.p. (BR, non P); *Mosén 113* p.p. (S, non S-PA); *Mosén 114* p.p. (S-PA, non S); Serra dos Orgãos, *Lüetzelburg 6915* (MICH). SAO PAULO: Campos do Jordão, *Harshberger 930* (US), *Leite 388* (GH). SANTA CATARINA: Sombrio, *Reitz C1159* (US); Lages, *Spannagel* (*Rosenstock 396*) (US), *Spannagel s.n.*, in 1920 (US). RIO GRANDE DO SUL: Hamburger Berg, *Lindman I.A. 493* (S, S-PA, US); São Leopoldo, *Rick s.n.* (GH); Silveira Martins, *Lindman A. 493½* (S).

PARAGUAY: Caaguazú, *Hassler 9084* (GH).

ARGENTINA: MISIONES: Yerbel Viejo, *Burkart 1584* (GH).

Superficially, *P. pectinatiforme* and *P. paradiseae* are very similar. The latter is considerably larger, however, with segments more gradually reduced at the base of the blade, and with characteristically more strongly crenate and falcate segments with marginal sori. The rhizome scales of *P. pectinatiforme* are larger and only inconspicuously comose.

Rosenstock's *P. pectinatiforme* var. *hirsutum* applies to specimens with a more villose rachis. This may be a distinct taxon, but I do not have sufficient material at hand to evaluate it satisfactorily.

21. *Polypodium paradiseae* Langsd. & Fisch., Icon. Fil. 11, *t. 11,* 1810.

P. pectinatum L. var. *paradiseae* (Langsd. & Fisch.) Baker in Mart., Fl. Bras. **1**(2): 517, 1870.

Rhizome long-creeping, 8 (6-10) mm in diam; rhizome paleae narrow-triangular, red-brown, lustrous, basifixed, acuminate, comose, non-clathrate, entire or with a few inconspicuous fimbriae; *fronds* 120 (70-170) cm long, spaced ca 2 cm apart on the rhizome; rachis 7 (4.5-11.5) times as long as the stipe; stipe and rachis red-brown, pilose with long, golden, acicular hairs, ctenoid hairs conspicuous; rachis paleae inconspicuous, filiform, entire; *blades* 100 (60-150) cm long, 16 (10-20) cm wide, narrow-rhombic, narrow-cuneate at the base; segments 80 (55-105) mm long, 6.5 (4-9) mm wide, linear-triangular, falcate, gradually shortened and deflexed to mere auricles at the blade base, coriaceous, acute, unequal at the base with the lower edge perpendicular to the rachis or incised, 24 (18-30) pairs of segments in the middle ¼ of the frond, crenate; lamina thinly pilose with golden, acicular hairs, ca 0.3 mm long and with scattered clavate hairs ca 0.25 mm long; costa perpendicular to or curved downward from the rachis, pilose with long, golden, acicular hairs ca 0.4 mm long; veins 2-3-forked, free; guard cells ca 43μ long; sori marginal to submarginal, round, with simple clavate paraphyses ca 0.25 mm long; *sporangia* without setae; spores reniform, tuberculate, ca 43μ long; $n = 37$.

Holotype: Brazil, Santa Catarina, Santa Catarina I, *Langsdorff s.n.* Herb. Fisch. LE; isotype Herb. Willd. B, photograph.

Habitat: terrestrial or occasionally epiphytic, in wet forests, up to 1600 m alt.

Distribution: southeastern Brazil.—Fig. 10.

RIO DE JANEIRO: Matto, Macieiras, Mt Itatiaya, *Smith 1764* (US); Monte Serrat, Mt Itatiaya, *Smith 2296* (GH); Serra do Itatiaio, *Dusén 467* (US). SAO PAULO: Alto da Serra, *Wacket* (US); Campos do Jordão, *Bailey 889* (US); Guarujá, *Dusén 14213* (US). PARANÁ:

Alexandra, *Dusén 17128* (GH); Serra do Mar, Desiro Ypiranga, *Dusén 14471* (GH); Tacarachý, *Dusén 6602* (GH, MO, US), *14743* (MO), *14743a* (GH, MO). SANTA CATARINA: Santa Catarina I, Itacorobí, *Rohr 1040* (US); Itajaí, Praia Braba, *Smith & Reitz 6093* (US); Joinville, *Müller* (US); Mun. Pôrto União, Pinheiral by new airport E of Pôrto União, *Smith & Reitz 8845* (US); Sombrio, *Reitz 1750* (US). RIO GRANDE DO SUL: São Leopoldo, *Leite 1462 (211), 1716, 1855* (GH), *Reitz C679?;* São Francisco do Paula, Vila Oliva, *Rambo 31204* (MO); São Salvador, *Leite 1934* (212) (GH).

This species appears to intergrade with *P. ptilodon* var. *robustum*. However, the marginal sori and the crenate, narrow segments, gradually reduced and deflexed at the base of the blade are characteristic of *P. paradiseae*. Also, if the total length of the blade is measured and then the numbers of pairs of segments counted in the middle fourth of the blade length, these two species are strikingly separated. In my test of this character *Polypodium paradiseae* had 24 (18-30) pairs of segments, whereas *P. ptilodon* (including all four varieties) had 16 (10-21) pairs. Applying a Mann Whitney-U test to samples of 10 fronds of each species, the two groups were found to be significantly different at the .002 level.

22. *Polypodium camptophyllarium* Fée, Mém. Foug. **8:** 86, 1857.

Rhizome short- to long-creeping, 5-10 mm in diam; rhizome paleae linear-triangular, dark red-brown, basifixed, filiform at the apex, comose, with linear non-clathrate cells, entire to slightly and inconspicuously fimbriate; *fronds* 1.6-16 dm long, closely spaced to approximate on the rhizome; rachis 1.5-7 times as long as the stipe; stipe and rachis light to dark red-brown, pilose with acicular hairs 0.4-1 mm long, ctenoid hairs present; rachis paleae inconspicuous, filiform, entire; *blades* narrow- to linear-ovate, 13-138 cm long, 4-17 cm wide, cuneate at the base; segments 20-90 mm long, 3-8 mm wide, perpendicular to the rachis, or slightly deflexed at the blade base, reduced to lobes or auricles at the blade base, slightly falcate to straight, herbaceous to coriaceous, obtuse to acute, the base expanded and symmetrical or the lower edge approaching a right angle with the rachis toward the base of the blade, or incised, entire; lamina pilose with pale acicular hairs up to 0.5 mm long, and with scattered, clavate, simple or forked hairs ca 0.2 mm long; costa decurrent on the rachis, with fine, pale, acicular hairs like those on the lamina or with coarser, longer and yellower hairs than those of the lamina; veins once- or twice-forked, free to completely anastamosing with a free included veinlet; guard cells 52-57μ long; sori medial to supramedial, with long, simple or forked, clavate paraphyses; *sporangia* with 0-3 multicellular capsular setae up to 250μ long; spores reniform, smoothish to tuberculate, 43-60μ long.

Polypodium camptophyllarium is a widespread and variable species, distinguished primarily by the long-pilose pubescence of the rachis and lamina. It is subdivided into four varieties showing varying degrees of similarity to *P. pectinatum*.

1. Fronds less than 30 cm long; veins once-forked, free throughout .... 22d. *P. camptophyllarium* var. *abbreviatum*
1. Fronds greater than 30 cm long; veins twice-forked, partially anastomosing.
    2. Veins completely anastomosing except at the segment apex; receptacular paraphyses and laminar hairs forked with a clavate and a setose branch; rachis 2.5 (1.5-3) times as long as the stipe; basal segments only slightly reduced and perpendicular to the rachis; plants of Bolivia and southern Brazil .... 22b. *P. camptophyllarium* var. *macedoi*

2. Veins only partially anastomosing; receptacular paraphyses and laminar hairs simple; rachis 4.5-(1.5-7) times as long as the stipe; basal segments reduced to auricles or strongly deflexed and only partially reduced; plants wide-ranging.
   3. Rachis and costa pilose with soft hairs up to 0.5 mm long, the lamina the same; sori occupying half the width of the segment or less .... 22a. *P. camptophyllarium* var. *camptophyllarium*
   3. Rachis and costa thinly pilose with scattered, harsh acicular hairs ca 0.75 mm long, the lamina thinly pilose with finer hairs ca 0.35 mm long; sori occupying most of the width of the segment .... 22c. *P. camptophyllarium* var. *lachniferum*

22a. *Polypodium camptophyllarium* var. *camptophyllarium.*

P. cinerascens Lindm., Ark. Bot. **1**: 238, *t. 11, fig.* 6, 1903. (Lectotype: Brazil, Rio de Janeiro, *Regnell I 474* S, isolectotypes BR, C, S, S-PA, US. Syntype: *Regnell I A99* S, S-PA)

P. robustum var. *cinerascens* (Lindm.) Hassl., Trab. Inst. Bot. Farm. Buenos Aires **45**: 69, 1928.

P. lachniferum Hieron., Bot. Jahrb. Engler **34**: 515, 1904, p.p., not as to lectotype. (for typification, see below under var. *lachniferum*)

Fronds 70 (25-165) cm long, spaced ca 1 cm apart on the rhizome; rachis 4 (1.5-5.5) times as long as the stipe; stipe and rachis light red-brown, pilose with pale, acicular hairs up to 0.75 mm long; *blades* 58 (23-138) cm long, 9 (3.5-17) cm wide; segments 45 (15-90) mm long, 5 (4-8) mm wide, perpendicular to the rachis, reduced to mere lobes at the blade base, slightly falcate to straight, herbaceous; lamina pilose with pale, acicular hairs, all ca 0.5 mm long; costa with trichomes like those on the lamina; veins twice (once)-forked, usually partially anastomosing; guard cells ca 52μ long; sori occupying half the width of the segment or less, with long simple clavate paraphyses; *sporangia* with 2 or 3 capsular setae ca 250μ long; spores reniform, tuberculate, ca 54 (47-60)μ long, mostly with 64 normal appearing spores per sporangium; $n = 74$.

Holotype: Colombia, Norte de Santander, Environs of Ocaña, in 1850, *Schlim 128, p.p.* P; isotypes BR, G, K photograph, not L.

Habitat: terrestrial, occasionally epiphytic, in rocky soil or on rocks in forests, often in openings or at the edge of the forest, 350-2100 m alt.

Distribution: Costa Rica, Cuba, Jamaica, northwestern South America to southern Brazil.—Fig. 10.

COSTA RICA: LIMÓN: Guápiles, *Standley 37291* (US).

PANAMA: PANAMA: 5 mi N of Cerro Azu, rd to Cerro Jefe, *Blum et al. 1692* (FSU).

CUBA: ORIENTE: El Cristo, *Ekman 1468* (US); Sierra Maestra, Termino del Cobre, *Clément 1129* (US), Finca Reunion to Loma del Gato, *Ekman 6925* (US); El Cobre, *Pollard & Palmer 412* (GH, MO, US).

DOMINICAN REPUBLIC: BARAHONA: Montiada Nueva, SE of Polo, *Howard 8431* (GH). SAN JUAN: Juán Santiago, *Howard 9288* (GH, US); Hondo Valle, *Howard 8753* (GH, US). SANTIAGO: Arroyo Juán Fino, Jicomé, *Valeur 655* (GH, US). LA VEGA: Salto de Constanza, *Jiménez 2215* (US); Salto de Jiménoa, Jarabacoa, *Jiménez 1533* (US).

HAITI: Bombardopolis, *Leonard 13457* (US); Dept l'Artibonite, Ennery, *Leonard 9576* (US); Furcy, *Leonard 4432* (GH, US); Massif du Nord, Hinche, *Ekman 6166* (US); Marc Sal, *Holdridge 1380* (US); Massif de la Selle, Petionville, *Ekman 10024* (US); Mission, Fonds Varettes, *Leonard 3958* (US); St. Louis du Nord, *Leonard 14469* (GH, US); Dept du Nord, St. Michel de l'Atalaye, *Leonard 7627* (GH, US).

JAMAICA: Abbey Green, *Maxon 10060* (GH, US); above Cedar Valley, Silver Hill Gap, *Maxon 10272* (GH, US); Cinchona, *Clute s.n.*, 21 Febr 1900 (US); Cinchona to Morce's

Gap, *Killip 204* (US); Port Royal Mts, Flamstead, *Maxon 8683a* (US); Mandeville, *Gilbert s.n.*, Febr 1895 (MO), *Maxon 2581* (US); Mocho, Catadupa, *Maxon & Killip 1551* (GH, US); Moneague, St. Ann, *Hunnewell 15217* (GH); Mt Diabolo, *Maxon & Killip 469* (GH, US); St. Helen's Gap, St. Andrew, *Maxon & Killip 631* (GH, US); Troy, *Underwood 2930* (US), *3296* (US).

Venezuela: monagas: Quebrada Colorado Grande, SW of Caripe, *Steyermark 61690a* (US). distrito federal: Quebrada de San Lázaro, nr Caracas, *Pittier 9760* (US).

Colombia: magdalena: *Haught 3942* (US); betw Pueblo Viejo & San Miguel, *Seifriz 359x* (US). bolívar: El Patico, Río Paez, *Lehmann K. 110* (US). santander: Pica-Pica Valley, above Tapatá, N of Toledo, *Killip & Smith 20191* (GH, US). valle: nr Corrales, *Lehmann 4424* (B); El Naranjo, Río Dagua, *Lehmann 5049* (B, US).

Peru: Cedrobamba, *Herrera 1580* (US). huánuco: Chinchao to Puerte Durand, *Coronado 91* (US). apurímac: Quebrada Nataza, *Vargas C. 2299* (US). cusco: Urubamba River, Machu Picchu, *Heller 2206* (US), *Herrera 3479* (US).

Bolivia: la paz: Apolo, *Williams 1124* (US); N Yungas, Milluhuaya, *Buchtien 4235* (MO, US); Sirupaya, Yanucachi, S Yungas, *Buchtien 482* (US); Tres Cruces, *Herzog 1616* (US).

Brazil: minas gerais: Mun. Ouro Preto, Andorinhas, *Macedo 2864* (MO); Mun. Ituiutaba, Aroeira, *Macedo 2383* (MO); Mun. Nova Lima, Serra do Curral, *Williams 6505* (GH); *Regnell I A 99* (S).

This is the central and widespread variety which ties the four together. The other three were not, however, necessarily derived from this variety, though var. *macedoi* very likely has been. The var. *abbreviatum* has considerably smaller spores, suggesting that it is a diploid and may have arisen by divergence. The var. *lachniferum* can, in most cases, be distinguished by the rather coarse golden scattered hairs on the rachis and costa, the slightly to strongly deflexed lower segments often reduced and auriculate, and the sori, which occupy the major portion of the segment. However, the collections which I have range from the West Indies to Peru and show little variation between range limits and considerable intergradation throughout its range with var. *camptophyllarium*. The range of this and related varieties is complicated by its extension over what I consider to be four geographical areas (see Figs. 8 & 10). At the overlapping of three of these distributional areas in northern South America, the representatives of the *P. pectinatum-plumula* complex in Colombia and Venezuela are often difficult to interpret.

The material of var. *camptophyllarium* from the West Indies and from Colombia is somewhat different. In the West Indies the segments tend to be more obtuse and the plants somewhat smaller, the spores more irregular, and a few evidences of apogamy are suggested, as discussed below. The material from Colombia tends to be larger with straighter and more acute segments. The laminar trichomes are essentially identical throughout the range. In Brazil the plants again begin to exhibit segments which are more obtuse and falcate as in the West Indian material, except that the stipe is considerably longer, and the anastomosing of the venation is more complete, as in var. *macedoi*. Because few collections from this area have been examined and because there does appear to be sufficient difference between the long-stiped materials which I have called var. *camptophyllarium* and var. *macedoi*, I am maintaining the latter as a distinct variety.

Throughout the range of this species the spores seem normal, though large and somewhat irregular. The spores are much like the large and somewhat irregular spores of *P. ptildon* var. *caespitosum*. A few of the specimens from Cuba and Jamaica have quite irregular reniform spores. They appear viable but are attached in pairs by the terminal ends; sometimes only by one end, thus making a double spore in a horseshoe shape; sometimes by both ends, making a deformed, dough-nut-shaped, double spore. These may be apogamous hybrids. Further cytological and populational studies of *P. camptophyllarium* are in progress, but it is suggested that these few plants may be isolated cases of apogamous reproduction. I have included these specimens with var. *camptophyllarium* as they represent only a small fraction of the total material, and they cannot at present be distinguished other than by a critical observation of the spores.

22b. *Polypodium camptophyllarium* var. **macedoi** (Brade) A. M. Evans, comb. nov.

P. macedoi Brade, Arq. Jard. Bot. Rio de Janeiro **11**: 30, *t. 10, 11, fig.* 3, 1951. (Holotype: Brazil, Estado de Minas Gerais, Ituiutaba, *Macedo 1098* RB-63398 not seen, isotypes G, MO)

Similar to var. *camptophyllarium*, except: rachis only 2.5 (1.5-3) times as long as the stipe; veins completely anastomosing or free at the apex only; lamina with forked, clavate-setose hairs; receptacular paraphyses consisting of forked hairs with one clavate and one setose branch; spores reniform, smoothish, ca 44μ long.

Habitat: terrestrial in humid forests and along river banks.

Distribution (Fig. 10): BOLIVIA: LA PAZ: Polo-Polo, Corioco, N Yungas, *Buchtien 3505* (US); Yungas, *Rusby* 357 (US).

BRAZIL: MINAS GERAIS: San Vicente, Mun. Ituiutaba, *Macedo 1894* (S, US), *2302* (MO, US), *2383* (US), *2864* (US).

This variety is distinguished from var. *camptophyllarium* on the basis of the completely anastomosing venation, longer stipes, and the presence of forked hairs on the lamina, as well as receptacular paraphyses consisting of one clavate and one setose branch.

Although in the original description Macedo considered this a goniophlebioid *Polypodium* because of its venation, in all other respects this variety is typical of the *P. pectinatum-plumula* complex. The extent of the anastomosing of the venation is only an extreme expression of what occurs to a lesser extent in var. *camptophyllarium* and in *P. pectinatum* s.s.

22c. *Polypodium camptophyllarium* var. **lachniferum** (Hieron.) A. M. Evans, comb. nov.

P. lachniferum Hieron., Bot. Jahrb. Engler **34**: 515, 1904. (Lectotype: Ecuador, Mt Tunguragua, 1500-2500 m, *Lehmann* 458 B, isolectotypes LE, US. Syntypes: Colombia, Cauca, Central Cordillera, nr Corrales, 2000-2800 m, *Lehmann 4424* B; Colombia, El Valle, nr El Naranjó, on Río Dagua, 300-1000 m, *Lehmann 5049* B, US) The Colombian collections are referable to var. *camptophyllarium*.

Rhizome as in var. *camptophyllarium* except the rhizome paleae with entire margins; *fronds* 46 (33-70) cm long, approximate on the rhizome; rachis 5 (1.7-7) times as long as the stipe; stipe and rachis light to dark red-brown, thinly pilose with coarse, golden, acicular hairs ca 1 mm long, ctenoid hairs conspicuous; rachis paleae inconspicuous, filiform, entire; *blades* narrow-ovate, 35 (25-60) cm long, 7.5 (5-11.5) cm wide, broad-cuneate at the base; segments 40 (25-60) mm long, 4.5 (3.5-5) mm wide, perpendicular to the rachis, slightly deflexed and reduced to auricles at the blade base, slightly falcate, herbaceous to coriaceous, acute, the lower edge perpendicular to the rachis or incised, entire; lamina thinly pilose with acicular hairs up to 0.35 mm long and with scattered clavate hairs; costa decurrent on the rachis, with scattered long hairs up to 0.75 mm long; veins twice-forked, free or occasionally partially anastomosing; guard cells ca 57μ long; sori medial, round, occupying most of the width of the lamina, with long, simple, clavate paraphyses; *sporangia* occasionally with one capsular seta ca 200μ long; spores reniform, smoothish, 54 (41-69)μ long; $n=74$.

Habitat: epipetric or terrestrial, montane, on and about rocks on wooded mountain sides, 600-2300 m alt.

Distribution: Cuba, Jamaica, northwestern South America.—Fig. 10.

CUBA: ORIENTE: La Perla, *Shafer 8474* (US); Loma del Gato, Cobre Range of Sierra Maestra, *León et al. 10530* (US).

JAMAICA: Arntully, *Orcutt 3105a* (US); Blue Mt Peak, *Hitchcock s.n.*, 13 Dec 1890 (MO); Chestervale, *Underwood 1148* (US), Cinchona, *Maxon 2596* (US), *Underwood 473* (US), Cinchona Plantation, *Underwood 1127* (US); Farm Hill, *Orcutt 3402* (US); Port Royal Mts, Flamstead, *Maxon 8683* (GH, US); Blue Mt range, Helen's Gap to Morce's Gap, *Chrysler 1741* (US); Mandeville, *Churchill s.n.*, 16 Mar 1897 (MO); Moody's Gap, *Maxon 1207* (US); Cedar Valley, rd to Silver Hill Gap, *Maxon 10306* (GH, US); *Churchill s.n.*, 26 Mar 1897 (GH).

VENEZUELA: MÉRIDA: Mucurubá, *Gehriger 195* (US); Páramo de la Sal, *Jahn 632* (US).

COLOMBIA: MAGDALENA: betw Pueblo Viejo & San Miguel, *Seifriz 378* (US), *384* (US). SANTANDER: California, *Killip & Smith 18488* (GH, US); betw Piedecuesta & Las Vegas, *Killip & Smith 15508* (GH, US). CUNDINAMARCA: Bogotá, Quebrada, *Ewan 15593* (US); Suba Hill, Sabana of Bogotá, *Schiefer 596* (US); Facatativa, *Ariste-Joseph A190* (US); Pandi, *Perez s.n.* (Col 552) (US); mts W of Salto de Tequendama, *Uribe Uribe 3382* (US). ANTIOQUIA: Bello, *Archer 161* (US); Boquerón, *Daniel 1634* (US); Copacabana, *Henri-Stanislas 1606* (US).

ECUADOR: Grubi, *Mille 14* (US). TUNGURAHUA: Baños, *Popenoe s.n.*, 6 Mar 1921 (US). AZUAY: Cuenca, nr union of Ríos Tarqui & Yanuncay, *Prieto*, (Camp E-2658) (US); Río Milchichic, 5 km N of Cuenca, *Prieto* (Camp E-2735) (US). LOJA: San Lucas, *Dodson & Thien 564* (US). NAPO-PASTAZA: betw Río Blanco & Río Verde, rd from Baños to Puyo, *Dodson & Thien 1970* (US).

PERU: CAJAMARCA: Las Juntas, *Rose 23221* (US). JUNÍN: Huacapistana, *Coronado 275* (GH); Manto to Yaupi, *Woytkowski 6518* (US), Manto, km 20, *Woytkowski 6521* (US); Prov Tarma, 5 km SW of Huacapistana, 25 km NE of Tarma, *Tryon 5426* (GH, US); nr Yaupi, *Woytkowski 6414* (US). AYACUCHO: Ccarrapa, betw Huanta & Río Apurimac *Killip & Smith 22473* (US).

This variety is closely related to var. *camptophyllarium*, the best differentiating characters being that var. *lachniferum* is generally a shorter plant, with distinctly deflexed, reduced and auriculate basal segments; and that there are two distinctly different sizes of acicular hairs on the frond. There are scattered but long and harsh hairs on the costa and rachis and shorter, finer hairs (not as dense as in var. *camptophyllarium*) on the limina. The sori cover almost the entire width of the segment, whereas in var. *camptophyllarium*, the sori, in most cases, cover only a half or less of the width of the segment.

22d. *Polypodium camptophyllarium* var. **abbreviatum** A. M. Evans, var. nov.—Fig. 18.

A var. *camptophyllario* simile, frondibus ca 23 cm latis, approximatis, laminis ca 18 cm longis et 6 cm latis, basi late cuneatis, segmentis ca 30 mm longis et 3 mm latis, rhachide perpendicularibus basalibus paullo deflexis exceptis, venis 1-furcatis, liberis, soris medialibus, laminam subtus fere tegentibus, sporangii cum setis 2-capsularibus differt.

Rhizome as in var. *camptophyllarium; fronds* 23 (15-30) cm long, approximate on the rhizome; rachis 4.5 (3.5-5) times as long as the stipe; stipe and rachis red-brown, pilose with clear, acicular hairs ca 0.4 mm long, ctenoid hairs present; rachis paleae inconspicuous, filiform, entire; *blades* narrow-ovate, 18 (13-25) cm long, 5.5 (4-7) cm wide, broadly cuneate at the base; segments 30 (20-40) mm long, 3 mm wide, perpendicular to the rachis except the lower few slightly deflexed, mostly expanded and symmetrical at the base except the lower few pairs of segments incised on the lower edge and gradually reduced to auricles, herbaceous, acute, entire, the laminar and costal trichomes as in var. *camptophyllarium* except shorter; costa decurrent; veins once-forked, free; sori medial, round, covering most of the width of the frond; *sporangia* with two capsular setae ca 0.14 mm long; spores reniform, slightly tuberculate, ca 43μ long.

Holotype: Peru, Cusco, Prov La Convención, Distr of Santa Ana, Hacienda Echarabi, 1300 m, Jan 1926, *Herrera* 872 US 1342112.

Habitat: terrestrial on rocky hillsides, 1300-1800 m alt.

Distribution (Fig. 10): Peru: cusco: 20 km N of Ollontaytombo, *Hitchcock 22516* (US); Pampakjahua, *Coronado 105* (US).

This is a local endemic. It is smaller than either var. *camptophyllarium* or var. *lachniferum*. It is related to the former by the trichomes of the lamina and rachis and to the latter by the reduction and constriction of the basal segments. Except for the overall small size and the smaller, regular spores, it could easily be considered as a hybrid of the other two varieties.

23. *Polypodium ptilodon* Kunze, Linnaea **9:** 42, 1834 (as "*ptiloton*," in error).

Rhizome long-creeping, 8 (5-12) mm in diam; rhizome paleae narrow-triangular, dark red-brown, lustrous, basifixed, acuminate, comose, non-clathrate, entire; *fronds* 27-170 cm long, closely-spaced to fasciculate on the rhizome; stipes 1-36 cm long; rachis 5-42 times as long as the stipe; stipe and rachis red-brown, with scattered acicular hairs up to 2 mm long, ctenoid hairs conspicuous; rachis paleae inconspicuous, filiform, entire to inconspicuously fimbriate; *blades* narrow- to linear-ovate, 25-130 cm long, 3.5-22 cm wide, narrow-cuneate at the base; segments 2-11 cm long, 3-10 mm wide, perpendicular to the rachis or slightly ascending, gradually reduced to lobes or auricles at the blade base, straight to subfalcate, acute to rounded, expanded at the base and symmetrical or with the lower edge perpendicular to the rachis, herbaceous to coriaceous, entire (crenulate), the spaces between the segments ½ to 1 times the width of the segments; 10-21 pairs of segments in the middle ¼ of the blade; lamina with scattered silvery acicular hairs up to 0.35 mm long, more densely pilose in an oblong area around the sorus and with scattered clavate hairs; costa decurrent on, or perpendicular to, the rachis, with ctenoid hairs, and with scattered, golden, acicular hairs up to 2 mm long; veins 1-3(4)-forked, free; guard cells 44μ long; sori medial, round or occasionally oblong, with simple and branched, clavate paraphyses up to 165μ long; *sporangia* with 1-3 capsular setae 45-140μ long; spores reniform, tuberculate, 41-52μ long.

This species is subdivided into four closely related varieties. *Polypodium ptilodon* var. *ptilodon* is known to be a diploid, with small spores. The var. *caespitosum* is a tetraploid, with larger spores; var. *robustum*, with similar spores is presumed to be a tetraploid. The var. *pilosum* has medium-sized spores, and is a smaller plant than the other varieties, with longer hairs on the rachis and costae.

1. Stipe 2 (1-5) cm long; segments rounded to obtuse; hairs of the rachis and costa 1.5-2 mm long .... 23d. *P. ptilodon* var. *pilosum*
1. Stipe 13 (3-36) cm long; segments obtuse to acute; hairs of the rachis and costa less than 0.75 mm long.
   2. Lower edge of the segments perpendicular to the rachis in the lower half of the blade; fronds 110 (50-170) cm long; spores ca 52μ long; Bolivia, Argentina, Paraguay, Uruguay, and southern Brazil ....23c. *P. ptilodon* var. *robustum*
   2. Upper and lower edges of the segments similar and equally expanded and adnate on the rachis; fronds 85 (30-115) cm long.
      3. Stipe 14 (12-17) cm long; fronds 95 (55-115) cm long; spores ca 41μ long; Peru and Bolivia .... 23a. *P. ptilodon* var. *ptilodon*
      3. Stipe 9 (3-13) cm long; fronds 70 (30-105) cm long; spores ca 52μ long; Florida, West Indies, Mexico and Honduras. .... 23.b. *P. ptilodon* var. *caespitosum*

23a. *Polypodium ptilodon* var. *ptilodon*.

Fronds 97 (55-115) cm long, spaced ca 1 cm apart on the rhizome; rachis 6 (4-7) times as long as the stipe; stipe and rachis pilose with golden acicular hairs ca 0.75 mm long; rachis paleae entire; *blades* narrow-ovate, 80 (45-100) cm long, 15 (10-18) cm wide; segments 70 (55-90) mm long, 9 (8-10) mm wide, gradually reduced to mere wings at the blade base, obtuse, expanded at the base and symmetrical, the spaces between segments approximately equal to the width of the segments, 14 (13-15) pairs of segments in the middle one-fourth of the blade; costa perpendicular to the rachis, with scattered acicular hairs up to 0.3 mm long; veins 2-or 3-forked, 41μ long; $n=37$.

Type: Peru, Dept San Martín, in woods at Pampayacu, July 1829, *Poeppig s.n.* Since the original in the Kunze Herbarium in Leipzig is presumed to have been destroyed, the duplicate at B is designated lectotype.

Habitat: dense forests, 1100-1700 m alt.

Distribution (Fig. 11): PERU: AMAZONAS: Río Utcubamba, Cerro Tapur, 40 km S of Bagua Grande, *Hutchison 1470* (MICH). JUNIN: Chanchosmayo Valley, *Schunke 126* (US); San Ramón, Schunke Hacienda, *Schunke A151* (US).

BOLIVIA: LA PAZ: Polo-Polo, Corioco, N Yungas, *Buchtien 3508* (MO, US), *3510* (US); Mapiri, *Rusby 356* (US); Simaco, Tipuani Valley, *Buchtien 5269* (GH).

This variety is a diploid with spores averaging ca 11μ shorter than either of the two other similar varieties. Inasmuch as var. *caespitosum* is known to be a tetraploid, one may presume that var. *robustum*, with the same spore size, is also a tetraploid. It would appear that var. *ptilodon* was the original parental stock in the species. The var. *caespitosum* is so similar to var. *ptilodon* that it could be an autotetraploid, although its smaller size indicates that it could also be of hybrid origin with any of several other Caribbean species.

23b. *Polypodium ptilodon* var. *caespitosum* (Jenman) A. M. Evans, Amer. Fern Jour. **58:** 170, 1968.

P. pectinatum auct., non L., 1753.
P. pectinatum var. *caespitosum* Jenman, Bull. Bot. Dept. Jamaica **4:** 125, 1897. (Holotype: Jamaica, Old England, 4000 ft, *Jenman s.n.* NY, not K which is *P. consimile* var. *consimile*)

As in var. *ptilodon* except: *fronds* 70 (30-105) cm long; rachis 9 (6-14) times as long as the stipe; stipe and rachis red-brown to blackish; *blades* 60 (27-90) cm long, 12 (6.5-18) cm wide; segments 65 (35-85) mm long, 7 (4-10) wide, obtuse to acute; guard cells 50μ long; *sporangia* with 1 or 2 two-celled capsular setae ca 140μ long; spores ca 56μ long; $n=74$.

Type: Based on *P. pectinatium* var. *caespitosum* Jenman.

Habitat: terrestrial or on mossy tree bases or logs, occasionally epipetric, usually in damp woods, mountain slopes or ravines, from sea level to 1500 m alt.

Distribution: Florida, Greater Antilles, eastern Mexico to Honduras.—Fig. 11.

FLORIDA: BREVARD CO: N of Titusville, Turnbull Hammock, *Small & DeWinkler 10799* (US). CITRUS CO: Homosassa Springs, *Correll 5798* (MO); 3 mi NE of Lake Lindsey, *Cooley 5488* (FLAS, US); Pineola grottoes, *Evans 2005* (MICH). COLLIER CO: Fakahatchee, *Eaton 1133* (GH); Deep Lake, Royal Palm Hammock, *Scull s.n.* (FLAS). DADE CO: Hattie Bauer Hammock, *Small 7421* (US). HERNANDO CO: Annutalagga Hammock, NW of Brooksville, R19E, T21S, Sect 20 & 29, *Evans 2011* (MICH), *Garrett s.n.*, 18 Sept 1953 (FLAS); Brooksville, Choochahattie Hammock, *St. John et al. s.n.*, 13 Jan 1935 (FLAS); Istachatta, *Curtiss s.n.*, Aug 1897 (US); Pineola, *McFarlin 3618* (MICH); Brooksville, Spring Lake, *Perkins 65* (MO). HIGHLANDS CO: Avon Pk Wildlife Management Area, N end of Bill Bay, *Evans 1158* (MICH); Sebring, Highlands Hammock, *Correll & McFarlin 6247* (US); Parker I, 4 mi E of Childs, *Ward et al. 2420* (FLAS), *Correll 6174* (GH). HILLSBOROUGH CO: Hillsborough River St Pk, R21E, T27S, Sect 8, *Evans 2018* (MICH). LAKE CO: Eustis, *Nash s.n.*, 25-27 July 1895 (US); Seminole Springs, *West s.n.*, 15 Oct 1929 (FLAS). MANATEE CO: Manatee, *Garber 15* (FLAS, US). MARION CO: *Stevens s.n.*, May 1883 (MICH). ORANGE CO: Rock Spring, *Harper s.n.*, 11 Febr 1915 (US). PASCO CO: Blanton, *Small et al. 10858* (US). POLK CO: Fort Meade, *Smith s.n.*, Mar 1880 (US); 7 mi S of Lakeland, Scott Lake, *Sheridan s.n.*, 28 Nov 1958 (FLAS); Peace Creek, *Smith s.n.*, Apr 1880 (US); Winter Haven, Faulkner Hammock, *McFarlin 3547* (FLAS, MICH). PUTNAM CO: 4 mi W of Interlachen, *West & Arnold s.n.*, 29 May 1942 (FLAS). SEMINOLE CO: Sanford, Orange Co, *Rapp s.n.*, Mar 1910 (FLAS). SUMTER CO: Indian Field Ledges, R21E, T20S, Sect 34, *Evans 2004* (MICH, TENN); Camp's Grove, *St. John s.n.*, 4 Dec 1933 (FLAS). VOLUSIA CO: Halifax R, *Reynolds s.n.*, in 1877 (US); 5 mi SW of Port Orange, *Freeman 59327* (US).

MEXICO: TAMULIPAS: Gómez Farías, *Palmer 306* (US). SAN LUIS POTOSÍ: Hacienda de Tamasopo, *Pringle 3974* (GH, MO, US); 4.2 mi E of Xilitla, *Mickel 602* (MICH). VERACRUZ: Atoyác River, *Copeland s.n.*, 3 Mar 1938 (US); Córdoba, *Conzatti & González 575* (GH), *Fink 74a* (US), *Woronow 3093* (US); Zacualpán, *Purpus 15728* (MICH), *3818* (US).

HONDURAS: CORTÉS: Río Lindo, N of Lake Yojoa, *Morton 7665* (US).

CUBA: Loma San Juán, *Hioram 7064* (US). LAS VILLAS: Buenos Aires, *Howard 5246* (GH, MO), *Morton 4154* (US); Arroyo de Manaca, Herradura, *Britton 4997* (US). ORIENTE: La Perla, *León 3849* (US); Loma del Gato, *Clément 1172* (GH), *Hioram & Clément 6490* (US); Santa Ana, 6 mi N of Jaguey, Yateras, *Maxon 4212* (GH, US). PINAR DEL RIO: source of Río Taco-Taco, *Morton 4304* (US).

HAITI: Plaisance, *Leonard 9383* (US); St. Louis du Nord, *Leonard 14314* (US).
JAMAICA: Cinchona, *Clute 321* (MO); Morce's Gap, *Hatch 30* (US); Mount James, *Maxon 8550* (US), *8608* (US); Silver Hill Gap, *Maxon 1143* (US), *Maxon 1145* (US); above Tweedside, *Maxon 933* (US).

The affinities of the variety are discussed above under var. *ptilodon.*

23c. *Polypodium ptilodon* var. **robustum** (Fée) A. M. Evans, comb. nov.

P. robustum Fée, Crypt. Vasc. Braz. **1**: 92, 1869. (Type: Brazil, Rio de Janeiro, Angra dos Reis, 16 June 1868, *Glaziou 2407* BR, C, K photo, P, S, US)
P. robustum var. *cinerascens* f. *majus* Hassl., Trab. Inst. Bot. Farm. Buenos Aires **45**: 70, 1928. (as "*major*"). (Holotype: Paraguay, Sierra de Amambay, *Hassler 11327* G)
P. robustum var. *cinerascens* f. *minus* Hassl., loc. cit. (As "minor"). (Lectotype: Paraguay, *Hassler 624* G. Syntype: Paraguay, nr Tobaty, *Hassler 6281* G)

As in var. *ptilodon* except: *fronds* 110 (50-170) cm long; *blades* 90 (45-130) cm long, 14 (9-22) cm wide; segments 70 (40-110) mm long, 8 (5-11) mm wide, gradually reduced to auricles at the blade base, expanded and symmetrical at the base in the upper part of the blade, with the lower edge perpendicular to the rachis in the lower half of the blade, 16 (10-21) pairs of segments in the middle one-fourth of the blade; costa decurrent on the rachis, thinly pilose with golden, acicular hairs ca 0.5 mm long; spores ca 52μ long.

Habitat: terrestrial, occasionally epiphytic or epipetric, in moist woods and along streams, up to 1400 m alt.

Distribution: Bolivia and eastern Brazil to northern Argentina.—Fig. 11.

BOLIVIA: LA PAZ: Tipuani, Hacienda Simaco, *Buchtien 5249* (US).
BRAZIL: CEARA: Sitio Pe de Ladeira, 3 km E of Guaramiranga, *Cutler 8324* (GH). MINAS GERAIS: Fazenda de Aguada, Viçosa, *Mexia 5180* (GH, MO, US). RIO DE JANEIRO: Meio de Serra, *Smith & Brade 2290* (GH); Monte Serrat, Mt Itatiaya, *Smith 2296* (GH); Nova-Friburgo, *Leite 4816* (MO); Petrópolis, *Drogo 324* (US); Rio de Janeiro, *Wilkes Exped.* in 1838-1842 (US); Tijuca, *Ball s.n.*, 22-23 July 1882 (GH); *Glaziou 1725* (BR, C); *Mosén 114* p.p (S, non S-PA). SAO PAULO: Igaupe, *Brade 7735* (US); Mun. Moji-Guacu, Fazenda Campininha, 6 km NNW of Padua Sales, *Eiten & de la Sota 2123* (US), PARANA: Tibagy, *Reiss 67* (GH). RIO GRANDE DO SUL: Mun. Rio Pardo, *Jürgens s.n.* (Rosenstock 422) (US); São Leopoldo, *Reitz 168* (US).
URUGUAY: Montevideo, no data (MO).
PARAGUAY: betw Río Apa & Río Aquidaban, San Luis, *Fiebrig 4417* (GH); Sierra de Maracajú, Igatimí, *Hassler 5511* (GH); *Villarica, Jörgensen 4605* (MO).
ARGENTINA: MISIONES: Iguazú, Puento Iguazú, *de la Sota & Cuezzo 1556* (US); Posadas, *Ekman s.n.*, in 1907-1908 (MO).

See under *P. paradiseae* and *P. ptilodon* var. *ptilodon* for comments regarding the affinities with var. *robustum.*

23d. *Polypodium ptilodon* var. **pilosum** A. M. Evans, var. nov.—Fig. 20.

A var. ptilodonte simile, frondibus approximatis vel fasciculatis, stipitibus brevibus pilis numerosis longis acicularibus (interdum pilis brevioribus) praeditis, rhachibus cum pilis eis stipitium similibus et paleis inconspicue fimbriatis praeditis, lamina lineari-elliptica, segmentis apice rotundatis, basi symmetricis, infimis numerosis reductis triangularibus, costis horizintalibus, pilis dissitis longis acicularibus praeditis, venis 1-vel 2-furcatis, sporangiis cum 2 vel 3 inconspiuis setis praeditis, sporis 47μ longis differt.

As in var. ptilodon except: *rhizome* long-creeping to suberect; *fronds* 49 (27-73) cm long, approximate to fasciculate on the rhizome; stipe 2 (1-5) cm long; stipe and rachis with numerous long acicular hairs 1.5-2 mm long, occasionally with shorter, acicular hairs; rachis paleae with inconspicuously fimbriate margins; *blades* linear-elliptic, 47 (26-70) cm long, 6.5 (3.5-9) cm wide; segments 32 (18-48) mm long, 5.5 (3-9) mm wide, reduced to numerous pairs of triangular lobes at the blade base, rounded at the apex, symmetrical at the base, the spaces between segments less than one-half the width of the segment; costa perpendicular to the rachis, with scattered long acicular hairs 1.5-2 mm long; veins once- or twice-forked; *sporangia* with 2 or 3 short, inconspicuous, capsular setae up to 45μ long; spores ca 47μ long.

Holotype: British Guiana, Demerara, Essequibo River, *Jenman s.n.* NY.

Habitat: epiphytic or occasionally epipetric in humid forests, 400-1000 m alt.

Distribution: TRINIDAD: Blanchisseuse Rd, *Hombersley 306* (US); Maracas, *Hombersley 30* (US), *88* (US), Morne Bleu, *Britton et al.* (US).

BRITISH GUIANA: Essequibo River, nr mouth of Onoro Creek, *Smith 2781* (GH); Shodikar Creek (Essequibo tributary), *Smith 3010* (GH).

VENEZUELA: NEUVA ESPARTA: Copey, *Gines 3799* (US). MIRANDA: Guinand Estate (Cárdenas), Siquire Valley, *Pittier 5949* (US). AMAZONAS: Cerro Duida, Cano Negro, *Steyermark 57993* (US).

PERU: SAN MARTIN: Tingo Mariá, *Allard 21541* (US). HUANUCO: Tingo Mariá, Río Huallaga, *Tryon 5334* (GH, US). JUNIN: Santa Rosa, Pichis Trail, *Killip & Smith 26201* (US).

BOLIVIA: LA PAZ: San Carlos, Mapiri region, *Buchtien 208* (US), *1072* (US). COCHABAMBA: Antahuacana, *Buchtien 2167* (US); Puerto Polonia, Río Coni, 14 km E of San Antonio, *Cárdenas & Cutler 8324* (GH, MO).

BRAZIL: CEARA: Sitio Pe da Ladeira, 3 km E of Guaramirango, *Cutler 8324* (GH, MO). RIO DE JANEIRO: Ilha Grande, *Rose 20350* (US).

This is the most distinct of the varieties of *P. ptilodon* because of the rounded segments, the conspicuously longer hairs of the rachis and costa, and the very short stipe. It is like the other varieties in the curious distribution of acicular hairs only around the sorus (a character found only in this species) and in the gradual reduction of the basal segments. Superficially it resembles *P. consimile*, but the harsher texture, the trichomes of the lamina and costa, and the rhizome scales are different.

24. *Polypodium consimile* Mett., Ann. Sci. Nat. (Paris) V, **2:** 253, 1864.

Rhizome short- to long-creeping, 5 (3-7) mm in diam; rhizome paleae linear-triangular to triangular, dark red-brown to blackish, lustrous, basifixed, attenuate to acute, non-clathrate to sub-clathrate, slightly comose to comose with hairs completely obscuring the paleae throughout the rhizome, entire; *fronds* 25-65 cm long, close-spaced to approximate on the rhizome; stipe short to almost lacking; rachis 6-20 times as long as the stipe; stipe and rachis light to dark red-brown, with few acicular hairs up to 0.75 mm long and with inconspicuous ctenoid and clavate hairs; rachis paleae inconspicuous, linear, entire; *blades* narrow-ovate, 23-60 cm long, 4-15 cm wide, narrow-cuneate at the base; segments 20-75 cm long, 5-11 mm wide, perpendicular to the rachis, reduced to numerous short lobes at the blade base, straight, herbaceous, obtuse to rounded, the base symmetrical, expanded and confluent throughout, entire, the spaces between segments narrower than the segments; lamina essentially glabrous, with occasional long, acicular hairs and small scattered, clavate hairs; costa decurrent on the rachis, with trichomes like those of the lamina; veins twice-forked, free; guard cells ca 43μ long; sori inframedial, round, small, with simple and branched, clavate paraphyses up to 160μ long; *sporangia* golden or brownish, with or without capsular setae; spores reniform, tuberculate, ca 40μ long.

As here construed, this species consists of the two varieties discussed below.

1. Sporangia setose; rhizome paleae narrow-triangular, not obscured by dorsal hairs; blade 6.5 (4-11) cm wide. ....24a. *P. consimile* var. *consimile*
1. Sporangia without setae; rhizome paleae broad-triangular, completely obscured by dorsal hairs; blade 12 (10-15) cm wide. ....24b. *P. consimile* var. *pastazense*

24a. *Polypodium consimile* var. *consimile.*

P. consimile Mett. ex D. C. Eaton, Mem. Amer. Acad., n.s., **8:** 198, 1860, nomen nudum. (Based on: Venezuela, propre colonia Tovar, *Fendler 220* B, GH, MO, US)
P. consimile Mett. var. *minus* Hieron., Bot. Jahrb. Engler **34:** 519, 1904 (as "*minor*"). (Lectotype: Colombia, Tolima, Río Ambica, 2000 m, *Lehmann 2353* B fragment, isolectotypes LE, US. Syntype: Venezuela, Aragua, Colonia Tovar, *Moritz 255,* p.p. These two collections were separated by Hieronymus as "Forma 1" and "Forma 2," without assigning formal names. The specimen of "Forma 1" is chosen lectotype)
P. pityrolepis Rosenst., Repert. Sp. Nov. **22:** 16, 1925. (Holotype: Costa Rica, Río Chris, Juán Vinas, 1200 m, 30 Mar 1910, *Brade & Brade 694* S-PA; isotypes NY, US)

Rhizome paleae linear- to narrow-triangular, comose hairs not obscuring the paleae; *fronds* 40 (25-60) cm long; rachis 12 (6-17) times as long as the stipe; *blades* 36 (23-50) cm long, 6.5 (4-11) cm wide; segments 34 (20-55) mm long, 5 (4-9) mm wide; *sporangia* mostly with 2 capsular setae up to 80μ long.

Holotype: Colombia, Ocaña, Norte de Santander, 6000-7000 ft. *Schlim 633* B; isotypes BR, G, L.

Habitat: mountain slopes, montane forest and ravines, terrestrial or on mossy tree bases, 300-2300 m alt.

Distribution: Hispaniola, Jamaica, Guatemala south to Colombia and Venezuela.—Fig. 8.

GUATEMALA: EL QUICHÉ: Chamá, *Johnson 206* (US). ALTA VERAPAZ: Cubilquitz, *von Tuerckheim s.n.,* Nov 1903 (US).

COSTA RICA: Cabeceras del Bkís, *Pittier 10572* (US); *Cooper 6057* (MO), *Cooper s.n.,* Nov 1886 (GH). ALAJUELA: Zarcero, *Smith 48/32, 48/137, 48/195, 48/242, 48/247* (US), *F72* (MO). SAN JOSÉ: La Hondura, *Standley 37801* (US); La Palma, rd to La Hondura, *Scamman 7763* (GH); Las Nubes, *Scamman 7229* (GH). CARTAGO: Cartago, *Cooper s.n.,* Apr 1888 (GH, MO, US); Cerro de la Carpintera, *Standley 34310, 35537* (US); Navarro, *Rorres R. s.n.,* 20 Dec 1923 (US).

PANAMA: CHIRIQUI: Bajo Mona, mouth of Quebrada Chiquero, *Woodson et al. 1028* (US); El Boquete, *Cornman 893, 1177, 1198* (US); "Camp I," Holcombs Trail, 10 mi above El Boquete, *Killip 5228, 5253* (US); above El Boquete, Río Panduro, *Killip 5419* (US), Roballo Trail, Río Piarnasta toward the Cordillera, *Killip 5424* (US).

DOMINICAN REPUBLIC: MONTE CRISTO: Las Rosas, *Ekman s.n.,* 6 June 1926 (US).

HAITI: Furcy, *Leonard 4611, 4728, 4776* (US); Massif de la Selle, Croix-des-Bouquets, *Ekman s.n.,* 2 Apr 1925 (US); Mission, Fonds Varettes, *Leonard 4022* (US).

JAMAICA: Clyde River, below Cinchona, *Underwood 435* (US).

VENEZUELA: MONAGAS: Cerro de Turumiquire, *Tate 103, 104* (US). DISTRITO FEDERAL: Cordillera del Avila, above Caracas, betw Los Venados & Papelón, *Steyermark 55070* (GH, MO, US). ARAGUA: Colonia Tovar, *Fendler 220* (B, GH, MO, US), *220B* (GH, US).

COLOMBIA: SANTANDER: Río Suratá, above Suratá, *Killip & Smith 16647* (GH, US). CUNDINAMARCA: Bogotá, *Ariste-Joseph* (GH, US).

Although superficially similar to *P. ptilodon* var. *pilosum,* this species differs in the shorter rachis hairs, the lack of the stiff hairs around the sori, and the segments with symmetrical bases.

There may be valid varieties in this species other than the var. *pastazense* discussed below. The plants from Central America, represented by *P. pityrolepis* Rosenst., tend to have a lighter brown, glabrous or subglabrous, narrower blade, shorter stipes, and darker brown sporangia than the material from elsewhere in the range. Venezuelan plants tend to have shorter, more clathrate, and less comose rhizome scales, almost golden sporangia, and darker brown rachises and longer stipes.

24b. *Polypodium consimile* var. **pastazense** (Hieron.) A. M. Evans, comb. nov.

P. pastazense Hieron., Hedwigia **48**: 257, *t. 13, fig. 22,* 1909. (Holotype: Ecuador, betw Baños & Jivaría de Píntuc in Pastaza Valley, *Stubel 1011* B)

Rhizome paleae short, triangular, dark red-brown, acute, non-clathrate, comose with hairs completely obscuring the scales throughout the rhizome; *fronds* 54 (42-65) cm long, spaced ca 1 cm apart on the rhizome; rachis 15 (12-20) times as long as the stipe; stipe and rachis red-brown, glabrescent with short, acicular hairs; *blades* 50 (40-60) cm long, 12 (10-15) cm wide; segments 60 (45-75) mm long, 9 (6-11) mm wide, obtuse at the apex; *sporangia* without setae.

Habitat: epiphyte in montane forests, 325-2300 m alt.

Distribution: Colombia and Ecuador.—Fig. 8.

Colombia: narino: betw Río Miraflores & Río San Martín, Volcán de Cumbal region, *Ewan 16157* (US).

Ecuador: napo-pastaza: Andes, *Spruce 5260* (US); betw Puyo & Canelos, *Mexía 6832* (US); Hacienda La Mascota, Canton Mera, *Mexía 7016* (US). zamora-chinchepe: Cordillera Cutucu, *Camp E-1393* (US).

In the original description, Hieronymus noted the similarity between his species and *P. consimile.* I believe that it is sufficiently distinct to maintain varietally, because of the more robust aspect, the more nearly glabrous lamina, non-setose sporangia, and particularly the complete obscuring of the rhizome scales by the dorsal hairs. The spore and guard cell sizes do not suggest hybridity or polyploidy, and it is probable that this is a local endemic variety just south of the broader range of var. *consimile* and undergoing allopatric speciation.

25. *Polypodium recurvatum* Kaulf., Enum. Fil. 106, 1824.

P. extensum Fée, Crypt. Vasc. Bras. **1**: 85, *t. 28, fig. 3,* 1869, non Forst., 1786. (Holotype: Brazil, Rio de Janeiro, *Glaziou 2403* B)

P. paradisiastrum Fée, Crypt. Vasc. Bras. **1**: 90, *t. 29, fig. 2,* 1869. (Lectotype: Brazil, Rio de Janeiro, Corcovado, *Glaziou 974* P, isolectotype BR. Syntypes: Brazil, Rio de Janeiro, Corcovado, *Glaziou 396* P, at BR is *P. pectinatiforme,* Brazil, Therezopolis, *Glaziou 1725 P. Glaziou 1725* at BR and C represent *P. ptilodon* var. *robustum*)

P. paraguayense Baker, Jour. Bot. 310, 1878. (Type: Paraguay, forests nr base of Cerro Telado, nr Villa Rica, *Balansa 388* G)

P. pectinatum L. var. *recurvatum* (Kaulf.) Sodiro, Crypt. Vasc. Quit. 335, 1893.

P. paradisiastrum f. *crenulatum* Rosenst., Hedwigia **46**: 140, 1906 (as "crenulata"). (Holotype: Brazil, Santa Catarina, Lages, *Spannagel 145* S-PA)

P. paradisiastrum forma *pectinatum* Rosenst., loc. cit. (as "*pectinata*"). (Holotype: Brazil, Rio Grande do Sul, Serra João, Rodriguez, *Jürgens 159* S-PA)

P. recurvatum var. *minus* Rosenst. ex Hassl., Trab. Inst. Bot. Farm. Buenos Aires **45**: 69, 1928. (Holotype: Paraguay, *Hassler 3990* G; isotype B)

P. recurvatum var. *paraguayense* (Baker) Hassl., loc. cit.

P. recurvatum var. *subbipinnatifidum* Rosenst. ex Hassl., loc. cit. (Holotype: Paraguay, *Hassler 12241b* G)

Rhizome long-creeping, 6 (5-7) mm in diam; rhizome paleae narrow-triangular, light red-brown, non-lustrous, basifixed or basally cordate, acute, inconspicuously comose, non-clathrate, the margins inconspicuously papillate; *fronds* 53 (22-90) cm long, spaced ca 1 cm or less apart on the rhizome; rachis 2 (1.5-3.5) times as long as the stipe; stipe and rachis red-brown, with scattered, short acicular silvery hairs, ctenoid hairs absent; rachis paleae inconspicuous, filiform, entire; *blades* triangular to narrow-triangular, 36 (16-65) cm long, 14 (10-24) cm wide, truncate at the base; segments 72 (30-120) mm long, 4.5 (3-6) mm wide, perpendicular to the rachis, occasionally slightly ascending, sometimes slightly shortened at the blade base, straight or occasionally slightly falcate, often slightly constricted toward the rachis, herbaceous or coriaceous, acuminate, expanded and symmetrical at the base, entire (rarely crenate), the spaces between segments 1-3 times as wide as the segments; lamina glabrous; costa perpendicular to the rachis, with scattered, short, acicular hairs; veins twice-forked, free; guard cells ca 39μ long; sori medial, round, with simple, clavate paraphyses; *sporangia* with 2 (1-5) short capsular setae; spores reniform, tuberculate, ca 43μ long; $n = 37$.

Type: Brazil, Santa Catarina, Santa Catarina I, *Chamisso s.n.* B, LE.

Habitat: epiphytic, occasionally epipetric or terrestrial, in forest, 50-1000 m alt.

Distribution: southeastern Brazil and Paraguay.—Fig. 8.

BRAZIL: Campo da Lanca, *Annies s.n.* (Rosenstock 113b) (US). BAHÍA: Toca de Onca, *Rose 20101* (US). RIO DE JANEIRO: Itatiaya, *Rose 20591* (US); Meio da Serra, *Smith & Brade 2289* (GH); Nova-Friburgo, *Leite 4232* (MO); Organ Mts, *Rose 20792* (US), *Wilkes U. S. South Pacific Exp. no. 15* (GH); Sumaré, *Brade 20607e* (MO); Rio de Janeiro, *Monroe s.n.*, in 1864-70 (GH). SAO PAULO: Campos do Jordão, *Leite 3570* (GH), *Leite 3498* (MICH), *Porto 3089* (MO). PARANÁ: Desvio Ypiranga, *Dusén 8337* (GH, MO, US). SANTA CATARINA: Mun. Blumenau, *Smith & Reitz 6287* (US), Hausa, *Lüdenvaldt 1.860* (US); Horto Florestal I. N. P. Ibirama, *Reitz & Klein 3090* (US); Joinville, *Schmalz 87* (MO); Lages, *Spannagel 5, 69, 118* (US); Marata, Pôrto União, *Reitz 4709* (US); São Bento, *Dutsch s.n.* (Rosenstock 113a) (US); Sierra da Pedra, Ararangua, *Reitz C279* (US). RIO GRANDE DO SUL: São Salvador, *Leite 2639 (209)* (GH).

PARAGUAY: Villarrica, *Jörgensen 4385, 4605* (MO), *Hassler 8781* (B, G); Colonia Presidente González, *Regnell I, A. 1813* (US).

This is a distinctive species because of its gray-green foliage, long-acuminate segments, strongly truncate blade, and bright, inconspicuously comose, rust-colored rhizome paleae. Its only really close relative is *P. hygrometricum*, which is smaller in all respects and has only once-forked veins and more obtuse segments.

Many of the specimens from Paraguay have a more herbaceous texture and wider and often deeply lobed segments. They are clearly *P. recurvatum*, although several specific, varietal, and formal names for these have been created. Even though the range of the Paraguayan materials might suggest it, these do not represent intermediates between *P. recurvatum* and *P. hygrometricum*, so far as I can determine.

26. *Polypodium hygrometricum* Splitg., Tijdschr. Nat. Gesch. **7**: 409, 1840.

P. pectinatum L. var. *caliense* Hieron., Bot. Jahrb. Engler **34**: 517, 1904. (Holotype: Colombia, El Valle, Cordillera Occidental de Cali, nr Las Juntas del Dagua, *Lehmann 7668* B; isotypes LE, US)

P. truncatulum Rosenst., Repert. Sp. Nov. **9**: 343, 1911. (Holotype: Bolivia, Antahuacana, valley of Río Espiritu Santo, *Buchtien 2168* S-PA; isotype US)

Rhizome long-creeping, 4 (3-5) mm in diam; rhizome paleae narrow-triangular, sometimes expanded and cordate at the base, light red-brown, basifixed, acuminate, inconspicuously comose, non-clathrate, the margins inconspicuously papillate; *fronds* 27 (10-50) cm long, close-spaced to approximate on the rhizome; rachis 7 (3-15) times as long as the stipe; stipe and rachis red-brown to dark red-brown, pilose with short to long, simple, acicular, silvery hairs, ctenoid hairs absent; rachis paleae inconspicuous, filiform, entire; *blades* 23 (8-40) cm long, 5 (2-9) cm wide, narrow-ovate to narrow-triangular, subtruncate to truncate at the base; segments 25 (10-45) mm long, 4 (2-5) mm wide, perpendicular to the rachis or slightly ascending throughout, narrow-ovate to linear-triangular, herbaceous, obtuse to acute at the apex, expanded and symmetrical at the base, entire; lamina pilose with simple, silvery, acicular hairs, clavate hairs absent; costa decurrent on the rachis, brown or occasionally stramineous or blackish, pilose as on the lamina; veins once-forked, free; guard cells ca 43μ long; sori medial, round, with short, simple, clavate paraphyses; *sporangia* with 2 (1-5) acicular capsular setae; spores reniform, tuberculate, ca 48μ long; $n = 37$.

Holotype: Surinam, Para, *Splitgerber 1069* L.

Habitat: epiphytic, occasionally epipetric or terrestrial, in humid forests, 30-1800 m alt.

Distribution: southern Mexico to western Bolivia.—Fig. 8.

MEXICO: CHIAPAS: Escuintla, Col. Cintalapa, *Matuda 18392* (US), Esperanza, *Matuda 18116* (US); Huixtla, *Purpus 7226* (GH, US).

GUATEMALA: RETALHULEU: Río Xibana, Finca San José Nil, *Hatch & Wilson 403* (US); Pueblo Nuevo, *Rojas 548* (US).

HONDURAS: COLÓN: Claura, *Spinden 38* (US).

NICARAGUA: MANAGUA: Sierras de Managua, *Chaves 7* (US).

COSTA RICA: Río Poás, *Pittier 2426* (US). LIMÓN: La Columbiana Farm, *Standley 36896* (GH, US). HEREDIA: La Selva, Río Puerto Viejo, *Scamman & Holdridge 8098* (GH), *Scamman 7518* (GH). SAN JOSÉ: El General, *Skutch 2667* (MICH, MO, US); San Isidro del General, *Chrysler & Roever 5318* (MICH, US). CARTAGO: Jesús María, *Lankester 617* (US).

PANAMA: Aquarubia, *Killip 2800* (US); Pecora, *Killip 2703* (US). CANAL ZONE: Barro Colorado I, *Bailey 525* (US), Barbour Lathrop Trail, *Wetmore & Woodworth 150* (GH); betw Frijoles & Monte Lirio, *Killip 12134* (GH, US); N of Frijoles, *Standley 27449* (US); Río Indio de Gatún, *Maxon 4815, 4849* (US). DARIEN: Cana, *Williams 931* (US). PANAMA: Juán Díaz, *Killip 2755, 2765* p.p. (US); Charavé River, Chepo, *Pittier 4721* (US); Pearl Archipelago, Canyon Rd, *Erlanson 414, 420* (US); Río Merino, *Erlanson 541* (US); below pumping station, *Johnston 383* (US), Area M, *Johnston 71* (US).

BRITISH GUIANA: Kanaku Mts, Mt Iramaikpang, *Smith 3670* (GH).

VENEZUELA: NUEVA ESPARTA: El Valle, Margarita I, *Miller & Johnston 163* (GH, MO, US). MIRANDA: Parque Nacional de Guatopo, *Steyermark 90178* (VEN). BOLÍVAR: El Morrocoy, Guayapo, Bajo Caura, *Williams 11807* (US); La Unión, Medio Caura, *Williams 11263* (US).

COLOMBIA: MAGDALENA: Codazzi, *Haught 3760* (GH, US); Quebrada Soraria, 6 km E of La Jagua, *Haught 3615* (GH, US); Santa Marta, Río Piedras, *Smith 1028* (GH, MICH, MO, US). SANTANDER: Barranca Bermeja, Magdalena Valley, betw Sogamoso & Colorado

Rivers, *Haught 1424* (MICH, US). CUNDINAMARCA: Sasaima, *González & Daniel 1885* (US). META: jct of Güejar & Zanza Rivers, *Smith & Idrobo 1499, 1506* (US). CHOCÓ: *Schott 1216* (MO); Lloró, 50 km S of Quibdó, jct of Río Atrato & Río Andágueda, *Archer 2066* (US); S of Río Condoto, betw Quebrada Guarapo & Mandinga, *Killip 35138* (US). VALLE DEL CAUCA: Las Juntas del Dagua, *Lehmann 7668* (US); Río Dagua, Quebrada del Río Blanco, *Cuatrecasas 13671* (US); Río Dagua, betw La Elsa & Río Blanco, *Killip 34734* (US).

PERU: LORETO: Río Santiago, above Pongo de Manseriche, *Mexía 6216* (MICH); betw Yurimaguas & Balsapuerto (lower Río Huallaga basin), *Killip & Smith 28164* (US). JUNÍN: Río Pinedo, N of La Merced, *Killip & Smith 23608* (US).

BOLIVIA: COCHABAMBA: Antacahuana, ca 160 km NE of Cochabamba, *Buchtien 2168* (US).

This species is easily recognized by its bright- or gray-green foliage, bright-ferruginous rhizome scales, truncate blades, and silvery pilose pubescence. It varies somewhat from north to south. Material from Central America is smaller, pale- or lime-green, sometimes with a stramineous rachis or costa and more blunt segments. The southern form is larger, more gray-green, and with more acute segments. The hairs of the blade vary in length throughout the range but are always characteristically silvery. Except for pubescence, which is most strongly expressed in the middle of the range (i.e. northern South America), the variation is evidently a cline ranging from smaller, more obtusely lobed plants in Central America to taller, acutely lobed ones in Peru.

The allied species *Polypodium recurvatum* from Paraguay and Brazil differs in being more glabrous and more robust and in having very long, almost acuminate segments, but it is otherwise quite similar. It is isolated geographically from the range of *P. hygrometricum,* and the differences between the two probably result from allopatric speciation.

SPECIES DUBIAE ET EXCLUDENDAE

Polypodium bolivianum Rosenst. var. *brevipes* Rosenst., Repert. Sp. Nov. **12:** 473, 1913 (Type: Bolivia, North Yungas, Polo-Polo, nr Corioco, 900 m alt, *Buchtien 3497* S-PA?). This is probably a small specimen of *P. bolivianum* Rosenst.

P. inversum Vell., Fl. Flum. **11:** 11, *t. 72,* 1827, nomen nudum; Arch. Mus. Nac. Rio **5:** 448, 1881. No Velloso types exist; the name must be based on the description and illustration of a plant from Rio de Janeiro, Brazil. It is usually considered a synonym of *P. plumula* (Morton, pers. comm.), but other similar species in that region include *P. dispersum, P. siccum* and *P. filicula.*

P. lomariiforme Kunze, Linnaea **9:** 42, 1834 (as "*lomariaeforme*") (Type: "in flor. Peruv. montibus aridioribus as Cassapi 1829, Lect. *Diar. 1152,* Herb. Poepp., Kze., etc."). I have seen a specimen at K labeled as having been sent to Kunze from Poeppig. It is dated 1830, but Mr. Morton (pers. comm.) indicates that Poeppig's Peruvian collections are often misdated. Kunze's herbarium at Leipzig is destroyed. The Kew specimen may be an isotype although Dr. Jarrett questions this (pers. comm.). There may be authentic material at Berlin. The specimen agrees with the protologue except that the frond is pinnatisect rather than pinnate, and it agrees with my *P. camptophyllarium* Fée var. *lachniferum* (Hier.) Evans. If a satisfactory determination of type material supports this, *P. lomariiforme* would take precedence.

P. maenurum Link, Hort. Reg. Bot. Berol. Descr. **2:** 96, 1833 (Type: none cited, probably at B). The protologue compares it to *P. paradiseae* Langsd. & Fisch., and it has been considered a synonym of *P. recurvatum.*

P. otites L., Sp. Pl. 1085, 1753 (Type: none in LINN; based on the illustration in Petiver, Pteridographia 32, *t. 1, fig. 16*). Although this name has been associated with *P. pectinatum* L., it is not a member of this complex, and is more nearly allied with *P. tenuifolium* Humb. & Bonpl. ex Willd. [in L., Sp. Pl., ed. 4, **5:** 185, 1810 (Type: Venezuela, Cumanacoa, *Humboldt* 437 B-photo)].

P. pectinatiforme var. *brevipes* Rosenst. in Buchtien, Contrib. Fl. Bolivia **1:** 38, 1910, nomen nudum.

P. pectinatiforme f. *parvum* Sehnen, Pesquisas, Bot. **10:** 33, 1960. No type is cited and the name is, therefore, invalidly published.

P. pectinatum var. *acuminatum* Baker, Jour. Bot. Brit. For. **25:** 25, 1887 (Type: Costa Rica, *Cooper* K). The specimen is incomplete and cannot be determined with confidence. It appears not to belong to this complex.

P. pectinatum L. var. *baezanum* Mille, Revista Col. Nac. Vic. Rocofuerte **9:** 202, 1927 (Type: none cited; authentic material may be at B or in Ecuador). It is not possible to place this name with confidence; it may be *P. consimile* Mett.

P. pectinatum L. var. *bourgaeanum* Fourn., Mex. Pl. 76, 1872. (Syntypes: "In valle Cordobensi, dec. sp. *Bourgeau 1431, 1436;* Guadalupa, Nova-Grenada *Lindig* 45; Brasilia."). No syntype has been seen, but the protologue indicates that the plant has ellipsoid sori and anastomosing veins, neither of which would place it in *P. pectinatum* L., and would tend to exclude it from the group altogether.

P. pectinatum L. var. *brachypus* Sodiro, Crypt. Vasc. Quit. 334, 1893 (Type: "Crece en los bosques de Gualea colectado por el Sr. D. Rodolfo Riofrio."). No type has been seen; the description is inconclusive.

P. pectinatum L. var. *hispidum* Christ in Pittier, Prim. Fl. Cost. 3: 15, 1901 (as "*hispida*") (Type: "El Paramó, 3000 m, versant E du massif de Buena Vista, Jan 1897, *Pittier 10474* P? or BR?). =*Ctenopteris semihirsuta* (Klotzch) Copeland, Phil. Jour. Sci. **84:** 450, 1955).

P. pectinatum L. var. *jürgensii* Rosenst., Hedwigia **43:** 229, 1904 (Syntypes: Brazil, Santa Cruz, auf Berg João Rodriquez, 200 m, *Jürgens & Stier* 82 S-PA?; Joinville, Santa Catharina, *Schmalz 56* S-PA?). *Schmalz 56* at MO is not a member of this complex, and other material has not been seen.

P. pectinatum. L. var. *paradisiae* Sodiro, Crypt. Vasc. Quit. 334. 1893, non Baker, 1870 (Type: "Crece en la region tropical y subtropical, en lugares secos y pedregosos; en la orilla del rio Pilatón."). This is presumed to be a new variety rather than a transfer as *P. paradiseae* Langsd. & Fisch. is cited only with a query, and does not occur in Ecuador. From the description, *P. bolivianum* suggests itself.

P. venustum Desv., Gesell. Naturf. Freund. Berlin Mag. **5:** 315, 1811 (Type: "Habitat in America calidiore Antillisque", Herb. Desv. P-photo). Although Christensen (1906) referred this name to *P. taxifolium* L., the photo of the type indicates that it is a eupolypodium. It would appear to be *P. camptophyllarium* Fée, over which it would take precedence, but I would have to see the the specimen to be sure that it was not *P. eurybasis* or *P. consimile.*

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Fig. 1. Morphology of the sporophyte. (A) Rhizome cross-section of *P. ptilodon* var. *robustum, de la Sota 10* (EVANS), ×5.5. (B) Vascular bundle from A, ×80. (C) Rhizome cross-section of *P. truncorum, de la Sota 21* (EVANS), showing only two vascular bundles and thick-walled cells of the inner ground parenchyma, ×5.5. (D) Cross-section of the blade segment of *P. ptilodon* var. *robustum, de la Sota 10* (EVANS), showing the mesophyll and the sclerified bundle sheath, ×80. (E) Localized distribution of laminar hairs around the sorus in *P. ptilodon* var. *ptilodon, Hutchison 1470* (MICH), ×6.5. (F) Ctenoid hairs of the rachis of *P. ptilodon* var. *ptilodon, Hutchison 1470* (MICH), ×6.5. (G) Rhizome palea of *P. dispersum, Evans 2007* (MICH), ×18. (H) Rachis palea of *P. dispersum, Evans 2007* (MICH), ×18. (I) Rhizome palea of *P. cupreolepis, Pringle-3353* (GH), ×18. (J) Rhizome palea of *P. plumula, Copeland 16059* (MICH), ×18. (K) Palea from the rhizome apex of *P. bolivianum,* (US 1007896), ×18. (L) Palea from the side of the rhizome of *P. bolivianum,* (US 675781), ×18.

Fig. 2. Gametophyte development and sporophyte juvenile leaves. (A) Stages of development of the young gametophyte of *P. dispersum, Evans 2008* (MICH). (B) Stomates on the gametophyte of *P. dispersum, Evans 2008* (MICH). (C) Stages of development of the young gametophyte of *P. ptilodon* var. *caespitosum, Evans 2002* (MICH). (D) Mature gametophytes and heteroblastic leaf series of juvenile leaves of *P. dispersum, Evans 2008* (MICH). (E) Heteroblastic series of juvenile leaves of *P. plumula, Evans 1187* (MICH). (F) Mature gametophytes and heteroblastic leaf series of juvenile leaves of *P. ptilodon* var. *caespitosum, Evans 2005* (MICH).

Fig. 3. Representative frond shapes. (A) *P. ptilodon* var. *robustum, Pabst s.n.* (MICH). (B) *P. paradiseae, Sehnen 2* (MICH). (C) *P. curvans, Stork, et al., 10626* (MO). (D) *P. truncorum, Pabst s.n.* (MICH). (E) *P. dispersum, Evans 2008* (MICH). (F) *P. plumula, Evans 1187* (MICH). (G) *P. recurvatum, Sehnen 4* (MICH).

Fig. 4. Epidermal cells, hairs and paraphyses of the lamina. Fig. A-G, Epidermal cells. (A) *P. dispersum* (US 1287974). (B) *P. filicula* (US 1280298). (C) *P. siccum,* (US 1516124). (D) *P. truncorum, Mexia 5105* (GH). (E) *P. hygrometricum, Chrysler & Roever 5318* (MICH). (F) *P. absidatum* (US 1833997). (G) *P. camptophyllarium* var. *macedoi* (US 2081770). (H) Transition of costal hairs to costal paleae in *P. plumula* (US 1049810). (I) Variation in the ctenoid hairs of *P. ptilodon* var. *caespitosum, McFarlin s.n.,* Nov. 4, 1930 (MICH): 1. Rachis; 2. Costa; 3. Lamina; 4. Receptacular paraphyses. Fig. J-P, Laminar hairs and paraphyses. (J) *P. dispersum*: 1. Capsular and receptacular paraphyses, *Wagner 62061* (MICH); 2. Clavate hairs of the costa and lamina (US 1287974); 3. Acicular hairs of the abaxial surface of the costa (US 1287974). (K) *P. filicula*: 1. Receptacular paraphyses, *Ahmuda & de la Sota 51* (EVANS); 2. Clavate hairs of the abaxial surface of the lamina (US 1280298); 3. Acicular hairs of the segment margin (US 1280298); 4. Acicular hairs of the abaxial surface of the costa (US 1280298). (L) *P. absidatum* (US 1833997): 1. Capsular setae; 2. Clavate hairs of the lamina; 3. Hairs of the abaxial surface of the costa; (M) *P. camptophyllarium* var. *macedoi* (US 2081770): 1. Clavate, short and long acicular and setose-clavate forked hairs of the lamina; 2. Acicular hairs of the segment margin; 3. Acicular hairs of the abaxial surface of the costa; 4. Capsular setae and receptacular paraphyses. (N) *P. venturii, Venturi 2970* (GH): 1. (Receptacular paraphyses; 2. Clavate and acicular laminar hairs. (O) *P. ptilodon* var. *robustum, de la Sota & Cuezzo 1556* (EVANS), Capsular seta and simple and branched receptacular paraphyses. (P) *P. sursumcurrens, Copeland 128* (MICH): 1. Clavate laminar hairs; 2. Receptacular paraphyses, showing the range from the simple hair to those with a multicellular subterminal expansion.

Fig. 5. Representative types of rachis paleae. (A) *P. plumula* from: 1. Jamaica, *Maxon et al. 1234* (GH); 2. Mexico *Copeland 16055* (MICH); 3. Mexico (US 1745606); 4. Panama, *Taylor 1390* (MICH); 5. Colombia (US 1692356); 6. Peru (US 2356738); 7. Brazil (US 762365). (B) *P. dispersum, Evans 2007* (MICH). (C) *P. atrum, Lundell 6639* (US). (D) *P. bermudianum, Brown 464* (GH). (E) *P. singeri, Ahmuda & de la Sota 53* (EVANS). (F) *P. ferrugineum, Copeland 125* (MICH). (G) *P. cupreolepis, Pringle 3353* (GH). (H) *P. ptilodon* var. *caespitosum* (FLAS-P1718). (I) *P. filicula, Ahmuda & de la Sota 51* (EVANS). (J) *P. dispersum* (FLAS-P1155, FLAS-P4879). (K) *P. ptilodon* var. *caespitosum* (FLAS-P4881). (L) *P. plumula* (FLAS-P1153, FLAS-P5166).

Fig. 6. Venation patterns and segment shapes. Most of the segments lack the expanded basal portion, M and N lack medial portions, and O and S_1 lack terminal portions. (A) *P. truncorum, Mexia 5105* (GH). (B) *P. siccum* (US 1516124). (C) *P. filicula* (US 1280298). (D) *P. cupreolepis, Pringle* 3353 (GH). (E) *P. sursumcurrens, Copeland 128* (GH). (F) *P. bermudianum* (sterile segment with portion of a fertile segment) (US 848332). (G) *P. dispersum, Evans 2007* (MICH). (H) *P. hygrometricum, Chrysler & Roever 5318* (MICH). (I) *P. plumula, Maguire 25005* (GH). (J) *P. atrum, Stoutamire* 3563 (MICH). (K) *P. ptilodon* var. *caespitosum, McFarlin s.n.*, 4 Nov. 1930 (MICH). (L) *P. pectinatiforme, Copeland 13601* (MICH). (M) *P. bolivianum* (US 675781). (N) *P. consimile var. pastazense* (US 2254236). (O) *P. recurvatum, Copeland 21561* (MICH). (P) *P. venturii, Venturi 2974* (GH). (Q) *P. camptophyllarium* var. *maceodi* (US 1081770). (R_1) *P. pectinatum,* from Guadeloupe (US 1712313). (R_2) *P. pectinatum,* from Surinam. (S_1) *P. camptophyllarium* var. *camptophyllarium,* from Haiti, with typical venation pattern (US 1783820. (S_2) *P. camptophyllarium* var. *camptophyllarium,* from Bolivia, with extreme venation pattern (US 1191631). (T) *P. choquetangense, Cárdenas 3161* (MICH).

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Fig. 9. Geographic distribution of species in the *Polypodium pectinatum-plumula* complex, (as represented by herbarium specimens). (A) *P. plumula, P. sursumcurrens.* (B) *P. atrum, P. dispersum, P. filicula.*

Fig. 10. Geographic distribution of species in the *Polypodium pectinatum-plumula* complex, (as represented by herbarium specimens). (A) *P. alfredii, P. paradiseae, P. pectinatiforme, P. pectinatum, P. venturii.* (B) *P. camptophyllarium* var. *abbreviatum,* var. *camptophyllarium,* var. *lachniferum* & var. *macedoi, P. cupreolepis, P. siccum.*

Fig. 11. Geographic distribution of species in the *Polypodium pectinatum-plumula* complex, (as represented by herbarium specimens). (A) *P. ptilodon* var. *caespitosum,* var. *pilosum,* var. *ptilodon,* var. *robustum.* (B) *P. absidatum, P. choquetangense, P. curvans, P. eurybasis* var. *eurybasis,* var. *glabrescens* & var. *villosum, P. truncorum.*

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Fig. 13. Stages in sporogenesis in *Polypodium dispersum, Wagner 62061* (MICH). (A) Mitosis in the eight pre-mother cells, ×160. (B) Cytokinesis in the eight pre-mother cells, ×160. (C) 16 spore mother cells, ×160. (D) Mitosis in the 16 spore mother cells, ×160. (E) 111 univalent chromosomes at metaphase in the spore mother cells, ×760. (F) Cytokinesis in the 16 diads of young diplospores, ×160. (G) Mature spores, one without a scar, the other with a monolete scar, ×760. (H) 32 young diplospores, ×160.

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Fig. 16. Specialization in the *Polypodium pectinatum-plumula* complex. (A) Rhizome long-creeping (0) to short-creeping or erect (1); (B) Rhizome paleae narrowly triangular (0) to cordate (1); (C) Rhizome paleae non-comose (0) to comose (1) to comose hairs completely obscuring the paleae (2.5); (D) Rachis brown (0) to black (1); (E) Rachis stiff (0) to elastic (1); (F) Rachis straight (0) to spiralled or circinate (1); (G) Rachis glabrous or thinly pilose (0) to densely villose (1); (H) Ctenoid hairs absent (0) to present (1); (I) Rachis paleae filiform (0) to non-filiform (1); (J) Fronds generally 25 cm to 150 cm (0) to less than 25 cm (1); (K) Frond stipitate (0) to sessile (1); (L) Base of the blade subtruncate or cuneate (0) to definitely truncate (1); (M) Basal segments perpendicular to the rachis (0) to occasionally deflexed (0.5) to regularly deflexed (1); (N) Segments perpendicular to the rachis (0) to ascending (1); (O) Perpendicular segment base symmetrical (0) to asymmetrical when the segment is perpendicular to the rachis (1); (P) Segment margin entire (0) to crenate (1) to pinnatifid (1.5); (Q) Lamina glabrous (0) to pubescent (1); (R) Pubescence evenly distributed (0) to localized (1); (S) Lateral veinlets forked (0) to simple (1); (T) Sori medial (0) to marginal (1); (U) Receptacular paraphyses simple (occasionally forked) and with uniform cells (0) to: U_1 paraphyses with a subterminal irregular multicellular expansion (1) or: U_2 paraphyses regularly branched—one branch tipped with a clavate cell and the other tipped with a setose cell (1); (V) Spores up to 50 mu long (0) to over 50 mu long (1); (W) Spores 64 per sporangium (0) to 32 per sporangium (1).

Solid dots represent extant taxa; hollow dots represent hypothetical ancestral intermediates. The character letter is given the first time the specialized condition appears in an evolutionary line. Small letters represent intermediate character states (0.5); capital letters followed by an apostrophe (') represent an extreme character state (1.5). The dotted lines leading to *P. dispersum* indicate its hybrid nature and probable parental types.

Fig. 17. Type specimens of new taxa. Left. *P. cupreolepis* A. M. Evans, *Pringle* 3353 (US 66004). Right. *P. bermudianum* A. M. Evans, *Brown 464* (US 84332), ×¼.

Fig. 18. Type specimens of new taxa. Left. *P. atrum* A. M. Evans, *Lundell 6639* (US 1638286). Right. *P. camptophyllarium* var. *abbreviatum* A. M. Evans, *Herrera 872* (US 1342112), ×¼.

Fig. 19. Type specimens of new taxa. Left. *P. eurybasis* var. *villosum* A. M. Evans, *Fosberg 19688* (US 2290492). Right. *P. ptilodon* var. *pilosum* A. M. Evans, *Jenman s.n.*, in 1897 (NY), ×¼.

Fig. 20. Type and representative specimens. Left. Type of *P. absidatum* A. M. Evans, *Killip & Smith 18518* (US 1353919). Right. Representative specimen of *P. pectinatum* L. s.s., *Evans 2587* (TENN), ×¼.

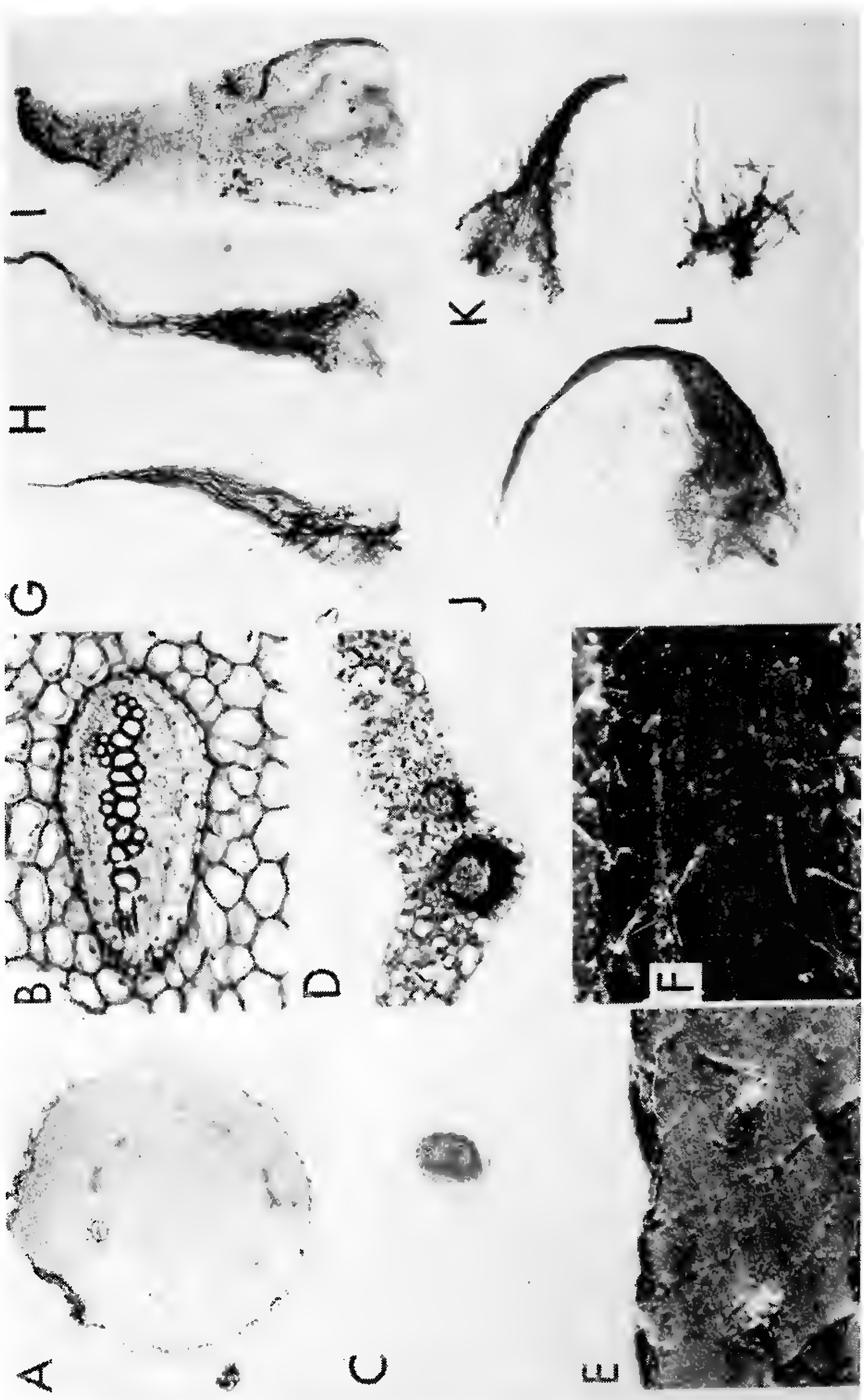


Fig. 1. Morphology of the sporophyte (legend p. 269).

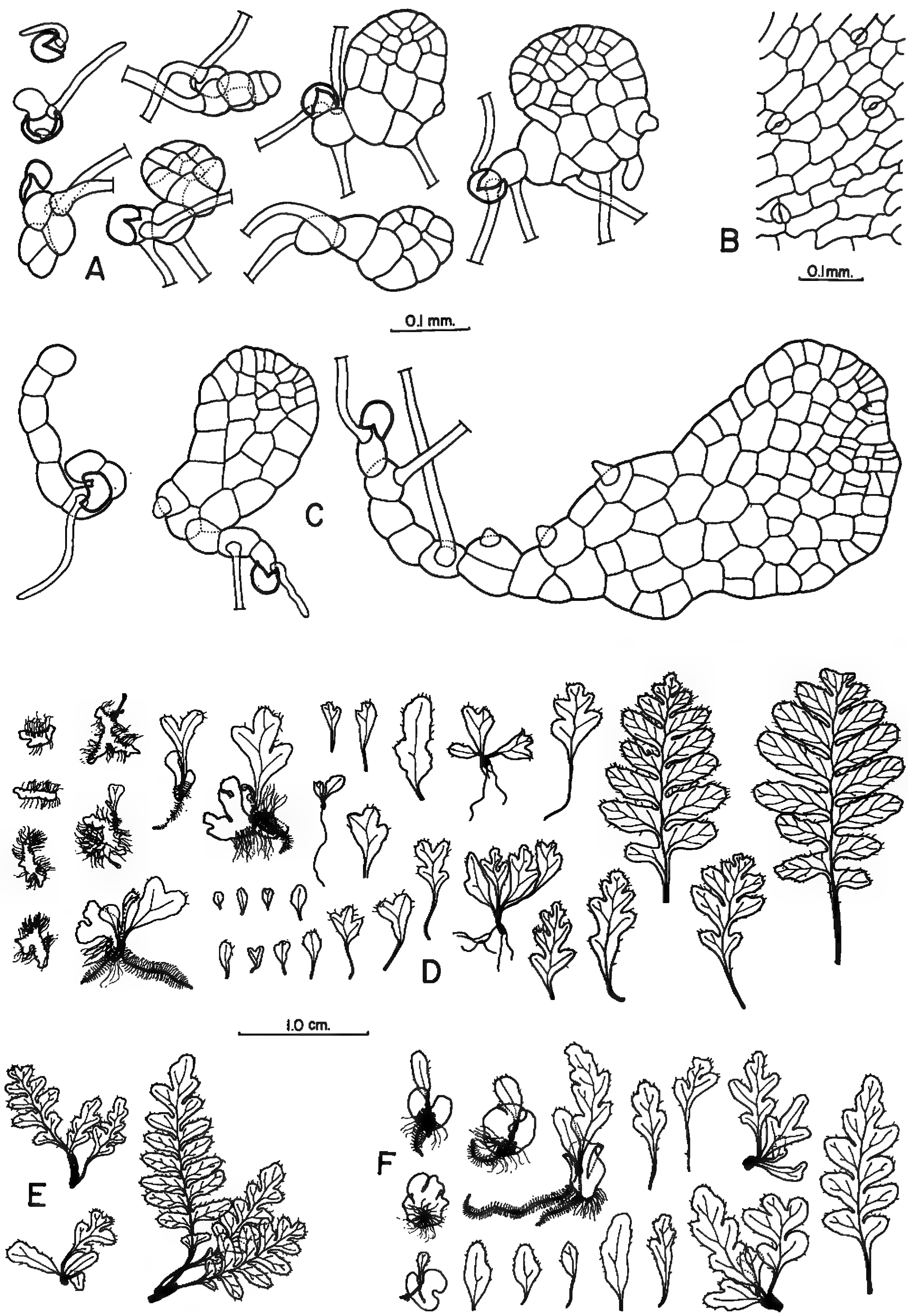


Fig. 2. Gametophyte development and sporophyte juvenile leaves (legend p. 269).

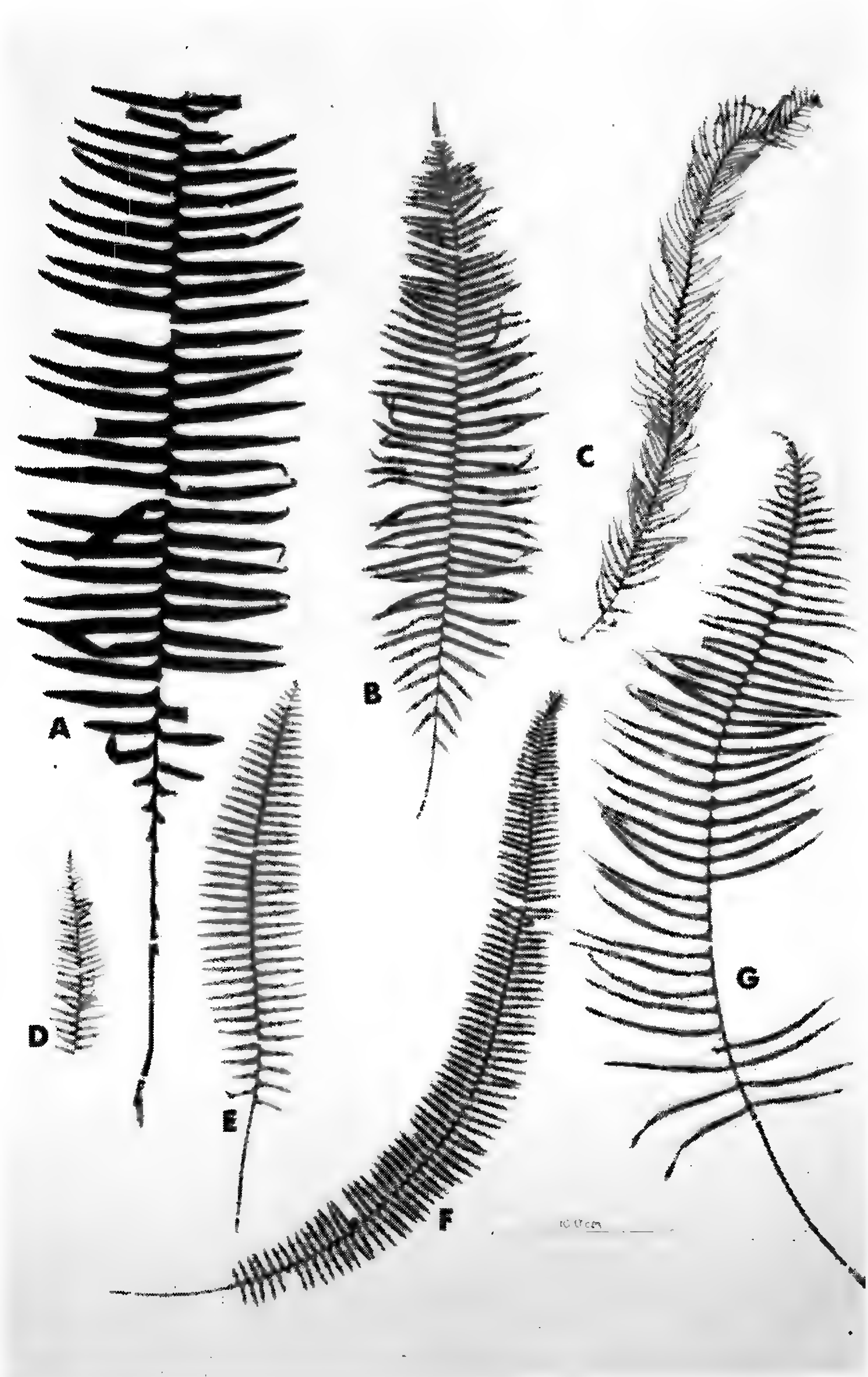


Fig. 3. Representative frond shapes (legend p. 269).

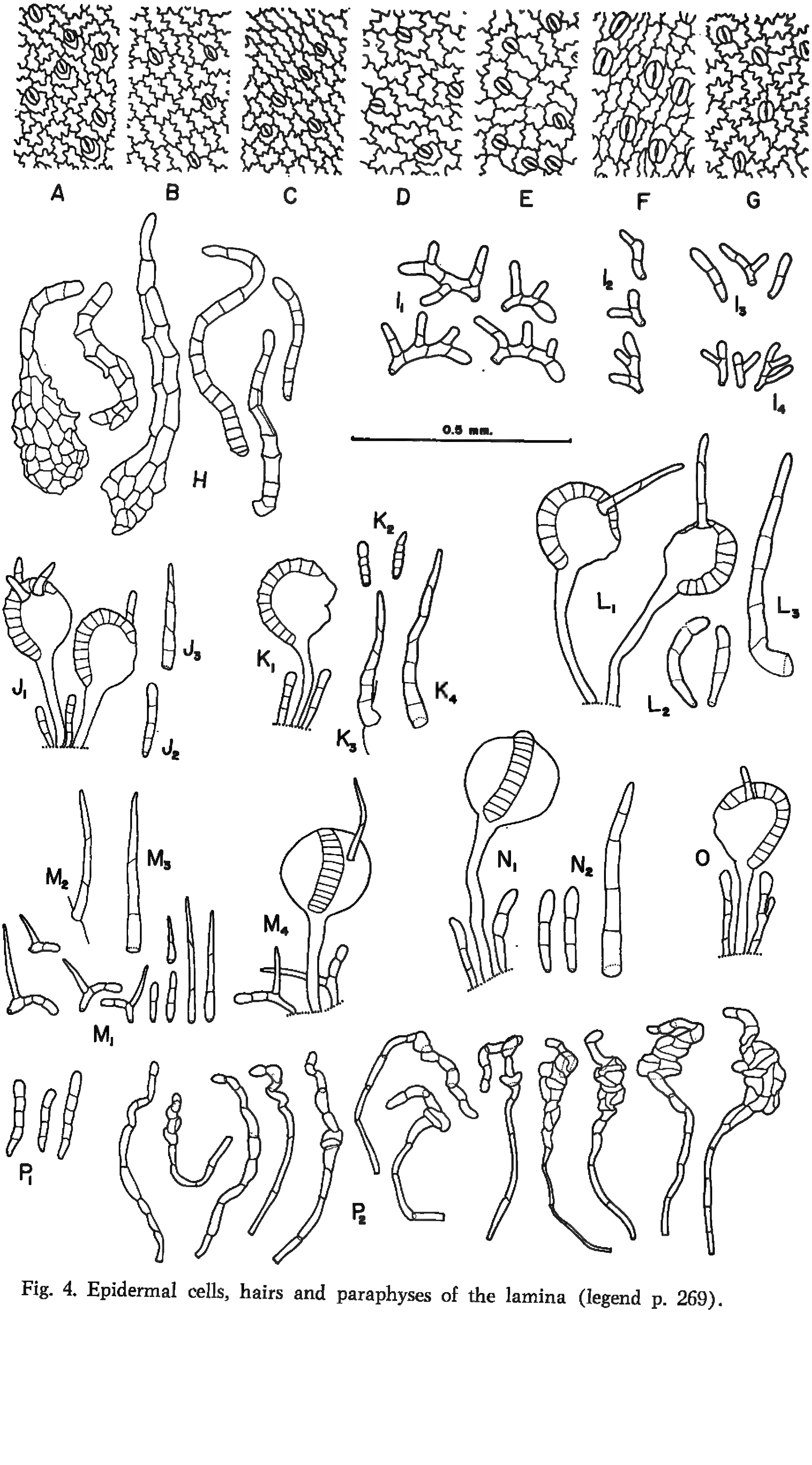


Fig. 4. Epidermal cells, hairs and paraphyses of the lamina (legend p. 269).

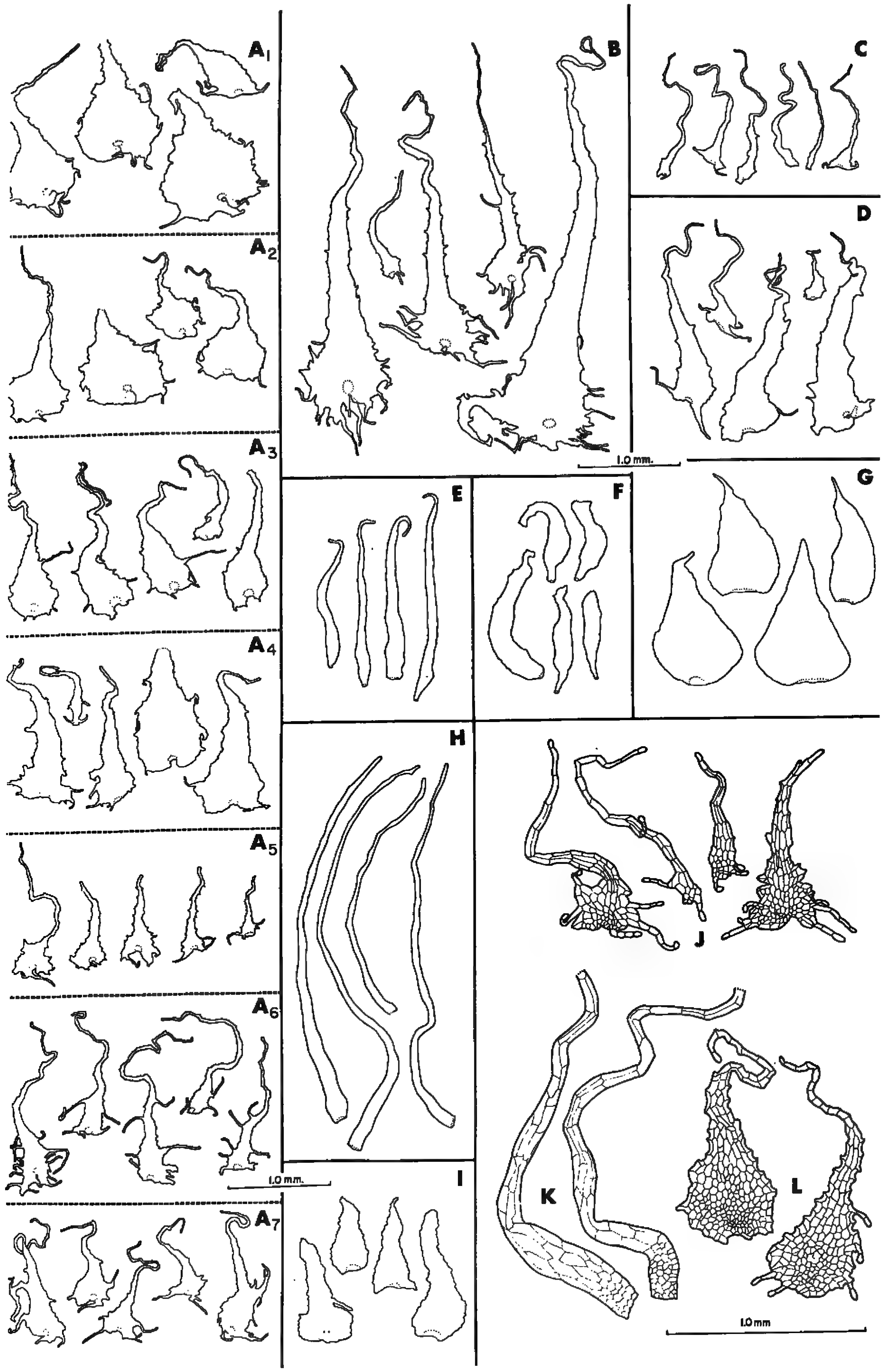


Fig. 5. Representative types of rachis paleae (legend p. 269).

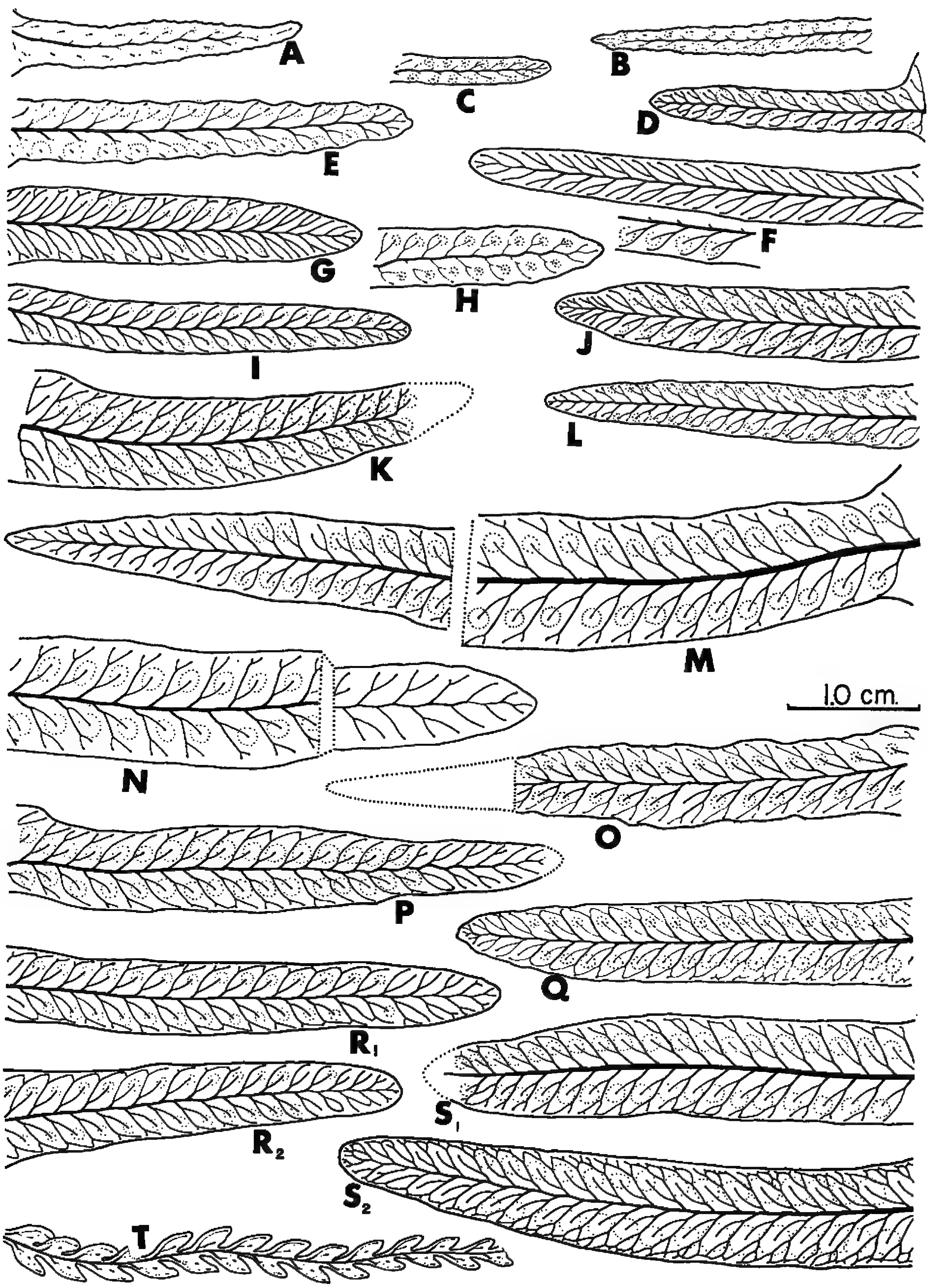
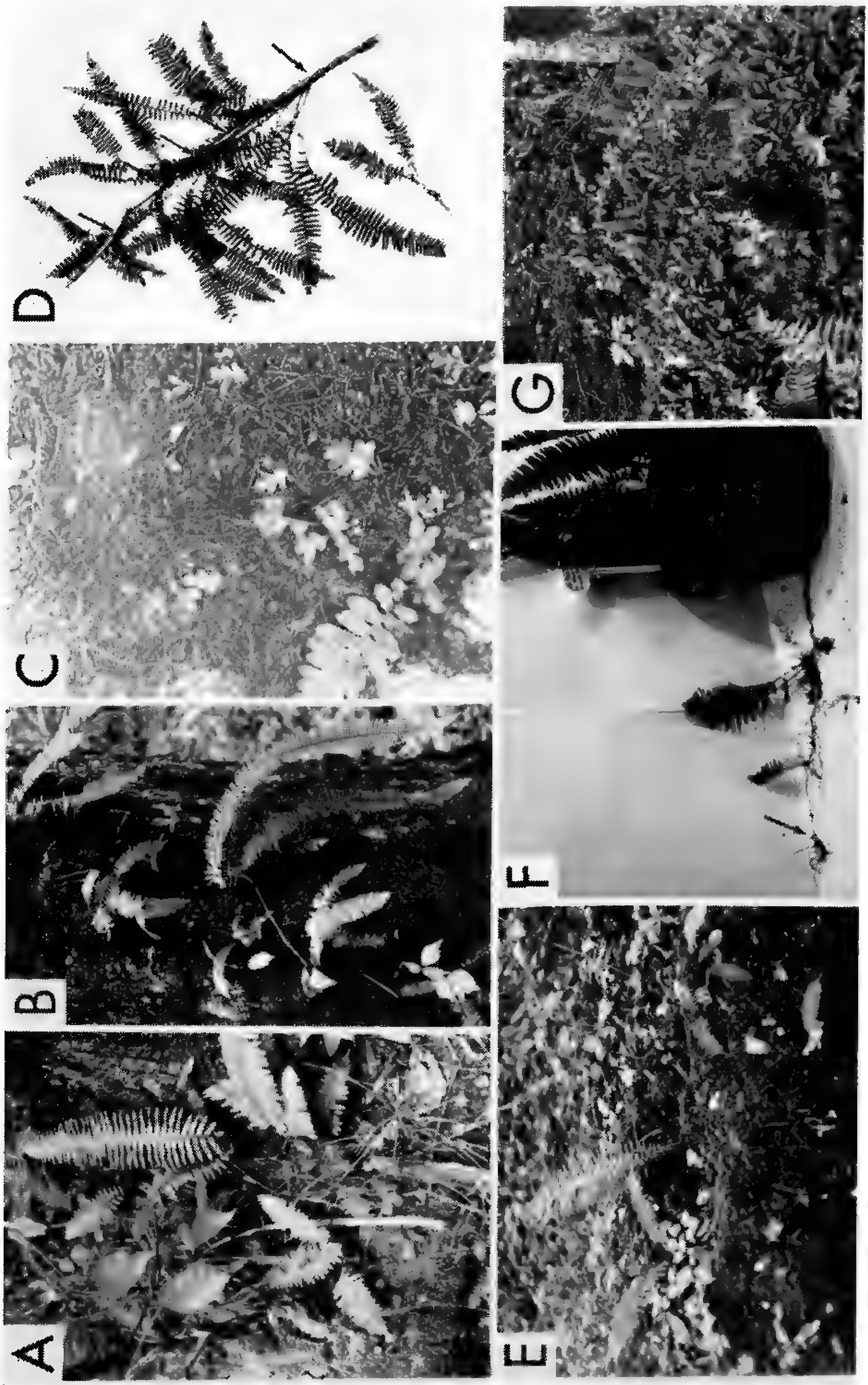


Fig. 6. Venation patterns and segment shapes (legend p. 270).



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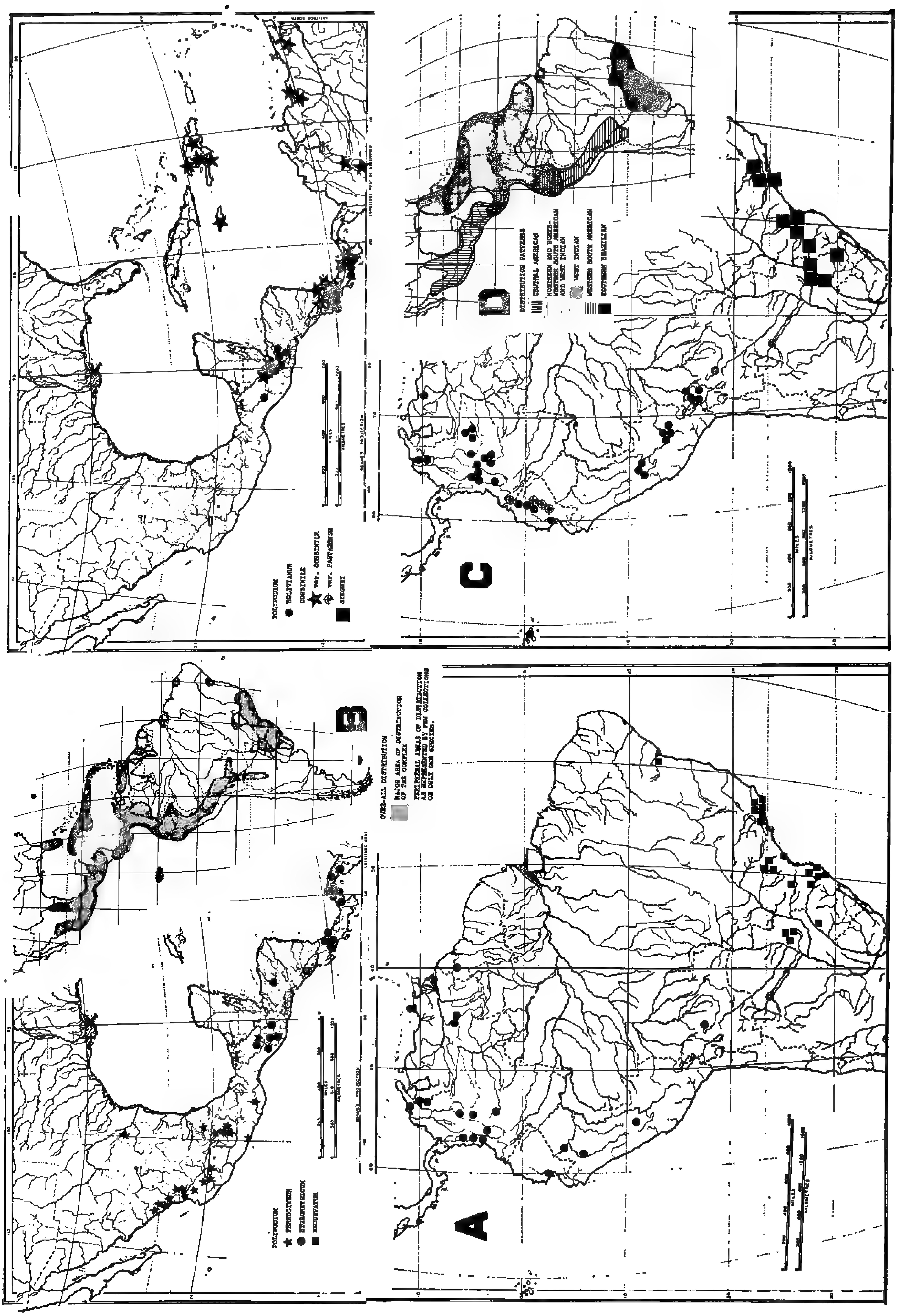


Fig. 8. Geographic distributions (legend p. 270).

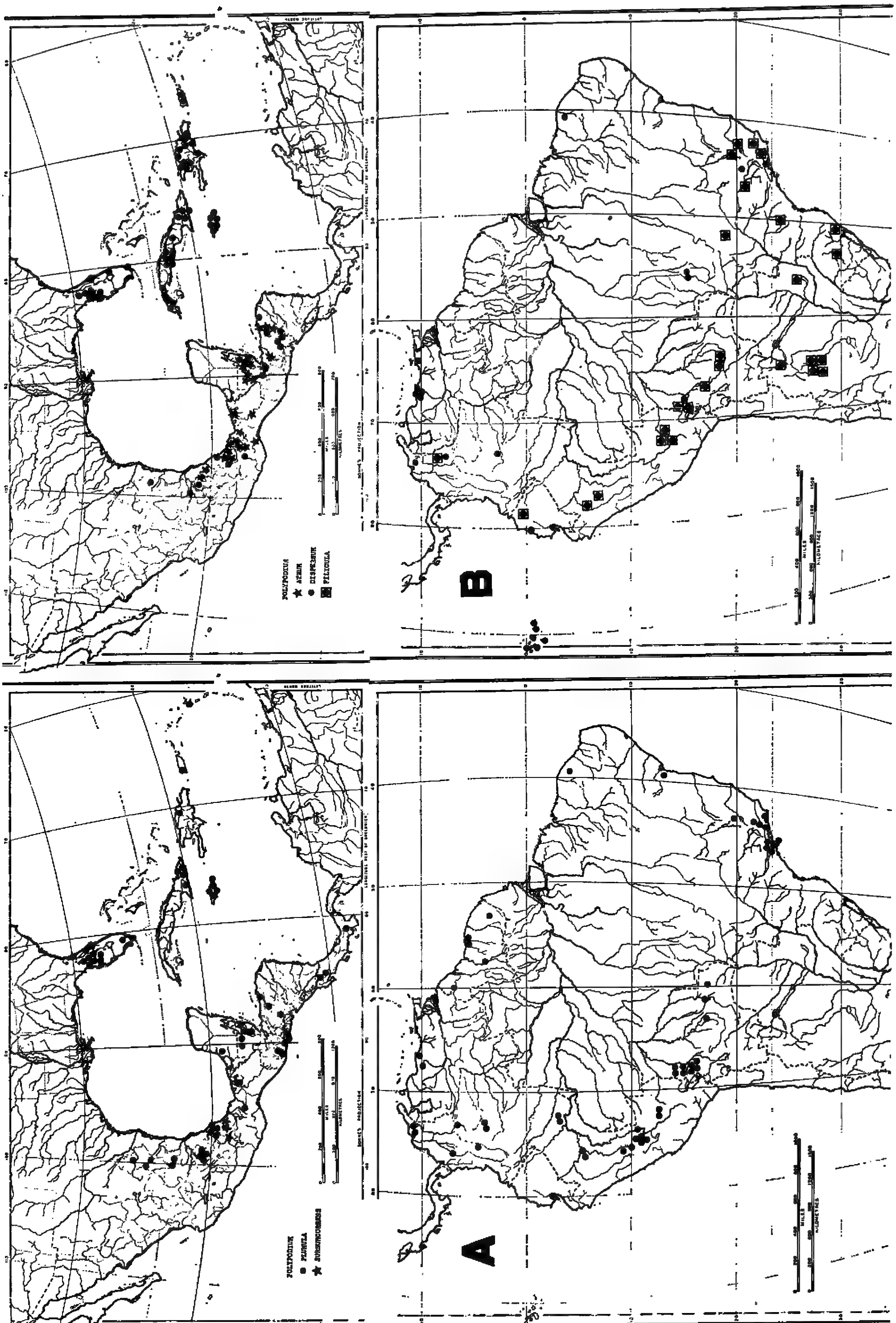


Fig. 9. Geographic distributions (legend p. 270).

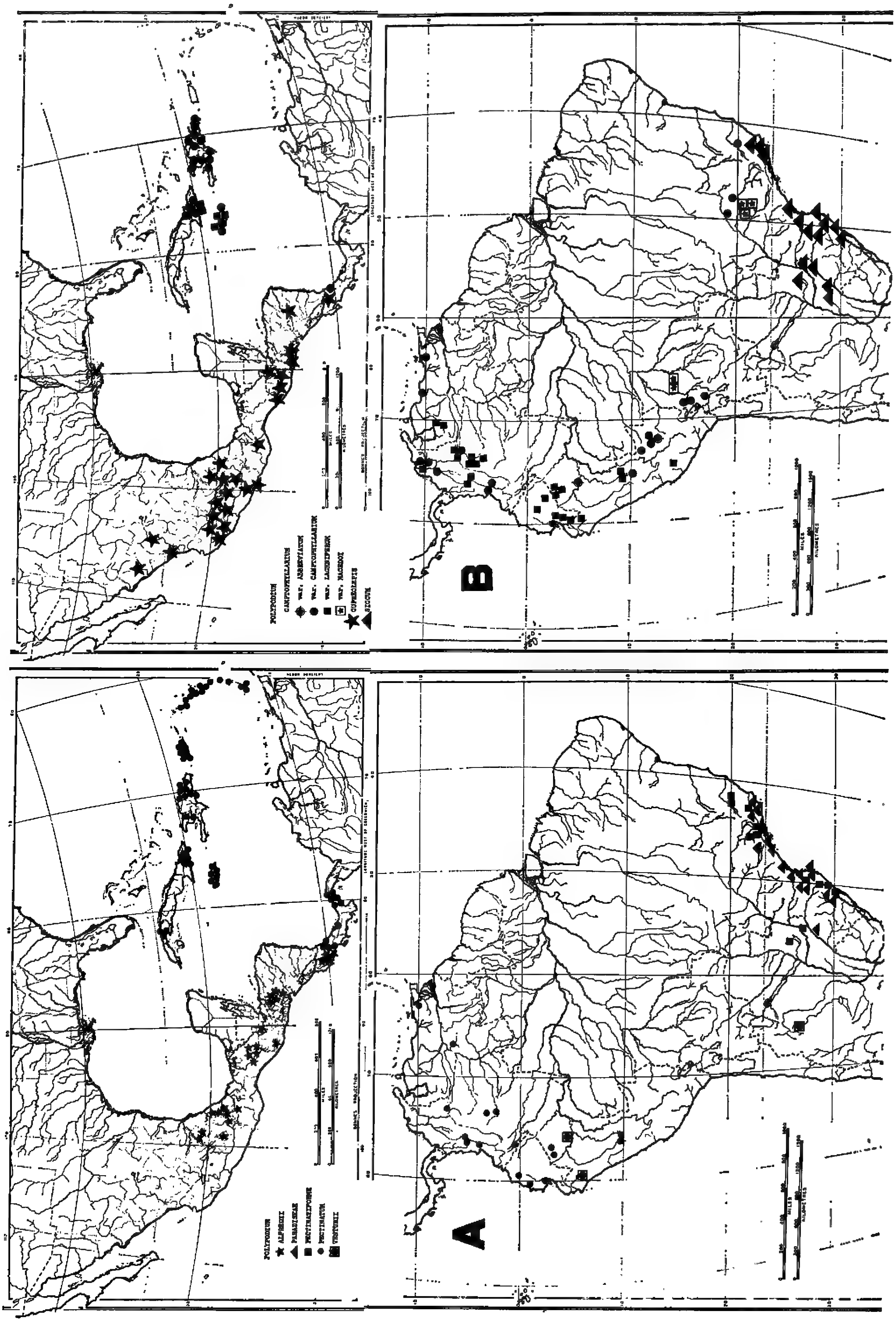
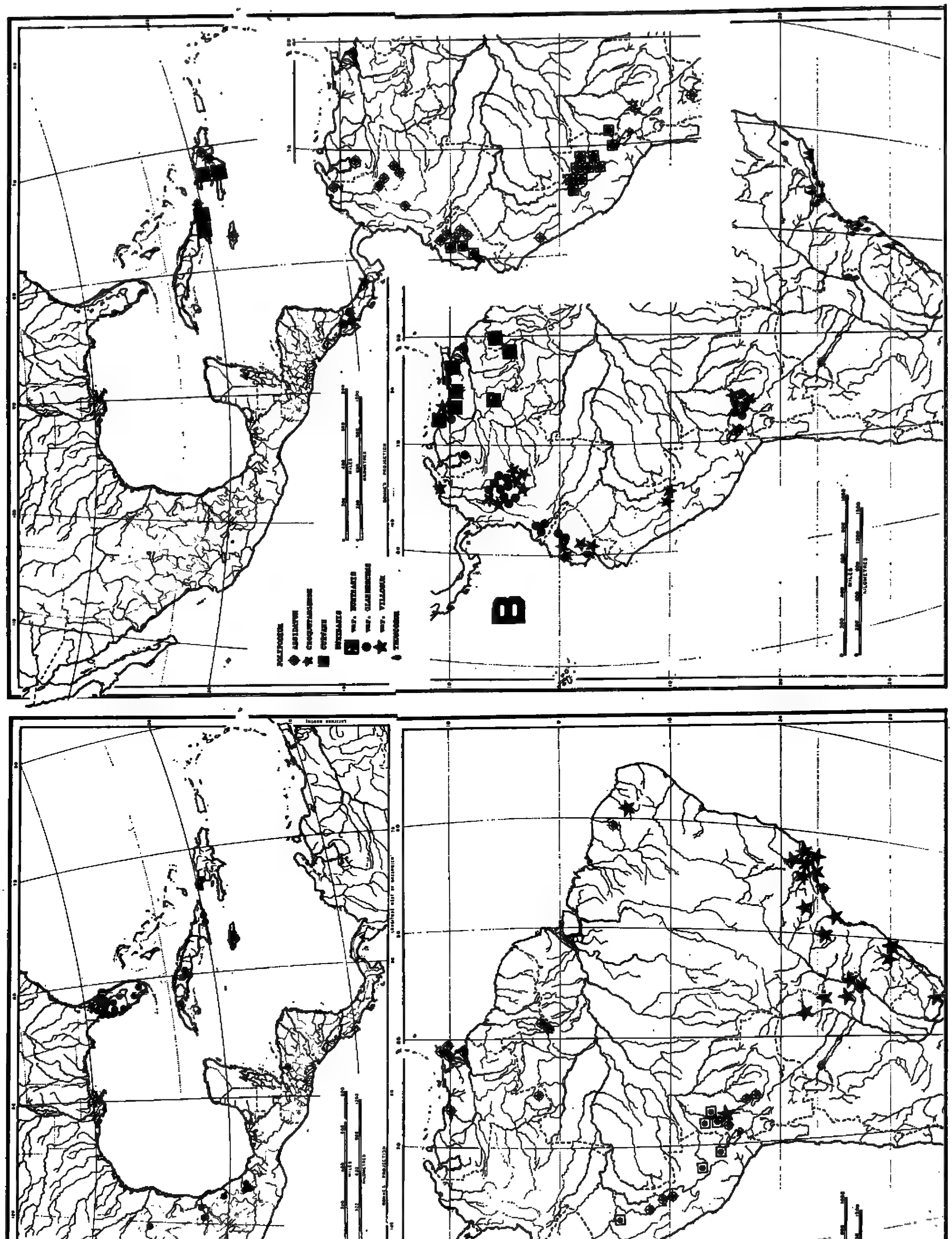


Fig. 10. Geographic distributions (legend p. 270).



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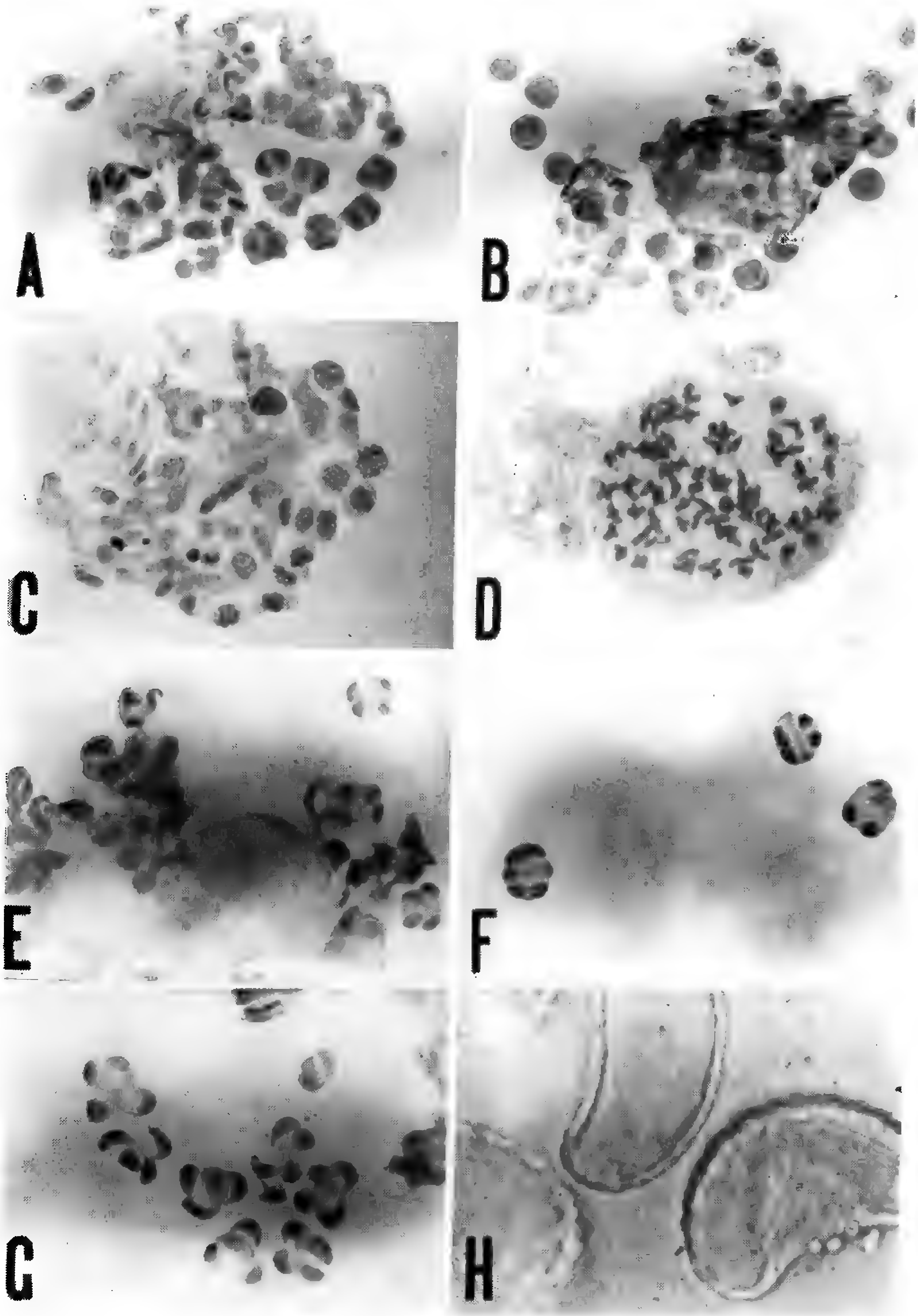


Fig. 12. Sporogenesis (legend p. 270).

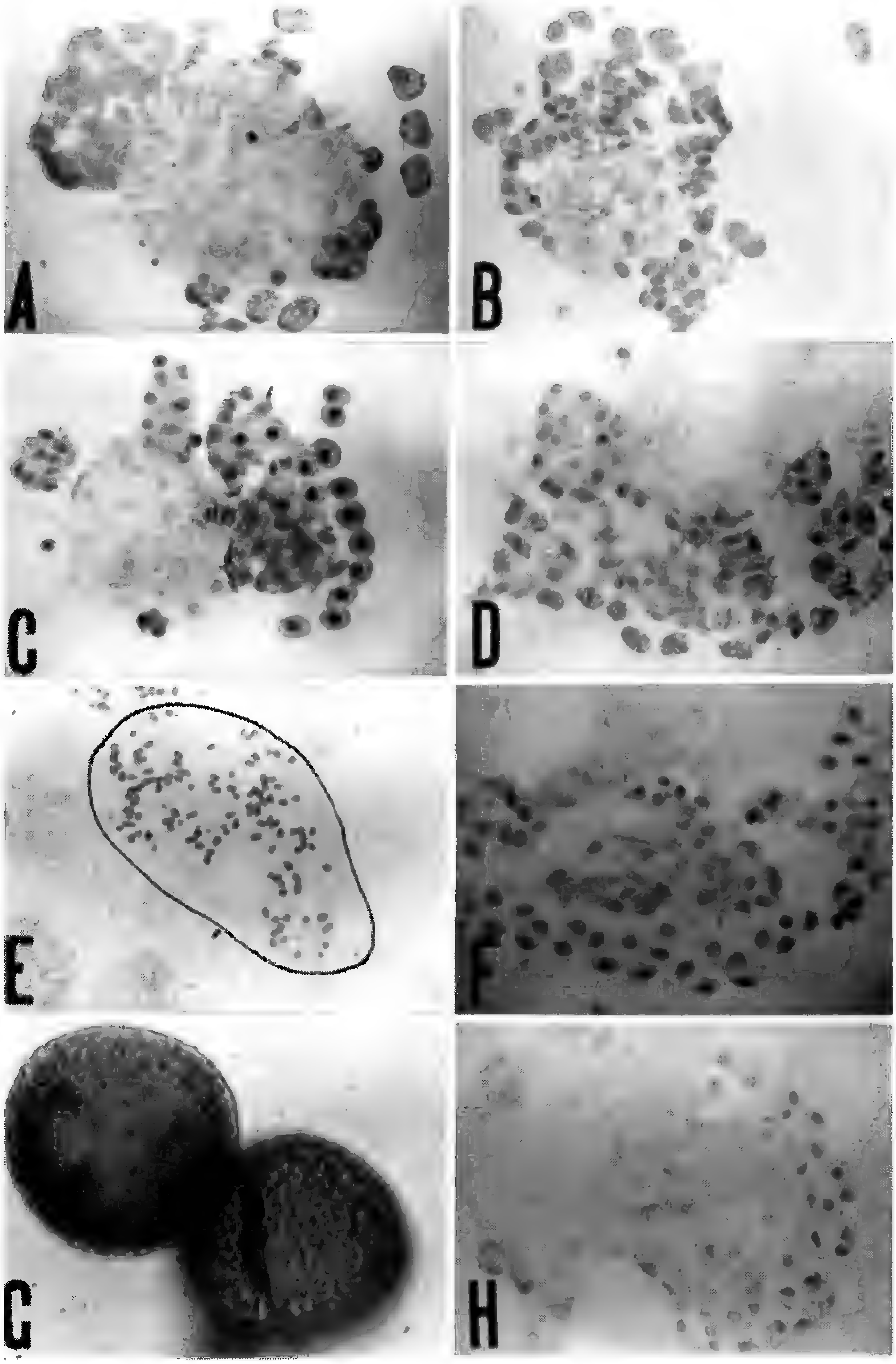
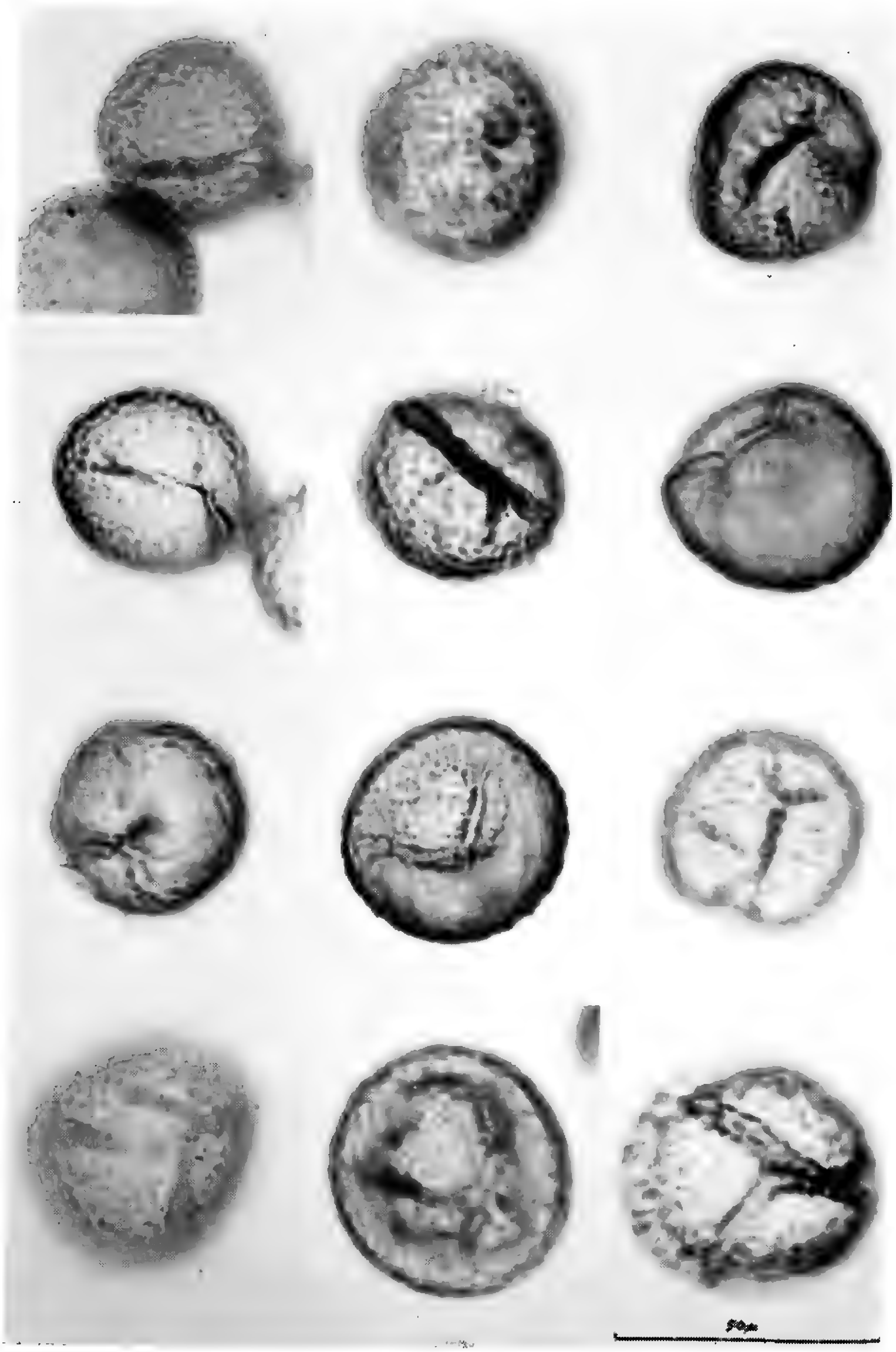


Fig. 13. Sporogenesis (legend p. 270).



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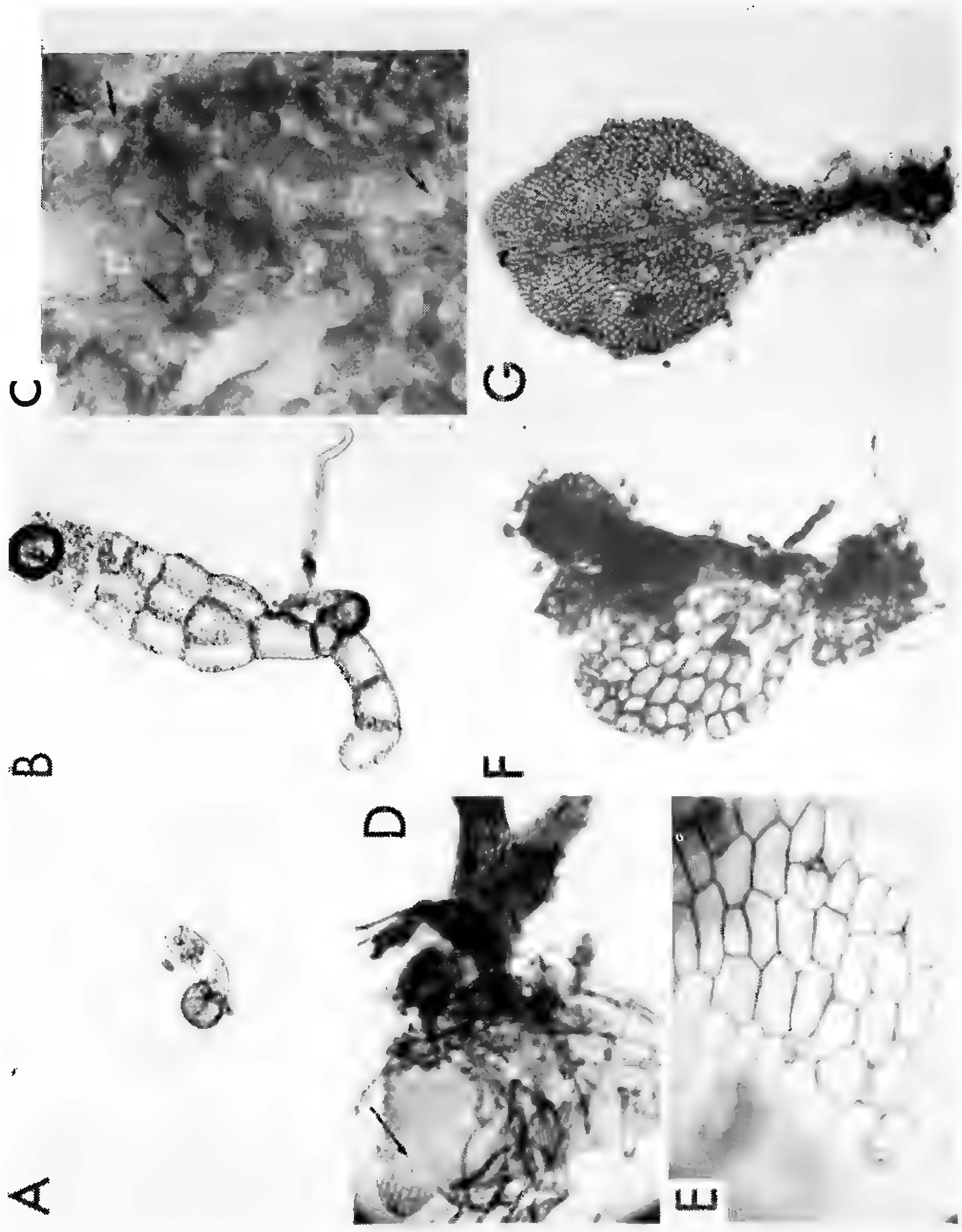

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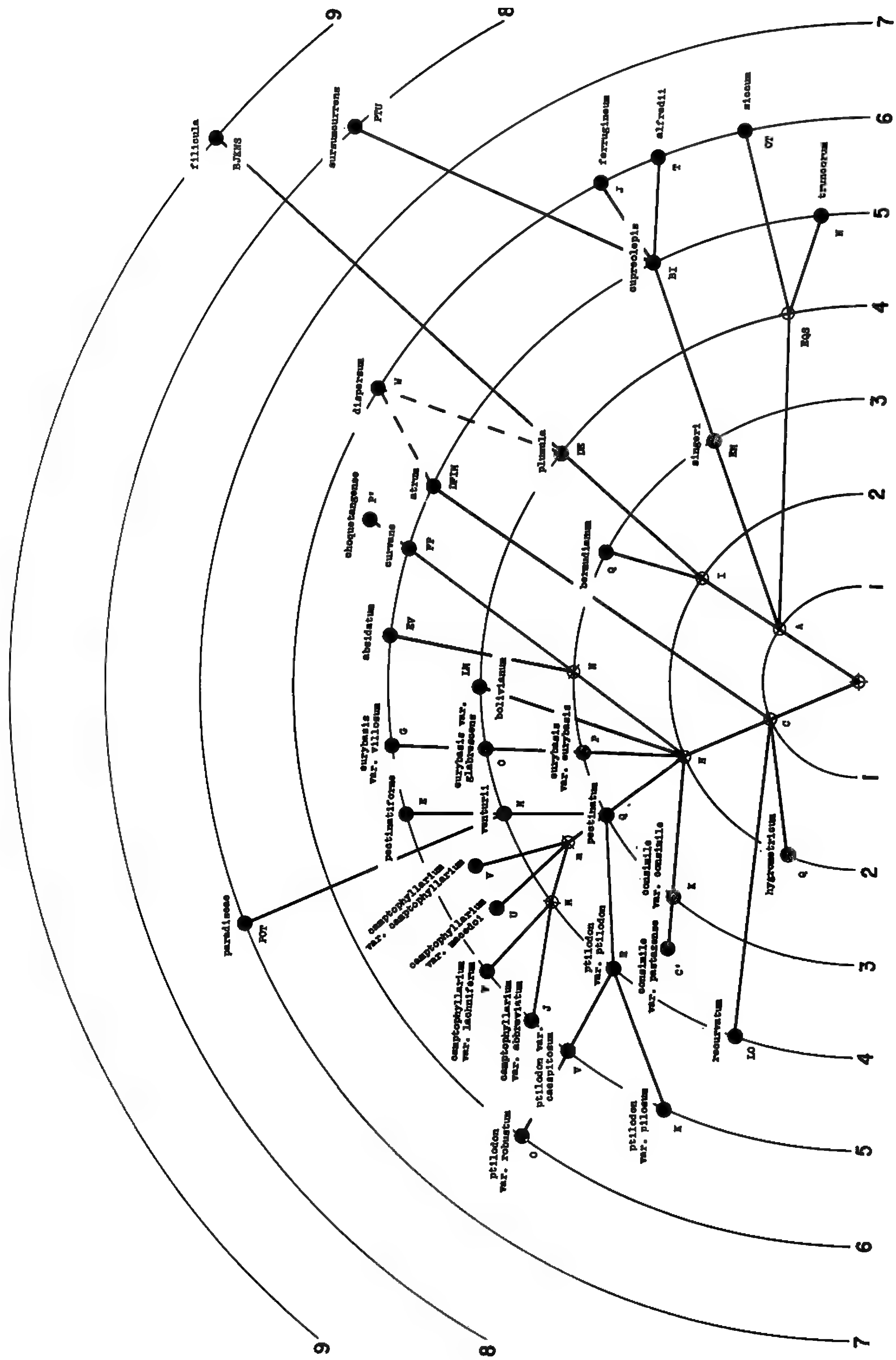

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Fig. 17. Type specimens (legend p. 271).

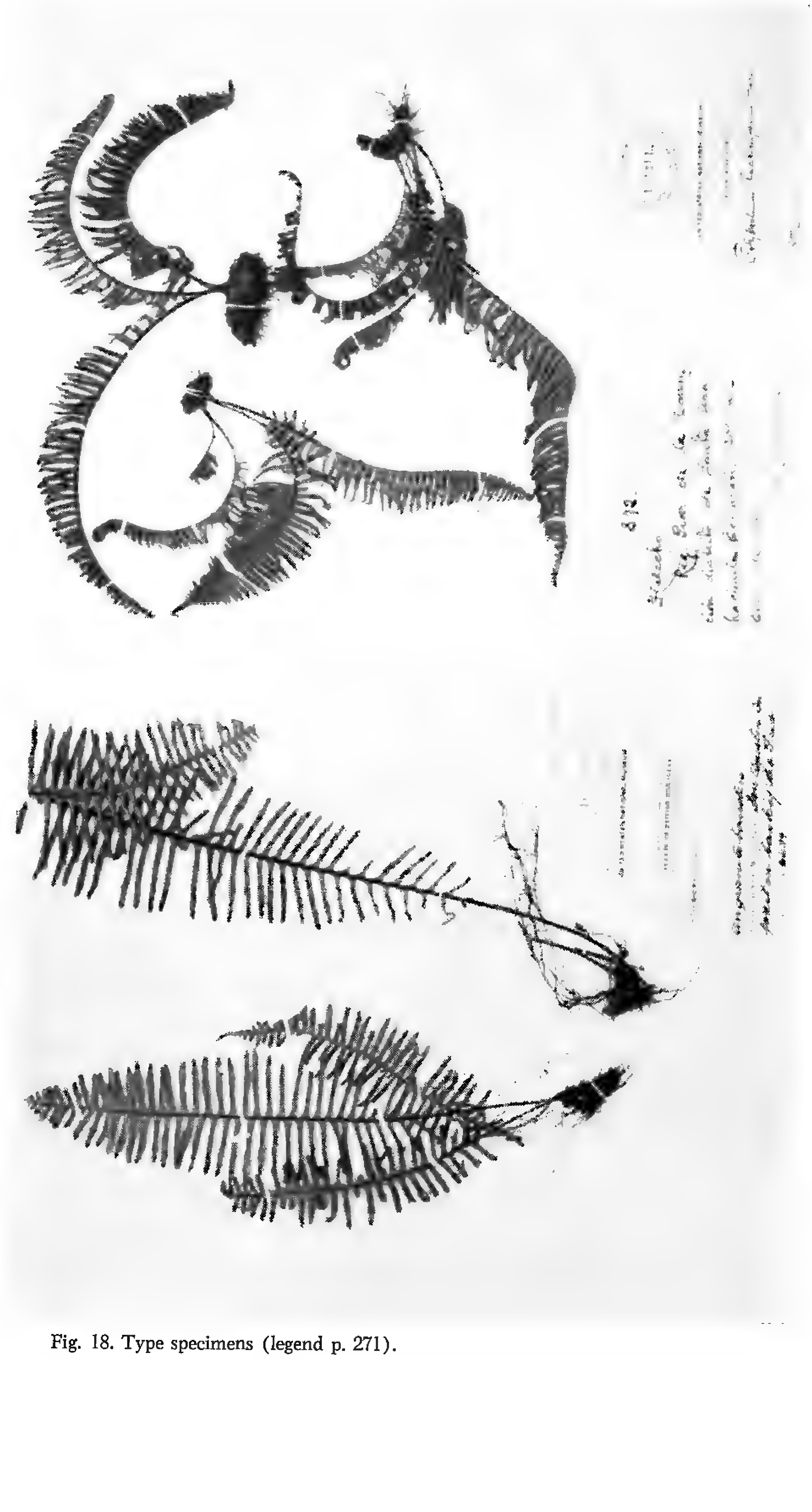

Fig. 18. Type specimens (legend p. 271).

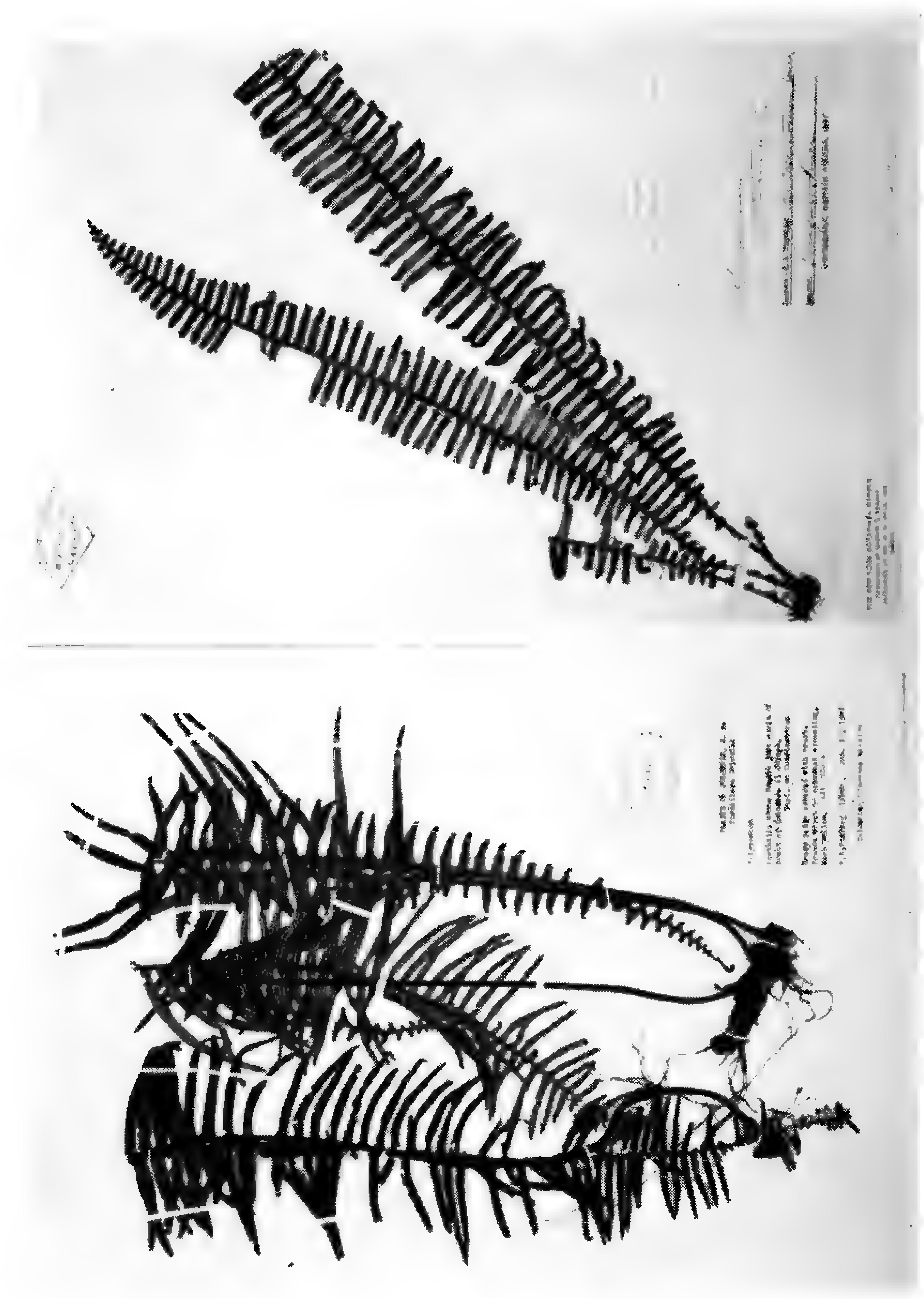

Fig. 19. Type specimens (legend p. 271).

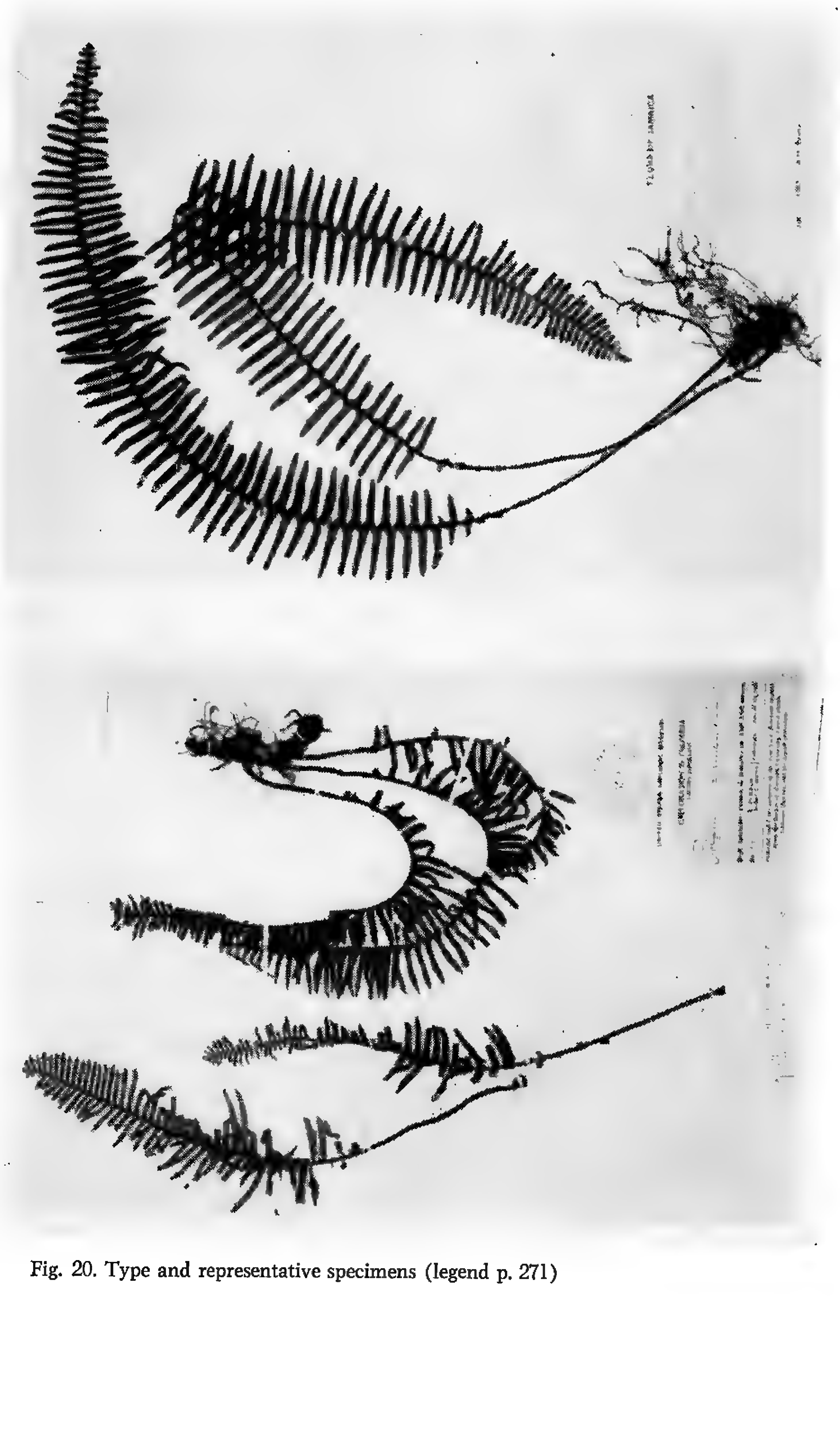

Fig. 20. Type and representative specimens (legend p. 271)

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PALYNOTAXONOMIC STUDY OF THE PHYTOLACCACEAE[1]

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ABSTRACT

The *Phytolaccaceae,* a largely tropical and subtropical plant family, are revised utilizing pollen morphology in addition to floral and vegetative morphology. Seventy-one species, including the novelty *Ercilla syncarpellata* Nowicke, are treated with descriptions of pollen and gross morphology; keys are provided to all major taxa and species. The 17 genera recognized (*Anisomeria, Ercilla, Phytolacca, Gallesia, Seguieria, Rivinia, Trichostigma, Schindleria, Hilleria, Petiveria, Ledenbergia, Monococcus, Agdestis, Microtea, Lophiocarpus, Stegnosperma,* and *Barbeuia*) are placed in six subfamilies (*Phytolaccoideae, Rivinoideae, Agdestioideae, Microteoideae, Stegnospermoideae,* and *Barbeuioideae*) three of which are newly established, with all subfamilies except the *Rivinoideae* (with *Seguierieae* and *Rivineae*) being monotribic. Four major pollen types are recognized: 3-colpate with variations of minor os formation or polar exine thickening; pantoporate; 12-colpate with four colpi forming a square at each pole and four perpendicular to the equator; and 15-colpate with five colpi forming a pentagon at each pole and five perpendicular to the equator. In terms of gross morphology the family is considered relatively primitive with only occasional examples of characters considered advanced. In terms of pollen morphology, the family has advanced types (those other than 3-colpate) well represented.

INTRODUCTION

The *Phytolaccaceae* comprise a weedy family of largely tropical and subtropical plants which have been placed, almost without exception, in the order *Centrospermae* (*Chenopodiales* of Hutchinson, 1959; *Caryophyllales* of Bessey, 1915). It is a relatively natural order, best characterized by its uniform placentation, ovule structure, perisperm storage tissue and the unique presence of betacynanins.

Heimerl (1889), in his survey of the *Phytolaccaceae* for the Pflanzenfamilien, recognized six tribes: *Rivineae* [*Gallesia* Casar., *Seguieria* Loefl., *Monococcus* F. Muell., *Phaulothamnus* A. Gray, *Ledenbergia* Klotzsch, *Rivina* L., *Petiveria* L., *Microtea* Swartz, *Hilleria* Vell. (as *Mohlana* Mart.), *Adenogramma* Reichb.], *Limeae* (*Polpoda* Presl, *Limeum* L., *Barbeuia* Thouars), *Stegnospermeae* (*Stegnosperma* Benth., *Psammotropha* Eckl. & Zey.), *Phytolacceae* (*Phytolacca* L., *Anisomeria* D. Don, *Giesekia* L.), *Gyrostemoneae* (*Didymotheca* Hook. f., *Gyrostemon* Desf., *Tersonia* Moq.), *Agdestideae* (*Agdestis* Moc. & Sesse). He did not recognize *Trichostigma* A. Rich., *Ercilla* Juss. (Ercilia), or *Schindleria* H. Walter as distinct genera, and *Lophiocarpus* Turcz. was not treated but rather included in the *Chenopodiaceae.*

Walter's (1909) monograph was the first comprehensive treatment of the family and he recognized two subfamilies, *Phytolaccoideae* containing 17 genera

[1] Based on a dissertation submitted to the Graduate School of Washington University in partial fulfillment of the requirements for the degree of Doctor of Philosophy. Assisted by a Junior Fellowship from the Center for the Biology of Natural Systems and by National Science Foundation Grant No. GB-5042 (Principle Investigator, Walter H. Lewis). Dr. Lewis is gratefully acknowledged for supervision of this research.

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(*Anisomeria, Ercilla, Phytolacca, Barbeuia, Didymotheca, Tersonia, Gyrostemon, Codonocarpus* A. Cunn., *Hilleria, Seguieria, Gallesia, Rivina, Trichostigma, Ledenbergia, Schindleria, Petiveria, Monococcus*), *Stegnospermoideae* with only *Stegnosperma, Agdestis* which is not placed in a subfamily or tribe, as well as three other anomalous genera (*Achatocarpus* Triana, formerly placed in the *Amaranthaceae* by Bentham & Hooker, 1883; *Microtea, Phaulothamnus*) with affinities to the *Chenopodiaceae* for a total of 22 genera. He removed six genera (*Limeum, Giesekia, Adenogramma, Psammotropha, Polpoda, Semonvillea* Gay, the last genus Heimerl had treated as a subgenus of *Limeum*) to the subfamily Ficoideae of the *Aizoaceae.* In addition to this major change, he recognized *Ercilla* as distinct from *Phytolacca, Trichostigma* as distinct from *Rivina,* and included his recently established genus, *Schindleria* (Walter, 1906).

In the second edition of Pflanzenfamilien, Heimerl (1934) divided the *Phytolaccaceae* into five tribes: *Rivineae, Phytolacceae, Agdestideae, Stegnospermeae,* and *Barbeuieae,* the last three being monogeneric; in addition he cited two genera, *Microtea* and *Lophiocarpus,* as connecting links to the *Chenopodiaceae.* He reduced the total number of genera to 17 by removing six previously included by Walter (1909) and adding *Lophiocarpus,* a genus formerly placed in the *Chenopodiaceae* (Bentham & Hooker, 1883), and placed by N. E. Brown (1909) in the *Phytolaccaceae* as congeneric with *Microtea.* Four of the genera which Heimerl separated from the *Phytolaccaceae* comprised the *Gyrostemonaceae* (*Gyrostemon, Codonocarpus, Didymotheca, Tersonia*) all of which have unisexual flowers and a high carpel frequency (rarely two or one). The *Achatocarpaceae* was constructed for two dioecious genera, *Achatocarpus* and *Phaulothamnus,* found in the American tropics and subtropics.

Hutchinson (1959) included the *Phytolaccaceae* in the *Chenopodiales;* the latter consists of 10 families of which four resulted from a further division of the *Phytolaccaceae.* The family was consequently reduced to three genera: *Phytolacca, Anisomeria,* and *Ercilla. Agdestis* and *Barbeuia* were placed in monotypic families and the remaining genera, with the exception of *Stegnosperma* which he placed as a monogeneric family in the *Pittosporales,* comprise the *Petiveriaceae* (*Gallesia, Hilleria, Ledenbergia, Lophiocarpus, Monococcus, Microtea, Petiveria, Rivina, Schindleria, Seguieria, Trichostigma*).

Eckardt (1964) made some changes in the larger taxa, recognizing three subfamilies, the *Phytolaccoideae* with four tribes, and the *Stegnospermatoideae* and the *Microteoideae* each with a single tribe. He does not cite all genera, but his treatment appears to follow closely that of Heimerl (1934).

The present work is the first major treatment and revision of the *Phytolaccaceae* in the generic concepts of Heimerl (1934). Although Walter's (1909) monograph is a competent treatment of the family, several serious flaws exist: the familial limits, i.e. inclusion of genera whch have since, justifiably, been removed; and the fact that in many instances, generic as well as specific, the exsiccatae listed could not possibly have permitted an adequate consideration of the wide variation which characterizes the family, with the result that many of the taxa established are invalid. This study, although incomplete in parts, attempts to coordinate morphological descriptions, including pollen, floral and vegetative, in order to revise the generic and specific limits.

SYNOPSIS OF THE PHYTOLACCACEAE

Phytolaccaceae Lindl., Nat. Syst. ed. 2, 210, 1836.

Petiveriaceae Link, Handb. **1**: 392, 1829[3].

Herbs, shrubs, or trees. *Leaves* simple, alternate, petiolate to ± sessile, entire, generally estipulate (stipules thorny in *Seguieria*). *Inflorescences* racemes, spikes, or irregular panicles rarely cymules. *Flowers* small, perfect or rarely unisexual (plants then dioecious), ± actinomorphic (weakly zygomorphic in *Hilleria* and *Anisomeria*); calyx composed of 4-5 free or slightly connate segments, dry and inconspicuous or occasionally corolla-like; corolla absent (staminodia petaloid in *Stegnosperma*); stamens 3-∞ (number variable within a species or even an inflorescence), frequently arranged in one or two whorls, sometimes deposited on a hypogynous disc but placed irregularly in relation to sepals or rarely alternate, the filaments linear, or awl-shaped, the anthers mostly linear, tetrasporangiate, introrse (extrorse in *Hilleria*), dehiscing longitudinally; ovary superior (semi-inferior in *Agdestis*), composed of 1-16 free or united carpels, each carpel with one basal, campylotropous ovule, the styles usually equal to the carpel number or absent, the stigmas capitate or ± penicellate or not apparent. *Fruit* a berry, capsule, drupe, utricle, achene or samara; seed one per carpel; embryo curved around a mealy perisperm.

A family of 17 genera and ca 70-80 species mostly in the New World tropics and subtropics, but also found in Africa, Australia and Hawaii.

Economically the family is of little importance, but some species contain partially toxic substances which are used medicinally. The roots and fruits of some contain Saponin, which can be utilized as a soap. *Phytolacca dioica* L. is frequently planted as a shade tree in the tropics because it is fast growing. The berries of some *Phytolacca* spp. have been utilized as an adulterant of red wine, and the young sprouts and leaves can be made into a "poke salad".

Pollen

Pollen grains single, prolate, subprolate or prolate spheroidal, ca 16-35μ (E) × ca 18-39μ (P), 3-colpate, 3-colporoidate, 12-colpate in a 4-4-4 pattern, 15-colpate in a 5-5-5 pattern, or pantoporate, exine ca 1.5-3μ in thickness, sometimes thickened at the poles to 5μ, sexine ± equal to or slightly thicker than nexine and sparsely small spinulose to ± smooth (see Appendix).

[3] The name *Phytolaccaceae* is conserved over *Petiveriaceae*.

Cytology

Relatively few chromosome counts are available for the family, but all evidence points to a base of $x = 9$ (18).

Hilleria latifolia H. Walter	$2n = 36$	(Mangenot & Mangenot, 1958).
Petiveria alliacea L.	$2n = 72$	(Sugiura, 1937).
Phytolacca acinosa Roxb.	$2n = 36$	(Sugiura 1936b).
P. americana L.	$2n = 36$	(Bostick, 1965, N. C.; Lewis et al., 1962, Texas).
P. australis Phil.	$n = 18$	(Heiser, 1963).
P. dioica L.	$2n = 36$	(Schnack & Covas, 1947).
P. octandra L.	$2n = 36$	(Sugiura, 1936a).
Rivina humilis L.	$2n = 108$	(Nowicke, 1967; Sugiura, 1936a).

Anatomy

The entire order *Centrospermae* is characterized by its distinctive stem structure (essentially anomalous secondary thickening) and according to Metcalfe & Chalk (1950) certain genera in the *Phytolaccaceae* (*Agdestis, Anisomeria, Barbeuia, Gallesia, Petiveria, Phytolacca, Seguieria*) have successive rings of vascular bundles in the inner parenchymatous portion of the pericycle. Concentric rings of xylem and phloem occur in sufficiently thick stems of *Ercilla, Gallesia, Phytolacca, Rivina* and *Seguieria.*

Another distinctive feature of the *Phytolaccaceae,* as well as the entire order, is found in the character of its pigments. It is one of the "beta-cyanin families" (Dreiding, 1961), which are closely related and characterized by their inability to produce anthocyanins which is replaced by the ability to synthesize betacyanins (and betaxanthins).

Taxonomy

In this treatment I recognize six subfamilies, all monotribic with the exception of *Rivinoideae* which is divided into two tribes based primarily on the striking differences in fruits and types of inflorescences.

I. *Phytolaccoideae* H. Walter—ovary of 3-16 carpels, free or united; fruit a drupe, achene or berry. 3 genera: *Anisomeria, Ercilla, Phytolacca.*

II. *Rivinoideae* Nowicke—ovary of one carpel and one seed; fruit an achene, drupe, utricle or samara. 9 genera: *Gallesia, Seguieria, Rivina, Trichostigma, Schindleria, Hilleria, Petiveria, Ledenbergia, Monococcus.*

III. *Microteoideae* Eckardt ex Nowicke—ovary of one carpel with 2-4 stigmas and one seed; fruit an achene. 2 genera: *Microtea, Lophiocarpus.*

IV. *Agdestioideae* Nowicke—ovary of 3-4 carpels, 3-4 stigmas, semi-inferior, and one seed. One genus: *Agdestis.*

V. *Stegnospermoideae* H. Walter—ovary of 3-5 united carpels, 3-5 seeds, petaloid staminoidia; fruit a capsule. One genus: *Stegnosperma.*

VI. *Barbeuioideae* Nowicke—ovary of 2 united carpels, 2 seeds; fruit a capsule. One genus: *Barbeuia.*

Key to the Subfamilies

a. Fruit(s) a capsule, 2 or 3-5 locular.
  b. Capsule 2-locular; inflorescences axillary cymules or fascicles; staminodia absent; plants drying black; endemic to the Malagasy Republic
  bb. Capsule 3-5 locular; inflorescences racemes, sometimes cymules; staminodia petaloid; plants drying green; Central America and the West Indies ....subf. V *Stegnospermoideae* (p. 356)
aa. Fruit(s) a berry, drupe, samara, achene, or utricle. ....subf. VI *Barbeuioideae* (p. 358)
  c. Ovary of 3-16 carpels, free or united.
    d. Ovary semi-inferior, with 3-4 united carpels and 3-4 stigmas; seed one; ± woody vines; leaves cordate ....subf. IV *Agdestioideae* (p. 355)
    dd. Ovary superior, 3-16 free or united carpels and one stigma per carpel; seeds as many as the carpels; herbs, shrubs or trees; leaves variable, but not cordate ....subf. I *Phytolaccoideae* (p. 298)
  cc. Ovary of one carpel, with one seed.
    e. Ovary with one stigma; fruit a samara, drupe or utricle, or if an achene then not globose, and conspicuously 4-6 hooked or covered with recurved spines ....subf. II *Rivinoideae* (p. 320)
    ee. Ovary with (2-)3-4 stigmas; fruit an achene, globose with pericarp wrinkled, glochidiate, warty or ridged ....subf. III *Microteoideae* (p. 346)

PHYTOLACCOIDEAE

I. Subf. *Phytolaccoideae* H. Walter, Pflanzenr. IV, 83 (Heft 39): 29, 1909. (Type *Phytolacca* L.)

Tribe *Phytolacceae* Reichb., Fl. Exc. 586, 1832. (Type *Phytolacca* L.)

a. Carpels distinctly free; sepals unequal and ± fleshy; leaves succulent-leathery; inflorescences mostly terminal ....1. *Anisomeria*
aa. Carpels free or united; sepals equal or only weakly unequal and thin; leaves not succulent-leathery; inflorescences axillary or terminal.
  b. Carpels usually free, rarely united; inflorescences dense, short, axillary spikes, rarely raceme-like; shrubs of Chile ....2. *Ercilla*
  bb. Carpels free or united, usually united; inflorescences racemes or ± long spikes; mostly herbs; cosmopolitan ....3. *Phytolacca*

1. ANISOMERIA

Anisomeria D. Don, Edinb. New Phil. Jour. **13:** 238, 1832. (Type *A. coriacea* D. Don)

Pircunia Bertero, Mercurio Chileno 744, 1829; Amer. Jour. Sci. **23:** 264, 1833, non Moq. (in DC., Prodr. **13**(2):29, 1849).

Herbs or shrubs, sometimes succulent, calcium oxalate crystals present. *Leaves* alternate or in fascicles of ca 3, ovate, ovate-elliptic, or ± spatulate, mucronate, retuse or rounded, entire or slightly undulate, the bases rounded to attenuated, glabrous, ± leathery; sessile to petiolate, petioles sometimes thickened at the base in fascicular arrangement and appearing stipular. *Inflorescences* spikes or spike-like racemes, mostly terminal. *Flowers* perfect, ± zygomorphic; sessile or pedicellate; bract single or absent; bracteoles 2 and fleshy, or absent; sepals 5, unequal, ± united at the base, orbicular, fleshy; stamens 10-20, appearing in two whorls, the filaments ± thickened; ovary 5-8 carpellate, free, the styles as many as the carpels, the stigmas inconspicuous to slightly thickened. *Fruit* a loose collection of drupelets (?), red to brown; seed one (Fig. 1).

This genus of three species has been described as restricted to Chile; however, some locations cited on herbarium specimens are from the Chilean-Argentinean border.

Pollen grains single, prolate, ca 26μ (E) $\times$ ca 34-39μ (P), 3-colpate, colpi ca 23-32μ long, the exine ca 2-3μ in thickness, sexine $\pm$ equal to or slightly thicker than nexine and finely reticulated (Fig. 4).

The publication of Bertero (1829) does predate that of Don, but the descriptions of the former author are seminude and until I see collections of Bertero which have definitely been determined by him as *Pircunia drastica,* and thus leave no doubt as to the plant described in the Mercurio Chileno publication, I think the generic name *Anisomeria* should remain.

Two names have deliberately been omitted from the following synonymy, namely, *Anisomeria coriacea* var. *petalifera* H. Walter (Pflanzenr. IV, 83 (Heft 39): 32, 1909) which may well be a variety of *A. fruticosa* Phil. judging from the thickened filaments of the latter; however, since I have not seen petaloid specimens, I withhold judgment. The other name, *A. densiflora* H. Walter (loc. cit.), does not apply in my opinion to a distinct species, but could, because of the immaturity of the inflorescence, be placed in synonomy under either *A. coriacea* D. Don or *A. fruticosa.* I tend to favor the former reduction because the leaves of the type (*Lechler s.n.* photo F, from B†) resemble those of *A. coriacea,* which agrees with Walter's (1909) description.

Fig. 1. Inflorescences of *Anisomeria* D. Don. A, *A. littoralis* (Poepp. & Endl.) Moq. (×1); B, *A. coriacea* G. Don (×½); C, *A. fruticosa* Phil. mature and immature inflorescences. A after *Grandjot s.n.* (MO); B after *Grandjot s.n.* (MO); C after *Werdermann 785* (MO).

The genus is clearly related to *Phytolacca* and is distinguished by its rather weak zygomorphic condition, fruit type and, to a greater or lesser extent, its general habit.

a. Flowers sessile ....1. *A. coriacea*
aa. Flowers pedicellate.
  b. Inflorescences < 8 cm long, pedicels mostly 4 mm or longer ....2. *A. littoralis*
  bb. Inflorescences > 10 cm long, pedicels mostly 2-2.5 mm at maturity ....3. *A. fruticosa*

1. *Anisomeria coriacea* D. Don, Edinb. New Phil. Jour. **13:** 238, 1832. (Type *Cuming s.n.* G?)

Pircunia drastica Bertero, Mercurio Chileno 744, 1829; Amer. Jour. Sci. **23:** 264, 1833.
Phytolacca drastica (Bertero) Poeppig & Endl., Nov. Gen. Sp. Pl. **1:** 26, *pl.* 43, 44, 1835.
Anisomeria drastica (Bertero) Moq. in DC., Prodr. **13**(2):25, 1849.

Shrubs, weak, or succulent herbs with woody bases. *Leaves* mostly alternate, ovate, rarely lanceolate or spatulate, mucronate, undulate, the bases attenuate, up to 6 cm long and 3 cm wide, succulent to leathery; petiole indistinct. *Inflorescences* spikes, up to 25 cm long, terminal. *Flowers* sessile; bract single, ca 2-2.5 mm long, lanceolate; bracteoles absent (?); sepals 5(-6), ± unequal, rounded, ca 3 mm long and 3-4 mm wide; stamens ca 20, in two irregular whorls, the filaments linear, ca 2.5-2.9 mm long, the anthers ca 1.7-1.9 mm long; ovary 5-6 carpellate, free, the styles as many as the carpels and ca 1.5-2 mm long, the stigma on the upper surface. *Drupelets* 5-6, red-brown, ca 8 mm long, style ± persistent (Fig. 1B).

CHILE[4]: COQUIMBO: s. loc., *Gay s.n.*, (G, NY). SANTIAGO: nr Juncal, *Elliot 631* (K); vic of Santiago, *Grandjot s.n.*, in 1932 (MO). WITHOUT PROVINCE: *Reed s.n.* (K); *Bridges 526* (K).

Pollen grains ca 39μ (P), colpi ca 32μ long, exine ca 3μ in thickness, sexine somewhat thicker than nexine.

Pollen examined: *Grandjot s.n.* (MO).

2. *Anisomeria littoralis* (Poepp. & Endl.) Moq. in DC., Prodr. **13**(2):25, 1849.

Phytolacca chilensis Miers, Trav. **2:** 532, 1826, nom. nud.
P. littoralis Poepp. & Endl., Nov. Gen. Sp. Pl. **1:** 27, *pl.* 45, 1835. (The plate is taken as the type)
Anisomeria chilensis Miers ex H. Walter, Pflanzenr. IV, 83(Heft 39):33, 1909, non *Phytolacca chilensis* (Miers ex Moq.) H. Walter [Pflanzenr. IV, 83 (Heft 39):45, 1909].

Shrubs. *Leaves* mostly fasciculate, ovate-elliptic, obtuse, mucronate or retuse, lamellate, the bases obtuse or rarely attenuate, up to 5 cm long and 2 cm wide, succulent to leathery; petioles to 1.5 cm long, becoming swollen and woody at the base. *Inflorescences* racemes (appearing as a spike in bud), mostly terminal, up to 7 cm long. *Flowers* with pedicels up to 6 mm long at maturity; bract absent; bracteoles two, ca 0.6-0.7 mm long, located ca midway on pedicel; sepals 5, unequal, somewhat united at the base, ca 2 mm long, and ca 0.6-2 mm wide,

[4] The geographical citation procedure is: large countries of S. America, the province or state, the location, then alphabetically by collector; Mexico and the United States, the state, then alphabetically by collector; large countries of Africa, Australia, and Asia, the location or province, then alphabetically by collector; all others, alphabetically by collector.

± orbicular; stamens 10-20, the filaments ca 2 mm long, stout, the anthers ca 1.2 mm long; ovary 5-8 carpellate, free, the styles as many as the carpels, thick, short, strongly recurved, the stigma on the upper surface. *Drupelets* 3-5, green-brown, ca 8-9 mm long (Fig 1A).

CHILE: COQUIMBO: vic of lower Choros River, *Reed s.n.* (K); estate of Frai Jorge, *Munoz B161* (GH), *B218* (GH); *Skottsberg & Skottsberg 763* (F, NY). SANTIAGO: vic of Santiago, *Grandjot s.n.*, in 1935 (MO). VALPARAISO: Algarrobo, *Kausel 4339* (F); Quillota, *Bertero 1233* (MO).

Pollen grains ca 34μ (P), colpi ca 23μ long, exine ca 2-2.5μ in thickness, sexine ± equal to nexine.

Pollen examined: *Grandjot s.n.* (MO); *Skottsberg & Skottsberg 763* (NY) (Fig. 4).

It is unfortunate that Walter (1909) applied the nude name *Phytolacca chilensis* Miers to two different taxa, a species of *Anisomeria* and one of *Phytolacca.* Since it is impossible as yet to determine to which entity Miers referred, even though I have seen Miers collections of *Anisomeria,* I have applied it to a bona fide species of *Phytolacca.*

3. *Anisomeria fruticosa* Phil., Linnaea **29:** 38, 1857-1858. (Type *Philippi 873* photo F, from B†)

Shrubs. Leaves mostly alternate, ovate, rounded to retuse, entire, the bases rounded to obtuse, up to 6 cm long and 4 cm wide, ± leathery; petioles to 12 mm long, the bases ± thickened and woody. *Inflorescences* spike-like racemes, up to 20 cm long, mostly terminal. *Flowers* with pedicels ca 2-2.5 mm long at maturity; bract absent; bracteoles two, ca 1 mm long; sepals 5, slightly united at the base, unequal, ± orbicular, ca 2.5-3 mm long and 0.6-2.2 mm wide; stamens 10-20, the filaments ca 2 mm long and ca 0.8 mm wide, fleshy, the anthers ca 1 mm long; ovary 6-7 carpellate, free, the styles as many as the carpels, short, thick and recurved, the stigmas on the upper surface. *Drupelets* 6-7, up to 1 cm long (Fig. 1C).

CHILE: ANTOFAGASTA: vic of Taltal, *Johnston 5195* (GH), *5611* (GH); *Werdermann 785* (F, K, MO, NY).

Pollen grains ca 34μ (P), colpi ca 24-25μ long, exine ca 2-2.5μ in thickness, sexine ± equal to nexine.

Pollen examined: *Werdermann* 785 (MO).

2. ERCILLA

Ercilla A. Juss., Ann. Sci. Nat. **25:** 11, 1832; Edinb. New Phil. Jour. **14:** 261, 1833. [Type *E. spicata* (Bert.) Moq.]

Suriana Domb. & Cav. ex D. Don, loc. cit. 13: 238, 1832.
Bridgesia Hooker & Arnott in Hooker, Bot Misc. **3:** 168, *pl. 102,* 1833, pro parte, non *B. incisifolia* Bertero, (*Bertero 1361* photo NY, from G).
Ercilia Endl., Gen. Sp. Pl. 977, 1840.
Apodostachys Turcz., Bull. Soc. Nat. Hist. Moscou **21**(1): 577, 1848.

Shrubs. Leaves ovate to ovate-orbicular to ovate-elliptic, acute to retuse-mucronate, entire to very finely undulate, the bases slightly cordate to obtuse, ±

papery to coriaceous, glabrous; petiolate. *Inflorescences* spikes or spike-like racemes, mostly axillary, rarely terminal, densely flowered. *Flowers* sessile to shortly pedicellate; bract single; bracteoles 2, closely appressed to sepals; sepals 5, ± equal free, ovate to ± elliptic, turning black on dessication; stamens 8-12, free, inserted on a hypogynous disc; ovary 4-8 carpellate, free or united, the styles as many as the carpels and free, slender, the stigmas not apparent. *Fruit* a loose collection of drupelets (?) or berry (?); seeds 1-7.

Chile.

Pollen grains single, prolate, ca 19-20μ (E) × ca 27μ (P), 3-colpate, colpi ca 20-22μ long, exine ca 2μ in thickness, sometimes thickened at the poles to ca 2.5-3μ, sexine ± equal to nexine and sparsely small spinulose.

Heimerl (1934) stated that *Ercilla spicata* (Bertero) Moq. is the sole species of the genus, for *E. volubilis* Juss. scarcely differs from it. Walter (1909) recognized both and separated the two by leaf texture, viz. coriaceous in *E. spicata* and papery in *E. volubilis*, and by the sunken condition of the midvein in the former. Both leaf texture as well as shape vary widely in the genus, although there are, admittedly, some very leathery-leaved specimens. Walter's description of *E. volubilis* is based on a single collection, *Dombey 944*, which he cites as being from Peru, and which Harms in a footnote (Heimerl, 1934) states as being a doubtful location for the genus, a conclusion with which I agree, especially since the NY specimen of this collection is marked Chile. This particular sheet of *Dombey 944* is unusual in that it may represent a mixed collection since the inflorescences of the two specimens are somewhat different, the one on the right having spike-like racemes, the left one having shorter spikes. For the present I am recognizing two species based on carpel condition, i.e. free or united, and am treating all free carpellate specimens as *E. spicata*.

a. Carpels free .... 1. *E. spicata*
aa. Carpels united, the styles free .... 2. *E. syncarpellata*

1. *Ercilla spicata* (Bertero) Moq. in DC., Prodr. **13**(2): 35, 1849. (Type *Dombey 944* G, NY)

Galvezia spicata Bertero, Mercurio Chileno 642, 1829.
Ercilla volubilis A. Juss., Ann. Sci. Nat. **25**: 11, *pl. 3, fig. 1*, 1832.
Suriana volubilis (A. Juss.) Domb. & Cav. ex D. Don, Edinb. New Phil. Jour. **13**: 238, 1832.
Bridgesia spicata Hooker & Arnott in Hooker, Bot Misc. **3**: 169, *pl. 102*, 1833. (Syntypes: *Bridges s.n.* BM; *Cuming* 349 K; *Mathews 244*, not seen)
Apodostachys densiflora Turcz., Bull. Soc. Nat. Moscou **21**(1): 577, 1848. (Type *Bridges s.n.* BM)
Phytolacca volubilis (A. Juss.) Heimerl, Pflanzenfam. **3**(1b): 11, 1889.

Shrubs. Leaves up to 8 cm long and 5.5 cm wide; petioles to 1.5 cm long. *Inflorescences* mostly spikes, rarely spike-like racemes, up to 10 cm long. *Flowers* mostly sessile, rarely with pedicels to 1 mm long; bract single, ca 2.2-2.8 mm long, ± elliptic; bracteoles two, ca 1.7-2.4 mm long; sepals ovate, ca 3.5-5 mm long; stamens 8-10(-12), the filaments 5-6 mm long, the anthers ca 1.6 mm long; ovary 4-8 carpellate, free, the styles ca 1.2-1.6 mm long, recurved. *Drupelets* 4-8, reniform, ca 4-5 mm long; seed ca 3.5-4 mm long, testa shiny black.

CHILE: CONCEPCIÓN: vic of Concepión, *Macrae s.n.* (K). MAULE: Cauquenes, *Joseph 1822* (US). O'HIGGINS: Donihue, *Bertero 289* (GH). VALDIVIA: Chinguil, *Hollermayer 1922* (NY, US); Coral, *Buchtien s.n.* (US); Panguipulli Lake, *Joseph 2405* (US); s. loc., *Philippi s.n.* (US). VALPARAISO: s. loc., *Cuming 349* (K); *Bertero 289* (GH). WITHOUT PROVINCE: *Gay 362* (NY, US), *s.n.* (K, NY, US); *Dombey 944* (NY); *Joseph 4398* (US).

Pollen grains ca 20μ (E), colpi ca 20μ long, exine thickened at the poles to ca 2.5-3μ in thickness.

Pollen examined: *Gay 362* (NY).

2. *Ercilla* **syncarpellata** Nowicke, sp. nov.

Inflorescentiae spicato-racemosae; flores pedicellis ca 1.5 mm longis; antherae ca 1.5-1.6 mm longae; ovarium brevi gynophoro, 5-7 carpellatum, carpellisque connatis.

Shrubs. Leaves ovate-elliptic, acute-mucronate, entire, the base obtuse to slightly cordate or oblique, up to 7 cm long and 3 cm wide, ± coriaceous, petioles up to 6 mm long. *Inflorescences* spike-like racemes, up to 8.5 cm long, mostly axillary. *Flowers* with pedicels ca 1.5 mm long; bract single, ca 2-2.8 mm long, awl-shaped; bracteoles two, ca 1-1.3 mm long; sepals 3-4 mm long; stamens ca 10, the filaments ca 5-6 mm long, the anthers ca 1 mm long; ovary on short gynophore, ca 0.5 mm long, 5-7 carpellate, united, the styles separate or closely appressed at the bases, recurved, the stigmas on the upper surface. *Fruit* unknown.

Holotype: Chile. Valdivia: La Aguade, *Gunckel 1837* (MO), 15 Nov 1930; isotype GH.

CHILE: VALDIVIA: Coral, *Gunckel 62* (BM); *Krause s.n.* (US).

Pollen grains ca 19μ (E), colpi ca 22μ long, exine not noticeably thickened at the poles.

Pollen examined: *Krause s.n.* (US).

3. PHYTOLACCA

Phytolacca L., Sp. Pl. 441, 1753. (Type *P. americana* L.)
Phytholacca Brot., Fl. Lusit. **2**: 224, 1804.
Sarcoca Raf., Fl. Tellur. **3**: 55, 1836.
Pircunia Moq. in D.C., Prodr. **13**(2): 29, 1849, non Bertero (Mercurio chileno 744, 1829).

Trees, shrubs or herbs; calcium oxalate crystals ± conspicuous. *Leaves* lanceolate to ovate or rarely ± deltoid, acute, acuminate, mucronate, retuse-mucronate, entire, rarely finely undulate, the bases rounded, obtuse, or attenuate, rarely ± oblique, ± glabrous; subsessile or petiolate. *Inflorescences* racemes or spikes, rarely racemes with thyrsiform bases, axillary or terminal, ± scurfy to pubescent. *Flowers* perfect, or unisexual and plants dioecious, mostly actinomorphic; sessile or pedicellate; bract single, rarely absent, narrowly-lanceolate to awl-shaped; bracteoles two, rarely absent, lanceolate to awl-shaped; sepals 5, rarely 4 (-9), narrow-oblong, oblong, elliptic, oblanceolate or ovate, white to red; stamens functional or rudimentary, 8-25, deposited irregularly in one or two whorls, generally on a hypogynous disc, the filaments sometimes widened at the bases; ovary absent, rudimentary or functional, sometimes on a short gynophore, 5-16 carpellate, free or united, the styles as many as the carpels, the stigmas on the upper surface.

Fruit a berry, ribbed, or a loose collection of drupelets (or achenes ?); seeds 5-16 for berry, one for drupelet, reniform, testa shiny black.

Cosmopolitan in distribution but principally in the warmer regions.

Pollen grains single, prolate spheroidal, subprolate, or prolate, ca 17-29μ (E) $\times$ ca 25-36μ (P), 3-colpate, colpi ca 17-26μ long, exine ca 2-2.5μ in thickness, sometimes slightly thickened at the poles, sexine $\pm$ equal to nexine, rarely 2$\times$ as thick, and finely reticulated to sparsely small spinulose (Fig. 7).

Without exception, *Phytolacca* is the most difficult genus in the *Phytolaccaceae* in which species can be accurately defined or classified. The problem lies principally with the fact that many taxa hybridize readily (Fassett & Sauer, 1950; Sauer, 1951), thus obscuring the characters by which they are recognized. In addition infraspecific variability and even extensive variation in the same specimen, e.g. inflorescences in which the flowers may have either one or two staminal whorls, contribute to the difficulty. An illustration of the type of problem encountered in species differentiation is the occurence of inflorescences which are thyrsiform at the base—a character supposedly best delimiting two South American species, *P. thyrsiflora* Fenzl. and *P. sanguinea* H. Walter. However this same character can be observed to a disturbing extent in *P. americana* L., to a lesser degree in *P. heterotepala* H. Walter and even in specimens collected in Asia.

The best characters to delimit taxa in this problematical genus should of course be qualitative, but it appears that many of these parameters are under weak genetic control. Heimerl (1934) noted that the approximately 35 species described are in part very closely related and are difficult to distinguish. In my opinion there are far less than 35 distinct species of *Phytolacca*; many names have undoubtedly been assigned to specimens of hybrid origin.

A discussion of all species which have been described is not feasible here, and I am, for the most part, revising and amending the species in the sense of Walter's (1909) treatment.

Walter (1909) placed 26 species of *Phytolacca* into three subgenera based on the degree of connation of the carpels: free, connate at the base with the apices free, or completely united carpels. Subgenus 1 *Pircunia* (Moq.) H. Walter contains *P. heptandra* Retz, *P. esculenta* van Houtte, *P. acinosa* Roxb., *P. latbenia* (Buch.-Ham.) H. Walter, and *P. cyclopetala* H. Walter in the sect. 1 *Pircuniastrum* Moq., characterized by hermaphroditic flowers, and *P. dodecandra* L'Herit, *P. goudotii* Briq., and *P. nutans* H. Walter in the sect. 2 *Pircunioides* H. Walter, characterized by dioecious plants. Subgenus 2 *Pircuniopsis* H. Walter, characterized by carpels connate at the base with the apices free, contains a hermaphroditic group, the sect. 1 *Pircuniophorum* H. Walter, with three species, *P. chilensis* (Miers ex Moq.) H. Walter, *P. sanguinea* H. Walter, and *P. rugosa* A. Br. & Bouche, as well as the sect. 2 *Pseudolacca* Moq., with two dioecious species *P. dioica L.* and *P. weberbaueri* H. Walter. Subgenus 3 *Euphytolacca* Moq., the largest group and characterized by carpels completely united contains a very large hermaphroditic sect. 1 *Phytolaccastrum* H. Walter with *P. thyrsiflora* Fenzl, *P. heterotepala* H. Walter, *P. brachystachys* Moq., *P. americana* L., *P. polyandra* Batalin, *P. rivinoides* Kunth & Bouche, *P. meziana* (J. D. Smith) H. Walter, *P.*

micrantha H. Walter, *P. australis* Phil., *P. octandra* L., *P. purpurascens* A. Br. & Bouche, and *P. icosandra* L., and a monotypic dioecious sect. 2 *Phytolaccoides* H. Walter containing *P. pruinosa* Fenzl.

The degree of carpel connation upon which Walter (1909) based the three subgenera functions well for recognition of the subg. *Pircunia,* with its completely separate carpels, a condition which is unmistakable in fruit, but for distinguishing the subg. *Pircuniopsis,* with carpels connate at the base, from subg. *Euphytolacca,* with carpels completely united, it is a difficult character. However, in view of the fact that I am not monographing the genus and do not wish to add further to the taxonomic and nomenclatural confusion by making an unmeaningful change, I think it best at this time to maintain the subgenera as outlined by Walter.

The dioecious species are a unique problem, not only in subgeneric classification of male specimens, but also because some species have female flowers with normal appearing stamens. These may be mistaken for functionally perfect flowered species.

A useful, if not essential, criterion for classifying material of *Phytolacca* is geographic location. It is unfortunate, however, that so many binomials seem to be based primarily on this feature; in some instances location is the key to rapid and accurate identification, e.g. Cyprus and *P. pruinosa.* A knowledge of the species commonly found in a particular region can also aid in recognition of hybrids. Specimens from the northern regions of South America are the most perplexing, due to the large number of species found there and to the almost continuous variability of their characteristics.

In this treatment I am recognizing 20 species, but in some instances do so with misgivings. Most of the latter involve specimens where geographic location is apparently the only feature which distinguishes them as species. Examples are *P. brachystachys* from the Hawaiian Islands, which is very similar to *P. rugosa* of Central and South America, and *P. purpurascens* from Haiti, which may very likely be a hybrid of *P. icosandra* and *P. americana* or *P. rivinoides.*

Following Walter's (1909) infrageneric classification in his subg. 1 sect. 1, I recognize *P. heptandra,* but have reduced *P. esculenta* to *P. acinosa.* To my knowledge, I have not seen *P. latbenia* or *P. cyclopetala,* but this does not deny their existence; they are unfortunately omitted. In his dioecious sect. 2 I recognize *P. dodecandra,* yet doubt the validity of *P. goudotii* and *P. nutans.*

In his subg. 2 sect. 1, I recognize *P. sanguinea, P. rugosa,* and *P. chilensis.* In the dioecious sect. 2, I recognize both species cited by Walter, *P. dioica* and *P. weberbaueri,* even though I have not included a description of the latter because I have seen only a male specimen. I am also including here *P. tetramera* Hauman-Merck, which Walter neglected.

In the subg. 3 sect. 1, I follow Walter's treatment rather closely, with the following exceptions: *P. polyandra* I have not seen and omit; *P. heterotepala* and *P. meziana* I include, but with reservations that they may be of hybrid origin; and *P. micrantha* and *P. australis* are reduced to *P. bogotensis* H.B.K. In the monotypic dioecious sect. 2, I recognize *P. pruinosa.*

In accordance with the Code, I have changed the subg. 3 *Euphytolacca* sect. 1 *Phytolaccastrum*, which contains the type species, to the subg. *Phytolacca*, sect. *Phytolacca*.

a. Carpels completely free .... subg. 1 *Pircunia*
  b. Flowers perfect .... sect. 1 *Pircunia*
    c. Slender herbs; inflorescences few-flowered spikes, rarely racemes; Africa. .... 1. *P. heptandra*
    cc. Robust herbs; inflorescences dense racemes; Asia .... 2. *P. acinosa*
  bb. Flowers functionally pistillate or staminate, but with rudimentary stamens or carpels .... sect. 2 *Pircunioides*
  3. *P. dodecandra*

aa. Carpels ± united.
  d. Carpels with apices ± free, styles not connivent .... subg. 2 *Pircuniopsis*
    e. Flowers perfect .... sect. 1 *Pircuniophorum*
      f. Inflorescences dense racemes, thyrsiform at the base .... 4. *P. sanguinea*
      ff. Inflorescences open racemes, not thyrsiform at the base, or elongate spikes.
        g. Inflorescences racemes; Central America & northern South America .... 5. *P. rugosa*
        gg. Inflorescences spikes; Chile .... 6. *P. chilensis*
    ee. Flowers pistillate or staminate .... sect. 2 *Pircuniopsis*
      h. Leaves spatulate, without a sharply defined petiole; sepals 4.. 7. *P. tetramera*
      hh. Leaves ± ovate, the petiole well-defined; sepals 5.
        i. Inflorescences ca 10 cm long or less; filaments 3.5 mm long .... 8. *P. dioica*
        ii. Inflorescences ca 25 cm long or more; filaments ca 6-6.5 mm long; very robust .... 9. *P. weberbaueri*
  dd. Carpels completely united, the styles ± connivent .... subg. 3 *Phytolacca*
    j. Flowers perfect .... sect. 1 *Phytolacca*
      k. Inflorescences spikes; flowers sessile to pedicels ca 1 mm long.
        l. Inflorescences longer than leaf lengths; usually two staminal whorls. .... 10. *P. icosandra*
        ll. Inflorescences equal to or less than leaf lengths; one staminal whorl. .... 11. *P. octandra*
      kk. Inflorescences racemes, sometimes thyrsiform, the flowers pedicellate.
        m. Racemes extended, thyrsiform at least at the base; chiefly Brazil. .... 12. *P. thyrsiflora*
        mm. Racemes not thyrsiform at the base, or if so then from North America.
          n. Flowers mostly with two staminal whorls.
            o. Sepals unequal, one noticeably more narrow; western North America. .... 13. *P. heterotepala*
            oo. Without the above combination.
              p. Sepals oblong, ca 4 mm long; Guatemala ....14. *P. meziana*
              pp. Sepals ± ovate, < 4 mm long.
                q. Racemes very long, ca 40-50 cm; pedicels ca 7-13 mm; carpels 10-16. .... 15. *P. rivinoides*
                qq. Racemes less than 30 cm long; pedicels < 7 mm long; carpels ca 9-10. .... 16. *P. purpurascens*
          nn. Flowers mostly with one staminal whorl.
            r. Plants of Hawaii; carpels mostly 5-6 .... 17. *P. brachystachys*
            rr. Plants of North or South America; carpels mostly 7-10.
              s. Inflorescences dense racemes; plants of South America .... 18. *P. bogotensis*
              ss. Inflorescences ± open racemes; plants of North America .... 19. *P. americana*
    jj. Flowers pistillate or staminate .... sect. 2 *Phytolaccoides*
    20. *P. pruinosa*

SUBG. 1 PIRCUNIA (Moq.) H. Walter, Pflanzenr. IV, 83 (Heft 39): 38, 1909. (Type *P. acinosa* Roxb.)

Pircunia Moq. in DC., Prodr. **13**(2): 29, 1849, non Bertero (Mercurio chileno 744, 1829).

SECT. 1 PIRCUNIA

sect. *Pircuniastrum* Moq. in D.C., Prodr. **13**(2): 29, 1849.

1. *Phytolacca heptandra* Retz., Obs. **6**: 29, 1791.

P. stricta Hoffm., Comm. Götting. **12**: 27, 1796.
P. resediformis Moq. in DC., Prodr. **13**(2): 30, 1849, nom. nud. pro syn. *Pircunia stricta* var. *residiformis.*
P. resedifolia Moq., loc. cit., nom. nud. pro syn. *Pircunia stricta* var. *residiformis.*
Pircunia stricta Moq., loc. cit. (Type *Ecklon & Zeyher s.n.* P)
P. stricta var. *resediformis* Moq., loc. cit. (Type *Ecklon & Zeyher s.n.* P)
P. stricta var. *latifolia* Moq., loc. cit. (Type *Drège s.n.* G, not seen, in IDC Micro-Edition, Candolle Prodromi Herbarium)

Herbs, slender, to ca 1 m. *Leaves* lanceolate-elliptic, rounded-mucronate, entire, the bases obtuse, up to 10 cm long and 2.5 cm wide; ± sessile to petioles 1 cm long. *Inflorescences* spikes or spike-like racemes, up to 13 cm long, sparsely flowered. *Flowers* ± sessile or with pedicels to ca 3-4 mm long; bract single, ca 1.4-1.6 mm long, linear-lanceolate, bracteoles two, ca 1 mm long, lanceolate; sepals 5, somewhat united at the bases, rounded, ca 2.5-3 mm long and 1.3-1.5 mm wide; stamens 6-7, in one whorl, the filaments ca 1.5-2 mm long, widened at the bases, the anthers ca 0.8 mm long; ovary 5-7 carpellate, free, the styles ca 0.8 mm long, ± straight. *Fruit* a collection of 5-7 drupelets, each 2-3 mm long.

SOUTH AFRICA: Albert Dist., *Cooper 1358* (K); 8 mi from Greytown, *Wylie 28018* (MO); Somerset East, *MacOwen 1453* (F, NY); s. loc., *Cooper 366* (K, NY), *Ecklon & Zeyher s.n.* (MO).

Pollen grains prolate spheroidal, ca 26μ (E) × ca 27μ (P), colpi ca 17μ long, exine ca 2μ in thickness, sexine ± equal to nexine and sparsely small spinulose.

Pollen examined: *MacOwan 1453* (NY).

2. *Phytolacca acinosa* Roxb., Hort. Bengal. 35, 1814.

P. esculenta Van Houtte, Fl. Serres **4**: 398 B, 1848.
Pircuinia esculenta (Van Houtte) Moq., loc. cit. **9**: 236, 1853-54.
Phytolacca kaempferi A. Gray, Mem. Amer. Acad. n.s. **6**: 404, 1858. (Type *Small s.n.* GH)
P. pekinensis Hance, Jour. Bot. **7**: 166, 1869. (Type *Williams 12648,* location unknown)

Herbs, stout, ca 2-3 m. *Leaves* ovate, ovate-elliptic, or rarely ovate-lanceolate, acute to ± mucronate, entire, the bases attenuate to slightly rounded, up to 35 cm long and 16 cm wide, ± glabrous; petioles to 6 cm long. *Inflorescences* racemes, up to 30 cm long, mostly axillary, rarely terminal, the peduncle ± smooth to scurfy. *Flowers* with pedicels 5-13 mm long, slightly winged at the base in some; bract single, (1-)2-4 mm long, lanceolate to awl-shaped; bracteoles two, ca 1.5 mm long; sepals 5, ± unequal, 3-4 mm long and 1.8-2.3 mm wide, ovate to rounded; stamens 7-15, sometimes in ± two whorls, the filaments ca 1.8-2 mm long, widened at the bases, the anthers ca 0.8-1 mm long; ovary sessile or on short gynophore, ca 0.5 mm long, 6-9 carpellate, somewhat united at the base in flower, mostly free in fruit, the styles ca 0.6-1 mm long, mostly straight, slightly recurved at the tip. *Fruit* an assemblage of drupelets, each up to 4 mm long.

Asia.

CHINA: CHANGYANG: *Wilson 873a* (K). CHIHLI: *Wang 20194* (NY). HUPEH: *Chow 532* (NY); *Henry 4351* (MO). KANSU: *Potanin s.n.* (K). KIANGSU: *Tsu 255* (K, MO). KWANGTUNG: *Tso 20891* (NY). LUNGCHOW: *Morse 576* (NY). SHANTUNG: *Chiao 2609* (F). SZECHAN: *Henry 5511A* (K). YUNNAN: *Forrest 5989* (K); *Henry 10705* (NY), *10705A* (MO). WITHOUT PROVINCE: *Henry 2045* (K); *Licent 1467* (K).

JAPAN: *Albrecht s.n.* (GH, NY); *Arimoto s.n.* (MO); *Dickens s.n.* (K, NY) *s.n.* (NY); *Higg s.n.* (NY); *Oldham 671* (GH, K); *Wright s.n.* (NY).

S. KOREA: *Yongsok 8063* (F).

INDIA: ASSAM: *Ward 8453* (K). HIMACHAL PRADESH: *Gammie 18587* (K). KASHMIR: *Stewart 7873* (MO). PUNJAB: *Jain & Bharadwaja s.n.* (NY). SIKKIM: *Watt 5709* (K). WITHOUT PROVINCE: *Griffith 4360* (K).

PAKISTAN: *Stewart s.n.* (NY).

Pollen grains subprolate, ca 23μ (E) $\times$ ca 28μ (P), colpi ca 23μ long, exine ca 2.5μ in thickness, sexine ca 2X as thick as nexine or $\pm$ equal to nexine and finely reticulated.

Pollen examined: *Henry 10705* (MO).

This Asian group of very robust herbs with conspicuously free-carpelled ovaries, is treated as an "aggregate species". Walter (1909) distinguished *P. acinosa* from *P. esculenta* primarily by the condition of the peduncle and inflorescence axis, scabrous in the former and glabrous in the latter, coloration of floral parts, and shape of sepals, all of which are not necessarily correlated in the manner described in his key. The individual characters, particularly coloration, are unsound bases for specific recognition.

SECT. 2 PIRCUNIOIDES H. Walter, Pflanzenr. IV, 83 (Heft 39): 42, 1909.

3. *Phytolacca dodecandra* L'Her., Stirp. Nov. 143, *pl. 69*, 1789. (Type *Bruce s.n.* K)

P. abyssinica Hoffm., Comm. Götting. **12**: 27, 1796.
P. elongata Salisb., Prodr. 345, 1796.
P. lutea Marsigl. ex Steud., Nom. ed. 1, 618, 1821.
Pircunia abyssinica (Hoffm.) Moq. in DC., 13(2): 30, 1849.
Phytolacca scandens Hilsenb. & Boj. ex Moq., loc. cit., nom. nud. pro syn. *Pircunia abyssinica.*

Shrubs or herbs, dioecious, $\pm$ scandent. *Leaves* ovate or rarely ovate-lanceolate or $\pm$ deltoid, acute-mucronate to retuse-mucronate, entire, the bases rounded, oblique-rounded, or $\pm$ obtuse, up to 14 cm long and 8.5 cm wide; petioles up to 3.5 cm long. *Inflorescences* racemes, pistillate or staminate, up to 30 cm long, axillary or terminal, pubescent. *Staminate flowers* with pedicels ca 4-6 mm long; bract single, ca 1-1.2 mm long, very narrow; two bracteoles, ca 0.6 mm long, very narrow; sepals 5, $\pm$ equal, narrow-oblong, ca 2-2.3 mm long and 0.7-0.9 mm wide; stamens 13-15, in two whorls, the filaments ca 2.5 mm long, widened at the base, the anthers ca 1 mm long; ovary rudimentary, 3-5 carpellate. *Pistillate flowers* with pedicels 5-7 mm long at maturity; bract single, ca 1 mm long, awl-shaped; two bracteoles, ca 0.6-0.8 mm long, $\pm$ awl-shaped; sepals 5, $\pm$ equal, oblong-ovate, ca 2.5 mm long and 1.5 mm wide; stamens rudimentary, ca 8-12, deposited in two (rarely one) whorls, the filaments ca 2 mm long, widened at the bases, the anthers ca 0.8 mm long; ovary 5 carpellate, ± free, the styles widened at the bases, the stigmas weakly penicellate. *Fruit* a collection of 5 or fewer drupelets, ca 3.5-4.5 mm long; seed 1, reniform, ca 3.5-4 mm long, testa shiny black.

Central and southern Africa and reported from Madagascar (Walter, 1909).

NIGERIA: Oban, *Talbot 1381* (MO).

REPUBLIC OF CONGO: Lake Kivu, *Linder 2032* (A); betw Sileko & Basoko, *Louis 11404* (MO); Yangambe, *Louis 264* (MO), *8638* (MO), *13890* (MO).

ETHIOPIA: s. loc., *Loccardo s.n.* (GH); *Schimper 131* (GH).

RUANDA: Biumba Terr, *Troupin 11819* (MO).

TANZANIA: Bezirk Bagamogo, *Schlieben 4136* (MO); N of Lake Nyasa, *Stolz 2265* (A).

UGANDA: s. loc., *Dummer 5405* (A).

RHODESIA: Headlands Dist, *Greenlow 88* (MO); Inyanga, *Whellan 672* (MO).

Pollen grains subprolate, ca 23μ (E) × ca 28-29μ (P), colpi ca 17-18μ long; exine ca 2μ in thickness, slightly thickened at the poles, sexine sparsely small spinulose.

Pollen examined: *Troupin 11819* (MO).

SUBG. 2 PIRCUNIOPSIS H. Walter Pflanzenr. IV, 83 (Heft 39): 45, 1909. (Type *P. dioica* L.)

SECT. 1 PIRCUNIOPHORUM H. Walter, loc. cit.

4. *Phytolacca sanguinea* H. Walter, Pflanzenr. IV, 83 (Heft 39): 46, 1909. (Lectotype selected: *Lehmann 4479* US, isolectotypes F, K. Syntypes: *Humboldt & Bonpland 822; Karsten s.n.; Linden 852;* all not seen)

Herbs, somewhat succulent, to 2 m. *Leaves* lanceolate-elliptic to elliptic to rarely ± ovate, acute, entire to very finely undulate, the bases obtuse to attenuate, up to 18 cm long and 6 cm wide, glabrous; subpetiolate to petioles ca 2.5 cm long. *Inflorescences* racemes, thyrsiform at the base, up to 15 cm long, the peduncle ⅓ to ½ this length, axillary or terminal, flowers crowded at maturity, scurfy. *Flowers* with pedicels to 1 cm long; bract single, ca 7-9 mm long, lanceolate; bracteoles two, sometimes appearing to be absent, ca 0.8-1 mm long, lanceolate; sepals 5, ± equal, oblong-elliptic, ca 4-5 mm long and 2-3 mm wide, ± red; stamens 8-11 (-15), deposited irregularly in one whorl, rarely two whorls, the filaments ca 2-2.5 mm long, the anthers ca 0.8-0.9 mm long; ovary ca 9 carpellate, almost completely united, the styles ca 1.5-2 mm long, recurved near the tip. *Fruit* a berry, ca 9 ribbed, black, ca 6 mm in diam.

Mostly northern South America.

COSTA RICA: *Hatheway 1358* (US).

COLOMBIA: CAUCA: El Tambo, *von Sneidern 1146* (F, NY, US); Popayan, *Lehmann 4479* (F, K, US); Mt Puracé, *Pennell & Killip 6510* (US); Quebrada del Río San Marcos, *Cuatrecasas 14776* (F, US). PUTUMAYO: Mts above Laguna de La Cocha, *Fosberg 20439* (NY, US); Valle de Sibundoy, *Cuatrecasas 11597* (F, US). SANTANDER: mts E of Las Vegas, *Killip & Smith 15783* (NY); Páramo Rico, *Killip & Smith 17703* (NY). TOLIMA: betw Cajamarca & summit of Divide, *Killip & Varela 34558* (US).

VENEZUELA: MÉRIDA: Páramo de las Lajas, *Hamburg-Tracy 141* (K).

Pollen grains prolate spheroidal, ca 25-26μ (E) × ca 28μ (P), colpi ca 22-23μ long, sexine ± equal to nexine and finely reticulated.

Pollen examined: *Killip & Smith 15783* (NY).

5. *Phytolacca rugosa* Br. & Bouche, Ind. Sem. Hort. Berol. 13, 1851. (Type *Warszewicz s.n.*, location unknown)

Herbs, woody at the bases, branches erect, angled, to 2 m. *Leaves* elliptic to elliptic-lanceolate, acute to long acuminate, entire, the bases attenuated or obtuse, up to 19 cm long and 6.5 cm wide; petioles to 5 cm long. *Inflorescences* racemes, to 15 cm long, mostly axillary. *Flowers* with pedicels, 3-7 mm long; bract single, ca 3-4 mm long, lanceolate; bracteoles two, < 1 mm long; sepals 5, ± equal, elliptic, 2-3 mm long, reflexed in fruit, white to pink; stamens 6-12, deposited on a hypogynous disc, the filaments ca 2 mm long, the anthers < 1 mm; carpels 4-9, united at the bases, styles not connivent and straight. *Fruit* a berry, sharply ridged, green-black, ca 6 mm in diam.

Mexico south to Colombia.

Mexico: guerrero: *Hinton 11082* (MO). jalisco: *Mexia 1661* (MO). michoacán: *Hinton 11896* (MO).

Costa Rica: *Dodge & Thomas 4351* (MO), *5320* (MO).

Panama: *Allen 311* (MO), *1511* (MO); *Blum et al. 2403* (MO); *Dwyer et al. 469* (MO); *Maurice 742* (MO); *Siebert 302* (MO); *Woodson & Schery 660* (MO); *Woodson et al. 884* (MO), *975* (MO).

Colombia: santa marta: *Smith 1160* (MO).

Pollen grains prolate, ca 24-26μ (E) × ca 34μ (P), colpi ca 24μ long, exine slightly thickened at the poles, sexine finely reticulated.

Pollen examined: *Hinton 11896* (MO).

6. *Phytolacca chilensis* (Miers ex Moq.) H. Walter, Pflanzeur. IV, 83 (Heft 39): 45, 1909, non H. Walter, loc. cit. 33.

P. chilensis Miers, Trav. **2**: 532, 1826, nom. nud.
Pircunia chilensis Miers ex Moq. in DC., Prodr. **13**(2): 29, 1849. (Type *Bridges s.n.* K)

Herbs, with woody bases. *Leaves* ovate-elliptic, mucronate, entire, the bases obtuse, up to 13 cm long and 5 cm wide; petioles to 3.5 cm long. *Inflorescences* spikes, to 20 cm long, axillary or terminal. *Flowers* sessile or with pedicels ca 1 mm long; bract single, ca 4-5 mm long, lanceolate; bracteoles two, ca 2 mm long, lanceolate; sepals 5, ± equal, ovate, rounded, ca 3-4 mm long and ca 2.5 mm wide; stamens 9-12, in 2 whorls, the filaments ca 2 mm long, the anthers ca 0.7 mm long; carpels 5-8, united only at the bases, the styles not connivent and straight. *Fruit* a weak berry, 5-8 ridged, ca 6-7 mm in diameter.

Chile: s. loc. *Bridges s.n.* (K).

No pollen examined due to paucity of flowering material.

Known only from the type collection, it nonetheless separates very easily from *P. sanguinea* and *P. rugosa* by its long spike. The possibility of hybrid origin from *P. icosandra* L. x *P. rugosa* (which could give the general characters of *P. chilensis*) are remote because of the geographical location. See also the discussion of *Anisomeria littoralis*.

Sect. 2 Pircuniopsis

sect. *Pseudolacca* Moq. in DC., Prodr. **13**(2): 30, 1849.

7. *Phytolacca tetramera* Hau. Mer., Apuntes Hist. Nat. **1**: 108, 1909. (Type *Hauman-Merck s.n.*, photo US, from B†)

Herbs, dioecious, to ca 0.5 m. *Leaves* spatulate to elongate lanceolate, mucronate, entire and finely undulate, the bases attenuate, up to 19 cm long and 5 cm wide, midrib prominent, up to 2 mm wide; subpetiolate to petioles 1-3 cm long. *Inflorescences* spikes, rarely spike-like racemes, staminate ca 4-5 cm long, the pistillate up to 10 cm long, mostly axillary. *Staminate flowers* sessile or with pedicels ca 2-3 mm long; bract single, present or absent, ca 2 mm long, closely appressed to sepals; bracteoles absent; sepals 4, unequal, ovate-elliptic, ca 2-2.5 mm long and 1.8-2.3 mm wide; stamens 12-15, irregularly deposited, the filaments ca 2.5-3.5 mm long, the anthers ca 1-1.5 mm long; ovary absent or of 2-3 carpels, thin and abortive. *Pistillate flowers* sessile or rarely with pedicels to 1 mm long; bract single, ca 2-2.5 mm long, sepal-like and keeled at the base, closely appressed to calyx; bracteoles absent; sepals 4, unequal, ovate, ca 2-2.5 mm long and 1.6-2.2 mm wide; stamens absent; ovary 6-9 carpellate, ± united, the styles somewhat connivent. *Berry* 6-9 ribbed, ca 4-6 mm in diam.

ARGENTINA: BUENOS AIRES: rd to Ignacio Correas, *Cabrera 5725* (NY); rd betw La Plata & Magdalena, *Cabrera 1641* (NY); Magdalena, *Parodi 6018* (GH); Monte Veloj, *Cabrera 626* (NY).

Pollen grains subprolate, ca 23μ (E) × ca 28-29μ (P), colpi ca 17-18μ long, sexine ± equal to nexine and finely reticulated.

Pollen examined: *Cabrera 626* (NY).

An easily identified species, not only because of the unique sepal number, but also because of the distinct leaf shape.

8. *Phytolacca dioica* L., Sp. Pl. ed. 2, 632, 1762. (Type *Alstroemer 129* LINN, not seen; from IDC Micro-Edition 607.5)

P. populifolia Salisb., Prodr. 345, 1796.
Pircunia dioica Moq. in DC., Prodr. **13**(2): 30, 1849.
Phytolacca arborea Moq., loc. cit., 31, nom. nud. pro syn *Pircunia dioica.*

Trees, dioecious, to 25 m. *Leaves* ovate, acute, entire to finely undulate, the bases rounded and sometimes decurrent, up to 12 cm long and 6 cm wide; petioles up to 7 cm long. *Inflorescences* racemes, up to 15 cm long, axillary or terminal. *Staminate flowers* with pedicels to 4 mm long; bract single, ca 1 mm long; bracteoles two, ca 1 mm long; sepals 5, ca 3 mm long; stamens 20-25, in two whorls, the filaments ca 4-5 mm long, the anthers ca 1.5-2 mm long; ovary occasionally present, 2-4 abortive carpels. *Pistillate flowers* with pedicels ca 3 mm long, ± stout; bract single, ca 0.5 mm long; bracteoles two, ca 0.5 mm long; sepals 5, ± equal, elliptic, ca 2-3 mm long, persistent in fruit; stamens ca 10, rudimentary; ovary 8-12 carpellate, incompletely united, the styles not connivent. *Fruit* a weak berry, ca 6-8 mm in diam.

South America.

ECUADOR: S Naranjapata, *Schimpff 534* (MO).

BRAZIL: PARANÁ: Desvio Ypiranga, *Dusen 16147* (MO, NY). SANTA CATARINA: Joinville, *Reitz & Klein 5701* NY); Vidal Ramos, *Klein 2222* (NY).

URUGUAY: Montevideo, *Herter 220* (MO).

Argentina: chaco: s. loc., *Jorgensen 1995* (MO); *Venturi 9825* (MO). corrientes: Santa Maria, *Pedersen 455* (MO, NY). misiones: Santo Pipo, *Schwarz 4844* (MO). tucumán: Quinta Lillo, *Descole-Borsini 35934* (NY).

Paraguay: guaira: Villarrico, *Jorgensen 3903* (MO). without province: *Hassler 447a* (MO, NY), *3379* (NY), *3380* (NY).

Pollen grains prolate, ca 17μ (E) $\times$ ca 25μ (P), colpi ca 17μ long, exine ca 2μ in thickness, sexine $\pm$ equal to nexine and finely reticulated.

Pollen examined: *Venturi 9825* (MO).

9. *Phytolacca weberbaueri* H. Walter, Pflanzenr. IV, 83 (Heft 39): 49, 1909. (Type *Weberbauer 4817*, photo F from B†).

Peru: cajamarca: vic of Casa Hacienda, *Hutchison & von Bismarck 6349* (F, MO, US).

Pollen grains prolate spheroidal, ca 21-22μ (E) $\times$ ca 24μ (P), colpi ca 17μ long, sexine $\pm$ equal to nexine and finely reticulated.

Pollen examined: *Hutchison & von Bismarck* 6349 (MO).

The description is omitted because of a lack of female specimens.

Subg. 3 Phytolacca.

Subg. *Euphytolacca* Moq. in DC., Prodr. **13**(2): 31, 1849.

Sect. 1 Phytolacca.

Sect. *Phytolaccastrum* H. Walter, Pflanzenr. IV, 83, (Heft 39): 50, 1909.

10. *Phytolacca icosandra* L., Sp. Pl. 631, 1753. (Type LINN, not seen; from IDC Micro-Edition 607.4)

P. malabarica Crantz, Inst. **2**: 484, 1769.
P. mexicana Gaertn., Fruct. **1**: 377, *pl. 77, t. 8*, 1788, non Crantz (Inst. **2**: 484, 1769)
P. triquetra Moench, Meth. Suppl. 107, 1802.
P. mexicana Sweet, Hort. Brit. ed. 1: 337, 1827, non Crantz (Inst. **2**: 484, 1769)
P. sessiliflora Kunth & Bouche, Ind. Sem. Hort. Berol. 15, 1848.
P. acuminata Moq. in DC., Prodr. **13**(2): 33, 1849, nom. nud. pro syn. *P. icosandra*.
P. longespica Moq., loc. cit. (Type *Bates s.n.* P)
P. icosandra L. var. *fraseri* Moq. in DC., Prodr. **13**(2): 34, 1849. (Type *Fraser s.n.* G, not seen, in IDC Micro-Edition, Candolle Prodromi Herbarium)
P. nova-hispania Millsp., Publ. Field Mus. Nat. Hist., Bot. Ser. **2**: 41, 1900. (Type *Millspaugh 1413* F)
P. icosandra var. *angustitepala* H. Walter, Pflanzenr. IV, 83 (Heft 39): 61, 1909. (Type *Kerber 216a*, location unknown)
P. icosandra var. *sessiliflora* (Kunth & Bouche) H. Walter, loc. cit.

Herbs, sometimes woody at the bases, stems angled or grooved, to ca 2 m. *Leaves* variable, elliptic, to obovate or rarely lanceolate, acute, entire, the bases obtuse to attenuate, up to 16 cm long and 8 cm wide, $\pm$ glabrous, subsessile to petioles ca 4 cm long. *Inflorescences* spikes or spike-like racemes, up to 30 cm long, mostly axillary. *Flowers* mostly sessile or rarely with pedicels to 4 mm long; bract single, lanceolate, ca 4 mm long; bracteoles two, ca 1 mm long; sepals 5, $\pm$ equal, broadly elliptic to $\pm$ lanceolate, ca 3 mm long and ca 2 mm wide, persistent in fruit, pink tinged; stamens ca 8-20, usually in two whorls, on a hypogynous disc, the filaments ca 2-2.5 mm long, widened at the bases, the anthers ca 1 mm long; ovary 6-9 carpellate, united, the styles connivent in flower and recurved. *Fruit* a berry, dark green to brown, rarely purple, ca 5-7 mm in diam.

Mexico, Central America, the West Indies and northern South America.

MEXICO: DURANGO: *Palmer 157* (MO). GUERRERO: *Hinton 9240* (MO). JALISCO: *Pringle 9525* (MO). MEXICO: *Ortenburger 16M650* (MO). MICHOACÁN: *Bro. Arsène 8703* (MO); *Hinton 12200* (MO), *12852* (MO); *Schery 124* (MO). NAYARIT: *Jones 23278* (MO). PUEBLA: *Pringle 6293* (MO). SINALOA: *Gentry 5911* (MO). SONORA: *Gentry 1423* (MO). VERA CRUZ: *Palmer 453* (MO).

COSTA RICA: *Godfrey 66075* (MO).
PANAMA: *Lewis et al. 321* (MO).
CUBA: *Wright 1392* (MO).
HAITI: *Holdridge 1630* (MO).
COLOMBIA: CAUCA: El Tambo, *Hultén 9* (GH).
VENEZUELA: MIRANDA: Los Mariches, *Pittier 11965* (MO).

Pollen grains prolate, ca 26μ (E) $\times$ ca 36μ (P), colpi ca 26μ long, exine ca 2μ in thickness, thickened at poles to ca 2.5μ, sexine $\pm$ equal to nexine and finely reticulated.

Pollen examined: Gentry *1423* (MO).

This is one of the more distinct species of *Phytolacca* perhaps best recognized by a combination of long inflorescences, almost sessile flowers and two staminal whorls, although any one of these three features alone is not sufficient.

11. *Phytolacca octandra* L. Sp. Pl. ed. 2, 631, 1763. (Type LINN, not seen; from IDC Micro-Edition 607.1)

P. mexicana Crantz, Inst. **2**: 484, 1796, non Gaertn. (Fruct. **1**: 377, *pl. 77, t. 8,* 1788) nec Sweet (Hort. Brit. ed. 1, 337, 1827)
P. decandra Descourt., Fl. Antill. **5**: 32, *pl. 312,* 1827, non L. (Sp. Pl. ed. 2: 631, 1763)
P. octandra var. *grandifolia* Moq. in DC., Prodr. **13**(2): 32, 1849. (Type *Galeotti 372* P)
P. acinosa Pope, Wayside Pl. Hawaii 61, *pl. 25,* 1929, non Roxb. (Hort. Bengal. 35, 1814).

Herbs, $\pm$ succulent, to 2 m. *Leaves* lanceolate, lanceolate-ovate, acute to acute-acuminate, sometimes mucronate, entire, the bases obtuse to attenuate, up to 22 cm long and 7.5 cm wide; subpetiolate to petioles ca 2.5 cm long. *Inflorescences* spikes or rarely spike-like racemes, up to 14 cm long, axillary or terminal, $\pm$ scurfy. *Flowers* sessile or with pedicels to 1 mm long; bract single, ca 2.2-2.5 mm long, lanceolate; bracteoles two, ca 1 mm long, narrow-lanceolate; sepals 5, subequal, oblong to ovate, ca 2-3 mm long and 1.2-2 mm wide; stamens 8-10, in one whorl, the filaments ca 1.5-1.8 mm long, the anthers $<$ 1 mm long; ovary 7-10 carpellate, united, the styles $\pm$ connivent. *Fruit* a berry, 7-10 ribbed, green-black, ca 4.5-6 mm in diam.

A $\pm$ cosmopolitan species.

MEXICO: FEDERAL DISTRICT: *Lyonnet 220* (K, MO). MORELOS: *Clark 7293* (MO). NUEVO LEÓN: *Kenoyer s.n.* (MO); *Meyer & Rogers 2738* (MO); *Taylor 195* (MO). SAN LUIS POTOSÍ: *Schaffner 887* (K). YUCATÁN: *Gaumer 674a* (MO). WITHOUT STATE: *Bourgeau 199* (K).
GUATEMALA: *Greenman & Greenman 5698* (MO).
COLOMBIA: NORTE DE SANTANDER: Mutiscua, *Killip & Smith 19651* (NY).
VENEZUELA: MÉRIDA: COLONIA TOVAR, *Fendler 1085* (MO, NY). Quebrada de Saisay, *Gehriger 26* (MO). MIRANDA: upper Pico de Naiguata, *Pittier 6272* (NY).
BOLIVIA: COCHABAMBA: Pocona, *Steinbach 8682* (K, MO, NY).
INDIA: Kodaikanal, *Matthew 1539* (K).

Java: preanger: *Schiffner 1932* (A).

Kenya: 18 mi S of Eldort, *Bogdan 1813* (K); Kakamega Forest, *Lucas 100* (K); Ngong Hills, *Kokwaro 312* (K); vic of Norfolk Hotel, *Kiwika 249* (K).

Rhodesia: Hondi View, *Noel 2341* (MO).

South Africa: Utrecht Natal, *Pole-Evans 3894* (K).

Australia: new south wales: *Constable 19105* (MO).

New Zealand: Rangitoto I, *Walker 4288* (MO).

Hawaii: oahu: *Degener 8892* (MO), *8893* (NY). Kauai: *Forbes 507* (K, MO).

Pollen grains prolate, ca 26μ (E) $\times$ ca 36μ (P), colpi ca 21-22μ long, exine ca 2.5μ in thickness and finely reticulated.

Pollen examined: *Gaumer 674a* (MO).

There are suggestions of characteristics of this species in many specimens; bona fide collections of *P. octandra* may be rather easily identified by the ± sessile flowers, inflorescences which are not conspicuously long (as in *P. icosandra* L.), and which have a relatively short peduncle and a single whorl of stamens.

12. *Phytolacca thyrsiflora* Fenzl ex J. A. Schmidt in Mart., Fl. Brazil. **14**(2): 343, *pl. 80,* 1872.

Herbs to 3 m. *Leaves* ovate-elliptic to elliptic, ± acute, entire or very finely undulate, the bases obtuse to attenuate, up to 14 cm long and 7 cm wide, glabrous; subpetiolate to petioles ca 3 cm long. *Inflorescences* raceme-like, thyrsiform near the base or often ± completely to tip, up to 30 cm long, axillary or terminal, the flowers not crowded at maturity, ± scurfy. *Flowers* with pedicels to 1.4 cm long; bract single, ca 2.5-4 mm long, lanceolate; bracteoles two, sometimes obsolete, ca 1.5-1.8 mm long, lanceolate; sepals 5, ± equal, oblong-ovate, ca 2-3 mm long and 1.5-2 mm wide; stamens 9-12, in one whorl, rarely a partial second whorl, the filaments ca 1.8-2 mm long, the anthers ca 0.8 mm long; ovary 7-9 carpellate and united. *Fruit* a berry, 7-9 ribbed, green to black, ca 5-7 mm in diam.

Brazil, French Guiana and Paraguay.

Brazil: espirito santo: Espirito Santo, *Robert s.n.* (K). goiás: S of Corumbá de Goiás, *Irwin et al. 10883* (MO); W of Veadeiros, *Irwin et al. 12793* (MO). maranhao: Maracassume River, *Froes 1997a* (K). minas geraes: betw Itamuri & Realeza, *Duarte & Castellanos 33176* (F); 4 km SE of Vicosa, *Irwin 2171* (US). pernambuco: Recife, *Tavares 985* (US). rio de janeiro: vic of Mangaratiba, *Monteiro 3107* (US); vic of Rio de Janeiro, *Glaziou 15354* (K). santa catarina: anitapolis: *Klein 435* (US); Brusque, *Smith 5800* (US); Caruru de Cacho, *Reitz 1889* (NY).

French Guiana: *Broadway 637* (US).

Paraguay: amambay: Sierra de Amambay, *Hassler 9909* (K, NY).

Pollen grains subprolate, ca 25μ (E) $\times$ ca 30μ (P), colpi ca 22-23μ long, sexine ± equal to nexine and finely reticulated.

Pollen examined: *Reitz 1889* (NY).

13. *Phytolacca heterotepala* H. Walter, Pflanzenr. IV, 83 (Heft 39): 51, 1909. (Syntypes: *Bourgeau 199* pro parte; *Ehrenberg s.n.; Hahn s.n.; Schiede s.n.; Schumann 1185* pro parte; all not seen).

Herbs to ca 2 m. *Leaves* ± lanceolate to ovate, acute to acute-mucronate, entire, the bases obtuse, up to 13 cm long and 6 cm wide; petioles up to 5 cm long. *Inflorescences* spike-like racemes, up to 25 cm long, mostly axillary, slightly scurfy.

Flowers with pedicels 1-4 mm long; bract single, ca 2.5-3 mm long, lanceolate; bracteoles two, ca 0.8-1 mm long, ± awl-shaped; sepals 5(-6-8), unequal, ± oblong, ca 3-4 mm long and 1.5-2.2 mm wide, stamens 15-22, in two whorls, the filaments ca 1.8 mm long, the anthers ca 0.9-1 mm long; ovary 8-9 carpellate and united. *Fruit* a berry, ca 8-9 ribbed, purple-black, ca 6-7 mm in diam.

Western United States and Mexico.

UNITED STATES: CALIFORNIA: Howell 34602 (US), 34604 (US), 35095 (US), 35121 (US). MEXICO: TAMAULIPAS: *Viereck* 333 (US).

Pollen grains subprolate, ca 28μ (E) × ca 35μ (P), colpi ca 24μ long, exine slightly thickend at the poles, sexine finely reticulated.

Pollen examined: *Howell 34602* (US).

The only collection listed in Walter's (1909) original description which I have seen is *Schumann 1185* (US), and I believe this to be *P. octandra* L. Nevertheless, the specimens from California possess the distinctive characters which Walter (1909) cited, i.e. unequal sepal size and two staminal whorls. Specimens collected by *Howell* in the vicinity of San Francisco, exhibit hybrid characters such as 8-9 sepals, sterility, and thyrsiform inflorescences, particularly *Howell 35122* (US), which because of the above anomalies, I do not cite (see Howell, 1960).

14. *Phytolacca meziana* H. Walter, Pflanzenr. IV, 83 (Heft 39): 57, 1909. (based on *P. icosandra* var. *octogyna*)

P. icosandra L. var. *octogyna* J. D. Smith, Bot. Gaz. **18**: 210, 1893. (Type *Heyde & Lux 3031* lectotype selected US).

Herbs, somewhat suffrutescent at the base. *Leaves* lanceolate-elliptic, acute, entire, the bases obtuse, up to 14 cm long and 4.5 cm wide, glabrous; petioles up to 5 cm long. *Inflorescences* racemes, up to 28 cm long, mostly axillary, ± scurfy. *Flowers* with pedicels to 1 cm long; bract single, ca 7-9 mm long, lanceolate; bracteoles two, ca 2 mm long, lanceolate; sepals 5, ± equal, oblanceolate to oblong, ca 4 mm long and 2 mm wide; stamens 15-20, in two whorls, the filaments ca 2-2.2 mm long, the anthers ca 0.9-1 mm long; ovary 7-8(-9) carpellate, united, the styles ca 1.5 mm long, slightly recurved at the tip, the stigma on the upper surface. *Fruit* a berry, 7-8 ribbed, black, ca 5-6 mm in diam.

Central America.

GUATEMALA: *Heyde & Lux 3031* (US).
COSTA RICA: *Standley 42697* (US).

Pollen grains subprolate, ca 24μ (E) × ca 30-31μ (P), colpi ca 19-21μ long, exine slightly thickened at the poles, sexine ± equal to nexine and finely reticulated.

Pollen examined: *Heyde & Lux 3031* (US).

15. *Phytolacca rivinoides* Kunth & Bouché, Ind. Sem. Hort. Berol. 15, 1848. (Type *Moritz s.n.*, location unknown)

P. icosandra Wright, Mem. 268, 1828, non L. (Sp. Pl. 631, 1753).
P. bogotensis Miq., Ser. Exot. *pl.* 6.3, 1842, non H.B.K. (Nov. Gen. Sp. Pl. **2**: 183, 1817).
P. macrostachya Willd. ex Moq. in DC. Prodr. **13**(2): 33, 1849, nom. nud. pro syn *P. icosandra*.
P. polystigma Benth. ex Moq., loc. cit.
P. polystyla Schomb. ex Moq., loc. cit., 460.

Herbs, succulent, robust, erect to 5 m. *Leaves* ovate-elliptic, rarely lanceolate, acute, acuminate, or rarely mucronate entire, the bases obtuse or rarely oblique, up to 21 cm long and 9 cm wide; petioles to 7 cm long. *Inflorescences* racemes, ca 40-50(-70) cm long, axillary or terminal, robust, the peduncle red-purple. *Flowers* with pedicels 7-13 mm long, filiform in some; bract single, ca 2 mm long, awl-shaped; bracteoles two, ca 0.5-0.7 mm long; sepals 5, ± equal, ovate, ca 2 mm long and 1.5 mm wide, white to pink, absent in fruit; stamens 10-17, in two whorls on a hypogynous disc, the filaments ca 1.5-2 mm long, the anthers ± globose, < 1 mm long; ovary 10-16 carpellate, united, the styles connivent at the base, free and recurved above. *Fruit* a berry, juicy, ribbed when dry, purple-black, 2-3 mm in diam and delicate appearing to 5-6 mm in diam and robust.

Mexico, south to Bolivia and Brazil, and the West Indies.

MEXICO: NUEVO LEÓN: *Frye & Frye 2548* (MO).
BRITISH HONDURAS: *Schipp 125* (MO).
HONDURAS: *Yuncker et al. 6166* (MO), *8459* (MO).
GUATEMALA: *Turckheim 11536* (MO).
COSTA RICA: *Dodge & Thomas 4367* (MO), *6406* (MO); *Godfrey 67290* (MO); *Rojas 205* (MO); *Skutch 2919* (MO), *3389* (MO).
PANAMA: *Blum 1259* (MO); *Duke 4351* (MO), *8104* (MO); *Ebinger 49* (MO); *Hunter & Allen 313* (MO); *Lewis et al. 874* (MO); *Tyson 2186* (MO), *3364* (MO); *Tyson et al. 2922* (MO); *von Wedel* 833 (MO), *2078* (MO), *2079* (MO), *2631* (MO); *Woodson et al. 1392* (MO).
DOMINICAN REPUBLIC: *Valeur 11* (MO).
GUADELOUPE: *Duss 2400* (MO).
JAMAICA: *Hespenheide 709* (MO).
PUERTO RICO: *Otero 645* (MO); *Stimson 1684* (MO).
TRINIDAD: *Broadway 6778* (MO).
COLOMBIA: PUTUMAYO: Río San Miguel, *Schultes 3646* (MO). SANTA MARTA: s. loc., *Smith 1161* (MO), *2664* (MO). VALLE: Jamundi, *von Sneidern 4558* (MO).
VENEZUELA: MÉRIDA: Colonia Tovar, *Fendler 1084* (MO).
SURINAME: *Irwin et al. 55120* (MO).
GUYANA: *De La Cruz 2085* (MO), *2132* (MO), *3221* (MO), *3639* (MO), *4481* (MO).
BRAZIL: ACRE: NW of Cruzeiro do Sul, *Prance 2796* (MO.) AMAPA: vic of Mt Bruyers, *Irwin et al. 47328* (MO).
BOLIVIA: BENÍ: *Werdermann 2165* (MO). LA PAZ: S Yungas, *Krukoff 10300* (MO). NORDYUNGAS: nr Coroico, *Buchtien 4117* (MO). SANTA CRUZ: Río Víbora, *Steinbach 7574* (MO). WITHOUT PROVINCE: *Buchtien 5403* (MO).
PERU: CUZCO: Quincemil, *Vargas 7779* (MO). LORETO: vic of Pongo de Manseriche, *Mexia 6231* (MO); Boqueron Padre Abad, *Woytkowski 34358* (MO). PUNO: trail betw Santo Domingo & Machu, *Metcalf 30655* (MO). SAN MARTÍN: vic of Moyobamba, *Klug 3494* (MO).

Pollen grains subprolate, ca 27μ (E) × ca 35μ (P), colpi ca 22-23μ long, sexine ± equal to nexine and finely reticulated (Fig. 7).

Pollen examined: *Frye & Frye 2548* (MO).

An easily recognized species because of the very robust racemes, long pedicels and high carpel number.

16. *Phytolacca purpurascens* A. Br. & Bouche, Ind. Sem. Hort. Berol., app. 13, 1851. (Type *Warszewicz s.n.*, location unknown)

Herbs. *Leaves* elliptic, lanceolate-elliptic, or rarely ± ovate, acute or mucronate, entire, the bases obtuse, up to 22 cm long and 8 cm wide; petioles to 7 cm long. *Inflorescences* spike-like racemes, up to 28 cm long, mostly axillary, lightly pubescent. *Flowers* with pedicels 3-6 mm long; bract single, ca 2.3-2.8 mm long, lanceolate; bracteoles two, ca 1.5-1.8 mm long, lanceolate; sepals 5, subequal, ± ovate, ca 2.5 mm long and 1.8-2 mm wide; stamens 13-17(-20), in two whorls, the filaments ca 1.5-1.7 mm long, the anthers ca 0.7-0.8 mm long; ovary (7-8-) 9-10 carpellate, ± completely united, the styles ± connivent. *Fruit* a berry, 7-10 ribbed, ca 6-7 mm in diam.

Sparsely distributed in the West Indies and reported from Central America (Walter, 1909).

HAITI: *Leonard & Leonard 11631* (MO, US), *13394* (US), *13912* (US), *15454* (US). GRAND BAHAMA I.: *Lewis 7166* (MO).

Pollen grains prolate spheroidal, ca 27μ (E) × ca 30μ (P), colpi ca 23μ long, sexine ± equal to nexine and finely reticulated.

Pollen examined: *Leonard & Leonard 13912* (US).

Phytolacca purpurascens is closely related to *P. icosandra* but can usually be distinguished from the latter by its longer pedicel, a somewhat unreliable character because of continuous graduation. This taxon may well be of hybrid origin from *P. icosandra* × *P. rivinoides* or *P. americana.*

17. *Phytolacca brachystachys* Moq. in DC., Prodr. **13**(2): 31, 1849. (Type *Beechey s.n.* K)

P. abyssinica Hook. & Arn., Bot. Beech. Voy. 94, 1832, non Hoffm. (Comm. Götting. **12**: 27, 1796).

P. bogotensis Mann, Proc. Amer. Acad. **7**: 198, 1867, non H.B.K. (Nov. Gen. Sp. Pl. **2**: 183, 1817).

Herbs. Leaves ± elliptic, acute or mucronate, entire, the bases obtuse, up to 17 cm long and 9 cm wide; petioles to 3.5 cm long. *Inflorescences* racemes, up to 16 cm long, mostly axillary, ± scurfy. *Flowers* with pedicels to 5 mm long; bract single, ca 2-2.5 mm long, lanceolate; bracteoles two, ca 1-1.5 mm long, lanceolate; sepals 5, ± equal, oblong, ca 3-4 mm long and ca 1.8-2 mm wide; stamens 7-9, in one whorl, the filaments ca 1.5 mm long, the anthers ca 0.8 mm long; ovary 5-7(-8) carpellate, united the styles connivent or sometimes free. *Fruit* a berry, 5-7 ribbed, ca 4-6 mm in diam.

HAWAII: *Degener 8891* (MO), *8896* (MO), *8897* (MO); *Degener & Wieblse 3302* (MO); *Forbes 184* (MO), *208* (MO), *1036* (F, MO); *Forbes & Rock s.n.* (MO); *Fosberg 10946* (F); *Heller 2772* (F, MO); *Mann & Brigham 426* (F, MO).

Pollen grains subprolate, ca 29μ (E) × ca 32μ (P), colpi ca 22-23μ long, exine ca 2.5μ in thickness, sexine ± equal to nexine and finely reticulated.

Pollen examined: *Heller 2772* (MO).

18. *Phytolacca bogotensis* H.B.K., Nov. Gen. Sp. Pl. **2**: 183, 1817.

P. australis Phil., Anal. Univ. Chil. **43**: 536, 1873. (Type *Philippi s.n.* photo NY, from B†)

P. micrantha H. Walter, Pflanzenr. IV, 83 (Heft 39): 57, 1909. (Type *Loretz & Hieronymus 947* B†)

P. parviflora Hau.-Mer., Apuntes Hist. Nat. **1**: 107, 1909. (Type *Hauman-Merck s.n.*, location unknown)

Herbs, ± succulent, to 2 m. *Leaves* lanceolate to elliptic, acute to ± acuminate, entire, the bases obtuse to attenuate, up to 18 cm long and 7 cm wide; subsessile to petioles ca 3.5 cm long. *Inflorescences* spike-like racemes, up to 20 cm long, axillary or terminal, scurfy. *Flowers* with pedicels ca 2-4 mm long; bract single, 2-3 mm long, lanceolate; bracteoles two, ca 1-1.2 mm long, narrow-lanceolate; sepals 5, subequal, oblong to ± ovate, ca 2-3 mm long and 1.2-2 mm wide; stamens 7-10, in one whorl, rarely a partial second whorl, the filaments ca 2 mm long, the anthers ca 0.8-0.9 mm long; ovary 7-10 carpellate, united, the styles thin. *Fruit* a berry, 7-10 ribbed, green-brown, ca 5-6 mm in diam.

South America.

COLOMBIA: CAUCA: Popayan, *Lehmann 616* (GH).

ECUADOR: E of Loja, *Espinosa 485* (NY); eastern Río Bamba, *Schimpff 791* (MO).

CHILE: VALDIVIA: S of José de La Mariquina, *Hollermayer 1205* (MO).

BOLIVIA: LA PAZ: vic of Sorata, *Mandon 1030* (NY); *Williams 828* (K, NY). WITHOUT PROVINCE: Yungas Mts, *Scolnik & Luti 502* (NY).

ARGENTINA: CATAMARCA: s. loc., *Jorgensen 1490* (MO). JUJUY: 25 km NW of Jujuy, *Eyerdam & Beetle 22227* (MO); Río Yala nr Yala, *West 6256* (MO). TUCUMÁN: Quebrada de Hules, *Venturi 9130* (MO).

Pollen grains prolate ca 25μ (E) × ca 34μ (P), colpi ca 23-24μ long, exine ca 2-2.5μ in thickness and finely reticulated.

Pollen examined: *Eyerdam & Beetle 22227* (MO).

Phytolacca bogotensis is very difficult to separate from *P. octandra*; the pedicel length, ± sessile in the latter species, appears to be the only consistent character.

19. *Phytolacca americana* L., Sp. Pl. 441, 1753.

P. decandra L., Sp. Pl. ed. 2, 631, 1763, non Descourt. (Flor. Med. Antilles **5**: *pl. 312*, 1827). (Type LINN, not seen; from IDC Micro-Edition 607.3)

P. vulgaris Crantz, Instit. **2**: 484, 1766.

P. rigida Small, Bull. N.Y. Bot. Gard. **3**: 422, 1904. (Type *Small & Wilson 1893* NY)

Herbs, ± succulent, to ca 3 m. *Leaves* lanceolate-elliptic, elliptic or rarely ± ovate, acute or sometimes mucronate, entire, the bases obtuse, up to 30 cm long and 12 cm wide (occasionally much larger); petioles to ca 6 cm long. *Inflorescences* racemes, sometimes thyrsiform at the bases, up to 30 cm long, mostly axillary, glabrous to lightly scurfy. *Flowers* with pedicels to 12 mm long; bract single, ca 2-3 mm long, lanceolate; bracteoles two, ca 1-1.5 mm long, lanceolate; sepals 5, ± equal ovate and rounded, ca 2.2 mm long and 2 mm wide; stamens ca 10, in one whorl, the filaments ca 2 mm long, the anthers ca 0.8 mm long; ovary ca 10 carpellate, united or sometimes the apices free, the styles mostly connivent in flower. *Fruit* a berry, ca 10 ribbed, ca 6-8 (-10) mm in diam.

Widely distributed in eastern North America and introduced into Europe, Africa and Asia; selected exsiccatae listed.

CANADA: ONTARIO: *Marie-Victorin et al. 56838* (MO); *Soper & Shields 377* (MO).

UNITED STATES: FLORIDA: *Hitchcock 301* (NY); *Moldenke 250* (MO); *O'Neill s.n.* (MO); *Small & Small 4120* (NY), *4682* (NY), *5439* (NY); *Small & Wilson 2010* (NY); *Tracy 7531* (NY). INDIANA: *Deam 18* (MO). LOUISIANA: *Ball 542* (MO). MASSACHUSETTS: *Churchill s.n.* (MO); *Seymour 265* (MO). MISSISSIPPI: *Pollard 1156* (MO). MISSOURI: *Eggert s.n.* (MO); *Fritchey s.n.* (MO); *Kellogg 1713* (MO). OKLAHOMA: *Houghton 3936* (MO). TENNESSEE: *Ruth 191* (MO). WEST VIRGINIA: *Berkley 840* (MO). WISCONSIN: *Fassett 27388* (MO).

Pollen grains ca 25μ (E) $\times$ ca 34μ (P), colpi ca 23-24μ long, exine ca 2μ in thickness, slightly thickened at the poles to ca 2.5μ, sexine equal to or greater than nexine and finely reticulated.

Pollen examined: *Soper & Shields* 377 (MO).

Although *P. rigida* Small has been considered conspecific with *P. americana* by many authors, including Sauer (1952), there does seem to be a higher frequency of certain characteristics in specimens from Florida, the type locality for *P. rigida.* These features include a shorter raceme, hence the specific epithet which refers to the erectness of the inflorescence, and pedicels which are, on the average, a little shorter and stouter than for most individuals of *P. americana.* Hardin (1964) in a study of the two taxa cited the above observation plus minor differences in leaves, bracteole width, number of fruits, etc., all of which, as his Table 1 (p. 163) indicates, have overlapping measurements. The most striking discovery was the difference in the xylem of the peduncle, in which *P. rigida* averages a 70% thicker cylinder. In spite of Hardin's results, and he makes no definite designation of the status of the Florida collections, I tend to favor a reduction of *P. rigida* to *P. americana* in view of the widespread morphological variation in the entire genus. Hardin's tentative conclusions and ideas are worthy of mention because of their applicability to the problem of speciation in *Phytolacca* in general (Hardin, 1964, p. 162): "*P. rigida* may represent an ecological variant of *P. americana* which is not yet distinct; i.e., an early stage in sympatric speciation. On the other hand, two distinct species may have existed at one time and with forced migration and sympatry during Pleistocene or before, the old barriers and discontinuities have been eliminated. A third possibility is that *P. americana* has been "contaminated" by introgression from a tropical or subtropical species such as *P. octandra* which has an erect raceme, by way of Mexico or the Caribbean."

SECT. 2 PHYTOLACCOIDES H. Walter, Pflanzenr. IV, 83 (Heft 39): 61, 1909.

20. *Phytolacca pruinosa* Fenzl., Del. Sem. Hort. Vindob 8, 1855. (Type *Kotschy s.n.* W, not seen)

Herbs, dioecious, stems $\pm$ succulent, mostly unbranched, to 1 m. *Leaves* ovate-lanceolate, acute, rarely mucronate, entire, the bases obtuse-attenuate, up to 10 cm long and 4 cm wide; petioles indistinct. *Inflorescences* racemes, the staminate up to 12 cm long, the pistillate up to 7 cm long and densely flowered. *Staminate flowers* with pedicels up to 6 mm long; bract single, ca 2.5-3 mm long, lanceolate; bracteoles two, ca 1 mm long, located ca midway on pedicel; sepals 5, $\pm$ equal, ovate ca 3.5-4 mm long and ca. 2.5 mm wide, green to pink; stamens 15-20, in two whorls, the filaments ca 2-2.5 mm long, widened at the base, the anthers ca 1-1.2 mm long; ovary rudimentary, 5-7 carpellate. *Pistillate flowers* with pedicels up to 3.5 mm long; single bract, ca 2.2-3 mm long; two bracteoles, ca 1.8-2 mm long; sepals 5, $\pm$ equal, ovate-triangular, ca 3-3.5 mm long and 2.5-3 mm wide, green to pink; stamens rudimentary and much reduced, 12-15, appearing to be deposited in two whorls; ovary 6-9 carpellate, united, the styles recurved. *Fruit* a berry, 6-9 ribbed, ca 5-6 mm in diam; seeds reniform, ca 3.5 mm long.

Endemic to Cyprus.

CYPRUS: *Haradjian 487* (MO); *Oswald 147* (K); *Young 7808* (K).

Pollen grains ca 27μ (E) $\times$ ca 34μ (P), colpi 20-23μ long, exine slightly thickened at the poles, sexine medium finely reticulated.

Pollen examined: *Young 7808* (K).

EXCLUDED SPECIMENS:

Horticultural specimens from Kew, the type collections of P. clavigera W. W. Smith (Bot. Mag. ***149:*** *pl. 8978, 1923).* At first glance this specimen appears to be the robust Asian species, *P. acinosa;* however, the carpels are definitely united. Since it is of horticultural origin, I hesitate to treat it as a distinct species until I have seen more collections.

Pittier 6272 (US). This is the type collection of *P. venezuelensis* O. C. Schmidt (Notizbl. Ber. **8:** 312, 1923), which in my opinion is a stunted specimen of *P. octandra.* The carpel connation is not characteristic of subg. *Pircuniopsis,* to which Schmidt assigned it.

RIVINOIDEAE

II. Subf. **Rivinoideae** Nowicke, subf. nov. Ovarium unicarpellatum et uniovulatum; achenium, drupa, samara, vel utriculus. (Type *Rivina* L.)

A. Tribe **Seguierieae** Nowicke, trib. nov. Inflorescentiae paniculiformes; samara. (Type *Seguieria* Loefl.)

a. Calyx of 4 sepals, becoming woody and remaining erect in fruit ....4. *Gallesia*
aa. Calyx of 5 sepals, herbaceous and becoming reflexed in fruit ....5. *Seguieria*

4. GALLESIA

Gallesia Casar., Stirp. Bras. Dec. **5:** 43, 1843.

Monotypic.

1. *Gallesia integrifolia* (Spreng.) Harms in Engler & Prantl, Nat. Pflanzenfam. **2**(16): 144, 1934. (Neotype selected: *Ducke 24211* US, isoneotypes G, S)

Thouinia integrifolia Spreng., Neue Entdeck. **2:** 155, 1821.
Crataeva gorarema Vell., Fl. Flum. **1:** 191; **5:** *pl. 4,* 1825.
Gallesia scorododendrum Casar., Nov. Stirp. Bras. Dec. **5:** 44, 1843.
G. gorazema (Vell.) Moq. in DC., Prodr. **13**(2): 8, 1849. (Type *Vauthier 146* G, P)

Trees to 30 m. *Leaves* ovate to ovate-elliptic, acute to acuminate, entire, the bases obtuse or slightly cordate, up to 12 cm long and 6.5 cm wide, glabrous, $\pm$ leathery; petioles ca 2-3 cm long. *Inflorescences* irregular panicles, ca 10-20 cm long, axillary or terminal, softly pubescent. *Flowers* perfect, $\pm$ actinomorphic, $\pm$ sessile; bract single, ca 1.2 mm long; bracteoles two, ca 1.2 mm long; sepals 4, somewhat unequal, ovate, ca 4 mm long and 1.4-2.5 mm wide, green-brown, leathery, pubescent, thickened at the base, erect in fruit and becoming enlarged and the margins split; stamens numerous, irregularly deposited, the filaments ca

1.5 mm long, the anthers ca 1.5 mm long; ovary 1-carpellate, compressed laterally, the style flattened, the stigma papillose on one edge. *Fruit* a samara, ca 2.5-3 cm long, brown, the non-stigmatic edge gradually curved or ± constricted at the base; seed one, ovoid to elliptic, compressed laterally.

Central South America: Bolivia, Brazil, Ecuador and Peru.

Pollen grains single, subprolate, ca 21-22μ (E) × ca 24-25μ (P), 3-colporoidate, colpi ca 9-10μ long, os irregular, ca 4μ wide and ± as long as colpi, exine ca 1.7μ in thickness, ca 2μ at the poles, sexine ± equal to nexine and ± smooth.

Although clearly related to the large genus *Seguieria* Loefl. by its almost identical flower plan and samara fruit, *Gallesia* is nevertheless easily identifiable by its 4-merous calyx, which has a woody texture and remains erect in fruit. *Gallesia ovata* O.C. Schmidt is here reduced to a variety of *G. integrifolia* (Spreng.) Harms for the following reasons: while there appears to be some variation in the shape of the samara wing, the condition is somewhat indeterminate, and the wider leaves cited for *G. ovata* do not constitute a distinguishing character.

a. Samara wing with gradual taper ....1a. *G. integrifolia* var. *integrifolia*
aa. Samara wing with a constricted basal portion ....1b. *G. integrifolia* var. *ovata*

1a. *Gallesia integrifolia* (Spreng.) Harms var. *integrifolia.*

BOLIVIA: LA PAZ: San Bartolomé, *Krukoff 10118* (G, S, US).

BRAZIL: ACRE: upper Rio Jurupary, *Krukoff 5216* (G, S, US); Seringal, *Ducke 24212* (S, US). AMAZONAS: Rio Purus, *Ducke 24211* (G, S, US). BAHIA: basin of Rio Grongogy, *Curran 7* (US). MATO GROSSO: Recreio, *Lutz 1427* (US). MINAS GERAES: Caldas, *Regnell III 1014* (S, US). PARANÁ: Patrimonio, *Dusen 16786* (S). RIO DE JANEIRO: Copacabana, *Glaziou 4753* (S).

ECUADOR: EL ORO: vic of Piedras, *Little 6621* (US).

PERU: JUNIN: *Satipo, Vasquez 16* (G).

Pollen examined: *Ducke 24211* (US).

1b. *Gallesia integrifolia* (Spreng.) Harms var. **ovata** (O.C. Schmidt) Nowicke, stat. nov.

G. ovata O. C. Schmidt, Repert. Sp. Nov. **32:** 97, 1933. (Type *Raimondi 11606* B†)

BRAZIL: ACRE: nr mouth of Rio Macauhan, *Krukoff 5405* (G, S, US).

The *Krukoff* collection is cited by Macbride in the Flora of Peru (1936) as *Gallesia integrifolia* even though he recognizes both "species." It differs, however, from all other collections of *Gallesia* in the constriction of the samara wing near the base.

5. SEGUIERIA

Seguieria Loefl., Iter Hispan. 191, 1758. (Type *S. americana* L.)
Seguiera Adans., Fam. Pl. **2:** 443, 1763.
Albertokuntzea O. Ktze., Rev. Gen. Pl. **2:** 550, 1891.

Trees, shrubs, or lianas. *Leaves* lanceolate, lanceolate-elliptic to ovate, acute to mucronulate, entire, the bases obtuse to slightly rounded, papery to ± leathery, mostly glabrous; petiolate or subpetiolate; stipular thorns present or absent on flowering branches, sometimes conspicuous on older branches. *Inflorescences* irregular panicles, rarely ± racemes, axillary or terminal, mostly pubescent. *Flowers* perfect, ± actinomorphic, pedicellate; bract single, awl-shaped, sometimes keeled at the base; bracteoles two, or rarely absent, mostly awl-shaped; sepals 5, ± equal, oblong to oblanceolate, somewhat veined, reflexed in fruit; stamens ∞, generally in 2-3 irregular whorls, the filaments ± filiform, the anthers linear; ovary 1-carpellate, compressed laterally, the styles flattened, the stigma lightly papillose on one edge. *Fruit* a samara, the base or ovary with or without a tubercle and ridges or winglets, green to black on drying, the stigmatic edge convex, straight, or concave; seed one, ovoid (Fig. 2).

South America.

Pollen grains single, prolate, ca 15-22μ (E) × ca 25-30μ (P), 3-colpate, colpi ca 18-25μ long, exine ca 1.5-2μ in thickness, sexine ± equal to nexine and almost smooth.

In 1909 Walter described the genus *Seguieria* with 23 species in two sections. The sect. 1 *Euseguieria* H. Walter, is characterized by a small tubercle and ridges at the base of the samara and includes 13 species. The sect. 2 *Seguieriella* H. Walter has samaras lacking the above characters and includes the remaining species. Specific alignments within the sections are very difficult and the flowers, and in most instances the fruits, do not yield good distinctive characters. My treatment of the genus is admittedly based on insufficient material, even though all

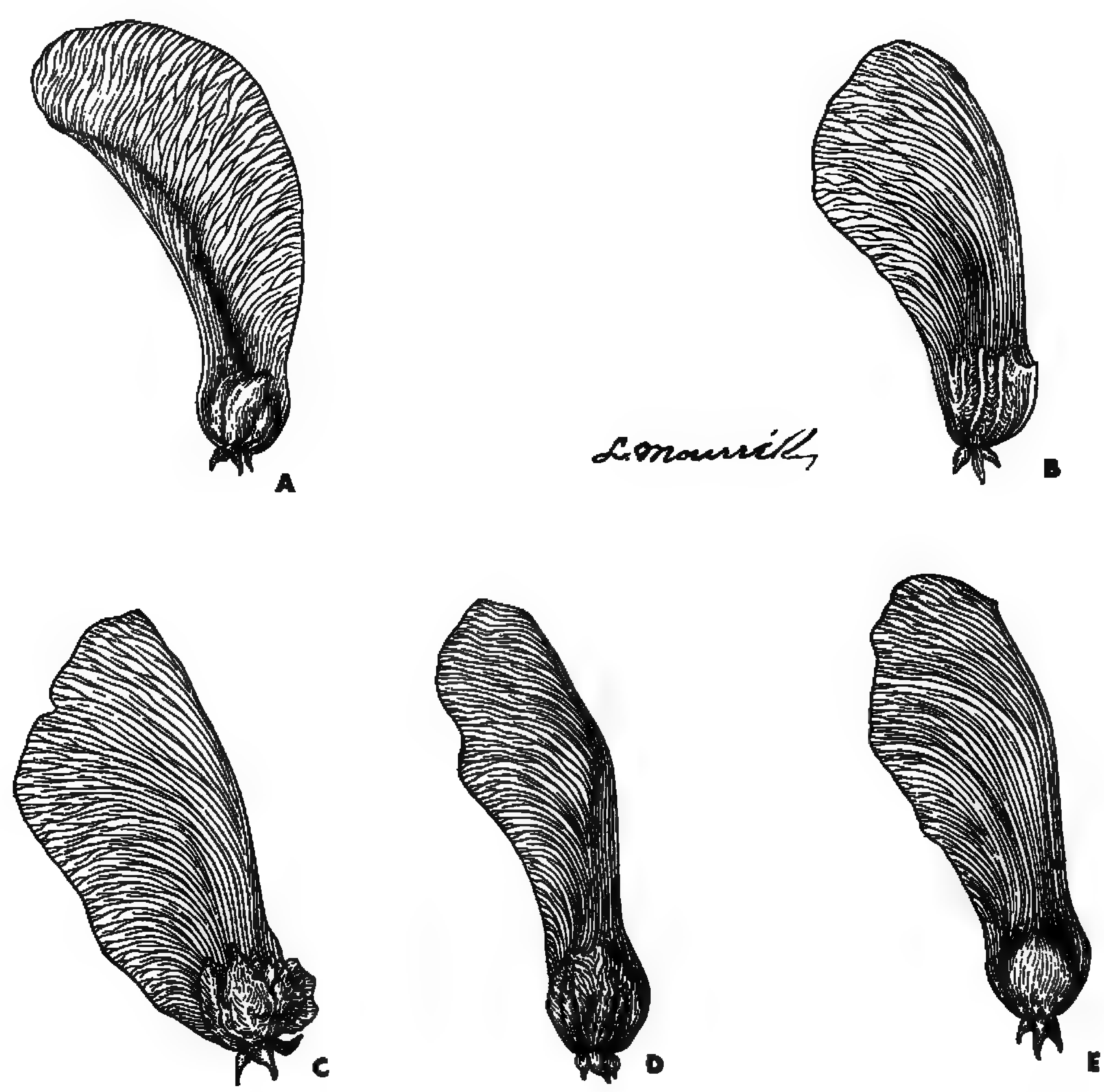

Fig. 2. *Seguieria* L. samara types. A, *S. coriacea* Benth.; B, *S. foliosa* Benth.; C, *S. vauthieri* Moq; D, *S. floribunda* Benth.; E, *S. parvifolia* Benth. A after *Regnell III 1013* (US); B after *Schomburgk 661* (K); C after *Vauthier 29* (K); D after *Gardner 722* (US); E after *Schwarz 4256* (MO).

loans from the world's major herbaria included a request for specimens. In view of Walter's high number of species, I think two conclusions are possible; firstly, that the group has not been well collected and distributed, or secondly, that as so many species are based on only one collection, they may represent extreme forms of polymorphic species. Undoubtedly both factors plus the lack of fruiting material have contributed to great difficulty with the genus. It is badly in need of monographic revision.

The original treatment of sect. 1 was severely limited by lack of material for many of the species which Walter authored. However, after an examination of type material at Kew and subsequent borrowing of many of these collections, I have recognized and described nine of the 13 species and transferred one, *S. brevithyrsa* H. Walter, to sect. 2. To my knowledge, I have not seen specimens of *S. inermis* H. Walter and *S. wangerinii* H. Walter and omit their treatment; and based on a photo of the type, *S. pachycarpa* H. Walter has been reduced to *S. foliosa* Benth. Even though most descriptions are from type material, I wish to emphasize that the entire treatment of the section is highly provisional due to lack of additional collections to reinforce the validity of species.

The sect. 2 *Seguieriella*, which included 10 species according to Walter (1909), is here reduced to six or possibly seven species, not including the transfer of *S. brevithyrsa*. *Seguieria paraguayensis* Morong, *S. macrophylla* Benth. and *S. glaziovii* Briq. are all rather distinct species. *Seguieria affinis* Heimerl (including *S. rigida* H. Walter) is very close to *S. glaziovii* and may prove to be conspecific; the former has very long stipules on the older stems, a character not specifically listed for *S. glaziovii*, which may be lacking on the latter specimens due simply to poor collecting techniques. Two wide ranging and very variable species, *S. parvifolia* Benth [including *S. votschii* H. Walter and *S. guaranitica* Speg.; the latter reduction agrees with Heimerl (1934)] and *S. americana* are very difficult to define, and the determiner must almost resort to utilizing these two complexes as "catch-alls" for specimens which are not readily identifiable as one of the more distinct species. Even so, I think in most instances the specimens would be correctly classified. *Seguieria mammifera* H. Walter is not treated due to lack of material. The photo of the type (*Riedel s.n.*) does very little to elucidate the species characteristics.

Following the Code, the sect. *Seguieriella*, which contains the type *S. americana*, must become sect. *Seguieria*, and sect. *Euseguieria* I have renamed sect. *Walteria*.

a. Samaras with ridges or winglets and/or a tubercle at the base .... Sect. 1. *Walteria*
  b. Leaves leathery.
    c. Leaves ± lanceolate, or if lanceolate-elliptic then at least some 10 cm long.
      d. Leaves crowded, the largest < 10 cm long; inflorescences mostly axillary and < 10 cm long .... 1. *S. langsdorffii*
      dd. Leaves not crowded, at least some > 10 cm long; inflorescences mostly > 10 cm long and axillary or terminal .... 2. *S. longifolia*
    cc. Leaves ± ovate, elliptic-ovate, or if rarely elliptic-lanceolate then < 10 cm long.
      e. The stigmatic edge of the samara wing convex, or if not distinctly so, then with the non-stigmatic edge arising from the base of the ovary.

f. Non-stigmatic edge of samara wing constricted near the top of the ovary, and wings < 15 mm at its widest point ....3. *S. floribunda*
ff. Non-stigmatic edge of samara wing arising conspicuously from the base of the ovary, at least some wings 16-20 mm at widest point ....4. *S. vauthieri*
ee. The stigmatic edge ± straight or concave, the non-stigmatic edge not noticeably arising from the base of the ovary ....5. *S. coriacea*
bb. Leaves not distinctly leathery.
g. At least some leaves with retuse tips.
h. Stipules small, < 2 mm long, straight; leaves ovate to ovate-rounded, the bases rounded ....6. *S. alberti*
hh. Stipules 2-3 mm long, recurved; leaves ovate-elliptic to ovate, the bases obtuse ....7. *S. emarginata*
gg. Leaves without retuse tips.
i. Leaves lanceolate-elliptic to ovate-lanceolate, at least some 10-11 cm long; flowering branches without stipules; inflorescences mostly terminal ....8. *S. laurifolia*
ii. Leaves ovate, the largest < 10 cm long; flowering branches with recurved stipules; inflorescences mostly axillary ....9. *S. foliosa*
aa. Samaras without protuberances at the base ....Sect. 2 *Seguieria*
e. Bracteoles absent; leaves ovate to ± rounded, pale green on drying ....10. *S. paraguayensis*
ee. Without the above combination of characters.
f. Leaves ± lanceolate-elliptic, conspicuously mucronate.
g. Samaras black on drying, the stigmatic edge ± straight, a small protuberance near the distal end ....11. *S. glaziovii*
gg. Samaras brown on drying, the stigmatic edge convex and gradually tapering at the distal portion ....12. *S. affinis*
ff. Leaves not lanceolate and not conspicuously mucronate.
h. Climbers; leaves ovate to ± elliptic, the stipules thick and recurved; samaras black or dark brown on drying, distal protuberance on wing absent.
i. Leaves large, ovate, the bases ± rounded; samaras brown on drying ....13. *S. macrophylla*
ii. Leaves smaller, ± elliptic, the bases ± obtuse; samaras black on drying ....14. *S. brevithyrsa*
hh. Without the above combination of characters.
j. Samara wing with protuberance; leaves generally elliptic or ovate-elliptic, the stipules ± straight; widespread. ....15. *S. parvifolia*
jj. Samara wing without protuberance; leaves more ovate, or ovate-rounded, the stipules recurved; mostly from Colombia ....16. *S. americana*

Sect. 1 **Walteria** Nowicke, nom. nov. (Type selected: *S. floribunda Benth.*)
sect. *Euseguieria* H. Walter, Pflanzenr. IV 83 (Heft 39): 87, 1909.

1. *Seguieria langsdorffii* Moq. in DC., Prodr. **13**(2): 6, 1849. (Type *Langsdorff s.n.* G, K)

Albertokuntzea langsdorffii (Moq.) O. Ktze., Rev. Gen. Pl. **2**: 550, 1891.

Trees to ca 15 m. *Leaves* crowded, lanceolate or lanceolate-elliptic, acute to mucronate, entire, the bases obtuse or attenuate, up to 10 cm long and 4 cm wide, ± leathery; petioles to ca 1 cm long; stipules to 5 mm long, erect, slender. *Inflorescences* ± racemes or weak panicles, up to 10 cm long, mostly axillary, sparsely pubescent. *Flowers* with pedicels to 5 mm long; bract single, ca 1-1.5 mm long, awl-shaped and keeled at the base; bracteoles two or none, ca 0.5 mm long; sepals oblong, ca 2.5-3 mm long and 1.8-2.3 mm wide; filaments ca 2 mm long, the anthers ca 1.5-1.8 mm long. *Samara* unknown.

BRAZIL: BRASILIA: s. loc., *Riedel s.n.* (GH). MINAS GERAES: s. loc., *Langsdorff s.n.* (K). RIO DE JANIERO: vic of Rio de Janeiro, *Glaziou 8259,* (K); s. loc., *Filho 98* (F, MO). WITHOUT STATE: *Gardner s.n.* (BM).

Pollen grains ca 15μ (E) $\times$ ca 25μ (P), colpi ca 18-19μ long.

Pollen examined: *Riedel s.n.* (GH).

2. *Seguieria longifolia* Benth., Trans. Linn. Soc. London **18:** 235, 1839. (Type *Pohl s.n.* K)

Albertokuntzea longifolia (Benth.) O. Ktze., Rev. Gen. Pl. **2:** 550, 1891.

Trees or shrubs? *Leaves* lanceolate to lanceolate-elliptic, acute, entire, the bases obtuse to slightly rounded, up to 13 cm long and 4 cm wide, ± leathery; petioles ca 4-7 mm long, stipules small, ca 1-2 mm on flowering branches and recurved. *Inflorescences* panicles, irregular, up to 17 cm long, axillary or terminal, sparsely to densely villous. *Flowers* with pedicels to 5 mm long; bract single, ca 0.5-0.7 mm long, awl-shaped; bracteoles two, ca 0.5 mm long, awl-shaped; sepals oblong, ca 3-4 mm long and 1.5-2.5 mm wide; filaments ca 2 mm long, the anthers ca 1.5-1.8 mm long; ovary with winged and/or ridged base. *Samara* unknown.

BRAZIL: BRASILIA: Mathea barboso, *Pohl s.n.* (K). WITHOUT STATE: *Pohl 3747* (F); *Sello s.n.* (K).

No pollen examined due to lack of suitable flowering material.

The specimens cited have minor variation in their leaf shape, i.e. the tip and the base. While I include the *Sello* collection with some reservation, I believe this to be the best decision until further collections are observed.

3. *Seguieria floribunda* Benth., Trans, Linn. Soc. London **18:** 235, 1839. (Type *Gardner* 722 BM, F, K, P, US)

Albertokuntzea floribunda (Benth.) O. Ktze., Rev. Gen. Pl. **2:** 550, 1891.

Shrubs or woody vines. *Leaves* elliptic-ovate to elliptic-lanceolate, acute, entire, the bases obtuse, up to 10 cm long and 6 cm wide; petioles ca 2-4 mm long; stipules 0.5-4 mm long, recurved. *Inflorescences* panicles, irregular, ca 18-22 cm long, axillary or terminal, pubescent. *Flowers* with pedicels to 6 mm long; bract single, < 1 mm long, awl-shaped; bracteoles two, < 1 mm long, awl-shaped; sepals oblong, ca 4.5-6 mm long and 2-3 mm wide; filaments ca 1.5-1.8 mm long, the anthers ca 1.5-1.8 mm long. *Samara* ca 3.5-4 cm long, brown, the base with prominent winglets, the stigmatic edge convex (Fig. 2D).

Brazil and Peru.

BRAZIL: MINAS GERAES: s. loc., *Regnell III 1013* (US, in 1845). WITHOUT STATE: *Gardner 722* (BM, F, K, P, US).

PERU: MADRE DE DIOS: Río Acre, *Ule 9487* (K, US).

No pollen examined due to lack of suitable flowering material.

The *Ule* specimens with the numbers *9487* and *9486* on the same sheet (K) are cited by Macbride in the Flora of Peru (1936) as *S. foliosa* Benth. I have seen the types of both species, and while the *Ule* collections are not identical to either, they are much closer to *S. floribunda* than to *S. foliosa*.

4. *Seguieria vauthieri* Moq. in DC., Prodr. **13**(2): 7, 1849. (Type *Vauthier 29* K)
Albertokuntzea vauthieri (Moq.) O. Ktze., Rev. Gen. Pl. **2**: 550, 1891.

Trees or shrubs? *Leaves* ovate, obtuse, entire and slightly inrolled, the bases obtuse, up to 3 cm long and 4 cm wide, somewhat leathery; petioles ca 3-4 mm long, the stipules very small, ca 1 mm long or absent. *Inflorescences* panicles, weakly so, ca 13 cm long, terminal, ± glabrous. *Flowers* with pedicels to ca 7 mm long; bract single, ca 1 mm long; bracteoles two, ca 0.8-1 mm long; sepals and stamens unknown. *Samara* ca 3.5-4 cm long and 1.6-2 cm wide, brown, the stigmatic edge ± convex, the non-stigmatic edge arising from the base of the ovary (Fig. 2C).

Known only from a single fruiting collection.

Brazil: Brasilia, *Vauthier 29* (K).

No pollen examined due to lack of suitable flowering material.

Walters (1909) concept of this species is erroneous. His description is based solely on one of the confusing *Regnell III 1013* collections (1864) of which there appear to be three, all collected on different dates, 1845, 1855 and 1864. The 1864 collection bears Walter's determination as well as the location of Caldas. This specimen differs markedly in samaral characters from that of *Vauthier 29* (K), the type collection of *S. vauthieri.* I have included *Regnell III 1013* (1864 & 1855), as well as an unnumbered *Regnell* collection from 1866, under *S. coriacea* Benth. because of their similarity in leaf shape, stipule size and direction, and inflorescence size and position, to that of the type for this species, *Blanchet 2908.*

5. *Seguieria coriacea* Benth., Trans. Linn. Soc. London **18**: 235, 1839. (Type *Blanchet 2908* BM; photo F, from G)
Albertokuntzea coriacea (Benth.) O. Ktze., Rev. Gen. Pl. **2**: 550, 1891.

Shrubs or small trees. *Leaves* elliptic-lanceolate, acute to slightly mucronulate, entire, the bases obtuse, up to 8 cm long and 3.5 cm wide, ± leathery; petioles ca 3-5 mm long; stipules up to 13 mm long, ± straight to slightly recurved. *Inflorescences* panicles, irregular, up to 40 cm long, axillary or terminal, lightly pubescent, ± woody. *Flowers* with pedicels to 6 mm long; bract single, ca 1 mm long, awl-shaped; bracteoles two, ca 0.8 mm long, awl-shaped; sepals oblanceolate, up to 4 mm long and 2-2.6 mm wide; filaments ca 1.8-2 mm long, the anthers ca 1.5 mm long. *Samara* ca 3.5-4 cm long and ca 1.7 cm wide, brown-green, the base with prominent winglets, the stigmatic edge concave (Fig. 2A).

Brazil: bahia: Acurua, *Blanchet 2908* (BM; photo F, from G). minas geraes: s. loc., *Regnell III 1013* (K, in 1855; US, in 1864), *s.n.* (US, in 1866).

Pollen grains ca 18μ (E) × ca 27μ (P), colpi ca 19μ long.

Pollen examined: *Regnell 1013* (K).

The specific epithet which Bentham (1839) applied to this species is perplexing with regard to the BM collection of *Gardner 2908.* Of the six species which he described, this specimen has perhaps the least coriaceous leaves. A photo (F from G) of a more mature portion of the type does appear to have the coriaceous leaves characteristic of the *Regnell* collections. For the present I am assuming, based on

Bentham's description of the leaves (Bentham, 1839, p. 235) "foliis subsessilibus oblongis obtusissimis coriaceis" and choice of names in light of the remaining collections on which he based five other species, that he saw extensive material of *Gardner 2908* and that the BM specimen represents an immature leaf stage. See also the discussion of *S. vauthieri.*

6. *Seguieria alberti* H. Walter, Repert. Sp. Nov. **8:** 79, 1910. (based on *S. elliptica*)
S. elliptica H. Walter, Pflanzenr. IV, 83 (Heft 39): 89, 1909, non Fries (Ark. Bot. Stockh. **8:** 20, 1909). (Type *Glaziou 8260* K)

Trees or shrubs? *Leaves* ovate to ovate-orbicular, entire, obtuse and ± retuse, the bases rounded or slightly obtuse in immature leaves, up to 6 cm long and 3.5 cm wide; petioles ca 3-6 mm long, stipules on flowering branches ca 2 mm long, horizontal to ± ascending. *Inflorescences* panicles, irregular, axillary or terminal, up to 10 cm long, ± villous. *Flowers* with pedicels to 5 mm long; bract single, ca 1 mm long, awl-shaped; bracteoles two, ca 1 mm long, awl-shaped; sepals oblong, ca 4-5 mm long and 2-2.5 mm wide; filaments 2.5-3 mm long, the anthers ca 1-1.2 mm long; ovary with ridges in mature flowers. *Samara* unknown.

BRAZIL: RIO DE JANEIRO, vic of Rio de Janeiro, *Glaziou 8260* (K, photos F, from B & G).
No pollen examined due to paucity of flowering material.

7. *Seguieria emarginata* H. Walter, Pflanzenr. IV, 83 (Heft 39): 89, 1909. (Type *Glaziou 5730* K)

Trees or shrubs? *Leaves* ovate-elliptic to ovate, entire, blunt-acute and retuse, the bases obtuse, up to 8 cm long and 5 cm wide; petioles 5-7 mm long, stipules on flowering branches ca 2-3 mm long and recurved. *Inflorescences* panicles, irregular, axillary or terminal, up to 8 cm long; ± glabrous. *Flowers* with pedicels to 5 mm long; bract single, ca 1 mm long, awl shaped; bracteoles two, ca 0.5 mm long, awl-shaped; sepals oblong, ca 4-5 mm long; filaments ca 3-4 mm long, the anthers ca 1.5 mm long; ovary with ridges in mature flowers. *Samara* unknown.

BRAZIL: RIO DE JANEIRO: s. loc., *Glaziou 5730* (K; photo F, from B).

No pollen examined due to paucity of flowering material.

When the type specimens of *S. emarginata* (*Glaziou 5730*) and *S. alberti* (*Glaziou 8260*), both from Kew, are compared, they are markedly different in leaf shape, *S. emarginata* being conspicuously more elongate. However, a photo (F) of the Berlin specimen of *Glaziou 5730* has very broad leaves, and at first glance is almost more similar to *Glaziou 8260* than it is to the Kew specimen of *Glaziou 5730.* Nevertheless I have treated the two as separate taxa based on leaf shape, and the stipule size and direction, but I admit that the distinction is somewhat obscure.

8. *Seguieria laurifolia* H. Walter, Pflanzenr. IV, 83 (Heft 39): 92, 1909. (Type *Glaziou 2488* K; photo F, from C)

Trees or shrubs? *Leaves* lanceolate-elliptic to ± ovate-lanceolate, acute, entire, the margins ± inrolled, the bases obtuse, up to 11 cm long and 4 cm wide; petioles up to 5 mm long, stipules absent on flowering branches. *Inflorescences* panicles, irregular, rarely ± racemes, up to 15 cm long, axillary or terminal, lightly villous. *Flowers* with pedicels to 6 mm long; bract single, < 1 mm long, awl-shaped; bracteoles two, < 1 mm long, awl-shaped; sepals oblong, ca 4 mm long and 2.2-2.5 mm wide; filaments ca 3 mm long, the anthers ca 1.8 mm long; ovary appearing to have prominent winglets. *Samara* unknown.

Known only from the type collection.

BRAZIL: RIO DE JANEIRO: Juiz de Fora, *Glaziou 2488* (K; photo F, from C).

No pollen examined due to lack of suitable flowering material.

9. *Seguieria foliosa* Benth., Trans. Linn. Soc. London **18:** 236, 1839. (Type *Schomburgk 661* BM, F, K)

S. pachycarpa H. Walter, Pflanzenr. IV, 83 (Heft 39): 93, 1909. (Type *Riedel s.n.*, photo F, from B†)

Trees or shrubs to ca 3 m. *Leaves* ovate-elliptic, entire, acute to slightly mucronulate, the bases obtuse to somewhat rounded, up to 12 cm long and 5 cm wide, mostly 6-8 cm long and ca 4 cm wide; petioles ca 3-5 mm long; stipules to 10 mm long, recurved. *Inflorescences* panicles, irregular, or ± racemes, up to 12 cm long, mostly axillary, lightly pubescent. *Flowers* with pedicels to 1 cm long; bract single, ca 1-1.5 mm long, awl-shaped; bracteoles two, ca 0.6-0.8 mm long, awl-shaped; sepals oblanceolate, ca 3-4 mm long and 1.5-2 mm wide; filaments ca 2 mm long, somewhat thickened at the base, the anthers ca 1 mm long. *Samara* up to 3.5 cm long, brown, the base ridged, the stigmatic edge ± straight to slightly convex, the non-stigmatic edge ± straight (Fig. 2B).

Brazil and Guyana.

BRAZIL: CEARA: Maracanau, *Ducke 2576* (NY).
GUYANA: Rupununi Dist, *Irwin 797* (US); s. loc., *Schomburgk 661* (BM, F, K).

Pollen grains ca 25μ (E) × ca 30-31μ (P), colpi ca 22-23μ long.

Pollen examined: *Ducke 2576* (NY).

SECT. 2 SEGUIERIA.

sect. *Seguieriella* H. Walter, Pflanzenr. IV, 83 (Heft 39): 94, 1909.

10. *Seguieria paraguayensis* Morong, Ann. N. Y. Acad. Sci. **7:** 210, 1893. (Type *Morong 690* MO)

Trees or shrubs. *Leaves* ovate, mucronate, entire, the bases obtuse to slightly rounded, up to 8.5 cm long and 6.5 cm wide, glabrous, ± leathery; petioles up to 1.5 cm long; stipules up to 3 mm long, ± straight to erect, mostly on older branches. *Inflorescences* panicles, ca 6 cm long, mostly axillary, few-flowered, lightly pubescent. *Flowers* with pedicel length variable, up to 7 mm long; bract single, ca 2.5-2.8 mm long, lanceolate; bracteoles absent; sepals ± equal, oblong. ca 4 mm long and ca 2 mm wide; filaments ca 2.5-3 mm long, the anthers ca 2 mm long. *Samara* up to 3 cm long, yellow-brown, the stigmatic edge convex.

PARAGUAY: San Bernardino, *Hassler 3712* (F, NY), *3887* (F, NY); vic of Ypacaray, *Hassler 12400* (MO, NY); s. loc., *Fiebrig 869* (A, F, US), *Hassler 1764* (NY), s.n. (F), *Morong 690* (MO).

Pollen grains ca 17μ (E) × ca 26μ (P), colpi ca 19μ long.

Pollen examined: *Hassler 12400* (MO).

11. *Seguieria glaziovii* Briq., Ann. Conserv. Jard. Bot. Geneve **4**: 214, 1900. (Type *Glaziou 13126* G, K)

Trees to 30 m. *Leaves* elliptic-lanceolate, mucronate, entire, the bases obtuse, up to 11 cm long and 4.5 cm wide, ± leathery; petioles ca 0.5-1 cm long; stipules ca 0.5 cm long, slender. *Inflorescences* irregular panicles, up to 18 cm long, mostly axillary, rarely terminal, rachis pubescent. *Flowers* with pedicels up to 8 mm long; bract single, up to 1.5 mm long, awl-shaped, keeled at the base; bracteoles two, ca 0.8 mm long, awl-shaped; sepals subequal, ca 4-5 mm long and 2-2.5 mm wide, veined, prominently so in fruit; filaments ca 3 mm long, the anthers ca 2.2 mm long. *Samara* ca 2.5-3 cm long, black on drying, the stigmatic edge ± straight.

BRAZIL: SANTA CATARINA: Brusque, *Klein 288* (NY), *290* (NY); *Reitz 3464* (US); Ibirama, *Reitz & Klein 1563* (NY); Itajai, *Klein 1183* (NY), *Reitz & Klein 2257* (NY, US), *2409* (NY, US).

Pollen grains ca 18-19μ (E) × ca 29-30μ (P), colpi ca 25μ long.
Pollen examined: *Reitz & Klein 2409* (NY).

12. *Seguieria affinis* Heimerl in von Wettstein, Ergebn. Exped. Sudbrasil 1901 **1**: 6, 1908. (Lectotype selected: *Novaes 1027* US; syntype *Novaes 1026* WU, not seen).

S. rigida H. Walter, Pflanzenr. IV, 83 (Heft 39): 98, 1909. (Syntypes *de Moura 985* LE, B†; *Riedel s.n.* LE, B†, all not seen)

Trees, to 18 m. *Leaves* lanceolate-elliptic, mucronulate, entire, the bases obtuse, up to 11 cm long and 5 cm wide, glabrous to slightly pubescent, ± leathery; petioles to 6-7 mm long; stipules to 4.5-5 cm long on older stems, slender. *Inflorescences* panicles or racemose, to 20-25 cm long, axillary or terminal, pubescent. *Flowers* with pedicels ca 6-7 mm long; bract single, ca 1-1.5 mm long, awl-shaped; bracteoles two, ca 0.6 mm long, ± triangular; sepals subequal, oblong and narrowed at the base, ca 4.5 mm long and 3-3.5 mm wide, veined; filaments ca 3.5 mm long, the anthers ca 1.7 mm long. *Samara* ca 3.5 cm long, brown, the base darkened, the stigmatic edge convex.

Brazil.

BRAZIL: MINAS GERAES: rd to Barroso, *Mexia 4444* (BM, F, MO); rd to São Miguel, *Mexia 4358* (BM, F, K, MO). SAO PAULO: Campinas, *Novaes 1027* (US).

Pollen grains ca 18-19μ (E) × ca 28-29μ (P), colpi ca 21-22μ long.
Pollen examined: *Mexia 4358* (F).

13. *Seguieria macrophylla* Benth., Trans. Linn. Soc. London **18**: 235, 1839. (Type *Schomburgk 348* K)

Albertokuntzea macrophylla (Benth.) O. Ktze., Rev. Gen. Pl. **2**: 550, 1891.

Lianas? Leaves ovate-elliptic, acute, entire, the bases rounded-obtuse, up to 17 cm long and 9 cm wide, leathery; petioles ca 0.5-1 cm long; stipules up to 6 mm long, recurved, stout. *Inflorescences* panicles, up to 40 cm long, axillary or terminal, pubescent. *Flowers* with pedicels ca 6 mm long; bract single, ca 1.2 mm long, awl-shaped; bracteoles two, ca 0.8 mm long, awl-shaped; sepals subequal, ca 4 mm long and 1.6-2.4 mm wide; filaments ca 2.5 mm long, the anthers ca 1.7 mm long.

Samara up to 3.1 cm long, brown-black on drying, the stigmatic edge ± straight.

Brazil, Guyana, Peru and Venezuela.

BRAZIL: AMAZONAS: nr mouth of Rio Embira, *Krukoff 5206* (A). MARANHAO: Maracassume River Basin, *Krukoff 1924* (A, BM, MO). PARÁ: Belem, *Archer 7936* (F, MO); Bouche de lac de Faro, *Ducke 8657* (US).

GUYANA: Essequibo River, *Schomburgk 348* (K); Kanuku Mts, *Smith 3650* (A).

PERU: LORETO: Yurimaguas, *Poeppig 2176* (F).

VENEZUELA: DELTA: Cano del Corisal, *Bond et al. 208* (GH). WITHOUT PROVINCE: Sacupana, *Rusby & Squires 57* (F, MO).

No pollen examined due to lack of suitable flowering material.

14. *Seguieria brevithyrsa* H. Walter, Pflanzenr. IV 83 (Heft 39): 87, 1909. (Type *Rusby 1353* BM, GH, NY)

S. inerensis Britton, Bull. Torrey Bot. Club **48**: 331, 1921. (Type *Britton, Freeman & Nowell 2527,* probably NY)

Shrubs, decumbent, or woody vines. *Leaves* elliptic-lanceolate, acute-acuminate, entire, the bases obtuse, up to 11 cm long and 4 cm wide, glabrous, ± leathery; petioles up to 1 cm long; stipules ca 4-6 mm long, recurved. *Inflorescences* racemes or weak panicles, up to 10 cm long, axillary, glabrous, black on drying. *Flowers* with pedicels up to 6 mm long; bract single, 3-4 mm long, lanceolate; bracteoles absent; sepals subequal, oblong, ca 5 mm long and 3.5 mm wide; filaments ca 3 mm long, the anthers ca 2 mm long. *Samara* up to 4.5 cm long, black on drying, ± slightly ridged at the base, the stigmatic edge straight or concave.

Reported only from Trinidad and Bolivia.

TRINIDAD: *Smith 2706* (US).

BOLIVIA: S. YUNGAS: San Bartolomé, *Krukoff 10166* (F, MO, US). WITHOUT PROVINCE: Guanai, *Rusby 1353* (GH, NY).

No pollen examined due to lack of suitable flowering material.

Walter (1909) included this species in his sect. 1, *Euseguieria,* characterized by the extra tubercle at the base of the fruit, a condition difficult to detect in flowers, and certainly not visible in the single collection from which he described the species. The collection of *Krukoff 10166,* in fruit only, which agrees with Rusby *1353* in leaf shape, stipule size and direction, inflorescence characters, and blackening on dessication, as well as in geographic location, has two slight ridges on the flattened sides of the ovary but no evidence of the tubercle. For this reason I have transferred this species to the sect. *Seguieria.*

15. *Seguieria parvifolia* Benth., Trans. Linn. Soc. London **18**: 235, 1839. (Type *Tweedie s.n.* K)

Seguieria guaranitica Speg., Anal. Soc. Cient. Argent **16**: 88, 1883.
Albertokuntzea parvifolia (Benth.) O. Ktze., Rev. Gen. Pl. **2**: 550, 1891.
Seguieria elliptica R. E. Fries, Ark. Bot. Stockh. **8**: 20, 1909, non H. Walter [Pflanzenr. IV, 83 (Heft 39): 89, 1909] (Type *Fries 313* US).

Shrubs, ± scandent. *Leaves* ovate-elliptic to ovate, mucronulate, entire, the bases obtuse, up to 11 cm long and 5 cm wide, ± leathery; petioles to 8-9 mm long; stipules to 1 cm long, ± straight, mostly on older branches. *Inflorescences* panicles or rarely racemose, up to 20 cm long, axillary or terminal, pubescent. *Flowers* with pedicels up to 6 mm long; bract single, ca 1-1.2 mm long, awl-shaped, membranaceous; bracteoles two, ca 0.8 mm long, awl-shaped, membranaceous; sepals subequal, ca 4.5 mm long and up to 3 mm wide, veined, conspicuously so at the base in fruit; filaments ca 3.5 mm long, the anthers ca 1.7 mm long. *Samara* up to 4 cm long, green-brown, the stigmatic edge convex, rarely ± straight, a small protuberance near the tip (Fig. 2E).

A variable species widely distributed in South America.

BRAZIL: PARANA: Iguacu Ntl Pk, *Pereira 5314* (F). RIO GRANDE DO SUL: Vila Elsa, *Rambo 41919* (F, MO).

ARGENTINA: MISIONES: Acaragua, *Bertoni 3172* (F); Campo Grande, *Schwarz 4419* (MO); Duranona, *Schwarz 4256* (MO); Puerto Iguazu, *Meyer 5354* (F); Puerto Rico, *Schwindt 578* (MO); Santo Pipo, *Schwarz 4267* (MO); Santa Rita *Schwarz 4204* (F). SALTA: Bosque al Sud, *Lillo 11266* (F); La Callera, *Pierotti 203* (F); betw El Piquete & Palmero, *Ragonese 88* (F).

PARAGUAY: CENTRAL DEPT: Villa Elisa, *Pedersen 3152* (MO, US). GAIRA: Villarrico *Hassler 3758* (F, MO); s. loc., *Hassler 1849e* (NY), *3786* (F, NY), *7055* (MO, NY), *Morong 645* (MO).

Pollen grains ca 21μ (E) × ca 28-29μ (P), colpi ca 17μ long, exine ca 1.5μ in thickness.

Pollen examined: *Hassler 7055* (MO).

16. *Seguieria americana* L., Syst. Nat. ed. 10, 1074, 1759. (Neotype selected: *Smith 342* MO, isoneotypes F, US)

S. aculeata Jacq., Select. Stirp. Amer. 170, 1763.
Albertokuntzea americana (L.) O. Ktze., Rev. Gen. Pl. **2:** 550, 1891.

Shrubs, scandent or climbers. *Leaves* ovate or ovate-elliptic, acute to slightly accuminate and emarginate, the bases obtuse, up to 10 cm long and 7 cm wide, glabrous, papery to slightly leathery; ± sessile to petioles 3 mm long; stipules up to 1 cm long, recurved. *Inflorescences* panicles, up to 15 cm long, axillary or terminal, pubescent. *Flowers* with pedicels 6-7 mm long, slender; bract single, ca 0.5 mm long, membranaceous; bracteoles two, ca 0.4 mm long, membranaceous; sepals ± unequal, oblong, ca 3.5-4 mm long and 1.2-2.5 mm wide; filaments ca 2-2.5 mm long, the anthers ca 1.2 mm long. *Samara* ca 3.5 cm long, green-brown, the stigmatic edge ± straight.

South America.

COLOMBIA: ATLANTICO: Barranquilla, *Dugand 106* (F), *474* (F), *1112* (F); betw Galapa & Baranca, *Dugand 272* (F, US); Puerto Colombia, *Bro. Elias 1020* (F, US); betw Pon-adera & Santa Rita, *Dugand 683* (F); Soledad, *Dugand 1128* (F). MAGDALENA: La Paz, *Haught 2330* (F). SANTA MARTA: s. loc., *Smith 342* (F, MO, US).

VENEZUELA: ARAGUA: Tuy Valley, *Pittier 12201* (US).

BOLIVIA: s. loc., *Williams 249* (BM, NY).

PARAGUAY: WITHOUT PROVINCE: *Fiebrig 776* (F), *Hassler 8393* (F), *11502* (F).

Pollen grains ca 21-22μ (E) × ca 30μ (P), colpi ca 20-21μ long.

Pollen examined: *Dugand 683* (F).

Excluded collection: *Broadway s.n.* (K). This is the type collection for *S. cordata* Britton (Bull. Torrey Bot. Club **48:** 331, 1921), which has neither flowers nor fruit and is impossible to describe or identify.

B. Tribe Rivineae Agardh, Aphor. 218, 1825. Inflorescences spikes or racemes; fruits not a samara. (Type *Rivina L.*)

a. Flowers unisexual; fruits covered with hooked spines; Australia ....12. *Monococcus*
aa. Flowers perfect, rarely unisexual; fruits not covered with hooked spines; South and Central America.
 b. Fruit a 4-6 hooked achene; inflorescences elongate spikes; calyx of 4 narrow-lanceolate, erect sepals ....11. *Petiveria*
 bb. Fruit an utricle or drupe not hooked; inflorescences racemes; calyx not of 4 narrow-lanceolate, erect sepals.
  c. Flowers ± zygomorphic; sepals connate at the base in late flower and fruit ....9. *Hilleria*
  cc. Flowers ± actinomorphic; sepals not becoming connate in late flower and fruit.
   d. Leaves ± deltoid; stamens 4; fruit a red, orange, or purple drupe ....6. *Rivina*
   dd. Without the above combination of characters.
    e. Racemes from woody stems, not pendulous; fruit a purple or black drupe ....7. *Trichostigma*
    ee. Racemes not from woody stems or if so, then pendulous; fruit an utricle.
     f. Racemes pendulous; flowers perfect or functionally unisexual, the pistillate with 4-6 rudimentary stamens, the sepals net-veined ....10. *Ledenbergia*
     ff. Racemes ± erect; flowers perfect, the stamens 12-25, the sepals with ca 3 parallel veins ....8. *Schindleria*

6. RIVINA

Rivina L., Sp. Pl. 121, 1753. (Type *R. humilis* L.)

Rivinia L., Gen. Pl. ed. 5, 57, 1754.
Piercea Mill., Gard. Dict. ed. 7, 1759.
Solanoides Moench, Meth. 307, 1794.
Tithonia L. ex. O. Ktze., Rev. Gen. Pl. **2**: 552, 1891.

Monotypic.

1. *Rivinia humilis* L., Sp. Pl. 122, 1753. (Type LINN, not seen; from IDC Micro-Edition 163.1)

R. laevis L., Mant. 41, 1767.
R. purpurascens Schrad., Gen. Pl. Illustr. 17, *pl. 5*, 1808.
R. portulaccoides Nutt., Trans. Amer. Phil. Soc. II, **5**: 167, 1837. (Type *Nuttall s.n.* BM)
For a complete synonomy list, see: Ann. Missouri Bot. Gard. **48**: 76, 1961, By K. Raeder.

Herbs or subshrubs, woody at the base, to 70 cm. *Leaves* deltoid to ovate, acuminate, entire, the bases truncate to rounded, rarely oblique, up to 12 cm long and 6 cm wide, glabrous to finely pubescent; petioles up to 6 cm long. *Inflorescences* racemes, up to 15 cm long at maturity, terminal or axillary. *Flowers* perfect, actinomorphic, with pedicels to 8 mm long in fruit; bract single, ca 1.3-2 mm long, awl-shaped, ± deciduous; bracteoles two, ca 0.2-0.3 mm long, closely appressed to the sepals; sepals 4, subequal, oblong, ca 2-3 mm long, white or pink; stamens 4, alternate, the filaments ca 1.2-2 mm long, the anthers ca 0.8-1 mm long; ovary globose to elliptic, compressed laterally, 1-carpellate, the style short but distinct, ca 0.3-0.5 mm long, the stigma capitate. *Fruit* a drupe, up to 4.5 mm in diam, ± globose, orange, red, or purple; seed one, lens shaped, ca 2.5-3.5 mm in diam, the testa pubescent.

Southwestern United States to Florida, south through Central and South America to Argentina; also introduced into Africa and reported from Asia and Australia (Heimerl, 1934).

UNITED STATES: ARIZONA: *Gilman 53* (MO); *Jones s.n.* (MO). FLORIDA: *Blanton 6426* (MO); *Curtiss 2340* (MO), *5383* (MO); *Hitchcock 302* (MO); *Hood s.n.* (MO); *Janish & Janish 454* (MO); *Moldenke 325* (MO); *Murrill s.n.* (MO); *Nash 1273* (MO); *O'Neill s.n.* (MO); *Palmer 458* (MO), *459* (MO), *27344* (MO), *Reynolds s.n.*, *11565* (MO); *Seibert 1239* (MO); *Small & Small 4162* (MO); *Tracy 6429* (MO), *9349* (MO); *Webber 376* (MO). LOUISIANA: *Riddell s.n.* (MO); *Short s.n.* (MO). OKLAHOMA: *Houghton 4049* (MO). TEXAS: *Bush 1128* (MO); *Chandler 7040* (MO); *Davis s.n.* (MO); *Eggert s.n.* (MO); *Ferris & Duncan 2632* (MO), *2890* (MO), *3151* (MO); *Heller 1422* (MO); *Jermy s.n.* (MO); *Joor s.n.* (MO); *Letterman 423* (MO); *Lindheimer 295* (MO), *374* (MO), *1113* (MO), *s.n.* (MO); *Mackenzie 48* (MO); *Moore & Steyermark 3014* (MO); *Mueller 8094* (MO), *s.n.* (MO); *Orcutt 5886* (MO); *Palmer 1170* (MO), *9835* (MO), *10170* (MO), *10194* (MO), *10357* (MO), *14351* (MO), *26782* (MO), *30521* (MO); *Parks 1359* (MO); *Reverchon 812* (MO), *1588* (MO); *Ruth 229* (MO), *s.n.* (MO); *Tracy 9351* (MO), *9421* (MO); *Traverse 1086* (MO); *Trelease s.n.* (MO); *Ward s.n.* (MO); *Wilkinson 155* (MO); *Young s.n.* (MO).

MEXICO: BAJA CALIFORNIA: *Gentry 4148* (MO); *Jones 24020* (MO). CHIHUAHUA: *Gentry 1846* (MO); *Palmer 254* (MO). COAHUILA: *Palmer 729* (MO); *Stewart s.n.* (MO); *Warnock & Barkley 14720* (MO); *Wynd & Mueller 292* (MO). COLIMA: *West 3529* (MO). HIDALGO: *Pringle 7428* (MO). NUEVO LEÓN: *Bro. Arsène 6138* (MO). SINALOA: *Gentry 6105* (MO). SONORA: *Gentry 1078A* (MO), *1606* (MO); *Wiggins & Rollins 340* (MO); *Wright 1729* (MO). TAMAULIPAS: *Clark 6622* (MO); *Meyer & Rogers 2484* (MO); *Palmer 127* (MO), *136* (MO). YUCATAN: *Gaumer 322* (MO), *1599* (MO); *Gaumer et al. 23419* (MO), *23561* (MO); *Lundell 858* (MO), *942* (MO). WITHOUT STATE: *Parry 776* (MO).

BRITISH HONDURAS: *Lundell 380* (MO); *Schipp 469* (MO).

HONDURAS: *Williams & Molina 10510* (MO).

GUATEMALA: *Steyermark 47631* (MO).

COSTA RICA: *Greenman & Greenman 5423* (MO); *Rojas 412* (MO); *Smith A667* (MO); *Thomas 6183* (MO).

PANAMA: *Allen 336* (MO), *889* (MO); *Carleton 52* (MO); *Cooper 77* (MO); *Duke 5365* (MO); *Hunter & Allen 579* (MO); *von Wedel 609* (MO), *256* (MO), *2882* (MO); *White & White 88* (MO); *Woodson & Schery 1028* (MO); *Woodson et al. 1807* (MO).

BAHAMAS: *Wilson 7981* (MO), *8016* (MO), *8138* (MO).

CUBA: *Combs 153* (MO), *186* (MO); *Curtiss 720* (MO); *Pollard 3* (MO); *Pollard et al. 190* (MO); *Van Hermann 335* (MO).

DOMINICAN REPUBLIC: *Valeur 486* (MO).

GRENADA: *Broadway s.n.* (MO).

GUADELOUPE: *Grisebach s.n.* (MO).

JAMAICA: *Crosby et al. 90* (MO); *Hitchcock s.n.* (Kingston) (MO), *s.n.* (Constant Springs) (MO); *Lloyd 1012* (MO); *Nichols 189* (MO); *Yuncker 17074* (MO).

MARTINIQUE: *Sieber 48* (MO).

PUERTO RICO: *Heller 4523* (MO), *6165* (MO); *Otero 385* (MO); *Sintenis 306* (MO), *1655* (MO); *5527* (MO).

ST. CROIX: *Eggers s.n.* (MO); *Ricksecker 134* (MO).

COLOMBIA: MAGDALENA: Rincon Hondo, *Allen 236* (MO), *375* (MO); Santa Marta, *Smith 1163* (MO). VALLE: N of Palmira, *Garcia 6394* (MO).

VENEZUELA: AMACURO: Lower Orinoco, *Rusby & Squires 80* (MO). MÉRIDA: Colonia Tovar, *Fendler 1088* (MO). MARGARITA I, *Miller & Johnston 263* (MO).

BRAZIL: CEARA: Baturite, *Schery 429* (MO). RIO DE JANEIRO: vic of Rio de Janeiro, *Dusen 105* (NY).

URUGUAY: *Herter 10078* (MO).

ARGENTINA: BUENOS AIRES: Zorate, *Krapovickas 3020* (MO). CHACO: Campo Bonazzola, *Rodrigo 2528* (NY), *2679* (NY); s. loc., *Jorgensen 1998* (MO). CÓRDOBA: Río Grande, *Job 469* (NY). ENTRE RIOS: Tezanos Pindo, *Huidobro 3641* (MO). FORMOSA: Espinilloa, *Morel 7196* (MO); La Frontera, *Morel 8380* (MO); Siete Palmas, *Morel 8448* (MO). MISIONES: Oro Verde, *Schwarz 7826* (MO); Posadas, *Schwarz 5649* (MO). SALTA: Balboa, *Cabrera 3135* (NY); Coronel Moldes, *Meyer 3748* (NY). SANTIAGO DEL ESTERO: Yutuyacu, *Legname 43* (MO).

PARAGUAY: Villarica, *Jorgensen 3904* (MO, NY). Ypacaray, *Hassler 12198* (MO); s. loc., *Morong 263* (MO).

BOLIVIA: LA PAZ: Coripata, *Bang 2083* (MO), *Buchtien 8257* (NY); Coroico, *Buchtien s.n.* (MO). SANTA CRUZ: Yorochito, *Steinbach 8146* (MO). WITHOUT PROVINCE: *Bang 574* (MO).

ECUADOR: Albermarle I, (Galápagos I) *Stewart 1434* (MO).

SIAM: *Zimmerman 146* (MO).

HAWAII: OAHU: *Fosberg 9388a* (MO).

Pollen grains single, prolate, spheroidal, ca 35μ (E) × ca 35μ (P), 15 colpate, 5 at each pole and 5 perpendicular to the equator, colpi ca 11μ long, exine ca 2-2.5μ in thickness, sexine ± equal to nexine and very finely reticulated.

Pollen examined: *Orcutt 5886* (MO); *Pringle 7428* (MO); *Ruth 229* (MO).

Rivina humilis is one of the most variable species in the *Phytolaccaceae*. Walter (1909) recognized three species, *R. humilis*, *R. portulaccoides* Nutt., and *R. purpurascens* Schrad., based on sepal color and size, erectness of the inflorescence, and relationship of leaf length to inflorescence length, all of which are overlapping characters. I have reduced all to synonomy under *R. humilis*. Some of the variability may result from the diverse weedy habitats in which *Rivina* is frequently found—some specimens are almost "stunted" in appearance, wiry, small leaves, short internodes, etc., and present a marked contrast to the more robust collections. However, to give each of these variants species rank is unsound.

7. TRICHOSTIGMA

Trichostigma A. Rich. in Sagra, Hist. Fis. Pol. Nat. Cuba, Part 2, Hist. Nat. **10:** 306, 1845. [Type *T. octandrum* (L.) H. Walter]

Rivinia Mill., Gard. Dict. Abridg. ed. 4, 3, 1754.
Villamilla Ruiz & Pavon ex Moq. in DC., Prodr. **13**(2): 10, 1849.

Shrubs or trailing vines. *Leaves* ovate to elliptic, acute to long acuminate, entire, the bases cordate to obtuse, punctate, ± glabrous to sparsely hairy on veins beneath; petiolate. *Inflorescences* racemes, axillary or terminal. *Flowers* perfect, ± actinomorphic, pedicellate; bract single, awl-shaped to lanceolate; bracteoles two, minute; sepals 4, ± equal, oblong, green to white; stamens 8-25, separate, irregularly deposited in two whorls, ± sessile or filaments filiform, the anthers linear; ovary 1-carpellate, cylindrical to ± globose, the style short or absent, the stigma generally penicellate. *Fruit* a drupe, ± globose, black to red-purple; seed 1, lens shaped, the testa red-brown.

Northern South America, Central America and the West Indies; a genus of three species.

Pollen grains subprolate or prolate spheroidal, ca 27-37μ (E) × ca 27-35μ (P), 3-colpate with colpi 22-23μ long, or 15 colpate, 5 at each pole and 5 perpendicular to the equator with colpi ca 4.5-6μ long, exine ca 2-2.3μ in thickness, sexine ± equal to nexine or slightly thicker than nexine, and ± smooth.

The results of pollen analysis, 3-colpate grains in *Trichostigma octandrum* L., and 15-colpate in a 5-5-5 pattern for *T. polyandrum* (Loes.) H. Walter and *T. peruvianum* (Moq.) H. Walter, are perplexing in view of the very similar floral and vegetative morphology, especially of *T. octandrum* and *T. polyandrum*. Although the two pollen types are very different in terms of aperture structure, I make no recommendation for division of the genus based solely on this feature.

a. Leaf bases cordate, petioles pubescent ....1. *T. peruvianum*
aa. Leaf bases obtuse, petioles glabrous.
  b. Stamens 20-25; inflorescences few and more than 10 cm long, the pedicels 10 mm or longer ....2. *T. polyandrum*
  bb. Stamens 8-10; inflorescences many and up to 10 cm long; the pedicels up to 10 mm long ....3. *T. octandrum*

1. *Trichostigma peruvianum* (Moq.) H. Walter, Pflanzenr. IV, 83 (Heft 39): 111, 1909.

Rivina peruviana Moq. in DC., Prodr. **13**(2): 10, 1849. (Type *Matthews 1455* G, K)
Villamilla tinctoria Ruiz & Pavon (Fl. Peru Chile, *pl. 402*) ex Moq., loc. cit.
Ledenbergia roseo-aenea Lem., Illustr. Hort. **16**: *pl. 591*, 1869.
Villamilla peruviana Hook. f. in Benth. & Hook. f., Gen. Pl. **3**: 81, 1880.
Rivina roseoaenea (Lem.) O. Ktze., Rev. Gen. Pl. **2**: 551, 1891.
Villamilla roseo-oenia (Lem.) Rusby, Mem. Torrey Bot. Club **6**: 110, 1896.

Shrubs to 2 m. *Leaves* ovate, acuminate, entire, the bases cordate, up to 27 cm long and 11 cm wide, sparsely hairy on veins beneath; petioles 2-3 cm long, conspicuously pubescent. *Inflorescences* mostly terminal, 25-30 cm long, rachis pubescent. *Flowers* with pedicels up to 8 mm long; bract single, 1.5 mm long; bracteoles two, ca 0.3-0.4 mm long, triangular; sepals ca 4 mm long; stamens 10-12, usually in two whorls, the filaments ca 1.5-2 mm long, the anthers ca 1.5-1.8 mm long; style short and thick or absent. *Drupe* ca 4-6 mm in diam, black.

Peru and rarely Ecuador.

ECUADOR: s. loc., *Mexia 7221* (US).
PERU: LORETO: Balsapuerto, *Killip & Smith 28690* (F); *Klug 2976* (F, MO); Soledad, *Killip & Smith 29696* (F); betw Yuramaguas & Balsapuerto, *Killip & Smith 28344* (F). SAN MARTÍN: San Roque, *Williams 6935* (F).

Pollen grains prolate spheroidal, ca 30-32μ (E) $\times$ ca 30-32μ (P), 15-colpate, 5 at each pole and 5 perpendicular to the equator, colpi ca 4.5-5.5μ long, exine ca 2μ in thickness, sexine $\pm$ equal to nexine and $\pm$ smooth.

Pollen examined: *Klug 2976* (MO); *Williams 6935* (F).

2. *Trichostigma polyandrum* (Loes.) H. Walter, Pflanzenr. IV, 83 (Heft 39): 112, 1909.

Rivina polyandra Loes., Bot. Jahrb. **23**: 123, 1896. (Type *Rothschuh 114* B†)
Villamilla polyandra (Loes.) H. Walter, loc. cit. **37**(Beibl. 85): 24, 1906.

Shrubs, $\pm$ erect or trailing vines. *Leaves* ovate to elliptic, acute to long acuminate, the bases obtuse, up to 16 cm long and 8 cm wide, $\pm$ glabrous; petioles 2-3 cm long. *Inflorescences* mostly terminal, occasionally axillary, up to 25 cm long. *Flowers* with pedicels to 15 mm long; bract single, ca 1.5-2 mm long; bracteoles two, ca 0.5 mm long; sepals 4-5 mm long, enlarging in fruit to ca 8-9 mm long; stamens 20-25, deciduous, sessile to filaments 0.6 mm long, the anthers ca 2 mm long; the style short, the stigma sparsely penicellate. *Drupe* ca 4.5-5.5 mm in diam, red-purple.

Central America.

Costa Rica: *Rojas 441* (MO); *Standley & Valedio 44442* (US), *46272* (US).
panama: *von Wedel 714* (MO), *752* (MO), *926* (MO), *940* (MO), *1439* (MO), *1547* (MO), *2571* MO); *Woodson et al. 1832* (MO).

Pollen grains prolate spheroidal, ca 27-29μ (E) $\times$ ca 27-29μ (P), 15 colpate, 5 at each pole and 5 perpendicular to the equator, colpi ca 5-6μ long, exine ca 2.3μ in thickness, sexine $\pm$ equal to nexine or slightly thicker than nexine, and $\pm$ smooth.

Pollen examined: *Standley & Valerio 44442* (US), *46275* (US).

3. *Trichostigma octandrum* (L.) H. Walter, Pflanzenr. IV, 83 (Heft 39): 109, 1909.

Rivina humilis var. *scandens* L., Sp. Pl. 122, 1753.
R. octandra L., Cent. Pl. **2**: 9, 1756. (Type LINN, not seen; from IDC Micro-Edition 163.3)
R. dodecandra Jacq. Obs. Bot. **1**: 6, 1764.
R. scandens Mill., Gard. Dict. ed. 8, Rivinia no. 2, 1768.
R. mutisii Willd. ex. Schultes, Mant. **3**: 305, 1827.
R. americana Raf., Fl. Tellur. **3**: 56, 1837.
Trichostigma rivinoides A. Rich. in Sagra, Hist. Cuba **10**: 306, 1845.
Rivina octandra L. var. *obtusifolia* Moq. in DC., Prodr. **13**(2): 11, 1849.
R. ehrenbergiana Klotzsch ex Moq., loc. cit., nom. nud. pro syn. *R. octandra*.
R. moritziana Klotzsch ex Moq., loc. cit., nom. nud. pro syn. *R. octandra*.
Villamilla octandra Hook. f. in Benth. & Hook. f., Gen. Pl. **3**: 81, 1880.

Shrubs, decumbent or woody vines. *Leaves* elliptic, acuminate, entire, the bases obtuse, up to 13 cm long and 6 cm wide, glabrous or pubescent; petioles ca 2-3 cm long. *Inflorescences* ca 10 cm long, mostly axillary. *Flowers* crowded, with pedicels ca 6-7(-10) mm long at maturity; bract single, ca 2-3 mm long, awl-shaped; bracteoles two, ca 0.4-0.5 mm long; sepals 2.5-4 mm long and 1.5-2.5 mm wide, white to green; stamens 8-10, the filaments ca 2-3 mm long, the anthers ca 1.5-2 mm long; style absent, the stigma penicellate. *Drupe* ca 4-5 mm in diam, black.

Widely distributed in Central America, the West Indies and South America.

United States: florida: *Small & Matthaus 9904* (MO).
Mexico: guerrero: *Hinton 14154* (MO). morelos: *Pringle 8491* (MO). sinaloa: *Lamb 418* (MO). tamaulipas: *Palmer 349* (MO). without state: *Rose 14677* (US).
British Honduras: *Gentle 4028* (MO).
Costa Rica: *Smith 1672* (MO).
Panama: *Allen 944* (MO), *17279* (MO); *Terry & Terry 1396* (MO).
Cuba: *Curtiss s.n.* (MO); *Pringle 90* (MO); *Wright 471* (MO).
Guadeloupe: *Duss 2399* (MO); *Bertero s.n.* (MO).
Haiti: *Leonard 9873* (MO); *Leonard & Leonard 13623* (MO).
Jamaica: *Harris 11966* (MO); *Yuncker 18185* (MO), *18345* (MO).
Puerto Rico: *Sintenis 3931* (MO), *1016b* (MO).
St. Croix: *Ricksecker 343* (MO); *Ricksecker 325* (MO).
Tobago: *Broadway 2967* (MO).
Trinidad: *Broadway 5118* (MO).
Colombia: magdalena: Santa Marta, *Smith 1718* (MO, NY).
Venezuela: mérida: Colonia Tovar, *Fendler 1087* (MO, NY). monagas: W of Santa Bárbara, *Steyermark 61768* (MO). without state: Punta Predra I, *Rusby & Squires 419* (MO).
Brazil: amazonas: mouth of Rio Embira, *Krukoff 4872* (MO); São Paulo de Olivença, *Ducke 404* (MO); Rio Solimoes, *Krukoff 4507* (MO).
Argentina: salta: nr Tariga River, *Eyerdam & Beetle 22800* (MO). misiones: Posadas, *Ekman 1884* (GH).

BOLIVIA: PANDO: jct of Beni & Madre de Dios Rivers, *Rusby 741* (MO). SANTA CRUZ: Missiones Guarayos, *Werdermann 2648* (MO).

PERU: SAN MARTÍN: Juan Jui, *Klug 4185* (MO), *4364* (MO).

Pollen grains subprolate, ca 28-29μ (E) $\times$ ca 34-35μ (P), 3-colpate, colpi ca 22-23μ long, exine ca 2μ in thickness, sexine $\pm$ equal to nexine and $\pm$ smooth.

Pollen examined: *Allen 944* (MO), *17279* (MO).

Excluded collection: Pollard & Palmer 340 (MO, NY). This is a fruiting specimen in which the robustness of the inflorescence, i.e. length of pedicel, size of sepals and overall inflorescence length, is characteristic of *T. polyandrum,* whereas the geographical location and intermediate stamen number, ca 13-14, are typical of *T. octandrum.*

8. SCHINDLERIA

Schindleria H. Walter, Bot. Jahrb. **37**(Beibl. 85): 24, 1906. [Lectotype selected: *S. racemosa* (Britton) H. Walter]

Shrubs, rarely herb-like with woody bases, drying black or yellow-green. *Leaves* elliptic or elliptic to ovate-elliptic, acuminate or acute-acuminate, entire, the bases obtuse, slightly cordate, or rarely $\pm$ oblique, glabrous, or sparsely to densely pubescent; petiolate. *Inflorescences* racemes, in some appearing as a delicate spike in bud, mostly axillary, or axillary and terminal. *Flowers* perfect, actinomorphic, pedicellate; bract single, lanceolate and keeled at the base or awl-shaped; bracteoles two, minute, closely appressed to sepals; sepals 4, $\pm$ equal, oblong and $\pm$ rounded, veins barely discernible or $\pm$ prominent; stamens 12-25, irregularly deposited, the filaments filiform, the anthers linear; ovary 1-carpellate, $\pm$ cylindrical to ovoid, $\pm$ compressed laterally, style absent, stigma penicellate. *Fruit* an utricle, compressed laterally, green-brown; seed 1, lens shaped, testa shiny black.

Two species in Peru and Bolivia.

Pollen grains single, subspheroidal, ca 17-21μ (E) $\times$ ca 17-21μ (P), 12-17 pantoporate, ora ca 3-3.5μ in diam, exine ca 2-2.5μ in thickness, sexine $\pm$ equal to nexine and finely reticulated.

I have reduced the six species listed by Heimerl (1934) to two, which are best separated by the striking color differences in the dried specimens. *Schindleria racemosa* (Britton) H. Walter has inflorescences and leaves drying black or brown-black and includes *S. glabra* H. Walter and *S. mollis* H. Walter, both of which were based on single collections.

Schindleria densiflora (O. Ktze) Monachino, retaining its green color or becoming yellow on drying, comprises a variable group of specimens in terms of leaf base and texture. In flower structure, however, the group is much more uniform and no character or set of characters serves to separate this complex into distinctive alliances. Monachino (1952) first proposed this treatment, although admittedly on insufficient material, and elucidated the nomenclatural problems involved with it. With the exception of *Bang 2607,* the type of *S. rivinoides* H. Walter and about which I maintain some reservations concerning conspecificity with *S. densiflora,* members of the group are coarse, weedy semi-shrubs found in southern Peru and northern Bolivia.

a. Plants turning black or brown-black upon dessication ....1. *S. racemosa*
aa. Plants remaining green or turning yellow upon dessication ....2. *S. densiflora*

1. *Schindleria racemosa* (Britton) H. Walter, Bot. Jahrb. **37**(Beibl. 85): 24, 1906. (Lectotype selected: *Bang 414* MO; isolectotypes F, NY, US; syntypes *Rusby 743* K, MO, NY)

Villamilla racemosa Britton in Rusby, Mem. Torrey Bot. Club **4**: 251, 1895. (Syntypes *Bang 414* NY; *Rusby 743* NY)
Schindleria glabra H. Walter, Bot. Jahrb. **37**(Beibl. 85): 24, 1906. (Type *Weberbauer 1168* B†, not seen)
S. mollis H. Walter, Pflanzenr. IV, 83 (Heft 39): 116, 1909. (Type *Lobb 691,* photo F, from W)

Shrubs, or herbs with woody bases, black on drying. *Leaves* elliptic, acute-acuminate, entire, the bases obtuse, up to 15 cm long and 6 cm wide, slightly to very pubescent, especially on the veins beneath; petioles ca 1.5-4 cm long. *Inflorescences* racemes, up to 28 cm long, axillary or terminal. *Flowers* with pedicels ca 6-8 mm long; bract single, ca 1.2-1.5 mm long, lanceolate and keeled at the base; bracteoles two, minute, ca 0.1-0.2 mm long, triangular and closely appressed to sepals; sepals ca 2-3.5 mm long and 1.5-1.7 mm wide, veins barely discernible; stamens ca 12-15, the filaments ca 1.2-2 mm long, the anthers ca 1.2-1.5 mm long; ovary slightly elongate. *Utricle* ca 2 mm in diam.

BOLIVIA: LA PAZ: Colaya, *Mexia 4302* (GH); Coroico, *Buchtien 3772* (NY, US); Yungas, *Bang 414* (F, MO, NY, US); *Rusby 743* (K, MO, NY, US). SANTA CRUZ: Bella Vista, *Buchtien 6291* (US).

Pollen grains ca 21μ (E) $\times$ ca 21μ (P), 12-15 pantoporate, ora ca 3μ in diam, exine ca 2.5μ in thickness.

Pollen examined: *Rusby* 743 (MO).

2. *Schindleria densiflora* (O. Ktze.) Monachino, Phytologia **4**: 39-41, 1952.

Rivina densiflora O. Ktze., Rev. Gen. Pl. **3**(3): 268, 1898. (Type *Kuntze s.n.* NY, not seen)
Schindleria rosea H. Walter, Bot. Jahrb. **37**(Beibl. 85): 24, 1906. (Type *Bang 1292* MO)
S. rivinoides H. Walter, loc. cit. (Type *Bang 2607* MO)
S. weberbaueri O. C. Schmidt, Notizbl. Berlin Bot. Gart. **8**: 313, 1923. (Type *Weberbauer 6758* F, GH, MO, NY)

Shrubs, or herbs with woody bases, to 3 m, green to yellow on drying. *Leaves* elliptic to ovate-elliptic, acuminate, entire, the bases obtuse, slightly cordate or rarely ± oblique, size variable, up to 20 cm long and 7 cm wide, mostly glabrous, some sparsely pubescent on veins beneath; petioles to 8.5 cm long. *Inflorescences* racemes (appearing as delicate spikes in bud), up to 35 cm long (in fruit), mostly axillary, rarely terminal. *Flowers* with pedicels ca 7-9 mm long at maturity; bract single, ca 1 mm long, awl-shaped; bracteoles two, ca 0.2 mm long, closely appressed to sepals; sepals 2-3 mm long, some prominently veined; stamens ca 15-25, the filaments ca 1.5 mm long, the anthers ca 1 mm long. *Utricle* ovoid, compressed laterally and ridged on the edges, ca 1.8-1.9 mm in diam, testa wrinkled, yellow-brown.

Bolivia and Peru.

BOLIVIA: COCHABAMBA: Chimore, *Cardenas 5482* (US); s. loc., *Steinbach 9361* (GH, NY). LA PAZ: Mapiri, *Buchtien 1694* (GH, US). SANTA CRUZ: Samaipata, *Steinbach 8201* (GH). WITHOUT PROVINCE: N Yungas, *Buchtien 4327* (US); s. loc., *Bang 2607* (F, GH, MO).

PERU: AYACUCHO: betw Huanta & Río Apurimac, *Killip & Smith 23092* (NY, US).

CUZCO: Lares Valley, *Weberbauer 7924* (F, GH, MO, NY); Manto-Lares, *Marin 2164* (F); Hacia Pilcopata, *Vargas 13282* (US); Quincemil, *Vargas 7746* (MO); betw Santo Isabel & Mistiana, *Scolnik 906* (NY). HUANUCO: Divisoria, *Woytkowski 34509* (MO); Tal des Mayro, *Weberbauer 6758* (F); Tingo María, *Asplund 12488* (US). MADRE DE DIOS: s. loc., *Vargas 16931* (US). PUNO: vic of Santo Domingo, *McCarroll 54* (NY).

Pollen grains ca 21μ (E) $\times$ ca 21μ (P), 12-17 pantoporate, ora ca 3-3.5μ in diam.

Pollen examined: *Woytkowski 34509* (MO).

9. HILLERIA

Hilleria Vell., Fl. Flumin. 47, **1:** *pl. 122,* 1825. [Type *H. latifolia* (Lam.) H. Walter]

Mohlana Mart., Nov. Gen. Sp. Pl. **3:** 171, *pl. 290,* 1829.

Herbs, robust, some species suffrutescent at the base, to 1.5 m. *Leaves* ovate to elliptic, acute, acuminate, or long acuminate, entire, the bases obtuse, ± glabrous above to sparsely hairy on the veins beneath; petiolate. *Inflorescences* racemes, axillary or terminal, ± black on drying. *Flowers* perfect, ± zygomorphic, pedicellate; bract single, awl-shaped; bracteoles two, minute, visible only in bud; sepals 4, unequal, the lowermost enlarging conspicuously in fruit and somewhat uniting at the base with the 2 laterals; stamens 4 or 8-13, alternate or deposited irregularly, the filaments filiform, the anthers 2× longer than broad; ovary spherical or slightly compressed laterally, 1-carpellate, the styles present or absent, the stigma feathery or capitate. *Fruit* an utricle, lens-shaped, ridged on the edges, pericarp wrinkled; seed one, testa shiny black.

Northern South America and introduced into Africa; a genus of 3 species.

Pollen grains single, subspheroidal, ca 23-29μ (E) $\times$ ca 23-29μ (P), 12-colpate, 4 at each pole and 4 perpendicular to the equator, colpi ca 6-9μ long, sometimes ± indistinct, exine ca 2-2.5μ in thickness, sexine ± equal to nexine and finely to very finely reticulated (Fig. 5).

Young specimens of *Hilleria,* i.e. those not in late flowering or fruit, can be confused with *Schindleria* H. Walter, especially that section of the latter genus which turns black upon dessication. However, the pollen of the two genera, 12-colpate in *Hilleria,* and polyporate in *Schindleria,* provides a means for unmistakable identification.

a. Stamens 8-13; stigmas feathery, ± sessile .... 1. *H. longifolia*
aa. Stamens ± 4; stigmas capitate.
  b. Style absent, stigma sessile .... 2. *H. latifolia*
  bb. Style short, ca 0.2-0.3 mm long, stigma not sessile .... 3. *H. secunda*

1. *Hilleria longifolia* (H. Walter) Heimerl, Oesterr. Bot. Zeitschr. **61:** 10, 1911.

H. latifolia (Lam.) H. Walter var. *longifolia* H. Walter, Pflanzenr. IV, 83 (Heft 39): 82, 1909. (Type *Poeppig 1541* W)

Herbs, erect, to 1-2.5 m. *Leaves* elliptic, ± long acuminate, entire, the bases obtuse, up to 23 cm long and 6 cm wide, glabrous above, coarsely hairy on veins beneath; petioles up to 6 cm long. *Inflorescences* up to 40 cm long, terminal or axillary. *Flowers* with pedicels to 6 mm long; bract single, up to 4 mm long;

bracteoles two, ca 0.2 mm long; sepals at maturity ca 3.5 mm long for lowermost, ca 3 mm long for remaining 3; stamens 8-13, irregularly deposited, the filaments ca 0.8-0.9 mm long, the anthers ca 1 mm; style absent, the stigma feathery. *Utricle* ca 2.5 mm in diam.

A rare species reported only from Peru and Bolivia.

BOLIVIA: SUR YUNGAS: Colaya, *Mexia 4302* (MO).

PERU: CUZCO: Quincemil, *Marín 1536* (US). SAN MARTIN: Margarita, *Ferreyra 1017* (US); vic of Tingo María, *Allard 22267* (US).

Pollen grains ca 23μ (E) $\times$ ca 23μ (P), colpi ca 8-9μ long, sexine medium finely reticulated.

Pollen examined: *Allard 22267* (US).

2. *Hilleria latifolia* (Lam.) H. Walter, Pflanzenr. IV, 83 (Heft 39): 81, 1909.

Rivina latifolia Lam., Encycl. Méth. Bot. **1**: 324, 1791. (Type *Martin s.n.* P)
R. affinis Nees & Mart., Nov. Acta Acad. Nat. Cur. **11**: 30, 1823.
Hilleria elastica Vell., Fl. Flumin. 47, **1**: *pl. 122,* 1825.
Rivina apetala Schum. & Thonn., Beskr. Guin. Pl. 84, 1827.
Mohlana nemoralis Mart., Nov. Gen. Sp. Pl. **3**: 171, *pl. 290,* 1829.
M. guineensis Moq. in DC., Prodr. **13**(2): 15, 1849. (Type *Schumann s.n.,* location unknown)
M. latifolia (Lam.) Moq., loc. cit. 16. (Type *Martin s.n.* P)
M. apetala (Schum. & Thonn.) Engler, Pflanzenwelt Ost-Afr. **5**: 175, 1895.

Herbs, slightly suffrutescent at the base, to ca 1 m. *Leaves* ovate to elliptic, acuminate to long acuminate, entire, the bases obtuse, up to 20 cm long and 6 cm wide, ± glabrous above, and coarsely hairy on the veins beneath; petioles to 8 cm long. *Inflorescences* up to 30 cm long, mostly axillary, rarely terminal. *Flowers* with pedicels up to 5 mm long; bract single, ca 2 mm long; bracteoles two, ca 0.2 mm long; sepals at maturity ca 4 mm long for lowermost, ca 3 mm long for remaining 3; stamens 4, alternate with the sepals, the filaments ca 0.8 mm long, the anthers ca 0.8 mm long; the style absent, the stigma capitate. *Utricle* ca 2 mm in diam.

South America and introduced into Africa.

COLOMBIA: CUNDINAMARCA: Quebrada Cabana, *Killip et al.* 38373 (US).

ECUADOR: GUAYAS: Hacienda Barcelona Trail, *Gilmartin 555* (US).

PERU: CUZCO: betw Victoria & Echarate, *Vargas 7555* (MO, US). HUANUCO: Pozuzo, *Macbride 4625* (US); Tingo María, *Asplund 12039* (US). JUNÍN: La Merced, *Soukup 3373* (US). LORETO: lower Río Huallaga, *Killip & Smith 28904* (US), *29079* (US). SAN MARTÍN: Rioja, *Woytkowski 6127* (US); Zepelacio nr Moyobamba, *Klug 3438* (MO, US).

BOLIVIA: BENÍ: vic of Rurrenabaque, *Cárdenas 1771* (US). SARA: Río Palometillas, *Steinbach 6799* (MO).

PARAGUAY: *Hassler 8287* (MO).

ARGENTINA: SALTA: Río Blanco, *Venturi 7634* (US); vic of Tartagal, *West 8417* (MO).

IVORY COAST: *Leeuwenberg 4142* (MO); *Roberty 12376* (MO).

GHANA: *Darko 631* (MO); *Oldeman 757* (MO).

NIGERIA: *Ross 153* (MO).

CAMEROONS: *Bates 673* (MO); *Staudt 922* (US); *Zenker 316* (MO, US), *4628* (MO); *Zenker & Staudt 15* (US).

REPUBLIC OF CONGO: *Corbisier 745* (MO); *Germain 229* (MO); *Louis 924* (MO), *7318* (MO, US), *11081* (MO), *11095* (MO).

UGANDA: *Dummer 327* (US), *459* (MO, US).

Pollen grains ca 29μ (E) $\times$ ca 29μ (P), colpi 6-7μ long, sexine very finely reticulated (Fig. 5).

Pollen examined: *Bates 673* (MO); *Dummer 459* (US); *Louis 924* (MO); *Woytkowski 6127* (US).

Hilleria latifolia and *H. secunda* (Ruiz & Pavon) H. Walter are very difficult to distinguish. Frequently the styles are broken and what appears at first glance to be *H. latifolia* may be classifiable as *H. secunda* when a sufficient number of flowers is examined. Also, some specimens are almost undeterminable because of the intermediate character of the style length, which is difficult at best to observe because of its small size.

3. *Hilleria secunda* (Ruiz & Pavon) H. Walter, Pflanzenr. IV, 83 (Heft 39): 82, 1909.

Rivina secunda Ruiz & Pavon, Fl. Peru Chile **1**: 65, *pl. 102*, 1794. (Type *Ruiz & Pavon s.n.* K)
R. acuminata H.B.K., Nov. Gen. Sp. Pl. **2**: 184, 1817.
Mohlana secunda (Ruiz & Pavon) Mart., Nov. Gen. Sp. Pl. **3**: 172, 1829.
Rivina inaequalis Hook., Icon. Pl., *pl. 130*, 1837. (Type *Mathews 1604*, location unknown)
Mohlana secunda var. *acuminata* (H.B.K.) Moq. in DC., Prodr. **13**(2): 15, 1849.
Hillera secunda (Ruiz & Pavon) O. Ktze., Rev. Gen. Pl. **2**: 551, 1891.
Mohlana meziana H. Walter, Bot. Jahrb. **37**(Beibl. 85): 25, 1906. (Type *Ule 6500* B†, K)
Hilleria meziana H. Walter, Pflanzenr. IV, 83 (Heft 39): 83, 1909. (Type *Ule 6500* B†, K)

Herbs, slightly suffrutescent at the base, erect, to ca 1 m. *Leaves* ovate to elliptic, acute to acuminate, entire, the bases obuse, up to 15 cm long and 6 cm wide, coarsely hairy on the veins beneath; petioles to 6 cm long. *Inflorescences* up to 20 cm long, mostly axillary. *Flowers* with pedicels ca 5 mm long; bract single, ca 1.5 mm long, much overtopping the flowers in bud; bracteoles two, ca 0.2 mm long; sepals at maturity ca 3.5 mm long for lowermost, ca 2.25 mm long for remaining 3; stamens 4-7, alternate with the sepals, or $\pm$ deposited irregularly, the filaments ca 0.8-1 mm long, the anthers ca 1 mm long; style ca 0.2-0.3 mm long, the stigma capitate. *Utricle* ca 2 mm in diam.

Northern South America.

COLOMBIA: CUNDINAMARCA: Icononzo, *Pennell 2762* (MO, US); La Mesa, *Fernandez & Mora 1386* (US). TOLIMA: vic of Totare River, *Haught 2395* (A, US).

VENEZUELA: WITHOUT STATE: Quebrada de Chacaito, *Pittier 12996* (MO, US).

ECUADOR: GUAYAS: Manglar Alto, *Anthony & Tate 14* (US). MANABÍ: El Recreo, *Eggers 15513* (US); N of La Tuna, *Haught 3364* (US).

PERU: CAJAMARCA: Monte Seco: *Soukup 3866* (US). HUANUCO: Tingo María, *Asplund 12129* (US). JUNIN: La Merced, *Sandeman 5037* (US). LORETO: Tarapoto, *Ule 6500* (K). SAN MARTÍN: Alto Río Huallaga, *Williams 5757* (US), *6884* (US); Río Mayo, *Ferreyra 7813* (US); San Roque, *Williams 7611* (US); N of Tingo María, *Allard 20923* (US), *21822* (US).

BOLIVIA: BENÍ: San Buenaventura, *Williams 343* (US). LA CRUZ: s. loc., *Kuntze s.n.* (US).

Pollen grains ca 25μ (E) $\times$ ca 25μ (P), colpi ca 8-9μ long, exine ca 2μ in thickness, sexine finely reticulated.

Pollen examined: *Ferreyra 7813* (US); *Haught 2395* (US); *Williams 7611* (US).

10. LEDENBERGIA

Ledenbergia Klotzsch ex Moq. in DC., Prodr. **13**(2): 14, 1849. (Type *L. seguierioides* Klotzsch ex Moq.)

Ladenbergia O. Ktze., Rev. Gen. Pl. **2**: 550, 1891.
Flueckigera O. Ktze., loc. cit.

Trees or shrubs. *Leaves* alternate, elliptic to ± ovate, acuminate to acute, entire, the bases obtuse, glabrous to slightly pubescent; petiolate. *Inflorescences* racemes, mostly axillary, pendulous. *Flowers* perfect, or unisexual and plants dioecious, ± actinomorphic, pedicellate; bract single, awl-shaped, absent at anthesis; bracteoles two, minute, closely appressed to sepals; sepals 4, ± oblanceolate, constricted at the base, prominently veined, papery, green to brown; stamens 10-15, or 4-6 and rudimentary, deposited irregularly, or 4 alternate and 2 opposite; ovary present or absent, subglobose, compressed laterally, 1-carpellate, style absent, stigma penicellate. *Fruit* an utricle, subglobose, compressed laterally, ridged at the edges, pericarp wrinkled, papery brown; seed one, black.

Central America and Venezuela; a small genus of two species.

Pollen grains single, prolate spheroidal, ca 23-24μ (E) × ca 23-24μ (P), 12-colpate, 4 at each pole and 4 perpendicular to the equator, colpi ca 8-10μ long, exine ca 1.5-2.0μ in thickness, sexine ± equal to nexine and smooth to very finely reticulated.

Schmidt (1923) described a new species, *Ledenbergia peruviana,* based on *Weberbauer 6413*. I have seen a specimen of the type collection (GH), and hesitate to include it in *Ledenbergia* for the following reasons: its ± erect, paniculate inflorescences are in contrast to the pendulous racemes of *L. macrantha* Standley and *L. seguierioides* Klotszch, and the pollen is 3-colpate, in contrast to 12-colpate for the above mentioned species. Another collection, *Hutchison & Wright 3471* (MO), also from Peru, appears almost identical to *Weberbauer 6413* in floral and pollen morphology. For the present time, however, I am uncertain as to their inclusion in *Ledenbergia,* to which they are undoubtedly related.

a. Flowers perfect ....1. *L. seguierioides*
aa. Flowers unisexual, pistillate flowers appearing as perfect with 4-6 rudimentary stamens ....2. *L. macrantha*

1. *Ledenbergia seguierioides* Klotzsch ex Moq. in DC., Prodr. **13**(2): 14, 1849. (Syntypes: *Klotzsch 350* G; *Plie 20* P; *Vargas 296* G, P)

Rivina seguierioides Klotzsch ex Moq., loc. cit.
Flueckigera seguierodes (Klotzsch ex Moq.) O. Ktze., Rev. Gen. Pl. **2**: 551, 1891.

Shrubs or small trees, to 3.5 m. *Leaves* elliptic, acuminate, entire, the bases obtuse to slightly cordate, up to 16 cm long and 7 cm wide, glabrous or slightly pubescent on veins beneath; petioles 2-4(-8) cm long. *Inflorescences* racemes, up to 35 cm long, mostly axillary, softly pubescent, pendulous. *Flowers* perfect, with pedicels to 4 mm long; bract single, 1.2 mm long, awl-shaped; bracteoles two, ca 0.5 mm long; sepals ca 4(-6) mm long and 1.5-2 mm wide, green to yellow; stamens 12-14, irregularly deposited in one-two whorls, the filaments ca 2 mm long, the anthers ca 1.2 mm long; ovary present, stigma profusely penicellate. *Utricle* ca 2 mm in diam.

Reported only from Venezuela.

VENEZUELA: BOLÍVAR: nr Las Trincheras, *Pittier 8884* (G, GH, US). FEDERAL: rd betw Caracas & La Guaira, *Aristequieta 2814* (US); *Tamayo 1490* (US). MÉRIDA: Colonia Tovar, *Fendler 1297* (GH), *2389* (GH). SUCRE: vic of quebrada tributary of Río Manzanares, *Steyermark 62767* (F). WITHOUT PROVINCE: *Curran & Hamman 1238* (GH, MO).

Pollen grains ca 24μ (E) $\times$ ca 24μ (P), colpi ca 9-10μ long.

Pollen examined: *Aristequieta 2814* (US); *Fendler 2389* (GH); *Tamayo 1490* (US).

2. *Ledenbergia macrantha* Standley, Jour. Wash. Acad. Sci. **13:** 350, 1925. (Holotype *Calderon 680* US)

Trees, dioecious, to 12 m. *Leaves* ovate to elliptic, acuminate, entire, the bases obtuse to slightly oblique, up to 13 cm long and 6 cm wide, softly pubescent on veins beneath; petioles elongated, 7-10 cm long. *Inflorescences* racemes, the staminate ca 10 cm long, the pistillate 15-25 cm long and pendulous, mostly axillary, the peduncle softly pubescent. *Staminate flowers* with pedicels ca 5 mm long; bract single, ca 1 mm long, triangular, brown, papery; bracteoles two, ca 0.8 mm long; sepals 4, $\pm$ equal, ca 3-4 mm long and 1.5-3 mm wide; stamens 15-20, the filaments ca 0.8-1 mm long, the anthers ca 0.8-0.9 mm long; ovary absent. *Pistillate flowers* with pedicels ca 8 mm long; bract single, ca 2 mm long, brown, papery, deciduous; bracteoles two, ca 1.2 mm long, papery; sepals 4, $\pm$ equal, 8-10 mm long and 4-5 mm wide, conspicuously net veined, green to yellow; stamens 4-6, rudimentary, alternate with the sepals or 4 alternate and 2 opposite, the filaments very short, the anthers ca 0.5 mm long; ovary subglobose, compressed laterally, style absent, stigma papillose. *Utricle* ca 2.5-2.8 mm in diam.

Central America.

MEXICO: JALISCO: *Rzedowski 21872* (F), *21873* (F).
GUATEMALA: *Steyermark 52148* (F).
EL SALVADOR: *Allen & Armour 6802* (MO); La Libertad, Puerta de la Laguna, *Calderon 680* (NY, US); *Standley 23656* (F, MO, US); *Padilla 195* (MO).

Pollen grains ca 23μ (E) $\times$ ca 23μ (P), colpi ca 8-9μ long. [Very rarely 15-colpate, grains then ca 30μ (E) $\times$ ca 30μ (P), colpi ca 7-8μ long.]

Pollen examined: *Rzedowski 21873* (F).

Originally described with perfect flowers, the specimens collected by Rzedowski definitely are otherwise. Upon close examination of other specimens the occasional flowers appearing as perfect can be seen to have only much reduced and rudimentary stamens. However, it is unusual that so few specimens of the male plant have been collected (*Rzedowski 21873* F is the only one I have seen); it must be very rare.

11. PETIVERIA

Petiveria L., Sp. Pl. 342, 1753. (Type *P. alliacea* L.)

Mapa Vell., Fl. Flumin. 59, 1825.

Monotypic.

1. *Petiveria alliacea* L., Sp. Pl. 342, 1753. (Type LINN, not seen; from IDC Micro-Edition 472.1)

P. octandra L., Sp. Pl. ed. 2, 486, 1762. (Type LINN, not seen; from IDC Micro-Edition 472.2)
P. foetida Salisb., Prodr. 214, 1796.
Mapa graveolens Vell, Fl. Flumin. 59, *pl. 153*, 1825.
Petiveria alliacea var. *grandifolia* Moq. in DC., Prodr. **13**(2): 9, 1849. (Type *Michaux s.n.* G, not seen, in IDC Micro-Edition, Candolle Prodromi Herbarium)
P. alliacea var. *octandra* (L.) Moq., loc. cit. 1849. (Syntypes: *Ledru s.n.* G; *Sagra 399* G, both not seen, in IDC Micro-Edition, Candolle Prodromi Herbarium)
P. ochroleuca Moq., loc. cit. 1849. (Type *Mociño & Sessé s.n.*, location unknown)
P. paraguayensis Parodi, Anal. Soc. Cient. Argent. **5**: 160, 1878.
P. hexandria Sessé & Moc., Fl. Mexic. ed. 2, 90, 1894.
P. corrientina Rojas, Bull. Geogr. Bot. **28**: 163, 1918.
P. graveolens (Vell.) Stellfeld, Trib. Farm. Bras. **12**: 114, 1944.

Herbs, slightly woody at the base, sparsely branched, to 2 m. *Leaves* elliptic to ovate, mucronate to acute, entire, the bases narrowed to obtuse, up to 20 cm long and 6 cm wide, ± glabrous; petioles to 1 cm long. *Inflorescences* spike-like racemes, up to 40 cm long, peduncle sparsely pubescent to ± glabrous, somewhat lax. *Flowers* ± sessile or with pedicels 2-3 mm long; bract single, ca 1.5 mm long, triangular; bracteoles two, < 1 mm long; sepals 4, ± equal, oblong, ca 4 mm long, 3 veined, persistent in fruit; stamens 4, 6 or 8, alternate or deposited irregularly, the filaments ca 2-3 mm long, the anthers ca 1.5-2 mm long; ovary 1-carpellate, flattened, 4-6 uncinate, style absent, stigma papillose and on one flattened side of ovary only. *Fruit* an achene, flattened, elongated, 4-6 hooked, green, up to 8 mm long; seed one, linear.

Widely distributed in the warmer regions of the New World.

Pollen grains subspheroidal, ca 23-28μ (E) × ca 23-28μ (P), 12 colpate or sometimes 15 colpate, with 4(-5) at each pole and 4(-5) perpendicular to the equator, colpi ca 5-7μ long, exine ca 1.7-1.9μ in thickness, sexine ± equal to nexine and finely reticulated.

Some samples of pollen, mostly from *Petiveria alliacea* L. var. *tetrandra* (Gomez) Nowicke, had pollen which appeared acolpate, indicating possible partial sterility of this group, notwithstanding the setting of fruit.

a. Fruits 4-hooked .... 1a. *P. alliacea* var. *alliacea*
aa. Fruits 5- or 6-hooked .... 1b. *P. alliacea var. tetrandra*

1a. *Petiveria alliacea* L. var. *alliacea.*

UNITED STATES: FLORIDA: *Chapman s.n.* (MO); *Curtiss 2339* (MO), *5520* (MO); *Garber 23* (MO); *Miller s.n.* (MO); *Moldenke 723* (MO), *727a* (MO).

MEXICO: CHIAPAS: *Matuda 139* (MO). GUERRERO: *Hinton 10850* (MO). MICHOACÁN: *Hinton 12300* (MO). SINALOA: *Gentry 4965* (MO); *Mexia 305* (MO). VERA CRUZ: *Purpus 2272* (MO). YUCATÁN: *Gaumer et al. 23418* (MO); *Steere 1074* (MO). WITHOUT STATE: *Orcutt 5338* (MO).

BRITISH HONDURAS: *Gentle 4953* (MO); *Schipp 426* (MO).

HONDURAS: *Molina 17* (MO); *Yuncker et al. 8194* (MO).

GUATEMALA: *Smith 4060* (MO).

NICARAGUA: *Baker 159* (MO); *Greenman & Greenman 5718* (MO); *Wright s.n.* (MO).

PANAMA: *Allen 940* (MO), *1291* (MO); *Blum & Tyson 1001* (MO); *Duke 3853* (MO), *3976* (MO), *4146* (MO), *5086* (MO); *Dwyer 1770* (MO); *Ebinger 555* (MO); *Hunter & Allen 694* (MO), *731* (MO); *MacBride 2791* (MO); *Tyson 1425* (MO), *1477* (MO); *von Wedel 636* (MO), *1323* (MO); *White 308* (MO); *Woodson & Schery 841* (MO), *900* (MO); *Woodson et al. 1470* (MO).

COLOMBIA: CUNDINAMARCA: betw Fusagasuga & Pandí, *Pennell 2720* (MO); La Mesa, *Garcia 12163* (MO). MAGDALENA: Santa Marta, *Smith 440* (MO).

VENEZUELA: AMACURO: Pedernales, *Curran & Haman 1315* (MO). CARABOBO: betw Maracay & Valencia, *Williams 11031* (MO). SUCRE: Margarita I, *Millier & Johnston 13* (MO).

BRAZIL: AMAZONAS: Tres Casas, *Krukoff 6500* (MO).

ARGENTINA: FORMOSA: Laguna Vera, *Morel 4975* (MO); s. loc., *Jorgensen 3074* (MO). MISSIONES: Puerto Viejo, *Schwarz 2294* (MO); San Javier, *Schulz 7011* (MO); *Schwarz 3756* (MO). SALTA: Campo Quijano, *Venturi 8210* (MO).

PARAGUAY: WITHOUT PROVINCE: vic of Pilcomayo River *Morong 948* (MO); Ypacaray, *Hassler 12112* (MO). s. loc., *Hassler 3586* (MO); *Morong 530* (MO).

BOLIVIA: SARA: Buena Vista, *Steinbach 5124* (MO). WITHOUT PROVINCE: Yungas, *Bang 506* (MO); *Buchtien 743* (MO).

PERU: HUANUCO: Tingo María, *Woytkowski 5384* (MO). SAN MARTÍN: Juan Jui, *Klug 3833* (MO).

ECUADOR: MANABÍ: betw Chone & Santo Domingo, *Dodson & Thien 1758* (MO).

CUBA: *Britton et al. 14922* (MO); *Combs 182* (MO); *Curtiss 611* (MO); *Pollard & Palmer 322* (MO); *Rugel 66* (MO); *Van Hermann 232* (MO).

DOMINICAN REPUBLIC: *Allard 13920* (MO).

HAITI: *Eyerdam 123* (MO); *Leonard 8950* (MO); *Leonard & Leonard 11626* (MO).

GRENADA: *Broadway s.n.* (MO).

GUADELOUPE: *Duss 2983* (MO).

JAMAICA: *Crosby et al. 98* (MO); *Harris 11007* (MO); *Hitchcock s.n.* (MO).

MARTINIQUE: *Kohaut 98* (MO); *Sieber 98* (MO).

PUERTO RICO: *Heller 4487* (MO), *6179* (MO); *Holm 261* (MO); *Otero 318* (MO); *Sintensis 3079* (MO).

ST. CROIX: *Ricksecker 27* (MO); *Ricksecker 132* (MO).

TOBAGO: *Broadway 4690* (MO).

TRINIDAD: *Broadway 5168* (MO); *Sieber 115* (MO).

Pollen examined: *Blum & Tyson 1001* (MO); *Crosby et al. 98* (MO); *MacBride 2791* (MO).

1b. *Petiveria alliacea* L. var. **tetrandra** (Gomez) Nowicke, stat. nov.

P. tetrandra Gomez, Obs. Med. Bot. Pl. Bras. 13, 1803.
P. hexaglochin Fisch. & Meyer, Ind. Sem. Hort. Petrop. 35, 1835; Linnaea **10**(Litt. Ber.): 99, 1836.

BRAZIL: CANOAS: s. loc., *Luis 8* (F). PARANÁ: s. loc., *Dusen 16339* (NY); *Fiebrig 5867* (F). WITHOUT PROVINCE: *Jorgensen 3908* (F).

Pollen grains in both samples appeared acolpate.

Pollen examined: *Fiebrig 5867* (F); *Luis 8* (F).

12. MONOCOCCUS

Monococcus F. Muell., Fragm. **1:** 46, 1858. (Type *M. echinophorus* F. Muell.) Monotypic.

1. *Monococcus echinophorus* F. Muell., Fragm. **1:** 46, 1858. (Type *Hill & Mueller s.n.* location unknown, but *Mueller s.n.* K)

Shrubs, dioecious or monoecious, subscandent to climbing. *Leaves* lanceolate-ovate, acute, uneven to finely undulate, the bases obtuse, up to 8 cm long and 3 cm wide, ± pubescent, more so on the veins beneath; petioles to ca 1 cm long. *Inflorescences* spike-like racemes, up to 15 cm long, mostly terminal, pistillate or staminate, or rarely both and the staminate flowers terminal. *Staminate flowers* with pedicels to ca 2 mm long; bract single, ca 2-2.5 mm long, awl-shaped, keeled; bracteoles two, ca 1-1.2 mm long; sepals 4, ± equal, ca 2-2.5 mm long, rounded; stamens 12-20, the filaments ca 2.5-3 mm long, the anthers ca 1.5 mm long; ovary absent. *Pistillate flowers* sessile or with pedicels to 1.5 mm long; bract single, ca 1-1.5 mm long, lanceolate, keeled; bracteoles two, ca 1 mm long, closely appressed to sepals; sepals 4, ± equal, somewhat united at the base, lanceolate, ca 1.2-1.5 mm long; stamens absent; ovary obovoid, 1-carpellate, spinulose, the style from one side, short, curved, the stigma profusely papillose. *Fruit* an utricle or achene (?), flattened, spinulose, spines recurved at the tip, up to 3 mm long; seed one.

Australia, New Caledonia, and New Hebrides.

AUSTRALIA: NEW SOUTH WALES: *Cunningham 191* (BM, MO). QUEENSLAND: *Bailey 214* (MO), *s.n.* (US); *Dietrich s.n.* (US); *Mueller s.n.* (BM, K, MO); *White 6580* (K).
NEW CALEDONIA: *Vieillard 3075* (BM).
NEW HEBRIDES: *Baker 163* (BM).

Pollen grains single, subspheroidal, ca 23μ (E) × ca 23μ (P), 7-11 pantoporate, the ora ca 3-3.5μ in diam, exine ca 1-1.5μ in thickness, the sexine ± equal to nexine and ± smooth.

Pollen examined: *Dietrich s.n.* (US).

MICROTEOIDEAE

III. Subf. **Microteoideae** Eckardt ex Nowicke, subf. nov. Ovarium unicarpellatum (?) stigmatitus 2-4, uniseminate; achenium. (Type *Microtea* Swartz)

a. Herbs; leaves not succulent, without calcium oxalate crystals; inflorescences spikes or racemes; flowers attached singly; stamens 5 or more, anthers globose; pollen pantoporate; S. America .... 13. *Microtea*
aa. Wiry herbs; leaves ± succulent, with calcium oxalate crystals; inflorescences spikes; flowers attached in groups of ca three; stamens 4; anthers longer than broad; pollen 3-colpate; Africa .... 14. *Lophiocarpus*

13. MICROTEA

Microtea Swartz, Prodr. **4**: 53, 1788. (Type *M. debilis* Swartz)

Schollera Rohr & Vahl, Skrivt. Naturh. Selsk. Kjoebenhavn **2**: 210, 1792.
Microthea Juss., Dict. **3**: 288, 1804.
Ancistrocarpus H.B.K., Nov. Gen. Sp. Pl. **2**: 186, *pl. 122,* 1817.
Potamophila Schrank, Pl. Rar. Horti. Monac. **2**: 62, 1819.
Ceratococa Willd. ex Roem. & Schult. in L., Syst. Veg. ed 15, **6**: 800, 1820.
Aphananthe Link, Enum. **1**: 383, 1821.

Herbs, slender, some species becoming suffrutescent at the base, erect or with branches descending or trailing, up to 60 cm, annuals. *Leaves* alternate or fasciculate, narrow-lanceolate, elliptic or deltoid, entire, the bases attenuate, obtuse or truncate; sessile or petiolate. *Inflorescences* spikes or spike-like racemes, terminal or axillary. *Flowers* perfect, actinomorphic, sessile or with pedicels to 5 mm long; bract single; bracteoles two, rarely absent; sepals 5, ± equal, one vein, dry and/or membranaceous, green to white; stamens 5-9, rarely 4, alternate with the sepals or irregularly placed, in some species appearing to be united into a ring at the base, the filaments of varying lengths, the anthers globose; ovary ± spherical, 1-carpellate (?), the styles absent or very abbreviated, the stigmas 2-4, filiform.

Fruit an achene, thin walled, muricate to spiny; seed one, spherical-lenticular, testa shiny black.

A genus of about 9 species well represented in the American tropics, particularly in South America. *Microtea scabrida* Urban has perhaps the most southerly distribution, being found in the northern provinces of Argentina.

Pollen grains single, subspheroidal, ca 17-23μ (E) $\times$ ca 17-23μ (P), pantoporate, (15-)20-25 apertures, ora ca 2-3μ in diam, exine ca 1.3-2μ in thickness, sexine $\pm$ equal to nexine and finely reticulated.

Microtea, as well as *Lophiocarpus* Turcz., with its minute, simplified flowers, scarious bracts and pollen type, represents a connecting link to the halophytic *Chenopodiaceae* and *Amaranthaceae.* The recognition of *Lophiocarpus* as distinct from *Microtea,* into which it had been incorporated by Brown (1909), is valid, based not only on a marked contrast in the pollen morphology, but on significant differences in the sporophyte generation as well. *Microtea* is distinguished from *Lophiocarpus* by its more herbaceous habit, strictly actinomorphic flowers which are singly attached, tendency to 5 stamens or more, globose anthers, and lack of calcium oxalate crystals or succulence in the leaves. The geographical distribution of the two groups, neotropics (*Microtea*) versus dry areas of southern Africa (*Lophiocarpus*), provides additional support for their separation as distinct genera.

Walter (1909) described the subg. *Schollera* containing the generic type, *M. debilis* Swartz, and one other species, *M. portoricensis* Urban, and subg. *Eumicrotea* to include the remaining species. In accordance with the Code, his subg. *Schollera* must become subg. *Microtea,* and his subg. *Eumicrotea* is renamed subg. *Moquinia.*

a. Inflorescences spikes less than 4 cm long; stamens (4-)5 ....subg. 1. *Microtea*
    b. Achenes wrinkled or muricate ....1. *M. portoricensis*
    bb. Achenes spiny ....2. *M. debilis*

aa. Inflorescences spikes or spike-like racemes greater than 4 cm long at maturity; stamens 6-9 ....subg. 2. *Moquinia*
    c. Flowers sessile or subsessile, pedicels < 1.5 mm long.
        d. One bract subtending each flower ....3. *M. longebracteata*
        dd. One bract and two smaller bracteoles subtending each flower.
            e. Leaf blades deltoid, petioles distinct ....4. *M. scabrida*
            ee. Leaf blades linear to lanceolate, the bases attenuate.
                f. Inflorescences delicate or filmy spikes; fruits ca 1 mm in diam; leaves thin and brittle when dry ....5. *M. paniculata*
                ff. Without the above combination of characters.
                    g. Leaf blades narrowly lanceolate; fruits ca 1.5 mm in diam ....6. *M. sulcicaulis*
                    gg. Leaf blades more variable; fruits ca 1.2 mm in diam ....7. *M. foliosa*
    cc. Flowers pedicellate, at least some pedicels 2 mm long.
        h. Plants suffrutescent at the base; leaves filiform, less than 2 mm wide and ca 1 cm long ....8. *M. tenuifolia*
        hh. Plants herbaceous; leaves lanceolate to elliptic, at least some greater than 5 mm wide and 3 cm long ....9. *M. maypurensis*

SUBG. 1 MICROTEA.

subg. *Schollera* (Rohr & Vahl) H. Walter, Pflanzenr. IV, 83 (Heft 39): 127, 1909.

1. *Microtea portoricensis* Urban, Ber. Deutsch. Bot. Ges. **3**(8): 324, 1885. (Type *Sintenis 717* NY, S)

Herbs, slender, trailing, primary stems abbreviated. *Leaves* at the base spatulate, appearing in some to form a basal rosette, up to 5 cm long and 2 cm wide, stem leaves smaller, oblanceolate to obovate, acute to slightly mucronate, entire, the bases long attenuate. *Inflorescences* spikes, < 3 cm long, 15-30 flowers. *Flowers* ± sessile; bract single, ca 0.8 mm long, lanceolate; bracteoles absent; sepals (4-)5, ca 0.8 mm long, oblong, dry; stamens 5, occasionally 4; the stigmas 2. *Achene* ca 1 mm in diam, testa muricate or wrinkled.

The Greater Antilles.

Cuba: *Ekman 11495* (S), *13408* (NY, S); *Leon 2609* (NY), *4340* (NY); *Leon & Eduard 8717* (NY); *Rugels 771* (NY); *Van Hermann 121* (BM, NY).

Dominican Republic: *Ekman 15330* (S).

Haiti: *Eckman 7279* (S).

Puerto Rico: *Sintenis 717* (BM, NY, S)

Pollen grains ca 21μ (E) × ca 21μ (P), ca 20 apertures, exine ca 2μ in thickness.

Pollen examined: *Ekman 13408* (NY); *Bro. Leon 2609* (NY), *4340* (NY).

Although a sharp distinction between this species and the wider ranging *M. debilis* Swartz is difficult to maintain, the characters of the exocarp, wrinkled in *M. portoricensis* Urban and spinulose in *M. debilis*, and the length of the spike, shorter in *M. portoricensis*, are the most constant. However, Urban's original description of 3-4 stamens does not appear to be correct; three stamens were never observed and four only occasionally.

2. *Microtea debilis* Swartz, Prodr. **4**: 53, 1788. (Type *Swartz s.n.*, location unknown)

Schollera debilis Rohr, Skirvt. Naturh. Selsk. Kjorb. **2**: 210, 1792.
Microtea ovata Delile, Hort. Monsp., 1827.
M. debilis var. ovata (Delile) Moq. in DC., Prodr. **13**(2): 17, 1849.
M. debilis var. rhombifolia Moq., loc. cit.

Herbs, ± decumbent, stems prominently grooved, to 45 cm. *Leaves* very variable but generally oblanceolate to rhomboid, ± acute, entire, the bases long attenuate, up to 8 cm long and 3 cm wide. *Inflorescences* spikes, < 4 cm long, 10-20(-24) flowers. *Flowers* ± sessile; bract single, ca 1 mm long, thin, lanceolate; bracteoles absent; sepals oblong; stamens 5, the filaments ca 0.5 mm long, the anthers 0.1 mm long; stigmas 2. *Achene* spiny, ca 1 mm in diam, much overtopping the persistent calyx at maturity.

Neotropics.

British Honduras: *Gentle 1487* (MO); *Schipp S-286* (MO).

Honduras: *Thieme 5427* (NY); *Wilson 384* (NY); *Yuncker et al. 8374* (BM, MO, NY); *Robertson 5* (BM).

Guatemala: *Bernoulli 877* (NY); *Deam 6042* (MO, NY); *Kellerman 7477* (NY); *Pittier 386* (NY).

El Salvador: *Calderon 1069* (NY).

Costa Rica: *Boissier 8712* (NY); *Brenes 12242* (NY).

Panama: *Allen 883* (MO), *1296* (MO); *Duke 4023* (MO), *4054* (MO); *Fendler 109* (MO); *Heriberto 115* (NY); *Killip 3423* (NY); *Pittier 2709* (NY); *Stern et al. 808* (MO).

ANTIGUA: *Box 1005* (MO, NY).
DOMINICA: *Lloyd 402* (NY).
DOMINICAN REPUBLIC: *Howard & Howard 9731* (NY).
GRENADA: *Broadway s.n.* (NY).
GUADELOUPE: *Bertero 93* (MO); *Duss 2401* (NY).
HAITI: *Leonard & Leonard 11346* (NY).
JAMAICA: *Britton & Hollick 2013* (NY); *Harris 10214* (NY).
MARTINIQUE: *Duss 2063* (NY); *Hahn 811* (NY).
PUERTO RICO: *Britton & Cowell 1495* (NY); *Britton et al. 6650* (NY); *Shafer 2431* (NY).
ST. EUSTATIUS: *Boldingh 569B* (NY).
ST. KITTS: *Britton & Cowell 275* (NY).
ST. LUCIA: *Box 1999* (NY).
ST. THOMAS: *Britton et al. 470* (NY).
ST. VINCENT: *Smith & Smith 178* (NY).
TOBAGO: *Broadway 4642* (MO, NY); *Eggers 5826* (NY).
TRINIDAD: *Britton & Britton 2170* (NY); *Broadway 5455* (MO); *Fendler 643* (NY); *Kuntze 748* (NY).
BRAZIL: RIO NEGRO: vic of Barra, *Spruce s.n.* (NY).
COLOMBIA: ANTIOQUÍA: Vuelta de Acuna, *Pennell 3815* (MO, NY). BOLÍVAR: Arjona, *Killip & Smith 14525* (NY); *Turbaco, Killip & Smith 14359* (NY). MAGDALENA: Chiriguana, *Allen 72* (MO); Rincon Hondo, *Allen 504* (MO); Santa Marta, *Smith 1246* (MO, NY). META: Villavicencio, *Pennell 1567* (NY). VALLE: Cali, *Fosberg 20540* (NY).
VENEZUELA: LARA: betw Yaritagua & Duaca, *Saer 355* (NY); WITHOUT STATE: Cristóbal Colon, *Broadway 70* (NY).
GUYANA: *De La Cruz 1143* (NY), *2093* (MO, NY), *2480* (NY), *2501* (MO, NY), *3548* (NY), *3650* (MO, NY), *4033* (MO, NY); *Gleason 18* (NY), *696* (NY); *Jenman 5277* (NY); *Mell & Mell 234* (NY).
FRENCH GUIANA: *Broadway 222* (NY).
SURINAM: *Samuels 115* (NY).
ECUADOR: MILAGRO, *Hitchcock 20282* (NY); Naranjito, *Camp E 3575* (NY); Río Pita, *Asplund 5253* (NY).
PERU: LORETO: Río Paranapura, *Klug 3959* (MO); Yurimaguas, *Killip & Smith 28215* (NY).

Pollen grains ca 23μ (E) $\times$ ca 23μ (P), ca 20-25 apertures, exine ca 2μ in thickness.

Pollen examined: *Allen 504* (MO), *Duke 4054* (MO).

Microtea debilis is widely distributed in Central America, the lesser Antilles, the Dominican Republic and Haiti, and northern South America, but is conspicuously absent in collections from Cuba, where *M. portoricensis* appears semi-endemic, notwithstanding Roig & Acuna's (1951) reference to it in the Flora de Cuba. However, as I have indicated, the two species are closely related and may prove to be conspecific.

SUBG. 2 **Moquinia** Nowicke, nom. nov. (Type *Microtea paniculata* Moq.)
subg. *Eumicrotea* H. Walter, Pflanzenr. IV, 83 (Heft 39): 127, 1909.

3. *Microtea longebracteata* H. Walter, Pflanzenr. IV, 83 (Heft 39): 129, 1909. (Type *Sellow 359* photo NY from B†)

Herbs, erect, stems grooved, sparsely branched, to 30 cm. *Leaves* lanceolate to oblanceolate, acute, entire, the bases attenuate, up to 6 cm long and 1.5 cm wide. *Inflorescences* spikes, 12-15 cm long, 25-30 flowers. *Flowers* ± sessile or with minute pedicels < 1 mm long; bract single, ca 1-1.2 mm long, lanceolate; bracteoles absent; sepals ca 1 mm long; stamens ca 8, ± united into a ring at the base, the filaments ca 0.3 mm long, the anthers ca 0.1-0.2 mm long; stigmas 2, recurved. *Achenes* muricate, ca 0.8-1 mm in diam, overtopping the persistent calyx at maturity.

BRAZIL: PARAIBA: Areia, *de Moraes 974* (NY). PERNAMBUCO: Recife, *Pickel 3589* (NY).

Pollen grains ca 21μ (E) × ca 21μ (P), ca 15-aperturate, ora ca 2.5μ in diam, exine 1.5-2μ in thickness.

Pollen examined: *Pickel 3589* (NY).

Microtea longebracteata is similar in general habit to *M. maypurensis* (H.B.K.) G. Don, but is easily distinguished by its sessile flowers and single bract.

4. *Microtea scabrida* Urban, Ber. Deutsch. Bot. Ges. **3**(8): 325, 1885. (Type *Sello s.n.* photo NY, from B†)

M. paniculata Moq. var. *latifolia* O. Ktze., Rev. Gen. Pl. **3**(2): 268, 1898.
M. scandens Rusby, Mem. N. Y. Bot. Gard. **7**: 239, 1927. (Type *Cardenas 1942* NY)

Herbs, erect, stems grooved, to 1 m. *Leaves* ± deltoid, acute-acuminate, entire, the bases truncate, up to 8 cm long and 4.5 cm wide; petioles to 2 cm long. *Inflorescences* spikes, ca 10-12 cm long, 30-40 flowers. *Flowers* ± sessile; bract single, ca 0.6 mm long; bracteoles two, ca 0.3 mm long; sepals ca 1.2 mm long, turning dark on dessication; stamens 8(-9), the filaments 0.7-0.8 mm long, the anthers ca 0.2 mm long; stigmas 2 and fimbriolate, or occasionally 3 by subdivision of one of original 2. *Achenes* sparsely spinulose, ca 1.8 mm in diam.

Northern Argentina and Bolivia, occasional from Brazil and Paraguay.

BRAZIL: PARANÁ: Therezina, *Dusen 11265* (NY, S). PERNAMBUCO: Caxauga, *Ridley et al. s.n.* (BM). RIO ACRE: São Francisco, *Ule 9361* (G).

ARGENTINA: CORRIENTES: Ita Ibate, *Schwarz 8262* (MO). MISIONES: Ora Verde, *Schwarz 7789* (G); Posadas, *Ekman 1976* (S); Puerto Piray, *Schwarz 6844* (NY); San Javier, *Schwarz 3754* (MO); Cerro San Pedro, *Schwarz 2892* (MO); Santa Ana, *Montes 1509* (MO).

PARAGUAY: Tobaty, *Hassler 6254* (S); s. loc., *Jorgensen 4008* (MO).

BOLIVIA: SANTA CRUZ: San Raphael, *Williams 222* (BM, NY); along Río Yapacani, *Kuntze s.n.* (NY), *Steinbach 7498* (BM, NY), WITHOUT STATE: *Cardenas 1942* (NY).

Pollen grains ca 22μ (E) × 22μ (P), 17-20-aperturate, ora ca 2-2.5μ in diam, exine ca 2μ in thickness.

Pollen examined: *Montes 1509* (MO).

5. *Microtea paniculata* Moq. in DC., Prodr. **13**(2): 18, 1849. (Lectotype selected: *Blanchet 2709* K)

M. celosioides Moq. in DC., loc cit. (*Salzmann 472,* photo NY, from G)
Chenopodium paniculatum Salzm. ex Moq. in DC., loc cit., nom. nud. pro syn. *M. paniculata.*

Herbs, erect, stems grooved, to 45 cm. *Leaves* narrow-lanceolate to lanceolate, acuminate, entire, the bases attenuate, up to 4 cm long and 1 cm wide; ± sessile. *Inflorescences* spikes, ca 9-10 cm long, slender, 20-25 flowers. *Flowers* ± sessile; bract single, 1-1.2 mm long; bracteoles two, ca 0.5 mm long; sepals ca 1-1.2 mm long; stamens 8, the filaments ca 0.3 mm long, the anthers ca 0.2 mm long; stigmas 2 or 3. *Achene* spiny, ca 1 mm in diam, overtopping the persistent calyx at maturity.

Brazil and Paraguay.

BRAZIL: BAHIA: Brasilia, *Irwin et al.* 9600 (MO); *Lützelburg 730* (NY); Paranoa, *Irwin et al. 11258* (MO). WITHOUT STATE: *Gardner 1138* (BM, G, NY), *Glaziou 11440* (MO).

PARAGUAY: s. loc., *Hassler 3981* (NY), *6407* (MO, NY), *Jorgensen 4009* (MO, NY).

Pollen grains ca 18μ (E) × ca 18μ (P), ca 15 apertures, ora ca 2.5-3μ in diam, exine ca 2μ in thickness.

Pollen examined: *Hassler 6407* (MO).

6. *Microtea sulcicaulis* Chodat, Bull. Herb. Boiss., sér. 2, **3:** 1903. (Type: *Hassler 4238* F, K, NY)

Herbs, robust, stems grooved, to 45 cm. *Leaves* narrow-lanceolate to lanceolate-elliptic, acuminate to ± mucronate, entire, the bases attenuate, up to 7 cm long and 0.5-1.3 cm wide. *Inflorescences* spikes, 12-15 cm long, 40-50 flowers. *Flowers* ± sessile; bract single, ca 0.8 mm long; bracteoles two, minute, 0.1 mm long; sepals ca 1.2 mm long; stamens 8, appearing in some to be united into a ring at the base, the filaments ca 0.8 mm long, the anthers 0.2 mm long; stigmas 2. *Achene* spiny, ca 1.5 mm in diam, much overtopping the persistent calyx at maturity.

PARAGUAY: AMAMBAY: s. loc., *Hassler 9879* (G). YERBALES: Montium, *Hassler 4328* (F, NY). IPACARAY: s. loc., *Hassler 12395* (F, MO, NY, US).

Pollen grains ca 21μ (E) × ca 21μ (P), ca 15-aperturate, ora ca 2.5-3μ in diam, exine ca 2μ in thickness.

Pollen examined: *Hassler 12395* (US).

7. *Microtea foliosa* Chodat, Bull. Herb. Boiss., pér. 2, **3:** 418, 1903, emend. Nowicke. (Lectotype selected: *Hassler* 7605 MO; isolectotypes F, G, NY, S)

Herbs, erect, stems grooved, to 40 cm. *Leaves* mostly lanceolate, mucronate, entire, the bases attenuate, up to 4 cm long and 1 cm wide; sessile or petioles to ca 8 mm long. *Inflorescences* spikes, 12-15 cm long, slender, 30-40 flowers. *Flowers* subtended by single bract, ca 0.8 mm long; bracteoles two, ca 0.2 mm long; sepals ca 0.9-1 mm long, prominently one-nerved; stamens 8, the filaments ca 0.5 mm long, the anthers ca 0.2 mm long; stigmas 2, spatulate. *Achenes* spiny, ca 1.2 mm in diam, overtopping the persistent calyx at maturity.

PARAGUAY: CONCEPCIÓN: Concepción, *Hassler 7605* (F, MO, NY, S).

Pollen grains ca 17μ (E) × ca 17μ (P), ± 15-aperturate, ora ca 2μ in diam, not well defined, exine ca 2μ in thickness.

Pollen examined: *Hassler 7605* (MO).

Sometimes difficult to separate from *M. paniculata* and *M. sulcicaulis, M. foliosa* differs from *M. paniculata* in its more robust habit, sturdy spikes and wider leaves, and from *M. sulcicaulis* in its smaller fruit size and shorter leaf length.

Chodat's exsiccatae (1903) of *Microtea foliosa* includes *Hassler 6254* and *7605.* Walter (1909) reduces *M. foliosa* to synonomy with *Microtea scabrida* Urban and cites both of the above collections. However, only *Hassler 6254* is a bona fide specimen of *M. scabrida; Hassler 7605* (MO) has been selected as the lectotype for an amended description of *M. foliosa.*

8. *Microtea tenuifolia* Moq. in DC., Prodr. **13**(2): 18, 1849. (Lectotype selected: *Claussen 392* P)

Herbs, erect, much branched, ± suffrutescent at the base, to 25 cm. *Leaves* filiform, up to 1 cm long and 1 mm wide, curling when dry. *Inflorescences* spike-like racemes, ca 8-10 cm long. *Flowers* with pedicels to 2 mm long; bract single, ca 0.6 mm long; bracteoles two, ca 0.2 mm long; sepals ca 0.6-0.8 mm long; stamens 8, the filaments 0.6 mm long, the anthers ca 0.2 mm long; stigmas 2(-3). *Achene* spiny, ca 1 mm in diam, much overtopping the persistent calyx at maturity.

BRAZIL: MINAS GERAES: Caldas, *Regnell II:11* (NY, US); vic of Lagoa Seca, *Williams 5447* (MO, US); Pico d'Habira, *Claussen 4* (P), *392* (P); Turvo, *Hoehne & Gehrt 17464* (NY); s. loc., *Riedel 48* (P).

Pollen grains ca 18μ (E) × ca 18μ (P), 17-20 apertures, ora ca 2μ in diam, exine ca 1.5-2μ in thickness.

Pollen examined: *Williams 5447* (MO).

The suffrutescent, much branched habit and very small, filiform leaves make this the most distinct species of *Microtea.*

9. *Microtea maypurensis* (H.B.K.) G. Don, Loud. Hort. Brit. ed. 2, 98, n. 6423, 1839.

Ancistrocarpus maypurensis H.B.K., Nov. Gen. Sp. Pl. **2**: 186, *pl. 122* 1817.
Galenia celosioides Spreng., Nov. Prov. Hort. Hal. 38, 1819.
Potamophila parviflora Schrank, Pl. Rar. Horti Monac. **2**: 63, 1819.
Ceratococca maypurensis (H.B.K.) Willd. ex Schult. in L., Syst. Veg. ed. 15, **6**: 800, 1820.
Aphananthe celosiodes Link, Enum. Hort. Berol. **1**: 383, 1821.
Ancistrocarpus schrankii Lebdeb., Ind. Sem. Hort. Dorp., 1822.
Microtea lanceolata Del., Hort. Monsp., 1827.
M. glochidiata Moq. in DC., Prodr. **13**(2): 18, 1849. (Syntypes: *Blanchet 2680* G, P; *Gardner 2311* K)
M. sprengelii Moq., loc cit. 19.
Ancistrocarpus hexander Gay ex Moq., loc. cit. 17, nom. nud. pro syn. (Type *Gay s.n.* P)

Herbs, stems grooved, moderately branched, erect, to 40 cm. *Leaves* lanceolate, acute to acuminate, entire, the bases attenuate, up to 5 cm long and 1 cm wide. *Inflorescences* spike-like racemes, ca 8-10 cm long. *Flowers* with pedicels to 5 mm long; bract single, ca 0.8-1 mm long; bracteoles two, ca 0.4 mm long; sepals ca 1.2 mm long; stamens 8, the filaments ca 0.5 mm long, the anthers ca 0.1 mm long; stigmas 2, or 4 by subdivision. *Achene* spiny, each spine having 3-5 hairs at the tip, ca 1-1.4 mm in diam, much overtopping the persistent calyx at maturity.

Brazil, Bolivia and Paraguay.

BRAZIL: AMAZONAS: Rio Uaupes, *Spruce 2546* (NY). BAHIA: *Blanchet 2680* (G), *s.n.* (NY). CEARÁ: Brasilia, *Lofgren 175* (S). RIO GRANDE DO SUL: Tapera, *Pickel s.n.* (NY). s. loc.: *Martius 428* (MO, NY).

PARAGUAY: s. loc., *Jorgensen 3846* (NY); *Hassler 3126* (NY, S).

BOLIVIA: BENÍ: Bení River, *Rusby 1379* (BM, MO, NY). LA PAZ: Tipuani, *Buchtien 7290* (MO, NY). WITHOUT STATE: vic of Guanai, *Bang 1589* (BM, NY). s. loc., *Williams 369* (NY).

Pollen grains ca 21μ (E) × ca 21μ (P), 20-25 apertures, ora ca 2-2.5μ in diam, exine ca 2μ in thickness (Fig. 6).

Pollen examined: *Buchtien 7290* (MO).

14. LOPHIOCARPUS

Lophiocarpus Turcz., Bull. Soc. Nat. Hist. Moscou **16:** 56, 1843. (Type *L. polystachyus* Turcz.)

Wallinia Moq. in DC., Prodr. **13**(2): 143, 1849.

Herbs, in some species markedly suffrutescent at the base, sparsely or profusely branched, annuals. *Leaves* alternate or fasciculate, filiform or linear, sometimes ± succulent, calcium oxalate crystals present; sessile. *Inflorescences* spikes, mostly terminal, rarely axillary, flowers in clusters of (2-)3. *Flowers* perfect, ± actinomorphic; bract single, trilobed, the central lobe largest, the bract of the central flower largest; sepals 5, ± equal, thin, membranaceous; stamens 4, 3 alternate and one opposite, the filaments short, the anthers longer than broad; ovary spherical, 1-carpellate(?), style short, the stigmas 4, filiform. *Fruit* an achene, muricate, warty, or ridged; seed one.

South West Africa and South Africa; a small genus of 3 species characteristic of dry, sandy habitats.

Pollen grains single, subprolate, ca 16-23μ (E) × ca 20-27μ (P), 3-colpate, colpi ca 16-17μ long and ca 1μ wide at mid-length, exine ca 1.7-2.9μ in thickness, sexine equal to or slightly thicker than nexine and very finely reticulated (Fig. 8).

a. Delicate herbs; some inflorescences small and lateral; achenes weakly 16-ribbed .... 1. *L. dinteri*
aa. Without the above combination of characters.
  b. Achenes ribbed, or sometimes muricate and ribbed .... 2. *L. polystachyus*
  bb. Achenes warty to muricate, but not ribbed .... 3. *L. tenuissimus*

1. *Lophiocarpus dinteri* Engl. in Engl. & Drude, Veg. Erde **9**(3): 138, 1915. (Neotype selected: *Dinter 6885* PRE)

Herbs delicate, to 40 cm. *Leaves* alternate to slightly fasciculate, filiform, up to 3.5 cm long and 1 mm wide. *Inflorescences* spikes to 30 cm long, mostly terminal but some smaller lateral ones, very slender. *Flowers* subtended by a trilobed bract, ca 0.7 mm long for central flower, ca 0.4-0.5 mm long for two lateral flowers; sepals ± lanceolate, ca 0.8 mm long; filaments ca 0.8-0.9 mm long, the anthers ca 0.4 mm long; stigmas free to base. *Achenes* weakly 16-ribbed, ca 0.6-0.7 mm in diam.

South West Africa: Karibib, *Dinter 6885* (BM, K, PRE); *Hardy 2061* (PRE).

Pollen grains ca 16μ (E) × 20μ (P), colpi ca 16μ long, very narrow, exine ca 1.7μ in thickness.

Pollen examined: *Dinter 6885* (PRE).

2. *Lophiocarpus polystachyus* Turcz., Bull. Soc. Nat. Hist. Moscou **16:** 56, 1843. (Type *Drège 2940* K, PRE)

Wallinia polystachya (Turcz.) Moq. in DC., Prodr. **13**(2): 143, 1849.
Lophiocarpus burchellii Hook. f. in Benth. & Hook. f., Gen. Pl. **3:** 50, 1883. (Type *Burchell 1934* K)
Microtea burchellii (Hook. f.) N.E.Br., Kew Bull. **1909:** 135, 1909.
M. polystachya (Turcz.) N.E.Br., loc. cit.
M. gracilis A. W. Hill, Kew Bull. **1910:** 56, 1910. (Type *Schlechter 11806* K, PRE)
Lophiocarpus gracilis (A. W. Hill) Engl. in Engl. & Drude, Veg. Erde **9:** 138, 1915.

Herbs, in some markedly suffrutescent at the base, to 40 cm, moderately to profusely branched. *Leaves* alternate to fasciculate, filiform to linear, in some slightly succulent, up to 3 cm long and 2 mm wide. *Inflorescences* spikes, to 25 cm long, terminal, and 50-70 flower clusters. *Flowers* subtended by a trilobed bract, ca 1.2 mm long for central flower, ca 0.9-1 mm long for two lateral flowers; sepals slightly unequal, 1.2-1.5 mm long; filaments 1.2 mm long, the anthers ca 0.6 mm long. *Achenes* ribbed, sometimes muricate between the ridges, ca 1.5 mm in diam.

South Africa and South West Africa.

South Africa: cape of good hope: Barkley West, *Acocks 168* (PRE); Kalahari-Gemsbok Park, *Barnard 761* (PRE); Kenhardt, *Acocks 12632* (PRE); Prieska, *Bryant 909* (PRE); Springbok, *Hardy 1710* (PRE); Upington, *Theron 759* (PRE); Vryburg, *Burtt-Davy s.n.* (PRE), *Mogg 8132* (PRE); Warrenton, *Leistner 1252* (PRE); s. loc., *Acocks H1311* (PRE), *Marloth 1426* (PRE). transvaal: Kimberly, *Wilman 20234* (PRE); Lydenburg, *Storey 4064* (PRE). without state: Asbestos Mts, *Marloth 2070* (PRE).

South West Africa: Gobabis, *Codd 5833* (PRE), *de Winter 2468* (PRE), *Schlieben 10395* (PRE); Kaoko Veld Reserve, *de Winter & Leistner 5786* (PRE); Keetmanshoop, *Liebenberg 5187* (PRE), Klein Karas, *Ortendahl 79* (PRE); Luderitz, *Kinges 2654* (PRE), *Merxmuller & Giess 3370* (PRE); Okambahe, *Liebenberg 5043* (PRE); Omaruru, *de Winter 3156* (PRE); Rehoboth, *Basson 37* (PRE); Spitzhopje, *Boss s.n.* (PRE); Windhoek, *Merxmuller 1003* (PRE).

Without Location: *Holub s.n.* (PRE).

Pollen grains ca 23μ (E) $\times$ ca 27μ (P), colpi ca 17μ long, exine ca 2.9μ in thickness (Fig. 8).

Pollen examined: *Ortendahl 79* (PRE); *Liebenberg 5043* (PRE), *5187* (PRE); *Schlieben 10395* (PRE).

Although a range of variation does exist in general habit, *Lophiocarpus burchellii* Hook. f. has been reduced to synonomy with *L. polystachyus* Turcz., since no specific character or set of characters consistently separates the two. Hill (1912) used the condition of the fruit wall, smooth in *L. polystachyus* and ribbed in *L. burchellii*, in attempting to validate separate specific status. However, all sheets examined, which had fruits, were ribbed to a greater or lesser degree, including the type for *L. polystachyus, Drège 2940* (PRE). Heimerl (1934) appears to agree with this conspecific treatment, as he states that the above species are scarcely separate from one another.

3. *Lophiocarpus tenuissimus* Hook. f., Ic. Pl. 1463, 1884. (Type *Rehman 4018* K)
Microtea tenuissima (Hook. f.) N.E.Br., Kew Bull. **1909**: 146, 1909.

Herbs slender, becoming suffrutescent at the base, to 25(-30) cm, sparsely branched. *Leaves* alternate or fasciculate, filiform, up to 2.5 cm long and 1 mm wide. *Inflorescences* spikes, to 15(-20) cm long, terminal, and 30-40 flower clusters. *Flowers* subtended by a trilobed bract, ca 0.8 mm long for central flower, ca 0.4 mm long for two lateral flowers; sepals lanceolate, ca 1 mm long; filaments ca 0.8 mm long, the anthers ca 0.5 mm long. *Achenes* muricate to warty, ca 1.2 mm in diam.

Southern Africa.

Bechuanaland: vic of Kang, *Wild 5035* (MO); Okavango Terr, *de Winter 4422* (PRE); s. loc., *Harbor 6553* (PRE).

South Africa: cape of good hope: Prieska, *Bryant 5234* (MO); Vryburg, *Mostert 1250* (PRE). transvaal: Louis Trichardt, *Schlieben & Strey 8381* (PRE); Middleburg, *Hewitt*

10437 (PRE); Pietersburg, *Bolus 11010* (PRE); Rustenburg, *Codd 2670* (PRE); Silverton, *Obermeyer & van Nowhuys 27698* (PRE); Warmbad, *Leenderter 6269* (PRE); Witbank, *Repton 1211* (PRE); s. loc., *Schlechter 2336* (PRE), *Sidey 1425* (PRE).

SOUTHERN RHODESIA: Beitbridge, *Wild 5329* (MO); Nuanetsi, *Drummond 7748* (PRE); Wonderbloom Reserve, *Repton 1633* (PRE), *Smith 6195* (PRE); s. loc., *Kirk 47* (PRE).

SOUTH WEST AFRICA: Grootfontein, *Schoenfelder S413* (PRE), *Wild & Drummond 6983* (PRE); Waterburg, *Galpin 515* (PRE).

Pollen grains ca 20μ (E) $\times$ ca 27μ (P), colpi ca 17μ long, exine ca 2.2μ in thickness.

Pollen examined: *Harbor 6553* (PRE), *Schlieben & Strey 8381* (PRE), *Wild 5035* (MO).

AGDESTIOIDEAE

IV. Subf. **Agdestioideae** Nowicke, subf. nov. Ovarium 3-4 carpellatum, stigmatibus 3-4, uniseminale. (Type *Agdestis* Moc. & Sessé)

Monogeneric.

15. AGDESTIS

Agdestis Moc. & Sessé in DC., Regni Veg. Syst. 1: 543, 1818. (Type *A. clematidea* Moc. & Sessé)

Monotypic.

1. *Agdestis clematidea* Moc. & Sessé in DC., Regni Veg. Syst. Nat. **1:** 543, 1818. (Type *Sessé & Mociño s.n.* MA, not seen)

A. teterrima De Not., Ind. Sem. Bot. Genuens 29, 1855.

Vines, semi-woody climbers. *Leaves* deltoid, mucronate, entire, the bases cordate, up to 5 cm long and 6 cm wide, $\pm$ glabrous, punctated by calcium oxalate crystals; petioles 2-3(-5) cm long. *Inflorescences* panicles, irregular, ca 12 cm long, terminal or axillary. *Flowers* perfect, actinomorphic; with pedicels 3-10 mm long; bract single, ca 1.2 mm long, variously placed; bracteoles two, minute, visible only in bud; sepals 4, $\pm$ equal, ca 4 mm long, yellow-green, net veined, enlarging to ca 8 mm in fruit and becoming brown, papery and translucent; stamens 15-20, irregularly deposited in a ring at the base, the filaments ca 3.2 mm long, filiform, the anthers ca 1 mm long; ovary semi-inferior, 4-carpellate, the style ca 0.5 mm long, the stigmas 4, papillose and recurved. *Fruit* an achene; seed one, by abortion of the other 3 ovules.

Mexico; reported also from Nicaragua and from southern Florida and parts of Texas (Heimerl, 1934).

MEXICO: COLIMA: *Worth et al. 8716* (MO). GUERRERO: *Mexia 8947* (MO). SAN LUIS POTOSÍ: *Palmer 50* (MO); *Pringle 3276* (BM, MO, US); *Purpus 5387* (MO). TAMAULIPAS: *Berlandier 2367* (MO); *Dressler 2278* (MO); *Palmer 420* (MO). VERA CRUZ: *Purpus 6004* (BM, MO).

Pollen grains single, subprolate, ca 23μ (E) $\times$ ca 27μ (P), 3-colpate, colpi ca 12-13μ long, exine ca 1.5μ in thickness, ca 2.5μ in thickness at the poles, sexine $\pm$ equal to nexine and finely reticulated.

Pollen examined: *Dressler 2278* (MO).

The habit, leaf shape and inferior ovary distinguish this genus readily from all other members of the *Phytolaccaceae*.

STEGNOSPERMOIDEAE

V. Subf. *Stegnospermoideae* H. Walter, Pflanzenr. IV, 83 (Heft 39): 122, 1909. (Type *Stegnosperma* Benth.)

Monogeneric.

16. STEGNOSPERMA

Stegnosperma Benth., Bot. Voy. Sulph. 17, *pl. 12,* 1844. (Type *S. halimifolium* Benth.)

Chlamydosperma A. Rich., Ess. Fl. Cuba **1:** 631, 1845.

Shrubs, sometimes vine-like or spreading. *Leaves* alternate, spatulate, elliptic or ovate-orbicular, acute, mucronate, or rounded, entire or ± lamellate, the bases obtuse, glabrous, some species ± leathery to slightly succulent, calcium oxalate crystals present; petiolate. *Inflorescences* racemes or few-flowered cymules. *Flowers* perfect, actinomorphic, with pedicels to 8 mm long; bract single, lanceolate, or elliptic and keeled; bracteoles two, smaller, lanceolate or elliptic and keeled; sepals 5, ± equal, elliptic to ovate, slightly united at the base; staminodia 5, elliptic to ovate, thin, adhering to the sepals; stamens 5, 8, or 10, the filaments widened at the base and united into a ring, the anthers 2× longer than broad; ovary spherical, 3-5 carpellate, style very short or absent, stigmas 3-5, recurved. *Fruit* a capsule, splitting by 3-5 seams; seeds 3-5, testa smooth, shiny, red-brown to ± black.

Mexico, south to Nicaragua and in the West Indies; a small genus of three species, easily distinguished from each other.

Pollen grains single, subspheroidal to subprolate, ca 28-31μ (E) × ca 30-35μ (P), 3-colpate, colpi ca 21-24μ long and ca 3.5μ wide at midlength, exine ca 3μ in thickness, ca 4.5-5μ in thickness at the poles, sexine ± equal to nexine and mediumly reticulated (Fig. 3).

Two important characteristics of the genus *Stegnosperma* are in marked contrast to the remaining *Phytolaccaceae:* presence of petaloid staminodia (often referred to as petals, the occasional presence of anthers indicates otherwise), and the compound ovary of 3-5 carpels, each of which generally forms a seed.

a. Inflorescences small axillary cymules .... 1. *S. watsonii*
aa. Inflorescences racemes, 5-7 cm long.
  b. Stigmas 5, capsule splitting by 5 seams .... 2. *S. halimifolium*
  bb. Stigmas 3-4, capsule splitting by 3-4 seams .... 3. *S. cubense*

1. *Stegnosperma watsonii* D. J. Rogers, Ann. Missouri Bot. Gard. **36:** 475, 1949. (Holotype *Palmer 1226* MO)

Shrubs, spreading or vine-like, to 5 m. *Leaves* spatulate to elliptic, rounded, acute, or rarely mucronate, entire, the bases obtuse, up to 2.5 cm wide and 3.5 cm long, glabrous, slightly leathery; petioles to 4 mm long. *Inflorescences* cymules, mostly axillary, rarely terminal, (1-)3-8 flowered. *Flowers* with pedicels to 6 mm long; bract single, ca 1.2 mm long, elliptic and keeled; bracteoles two, ca 0.8 mm long, elliptic and keeled; sepals ca 5 mm long and ca 3 mm wide; staminodia ca 5 mm long and 3 mm wide, constricted at the base; stamens ca 10, the filaments ca 4 mm long, the anthers ca 1.5 mm long; ovary 5-carpellate, the stigmas 5. *Capsule* ca 5 mm in diam, splitting by 5 seams; seeds (4-)5, testa red-brown.

Restricted to Baja California and northwestern coastal regions of Mexico.

MEXICO: BAJA CALIFORNIA: *Wiggins 7681* (F, US). SINALOA: *Jones s.n.* (F). SONORA: *Coville 1646* (US); *Gentry 2195* (F, MO, US), *2975* (F, MO); *Goldman 399* (US); *Keck 4067* (US); *Palmer 1226* (MO); *Rose 1211* (US); *Rose et al. 12390* (US), *12566* (US), *13231* (US), *15047* (US); *Shreve 5992* (F); *Wiggins 6247* (US).

Pollen grains subspheroidal to subprolate, 29-31μ (E) $\times$ 30-33μ (P), colpi ca 21μ long, exine ca 3.5μ in thickness, thickened at poles to ca 5μ.

Pollen examined: *Gentry 2975* (MO).

2. *Stegnosperma halimifolium* Benth., Bot. Voy. Sulph. 17, *pl. 12,* 1844. (as *S. halimifolia*)

Shrubs, coarse, to 4 m. *Leaves* ovate, apiculate to ± mucronate, entire, the bases obtuse, up to 4 cm long and 2.5 cm wide, glabrous, somewhat succulent or leathery; petioles 2-6 mm long. *Inflorescences* racemes, 5-7 cm long, terminal, sometimes a smaller lateral raceme near the base of the primary one. *Flowers* subtended by a single bract, 1.6 mm long, lanceolate; bracteoles two, ca 1.4 mm long, lanceolate; sepals ca 4 mm long and 2.5 mm wide; stamens ± 10, the filaments ca 4 mm long, the anthers ca 1.5 mm long; ovary 5-carpellate, the stigmas 5. *Capsules* 5-7 mm in diam, splitting by 5 seams; seeds 5, red-brown.

A distribution similar to *S. watsonii;* Baja California and northwestern states of Mexico.

MEXICO: BAJA CALIFORNIA: *Carter et al. 2115, 2497* (MO); *Constance 3139* (MO); *Fisher s.n.* (MO), *Gentry 4032* (MO); *Johnston 3166* (MO), *3488* (MO); *Jones 27465* (MO), *24481* (MO); *Purpus s.n.* (MO); *Sharsmith & Sharsmith 1436* (MO); *Shreve 6973* (MO).

Pollen grains ca 29μ (E) $\times$ ca 34μ (P) and colpi ca 23μ long (Fig. 3).

Pollen examined: *Purpus s.n.* (MO).

3. *Stegnosperma cubense* A. Rich. in Sagra, Hist. Fis. Pol. Nat. Cuba, Part 2, Hist. Nat. **10:** 309, **12:** *pl. 44,* 1845.

Shrubs to 4 m. *Leaves* ovate to orbicular, mucronate to retuse, lamellate, the bases rounded or obtuse, up to 6 cm long and 3 cm wide, or up to 3.5 cm in diam, glabrous; petioles 6-8 mm long. *Inflorescences* racemes, 5-7(-10) cm long. *Flowers* subtended by a single bract, ca 1.6 mm long, lanceolate; bracteoles two, ca 0.8 mm long, lanceolate; sepals ca 3.7 mm long and 2 mm wide; stamens 5, 8, or 10, the filaments 4 mm long, the anthers 1.6 mm long; ovary 3(-4) carpellate, the stigmas 3(-4). *Capsules* ca 5 mm in diam, splitting by 3(-4) seams; seeds 1-2(-3), black.

Central America, north to Baja California and south to Nicaragua, and the West Indies.

MEXICO: CHIAPAS: *Morley 710* (MO). COLIMA: *Goldsmith 99* (MO). GUERRERO: *Hinton 5719* (MO). MICHOACÁN: *Hinton 12627* (MO); *Leavenworth & Hoogstraal 1394* (MO). OAXACA: *Orcutt 3307* (MO). SINALOA: *Lamb 465* (MO); *Mexia 152* (MO); *Ortega 7488* (MO). VERA CRUZ: *Purpus 8959* (MO), *13066* (MO).

NICARAGUA: *Baker 2065* (MO).

CUBA: *Wright 2027* (MO).

DOMINICAN REPUBLIC: *Bertero s.n.* (MO); *Howard 12507* (MO).

Pollen grains ca 28μ (E) $\times$ 35μ (P) and colpi ca 24μ long.

Pollen examined: *Purpus 8959* (MO).

BARBEUIOIDEAE

VI. Subf. **Barbeuioideae** Nowicke, subf. nov. Ovarium 2-carpellatum, carpellisque connatis, biseminale; capsula. (Type *Barbeuia* Du Petit-Thouars)

Monogeneric.

17. BARBEUIA

Barbeuia Du Petit-Thouars, Gen. Nov. Madagasc. 6, 1806. (Type *B. madagascariensis* Steud.)

Monotypic.

1. *Barbeuia madagascariensis* Steud., Nom. ed. 2, **1**: 186, 1841.

Lianas, branched, drying black. *Leaves* elliptic, acute, entire, the bases obtuse, up to 8.5 cm long and 4 cm wide, glabrous, somewhat leathery; petioles ca 1-1.5 cm long. *Inflorescences* axillary fascicles or cymes, 2-10 flowered, rarely 1. *Flowers* perfect, actinomorphic; with pedicels ca 2.5-4 cm long; bract single, ca 1-1.5 mm long; bracteoles absent; sepals 5, subequal, ovate, ca 4-4.5 mm long and ca 3 mm wide, ± leathery; stamens 20-25, inserted on a disc at the base of ovary, the filaments ca 2-2.2 mm long, the anthers ca 1.4 mm long; ovary globose, 2-carpellate, the style absent, the stigmas 2, somewhat flattened, the inner margin lightly papillose. *Fruit* a capsule, 2 loculed; seeds two.

MALAGASY REPUBLIC: *Elliot 2748* (BM); *Guillot 25* (G); *Humbert 3324* (A); *Schlieben 8039* (BM, G, K).

Pollen grains single, subprolate, ca 21μ (E) × ca 25μ (P), 3-colporoidate, colpi ca 10-11μ long, exine ca 2-2.5μ in thickness, sexine ± equal to nexine and finely reticulated.

Pollen examined: *Guillot* 25 (G).

The relationship of *Barbeuia* to the remaining *Phytolaccaeceae* is tenuous. The ovary structure with two functional united carpels and the striking inflorescence type are unique. According to Walter's (1909) description of the ovule, it appears to be characteristic of the *Centrospermae* and should remain in the order, and, while I am inclined to agree with Hutchinson's (1959) treatment of this species as a monotypic family, I think that until *Barbeuia* is treated monographically it should be regarded as an anomalous member of the *Phytolaccaceae*.

SPECIES EXCLUDED FROM FAMILY

Hilleria subcordata Standley & Williams, Ceiba **3**: 199, 1953. (Type *León* 3488 US)

DISCUSSION AND CONCLUSION

This revision of the *Phytolaccaceae* does not change the familial limits as outlined by Heimerl in 1934. It does, however, change the intrafamilial categories and groupings as follows: the *Rivineae* now become the subf. *Rivinoideae* and contain two tribes, the *Seguierieae* and the *Rivineae*. The differences in fruit and inflorescence type between the two tribes are striking, and justify the recognition of the *Seguierieae*. The pollen, 3-colpate or 3-colporoidate in the *Seguierieae*, and

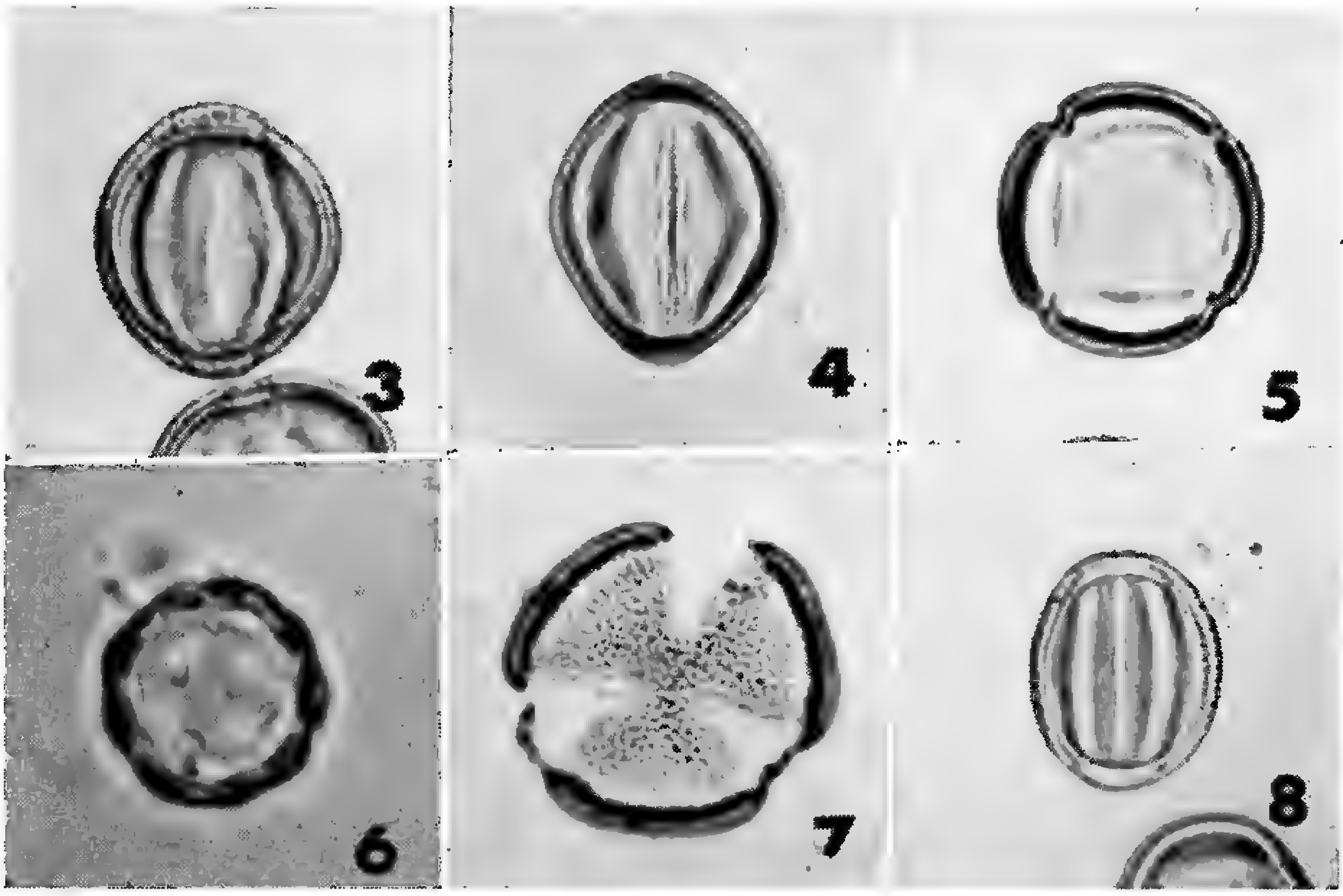

Fig. 3-8. Pollen in the *Phytolaccaceae*. Fig. 3 *Stegnosperma halimifolium* Benth., 3-colpate, equatorial view, ×680. Fig. 4 *Anisomeria littoralis* (Poepp. & Endl.) Moq., 3-colpate, equatorial view, ×700. Fig. 5 *Hilleria latifolia* (Lam.) H. Walter, 12-colpate, polar view, ×760. Fig. 6 *Microtea maypurensis* (H.B.K.) G. Don, pantoporate, ×850. Fig. 7 *Phytolacca rivinoides* Kunth & Bouché, 3-colpate, polar view, ×1000. Fig. 8 *Lophiocarpus polystachyus* Turcz., 3-colpate equatorial view, ×870.

Fig. 3 after *Purpus s.n.* (MO); Fig. 4 after *Grandjot s.n.* (MO); Fig. 5 after *Bates 673* (MO); Fig. 6 after *Buchtien 7290* (MO); Fig. 7 after *Frye & Frye 2548* (MO); Fig. 8 after *Liebenberg 5043* (PRE).

pantoporate, 12-colpate or 15-colpate in most of the *Rivineae*, also supports this distinction (Fig. 3-8).

All of Heimerl's tribal groups, *Barbeuieae*, *Phytolacceae* (*Euphytolacceae*), *Agdestideae*, and *Stegnospermeae*, now become monotribic subfamilies containing the same genera. The *Phytolaccoideae*, with their multiple, functional carpels as well as 3-colpate pollen, represent the base of the family and contain three closely related genera, *Anisomeria*, *Ercilla*, and *Phytolacca*, the first two having been placed within *Phytolacca* by various early authors. The *Agdestioideae*, with a unique semi-inferior ovary, well-defined cordate leaves and 3-4 stigmas, represent a distinct group, but the similarity between it and some genera in the *Rivineae*, i.e. *Ledenbergia*, cannot be denied. However, no clear morphological relationships exist for either the *Stegnospermoideae* or the *Barbeuioideae* to the remaining *Phytolaccaceae*, especially in the latter subfamily. In the case of the *Stegnospermoideae*, the general habit, inflorescence type, and absence of a true corolla are representative characters of most *Phytolaccaceae*, but the capsular fruit is not. The inclusion of the *Barbeuioideae in the Phytolaccaceae*, however, is difficult to justify. Its inflorescence type, ovary structure, and endemism to Madagascar, are all unique for the family. Its evidences of relationship to the other *Phytol-*

accaceae, i.e. lack of corolla, stamen number and attachment, and blackening on dessication, are all vague; certainly its 3-colporoidate pollen adds no evidence for a true connection within the family.

For *Microtea* and *Lophiocarpus* I follow Eckhardt (1964) and include these genera in the subf. *Microteoideae,* rather than treat them as anomalous genera as heretofore. The relationship between these two taxa may indeed prove to be superficial, but the relationship of the *Rivineae* to *Microtea,* e.g. general habit, geographical location, and pollen morphology, is certainly much closer than to *Lophiocarpus.* The connection of the *Phytolaccaceae* to the *Chenopodiaceae* and *Amaranthaceae* is best illustrated by *Lophiocarpus* with its tendency towards succulence, reduction in stamen number, scarious bracts, habitat, etc.

Within the family, even within genera, e.g. *Phytolacca,* there exists a wide variability, from primitive to somewhat advanced characters. The primitive features include: alternate, simple, entire leaves; ± simple inflorescence types; an absence of a corolla not due to reduction; actinomorphic and perfect flowers; a tendency to many stamens irregularly deposited; superior ovary placement; separate and many carpels; and 3-colpate pollen. The more advanced characters observable in some groups include: reduction of carpel and stamen numbers, and loss, either physical or functional, of the androecium or gynoecium, leading to a dioecious condition. More rarely, a tendency to zygomorphy and inferior ovary position are present. Many more genera have advanced pollen types, i.e. pantoporate, 12-colpate and 15-colpate, and chromosome data for the family indicate many polyploid genera. As might be expected, there is not necessarily a correlation between advanced pollen morphology and advanced floral morphology, nor is there a correlation between the different evidences of advanced floral morphology, e.g. *Anisomeria* exhibits a tendency towards zygomorphy but is primitive in most other floral characters. In conclusion I consider the floral morphology on the whole as moderately primitive, but the pollen shows a wide range of variation from a primitive 3-colpate type, to more advanced types, 12-colpate, 15-colpate and pantoporate, which are well represented.

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Appendix

Materials and Methods for Preparing Slides of Pollen by Acetolysis (modified from Erdtman, 1952).

Dried anthers from large flowers or whole dried immature buds of small flowers were dissected and placed in centrifuged tubes and the following procedure was utilized.

1. To the centrifuge tube containing the flower material was added about 5 cc of a mixture 8 parts of acetic anhydride and 1 part concentrated sulfuric acid.

2. It was then heated in a water bath to 98°C for 2 minutes, with gentle stirring.

3. Material was cooled for about 5 minutes, centrifuged[5], and decanted.

[5]Speed and time of centrifugation will vary depending upon the size of the pollen; about 45 seconds at 1000 rpm were used here.

4. To the sediment was added 2-3 cc of 95% ethyl alcohol and sufficient water to fill approximately half the centrifuge tube.

5. The sediment was rinsed through a bronze filter, 200 mesh, then centrifuged, and decanted.

6. The sediment was rinsed twice more with tap water.

7. To the sediment was added about 10 drops of 50% glycerin for about 15 minutes.

8. Material was then centrifuged, decanted, and inverted on filter paper overnight or for 2 hours at 60°C.

9. Using a platinum needle, a small piece of glycerin jelly[6] was rotated in the sediment and placed on a slide.

10. The slide was placed on a warmer at about 80°C; when the jelly melted a cover slip was added, and melted paraffin then added at the cover slip edge, sealing all edges and removing all air.

11. Slides were cooled and excess paraffin removed with xylene.

INDEX OF LATIN NAMES

New taxa are in **boldface** type, all other taxa are in roman type; numbers in **boldface** type refer to descriptions, numbers in roman type refer to synonyms, numbers with dagger (†) refer to names incidentally mentioned.

[6]Glycerin jelly was prepared as follows: gelatin 50 gm, distilled water 175 ml, glycerin 150 ml, phenol (crystals) 7 gm, and heated until clear and stored in refrigerator.

TWO NEW SPECIES OF POLYGALA ENDEMIC TO PANAMA

BY WALTER H. LEWIS[1]
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ABSTRACT

Two species of *Polygala* belonging to the *Timutua* of Blake are described as new. *Polygala wurdackiana* and *P. jefensis* are endemic, respectively, to isolated and extremely rich Panamanian cloud forests at El Valle de Antón in the Province of Coclé and to Cerro Jefe in the Province of Panama.

Still another genus can be added to a long list now accumulating of species endemic either to El Valle de Antón, about 50 miles west of the Canal Zone in the Province of Coclé, or to Cerro Jefe, just east of the Zone in the Province of Panama (cf. Dwyer, Taxon **16:** 159, 1967). These and other cloud forests, largely from about 2500-3500 ft in elevation, apparently have been the sites of evolution of many taxa, following their isolation from the main North American cordillera, which now vacillates to sea level throughout the length of the isthmus. To the rich cloud forest floras are added two new species of *Polygala*, one to each area noted, and both closely allied yet quite unlike any others from the New World (for a full comparison with other Panamanian species, see the treatment of the *Polygalaceae* in the *Flora of Panama* by Lewis & MacBryde, Ann. Missouri Bot. Gard. **56**(1), 1969, in press).

Polygala **wurdackiana** W. H. Lewis, sp. nov.—Fig. 1A-D.

Inter species *Timutuae* Blake remote affinis *P. aparinoidi* Hooker et Arnott differt habitu suffrutescenti, foliis grandibus usque 3 cm latis, floribus albis pedicellis usque 3 mm longis, sepalis et petalis grandioribus, cristis 8-22 lobis vel furcatis, seminibus ovatis curvis 4 mm longis, arillis obovatis 2.5-3 mm longis.

Suffrutescent *perennials* to 1.3 m, branched above, often with 2-4 branchlets at a node, glabrous, angular, green. *Leaves* (2-)3-5 in whorls; petioles 4-10 mm long, glabrous; blades elliptic to less commonly ovate, basally somewhat attenuated, apically acute, the margins remotely crenate, glabrous, sparingly punctate, 4-7.5 cm long and 1.8-3 cm wide decreasing in size apically. *Inflorescences* terminal, racemose, glabrous, the axis elongating to ca 9 cm, the flowers loose; bracts ovate, glabrous, deciduous, 0.8-1 mm long. *Flowers* white, the pedicels to 3 mm long; outer sepals 3, marginally ciliate, the larger ovate, concave, 2.3-2.5 mm long, the smaller pair ovate to oblong, usually short-connate at the base, sometimes free, 1-1.5 mm long; inner sepals (wings) 2, obovate to oblong-elliptic, apically rounded, basally short-clawed, marginally ciliate, persistent, 3.2-3.8 mm long; petals 3, the keel 2.5-2.8 mm long with a crest 8-22 lobed (often irregularly forked and varying in size), the upper pair obovate, rounded, equaling the keel. *Capsules* widely oblong, glabrous, 4-5 mm long, 3.2-4 mm wide; seeds 2, ovate, 4 mm long,

[1]Supported by the Air Force Office of Scientific Research (Contract No. F44620-67-C-0055).

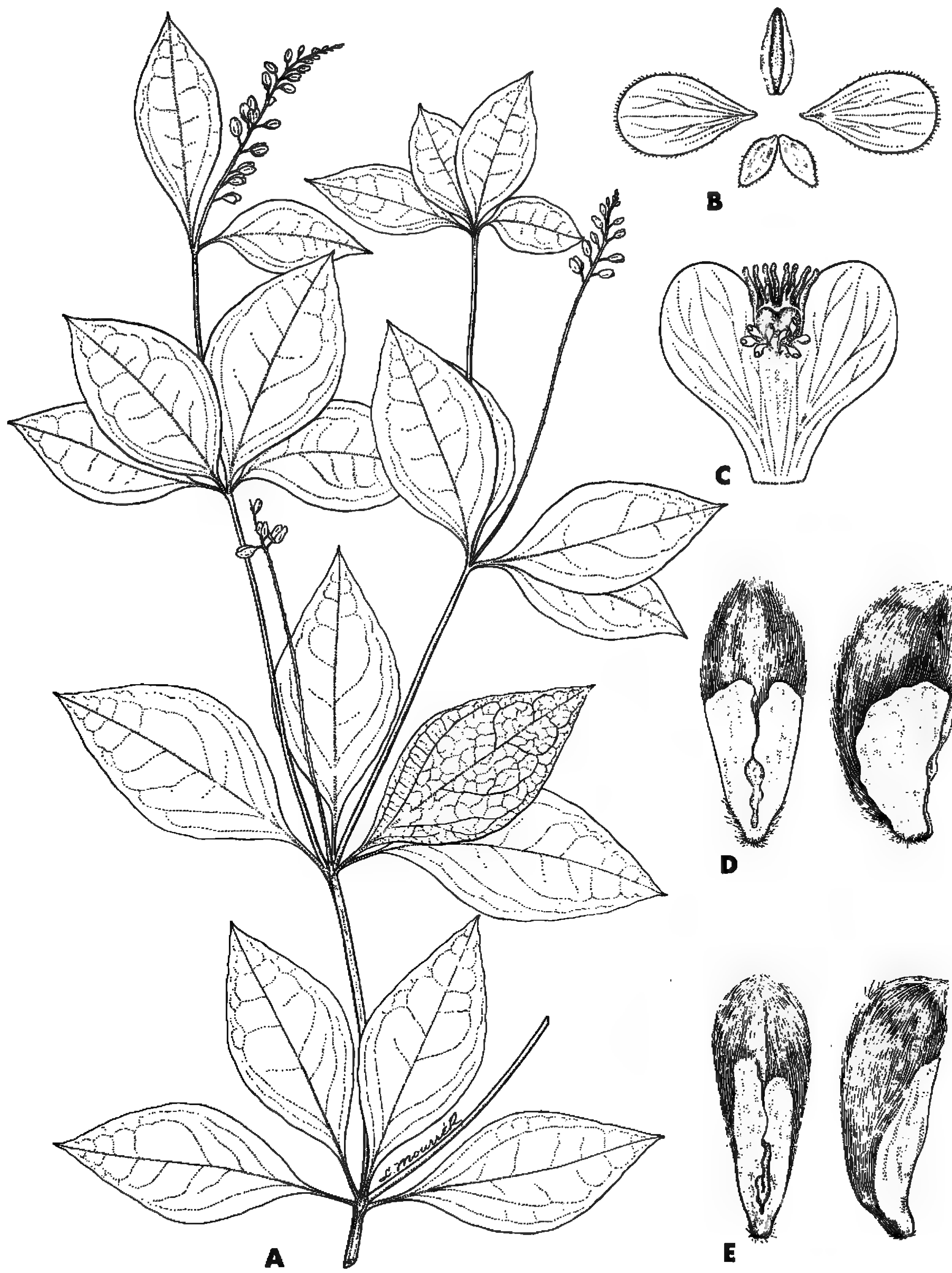

Fig. 1. *Polygala wurdackiana* W. H. Lewis (A-D) and *P. jefensis* W. H. Lewis (E). A. Habit, ×⅔. B. Three outer and two inner larger sepals (wings), ×5. C. Keel with crest of 12 lobes, upper paired petals and anthers, ×10. D. Seed of *P. wurdackiana* showing obovate aril, ×10. E. Seed of *P. jefensis* showing oblong aril, ×10. A-D after *Lewis et al. 1723* (MO); E after *Bouché s.n.* (MO).

densely pubescent with hairs copper colored at maturity; arils 2.5-3 mm long, the 2 lobes broadly obovate, appressed. *Pollen* ca 50μ (E) $\times$ 29μ (P), sexine smooth, 6-8 colporate, the colpi 33μ long, 5μ wide with thick nexinous regions 4μ wide between the colpi and thickening to 4μ equatorially where the nexine abruptly thins, synorate, the ora broad; after acetolysis grains readily shatter at the equator. *Flowering* Jan-May.

Apparently endemic to the cloud forest above 2500 ft in the vicinity of El Valle de Antón, Panama.

COCLÉ: Cerro Pajita, hills N of El Valle de Antón, 1000-1200 m, common, 7 Febr 1947, *Allen & Allen 4170* (MO); Cerro Caracoral (vic of El Valle de Antón), alt ca 1000 m, elfin forest, 19 Jan 1968, *Duke & Dwyer 15101* (MO, NY); mountains N of El Valle de Antón, alt 2500-3000 ft, cloud forest, 28 May 1967, *Lewis, MacBryde, Oliver & Ridgway 1723* (holotype MO, isotypes DUKE, K, UC, US).

Polygala wurdackiana is named for Dr. John J. Wurdack, Department of Botany, Smithsonian Institution, Washington, D. C., a student especially of South American members of the family.

Polygala **jefensis** W. H. Lewis, sp. nov.—Fig. 1E.

Polygala wurdackiana affinis sed differt laminis acuminatis et dense punctatis, sepalis parvioribus uterque praebens glanes grandiores binatas, arillis lobis oblongis.

Herb to shrub 2 m high (*Duke 9431*), branched above with 2-3 branchlets per node, glabrous, angular. *Leaves* 4-5 in whorls; petioles usually 4-7 mm long, glabrous; blades elliptic, somewhat attenuated basally, acuminate apically, the margins remotely crenate, glabrous, densely punctate, the more mature 4-5.5 cm long and 2-2.5 cm wide. *Inflorescences* terminal, racemose, glabrous, the axis to 7 cm long, the flowers ± loose; bracts ovate-lanceolate, ciliate, deciduous, 0.8-1 mm long. *Flowers* greenish white, the pedicels to 2 mm long; outer sepals 3, marginally ciliate, the larger ovate, concave, 2 mm long, the smaller pair ovate to oblong, 1 mm long, usually shortly connate at the base, each with 2 large glands; inner sepals (wings) 2, broadly obovate, apically rounded, basally short-clawed, persistent, marginally ciliate, 3.5 mm long, 2.5 mm wide; petals 3, the keel 3 mm long with a crest 6-20 lobed (mostly 6), the upper pair obovate, rounded, 3 mm long, glabrous. *Capsules* widely oblong to subglobose, glabrous, 4 mm long, 3-3.5 mm wide; seeds 2, ovate, curved, 4 mm long, pubescent with hairs copper colored at maturity; arils 2.8-3 mm long, the 2 lobes oblong, appressed. *Flowering* Jan-July.

Endemic to Cerro Jefe, Province of Panama; closely allied to *P. wurdackiana.*

PANAMA: Cerro Jefe, alt 3400 ft, *Bouché s.n.*, 31 Jan 1954 (holotype MO); *Duke 9431* (MO), 21 Jan 1967; alt 2700-3000 ft, *Tyson et al. 4397* (MO), 9 July 1966.

PSIDIUM (MYRTACEAE) IN THE GALAPAGOS ISLANDS[1]

BY DUNCAN M. PORTER
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ABSTRACT

The three insular taxa of *Psidium* are described, and a key to them is provided. The relationships of the endemic *Psidium galapageium* are discussed, and *P. galapageium* var. *howellii* is described as new.

In a survey of the Myrtaceae for the *Flora of the Galápagos Islands,* it has become increasingly obvious that three taxa of *Psidium* are present in the archipelago. The first is *P. guajava* L., the cultivated guava, which has escaped and become naturalized on several of the islands. The second is the endemic *P. galapageium* Hook. f., a common tree of the transition and *Scalesia* forests of the larger islands. The third proves to be an undescribed variety of *P. galapageium.* These three taxa may be distinguished by means of the following key:

a. Flowers ca 2.5 cm in diam, in 1(-3)-flowered dichasia; buds 7-10 mm long; leaves ovate to ovate-lanceolate, slightly inequilateral, 5-14 cm long, 2-6 cm wide, persistent .... 1. *P. guajava*
aa. Flowers ca 1-1.5 cm in diam, solitary; buds 4-5 mm long; leaves elliptic to ovate or occasionally suborbicular, equilateral, 1.8-5.5 cm long, 0.9-2.6 cm wide, deciduous.
  b. Buds unlobed, closed at anthesis except for a terminal pore, distally glabrous; calyx opening by a circumscissile calyptra .... 2a. *P. galapageium* var. *galapageium*
  bb. Buds 5-lobed apically, open at anthesis, tomentose; calyx splitting irregularly into 4 unequal lobes .... 2b. *P. galapageium* var. *howellii*

1. *Psidium guajava* L., Sp. Pl. 470, 1753.

Small trees to 8 m high; branchlets 4-angled to slightly 4-winged, inconspicuously punctate-glandular, tomentose with white or gray trichomes. *Leaves* opposite, ovate to ovate-lanceolate, slightly inequilateral, apex obtuse to apiculate, usually abruptly rounded or occasionally narrowed to an obtusely pointed or rounded tip, base abruptly rounded or obtuse, decurrent on petiole, inconspicuously punctate-glandular and thinly pubescent to glabrate above, thickly and more conspicuously punctate-glandular and tomentose beneath, especially on veins, main veins reddish and prominent beneath, impressed above, 5-14 cm long, 2-6 cm wide, persistent; petioles tomentose, 4-5 mm long. *Buds* tomentose, punctate-glandular, constricted below calyx, distal portion enlarged and ovoid to ellipsoid, apex acute, completely closed before anthesis, 7-10 mm long; bracteoles 2, subulate, tomentose, 2-2.5 mm long. *Flowers* on branches of recent growth, ca 2.5 cm in diam, in a 1(-3)-flowered dichasium, terminal flower sessile, laterals on tomentose pedicels 10-12 mm long; peduncles tomentose, 10-20 mm long; hypanthium tomentose, punctate-glandular, slightly constricted above ovary, 4-6

[1]Dr. Rogers McVaugh, University of Michigan, and Dr. Ira L. Wiggins, Stanford University, have both kindly read and commented on the manuscript for this paper. Field studies in the Galápagos Islands were accomplished under National Science Foundation Grant GB-5254, administered by the California Academy of Sciences, San Francisco.

mm long; calyx appressed-pubescent, basally punctate-glandular, at anthesis splitting irregularly into 4-5 lobes ca 1 cm long, whitish and sericeous within, persistent on fruit apex; petals 5, thin, delicate, broadly oval to elliptic, concave, 12-19 mm long, 6-10 mm wide, caducous; filaments white, spreading, longest as long as style; anthers versatile; style glabrous, 8-11 mm long; stigma capitate, slightly 2-lobed. *Berry* globose, glabrous, roughened with punctate glands, pale yellow and ca 2 cm in diam at maturity.

Citation of the complete synonomy for this species is impossible at present.

ISLA FLOREANA: wet meadow, rain forest E Floreana Peak, *Howell 8898* (CAS). ISLA SAN CRISTÓBAL: tree to 8 m, along Wreck Bay-El Progreso rd, *Wiggins & Porter 410* (CAS); nr village above Wreck Bay, *Willows s.n.*, 18 Apr 1932 (CAS). ISLA SANTA CRUZ: S outskirts Bella Vista, 490-500 ft, common to 1800 ft, *Wiggins & Porter 624* (CAS).

This native of tropical America is widely cultivated and has become naturalized throughout the tropics. In the Galápagos Islands it has escaped from cultivation and has become common in the more mesic forests on several of the larger islands.

2a. *Psidium galapageium* Hook. f. (Trans. Linn. Soc. **20:** 224, 1847) var. *galapageium.*

Small trees or shrubs, to 8 m high; trunk to ca 1 m in diam, bark smooth, pinkish-gray; branches divaricate; branchlets terete, gray, punctate-glandular, tomentose to lanate with reddish to white or yellowish trichomes, becoming glabrate, bark becoming stringy, ultimate branchlets and leaves sometimes covered with a scurfy reddish bloom. *Leaves* opposite, elliptic to ovate, equilateral, apex acute to acuminate, base narrowly cuneate, decurrent on petiole, drying flat and usually black above and paler beneath or sometimes reddish-brown, subcoriaceous, shortly appressed-pubescent to glabrate, except for sparingly pubescent reddish ± prominent midvein, both surfaces punctate-glandular, paler and more prominently so beneath, margins slightly revolute, 21-54 mm long, 9-26 mm wide, deciduous; petioles tomentose, flattened, slightly twisted, 1-3 mm long. *Buds* pyriform, punctate-glandular, contracted basally into a conic ± pubescent pseudostalk 1-1.5 mm long, distal portion subglobose and glabrous, apex obtuse, at anthesis closed except for a minute apical pore bearing some projecting trichomes, 4-5 mm long; bracteoles 2, linear, tomentose, 3-3.5 mm long, caducous. *Flowers* on branches of recent growth, ca 1-1.5 cm in diam, solitary; peduncles opposite, slightly curved, spreading, tomentose, 6-10 mm long; hypanthium slightly constricted above ovary, tomentose below constriction, punctate-glandular, ca 2 mm long; calyx calyptrate, circumscissile ca 1 mm above ovary summit, calptra glabrous, ± persistent by one side, pubescent and punctate-glandular within, calyx further splitting longitudinally into several segments following anthesis, forming a lobed persistent ring ca 1 mm high on fruit summit; petals 5, obovate, concave, 8-9 mm long, punctate-glandular, caducous; filaments filiform, white, spreading, to 4 mm long, inserted on tomentose punctate-glandular inner wall of hypanthium; anthers versatile, ovoid; ovary 3-loculed; style as long as stamens, lower ¾ pilose, base persistent; stigma capitate. *Berry* globose to subglobose, glabrous, roughened with punctate glands, yellow at maturity, drying black to reddish-brown, 6-13 mm in diam, pericarp 1 mm thick; seeds several per locule, angular, dark, ca 5 mm long, testa bony.

ISLA FERNANDINA: meadow on SW part of island, alt ca 300-310 m, *Hendrickson H-61* (DS). ISLA ISABELA: Iguana Cove, *Snodgrass & Heller 126* (DS, GH); bushes at 100 ft, low forest trees common at 350-600 ft, Villamil, *Stewart 3025* (CAS, GH, MO). ISLA PINTA: occas small trees, 500-1000 ft, SE side, *Stewart 3030* (CAS, GH). ISLA SAN SALVADOR: *Darwin s.n.*, Oct 1835 (CGE), *Scouler s.n.* (lectotype K), forest belt, 1000-1500 ft, *Ericsson s.n.*, 7 Sept 1947 (CAS); occas small trees, 350-2800 ft, James Bay, *Stewart 3029* (CAS); ridge leading to main peak at W end, nr NE end of James Bay, slender tree to 8 m, ca 300 m, *Wiggins & Porter 272* (CAS, MO), common second level tree among *Bursera*, ca 355 m, *Wiggins & Porter 273* (CAS, MO). ISLA SANTA CRUZ: lower part of forest belt, *Howell 9286* (CAS, GH); bushes at 300 ft, gradually increasing in size to 600 ft where abundant forest trees, Academy Bay, *Stewart 3028* (CAS); Transition Zone, among *Pisonia*, ca 70 m, Academy Bay-Bella Vista trail, *Itow 31* (DS); tree 6 m, Transition Zone, 100 m, "Old Trail" Academy Bay-Bella Vista, *Wiggins 18399* (DS, MO); small tree ca 6-8 m, Transition Zone, ca 50 m, "new road" Academy Bay-Bella Vista, *Wiggins 18760* (DS, MO); shrub or small tree, ca 200-300 m, El Chato, 15-18 km W Bella Vista, *Hendrickson H-38* (DS); above Fortuna, upper part forest belt, *Howell 9266B* (CAS), upper part *Scalesia* Zone, ca 420 m, *Itow 102* (DS).

Following his description of *Psidium galapageium*, Hooker (1847) cited both the Darwin and Scouler collection from Isla San Salvador. He did not indicate which was the type. Scouler's specimen is in bud, while that of Darwin bears mature fruits. The Scouler specimen is chosen as the lectotype, as it clearly exhibits the characters that differentiate var. *galapageium* from var. *howellii*. The two varieties are virtually indistinguishable in collections bearing only mature fruits.

The fruits of *Psidium galapageium*, like those of *P. guajava*, are edible. The label of *Ericsson*, 7 Sept 1947, bears the notation, "Fruits yellow, with a slight taste of turpentine; said to be poisonous, but I ate them and they did me no harm. Liked by birds. A goose we killed was full of them."

2b. *Psidium galapageium* var. **howellii** D. M. Porter, var. nov.

A var. *galapageio* gemmis 5-lobis apicibus et calycibus dehiscentes irregulariter in 4 segmentis differt.

Differing from var. *galapageium* in being shrubs or *small trees* 2-6 m high. *Leaves* elliptic to ovate, occasionally suborbicular, apex acute to acuminate or rarely obtuse or retuse, base obtuse to narrowly cuneate, usually decurrent on petiole, shortly appressed-pubescent, especially along midvein, sometimes becoming glabrate except for midvein, 18-55 mm long, 10-21 mm wide; petioles 2-3 mm long. *Buds* tomentose, more thickly so below, distal portion ovoid, apically 5-lobed, acute, open at maturity. *Flowers* ca 1 cm in diam; hypanthium tomentose; calyx open in bud, 5-lobed, lobes free in mature bud, tomentose, tomentose within, at anthesis irregularly splitting between 4 lobes into 4 persistent segments 2.5-3 mm long, 1 segment larger and terminated by 2 lobes; petals 4-5.5 mm long, ca 3 mm wide; filaments white, greenish basally, 4-5 mm long; style pilose basally. *Berry* drying reddish-brown, 8-11 mm in diam; seeds reddish-brown.

ISLA SAN CRISTÓBAL: common bushes & low trees, 150-400 ft, Wreck Bay, *Stewart 3026* (CAS, GH, MO); tree 5-6 m, impt in forest betw Wreck Bay & El Progreso, *Wiggins & Porter 370* (CAS, MO); shrub 2 m, forest ca 3.5 km above Wreck Bay along rd to El

Progreso, *Wiggins & Porter 398* (holotype MO, isotype CAS). ISLA SANTA CRUZ: shrub 8-9 ft, in forest with *Scalesia & Psidium* dominant, 6 mi NW Academy Bay, *Taylor TT46* (CAS).

This endemic variety is named for Mr. John Thomas Howell, recently retired Curator of the Department of Botany, California Academy of Sciences, indefatigable collector of the Galápagos flora.

The character of a circumscissile versus an irregularly dehiscent calyx is exceedingly variable in *Psidium*, even within individual species (Amshoff, 1956; McVaugh, 1963a, b). However, in the case of *P. galapageium*, this character does not appear to vary within the different populations on separate islands. Specimens from Isla San Cristóbal have lobed calyces; those from the islands of Fernandina, Isabela, Pinta, San Salvador, and Santa Cruz (with one exception) have calyptrate calyces. The two varieties are allopatric in distribution, except for the collection of *P. galapageium* var. *howellii* known from Isla Santa Cruz (*Taylor TT46*). The label of this specimen bears the notation, "Perhaps a shrubby form of *Ps. galapageium*, a common tree in the forest." Thus, the two varieties may prove to differ in habit as well as in the morphology and dehiscence of the calyx and the pubescence of the buds and leaves. Further field study is needed to ascertain the biological and ecological relationships between the varieties in this area where they are geographically sympatric.

Johnston (1931) indicated that certain populations of *Psidium* on Socorro Island, off western Mexico, were doubtfully referable to *P. galapageium*. Others were referred to a new species, *P. soccorense* Johnst. Stebbins (1966, p. 49) has ventured the opinion that, "In many respects the Galápagos *P. galapageium* appears to me to be as similar to the widespread tropical American *P. sartorianum* (Berg) Ndzu. as to the plant from the Revillagigedos, while the latter bears a considerable resemblance to *P. salutare* (H.B.K.) Berg, of southern Mexico." *Psidium sartoranium* is found in forests and savannas below 1500 m from Mexico to northern Colombia and Venezuela, while *P. salutare* occurs in savannas below 1000 m from Mexico to the Guianas (McVaugh, 1963a, b). McVaugh (pers. comm.), however, indicates that both the Galápagos Islands and Socorro Island collections show close affinities with *P. sartorianum*, perhaps representing insular populations of the later. *Psidium salutare* is a very different species, showing no close relationships to these insular populations. This whole complex is badly in need of taxonomic revision.

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A REVISION OF THE PANAMANIAN SPECIES OF RONDELETIA (RUBIACEAE)[1]

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ABSTRACT

A key to and descriptions of the Panamanian taxa of *Rondeletia* are given; two new taxa are described.

INTRODUCTION

The genus *Rondeletia* was first described by Plumier (1703) and named in honor of the physician Gulliaume Rondelet of Montpellier, and it was subsequently taken up by Linnaeus (1753). Several other generic names were introduced after this.

Planchon (1849) divided *Rondeletia* into three genera, creating two new ones, *Rogiera* and *Arachnothryx*. He based the separation principally on the condition of the orifice of the corolla and the number of floral limbs. *Rondeletia* was 5-merous with an annular callosity at the orifice of the corolla, *Rogiera* was 5-merous with the orifice of the corolla yellow-bearded, and *Arachnothryx* was 4-merous with the orifice of the corolla nude and the indumentum generally arachnoid-tomentose.

Hooker (1873) reduced *Rogiera* to synonymy under *Rondeletia* and made *Arachnothryx* a section of the genus. Schumann (1891) followed his lead. Standley (1918), in his revision of *Rondeletia* in North America, reduced both genera to synonymy, establishing the generic limits that have been accepted to the present. Steyermark (1967) resurrected *Arachnothryx* and transferred many South American species into it. He did not consider the species from Central America, Mexico, or the West Indies, which seem to form the major evolutionary centers of the genus. To evaluate the situation properly, it is essential that the species in these areas be studied critically.

Since Standley's revision of the genus for North America, six new species of *Rondeletia* have been described from Panama, three by Standley and three by Dwyer & Hayden.

FLORAL AND FRUIT MORPHOLOGY

The flowers provide the majority of the diagnostic characters. The number of floral limbs can be important, but it must be used with caution due to the

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[1] Rewritten portion of a thesis submitted to the Department of Biology and Graduate School of Saint Louis University in partial fulfillment of the requirements for the degree Master of Science (research).

[2] I wish to express appreciation to the Society of the Sigma XI for their support, in part, of the field work that went into the preparation of this paper. I also wish to thank the curators of the herbaria at A, ECON, F, GH, MO, NY, US and Y who furnished specimens for study or who aided in other ways, and I am deeply grateful to the Missouri Botanical Garden for the privilege of using its herbarium, library and other facilities.

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variability in the number of limbs. The calyx lobes are the most valuable character at the specific level in Panama. They are extremely variable between species in size and shape and are stable enough within the species to make adequate specific determinations. The corolla is also used at both group and specific levels based on its indumentum, length, condition of the orifice, and number of limbs. Heterostyly has been found in one taxon from Panama, *R. salicifolia* Dwyer & Hayden subsp. *salicifolia*. Presumably it is rare in the genus, although readily occurring throughout the rest of the family without regard to phylogenetic relationships (Vuilleumier, 1967). The placenta shape is variable enough to separate some taxa and show relationships.

The mature fruit is one of the principal characters for generic determination. The shape and dehiscence are used at the group level, but at the specific level the fruit is of little use across the full range of the genus, although it has practical value in a key to the Panamanian species. It appears that the morphology of the ovules or seeds might be useful at the group level; they are either winged at one or both ends, or not winged.

Discussion

Rondeletia is confined to the neotropics except for several species reported from the Himalayas. The two main evolutionary and distributional areas of the genus are Mexico-Central America and the West Indies. There is also a smaller center in northern South America. Panama is at the edges of the Mexico-Central American and the South American complexes having affinities with both.

The Panamanian species fall into two general phylogenetic patterns: 1) those species which while obviously related, as evidenced by morphological characters, represent the products of strongly divergent evolutionary lines; 2) a group of endemics whose close phylogenetic inter-relationships are currently extremely difficult to determine. Except for their calycine lobation, these endemics, viz. *R. salicifolia, R. cooperi, R. secunda, R. bertieroides,* and *R. platysepala,* are difficult to delimit as species. They exhibit certain similarities of structure in the following characters: 4-merous condition, septicidal capsules (*R. secunda* excepted), fruits up to 4 mm in diameter, corolla naked at the throat, ovules not winged, and one or more calyx lobes expanded.

The remaining seven Panamanian species of *Rondeletia* fall into the former phylogenetic pattern. Even *R. odorata* var. *breviflora, R. hamelifolia,* and *R. panamensis,* presumably closely related, show strong divergence in certain features: amount of pubescence, type of leaf, type of inflorescence, length of the calyx lobes, length of the corolla tube, shape of the fruit, and appendages on the ovules. In the Panamanian members of the genus, it is this type of divergence which allows the taxonomist to easily segregate these taxa as species. A world revision of *Rondeletia* may permit a more critical evaluation of the strength of these characters at the species level[3].

[3] The need for an overall monograph of this large genus and related taxa is obvious; what this study emphasizes first, however, is the necessity for major collecting particularly at higher elevations so that some understanding of the variation of *species* populations is possible.—*Editor.*

In his recent South American revision of *Rondeletia,* Steyermark (1967) resurrected the genus *Arachnothryx* Planchon. He effectively divided the species formerly assigned to *Rondeletia* between *Rondeletia* (12 species) and *Arachnothryx* (21 species). Because his generic key is so important in modern *Rondeletia* research, it is given below:

"Capsule loculicidally dehiscent; seeds fusiform, winged, caudate at one or both ends, the testa shallowly reticulate with elongated cells; orifice of corolla with a conspicuous thickened annular callosity; tube of corolla glabrous within; corolla-lobes 5; calyx-lobes 5; disk densely hirsutulous, projecting above the sinus at the base of the calyx-lobes, the calyx-tube not developed or obsolete; stipule inconspicuous, triangular or deltoid; pubescence of hypanthium, outer surface of corolla, or vegetative parts usually not pannose nor arachnoid-pubescent.
Rondeletia.

Capsule septicidally dehiscent; seeds rhomboidal to triangular, compressed, not winged nor caudate, the testa deeply foveolate and rugulose thickened with sunken pentagonal or hexagonal cells; orifice of corolla naked, without a thickened callosity; tube of corolla pubescent within in basal portion; corolla-lobes 4; calyx-lobes 4; disk usually glabrous, sunken below sinus at the base of the calyx-lobes, the calyx-tube obviously manifest; stipule conspicuously developed, oblong or oblong-lanceolate; pubescence of hypanthium or vegetative parts usually pannose or arachnoid-pubescent.
Arachnothrix."

This key effectively deals with the species of *Rondeletia* in South America, but is open to criticism in the case of the Panamanian species. *Rondeletia secunda* matches the key for *Arachnothryx* except that it has loculicidally dehiscent fruit. Also, the key is not effective in separating those species which are bearded in the throat of the corolla such as *R. amoena* and *R. dukei.*

SYSTEMATIC TREATMENT

Rondeletia L., Sp. Pl. 172, 1753.

Petesia P. Br., Hist. Jamaica, 143, *tab.* 2 & 3, 1756.
Lightfootia Schreb., Gen. 122, 1789, non L'Her. (Sert. Angl. *t. 4,* 1788).
Willdenovia J. F. Gmel., Syst. **2:** 362, 1791, non Thunb. (Vet. Akad. Handl. Stock. **11:** 26, *t.* 2, 1790).
Arachnimorpha Desv. in Hamilt., Prodr. 28, 1825.
Rogiera Planchon, Fl. Serres **5:** 442, 1849.
Arachnothryx Planchon, loc. cit.

Shrubs or trees, the branchlets terete or angular. *Stipules* interpetiolar, variable in length and width, rostrate, acute, acuminate, obtuse or cuspidate at the apex, entire or very rarely bilobate, usually persistent, erect or rarely reflexed. *Leaves* opposite, simple, sessile to pedicellate, the blade ovate, elliptic, obovate, oblong, or very rarely circular, obtuse, acute or acuminate at the apex, variable at the base, the venation pinnate with the secondary veins arcuate, anastomosing near the margin of the leaf, very rarely bullate between the secondary veins, tertiary veins running at right angles to the secondary veins or open reticulate, pubescent to glabrous above, densely pubescent to glabrous and the midrib and secondary veins generally raised beneath, entire, very rarely revolute at the margin, coriaceous, chartaceous or membranaceous. *Inflorescences* terminal or axillary, commonly paniculate, rarely thyrsoid or of compound dichasia or racemose or spike-like, pedunculate. *Flowers* pedicellate to sessile; hypanthium rotund or oblong, with an annular disk; calyx-lobes 4-6(-7) often unequal, sometimes foliaceous, often basally connate, variable in length and width; corolla with the tube usually slender, variable in length, the throat bare, bearded or with an annular callosity, the 4-6 lobes usually spreading, obtuse, imbricate in the bud; stamens 4-6, alternate with the corolla-lobes, variably attached in the tube, the filaments sometimes of variable length, the anthers oblong, dorsifixed, introrse, with 4 thecae, included or rarely excluded; style rarely variable in length; stigma bilobate or very rarely trilobate; ovary 2- or very rarely 3-loculate, the septum fully fused or rarely incompletely fused; placenta axile, polymorphic interspecifically; ovules many. *Fruit* a capsule, globose or rotund or rarely transverse elliptic or ovoid, 2-celled, loculicidally or septicidally bivalvate, the valves often bipartite, the seeds many, minute, sometimes winged at one end or at both ends.

Key to the Panamanian Species of Rondeletia

a. Leaves coriaceous. bullate, the margin revolute .... 1. *R. odorata* var. *breviflora*

aa. Leaves subcoriaceous, chartaceous, or membranaceous, non-bullate, the margin not revolute.

  b. Leaves with the lower surface with a dense whitish- or grayish-indumentum.

    c. Leaves densely grayish arachnoid-tomentose beneath; inflorescence a few-flowered modified thyrse, 4-5 cm long; calyx-lobes lanceolate, 10-13 mm long .... 2. *R. darienensis*

    cc. Leaves densely white-tomentose beneath; inflorescence racemose, 2.5-32 cm long; calyx-lobes triangular or oblong, 0.5-1.7 mm long .... 3. *R. buddleioides*

  bb. Leaves with the lower surface with a moderate to sparse indumentum, glabrate, or glabrous.

    d. Stipules reflexed; leaves subcoriaceous; corolla-tube densely yellow-pilose in the throat .... 4. *R. amoena*

    dd. Stipules erect; leaves chartaceous or membranaceous; corolla-tube never yellow-pilose in the throat.

      e. Flowers 4-merous; mature capsule to 4 mm in diam, septicidal (except *R. secunda*); seeds rectangular.

        f. One calyx-lobe 2 or more times longer than the other 3 lobes; capsule globose, rotund or ovoid, costate or rugose, sparsely strigose, glabrate or glabrous.

          g. Large calyx lobe 6-11.5 mm long, 3.5-6.5 mm wide, capsule globose, costate, glabrate when mature .... 5. *R. salicifolia*

          gg. Large calyx-lobe 2-7.4 mm long, 0.7-2.2 mm wide; capsule globose, rotund, or ovoid, costate or rugose, sparsely strigose or glabrous.

            h. Hypanthium densely strigose; capsule ovoid, costate, sparsely strigose .... 6. *R. cooperi*

            hh. Hypanthium arachnoid-tomentose; capsule globose or rotund, costate or rugose, glabrous.

              i. Small calyx-lobes linear or narrowly oblong, 1.7-4 mm long, 0.2-0.6 mm wide; capsule rotund, rugose when mature, glabrous, loculicidal .... 7. *R. secunda*

              ii. Small calyx-lobes triangular to broadly triangular or oblong, 0.3-1.8 mm long, 0.5-0.9 mm wide; capsule globose, costate, glabrous, septicidal .... 8. *R. bertieroides*

        ff. Calyx-lobes ca equal in length; (fruit not known) .... 9. *R. platysepala*

      ee. Flowers 5-merous or 5- & 6-merous; mature capsule (not seen for *R. dukei*) 8-10 mm in diam, loculicidal; seeds winged.

j. All calyx-lobes on the inflorescence 1-9.5 mm long; annular callosity at the orifice of the corolla; placenta hemispherical.
  k. Calyx-lobes 5 or 6, 1-2 mm long; corolla-tube 6-9 mm long; capsule transversely elliptic in radial section ....10. *R. hamelifolia*
  kk. Calyx-lobes 5, ca 8.5 mm long; corolla-tube 13-18 mm long; capsule globose ....11. *R. panamensis*
jj. Several calyx-lobes on the inflorescence to 3.8 cm long; no annular callosity at the orifice of the corolla; placenta oblong ....12. *R. dukei*

1. *Rondeletia odorata* Jacquin var. *breviflora* Hooker, Curtis Bot. Mag. *tab. 6350,* 1878.

Shrub with the branchlets terete, the younger portions ferrugineous-hirsute, the older portions brown and glabrous. *Stipules* broadly triangular with a rostrate apex, 2.2-3.9 mm long, 1.3-4 mm wide. *Leaves* sessile or subsessile, the petioles to 2 mm long; blade subovate to elliptic or subobovate, 1.8-4.7 cm long, 1-2.8 cm wide, subacute at the apex, subcordate at the base, coriaceous, densely scabrous above when young, sparsely scabrous above when older, bullate between the secondary veins, sparsely hirsute on the veins and the midrib and secondary veins prominently raised beneath, the tertiary veins open-reticulate, the margin revolute. *Inflorscences* terminal, contracted thyrses, 1-2.2 cm long, the floriferous portion of the axes with 2 basal foliar bracts 3-8 mm long and 2.5-5 mm wide; peduncles 3.2-7 mm long; axes ferrugineous-hirsute. *Flowers* pedicellate, the pedicels ca 2 mm long, with a linear bractlet to 4 mm long and ca 0.5 mm wide; hypanthium ferrugineous-tomentose, rotund, ca 2 mm long, the disk ca 1 mm in diam, sparsely puberulent; calyx-lobes 6, narrowly oblong, ca 4 mm long, ca 1 mm wide, very sparsely tomentose outside, glabrous inside; corolla bright red, the tube 5 to 7 mm long, very sparsely tomentose outside, glabrous inside, the 5 lobes obtuse, ca 2.5 mm long, with an annular callosity at the orifice of the corolla, ca 0.4 mm thick; stamens 5, the filaments ca 1 mm long, attached at the middle of the tube, the anthers oblong, ca 2 mm long; stigma bilobate or trilobate, the style thick and glabrous; ovary 2- or 3-loculate, as indicated by the stigma; placenta obovate, ca 1.3 mm long, ca 1 mm wide, with rectangular ovules. *Fruits* not seen.

CANAL ZONE: Matachin to Las Cascadas, *Cowell 359* (NY).

This variety is confined to Cuba, except for one collection from the Canal Zone. It is odd that it has not been recollected in the Canal Zone, one of the most thoroughly collected areas in Panama.

2. *Rondeletia darienensis* Standley, N. Amer. Fl. **32:** 53, 1918.

Branchlets terete, arachnoid-tomentose when young. *Stipules* narrowly ovate, 7-8 mm long, 1.5-2.5 mm wide, with a sheathing base 5-6 mm wide, abaxially glabrous, adaxially tomentose along the margin and sericeous in the center, the sheathing base tomentose when young. *Leaves* with the petioles 3-18 mm long, arachnose when young; blade elliptic or narrowly ovate, 7.5-17 cm long, 2.5-7 cm wide, acuminate at the apex, cuneate or obtuse at the base, densely grayish arachnoid-tomentose and the midrib and secondary veins raised beneath, the tertiary veins running at right angles to the secondary veins. *Inflorescences* axillary, modified thyrses, 4-5 cm long, few-flowered, subtended by 2 bracts 3-4 mm long; peduncle 1-1.5 cm long, sparsely arachnoid-tomentose. *Flowers* 4-merous, with 1 or 2 bractlets, pedicellate, the pedicels densely white-arachnoid-tomentose, 1-11 mm long; hypanthium densely white-tomentose, oblong, ca 3 mm long, ca 2 mm wide; calyx-lobes lanceolate, 1-1.3 cm long, 0.2-0.4 cm wide, acute at the apex, arachnoid-tomentose outside, glabrous inside, with 3 parallel veins; corolla (fide Pittier) with the tube 15 mm long, white-woolly-tomentose on the outside, yellow in the throat, the lobes rounded, irregular, ± 5 mm long; stamens (fide Pittier) attached in the upper ½ of the tube. *Capsules* (fide Standley) ca 4 mm long.

DARIEN: Boca de Paurando, on Sambu River, S Darien, alt 20 m, *Pittier 5684* (holotype US, isotype F).

The inflorescence is a modified thyrse composed of three dichasia of which two flowers have been lost from each of the basal dichasia. This species is distinguished by all four calyx-lobes, not just one being expanded, with the lobes lanceolate and 1-1.3 cm long; in addition the under surface of the leaves is densely grayish arachnoid-tomentose. It is known only from the type collection.

3. *Rondeletia buddleioides* Bentham, Pl. Hartw. 69, 1840.—Fig. 1.

Arachnothryx buddleioides (Bentham) Planchon, Fl. Serres **5**: 442, 1849.
Rondeletia affinis Hemsley, Diag. Pl. Nov. 28, 1879.

Tree or shrub to 15 m high with trunk diam to 15 cm, the branchlets terete or angular, terminally white-tomentose, the older portions brown and glabrous. *Stipules* erect, oblong to narrowly oblong to linear or rarely ovate to broadly ovate to ovate at the base and triangular at the apex, 4-10 mm long, 0.5-5 mm wide. *Leaves* with the petioles 0.3-2 cm long, the younger white-tomentose, the older glabrous; blade ovate to elliptic or obovate, 2.5-21 cm long, 1-7 cm wide, acute to abruptly acuminate at the apex, subobtuse to cuneate or attenuate at the base, sparsely arachnoid-tomentose when young but soon glabrous and asperous or non-asperous above, densely white-tomentose and the midrib raised beneath, the tertiary veins running at right angles to the secondary veins. *Inflorescences* terminal and pseudo-axillary, racemose with equally pedunculate cymules or helicoid-cymules, 2.5-32 cm long; peduncle 0.4-8.5 cm long; main axes densely white-tomentose when young, but soon glabrous. *Flowers* sessile or subsessile, 4-merous; hypanthium densely white arachnoid-tomentose, rotund, 1-1.5 mm long, the disk ca 0.1 mm thick, 0.2-0.6 mm in diam, glabrous; calyx-lobes equal or unequal, basally connate for ca 0.5 mm, triangular or oblong, 0.5-1.7 mm long, ca 0.7 mm wide, reflexed at maturity; corolla with the tube 6-11 mm long, arachnose outside, the basal ½ sparsely villous inside, the lobes 2-3 mm long and wide, irregularly shaped, arachnoid-tomentose outside, papillate inside; stamens subsessile, attached above the indumentum, the anthers oblong, ca 1.5 mm long; placenta obovate, rarely elliptic, 0.5-0.9 mm long, 0.5-0.7 mm wide, with rectangular ovules. *Capsules* oblong-globose, 3-4 mm long, sparsely tomentose when mature, septicidal.

This is a mountainous species found about 300 m growing in cloud forest. So far, it has been collected on the Pacific slope from Chiriquí to east of the Canal Zone and on the Atlantic slope in Bocas del Toro. It probably will be found along

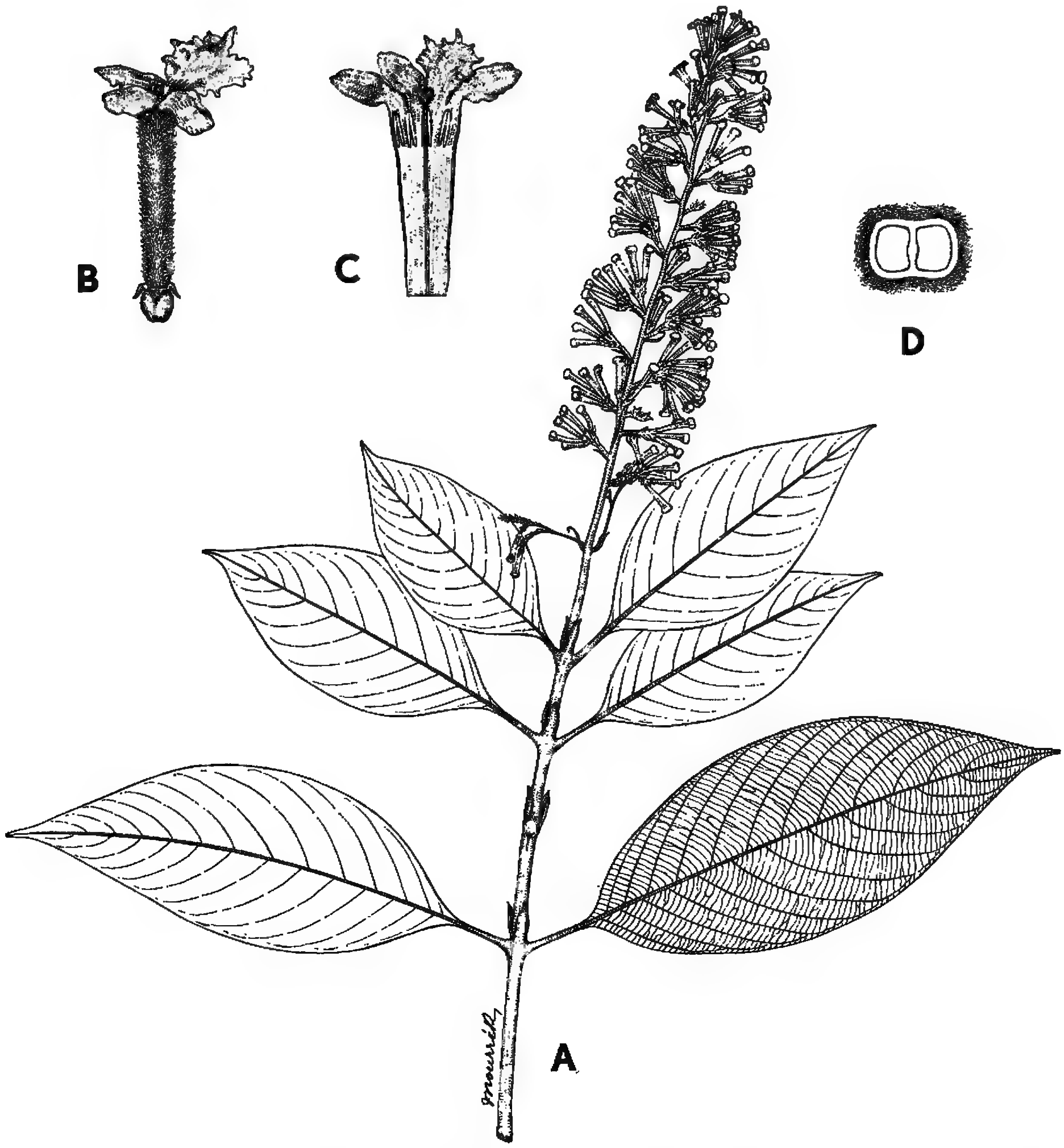

Fig. 1. *Rondeletia buddleioides* Bentham: A, flowering branch (×½); B, flower (ca×2½); C, opened corolla-tube (ca×2½); D, ovary cross section with placenta and ovules omitted (ca×10).

the entire corresponding Atlantic slope also. It ranges from east of the Canal Zone to Mexico, and, judging from the number of collections, is as common at higher elevations across its entire range as it is in Panama.

The isotypes collected in Mexico and deposited in the New York Botanical Garden differ from the Panamanian collections in leaf size, stipule shape, and the length of the peduncles of the cymules. Certain collections from the entire range of the speices also show a great deal of variation. A representative sampling of the species across its entire range is necessary before it will be possible to understand its variation and consequent taxonomic ramifications.

The stem bearing a terminal fruiting inflorescence shows at the time of fruit dehiscence, at the uppermost node, a short branchlet from an axillary bud of several nodes. This eventually develops into a full-size terminal inflorescence. I have used the term pseudo-axillary to describe it.

This species is represented in Panama by two varieties:

a. Upper surface of the leaf blade non-asperous .... var. *buddleioides*
aa. Upper surface of the leaf blade asperous .... var. *aspera*

3a. *Rondeletia buddleioides* var. *buddleioides.*

CHIRIQUÍ: rocky plains ca 5 mi S of Boquete, *Allen 4699* (F); elevated gravel benches 1 mi SW of Boquete, *Allen 4718* (F); Finca Lérida, *Allen 4753* (MO), *Woodson & Schery 222* (F, GH, MO); Bajo Mono-Robalo Trail, *Allen 4785* (F, NY), *4829* (F); Finca Collins, *Blum & Dwyer 2423A* (MO), *Ebinger 717* (MO), *Stern et al. 1128* (GH, MO, US), *2037* (MO), *2044* (MO); Bajo Charro, *Davidson 231* (A, F, MO, US); Volcán de Chiriquí, *Davidson 918* (A, F, MO, US); Boquete, *Davidson 1060* (A, F, MO, US), *Dwyer 6955* (MO), *7004* (MO); Cerro Horqueta, *Dwyer et al. 551* (GH, MO, US), *von Hagen & von Hagen 2151* (MO), *Kirkbride 155* (MO, NY); Llanos Francia, *Dwyer & Hayden 7592* (MO), *Stern et al. 1199* (GH, MO); 1.5 mi from Boquete towards David, *Dwyer & Hayden 7626* (MO); nr Pinola on the Chiriquí Trail, *Kirkbride & Duke 864* (MO, NY); betw Pinola & Quebrada Hondo on the Chiriquí Trail, *Kirkbride & Duke 905* (MO); betw Pinola & Quebrada Seco on the Chiriquí Trail, *Kirkbride & Duke 1023* (MO, NY); valley of the upper Río Chiriquí Viejo, *Seibert 240* (A, F, NY), *White & White 28* (A, F, MO, NY), *30* (A, F, MO, NY); Callejon Seco, *Woodson & Schery 493* (F, GH, MO); Casita Alta, *Woodson et al. 885* (A, F, NY), *930* (A, F, NY). COCLÉ: betw Cerro Pilón & El Valle de Antón, *Duke & Dwyer 13945* (GH, MO, US); betw Las Margaritas & El Valle, *Woodson et al. 1280* (F, MO, NY), *1757* (A, F, MO, NY). PANAMA: Cerro Campana, *Allen 2650* (MO, US), *Duke 8680* (MO), *Dwyer & Kirkbride 7814* (MO), *Lewis et al. 1912* (GH, MO, US), *McDaniel 6812* (MO); Cerro Azul, *Dwyer 1495* (F), *1880* (MO, US), *2069* (MO), *Ebinger 394* (MO); Fort Sherman, Piña Highlands, *Hayden 120* (MO); Cerro Azul to Cerro Jefe, *Tyson et al. 4328* (MO).

3b. *Rondeletia buddleioides* var. **aspera** Kirkbride, var. nov.

Differt a var. *buddleioide* superficie laminae folii aspera.

BOCAS DEL TORO: Buena Vista Camp on the Chiriquí Trail, alt 1000 m, *Cooper 615* (F, NY, Y); betw Criollo (just above Buena Vista) & Quebrada Higueron on the Chiriquí Trail, *Kirkbride & Duke 780* (holotype MO, isotype NY), *796* (MO, NY).

Standley placed the first collection of this taxon, made by G. Proctor Cooper, in *R. buddleioides* Bentham. It has only very immature floral buds and Thomas A. Sprague of Kew (in correspondence with S. J. Record) challenged this specific identification. My recent collection, which bears fruit and more mature floral buds, leaves no doubt that it belongs to *Rondeletia.* Inflorescence, floral, foliar, and stipule characters place it in *R. buddleioides,* but the asperous condition of the upper leaf surface warrants establishing it as a separate variety.

A population of eight to ten trees, to 30 m high with a 3-10 cm diam, is located on the Chiriquí Trail just above Buena Vista. The diagnostic character of the new variety, the asperous leaf-surface, is obvious in the field.

4. *Rondeletia amoena* (Planchon) Hemsley, Diag. Pl. Nov. 26, 1879.—Fig. 2.

Rogiera amoena Planchon, Fl. Serres **5**: 442, 1849.
R. *menechma* Planchon, loc. cit.
Rondeletia versicolor J. Smith, Bot. Mag. *tab. 4579,* 1851.
R. latifolia Oersted, Kjoeb. Vidensk. Meddel. **1852**: 43, 1852.
R. rugosa Bentham ex Oersted, loc. cit.

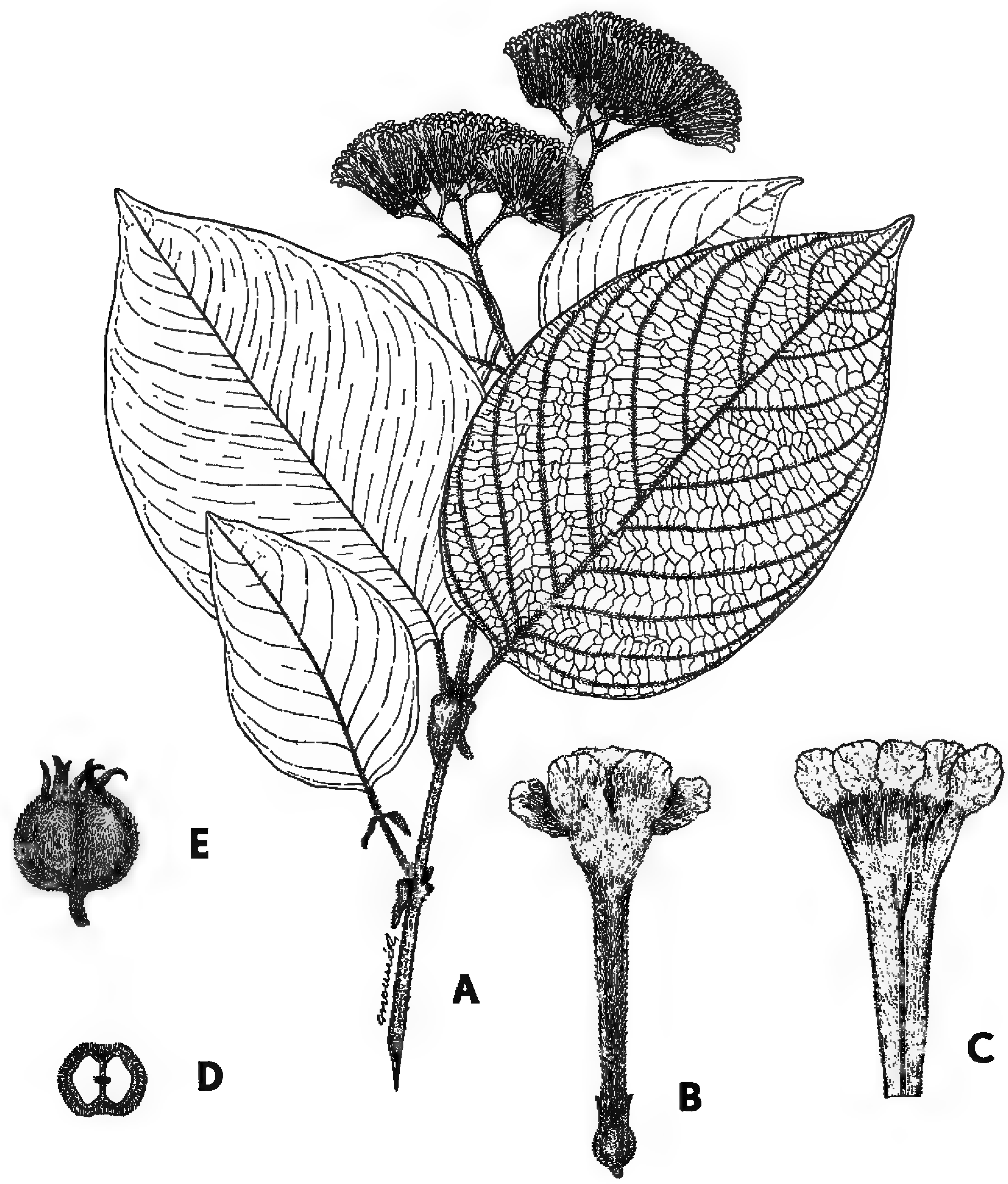

Fig. 2. *Rondeletia amoena* (Planchon) Hemsley: A, flowering branch (×½); B, flower (ca×2); C, opened corolla (ca×2); D, ovary cross section with placenta and ovules omitted (ca×3½); E, immature fruit (ca×2).

Rogiera latifolia Decaisne, Rev. Hort. sér. 4, **2**: 121, 1853.
R. versicolor Lindley & Paxton, Fl. Gard. **2**: 69, 1853.
Rondeletia schumanniana K. Krause, Bot. Jahrb. **40**: 315, 1908.

Shrub or tree to 14 m high and 10 cm in diam, the branchlets terete, terminally ferrugineous-pilose, the older portions brown and glabrous. *Stipules* reflexed, triangular to broadly triangular, 4-17 mm long, 3-10 mm wide, obtuse at the apex, sericeous outside, sericeous or puberulous along the edge and glabrous in the center on the inside. *Leaves* with the petioles 3-18 mm long, ferrugineous-pilose when young but soon brown and glabrous; blade subovate to elliptic or very rarely circular, 5.5-20 cm long, 2.7-12.8 cm wide, acute to abruptly acuminate at the apex, obtuse, subtruncate, or subcordate at the base, subcoriaceous, the midrib and secondary veins above with the pubescence strigose and the intercostal areas with a sparsely strigose pubescence or glabrous, the midrib and secondary veins beneath with the pubescence sericeous or strigose and the intercostal areas sparsely pilose or glabrate, the midrib and secondary veins prominently raised beneath, the tertiary veins open-reticulate. *Inflorescences* terminal and axillary, paniculate, 3.5-16 cm long, ca as broad or broader than long; peduncle 1.5-8.5 cm long; floral axes ferrugineous-pilose, the mature fruiting axes glabrate. *Flowers* with several bractlets, sessile or subsessile, the pedicels white-velutinous, 1-2 mm long; hypanthium densely ferrugineous- or white-tomentose, rotund, ca 2 mm long, the disk ca 0.1 mm thick, ca 0.7 mm in diam, glabrous; calyx-lobes 5-6(-7), unequal, basally connate for ca 0.5 mm, broadly triangular to triangular-oblong, 0.5 mm long, 0.25-0.75 mm wide; corolla with the tube 9-14 mm long, tomentose on the outside, densely yellow-pilose in the throat, with the hairs septate, glandular-pubescent below inside, the lobes 5-6, obtuse, 2-3.5 mm long, sparsely tomentose outside, glabrous inside; stamens attached at ca the middle of the tube, the filaments 1.5-2.5 mm long, the anthers oblong, ca 2 mm long; placenta hemispherical, ca 1.5 mm in diam, with many winged ovules. *Capsules* broadly transverse to transverse elliptic, to 6 mm in diam, tomentose when young, very sparsely tomentose or glabrate when mature, loculicidal.

CHIRIQUÍ: llanos on slopes of Volcán de Chiriquí Viejo & along Río Chiriquí Viejo, *Allen 994* (GH, MO); "New Switzerland," *Allen 1350* (F, GH, MO, NY, US); Llano del Volcán, *Allen 3469* (MO); N forested face of Cerro Copete, *Allen 4866* (MO); Finca Collins, *Blum & Dwyer 2553* (MO), *Dwyer & Hayden 7669* (MO), *Stern et al. 2002* (MO); Bajo Mono, *Davidson 471* (F); Volcán de Chiriquí, *Davidson 951* (A, F, MO, US); Cerro Horqueta, *Duke et al. 13650* (MO); betw Pinola & Quebrada Seco on the Chiriquí Trail, *Kirkbride & Duke 1026* (MO, NY), *1036* (MO, NY); Alto Lino, *Bro. Maurice 839* (MO); forests around El Boquete, *Pittier 2917* (GH, NY, US); Cerro de Lino, *Pittier 3024* (US); Camp Aguacatal, E slope of Chiriquí Volcano, *Pittier 3120* (US); betw Cerro Vaca & Hato del Loro, *Pittier 5388* (US); valley of the upper Río Chiriquí Viejo, *White & White 19* (ECON, F, MO); vic of Cerro Punta, *White 35* (F, GH,); Río Chiriquí Viejo Valley, *White 231* (F, GH, MO); Finca Lérida, *Woodson & Schery 227* (F, MO); Finca Lérida to Peña blanca, *Woodson & Schery 311* (F, MO); Casita Alta, *Woodson et al. 810* (A, F, MO, NY).

This species occurs between 1000 and 3000 m elevation from Chiapas, Mexico, to Chiriquí, Panama. It is distinguished by its large reflexed stipules, subcoriaceous leaves, and paniculate inflorescences.

5. *Rondeletia salicifolia* Dwyer & Hayden, Phytologia **15:** 58, 1967.

Shrub or tree to 8 m high and 6 cm in diam, the branchlets terete, white-tomentose when young, the older portions glabrate. *Stipules* erect, narrowly triangular to triangular or rarely broadly triangular, 3-9.5 mm long, 2-4 mm wide, cuspidate with the cusp 0.5-6.5 mm long, tomentose to glabrate on the outside, sericeous on the inside with several finger-like structures, these ca 0.5 mm long and 0.07 mm in diam, dark red or black when dry. *Leaves* petiolate with the petioles 2-15 mm long, tomentose when young but soon glabrate; blade elliptic to narrowly elliptic, rarely narrowly oblong, narrowly ovate, or narrowly subobovate, 3.5-21 cm long, 1-9 cm wide, long-acuminate at the apex with the acumen 0.5-2 cm long, attenuate to cuneate or subacute at the base, arachnoid-tomentose above and tementose below when young but soon glabrate above and glabrate or sparsely tomentose on the veins and the midrib and secondary veins raised beneath, the tertiary veins open reticulate or running at right angles to the secondary veins. *Inflorescences* terminal, axillary and psuedo-axillary, paniculate with the branches helicoid-cymose and often secund, 3.5-12 cm long; peduncle 0.5-6 cm long; axes white-arachnoid-tomentose when young, sparsely tomentose when fruit mature. *Flowers* 4-merous, sessile or pedicellate with the pedicels to 2 mm long, white arachnoid-tomentose; hypanthium sparsely tomentose, rotund, 1.2-2.3 mm long, the disk ca 0.1 mm thick, ca 0.5 mm in diam, glabrous; calyx-lobes glabrous on the inside, with a few appressed hairs on the outside, unequal, basally connate for ca 0.5 mm with 1 lobe 3 or more times longer than the other 3, the larger lobe elliptic or subovate, 6-11.5 mm long, 3.5-6.5 mm wide, acute at the apex, the small lobes elliptic or oblong or triangular, 0.7-3.5 mm long, 0.5-2.7 mm wide, acute at the apex; corolla with the tube 8-15 mm long, with a few appressed hairs on the outside and $\frac{1}{5}$-$\frac{1}{2}$ basally puberulent below the anthers inside, the lobes obtuse, 3-4 mm long and wide. glabrous inside, with a few appressed hairs on the outside; stamens variably attached in the tube, the filaments 0.5-2 mm long, the anthers ca 3 mm long; style 6-14 mm long; ovary with a thick septum fused only at the base or completely fused, the placenta V-shaped or elliptic with rectangular ovules. *Capsules* globose, 3-4 mm in diam, costate, glabrate when mature, septicidal, the calyx persistent.

This species is presumbly endemic to Panama. It appears to spread over the mountains of the Cerro Jefe region and is found in the western river valleys of Bocas del Toro. Probably, it will be found in the neighboring river valleys of Costa Rica. It appears to be closely related to *R. aetheocalymma* J. D. Smith of Guatemala, which has narrowly oblong stipules, subcoriaceous leaves and larger fruits.

a. Cusp of the stipule 0.5-2 mm long; mature leaves glabrate beneath, the tertiary veins open reticulate; tube of the corolla ca 15 mm long; septum of the ovary fused only at the base, the placenta V-shaped .... subsp. *salicifolia*
aa. Cusp of the stipule 3-6.5 mm long; mature leaves sparsely tomentose on the veins beneath, the tertiary veins running at right angles to the secondary veins; tube of the corolla ca 8 mm long; septum of the ovary completely fused, the placenta elliptic .... subsp. *brevicorolla*

5a. *Rondeletia salicifolia* subsp. *salicifolia*.

PANAMA: betw Cerro Jefe & Eneida, alt 700-966 m, *Dwyer et al. 8215* (MO); Altos de Río Pacora, alt 833 m, *Lewis et al. 2315* (MO); Cerro Jefe, alt 900-1000 m, *Tyson et al. 3319* (holotype MO).

This subspecies exhibits a complicated form of heterostyly. When the style is ca 13 mm long, the stigma is ca 1.3 mm long, the stigmatic surface is smooth, the filaments are ca 2 mm long, the stamens are attached ca $\frac{1}{3}$ of the way up from the base of the tube, and the tube is puberulent ca $\frac{1}{5}$ of the way up from the base inside. When the style is ca 6 mm long, the stigma is ca 2.5 mm long, the stigmatic surface is densely granulate, the filaments are ca 0.5 mm long, the stamens are attached ca $\frac{3}{4}$ of the way up the tube from the base, and the tube is puberulent ca $\frac{1}{2}$ of the way up from the base inside. Heterostyly is also known to occur in a number of other genera of the *Rubiaceae* (Vuilleumier, 1967).

The inflorescences of the holotype are presumably immature. In the maturation of the inflorescence the ovary and calyx lobes develop first, with the floral axes being very short and the corolla only 1-3 mm long. Subsequently, both the corolla and the floral axes lengthen as much as five times. Thus a mature inflorescence is twice the size of the immature inflorescences as represented by those found on the holotype.

5b. *Rondeletia salicifolia* subsp. **brevicorolla** Kirkbride, subsp. nov.

Differt a subsp. *salicifolia* cuspide stipulae 3-6.5 mm longa, foliis maturis sparsim tomentosis in venis subter, venis tertiariis currentibus in angulis rectis venis secundaris, tubo corollae crca 8 mm longo, septo ovarii omino connato, placenta elliptica.

BOCAS DEL TORO: Changuinola Valley, *Cooper & Slater 98* (F); Río Teribe betw Quebrada Huron & Quebrada Schlunjik, alt ca 100 m, *Kirkbride & Duke 467* (MO, NY); cloud forest above Quebrada Huron on Cerro Bonyik, alt 166-400 m, *Kirkbride & Duke 597* (holotype MO, isotype NY).

This taxon does not appear to be heterostylous. The stamens are attached at ca the middle of the corolla-tube.

6. *Rondeletia cooperi* Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. **4**: 267, 1929.

Tree or shrub to 7 m high and 5 cm in diam, the branchlets terete, terminally densely white-strigose, the older portions sparsely strigose, the internodes unequal, 1.5-25 cm long. *Stipules* erect, triangular to very depressed triangular, 3-4 mm long, 2-7.5 mm wide, abruptly acuminate with the acumen 0.5-1(-1.5) mm long, strigose or sericeous-strigose on the outside, sericeous on the inside with several finger-like structures, these ca 0.7 mm long and 0.1 mm in diam, dark red when dry. *Leaves* petiolate with the petioles 0.2-3 cm long, densely strigose when young but sparsely so when mature; blade narrowly elliptic to elliptic, 11-21 cm long, 4.5-9 cm wide, acuminate at the apex with the acumen (1-)1.5-2.5 cm long, attenuate to short-attenuate or cuneate at the base, densely to sparsely strigose on the veins when young but soon glabrate above, strigose to densely white-strigose on the veins when young but soon strigose beneath, the midrib and secondary veins raised beneath, the tertiary veins running ± at right angles to the secondary veins. *Inflorescences* terminal, paniculate with the branches modified compound dichasia, 9-25 cm long; peduncles unequal, 3-16.5 cm long; peduncle and secondary axes strigose. the floral axes densely strigose. *Flowers* 4-merous, sessile or pedicellate with the pedicels to 1(-3) mm long, densely strigose; hypanthium densely ferrugineous-strigose, oblong, to 2 mm long and 1.3 mm in diam, sericeous-strigose; calyx-lobes basally connate for ca 0.5 mm, 1(or 2) lobes 3 or more times longer than the other (2 or) 3 lobes, the large lobe narrowly elliptic to elliptic or ovate, 3.4-4.3 mm long, 1.2-2.2 mm wide, obtuse at the apex, sparsely strigose on both sides, the small lobes narrowly oblong to oblong or triangular, 0.9-1.3 mm long, 0.3-0.6 mm wide, acute at the apex, sparsely strigose inside, strigose outside; corolla with the tube 9-11 mm long, strigose outside, the lobes obtuse, ca 4 mm long, sericeous-strigose outside near the base. *Capsules* ovoid, to 4.5 mm long, to 3.5

mm in diam, costate, sparsely strigose when mature, septicidal to ca the middle, calyx lobes persistent; seeds rectangular.

BOCAS DEL TORO: Buena Vista Camp, Chiriquí Trail, alt 416 m, *Cooper 600* (holotype F, isotypes NY, Y); betw Buena Vista coffee finca & Cerro Pilón, Chiriquí Trail, *Kirkbride & Duke 703* (MO, NY); Punta Peña, alt ca 333 m, *Lewis et al. 2158* (MO).

This species is known only from the vicinity of the type locality, an area of rain forest on the Atlantic slope with no appreciable dry season.

Kirkbride & Duke 703 bears what appear to be two types of fruit, capsules and berries. They have similar internal structures: 2 locules, many ovules, and axile placentation. However, the septum of the baccate fruit has increased in thickness tremendously and the tissues of the septum appear to be abnormal. This abnormal development of the fruit is probably caused by an exterior agent, such as a virus.

7. *Rondeletia secunda* Standley, Contr. U.S. Nat. Herb. **18:** 141, 1916.

Shrub with the branchlets terete, terminally sparsely tomentose, the older portions glabrous. *Stipules* erect, triangular, 3-6 mm long, 2-3.5 mm wide, cuspidate with the cusp 1.5-3.5 mm long, connate at the base, glabrous on the outside. *Leaves* subsessile with the petioles 1.5-4.5 mm long, glabrous; blade narrowly elliptic to elliptic or rarely subovate, 7.5-16 cm long, 3.3-6 cm wide, acuminate or rarely abruptly acuminate at the apex, acute or rounded at the base, glabrate on both surfaces, the midrib and secondary veins raised beneath, the tertiary veins running ± at right angles to the secondary veins. *Inflorescences* terminal, paniculate with the branches helicoid-cymose and secund, 6-9 cm long; peduncle 4-6 cm long; axes sparsely arachnoid-tomentose but glabrate when the fruit is mature. *Flowers* 4-merous, subsessile, the pedicels to 0.5 mm long, sparsely arachnoid-tomentose; hypanthium very sparsely arachnoid-tomentose, rotund, 0.8-1.5 mm long, the disk ca 0.1 mm thick and 0.5 mm in diam, glabrous; calyx-lobes with a few hairs or glabrous on both sides, unequal, basally connate for ca 0.2 mm, with 3 lobes linear or narrowly oblong, acute or obtuse at the apex, 1.7-4 mm long, 0.2-0.6 mm wide, 1 lobe narrowly obovate, acute or obtuse at the apex, 3.6-7.4 mm long, 0.7-1.4 mm wide, this lobe twice as long as the other 3 lobes; corolla with the tube 9-12 mm long, sparsely villous on the outside, the lobes obtuse, 2-3 mm long, with a few hairs on the outside, papillate on the inside; stamens attached below the middle of the tube. *Capsules* rotund, ca 4 mm in diam and high, when young faintly costate when dry, when mature glabrous and rugose when dry, loculicidal, the calyx lobes persistent until dehiscence; seeds rectangular.

SAN BLAS: Permé *Cooper 229* (F, NY, US); headwaters of Río Cuadí, along the river, alt 91 m, *Duke et al. 3657* (MO); forests around Puerto Obaldía, alt 0-50 m, *Pittier 4279* (holotype US, isotype NY).

This endemic species is known only from the eastern end of San Blas, but it will probably be found in the western end of the province and in Colombia in the area adjacent to San Blas. It is distinguished by its one enlarged calyx-lobe and three linear to narrowly oblong calyx-lobes, 1.7-4 mm long, which persist on the rugose fruit.

8. *Rondeletia bertieroides* Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. **4**: 267, 1929.

Tree or rarely shrub with the branchlets terete or subterete, terminally arachnoid-tomentose, the older portions glabrous. *Stipules* erect, triangular to ovate, 4-7 mm long, 2.5-4.5 mm wide, cuspidate with the cusp 1-3 mm long, connate at the base, glabrous on the outside, sericeous on the inside with several finger-like structures, these ca 0.5 mm long and 0.1 mm in diam, red when dry. *Leaves* petiolate with the petioles 0.2-3 cm long, arachnoid-tomentose when young but soon glabrate; blade narrowly elliptic or very rarely elliptic or subovate, 5.5-22.5 cm long, 1.7-6 cm wide, long-acuminate to rarely acute at the apex, attenuate to cuneate or rarely acute at the base, sparsely arachnulose above and arachnose beneath when young, glabrate when mature, the tertiary veins running ± at right angles to the secondary veins. *Inflorescences* terminal or very rarely axillary, paniculate with the branches helicoid-cymose or bearing reduced compound dichasia, 7-20 cm long, pedunculate with the peduncles 2.5-5 cm long, or sessile with 2 basal branches (fide Standley) 1-8 cm long, the axes tomentose when young but glabrate when fruit mature. *Flowers* 4-merous, subsessile, the pedicels to 0.5 mm long, tomentose; hypanthium arachnoid-tomentose, rotund, 1.3-1.5 mm long, the disk 0.1-0.2 mm thick, 0.5-0.7 mm in diam, with a few straight erect hairs ca 0.5 mm long or glabrous; calyx-lobes glabrous on the inside, with a few hairs or glabrous on the ouside, unequal, basally connate for ca 0.5 mm, with 3 lobes triangular to broadly triangular or oblong, 0.3-1.8 mm long, 0.5-0.9 mm wide, 1 lobe elliptic or narrowly obovate or rarely oblong, acute or very rarely obtuse at the apex, (1.3)2-4.2 mm long, 0.8-2.7 mm wide, this lobe 3 or more times longer than the other 3 lobes, the 3 small lobes reflexed after loss of the corolla; corolla with the tube 9-12 mm long, sparsely strigose on the outside, puberulent on the inside below the anthers, the lobes obtuse, ca 2.5 mm long; stamens subsessile, the filaments of equal length but variably attached, all at the same level in each flower. from below the mouth to the middle of the tube, the anthers 2-2.7 mm long; ovary with a thick entire or incompletely fused septum, the basal fusion ca ¼ of the way up, the placenta elliptic or V-shaped with rectangular ovules. *Capsules* globose, ca 4 mm in diam, costate, glabrous when mature, septicidal, the calyx-lobes persistent.

BOCAS DEL TORO: Buena Vista Camp, Chiriquí Trail, alt 1000 m, *Cooper 598* (holotype F, isotypes NY, Y); betw Buena Vista coffee finca & Cerro Pilón, cloud forest, Chiriquí Trail, *Kirkbride & Duke 712* (MO, NY), *713* (MO, NY); betw Criollo (just above Buena Vista) & Quebrada Higueron, Chiriquí Trail, *Kirkbride & Duke 798* (MO, NY), *799* (MO, NY). COCLÉ: El Valle de Antón, alt 1000 m, *Allen 3409* (F); cloud forest on slopes of Cerro Pilón nr El Valle de Antón, alt 700-900 m, *Duke 12161* (MO); rain forest on Cerro Caracoral below the elfin forest, *Kirkbride 1124* (MO, NY). VECAGUAS: forested slopes of Cerro Tute, vic Santa Fe, alt 800 m. *Allen 4368* (F), *4369* (NY).

This endemic species is very heterogeneous. The collections from El Valle generally have smaller leaves, a shorter inflorescence, and more indumentum than do the collections from Bocas del Toro and Cerro Tute, but these characters all overlap, making them useless as key characters. In addition to these differences between the two groups is the fact that the septum of flowers from El Valle was entire, while the septum of those from Bocas del Toro and Cerro Tute was incompletely fused. My field observations in Bocas del Toro and at El Valle tend to support the separation of the two groups.

It appears that two taxa are involved here, but I am unable at this time to determine any characters in each which would make them readily separable in a key. Perhaps more intensive field work and collecting at all three areas will provide the necessary characters for an adequate separation or for a more positive description of this taxon as a heterogeneous one.

The collections from El Valle also resemble *Rondeletia platysepala* Standley, but *R. platysepala* has all 4 calyx-lobes ca equally expanded.

9. *Rondeletia platysepala* Standley, Ann. Missouri Bot. Gard. **27:** 343, 1940.

Tree to 6 m high, the branchlets terete, terminally sparsely strigose, the older portion glabrous. *Stipules* erect, triangular, 2-3 mm long, 1-1.8 mm wide, cuspidate with the cusp ca 0.75 mm long, glabrous on the outside, strigose on the inside with several narrowly elliptic finger-like structures near the apex, these ca 0.5 mm long and 0.2 mm in diam, black when dry. *Leaves* subsessile with the petioles 1-3 mm long, strigose; blade narrowly elliptic or narrowly oblong, 4.4-8 cm long, 1.3-2.3 cm wide, abruptly long-acuminate at the apex, acute at the base, very sparsely tomentose above when young but soon glabrous, the midrib and secondary veins sparsely strigose and the intercostal areas glabrous beneath when mature, the midrib and secondary veins raised beneath, the tertiary veins open-reticulate. *Inflorescences* terminal, paniculate with the branches cymose or helicoid-cymose, 3-9 cm long; peduncle 1.5-4 cm long; axes tomentose. *Flowers* 4-merous, sessile or pedicellate, the pedicels to 5 mm long; hypanthium tomentose, oblong, ca 1.5 mm long, the disk ca 0.3 mm thick and 0.8 mm in diam, glabrous; calyx-lobes ca equal on each flower, laminar-like, elliptic, the apex acute or obtuse, 1.7-4.2 mm long, 0.6-2.5 mm wide, very sparsely tomentose on the outside, very sparsely tomentose to glabrous on the inside; corolla with the tube 7-11 mm long, tomentose on the outside, sparsely puberulous below the middle inside, the lobes obtuse, ca 2.5 mm long; stamens subsessile, the anthers oblong, ca 2 mm long, attached above the middle of the tube; placenta subobovate, ca 1.3 mm long, ca 0.7 mm wide, ca 0.2 mm thick. *Fruits* not seen.

COCLÉ: vic of El Valle, N rim (wet), *Allen 1791* (holotype F, isotypes GH, MO, NY).

This endemic resembles *Rondeletia bertieroides* Standley, but it is readily distinguished by its four ca equally expanded calyx-lobes. *Rondeletia bertieroides* has one lobe ca 3 times longer than the other three lobes.

10. *Rondeletia hamelifolia* Dwyer & Hayden, Phytologia **15:** 58, 1967.

Shrub 3-8 m high, to 5 cm in diam, the branchlets terete, terminally sparsely tomentose, the older portion glabrous, the internodes of variable length, 0.5-6 cm long. *Stipules* erect, triangular, 4-8 mm long, 2-4 mm wide, cuspidate with the cusp 2-4 mm long, sericeous on the outside and the inside with several narrowly oblong finger-like structures on the inside, ca 1 mm long and 0.2 mm in diam, black when dry, the stipules below the terminal inflorescence often bilobate. *Leaves* with the petioles to 8 mm long, white-tomentose when young, but soon glabrate; blade narrowly elliptic to elliptic, 4.5-20 cm long, 1.5-6.5 cm wide, acute to acuminate at the apex, attenuate at the base, membranous, very sparsely sericeous on the veins above, tomentose on the midrib and secondary veins and sparsely tomentose on the tertiary veins and the midrib and secondary veins raised beneath, the tertiary veins open reticulate. *Inflorescences* terminal and axillary, paniculate, 2-7(-13) cm long; peduncle 1.5-6 cm long with 2 foliaceous bracts at the apex, narrowly elliptic to elliptic, 1.2-3 cm long, 4-12 mm wide; axes white-tomentose becoming glabrate as the fruit matures. *Flowers* sessile or pedicellate, the pedicels to 3 mm long, white-tomentose; hypanthium white-strigose, rotund, 1.5-2 mm long, the disk ca 0.2 mm thick and 0.8 mm in diam, puberulent; calyx-lobes 5 or 6, unequal, narrowly oblong, the apex acute, 1-2 mm long, very sparsely tomentose outside, sparsely and minutely strigose inside, becoming reflexed at maturity; corolla with the tube 6-9 mm long, white-strigose outside, glabrous inside, the lobes 5, obtuse, ca 2.5 mm long and wide, with an annular callosity ca 0.5 mm thick at the orifice of the corolla; stamens with the filaments ca 1 mm long, attached at the middle of the tube, the anthers oblong, ca 2.5 mm long; placenta hemispherical, ca 0.5 mm in diam, with winged ovules. *Capsules* transversely elliptic in radial section, to 8 mm in diam and 5 mm thick, sparsely puberulous, lightly costate, loculicidal.

LOS SANTOS: Cañfístulo, *Dwyer 2458* (MO). VERAGUAS: Santiago, *Dwyer 1350* (holotype MO); 4 mi from Pan-Amer Hwy toward Atalaya, *Dwyer & Kirkbride 7410* (GH, MO, US), *7422* (MO); nr Ponuga, *Dwyer & Kirkbride 7443* (GH, MO); 2 mi W of Santiago on Pan-Amer Hwy, *Dwyer et al. 7556* (GH, MO, US); 50 mi W of Santiago on Pan-Amer Hwy, down embankment, *Kirkbride & Hayden 164* (MO, NY); Cañazas, *Tyson 3638* (MO).

This endemic species is found in savanna areas of the Azuero Peninusla and Veraguas Province. These areas undergo a very marked dry season each year.

11. *Rondeletia panamensis* DC., Prodr. **4**: 408, 1830.—Fig. 3.

Shrub or tree to 6 m high and 5 cm in diam, the branchlets terete, terminally white-tomentose, the older portions glabrous. *Stipules* erect, triangular to broadly triangular, 3-5 mm long, 2-7 mm wide, cuspidate with the cusp ca 2 mm long, tomentose on the outside but glabrate when older. *Leaves* with the petioles 2-6(-13) mm long, the younger white-tomentose, the older glabrate; blade narrowly elliptic to broadly elliptic or subovate, 2.5-15 cm long, 1.5-7 cm wide, acute to subacuminate at the apex, subattenuate to attenuate at the base, very sparsely tomentose on the veins and the midrib raised beneath, the tertiary veins running ± at right angles to the secondary veins. *Inflorescences* terminal and axillary, of compound dichasia with the secondary axes compressed, 1.5-7 cm long; peduncle 0.5-4 cm long; axes white-tomentose becoming sparsely tomentose as the fruit matures. *Flowers* 5-merous, with several bractlets, sessile or pedicellate, the pedicels to 7 mm long, white-tomentose; hypanthium densely white-tomentose, rotund, ca 2.5 mm long and 3 mm in diam, the disk ca 0.25 mm thick and 0.75 mm in diam, puberulent; calyx basally connate for ca 1.5 mm, the lobes narrowly ovate,

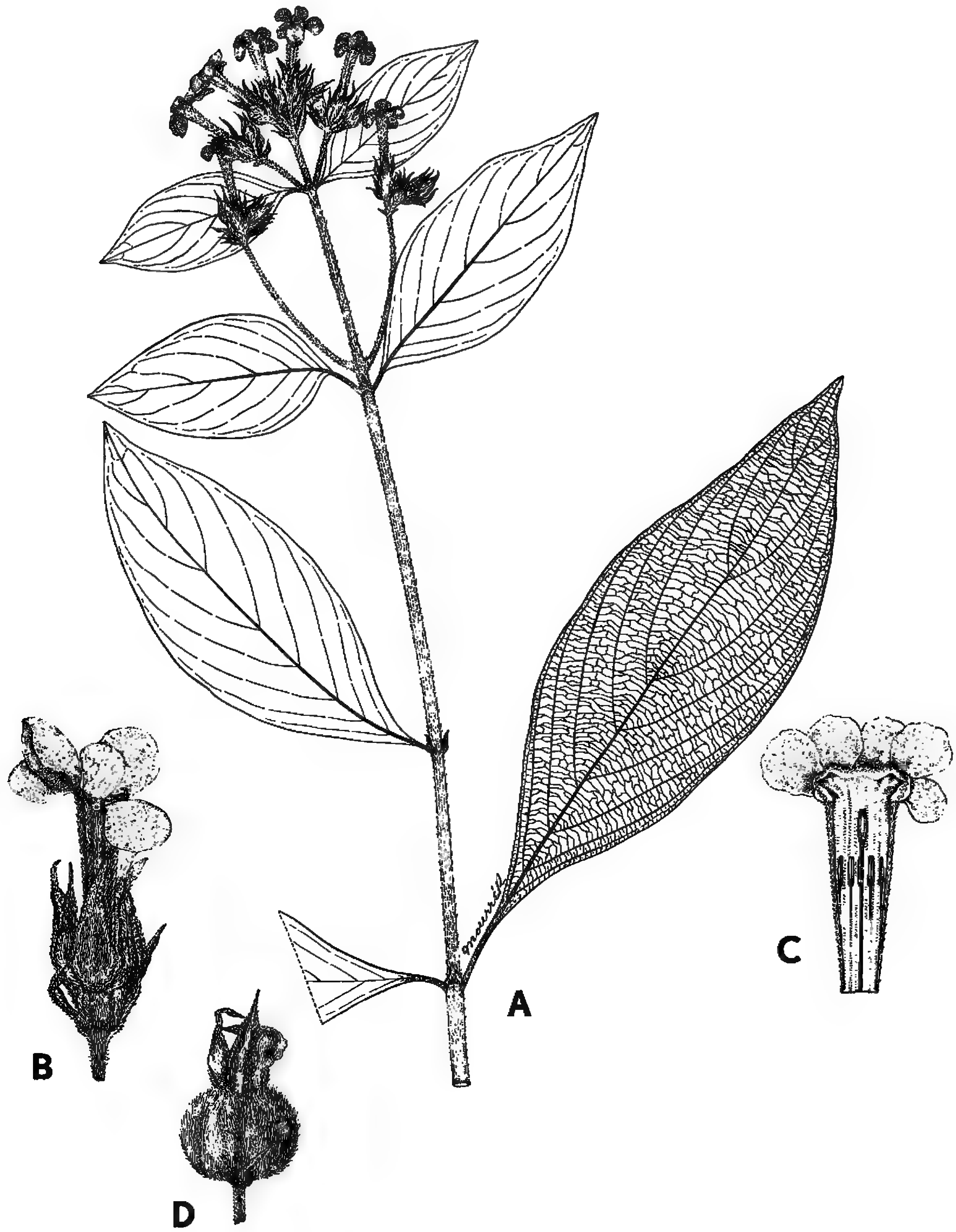

Fig. 3. *Rondeletia panamensis* DC.: A, flowering branch ($\times\frac{1}{2}$); B, flower ($\times 1\frac{3}{5}$); C, opened corolla ($\times 1\frac{3}{5}$); D, immature fruit ($\times 2$).

with the apex acute, ca 8.5 mm long and 2.5 mm wide, ca 1 mm thick near the base, sparsely tomentose outside, densely sericeous at the base and glabrous at the apex inside; corolla with the tube 13-18 mm long, villous-sericeous outside, glabrous inside, the lobes unequal, obtuse, 4 lobes ca 5 mm long and wide, 1 lobe ca 3 mm long and wide, sparsely sericeous in the center outside, sparsely puberulous inside, with an annular callosity ca 0.5 mm thick at the orifice of the corolla; stamens with the filaments ca 2 mm long, attached above the middle of the tube, the anthers oblong, ca 2 mm long; placenta hemispherical, ca 0.5 mm in diam, with winged ovules. *Capsules,* globose, to 10 mm in diam, sparsely tomentose when mature, loculicidal, 2-valvate, the calyx-lobes persistent.

CANAL ZONE: 2 mi W of Balboa, *Correll 12257* (GH, NY); forests along banks of Quebrada Fea, Quebrada Pura, & Cañon de Río Chagres, alt 70-100 m, *Dodge & Allen 17413* (MO); Albrook Site, U.S. Army Tropic Center, *Dwyer 7123* (MO); Ancón Hill, alt 200 m, *Killip 3004* (GH, NY), *3054* (US), *12061* (GH), *Piper 5569* (GH, NY, US), *Williams 24* (NY); Thunder Hill, Curundu, *McDaniel 5189* (MO); Sosa Hill, Balboa, *Standley 25272* (US); Balboa, *Standley 26996* (A, US); Las Cruces Trail betw Fort Clayton & Corozal, *Standley 29060* (US); betw Tumba Vieja & Salamanca, alt 66 m, *Steyermark & Allen 16757* (MO); nr Tropic Survival School, Curundu, *Tyson & Dwyer 4464* (MO); vic Salamanca Hydrographic Station, Río Pequení, alt ca 80 m, *Woodson et al. 1562* (A, F, NY). DARIEN: Chepigana, *Duke 277* (MO); vic Pinas, *Duke 10626* (MO); Puerto St. Dorotea, *Dwyer 2203* (MO), *2259* (US). PANAMA: Pan-Am Hwy nr Jenine, *Duke 3843* (MO); Río Chagres, 1 mi above Madden Lake, *Duke 4482* (GH, MO); gallery along Río Mamoni, *Duke 5686* (GH, MO); Río Charco-Espiritu, Tocumen Hwy, *Duke 5706* (GH, MO); forests of upper Río Mamoni, alt 150-400 m, *Pittier 4475* (NY, US); Río Tapia, *Standley 28083* (US). PROVINCE UNKNOWN: *Duchassaing s.n.* (F, GH).

This is a lowland endemic known only from the Canal Zone, the Pacific lowlands of the Province of Panama from the Canal Zone to the Río Bayano, and central Darien. It will probably be found in the Pacific lowlands from the Canal Zone to Darien and possibly in the Choco area of Columbia. It is readily distinguished from other species by its large tomentose fruits bearing the persistent calyx-lobes and its large pubescent flowers.

12. *Rondeletia dukei* Dwyer & Hayden, Ann. Missouri Bot. Gard. **54**: 144, 1967. —Fig. 4.

Shrub ? with the young portions of the branchlets purplish-black when dry, angular, and glabrous, the older portions of the branchlets brown, terete, and glabrous. *Stipules* erect, triangular to broadly triangular, 3-6 mm long, 2-4 mm wide, glabrous. *Leaves* with the petioles 0.7-3 cm long, purplish-black when dry, ciliate in the axil; blade elliptic-obovate, 5.5-10 cm long, 3.5-6 cm wide, obtuse at the apex, cuneate at the base, rigidly membranous, glabrous, the midrib purplish-black, raised beneath, the tertiary veins open-reticulate. *Inflorescences* terminal or axillary, spike-like, 3.5-8 cm long; peduncle (0.2-)2-4.5 cm long, to 1.5 mm in diam, angular, minutely farinose. *Flowers* with several bractlets, mostly sessile, the occasional pedicels white, to 3 mm long; hypanthium densely white-sericeous, rotund, 1.5-2 mm long, the disk ca 0.4 mm thick and 1 mm in diam; calyx lobes 5(-6), basally connate for ca 0.5 mm, rotund to broadly ovate, ca 1.5 mm long, 1.5-2 mm wide, 1 or 2 calycine lobes of the lowest flowers disposed as broad foliose blades, the stalk linear, to 3 mm long, the blade broadly ovate, to 3.5 cm long, cuneate, brownish-yellow when dry; corolla with the tube 1-8 mm long, strigose outside, villous at the throat, the lobes 5-6, 2-3 mm long, obtuse, puberulent outside, papillate and purple when dry inside, patulous at anthesis; filaments unequal, 0.3-3 mm long, attached at the throat of the corolla-tube; anthers 5 or 6, oblong, 1.5-5 mm long, subversatile, some subsessile, some exserted; stigma exserted; placenta oblong, ca 1.5 mm long, ca 0.1 mm wide, ca 0.25 mm high, with the ovules winged when immature. *Fruits* not seen.

DARIEN: Río Pirre, *Duke 8329* (holotype MO, isotype NY).

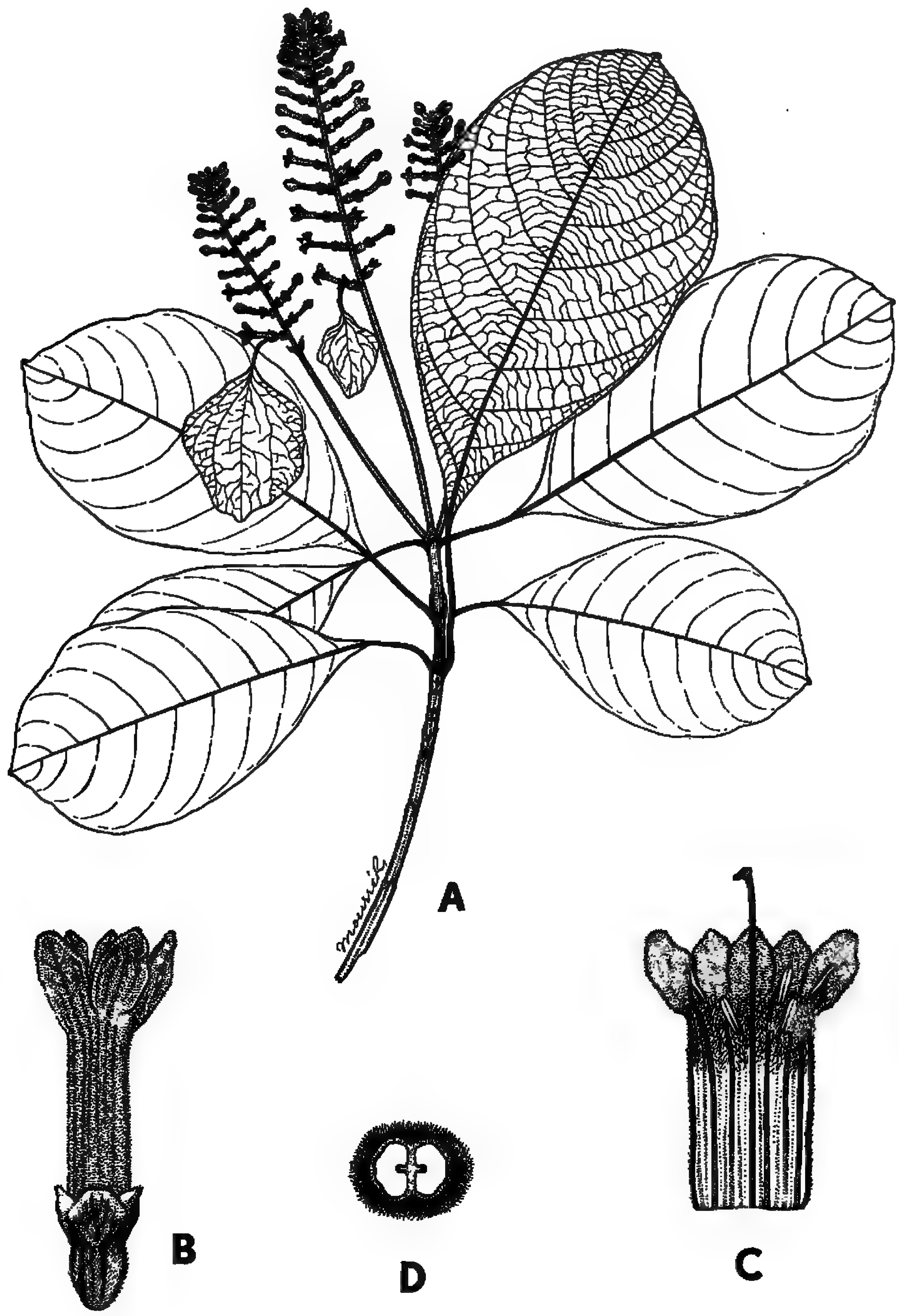

Fig. 4 *Rondeletia dukei* Dwyer & Hayden: A, flowering branch (×½); B, flower (×3½); C, opened corolla (×3½); D, ovary cross section with placenta and ovules omitted (×8½).

This species differs from the others in Panama by its extremely large foliar calyx-lobes on the lowest flowers of the inflorescence and its filaments of variable length. On the specimens observed, 10 of the 12 leaves had deformed apices of their blades.

This species is known only from the type collection. The common name found on the label, *madroño* according to the collector probably denotes the large foliar calyx-lobes, and is probably not species specific.

Excluded Species

Rondeletia laniflora Bentham, Pl. Hartw. 85, 1841.

Arachnothryx laniflora (Bentham) Planchon, Fl. Serres **5:** 442, 1849.

This taxon resembles *Rondeletia buddleioides* Bentham somewhat. It is reported by Seemann (1854) to have been collected on Chiriquí Volcano; the specimen was not available for examination, but may be a misidentified *R. buddleioides.*

Rondeletia nicaraguensis Oersted, Kjoeb. Vidensk. Meddel. **1852:** 43, 1852.

This taxon was described from Nicaragua and reported from Panama by Oersted. The description of the corolla and leaves seems unusual for *Rondeletia,* and neither the ovarian nor the fruit structure was described. No specimen was available for examination.

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A NEW SPECIES OF CUCURBITA FROM ECUADOR

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La Jolla, California

ABSTRACT

A new species of *Cucurbita* from South America is described. This species, *Cucurbita ecuadorensis,* is the first wild species of *Cucurbita* described from northwestern South America. *Cucurbita ecuadorensis* has been excavated from pre-ceramic, pre-maize levels in Coastal Peru. It appears to be more closely related to the South American *C. maxima* and *C. andreana* than to other species in the genus.

Recent interest in the solitary bees of the genera *Peponapis* Robertson and *Xenoglossa* Smith stimulated an intensive search for species of *Cucurbita* and the bees associated with each species (Hurd & Linsley, 1964, 1966, 1967). On a collecting trip for solitary bees, Dr. and Mrs. A. E. Michelbacher were in Ecuador from January 27 to February 16, 1965. They made three collections of a large, wild gourd. Through the courtesy of the Michelbachers, seeds from these collections were grown in experimental gardens and greenhouses at Tucson, Arizona, and La Jolla, California. These collections belong to an undescribed species of *Cucurbita.*

Cucurbita **ecuadorensis** Cutler & Whitaker, sp. nov.—Fig. 1-3.

Plants scandens ad 10 m fortasse plus alta, spicula et trichomata diffusa, interdum ad nodos radicans, cirrhi crassi, saepe tripartiti et plerumque circinati; folia plerumque 12-32 cm lata, lato-ovato ad reniforma, lamina opaco-viridis, plerumque superficie pallido-viridis, basi lato-cordata, quinquelobata, lobi laterales saepe vadosiores, lobi basales circiter ad dimidium distantiae versus costam divisi, apice mucronati, supra diffuso-ciliati, subtus pubescentes, margines irregulares, petioli maturi, 8-16 cm longi, plerumque laminam aequantes, trichomatibus et apiculis ornati; flores solitarii campanulati aurantiaco-fulvi; flores staminati pedicellati, pedicellis brevibus ciliatis, 2-5 cm longis, corolla 5-8 cm longa, tubus 3-5 cm longus, calyx ciliatus, lobi angusti et acuti, 1-2 cm longi; flores pistillati pedicellati, pedicellis brevibus, ciliatis, 2-5 cm longis, corolla 5-9 cm longa, tubus 3.5-5 cm longus, lobi calycis filiformes, 1 cm longi, pedunculi graciles, 4-8 cm longi angulati, apiculati, origine vix turgidi; pepo globosus vel subglobosus, 16 cm diametro, cremeus ad opaco-viridis, plerumque cremeus et lineis viridibus maculisque ornatus, interdum maturite fulvi, pulpa alba, saepe acris sed magis sapore placenti parata,

[1] We are pleased to acknowledge the cooperation of Dr. and Mrs. A. E. Michelbacher and Professor Paul D. Hurd, Jr. of the University of California, Berkeley, for making collections and contributing the materials that made this study possible. The Latin description was prepared by Dr. John D. Dwyer, St. Louis University, the chromosome counts and information on species hybridization were furnished by Dr. W. P. Bemis, University of Arizona, and the electrophoretic analyses by Dr. J. R. Wall, Texas Technological College.

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Fig. 1. Typical mature leaves of *Cucurbita ecuadorensis* grown at La Jolla from seed collection in Guayaquil, Ecuador; note 5-lobed leaves with traces of secondary lobing; × 3/10.

loculi 3, semina ovata, 1.1-1.5 cm longa, 0.7-0.8 cm lata, corpus album ad brunneolum, margo quam corpore conspicue opacior.

Annual when grown in California and Arizona; *vine* up to 10 m or more, often clambering over shrubs; *stems* striate *with* scattered spicules and hairs, sometimes rooting at the nodes; *tendrils* thick, usually tripartite, often coiled on themselves; *leaves* usually 12-32 cm wide, broadly ovate to nearly reniform in outline; *blade* dark green, usually with light green blotches on upper surface, base broadly cordate, deeply 5-lobed, lateral lobes often shallower, basal lobes often divided nearly ½ way to mid-vein, tips of lobes mucronate, upper surface with scattered hairs, lower surface pubescent; margins irregular, denticulate at vein ends; *petiole* 8-16 cm long when mature, usually as long as blade, with hairs and spicules; *flowers* solitary, campanulate, orange-yellow; staminate on short, hairy pedicels 2-5 cm long; corolla 5-8 cm long; tube 3-5 cm long; calyx hairy, lobes narrow and pointed, 1-2 cm long; pistillate on short, hairy pedicels, 5 cm long; corolla 5-9 cm long; tube 3.5-5 cm long; calyx-lobes filiform, 1 cm long; *peduncle* slender, 4-8 cm long, angled, spiculate, slightly enlarged at attachment; pepo to 16 × 16 cm, creamy to dark green, usually creamy with green lines and spots, sometimes turning yellow at maturity; flesh white, stringy, sometimes bitter, but usually with pleasant cucumber-like flavor; locules 3; *seeds* ovate, 1.1-1.5 cm long, 0.7-0.8 cm wide; body white to tan; margin conspicuous, darker than body.

Ecuador: 5 mi W of Guayaquil; abundant, no bloom; dry gourds of previous year hanging from shrubs, 2 Febr 1965 (holotype MO, isotype US). 19 mi N of Balzar, ca 60 mi N of Guayaquil, fruits from previous years hanging from shrubs, 4 Febr 1965 (MO, US). On the river nr Ambuqui, NE of Ibarra, in deep hot valley, alt ca 2,500 ft, 14 Febr 1965

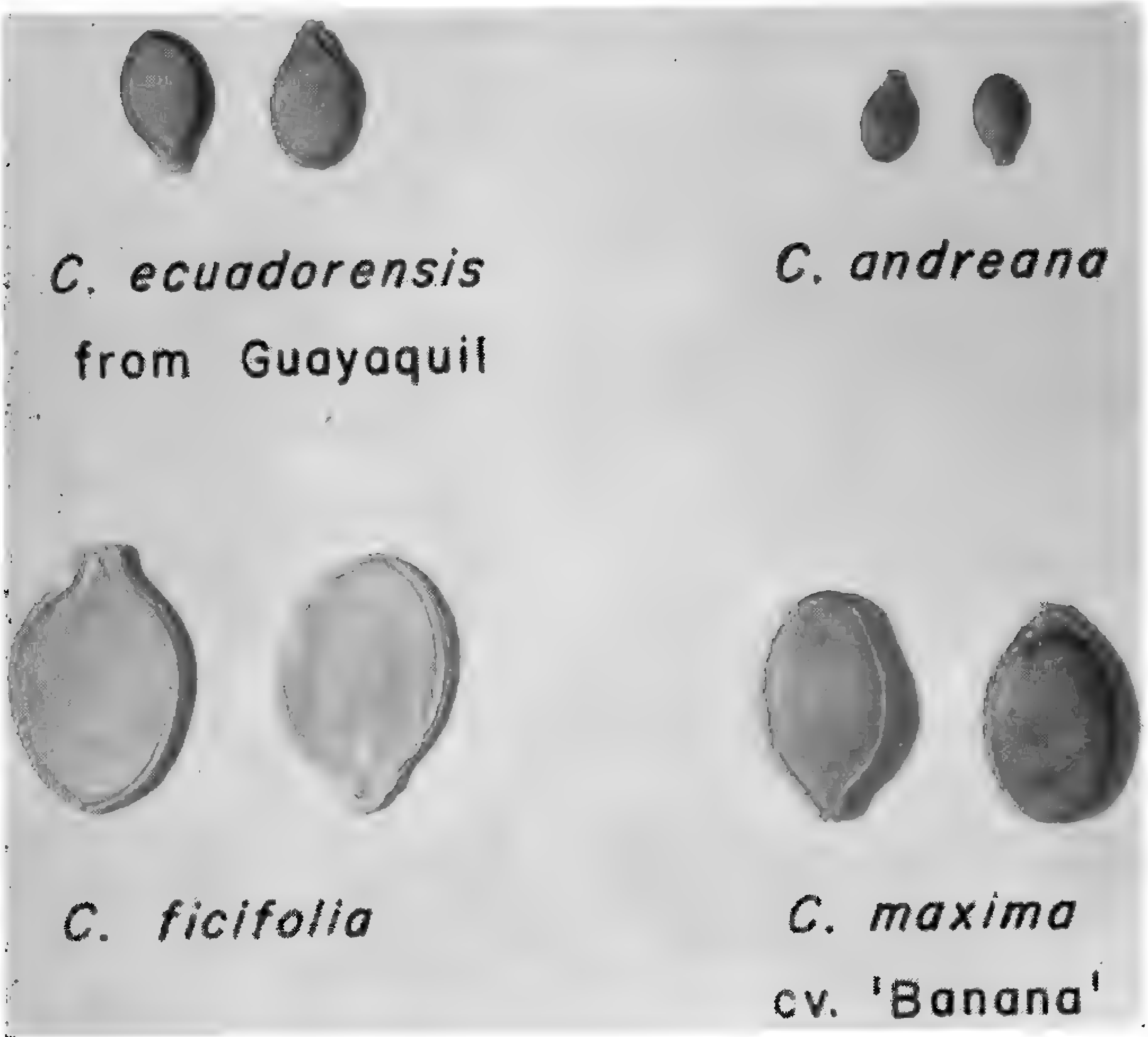

Fig. 2. Seeds of *Cucurbita ecuadorensis* compared with those of celosely related species: *C. andreanna, C. maxima* & *C. ficifolia;* × 1½.

(MO). Nr Ambuqui, hway 1, 14 Febr 1965 (MO). 10 mi N of Guayaquil, 15 Febr 1965. All by *Michelbacher & Michelbacher s.n.*

Peru: Site PV45-136 on Bay of Ventanilla, cut 1, level 7, and cut 1A, level 6. Estimated to be from 3000 B.C., *Edward P. Lanning s.n.* (MO).

California: La Jolla, grown from seeds collected by the Michelbachers at the type locality (MO, US). La Jolla, grown from seeds collected by the Michelbachers nr Ambuqui; Highway 1, (MO, US). Both by *Whitaker s.n.*

The species differs from the weedy *Cucurbita andreana* Naud. in having large, deeply lobed leaves, and a large, globular non-bitter fruit. The only other pre-Columbian species of *Cucurbita* from South America are the cultivated ones, *C. ficifolia* Bouche, *C. moschata* Duchesne ex Poir. and *C. maxima* Duchesne. *Cucurbita ecuadorensis* differs from wild Central American and North American species by the large leaves and fruit, by the virtual absence of bitter taste in the flesh of the fruit, and by the prominent seed margins. The margins are slightly darker than the cream color or light tan seed body.

Rinds, seeds and peduncles of a species of *Cucurbita*, similar to *C. ecuadorensis*,

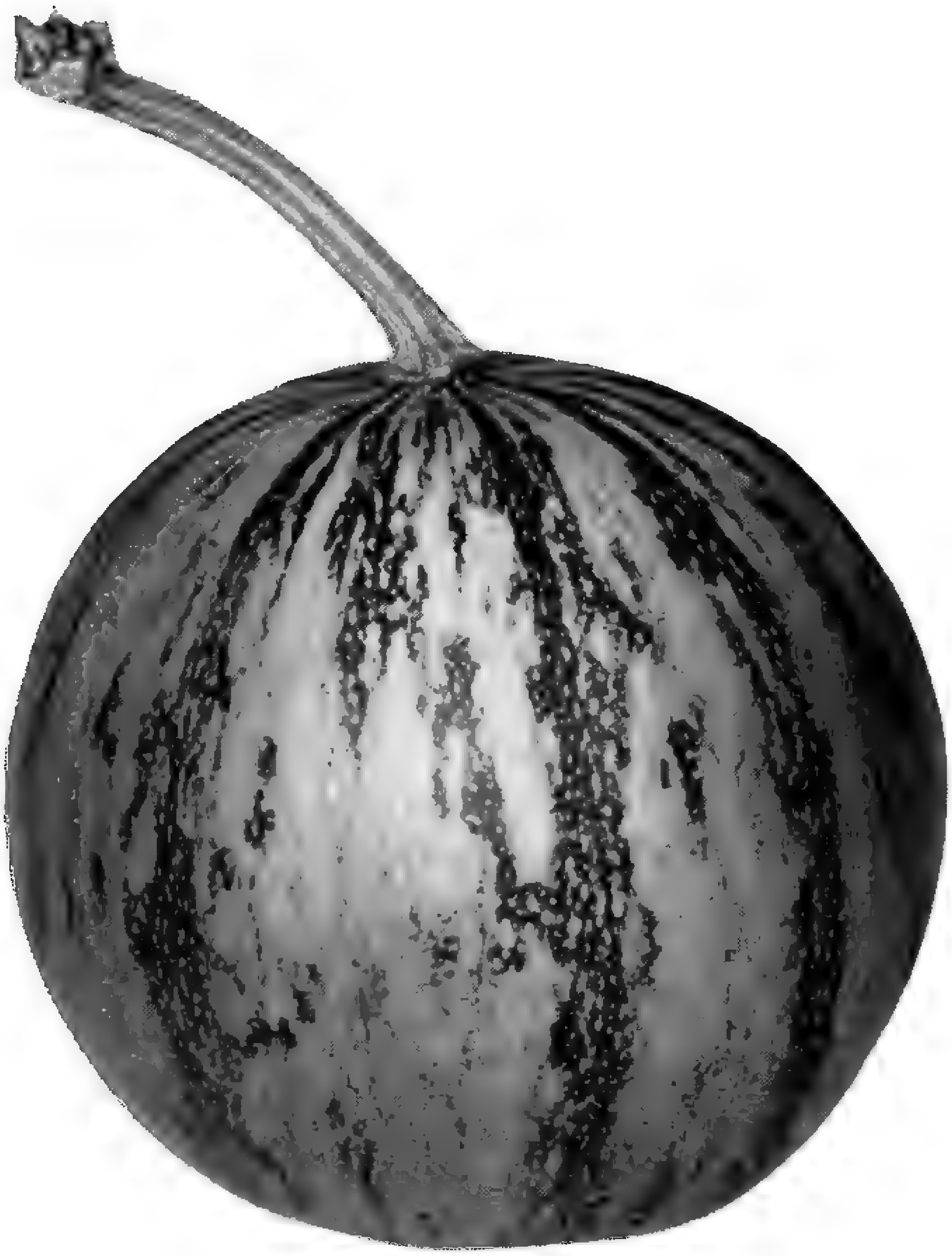

Fig. 3. Fruit of *Cucurbita ecuadorensis;* × 3/5.

have been excavated by Lanning (1967) from pre-Columbian pre-ceramic and pre-maize sites in coastal Peru. He lists these specimens as *C. andreana* and as a wild cucurbit.

Cucurbita ecuadorensis has 20 pairs of chromosomes, the same as other species of *Cucurbita.* It hybridizes readily with *C. maxima* (Whitaker, Bemis & Wall, unpublished data). Fertility decreases to about 50% in the F_1 plants, but F_2 progenies, and backcrosses to either parent can be obtained. Fertility is greatly decreased in most individuals in the F_2 and backcross progenies. Some individuals in these progenies are characterized by complete sterility of the staminate or pistillate flowers. Also, various patterns of chlorophyll deficiencies of both leaves and stems occur.

Hybrids between *Cucurbita ecuadorensis* and the following species have been made and F_1 plants grown: *C. moschata, C. lundelliana* Bailey, and *C. okeechobeensis* Bailey. The fertility of these hybrids has not yet been determined. *Cucurbita ecuadorensis* was included in a numerical taxonomic study of *Cucurbita* (Rhodes *et al.,* 1968). The results indicate it was *not* closely associated with other species of *Cucurbita* or with interspecific hybrids, but it did show some affinity with the *lundelliana* group (*C. lundelliana, C. okeechobeensis* and *C. martinezii Bailey*). There was also an indication of association with *C. ficifolia,* a cultivated species, sympatric in part of its range with *C. ecuadorensis.*

J. R. Wall (unpublished data) has studied the electrophoretic characterization of nine populations of *Cucurbita* species and the hybrid of *C. ecuadorensis* × *C. maxima* cv. 'Pink Banana'. He has demonstrated that, on the basis of electrophoretic mobilities of leucine amino-peptidase (LAP) and alpha-napthyl acetate esterase (Est), *E. ecuadorensis* can be separated from other species of *Cucurbita.*

Aside from its interest as an important factor in the co-evolution of the bee, *Peponapis* in South America, *C. ecuadorensis* appears to be the first truly wild species of *Cucurbita* described from South America. The feral species, *C. andreana* Naud. (Crovetto, 1965), and the closely related cultivated species, *C. maxima* Duch., are the only other species of the genus thought to have originated in South America. The discovery of this new species suggests that insects may be useful guides to unreported species in *Cucurbita.* Furthermore, some modification of current ideas of the origin, domestication, and dispersal of the cultivated *Cucurbita* may be in order.

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NOTES

HEDYOTIS ACEROSA VAR. BIGELOVII, COMB. NOV. (RUBIACEAE)

The name *Hedyotis acerosa* Gray var. *polypremoides* (Gray) W. H. Lewis in Ann. Missouri Bot. Gard. **55**: 31, 1968, is superfluous. Clearly the earliest available is *Houstonia polypremoides* var. *bigelovii* Greenman so that the correct name for the atypical variety of this species is *Hedyotis acerosa* Gray var. **bigelovii** (Greenman) W. H. Lewis, comb. nov., based on *Houstonia polypremoides* var. *bigelovii* Greenman, Proc. Amer. Acad. **32**: 291, 1897 (Type *Bigelow* 437 GH).—*Walter H. Lewis, Missouri Botanical Garden, St. Louis.*

SISYRINCHIUM DIMORPHUM (IRIDACEAE), A NEW SPECIES FROM TEXAS AND MEXICO

Sisyrinchium **dimorphum** R. Oliver, sp. nov. Herba perennis glabra, caule interdum sine bracteis foliacea, floribus azureis parvis, filamentis connatis, capsulis globesis.

Perennial 9-32 cm tall; roots coarse from a short rhizome. *Leaves* 1.5-3.5 mm wide, 5-30 cm long. *Stems* 0.3-1.3 mm wide, wings 0.2-0.4 mm wide, usually less than ½ the width of the stem. *Leafy bract* 4-14 cm long. *Floral bracts* equal or the outer bract to 10 mm longer than the inner, outer bract 12-30 mm long, connected 4-7 mm at base, inner 11-19 mm long. *Flowers* blue, tepals alternating wide and narrow, 6-9 mm long, 1.5-4 mm wide; anthers 0.8-1.3 mm long. *Capsules* globose 4-5 mm high. Plants dry olive-green.

MEXICO: Tamaulipas: betw Guamos & Padilla, abundant on moist river bank, 25 Mar 1925, *Runyon* 773 (US).

TEXAS: Bandera Co: 2 mi N of Utopia, Sabinal River, open wet pasture nr river, 3 July 1963, *Correll et al. 28230* (LL); Sabinal River Valley, 3 mi N of Vanderpool, in seepy ground of dark calceareous clay, 13 May 1956, *McCart 5761* (SMU). Burnet Co: 7 mi S of Burnet on Hwy 281, rocky creek bed, 1 May 1947, *Whitehouse 18427* (SMU). Llano Co: W of Inks Dam, on gentle slope in granitic area, 28 Apr 1946, *Lundell & Lundell 14549* (LL). Travis Co: Austin, University of Texas Campus, shady area in wild flower garden, 7 May 1957, *McCart 5734* (SMU); 1 mi W of Austin Dam, infrequent along stream in limestone hills, 14 Apr 1946, *Warnock 46121* (LL), *46113* (LL). Uvalde Co: nr Laguna, edge of Nueces River, 3 Apr 1942, *Lundell 10967* (LL); "Chalk Bluff", moist rocky bank of Nueces River, 11 Apr 1918, *Palmer 13328* (MO); Sabinal River Bank, 9 Apr 1917, *Palmer 11509* (MO). Val Verde Co: Devil's River W of Del Rio, grassy slope, 18 Apr 1957, *Correll et al. 15996* (LL); San Felipe Springs, Del Rio, infrequent along stream, alt 950 ft, 7 Apr 1951, *Warnock & Cameron 9889* (LL, SMU); frequent in limestone soil at San Felipe Springs, Del Rio, 7 Apr 1951, *Warnock & Cameron 9894* (holotype SMU, isotype LL).

Sisyrinchium dimorphum seems most closely related to *S. demissum* Greene with stems both scapose and foliaceous, and pedicels longer than the spathes; but can be distinguished by the smaller flowers, narrower tepals, and plants drying olive-green.—*Royce L. Oliver, Missouri Botanical Garden, St. Louis.*

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NOTES ON SOME AMERICAN SPECIES OF VOYRIA (GENTIANACEAE)

Voyria **bilobata** A. Robyns, sp. nov.; ab omnibus speciebus *Voyriae* neotropicis calyce intus basi squamellis 5 instructo, ovario supra basin glandulis 2 oppositis anguste ellipticis donato stigmateque 2-lobato primo visu sat differt.—Fig. 1.

Herbula saprophytica, chlorophyllo carens, usque ad 15 cm alta, caule erecto gracili tereti aurantiaco-rubro simplici vel parte inferiore bifurcato glabroque. *Folia* squamiformia, opposita, decussata, sessilia, vaginantia, membranacea glabraque; squamae caulis parte superiore remotae, usque ad 5 mm longae, internodiis multo breviores, ovatae, apice acuminatae, squamis oppositis basi ca 2 mm connatis; squamae caulis parte inferiore vix breviores, internodiis ± aequantes. *Flores* terminales, solitarii, usque ad 17 mm longi; calyx tubuloso-campanulatus, hyalinus, obtuse 5-angulatus, 5-lobatus, ca 4 mm longus, intus basi 5 squamellis lobis oppositis transverse ellipticis apice emarginatis ca 0.5-0.6 mm latis instructus, lobis subaequalibus apice subacutis ca 1 mm longis et basi ca 0.8 mm latis, sinibus rotundatis; corolla aurantiaca, tubo anguste cylindrico circa ovarium leviter ventricoso fauce vix dilatato ca 10.5 mm longo et ca 2 mm diam, lobis ut videtur patentibus anguste oblongis apice acutis ca 6-6.5 mm longis et ca 1.3 mm latis; antherae sessiles, sub corollae tubi fauce insertae, introrsae, cohaerentes, basi bilobatae, ca 1.5 mm longae (appendicibus inclusis), thecis apice rotundatis basi brevissime appendiculatis appendicibusque vix 0.5 mm et inconspicue puberulis; gynoecium ca 8-9 mm longum, ovario sessili anguste oblongo ca 4.5-5 mm longo et ca 0.5 mm supra basin glandulis 2 oppositis anguste ellipticis ca 1.5 longis instructo, stylo filiformi et ca 3.5-4 mm longo, stigmate 2-lobato et ca 2 mm diam.

PANAMA: BOCAS DEL TORO: Punta Peña, vic of Chiriquicito, alt ca 1000 ft, rain forest, 7 June 1967, *Lewis, Escobar, MacBryde, Oliver & Ridgway 2181* (holotype MO).

The small scales at the base within the calyx, the ovary with 2 basal, narrowly ovoid, opposite glands, and the 2-lobed stigma readily separate *V. bilobata* from all other neotropical species of *Voyria* Aubl. Except for the bilobed stigma, this new species fits very well within the definition of the genus *Voyria* given by A. Raynal in 1967 [Étude critique des genres *Voyria* et *Leiphaimos* (*Gentianaceae*) et révision des *Voyria* d'Afrique. Adansonia, sér. 2, **7**: 53-71]. According to Raynal (p. 64), the stigma of *Voyria* is always entire ("jamais bilabié"), while the stigmas of *Leiphaimos* Schlecht. & Cham. and *Voyriella* (Miquel) Miquel are 2-lobed.

The characters used for separating the saprophytic gentians into supraspecific units differ from one author to another. For Raynal, the genus *Leiphaimos* is separated from *Voyria* by the burmannioid habit of the inflorescence and mainly by the special structure of the stigma (loc. cit. pp. 64-65). For L. O. Williams (Fieldiana: Bot. **31**: 411-415, 1968), *Leiphaimos* can easily be separated from *Voyria* by the winged seeds and the elator-like hairs along the sutures inside the capsule, *Voyria* having wingless seeds and no elator-like hairs in the capsule. The seed character is considered by Raynal to be quite variable (loc. cit. p. 60). In view of these different opinions concerning the delimitation of the saprophytic genera *Voyria* and *Leiphaimos* and in abscence of a comprehensive revision of the

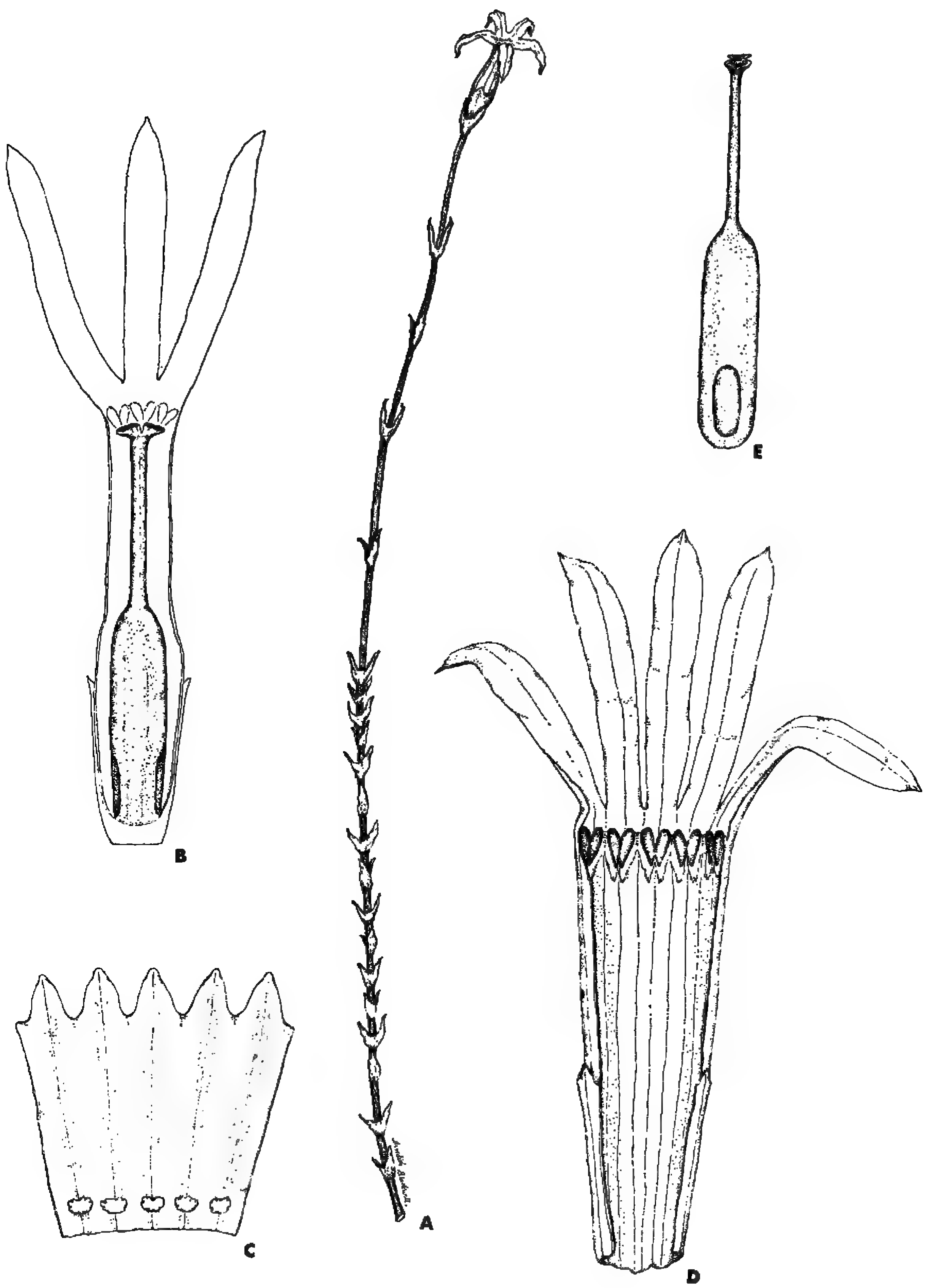

Fig. 1. *Voyria bilobata* A. Robyns: A habit (×1); B, flower, longitudinal section (× 5); C, calyx spread out showing the 5 small scales (× 7½); D, corolla spread out showing the 5 stamens (× 5); E, gynoecium showing 1 gland (× 5). After *Lewis et al. 2181*.

New World saprophytic gentians, I shall treat the genus *Voyria* in the broad sense (sensu lato) in my forthcoming revision of the *Gentianaceae* for the Flora of Panama. Therefore, the following transfer from *Leiphaimos* to *Voyria* is needed:

Voyria **stellata** (Standley) A. Robyns, comb. nov., based on *Leiphaimos stellatus* Standley, Contr. U. S. Nat. Herb. **20:** 197, 1919 (Panama, Venezuela, Brazil, and Peru).—*André Robyns, National Foundation for Scientific Research, Belgium.*

THE FIRST JESSE M. GREENMAN AWARD

The 1968 and first Jesse M. Greenman Award for the best Ph. D. dissertation published in 1967 in plant systematics was awarded to Dr. Carl S. Keener, Assistant Professor of Botany and Curator, Pennsylvania State University. Dr. Keener's paper on "A biosystematic study of *Clematis* subsection *Integrifoliae* (*Ranunculaceae*)" was completed at North Carolina State University at Raleigh and published in the Journal of the Elisha Mitchell Scientific Society **83:** 1-41, 1967.

The Greenman Award of $100 is given annually at the AIBS meetings by the Alumni Association of the Missouri Botanical Garden in honor of Dr. Jesse M. Greenman, the dedicated scholar and teacher who was Curator of the Herbarium from 1913-1945. Papers published in 1968 are being received for consideration by Dr. David M. Gates, Director of the Missouri Botanical Garden, 2315 Tower Grove Avenue, St. Louis, Missouri 63110, until 1 May 1969.—*Editor.*

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ERRATUM

Page 36, line 35. For '*Lewis et al. 1759* (MO)' read '*Lewis et al. 1759* (holotype MO).'

The previous issue of the ANNALS OF THE MISSOURI BOTANICAL GARDEN, Vol. **55**, No. 2, pp. 81-170, was published on October 22, 1968.

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