

REVISED SYNOPSIS OF PANAMANIAN EUPHORBIACEAE¹

Grady L. Webster² and Michael J. Huft³

ABSTRACT

Collections made in the last two decades have added 9 genera and 42 species to the 35 genera and 100 species included in the *Flora of Panama* treatment of the Euphorbiaceae published in 1968. The new taxa and combinations proposed in this paper are *Richeria dressleri* Webster, *Phyllanthus gentryi* Webster, *Tragia correae* Huft, *Dalechampia canescens* Kunth subsp. *friedrichsthali* (Muell. Arg.) Webster & Huft, *Tetrorchidium costaricense* Huft, *Tetrorchidium microphyllum* Huft, *Croton pachypodus* Webster, *Croton speciosus* Muell. Arg. subsp. *tacarcunensis* Webster, *Croton draco* Cham. & Schldl. subsp. *panamensis* (Klotzsch) Webster, *Croton billbergianus* Muell. Arg. subsp. *pyramidalis* (J. D. Smith) Webster, *Croton santaritensis* Huft, *Sebastiania panamensis* Webster, *Gymnanthes dressleri* Webster, and *Gymnanthes farinosa* (Griseb.) Webster. In addition, new or updated keys are provided where appropriate, as well as descriptions and specimen citations.

When the treatment of the Euphorbiaceae for the *Flora of Panama* was originally published (Webster & Burch, 1968), it was anticipated that it would prove to be incomplete, but collections made during the past 20 years show that it was even more provisional than we had thought. Not only has *Pausandra* been found as predicted, but no fewer than nine other genera new to Panama: *Adenophaedra*, *Astrocasia*, *Croizatia*, *Drypetes*, *Gymnanthes*, *Maprounea*, *Richeria*, and *Senefeldera*, and an unpublished genus from Cerro Tacarcuna in Darién; this brings the number of native genera to 45. In addition, species new to Panama have been found in a number of genera, including *Acalypha*, *Alchornea*, *Cleidion*, *Croton*, *Dalechampia*, *Euphorbia*, *Hyeronima*, *Mabea*, *Manihot*, *Sapium*, *Sebastiania*, *Tetrorchidium*, and *Tragia*. The arrangement of genera within the family has become obsolete since the publication of a new classification (Webster, 1975); there are now five subfamilies recognized, of which four occur in Panama. This new treatment, with the order of the genera now following the revised classification, includes the taxa new to Panama as well as references to recent publications on these taxa.

In order to incorporate all of these additions and changes, the generic key has been revised, and new keys to species have been made for several genera. Citations of specimens are not given for species already included in the original treatment unless they represent new records for provinces or considerable range extensions. Descriptions are provided for most species new to Panama, but in a few cases, if the Panamanian material is not adequate for description or if the species has been recently described elsewhere, a literature reference is given in lieu of a description.

The preparation of this paper has involved us in the study of much extra-Panamanian material and has led to the resolution of a number of ancillary taxonomic and distributional problems. We have not hesitated to discuss these additional items where appropriate. The central position of Panama in the Neotropics certainly renders this account of Panamanian Euphorbiaceae of value to an understanding of the family throughout Central America and northern South America. It seems appropriate, therefore, to include peripheral items that, while not concerning Panamanian species directly, are definitely of relevance.

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² Department of Biology, University of California, Davis, California 95616, U.S.A.; primarily responsible for key to genera and new treatments of genera 1, 3, 4, 5, 6, 8, 9, 23, 27, 32, 34, 36, and 37. The treatment of genus 28, *Cnidoscolus*, is furnished by Dr. Gary Breckon, University of Puerto Rico, Mayagüez.

³ Missouri Botanical Garden. Mailing address: Department of Botany, Field Museum of Natural History, Chicago, Illinois 60605, U.S.A.; primarily responsible for new treatments of genera 2, 12, 13, 14, 17, 19, 20, 26, 30, 33, 39, and 42; the treatments of genera 16, 22, and 35 are the joint responsibility of both authors.

KEY TO THE GENERA OF EUPHORBACEAE IN PANAMA

- 1a. Ovules paired in each cell of the ovary; seeds ecarunculate; milky latex absent; leaves unlobed, entire or obscurely toothed, usually without embedded laminar glands; indumentum simple or lepidote. [Subfamily Phyllanthoideae.]
- 2a. Petals present.
- 3a. Petals equalling or longer than the sepals; filaments connate; seeds with copious endosperm 1. *Astrocasia*
- 3b. Petals much shorter than sepals; filaments free or connate; seeds with endosperm scanty or absent.
- 4a. Monoecious; stipules intrapetiole; petals glabrous; styles dilated, bifid; columella tapering from base, not apically winged 2. *Ananoa*
- 4b. Dioecious; stipules not projecting between petiole and stem; petals pubescent; styles twice bifid; columella distally expanded into 3 papery wings 3. *Croizatia*
- 2b. Petals absent.
- 5a. Dioecious; staminate flowers in spikes or racemes, with prominent pistillode.
- 6a. Indumentum simple; calyx deeply lobed, nearly chorisepalous; anther sacs not pendulous; carpels 2 or 3; fruits capsular; seeds fleshy 4. *Richeria*
- 6b. Indumentum mainly lepidote; calyx distinctly gamosepalous; anther sacs pendulous; carpels 2; fruits drupaceous 5. *Hyeronima*
- 5b. Monoecious or dioecious; staminate flowers in axillary clusters (or if racemose, then branchlets deciduous), lacking a prominent pistillode.
- 7a. Staminate flowers with a central (intra-staminal) disk; carpels 1 or 2; styles obsolete, the stigmas dilated; fruits drupaceous; seeds solitary in each locule 6. *Drypetes*
- 7b. Staminate flowers without a central disk; carpels 3–5 or more; styles distinctly bifid, the stigmas slender to dilated; fruits mostly dehiscent; seeds 2 per locule.
- 8a. Carpels 4 or 5 (rarely 3 or 6), irregularly dehiscent; seeds with fleshy bluish outer coat and bony inner coat; staminate flower with annular disk and 4 free stamens; dioecious tree 7. *Margaritaria*
- 8b. Carpels 3 (rarely 2), dehiscent into valves (except in *P. elsiæ*); seeds neither fleshy nor bony; stamens 2 or 3 (or if 4, then disk absent); monoecious or dioecious, the habit various 8. *Phyllanthus*
- 1b. Ovules solitary in each cell of the ovary; seeds carunculate or ecarunculate; sap often colored or milky; leaves often dentate and/or palmately veined or lobed, often with laminar or petiolar glands; indumentum various.
- 9a. Floral bracts not glandular at base (except in *Tetrorchidium*); sepals imbricate to valvate, usually completely covering the anthers in bud; petals present or absent; disk often present; indumentum various; leaves simple to palmately lobed or compound.
- 10a. Petals absent, or if present then leaves pinnately veined; stalked petiolar glands absent (embedded laminar glands often present); pollen grains mostly 3-colporate; seeds mostly ecarunculate (carunculate only in *Ricinus* and *Pera*); indumentum simple or malpighiaceus (lepidote in *Pera*); flowers in axillary clusters, racemes, or spikes (these sometimes aggregated into panicles). [Subfamily Acalyphoideae.]
- 11a. Petals present; flowers in racemes; stamens 10; seeds more or less foveolate.
- 12a. Leaves finely serrate, the lateral veins distinctly parallel; hairs simple or glandular; staminate flowers with pistillode 9. *Caperonia*
- 12b. Leaves entire, the lateral veins not distinctly parallel; hairs malpighiaceus (at least in part); staminate flowers without pistillode 10. *Argythamnia*
- 11b. Petals absent.
- 13a. Flowers neither sessile nor enclosed in a stalked involucre; seeds not carunculate, black, or shiny.
- 14a. Flowers not enclosed in a bilabiate involucre formed by 2 palmately veined bracts.
- 15a. Stamens fasciculate-ramified, anthers numerous; leaves peltate, palmately lobed; inflorescences terminal, paniculate, the pistillate flowers distal; seeds carunculate 18. *Ricinus*
- 15b. Stamens not branched; leaves neither peltate nor palmately lobed; inflorescences otherwise; seeds ecarunculate or the caruncle very small.
- 16a. Staminate sepals valvate; stamens mostly 3 or more (if 2, connectives not enlarged); latex not distinctly reddish or purplish; fruit less than 8 cm across.
- 17a. Stinging hairs absent.
- 18a. Styles free or basally connate; inflorescences unisexual; carpels 2 or 3, not prominently carinate; trees or shrubs, not climbing.

- 19a. Anthers not vermiform; pistillate bracts not strikingly larger or differently shaped from staminate bracts; styles various, often bifid or unlobed (but not slender and lacerate except in *Adelia*).
- 20a. Carpels 3; styles bifid (or if unlobed, then seeds fleshy).
- 21a. Stamens fewer than 10; stipules absent or caducous; dioecious.
- 22a. Pistillode present in staminate flowers; inflorescences axillary; seed coat fleshy; leaves triplinerved 11. *Alchorneopsis*
- 22b. Pistillode absent; inflorescences terminal (at least in part); seed coat not fleshy; leaves pinnately veined.
- 23a. Leaves with laminar glands; staminate disk massive, pulviniform; stamens 4-7; styles elongate; seeds over 1 cm long 12. *Caryodendron*
- 23b. Leaves eglandular; staminate disk absent; stamens 3; styles broadly dilated, stig-
matiform; seeds less than 1 cm long 13. *Adenophaedra*
- 21b. Stamens more than 10; stipules sometimes persistent.
- 24a. Stamens less than 30; anther connective not enlarged; pistillate disk present; stipules thin.
- 25a. Styles 1 or 2 times bifid; pistillate flowers sessile or with short pedicels (less than 5 mm long); leaves with conspicuous foliar glands near base 14. *Bernardia*
- 25b. Styles lacinate; pistillate flowers with long pedicels (at least 20 mm); leaves eglandular 15. *Adelia*
- 24b. Stamens more than 50; anther connective enlarged; pistillate disk absent; stipules indurate 17. *Cleidion*
- 20b. Carpels 2; styles elongate, free, entire; stamens usually 8; seeds tuberculate, ecarunculate, dry; indumentum minutely stellate (at least in part) 16. *Alchornea*
- 19b. Anthers vermiform; styles lacinate; inflorescences spicate; pistillate bracts much larger than the staminate bracts, or else the ovary densely verrucose 19. *Acalypha*
- 18b. Styles connate into a long column; inflorescences bisexual, axillary; carpels 4, prominently carinate; leaves biglandular at base; lianas 20. *Plukenetia*
- 17b. Stinging hairs present; styles unlobed, connate below; disk absent; seeds smooth, ecarunculate.
- 26a. Anthers with apical tuft of stinging hairs; dioecious shrubs or trees; leaves cuneate at base, glabrescent 21. *Acideton*
- 26b. Anthers not apically tufted; monoecious twining vines; leaves cordate at base, copiously pubescent with stinging hairs 22. *Tragia*
- 16b. Staminate sepals 4, imbricate (in 2 whorls); stamens 2, the anther connectives greatly enlarged and fleshy; latex purplish or reddish; fruit pomiform, 8-12 cm across 24. *Omphalea*
- 14b. Inflorescences pseudanthial, bisexual; flowers subtended by a bilabiate involucre of 2 palmately veined (or lobed) bracts; styles connate to the stigmas; ovary and fruit armed with irritating hairs; twining or clambering vines with palmately veined, lobed, or dissected leaves 23. *Dalechampia*
- 13b. Flowers sessile in a stalked globose 2-valved involucre; seeds smooth, black, and shiny, carunculate; dioecious trees, indumentum lepidote 25. *Pera*
- 10b. Petals present, at least in staminate flowers, or else calyx petaloid (except in *Tetrorchidium*, with raised foliar glands, and in *Croton punctatus*); leaves often palmately veined or lobed; petioles or leaf bases often with raised or stalked glands; pollen grains with clavate exine, porate or inaperturate (3-colporate in *Tetrorchidium*); seeds carunculate or fleshy (except in *Garcia*); indumentum simple, malpighiaceae, stellate, or lepidote; latex clear, colored, or milky. [Subfamily Crotonoideae.]
- 27a. Petals absent; stamens 3, the anthers peltate and appearing 4-locellate; pollen grains 3-colporate; seeds fleshy; dioecious shrubs or trees; leaves with stalked petiolar glands and malpighiaceae hairs 26. *Tetrorchidium*

- 27b. Petals present (or else calyx petaloid or indumentum lepidote); stamens 8 or more, the anthers not appearing 4-locellate; pollen grains porate or inaperturate; seeds carunculate (except in *Garcia*), not fleshy.
- 28a. Petals absent; calyx petaloid; leaves palmately lobed; indumentum simple; latex milky; pollen grains porate; monoecious, the inflorescences terminal, dichasial or paniculate.
- 29a. Stinging hairs absent; calyx yellowish or greenish to purplish; stamens free; disk central and intrastaminal 27. *Manihot*
- 29b. Stinging hairs present (sometimes very sparse); calyx whitish; stamens connate; disk extrastaminal 28. *Cnidoscolus*
- 28b. Petals present (or else indumentum lepidote); latex not distinctly milky; pollen grains inaperturate.
- 30a. Anthers more or less erect in bud; indumentum neither stellate nor lepidote.
- 31a. Calyx of imbricate sepals; stamens not more than 12; staminate petals normally 5; seeds carunculate.
- 32a. Leaves palmately veined or lobed; stamens mostly 8-12, the filaments connate; monoecious, the inflorescences terminal, dichasial; indumentum simple or of more or less branched glandular setae 29. *Jatropha*
- 32b. Leaves pinnately veined; stamens 3-7, the filaments free; dioecious, the inflorescences axillary, spiciform; indumentum malpighiaceus 30. *Pausandra*
- 31b. Calyx rupturing into valvate segments; stamens 30-100 or more; staminate petals 6-13; seeds ecarunculate; monoecious shrubs or trees; indumentum simple 31. *Garcia*
- 30b. Anthers inflexed in the bud, the stamens 8-50 or more, free; indumentum (at least in part) stellate or lepidote; monoecious (in Panamanian taxa), the inflorescences mostly bisexual, racemose or spicate; seeds carunculate 32. *Croton*
- 9b. Floral bracts biglandular at base; sepals imbricate or reduced; anthers mostly not covered in the bud; petals absent; calyx not petaloid; disk reduced or absent; leaves unlobed; indumentum simple or absent (dendritic in *Mabea*); pollen grains tricolporate, tectate; styles unlobed (or else inflorescence a pseudanthium). [Subfamily Euphorbioideae.]
- 33a. Inflorescences spicate, racemose, or paniculate, not pseudanthial with a gamophyllous involucre; styles unlobed.
- 34a. Inflorescences thyrsoid or paniculate; stamens subsessile on an elevated receptacle.
- 35a. Indumentum dendritic; stylar column elongated; staminate flowers long-pedicellate, 2 or more per node; stamens (in ours) 10 or more 33. *Mabea*
- 35b. Indumentum absent; styles nearly free; staminate flowers subsessile, solitary at each node; stamens (in ours) 5 34. *Senefeldera*
- 34b. Inflorescences spicate or racemose; stamens with filaments mostly well developed.
- 36a. Stylar column less than 2.5 cm long, diverging into slender tips; staminate flowers in glomerules, not rupturing bracts at anthesis.
- 37a. Ovary (2-3-locular; fruits capsular).
- 38a. Seeds carunculate, the seed coat dry; petioles eglandular; pistillate sepals free.
- 39a. Columella without persistent 3-pronged gynobase; milky latex scanty (or perhaps sometimes absent); leaves without raised or stalked glands.
- 40a. Staminate part of inflorescence elongated; seeds with small caruncle.
- 41a. Spikes terminal or opposite the leaves; staminate calyx 3-lobed; ovary 6-cornute; fruiting pedicels less than 5 mm long 35. *Sebastiania*
- 41b. Spikes axillary; staminate calyx of 1 segment or absent; ovary smooth; fruiting pedicels more than 10 mm long 36. *Gymnanthes*
- 40b. Staminate part of inflorescence contracted, subglobose; stamens and styles distinctly connate; seeds foveolate, with large calyprate caruncle 37. *Maprounea*
- 39b. Columella with persistent 3-pronged gynobase; milky latex usually copious; leaves with paired basal cyathiform glands; seeds (in ours) with small caruncle 38. *Stillingia*
- 38b. Seeds ecarunculate, the coat fleshy; petioles usually with a pair of projecting or stipitate glands; calyces distinctly gamophyllous; stamens 2 39. *Sapium*
- 37b. Ovary 6-9-locular; fruits drupaceous; seeds ecarunculate; pistillate calyx 3-parted 40. *Hippomane*
- 36b. Stylar column at least 2.5 cm long, terminating in a lobed, fleshy disk 2-3 cm wide; staminate flowers aggregated into a fleshy cone; carpels more than 5 41. *Hura*

- 33b. Inflorescences pseudanthial, i.e., the 5 involucre bracts fused into a cupular cyathium; pistillate flower solitary, terminal, the staminate flowers each with a single stamen, in 5 lateral cymes; styles usually bifid; milky latex copious; seeds (in Panamanian taxa) ecarunculate or minutely carunculate.
- 42a. Cyathia more or less radially symmetrical, with glands alternating with bract tips (lobes) around rim; styles free or nearly so.
- 43a. Leaves alternate, opposite, or whorled (but if opposite then not inequilateral at base); stipules (in Panamanian taxa) obsolete or glanduliform; veins not chlorenchyma-sheathed; main axis not precociously aborting 42. *Euphorbia*
- 43b. Leaves opposite, stipulate, inequilateral at base, the veins with chlorenchyma sheaths; main axis aborting just above the cotyledons 43. *Chamaesyce*
- 42b. Cyathia reddish, bilaterally symmetrical, the involucre glands hidden within the nectar spur; styles connate into a long column 44. *Pedilanthus*

ENUMERATION OF TAXA

Subfamily I. PHYLLANTHOIDEAE Asch.

1. *Astrocasia*

Astrocasia Robinson & Millsp., Bot. Jahrb. Syst. 36, Beibl. 80: 19. 1905. TYPE: *Astrocasia phyllanthoides* Robinson & Millsp. = *Astrocasia tremula* (Griseb.) Webster.

Diocious, glabrous trees or shrubs. Leaves alternate, petiolate; stipules ribbed, deciduous; blades entire, pinnately veined. Inflorescences axillary; flowers in clusters. Staminate flowers pedicellate; sepals 5, sometimes unequal; petals 5, longer than the sepals; disk annular; stamens 3 or 5, the filaments connate into a column, anthers extrorse in bud, dehiscing horizontally; pollen grains tricolporate, reticulate; pistillode dilated at tip into a peltate disk capping the staminal column. Pistillate flowers long-pedicellate; sepals 5, articulated, deciduous; petals 5, longer than sepals; disk cupuliform, surrounding the ovary; ovary of 3 or 5 carpels; ovules 2 per locule, anatropous; styles free, bifid. Fruits capsular; columella slender, persistent; seeds 1 or 2 per locule, ecarunculate; seed coat dry, thin, smooth; raphe conspicuous; endosperm copious; embryo straight; cotyledons thin, flat, much longer and broader than the radicle.

This neotropical genus of four species was not reported from Panama in the original treatment. *Astrocasia* is one of the more primitive genera of Euphorbiaceae and has its closest relatives in Africa and Madagascar (*Heywoodia* Sim, *Wielandia* Bailon).

1.1. *Astrocasia tremula* (Griseb.) Webster, J. Arnold Arbor. 39: 208. 1958. *Phyllanthus tremulus* Griseb., Fl. Brit. W.I. 34. 1859. TYPE: Jamaica: Purdie, Wulfschlaegel (syn-types, K).

Astrocasia phyllanthoides Robinson & Millsp., Bot. Jahrb. Syst. 36, Beibl. 80: 19. 1905. TYPE: Mexico. Yucatán: Mérida, Seler 3943 (holotype, F).

Shrub or tree 2–10 m high; branches terete or obscurely angled, pale; foliage deciduous. Leaves with slender petioles 2–6 cm long; stipules lanceolate, chartaceous, 4–6 mm long; blades chartaceous, ovate, acute or obtuse at tip, broadly cuneate at base, 5–12 cm long, 3–7.5 cm broad; major veins 5–8 on a side, ascending, brochidodromous; veinlets prominulous beneath; margins narrowly revolute. Flower clusters axillary, staminate and pistillate on separate plants (or on separate branches of the same plant). Staminate flow-

ers with pedicels 8–15 mm long; sepals broadly elliptic to obovate, entire, 1.2–1.5 mm long, 1.2–1.8 mm broad; petals elliptic-lanceolate, 2.4–2.7 mm long, 0.8–1.1 mm broad; disk cupuliform, fluted, 0.4–0.5 mm high, 0.9–1 mm broad; androecium 0.7–0.9 mm across; stamens 5; anthers 0.4 mm across; pistillode head circular, 0.5–0.6 mm across. *Pistillate flowers* with slender pedicels becoming 2.5–5.5 cm long; sepals suborbicular to elliptic, 2–2.2 mm long, 1.8–2 mm broad; disk cupuliform, its margin undulate, ca. 1 mm high and 2 mm broad; styles thickened, 0.6 mm long, bifid, the tips clavate. *Fruits* obovate, 3-angled, reticulate-venose, cocci ribbed on back; columella cylindric, 3.2–3.5 mm long; seeds plano-convex, smooth, yellowish, 4.4–5 mm long, 3.8–4 mm broad.

The recent discovery of *Astrocasia* in Panama is one of the most surprising additions to the flora, particularly since it was found near Madden Dam in what is surely one of the most heavily botanized locations in the country. *Astrocasia tremula* has a broad but greatly disjunct distribution from Mexico and Jamaica to Colombia, Venezuela, and Brazil. The Madden Dam locality, however, is the only known station in Central America south of Belize and Guatemala.

Specimens examined. PANAMA. COLÓN: forests along shores of Madden Lake, near Madden Dam, 50 m, *Knapp 1299* (DAV, F, MO), *Witherspoon 8805* (DAV, MO); 6 km N of Chilibre, along Madden Lake, *Knapp 2715* (MO).

2. *Amanoa*

Amanoa Aublet, Hist. Pl. Guiane 256. 1775.
TYPE: *Amanoa guianensis* Aublet.

2.1. *Amanoa guianensis* Aublet, Hist. Pl. Guiane 256. 1775. TYPE: French Guiana: *Aublet* (possibly at BM, not seen).

Additional specimens examined. PANAMA. COLÓN: along Río Chagres and associated tidal channels off side road 9 km from Fort Lorenzo turnoff, 9°40'N, 80°03'W, sea level, *Knapp 1329* (F, MO). SAN BLAS: along Río Armilo, W of Puerto Obaldía, ca. 8°40'N, 77°25'W, sea level, *McPherson 6944* (F, MO).

3. *Croizatia*

Croizatia Steyerl., Fieldiana, Bot. 28: 308, fig. 57. 1952. TYPE: *Croizatia neotropica* Steyerl.

Dioecious trees or shrubs; indumentum simple. Leaves alternate, petiolate; stipules persistent or deciduous; blades entire, pinnately veined, without

embedded glands. *Flowers* in axillary clusters. *Staminate flowers* pedicellate; sepals 5, imbricate; petals 5, much shorter than sepals, pubescent; disk annular; stamens 5, free or connate, the anthers $\pm$ introrse; pollen grains 3-colporate, the sexine echinate; pistillode 3-fid. *Pistillate flowers* pedicellate; sepals 5, imbricate; petals 5, much shorter than sepals, pubescent; disk annular; ovary pubescent; styles free, twice bifid; ovules paired in each locule, hemitropous. *Fruits* capsular; columella distally expanded into 3 broad papery wings; seeds paired or solitary in each locule, smooth, not fleshy, ecarunculate; endosperm absent; cotyledons greenish, contortuplicate, much broader than and about as long as the radicle.

LITERATURE

WEBSTER, G. L., L. GILLESPIE & J. STEYERMARK. 1987. Systematics of *Croizatia* (Euphorbiaceae). Syst. Bot. 12: 1–8.

The affinities of this small neotropical genus of three species have remained questionable because of fragmentary material. The recent discovery of staminate flowers of *Croizatia naiguatensis* Steyerl. (Webster et al., 1987) has not made it possible to determine the affinities of the genus more closely. In the protologue to the original description of *Croizatia*, Steyerl. proposed a relationship to the Old World genus *Actephila* Blume on the basis of a suggestion by Dr. Leon Croizat. That suggestion seems very perceptive, as there is a clear resemblance to that genus in details of habit, flower, and fruit. On the basis of gross morphology, *Croizatia* can be maintained as a genus distinct from *Actephila*, especially by virtue of its pubescent petals and ovary and its twice-bifid styles. In this latter character it is similar to the African *Pentabrachium* Muell. Arg.; however, in the African genus the seeds have abundant endosperm and the embryo is not contorted as in *Croizatia*. The echinate pollen grains of *Croizatia* are very different from those of *Actephila* or *Pentabrachium* and indicate a possible closer affinity to genera in subfamily Oldfieldioideae.

3.1. *Croizatia panamensis* Webster, Syst. Bot. 12: 7. 1987. TYPE: Panama. Panamá: primary forest along road from El Llano to Cartí-Tupile, 300–500 m, 30 Mar. 1973, *Liesner 1279* (holotype, MO; isotype, DAV).

Shrub or small tree 1–6 m high, usually with a single main stem. Leaves with petioles 0.5–1 cm long, 3–4 mm thick; stipules $\pm$ persistent, oblong-lanceolate, acuminate, ribbed, sericeous, 10–20

mm long, 6–7 mm broad; blades chartaceous, glabrous or sparsely strigose-hispidulous beneath, obovate, abruptly short-acuminate, basally attenuate, 22–47 cm long, 5–15 cm broad, with ca. 15 arcuate-ascending lateral nerves connected by intramarginal loops, the veins and (to some extent) veinlets prominent beneath. *Staminate flowers* with sparsely pubescent pedicels 3–4 mm long; sepals (4–)5, elliptic, entire, 1.7–2.5 mm long, 1–1.5 mm broad; stamens 5, the filaments 2–4 mm long, connate at the base for 0.5–1.5 mm, the column long-pubescent; anthers 0.6–0.8 mm long; pistillode 1.5–2.5 mm long. *Pistillate flowers* with pubescent pedicels ca. 1.5 cm long, becoming 2.5–3.5 cm long in fruit; sepals 5, elliptic-lanceolate, $\pm$ acute, 8–12 mm long, 3–4 mm broad, hispidulous without, persistent and becoming reflexed in fruit; ovary 3.5–5 mm diam., densely hirsutulous; styles 3, 3–4 mm long, connate basally into a column ca. 1 mm high, three times bifid. *Fruit* capsular, 10–15 mm broad; columella ca. 8–9 mm high, 10–11 mm broad; seeds trigonous, smooth, brownish, 7.2–10 mm long, 5.3–6.5 mm broad.

Rainforests, Panama and Colombia.

This more complete species description of *Croizatia panamensis* has been made possible by recently collected flowering specimens and data provided by Dr. Gordon McPherson. It is now apparent that *C. panamensis* is clearly different from *C. naiguatensis* in floral characters: staminate flowers with stamens connate in *C. panamensis* (free in *C. naiguatensis*), staminate petals more long-ciliate and styles more divided in *C. panamensis*. Since flowering material of *C. neotropica* is still unknown, it remains difficult to assess its relationships with *C. panamensis*.

Additional specimens examined. PANAMA. SAN BLAS: near road from El Llano to Cartí, beyond Nusagandí, along divide trail to east, 9°15'N, 79°00'W, ca. 300 m (fr), McPherson 11037 (DAV, MO), (fl, pistillate), 11040 (DAV, MO), (fl, staminate), 11041 (DAV, MO).

4. *Richeria*

Richeria Vahl, *Eclog. Amer.* 1: 30, tab. 4. 1797.
TYPE: *Richeria grandis* Vahl.

Trees or shrubs; dioecious; indumentum simple or absent. *Leaves* alternate, petiolate; stipules deciduous; blades entire or distantly crenulate, pinately veined, sometimes with basal laminar glands. *Inflorescences* axillary, racemose or spicate; staminate flowers several per bract in sessile or pedunculate glomerules; pistillate bracts subtending solitary flowers; flowers apetalous. *Staminate flow-*

ers sessile; calyx 3–5-lobed, the lobes imbricate; disk segments 3–5; stamens 3–6, free; filaments exerted from calyx; anthers introrse, $\pm$ versatile, dehiscing longitudinally; connective not enlarged; pollen grains prolate, 3-colporate, semitectate, reticulate; pistillode present. *Pistillate flowers* pedicellate; calyx 3–5-lobed, the lobes imbricate; disk cupulate; ovary 3-locular, glabrous or pubescent; styles short, bifid; ovules 2 per locule, anatropous. *Fruits* capsular (somewhat fleshy and tardily dehiscent); columella slender, upwardly dilated, with papery wings; seeds solitary in each locule, ecarunculate, the outer testa fleshy; endosperm present; cotyledons broad, plane, basally cordate.

A neotropical genus of five closely related species, previously unreported from mainland North America. *Richeria* appears to be most closely related to the African genus *Maesobotrya* Benth. and to *Aporosa* Blume of southeastern Asia and Malaysia. The circumscription of the genus adopted here differs from that of Mueller (1866) and Jablonski (1967), since section *Podocalyx* (Klotzsch) Muell. Arg. (based on *Richeria loranthoides* (Klotzsch) Muell. Arg.) should be segregated as the monotypic genus *Podocalyx* Klotzsch, which, in fact (as indicated by the spinose pollen), belongs in the subfamily Oldfieldioideae rather than the Phyllanthoideae.

There are two species of *Richeria* in Panama, neither previously reported.

KEY TO THE SPECIES OF *RICHERIA* IN PANAMA

- 1a. Carpels 3; capsules glabrous; styles suppressed (stigmas sessile); leaves obtuse or rounded at tip, glabrous or nearly so; stipules less than 1 cm long, lanceolate 1. *R. obovata*
- 1b. Carpels 2; capsules distinctly puberulent; styles ca. 1.5 mm long; leaves acuminate at tip, pubescent abaxially; stipules over 1 cm long, foliaceous 2. *R. dressleri*

4.1. *Richeria obovata* (Muell. Arg.) Pax & K. Hoffm., *Pflanzenreich* IV. 147. XV(Heft 81): 29. 1922; Jablonski, *Mem. New York Bot. Gard.* 17(1): 126. 1967. *Richeria grandis* $\S$ *obovata* Muell. Arg. in DC., *Prodr.* 15(2): 468. 1866; Fl. Bras. 11(2): 16. 1873. TYPE: "Brazil," Rio Casiquiari, *Spruce* 3526 (not seen).

A species description is not offered here, since the Panamanian specimens are incomplete, and it is not possible to expand the description of Pax & Hoffmann. In the absence of flowers, it is not entirely certain that the Panamanian specimens belong with those cited by Jablonski from montane

rain forests in the states of Bolívar and Amazonas, Venezuela.

Specimens examined. PANAMA. PANAMÁ: ca. 5–6 mi. N of El Llano, 1,300 ft., *Gentry 5796* (GH, MO, SCZ). VERAGUAS: cloud forest, Cerro Tute, NW of Santa Fe, *Mori & Kallunki 5264* (DAV, MO).

4.2. *Richeria dressleri* Webster, sp. nov. TYPE:

Panama. Panamá: Santa Rita Ridge, road to Estación Calibrar el Agua Clara, 9°22'N, 79°42–45'W, 1,000–1,500 ft., 26 June 1971, *Webster & Dressler 16744* (holotype, DAV; isotype, MO).

Species haec ab congeneribus differt stylis elongatis, capsulis 2-locularis; foliis acuminatis eglandulosis, integris, subtus puberulis; ovario sericeo-hispido.

Tree to 15 m high, 3.5 dm thick; twigs terete, mostly densely appressed-hirtellous when young, eventually glabrate; foliage evergreen. *Leaves* with hirtellous petioles 1.5–5 cm long; stipules lanceolate, 1–1.5 cm long, densely sericeous, caducous; blades chartaceous, obovate, mostly abruptly acuminate, at base narrowly cuneate and decurrent on the petiole, 10–30 cm long, 4–14 cm broad; major veins mostly 10–12 on a side, straight, brochidodromous, the midrib saliently raised beneath; secondaries archingly and irregularly scalariform; ultimate veinlets fine, scarcely prominent; surface of blade above glabrous and flecked or pitted with minute colored spots, beneath bronze-colored and densely to sparsely hirtellous (becoming glabrate in age except along midrib and larger veins); margins entire, plane or recurved. *Inflorescences* spiciform; staminate spikes 1.5–5.5 cm long, pistillate spikes 1.5–7 cm long; axes densely hirsutulous without. *Staminate flowers* sessile; calyx deeply 4–5-lobed, densely hirsutulous without; calyx lobes oblong to obovate or suborbicular, unequal, the larger ones 1.4–1.8 mm long, 1.2–1.5 mm broad, the smaller ones 1.2–1.5 mm long, ca. 1 mm broad; disk segments 5, erect, cylindrical-prismatic, apically hirtellous, 0.2–0.3 mm high; stamens 5(–6); filaments free, 2–3 mm long; anthers ellipsoid, ca. 0.4 mm long; pistillode cylindrical, densely hirtellous, 1–1.2 mm high, 0.6–0.9 mm broad. *Pistillate flowers* subsessile; sepals mostly 4(–5), elliptic, tomentulose outside, sericeous within, 1.5–2 mm long, 0.8–1.3 mm broad; disk entire, adnate, ciliate-margined, ca. 1.5 mm across; ovary of 2 carpels, sericeous; styles stout, 2- or 3-fid, 1.5–1.7 mm long. *Capsules* ellipsoid, reddish, smoothish (not venose), ca. 10–13 mm long, 6–9 mm broad; columella flattened, papery-winged, 11–12 mm long; seeds somewhat asym-

metrically ovoid-ellipsoid, tapering to an obtuse beak, with reddish, fleshy ribbed-striate exotesta, 8.3–9 mm long, 4.8–5.3 mm broad.

This species is sharply characterized within *Richeria* by its 2-carpellate densely sericeous gynoecium with distinct styles; the staminate flowers are similar to those of *Richeria grandis* but differ in the more slender cylindrical pistillode. The acuminate leaves often copiously hirtellous beneath and the large foliaceous stipules also appear distinctive. The collections from Costa Rica are morphologically divergent but may tentatively be grouped with the Panamanian plants. It seems appropriate to name this species in honor of the collector of the type specimen, Dr. Robert Dressler, formerly of the Smithsonian Tropical Research Institute, since he has made a significant contribution to our knowledge of Mesoamerican Euphorbiaceae through his many collections and his monographs of *Pedilanthus* (Dressler, 1957) and *Euphorbia* subgenus *Poinsettia* (Dressler, 1961).

Additional specimens examined. COSTA RICA. HEREDIA: Finca La Selva, the OTS Field Station on the Río Puerto Viejo just E of its junction with the Río Sarapiquí, 100–450 m, *Grayum & Perry 1447* (F), *Hammel 8689*, 8833 (F), *Jacobs 2179* (F). PUNTARENAS: on road to radio and telecommunications tower 6 km N of Golfito, 300–400 m, *Utley & Utley 4902* (F). PANAMA. COCLÉ: near El Valle de Antón, ca. 8°37'N, 80°07'W, ca. 550 m, *McPherson 7616* (F). COLÓN: Santa Rita lumber road, 15 km E of Colón, *Dressler & Williams 3968* (MO). PANAMÁ: rainforest along El Llano-Cartí road, 4.6–8.2 mi. N of Panamerican Highway, 350–450 m, *D'Arcy 11496* (MO, dupl. at SCZ seen by M. Huft), *Gentry 5076* (MO), *Hammel 7350* (MO), *Knapp 5929* (DAV, F, MO), *McPherson 9959* (F, MO), *Mori & Kallunki 5607* (DAV, MO). SAN BLAS: Cerro Brewster, 9°18'N, 79°16'W, 850 m, *de Nevers et al. 5414* (F).

5. *Hyeronima*

Hyeronima Allemão, Pl. Novas Brasil 1. 1848.

TYPE: *Hyeronima alchorneoides* Allemão.

A number of collections made in cloud forests in Panama indicate that there is at least one additional taxon of *Hyeronima* besides the lowland *H. laxiflora*. However, as often happens, these additional specimens have increased the difficulties taxonomically; the following revised treatment is highly tentative pending revisionary studies of this poorly understood genus.

KEY TO THE SPECIES OF *HYERONIMA* IN PANAMA

- 1a. Stamens 4; pistillode slender, bifid, 0.7–0.8 mm high; leaves sparsely lepidote; blades mostly 10–30 cm long with petioles of 3–9 cm; stipules

5–15 mm long; ovary densely lepidote; endocarp of fruit not over 3.5 mm long

..... 1. *H. laxiflora*

- 1b. Stamens 5; pistillode stout, not bifid, to 0.5 mm high; leaves sparsely to densely lepidote beneath; blades mostly 5–10 cm long with petioles of 1–2 cm; stipules apparently obsolete; ovary glabrous to lepidote; endocarp of fruit at least 4 mm long 2. *H. oblonga*

5.1 *Hyeronima laxiflora* (Tul.) Muell. Arg., Linnaea 34: 67. 1865. *Stilaginella laxiflora* Tul., Ann. Sci. Nat. Bot. III, 15: 244. 1851. TYPE: Guyana: “British Guiana,” Schomburgk 879, Hostmann 391 (syntypes, P).

The specimens originally cited under this name were correctly referred to *H. laxiflora*, which is apparently widespread in lowland rain forests in northern South America. All of the lowland populations of *Hyeronima* in Panama belong to this species.

5.2 *Hyeronima oblonga* (Tul.) Muell. Arg., Linnaea 34: 66. 1865; in DC., Prodr. 15(2): 271. 1866. *Stilaginella oblonga* Tul., Ann. Sci. Nat. Bot. III, 15: 248. 1851. TYPE: Guyana: “British Guyana,” Schomburgk 805 (P, not seen).

Stilaginella benthamii Tul., Ann. Sci. Nat. Bot. III, 15: 247. 1851. *H. oblonga* (Tul.) Muell. Arg. var. *benthamii* (Tul.) Muell. Arg., Linnaea 34: 66. 1865. SYNTYPES: Mexico. Oaxaca: Hartweg 513 (P), Galcott 7240 (P).

Hieronyma guatemalensis J. D. Smith, Bot. Gaz. (Crawfordsville) 54: 241. 1912. TYPE: Guatemala. Alta Verapaz: Tuerckheim 423, II 2228 (not seen).

Tree to 10 m high; young twigs angled, densely lepidote (scales ca. 0.15–0.25 mm across). Leaves with petioles mostly 10–15 mm long; stipules apparently absent; blades mostly obovate, abruptly cuspidate or short-acuminate, cuneate at base, generally 4–8 cm long, 2.5–5 cm broad; major veins ca. 5–7 on a side, divergent, straight, brochidodromous; midrib and veins raised beneath and $\pm$ hirsutulous, the veins and veinlets distinctly prominent above (upper surface scabrous to the touch); lepidote scales on upper surface scattered to absent, ca. 0.1–0.2 mm across, with reddish center, beneath sparse to dense and overlapping, ca. 0.2–0.25 mm across, with pale center (lower leaf surface much paler than upper). Panicles densely lepidote with whitish scales; lateral axes mostly 2–4, the staminate ones 5–10 cm long, the pistillate ones ca. 1.5–2.5 cm long; bracts densely lepidote, acute, ca. 0.7–1 mm long. Staminate flowers with rigid stout pedicels ca. 0.4–1.2 mm long; calyx

cupulate, shallowly 5-lobed, 1–1.4 mm high, densely lepidote; disk massive, 0.6–0.8 mm high, densely lepidote on top. Pistillate flowers subsessile (pedicels equaling or shorter than the bracts); calyx cupulate, shallowly 5-lobed, densely lepidote, 1–1.3 mm high; disk cupulate, subentire, glabrous, ca. 0.4–0.5 mm high; ovary ovoid, ca. 1.5 mm high, glabrous or nearly so; stigmas punctiform. Fruits ellipsoid, acute at both ends, coarsely bullate-rugose, 5–6 mm long (endocarp 4–5.5 mm long).

Montane rainforests, Guatemala to Panama and South America.

With some reluctance we are referring all of the high-elevation (cloud forest) populations of *Hyeronima* in Panama to a single species. There is a striking amount of variation in pubescence, and the literature might lead one to recognize two, three, or even more species. Plants with densely lepidote leaves, pale inflorescence axes, and the ovary glabrous or nearly so could be referred to *H. scabrida* (Tul.) Muell. Arg., and plants with sparsely lepidote leaves and densely lepidote ovary to *H. oblonga* s. str. However, specimens from Darién in particular have the pale inflorescence axes of *H. scabrida* combined with the sparsely lepidote leaves of *H. oblonga*. Both “species” occur in the vicinity of El Valle. Plants from the vicinity of Cerro Campana, divergent in having densely lepidote leaves (with prominent venation above) and larger flowers, appear to match the descriptions of *H. oblonga* var. *benthamii* (Tul.) Muell. Arg. However, it is not clear whether that variety can be satisfactorily delimited from other populations. Only critical field studies can establish whether the broad delimitation of *H. oblonga* adopted here is correct.

Representative specimens examined. PANAMA. BOCAS DEL TORO: between Criollo and Quebrada Higuérón on Chiriquí Trail, Kirkbride & Duke 783 (MO). CHIRIQUÍ: Cerro Hornitos, ca. 40 km NW of Gualaca, 2,238 m, Mori & Bolten 7505, 7514 (DAV, MO); Cerro Pate Macho, 4 km NE of Boquete, Sytsma et al. 4868 (MO). COCLÉ: La Mesa, 2.5 km N of El Valle, 850 m, Mori et al. 6610 (DAV, MO); hill 3 km E of El Valle, 2,500 ft., Hammel 4776 (MO); swampy area 5 mi. from El Valle, Gentry & Dwyer 3622 (DAV, MO); foothills of Cerro Pilón, Duke & Correa 14675 (MO). DARIÉN: Cerro Mali, 1,400 m, Gentry & Mori 13629 (DAV, MO); Cerro Tacarcuna, 1,800–1,850 m, Gentry & Mori 13989, 14025 (DAV, MO). PANAMÁ: Cerro Campana, Webster & Breckon 16490 (DAV). VERAGUAS: 3–4 km W of Santa Fe, 2,500 ft., Nee 11315 (DAV, MO); summit of Cerro Arizona, N of Santa Fe, 4,700 ft., Hammel 4741 (MO); Cerro Tute, just W of Santa Fe, Knapp & Dressler 5390 (MO).

6. *Drypetes*

Drypetes Vahl, *Eclog. Amer.* 3: 49. 1807. TYPE:
Drypetes glauca Vahl.

Trees or shrubs, dioecious; indumentum absent or of simple hairs. Leaves alternate, short-petiolate, stipulate; the blades often coriaceous, entire to serrate. Inflorescences axillary; flowers in axillary clusters, sometimes cauliflorous. Flowers apetalous; sepals usually 4 or 5, imbricate, deciduous. Staminate flowers sessile to pedicellate, with intrastaminal disk; stamens mostly 4–5(–50), filaments free; anthers basifixed, extrorse to introrse; pollen grains tricolporate, reticulate; pistillode present or absent. Pistillate flowers pedicellate; disk cupuliform; ovary of 1 or 2 (rarely 3 or 4) carpels; styles obsolete or nearly so, dilated stigmas capping the ovary; ovules 2 in each locule, anatropous. Fruits indehiscent, $\pm$ drupaceous, the exocarp fleshy or leathery, the endocarp crustaceous or bony; seeds usually solitary in each locule, ecarunculate, the testa smooth; endosperm copious; embryo straight, the cotyledons broad and flat.

A large circumtropical genus of about 150 species, best represented in the Old World; about 20 neotropical species have been described. The single Panamanian species was discovered on Barro Colorado Island shortly after the publication of our original treatment.

LITERATURE

WEBSTER, G. L. 1977. A new species of *Drypetes* (Euphorbiaceae) from Panama. *Madroño* 24: 65–68.

6.1. *Drypetes standleyi* Webster, *Madroño* 24: 65, fig. 1. 1977; Croat, *Fl. Barro Colorado I.* 529, fig. 321. 1978. TYPE: Panama. Canal Zone: Barro Colorado I., Armour Trail, Foster & Croat 2307 (holotype, DAV; isotypes, DUKE, F, F neg. 62358, MO).

Recent collections indicate that *Drypetes standleyi* may occur over a broad area in Panama. A barren collection from the Burica Peninsula, Chiriquí Province (Busey 602, MO) may possibly represent *D. standleyi*, although it differs from the other collections in its stiffer leaves with a more prominent veinlet reticulum. The species may also occur in Costa Rica; a specimen from La Selva (Hartshorn 1009, DAV) resembles *D. standleyi*, although it is divergent in having more slender pistillate pedicels.

Additional specimens examined. PANAMA. PANAMÁ: Barro Colorado I., Armour Trail, Foster & Croat 2308 (DAV); vicinity of Armour Trail, Croat 14843, 14849, 16516 (DAV, MO); S of Zetek 11, Foster 1122 (DAV, DUKE, MO). COLÓN: Santa Rita lumber road, 9.4 km from Transisthmian Highway, Dressler 3810 (MO). VERAGUAS: Alto Piedra Santa Fe, Lao & Maasola 480 (MO); Cerro Tute, Mori et al. 7541 (MO).

7. *Margaritaria*

Margaritaria L. f., *Suppl. Pl.* 66. 1782. TYPE:
Margaritaria nobilis L. f.

RECENT LITERATURE

WEBSTER, G. L. 1979. A revision of *Margaritaria* (Euphorbiaceae). *J. Arnold Arbor.* 60: 403–444.

8. *Phyllanthus*

Phyllanthus L., *Sp. Pl.* 981. 1753. LECTOTYPE:
Phyllanthus niruri L. (chosen by Small in Britton & Brown, Ill. Fl. N. U.S. edition 2, 2: 453. 1913).

RECENT LITERATURE

BANCILHON, L. 1971. Contribution à l'étude taxonomique du genre *Phyllanthus* (Euphorbiacées). *Boissiera* 18: 1–81.

8.11. *Phyllanthus anisolobus* Muell. Arg. in DC., *Prodr.* 15(2): 382. 1866. TYPE: Peru: Pavón (holotype, G).

The collection from La Palma, Darién (Pittier 6600, US) mentioned with doubt in 1968 now appears to represent *Phyllanthus anisolobus* on the basis of its resemblance to the Darién specimens cited below.

Additional specimens examined. PANAMA. BOCAS DEL TORO: Río Teribe, below Puerto Palenque, Kirkbride & Duke 553 (MO). DARIÉN: Manené, Kirkbride & Bristan 1592 (MO); Río Balsa, between Manené and Guayabo, Duke & Nickerson 14958 (MO); Río Pucuro, between Cerro Mali and Cerro Tacarcuna, Gentry & Mori 13861 (MO). VERAGUAS: 2–5 km NW of Santa Fe on road to Río Calovébora, 500–700 m, Hernández et al. 744 (F).

8.12. *Phyllanthus gentryi* Webster, sp. nov.
TYPE: Panama. Darién: lower slopes of Cerro Pirre, 200–500 m, Gentry & Clewell 7017 (holotype, F, F neg. 62354; isotypes, DAV, MO). Figure 1.

Species haec aff. *P. juglandifolio* sed ab subsp. *juglandifolio* differt foliis seminibus grandioribus, ab subsp. *cornifolio* differt staminibus 3, stipulis longioribus, ab ambibus differt disco non rugoso, columna stylari brevior.

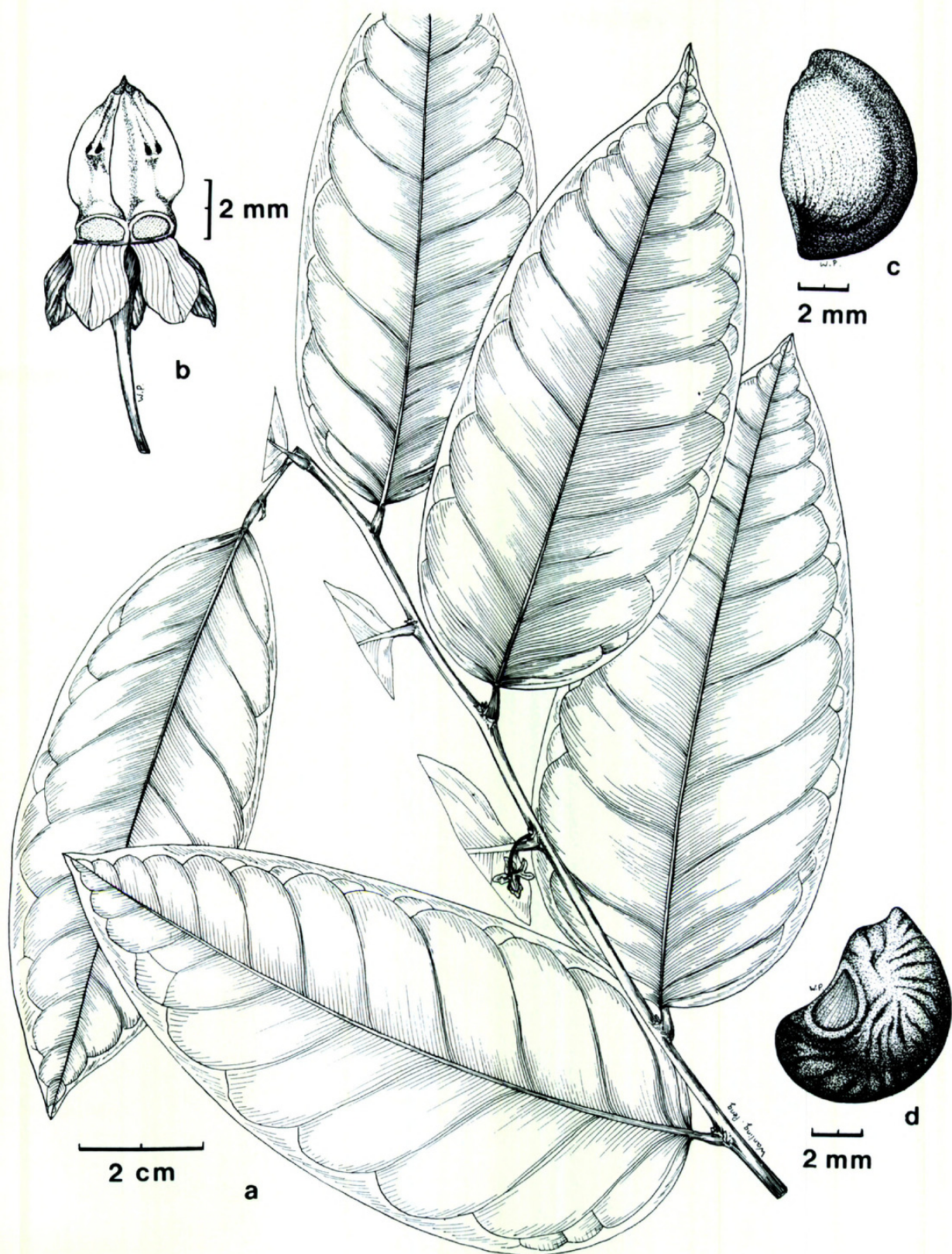


FIGURE 1. *Phyllanthus gentryi*.—*a*. Habit.—*b*. Columella of fruit, showing seed scars and persistent calyx.—*c*. Seed, dorsal view.—*d*. Seed, ventral view. Based on Gentry 4589. Illustration by Wan-Ling Peng.

Shrub or small tree to 5 m high; monoecious; deciduous branchlets pinnatifid, at least 5 dm long, obtusely angled, brownish, minutely scabridulous. *Leaves* with petioles 5–8 mm long; stipules cordate, acuminate, brownish, scarious, ca. 3.5 mm long; blades chartaceous, elliptic-lanceolate, 12–28 cm long, 6–7.5 cm broad, acuminate, rounded to cuneate at base, glabrous on both faces. *Cymules* each of 1 pistillate and several staminate flowers. *Staminate flowers* with pedicels 15–20 mm long; sepals 5, broadly elliptic or oblong; 2.5–3 mm long, 2.2–2.7 mm broad; disk entire, angled, not pitted, 1.8–2.2 mm across; stamens 3, the filaments connate into a column 0.7–0.8 mm high and ca. 0.5 mm broad; anthers suborbicular, flattened, dehiscing horizontally, 0.8–0.9 mm long and broad. *Pistillate flowers* with pedicels 8–13 mm long; sepals 5, elliptic-oblong, blunt, mostly 3–4 mm long, 2.5–3 mm broad; disk massive, angled, not pitted, 2.2–2.5 mm across; ovary smooth, of 3 carpels; styles nearly free, dilated, 1–1.2 mm long, 0.7–1 mm across. *Capsules* reddish, valves 12.5–13 mm long; columella massive, 4.5–5 mm long, 4.2–4.5 mm broad; seeds trigonous-umbonate, 6.5–7.1 mm long, 5.2–5.3 mm broad, smooth, with irregular wavy horizontal dark brown bands on a light brown background, the apex sometimes with a small whitish caruncular outgrowth (ca. 0.5 mm across); hilum triangular, broad, ca. 3 mm long and broad.

Additional specimens examined. PANAMA. DARIÉN: trail up Cerro Pirre, *Gentry* 4589 (MO); razorback ridge on Cerro Pirre, *Duke* 6556 (MO); Serranía de Pirre, trail from Q. Perecingo to Cerro Pirre, ca. 10 km airline SSE of El Real, in subtropical moist-to-wet forest, 300–750 m, *Reveal & Duke* 4919 (MARY, MO); around Rancho Frío, halfway up slope of Cerro Pirre from Piji Vasal, *Folsom* 6245 (F, MO); S of El Real on trail up Cerro Pirre, ca. 8°00'N, 77°45'W, 550–1,030 m, *McPherson* 7051 (F, MO).

Phyllanthus gentryi is the first representative of subgenus *Xylophylla* (L.) Pers. discovered in Panama. It clearly belongs in section *Asterandra* (Klotzsch) Muell. Arg. by virtue of its confluent staminate disk and dilated styles, and it resembles *P. juglandifolius* Willd. in general aspect. Although it could be interpreted as a subspecies of *P. juglandifolius*, it is distinctive in its large seeds, smooth (nonpitted) disk, and nearly free styles.

In order to accommodate this species in the *Flora of Panama* treatment, the key on p. 221 must be revised as follows:

e. Branchlets pinnatifid.

e'. Plants (in Panama) herbaceous; leaves less

than 3 cm long; seeds less than 3 mm long; pollen grains prolate, 3–4-colporate (subg. *Phyllanthus*).

ee'. Plants woody; leaves more than 3 cm long; seeds over 3 mm long; pollen grains globose, areolate (subg. *Xylophylla*) 12. *P. gentryi*

Subfamily II. ACALYPHOIDEAE Asch.

9. *Caperonia*

Caperonia A. St. Hil., Hist. Pl. Remarq. Bresil 244. 1826. LECTOTYPE: *Caperonia castaneifolia* (L.) A. St. Hil. (*Croton castaneifolius* L.) (chosen by Britton & Wilson, Bot. Porto Rico 6: 486. 1925).

No additional Panamanian species have been discovered. However, examination of additional specimens indicates that we may not have gone far enough in reducing the taxa proposed under *C. paludosa* Klotzsch. It is extremely difficult to separate that species from *C. castaneifolia* (L.) A. St. Hil., and we now believe that our Panamanian specimens of *C. paludosa* probably represent only forms of that more wide-ranging species. However, the narrower leaves of plants referred to *C. paludosa* are distinctive, and further study in the field is required to establish whether that species concept can be upheld.

10. *Argythamnia*

Argythamnia P. Browne, Civ. Nat. Hist. Jamaica 338. 1756. TYPE: *Argythamnia candicans* Sw.

11. *Alchorneopsis*

Alchorneopsis Muell. Arg., Linnaea 34: 156. 1865: TYPE: *Alchorneopsis floribunda* (Benth.) Muell. Arg. (*Alchornea glandulosa* var. ?*floribunda* Benth.).

11.1 *Alchorneopsis floribunda* (Benth.) Muell. Arg., Linnaea 34: 156. 1865; in DC., Prodr. 15(2): 765. 1866. *Alchornea glandulosa* Poeppig var. *floribunda* Benth., Hooker's J. Bot. Kew Gard. Misc. 6: 331. 1854. TYPE: Brazil. Amazonas: *Spruce* 2681 (holotype, K, not seen).

The single collection of this species cited in the original treatment, from Darién, was the only Central American record known at the time and was likewise a range extension of over 800 miles. The specimens cited below extend the range to western Panama as well as to Costa Rica.

Additional specimens examined. COSTA RICA. CARTAGO: 24 km NE of Turrialba on hwy. to Limón, then E at Tres Equis on jeep road 1.5 km, 9°58'N, 83°34'W, 450–525 m, *Liesner et al.* 15354 (MO). HEREDIA: Finca La Selva, the OTS Field Station on the Río Puerto Viejo just E of its junction with the Río Sarapiquí, ca. 100 m, *Hammel* 9425, 11083 (F, MO); Istarú Farm, Tirimbina, Sarapiquí, 220 m, *Lent* 2320 (F, MO). LIMÓN: S end of Lomas de Sierpe, NE of terminus of road from Villa Franca, 10°19'N, 83°34'W, *Grayum et al.* 3520 (F, MO). SAN JOSÉ: 2 km N of Dominical along CR 223, 40–100 m, *Uley & Uley* 4938 (F). PANAMA. BOCAS DEL TORO: Cerro Pila de Arroz, along road to Chiriquí Grande, 10 road-mi from Continental Divide and 2 mi. along pipeline access road E of highway, ca. 8°55'N, 82°08'W, 350–500 m, *McPherson* 8750 (F).

12. *Caryodendron*

Caryodendron Karsten, Fl. Columb. 1: 91, tab. 45. 1860. TYPE: *Caryodendron orinocense* Karsten.

12.1. *Caryodendron angustifolium* Standley, Publ. Field Columbian Mus., Bot. Ser. 4: 217. 1929. TYPE: Panama. Chiriquí: Progreso, *Cooper & Slater* 192 (holotype, F, F neg. 59913).

The collection cited from Darién under this name in the original collection is now known to be *Senefeldera testiculata* Pittier (q.v.). No additional collections of *Caryodendron angustifolium* are known from Panama or elsewhere.

13. *Adenophaedra*

Adenophaedra (Muell. Arg.) Muell. Arg. in Mart., Fl. Bras. 11(2): 385. 1874. *Bernardia* sect. *Adenophaedra* Muell. Arg., Linnaea 34: 172. 1865; in DC., Prodr. 15(2): 918. 1866. TYPE: *Bernardia ?megalophylla* Muell. Arg. = *Adenophaedra megalophylla* (Muell. Arg.) Muell. Arg.

Dioecious trees and shrubs; indumentum of simple trichomes. Leaves alternate, petiolate, stipulate; blades pinnately veined, without embedded laminar glands, dentate. Inflorescences axillary or terminal, spiciform, the staminate often compound; bracts eglandular, subtending 1 pistillate or several staminate flowers. Staminate flowers pedicellate; calyx splitting into 3 valvate lobes at anthesis; petals and disk absent; stamens 2(–3); filaments short; anthers with enlarged connectives, dehiscing introrsely and longitudinally; pistillode absent. Pistillate flowers pedicellate; calyx lobes 6, biseriate, imbricate; petals absent; disk 3-lobed; ovary of 3

carpels; ovules 1 per locule; styles contracted into sessile stigmas. Fruits capsular, 3-lobed; seeds 1 per locule, smooth, ecarunculate.

LITERATURE

CROIZAT, L. 1946. Nomenclatural transfers and corrections in the Euphorbiaceae. Trop. Woods 88: 30–32.

This poorly known genus, hitherto considered to be South American, includes only three species. Croizat (1946) reported *Adenophaedra* from Panama on the basis of *Adenophaedra woodsoniana*; but in the original treatment (Webster & Burch, 1968: 278) it was pointed out that his original generic disposition (J. Arnold Arbor. 24: 167. 1943) of this plant as *Cleidion woodsonianum* was correct, although that species is now known to be synonymous with *C. membranaceum* Pax & K. Hoffm. (q.v.). Several recent collections of *A. grandifolia* from Panama and Costa Rica, however, firmly establish the presence of *Adenophaedra* in southern Central America. In addition, it now appears that the plant called *Bernardia denticulata* in the original treatment is actually *A. grandifolia*.

13.1. *Adenophaedra grandifolia* (Klotzsch) Muell. Arg. in Mart., Fl. Bras. 11(2): 386. 1874. *Tragia grandifolia* Klotzsch, London J. Bot. 2: 46. 1843. TYPE: Guyana: “British Guiana,” *Schomburgk* 948 (presumably K, not seen). *Bernardia ?grandifolia* (Klotzsch) Muell. Arg., Linnaea 34: 173. 1865; in DC., Prodr. 15(2): 918. 1866.

Cleidion denticulatum Standley, Publ. Field Columbian Mus., Bot. Ser. 4: 218. 1929. *Bernardia denticulata* (Standley) Webster, Ann. Missouri Bot. Gard. 54: 200. 1967. TYPE: Panama. Bocas del Toro: Chiriquí Trail, Buena Vista Camp, 1,250 ft., *Cooper* 606 (holotype, F, F neg. 52608; isotypes, NY, Y).

Shrub or small tree to 8 m; twigs smooth, reddish, thinly puberulent, tardily glabrate. Leaves with petiole 3–6 mm long; stipules lanceolate, ca. 1 mm long, ca. 1 mm broad, caducous; blades chartaceous, oblanceolate, acuminate at the tip, attenuate at the base, 12–35 cm long, 3–12 cm wide, 2.5–4.5 times as long as broad, glabrous, or sometimes thinly villous below on the principal veins, the secondary veins 7–9 per side, arcuate, prominent below, the tertiaries reticulate, prominulous; margins remotely denticulate. Inflorescences axillary, densely villous, the bracts deltate, 1–2 mm long, densely villous; staminate spikes slender, flexuous, to 15 cm long, the glomerules widely spaced,

to 25; pistillate spikes thicker, not flexuous, 5–12 cm long, with 4–7 solitary flowers. *Staminate flowers* to 12 per glomerule, early dehiscent, leaving persistent pedicels ca. 1 mm long; calyx lobes membranous, deltate, spreading at anthesis, ca. 0.5 mm long. *Pistillate flowers* not seen; pedicels at maturity ca. 4 mm long, reflexed, sericeous. *Capsules* depressed-globose, deeply 3-lobed, 6–8 mm high, 12–18 mm diam., sericeous, glabrate at maturity, the persistent calyx lobes ca. 2 mm long, deltate, sericeous; seeds subglobose to ovoid, ca. 1 mm long, ca. 0.7 mm diam., yellowish, mottled.

Additional specimens examined. COSTA RICA. LIMÓN: 7 km SW of Bribri, 100–150 m, *Gómez et al.* 20422 (F); camino entre la finca de don Calixto Kiamble y el antiguo camino a Katsi, subiendo hasta el Cerro Kikirchabata, *Gómez et al.* 23800 (F); camino de Fila Dimat (casa de Hermógenes Pereira) hasta Soki pasando por la quebrada Sha, *Gómez et al.* 23859 (F). PANAMA. BOCAS DEL TORO: along road from Fortuna Dam to Chiriquí Grande, ca. 8°45'N, 82°15'W, ca. 700 m, *McPherson* 8430 (F); Cerro Pila de Arroz along road to Chiriquí Grande, 10 road-miles from Continental Divide and 2 mi. along pipeline access road E of highway, ca. 8°55'N, 82°08'W, 350–500 m, *McPherson* 8752 (F), 8775 (F, distributed as *Cleidion woodsonianum*). VERAGUAS: 5 mi. NW of Santa Fe, 700–1,200 m, *Liesner* 976 (GH, MO).

14. *Bernardia*

Bernardia Miller, Gard. Dict. abr. ed. 4, 28. 1754. LECTOTYPE: *Bernardia carpinifolia* Griseb. (see Buchheim, 1962).

Following the reduction of *Bernardia denticulata* to the synonymy of *Adenophaedra grandifolia* (q.v.), this genus is now represented in Panama by a single species.

LITERATURE

- BUCHHEIM, G. 1960. Nomenklatorische und systematische Bemerkungen über die Gattung *Bernardia* (Euphorbiaceae). Willdenowia 2: 291–318.
———. 1962. Über die Typusart der Gattung *Bernardia* (Euphorbiaceae). Willdenowia 3: 217–220.

KEY TO THE SPECIES OF *ALCHORNEA* IN PANAMA

- 1a. Pistillate spikes less than 25 cm long; leaves less than 25 cm long (or else copiously stellate-pubescent beneath), with 2 or more basal laminar glands; seeds (where known) not over 7 mm long.
 - 2a. Leaves (except on sprout shoots) not over ca. 20 cm long, glabrate, the veinlet reticulum only moderately prominulous beneath.
 - 3a. Leaves chartaceous, abruptly cuspidate-acuminate; vein axils not barbate beneath; basal foliar glands usually 2; staminate spikes unbranched, mostly axillary 1. *A. costaricensis*
 - 3b. Leaves not abruptly cuspidate (or else coriaceous); vein axils often barbate beneath.
 - 4a. Styles 5–20 mm long, relatively slender.
 - 5a. Leaves coriaceous, usually with 2–4 basal glands; spikes mostly cauliflorous.
 - 6a. Leaves mostly 8–20 cm long, acuminate, with mostly 5–8 main lateral veins, entire or crenate-dentate; foliar glands mostly 2(–4); pistillate sepals 2–2.8 mm long 2. *A. latifolia*

14.1. *Bernardia macrophylla* Standley, J. Wash. Acad. Sci. 15: 103. 1925. TYPE: Panamá: Río Tocumen, near sea level, 3 Jan. 1924, *Standley* 29389 (holotype, US).

No Panamanian specimens of this species have been found in addition to those cited in the original treatment. The recent collection cited below extends the range to Costa Rica. That specimen has somewhat more acuminate leaf apices than the Panamanian collections and was taken at a considerably higher altitude but seems otherwise identical. As indicated in the original treatment, the closest relative of *Bernardia macrophylla* seems to be *B. jacquiniana* Muell. Arg. of Venezuela, but the latter differs in having retrorse rather than ascending pubescence on the stems, more prominent venation on the undersurface of the leaves, and 9–12 vs. 14 stamens.

Additional specimen examined. COSTA RICA. PUNTARENAS: foothills of the Cordillera de Talamanca, around Tres Colinas, 9°07'N, 83°04'W, 1,800–1,850 m, *Davidse et al.* 25611 (F).

15. *Adelia*

Adelia L., Syst. Nat. ed. 10, 1298. 1759, nom. cons. TYPE: *Adelia ricinella* L. (typ. cons.).

16. *Alchornea*

Alchornea Sw., Prodr. 98. 1788; Fl. Ind. Occ. 2: 1153. 1800. TYPE: *Alchornea latifolia* Sw.

Several recent collections of *Alchornea* indicate that there are some additional taxa in Panama, but the material is still inadequate for a satisfactory treatment. The taxa that appear to be present may be treated as follows.

LITERATURE

- PAX, F. & K. HOFFMANN. 1914. Euphorbiaceae—Acalypheae—Mercurialinae. In: A. Engler, Das Pflanzenreich IV. 147. VII(Heft 63): 1–473 (*Alchornea*, pp. 220–253).

- 6b. Leaves mostly 2–7 cm long, acute, with mostly 3 or 4 main lateral veins; foliar glands 2–4; pistillate sepals shorter than 2 mm long 3. *A. triplinervia*
 5b. Leaves chartaceous, usually with 5–10 basal glands, with 5–8 main lateral veins; spikes mostly axillary; pistillate sepals 1–1.5 mm long 4. *A. glandulosa*
 4b. Styles 3–7 mm long, thick; leaves coriaceous, acuminate, with 5–7 main lateral veins; foliar glands 2–4; spikes axillary 5. *A. grandiflora*
 2b. Leaves over 20 cm long, copiously stellate-pubescent beneath, with veinlet reticulum corrugate-impressed above and distinctly raised beneath; spikes cauliflorous 6. *A. grandis*
 1b. Pistillate spikes mostly 25 cm long or longer, cauliflorous; leaves coriaceous, oblanceolate, ca. 25–40 cm long, glabrescent beneath; basal foliar glands obscure or absent; seeds 9–11 mm long 7. *A. megalophylla*

16.1. *Alchornea costaricensis* Pax & K. Hoffm., Pflanzenreich IV. 147. VII(Heft 63): 235. 1914. TYPE: Costa Rica: Palmar, Tonduz 6757 (not seen).

Recent collections show that *Alchornea costaricensis* is not confined to western Panama; it extends into South America, where there is at least one record from Colombia (Chocó: *Ordóñez et al.* 58, MO). The plant described from Colombia by Croizat (*Caldasia* 2: 357. 1944) as *A. umboensis* may prove to be a form of *A. costaricensis*.

Additional specimens examined. PANAMA. CHIRIQUÍ: vicinity of San Bartolo Limite, 11 mi. W of Puerto Armuelles, *Croat* 21973a (MO). COCLÉ: along Río San Juan below its junction with Río Tife, *Hammel* 3405 (MO). COLÓN: Río Boquerón near juncture with Río Escandaloso, *Hammel* 2743 (MO, determination somewhat dubious); along Río Guanche toward Cerro Bruja, *Huft & Knapp* 1789 (MO); 3 mi. from Portobelo, *Correa & Dressler* 1749 (GH, MO). DARIÉN: Río Ucugantí, *Bristan* 1137 (MO); Río Tuqueza, below Quebrada Venado, *Bristan* 1065 (DAV, MO). LOS SANTOS: Loma Prieta, Cerro Grande, *Duke* 11859, *Lewis et al.* 2208 (MO). PANAMÁ: Chiltepe, *Holdridge* 6471 (MO). SAN BLAS: Canagangí, forest upstream of village, 9°24'N, 79°24'W, 100 m, *de Nevers et al.* 5720 (F).

16.2. *Alchornea latifolia* Sw., Prodr. 98. 1788. TYPE: Jamaica: Swartz (not seen).

Southern Mexico to Venezuela and Peru.

Further botanical exploration has shown that *Alchornea latifolia* is widely distributed in Panama, including Barro Colorado Island, whence it was correctly recorded by Croat (1978). On several peaks and ridges in central Panama occur montane forms that appear very different from typical *A. latifolia* of lowland Central America and the West Indies. For example, plants with entire leaves and unusually short petioles are found on Cerro Jefe and Santa Rita Ridge (e.g., *Gentry & Dwyer* 5536, *Croat* 15309). These specimens somewhat suggest the South American *A. pearcei* Britton, but their relatively long petioles and short spikes bring them closer to *A. latifolia*. Specimens with very unusual narrowly obovate leaves have been collected on Santa Rita Ridge (e.g., *Croat* 13844, *Duke* 15264);

however, since plants with this leaf form occur in the same area as plants with more typical leaves, it seems probable that they are merely local variants. At present, it seems best to include all of these variants within *A. latifolia*, but it must be admitted that the species so conceived has an extraordinary amplitude of foliar variation; until critical studies in the field are made, the situation will remain unsatisfactory.

Additional specimens examined. PANAMA. CHIRIQUÍ: San Félix, *Croat* 33416 (MO). PANAMÁ: Cerro Campana, *Croat* 14673, *Duke* 10742, *Sullivan* 434 (MO), *Méndez* 19, 49 (F); Cerro Jefe, *Dwyer et al.* 5048, 5049, *Gentry* 4938 (MO), *Gentry & Dwyer* 5536 (GH, MO), *Webster & Dressler* 16454 (DAV); between Cerro Jefe and Cerro Azul, *Tyson et al.* 4325, *Mori et al.* 6543 (MO); Cerro Azul, *Dwyer* 5042 (MO), *Lao & Holdridge* 33 (DAV, MO), *Stimson et al.* 5158 (GH, MO), *Tyson & Blum* 4081 (MO); N of El Llano, *Gentry* 5105 (MO); El Llano-Cartí road, 7.8–8.6 mi. from Pan-American Hwy., *Folsom* 3572, *Mori & Kallunki* 6405 (MO).

16.3. *Alchornea triplinervia* (Sprengel) Muell. Arg. in DC., Prodr. 15(2): 909. 1866; Pax & K. Hoffm., Pflanzenreich IV. 147. VII(Heft 63): 227. 1914. *Antidesma triplinervium* Sprengel, Neue Entdeck. 2: 116. 1821. TYPE: Brazil. Rio de Janeiro: Serra do Mar, *Gardner* 617 (neotype, G; chosen here).

This species is tentatively added to the Panamanian flora on the basis of two recent collections from a single locality. The collection of Knapp has only staminate flowers, but the small coriaceous leaves with only three or four main veins and the cauliflorous spikes match those of *Alchornea triplinervia* better than those of any of the species of *Alchornea* previously known from Panama. Another collection that may represent *A. triplinervia* is *Hammel* 7252 (MO) from Cerro Sapo, Darién; this has much larger leaves and somewhat resembles some of the aberrant forms here treated as *A. latifolia*; for the present, its assignment must be regarded as dubious.

The collections from Coclé do not fit any of the varieties recognized by Pax & Hoffmann (1914: 228–230), but the variation within *A. triplinervia*

has not yet been critically studied, and it would certainly be premature to assign the Panamanian material to a new variety. The typification of *Alchornea triplinervia* requires some comment, since Sprengel apparently left no type specimen. Mueller (1866: 909) designated what may be regarded as the typical element of the species as *Alchornea triplinervia* var. *genuina* forma *psilorhachis*. Since there is a good microfiche image (G, Prodr. 15(2) of *Gardner 617*, probably from the general area of the collection that was available to Sprengel, it seems appropriate to designate that as neotype.

Specimens examined. PANAMA. COCLÉ: hills N of El Valle, E slope of Cerro Gaital, 900–1,000 m, *Knapp 5351* (MO), *McPherson 11242, 11260* (MO).

16.4. *Alchornea glandulosa* Poeppig var. *pittieri* (Pax) Pax, Pflanzenreich IV. 147. VII(Heft 63): 235. 1914. *Alchornea pittieri* Pax, Bot. Jahrb. Syst. 33: 291. 1903. TYPE: Costa Rica: Cañas Gordas, *Pittier 11101* (isotype, US).

Since the Darién collection of Terry & Terry was reported in our original treatment, a number of additional specimens have accumulated; these confirm the widespread occurrence of *Alchornea glandulosa* in montane forests of Panama. Examination of this expanded suite of specimens now shows that the Panamanian plants represent var. *pittieri*, originally described from Costa Rica. This variety is very similar to var. *glandulosa* of the upper Amazon but differs in the smaller glandular spots at the base of the leaf (mostly 0.5 mm long or less in var. *pittieri*, reaching 1–1.5 mm long in var. *glandulosa*). At present, var. *pittieri* is known only from Costa Rica, Panama, and adjacent Colombia (Chocó).

Additional specimens examined. PANAMA. BOCAS DEL TORO: headwaters of Río Mali, between Q. Gutiérrez and La Zorra, *Kirkbride & Duke 726* (MO); along pipeline road in area of Fortuna Dam, near end of road, ca. 8°48'N, 82°15'W, 900–950 m, *McPherson 8691, 8699* (F). DARIÉN: Cana-Cuasí Trail, *Terry & Terry 1575* (MO); Cerro Pirre, *Bristan 620* (MO); Alto de Nique, Cerro Pirre massif, 1,300–1,520 m, *Gentry et al. 28647* (DAV, MO); Cerro Tacarcuna, lower montane wet forest, 1,500 m, *Gentry & Mori 13793* (DAV, F, MO, PMA). VERAGUAS: lower montane wet forest, 7 km W of Santa Fe, ca. 900 m, *Nee 11183* (MO, US); NW of Santa Fe, 2.8 km from Escuela Agrícola, Alto de Piedra, *Mori & Kalunki 6219* (MO).

16.5. *Alchornea grandiflora* Muell. Arg., Linnaea 34: 170. 1865; in DC., Prodr. 15(2): 907. 1866. SYNTYPES: Venezuela: *Fendler 1272* (G), *Moritz 1497a* (G). Costa Rica: *Hoffman 530* (G, not seen).

Although it has been confused with *A. glandulosa*, the relatively short thick styles and stiff glandular leaves distinguish *A. grandiflora* from *A. glandulosa* and from *A. latifolia*. Mueller (loc. cit.) reported *A. grandiflora* from Costa Rica and Venezuela, so its occurrence in Panama is not surprising.

Specimens examined. PANAMA. CHIRIQUÍ: Cerro Colorado, 1,690 m, *Croat 37195* (MO). DARIÉN: Cerro Tacarcuna, elfin forest, 1,800–1,850 m, *Gentry & Mori 13995* (DAV, F, MO).

16.6. *Alchornea grandis* Benth., Bot. Voy. Sulphur 164. 1844. TYPE: Colombia. Nariño: Tumaco, *Barclay & Hinds* (K, not seen).

The specimens cited below, and several collections from Chocó Province, Colombia (*Fernández 206*, *Killip & Cuatrecasas 39076*, both UC) furnish previously unknown characters for the staminate plant: staminate spikes mostly compound, 4–12 cm long, with 1–6 lateral axes; staminate calyx glabrous, sepals ca. 1.2 mm long; stamens 8, anthers 0.7–0.8 mm long, blunt.

Specimens examined. PANAMA. VERAGUAS: Isla de Coiba, road from Campamento Juncal to Colonia Penal, *Antonio 2417* (MO); Playa Hermosa, *Antonio 2342* (MO).

16.7. *Alchornea megalophylla* Muell. Arg., Flora 47: 343. 1864; in DC., Prodr. 15(2): 911. 1866. TYPE: Colombia. Antioquia: *Purdie* (K, not seen).

Tree to ca. 10 m high; trunk 1.5 dm diam.; twigs subterete, smooth, glabrous. *Leaves* with stout petioles 0.5–1.5 cm long, glabrous, plicate; stipules inconspicuous, ca. 1.5 mm long or shorter, dark, triangular, pubescent; blades becoming subcoriaceous or coriaceous, elliptic to obovate, abruptly short acuminate at apex (the acumen ca. 1–2 cm long), ca. 25–40 cm long, 7–15 cm broad, glabrous or glabrescent (minute scattered stellate hairs on underside of lamina or confined to midrib); basal foliar glands obscure or absent; major lateral veins ca. 10–15 on a side, straight, ascending, raised beneath, connected by ladderlike prominulous veinlets, contracted to an obtuse base; margins distantly crenulate-dentate (ca. 10–15 glandular teeth on a side), apex abruptly short-acuminate (acumen ca. 1–2 cm long). *Spikes* cauliflorous, pendulous, stellate-pubescent; staminate spikes not seen; pistillate spikes ca. 50–75 cm long, with ca. 20–30 flowers. *Staminate flowers* not seen. *Pistillate flowers* sessile; calyx ca. 3.5 cm broad, 4-lobed, pubescent; ovary copiously pubescent with minute stellate hairs; styles slender, unlobed, ca. 20–25 mm long,

basally connate for 2–4 mm, basally stellate, apically smooth and long-attenuate. *Capsules* reddish brown, stellate-pubescent, not seen entire; seeds elliptic, plump, pale brown, coarsely tuberculate, 9–11 mm long.

Rainforests, Panama and Colombia.

This striking species stands out from all other Panamanian taxa by virtue of its long, pendulous, cauliflorous inflorescences and its large, coriaceous, more or less oblanceolate leaves. It resembles *A. grandis* in a number of respects but differs in leaf shape and sparseness of the laminar pubescence.

Specimens examined. PANAMA. DARIÉN: La Laguna, ridge between Pucuro and Tapalisa rivers, 820–840 m, *Gentry & Mori 13560* (DAV, MO); top of Cerro Mali, 1,400 m, *Gentry & Mori 13693* (DAV, MO); Cerro Tacarcuna, *Gentry & Mori 13938* (MO); Alturas de Nique, S of El Real, 900–1,250 m, *McPherson 11614* (MO).

17. *Cleidion*

Cleidion Blume, *Bijdr. Fl. Ned. Ind.* 612. 1826.

TYPE: *Cleidion javanicum* Blume.

Recent collections in Panama and further study of the South American species have greatly altered the picture of *Cleidion* in Panama. Largely as a result of problems encountered in the preparation of this account, the junior author has undertaken a revisionary study of the neotropical species of *Cleidion*, and until its completion, some of the conclusions expressed here must remain tentative.

In addition to the two species treated here, a recent collection in Darién by Dr. Gordon McPherson may belong to *Cleidion prealtum* Croizat (J. Arnold Arbor. 24: 167. 1943), a species otherwise known only from material collected in the basin of the upper Rio Madeira in Amazonian Brazil. The poorly known *Polyandra bracteosa* Leal (Arch. Jard. Bot. Rio de Janeiro 11: 64. 1951), described from staminate material, also from the Rio Madeira, now appears to be synonymous with *C. prealtum*.

LITERATURE

VAN DER WERFF, H. & A. R. SMITH. 1980. Pteridophytes of the State of Falcon, Venezuela. *Opera Bot.* 56: 1–34.

KEY TO THE SPECIES OF *CLEIDION* IN PANAMA

1a. Fruiting spikes slender, (5–)8–18 cm long; capsules 3–6, remote, 5–8 mm in diameter; leaves up to 13 cm long; leaf vein axils barbate beneath; veins 7 or 8 on a side; staminate thyrses ca. 1 cm long 1. *C. membranaceum*

1b. Fruiting spikes thick, 2–3 cm long; capsules 1–3, 13–15 mm in diameter; leaves over 15 cm long; leaf vein axils not barbate beneath; veins 8–10 on a side; staminate thyrses 5–9 cm long 2. *C. castaneifolium*

17.1. *Cleidion membranaceum* Pax & K. Hoffm. in Engler, *Pflanzenreich* IV. 147. XIV(Heft 68): 23. 1919. TYPE: Venezuela. Lara: around Palmosola, in forest along Río Aroa, near sea level, 26–28 June 1913, *Pittier 6375* (US, photo F neg. 44609).

Cleidion woodsonianum Croizat, J. Arnold Arbor. 24: 167. 1943. TYPE: Panama. Panamá: vicinity of Salamanca Hydrographic Station, Río Pequení, ca. 80 m, *Woodson et al. 1587* (holotype, A; isotypes, F, F neg. 62417, MO, F neg. 62356, NY).

There appear to be no differences between the Panamanian plants and the Venezuelan collections of *Cleidion membranaceum*. The three known Venezuelan collections are all from a restricted area near the junction of the provinces of Falcón, Yaracuy, and Lara. No substrate is indicated on the labels of these collections, but it is known that much of this area is underlain by limestone (van der Werff & Smith, 1980), which is also true of the Panamanian collections. The recent disjunct collection from Peru strengthens the probability that this species is restricted to limestone, and that this accounts for the peculiar disjunctions in its range.

Further study may show that *Cleidion membranaceum* is synonymous with *C. tricoccum* (Casar.) Baillon, of eastern Brazil from Bahia to São Paulo, which has leaves similar in shape and size to those of the Panamanian plant, similar long, nearly filiform pistillate inflorescences, and similar capsules.

Additional specimens examined. PANAMA. PANAMÁ: Majé, second growth on limestone hillsides, along Chocó Indian trail, ca. 5 mi. up from village of Majé, *Foster & Kennedy 2021* (MICH, MO, PMA). PERU. HUÁNUCO. LEONCIO PRADO: Distrito Rupa Rupa, Tingo María, ca. 9°18'S, 75°59'W, limestone hills opposite airport, *Plowman et al. 11246* (DAV, F, K). VENEZUELA. FALCÓN: Parque Nacional Quebrada de la Cueva El Toro, steep wet valley along river, 10°50'N, 69°07'W, *Liesner et al. 7722* (F, MO). YARACUY-FALCÓN: Reserva Forestal "Rio Tocuyo," a 4 km del Campto. "Canelon," via Tucacas, *Blanco 895* (MO).

17.2. *Cleidion castaneifolium* Muell. Arg., *Linnaea* 34: 184. 1865. TYPE: Peru: *Pavon* (holotype, G, F neg. 7159).

Alchornea oblongifolia Standley, Carnegie Inst. Wash. Publ. 461(Botany of the Maya Area 4): 66. 1935. *Cleidion oblongifolium* (Standley) Croizat, J. Arnold Arbor. 24: 166. 1943. TYPE: Guatemala. Petén:

Camp 35, boundary with Belize, 750 m, *Schipp S-279* (holotype, F, F neg. 52594).

Trees to 10 m high; dioecious; twigs glabrous. *Leaves* with petioles 1.5–4 cm long, glabrous or sparsely pubescent with short, white, appressed hairs, swollen toward apex; stipules not evident; blades membranous or thinly chartaceous, elliptic, abruptly caudate-acuminate at tip, acute or cuneate at the somewhat inequilateral base, 15–26 cm long, 6.5–9.5 cm broad, minutely pustulate, glabrous, the veins 8–10 on a side; margins shallowly dentate, the teeth callose, 15–28 on a side. *Inflorescences* unisexual, axillary; pistillate racemes to 16 cm long, widely divergent from the stem, the rachis glabrous, or puberulent toward the apex, with ca. 3 flowers occurring singly (3 fruits on only complete pistillate raceme seen); staminate thyrses 5–9 cm long, with 7–12 flowers crowded at each of the 20–50 nodes, the rachis densely puberulent. *Staminate flowers* on pedicels to 1 mm long; calyx lobes cucullate, reflexed, 1.5–2 mm long, glabrous, ovate, the apex acute or acuminate; stamens ca. 60–80. *Pistillate flowers* not seen; bracts narrowly lanceolate, rigid, divergent, ca. 2 mm long, puberulent; fruiting pedicels 10–12 mm long, slightly clavate, puberulous, jointed; calyx lobes (in fruit) 3–5, somewhat reflexed, deltate, 2–3 mm long, acute, canescent below, ciliate on the margins; styles (persistent on mature fruits) 7–12 mm long, deeply bifid, densely strigose. *Capsules* 3-locular (of which often only 2 fully developed), deeply lobed, dorsally carinate, ca. 1 cm high, 14–18 mm diam., densely puberulent, drying black; columella 6–8 mm long, trigonous, narrowly winged, the seed scars elongate, conspicuous; seeds globose, smooth, not beaked, ca. 9 mm long, mottled light and dark brown.

Rainforests, southern Mexico to Panama, Ecuador.

The Panamanian collections of *Cleidion castaneifolium* match perfectly the type photograph as well as the original description except for the curious statement in the latter that the capsule is six-lobed. Since all other species of *Cleidion* have three-lobed capsules (as do the Panamanian collections), and since the one capsule on the type photo appears crushed and misshapen (and thus made to appear six-lobed), it seems that Mueller was merely careless in his description. Since these collections are in perfect agreement with all other distinguishing characteristics of this species (large elliptic-ovate leaves, petioles 3–5 cm long and glabrous except for the subpuberulous tips, long un-

divided pistillate racemes, and large capsules with dorsally carinate lobes), their identification seems certain. The only other Panamanian species of the genus, *C. membranaceum*, and the Peruvian *C. amazonicum* Pax both differ from *C. castaneifolium* in their smaller leaves, much shorter petioles (2–5 mm long), and smaller capsules. *Cleidion prealtum* Croizat of Amazonian Brazil differs from all of these in its obovate and coriaceous leaves.

Cleidion castaneifolium was described from "Peru," but a possible isotype sheet at F (Ruiz & Pavón s.n.) is labeled as having been collected at Guayaquil, Ecuador (another Ruiz & Pavón specimen at F has no locality data). The species is not definitely known from Peru, but there are two modern collections from between Santo Domingo and Quinindé in Esmeraldas Province, Ecuador (*Acosta Solís 13649*, *Little 6196*, both at F, both distributed as *Alchornea*).

There appear to be no salient differences separating *Cleidion castaneifolium* from Panama and South America from the Mexican and Central American populations that have long been referred to *C. oblongifolium*. In addition to the common characters given in the key, these populations all frequently exhibit a characteristic purplish cast to the leaves.

Specimens examined. PANAMA. DARIÉN: Serranía de Pirre, on the NW slope of the mountain range dominated by Cerro Pirre, along Q. Perecingo (Parasénico), a tributary to Río Pirre, ca. 10 air km S of El Real, 8°03'N, 77°43'W, *Reveal & Duke 4875* (MARY, MO); 2–3 mi. SE of Pijibasal on Río Perasénico, ca. 9–10 mi. S of El Real, *Hartman 12038* (F, MO).

18. *Ricinus*

***Ricinus* L., Sp. Pl. 1007. 1753. TYPE: *Ricinus communis* L.**

19. *Acalypha*

***Acalypha* L., Sp. Pl. 1003. 1753. LECTOTYPE: *Acalypha virginica* L. (chosen by Small in Britton & Brown, Ill. Fl. N. U.S. ed. 2, 2: 457. 1913).**

19.10. *Acalypha cuneata* Poeppig in Poeppig & Endl., Nov. Gen. Sp. Pl. 3: 22. 1841. TYPE: Peru. Maynas: Yurimaguas, *Poeppig* (not seen).

Acalypha obovata Benth. in Seemann, Bot. Voy. Sulphur 163. 1844. TYPE: Ecuador. Esmeraldas: Atacames, *Hinds* (BM, not seen). *A. cuneata* Poeppig var. *obovata* (Benth.) Muell. Arg. in DC., Prodr. 15(2): 816. 1866.

Shrub or small tree 2–5(–8) m high; monoecious; stems nearly glabrous. *Leaves* with petioles 1–7 cm long, glabrous; stipules lanceolate, 4–7 mm long, strongly keeled, caducous; blades obovate or obovate-oblong, cuspidate-acuminate at the tip (the acumen 1.5–3 cm long), acute at the base, 15–30 cm long, 5–13 cm broad, 2–3.2 times as long as broad, glabrous, pinnately veined, the secondary veins 11–15 per side, arcuate, prominent above and below, connected by a prominulous reticulum; margins shallowly crenate-denticulate. *Inflorescences* axillary, spicate, unisexual; staminate spikes to 15 cm long, densely flowered, densely puberulent, solitary and pedunculate or 2–4 and sessile on a slender rachis; pistillate spikes 7–15 cm long, 4–7 mm thick, loosely flowered with 15–50 bracts, the rachis glabrous to densely puberulent. *Pistillate flowers* solitary; bracts $\pm$ reniform, 3–4 mm long, 6–7 mm wide, inconspicuously 8–10-lobed, each lobe with a short tuft of bristles, the bracts otherwise glabrous or lightly short-strigose; calyx lobes obscure; ovary densely hispid, the styles free, lightly strigose, pinnatifid along entire length into 8–12 narrow segments. *Capsules* 4–5 mm diam., hispid, verrucose; seeds obovoid-ellipsoid, 3–3.5 mm long, ca. 2.5 mm diam., smooth, brown, the caruncle nearly obsolete.

This is a widespread species of lowland rainforests in northern South America, and its discovery in eastern Panama is not surprising. It is easily recognized by the long-petiolate obovate leaves with pinnate venation and axillary pistillate inflorescences. In order to accommodate this species in the *Flora of Panama* treatment, the key on p. 300 must be revised as follows:

- ee. Leaves pinnately veined; pistillate bracts subentire or shallowly dentate.
 - e'. Spikes mostly bisexual, 3–8 cm long, with 1 or 2 pistillate bracts at base, these subtending 2 or 3 flowers *A. diversifolia*
 - ee'. Spikes unisexual, to 15 cm long, the pistillate ones toward the apex of the branch, the staminate below; pistillate bracts subtending a single flower *A. cuneata*

Specimen examined. PANAMA. DARIÉN: S of El Real on trail to Cerro Pirre, disturbed forest along Cerro Percecénega, ca. 8°00'N, 77°45'W, ca. 50 m, McPherson 6977 (F).

20. *Plukenetia*

Plukenetia L., Sp. Pl. 1192. 1753. TYPE: *Plukenetia volubilis* L.

The discovery of a second species of *Plukenetia* in Panama makes it necessary to provide the following key.

KEY TO THE SPECIES OF *PLUKENETIA* IN PANAMA

- 1a. Leaves palmately veined; stylar column cylindrical, slender, 10–25 mm long; capsules to 3.5 mm broad 1. *P. volubilis*
- 1b. Leaves pinnately veined; stylar column obovoid, to 2 mm long; capsules to 1.5 mm broad 2. *P. penninervia*

20.1. *Plukenetia volubilis* L., Sp. Pl. 1192. 1753. TYPE: West Indies, *Plumier* (perhaps at BM).

This species is more widespread in eastern Panama than was indicated by the single collection cited in the original treatment. These new collections also confirm the identity of the Panamanian species with *Plukenetia volubilis* of the Antilles and South America. Recent collections have also extended the range to Costa Rica (*Gómez et al. 19184*, F), Nicaragua (*White 5323*, F), and Veracruz, Mexico (*Calzada 1034*, F).

Additional specimens examined. PANAMA. COLÓN: upstream from bridge over Río Guanche, 0–100 m, *Antonio 3351* (F, MO); near Portobelo, *Croat 12969* (MO); Portobelo, along stream running into Río Buena Ventura, S of Portobelo, 0–10 m, *Foster 2060* (F, MO); along Río Guanche, 6 km S of Portobelo, 0–10 m, *Nee & Gentry 8686* (MO). DARIÉN: Cerro Pirre, valley between Pirre and next most southerly peak, *Folsom 4426* (F, MO). PANAMÁ: 4–5 hours walk upriver from Tortí Arriba, 200–300 m, *Folsom et al. 6845* (F, MO).

20.2. *Plukenetia penninervia* Muell. Arg., Linnaea 34: 158. 1864; in DC., Prodr. 15(2): 770. 1866. TYPE: Venezuela, near Biscaina, *Fendler 2412* (holotype, G, not seen; photo F neg. no. 7110).

Plukenetia angustifolia Standley, Publ. Field Columbian Mus., Bot. Ser. 4: 314. 1929. TYPE: Honduras. Atlántida: Lancetilla Valley, 8 Mar. 1928, *Standley 56708* (holotype, F, F neg. 52742).

Liana; twigs spreading-puberulent, glabrescent. *Leaves* with petioles ca. 1 cm long, puberulent; stipules brownish, glabrous, rigid, deltate-lanceolate, 1–1.7 mm long; blades chartaceous-oblong, oblong-elliptic, or oblong-lanceolate, acute to acuminate at tip, abruptly acuminate-truncate at base, 5–10 cm long, 2–4.5 cm broad, glabrous and shining above, glabrate or with a few hairs along the nerves and paler below, with 2 prominent glands above at the base, often with 1–3 pairs of smaller ones in a row above them, pinnately veined, the midrib and secondary veins (6–11 on a side) prominent below; margins shallowly crenate-denticulate. *Inflorescences* axillary, bisexual or staminate, 0.5–3 cm long; pistillate flowers solitary at lower nodes of bisexual inflorescences, the staminate flowers

few at the distal nodes. *Staminate flowers* with pedicels short-pilose, 4–7 mm long; calyx segments generally 3, obovate, acute, 1.2–1.6 mm long; receptacle cylindrical, 1.6–1.8 mm high; disk obsolete; stamens ca. 18–25, inserted spirally on the receptacle, the filaments ca. 0.1 mm long, the anthers 0.1–0.2 mm long. *Pistillate flowers* with pedicels becoming 12–20 mm long, these narrowly clavate, strigose when young, glabrate to sparsely short-pubescent at maturity; calyx lobes lanceolate, 1–1.2 mm long, ca. 0.5 mm broad, strigose in a band along the center; ovary of 4 carinate carpels, strigose on the keels, otherwise glabrous, the stylar column to 2 mm long, obovoid, the stigmas thick, unlobed. *Capsules* deeply 4-lobed, oblate, to ca. 1 cm high, 1.5 cm broad, the cocci thick and rigid; seeds subglobose, only slightly compressed laterally, reticulate-venose, brownish mottled, ca. 5 mm long, 3–4 mm thick.

Lowland evergreen rainforests, Mexico (Oaxaca, Yucatán Peninsula) to Colombia and Northern Brazil (Pará); here reported from Panama for the first time.

The discovery of *Plukenetia penninervia* in Panama is not surprising, although it is still unknown in Costa Rica, and the reason for its apparent scarcity in southern Central America is not clear. The populations from northern Central America, where the species is much better known, were described by Standley as *P. angustifolia*, but no salient differences between these plants and those of South America are apparent.

Specimens examined. PANAMA. COLÓN: Santa Rita Ridge, in ravine bottom near Agua Clara rainfall station, 400–500 m, *Foster & Morton* 2222 (F); Santa Rita Ridge, ca. 9°20'N, 79°45'W, ca. 500 m, *McPherson* 8461 (F). PANAMÁ: 1–2 mi. S of Pan American Highway, 3.0 mi. E of Cañazas checkpoint, foothills of Serranía de Cañazas, 8°52'N, 78°15'W, 0–50 m, *Knapp* 3887 (F, MO).

21. *Acidoton*

Acidoton Sw., Prodr. 84. 1788. TYPE: *Acidoton urens* Sw.

21.1 *Acidoton nicaraguensis* (Hemsley) Webster, Ann. Missouri Bot. Gard. 54: 191. 1967. *Cleidion ?nicaraguensis* Hemsley, Biol. Cent.-Amer., Bot. 3: 130. 1883. TYPE: Nicaragua. Chontales: *Tate* 352, 455 (syntypes, presumably K, not seen).

Additional specimens examined. PANAMA. COLÓN: Santa Rita, *Correa & Dressler* 607 (MO); Santa Rita Ridge Rd., 20 km from Transisthmian Hwy., 9°24'N,

79°39'W, *Sytsma* 1117 (F, MO). PANAMÁ: along the El Llano–Cartí rd., ca. 10 mi. N of Pan Am Hwy., 500 m, *Gentry et al.* 8878 (MO). SAN BLAS: El Llano–Cartí road, km 26.5, 9°19'N, 78°55'W, 300–400 m, *de Nevers et al.* 5292 (F); Nusagandí, along trail to Quebrada de Nusagandí, *van der Werff* 7029 (F).

22. *Tragia*

***Tragia* L., Sp. Pl. 980. 1753. LECTOTYPE: *Tragia volubilis* L. (chosen by Small in Britton & Brown, Ill. Fl. N. U.S. ed. 2, 2: 458. 1913).**

The discovery of three additional species in Panama makes it necessary to provide a key to the Panamanian species.

LITERATURE

PAX, F. & K. HOFFMANN. 1919. Euphorbiaceae—Acalypheae—Plukenetia. In: A. Engler, Das Pflanzenreich IV. 147. IX (Heft 68): 1–108 (*Tragia*, pp. 32–101).

KEY TO THE SPECIES OF *TRAGIA* IN PANAMA

- 1a. Leaf blades 12–25 cm long, 11–18 cm broad, often 3-lobed; stamens ca. 40 1. *T. bailloniana*
- 1b. Leaf blades 6–16 cm long, less than 10 cm broad, unlobed; stamens 2–12.
 - 2a. Inflorescence bifurcate, the pistillate flowers 5–10 on lower branch; stamens 8–12 2. *T. fendleri*
 - 2b. Inflorescence racemose, not bifurcate; pistillate flowers solitary at basal node; stamens 2 or 3.
 - 3a. Pistillate flower long-pedicellate; styles connate 3. *T. volubilis*
 - 3b. Pistillate flower subsessile; styles free 4. *T. correae*

22.1. *Tragia bailloniana* Muell. Arg., Linnaea 34: 178. 1865; in DC., Prodr. 15(2): 927. 1866. TYPE: Mexico. Tabasco: Teapa, *Linden* (P, not seen). *Zuckertia cordata* Baill., Etud. Euphorb. 496, pl. 4, 1858, not *Tragia cordata* Michx., 1803.

Twining vine; stamens and foliage ± densely covered with stinging hairs. *Leaves* with petioles 8–14 cm long; stipules ovate-lanceolate, acuminate, greenish, 7–10 mm long; blades membranous, broadly ovate, unlobed, with a single lateral lobe, or shallowly 3-lobed, acuminate or caudate at tip, deeply cordate at base, 12–25 cm long, 11–18 cm wide, sparsely beset above and below with stinging hairs, usually 7-veined at the base, the margins remotely denticulate. *Inflorescences* opposite the leaves, bifurcate; peduncle 3–10 cm long; staminate branch to 20 cm long, many-flowered; pistillate branch 15–25 cm long, 7–15-flowered. *Staminate flowers* 1–3 per bract; bracts

foliaceous, ovate-lanceolate, acuminate, 3–5 mm long, reflexed; pedicels 8–10 mm long, divergent, glabrate; sepals 5, linear-lanceolate, acuminate, ca. 6 mm long; stamens ca. 40; buds pyriform, acute. *Pistillate flowers* solitary in the axil of each bract; bracts similar to those of the staminate flowers; pedicels 1–4 mm long, hirsute; sepals deltate to lanceolate, acute to acuminate, 4–5 mm long; margins ciliate with long, stiff hairs; ovary densely hirsute with stiff hairs ca. 1 mm long; styles black, 6–8 mm long, fused ca. $\frac{2}{3}$ their length, the style branches slightly spreading. *Capsules* deeply 3-lobed (one lobe sometimes abortive), ca. 15 mm diam., ca. 8 mm high, densely hirsute with stiff hairs; columella 6–7 mm long, with 3 prominent, narrow wings at tip; seeds nearly globose, ca. 6 mm diam., smooth, with 8 or 9 light longitudinal striations.

Forests, southern Mexico to western Panama.

This distinctive species is the only member of *Tragia* section *Zuckertia* (Baill.) Muell. Arg., distinguished from all other American species of the genus by its numerous stamens (ca. 40 vs. 2 or 3 or rarely up to 20) and its large, usually lobed leaves. The Panamanian collection represents a considerable range extension, for the species had previously been known only from southern Mexico (Veracruz, Chiapas, Yucatán Peninsula) to Honduras. Earlier reports of *Tragia bailloniana* from Costa Rica (Standley, 1937: 622) are erroneously based on collections of *Dalechampia shankii* (see discussion in Huft, 1984); however, several recent collections establish the presence of the former there.

Specimens examined. COSTA RICA. ALAJUELA: along upper Río Sarapiquí, near Cariblanco and along the road to Colonia Virgen del Socorro, 10°18'N, 84°10'W, ca. 800 m, *Burger et al.* 11850 (F); lower NE slope of Arenal Volcano, 10°29'N, 84°42'W, 500 m, *Lent* 2947 (F). LIMÓN: hills 2 airline km SSE of Islas Buena Vista in the Río Colorado, 14 airline km SW of Barro del Colorado; 83°40'W, 10°40'N, 10–120 m, *Davidse & Herrera* 31023 (F, MO); southwesternmost ridge of Cerro Coronel, NW-facing slope, just S of the Río Colorado, 10°40'30"N, 83°39'30"W, 10–80 m, *Davidse & Herrera* 31388 (F, MO); Cerro Coronel, E of Laguna Danto; 10°41'N, 83°38'W, 20–170 m, *Stevens* 24383 (F, MO). PANAMA. CHIRIQUÍ: Fortuna Dam site, 1,400–1,600 m, *Folsom et al.* 5612 (MO).

22.2. *Tragia fendleri* Muell. Arg., Linnaea 34: 178. 1865; in DC., Prodr. 15(2): 928. 1866.
TYPE: Venezuela: Biscaina, *Fendler* 1208 (G).

Twining vine; stems and petioles hirsutulous or strigose with mostly nonstinging hairs. *Leaves* with

petioles 4–11 cm long; stipules lanceolate, 5 mm long or more; blades thinly chartaceous, oblong- or elliptic-obovate, rather abruptly short-acuminate at tip, distinctly cordate at base with open to closed sinus, mostly 8–16 cm long, 4–7 cm broad, sparsely hispidulous on both faces with stinging and nonstinging hairs, mostly 5-nerved at base; the margins bluntly and coarsely crenate (teeth 15–25 on a side). *Inflorescences* opposite the leaves, becoming ca. 10–15 cm long, distinctly bifurcate and protogynous, the lower pistillate branch with 5–10 flowers; pistillate bracts entire, 3–4 mm long, the staminate ones entire, 1.5–2 mm long. *Staminate flowers* with minutely hispidulous pedicels ca. 1.5–2 mm long, articulate near the base (stumps remaining after dehiscence of flower much shorter than subtending bract); sepals 3 or 4, obovate, acute, strigose without, 1.5–3 mm long, 1.8–2.2 mm broad; disk glands 5, erect, cylindric, thicker than filaments, 0.5–0.8 mm high; stamens 8–12; filaments free; anthers 1–1.2 mm long. *Pistillate flowers* with hispidulous pedicels up to 2.5 mm long in fruit; sepals 6, lanceolate, asymmetric, green, reflexed in fruit, becoming 3.5–6 mm long, 1–1.5 mm broad; ovary densely hispidulous with stinging hairs; styles basally connate or nearly free, 2–2.5 mm long, distinctly papillate. *Capsules* copiously hispid with stinging hairs, cocci ca. 8 mm long; columella 2.4–2.7 mm long; seeds globose, mottled brownish and gray, 3.6–3.7 mm across.

The single specimen of this species, previously unrecorded from Panama, is in poor condition and without flowers, so there is some doubt regarding its assignment. The Bristan collection matches a photograph of the type specimen from Venezuela, although the basal leaf sinus is not as open in the Panamanian plant. There is also some resemblance to *T. japurensis* Muell. Arg., described from Amazonian Brazil. However, it seems probable that the Brazilian species is synonymous with the one from Venezuela; at least, no convincing differences are given by Pax & Hoffmann (1919: 36).

Specimen examined. PANAMA. DARIÉN: Río Uruceca, *Bristan* 1444 (MO).

22.4. *Tragia correae* Huft, sp. nov. TYPE: Panama. Panamá: Picada da Estrada Panamá–San Blas entre 320–420 m, 9.1.1973, *Sucre, Braga, Dressler & Correa* 9832 (holotype, RB-165572, F neg. 62359).

Caulis volubilis lignosus; ramunculi rubelli dense pilosi. *Folia* alterna elliptica-oblonga 6–12 cm longa septemnervia, infra dense pilosa supra sparsa, basi cordata, margine remote denticulata. *Inflorescentia* racemosa unico flore

femineo infime, ceteris floribus (20–25) masculis; flores masculi calyce trilobo, staminibus 3, filamentis crassis, antheris extrorsis; flores feminei calyce 5-lobo, ovario dense hispiduloso, stylis papillatis.

Twining woody vine; twigs reddish, densely pilose, tardily glabrate, the older twigs with loose, exfoliating bark. *Leaves* with petioles 0.5–4 cm long, densely pilose; stipules deltate-lanceolate, acute, 6–10 mm long, pilose below, glabrous above; blades membranous, elliptic-oblong, acuminate at tip, cordate at base, 6–12 cm long, 3–4.5 cm broad, 2.2–2.7 times as long as broad, sparsely pilose above, more densely so below, usually 7-nerved at base; margins remotely denticulate (teeth 18–22 on a side). *Inflorescences* opposite the leaves, racemose, ca. 3 cm long (immature), with a single basal pistillate flower, the remaining nodes (ca. 20–25) with staminate flowers; bracts trifid; bracts entire. *Staminate flowers* on short, hispidulous pedicels; calyx lobes 3, obovate, acute, ca. 1.3 mm long, ca. 1.2 mm broad, hispidulous without, cucullate; stamens 3, the filaments thick and fleshy, free, ca. 0.8 mm long; anthers elliptic, 0.2–0.3 mm long, extrorse. *Pistillate flowers* with pilose pedicels ca. 2 mm long; calyx lobes 5, lanceolate, acute, ca. 3 mm long; ovary densely hispidulous with stinging hairs, the styles free to the base, spreading, papillate, ca. 2 mm long. *Mature capsules* not seen.

In aspect *Tragia correae* resembles the species that Pax & Hoffmann (1919) placed in section *Bia*, particularly such species as *T. fendleri*, *T. japurensis* Muell. Arg., and *T. fallax* Muell. Arg. The new species is excluded from that affinity, however, by its racemose rather than bifurcate inflorescences and staminate flowers with three (vs. 8–20) stamens. The entire sepals and extrorse anthers dictate its placement in section *Tragia*

(section *Eutragia* Muell. Arg. of Pax & Hoffmann, 1919). This species bears some similarity to *T. volubilis* but differs by a much woodier habit, densely pilose leaves, and persistently sessile pistillate flowers.

It is a pleasure to name this distinctive new species for Profesora Mireya Correa of the University of Panama. *Tragia correae* is known only from the type collection. Dra. Correa has kindly searched for a duplicate at the herbarium of the University of Panama (PMA), but so far, unfortunately, none has been found.

23. *Dalechampia*

***Dalechampia* L., Sp. Pl. 1054. 1753. TYPE: *Dalechampia scandens* L.**

LITERATURE

- ARMBRUSTER, W. S. 1984. Two new species of *Dalechampia* (Euphorbiaceae) from Mesoamerica. *Syst. Bot.* 9: 272–278.
 ——— & A. HERZIG. 1984. Partitioning and sharing of pollinators by four sympatric species of *Dalechampia* (Euphorbiaceae) in Panama. *Ann. Missouri Bot. Gard.* 71: 1–16.
 HUFT, M. J. 1984. A new combination in *Dalechampia* (Euphorbiaceae). *Ann. Missouri Bot. Gard.* 71: 341.
 PAX, F. & K. HOFFMANN. 1919. Euphorbiaceae—*Dalechampia*. In: A. Engler (editor), *Das Pflanzenreich* IV. 147. XII (Heft 68): 1–59.
 WEBSTER, G. L. & B. WEBSTER. 1972. The morphology and relationships of *Dalechampia scandens* (Euphorbiaceae). *Amer. J. Bot.* 59: 573–586.

As a result of additional collecting in Panama, the species of *Dalechampia* are now considerably better understood, and the number of species has increased from five to seven, necessitating a new key. The order of species has been modified to reflect better their systematic relationships (Webster & Armbruster, unpubl. synopsis).

KEY TO THE SPECIES OF *DALECHAMPIA* IN PANAMA

- 1a. Leaves lobed or unlobed, never compound.
 - 2a. Stem tips and inflorescences densely golden-hirsute; leaves unlobed to 3-lobed, mostly 15–30 cm long, with broad, open sinus at base; stamens 60–70 (involucral bracts narrowly spatulate and apically trifid, dull yellowish; bracts of staminate involucre free) 1. *D. shankii*
 - 2b. Stem tips and inflorescences with appressed to spreading hairs, these never golden; leaves mostly smaller, variously shaped; stamens 15–45.
 - 3a. Bracts of staminate involucre free and disarticulating separately; bractlets within staminate involucre apically lacerate; leaves unlobed (occasionally with 1 or 2 small lateral teeth); involucral bracts creamy or pinkish, marginally lacerate; seeds more or less rugulose.
 - 4a. Stigma asymmetric, slightly dilated, not over 1.2 mm across; involucral bracts creamy or white with greenish veins; hairs of stem spreading at least in part; leaves persistently pubescent beneath, attenuate-acuminate, basal sinus narrow or lobes overlapping 2. *D. canescens* subsp. *friedrichsthali*
 - 4b. Stigma peltate, 1–3.5 mm across; involucral bracts pink or purple to white with pink veins (rarely white with greenish veins); hairs of stem appressed; leaves glabrate beneath, cuspidate, with broad open sinus 3. *D. dioscoreifolia*
 - 3b. Bracts of staminate involucre more or less connate into a cup, not disarticulating separately; leaves

lobed, at least in part; involucre bracts creamy or white, with entire denticulate margins; seeds smooth.

5a. Unlobed leaves often present with lobed leaves; involucre bracts merely 3-dentate at apex, 7-9-nerved, 3-6.5 cm long; bractlets within staminate involucre apically lacerate 5. *D. tiliifolia*

5b. Unlobed leaves rare or absent, the leaves all 3- or 5-lobed; involucre bracts 3-lobed at least to the middle, 5-nerved, 1.5-3 cm long; bractlets within staminate involucre entire, laminar 7. *D. scandens*

1b. Leaves compound, 3-foliolate (rarely 5-foliolate).

6a. Young stems and lower leaf surfaces spreading-hirsute; leaflet tips cuspidate-acuminate; involucre bracts white; staminate involucre of 4 separate bracts, staminate bractlets lacerate; central fruiting pedicel ca. 3 cm long 4. *D. websteri*

6b. Young stems retrorsely pubescent; leaf blades glabrate; leaflet tips acute to evenly acuminate; involucre bracts green; staminate involucre 2-lipped (bracts confluent); staminate bractlets truncate, laminar; central fruiting pedicel ca. 1 cm long 6. *D. cissifolia* subsp. *panamensis*

23.1. *Dalechampia shankii* (A. Molina) Huft, Ann. Missouri Bot. Gard. 71: 341. 1984. *Tragia shankii* A. Molina, Ceiba 11: 68. 1965. TYPE: Costa Rica. Limón: Río Reventazón, 15 m, 23 Oct. 1951, *Shank & Molina* 4427 (holotype, F).

This species, originally described from Costa Rica, has now been recorded from Nicaragua to Colombia. It may easily be distinguished from our other Panamanian species by its large and distinctive golden hairs, as well as yellowish, narrowly spatulate, trifold involucre bracts. The free bracts of the staminate involucre and the lacerate staminate bractlets indicate that the species belongs to section *Dioscoreifoliae* in the emended sense (Webster & Armbruster, ined.), along with the two following Panamanian taxa. The collections of Barry Hammel show that *D. shankii* is polymorphic in leaf shape, since leaf blades from the single locality vary from unlobed to having one lateral lobe to three-lobed. Additional collections from Costa Rica, Panama, and Colombia are cited by Huft (1984).

Specimens examined. PANAMA. COCLÉ: near sawmill, 16.7 km N of turnoff to Coclesito from Llano Grande, 700 ft., *Hammel* 1811, 1812, 1813 (MO); 12 mi. from Llano Grande, 200 m, *Churchill et al.* 4148 (F, MO).

23.2. *Dalechampia canescens* Kunth subsp. *friedrichsthalii* (Muell. Arg.) Webster & Huft, stat. nov. *Dalechampia friedrichsthalii* Muell. Arg., Flora 55: 45. 1872. TYPE: Nicaragua. Río San Juan: *Friedrichsthal* 683 (not seen; locality erroneously cited by Mueller as Guatemala).

Several additional collections of this plant have now been made in Panama.

Specimens examined. PANAMA. COLÓN: along Río Mendosa, 8 km NW of Gamboa *Nee & Smith* 11370 (MO); Río Fato, *Pittier* 3866 (GH, NY, US); Río Bo-

querón, 6-8 km upstream from Peluca Hydro Station, *Siri* 1005 (DAV). SAN BLAS: Puerto Obaldía, sea level, *Knapp & Mallet* 4627 (DAV, MO).

It now appears that *Dalechampia friedrichsthalii* is excessively close morphologically to *D. canescens* Kunth (Nov. Gen. Sp. 2: 98. 1817). The collection from San Blas in particular seems somewhat intermediate, and it makes more sense biologically to treat the two taxa as allopatrically replacing subspecies of a single species. The two subspecies may be keyed out as follows:

1a. Leaf blades mostly attenuate-acuminate, sparsely to moderately pubescent beneath (hairs mostly 0.1-0.2 mm long, not overlapping in sinuses between veinlets) subsp. *friedrichsthalii*

1b. Leaf blades mostly abruptly cuspidate, softly pubescent beneath (many hairs over 0.2 mm long, overlapping in sinuses between veinlets) subsp. *canescens*

The Colombian taxon, subsp. *canescens*, was described from Tolima Province (Mariquita) and cited from Nariño by Pax & Hoffmann (1919: 52). The additional collections cited below indicate that subsp. *canescens* is widely distributed in the lowlands and foothills of the western Andean region in Colombia.

Specimens examined. COLOMBIA. CALDAS: Quebrada Yeguas, 20 km N of Honda, 300 m, *Gentry et al.* 18167 (DAV, MO). CAUCA: Río Patía, 590 m, *Plowman & Vaughan* 5354 (DAV). SANTANDER: 29 km W of San Vicente de Chucurí, 200 m, *Gentry & Aguirre* 15429 (MO).

23.3. *Dalechampia dioscoreifolia* Poeppig in Poeppig & Endl., Nov. Gen. Sp. Pl. 3: 20. 1841. TYPE: Peru. Maynas: *Poeppig* 2163 (W).

One additional locality merits noting: PANAMA. DARIÉN: near Río Canglón, *Duke & Bristan* 378 (MO).

An unusual specimen from Playón Chico, San

Blas (*Gentry 6365*, MO) appears to be intermediate between *D. dioscoreifolia* and *D. canescens* subsp. *friedrichsthali*, having the broad stigma of the former and the pubescent attenuate-acuminate leaves of the latter.

23.4. *Dalechampia websteri* Armbruster, Syst. Bot. 9: 272. 1984. TYPE: Costa Rica. Heredia: La Selva, 3 km SE of Puerto Viejo, Armbruster & Herzig 79-207 (DAV).

This species, recently described from Costa Rica, has been identified from Panama on the basis of the single record that was attributed (with doubt) to *D. cissifolia* in our treatment of 1968.

Specimen examined. PANAMA. BOCAS DEL TORO: Chiriquito, Lewis et al. 2123 (MO).

23.5. *Dalechampia cissifolia* Poeppig subsp. **panamensis** (Pax & K. Hoffm.) Webster, Ann. Missouri Bot. Gard. 54: 193. 1967. *D. panamensis* Pax & K. Hoffm., Pflanzenreich IV. 147. XII (Heft 68): 19. 1919. SYNTYPES: Costa Rica: *Tonduz 8089*, Guatemala: Cubilgüitz, *Tuerckheim II. 244*, 7978, Mexico. Chiapas: Escuintla, *Donnell Smith 2079*. Panama: *Oersted; Pittier 2311*, 3775.

This species still requires additional study. A variant with simple, unlobed leaves mixed with the compound ones, to which the name *Dalechampia heteromorpha* Pax & K. Hoffm. has been applied, occurs in Panama and throughout Central America but does not appear to be specifically distinct from the South American subsp. *cissifolia*.

There is one new provincial record for *D. cissifolia* subsp. *panamensis*.

Additional specimen examined. PANAMA. BOCAS DEL TORO: 10 mi. NW of Almirante, *D'Arcy 11204A* (MO).

24. *Omphalea*

Omphalea L., Syst. Nat. ed. 10. 1264. 1759. Nomen conserv. TYPE: *Omphalea triandra* L. (typ. conserv.).

24.1. *Omphalea diandra* L., Sp. Pl. ed. 2. 1377. 1763. TYPE: Jamaica, *Browne* (presumably BM, not seen).

Additional specimen examined. PANAMA. CHIRIQUÍ: Burica Peninsula, 2–4 mi. SW of Puerto Armuelles, *Croat 22045*, *Liesner 409* (MO).

25. *Pera*

Pera Mutis, Kongl. Vetensk. Akad. Nya. Handl.

5: 299, tab. 8. 1784. TYPE: *Pera arborea* Mutis.

Subfamily III. CROTONOIDEAE Pax

26. *Tetrorchidium*

Tetrorchidium Poeppig in Poeppig & Endl., Gen. Nov. Sp. Pl. 3: 23, tab. 227. 1841. TYPE: *Tetrorchidium rubrivenium* Poeppig.

The discovery of two distinctive new species in western Panama makes it necessary to provide a revised key. New province records are also recorded.

KEY TO THE SPECIES OF *TETROCHIDIUM* IN PANAMA

- 1a. Stems knobby, the apex densely hirsute or strigose.
 - 2a. Stems with persistent swollen stipules; leaves less than 7 cm long, the paired glands toward the apex of the petiole 1. *T. microphyllum*
 - 2b. Stems with raised leaf scars, the stipules persistent or not, rarely swollen; leaves usually over 10 cm long, the paired glands near the middle of the petiole 2. *T. costaricense*
- 1b. Stems smooth, the apex appressed-pubescent or glabrescent; leaves mostly more than 7 cm long; staminate inflorescence usually more than 4 cm long.
 - 3a. Basal foliar glands ca. 0.5–0.6 mm thick, definitely attached on laminar tissue; leaves mostly 15 cm long or more, with 6 or 7 prominent lateral veins; pistillate flowers sessile 3. *T. euryphyllum*
 - 3b. Basal foliar glands ca. 0.15–0.3 mm thick, attached at junction of lamina and petiole or well down on petiole; leaves 7–12 cm long, mostly with only 4 or 5 prominent lateral veins; pistillate flowers with distinct pedicels mostly 1.5–2 mm long 4. *T. gorgonae*

26.1. *Tetrorchidium microphyllum* Huft, sp. nov. TYPE: Panama. Chiriquí: 3.5 mi. NE of Boquete, end of road along Río Alto, 6,200 ft., 18 Nov. 1978, *Hammel 5721* (holotype, MO; isotype, F, F neg. 62357). Figure 2.

Arbor mediocris, gracilis, dioecia; ramulis junioribus fragilibus, praeter apicem dense hirsutum, glabris; foliis oblanceolatis, 2.5–7 cm longis, sparsim pubescentibus utrinque pilis malpighiaceis vel glabris, margine integris, apice acuminatis; petiolis brevibus, dense appressis pubescentibus pilis malpighiaceis; stipulis glanduliformibus, tumidis, persistentibus; floribus masculis in thyrsis axillaribus ad 3 cm longis; floribus femineis et capsulis ignotis.

Dioecious tree to 10 m; branches brittle, glabrous except at tips where densely hirsute, appearing warty by the presence of persistent, swollen

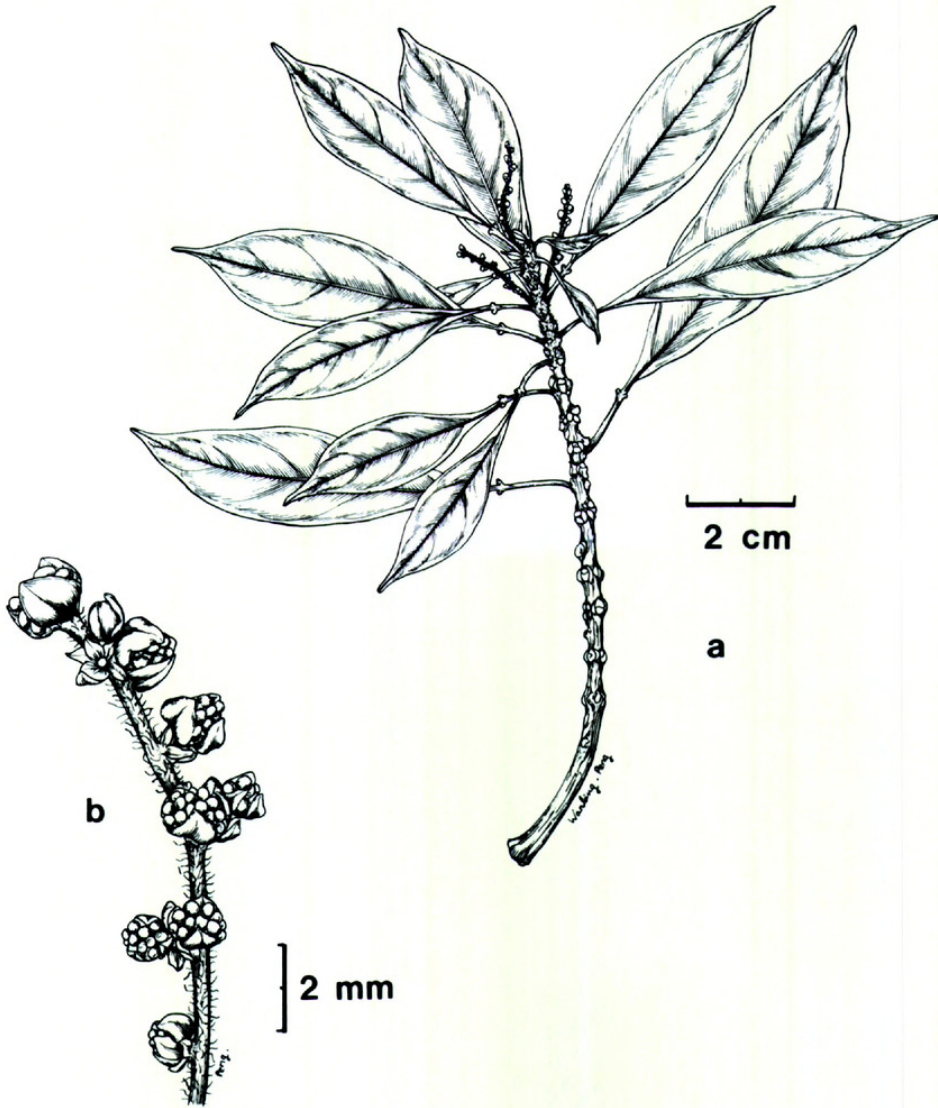


FIGURE 2. *Tetrorchidium microphyllum*.—*a*. Habit.—*b*. Detail of staminate inflorescence. Based on Hammel 6039. Illustration by Wan-Ling Peng.

stipules. *Leaves* short-petiolate, crowded near ends of branches; petioles 0.5–1.2(–1.5) cm long, densely appressed-pubescent with malpighiaceus hairs to glabrate, with massive, paired, thick-stalked, opposite or subopposite glands near the tip, these 0.6–0.8 mm long, 0.8–1 mm thick, stipules glanduliform, tumid, broadly triangular, 1.5–2 mm long, densely pubescent, persistent, glabrate soon after leaf-fall; blades chartaceous, oblanceolate, acuminate at tip, cuneate at base, (2.5–)4–5.5(–7) cm long, (0.9–)1.2–2 cm broad, sparsely pubescent with malpighiaceus hairs to glabrate on both sides, the midrib and primary veins (3–4 on a side) prominently raised below, the veinlets forming a prominent reticulum; margins entire. *Inflorescences* axillary; staminate thyrses unbranched, 1.5–3 cm long, the rachis densely strigose; pistillate inflorescences unknown. *Staminate flowers* subsessile; calyx lobes 3, triangular, glabrous, ca. 1–1.2 mm long; petals lacking; anthers subsessile, 0.8–0.9

mm long. *Pistillate flowers* unknown. *Fruits* unknown.

Cloud forests, western Panama.

This distinctive new species of *Tetrorchidium* appears to be most closely related to *T. brevifolium* Standley & Steyerf., described from the province of Alta Verapaz, Guatemala (Publ. Field Mus. Nat. Hist., Bot. Ser. 23: 126. 1944), from which it differs by the smaller leaves (7–12 cm long in *T. brevifolium*), densely pubescent shoot apices and inflorescences (both glabrous in *T. brevifolium*), and shorter inflorescences (4–7 cm long in *T. brevifolium*). The type specimen of the Guatemalan species (Rubelpec, Finca Seamay, Wilson 188, F) lacks the persistent tumid stipules that are so characteristic of *T. microphyllum*, but these are present on several collections of the former species made in 1974 and 1975 from Baja Verapaz, Guatemala (Lundell & Contreras 19173, 19436 (both

F, LL); *Williams et al.* 43277, F). The type specimen consists only of branchlet tips with a few leaves and staminate inflorescences that appear to have been taken from rapidly growing long shoots. *Tetrorchidium molinae* L. Williams, described from cloud forests in the mountains above San Juancito, Honduras (Fieldiana, Bot. 29: 348. 1961, based on *Williams & Molina* 17068, F), is similar in all respects to *T. brevifolium* and should be relegated to the synonymy of that species. A paratype specimen of *T. molinae* from the same area, *Williams & Molina* 13980 (F), has long shoots without stipules attached to a normal shoot with persistent stipules. This matches the pattern of the type collection of *T. brevifolium*, thus confirming the suspicion voiced above concerning the nature of that collection.

Additional specimen examined. PANAMA. CHIRIQUÍ: end of road past Palo Alto NE of Boquete in forest along ridge, 6,200–6,800 ft., *Hammel* 6039 (F, MO).

26.2. *Tetrorchidium costaricense* Huft, sp. nov. TYPE: Costa Rica. Puntarenas: Cordillera de Tilarán, Monteverde Reserve, near Continental Divide on Pacific side, 1,520–1,580 m, *Dryer* 1403 (holotype, CR, F neg. 62351; isotypes, F, F neg. 62350, MO, F neg. 62349).

Arbor ad 16 m alta, dioecia; ramulis junioribus dense strigosus; foliis anguste oblongis, 8–16 cm longis, apice abrupte cuspidatis; petiolis longis, prope medium glandibus binatis; floribus masculis sessilibus, in thyrsis axillaribus 4–9 cm longis; floribus femineis subsessilibus, ad fructus maturitatem brevipedicellatis, segmentis disci discretis ligulatis; ovariis 2-locularibus; seminum ovoideis, grosse reticulatis.

Dioecious tree to 16 m; branches densely strigose toward tip, appearing knobby from the raised leaf scars and occasionally from persistent, indurate stipules. Leaves long-petiolate, not crowded toward ends of branches; petioles 2.5–6 cm long, glabrous or minutely strigose, with paired, subopposite, sessile, patelliform glands near the middle, these ca. 1 mm (rarely to 2.2 mm) diam.; stipules oblong, 1.5–2.5 mm long, 1–1.5 mm broad, densely strigose, persistent, sometimes indurate after leaf-fall; blades membranous, narrowly oblong, 8–16 cm long, 3–7 cm broad, 2.2–3.3 times as long as broad, abruptly cuspidate at tip with an acumen 5–10 mm long, acute to attenuate at base, minutely puberulent below with scattered short malpighiaceae hairs, glabrous or nearly so above, the midrib prominent below, the secondary veins 6–8 on a side, arcuate, prominent below, obscure above; margin entire, eglandular. Inflorescences axillary, the axes densely strigose with short malpighiaceae hairs; staminate thyrses 4–9 cm long, freely

branched, the lateral branches to 3.5 cm long; pistillate racemes to 5 cm long. Staminate flowers in glomerules of 2–5, sessile; sepals 3, obovate, cucullate, glabrous without, pilose within; anthers subsessile, 1.3–1.5 mm broad. Pistillate flowers subsessile, the pedicels becoming 0.5–3 mm long in fruit; sepals broadly ovate, obtuse, 3–3.5 mm long, glabrous or sparingly short-strigose without, densely hispid toward base within; disk segments free, narrowly ligulate, ca. 2 mm long; ovary smooth, 2-locular, glabrous above, densely long-strigose below; style cap at maturity 0.5–0.8 mm high, 1.5–1.8 mm diam. Capsule 3–5 mm high, 5–6 mm diam., glabrous, oblate to globose; seeds ovoid-lenticular, 5–6 mm long, prominently and coarsely reticulate, the caruncle an irregular yellow papery keel running halfway from the hilum to the apex.

Known only from Costa Rica and extreme western Panama, this distinctive species is easily distinguished by the large, dark green, lanceolate leaves that are conspicuously venose, the paired glands near the middle of the rather long petioles, and the densely and minutely strigose branchlet tips, petioles, and leaves.

Tetrorchidium costaricense belongs to the group of species with free ligulate disk segments in the pistillate flower that includes *T. rotundatum* Standley and *T. brevifolium* Standley & Steyermark in northern Central America. Like *T. costaricense*, *T. rotundifolium* has paired glands near the middle of long petioles, but differs in its completely glabrous stems and leaves, mostly unbranched staminate thyrses that have larger glomerules, densely pubescent pistillate calyces, and distinctly pedicellate fruits. *Tetrorchidium brevifolium* differs in its glabrous stems, leaves, and calyces, short petioles with paired glands near the tip, and unbranched staminate thyrses. The widespread South American species *T. rubrivenium* Poeppig also belongs to this group but has glabrous stems and leaves, crenate or denticulate leaf margins, sometimes long petioles with the paired glands near the tip, densely pubescent pistillate calyces, uniformly puberulent ovary and capsule, and pedicellate fruits.

Additional specimens examined. COSTA RICA. ALAJUELA: Cordillera de Tilarán, Monteverde Reserve, Atlantic side, 1,500–1,580 m, *Dryer* 1071 (CR, F). CARTAGO: Reserva de Tapantí, 1,300–1,800 m, *Gómez* 18752 (F). PUNTARENAS: Cordillera de Tilarán, Monteverde Reserve, Pacific side, en orilla de Pantano Chomogo, 1,600–1,620 m, *Dryer* 659 (CR), 887 (CR, F); Monteverde Reserve, at field station, 1,500 m, *Haber* 491 (F); Monteverde Reserve, 1,570 m, *Haber & Bello* 1640 (F), 1,500 m, *Haber & Bello* 2457 (F). ALAJUELA/PUNTARENAS: on and near the Continental Divide, ca. 2–5 km

E and SE of Monteverde, 10°18'N, 84°46'W, 1,580–1,700 m, *Burger & Gentry 8608* (F); Monteverde, *Dryer 1731* (F). SAN JOSÉ: bajo de La Hondura, *Poveda 862* (CR, USJ). PANAMA. BOCAS DEL TORO: along Continental Divide, trail to headwaters of Río Mali, to W of Oleoducto Road, 8°47'N, 82°13'W, 1,200 m, *Churchill 5276* (F); Fortuna Dam region, along Continental Divide W of highway pass, ca. 8°45'N, 82°15'W, ca. 1,200 m, *McPherson 9695* (F).

26.3. *Tetrorchidium euryphyllum* Standley, Publ. Field Columbian Mus., Bot. Ser. 4: 219. 1929. TYPE: Panama. Bocas del Toro: vicinity of Almirante, 1928, *Cooper 621* (holotype, F).

When the original treatment was written, this species was known only from Costa Rica and extreme western Panama, but recent collections in Panama have now extended its range eastward to Darién.

Additional specimens examined. PANAMA. BOCAS DEL TORO: between Quebrada and Buena Vista, *Kirkbride & Duke 662* (MO). CHIRIQUÍ: Fortuna Dam region, along Quebrada Arena, ca. 8°45'N, 82°15'W, ca. 1,100 m, *McPherson 8394* (F). COCLÉ: slopes of Cerro Pilón near El Valle, 700–900 m, *Duke 12196* (MO, 2 sheets); Cerro Pilón, *Dwyer 8330* (MO); La Mesa, 8.5 mi. from Club Campestre (El Valle), *Dwyer 10515* (MO); Margarita near chicken farm, *Dwyer & Duke 8280* (MO); La Mesa, above El Valle, *Dwyer & Nee 11938* (MO); La Mesa, 4 km N of El Valle, 850–875 m, *Nee & Dwyer 9212* (MO). DARIÉN: Cerro Sapo, ca. 2,500 ft., *Hammel 1240* (MO). SAN BLAS: Cerro Brewster, 9°18'N, 79°16'W, 850 m, *de Nevers et al. 5408* (F). VERAGUAS: Caribbean slope above Río Primero Brazo, 5 mi. NW of Santa Fe, 700–1,200 m, *Croat 23233* (MO); NW of Santa Fe, 4.2 km from Escuela Agrícola Alto de Piedra, *Mori & Kallunki 4831* (MO); ca. 2.7 km from Escuela Agrícola Alto de Piedra, *Mori & Kallunki 5359, 6208* (MO); 7 km W of Santa Fe on road past agricultural school, 2,900 ft., *Nee 11216* (MO).

26.4. *Tetrorchidium gorgonae* Croizat subsp. **robledoanum** (Cuatrec.) Webster, Ann. Missouri Bot. Gard. 54: 199. 1967. *T. robledoanum* Cuatrec., Brittonia 9: 81. 1957. TYPE: Colombia. Antioquia: 23 Jan. 1947, *Gutiérrez 35556* (holotype, CAL, not seen).

This species is still unknown in Central America outside of Central Panama. Several recent collections allow a description of the fruit to be made for the first time. They are on densely strigose pedicels 7–10 mm long and jointed below the middle. The capsule is green, drying to brown, globose, shallowly 3-lobed, rugulose, 4–6 mm high, 4.5–7 mm in diameter, more or less densely strigose with short (0.2–0.6 mm) malpighiaceous hairs. The 3 styles are deeply bifid, 0.6–0.7 mm long, and tumid. The seeds are ovoid, 4–5 mm long, 3–4 mm

in diameter, black, coarsely and shallowly pitted, and completely surrounded by bright red, juicy arils.

Additional specimens examined. PANAMA. COLÓN: Santa Rita Ridge Road 1.5 mi. from Transisthmian Hwy., *Dwyer & Gentry 9338* (MO, 2 sheets); Santa Rita Ridge Road 4 mi. from Transisthmian Hwy. to Agua Clara weather station, ca. 500 m, *Gentry et al. 8841* (MO, 2 sheets); in forest along Río Guanche 3–7 km above bridge, 300–700 ft., *Hammel 4894* (MO). PANAMÁ: El Llano–Cartí highway, 17–20 km N of El Llano, *Dressler 4629* (F, MO); 10 km N of Margarita on road to Madroño, then 3 km W on ridgetop road, 1,800 ft., *Hammel 6014* (MO); Cerro Jefe region 2.5 mi. N of turnoff to radio tower along road, 2,400 ft., *Hammel 6300* (MO); El Llano–Cartí road, 9.6–11 km from Inter-American Hwy., 350 m, *Mori & Kallunki 3531* (MO); 5–10 km NE of Altos de Pacora on trail at end of road, 700–800 m, *Mori & Kallunki 6058* (MO); El Llano–Cartí road, 8 km N of Pan Am. Hwy. at El Llano, ca. 450 m, *Nee & Warmbrodt 10391* (MO).

27. *Manihot*

Manihot Miller, Gard. Dict. abr. ed. 4. 1754.
TYPE: *Manihot esculenta* Crantz (*Jatropha manihot* L.).

RECENT LITERATURE

ROGERS, D. J. & S. G. APPAN. 1973. *Manihot; Manihotoides*. Fl. Neotropica 13: 1–272.
——— & H. S. FLEMING. 1973. A monograph of *Manihot esculenta* — with an explanation of the taxonomic methods used. Econ. Bot. 27: 1–113.

The discovery of an additional Panamanian species necessitates a revised key and enumeration.

KEY TO THE SPECIES OF *MANIHOT* IN PANAMA

- 1a. Leaves glabrous, mostly with 7–9 lobes; calyx glabrous within (12–14 mm long; disk entire; anthers glabrous; ovary not sharply ribbed or winged) 1. *M. aesculifolia*
- 1b. Leaves pubescent or with fewer lobes; calyx pubescent within.
 - 2a. Leaves pubescent, mostly with 5 or more lobes; ovary distinctly ribbed or winged; staminate calyx 3–4.5 mm long; anthers pubescent; shrubs with erect stems 2. *M. esculenta*
 - 2b. Leaves glabrous, strictly 3-lobed; ovary not ribbed or winged; staminate calyx 10–20 mm long; anthers glabrous; clambering vine 3. *M. brachyloba*

27.1. *Manihot aesculifolia* (Kunth) Pohl, Pl. Bras. Icon. Descr. 1: 55. 1827. *Janipha aesculifolia* Kunth, Nov. Gen. Sp. 2: 85, tab. 109. 1817. TYPE: Mexico. Campeche: *Humboldt & Bonpland* (P, not seen).

This plant was called *M. gualanensis* Blake in our original treatment, but that name has been

reduced to a synonym of *M. aesculifolia* in the recent monograph of the genus by Rogers & Appan cited above.

27.3. *Manihot brachyloba* Muell. Arg., Fl. Brasil 11(2): 451. 1874; Rogers & Appan, Fl. Neotrop. 13: 190–192. 1973. TYPE: Brazil. Pará: *Martius* (syntype, G; microfiche seen).

The Bristan specimens have very young inflorescences but vegetatively match the description and illustration given by Rogers & Appan. However, contrary to their description and that of Mueller, the staminate buds in the Panamanian specimens are pubescent externally.

Specimens examined. PANAMA. DARIÉN: headwaters of Río Tuqueza, between Quebrado Venado and Peje Swamp, *Bristan 1001* (DAV, MO); between Manené and Río Coasí, *Hartman 12127* (MO).

28. *Cnidoscolus*⁴

Cnidoscolus Pohl, Pl. Brasil. Icon. Descr. 1: 56. 1827. LECTOTYPE: *Cnidoscolus hamosus* Pohl (chosen by Small in Britton & Brown, Illust. Fl. N. U.S. ed. 2, 2: 462. 1913).

28.1. *Cnidoscolus urens* (L.) Arthur, Torrey 21: 11. 1921. *Jatropha urens* L., Sp. Pl. 1007. 1753. TYPE: “America calidiori, in Brasilia & c.” (not seen, possibly in Hortus Cliffortianus Herbarium, BM).

Since the treatment of 1968, further study of the Panamanian specimens of *C. urens* leads to the conclusion that the two variants discussed there merit taxonomic recognition. Pending a more detailed revision of the *C. urens* complex (Breckon, ined.), the Panamanian plants may be disposed of as follows.

28.1a. *Cnidoscolus urens* (L.) Arthur subsp. *urens*.

Specimens examined. PANAMA. PANAMÁ: Farfan Beach area, *Correa et al. 1586*, *Dwyer 3065*, *Tyson 1803* (MO). COCLÉ: between Aguadulce and San Antón, *Woodson et al. 1226a* (MO); between Antón and Natá, *D’Arcy & Croat 4117* (MO); banks of Río Grande, *Burch et al. 1157* (MO). HERRERA: Chitré to Divisa, *Burch et al. 1357* (MO); Sal Salinas de Chitré, *Croat 9692* (MO). PANAMÁ: San Carlos, *de McPherson 11* (MO).

28.1b. *Cnidoscolus urens* subsp. ***adenophilus*** (Pax & K. Hoffm.) Breckon, stat. nov. *Jatropha adenophila* Pax & K. Hoffm., Pflanzenreich IV. 147. VII(Heft 63): 409. 1914. *Cnidoscolus adenophilus* (Pax & K. Hoffm.) Pax & K. Hoffm., Nat. Pflanzenfam. ed. 2, 19c: 166. 1931. TYPE: Panama. Panamá: Chepo, *Pittier 4740* (isotype, US).

Specimens examined. PANAMA. CANAL ZONE: Miraflores Locks, *Stern et al. 81* (MO); Pipeline Road, *Croat 12732* (MO); Curundú, *McDaniel 5180* (MO), *Tyson 1045* (MO); Ft. Amador Islands, *Tyson 5413* (MO). DARIÉN: El Real, *Lazor & Correa 3364* (MO), *Stern et al. 454* (MO). LOS SANTOS: 5 mi. NW of Guararé, *Wilbur et al. 12054* (MO); Monagre Beach, *Lewis et al. 1673* (MO). PANAMÁ: Jenine, Río Cañita, *Duke 3821* (MO); between Las Margaritas and Río Mamoní, *Duke 5867* (MO); Puente de Pacora, *De Hoyos 18* (MO). VERAGUAS: 2–4 mi. E of Santiago, *Duke 12354* (MO); 12 km E of Santiago, *Dwyer & Kirkbride 7450* (MO).

28.2. *Cnidoscolus aconitifolius* (Miller) I. M. Johnston, Contr. Gray Herb. 68: 86. 1923. subsp. ***aconitifolius***. *Jatropha aconitifolius* Miller, Gard. Dict. ed. 8. 1768. TYPE: *Herb. Miller* (presumably at BM, not seen).

In the present interpretation, the Panamanian specimens of *Cnidoscolus aconitifolius* all belong to the nominate subspecies, which is not native to Panama.

29. *Jatropha*

Jatropha L., Sp. Pl. 1006. 1753. LECTOTYPE: *Jatropha gossypifolia* L. (see McVaugh, 1944: 459).

RECENT LITERATURE

- DEHGAN, B. 1982. Comparative anatomy of the petiole and infrageneric relationships in *Jatropha* (Euphorbiaceae). Amer. J. Bot. 69: 1283–1295.
———. 1984. Phylogenetic significance of interspecific hybridization in *Jatropha* (Euphorbiaceae). Syst. Bot. 9: 467–478.
——— & G. L. WEBSTER. 1979. Morphology and infrageneric relationships of the genus *Jatropha* (Euphorbiaceae). Univ. Calif. Publ. Bot. 74: 1–73.
MCVAUGH, R. 1944. The genus *Cnidoscolus*: generic limits and intrageneric groups. Bull. Torrey Bot. Club 71: 457–474.

30. *Pausandra*

Pausandra Radlk., Flora 53: 92, tab. 2. 1870. TYPE: *Pausandra morisiana* (Casar.) Radlk. (*Thouinia morisiana* Casar.).

Diocious trees or shrubs; stems with reddish latex; indumentum malpighiaceous. Leaves alter-

⁴ Contributed by Dr. Gary Breckon, University of Puerto Rico, Mayagüez.

nate, simple; petioles swollen distally; blades pinately veined, biglandular at base, the margins serrate. *Inflorescences* axillary, spiciform; staminate flowers in glomerules; pistillate flowers solitary at each node; bracts inconspicuous, eglandular. *Staminate flowers* subsessile; calyx lobes 5, imbricate; petals 5 or rarely 6, connate (at least below), adaxially villous; disk extrastaminal, urceolate, lobate, glabrous; stamens (3-)5-7; filaments free; anthers dehiscent introrsely and longitudinally, the connective not enlarged; pollen grains globose, inaperturate, clavate; pistillode absent. *Pistillate flowers* subsessile; sepals 5, imbricate; petals 5, free, adaxially villous; disk urceolate, sometimes lobate, glabrous; ovary of 3 carpels; ovules 1 per locule; styles free, bifid. *Fruits* capsular; seeds smooth, carunculate; endosperm copious; embryo straight, cotyledons palminerved, much longer than radicle.

This primarily South American genus is here reported from Panama for the first time.

LITERATURE

- BAILLON, H. 1873. Nouvelles observations sur les Euphorbiacées. *Adansonia* 11: 72-138.
LANJOUW, J. 1936. The genus *Pausandra* Radlk. *Recueil Trav. Bot. Néerl.* 33: 758-769.

30.1. *Pausandra trianae* Baillon, *Adansonia* 11: 92. 1873, proposed without reference to *Pogonophora trianae* Muell. Arg. TYPE: Colombia: Bogotá, plains of San Martín, Río Meta, *Triana* 2597 (holotype, P, not seen; isotypes, G, not seen, photo F neg. 24574, K, not seen, holotype of *Pogonophora trianae* Muell. Arg.).

Pogonophora trianae Muell. Arg., *Flora* 47: 434. 1864. TYPE: Colombia. Bogotá: plains of San Martín, Río Meta, *Triana* 2597 (holotype, K, not seen, isotypes, G, not seen, photo F neg. 24574, P, not seen, holotype of *Pausandra trianae* Baillon).

Pausandra quadriglandulosa Pax & K. Hoffm., *Pflanzenreich* IV. 147. XIV(Heft 68): 43. 1919. TYPE: Brazil: Rio Acre, Seringal S. Francisco, *Ule* 9538 (holotype, B, not seen, photo F neg. 5406).

Pausandra extorris Standley, *Trop. Woods* 17: 24. Mar. 1929; *Publ. Field Columbian Mus., Bot. Ser.* 4: 219. Oct. 1929. TYPE: Nicaragua: Bragman's Bluff, *Englesing* 216 (holotype, F, F neg. 52719; wood sample, Y no. 13301).

Clavija septentrionalis L. O. Williams, *Fieldiana, Bot.* 32: 205. 1970. TYPE: Nicaragua: Cabo Gracias a Dios, Laimos Creek, ca. 15 km SW of Waspam, 7 Mar. 1961, *Bunting & Licht* 390 (holotype, F; isotypes, NY, US).

Tree to 30 m; branching pagodiform; sap dark red-brown; twigs and buds $\pm$ densely brown-puberulent with malpighiaceae hairs; leaf scars

prominent. *Leaves* horizontally aligned; petiole 1.5-3.5 cm long, 2-4 mm thick, terete, strigose with short (to 0.5 mm long) malpighiaceae hairs; glands at apex of petiole (3-)4, cylindrical, 1-1.5 mm long, ca. 1 mm thick; blade chartaceous, obovate to oblanceolate, rounded, obtuse, or abruptly short-cuspidate at tip, long-attenuate at base, 20-50 cm long, 7-18 cm broad, 2.6-4 times as long as broad, glabrous above, glabrate or thinly puberulent with short malpighiaceae hairs below, the secondary veins prominent, 15-23 per side; margin remotely denticulate. *Inflorescences* spicate, arising singly in the upper axils, 10-25 cm long, the rachis densely puberulent. *Staminate flowers* 6-12 per glomerule, these sessile, widely spaced; sepals 5, imbricate, densely puberulent, obovate, ca. 1.5 mm long, ca. 1.5 mm broad, rounded at apex; petals 5, white, narrowly obovate, ca. 6 mm long, glabrous without, densely hirsute toward base within; stamens 6, exserted, the filaments 5-6 mm long; disk cupulate. *Pistillate flowers* not seen. *Capsule* smooth, strigose with short malpighiaceae hairs, apparently subglobose, ca. 1 mm diam. (fragments only seen); columella 7-8 mm long; seeds subglobose, brown with irregular white striations, 8-9 mm long, ca. 6 mm diam.; caruncle a flattened irregular mass near hilum.

Rainforests, Honduras to western Brazil.

The description is based on the Panamanian specimens cited below and supplemented by collections at F from Costa Rica and Nicaragua.

The genus *Pausandra* remains poorly understood. The most recent revision (Lanjouw, 1936) was based upon only 33 collections and resulted in the recognition of nine species, most known from only a single sex. Lanjouw admitted that several of the species might need to be united as more material became available. *Pausandra trianae* does appear, however, to be one of the better-delimited species in the genus and is certainly the most widespread. The Central American plants readily key to that species in Lanjouw's revision, where *P. extorris* and *P. quadriglandulosa* are reduced to synonymy. The identity of *Clavija septentrionalis* as *P. trianae* was first pointed out by R. L. Liesner of the Missouri Botanical Garden (pers. comm.).

The author citation for *Pausandra trianae* has been almost universally given for the last century as *Pausandra trianae* (Muell. Arg.) Baillon, carrying the implication that Baillon had transferred *Pogonophora trianae* Muell. Arg. to its correct place in *Pausandra*. It is clear from Baillon's text,

however, that he intended to describe a new species; there is no indication that he was aware of Mueller's name. Baillon's paper (1873) is a series of miscellaneous notes on the Euphorbiaceae. Under *Pausandra* (pp. 92–93), he stated that the genus was described in 1870 and was known by a single species, *P. morisiana*. He then indicated that a collection from Colombia (*Triana* 2597) represented an additional species in the genus, which may be given the name *P. trianae*. ("Ce genre est aussi représenté à la Nouvelle-Grenade, par une plante qui est bien voisin de celle de Brésil, qui n'en est peut-être même qu'une forme; je lui donnerai provisoirement le nom de *P. Trianae*.") No reference whatever was made to Mueller's name, and none would be expected. One would not normally look in *Pogonophora* for species pertaining to *Pausandra*; the genera are too different for that.

The fact that the names of Mueller and of Baillon are both based on the same collection, although on different specimens, is merely a coincidence. That both chose the same epithet is also coincidental, but not very surprising, given the common practice of naming species after the collector of the type.

Thus, although Baillon ideally should have made a transfer of Mueller's name, he was understandably unaware that Mueller had previously described the species at hand, and did not make the transfer. Had the two authors chosen different epithets, then the rules would mandate a transfer of Mueller's epithet to create a new combination in *Pausandra* supplanting Baillon's name. But that solution is closed because it would create a later homonym. Article 63 of the Code (Voss, 1983) might mislead one to reject Baillon's name as superfluous, because it seems to be based on the type of a name whose epithet ought to have been adopted under the rules. A correct reading of the Code, however, makes it clear that a type is a *specimen*, and not a gathering, which usually consists of several duplicate specimens. An isotype has no official standing as long as the holotype exists, although its value is unquestioned. Thus, for a name to be rejected as

superfluous, it must be based upon the same specimen as an earlier name whose epithet ought to have been adopted. This is not the case with *Pausandra trianae* Baillon. There is therefore no bar to the acceptance of that name as the correct one for this species.

Additional specimens examined. PANAMA. BOCAS DEL TORO: premontane rainforest between Q. Lugron and Cerro Bonyic, near Terebe, 300–900 ft., *Kirkbride & Duke* 647 (MO). SAN BLAS: Río Taindi (Taimdi of maps) 6 km above confluence with Río Mandinga, 9°25'N, 79°11'W, 30–100 m, *de Nevers & Herrera* 7674 (F); along newly cut road from El Llano to Cartí-Tupile, near Continental Divide, 300–500 m, *Liesner* 1289 (DAV, F, MO), *Mori & Kallunki* 5535 (MO); seasonal lowland rainforest on the Aila Tilar (Río Acla), 8°48'N, 77°40'30"W, 25–100 m, *Sugden* 424, 588 (MO).

31. *Garcia*

Garcia Vahl in Rohr, Skr. Naturhist.-Selsk. 2: 217. 1792. TYPE: *Garcia nutans* Vahl.

31.1. *Garcia nutans* Vahl in Rohr, Skr. Naturhist.-Selsk. 2: 217, tab. 9. 1792. TYPE: Colombia. Magdalena: near Santa Marta, *von Rohr* (C, not seen).

Additional specimens examined. PANAMA. CANAL ZONE: Barro Colorado I., *Knight* 1090 (MO). LOS SANTOS: between Tonosí and Guánico, *Tyson et al.* 3126 (MO).

32. *Croton*

Croton L., Sp. Pl. 1004. 1753. LECTOTYPE: *Croton aromaticus* L. (chosen by Webster, J. Arnold Arbor. 48: 354. 1967).

Seven species new to Panama (including two new species and one new subspecies) are reported here; a few new province records are indicated as well. These additions make it necessary to provide a revised key.

LITERATURE

LANJOUW, J. 1931. The Euphorbiaceae of Surinam. Amsterdam.

KEY TO THE SPECIES OF *CROTON* IN PANAMA

- 1a. Staminate flowers apetalous; stipules and petiolar glands absent; leaves with stellate-lepidote indumentum above, lepidote beneath (stamens 10–12; filaments hirsutulous; styles usually 3 times bifid; seeds deciduously stellate, 5–6 mm long) 20. *C. punctatus*
- 1b. Staminate flowers petaliferous; leaves stipulate (stipules sometimes early deciduous); indumentum various.
 - 2a. Indumentum lepidote.
 - 3a. Leaves without basal laminar or petiolar glands; petals in flowers not reduced; pistillate calyx lobes valvate but not reduplicate.
 - 4a. Stamens 9–12; filaments glabrous; anthers 0.6–0.8 mm long; petals of staminate flowers not lepidote or with only 1 or 2 scales; seeds mostly 7 mm long or shorter.

- 5a. Leaves more or less oblong-elliptic, pinnately veined; inflorescences mostly 2 cm long or longer; pedicels of pistillate flowers mostly 10 mm long or longer 1. *C. schiedeanus*
- 5b. Leaves ovate, more or less cordate, (3-)5-veined at base; inflorescences 1 cm long or shorter; pedicels of pistillate flowers 1-2 mm long 2. *C. pseudoniveus*
- 4b. Stamens 14-17, or if fewer, then filaments hirsutulous; anthers 1-1.2 mm long; petals of staminate flowers lepidote; seeds 15 mm long or longer.
 - 6a. Stamens (10 or) 11-13; leaves pinnately veined; pistillate flowers mostly 3 or 4 per raceme; seeds 20-22 mm long 3. *C. tenuicaudatus*
 - 6b. Stamens 15; leaves 3-5-veined at base; pistillate flowers mostly 1 or 2 per raceme; seeds 15-18 mm long 4. *C. pyriticus*
- 3b. Leaves with basal laminar glands; petals in pistillate flowers reduced; pistillate calyx lobes reduplicate-valvate.
 - 7a. Seeds 3-5 mm long; fruiting pedicels 8-15 mm long 5. *C. lanjouensis*
 - 7b. Seeds 16-17 mm long; fruiting pedicels not over 7 mm long 6. *C. pachypodus*
- 2b. Indumentum not lepidote, the trichomes mostly or entirely stellate or dendritic; petals in pistillate flowers distinctly reduced or absent (sometimes fairly well developed in *C. draco*); petioles with prominent glands at junction with blade (except sometimes in *C. hircinus*); inflorescence (at least in part) terminal.
 - 8a. Leaves deeply 3-5-lobed; staminate calyx lobes distinctly imbricate in bud; staminate receptacle glabrous; seeds tetragonal; annual herb 19. *C. lobatus*
 - 8b. Leaves unlobed or shallowly lobed (less than halfway); staminate calyx lobes mostly valvate in bud; staminate receptacle sparsely to densely villose (glabrous in *S. santaritensis*); seeds not tetragonal.
 - 9a. Stamens over 50; styles more than 5 mm long, twice bifid; stipules tomentose, dentate, 3-6 mm long; seeds ventrally ribbed 7. *C. speciosus*
 - 9b. Stamens fewer than 50; styles less than 5 mm long.
 - 10a. Lower cymules of inflorescence with both staminate and pistillate flowers at the same nodes; seeds coarsely ribbed.
 - 11a. Styles bifid; pistillate calyx lobes not reduplicate-valvate; stamens 13 or more; filaments glabrous or nearly so; leaves unlobed, without scattered laminar glands.
 - 12a. Pistillate flowers distinctly pedicellate, the pedicels mostly 3-6 mm long; inflorescences mostly 2-4 dm long; stamens 13-20; styles glabrous or nearly so; seeds less than 5 mm long 8. *C. draco*
 - 12b. Pistillate flowers subsessile, the pedicels in fruit not over 2 mm long; inflorescences mostly 1-2 dm long; stamens 25-45; styles distinctly stellate-pubescent; seeds at least 5 mm long 9. *C. pungens*
 - 11b. Styles multifid, stellate-pubescent; pistillate calyx lobes reduplicate-valvate; stamens 11 or 12; filaments hirsutulous; leaves more or less 3-lobed, with scattered peltate laminar glands above 10. *C. smithianus*
 - 10b. Lower nodes of bisexual inflorescences with solitary pistillate flowers (not with staminate flowers at the same nodes), or inflorescences unisexual.
 - 13a. Styles twice bifid to multifid.
 - 14a. Shrubs or trees; pistillate calyx lobes not strongly unequal, the abaxial ones not deeply lacerate.
 - 15a. Pistillate bracts not deeply lacerate; staminate receptacle villose.
 - 16a. Stamens 14-16; seeds costate or verrucose.
 - 17a. Pistillate calyx lobes elliptic to oblong, valvate, neither reduplicate nor accrescent, glabrous within, less than 5 mm broad; staminate petals not over 4 mm long; leaves mostly 7-9-veined at base, entire; petioles mostly 5-20 cm long 11. *C. billbergianus*
 - 17b. Pistillate calyx lobes ovate, reduplicate-valvate, accrescent, stellate-tomentose within, becoming 7-8 mm long and broad; staminate petals 4.5-5 mm long; leaves mostly 5-veined at base, entire to denticulate; petioles 1-4 cm long 12. *C. fragrans*
 - 16b. Stamens 10-12; seeds smooth; staminate receptacle sparsely villose.
 - 18a. Leaves mostly alternate (occasionally opposite at 1 or 2 distal nodes), 7-9-veined at base, the margins distinctly dentate (teeth 15-40 on a side), the basal laminar glands small or absent; stipules, bracts, and pistillate calyx lobes coarsely glandular-dentate; inflorescence with 3-12 pistillate flowers; filaments densely hirsutulous below; ovary usually densely stellate-tomentose 13. *C. hircinus*
 - 18b. Leaves alternate below, opposite or ternate distally, pinnately veined or obscurely triplinerved, the basal laminar glands long-stipitate; stipules and bracts entire; pistillate

- calyx lobes entire or obscurely dentate; inflorescence with 1 or 2 (rarely 3) pistillate flowers; filaments glabrous; ovary sparsely stellate-pubescent apically ... 15. *C. brevipes*
- 15b. Pistillate bracts deeply lacerate; staminate receptacle glabrous; stamens 12–15 14. *C. santaritensis*
- 14b. Annual herbs; pistillate calyx lobes very unequal, the adaxial ones greatly reduced or obsolete, the abaxial ones lacerate, accrescent (6–8 mm long in fruit); seeds smooth 16. *C. argenteus*
- 13b. Styles once bifid; annual herbs.
- 19a. Leaves coarsely and sharply serrate (major teeth usually not over 10 per side); stamens 8–10; styles less than 1.5 mm long, spreading 17. *C. trinitatis*
- 19b. Leaves more finely and/or bluntly toothed; stamens mostly 11 or 12; styles 1.5 mm long or more, ascending or erect; seeds minutely beaked.
- 20a. Stems coarsely hispid; leaves mostly ovate, pointed at the tip, petiolar glands stipitate; bracts with long gland-tipped processes 18. *C. hirtus*
- 20b. Stems not coarsely hispid; leaves mostly elliptic or oblong, blunt at tip, the petiolar glands sessile; bracts eglandular [*C. glandulosus*]

32.3. *Croton tenuicaudatus* Lundell, *Phytologia* 1: 451. 1940. TYPE: Costa Rica. San José: vicinity of El General, *Skutch* 2575 (holotype, MICH).

Additional specimen examined. PANAMA. BOCAS DEL TORO: along road to Chiriquí Grande, 10 road mi. from Continental Divide and 2 mi. along pipeline access road E of highway, ca. 8°55'N, 82°08'W, 350–500 m, *McPherson* 8767 (F).

32.5. *Croton lanjouwensis* Jabl., *Mem. New York Bot. Gard.* 12: 158. 1965. *C. matourensis* Aublet var. *benthamianus* Muell. Arg., *Linnaea* 34: 95. 1865. *C. benthamianus* (Muell. Arg.) Lanjouw, *Euphorb. Surinam* 17. 1931, non *C. benthamianus* Muell. Arg., *Fl. Bras.* 11(2): 106. 1874. TYPE: Brazil: Río Negro, *Spruce Croton* 2 (isotype, NY).

Tree to ca. 12 m high; monoecious; twigs densely lepidote. *Leaves* with petioles lepidote, 1.5–3.5 cm long, distally with 2 large yellowish, subsessile, patelliform glands ca. 1.5–2 mm across; stipules linear-lanceolate, entire, densely lepidote, 8–10 mm long, early deciduous; blades chartaceous, elliptic to elliptic-oblong, acute to short-acuminate at tip, cuneate at base, mostly 8–15 cm long, 3.5–6.5 cm broad, smooth and glabrous above, densely lepidote beneath (scales denticulate-margined, ca. 0.25–0.4 mm across and nearly or quite contiguous); venation distinctly pinnate, the major lateral veins (ca. 11–15 on a side) straight; margins entire and lepidote-marginate. *Inflorescences* terminal, racemose, 13–15 cm long, bisexual; pistillate flowers solitary at 3–6 proximal axils; staminate flowers in cymes of 2 or 3 at distal axils; bracts entire, lepidote, up to 3 mm long. *Staminate flowers* with lepidote pedicels 2–5 mm long; calyx lobes 5, valvate, ovate-triangular, lepidote, 2–2.5 mm long;

receptacle villose; petals obovate or narrowly elliptic, ca. 2 mm long, glandular-punctate, densely villose on margins, glabrous on back; stamens 12 or 13; filaments glabrous or sparsely hirsutulous; anthers elliptic, 0.6–0.7 mm long. *Pistillate flowers* with stout lepidote pedicels becoming 8–15 mm long; calyx lobes 5, equal, triangular, ± reduplicate-valvate, lepidote without, ± stellate-lepidote within on the recurved margins, 4.5–5 mm long; disk 5-lobed, adnate to calyx; petals rudimentary (shorter than 1 mm long); ovary densely lepidote (scales ca. 0.6–0.8 mm across); styles twice-bifid, ca. 4 mm long, stellate proximally (branches glabrous). *Capsules* not seen entire; cocci lepidote, ca. 5 mm long; columella slender, ca. 4 mm long; seeds plump, scarcely compressed, brownish, smooth, ca. 3.5 mm long.

The Panamanian plants appear to agree in most respects with *C. lanjouwensis* as defined by Lanjouw (1931: 12–17; as *C. benthamianus*); the broad pistillate calyx with adaxially stellate lobes is apparently diagnostic in separating the species from *C. matourensis* Aublet. However, the Panamanian plants occurring in cloud forest at 800–1,000 m would appear to differ ecologically from the Amazonian plants, which have been collected in lowland rainforests. Jablonski (1965: 157–158) cited *C. matourensis* from comparable altitudes in Venezuela; further comparisons of plants from Panama with the South American plants evidently are needed. The specimens from Panamá Province differ rather strikingly in their duplex petiolar glands, sparsely lepidote upper leaf surfaces, and shorter pistillate pedicels.

Specimens examined. PANAMA. BOCAS DEL TORO: along road to Chiriquí Grande, ca. 1.5 mi. along road E of highway, ca. 8°55'N, 82°10'W, 250–350 m, *McPherson & Allen* 9640 (F). COCLÉ: Cerro Pilón, near El

Valle, ca. 900 m, *Duke & Correa 14718* (DAV, MO); cloud forest, hills N of El Valle de Antón, *Dressler 4083* (DAV, MO); cloud forest, El Valle, 800–1,000 m, *Duke 13166* (DAV, MO), *Dwyer & Correa 7951* (DAV, MO), *Correa 311* (MO). PANAMÁ: primary forest, road from El Llano to Cartí-Tupile, 200–500 m, *Croat 22905* (DAV, MO).

32.6. *Croton pachypodus* Webster, sp. nov.

TYPE: Panama. San Blas: km 18 of El Llano–Cartí road, 9°19'N, 78°55'W, 350 m, 1 Oct. 1984, *de Nevers & Herrera 3980* (holotype, MO; isotypes, DAV, F).

Species haec ab *C. pyritico* differt foliis supra glabris petiolo glandulato, ab *C. lanjouwense* differt seminibus majores, ab aliis speciebus Centroamericanis differt pedicellis valde incrassatis.

Tree 7–25 m high; twigs obtusely angular, glabrate. *Leaves* with petioles lepidote, 0.8–1.5 cm long, distally (near base of blade) with 2 subsessile or short-stipitate (to 0.7 mm) blackish patelliform glands 0.5–1 mm across; stipules linear-lanceolate, entire, densely lepidote, 4–10 mm long, 0.9–1.2 mm broad, $\pm$ persistent; blades chartaceous, elliptic-oblong to somewhat obovate, subacute or acute to abruptly short-acuminate at tip, cuneate to rounded at base, 8–22 cm long, 3.5–7 cm broad, smooth and glabrate above (with sparse scales on major veins when young), evenly and sparsely lepidote beneath (scales 0.25–0.4 mm across, denticulate, with ca. 50 radii), the scales widely separated; venation distinctly pinnate, the major lateral veins (9–13 on a side) straight or slightly curving, the veinlet reticulum prominulous beneath; margins entire, smooth, without lepidote rim. *Inflorescences* terminal and axillary, racemose, (5–)10–15 cm long, bisexual or staminate; pistillate flowers solitary at lowermost (1–)2–4(–5) nodes of bisexual inflorescences, staminate flowers solitary or paired at distal axils; bracts triangular, blackish, sparsely lepidote, 0.5–1 mm long. *Staminate flowers* (buds only observed) with lepidote pedicels 1.5–2.5 mm long; calyx lobes 5, valvate, triangular, lepidote, ca. 3 mm long; receptacle villose; petals narrowly elliptic, ca. 2.5 mm long, densely villose on margins, sparsely lepidote (often a single scale) on the back, densely hirsutulous adaxially; stamens 14–16, the filaments glabrous, the anthers 0.8–0.9 mm long. *Pistillate flowers* with stout lepidote pedicels ca. 2.5–3.5 mm long, becoming in fruit 4.2–6.5 mm long, 3.2–4 mm broad; calyx lobes 5, equal, triangular-ovate, reduplicate-valvate, densely lepidote without, densely tomentose-villose within, 3–3.5 mm long, 2.5–3 mm broad; disk shallowly 5-lobed, nearly 4 mm across, smooth and

glabrous; petals obsolete, represented by whitish tufts of hairs; ovary densely lepidote (scales 0.5–0.8 mm across, denticulate, 50–70-radiate, with 20–30 darkened radii); styles blackish, twice-bifid, 3.5–4 mm long, nearly glabrous. *Capsules* not seen entire; valves of cocci ca. 23–25 mm long; columella slender, ca. 20 mm long; seeds elliptic, somewhat compressed, flattened and obscurely carinate on the back, distinctly keeled on inner face, grayish brown, smooth and shining, 16.2–17.2 mm long, 10.3–11.3 mm broad; caruncle hippocrepiform, obscure, tenuous, ca. 2.5 mm long, 1.5 mm broad.

Collections of this species have been determined as *C. lanjouwensis*, to which indeed it is related and superficially very similar. However, it is distinguished by leaves very sparsely lepidote beneath and with margins free of scales, shorter petioles with smaller darker glands, and especially by the much larger fruits borne on greatly thickened pedicels. Among species earlier reported from Panama, the new species resembles *C. tenuicaudatus*; however, that species has eglandular leaves lepidote on both faces, strongly lepidote staminate petals, and more slender pistillate pedicels. *Croton pyriticus* appears to be even less similar because of its ovate palmately veined eglandular leaves, longer and more slender (1.5 mm or thinner) pistillate pedicels, and verruculose capsules; however, the seeds, although larger, are similar in shape to those of *C. pachypodus*.

Additional specimens examined. PANAMA. SAN BLAS: 12 mi. above Pan-American Hwy., 200–500 m, *Croat 22905* (MO); 20.7 km from Pan-American Hwy., 350 m, *Mori & Kallunki 5116* (MO).

32.7. *Croton speciosus* Muell. Arg. [Linnaea 34: 83. 1865] subsp. *tacarcunensis* Webster, subsp. nov. TYPE: Panama. Darién: Cerro Tacarcuna, S slope, premontane wet forest on ridge below summit, 1,250–1,450 m, *Gentry & Mori 13925* (holotype, MO; isotype, DAV).

Haec a subsp. *specioso* differt stipulis minoribus, glandulis petioli brevioribus, carunculo seminis ca. 2 mm lato.

Monoecious tree 5 m high; twigs subterete, densely tawny-villose with dendritic hairs. *Leaves* with petioles (2–)3–11 cm long, tomentose, apically with 4–6 stalked glands on ventral side, the glands ca. 0.8–1.5 mm long, 0.3–0.4 mm across; stipules lanceolate, densely tomentose, toothed, 3–6 mm long; blades membranous, mostly ovate, long-acuminate at tip, rounded to subcordate at base, the larger ones shallowly 3-lobed, 12–21 cm long, 7–12 cm broad; lamina above copiously pu-

bescent with stellate-tufted hairs, beneath copiously tomentose with whitish dendritic hairs ca. 0.5–1 mm across, 3–5-nerved at base, with 7–10 major lateral veins on each side, connected by a scalariform reticulum of straightish veinlets; margins subentire (obscurely denticulate). *Inflorescences* terminal (or pseudolateral), bisexual, racemose, 2.5–6 cm long, with 1 or 3 proximal flowers and 3–7 distal flowers; flowers solitary at each node; bracts 5–7 mm long, attenuate-acuminate, tomentose, with subulate stipules ca. 3–5 mm long. *Staminate flowers* with stellate-tomentose pedicels 5–8 mm long; receptacle densely tomentose; calyx lobes 5, fulvous-tomentose, obtuse, entire, 3.5–5 mm long; petals obovate, 4.5–5 mm long, densely appressed-pubescent without, glabrous within, woolly-villose along margins; stamens ca. 60–70; filaments slender, glabrous, ca. 4–5 mm long; anthers oblong, apiculate, 1.2–1.6 mm long, 0.5–0.7 mm broad. *Pistillate flowers* with stout tomentose pedicels ca. 2–4 mm long at anthesis (becoming up to 1 cm long in fruit); calyx segments 5, valvate, oblong, densely whitish- to fulvous-tomentose without, sparsely tomentose in distal third within, ca. 10 mm long, 3–5 mm broad; disk inconspicuous, adnate to base of calyx, crenulate, stellate-pubescent, ca. 5 mm across; petals rudimentary, densely hirsute, ca. 1–1.5 mm long; ovary densely fulvous-tomentose; styles twice-bifid near the base, densely stellate-pubescent below (and with scattered stellate hairs distally nearly to tips), ca. 7–9 mm long, the branches dark reddish, dilated and crenulate at tips. *Capsules* subglobose, fulvous-hispidulous, ca. 1 cm long and broad; seeds plump, plumbeous brown, distinctly costate ventrally, obscurely costate on back, ca. 7 mm long, 5 mm broad; caruncle roundish, low, ca. 2 mm across.

This striking *Croton* from the cloud forests at the crest of Cerro Tacarcuna appears to be conspecific with *C. speciosus*, which was described from specimens collected near Caracas, Venezuela. I have examined *Moritz 1329* (A, GH) from Galipán, near Caracas, one of the syntypes cited by Mueller (incorrectly located by him as in Colombia rather than Venezuela), as well as three other collections from near Galipán (*Allart s.n.*, *Pittier 221*, 9577, A, GH). These plants in general rather closely resemble the Cerro Tacarcuna specimens in leaf shape and pubescence, flower configuration, and seeds; there can be little doubt that we are dealing with a single species. The stamen number in the Venezuelan plants varies from 40 to 80 and hence includes the number for the Cerro Tacarcuna plants.

Mueller gave the stamen number of *C. speciosus* as ca. 150, which certainly does not agree with *Moritz 1329*, in which two buds yielded ca. 70 and ca. 80 stamens. Possibly the number may become higher in some Venezuelan plants, as Mueller (1866: 529) also cited two other collections from near Caracas, *Fendler 34* and *231* (cited as *Linden 34* and *201*), which we have not seen.

The publication of a separate subspecies for the Tacarcuna population is made diffidently, as intervening collections may close the gap. However, the Panamanian plants differ strikingly in their much smaller and less lacerate stipules, as well as in having distinctly shorter stalked glands at the apex of the petiole. Furthermore, the caruncle in seeds from Panama is roundish and ca. 2 mm broad, whereas it is distinctly laterally expanded and ca. 3 mm broad in seeds from Venezuela. Provisionally, therefore, it seems best to designate the Cerro Tacarcuna plants as a distinct subspecies.

Additional specimens examined. PANAMA. DARIÉN: S slope of westernmost peak of Cerro Tacarcuna, 1,100–1,300 m, *Gentry et al. 16877* (MO); ridgetop below Alto de Nique base camp, *Gentry et al. 28727* (MO).

32.8. *Croton draco* Cham. & Schltdl. [*Linnaea* 6: 360. 1831] subsp. **panamensis** (Klotzsch) Webster, stat. nov. *Cyclostigma panamense* Klotzsch in Seem., Bot. Voy. Herald 105. 1853. *Croton panamensis* (Klotzsch) Muell. Arg. in DC., Prodr. 15(2): 546. 1866. TYPE: Panama. Chiriquí: Volcán Chiriquí, *Seemann* (K, not seen). (see Webster & Burch, 1968: 254 for additional synonymy.)

Further examination of Mexican and Central American specimens of *Croton draco* indicates that the Panamanian plants cannot reasonably be maintained as a separate species. Except for the larger, broader stipules (mostly 2 mm or more across), the Mexican populations here assigned to subsp. *draco* show no essential differences from plants with narrow stipules that occur from Guatemala (and sporadically in southern Mexico) to Panama and Colombia.

32.10. *Croton smithianus* Croizat, J. Arnold Arbor. 21: 93. 1940. TYPE: Colombia. Santander: Mesa de los Santos, *Killip & Smith 15283* (holotype, A; isotype, US).

Tree to 18 m high; twigs angled or sulcate, yellowish-scurfy with pedicellate stellate hairs. *Leaves* with petioles mostly 5–15 cm long; patel-

liform glands at apex of petiole sessile, 0.9–1.2 mm across; stipules linear-lanceolate to spatulate, 5–9 mm long, 1–2 mm broad; blades mostly ovate, sometimes 3-lobed, blunt to acuminate at the tip, cordate to subcordate at base, the larger ones 15–35 cm long, 10–30 cm broad; venation palmate, with 5(–7) major veins at base, 5–8 laterals on each side above the base, the laterals sometimes dichotomizing towards the margin; veins and veinlets prominent on both sides, the veinlets scalariform; trichomes on upper surface pedicellate-stellate, 0.2–1 mm across, with stalks 0.1–0.5 mm high, beneath denser and $\pm$ floccose; small patelliform glands (0.4–1 mm across) occasional on upper surface; margins denticulate, with occasional small stalked glands. *Inflorescences* terminal, mostly 20–50 cm long; 5–15 proximal cymes bisexual, distal ones staminate; staminate bracts subulate, entire, deciduous, ca. 1–2.5 mm long, subtending several flowers. *Staminate flowers* with stellate-tomentose pedicels 1.5–5 mm long; calyx distinctly gamophyllous, 3.5–4 mm long; calyx lobes ovate, acute, valvate, 2.2–3.7 mm long, 2–2.8 mm broad; petals narrowly spatulate, 3.2–4.5 mm long, 0.5–1 mm broad, densely villose ventrally, strigose-hirsutulous dorsally; receptacle densely villose; stamens 11 or 12; filaments flattened, densely hirsutulous in lower $\frac{3}{4}$, 3–4.5 mm long; anthers elliptic, the connective glandular-pustulate, 1.1–1.5 mm long. *Pistillate flowers* with stellate-lepidote pedicels becoming 9–14 mm long; calyx lobes 5, valvate (not distinctly reduplicate), elliptic to ovate, entire, stellate-lepidote (trichomes 0.1–0.4 mm across) outside, stellate inside near tip and along margins, 5–7.5 mm long, 3.5–6.5 mm broad; disk entire, thickish, ca. 1.7 mm across; ovary yellowish-stellate or stellate-hispid, trichomes 0.5–1.5 mm across in fruit; styles free, multifid, sparsely to copiously stellate-hispid, ca. 5 mm long. *Capsules* subglobose, yellowish with appressed scales; columella ca. 4 mm long; seeds plump, lenticular, brownish, finely costate-rugulose, bluntly pointed at both ends, 3.9–4.1 mm long, 3.3–3.5 mm broad; caruncle flat, bilobed, 1.7–2.1 mm broad.

Croton smithianus is found in lowland and lower montane forests, up to ca. 1,500 m elevation, Nicaragua to Colombia, flowering July to September.

The Panamanian representative of the widespread and variable South American species complex centering on *Croton palanostigma* Klotzsch is here referred to *C. smithianus* Croizat because

of its characteristic indumentum of pedicellate stellate trichomes. The populations in Colombia are rather variable and poorly understood; the isotype at US, which is a fruiting specimen, has the characteristic indumentum, and a specimen from Chocó (Archer 2062, US) has the characteristic leaf form and margin, but the trichomes are not distinctly pedicellate as in the Panamanian plants. The Panamanian and Colombian plants somewhat resemble *Croton killipianus* Croizat, described from Boyacá; however, the type collection of that species (Lawrance 588; isotype, US) has subtire leaf margins and an appressed, rather sparse indumentum more characteristic of *C. benthamianus* Muell. Arg. *Croton nuntians* Croizat from Guyana is somewhat similar but differs in its smaller fruiting calyx and shorter fruiting pedicel. Until this species complex is revised, it seems best to refer our plants to *C. smithianus*. Several collections from Nicaragua and Costa Rica are also referred to that species.

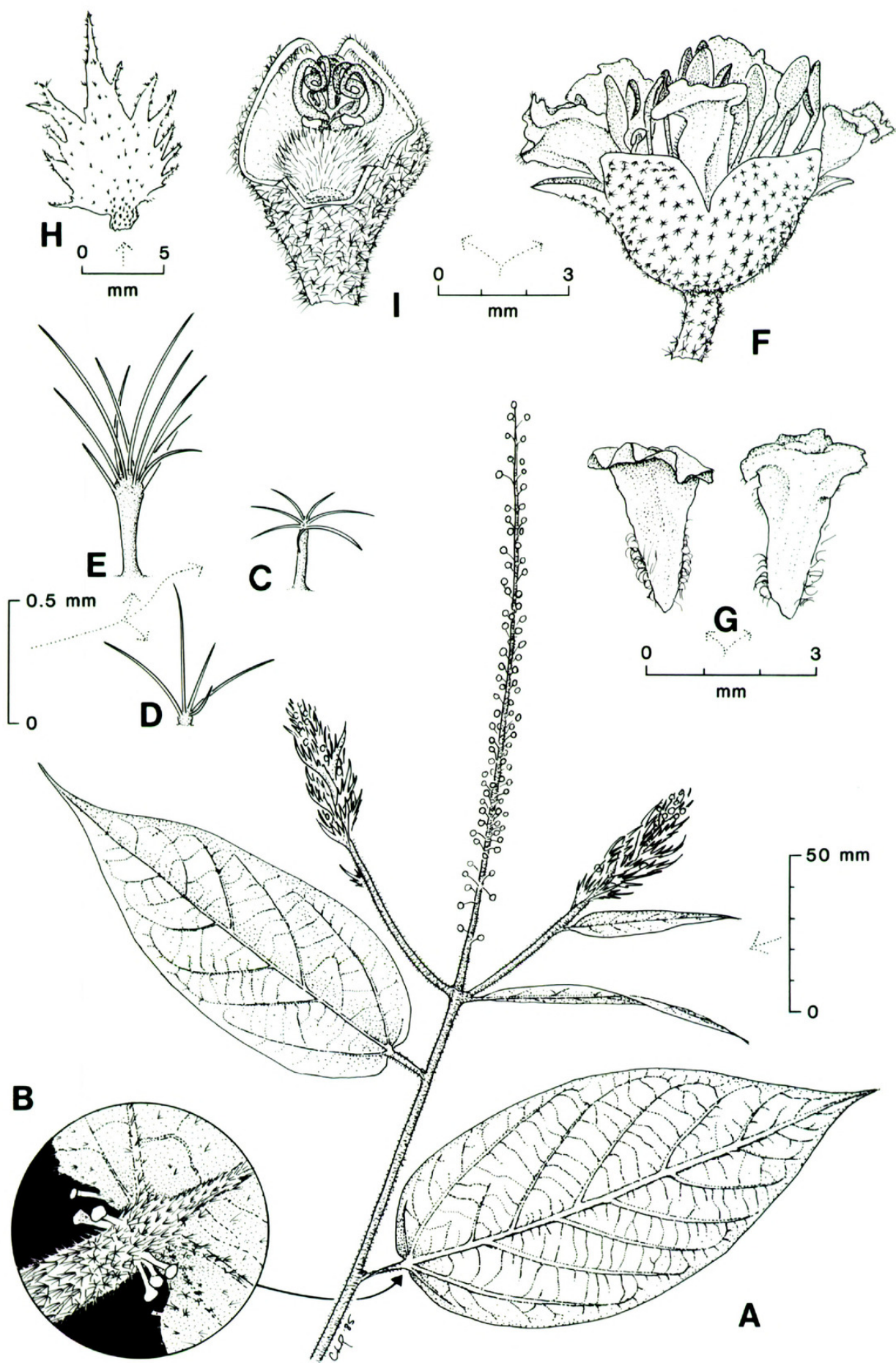
Specimens examined. COSTA RICA. HEREDIA: Finca La Selva, Hammel & Trainer 12849, 13044 (DAV, DUKE). PUNTARENAS: forest remnants along highway 4 mi. SE of turnoff to Buenos Aires, 9°07'N, 83°17'W, 400 m, Webster 21883 (DAV, MO); rainforest 17 mi. SE of San Isidro General, 700 m, Webster & Miller 12394 (DAV). NICARAGUA. RÍO SAN JUAN: Sábalo, Araquistain 3223 (DAV, MO). ZELAYA: Bluefields, Neill 2598 (DAV, MO). PANAMA. COLÓN: Río Salud, Howell 128, Lao & Holdridge 224 (MO). DARIÉN: between Manené and Tusijuanda, Duke 13576 (DAV). PANAMÁ: SE slopes of Cerro Trinidad, Kirkbride & Duke 1665 (MO).

32.11. *Croton billbergianus* Muell. Arg., Linnaea 34: 98. 1865; subsp. *billbergianus*.
TYPE: Panama. Colón: Portobelo, Billberg 316 (not seen).

This species has been collected in three additional provinces.

Additional specimens examined. PANAMA. BOCAS DEL TORO: Súrsuba, Río Changuinola, Dwyer s.n. (MO). SAN BLAS: Puerto Obaldía to La Bonga, Knapp & Mallet 4667 (MO). VERAGUAS: Coquyito mine to Río Barrera, Hammel 5221 (MO); Santa Fe, Folsom & Edwards 3392 (MO).

The description in the original treatment (Webster & Burch, 1968: 257–258) applies only to subsp. *billbergianus*. As suggested at that time, *C. pyramidalis* J. D. Smith, extending from Veracruz, Mexico, to Honduras, does not appear to be a distinct species. It may be retained at the subspecific level because of its apparently larger seeds (5.7–6.2 mm in the Veracruz population vs. 4.3–5.5 mm in the Panamanian plants) and longer



stipules (7–15 mm long vs. 5–7 mm in the Panamanian plants). A new combination for the Mexican plant is therefore necessary.⁵

32.13. *Croton hircinus* Vent., Jard. Malmaison 1: 50, pl. 50. 1804. TYPE: cultivated specimen, *Ventenat* (presumably at G, not seen).

An additional provincial record is cited.

Additional specimen examined. PANAMA. CHIRIQUÍ: Río Cobre bridge, 25 mi. W of Tole, *Dwyer & Hayden* 7542 (MO).

32.14. *Croton santaritensis* Huft, sp. nov.
TYPE: Panama. Colón: Santa Rita Ridge Road, 21–26 km from Transisthmian Highway, tropical wet forest, 500–550 m, 9°25'N, 79°37'W, 4 July 1982, *Knapp 5882* (holotype, MO; isotypes, DAV, F, F neg. 62353, PMA). Figure 3.

Frutex monoecus dense villosus, pilis castaneis stellatis. Folia ovata-oblonga vel lanceolata, basi subcordata vel rotundata, apice longicaudata; glandulae petiolares aliquot tubaeformes, stipulae ovatae-deltatae margine fimbriatae. Inflorescentiae unisexuales racemosae, masculinae terminales, femineae axillares; bractae femineae flabellatae profunde laciniatae flores includentes.

Shrub ca. 1.5 m high; monoecious; twigs subterete, densely villous with brownish stellate hairs. *Leaves* with petioles densely villous as the twigs, 5–20 mm long; petiolar glands several at apex of petiole, stipitate, trumpet-shaped, 0.5–1.5 mm long, 0.3–0.5 mm across; stipules ovate-deltate, membranous, eglandular, appressed, 8–11 mm long, 4–6 mm broad, the margins fimbriate; blades chartaceous, ovate, ovate-oblong, or lanceolate, longicaudate at apex, rounded to subcordate at base, 10–15 cm long, 4–8 cm broad, 1.7–3 times as long as broad, sparsely to moderately stellate pubescent above, sparsely tomentose below, 3–7-

nerved at base, the secondary veins 5–8 per side; margin entire to remotely denticulate. *Inflorescences* unisexual, racemose, the staminate ones terminal, the pistillate ones axillary, occurring only at the two subopposite nodes immediately below the terminal staminate raceme; staminate inflorescences 17–22 cm long, densely brown stellate-villous; nodes 15–30; flowers 1–3 at each node on stellately pubescent pedicels 6–9 mm long, the bracts subulate, 2–3 mm long, stellate below, glabrous above; pistillate inflorescences 5–11 cm long, densely brown-villous; bracts flabellate, deeply lacinate, 10–12(–14) mm long, at least the lower ones loosely enclosing the flower buds. *Staminate flowers*: sepals 5, deltate, joined at base, valvate, stellately pubescent, the lobes 2.5–3 mm long, ca. 2 mm broad; petals 5, only slightly exceeding the calyx lobes, ca. 6 mm long, ca. 2 mm broad below the tip, the tip abruptly expanded, ca. 2.5 mm broad, coarsely erose; stamens 12–15; disk consisting of 5 nearly separate glands; receptacle glabrous. *Pistillate flowers* (immature): sepals 5, deltate, fleshy; ovary densely stellate-hispidulous; styles twice-divided. Mature fruits and seeds not seen.

This species may easily be distinguished from all other Central American species of *Croton* by the peculiar arrangement of the inflorescences, the conspicuous fimbriate stipules, and the oblong, lacinate bracts that loosely enclose the young pistillate flowers.

No close relative of *C. santaritensis* is known. Because of its combination of pentamerous calyces in both pistillate and staminate flowers, five petals and glabrous receptacles in the staminate flowers, and the large fimbriate stipules and bracts, it is not easily accommodated in any of the sections recognized by Mueller (1866: 511–700) in the most recent worldwide account of *Croton*. No species closely resembling *Croton santaritensis* has been found among the large holdings of South American *Croton* at the Field Museum or the Missouri Botanical Garden.

32.15. *Croton brevipes* Pax, Bot. Jahrb. Syst. 33: 290. 1903. TYPE: Costa Rica. Río del Convento, *Pittier 12117* (isotype, US, photo, F).

⁵ *Croton billbergianus* subsp. *pyramidalis* (J. D. Smith) Webster, stat. nov. *Croton pyramidalis* J. D. Smith, Bot. Gaz. 35: 7. 1903. TYPE: Guatemala. Alta Verapaz: Río Dolores near Cubilgüitz, *Tuerckheim 7974* (holotype, US; not seen).

FIGURE 3. *Croton santaritensis*.—A. Habit, with staminate and pistillate inflorescences.—B. Detail of leaf base, showing glands.—C. Trichome from upper leaf surface.—D. Trichome from lower leaf surface.—E. Trichome from stem.—F. Staminate flower.—G. Staminate petals, abaxial view on left, adaxial on right.—H. Pistillate bract, abaxial view.—I. Pistillate flower in bud, cut-away view. Based on *Knapp 5882*. Illustration by Clara Richardson.

Shrub 1–3 m high; monoecious; twigs pale, appressed-stellate. *Leaves* alternate below, mostly opposite or ternate above; petioles densely appressed-stellate, 3–20(–30) mm long (less than $\frac{1}{4}$ length of blade); petiolar glands (at base of blade) conspicuous, cylindrical, apically truncate and dilated, 1–2.5 mm long, 0.3–0.5 mm across; stipules subulate to narrowly lanceolate, dark, entire, eglandular, stellate-pubescent, 1.4–2.8 mm long; blades thinly chartaceous, elliptic to ovate-elliptic or obovate, acute to acuminate at tip, cuneate to obtuse at base, 4–13 cm long, (1–)2–5 cm broad, sparsely stellate or appressed-hispid above with few-rayed trichomes, sparsely appressed-stellate and inconspicuously glandular-punctate beneath, pinnately veined (or inconspicuously triplinerved) with mostly 5–7 veins on each side; margins subentire to rather coarsely and irregularly dentate (teeth ca. 8–15 on a side), with stalked glands between some of the teeth. *Inflorescences* mostly terminal and bisexual (some also lateral and staminate), racemose, 1.5–3(–4.5) cm long, with 1 or 2 (rarely 3) basal solitary pistillate flowers, the staminate flowers 1 or 2 per bract at distal axils; bracts narrow, entire, eglandular, stellate-pubescent, mostly 1.5 mm long or shorter. *Staminate flowers* with sparsely stellate or nearly glabrous pedicels 1–2 mm long; calyx lobes 5, elliptic-lanceolate, acute, stellate-pubescent, glandular-punctate, 1.2–1.7 mm long, 0.9–1.1 mm broad; receptacle moderately villose; petals obovate-spathulate, 1.4–1.8 mm long, glandular-punctate, barbate-hirsute on lower margins; stamens 10–12; filaments glabrous, 1.8–2.5 mm long; anthers ovate, 0.5–0.7 mm long. *Pistillate flowers* with stout appressed-stellate pedicels becoming 1.3–3.5 mm long; calyx lobes 5, subequal, narrowly oblong-lanceolate or spathulate, subentire (with 1 or 3 obscure teeth), sparsely stellate outside, glabrous inside, 3.5–6.5 mm long, 1–1.5 mm broad; petals rudimentary, subulate; disk entire, glabrous; ovary sparsely stellate-pubescent apically, glabrous below; styles free, ca. 2 mm long, twice bifid, glabrous to hispidulous. *Capsules* subglobose, sparsely stellate-pubescent or glabrescent, ca. 5 mm diam.; columella slender, 3.2–4 mm long; seeds broadly ellipsoid, compressed, apically beaked, brownish, nearly smooth (minutely striolate), 3.8–4.1 mm long, 2.8–3.4 mm broad, the caruncle small, ca. 0.5–0.8 mm across.

Rainforest below 1,000 m, Costa Rica and Panama.

This plant bears a considerable resemblance in habit to *C. hircinus* but differs in having (distally) opposite or ternate pinnately veined leaves with

larger laminar glands; the stipules, bracts, and calyx lobes lack the glandular serrations of *C. hircinus*. Examination of material of *Croton macrodontus* Muell. Arg. from Mexico shows that it is extremely close to *C. brevipes*. Although specimens from Costa Rica and Panama may be easily recognized by their distally opposite, less coarsely toothed leaves with more rounded bases and shorter petioles, they are very similar to the Mexican plants in most details, including pubescence, floral details, and fruits. The seeds of the Mexican plants are somewhat larger, but this difference may disappear upon further sampling. Provisionally, the two species may be kept distinct on the basis of the foliar characters, and because no intermediate populations have yet been discovered in Central America between Costa Rica and Mexico.

Specimens examined. PANAMA. COLÓN: Santa Rita Ridge, ca. 300 m, Antonio 3739 (DAV, F, MO), Correa & Dressler 912 (F, MO), Croat 13898 (MO), Duke 15291 (MO), Dwyer 8543 (MO), Dwyer & Gentry 9395 (F, MO), Foster 1751 (DAV, DUKE, F), Gentry 1874 (DAV, F, MO), Kennedy 2756 (MO), Knapp 5845 (DAV, F, MO), Sytsma 2047 (MO), 2054 (F, MO), Webster & Dressler 16727 (DAV, MO, US); East Ridge, Duke 15291 (DAV). PANAMÁ: Cerro Jefe, 700–750 m, Dressler 3844 (DAV, MO, US), Webster & Dressler 16477 (DAV, DUKE, MO, US); Tortí Arriba, Folsom et al. 6644 (DAV, MO).

32.16. *Croton argenteus* L., Sp. Pl. 1004. 1753. *Julocroton argenteus* (L.) Didr., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1857(8–10): 134. 1857; Muell. Arg. in DC., Prodr. 15(2): 703. 1866; Croizat, Revista Argent. Agron. 10: 125. 1943; Correll & Johnston, Man. Vasc. Plants Texas 939. 1970. TYPE: America (not seen; presumably in Hortus Cliffortianus Herbarium, BM; 1140.8 in LINN).

Annual herb 2–10 dm high; stems pseudodichotomizing, with long internodes and pseudover-ticels of leaves, appressed stellate-puberulent. *Leaves* with petioles 1–5 cm long, these without paired apical glands; stipules subulate, (2.5–)5–10 mm long; blades chartaceous, ovate or the upper ones oblong-ovate, obtuse or rounded to subacute at tip, cuneate to rounded at base, mostly 3–7(–15) cm long, 2.5–5 cm broad, 5-veined at base; lateral veins above base 3 or 4 on each side, not prominent; above green and finely appressed-stellate, beneath grayish and more densely stellate; margins finely serrulate. *Inflorescences* terminal, bisexual, ca. 1–4 cm long; bracts subtending solitary flowers, the pistillate flowers 4–6 at base of spike; staminate bracts subulate, entire, ca. 3 mm

long. *Staminate flowers* with pedicels ca. 1.5–2.5 mm long; calyx lobes lanceolate, acute, valvate, ca. 1.5–2 mm long; petals linear, 2.1–2.3 mm long, 0.3–0.4 mm broad, glabrous except for the ciliate margins; receptacle copiously villose; stamens usually 11; filaments sparsely to rather copiously appressed-hirsutulous, ca. 2–2.5 mm long; anthers elliptic-oblong, 0.6–0.8 mm long. *Pistillate flowers* with short pedicels ca. 1–1.5 mm long, becoming 3–5 mm long in fruit; calyx lobes 5, imbricate, very unequal, the 3 abaxial lobes much larger, in fruit 6–8 mm long, 2.5–6 mm broad, oblong, laciniate, provided on each side with 5–10 teeth ca. 0.5–3 mm long, the 2 abaxial lobes much smaller, nearly or quite obsolete; petals absent; disk strongly asymmetrical, with larger adaxial lobes 0.9–1.2 mm long, 0.5–0.7 mm broad, the 2 adaxial lobes very small; ovary stellate-tomentellous; styles erect, distally quadrifid, hispid-stellate, ca. 2–4 mm long. *Capsules* ca. 5 mm long; columella 3–4.5 mm long; seeds ellipsoid, smooth, mottled gray and brown, apically beaked, 3.1–4 mm long, 2.4–2.9 mm broad; caruncle ca. 1.5 mm broad.

Scattered in weedy habitats from extreme southern Texas to Panama, reappearing in Venezuela, Paraguay, and Argentina, but not reported from most of tropical South America. The two Panamanian collections may represent recent introductions.

Specimens examined. PANAMA. PANAMÁ: marsh area 2 mi. S of Tocumen Airport, *Tyson & Clewell 5899* (MO); Río Tapia, *Bartlett & Lasser 16629* (MO).

Subfamily IV. EUPHORBIOIDEAE

33. *Mabea*

***Mabea* Aublet, Hist. Pl. Guiane 867. 1775. TYPE: *Mabea piriri* Aublet.**

RECENT LITERATURE

HUFT, M. J. 1987. Notes on *Mabea* (Euphorbiaceae) in Central America, together with comments on sect. *Apodae* in Brazil. *Phytologia* 62: 339–343.

STEINER, K. E. 1983. Pollination of *Mabea occidentalis* (Euphorbiaceae) in Panama. *Syst. Bot.* 8: 105–117.

The discovery of a distinctive new species of *Mabea* in Panama makes it necessary to provide a new key to the three species now known from the country.

KEY TO THE SPECIES OF *MABEA* IN PANAMA

- 1a. Leaves acute or subacuminate at apex, usually 3–5 times as long as broad; bracteal glands of the staminate cymules not elevated above the

rachis; stamens 15–20 per staminate flower ...

- 1. *M. montana*
1b. Leaves cuspidate to long-acuminate at apex, usually less than 3 times as long as broad.
2a. Bracteal glands of the staminate cymules not elevated above the rachis; stamens more than 30 per staminate flower; undivided portion of the style at maturity 12–20 mm long 2. *M. occidentalis*
2b. Bracteal glands of the staminate cymules elevated above the rachis; stamens 10–15 per staminate flower; undivided portion of the style at maturity 4–9 mm long
..... 3. *M. jefensis*

33.1. *Mabea montana* Muell. Arg. in DC., Prodr. 15(2): 1151. 1866. TYPE: Colombia: Schlim 1132. Venezuela: Fendler 24. Panama: Sutton Hayes 715 (syntypes, not seen).

Additional collections examined. PANAMA. VERAGUAS: roadside between Santa Fe and San José, *D'Arcy 10314* (MO); 5 km S of Santa Fe, below 500 m, *Folsom & Collins 1644* (MO); a 1 km del puente sobre el desvío del Río San Juan, *Luna 47* (MO).

33.3. *Mabea jefensis* Huft, Phytologia 62: 341. 1987. TYPE: Panama. Panamá: newly bulldozed trail off Cerro Jefe Road, 0.4 km beyond turnoff to Alto de Pacora, 29 Sep. 1975, *J. T. & F. Witherspoon 8570* (holotype, MO, F neg. 62352). Figure 4.

Montane and premontane rainforests of Central Panama, 350–1,000 m.

Mabea jefensis is known from abundant collections from both the Cerro Jefe area and from the Continental Divide north of El Llano in eastern Panamá Province, as well as from a single collection from the Cañazas mountain range in the western part of the province. It seems likely that this species will prove to be common in the mountainous region along the border of Panamá and San Blas provinces as this area becomes more thoroughly explored.

Additional specimens examined. PANAMA. PANAMÁ: Cerro Jefe area, *Antonio et al. 3399* (F), *Correa et al. 1601, 1610* (MO), *Croat 13031, 14438* (MO), *D'Arcy & D'Arcy 6253* (MO, 2 sheets), *D'Arcy 12185* (MO), *12201* (F), *D'Arcy & Sytsma 14733* (F, MO), *Duke 9474* (MO), *Dwyer et al. 7296* (MO, 2 sheets), *7364* (MO), *Folsom et al. 6709, 7105* (MO), *Hammel 3735* (MO), *Knapp 867* (F), *Liesner 531* (MO), *Porter et al. 5072* (MO), *Sytsma 1475, 4112* (F), *Sytsma et al. 2849* (F), *Sytsma & D'Arcy 3660* (F), *Tyson et al. 3204* (MO), *4355* (MO, 2 sheets), *Tyson 3399* (MO, SCZ), *Wilbur & Weaver 11360* (MO); La Eneida, *Correa & Dressler 824* (MO), *Maas et al. 1567* (MO); El Llano-Cartí road, 6–22 km N of Inter-American Highway, 300–500 m, *Croat 25127, 33805* (MO), *Hammel 867* (MO), *Huft & Knapp 1594, 1613* (MO), *Huft et al. 1868*

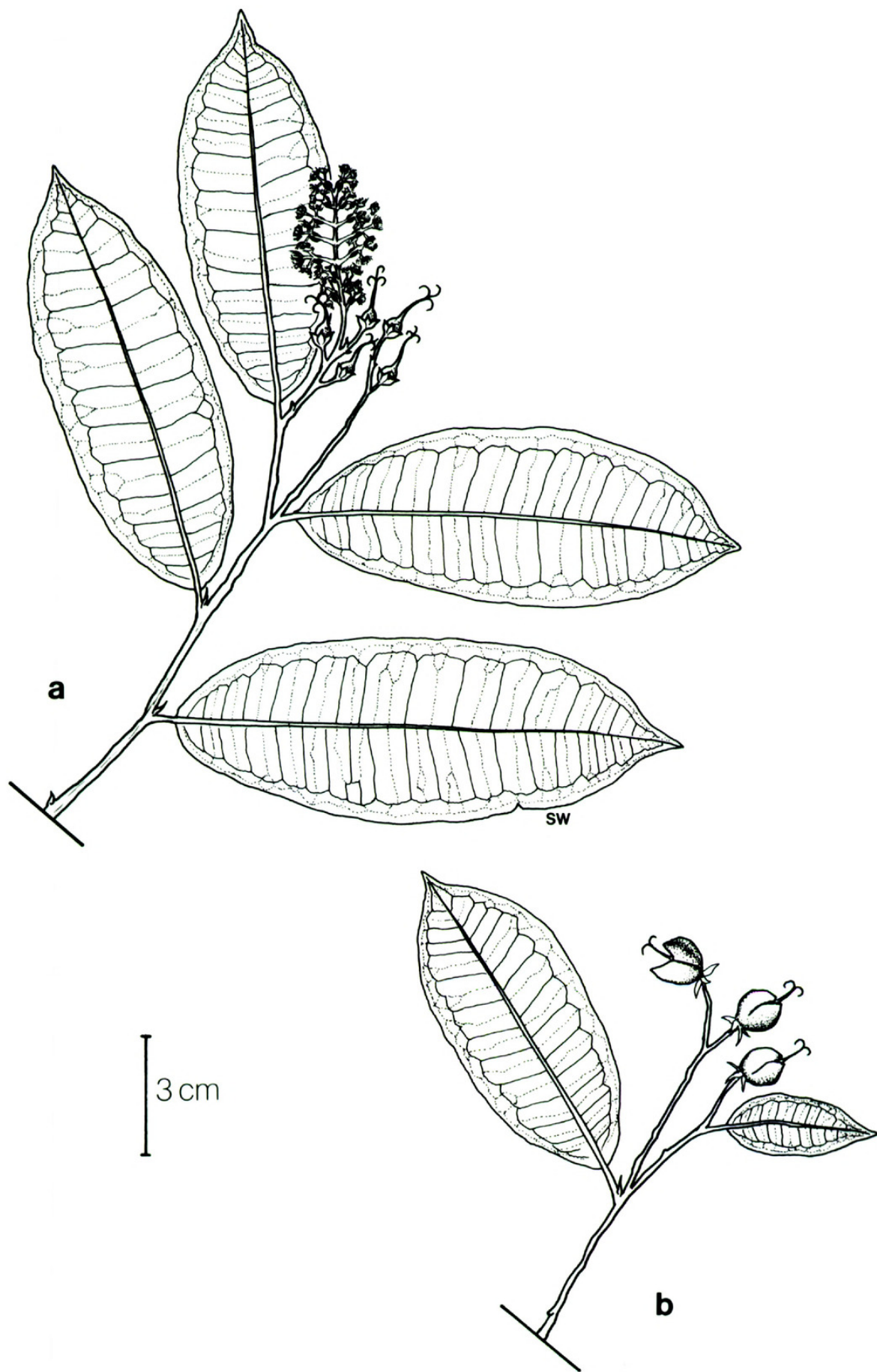


FIGURE 4. *Mabea jefensis*.—*a*. Branch with inflorescence at anthesis and with young fruits.—*b*. Branch with mature fruits. Based on Correa et al. 1601 (*a*), D'Arcy & Sytsma 14733 (*a* & *b*). Illustration by Steve Wilson.

(MO), Knapp 1396 (F), Knapp et al. 4728 (F), Liesner 1303 (MO), Maas et al. 1758 (MO), Mori & Kallunki 1864 (MO), Nee et al. 8752 (MO), Sytsma 960 (F, MO); Cañazas mountain chain, near Rancho Chorro, above Tortí Arriba, 400–700 m, Folsom et al. 6709 (MO).

34. *Senefeldera*

Senefeldera C. Martius, Flora 24 (Beibl.): 29. 1841. TYPE: *Senefeldera multiflora* C. Martius.

Monoecious *shrubs* or trees without evident milky latex; glabrous throughout. *Leaves* alternate (or pseudoverticillate at ends of branches), simple, petiolate; stipules deciduous; blades $\pm$ entire, pinnately veined, usually glandular on midrib at base; margins entire. *Inflorescences* terminal, paniculate (of compound spikes or racemes), bisexual. *Staminate flowers* solitary or in glomerules at distal axils of inflorescence axes, subtended by biglandular bracts; calyx 3–5-lobed, sometimes asymmetrical, not covering anthers in bud; petals and disk absent; stamens 5–12; anthers subsessile on an elevated receptacle, extrorse, dehiscing longitudinally; pollen grains subglobose, tectate, 3-colporate; pistillode absent. *Pistillate flowers* solitary at proximal nodes of inflorescence, sessile; calyx 3-parted, segments distinctly imbricate; petals and disk absent; carpels 3, unappendaged, each with a single ovule; styles unbranched, free, or basally connate. *Fruits* capsular, thin-walled; columella slender, usually not persistent; seeds solitary in each locule, plump, carunculate; endosperm copious.

As treated by Jablonski (1965: 171–174), *Senefeldera* is a genus of nine rather poorly understood South American species. It is here recorded from North America for the first time.

34.1. *Senefeldera testiculata* Pittier, Contr. Fl. Venez. 2: 31. 1923. TYPE: Venezuela. Zulia: Perijá, Pittier 10910 (US).

Shrub or small tree to ca. 4 m high; twigs subterete, channeled, smooth. *Leaves* with petioles variable in length, 0.5–4 cm long, adaxially channeled; stipules triangular, ca. 2 mm long, deciduous (leaving conspicuous scars); blades chartaceous, elliptic-lanceolate, acuminate at apex, cuneate at base, 12–24 cm long, 4–10 cm broad, usually with a ventral median swollen gland ca. 0.5–1 mm long; major lateral veins ca. 10–15 on a side, slightly curving to margins, the veinlets prominulous on both sides; margins plane to slightly reflexed, entire. *Inflorescences* usually bisexual, mostly 7–20

cm long; lateral axes 5–8, the peduncles 5–11 mm long. *Staminate flowers* 2 or 3 per node; bracts ca. 1–1.5 mm long, acute, the glands infolded on adaxial side; pedicels 0.5 mm long or shorter, subtended by 1 or more bractlets within the bract; calyx segments 3, unequal, acute, as broad as or broader than long, ca. 0.5–0.7 mm long; stamens 5; anthers apiculate, ca. 0.4–0.5 mm long (much longer than the very short filaments). *Pistillate flowers* solitary at the 2 or 3 lowermost nodes of each lateral axis, sessile; bracts apiculate, 1–1.3 mm long, with glands 0.8–1 mm across; calyx segments 3, slightly imbricate, broadly ovate, apiculate, ca. 1.2–1.3 mm long; ovary smooth and unappendaged, 3-locular, carinate; styles nearly free, ca. 1.5 mm long, falcate, thickened below and tapering to an acute tip, ventrally papillate. *Capsules* oblate, ca. 11.5–12 mm diam., 3-lobed, inconspicuously reticulate and ribbed, cocci ca. 7 mm long; columella ca. 5 mm high, unthickened, not persistent; seed plump, ovoid, ca. 5–6 mm long, brownish, streaked or mottled, smooth, $\pm$ notched at base; caruncle small; hilum subapical, raphe conspicuous.

Lowland evergreen rainforest, Panama to Venezuela; here reported from Panama for the first time.

The Panamanian specimens are a rather good match for collections of *S. testiculata* from Zulia, Venezuela (Steyermark 99576, 99917, VEN). Although they differ from the South American plants in having more acute leaf bases and shorter inflorescences, there seems little doubt that they are conspecific.

Specimens examined. PANAMA. DARIÉN: Río Canglón, Duke & Bristan 363 (DAV, MO); Río Perrecénico off Río Pirre, Duke & Bristan 8236 (DAV, MO); ridge 2 hours by piragua upstream above Tucutí, Duke 5261 (DAV, MO; incorrectly cited as *Caryodendron angustifolium* in the original treatment); Estero Grande off Río Marea, Duke 10962 (F, MO); Río Ucurgantí, Bristan 1148 (F, MO); Manené to Río Coasí, Hartman 12213 (F, MO).

35. *Sebastiania*

Sebastiania Sprengel, Neue Entd. Pflanzenk. 2: 118, pl. 3. 1821. TYPE: *Sebastiania brasiliensis* Spreng.

The discovery of an additional species of *Sebastiania* makes it necessary to provide a key to the two Panamanian species. A third Panamanian species, too fragmentary for identification, is discussed but not included in the key.

KEY TO THE SPECIES OF *SEBASTIANIA* IN PANAMA

- 1a. Annual herb; leaves linear-lanceolate; staminate flowers borne distichously on the rachis; seeds not over 2.5 mm long 1. *S. corniculata*
 1b. Shrub 2–3 m high; leaves elliptic-lanceolate; staminate flowers borne spirally on the rachis; seeds ca. 4 mm long 2. *S. panamensis*

35.2. *Sebastiania panamensis* Webster, sp. nov. TYPE: Panama. Chiriquí: N of San Félix at Chiriquí–Bocas del Toro border, on Cerro Colorado copper mine road, 5,000–5,500 ft., 3 May 1975, *Mori & Kallunki 5786* (holotype, DAV; isotype, MO).

A speciebus sect. *Microstachydi* recedit floribus masculinibus spiralibus, seminibus longioribus; a speciebus sect. *Elachocrotoni* differt habitu; a speciebus sect. *Sebastiania* differt ovario armato.

Shrub ca. 2–3 m high, the trunk $\pm$ unbranched; twigs slender, subterete, antrorsely $\pm$ appressed pubescent. *Leaves* with petioles 3–7 mm long, appressed-pubescent; stipules triangular-lanceolate, dark, 0.8–1.2 mm long; blades thinly chartaceous or membranous, elliptic-lanceolate, $\pm$ caudate-acuminate at tip, cuneate at base, (2.5–)5–12 cm long, (1–)2–4 cm broad, concolorous, without laminar glands, glabrous to distinctly hirsutulous on both faces; midrib plane above, distinctly raised beneath; major lateral veins ca. 8–20 on a side, straightish, slightly prominulous beneath, distally anastomosing into intramarginal loops; veinlets forming a delicate inconspicuous reticulum; margins finely crenulate with ca. 8–25 appressed teeth on a side. *Inflorescences* opposite leaves (sometimes pseudoterminal), spiciform, usually bisexual, 2–3 cm long, rachis $\pm$ hirtellous; pistillate flowers solitary at base, staminate flowers 1 or 2 per distal bract; bracts spirally arranged, lanceolate, dark, ca. 1 mm long, on each side with a short-stipitate (ca. 0.5 mm) cyathiform gland 0.5–0.8 mm across. *Staminate flowers*: pedicel less than 0.5 mm long; calyx 3-lobed, the lobes obovate, ca. 0.6–0.8 mm long, the anthers ca. 0.3 mm long. *Pistillate flowers*: subsessile or the pedicel up to 1.5 mm long at anthesis, becoming up to 4 mm long in fruit; calyx lobes 3, imbricate (covering ovary in bud), 0.7–1 mm long, eglandular within; ovary glabrous, 3-carpellate, each carpel with a pair of subapical horns; styles nearly free, spreading, tapering, ca. 1.5–2.5 mm long. *Capsules* ca. 6 mm high, ca. 7 mm broad, with 6 subapical lower triangular processes; columella ca. 4.5 mm high; seeds ovoid-ellipsoid, reddish brown and mottled, smooth, ca. 4 mm long; caruncle nearly 1 mm broad.

Montane rainforests or cloud forests, western Panama.

This shrubby species, now represented by several collections from montane rainforests in Chiriquí and Veraguas, does not appear to have been previously described. In overall appearance and floral characteristics it resembles the weedy *S. corniculata* of section *Microstachys* (Adr. Juss.) Muell. Arg. but differs in its woody habit. Its spirally arranged staminate flowers separate it from the woody species of that section. In the treatment of Pax (*Pflanzenreich* 85: 89ff. 1912) it would key to section *Elachocroton* (F. Muell.) Pax, but it does not resemble any of the species in that section except possibly *S. stipulacea* (Muell. Arg.) Muell. Arg.; that species, however, is entirely glabrous, with broader leaves and multicornute ovaries. The Panamanian plants do not fit into section *Adenogyne* (Klotzsch) Benth. because the staminate calyx is not asymmetric, the fruit is echinate, and the branches are not spiny. Nor do the Panamanian plants agree with species in section *Sebastiania*, because of their leaf-opposed spikes, broader staminate calyx lobes, and echinate fruits.

The sectional divisions used by Pax do not seem to be very well founded, so that a satisfactory systematic placement of *S. panamensis* does not seem to be feasible until the genus is monographed. At present, it appears that *S. panamensis* may represent a possible connecting link between the species of section *Microstachys*, with leaf-opposed spikes and echinate fruits, and the sections with terminal or axillary spikes and usually unarmed fruits.

Additional specimens examined. PANAMA. CHIRIQUÍ: Cerro Colorado, 1,200–1,500 m, *Mori & Dressler 7827* (MO, dupl. at SCZ seen by M. Huft), *Sullivan 391* (MO), *Antonio 1409* (MO, dupl. at PMA seen by M. Huft); above San Félix along mining road, above Chame, 1,200–1,500 m, *Croat 33044* (DAV, MO); near San Félix, 800–1,200 m, *Croat 33437* (MO); Chiriquí Trail, premontane rainforest between Pinola and Quebrada Honda, *Kirkbride & Duke 898* (DAV, MO), *Churchill & Churchill 6083* (F, MO); La Fortune hydroelectric project, 1,100–1,200 m, *Hammel 2165* (DAV, MO), *Knapp 4980* (MO), *Mendoza et al. 110* (MO); E of Fortuna campsite, *Folsom & Dressler 5299* (DAV, MO). VERAGUAS: Cerro Tute, 750–1,400 m, *Antonio 1817* (MO), *Knapp & Kress 4359* (F, MO), *Knapp & Sytsma 2562* (F, MO), *Mori & Kallunki 5232* (DAV, MO), *Mori et al. 7609* (DAV, MO).

35.3. *Sebastiania* sp. A.

Several fruiting collections from the dry Pacific coast of Panama and Costa Rica and from thorn

scrub on the Caribbean coast of Colombia represent a species otherwise unknown in Central America. In its membranous, venose, broadly ovate to rhombiform leaves with crenate to crenulate margins, it closely resembles such species of sect. *Sebastiania* from southern Brazil and Argentina as *S. brasiliensis* Sprengel, *S. anisandra* (Griseb.) Lillo, and *S. warmingii* (Muell. Arg.) Pax. Even closer is *S. macrocarpa* Muell. Arg. of Ceara in north-eastern Brazil, with which it shares a large capsule (to 15 mm in diameter).

Until flowering material becomes available, it will remain uncertain whether the Panamanian plant represents an undescribed species or belongs to one of the Brazilian species.

The Costa Rican specimen cited below is the basis for the record of *Ophellantha spinosa* Standley cited by Standley from Costa Rica (Standley, 1938: 1557). That species is definitely known only from northwestern Mexico to Honduras. One of the Colombian collections (Gentry & Cuadros 47466A, MO) has an immature inflorescence with a single pistillate flower and the multiparted bracteal glands that are characteristic of several species of section *Sebastiania*.

Specimens examined. COSTA RICA. ALAJUELA: vic. of San Ramón, Los Loros, Brenes 22679 (CR, NY). PANAMA. LOS SANTOS: 1–2 mi. W of Candelaria, Duke 12443 (MO, US); Las Tablas, Dwyer 1100 (MO); Los Santos, 30 m, Lao 320 (MO). COLOMBIA. ATLÁNTICO: Puerto Colombia, 50–100 m, Dugand 626 (F, distributed as *S. granatensis* Muell. Arg.). BOLÍVAR: Galerazamba, N tip of Bolívar, thorn scrub forest, 10°48'N, 75°15'W, Gentry & Cuadros 47456, 47466A, 47474 (F, MO).

36. *Gymnanthes*

***Gymnanthes* Sw., Prodr. 95. 1788. LECTOTYPE:**
Gymnanthes lucida Sw. (chosen by Grisebach, Fl. Br. W. Ind. 50. 1859).

Actinostemon Klotzsch, Arch. Naturgesch. 7: 184. 1841.
TYPE: *A. concolor* (Sprengel) Muell. Arg. (*Gussonia concolor* Sprengel).

Dactylostemon Klotzsch, Arch. Naturgesch. 7: 181. 1841.
TYPE: not designated.

Monoecious (rarely dioecious) shrubs or trees; latex scanty and scarcely milky; indumentum absent or of simple hairs. Leaves alternate, simple, petiolate; stipules small, mostly persistent; blades pinnately veined, entire or crenulate, glandular or eglandular. Inflorescences terminal or axillary, bisexual (or less commonly unisexual), spiciform, of 1–several basal solitary pistillate flowers and many distal staminate cymes; bracts mostly biglandular, subtending solitary pistillate flowers and 1–several

staminate flowers. Staminate flowers mostly pedicellate; calyx of 1 lobe or rudimentary or absent; petals and disk absent; stamens mostly 2–5; filaments free or basally connate; anthers extrorse, dehiscent longitudinally; pollen grains subglobose, tectate, 3-colporate; pistillode absent. Pistillate flowers sessile or pedicellate; calyx mostly 3-lobed, the lobes sometimes reduced or obsolete, eglandular within; petals and disk absent; carpels 3, each with a single ovule; styles free or basally connate, unbranched. Fruits capsular; columella $\pm$ persistent; seeds solitary in each locule, carunculate; testa smooth; endosperm copious.

As here circumscribed, *Gymnanthes* includes *Actinostemon* Klotzsch and *Dactylostemon* Klotzsch. Although most authors have upheld at least *Actinostemon* as a distinct genus, this seems to have been due more to inertia rather than to critical assessment of diagnostic characters. Pax & Hoffmann (1912: 13) did not provide any convincing distinctions in their key, nor did Jablonski (1967: 164, 178), who candidly stated that “the distinction between *Actinostemon* and *Gymnanthes* is very vague.” Even when *Actinostemon* is merged with *Gymnanthes*, the enlarged genus is difficult to distinguish from *Sebastiania*. Mueller (1866: 1164–1165), in fact, combined the two, but called the composite genus *Sebastiania* because the name *Gymnanthes* (which has priority) seemed inappropriate to him. The distinctly reduced staminate calyx of *Gymnanthes* furnishes only a tenuous difference from *Sebastiania*, in which the staminate calyx is presumably usually well developed. As Pax & Hoffmann (1912: 89–90) pointed out, *Sebastiania* may be an unnatural genus, part of which should be combined with *Gymnanthes*. Clarification of these difficulties will have to await the efforts of a very intrepid monographer.

Rothmaler (1944), following a suggestion by Hallier (1918), adopted the name *Ateramnus* P. Browne (1756: 338) in place of *Gymnanthes*. However, this is not justifiable, as has been shown recently (Webster, 1983); *Ateramnus* is best disposed of by lectotypifying it so that it becomes a synonym of *Sapium*.

As here construed, *Gymnanthes* is then a neotropical genus of about 40 species; the two Panamanian species are reported here for the first time.

LITERATURE

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WEBSTER, G. L. 1983. A botanical gordian knot: the case of *Ateramnus* and *Gymnanthes* (Euphorbiaceae). Taxon 32: 304-305.

KEY TO THE SPECIES OF *GYMNANTHES* IN PANAMA

- 1a. Staminate bracts each with 1 gland on each side, subtending 3 flowers; leaves glandular on margins; staminate calyx of 1 segment; fruiting pedicels 13-21 mm long; seeds 6.3-6.6 mm long 1. *G. actinostemoides*
- 1b. Staminate bracts (at least in part) with paired glands on each side, each bract subtending 1 flower; leaves eglandular on margins; staminate calyx absent; fruiting pedicels 40-50 mm long; seeds ca. 5.5 mm long 2. *G. dressleri*

36.1. *Gymnanthes actinostemoides* Muell.

Arg., Linnaea 32: 103. 1863; Pax & Hoffmann, Pflanzenreich IV. 147. V(Heft 52): 85. 1912 (as *G. actinostemonoides*). *Sebastiania actinostemoides* Muell. Arg. in DC., Prodr. 15(2): 1184. 1866. TYPE: Mexico. Veracruz: Zacuapan, Linden 1357 (holotype, G, microfiche seen).

Tree to 10-12 m high; twigs of current year obtusely angled, short-puberulent (glabrate in age). *Leaves* with petioles 3-10 mm long, $\pm$ puberulent; stipules lanceolate, ca. 1-2 mm long; blades chartaceous, elliptic-oblong, mostly caudate-acuminate at tip (the acumen acute, ca. 0.5-1.5 cm long), acutely cuneate at base, ca. 6-16 cm long, 2-6 cm broad, without laminar glands but with 1-3 depressed cyathiform glands at proximal marginal crenulations; midrib raised on both sides and puberulent proximally; major lateral veins ca. 10-15 on a side, arcuate; veinlets distinctly prominent beneath (slightly so above), forming irregular areoles; margins plane, remotely crenulate (teeth mostly 12-17 on a side), the distal teeth with a minute deciduous glandular tip, the proximal teeth with depressed cyathiform glands. *Inflorescences* axillary, racemiform, unisexual or bisexual, 2-7 cm long, the rachis puberulent. *Staminate flowers* in cymes of 3, subtended by umbonate bracts ca. 1 mm long, each bract with a pair of cyathiform glands 0.6-0.8 mm across attached above the base (subapical); pedicels 0.5-1.5 mm long (longer in central flower); calyx usually of 1

triangular segment ca. 0.5-0.7 mm long; stamens 2 or 3; filaments free, ca. 0.8-1.2 mm long; anthers ca. 0.4 mm long. *Pistillate flowers* solitary, 1 or 2 per raceme; bract eglandular; pedicel puberulent, ca. 2-4 mm long at anthesis, increasing to 13-21 mm long in fruit; calyx segments 3, pointed, not imbricate, 0.6-0.7 mm long; ovary unappendaged, smooth, puberulent; styles 3, basally connate for ca. $\frac{1}{4}$ - $\frac{1}{2}$ their length, 2.5-5 mm long. *Capsules* not seen entire; cocci 11-13 mm long, smooth; seeds plump, ovoid, ca. 6.3-6.6 mm long, 5.8-6 mm broad, brownish, smooth, obscurely beaked; caruncle 0.8-1.3 mm broad.

Montane and perhaps also lowland rainforests, eastern Mexico (Veracruz) to Panama.

The single Panamanian collection of this species bears only fruits, so the identification of Britton's plant with a Mexican species must be provisional. However, the characteristic leaf venation and especially the distinctive marginal foliar glands suggest that our plant is conspecific with specimens from Veracruz, Mexico (such as *Purpus* 3795, 8060 from Zacuapan, 4410 from Fortín, all at UC, from which the floral characters have been taken).

Specimen examined. PANAMA. DARIÉN.: Río Pirre, Britton 1466 (DAV, MO).

36.2. *Gymnanthes dressleri* Webster, sp. nov.

TYPE: Panama. Panamá: La Eneida, region of Cerro Jefe, 3 Jan. 1968, Dressler 3323 (holotype, MO; isotype, DAV).

Species haec aff. *G. granatensi*, differt foliis integris late ellipticis, cuspidato-acuminatis, glandulis bractearum masculinis duplicatis, calyce nullo.

Tree 2 m or more, glabrous; twigs slender, subterete, smooth, brownish. *Leaves* with petioles 3-5 mm long; stipules ovate, rounded, scarious, ca. 1 mm long; blades chartaceous, broadly elliptic, rather abruptly cuspidate-acuminate at tip (the acumen obtuse, 0.5-1 cm long), cuneate at base, 3-8 cm long, 1.5-4 cm broad, appearing eglandular but sometimes with a few scattered minute (diam. ca. 0.2 mm) embedded laminar glands, distinctly paler and glaucous beneath; major lateral veins ca. 6-8 on a side, straightish or distally arcuate; veinlets distinctly prominent beneath, often as prominent as the laterals, forming areoles partly parallel to the laterals; margins entire, with a plane or slightly reflexed subcartilaginous rim. *Inflorescences* axillary, mostly at the base or lower axils of annual increments, racemiform, unisexual or bisexual, where bisexual with 1 or 2 basal pis-

tillate flowers and ca. 8–13 distal staminate flowers; bracts all subtending solitary flowers, ovate, scarious, ca. 0.5–0.7 mm long, mostly with paired subsessile cyathiform glands on each side at base, the larger gland of each pair ca. 0.3 mm across. *Staminate flowers* with pedicels ca. 0.4–1.2 mm long, articulated at the top; calyx, petals, and disk absent; stamens 2–4; filaments free or basally united, 0.4–0.7 mm long; anthers 0.4–0.5 mm long. *Pistillate flowers* with pedicels ca. 3–5 mm long at anthesis, increasing to 40–50 mm long in fruit; calyx lobes 3, ovate, not overlapping, ca. 0.5–0.7 mm long, eglandular within, the margins minutely crenulate; ovary smooth and unappendaged; styles 3, ca. 1.5–2 mm long, thickish, recurved, slightly connate at base. *Capsules* not seen entire; columella 5.5–6 mm long, subpersistent; seeds ovoid-oblong, ca. 5.5 mm long, ca. 4–4.5 mm broad, essentially smooth, dark brown, shiny, apically beaked; caruncle ca. 1 mm across.

This new species from Cerro Jefe appears to be closely related to *G. granatensis* Muell. Arg., which was described (Linnaea 32: 107. 1863) from the vicinity of Ocaña in northern Colombia. Although the type collection of *G. granatensis* (Schlim 586) has not been examined, study of a photograph of the type and Mueller's description (in DC., Prodr. 15(2): 1189–1190. 1866) suggests that the Panamanian plant differs in some important particulars: the leaves are broader, more abruptly cuspidate, distinctly glaucous beneath, and entire at the margins. The staminate flowers completely lack a calyx, whereas there are two subulate calyx lobes in *G. granatensis*, and the staminate bracts have duplex glands on each side, while in the Colombian species (judging from Mueller's description), the bracteal glands are single on each side.

In the system of Pax & Hoffmann, *G. granatensis* would probably fit best into the "genus" *Actinostemon*, although they listed it under *Sebastiania* (Pax & Hoffmann, 1912: 150). However, because of its glabrous inflorescence and well-developed pistillate calyx, it would not readily fit into either of the sections of *Actinostemon*. Within *Gymnanthes* (sensu Pax), perhaps the species most similar to *G. dressleri* and *G. granatensis* is *G. farinosa* (Griseb.) Webster⁶. That West Indian species has somewhat similar leaves but differs in its three-flowered staminate bracts with a single

gland on each side, and in its well-developed staminate calyx. Among the species with bracts subtending solitary flowers, the closest to *G. dressleri* appears to be the Cuban species *G. albicans* (Griseb.) Urban; however, in that species the leaves are more elongated and lack cuspidate tips, the bracts are eglandular, and the staminate flowers have 5–12 stamens.

37. *Maprounea*

Maprounea Aublet, Hist. Pl. Guiane 2: 895. 1775.

TYPE: *Maprounea guianensis* Aublet.

Shrubs or trees, glabrous throughout; latex neither copious nor milky; monoecious. *Leaves* alternate, simple, petiolate; stipules small, persistent; blades pinnately veined, entire, glandular or eglandular. *Inflorescences* terminal, usually bisexual, of 1–4 solitary, pedicellate, pistillate flowers at basal nodes, the staminate flowers densely aggregated in a strobiliform mass at the end of the fleshy enlarged rachis, separated from the pistillate portion by an elongated internode (pseudopeduncle); bracts biglandular. *Staminate flowers* mostly 3 per bract; pedicel very short; calyx $\pm$ 3-lobed, distinctly gamophyllous, the lobes imbricate, $\pm$ covering the stamens in bud; petals and disk absent; stamens usually 2; filaments completely connate into a slender tube that is exerted from the calyx at anthesis; anthers bluntly apiculate, dehiscing extrorsely and longitudinally; pollen grains subglobose, tectate-perforate, 3-colporate, colpi marginate; pistillode absent. *Pistillate flowers* solitary to each bract, distinctly pedicellate; calyx 3-parted, segments imbricate, eglandular within; petals and disk absent; carpels 3, each with a single ovule; ovary unappendaged; styles connate into a column, the tips unbranched, spreading. *Fruits* capsular; columella not persistent; seeds solitary in each locule, the testa distinctly foveolate; caruncle large and partly occluding top of seed; endosperm copious.

A well-marked genus of three or four species, one or two in tropical America and two in tropical Africa, easily distinguished from the genera in the *Gymnanthes-Sebastiania* complex by its characteristic headlike staminate inflorescence, elongated staminal column, and hypertrophied caruncles on the seeds. *Maprounea* is here reported from North America for the first time.

RECENT LITERATURE

ALLEN, A. C. 1976. Uma especie unica de *Maprounea* (Euphorbiaceae) na America do Sul. Acta Amazonica 6: 417–422.

⁶ *Gymnanthes farinosa* (Griseb.) Webster, comb nov. *Excoecaria farinosa* Griseb., Abh. Ges. Wiss. Goettingen 7: 169. 1857. TYPE: Guadeloupe: *Duchassaing* (presumably GOET, not seen).

- secondary foliar veins straight, slightly arcuate near margin 3. *S. jamaicense*
- 4b. Spikes solitary at tips of branchlets; secondary foliar veins strongly arcuate-ascending.
- 5a. Leaves oblong or oblong-elliptic, less than 2.5 times as long as broad; the secondary veins usually 10–15 per side 3. *S. oligoneurum*
- 5a. Leaves usually elliptic-lanceolate, more than 3 times as long as broad, usually longer than 10 cm, the secondary veins usually more than 20 per side 1. *S. aucuparium*

39.1. *Sapium aucuparium* Jacq., Select. Stirp. Amer. Hist. 249. 1763. LECTOTYPE: Jacquin, Select. Stirp. Amer. Hist., pl. 158 (chosen here).

?*Sapium biglandulosum* (L.) Muell. Arg. (Linnaea 32: 116. 1863) sensu auctt. *Hippomane biglandulosa* L., Sp. Pl. ed. 2, 1431. 1762, correction of *H. glandulosa* L., Sp. Pl. ed. 1, 1191. 1753. *Excoecaria biglandulosa* (L.) Muell. Arg. in DC., Prodr. 15(2): 1204. 1866.

Sapium salicifolium Kunth, Nov. Gen. Sp. Pl. 2: 65. 1817. TYPE: Colombia: *Humboldt & Bonpland* (P, not seen).

Sapium moritzianum Klotzsch in Seem., Bot. Voy. Herald 100. 1853. *Sapium biglandulosum* (L.) Muell. Arg. var. *moritzianum* (Klotzsch) Muell. Arg., Linnaea 32: 119. 1863. *Excoecaria biglandulosa* (L.) Muell. Arg. var. *moritziana* (Klotzsch) Muell. Arg. in DC., Prodr. 15(2): 1206. 1866. *Sapium aucuparium* Jacq. subsp. *moritzianum* (Klotzsch) Pittier, Contr. U.S. Natl. Herb. 20: 127. 1918. TYPE: presumably Colombia: *Moritz* 236. Panama: *Seemann* 1243 (syntypes, not seen); no specimens cited in protologue.

Sapium caudatum Pittier, Contr. U.S. Natl. Herb. 20: 127. 1918. LECTOTYPE: Panama. Canal Zone: hill near Gamboa, 25 June 1911, *Pittier* 3713 (US) (chosen by Jablonski, 1968).

Sapium giganteum Pittier, Contr. U.S. Natl. Herb. 20: 128. 1918. TYPE: Panama. Colón: Fato, sea level, 10 Aug. 1911, *Pittier* 4141 (holotype, US).

Stillingia haematantha Standley, Ann. Missouri Bot. Gard. 27: 314. 1940. TYPE: Panama. Coclé: N rim of El Valle, 9 July 1939, *Allen* 1915 (holotype, F; isotype, MO, F neg. 62368).

Monoecious tree to 10 m. Leaves membranous to chartaceous, rarely coriaceous; petiole 1–5 cm long, the 2 apical glands prominent, cylindrical, ca. 1 mm long; stipules ovate-deltate, 1–1.5 mm long, 1.5–2 mm broad, persistent; blades elliptic-lanceolate to oblong-obovate, 5–40 cm long, 1.5–8 cm broad, 3–5 times as long as broad, the base rounded to acute, the margins entire, obscurely toothed or coarsely serrate, the apex short-acuminate or cuspidate, strongly cucullate. Spikes sol-

itary, terminal, to 22 cm long, bisexual or staminate. Staminate flowers in groups of 7–10, the subtending bract flabellate, ca. 0.5 mm long, biglandular, the glands circular to oblong, 0.5–3 mm long, 0.5–1 mm broad; calyx ca. 1 mm long, cupular, 2-lipped; stamens 2. Pistillate flowers to 10, solitary at basal nodes, the bracts and glands as those of the staminate flowers; calyx cupular, 2-lobed; ovary orbicular, the style simple, the style-branches strongly reflexed, the tips expanded. Capsules ovoid, to 1 cm long, smooth; seeds ovoid, flattened laterally, the surface warty.

There has been considerable controversy concerning the proper name of this species. The name *S. aucuparium* Jacq. had long been applied to it, but Croizat (1943: 175), whom Burch followed in the original treatment, referred that name to the species usually known as *S. jamaicense* Sw. and resurrected *S. biglandulosum* for this species. Jablonski correctly restored Jacquin's name to the present species, but rejected the name *S. biglandulosum* as a *nomen confusum*, leaving *S. aucuparium* as the earliest available name. It would seem, however, that the application of *S. biglandulosum* can be fixed by a proper lectotypification. More study is needed before that can reasonably be done, and, in any case, it is not clear to the present author whether any of the elements originally cited under *S. biglandulosum* actually belong to this species. The best course, then, seems to be the tentative acceptance of *S. aucuparium* Jacq. for this species until the matter can be satisfactorily resolved.

We are following Jablonski (1968) in uniting *Sapium caudatum* and *S. biglandulosum* (sensu Croizat and Burch) under *S. aucuparium*. Examination of a wide range of collections from Panama and from northern South America shows that the leaf characters used by Burch to distinguish these species are continuously variable and do not correlate with other characters. This is a commonly collected, highly variable species of lowland tropical forests.

39.2. *Sapium eglandulosum* Ule, Bot. Jahrb. Syst. 35: 673. 1905. TYPE: Brazil. Amazonas: Bom Fin on the Rio Juruá, Nov. 1900, *Ule* 5356 (holotype, B, F neg. 5522).

The following collection records a considerable westward range extension for this species, which was previously known in North America only from eastern Darién.

Additional specimen examined. PANAMA. PANAMÁ: Cerro Jefe region, 2 km N of turnoff to radio tower on roadside of Alto de Pacora, 2,600 ft., *Hammel 4868* (F, MO).

39.3. *Sapium jamaicense* Sw., Adnot. Bot.
62. 1829. TYPE: Jamaica: *Swartz s.n.* (BM, not seen).

Sapium aucuparium sensu Croizat, J. Arnold Arbor. 24: 174. 1943, sensu Burch, Ann. Missouri Bot. Gard. 54: 325. 1967, non Jacq. 1763.

Sapium pleiostachys Schumann & Pittier, Contr. U.S. Natl. Herb. 12: 164. 1908. TYPE: Costa Rica. Puntarenas: Golfito de Osa, near seashore, Mar. 1896, *Pittier s.n.*, *Inst. Fis. Geog. Costa Rica no. 9906* (holotype, US-578902; isotypes, F, F neg. 62366, GH, F neg. 62360).

Sapium anadenum Pittier, Contr. U.S. Natl. Herb. 12: 164. 1908. TYPE: Costa Rica. Cartago: Hacienda Valverde at Orosi, 1,200 m, Mar. 1902, *Pittier s.n.*, *Inst. Fis. Geog. Costa Rica no. 16366* (holotype, US-578045; isotype, F, F neg. 62364).

Rainforests, West Indies, Mexico to Panama, and recently discovered in Colombia.

The correct name of this species has also been a matter of some confusion. *Sapium jamaicense* had been used universally until Croizat (1943: 174) asserted that *S. aucuparium* sensu Jacq., *Enum. Pl. Carib.* 31, 1760, properly refers to this plant, in contradistinction to Jacquin's intention stated in his *Selectarum Stirpium Americanum Historia* (1763), which had been followed by most other authors, who had applied the name *S. aucuparium* as in this paper. Jablonski (1968), however, correctly pointed out that Jacquin's publication of *S. aucuparium* in 1760 is invalid, since a description is lacking, and that the traditional application of *S. aucuparium* as published by Jacquin in 1763 is correct.

Jablonski (1968) recognized *Sapium pleiostachys* as distinct from *S. jamaicense*, referring all collections from Panama and Costa Rica, as well as a few from Guatemala and Chiapas, to the former species, and restricting the latter to the West Indies and northern Central America. The only difference he adduced was the presence of petiolar glands on *S. pleiostachys* and their absence on *S. jamaicense*. Even granting this difference, recognition of *S. pleiostachys* would be tenuous indeed, given the inadvisability of maintaining a species on the basis of a single morphological feature and the assertion that both variants occur in northern Central America (indeed, specimens collected by Matuda at Escuintla, Chiapas, are cited under each species by Jablonski). A thorough examination of collections from throughout the range, however,

shows that even these meager grounds are untenable. Plants with petiolar glands occur commonly in the West Indies (cf. *Ekman 5512* from Hispaniola, *Harris 9156* from Jamaica, and *Pringle 104* from Cuba, all F), and thus there is no morphological discontinuity. *Sapium jamaicense* is simply a variable species in regard to the presence or absence of petiolar glands, and there is no justification for recognition of *S. pleiostachys*.

A few new provincial records are recorded below.

Additional specimens examined. PANAMA. DARIÉN: Río Pirre, *Bristan 1475* (MO). PANAMÁ: N of highway ca. 2 mi. E of El Llano, 200 m, *Foster & Kennedy 1971* (F, NY). VERAGUAS: Isla de Coiba (Penal Colony), *Dwyer 1566* (MO). COLOMBIA. ANTIOQUIA: Municipio de San Luis, Cañon del Río Claro, 330–425 m, *Cogollo 965, 1232* (MO).

39.4. *Sapium oligoneurum* Schumann & Pittier, Contr. U.S. Natl. Herb. 12: 168. 1908.
Sapium biglandulosum (L.) Muell. Arg. var. *oligoneurum* (Schumann & Pittier) Monach., Bull. Torrey Bot. Club 67: 772. 1940. TYPE: Costa Rica: near San Rafael on road from Cartago to Cot, 1,500 m, July 1899, *Pittier s.n.*, *Inst. Fis. Geog. Costa Rica no. 13403* (holotype, US-578903).

Sapium sulciferum Pittier, Contr. U.S. Natl. Herb. 12: 169. 1908. *Sapium biglandulosum* (L.) Muell. Arg. var. *sulciferum* (Pittier) Monach., Bull. Torrey Bot. Club 67: 772. 1940. TYPE: Costa Rica. La Palma, 1,500 m, 15 Aug. 1898, *Tonduz s.n.*, *Inst. Fis. Geog. Costa Rica no. 12428* (holotype, US-577588; isotype, NY).

Sapium schippii Croizat, Amer. Midl. Nat. 29: 477. 1943. TYPE: Belize. Toledo District: Forest Home, Punta Gorda, *Schipp 1049* (holotype, A, F neg. 62361; isotypes, F, F neg. 62365, MO, F neg. 62363).

Monoecious tree to 20 m. Leaves membranous or chartaceous; petiole 1–3(–6) cm long, the two glands near the apex opposite or subopposite, cylindrical, 1–2 mm long; stipules ovate-deltate, oblique, 2–3 mm long, 1.5–2 mm broad, appressed, persistent; blade oblong or elliptic-oblong, 4–10(–18) cm long, 2.5–4.5(–8) cm broad, 1.2–2.4 times as long as broad; midvein prominent, the secondary veins 10–15(–20) per side, somewhat inconspicuous; base rounded to obtuse; margin appearing entire, remotely denticulate with minute glandular teeth; apex acute or more often abruptly short-cuspidate, conspicuously and tightly cucullate. Spikes solitary, terminal, to 22 cm long, bisexual or staminate. Staminate flowers in groups of 5–7, the subtending bract short, broad, 1–1.2

mm long, 1.8–2.1 mm broad, rounded, hyaline, slightly erose, biglandular, the glands suborbicular to oblong, 1.8–3 mm long, 1.8–2.5 mm broad, flattened; calyx cupular, 1.7–2 mm long, 2-lipped; stamens 2, the filaments free. *Pistillate flowers* 10–22, borne singly at basal nodes of bisexual spikes; bracts and calyces as in the staminate flowers; ovary globose; styles simple. *Capsules* subglobose to slightly obovoid, subsessile, 5–9 mm long, 5–12 mm diam., smooth; seeds subglobose, slightly compressed, yellowish, the surface warty.

Montane and cloud forests, forest edges, and clearings, Chiapas, Mexico, to Panama.

Specimens examined. PANAMA. BOCAS DEL TORO: region of Cerro Colorado, 3.3 mi. above Camp Chamí, 8°35'N, 81°45'W, ca. 1,350 m, *McPherson* 9587 (F). CHIRIQUÍ: E of Boquete on Cerro Azul near Quebrada Jaramillo, 1,500–1,620 m, *Croat* 26820 (MO, NY); along road between Gualaca and Fortuna Dam site, 10.1 mi. NW of Los Planes de Nornito, 8°45'N, 82°17'W, 1,250 m, *Croat* 50032 (MO); Boquete, 4,000 ft., *Davidson* 852 (MO, US; cited in the original treatment as *S. aucuparium* sensu Burch); near Cerro Colorado, ca. 3.5 mi. along road from Chamí Camp, ca. 8°35'N, 81°45'W, ca. 1,350 m, *McPherson* 8997 (F); pastures around El Boquete, 1,000–1,300 m, *Pittier* 2880 (F, US); valley of the upper Río Chiriquí Viejo, G. & P. *White* 95 (MO).

These specimens have been distributed under the names *S. caudatum*, *S. aucuparium*, *S. oligoneurum*, or *S. sulciferum*.

39.5. *Sapium pachystachys* Schumann & Pittier, Contr. U.S. Natl. Herb. 12: 168, tab. 16. 1908. TYPE: Costa Rica. San José: Dota Mountains, El Copey, 1,800 m, Feb. 1898, *Tonduz s.n.*, *Inst. Fis. Geog. Costa Rica no. 11875* (holotype, US-333961; isotype, F, F neg. 62367).

Monoecious tree to 25 m; older twigs covered with crowded persistent stipules. *Leaves* membranous or chartaceous; petiole 2–5 cm long, the 2 glands near the apex subopposite, cylindrical, 1–3 mm long; stipules deltate, 4–6 mm long, 2–3 mm broad, appressed, persistent; blade elliptic, elliptic-obovate, or elliptic-lanceolate, 5–20 cm long, 2.5–7.5 cm broad, 1.6–2.4(–4.5) times as long as broad; base rounded or obtuse, rarely acute; margins entire or obscurely crenate; apex obtuse or acute, occasionally short-acuminate, plane. *Spikes* solitary at the apex of smooth lateral shoots, to 20 cm long, bisexual. *Staminate flowers* in groups of 7–10(–12), the subtending bract short, broad, to 2 mm long, hyaline, erose, biglandular, the glands oblong, 2.5–3 mm long, 1–1.5 mm broad, flattened, calyx 1–1.5 mm long, cupular, 2-lipped;

stamens 2, the filaments free. *Pistillate flowers* 14–22, solitary at basal nodes; bracts as in the staminate flowers; calyx 1–1.5 mm long, cupular, 2-lipped; ovary globose; styles simple, fused for $\frac{1}{3}$ – $\frac{1}{2}$ their length, the free portion strongly coiled. *Capsules* globose, subsessile, 7–10 mm long, smooth; seeds subglobose, flattened laterally, ca. 4 mm diam., the edges short-winged, the surface somewhat warty.

Montane rainforest and cloud forest, 700–2,000 m, Costa Rica and Panama.

The twigs densely covered with persistent stipules and the large, broad leaves with noncucullate apices are characteristic features of this species. A related species, *S. allenii* Huft, has recently been described from eastern Costa Rica (Huft, 1987) and may eventually be discovered at lower elevations in western Panama. It differs from *S. pachystachys* in having axillary spikes, smaller, stipitate capsules, and a small membranous calyx that does not persist on the mature capsules.

Specimens examined. PANAMA. BOCAS DEL TORO: border with Chiriquí, Cerro Colorado mine area, from Chamí Station to ca. 9 mi. along road, 8°35'N, 81°54'W, 1,100–1,700 m, *Hammel & Trainer* 15004 (F). CHIRIQUÍ: Boquete, Finca Collins, *Blum & Dwyer* 2558 (MO); SO de campamento Fortuna (8°45'N, 82°15'W), sitio de presa, desde la finca Pitti hasta e filo del Cerro Fortuna, 1,000–1,200 m, *Correa et al.* 2797 (MO, 2 sheets); Cerro Colorado, along road to copper mine 24.1 km beyond bridge over Río San Félix (13.1 km beyond turnoff to Escopeta), 1,390 m, *Croat* 37305 (MO); Cerro Punta, 2,000 m, *Lao* 328 (MO); above Los Llanos, 8°47'N, 82°38'W, ca. 2,100 m, *McPherson* 9258 (F, MO); Cerro Colorado, 50 km N of San Félix on the Continental Divide, 1,200–1,500 m, *Mori & Dressler* 7819 (MO, NY); between Río Ladrillo and Las Siquas Camp, southern slope of Cerro de la Horqueta, 1,200–1,700 m, *Pittier* 3165 (US); slopes of Volcán Barú near town of Cerro Punta, 6,300 ft., *Stern & Chambers* 97 (MO, US). COCLÉ: N of El Copé on road past sawmill, 2,400 ft., *Antonio* 3264 (F, MO). PANAMÁ: 5–10 km NE of Altos de Pacora, on trail at end of road, 700–800 m, *Mori & Kallunki* 6065 (MO, NY, 2 sheets).

39.6. *Sapium rigidifolium* Huft, Phytologia 63: 444. 1987. TYPE: Costa Rica. Heredia: pastures above San Rafael, 30 km W of Vaca Blanca, 1,750 m, 8 Aug. 1971, *Lent* 2041 (holotype, F; isotypes, MO, NY, US), distributed as *Sapium thelocarpum* Schumann & Pittier. Figure 5.

Sapium rigidifolium, which is known only from high altitudes in Costa Rica and Chiriquí Province in Panama, belongs to the otherwise wholly South American subsection *Emmenostylum* (Hemsley)

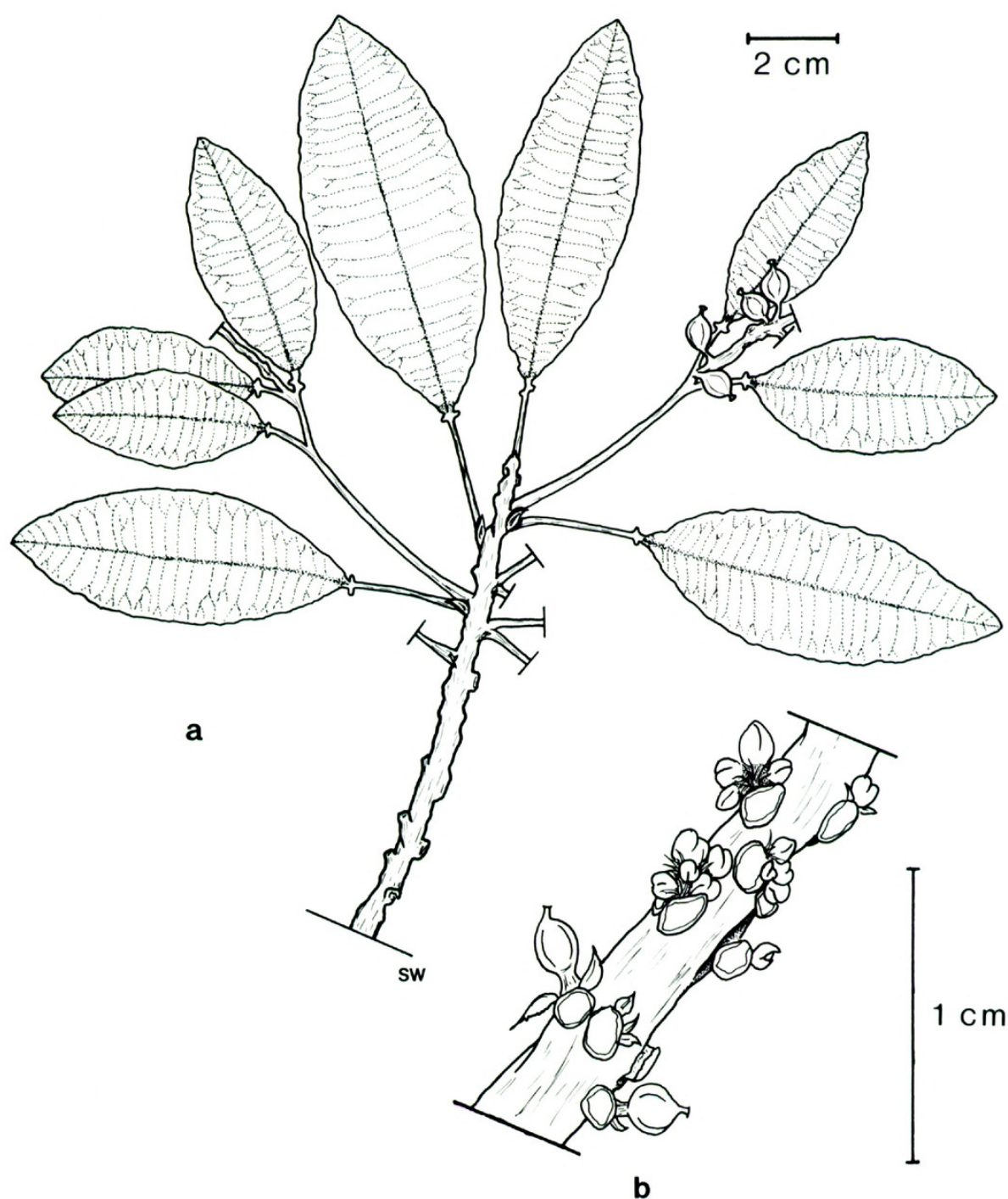


FIGURE 5. *Sapium rigidifolium*.—*a*. Branch with mature capsules.—*b*. Detail of portion of inflorescence, showing staminate flowers at anthesis and pistillate flowers in young fruit. Based on Lent 2041. Illustration by Steve Wilson.

Pax (Pflanzenr. IV. 147. V(Heft 52): 211. 1912), characterized by styles that are connate for most of their lengths and whose columns persist on the mature capsule, and by leaves with planar apices and nearly horizontal, prominent, closely spaced secondary veins. The South American representatives are restricted to high altitudes in the northern Andes and include such species as *S. verum*

Hemsley, *S. stylare* Muell. Arg., and *S. putumayense* Croizat.

Specimens examined. PANAMA. CHIRIQUÍ: Guadalupe Arriba, above Cerro Punta, 8°52'N, 82°33'W, 2,100 m, *de Nevers & Charnley* 6057 (F); Boquete, Cerro Horqueta, 5,000–6,000 ft., *Dwyer & Hayden* 7685 (MO); Cerro Punta, 2,000 m, *Lao* 391 (MO, PMA); slopes of Volcán Barú, near town of Cerro Punta, 6,000 ft., *Stern & Chambers* 85 (A, MO, US).

40. *Hippomane*

Hippomane L., Sp. Pl. 1191. 1753. TYPE: *Hippomane mancinella* L.

41. *Hura*

Hura L., Sp. Pl. 1008. 1753. TYPE: *Hura crepitans* L.

42. *Euphorbia*

Euphorbia L., Sp. Pl. 450. 1753. LECTOTYPE: *Euphorbia antiquorum* L. (chosen by Millspaugh, Publ. Field Columbian Mus., Bot. Ser. 2: 306. 1909).

Poinsettia Graham, Edinburgh New Philos. J. 20: 412. 1836. *Euphorbia* sect. *Poinsettia* (Graham) Baillon, Etud. 284. 1858. *Euphorbia* subg. *Poinsettia* (Graham) House, New York State Mus. Bull. 254: 472.

1924. TYPE: *Poinsettia pulcherrima* (Willd. ex Klotzsch) Graham.

Four species new to Panama are reported here. In addition, the Panamanian endemic, *Euphorbia apocynoides*, which was merely mentioned in passing in the original treatment, is here treated in full. These changes make it necessary to provide a new key. Both of the present authors are agreed that *Poinsettia*, treated as a separate genus in the original treatment, is best regarded as a subgenus of *Euphorbia*; thus *Poinsettia* is suppressed in the generic key, and the two Panamanian species are included in the key to *Euphorbia*.

LITERATURE

DRESSLER, R. L. 1961. A synopsis of *Poinsettia* (Euphorbiaceae). Ann. Missouri Bot. Gard. 48: 329–341.

KEY TO THE SPECIES OF *EUPHORBIA* IN PANAMA

- 1a. Leaves more than 15 cm long, leathery; cyathia 4–6 mm long 3. *E. elata*
- 1b. Leaves less than 8 cm long, membranous; cyathia less than 3 mm long.
- 2a. Gland of cyathium 1; floral bracts usually with pale or colored spots; seeds coarsely tuberculate.
- 3a. Involucral gland cup-shaped; floral leaves green, white, or purple-spotted at base, never red; seeds angulate, coarsely tuberculate 1. *E. heterophylla*
- 3b. Involucral gland bilabiate; floral leaves red, at least at base; seeds ovoid-cylindrical, finely and sharply tuberculate 2. *E. cyathophora*
- 2b. Glands of cyathium 4 or 5 (rarely 2).
- 4a. Leaves all whorled; stems articulate; trees or large shrubs.
- 5a. Floral leaves white 4. *E. leucocephala*
- 5b. Floral leaves green (unknown in *E. apocynoides*).
- 6a. Leaf blades ovate, 3–5 cm broad; petioles 2–6 cm long 5. *E. cotinifolia*
- 6b. Leaf blades oblong or narrowly obovate, 1.5–2 cm broad; petioles to 1 cm long 6. *E. apocynoides*
- 4b. Leaves alternate; herbs.
- 7a. Involucres and capsules pubescent.
- 8a. Inflorescence glandular-pilose; leaf blades mostly 1 cm long or shorter 7. *E. ocymoidea*
- 8b. Inflorescences nonglandular; leaf blades mostly longer than 2 cm.
- 9a. Cyathial glands 4 or 5, plane 8. *E. xalapensis*
- 9b. Cyathial glands 2, bilabiate 9. *E. oerstediana*
- 7b. Involucres and capsules glabrous.
- 10a. Cyathial appendages obsolete; glands with 2 conspicuous lateral horns 10. *E. peplus*
- 10b. Cyathial appendages present; glands elliptic.
- 11a. Seeds terete, the surface smooth; cyathia ca. 2 mm in diameter; glands 4, dark; appendages equaling glands, ciliate-pubescent above 11. *E. dwyeri*
- 11b. Seeds strongly angled, the surface deeply punctate with pits in regular longitudinal rows; cyathia ca. 1 mm in diameter; glands 4 or 2, green; appendages obsolete (Panamanian specimens) to prominent and white, several times size of gland, glabrous 12. *E. graminea*

42.3. *Euphorbia elata* Brandege, Univ. Calif. Publ. Bot. 6: 55. 1914. TYPE: Mexico. Chiapas: Finca Irlanda, *Purpus* 7026 (holotype, UC; isotypes, A, BM, F, GH, MO, F neg. 62362, UC, US).

near Tilarán, 600–700 m, Standley & Valerio 45338 (holotype, US; isotype, US).

Shrub or small tree to 3.5 m high, glabrous; branches few or none. *Leaves* alternate, clustered at apex of stem; petioles 2–4(–6) cm long, ca. 2 mm thick; stipules fleshy, light-colored, deltate to rounded, 3–4 mm long, 3–4 mm broad; blades

Euphorbia valerii Standley, J. Wash. Acad. Sci. 17: 11. 1927. TYPE: Costa Rica. Guanacaste: Los Ayotes,

coriaceous, glabrous, oblanceolate or narrowly elliptic, the apex rounded to bluntly short-acuminate at tip, acute to cuneate at base, 15–35 cm long, 4–10(–12) cm broad, 3–5(–7) times as long as broad; midrib prominent below, to 2 mm thick; lateral veins 17–30 pairs on a side, obscure, nearly at right angles to midrib; margin entire. *Inflorescences* single, terminal or rarely axillary, long-pedunculate, cymose; peduncle 10–30 cm long, glabrous, minutely brown-puberulent, or covered with a waxy brown reticulum; cyme up to 5 times divided, the cyathia ultimately in 2–4 compact groups; bracts opposite, scalelike, attached to the stem along a broad base, deltate, ca. 4 mm long, 2.5–3 mm broad; margin entire, sometimes ciliate, hyaline; apex blunt, somewhat cucullate. *Involucres* campanulate, glabrous, minutely brown-puberulent or covered with a waxy brown reticulum, green, drying to brown, 4–6 mm high, (3–)4–5.5 mm diam.; pedicels 1.5–3 mm long, 1–1.5 mm thick; lobes 5, 1.5–2 mm long, ca. 2 mm broad, erose to fimbriate, rarely entire, erect, concolorous or dark red; glands 5, round, 1.7–2 mm diam., placed vertically on rim of involucre, looking outwards, but positions of lobes making glands appear below rim; gland sometimes erect and thick-stalked so that surface is flat with respect to orifice, the margin then crisped; appendages none. *Capsules* exserted from the cyathium no more than 1 mm (the gynophore erect), green, glabrous, 8–9 mm high, 10–11 mm diam.; styles ca. 1.5 mm long, united at base for ca. $\frac{1}{3}$ of their length, strongly recurved, bifurcate; seeds subglobose, truncate at apex, 4.7–5 mm diam., ca. 4.5 mm long, ecarunculate, dark brown, with lighter, low, broken, irregular longitudinal ridges.

Euphorbia elata, which occurs in moist evergreen forests of low to middle elevations, is definitely known to range from southern Veracruz, Mexico, to Colombia, and may occur as far south as Bolivia. It is the most widespread species of sect. *Adenorima* (Raf.) Webster, a group of several highly divergent species of trees and shrubs from the West Indies, western and southern Mexico, and the northern Andes. The species closest to *E. elata* are all highly restricted in range and are poorly understood. *Euphorbia sinclairiana* Benth. (in Seemann, Bot. Voy. Sulphur 163. 1844), known only from the island of Gorgona off the Pacific coast of Colombia, is characterized by a deeply bifurcate and much-branched inflorescence with conspicuous foliaceous bracts, but is otherwise similar to *E. elata*. The Peruvian *E. tessmannii* Mansf. (Ber. Deutsch Bot. Ges. 46: 674. 1929; Notizbl.

Bot. Gart. Berlin-Dahlem 11: 137. 1931) is known only from the type collection, and no original material is definitely known to be extant. Until either new or original material is available, the status of that species cannot be determined. *Euphorbia capansa* Ducke (Arq. Inst. Pesq. Agron. 1: 21. 1938), described from western Amazonian Brazil, appears to be synonymous with *E. elata*. Another collection from Bolivia (Bang 619, MO, NY, US) was given an unpublished name but will probably also prove to be *E. elata*.

Specimens examined. PANAMA. BOCAS DEL TORO: road to Chiriquí Grande, 300 m, *McPherson 10085* (MO). COLÓN: trail from end of Santa Rita Ridge Rd. to Río Pedros, 600 m, *Antonio 3750* (F, MO); Distr. Portobelo, stream off N slope of Río Gatún, 2,200 ft., *Antonio 3804* (MO); Santa Rita, E of mountainous zone, *Correa & Dressler 973* (PMA); Santa Rita Ridge, E of Colón, *Dressler 3338* (PMA), 3348 (F, PMA); Santa Rita lumber road, ca. 15 km E of Colón, *Dressler & Lewis 3728* (MO, PMA); Santa Rita Ridge, 4 hour walk from end of road, *Hammel 6318* (MO); ca. 2–3 mi. up the Río Guanche, 10–20 m, *Kennedy & Foster 2170* (MO); Santa Rita Ridge Rd., ca. 6 km from Boyd-Roosevelt Hwy., *Mori & Kallunki 2151* (MO, NY); Santa Rita Ridge, on fork in road on main Santa Rita Ridge Road, *Mori & Kallunki 3053* (MO, NY). DARIÉN: Cerro Pirre, valley between Pirre and next most southerly peak, sloping hillside, *Folsom 4385* (MO). PANAMÁ: on road near slopes of Cerro Jefe, 2,400 ft., *Antonio et al. 3426* (F, MO); just before La Eneida along new trail beside Lopez House, *Correa & Dressler 724* (DUKE, 2 sheets), *Correa et al. 816* (MO); El Llano-Cartí road, 14–18 km from road to Chepo, 400 m, *Correa et al. 1867* (PMA); El Llano-Cartí road, 12 mi. above Pan-Am Hwy., *Liesner 1244* (MO); El Llano-Cartí road, 11 km from Pan-Am Hwy., *Mori & Kallunki 3057* (MO, NY). VERAGUAS: Escuela Agricultura, Alto Piedra near Santa Fe, 0.3 mi. beyond fork in road near school, toward Atlantic slope along trail to top of Cerro Tute, 3,400–3,800 ft., *Antonio 3498* (MO); 6.4 km outside of Santa Fe on road past agricultural school, toward the cordillera, *Folsom 2970* (F, MO).

42.4. *Euphorbia leucocephala* Lotsy, Bot. Gaz. (Crawfordsville) 20: 350, pl. 24. 1895. LECTOTYPE: Guatemala. Huehuetenango: Cuilco, Dec. 1891, *Shannon 305* (presumably US, not seen; chosen by Standley & Steyermark, Fieldiana, Bot. 24(6): 107. 1949).

Shrub to 3 m high; branches terete, glabrous, swollen at the nodes. *Leaves* verticillate; petioles (1–)2–6 cm long, slender, glabrous; stipules glanduliform, 0.3–0.5 mm long; blades glabrous, elliptic to linear-elliptic, mucronate and rounded or bluntly acute at tip, acute at base, (2–)3–7 cm long, (0.7–)1.5–2.7 cm broad, 2–3(–4) times as long as broad; margin entire. *Inflorescences* terminal, cymose; bracts white, narrowly spatulate; petioles 3–7 mm long, thinly pilose; blades 5–10

mm long, 1.2–2 mm broad; base narrowly acute; margin entire; apex rounded, mucronate. *Cyathia* on peduncles 1–2.5 mm long; involucre campanulate, 1–1.8 mm high, 1.1–1.7 mm diam., densely tomentose just below the glands, otherwise sparsely pilose; glands 5, green, 0.8–1 mm long parallel to the rim of the cyathium, 0.4–0.5 mm broad, the center of the inner margin strongly inflexed forming a deep convex trough; appendages white, linear-lanceolate, exceeding glands by 2–3(–3.5) mm, 0.5–1 mm broad, the apex narrowly rounded. Gynophore erect, exserted from cyathium 1–1.5 mm. *Capsules* glabrous, smooth, 5–6 mm high, 4.5–5.5 mm diam., shallowly 3-lobed, the cocci distinctly 3-angled; styles 0.6–0.7 mm long, united at base, deeply trifid, the style branches strongly recurved; seeds (immature) ca. 3.5 long, trigonous, ca. 1.8 mm wide, carunculate.

The reports of this species from central Panama represent a considerable range extension; the previously known range is from western and southern Mexico to Honduras. *Euphorbia leucocephala* is a commonly cultivated ornamental in Central America, and the Panamanian collections may be from cultivated trees, but the label data are not clear on this point.

Capsules are unknown in Panamanian collections and are scarce in the numerous collections from northern Central America. Our description of the capsules is taken from a specimen collected in Depto. Huehuetenango, Guatemala (*Molina* 21389, F).

Specimens examined. PANAMA. COCLÉ: El Valle de Antón, 1,000–2,000 ft., *Lewis et al.* 2570 (MO); El Valle, *Ramos* 19 (MO, PMA). PANAMÁ: Panama Viejo, *Girón* 1 (MO); near Cerro Azul, *Cambra* 49 (MO, PMA).

42.6. *Euphorbia apocynoides* Klotzsch in Seemann, Bot. Voy. Herald 99. 1853. TYPE: Panama. Darién: Punta Garachiné, *Seemann* 1096 (holotype, BM; isotype, K; photo of isotype, K, MO).

Shrub to 2 m high; stems glabrous, terete, swollen at nodes; internodes 2–4 cm long. *Leaves* ternate; petioles slender, 7–10 mm long, very sparsely pilose; blades membranous or chartaceous, dark green above, lighter or even somewhat glaucous below, oblong to narrowly obovate, rounded at tip, acute at base, 4.5–6 cm long, 1.5–2 cm broad, 3–3.5 times as long as broad, glabrous or with very few hairs below; margin entire. *Inflorescences* unknown. *Cyathia* turbinate, ca. 2.5 mm high, ca. 2.5 mm diam. below the appendages, sparingly to

evenly appressed-pubescent, the hairs short, straight, nonoverlapping; peduncles 3–4 mm long, subglabrous; appendages 5, narrowly flabellate, white, pubescent as the involucre below toward the base, ciliate on the margins near the juncture with the involucre, otherwise glabrous, entire in the lower half, deeply and coarsely crenellate along the distal margin. *Flowers* and *fruits* not seen.

This poorly known species is apparently endemic to Panama and is still known only from the fragmentary type collection and an equally fragmentary recent collection from the type locality. The type is sufficiently complete, however, to enable the species to be placed with reasonable certainty in section *Alectoroxtonum* (Schldl.) Boissier, a group characterized by verticillate branching and swollen nodes, and to say that it is unlike any other species in the section. Contrary to the statement in the original treatment (Webster & Burch, 1968: 335), the cyathium is quite unlike that of sect. *Dichilium* Boissier, which is characterized by a reduced number (usually 2) of bilabiate glands and small, erect, or often obsolete, appendages. The species of sect. *Dichilium* are also characterized by alternate leaves and stems that are pinched just above the nodes.

A plant vegetatively very similar to *Euphorbia apocynoides*, collected near Puerto Colombia on the Caribbean coast of Colombia (*Elias* 1197, F), has been identified as *E. nudiflora* Jacq., a West Indian species. The cyathium, however, differs from that of *E. apocynoides* in that it is campanulate, the pubescence is crisped with overlapping hairs, and the appendages are completely glabrous, obovate, and with smaller and more numerous crenellations on the distal margin. In all of these characters it matches *E. nudiflora*, which differs vegetatively in its more highly branched habit and shorter, broader leaves. An elucidation of the relationship of the Colombian plant to the Panamanian one, and of both to *E. nudiflora*, must await fuller collections from Panama and Colombia.

We are indebted to Mr. A. Radcliffe-Smith of Kew for providing a description and a sketch of the cyathium from the isotype of *E. apocynoides* at K, from which our description has been taken.

Additional collection examined. PANAMA. DARIÉN: thorn forest near Punta Garachiné, *Duke* 10485 (MO, 2 sheets).

42.7. *Euphorbia ocymoidea* L., Sp. Pl. 453. 1753. TYPE: Mexico. Campeche: *Houston* s.n. (BM, not seen).

E. astroites Fisch. & Mey., Index Sem. Hort. Petrop.

10: 44. 1845. TYPE: Mexico: Tampacoala, *Karwinsky* (LE, not seen).

A thorough examination of collections from throughout the range of this species (western Mexico to Panama) makes it clear that *Euphorbia astroites* cannot be separated from *E. ocymoides*. The only consistent character separating the two is the glandular-pilose stems of the former, as opposed to the glabrous or short-pilose, eglandular stems of the latter. The two forms occupy roughly the same geographical range (the glandular form is not yet known from western Mexico, and the eglandular form has not been collected south of Nicaragua) and the same habitats, and they exhibit similar variation patterns, particularly in the shape of the leaves, which range from broadly ovate or deltate to somewhat reniform. As suggested by McVaugh (1961: 177), several names based on collections from western Mexico, particularly *E. subreniformis* S. Watson, undoubtedly belong here.

The only known Panamanian collections are glandular-pilose, a fact that was omitted from the original treatment, and thus would have been placed under *E. astroites*. The species has apparently not been collected in Panama since the appearance of the original treatment.

42.8. *Euphorbia xalapensis* Kunth, Nov. Gen. Sp. Pl. 2: 61. 1817. *Poinsettia xalapensis* (Kunth) Klotzsch & Garcke, Monatsber. Königl. Preuss. Akad. Wiss. Berlin 1859: 253. 1859. TYPE: Mexico. Veracruz: near Xalapa, *Humboldt & Bonpland s.n.* (P, not seen).

Euphorbia enalla Brandegee, Univ. Calif. Publ. Bot. 6: 54. 1914. TYPE: Mexico. Chiapas: Cerro del Boquerón, *Purpus 7035* (holotype, UC; isotypes, F, F neg. 60269, GH, MO, NY; distributed under an unpublished name).

Euphorbia amphimalaca Standley, Publ. Field Columbian Mus., Bot. Ser. 4: 313. 1929. TYPE: Honduras. Comayagua: near Siguatepec, Feb. 1928, *Standley 56341* (holotype, F; isotypes, F, F neg. 60244, US).

Perennial rhizomatous *herb* to 50 cm high, the stems shaggy brown-pilose. *Leaves* opposite or verticillate above, alternate below; petioles 1.5–2.5 cm long, brown curly-pubescent; stipules glanduliform, brown or black, minute, 0.1–0.2 mm long; blades ovate, acute at tip, rounded to obtuse at base, dark green, 1.5–3.5 cm long, 1–2 cm broad, 1.5–1.8 times as long as broad, densely shaggy-pilose below, more sparsely so above, base rounded to obtuse; margins entire, ciliate, acute. *Inflorescences* terminal, cymose, often appearing one-sided by the abortion of one branch at a node, shaggy-pubescent; bracts similar to the leaves but greatly

reduced, often aborting. *Cyathia* on pedicels 1–3 mm long; involucre campanulate, 0.7–1.3 mm high, 0.5–1.3 mm diam., crisp-pubescent; glands 5, green, elliptic to reniform; appendages whitish or greenish, broadly ovate, exceeding the gland by 1–2 mm, 1.5–2 mm broad, the margin entire or crenate; gynophore glabrous, erect or somewhat recurved, exerted from the cyathium 1.5–2 mm. *Capsules* sparsely to densely pilose, 1.5–1.9 mm high, 1–1.5 mm diam.; styles 0.7–0.8 mm long, free to the base, deeply bifid, thinly pilose; seeds ca. 1.5 mm long, 0.9–1 mm diam., ovoid, grayish, coarsely pitted, tuberculate, ecarunculate.

Euphorbia xalapensis is a common species of forest borders and thickets that ranges from western Mexico to Honduras, and thus the new reports cited here from Panama and Costa Rica represent a considerable range extension. This species was erroneously treated in the *Flora of Guatemala* (Fieldiana, Bot. 24(part 6): 108. 1949) as *E. oerstediana* (Klotzsch & Garcke) Boissier, a very different species that has mostly glabrous stems, articulated nodes, two cyathial glands that are more or less bilabiate and that have inconspicuous or obsolete appendages, and densely white-pubescent capsules. The latter species, which belongs to section *Dichilium* Boissier, is very rare in Central America and is somewhat better known from the West Indies and northern South America. It is still unknown from Guatemala, and nearly all of the putative collections from there are referable to *E. xalapensis*. It has not been re-collected in Panama since the collection cited in the original treatment.

Euphorbia xalapensis is also frequently confused with *E. graminea*, a highly variable and widespread species of the same section, *Cyttarospermum* Boissier, and the two are indeed very similar in aspect. *Euphorbia xalapensis*, however, can be distinguished by the distinctly perennial and often strongly rhizomatous habit; the shaggy brown pubescence of the stems, leaves, and inflorescence; the one-sided appearance of the inflorescence, which is due to the frequent abortion of one branch at a node; and the five glands that have ample, usually greenish appendages.

Additional specimens examined. COSTA RICA. SAN JOSÉ: along Quebrada Tablazo and on forested slope above creek, NE part of Altos Tablazo, 9°50'N, 84°03'W, 1,700–1,800 m, *Grayum & Schatz 5157* (MO). PANAMA. CHIRIQUÍ: Volcán Chiriquí above Boquete, roadside, *D'Arcy 9805* (DAV, MO), distributed as "*Euphorbia graminea* Jacq. (s. lat.)."

42.10. *Euphorbia peplus* L., Sp. Pl. 456. 1753. TYPE: Europe (presumably in Hortus

Cliffortianus Herbarium, BM, not seen; 630.24 in LINN).

Annual glabrous *herb* 18–35 cm high. *Leaves* alternate below, opposite or ternate above, sessile or short-petiolate, numerous, early deciduous below; stipules obsolete; blades bright green, membranous, spatulate, rounded at tip, acute or cuneate at base, 10–14 mm long, 8–12 mm broad; margins entire; floral leaves slightly smaller, somewhat reflexed, congested. *Cyathia* solitary in forks of upper branches, on peduncles 0.6–1 mm long; involucre campanulate, light green, ca. 1 mm high, 0.5–0.7 mm diam.; glands 4, green, crescent-shaped, exappendiculate, ca. 0.5 mm long parallel to the rim of the involucre, with prolonged narrow horns 0.5–0.7 mm long; gynophore exerted, ca. 1.3 mm long, recurved. *Capsules* green, 1.8–2 mm high, 2–2.2 mm diam., broadest below the middle, shallowly 3-lobed, the cocci each with 2 narrow longitudinal ridges; styles ca. 0.1 mm long, bifurcate, the style branches bifurcate; seeds ovoid-oblong, weakly 6-angled, gray, ca. 1.5 mm long, ca. 0.8 mm diam., carunculate, deeply pitted, minutely white-tuberculate.

This is apparently the first report from southern Central America of this cosmopolitan weed of temperate Eurasian origin.

Specimens examined. PANAMA. CHIRIQUÍ: trail from Paso Respingo to Bajo, Chorro Cerro Punta to Boquete, along stream near Guadalupe, *Hammel et al.* 7077 (MO); forest remnant beside Las Cumbres, 1 mi. from road near Cerro Punta dairy, 8,000 ft., *D'Arcy et al.* 13193 (F, MO); Cerro Punta, *Tyson* 7058 (MO, PMA).

42.11. *Euphorbia dwyeri* Burch, *Ann. Missouri Bot. Gard.* 54: 182. 1967. TYPE: Panama. Chiriquí: Cerro Horqueta, NW of Boquete, *Dwyer et al.* 434 (holotype, MO; isotypes, GH, K, US).

A second collection of this species has been found, misidentified as *E. caracasana* Boissier.

Additional specimen examined. PANAMA. CHIRIQUÍ: humid forest of Cuesta de Las Palmas, southern slope of Cerro de la Horqueta, 1,700–2,100 m, *Pittier* 3216 (US).

43. *Chamaesyce*

Chamaesyce Gray, *Nat. Arr. Brit. Pl.* 2: 260. 1821. TYPE: *Chamaesyce maritima* Gray = *C. peplis* (L.) Prokh. (*Euphorbia peplis* L.) (See Wheeler, 1943: 461, for a discussion of the type.)

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INDEX TO LATIN NAMES

Numbers in boldface type refer to descriptions or principal entries; numbers with ! refer to illustrations; names in boldface type refer to new taxa or combinations; names in italic refer to synonyms.

- Acalypha* L. 1087, **1104**
cuneata Poeppig **1104**
 var. *obovata* (Benth.) Muell. Arg. 1104
obovata Benth. 1104
virginica L. 1104
- Acidoton* Sw. **1106**
nicaraguensis (Hemsley) Webster **1106**
urens Sw. 1106
- Actephila* Blume 1092
- Actinostemon* Klotzsch 1129
concolor (Sprengel) Muell. Arg. 1129
- Adelia* L. **1100**
ricinella L. 1100
- Adenophaedra* (Muell. Arg.) Muell. Arg. 1087, **1099**
grandifolia (Klotzsch) Muell. Arg. **1099**, 1100
megalophylla (Muell. Arg.) Muell. Arg. 1099
woodsoniana (Croizat) Croizat 1099
- Alchornea* Sw. 1087, **1100**
costaricensis Pax & K. Hoffm. **1101**
glandulosa Poeppig
 var. *floribunda* Benth. 1098
 var. *glandulosa* 1102
 var. *pittieri* (Pax) Pax **1102**
grandiflora Muell. Arg. **1102**
grandis Benth. **1102**, 1103
latifolia Sw. 1100, **1101**, 1102
megalophylla Muell. Arg. **1102**
oblongifolia Standley 1103
pearcei Britton 1101
pittieri Pax 1102
triplinervia (Sprengel) Muell. Arg. **1101**
 var. *genuina* f. *psilorhachis* Muell. Arg. 1102
umboensis Croizat 1101
- Alchorneopsis* Muell. Arg. **1098**
floribunda (Benth.) Muell. Arg. **1098**
- Amanoa* Aublet **1092**
guianensis Aublet **1092**
- Antidesma* L.
triplinervium Sprengel 1101
- Aporosa* Blume 1093
- Argythamnia* P. Browne **1098**
candicans Sw. 1098
- Astrocasia* Robinson & Millsp. 1087, **1091**
phyllanthoides Robinson & Millsp. 1091
tremula (Griseb.) Webster **1091**
- Ateramnus* Browne 1129
- Bernardia* P. Miller **1100**
 section *Adenophaedra* Muell. Arg. 1099
carpinifolia P. Miller 1100
denticulata (Standley) Webster 1099, 1100
 ?*grandifolia* (Klotzsch) Muell. Arg. 1099
jacquiniana Muell. Arg. 1100
macrophylla Standley **1100**
 ?*megalophylla* Muell. Arg. 1099
- Caperonia* St. Hil. **1098**
castaneifolia (L.) St. Hil. 1098
paludosa Klotzsch 1098
- Caryodendron* Karsten **1099**
angustifolium Standley **1099**
orinocense Karsten 1099
- Chamaesyce* Gray **1141**
maritima Gray 1141
peplis (L.) Prokh. 1141
- Clavija* Ruiz Lopez & Pavon
septentrionalis L. O. Williams 1115
- Cleidion* Blume 1087, **1103**
amazonicum Pax 1104
castaneifolium Muell. Arg. **1103**
denticulatum (Standley) Webster 1099
javanicum Blume 1103
membranaceum Pax & K. Hoffm. 1099, **1103**, 1104
 ?*nicaraguensis* Hemsley 1106
oblongifolium (Standley) Croizat 1103, 1104
prealtum Croizat 1103, 1104
tricoccum (Casar.) Baillon 1103
woodsonianum Croizat 1099, 1103
- Cnidioscolus* Pohl **1114**
aconitifolius (Miller) I. M. Johnston **1114**
 subsp. *aconitifolius* **1114**
adenophilus (Pax & K. Hoffm.) Pax & K. Hoffm. 1114
hamosus Pohl 1114
urens (L.) Arthur **1114**
 subsp. *adenophilus* (Pax & K. Hoffm.) Breckon **1114**
 subsp. *urens* **1114**
- Croizatia* Steyerf. 1087, **1092**
naiguatensis Steyerf. 1092, 1903
neotropica Steyerf. 1092, 1093
panamensis Webster **1092**
- Croton* L. **1116**
argenteus L. **1124**
aromaticus L. 1116
benthamianus Muell. Arg. 1118, 1121
benthamianus (Muell. Arg.) Lanjouw 1118
billbergianus Muell. Arg.
 subsp. *billbergianus* **1121**
 subsp. *pyramidalis* (J. D. Smith) Webster 1123
brevipes Pax **1123**
castaneifolius L. 1098
draco Cham. & Schldl. 1120
 subsp. *draco* 1120
 subsp. *panamensis* (Klotzsch) Webster **1120**
hircinus Vent. **1123**, 1124
killipianus Croizat 1121
lanjouwensis Jabl. **1118**, 1119
macrodonatus Muell. Arg. 1124
matourensis Aublet 1118
 var. *benthamianus* Muell. Arg. 1118
nuntians Croizat 1121
pachypodus Webster **1119**
palanostigma Klotzsch 1121
panamensis (Klotzsch) Muell. Arg. 1121
pyramidalis J. D. Smith 1121
pyriticus Croizat 1119
santaritensis Huft 1122!, **1123**
smithianus Croizat **1120**
speciosus Muell. Arg. 1120
 subsp. *tacarcunensis* Webster **1119**
tenuicaudatus Lundell **1118**, 1119
- Cyclostigma* Klotzsch
panamensis Klotzsch 1120
- Dactylostemon* Klotzsch 1129
- Dalechampia* L. 1087, **1108**
 section *Dioscoreifoliae* Pax & K. Hoffm. 1109
canescens Kunth
 subsp. *friedrichsthalii* (Muell. Arg.) Webster &

- Huft **1109**, 1110
 subsp. *canescens* 1109
cissifolia Poeppig 1110
 subsp. *panamensis* (Pax & K. Hoffm.) Webster **1110**
dioscoreifolia Poeppig 1109
friedrichsthali Muell. Arg. 1109
heteromorpha Pax & K. Hoffm. 1110
panamensis Pax & K. Hoffm. 1110
scandens L. 1108
shankii (A. Molina) Huft 1107, **1109**
websteri Armbruster **1110**
Drypetes Vahl 1087, **1096**
glauca Vahl 1096
standleyi Webster **1096**
Euphorbia L. 1087, **1137**
 section *Adenorima* (Raf.) Webster 1138
 section *Alectoroctonum* (Schldl.) Boissier 1139
 section *Cyttarospermum* Boissier 1140
 section *Dichilium* Boissier 1139, 1140
 section *Poinsettia* (Graham) Baillon 1137
 subgenus *Poinsettia* (Graham) House 1094, 1137
amphimalaca Standley 1140
antiquorum L. 1137
apocynoides Klotzsch 1137, **1139**
astroites Fisch. & Mey. 1139
capansa Ducke 1138
caracasana Boissier 1141
dwyeri Burch **1141**
elata Brandegee **1137**
enalla Brandegee 1140
graminea Jacq. 1140
leucocephala Lotsy **1138**
nudiflora Jacq. 1139
ocymoidea L. **1139**
oerstediana (Klotzsch & Garcke) Boissier 1140
peplus L. **1140**
peplis L. 1141
sinclairiana Benth. 1138
subreniformis S. Watson 1140
tessmannii Mansf. 1138
tithymaloides L. 1141
valerii Standley 1137
xalapensis Kunth **1140**
Excoecaria L.
biglandulosa (L.) Muell. Arg. 1133
 var. *moritziana* (Klotzsch) Muell. Arg. 1133
farinosa Griseb. 1131
Garcia Vahl **1116**
nutans Vahl **1116**
Gussonia Sprengel
concolor Sprengel 1129
Gymnanthes Sw. 1087, **1129**, 1131
actinostemoides Muell. Arg. **1130**
albicans (Griseb.) Urban 1131
dressleri Webster **1131**
farinosa (Griseb.) Webster 1131
granatensis Muell. Arg. 1131
lucida Sw. 1129
Heywoodia Sims 1091
Hippomane L. **1137**
biglandulosa L. 1133
glandulosa L. 1133
mancinella L. 1137
Hura L. **1137**
crepitans L. 1137
Hyeronima Allemão 1087, **1094**
alchorneoides Allemão 1094
guatemalensis J. D. Smith 1095
laxiflora (Tul.) Muell. Arg. 1094, **1095**
oblonga (Tul.) Muell. Arg. **1095**
 var. *benthamii* (Tul.) Muell. Arg. 1095
scabrida (Tul.) Muell. Arg. 1095
Janipha Kunth
aesculifolia Kunth 1113
Jatropha L. **1114**
aconitifolius Miller 1114
adenophila Pax & K. Hoffm. 1114
gossypifolia L. 1114
manihot L. 1113
urens L. 1114
Julocroton C. Martius
argenteus (L.) Didr. 1124
Mabea Aublet 1087, **1125**
jefensis Huft **1125**, 1126!
montana Muell. Arg. **1125**
piriri Aublet 1125
Maesobotrya Benth. 1093
Manihot Miller 1087, **1113**
aesculifolia (Kunth) Pohl **1113**
brachyloba Muell. Arg. **1114**
esculenta Crantz 1113
gualanensis Blake 1113
Maprounea Aublet 1087, **1131**
guianensis Aublet 1131, **1132**
Margaritaria L.f. **1096**
nobilis L.f. 1096
Omphalea L. **1110**
diandra L. **1110**
triandra L. 1110
Ophellantha Standley
spinosa Standley 1129
Pausandra Radlk. 1087, **1114**
extorris Standley 1115
morisiana (Casar.) Radlk. 1114
quadriglandulosa Pax & K. Hoffm. 1115
 trianae Baillon **1115**
Pedilanthus Necker ex Poit. 1094, **1141**
tithymaloides (L.) Poit. 1141
Pentabrachium Muell. Arg. 1092
Pera Mutis **1110**
arborea Mutis 1110
Phyllanthus L. **1096**
 subgenus *Xylophylla* (L.) Pers. 1098
 section *Asterandra* (Klotzsch) Muell. Arg. 1098
anisolobus Muell. Arg. **1096**
gentryi Webster **1096**, 1097!
juglandifolius Willd. 1098
niruri L. 1096
tremulus Griseb. 1091
Plukenetia L. **1105**
angustifolia Standley 1105
penninervia Muell. Arg. **1105**
volubilis L. **1105**
Podocalyx Klotzsch 1093
Pogonophora Miers 1116
 trianae Muell. Arg. 1115
Poinsettia Graham 1137
pulcherrima (Willd. ex Klotzsch) Graham 1137
xalapensis (Kunth) Klotzsch & Garcke 1140
Polyandra Leal
bracteosa Leal 1103
Richeria Vahl 1087, **1093**
dressleri Webster **1094**
grandis Vahl 1093, 1094

- grandis* Vahl ζ *obovata* Muell. Arg. 1093
loranthoides (Klotzsch) Muell. Arg. 1093
obovata (Muell. Arg.) Pax & K. Hoffm. **1093**
Ricinus L. **1104**
communis L. 1104
Sapium P. Browne 1087, 1129, 1132
 subsection *Emmenostylum* (Hemsley) Pax 1135
 allenii Huft 1135
 anadenum Pittier 1134
 aucuparium Jacq. 1132, **1133**, 1134, 1135
 var. *moritzianum* (Klotzsch) Pittier 1133
 aucuparium sensu Croizat 1134
 biglandulosum (L.) Muell. Arg.
 var. *moritzianum* (Klotzsch) Muell. Arg. 1133
 var. *oligoneurum* (Schumann & Pittier) Monach. 1134
 var. *sulciferum* (Pittier) Monach. 1134
 caudatum Pittier 1132, 1133, 1135
 eglandulosum Ule 1132, **1133**
 giganteum Pittier 1133
 jamaicense Sw. 1132, 1133, **1134**
 moritzianum Klotzsch 1133
 oligoneurum Schumann & Pittier **1134**
 pachystachys Schumann & Pittier **1135**
 pleiostachys Schumann & Pittier 1134
 putumayense Croizat 1136
 rigidifolium Huft **1135**, 1136!
 salicifolium Kunth 1133
 schippii Croizat 1134
 stylare Muell. Arg. 1136
 sulciferum Pittier 1134, 1135
 thelocarpum Schumann & Pittier 1135
 verum Hemsley 1136
Sebastiania Sprengel 1087, **1127**, 1129, 1131
 section *Adenogyne* 1128
 section *Elachocroton* (F. Muell.) Pax 1128
 section *Microstachys* (Adr. Juss.) Muell. Arg. 1128
 section *Sebastiania* 1128, 1129
 actinostemoides (Muell. Arg.) Muell. Arg. 1130
 anisandra (Griseb.) Lillo 1129
 brasiliensis Sprengel 1127, 1129
 corniculata (Vahl) Muell. Arg. 1128
 macrocarpa Muell. Arg. 1129
 panamensis Webster **1128**
 stipulacea (Muell. Arg.) Muell. Arg. 1128
 warmingii (Muell. Arg.) Pax 1129
Senefeldera C. Martius 1087, **1127**
 multiflora C. Martius 1127
 testiculata Pittier 1099, **1127**
Stilaginella Tul.
 benthamii Tul. 1095
 laxiflora (Tul.) Muell. Arg. 1095
 oblonga Tul. 1095
Stillingia Garden ex L. **1132**
 haematantha Standley 1133
 sylvatica L. **1132**
Tetrorchidium Poeppig 1087, **1110**
 brevifolium Standley & Steyerf. 1111, 1112
 costaricense Huft **1112**
 euryphyllum Standley **1113**
 gorgonae Croizat
 subsp. *robledoanum* (Cuatr.) Webster **1113**
 microphyllum Huft **1110**, 1111!
 molinae L. O. Williams 1112
 robledoanum Cuatr. 1113
 rotundatum Standley 1112
 rubrivenium Poeppig 1110, 1112
Thouinia Poit.
 morisiana Casar. 1114
Tragia L. 1087, **1106**
 section *Bia* (Klotzsch) Muell. Arg. 1108
 section *Eutragia* Muell. Arg. 1108
 section *Tragia* 1108
 section *Zuckertia* (Baillon) Muell. Arg. 1107
 bailloniana Muell. Arg. **1106**
 cordata Michx. 1106
 correae Huft **1107**
 fallax Muell. Arg. 1108
 fendleri Muell. Arg. **1107**, 1108
 grandifolia Klotzsch 1099
 japurensis Muell. Arg. 1107, 1108
 shankii A. Molina 1109
 volubilis L. 1106, 1108
Wielandia Baillon 1091
Zuckertia Baillon
 cordata Baillon 1106



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