

THE VASCULAR FLORA OF THE LA SELVA BIOLOGICAL
STATION, COSTA RICA*
RUBIACEAE

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Usually hermaphroditic or sometimes monoecious or dioecious, usually terrestrial or rarely epiphytic trees, shrubs, herbs, or lianas, frequently with raphides, stems often quadrate and usu-

ally becoming terete, wood hard and frequently brittle. *Leaves* opposite or rarely verticillate, decussate or rarely distichous; blades entire or rarely pinnatifid, sometimes with pit-like acarodomatia on abaxial surface; axils of midrib and secondary veins frequently barbate, fine venation rarely lineolate (closely and finely subparallel within individual reticulations); stipules persistent or deciduous, connate interpetiolarly and sometimes also intrapetiolarly or rarely apparently free, the interpetiolar portion triangular or bilobed or truncate with two triangular lobes or awns. *Inflorescences* terminal or sometimes axillary (present in both axils of a node) or pseudoaxillary (present in only one axil of a node), generally cymose, open, contracted to a capitulum, or reduced to a single flower, bracteate, the bracts sometimes reduced or caducous; *flowers* usually hermaphroditic or sometimes unisexual, monomorphic or frequently distylous, actinomorphic or rarely somewhat zygomorphic, (3-)4-5(-9)-merous; calyx gamosepalous, aestivation valvate or open; corolla gamopetalous, salverform or tubular to funnelform or campanulate, aestivation valvate or convolute or imbricate; stamens alternate with and equal in number to corolla lobes or rarely 1-3 more, epipetalous; anthers bithecal, dorsifixed or basifixed, dehiscent by longitudinal slits or rarely by pores; ovary syncarpous, inferior or rarely becoming superior in fruit, locules 2(-12) or incompletely 1; ovules 1 or several to many in each locule, basal or axile or borne on expanded axile placentas or rarely parietal; disk usually present. *Fruit* simple or sometimes schizocarpous or multiple, septicidal or rarely loculicidal capsules, berries, drupes, or achenes; seeds angled to flattened, sometimes winged, rarely comose; pyrenes planoconvex or concavoconvex, frequently ribbed on convex abaxial ("dorsal") side and with a median sulcus on the planar or concave adaxial ("ventral") side.

This family includes ca. 450 genera with about 8,000 species found throughout the world. Thirty-eight genera with 96 species are known from the La Selva field station. The trees and shrubs of the Rubiaceae are important components of the vegetation in tropical forests throughout the

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world, particularly in the Neotropics. The family has its greatest number of species and genera in the Neotropics, where it is well-represented at both low and high elevations. The largest genus in the family by far is *Psychotria*; also particularly numerous in Central America are species of *Coussarea*, *Faramea*, *Hoffmannia*, *Palicourea*, and *Randia*.

Members of the Rubiaceae can be recognized by their opposite leaves with interpetiolarly fused stipules and entire (or rarely pinnatifid) margins, combined with their flowers with inferior ovaries and sympetalous corollas. Many species also have raphides in their tissues. Some species of Chloranthaceae and Urticaceae may have opposite leaves with interpetiolar stipules, but these also have dentate leaf margins. *Cassipourea* (Rhizophoraceae) resembles some Rubiaceae vegetatively, but its petals are separate and its ovary is superior. Some sterile Rubiaceae with caducous stipules and a resulting scar may be confused with members of the Acanthaceae, which frequently have a scar-like line connecting opposite petioles. Acanthaceae can usually be separated by the pulvinal swellings on young twigs (sometimes seen as constrictions on dried specimens), which are located above the nodes in Acanthaceae in contrast to below the nodes in Rubiaceae.

Important commercial products derived from members of the Rubiaceae are the alkaloid substances in coffee, from *Coffea*; quinine, today synthesized but originally obtained from South American species of *Cinchona*; and ipecac, from species of *Psychotria*. Some fruits, including those

of *Genipa*, are collected or cultivated on a local scale.

Many species in several genera bear acarodomatia on the undersides of the leaf blades. These are structures that house mites (Pember-ton & Turner, 1989). They are usually situated at the junction of the midrib and the secondary veins.

Species in several genera are distylous (Ganders, 1979). Both distylous and monomorphic species may be found in the same genus. The term "homostylous," in the sense of non-distylous, is equivalent to the term "monomorphic" used here. The characterizations of breeding systems presented here are based on the observations of Bawa and Beach (1983) and on the study of dried specimens, and are not complete.

The descriptions presented here are based primarily on material from the La Selva Biological Station and nearby areas. Descriptions of stipule shape apply to the interpetiolar portion. Bracts of about 0.5–1.5 mm length are present in most species; only larger bracts or the absence of bracts is described. Number of flower parts (for example "4-merous," "5-merous") refers to the number of calyx lobes, corolla lobes, and stamens. For alternate states of most characteristics, the most common condition is assumed, and only the condition described as "sometimes," "unusual," or "rare" in the family or generic description is mentioned in the species description. Taxonomic synonyms are cited here as references to other floras; they are included only when a different name has been commonly or recently used for a particular species.

KEY TO THE GENERA

1. Plants vining, climbing, or extensively clambering.
 2. Woody lianas climbing to the canopy, armed with recurved thorns 1–2 cm long.
 3. Stipules 8 mm long; flowers numerous (30 or more) in globose pedunculate heads; corolla tubes 5–6 mm long; fruits dry, capsular, 7–9 mm long; seeds winged. 38. *UNCARIA*.
 3. Stipules 2–5 mm long; flowers 1–3, subsessile on stems; corolla tubes 30–45 mm long; fruits fleshy, baccate, 5–9 cm long; seeds not winged. 31. *RANDIA* (*R. pepoformis*).
 2. Woody or herbaceous low vines, unarmed.
 4. Herbaceous, puberulent to glabrous; stipules truncate to triangular, ca. 1 mm long; peduncles 1–2.5 cm long; pedicels 1–2.5 cm long; fruits dry, capsular. 24. *MANETTIA*.
 4. Suffrutescent to woody, strigose to pilose; stipules ovate, 4–10 mm long; peduncles 0–8 mm long, pedicels 0–8 mm long; fruits fleshy, indehiscent. 34. *SABICEA*.
1. Plants erect to decumbent or sometimes clambering or creeping, terrestrial or epiphytic.
 5. Epiphytes, usually succulent.
 6. Stipules persistent, connate around the stem into a truncate sheath 1–4 mm long; corolla tubes 1.5–2 mm long; fruits fleshy, indehiscent, ca. 5 mm in diameter with 4–6 seeds. 30. *PSYCHOTRIA* (*P. guadalupensis*).
 6. Stipules quickly deciduous, connate interpetiolarly, obovate to ligulate, 15–40 mm long; corolla tubes 43–80 mm long; fruit dry, capsular, 7–10.5 cm long, with numerous (30 or more) seeds.
 7. Stipules 15–20 mm long; pedicels 1–2 cm long; flowers 5-merous; calyx lobes 2–4 mm long; seeds winged but not comose. 8. *COSMIBUENA*.
 7. Stipules ca. 40 mm long; flowers subsessile, 6-merous; calyx limb truncate, ca. 0.5 mm long; seeds with trichomes attached at one end. 18. *HILLIA*.

5. Plants terrestrial, sometimes succulent.
8. Herbs or sometimes suffrutescent, stems to 1 m tall and usually less than 0.6 m tall, erect to decumbent or creeping, sometimes rooting at successive nodes.
9. Creeping herbs, frequently rooting at the nodes.
10. Leaf blades cordate at base; stipules triangular, sometimes fimbriate; corollas white; fruit red or purple-black, solid, with two seeds. 14. *GEOPHILA*.
10. Leaf blades truncate to cuneate at base; stipules with one large central and 4–7 smaller side lobes; corolla blue; fruit blue, hollow, with numerous (20 or more) seeds. 6. *COCCOCYPSELUM*.
9. Erect or decumbent soft to suffrutescent herbs, sometimes stoloniferous but not rooting at nodes.
11. Stipules persistent, with 3–10 lobes or setae.
12. Petioles 1.5–5 cm long; stipule lobes 1–4 cm long. 1. *AMPHIDASYA*.
12. Petioles 0–0.5 cm long; stipule teeth 2–13 mm long.
13. Petioles ca. 5 mm long; leaf blades 10–15 cm long. 30. *PSYCHOTRIA* (*P. ipecacuanha*).
13. Leaf blades subsessile, 1–10 cm long.
14. Inflorescences terminal, subtended by 1–2 pairs of foliaceous bracts 1–3 cm long; fruit separating into (2–)3 tuberculate mericarps. 32. *RICHARDIA*.
14. Inflorescences axillary and terminal, bracts 1 cm long or shorter or lacking; fruit dehiscent or separating into 1–2 smooth segments.
15. Calyx lobes 2–2.5 mm long; capsules circumscissile. 25. *MITRACARPUS*.
15. Calyx lobes 0.5–1 mm long; fruit septically or loculicidally dehiscent.
16. Stipule teeth 5–13, 3–8 mm long; capsules dehiscent acropetally. 17. *HEMIDIODIA*.
16. Stipule teeth 2–7, these 1–4 mm long; capsules dehiscent basipetally. 37. *SPERMACOCE*.
11. Stipules triangular or bidentate or bilobed, persistent or quickly deciduous and not observed.
17. Leaf blades 2–5 mm wide; flowers solitary or paired on axillary peduncles 5–20 mm long; corolla tube ca. 1 mm long; stipules 1–2 mm long. 26. *OLDENLANDIA*.
17. Leaf blades 3–7 cm wide; flowers 3 or more on axillary or terminal pedicels 0–5 mm long; corolla tubes 2–3 mm long; stipules 2–10 mm long.
18. Petioles 1–9 mm long; plants pilose; fruits with 3–8 seeds. 23. *LASIANTHUS*.
18. Petioles 1.5–10 cm long; plants pilose or glabrescent; fruit with seeds either 2 or numerous (30 or more).
19. Fruit with 2 pyrenes; corolla white to greenish or yellowish white. 30. *PSYCHOTRIA*.
19. Fruit with numerous seeds; corolla red or yellow. 20. *HOFMANNIA*.
8. Woody shrubs or trees, stems usually 1 m or more tall, erect, not rooting at nodes.
20. Stipules 5–7 cm long; leaf blades 40–80 cm long. 28. *PENTAGONIA*.
20. Stipules 0.5–30 mm long; leaf blades 5–40 cm long.
21. Stipules 14–30 mm long.
22. Underbark and wood tan or white becoming red-purple when exposed to air.
23. Leaf blades 12–28 cm wide; stipules triangular. 35. *SIMIRA*.
23. Leaf blades 5–9(–12) cm wide; stipules bilobed. 30. *PSYCHOTRIA* (*P. suerrensis*).
22. Underbark and wood pale becoming rusty brown, black, or grey or not changing color when exposed to air.
24. Fine leaf venation lineolate.
25. Calyx limb spathaceous, 25–35 mm long. 19. *HIPPOTIS*.
25. Calyx limb regularly lobed, (1)2–4(5) mm long. 36. *SOMMERA*.
24. Fine leaf venation not lineolate.
26. Flowers numerous (12 or more), usually congested; pedicels 0–1 mm long; corolla tubes 1–3.5 mm long; fruits 1–10 mm long.
27. Inflorescences racemiform, 20–60 cm long, each cymule with a red petaloid sepal 4–10 cm long; corolla yellow to orange; fruits capsular, 2–2.5 mm long. 39. *WARSZEWICZIA*.
27. Inflorescences paniculiform, pyramidal to rounded, 5–15 cm long; without petaloid sepals; corollas pale green to creamy or pure white; fruits fleshy, 3–10 mm in diameter. 30. *PSYCHOTRIA*.
26. Flowers fewer (ca. 1–12) in open inflorescences; pedicels 0–10 mm long; corolla tubes 18–90 mm long; fruits 3–9 cm long.

28. Leaves clustered near ends of branches; fruit baccate, fleshy, globose; calyx limb 18–35 mm long; flowers unisexual. 31. *RANDIA* (*R. sp. A*).
28. Leaves distributed along stem, internodes expanded; fruit capsular, woody, cylindrical; calyx limb 0.5–6 mm long; flowers hermaphroditic.
29. Calyx limb ca. 0.5 mm long; corolla tubes 18–25 mm long; leaf blades 4–7.5 cm wide. 12. *FERDINANDUSA*.
29. Calyx limb 5–6 mm long; corolla tubes 42–50 mm long; leaf blades 8–15 cm wide. 22. *LADENBERGIA*.
21. Stipules 0.5–18 mm long, or very quickly deciduous and not observed.
30. Leaves subsessile on petioles 0–3 mm long, bases truncate to auriculate.
31. Stipules persistent, truncate to somewhat rounded, with 5–8 deciduous teeth ca. 1 mm long. 33. *RUDGEA*.
31. Stipules quickly deciduous, triangular, entire.
32. Leaves with pit-like domatia in axils of midrib and secondary veins on undersurface; peduncles 3–10 cm long; corolla tubes 1.5–2 mm long; fruit 3–10 mm in diameter, smooth. 30. *PSYCHOTRIA* (*P. laselvensis*).
32. Leaves barbate in axils of midrib and secondary veins on undersurface; peduncles 1–2 cm long; corolla tubes 13–14 mm long; fruits 1.5 cm long, lenticellate. 9. *COUSSAREA* (*C. impetiolaris*).
30. Leaves with petioles 0.3–12 cm long; leaf bases cuneate or acute to attenuate.
33. Cauliflorous trees; flowers solitary, unisexual, 6–7-merous; bark red-brown. 31. *RANDIA* (*R. mira*).
33. Inflorescences terminal or axillary on youngest stems; flowers solitary to numerous, bisexual or unisexual, 4–6-merous; bark grey to brown.
34. Inflorescences axillary.
35. Flowers subsessile in sessile glomerules in leaf axils; fruit fleshy. 7. *COFFEA*.
35. Flowers sessile or pedicillate but with peduncles 0.2–5 cm long, not glomerulate; fruit fleshy or capsular.
36. Flowers sessile in capitate heads 5–10 mm in diameter; inflorescences (1–)2–3 per axil. 30. *PSYCHOTRIA* (*P. erecta*).
36. Pedicels 0.5–1 mm long, inflorescences congested, 1–6 cm long, 1 per axil.
37. Corollas red to yellow; fruit fleshy, indehiscent. 20. *HOFFMANNIA*.
37. Corollas pale green to white or pink; fruit capsular, dehiscent.
38. Flowers 6-merous; calyx limb 6–7 mm long; pedicels 2–5 mm long; capsules 30–35 mm long. 10. *COUTAREA*.
38. Flowers 4–5-merous; calyx limb 0.5 mm long; pedicels 0.5–1 mm long; capsules 1–1.5 mm long. 4. *CHIMARRHIS*.
34. Inflorescences terminal, sometimes pseudoaxillary later by growth of axillary buds.
39. Leaves clustered at ends of branches. 31. *RANDIA* (*R. grandifolia*).
39. Leaves distributed along stems, internodes developed.
40. Inflorescences or flowers enclosed in 2 or more enlarged, sometimes connate, ligulate to triangular involucre bracts 5–150 mm long; fruit fleshy.
41. Bracts partially fused; flowers unisexual, 1–6 on peduncles 0–3 mm long; fruit ca. 4.5 cm in diameter with pericarp 8–12 mm thick; seeds numerous (30 or more). 3. *BOROJOA*.
41. Bracts free; flowers unisexual or bisexual, 10 or more in capitate heads, usually with peduncles 5 mm long or longer; fruits to 1 cm in diameter with pericarp 1–2 mm thick; pyrenes 1–2. 30. *PSYCHOTRIA*.
40. Inflorescences bracteate or not but without involucre bracts, bracts 0.5–15 mm long; fruit fleshy or dry.
42. Corolla tubes 45–330 mm long; fruits 3–10 cm long.
43. Corolla tubes 45–60 mm long, funnelform; fruits capsular, 3–3.5 cm long. 10. *COUTAREA*.
43. Corolla tubes 100–330 mm long, salverform, tube slender; fruit fleshy, 5–10 cm in diameter. 29. *POSOQUERIA*.
42. Corollas with tubes 1–44 mm long; fruit 0.3–11 cm long.
44. Stipules bilobed or dentate; fruit fleshy with 1–5 seeds.
45. Corollas bright yellow to red; pedicels 0.5–5 mm long. 27. *PALICOUREA*.
45. Corollas pale green to white or flushed with yellow or rose; flowers sessile or on pedicels to 2 mm long. 30. *PSYCHOTRIA*.
44. Stipules triangular, rounded to mucronate.
46. Flowers blue and either leaf blades with strong submarginal veins similar to the midvein and the lesser venation oriented at right angles, or inflorescence bracts ovate, stipitate, white, 12–15 mm long, caducous. 11. *FARAMEA*.

46. Flowers white, green, yellow, red, or rose; leaf blades without strong submarginal veins; inflorescence bracts not stipitate.
47. Calyx limb 6–10 mm long; fruit 5–11 cm in diameter. 13. *GENIPA*.
47. Calyx limb 5 mm long or shorter; fruit 3 cm or less in diameter.
48. Corollas red or yellow with tubes 2–3 cm long. 16. *HAMELIA*.
48. Corollas white to yellow, rose, or pale green with tubes 1–15(–44) mm long.
49. Fruit present, fleshy; corollas not seen.
50. Fruit 1–3 cm in diameter; pyrenes 1–2.
51. Fruit ellipsoid to fusiform, usually curved; pyrene solitary with 2 chambers. 5. *CHIONE*.
51. Fruit ellipsoid to ovoid or globose, straight, sometimes flattened; pyrenes 1–2 each with one chamber. 9. *COUSSAREA*.
50. Fruit 3–9 mm in diameter; seeds 1–numerous (10 or more).
52. Seeds numerous, embedded in pulp or inside 1–4 pyrenes.
53. Fruits aerenchymatous with 1–4 pyrenes, these each containing several seeds. 15. *GONZALAGUNIA*.
53. Fruits soft throughout with seeds embedded in the pulp. 2. *BERTIERA*.
52. Pyrenes 1–2 per fruit.
54. Mature fruits blue-black; leaf blades without domatia; stipules triangular, acuminate or mucronate, persistent. 21. *IXORA*.
54. Mature fruits white, red, or blue-black; leaf blades sometimes with domatia; stipules triangular and caducous, or not triangular: bidentate, caplike, succulent and divergent, or truncate with one lobe. 30. *PSYCHOTRIA*.
49. Flowers present; fruits not seen.
55. Corolla tubes 10–25 mm long. 9. *COUSSAREA*.
55. Corolla tubes 1–9 mm long.
56. Corolla lobes valvate in aestivation.
57. Inflorescences racemiform, with contracted cymules on a long central axis. 15. *GONZALAGUNIA*.
57. Inflorescences capitate to open paniculate with the side branches expanded.
58. Corolla lobes ca. 4 mm long, tubes ca. 5 mm long. 9. *COUSSAREA* (*C. talamancana*).
58. Corolla lobes 1–3 mm long, if more than 2 mm long then half as long as or shorter than the corolla tubes. 30. *PSYCHOTRIA*.
56. Corolla lobes imbricate or convolute in aestivation.
59. Corolla lobes imbricate in aestivation. 5. *CHIONE*.
59. Corolla lobes convolute in aestivation.
60. Peduncles 4–10 cm long; inflorescence branches helicoid. 2. *BERTIERA*.
60. Peduncles 0–5 mm long; inflorescences open paniculate with the branches cymose. 21. *IXORA*.

1. *AMPHIDASYA* Standley

Erect shrubs or suffrutescent herbs. *Leaves* without domatia; stipules interpetiolarly connate, persistent, entire or with several lobes. *Inflorescences* terminal or axillary, cymose or subcapitate, subsessile; flowers apparently monomorphic, 4–6-merous; corollas tubular, aestivation valvate; ovules numerous on axile placentas. *Fruits* baccate, fleshy; seeds angled.

Amphidasya is a genus of about 6–7 species found from Costa Rica through northern Brazil, with one species in Costa Rica.

1. *Amphidasya ambigua* (Standley) Standley

Suffrutescent glabrescent herbs to 0.4 m tall. *Leaves* opposite or sometimes subopposite by displacement due to growth of lateral buds; blades

elliptic to oblanceolate, 12–28 cm long, 4.5–8.5 cm wide, acute to acuminate at apex, cuneate to somewhat attenuate at base, membranaceous to chartaceous, very minutely puberulent to glabrescent, pale below; secondary veins 15–21 pairs, looping to interconnect distally; petioles 1.5–5 cm long; stipules 3–5 mm long with 5 narrowly triangular to subulate lobes 1–4 cm long, acute. *Inflorescences* axillary contracted cymes or capitula to 5 cm long with 4–20 flowers; bracts triangular, acute, 1–5 mm long; *flowers* sessile or subsessile, 5–6-merous; calyx puberulent, limb membranaceous, green, divided to the base, lobes narrowly triangular to oblanceolate, 8–12(–18) mm long, usually unequal, acute; corolla salverform, puberulent to pilosulous externally, bright white, tube 4–5 cm long, lobes triangular, 15–17 mm long, acute. *Fruits* ellipsoid to obconic, 8–12 mm long, carnosose, green at maturity; seeds

globose, 0.3–0.4 mm in diameter, coarsely foveolate. At La Selva collected in flower August and November, in fruit March, June–July, September, and November. Costa Rica to Colombia in wet forests of Caribbean and Pacific lowlands.

FIGURE 1a.

This species is uncommon on steep banks along streams in primary forest. The plants are usually found with fruit, but flowers are seldom seen. The flowers probably open for one night. There is marked variation in the length of the calyx and corolla lobes across the geographic range of this species; the status of the Costa Rican plants probably deserves more study.

2. BERTIERA Aublet

Erect shrubs or small trees. *Leaves* distichous, sometimes with domatia; stipules connate interpetiolarly and intrapetiolarly, persistent, triangular. *Inflorescences* terminal, paniculate, the branches often helicoid; flowers apparently monomorphic, 4–5(6)-merous; corollas funnel-form, aestivation convolute; ovules numerous on axile placentas. *Fruits* baccate, fleshy, purple-black; seeds angled.

Bertiera includes about 30 species in tropical America and Africa, two of which occur in mainland Costa Rica.

1. *Bertiera guianensis* Aublet

Strigose shrubs to 5 (10) m tall. *Leaf* blades elliptic to slightly ovate, 10–18 cm long, 2–6.5 cm wide, acute at apex, acute to obtuse at base, chartaceous; secondary veins 6–8 pairs, without domatia; petioles 3–10 mm long; stipules 5–15 mm long, acuminate and rarely slightly bifid. *Inflorescences* drooping to pendulous; cymes pyramidal, 6–20 cm long, 3–7 cm broad; branches helicoid; peduncles flexuous, 4–10 cm long; bracts narrowly triangular to linear, 1–15 mm long, acute; *flowers* sessile or subsessile; calyx glabrescent or strigillose, limb green, divided to base, lobes triangular, 0.5–1 mm long, acute to shortly acuminate; corolla white, strigose to glabrescent externally, barbate in throat, tube 3–4 mm long, lobes ovate to lanceolate, 1.5–2.5 mm long, acuminate. *Fruits* globose, 3–4 mm in diameter, longitudinally slenderly 6–10 costate; seeds 1–2 mm long. At La Selva collected in flower March–August, in fruit March–August and October and December. Mexico and the western Greater Antilles through South America in wet forests at 0–300 m.

FIGURE 4p.

These occasional shrubs are most frequent on ridges in primary forest.

3. BOROJOA Cuatrecasas

Dioecious, erect small trees. *Leaves* sometimes with domatia; stipules interpetiolarly and sometimes also intrapetiolarly connate, persistent, ligulate to triangular. *Inflorescences* terminal, subtended by 1–3 pairs of bracts, staminate *flowers* cymose or capitulate, 4–5-merous, pistillate *flowers* solitary, 6–8-merous; corollas salverform to funnel-form, aestivation convolute; ovary 6–8-locular; ovules numerous and horizontal on axile placentas. *Fruits* baccate, fleshy, with thick pericarp and mucilaginous endocarp; seeds flattened.

Borojoa includes perhaps as many as 10 species found from Costa Rica to Colombia and Venezuela. These plants are infrequently collected, particularly pistillate plants with flowers. The fruits of some species are eaten by local people.

1. *Borojoa panamensis* Dwyer

Glabrescent trees to 10 m tall. *Leaf* blades broadly elliptic to elliptic-oblong, 12–25 cm long, 6–13 cm wide, acuminate at apex, cuneate at base, subcoriaceous; secondary veins 8–9 pairs, with domatia; petioles 5–15 mm long; stipules 12–16 mm long, fused for 2–5 mm, acute to acuminate. *Staminate inflorescences* cymose with 2–6 flowers; bracts connate similarly to stipules, 6–16 mm long, acuminate to mucronate; pedicels to 3 mm long; *staminate flowers* 5-merous; calyx glabrous, the limb green, 8–10 mm long, shallowly lobed, lobes triangular, 0.5–1 mm long, acute; corolla thickly carnosose, cream to yellowish white, externally and internally sericeous to pilosulous, tube ca. 1 cm long, lobes triangular, 12–15 mm long, acute to acuminate. *Pistillate flowers* not seen. *Fruit* globose to slightly ovoid, ca. 4.5 cm in diameter, smooth, yellowish brown, subtended by persistent bracts, with pericarp 8–12 mm thick; seeds orbicular, 4–5 mm in diameter. At La Selva collected in flower July, in fruit August. Costa Rica and Panama in wet forests throughout at 0–1,600 m.

FIGURE 5l.

This occasional species is most frequently found on ridges in primary forest.

4. CHIMARRHIS Jacquin

Erect trees. *Leaves* sometimes with domatia; stipules interpetiolarly connate, persistent or caducous, triangular. *Inflorescences* axillary open cymes; flowers monomorphic, protogynous, 4–5-merous; corollas funnel-form, aestivation valvate; ovules numerous and horizontal on axile placentas. *Fruits* capsular, septicidally and basipetally dehiscent, woody; seeds angled.

Chimarrhis is a genus of about 14 species found in the Antilles and from Costa Rica to central South America; two occur in Costa Rica. The trees frequently have well-developed buttresses, and hard yellow wood that is valued for lumber.

1. *Chimarrhis parviflora* Standley

Puberulent to glabrescent trees to 25 m tall. *Leaf* blades elliptic, 8–18 cm long, 3–7 cm wide, acute to acuminate at apex, acute at base, chartaceous; secondary veins 5–10 pairs, without domatia; petioles 5–15 mm long; stipules caducous, triangular, 5–10 mm long, acute. *Inflorescences* densely many-flowered; cymes pyramidal to rounded, 2–3.5 cm long, 3.5–6 cm wide, puberulent; peduncles 2–5 cm long; bracts triangular, to 0.5 mm long but usually lacking or caducous; pedicels 0.5–1 mm long; calyx limb green, to 0.5 mm long, shallowly lobed, lobes broadly triangular, to 0.2 mm long, acute to rounded; corolla white, glabrous externally, barbate in throat, tube stout, 1.5–2 mm long, lobes ligulate, 1.5–2 mm long, rounded. *Fruits* obconic, 1–2.5 mm long; seeds ca. 1 mm long, reticulate. At La Selva collected in flower in May, in fruit in September. Costa Rica and Panama, in wet forest at 30–900 m. FIGURE 4q.

This species is known only from a few individuals in swampy areas and stream edges in the primary forest. Smooth ellipsoid or globose galls 3–5 mm long are frequently found in the infructescences of this species, and may be mistaken for capsules.

5. *CHIONE* de Candolle

Erect shrubs or small trees. *Leaves* sometimes with domatia; stipules interpetiolarly connate, caducous, triangular. *Inflorescences* terminal, open cymose to corymbose; *flowers* apparently monomorphic, 5–6-merous; corollas funnelliform to salverform, aestivation imbricate; ovules solitary, pendulous from apex. *Fruit* drupaceous, fleshy; pyrene solitary, ridged, two-celled; seeds ellipsoid.

Chione includes about 10–15 species in southern Mexico, Central America, and the Greater Antilles. One variable species is known from Costa Rica.

1. *Chione sylvicola* (Standley) W. C. Burger (=*Chione costaricensis* Standley; *Chione allenii* L. O. Williams)

Glabrescent shrubs or small trees to 15 m tall. *Leaf* blades elliptic to ovate, 7–18 cm long, 4.5–8.5 cm wide, acute to acuminate at apex, cuneate to truncate at base, chartaceous; secondary veins 4–9 pairs, with domatia; petioles 5–20 mm long;

stipules 3–8 mm long. *Inflorescences* with cymes 2–5 cm long, 3–8 cm broad; peduncles 1.5–4 cm long; pedicels 2–10 mm long; calyx limb green, divided to base, lobes to 0.5 mm long, broadly rounded to angled or sometimes slightly emarginate; corolla white, glabrous, tube ca. 5 mm long, lobes 2–3 mm long, broadly rounded. *Fruits* ellipsoid to fusiform, usually somewhat curved, 18–22 mm long, becoming red then purple-black. At La Selva collected in flower February–April and September, in fruit April–May and August–September. Southern Nicaragua to Panama in wet forests of Caribbean and Pacific slopes at 0–2,000 m. FIGURE 4f.

This species is locally common in low areas and along streams in primary forest, particularly along the upper Quebrada El Salto.

6. *COCCOCYPSELUM* P. Browne

Creeping herbs. *Leaves* without domatia; stipules interpetiolarly connate, persistent, truncate with one subulate central lobe and 2–8 smaller lateral lobes. *Inflorescences* terminal or pseudoaxillary, capitulate; *flowers* 4-merous, monomorphic or distylous; corollas funnelliform, aestivation valvate; ovules numerous and horizontal on axile placentas. *Fruits* baccate, fleshy to rather dry, hollow, bright blue; seeds angled or flattened.

Coccocypselum includes about 10–20 species found from Mexico through South America, four known from Costa Rica.

1. *Coccocypselum herbaceum* P. Browne (=*Coccocypselum hispidulum* Standley; *Coccocypselum repens* Swartz, but not Humboldt, Bonpland, & Kunth)

Prostrate or trailing, sparsely pilose to glabrescent herbs. *Leaf* blades ovate, 2–5.5 cm long, 1.5–3.5 cm wide, acute at apex, obtuse to truncate and often attenuate at base, membranaceous; secondary veins 5–8 pairs; petioles 5–15 mm long; stipule sheath to 0.2 mm long, subulate central lobe 3–4 mm long, lateral lobes 2–4, 0.5–1 mm long, acute. *Inflorescences* pseudoaxillary and terminal; capitulae ca. 1 cm in diameter; peduncles 0–8 mm long; *flowers* ca. 3–6, sessile, monomorphic; calyx pilose, limb green, divided to base, lobes linear, 4 mm long, acute; corolla dark blue to purple, glabrous, tube 6–8 mm long, lobes triangular, 1–2 mm long, acute. *Fruits* globose to ellipsoid, ca. 1 cm in diameter; seeds orbicular to angled, 0.5–1 mm in diameter, flattened, smooth. At La Selva collected in flower and in fruit concurrently March, May, July, and December. Greater Antilles and Central America, in cool montane areas in the

Greater Antilles but hot lowland forests and *Manicaria* swamps in Central America.

FIGURE 1f.

These herbs are local in secondary forest. The bright blue corollas and fruits are distinctive.

7. COFFEA Linnaeus

PURSEGLOVE, J. W. 1984. Tropical crops: dicotyledons, Vol. II. Longman Group, Ltd., Harlow, Essex, England. 719 pp.

STANDLEY, P. A. AND L. O. WILLIAMS. 1972. *Coffea*. In Flora of Guatemala. Fieldiana Bot 9: 44-48.

Erect shrubs or small trees. *Leaves* opposite or verticillate, decussate to somewhat distichous, sometimes with domatia; stipules interpetiolarly connate, persistent, triangular. *Inflorescences* axillary, glomerulate; *flowers* monomorphic, 4-8-merous; corollas salverform to funnellform, aestivation convolute; ovules solitary, axile. *Fruits* drupaceous, fleshy; pyrenes two, planoconvex, grooved on inner face; seeds ellipsoid.

Coffea includes about 90 species native to the tropics of Africa, Madagascar, and the Mascarenes. Several species and hybrids are widely cultivated throughout the tropics of both hemispheres for their seeds, which are roasted and brewed to make coffee. *Coffea arabica* is also grown in Costa Rica, and is the preferred coffee bean.

1. *Coffea liberica* Hiern

Glabrescent shrubs or small trees to 4 m tall. *Leaves* opposite, decussate; blades elliptic to elliptic-oblong, 12-25 cm long, 5-10 cm wide, acuminate at apex, cuneate at base, chartaceous to subcoriaceous; secondary veins 7-10 pairs on each side, sometimes with domatia; petioles 1-1.5 cm long; stipules 4-6 mm long, acute. *Inflorescences* ca. 2-5 cm in diameter; bracts narrowly elliptic to lanceolate, 3-8 mm long, acute; *flowers* ca. 5-10, 5-merous; calyx limb green, divided to base, lobes triangular, to 0.5 mm long, acute to rounded; corolla white, funnellform, tube 5-8 mm long, lobes ligulate, 1-2 cm long, acute. *Fruits* ellipsoid to ovoid, 1-1.5 cm long, red. At La Selva collected in flower in March, in fruit in August. Native to west Africa but cultivated throughout the tropics at low elevations.

FIGURE 4b; Purseglove, 1984: fig. 75.

"Liberica" coffee persists in secondary forest near the end of the West River Road, where it was once cultivated.

8. COSMIBUENA Ruiz López & Pavón

Erect terrestrial or usually epiphytic shrubs or small trees. *Leaves* without domatia; stipules in-

terpetiolarly and partially intrapetiolarly connate, caducous, obovate. *Inflorescences* terminal few-flowered cymes or rarely solitary flowers; flowers monomorphic, 5-6-merous; corolla salverform, white becoming yellow when old, aestivation imbricate with 3-4 lobes external; ovules numerous and vertical on axile placentas. *Fruits* capsular, septicidally and basipetally dehiscent, woody; seeds flattened, fusiform, with a membranaceous marginal wing.

Cosmibuena comprises four species found from Mexico to central South America; three are known from Costa Rica. Two other epiphytic species of Rubiaceae are known from the La Selva station, in *Psychotria* and in *Hillia*.

1. *Cosmibuena macrocarpa* (Benth) Klotzsch (= *Cosmibuena skinneri* auctt.)

Glabrous shrubs or small trees to 10 m tall. *Leaf* blades obovate, 7-17 cm long, 4-8.5 cm wide, rounded at apex, cuneate to acute at base, coriaceous; secondary veins 4-5 pairs, obscure; petioles 8-10 mm long; stipules 15-20 mm long, somewhat stipitate, rounded. *Inflorescences* with peduncles 5-15 mm long; bracts caducous; pedicels 1-2 cm long; *flowers* ca. 3-8, 5-merous; calyx glabrous, limb green, 4-10 mm long, partially lobed, lobes 2-4 mm long, acute; corolla glabrous, tube 5-8 cm long, lobes elliptic to ligulate, 25-30 mm long, rounded. *Fruits* cylindrical, 7-8 cm long, 7-8 mm in diameter, brown; seeds 7-9 mm long, sparsely fimbriate or erose. At La Selva collected in fruit in August. Nicaragua to Panama at 0-500 m elevation; elsewhere known to flower from July to September. FIGURE 6c;

Dwyer, 1980: fig. 27; Croat, 1974: fig. 518.

This species is known only from a few individuals in the swamp forest along the Holdridge Trail. It is most frequently an epiphyte but may also be terrestrial, particularly in saturated soils.

9. COUSSAREA Aublet

Hermaphroditic or rarely dioecious erect shrubs or trees. *Leaves* opposite or verticillate, sometimes with domatia; stipules interpetiolarly and sometimes also intrapetiolarly connate, persistent or caducous, the interpetiolar portion triangular or bilobed. *Inflorescences* terminal or sometimes axillary, open cymose to capitatae, paniculate to umbelliform; *flowers* hermaphroditic or rarely unisexual, monomorphic or distylous, 4-5-merous; corollas salverform or tubular, aestivation valvate; ovary unilocular or incompletely to completely bilocular; ovules two or one by abortion or fusion, erect, basal. *Fruits* drupaceous, fleshy, becoming blue-black or white; pyrenes 1-2, smooth; seeds ellipsoid.

Coussarea includes about 100 poorly known species found from Mexico throughout moist Central America, the Greater Antilles, and South America. About ten species are known from Costa Rica. This genus is similar to *Psychotria*, which can be separated by its pyrenes with hard-ridged walls, in contrast to thin, smooth walls in *Coussarea*; to *Faramea*, which can be recognized by its leathery fruits, in contrast to succulent in *Coussarea*, and its leaves held in a distichous rather than decussate attitude; and to *Rudgea*, which can be recognized by its pectinate stipules.

KEY TO THE SPECIES

1. Petioles 1–2 mm long; secondary veins barbate in axils on lower surface. 2. *C. impetiolearis*.
1. Petioles 10–20 mm long; secondary veins with axils not barbate.
 2. Stipules 8–12 mm long; leaves 5–14 cm wide.
 3. Inflorescences racemiform (i.e., cylindrical); stipules interpetiolarly and intrapetiolarly connate, caducous; corolla tube ca. 5 mm long. 5. *C. talamancana*.
 3. Inflorescences corymbiform (i.e., rounded to pyramidal); stipules interpetiolarly connate, persistent; corolla tube 15–20 mm long. 1. *C. hondensis*.
 2. Stipules 0.5–2 mm long; leaves 2.5–6 cm wide.
 4. Stipules 1.5–2 mm long, persistent; plants puberulent, drying black; corolla tubes 22–24 mm long. 3. *C. nigrescens*.
 4. Stipules 0.5–1 mm long; plants glabrescent, usually drying grey or green; corolla tubes 12–15 mm long. 4. *C. psychotrioides*.

1. ***Coussarea hondensis*** (Standley) C. M. Taylor & W. Burger
(=*Psychotria hondensis* Standley; *Psychotria ostaurea* Dwyer & Hayden)

Puberulent shrubs or understory trees to 10 m tall. *Leaves* opposite; blades broadly elliptic to obovate, 15–25 cm long, 9–14 cm wide, acute to acuminate at apex, cuneate at base, chartaceous; secondary veins 7–10 pairs, without domatia; petioles 1–2 cm long, puberulent; stipules interpetiolarly connate, persistent at least on uppermost nodes, triangular, 8–12 mm long, emarginate to bidentate, the teeth to 2 mm long. *Inflorescences* terminal, puberulent; cymes corymbiform, 4–8 cm long, 8–15 cm wide; peduncles 3–9 cm long; bracts triangular, 0.5–2 mm long; *flowers* hermaphroditic, distylous, 4-merous; calyx puberulent, limb green, 1.5–2 mm long, shallowly lobed, lobes obtusely angled; corolla salverform, white, minutely puberulent externally, glabrous internally, tube 15–20 mm long, lobes narrowly triangular to ligulate, 8–12 mm long, acute. *Fruits* globose to obovoid, 12 mm

long, smooth, purple-black; pyrenes two, planoconvex, smooth with a median ventral sulcus. At La Selva collected in flower August–September, in fruit in December. Widespread in Costa Rica, in moist and wet lowland forest to 1,000 m elevation. FIGURE 5b.

This species is occasional in low areas in primary forest.

2. *Coussarea impetiolearis* J. Donnell Smith

Glabrescent understory trees to 15 m tall. *Leaves* opposite; blades elliptic to oblanceolate, 8–15 cm long, 3–6 cm wide, acute to acuminate at apex, truncate to auriculate at base, chartaceous; secondary veins 4–7 pairs, sometimes barbate in axils; petioles 1–2 mm long; stipules interpetiolarly connate, caducous, triangular, 1.5–2 mm long, acute to mucronate. *Inflorescences* terminal, open; cymes pyramidal, 2.5–3 cm long, 5–7 cm wide; peduncles 1–2 cm long; *flowers* subsessile in glomerules of 2–3, hermaphroditic, apparently monomorphic, 4-merous; calyx densely puberulent to glabrescent, limb green, truncate to shallowly lobed, 2–3 mm long; corolla salverform, white, densely puberulent externally, glabrous internally, tube 13–14 mm long, lobes narrowly triangular to ligulate, 6–8 mm long, acute. *Fruits* ellipsoid, 15–20 mm long, 14–15 mm in diameter, flattened, spongy, lenticellate; pyrene solitary, ellipsoid, flattened, smooth. At La Selva collected in flower in May, in fruit in January, June, and August. Costa Rica and Panama, in wet Caribbean lowlands and on the Osa Peninsula at 0–500 m. FIGURE 3w.

This species is occasional in forest understory.

3. *Coussarea nigrescens* C. M. Taylor & Hammel

Puberulent trees to 7 m tall. *Leaves* opposite; blades elliptic, 8–20.5 cm long, 3.5–9 cm wide, acute to slightly acuminate at apex, cuneate at base, thinly chartaceous; secondary veins 9–11 pairs, without domatia; petioles 10–35 mm long; stipules interpetiolarly and intrapetiolarly connate, persistent, broadly triangular, 1.5–2 mm long, broadly and shallowly bilobed. *Inflorescences* terminal; cymes rounded to pyramidal, 1–2 cm long; peduncles ca. 2 cm long; bracts triangular to ovate, 1–3 mm long, caducous; *flowers* sessile in glomerules of 3–7, hermaphroditic, 5-merous; calyx minutely puberulent, limb green, ca. 0.5 mm long, shallowly lobed; corolla salverform, white, glabrous, tube 22–24 mm long, lobes ligulate, 6–8 mm long. *Fruits* globose to ellipsoid, ca. 1 cm in diameter, black; pyrenes 1–2. At La Selva collected in flower in November. Wet forests of Caribbean lowlands

and the Osa Peninsula region of Costa Rica at 20–850 m.

FIGURE 3k; Taylor et al., 1991: fig. 1.

This species is known from along the Holdridge Trail just north of the Quebrada Esquina.

4. *Coussarea psychotrioides* C. M. Taylor & Hammel

Glabrescent understory trees to 12 m tall. *Leaves* opposite; blades elliptic, 8–18 cm long, 2.5–6.5 cm wide, acute to slightly acuminate at apex, cuneate at base, chartaceous; secondary veins 7–9 pairs, without domatia; petioles 1–2 cm long; stipules interpetiolarly and intrapetiolarly connate, caducous, truncate to slightly bilobed, 0.5–1 mm long. *Inflorescences* terminal; cymes rounded to pyramidal, 3–7 cm long, 5–8 cm wide; peduncles 1–3 cm long; bracts triangular, 0.5–3 mm long; *flowers* subsessile in glomerules of 3–7, hermaphroditic, 5-merous, distylous; calyx glabrous, limb green, 0.3 mm long, subtruncate, mucronate; corolla salverform to somewhat funnellform, white or often tinged with rose, glabrous, tube often curved, 12–15 mm long, lobes ligulate, 10–12 mm long. *Fruits* ellipsoid, 1.5–2 cm long, 12–13 mm in diameter, smooth, purple-black; pyrenes 1–2, ellipsoid to planoconvex, smooth or with a slight groove on the inner face. At La Selva collected in flower June–July, in fruit September–October and in December. In wet lowland forest of the Caribbean slopes of Costa Rica, to about 1,000 m. FIGURE 31;

Taylor et al., 1991: fig. 2.

This species is occasional in low areas in the primary forest. The crushed leaves reportedly have a slight fragrance of wintergreen. This species strongly resembles *Psychotria eurycarpa* Standley; the latter species can be distinguished by its more densely flowered inflorescences, shorter corolla lobes, shiny usually broader leaves, persistent longer stipules, pyrenes that are angled with a well-marked groove, and March–April flowering period. The reproductive biology of *Coussarea psychotrioides* was studied by Bawa and Beach (1983), as “*Coussarea* sp. voucher #JHB 1467.”

5. *Coussarea talamancana* Standley

Diocious glabrescent shrubs or small trees to 4 m tall. *Leaves* opposite; blades broadly elliptic to obovate, 12–20 cm long, 5–13 cm wide, acuminate and usually abruptly so at apex, acute to cuneate at base, chartaceous; secondary veins 7–10 pairs, without domatia; petioles 5–10 mm long; stipules interpetiolarly and intrapetiolarly connate, caducous, ligulate to broadly triangular, 8–10 mm long, rounded to shortly acuminate. *Inflorescences* terminal; cymes racemiform, cy-

lindrical, 4–8 cm long, 3–5 cm wide; peduncles 5–13 mm long; involucre bracts (or stipules) 15 mm long, sheathing, splitting along one side, floral bracts minute or lacking; pedicels 1–3 mm long; *flowers* unisexual, 4-merous; calyx glabrous, limb green, truncate to shallowly lobed, ca. 2 mm long; corolla salverform, white, glabrous, tube ca. 5 mm long, lobes lanceolate, ca. 4 mm long, acute. *Fruits* obovoid to globose, 1.5–2 cm long, somewhat flattened, spongy, smooth, becoming white; pyrene solitary, ellipsoid, smooth. At La Selva collected in flower May–July, in fruit in February, April, and July–August. Widespread in Costa Rica in moist and wet lowland forest to 700 m elevation. FIGURE 5m.

This species is common in low areas throughout the primary forest at La Selva.

10. *COUTAREA* Aublet

Erect shrubs or trees. *Leaves* decussate to somewhat distichous, sometimes with domatia; stipules persistent, interpetiolarly connate, triangular. *Inflorescences* terminal or sometimes pseudoaxillary, cymose or a solitary flower; *flowers* monomorphic, 5–6(8)-merous; corollas funnellform to campanulate, curved, somewhat zygomorphic, greenish-white to pink, aestivation imbricate; stamens held asymmetrically; ovules numerous and vertical on axile placentas. *Fruits* capsular, septically and basipetally dehiscent, woody; seeds flattened, winged.

Coutarea includes about half a dozen species found from Mexico to southern Brazil and Argentina; one is found in Central America and Mexico.

1. *Coutarea hexandra* (Jacquin) K. Schumann

Puberulent to glabrescent shrubs or small trees to 18 m tall. *Leaf* blades elliptic to ovate, 5–12 cm long, 2.5–6 cm wide, acute at apex, cuneate to truncate at base, membranaceous; secondary veins 6–10 pairs, barbate in axils; petioles 5–10 mm long; stipules 1–3 mm long, acute. *Inflorescences* with peduncles 3–30 mm long; bracts narrowly triangular to linear, 1–5 mm long, acute; pedicels 2–5 mm long; *flowers* (1)3–9, 6-merous; calyx puberulent, limb green, divided to base, lobes narrowly triangular, 6–7 mm long, acuminate; corolla glabrous, tube 45–60 mm long, lobes 15–20 mm long, acute. *Fruits* ellipsoid to ovoid, 30–35 mm long, 20–25 mm wide, laterally compressed, lenticellate; seeds oblong, ca. 1 cm long, 6–7 mm wide, brown. At La Selva collected in flower in August. Mexico to Argentina, more common in dry deciduous forests but also in moist and wet areas at 0–700 m. FIGURE 4e;

Croat, 1978: fig. 519; Haber & Frankie, 1989: fig. 3b.

This rare species is known only from one individual along the Southwest Trail. The floral biology is discussed by Haber and Frankie (1989).

11. FARAMEA Aublet

Erect shrubs or small trees. *Leaves* decussate but distichous in attitude, without domatia, frequently with strongly marked submarginal veins; stipules connate interpetiolarly and sometimes also intrapetiolarly, persistent or caducous, triangular to ovate, usually with a terminal awn. *Inflorescences* terminal or rarely axillary, open to congested, pyramidal to rounded or rarely a solitary flower; *flowers* monomorphic or distylous, 4(–5)-merous; corollas funnelform to salverform, aestivation valvate; ovary unilocular or partially to completely bilocular; ovules two or one by abortion or fusion, erect, basal. *Fruits* drupaceous, leathery, dull to usually bright blue; pyrenes 1(–2), globose to oblate, smooth.

Faramea includes about 120–130 species found throughout the moist and wet neotropics, about fifteen in Costa Rica. This genus is similar to *Coussarea*, and can be difficult to separate from it; the distinctions between them are summarized in the discussion of *Coussarea*. The flowers and fruits of *Faramea* are frequently bright distinctive cobalt blue.

KEY TO THE SPECIES

1. Stipules caducous.
 2. Inflorescences fasciculate to umbellate but sessile, bracts subtending flowers 10–12 mm long, ovate, white; corollas white; leaves glossy above. 2. *F. parvibractea*.
 2. Inflorescences pedunculate, paniculate; bracts subtending flowers to 0.5 mm long, triangular, green or blue; corollas blue; leaves dull above. 3. *F. stenura*.
1. Stipules persistent at least on uppermost 3–4 nodes.
 3. Submarginal veins strongly marked, straight; leaves stiffly chartaceous to subcoriaceous. 4. *F. suerrensis*.
 3. Submarginal veins not well marked, looping; leaves chartaceous. 1. *F. multiflora*.

1. *Faramea multiflora* A. Richard (=*Faramea talamancarum* Standley)

Glabrous shrubs to 4 m tall. *Leaf* blades elliptic to oblong, 6–15 cm long, 2–7 cm wide, slenderly acuminate at apex, acute to cuneate at base, chartaceous; secondary veins 6–12 pairs, submarginal veins looping ca. 2–5 mm from margins, obscure; petioles 5–10 mm long; stipules connate interpetiolarly and intrapetiolarly, persistent, 6–10 mm long, awned. *Inflorescences* terminal; cymes open, rounded, corymbiform, 3–6

cm long, 4–9 cm wide, bright blue; peduncles 1–6.5 cm long; pedicels 4–10 mm long; *flowers* 4-merous; calyx limb blue to green, divided to base, lobes broadly triangular, to 1 mm long, acuminate; corolla salverform, bright blue, glabrous, tube slender, 8–10 mm long, lobes ovate, 4–9 mm long, acute. *Fruits* oblate, 5–6 mm long, 8–12 mm wide, laterally compressed, smooth; pyrenes solitary. At La Selva collected in flower April–June and August, in fruit June–July. Costa Rica and Panama, in wet forests at 0–1,500 m.

FIGURE 40.

This tree is common in primary forest, particularly on ridges along the Southwest Trail.

2. *Faramea parvibractea* Steyermark

Glabrous understory trees to 10 (20) m tall. *Leaf* blades elliptic to elliptic-oblong, 9–16 cm long, 2.5–5.5 cm wide, acuminate at apex, cuneate at base, chartaceous; secondary veins 6–10 pairs, submarginal veins looping ca. 3–5 mm from margins, obscure; petioles 5–10 mm long; stipules interpetiolarly and intrapetiolarly connate, caducous, 12–15 mm long, acute. *Inflorescences* terminal, fasciculate to sessile; cymes umbellate, 2.5–4 cm long, 5–6 cm wide, white; branches (rays) ca. 3–15, 1–3 cm long, each bearing glomerules of 1–3 flowers enclosed by 2 bracts; bracts caducous, white, ovate, 10–12 mm long, acuminate, stipitate; pedicels 1–3 mm long; *flowers* 4-merous; calyx limb pale green, ca. 0.5 mm long, truncate to broadly lobed; corolla funnelform, white, glabrous, tube 5–7 mm long, lobes lanceolate to triangular, 6–7 mm long, acute. *Fruits* oblate, ca. 5 mm long, 8–12 mm wide, smooth; pyrene solitary. At La Selva collected in flower February–June, in fruit in February, July, and August. Costa Rica and southern Venezuela in wet forests at 0–300 m. FIGURE 4j.

This species is occasional throughout the primary forest, but more common near the southern end of the property. The crushed leaves reportedly have an almond fragrance.

3. *Faramea stenura* Standley

Glabrous shrubs or trees to 7 m tall. *Leaf* blades elliptic to oblong, 9–15 cm long, 2.5–4 cm wide, slenderly acuminate at apex, acute to cuneate at base, chartaceous; secondary veins 8–12 pairs, submarginal veins looping ca. 2–10 mm from margins, obscure; petioles 5–10 mm long; stipules connate interpetiolarly and intrapetiolarly, caducous, 6–10 mm long, awned. *Inflorescences* terminal; cymes open, pyramidal, 3–5.5 cm long, 4–7 cm wide, bright blue; peduncles 1.5–5 cm long; bracts triangular, to 0.5 mm long or those subtending primary branches some-

times with expanded blades; pedicels 2–4 mm long; *flowers* 4-merous; calyx limb green to blue, subtruncate to lobed, ca. 0.5 mm long; corolla salverform, pale to deep blue, glabrous, tube ca. 6 mm long, lobes elliptic to ovate, ca. 4 mm long, acute. *Fruits* oblate, 5–8 mm long, 12–15 mm wide, laterally compressed, smooth; pyrenes solitary. At La Selva collected in flower March–April, in fruit June–August. Honduras to eastern Panama in wet forests of Caribbean slopes at 20–600 m. FIGURE 5h.

These trees are occasional in low areas, particularly on alluvial soils in the northeastern part of the property.

4. *Faramea suerrensii* J. Donnell Smith

Glabrous shrubs to 4 m tall. *Leaf* blades elliptic to oblong, 10–25 cm long, 4–9 cm wide, slenderly acuminate at apex, cuneate to rounded at base, stiffly chartaceous to subcoriaceous; secondary veins 8–16 pairs, submarginal veins ca. 4–10 mm from margins, straight, sulcate, well-marked; petioles stout, 5–15 mm long; stipules connate interpetiolarly and intrapetiolarly, persistent or with the uppermost portion breaking off, 5–10 mm long, obtuse, mucronate. *Inflorescences* terminal; cymes open, rounded, corymbiform, 5–10 cm long, 8–15 cm wide, bright blue to purple; peduncles 3–7 cm long; pedicels 2–7 mm long; *flowers* 4-merous, distylous; calyx limb blue to green, divided to base, lobes triangular, to 0.5 mm long, acute; corolla salverform, deep bright blue, glabrous, tube slender, 7–9 mm long, lobes elliptic to ovate, 3–5 mm long, acute. *Fruits* oblate, 8–10 mm long, 12–15 mm wide, laterally compressed, sometimes glaucous, smooth; pyrenes solitary. At La Selva collected in flower February–March, May–August, and in November, in fruit January–March and in November. Southern Nicaragua to Colombia in wet forests at 0–1,000 m. FIGURE 4l.

This species is occasional in primary forest. Its breeding biology was studied by Bawa and Beach (1983).

12. *Ferdinandusa* Pohl

Erect shrubs or trees. *Leaves* opposite or verticillate, decussate or distichous, without domatia; stipules connate interpetiolarly, caducous, triangular. *Inflorescences* terminal, open cymose; flowers monomorphic, 4–5-merous, frequently somewhat zygomorphic; corollas funnelform to salverform, aestivation imbricate; ovules numerous and vertical, attached peltately to axile placentas. *Fruits* capsular, septicidally and basipetally dehiscent, woody; seeds flattened, winged.

Ferdinandusa includes about 20–25 species found from Costa Rica to Brazil, most in Brazil; one species is known from Costa Rica and Panama.

1. *Ferdinandusa panamensis* Standley & L. O. Williams

Pilosulous to glabrescent trees to 20 m tall. *Leaves* opposite or sometimes 3 per node, decussate; blades elliptic, 7.5–17 cm long, 4–7.5 cm wide, acuminate at apex, rounded to slightly cordate at base, chartaceous; secondary veins 6–9 pairs; petioles 5–8 mm long; stipules triangular, ca. 20 mm long, acute to acuminate. *Inflorescences* with cymes pyramidal to rounded and sometimes three-parted, 6–15 cm long, 8–22 cm wide; peduncles 2–5 cm long; pedicels 5–10 mm long; *flowers* 5-merous; calyx glabrous, limb green, divided to base, lobes triangular, to 1 mm long, acute; corolla funnelform, yellowish green to white, glabrous, tube 18–25 mm long, swollen at base, lobes 5–6 mm long, rounded. *Fruits* cylindrical, 4–6.5 cm long, 5–10 mm in diameter; seeds elliptic, 1–2 cm long. At La Selva collected in flower March–April, in fruit March–April and June–July. Costa Rica and Panama in wet forests of Caribbean lowlands at 0–200 m. FIGURE 5i.

This species is known from ridgetops in the southern corner and from along the Southwest, Holdridge, and Lost Passage Trails. The branches are reported to be drooping and bare except for leaf apices. The wood is very hard, and saplings are sought locally for boat poles.

13. *Genipa* Linnaeus

Hermaphroditic or sometimes monoecious or dioecious erect trees. *Leaves* without domatia; stipules interpetiolarly and sometimes also intrapetiolarly connate, persistent or deciduous, triangular. *Inflorescences* terminal or axillary, cymose or a solitary flower; flowers hermaphroditic or unisexual, monomorphic, 5–6-merous; corollas salverform to funnelform, aestivation convolute; ovules numerous and horizontal on parietal placentas. *Fruits* baccate, fleshy, grey to yellow-brown, with pericarp thick; seeds flattened, smooth.

Genipa includes about 5–10 species found from southern Florida, Mexico, and the West Indies through South America, with two in Costa Rica.

1. *Genipa americana* Linnaeus

Glabrescent trees to 25 m tall. *Leaf* blades elliptic to oblanceolate, 10–36 cm long, 4–15 cm wide, acute to acuminate at apex, acute at base, subcoriaceous; secondary veins 9–18 pairs; pet-

ioles 5–10 mm long; stipules connate interpetiolarly, deciduous, 12–15 mm long, acute to acuminate. *Inflorescences* terminal; cymes to 10 cm long and wide; peduncles 5–20 mm long; bracts caducous, triangular, 3–5 mm long, acute; pedicels 5–10 mm long; *flowers* 1–7, morphologically hermaphroditic but apparently functionally unisexual, 5–6-merous; calyx glabrescent externally, sericeous to pilosulous internally, limb green, 6–10 mm long, truncate to slightly lobed; corolla white turning yellow with age, thickly carinose, densely appressed-sericeous externally, densely pilose to villose internally, tube 10–15 mm long, lobes ovate to obovate, 10–28 mm long, rounded. *Fruits* globose to ellipsoid or obovoid, 4–11 cm long, 5–11 cm in diameter, smooth or lenticellate; seeds elliptic to ovate, flattened, 6–12 mm long, 4–7 mm wide, smooth. At La Selva collected in flower April–August. Florida, Mexico, and the West Indies to Paraguay, in wet and seasonally dry forest at 0–900 m; fruits are produced by most trees during most of the year. FIGURE 5c; Croat, 1978: fig. 520.

This species is rare at La Selva, where it is known only from a few individuals in low areas in the northeastern part of the property. The sap turns blue when exposed to air, and is used as a dye or body paint in many regions. Dried specimens frequently have a blue-black cast. The fruits are edible, and thought to have medicinal properties in some areas; this tree is widely though not intensively cultivated throughout the tropics. The typical variety is represented by the collections from La Selva; var. *caruto* (Humboldt, Bonpland, & Kunth) K. Schumann is also known from Costa Rica and sporadically throughout most of the range of this species. This variety can be recognized by its densely pilose lower leaf surfaces; it is of questionable taxonomic significance.

14. GEOPHILA D. Don

WILLIAMS, L. O. 1973. *Geophila* (Rubiaceae) in North America. *Phytologia* 26: 263.

Creeping herbs. *Leaves* without domatia; stipules interpetiolarly connate, persistent or caducous, triangular to ovate. *Inflorescences* terminal or pseudoaxillary, capitulate, the subtending bracts usually fused; flowers monomorphic or distylous, 4–7-merous; corollas funnelliform to salverform, aestivation valvate; ovules solitary, basal. *Fruits* drupaceous, fleshy; pyrenes 2, planoconvex, twisted, ribbed or smooth dorsally, with a ventral groove.

Geophila includes about 30 species in both the New and Old World tropics, most in the Old World; four occur in Costa Rica.

KEY TO THE SPECIES

1. Plants pilose. 1. *G. cordifolia*.
1. Plants glabrescent or puberulent, the petioles sometimes with ciliate lines.
 2. Mature fruit dark blue to black; leaf blades 2.5–6 cm long, 2–5.5 cm wide, the basal lobes not touching or overlapping; peduncles borne on leafless erect stems or directly on the primary creeping stem. 2. *G. macropoda*.
 2. Mature fruit orange or red; leaf blades 1–3 cm long, 1–2.3 cm wide, the basal lobes touching or overlapping; peduncles borne on leafy erect stems. 3. *G. repens*.

1. *Geophila cordifolia* Miquel

Plants pilose with trichomes to 2 mm long. *Leaf* blades ovate, 2.5–7 cm long, 1.5–5.5 cm wide, acute at apex, cordate at base with sinus 3–15 mm deep, chartaceous to membranaceous; secondary veins 3–5 pairs; petioles 1–13 cm long, sometimes with ciliate lines; stipules persistent, 2–4 mm long, angled to rounded. *Inflorescences* with capitulae 1–3 cm in diameter; peduncles 5–50 mm long; bracts linear, 3–10 mm long, acute; *flowers* 5–15, 5-merous; calyx limb green, divided to base, lobes 3 mm long, acute; corolla funnelliform, white, glabrous externally, barbate in throat, tube 2–4.5 mm long, lobes triangular, 1.5–2.5 mm long, acute. *Fruits* ellipsoid, ca. 8 mm long, 3–4 mm in diameter, orange to red; pyrenes ellipsoid, ribbed. At La Selva collected in flower and fruit February–May and July–October. Belize and Guatemala to Amazonian Brazil and eastern Peru; in Costa Rica in wet forests of Caribbean slopes at 0–500 m. FIGURE 3p.

This species is common along trails, particularly the Far Loop and South Boundary Trails.

2. *Geophila macropoda* (Ruiz López & Pavón) de Candolle

Plants glabrescent. *Leaf* blades broadly ovate, 2.5–6 cm long, 2–5.5 cm wide, acute at apex, cordate at base with sinus 2–15 mm deep, membranaceous to chartaceous; secondary veins 3–5 pairs; petioles 2–10 cm long, usually with ciliate lines; stipules caducous, 5–6 mm long. *Inflorescences* with capitulae 2–4 cm in diameter; peduncles 2–7.5 cm long; bracts narrowly triangular, 3–5 mm long, acute; *flowers* 3–7, 5-merous; calyx limb green, divided to base, lobes 2–3 mm long, acute; corolla white, funnelliform, glabrous externally, barbate in throat, tube ca. 3 mm long, lobes triangular, ca. 3 mm long, acute. *Fruits* ellipsoid to ovoid, ca. 5 mm long, ca. 3 mm in diameter, blue-black; pyrenes ellipsoid, smooth. At La Selva collected in flower and fruit April and June–September. Southern Mexico to Ar-

gentina; in Costa Rica in wet forests of Caribbean slopes at 0–500 m. FIGURE 3q.

This species is known only from along the West River Road.

3. *Geophila repens* (Linnaeus) I. M. Johnston
[=*Geophila herbacea* (Jacquin) K. Schumann]

Plants glabrescent. *Leaf* blades broadly ovate, 1–3 cm long, 1–2.3 cm wide, acute to rounded at apex, cordate at base with sinus 1–7 mm deep, membranaceous; secondary veins 3–5 pairs; petioles 1–6 cm long, usually with ciliate lines; stipules persistent, ca. 1.5 mm long, usually emarginate. *Inflorescences* with capitulae 1–3 cm in diameter; peduncles 1–3 cm long; bracts narrowly triangular to elliptic, 3–5 mm long, acute; *flowers* ca. 5, 5-merous, monomorphic; calyx limb green, divided to base, lobes ca. 2 mm long, acute; corolla white, funnelliform, glabrous externally, barbate in throat, tube ca. 7 mm long, lobes triangular, 4–5 mm long, acute. *Fruits* ovoid to ellipsoid, 8–10 mm long, 3–4 mm in diameter, orange to red; pyrenes ellipsoid, with 3 longitudinal ridges. At La Selva collected in flower and fruit August–October. Mexico and the West Indies to Paraguay, and in West Africa and islands of the western Pacific; in Costa Rica frequent in wet or moist forests at 0–800 m.

FIGURE 3j; Croat, 1978: fig. 522.

This species is found in clearings and along trails throughout, and is particularly common in the lab clearing. Its breeding biology was investigated by Bawa and Beach (1983).

15. GONZALAGUNIA Ruiz López & Pavón

Duggenia West
Gonzalea Standley

Erect shrubs or trees. *Leaves* distichous, without domatia; stipules interpetiolarly and sometimes also intrapetiolarly connate, persistent, triangular. *Inflorescences* terminal, racemiform with a long central axis bearing contracted lateral cymes; *flowers* monomorphic or distylous, 4–5-merous; corollas funnelliform to salverform, aestivation imbricate; ovary 2–4-locular; ovules numerous and horizontal on axile placentas. *Fruits* drupaceous, dry to fleshy; pyrenes 1–4, each containing several seeds; seeds angled.

Gonzalagunia includes about 25–35 species found throughout tropical America; eight are known from Costa Rica.

1. *Gonzalagunia bracteosa* (J. Donnell Smith) B. L. Robinson

Slender shrubs to 4 m tall, strigose to pilose. *Leaf* blades narrowly elliptic to oblanceolate, 12–

22 cm long, 4–8.5 cm wide, acute to acuminate at apex, cuneate to rounded at base, chartaceous; secondary veins 5–7 pairs; petioles 3–10 mm long; stipules intrapetiolarly and interpetiolarly connate, 19–22 mm long, acute to acuminate. *Inflorescences* with racemiform cymes 6–12 cm long, 1.5–3 cm wide; peduncles 3.5–5 cm long; lateral cymes subsessile, contracted, helicoid, separated; bracts narrowly triangular to ligulate, 2–8 mm long, acute; *flowers* 5-merous, sessile or subsessile; calyx limb green, divided to base, lobes triangular, 0.5–0.8 mm long, acute; corolla funnelliform, white, sericeous externally, barbate in throat, tube ca. 3 mm long, lobes to 1 mm long, acute. *Fruits* globose, 3–5 mm in diameter, blue-black, aerenchymatous; pyrenes 2–4. At La Selva collected in flower June–September, in fruit in March and August. Costa Rica to Colombia in wet forests of Caribbean slopes at 0–850 m.

FIGURE 5g.

This species is occasional in forests, particularly near streams. The plants from the La Selva station and adjacent forests in the area of the Parque Nacional Braulio Carrillo have inflorescences with relatively more developed bracts and branches than plants found further south and east. *Gonzalagunia bracteosa* is similar vegetatively to *Psychotria pilosa*, but that species can be distinguished by its more numerous secondary leaf veins and strong submarginal veins.

Gonzalagunia kallunkiae Dwyer should also be expected; this species can be separated from *G. bracteosa* by its inflorescences 15–30 cm long with linear bracts 1–4 mm long.

16. HAMELIA Jacquin

ELIAS, T. 1976. A monograph of the genus *Hamelia* (Rubiaceae). Mem. N.Y. Bot. Gard. 26: 81–144.

Erect shrubs or small trees. *Leaves* opposite or verticillate, sometimes with domatia; stipules connate interpetiolarly, persistent or caducous, triangular to trilobed. *Inflorescences* terminal, open cymose to frequently dichasial with helicoid branches; flowers monomorphic, 5-merous; corollas tubular to funnelliform, aestivation imbricate; ovary 4–5-locular; ovules numerous on axile placentas. *Fruits* baccate, fleshy; seeds angled.

Hamelia includes about 16 species found from southern Florida and Mexico through the West Indies and Central America to Chile and Argentina; seven are known from Costa Rica. *Hoffmannia* is similar but is separated by its axillary inflorescences.

KEY TO THE SPECIES

1. Corollas tubular, orange to red; inflorescence branches and calyces glabrate to minutely puber-

- ulent; calyx lobes 0.5–1 mm long; stipules 2–6 mm long. 1. *H. patens*.
 1. Corollas funnelform, yellow; inflorescence branches and calyces pilosulous; calyx lobes 1–2 mm long; stipules 6–15 mm long. 2. *H. xerocarpa*.

1. *Hamelia patens* Jacquin

Shrubs or small trees to 7 m tall, glabrous to sparsely pilosulous. *Leaves* (2–)3(–4) per node; blades elliptic to oblanceolate, 5.5–18 cm long, 2.5–8 cm wide, acute to acuminate at apex, acute to rounded at base, membranaceous to chartaceous; secondary veins 7–10 pairs, barbate in axils; petioles 5–40 mm long; stipules caducous, narrowly triangular to subulate, 2–6 mm long. *Inflorescences* with cymes dichasial, 3–10 cm long, 5–20 cm wide, orange to red; peduncles 5–40 mm long; branches helicoid; bracts triangular, to 1 mm long; pedicels to 1 mm long; calyx limb green to red, divided to base, lobes ovate, 0.5–1 mm long, acute; corolla tubular, orange to red, glabrous to villous externally, glabrous internally, tube 15–20 mm long, lobes triangular, 1.5–2.5 mm long, acute. *Fruits* ellipsoid to globose, 7–10 mm in diameter, becoming red then blue-black; seeds 0.5–1 mm long. At La Selva collected in flower and fruit in February, April–September, and November–December. Southern Florida, Mexico, and the West Indies to Argentina, common in secondary growth in wet and deciduous forest at 0–1,500 m. FIGURE 4d.

This species is common. The number of leaves per node apparently varies at least in part with age and vigor of the branch. The fruits are edible. Its breeding biology was studied by Bawa and Beach (1983).

2. *Hamelia xerocarpa* O. Kuntze (=*Hamelia costaricensis* Standley)

Shrubs or small trees to 5 m tall, densely pilosulous with yellow trichomes at least on stem apices, to glabrescent with age. *Leaves* (2–)3(–4) per node; blades ovate to broadly elliptic, 8–25(–37) cm long, 4–14 cm wide, acuminate at apex, acute to rounded at base, membranaceous to chartaceous; secondary veins 9–18 pairs; petioles 1–8.5 cm long; stipules triangular, 7–17 mm long, mucronate, caducous. *Inflorescences* with cymes dichasial, 3–12 cm long, 5–15 cm wide, greenish yellow; peduncles 1.5–5.5 cm long; pedicels 0–2 mm long; calyx limb green, divided to base, lobes 1–2 mm long, acute; corolla funnelform, yellow, glabrescent to pilosulous externally, glabrous internally, tube 2–3 cm long, lobes 4–8 mm long. *Fruits* globose, 11–14 mm in diameter, purple-black; seeds 0.5–1 mm long. At La Selva collected in flower May–August and November, in

fruit June–August and November. Nicaragua to Colombia in wet and deciduous forests of both coasts at 0–800 m. FIGURE 4r.

This species is occasional in primary forest along the Quebrada El Salto and in secondary forest along the Río Puerto Viejo. Its breeding biology was studied by Bawa and Beach (1983).

17. *HEMIDIODIA* K. Schumann

Erect to clambering, sometimes suffrutescent herbs. *Leaves* without domatia; stipules connate interpetiolarly and adnate to petioles, persistent, truncate and setaceous or with 5–15 subulate lobes. *Inflorescences* axillary, glomerulate, subsessile; flowers monomorphic, 4-merous; corollas funnelform, aestivation valvate; ovules solitary, erect, axile. *Fruits* capsular, septicidally and acropetally dehiscent; seeds ellipsoid.

Hemidiodia is monotypic. This genus is sometimes combined with *Diodia* Linnaeus, which differs only in its basipetally dehiscent capsules composed of two indehiscent valves. *Hemidiodia* can also be confused with *Spermacoce*, which differs in its basipetally dehiscent capsules with one or both of the valves then dehiscent.

1. *Hemidiodia ocimifolia* (Willdenow) K. Schumann [=*Diodia ocimifolia* (Willdenow) Bremekamp]

Glabrescent to pilosulous or scaberulous herbs to 1 m tall. *Leaves* sessile or subsessile; blades lanceolate or oblanceolate to narrowly elliptic, 4–10 cm long, 1–2 cm wide, acute at apex, acute to attenuate at base, chartaceous; secondary veins 3–6 pairs; stipules 2–5 mm long with setae 6–10, subulate, 3–8 mm long. *Inflorescences* with glomerules 6–15 mm in diameter; bracts 2–3 mm long; calyx pilosulous, limb green, divided to base, lobes to 0.5 mm long, acute; corolla white, glabrous externally, barbate in throat and often also pilosulous on apices of lobes, tube 2–2.5 mm long, lobes 1–1.5 mm long, acute. *Fruits* ellipsoid to obconic, laterally compressed, papyraceous, 2–3 mm long, 1–2 mm wide; seeds tuberculate with a median longitudinal sulcus. At La Selva collected in flower and fruit March–November. Weedy from central Mexico and the Antilles to Paraguay at 0–1,200 m and reportedly adventive in Malaya. FIGURE 1d.

This species is common in open disturbed areas.

Diodia sarmentosa Swartz may also be expected; it can be separated by its scabrous leaves, corollas with tubes about 1–1.5 mm long, calyx lobes about 2 mm long, and indehiscent capsule valves.

18. **HILLIA** Jacquin*Ravnia* Oersted

TAYLOR, C. M. 1989. Revision of *Hillia* subg. *Ravnia*, subg. nov. (Rubiaceae: Cinchonoideae). *Selbyana* 11: 26–34.

Erect succulent epiphytic shrubs. *Leaves* without domatia; stipules interpetiolarly connate, caducous, ligulate. *Inflorescences* terminal, cymose, with 1–3 flowers; *flowers* monomorphic, 4–6(–9)-merous; corollas tubular or salverform to funnellform or swollen, aestivation convolute; ovules numerous and vertical on axile placentas. *Fruits* capsular, septicidally and basipetally dehiscent, cylindrical, papery; seeds rhombic, flattened, with a marginal wing and a tuft of trichomes at one end.

Hillia includes about 25 species found from southern Mexico through Peru and Brazil; seven are known from Costa Rica. Two other species of epiphytic Rubiaceae are known from the La Selva station, one in *Psychotria* and one in *Cosmibuena*.

1. **Hillia grayumii** C. M. Taylor

Glabrous shrubs to 1 m tall. *Leaf* blades elliptic, 9–16 cm long, 1.5–5 cm wide, acuminate at apex, acute at base, coriaceous; secondary veins 3–4 pairs; petioles 3–20 mm long; stipules ca. 4 cm long, acute. *Flowers* solitary, 6-merous; peduncles 2–3 mm long; bracts 2–3 mm long, acute; pedicels 2–3 mm long; calyx limb green, ca. 0.5 mm long, truncate; corolla funnellform, pale green to yellow, tube 43–50 mm long, lobes triangular, 8–9 mm long, broadly angled to rounded. *Fruits* ca. 10.2 cm long, ca. 8 mm in diameter. At La Selva collected in flower and fruit May–June. In wet forests of Caribbean slopes of Costa Rica at 100–600 m.

FIGURE 6h; Taylor et al., 1991: fig. 3.

This species is known from disturbed forest in the Arboretum and the La Guardia Annex. The plants apparently have a short life span.

19. **HIPPOTIS** Ruiz López & Pavón

Erect shrubs or small trees. *Leaves* without domatia, fine venation lineolate; stipules interpetiolarly connate, caducous, triangular to obovate. *Inflorescences* terminal or pseudoaxillary, capitate to open, cymose or reduced to a single flower; *flowers* monomorphic, 5-merous; calyx bilabiate to spatheaceous (splitting down one side); corollas tubular to funnellform, aestivation valvate with lobes plicate; ovules numerous and horizontal on axile placentas. *Fruits* baccate, fleshy; seeds angled.

Hippotis includes about 10–12 species found from Costa Rica through northern South America; one species occurs in Costa Rica.

1. **Hippotis albiflora** H. Karsten

Pilose trees to 10 m tall. *Leaf* blades elliptic to obovate, 12–35 cm long, 5.5–18 cm wide, acuminate at apex, cuneate at base, chartaceous; secondary veins 7–10 pairs; petioles 1–3.5 cm long; stipules 20–28 mm long, acute to rounded. *Flowers* solitary (–3); peduncles 0–1 cm long; bracts ovate, 3–5 mm long; calyx densely pilose, limb green, 25–35 mm long; corolla pilose to sericeous externally, glabrous internally, white, tube curved, 40–45 mm long, lobes 5–6 mm long, obtuse. *Fruits* ellipsoid, 3–4 cm long, 1–3 cm in diameter, becoming purple; seeds 2 mm long, foveolate. At La Selva collected in flower February, April, July–August, and October, in fruit May–June and August. Costa Rica to Venezuela and Colombia; in Costa Rica in wet forests of Caribbean slopes at 0–200 m. FIGURE 6f.

This species is occasional on steep slopes along streams in primary forest, particularly along the Quebrada Esquina in the southern part of the property. The lineolate fine leaf venation is distinctive.

20. **HOFFMANNIA** Swartz

Erect herbs or shrubs. *Leaves* opposite or verticillate, sometimes with domatia or ant vesicles; stipules interpetiolarly connate, persistent or caducous, triangular or bilobed. *Inflorescences* axillary, open cymose to subcapitate, frequently dichasial; *flowers* monomorphic, 4–5-merous; corollas salverform to funnellform, aestivation imbricate; ovules numerous and vertical on axile placentas. *Fruit* baccate, fleshy; seeds angled.

Hoffmannia includes about 100 species found from Mexico and the West Indies through South America, most in Central America. At least 25 species are known from Costa Rica, most from wet montane forest.

KEY TO THE SPECIES

1. Stems strongly quadrate, often channelled; leaf blades 8–15 cm wide; petioles 5–12 cm long; plants puberulent or strigillose, usually becoming glabrescent; inflorescences strongly dichasial; peduncles 1–5 cm long; corollas red to red-brown, the lobes 6–7 mm long. 1. *H. liesneriana*.
1. Stems slightly quadrate to terete, not channelled; leaf blades 3–8 cm wide; petioles 1.5–6 cm long; plants hirtellous to villous, usually rather densely so; inflorescences umbellate to open cymose; peduncles 1–5 mm long; corollas yellow to yellow-green, the lobes 3–4 mm long. 2. *H.* sp. A.

1. *Hoffmania liesneriana* L. O. Williams

Succulent, strigillose to glabrescent, sometimes suffrutescent herbs to 1 m tall, sometimes rooting at nodes. *Leaves* opposite; blades elliptic to oblong, 12–25 cm long, 8–15 cm wide, acute to acuminate at apex, cuneate to truncate at base, chartaceous; secondary veins 10–18 pairs; petioles 5–12 cm long; stipules caducous, succulent, divergent, 1–3 mm long, bilobed, lobes acute to rounded. *Inflorescences* with cymes open, strongly dichasial, 1–6 cm long and wide, usually borne below leaves; peduncles 1–5 cm long; bracts minute or lacking; pedicels 1–4 mm long; *flowers* 4-merous; calyx hirtellous, limb green, divided to base, lobes 2–5 mm long, acute; corolla salverform, red to red-brown, puberulent externally, glabrous internally, tube 2–3 mm long, lobes 6–7 mm long, acute. *Fruits* narrowly ellipsoid, 4–6 mm long, 2–3 mm wide, red; seeds foveolate, ca. 0.2 mm long. At La Selva collected in flower and fruit March, May–August, October, and November. In wet forests of Costa Rica at 0–500 m.

FIGURE 5j.

This species is common in secondary forest, particularly in the old cacao grove along the West River Road. In general aspect it resembles *Psychotria capacifolia*, which has white flowers and fruit with two pyrenes.

2. *Hoffmannia* sp. A

Hirtellous to villous herbs or shrubs to 1.5 m tall, sometimes clambering. *Leaves* opposite; blades elliptic, 6–18 cm long, 3–8 cm wide, acute to acuminate at apex, acute to cuneate at base, membranaceous to chartaceous; secondary veins 9–12 pairs; petioles 1.5–6 cm long; stipules caducous, succulent, divergent, triangular, 1.5–3 mm long, acute. *Inflorescences* with cymes open to umbellate, 1–2 cm long and wide; peduncles 1–5 mm long; bracts minute to lacking; pedicels 3–10 mm long; *flowers* 4-merous; calyx hirtellous to villous, limb green, divided to base, lobes 1–3 mm long, acute; corolla salverform, yellow to yellow-green, puberulent to pilosulous externally, glabrous internally, tube ca. 2 mm long, lobes 3–4 mm long, acute. *Fruits* obconic, 3–5 mm long, 2–4 mm in diameter, red; seeds foveolate, ca. 0.2 mm in diameter. At La Selva collected in flower and fruit April–August. Wet forests of Costa Rica at 100–200 m.

FIGURE 5k.

This species is common in open swampy areas along streams. It will be formally described and named by Dr. John Dwyer.

21. *IXORA* Linnaeus

Erect shrubs or small trees. *Leaves* opposite or verticillate, without domatia; stipules interpetio-

larly connate, persistent, triangular. *Inflorescences* terminal or axillary, cymose to capitulate; *flowers* monomorphic, 4–5-merous; corollas salverform, aestivation convolute; ovules solitary, axile. *Fruits* drupaceous, fleshy; pyrenes 1–2, smooth, planoconvex.

Ixora includes about 400 species of the Old and New World tropics, most in the Old World. Two native species are found in Costa Rica, and several others are cultivated for ornament. The flowers are protandrous in a distinctive manner: pollen is released from the anthers onto the outside of the stigma, and then the style elongates and the pollen is dispersed. Later the stigma lobes open to reveal the receptive surfaces.

1. *Ixora nicaraguensis* Standley

Glabrescent trees to 6 m tall. *Leaves* opposite; blades elliptic to obovate, 5–12 cm long, 2–4.5 cm wide, acute to acuminate at apex, cuneate to attenuate at base, chartaceous to subcoriaceous; secondary veins 8–10 pairs; petioles 5–10 mm long; stipules 4–6 mm long, acuminate to mucronate. *Inflorescences* terminal, with cymes open, pyramidal, 4–10 cm long, 4–9 cm broad; peduncles 0–5 mm long; pedicels 0–4 mm long; *flowers* 4-merous; calyx puberulent, limb green, divided to base, lobes triangular, ca. 0.5 mm long, acute; corolla salverform, white, glabrous, tube 5–6 mm long, lobes ligulate, 3.5–4.5 mm long, rounded. *Fruits* ellipsoid, 5–6 mm long and in diameter, purple-black. At La Selva collected in flower June and August–September, in fruit September. Belize to Panama in wet forests of Caribbean slopes and Osa Peninsula at 0–300 m.

FIGURE 4i.

This species is rare in swamp forest.

22. *LADENBERGIA* Klotzsch

Erect shrubs or trees. *Leaves* opposite or verticillate, sometimes with domatia; stipules interpetiolarly and sometimes intrapetiolarly connate, caducous, triangular to obovate. *Inflorescences* terminal, open cymose; *flowers* monomorphic, 5–6-merous; corollas salverform to funnellform, aestivation valvate; ovules numerous and vertical on axile placentas. *Fruits* capsular, septicidally and basipetally dehiscent, cylindrical, woody; seeds fusiform, flattened, with a marginal wing.

Ladenbergia includes about 30 species found from Costa Rica to Bolivia, most in the Andes. Three species are known from Costa Rica. Fertile material of *Ladenbergia* is infrequently collected and consequently the plants are poorly known.

1. *Ladenbergia sericophylla* Standley

Sericeous to glabrescent trees to 15 (30) m tall.

Leaves opposite; blades elliptic to broadly elliptic, 14–30 cm long, 8–18 cm wide, acute to acuminate at apex, acute at base, chartaceous to subcoriaceous; secondary veins 5–8 pairs, barbate in vein axils; petioles 3–4 cm long; stipules interpetiolarly and shortly intrapetiolarly connate, obovate, 15–25 mm long, acute. *Inflorescences* with cymes pyramidal, ca. 15 cm long, ca. 18 cm wide; peduncles ca. 5 cm long; pedicels 5–10 mm long; calyx strigillose to glabrescent, limb green, 5–6 mm long, shallowly lobed, lobes 0.5–1 mm long, broadly angled to rounded; corolla salverform, white, sericeous externally, glabrous internally, tube 42–50 mm long, lobes narrowly ligulate, 25–30 mm long, rounded. *Fruits* 6–9 cm long, 1–2 cm in diameter; seeds 11–14 mm long, 4–5 mm wide. At La Selva collected in flower July. Costa Rica in wet forests at 10–1,000 m.

FIGURE 6g.

This species is known only from primary forest near Plot III; it is also found on the ridge along the Río Peje.

23. LASIANTHUS W. Jack

Dressleriopsis Dwyer

ROBBRECHT, E. 1982. The identity of the Panamanian genus *Dressleriopsis* (Rubiaceae). *Ann. Missouri Bot. Gard.* 69: 427–429.

Erect, hermaphroditic or rarely monoecious trees, shrubs, or suffrutescent herbs. *Leaves* without domatia; stipules interpetiolarly connate, persistent or deciduous, triangular. *Inflorescences* axillary, open cymose to usually glomerulate; *flowers* hermaphroditic or unisexual, monomorphic or sometimes distylous, 3–6-merous; corollas salverform to funnelliform, aestivation valvate; ovary 4–12-locular; ovules solitary, basal. *Fruits* drupaceous, fleshy; pyrenes 4–12, 1-seeded, 3-angled, indehiscent or rarely dehiscent by a basal operculum.

Lasianthus includes about 150 species, most in tropical Asia and Africa. Two species are found in the West Indies and one in Central and South America. The broken leaves and stems of some species have a foul musky odor.

1. *Lasianthus panamensis* (Dwyer) Robbrecht (= *Dressleriopsis panamensis* Dwyer)

Pilose, suffrutescent, rhizomatous herbs to 0.4 m tall. *Leaf* blades elliptic to oblanceolate, 10–18 cm long, 4–7 cm wide, acute to acuminate at apex, truncate to rounded at base, chartaceous; secondary veins 9–14 pairs; petioles 1–9 mm long; stipules persistent, 3–8 mm long, acute. *Inflorescences* 5–10 mm in diameter; *flowers* mono-

morphic, (4–)5–6-merous; calyx pilose, limb green, 3–4 mm long, divided to base, lobes elliptic to ovate, acute; corolla white, pilose externally, barbate in throat, tube 3–4 mm long, lobes triangular, 1–2 mm long. *Fruits* globose to ellipsoid, 8–11 mm in diameter, purple-black; pyrenes ca. 8. At La Selva collected in flower and fruit July. Costa Rica to Colombia in wet forests at 100–1,000 m.

FIGURE 3o.

This species is known only from primary forest on the slopes along the Quebrada Paralelo.

24. MANETTIA Linnaeus

Sometimes suffrutescent vines or herbs. *Leaves* without domatia; stipules interpetiolarly and sometimes also intrapetiolarly connate or adnate to petioles, persistent, triangular to lacinate, the teeth sometimes caducous. *Inflorescences* axillary, open cymose or reduced to a solitary flower; *flowers* monomorphic or distylous, 4–8-merous; corollas tubular to funnelliform, aestivation valvate; ovules numerous and vertical on axile placentas. *Fruits* capsular, septically and basipetally dehiscent, obconic to turbinate, somewhat dicocous and laterally compressed, papery; seeds orbicular, flattened, with a marginal wing.

Manettia includes about 100–130 species found throughout tropical America, most in South America. This genus is in need of study, although the variability of the plants presents a challenge.

1. *Manettia reclinata* Linnaeus

Glabrescent to retrorsely hispidulous, extensively twining vines. *Leaf* blades elliptic to ovate or broadly lanceolate, 3–12 cm long, 1.5–5 cm wide, acuminate at apex, cuneate to truncate at base, membranaceous; secondary veins 4–6 pairs; petioles 5–15 mm long; stipules triangular, ca. 1 mm long, with 4–8 cartilaginous teeth or triangular appendages, these often caducous and stipules appearing truncate. *Inflorescences* with peduncles 1–2.5 cm long; bracts triangular, to 2.5 mm long, scarious; pedicels 1–2.5 cm long; *flowers* monomorphic, 4–6-merous; calyx glabrescent, limb green, ca. 2 mm long, divided to base, lobes narrowly triangular, acute; corolla tubular, externally glabrous, internally pilose, green to pink, tube 6–10 mm long, lobes ovate, 3–4 mm long, acute. *Capsules* 5–9 mm long and wide, sulcate; seeds ca. 2 mm in diameter. At La Selva collected in flower and fruit February–May and December. West Indies and Central and South America in secondary growth at 0–1,500 m.

FIGURE 1g.

This species is occasional in thickets along large streams.

25. **MITRACARPUS** Zuccarini

Erect to decumbent, sometimes suffrutescent herbs. *Leaves* without domatia; stipules connate interpetiolarly and adnate to petioles, persistent, truncate, setaceous or fimbriate. *Inflorescences* axillary and terminal, glomerulate, sessile; *flowers* monomorphic, (3-)4-5-merous; corollas funnelform, aestivation valvate; ovary 2-3-locular; ovules solitary, axile. *Fruits* capsular, circumscissile, subglobose, papery; seeds ellipsoid, smooth with cruciform attachment scar.

Mitracarpus includes about 30-45 species found throughout tropical America, most in Brazil, one naturalized in Africa and Asia; one species is known from Costa Rica.

1. **Mitracarpus hirtus** (Linnaeus) de Candolle
(=*Mitracarpus villosus* (Swartz) de Candolle)

Hispidulous to pilose plants to 1 m tall. *Leaf* blades lanceolate to narrowly elliptic, 1-5 cm long, 3-18 mm wide, acute at apex, acute and often attenuate at base, chartaceous; secondary veins 3-4 pairs; petioles 0-3 mm long; stipule sheaths 1-4 mm long, lobes and setae 8-15, 2-4 mm long. *Inflorescences* 5-20 mm in diameter; bracts 2-4 mm long; *flowers* 4-merous; calyx glabrescent, limb green, divided to base, lobes narrowly triangular, unequal in pairs, the larger 2-2.5 mm long, the smaller about half as long, acute; corolla white, glabrous externally or sometimes sparsely pilosulous on lobes, barbate in throat, tube 0.5-2 mm long, lobes 0.5-1 mm long. *Capsules* ellipsoid, 1-2 mm long; seeds ca. 0.5 mm long. At La Selva collected in flower and fruit May and July. Weedy in tropical America at 0-1,300 m and naturalized in Africa and Asia. FIGURE 1e.

This species is uncommon in open disturbed sites.

26. **OLDENLANDIA** Linnaeus

Erect to decumbent, sometimes suffrutescent herbs. *Leaves* without domatia; stipules connate interpetiolarly and sometimes also adnate to petioles, persistent, triangular, sometimes setose. *Inflorescences* terminal and axillary, open cymose or reduced to a solitary flower; *flowers* monomorphic or distylous, 4-8-merous; corollas rotate to funnelform, aestivation valvate; ovules numerous and horizontal on axile placentas. *Fruits* capsular, loculicidally and basipetally dehiscent, ellipsoid to subglobose, often beaked, papery; seeds angled, reticulate to foveolate.

Oldenlandia includes in its traditional sense about 150 species, many of them weedy, most in tropical Africa. Some authors have combined

Oldenlandia or parts of it with *Hedyotis*, which includes 150 more temperate, neotropical, and tropical Asian species. The relationships of these groups are not well resolved.

1. **Oldenlandia lancifolia** (Schumacher) de Candolle
(=*Oldenlandia herbacea* auctt.)

Glabrous to strigillose plants to 1 m tall. *Leaf* blades narrowly elliptic to linear, 1.5-4 cm long, 2-5 mm wide, acute and mucronate at apex, acute at base, chartaceous; secondary veins 3-5 pairs; stipule sheath 1-1.5 mm long, adnate to petioles, with two subulate to narrowly triangular lobes 1-1.5 mm long and often marginally setose as well. *Flowers* 1-2, monomorphic, 4-merous, solitary on each peduncle; peduncles 5-20 mm long; calyx glabrous, limb green, divided to base, lobes triangular, 1-1.5 mm long, acute; corolla funnelform to rotate, white to flushed with pink, glabrous, tube ca. 1 mm long, lobes triangular, 1-2 mm long. *Capsules* subglobose to somewhat didymous, 1.5-2.5 mm long, beak ca. 0.5 mm long; seeds 0.1-0.2 mm long. At La Selva collected in flower and fruit March, May, July-August, and October. Widespread in tropical Africa and adventive in wet to moist areas of the West Indies and Central and South America at 0-1,500 m. FIGURE 1m.

This species is common, particularly on the banks of the Río Puerto Viejo.

Another widely naturalized weedy African species, *Oldenlandia corymbosa* Linnaeus, has also been reported from the La Selva Biological Station (M. H. Grayum, pers. comm.); it can be separated by its few-flowered cymes, pink corollas, and capsules about half as large.

27. **PALICOUREA** Aublet

TAYLOR, C. M. 1989. Revision of *Palicourea* (Rubiaceae) in Mexico and Central America. Syst. Bot. Monogr. 26: 1-102.

Erect shrubs or small trees. *Leaves* opposite or verticillate, axils of veins usually barbate; stipules connate interpetiolarly and usually also intrapetiolarly, persistent, bidentate or awned to truncate with two lobes. *Inflorescences* terminal, open paniculate, usually brightly colored; *flowers* distylous or rarely monomorphic, 5-merous; corollas tubular to funnelform, swollen and often gibbous at base, glabrous internally except for a ring of pilose trichomes near base, aestivation valvate; ovary 2(-6)-locular; ovules solitary, basal. *Fruits* drupaceous, fleshy, blue to purple-black; pyrenes 1, planoconvex, usually ribbed on the back and with a longitudinal furrow on the inner face; seeds ellipsoid, smooth.

Palicourea includes about 200 species found from central Mexico and the West Indies to Paraguay, most in South America; 31 are known from Costa Rica. This genus probably represents a line derived from *Psychotria* with adaptations for hummingbird pollination.

KEY TO THE SPECIES

1. Stipule lobes rounded, 7–10 mm long; leaves 6–18 cm broad. 2. *P. guianensis*.
1. Stipule lobes acute, 1–15 mm long; leaves 3–8 cm broad.
 2. Leaves paired or usually ternate; stipule lobes 5–15 mm long; pedicels 1–5 mm long. 3. *P. triphylla*.
 2. Leaves paired; stipule lobes 1–3 mm long; pedicels 4.5–10 mm long. 1. *P. crocea*.

1. *Palicourea crocea* (Swartz) Roemer & Schultes

Glabrescent to hirtellous shrubs to 5 m tall. *Leaves* opposite; blades elliptic, 4.5–19 cm long, 2–6.5 cm wide, acute at apex and base, membranaceous; secondary veins 8–14 pairs; petioles 2–20 mm long; stipule sheaths 0.1–1 mm long, lobes 1–3 mm long. *Inflorescences* with cymes pyramidal to rounded, 3–10.5 cm long, 1.5–6.5 cm wide, red to orange; peduncles 1.5–11.5 cm long; bracts triangular to linear, 0.5–10 mm long; pedicels 4.5–10 mm long; *flowers* distylous; calyx limb green to orange, divided to base, lobes ovate to triangular, to 0.5 mm long, acute; corolla tubular, externally glabrous to puberulent, red to red-orange, tube 7–9 mm long, lobes triangular, 1–2.5 mm long; ovary bilocular. *Fruits* ovoid to globose, 4–6 mm long and wide, purple-black. At La Selva collected in flower and fruit March and May. Central Mexico and the West Indies to Paraguay in swampy areas at 0–600 m.

FIGURE 2m; Taylor, 1989: fig. 5g, h.

This species is infrequent in secondary growth.

2. *Palicourea guianensis* Aublet

Glabrous to puberulent shrubs or small trees to 10 m tall. *Leaves* opposite; blades elliptic to somewhat ovate, 12–30 cm long, 6–18 cm wide, acute to acuminate at apex, cuneate at base, membranaceous to chartaceous; secondary veins 14–16 pairs; petioles 5–20 mm long; stipule sheaths 1–2 mm long, lobes elliptic to broadly triangular, 7–10 mm long, rounded. *Inflorescences* pyramidal, 5–12 cm long, 3.5–12 cm wide, yellow to orange or red; peduncles 4–12 cm long; bracts triangular, 0.5–6 mm long; pedicels 2–5 mm long; *flowers* monomorphic; calyx minutely puberulent, limb green, divided to base, lobes triangular, to 0.6 mm long, acute to rounded; corolla tubular, externally puberulent with stout

multicellular hairs, yellow to yellow-orange, tube 9–25 mm long, lobes triangular, 1–2 mm long, acute; ovary bilocular. *Fruits* ovoid to ellipsoid, 5–7 mm long, 3.5–5 mm wide, purple-black. At La Selva collected in flower May–July, in fruit June. Southern Mexico and the West Indies to southern Brazil in wet thickets at 0–1,000 m.

FIGURE 2g; Croat, 1978: fig. 524; Taylor, 1989: fig. 20d–f.

This species is frequent in open secondary vegetation near the Río Sarapiquí on the Guaría Annex.

3. *Palicourea triphylla* de Candolle

Glabrate to pilosulous suffrutescent herbs or shrubs to 5 m tall. *Leaves* (2–)3(–4) per node; blades elliptic to slightly obovate or lanceolate, 6–20 cm long, 3–8 cm wide, acuminate at apex, cuneate to rounded at base, chartaceous to subcoriaceous; secondary veins 7–11 pairs; petioles 1–15 mm long; stipule sheaths 1–2 mm long, lobes lanceolate, 5–15 mm long, acute. *Inflorescences* with cymes pyramidal, 2–15 cm long, 3–10 cm broad, red to orange; peduncles 5–18 cm long; bracts narrowly triangular to linear, 0.5–30 mm long; pedicels 1–5 mm long; *flowers* distylous; calyx glabrescent, limb green to red-orange, divided nearly to base, lobes broadly triangular, 0.3–1 mm long, obtuse; corollas tubular, externally puberulent with stout multicellular trichomes, yellow to red-orange, tube 9–14 mm long, lobes triangular, 1–2 mm long, acute; ovary bilocular. *Fruits* ovoid, laterally flattened, 3.5–5 mm long, 3.5–4 mm wide, blue-black. At La Selva collected in flower April–June. Central Mexico and Cuba to Brazil in moist thickets at 0–1,000 m. FIGURE 2f; Taylor, 1989: fig. 20a–c.

This species is known from open swampy areas in the La Guardia Annex.

28. PENTAGONIA Benth

ERNST, K. A. 1989. Insect herbivory on a tropical understory tree: effects of leaf age and habitat. *Biotropica* 21: 194–199.

MCDADE, L. M. 1986. Protandry, synchronized flowering, and sequential phenotypic unisexuality in neotropical *Pentagonia macrophylla* (Rubiaceae). *Oecologia* (Berl.) 68: 218–223.

Erect, frequently monopodial shrubs or small trees. *Leaves* entire or pinnatifid, without domatia; stipules connate interpetiolarly, caducous, triangular. *Inflorescences* axillary, contracted cymose to glomerulate; *flowers* monomorphic, 5–6-merous; corollas tubular to funnellform, aestivation valvate; ovules numerous and horizontal on axile placentas. *Fruits* baccate, fleshy to hard; seeds angled.

Pentagonia includes about 20–25 species found

from Mexico to northwestern South America; about five occur in Costa Rica. These plants make unwieldy specimens, and consequently are infrequently collected and poorly known.

1. *Pentagonia donnell-smithii* Standley

Glabrescent to sericeous, to 6 m tall. *Leaf* blades entire, elliptic to obovate, 40–70 cm long, 25–50 cm wide, acute at apex, cuneate to truncate at base, subcoriaceous; secondary veins 10–14 pairs; petioles 4–12 cm long; stipules 50–70 mm long, acute, sericeous. *Inflorescences* with cymes contracted, 2–3 cm long and wide; peduncles 1–2 cm long; pedicels 1–5 mm long; *flowers* 5-merous; calyx sericeous, limb green, 8–16 mm long, divided for about half its length, lobes imbricate, obovate, unequal, broadly rounded; corolla tubular, cream to pale yellow, externally densely and finely sericeous, barbate in throat, tube 25–30 mm long, lobes triangular to ligulate, 8–10 mm long, acute. *Fruits* globose, 1.5–4 cm long, yellow to orange; seeds ellipsoid, 3–5 mm long. At La Selva collected in flower April–July and October, in fruit February–March and October–November. Guatemala to Costa Rica in wet forests of Caribbean slopes at 0–1,200 m.

FIGURE 6k.

This species is occasional along streams and forest edges and in secondary forest. The lineolate fine venation is distinctive. The petioles are reportedly sometimes hollow and house ants.

29. *POSOQUERIA* Aublet

Erect shrubs or trees. *Leaves* usually with domatia; stipules connate interpetiolarly, caducous, triangular. *Inflorescences* terminal, open to contracted cymose; *flowers* monomorphic, (4–) 5-merous; corollas salverform with long tubes, white, aestivation imbricate; ovary incompletely to fully bilocular; ovules numerous and vertical on axile placentas. *Fruits* baccate, fleshy to hard; seeds angled to flattened, arillate, smooth.

Posoqueria includes about 15 species found throughout tropical America; three occur in Costa Rica. Several species are cultivated as ornamentals, and probably for their fruit by local people. The flowers are white and very strongly fragrant at night, but become yellowed and odorless when old. In some species the stamens are held under tension asymmetrically over the mouth of the corolla tube until they are disturbed, when they spring forward with some force.

KEY TO THE SPECIES

1. Corolla tubes 30–36 cm long; leaf blades (10–)18–46 cm long, densely pilosulous beneath. 2. *P. grandiflora*.

1. Corolla tubes 8–20 cm long; leaf blades 10–20(–24) cm long, glabrous beneath.
2. Leaf blades shiny above with tertiary venation marked and sometimes slightly raised; fruit subglobose, orange, with pericarp brittle and hard, 1–3 mm thick. 3. *P. latifolia*.
2. Leaf blades dull above with tertiary venation not readily discernible, not raised; fruit dull yellow to orange, ellipsoid to ovoid, with pericarp leathery, 10–15 mm thick. 1. *P. coriacea*.

1. *Posoqueria coriacea* M. Martens & Galeotti

Glabrescent shrubs or small trees to 8 m tall. *Leaf* blades narrowly elliptic to ovate, 10–20(–24) cm long, 5–12 cm wide, acute at apex, cuneate to rounded at base, coriaceous; secondary veins 4–8 pairs; petioles 1–2 cm long; stipules 8–10 mm long, acute. *Inflorescences* with cymes 2–3 cm long and wide excluding corollas; peduncles 1–2 cm long; pedicels 5–10 mm long; *flowers* 5-merous; calyx papillose, limb green, 2–7 mm long, shallowly lobed, lobes rounded; corolla greenish white, externally glabrous, pilose in throat and on bases of lobes, tube 15–20 cm long, lobes 15–25 mm long, unequal, rounded. *Fruits* ellipsoid to ovoid, 7–10 cm in diameter, pericarp leathery, 5–10 mm thick, brown; seeds angled, 10–12 mm in diameter, aril white. At La Selva collected in flower February–March, in fruit March–April, June–August, and October–November. Mexico to Brazil in wet forests of Caribbean slopes at 0–1,200 m. FIGURE 4h.

This species is occasional on ridges in primary forest. Its breeding system was studied by Bawa and Beach (1983).

2. *Posoqueria grandiflora* Standley

Glabrescent trees to 17 m tall. *Leaf* blades broadly elliptic, 10–46 cm long, 8–23 cm wide, acute at apex, cuneate to rounded at base, subcoriaceous; secondary veins 4–8 pairs; petioles 7–20 mm long; stipules 8–15 mm long, acute. *Inflorescences* with cymes 3–6 cm long and wide excluding corollas; peduncles 1–2 cm long; pedicels 2–12 mm long; *flowers* 5-merous; calyx glabrous, limb green, 4–7 mm long, shallowly lobed, lobes rounded; corolla glabrous externally, barbate in throat, tube 30–36 cm long, lobes ligulate, 20–38 mm long, unequal, rounded. *Fruits* ovoid to ellipsoid, 7–12 cm long, 4–7 cm in diameter, brown to dull orange, pericarp leathery, 8–12 mm thick; seeds angled, 6–10 mm in diameter, arils orange to white. At La Selva collected in flower in February, April, July, and September–October, in fruit January, March–April, June–August, and October–November. Costa Rica to Panama in wet forests of Caribbean slopes at 100–1,000 m.

This species is infrequent near the south end of the property.

2. *Posoqueria latifolia* (Rudge) Roemer & Schultes

Glabrescent shrubs or small trees to 20 m tall. *Leaf* blades elliptic to ovate, 7–20 cm long, 3.5–12 cm wide, acute at apex, cuneate to truncate at base, chartaceous to subcoriaceous; secondary veins 5–7 pairs; petioles 5–20 mm long; stipules 12–18 mm long, acute to rounded. *Inflorescences* with cymes 1–2.5 cm long and wide excluding corollas; peduncles 1–2 cm long; pedicels 5–10 mm long; *flowers* protandrous, (4–)5-merous; calyx glabrous, limb green, 1–2 mm long, shallowly lobed, lobes broadly rounded; corolla glabrous externally, barbate in throat, tube 8–15 cm long, lobes ligulate, 12–20 mm long, unequal, rounded. *Fruit* globose, ca. 5 cm in diameter, yellow externally, yellow to orange internally, pericarp brittle and hard, 1–3 mm thick; seeds angled, 8–10 mm long, arils white to yellow or yellow-orange. At La Selva collected in flower March–April, June, September, and October, in fruit May, July, and September. Central to South America in wet forests at 0–1,200 m.

FIGURE 4g; Croat, 1978: fig. 525.

This species is occasional along the Ríos Puer-to Viejo and Sarapiquí. The fruits are edible.

30. **PSYCHOTRIA** Linnaeus*

Cephaelis Swartz

BREMEKAMP, C. E. B. 1934. Notes on the Rubiaceae of Surinam. Meded. Bot. Mus. Herb. Rijks. Univ. Utrecht 11: 248–308.

HAMILTON, C. E. 1989. A revision of Mesoamerican *Psychotria* subg. *Psychotria* (Rubiaceae). Part I: introduction & species 1–16. Ann. Missouri Bot. Gard. 76: 67–111. Part II: species 17–47. Ann.

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Missouri Bot. Gard. 76: 386–429. Part III: species 48–61 & appendices. Ann. Missouri Bot. Gard. 76: 863–911.

TAYLOR, C. M. 1984. *Psychotria hebeclada* (Rubiaceae), an overlooked species from Central America. Ann. Missouri Bot. Gard. 71: 169–175.

Erect terrestrial or rarely epiphytic shrubs, trees, or herbs. *Leaves* sometimes with domatia; stipules connate interpetiolarly and frequently also intrapetiolarly, persistent or deciduous, interpetiolar portion triangular to bidentate or awned or truncate with two lobes. *Inflorescences* terminal, axillary, or pseudoaxillary, open to capitate; *flowers* hermaphroditic in our species, distylous or sometimes monomorphic, (4–)5-merous; corollas tubular to funnelliform or campanulate; aestivation valvate; ovary 2(–6)-locular; ovules solitary in each locule, basal. *Fruits* drupaceous, fleshy, becoming succulent or aerenchymatous, blue, purple-black, white, red, or orange; pyrenes 2(–6), planoconvex to concavoconvex, frequently with longitudinal ribs on the back and a median longitudinal sulcus on the inner face.

Psychotria is the largest genus of Rubiaceae with about 1,650 species found throughout the tropics (Hamilton, 1989); about 100 are known from Costa Rica. This genus is similar to *Coussarea* and *Rudgea*; the distinctions among them are summarized in the discussion of *Coussarea*. “*Cephaelis*” was originally distinguished by its capitate inflorescences and relatively large floral and inflorescence bracts. These plants are not clearly separable from *Psychotria*, however, and in addition apparently represent a widely polymorphic assortment of species with similar inflorescence structures derived in parallel (Steyermark, 1972). Therefore, “*Cephaelis*” is here included in *Psychotria*.

Species of *Psychotria* are an important component of the understory of wet and moist tropical forests. *Psychotria emetica* and *P. ipecacuanha* are sources of the emetic drug ipecac. Most species of *Psychotria* are distylous; the condition is described here only when known. The fruits mature a few at a time and disappear quickly.

KEY TO THE SPECIES

1. Plants epiphytic; leaves succulent, secondary veins indistinct, 4–7 pairs; inflorescences terminal; fruits usually with 4–6 pyrenes. 29. *P. orchidearum*.
1. Plants terrestrial; leaves succulent to membranaceous, secondary veins distinct or indistinct, 4–30 pairs; inflorescences terminal, pseudoaxillary, or axillary; fruits with 1–2 pyrenes (to 5 in *P. racemosa*).
2. Inflorescences axillary or all pseudoaxillary; plants 1 m tall or shorter (to 8 m tall in *P. erecta*); stipules triangular to acicular, entire or sometimes shortly bifid at apex, membranaceous to succulent.
3. Inflorescences axillary (present in both axils of a node); mature fruits bright to dark blue.
4. Rhizomatous, pilosulous, suffruticose herbs 1 m tall or shorter; stipules ca. 2 mm long; inflorescences 1 per axil; corolla tubes 2 mm long; fruit blue. 13. *P. emetica*.

4. Non-rhizomatous, puberulent to glabrous shrubs to 3(–8) m tall; stipules 2–7 mm long; inflorescences (1–)2–3 per axil; corolla tubes 3–4 mm long; fruit dark blue to black. 14. *P. erecta*.
3. Inflorescences all pseudoaxillary (present in only one axil of a node); mature fruits blue-black, red, or white.
 5. Leaf blades rounded at apex, corrugated; secondary veins 20–30 pairs. . . 34. *P. polyphlebia*.
 5. Leaf blades acute at apex, planar or only slightly corrugated; secondary veins 9–20 pairs.
 6. Leaves pilose to tomentose, at least on lower surface of young leaves.
 7. Leaf blades 25–40 cm long, with 18–25 pairs of secondary veins; inflorescences 10–20(–50) cm long; mature fruits greenish yellow. 8. *P. capacifolia*.
 7. Leaf blades 12–20 cm long, with 10–12 pairs of secondary veins; inflorescences 2(–8) cm long; mature fruits red. 37. *P. siggersiana*.
 6. Leaves puberulent to glabrescent.
 8. Leaves succulent, coriaceous, dark green on upper surface, lower surface pale and this often drying tan or brown; mature fruit red or black.
 9. Secondary leaf veins 9–11 pairs; inflorescences capitate, 5–10 mm in diameter; bracts 6–10 mm long. 7. *P. camponutans*.
 9. Secondary leaf veins 15–20 pairs; inflorescences branched, 2–3 cm long and wide; bracts 0.5–1.5 long. 39. *P. uliginosa*.
 8. Leaves membranaceous to subcoriaceous, with both surfaces similarly green or somewhat paler below, drying green; mature fruit white.
 10. Inflorescences open, 3–10 cm long, 4–6 cm wide, with peduncles 1.5–10(–14) cm long; stems rounded. 25. *P. macrophylla*.
 10. Inflorescences contracted to subcapitate (the branches sometimes developing in fruit), 1–2 cm in diameter, sessile; stems quadrate. 2. *P. aggregata*.
2. Inflorescences terminal, sometimes becoming pseudoaxillary in fruit; plants 0.5–10 m tall; stipules narrowly triangular to ovate, entire to deeply bilobed or truncate with two lobes, membranaceous to foliaceous.
 11. Stipules fused interpetiolarly and intrapetiolarly into a conical cap, caducous, 20–45 mm long. 30. *P. panamensis*.
 11. Stipules fused interpetiolarly and sometimes also intrapetiolarly but not forming a closed cap, persistent to caducous, 0.5–20 mm long.
 12. Plants pilose, tomentose, or hirsute, at least on distal 2–3 internodes of stem.
 13. Plants ferruginous (reddish)-tomentose on young stems; stipules quickly deciduous, ca. 1 cm long with a single awn 5 mm long on each side. 35. *P. psychotriifolia*.
 13. Plants pilose to tomentose or hirsute with white or pale yellow trichomes; stipules more or less persistent, bilobed or truncate with two awns.
 14. Inflorescences capitate, surrounded by two ovate red involucre bracts 20–30(–60) mm long, with floral bracts 10–15 mm long; stipules with truncate sheath 2–6 mm long and two awns 5–11 mm long. 33. *P. poeppigiana*.
 14. Inflorescences open, without involucre bracts, with floral bracts 1–5 mm long; stipules with truncate sheath 2 mm long and two lobes 2 mm long, or shortly bilobed and 15–20 mm long with an acute sinus.
 15. Stipules 15–20 mm long; floral bracts 4–5 mm long; leaf blades (5–)7–11 cm long, with 16–22 pairs of secondary veins; corollas yellowish white. . . 31. *P. pilosa*.
 15. Stipules ca. 4 mm long; floral bracts 1 mm long or shorter; leaf blades 2.5–4(5.5) cm wide, with 12–17 pairs of secondary veins; corollas white to cream. 32. *P. pittieri*.
 12. Plants glabrescent or scaberulous to puberulous, at least on distal 2–3 nodes of stem.
 16. Suffruticose, often rhizomatous herbs to 1 m tall, usually smaller.
 17. Inflorescences somewhat open to condensed, with some flowers always pedicellate; pedicels 0–5 mm long; floral bracts 0.5–6 mm long; calyx limb 1–3 mm long.
 18. Stipules quickly deciduous, usually present only on distal 1–2 nodes, (7–)8–18 mm long; inflorescences globose; floral bracts 0.5–1 mm long. . 3. *P. alfaroana*.
 18. Stipules persistent at least on distal 3–6 nodes, 1.5–4.5 mm long; floral bracts 1–6.5 mm long. 21. *P. hebeclada*.
 17. Inflorescences capitate, flowers all sessile; floral bracts 6–10 mm long; calyx limb ca. 1 mm long.
 19. Inflorescences ca. 1 cm in diameter; bracts pale green; petioles ca. 5 mm long; secondary leaf veins 5–8 pairs. 22. *P. ipecacuanha*.
 19. Inflorescences 1.5–5 cm in diameter; bracts green to purple; petioles 2–6 cm long; secondary leaf veins 10–14 pairs. 19. *P. guapilensis*.
16. Shrubs or trees 1–10 m tall, not rhizomatous.
 20. Inflorescences capitate, flowers all sessile in a single head enclosed by 1–3 involucre bracts 10–25 mm long.

21. Stipules deciduous, triangular to shortly bilobed, (3-)5-10 mm long; inflorescences sessile, 5-8 mm in diameter, bracts green. 9. *P. chagensis*.
21. Stipules persistent, composed of a truncate sheath 1-3 mm long and two lobes 1-5 mm long; inflorescences subsessile or usually with peduncles to 15 cm long, 1-20 cm in diameter, bracts orange to red or purple.
22. Peduncles 0-15 mm long; inflorescence bracts pale green to purple, involucrel bracts 10-15 mm long; stipule lobes ca. 1 mm long. 16. *P. glomerulata*.
22. Peduncles 2-15 cm long; inflorescence bracts orange to bronze red, involucrel bracts 10-25 mm long; stipule lobes 2-5 mm long. 12. *P. elata*.
20. Inflorescences branched at least once, flowers sessile or pedicellate in three or more heads, not enclosed by 1-3 unusually large involucrel bracts.
23. Stipules 15-20 mm long, triangular to ovate, very shortly bifid or entire; floral bracts 0-2 mm long.
24. Leaf blades 3-6 cm wide, with domatia (pits) well developed; stipules 5-12(-16) mm long, lanceolate, without midrib; floral bracts 0.5 mm long or shorter. 26. *P. marginata*.
24. Leaf blades 4-13 cm wide, with domatia (pits) absent or rare; stipules (15-)20 mm long, ovate, with well-developed midrib; floral bracts ca. 2 mm long. 18. *P. grandis*.
23. Stipules 1-20 mm long, bilobed to $\frac{1}{3}$ or more of their length, frequently with a truncate sheath, or if entire then 10 mm long or shorter; floral bracts 0-15 mm long.
25. Floral bracts 6-15 mm long, obovate to elliptic or ligulate.
26. Corolla tubes 30-40 mm long; fruits 10-20 mm long. 10. *P. chiapensis*.
26. Corolla tubes 2-10 mm long; fruits 2-8 mm long.
27. Stipule lobes 3-5 mm long; floral bracts 10-15 mm long; corolla tubes ca. 10 mm long; underbark and wood frequently becoming red-purple when exposed to air. 38. *P. suerrensii*.
27. Stipule lobes 1-2.5 mm long; floral bracts 3-5 mm long; corolla tubes 2-3 mm long; underbark and wood not changing color or becoming grey when exposed to air. 28. *P. officinalis*.
25. Floral bracts 0-5 mm long, triangular to elliptic, ligulate, ovate, or obovate.
28. Floral bracts 3-5 mm long, obovate to elliptic or ligulate.
29. Corolla tubes 30-40 mm long; fruits 10-20 mm long. 10. *P. chiapensis*.
29. Corolla tubes 1-15 mm long; fruits 2-8 mm long.
30. Inflorescences congested to subcapitate, to 1 cm in diameter; corolla tubes 1.5-2 mm long. 6. *P. brachybotrya*.
30. Inflorescences pyramidal, 1.5-12(-17) cm long, 2.5-9 cm wide; corolla tubes 1.5-5 mm long.
31. Calyx limb to 0.5 mm long; floral bracts ligulate. 28. *P. officinalis*.
31. Calyx limb 1-1.5 mm long; floral bracts triangular to ovate.
32. Floral bracts narrowly triangular; corolla tubes 3-4 mm long; pyrenes with broad angles on back. 21. *P. hebeclada*.
32. Floral bracts ovate; corolla tubes 5 mm long; pyrenes with narrow rounded ridges on back. 5. *P. brachiata*.
28. Floral bracts 0-2 mm long, triangular to ovate.
33. Pyrenes usually 5 per fruit; stipules 8-20 mm long, with truncate sheath 1-4 mm long and two narrow lobes 7-15 mm long. 36. *P. racemosa*.
33. Pyrenes (1-)2 per fruit; stipules 6 mm long or shorter, or if longer (to 20 mm) then triangular to shortly bilobed with the sinus acute.
34. Inflorescences 5-20 cm wide.
35. Corolla tube 10-15 mm long; fruits 15-25 mm in diameter. 15. *P. eurycarpa*.
35. Corolla tube 1.5-5 mm long or shorter; fruits 3-10 mm long.
36. Petioles 0-2(-5) mm long; leaf bases truncate to cordate or rarely acute. 23. *P. laselvensis*.
36. Petioles 5-60 mm long; leaf bases attenuate to cuneate.

37. Leaf blades with at least a few domatia (pits); stipules deciduous after first 1–2 nodes. 26. *P. marginata*.
37. Leaf blades without domatia; stipules persisting on at least the distal 3–8 nodes.
38. Stipules 10–20 mm long, bilobed for $\frac{1}{2}$ – $\frac{2}{3}$ this length. 27. *P. microbotrys*.
38. Stipules 4–9 mm long, triangular to ovate, bilobed for $\frac{1}{4}$ or less of this length.
39. Corolla tubes 1.5–3 mm long; inflorescences 9–15 cm long. 24. *P. luxurians*.
39. Corolla tubes 5–6 mm long; inflorescences 15–20 cm long. 4. *P. angustiflora*.
34. Inflorescences 5–48 mm wide.
40. Peduncles 0–8 mm long.
41. Stipules 2–3.5 mm long, with lobes very narrowly triangular; inflorescences with 2–12 flowers; mature fruits red. 20. *P. haematocarpa*.
41. Stipules 5–7 mm long, with lobes rounded; inflorescences with 20 or more flowers; mature fruit purple-black. 11. *P. cooperi*.
40. Peduncles 10–100 mm long.
42. Peduncles 3–10 cm long; petioles 0–2(–5) mm long. 23. *P. laselvensis*.
42. Peduncles 1–2.5 cm long; petioles 3–20 mm long.
43. Leaf blades 1–1.5 cm wide, with one pair of domatia (pits) per leaf. 17. *P. graciliflora*.
43. Leaf blades (2.5–)6–9 cm wide, without domatia. 1. *P. acuminata*.

1. *Psychotria acuminata* Bentham
(=*Psychotria cuspidata* auctt.)

Erect glabrescent shrubs 1–2 m tall, much branched; stems quadrate. *Leaf* blades elliptic, (10–)15–22 cm long, (2.5–)6–9 cm wide, acuminate at apex with curved tip 1.5–3 cm long, acute at base, thinly chartaceous, somewhat bulate, green above and below; secondary veins 10–12 pairs, looping to interconnect near margins, prominulous above and below, sometimes with domatia; petioles 1–2 cm long; stipules persistent, membranaceous, appressed, connate interpetiolarly and intrapetiolarly, truncate, 0.5–1 mm long, with two awns 1.5–3 mm long. *Inflorescences* terminal, with cymes open, pyramidal, 1–3 cm long and wide, puberulent, green, ebracteate; peduncles 1.5–2.5 cm long; *flowers* subsessile, distylous, 5-merous; calyx limb 0.5–1 mm long, slightly dentate; corolla white drying yellow-orange, tubular, glabrous, tube 3–5 mm long, lobes ca. 1.5 mm long. *Fruits* oblate to subglobose, didymous, ca. 8 mm in diameter, succulent, blue-grey to purple; pyrenes planoconvex, 2.5 mm in diameter, smooth dorsally, smooth with a median sulcus ventrally. At La Selva collected in flower May–June, in fruit July–December. Central Mexico and the West Indies to Peru, in wet forests of Caribbean slopes at 100–1,400 m. FIGURE 20; Croat, 1978: fig. 526.

This species is common in forest edges and gaps. Its breeding biology was studied by Bawa and Beach (1983).

2. *Psychotria aggregata* Standley
(=*Psychotria tonduzii* Standley; *Montamans panamensis* Dwyer)

Erect, glabrous suffruticose herbs 1–1.5 m tall, unbranched; stems quadrate with blunt angles. *Leaf* blades elliptic-oblong to obovoid-oblong, 20–38 cm long, 7–17 cm wide, acute to acuminate at apex, acute to attenuate at base, membranaceous to thinly succulent, green on both surfaces or paler below; secondary veins 15–17 pairs, looping to interconnect at least near apex, prominulous below, without domatia; petioles 3–10(–13) cm long; stipules deciduous, succulent, divergent, connate interpetiolarly and intrapetiolarly, broadly triangular, 3 mm long, with bifid conical appendage 4–7 mm long. *Inflorescences* pseudoaxillary, with cymes contracted to subcapitate, globose, green, 1–2 cm in diameter, puberulent, subsessile in flower but peduncle and branches elongating somewhat in fruit; floral bracts triangular, 3–4 mm long; *flowers* sessile, 5-merous; calyx 0.5–2 mm long, dentate; corolla white, puberulent, funnellform, tube ca. 4 mm long, lobes to 1 mm long. *Fruits* globose, ca. 10

mm in diameter, spongy, white; pyrenes flattened, ca. 6 mm in diameter, with margin and median keel thickened dorsally, smooth or with obscure median keel ventrally. At La Selva collected in flower and fruit throughout the year. Costa Rica and western Panama, in wet forests of the Caribbean slopes at 100–1,800 m.

FIGURE 6n, o.

This species is common in shady secondary forest, notably along the West River Road.

3. *Psychotria alfaroana* Standley

Erect glabrescent suffruticose herbs 0.3–0.6(–1) m tall, little branched; stems terete. *Leaf* blades obovate-oblong, 12–30 cm long, 4–11 cm wide, acute at apex, attenuate at base, membranaceous to somewhat chartaceous, frequently bullate, green on both sides; secondary veins 12–18 pairs, looping to interconnect near margins, prominulous below, without domatia; petioles ca. 1 cm long; stipules deciduous, membranaceous, appressed, connate interpetiolarly, oblong-ovate, (7–)8–18 mm long, bilobed for ca. ½ their length, lobes acuminate. *Inflorescences* terminal or pseudoaxillary, with cymes contracted, globose, green, (1.5–)2–4 cm in diameter; peduncles 0–3 cm long; pedicels ca. 1 mm long; *flowers* 5-merous; calyx limb ca. 2 mm long, lobed for ca. ½ its length; corolla funnellform, white, glabrous, tube ca. 4 mm long, lobes ca. 1 mm long. *Fruits* narrowly ovoid, 8–10 mm long, 4–5 mm wide, succulent, red; pyrenes planoconvex, ca. 7 mm long, 5-ribbed dorsally, smooth or with a faint median sulcus ventrally. At La Selva collected in flower March–May, in mature fruit late August. Costa Rica and western Panama in wet forests most frequently on Caribbean slopes at 100–900 m.

FIGURE 2b.

This species is known from a few plants in old secondary forest in the abandoned cacao plantation along the West River Road, and from the ridge just off the southwest corner of the Western Annex.

4. *Psychotria angustiflora* K. Krause (=*Psychotria mima* Standley)

Erect glabrous shrubs or trees 2–3(–5) m tall, much-branched; stems terete. *Leaf* blades broadly elliptic to oblong, 12–20 cm long, 4–10 cm wide, acute to acuminate at apex, acute at base, membranaceous, green on both sides; secondary veins 9–12 pairs, looping to interconnect near margins at least distally, prominulous, without domatia; petioles 15–25(–60) mm long; stipules persistent, membranaceous, appressed, connate interpetiolarly and intrapetiolarly, ovate, ca. 5 mm long, bilobed, lobes ca. 1 mm long. *Inflo-*

rescences terminal, with cymes open, pyramidal, 5–20 cm long, 15–20 cm wide, puberulent; peduncles 0–10 cm long; *flowers* subsessile, not strongly clustered, distylous, 5-merous; calyx limb to 0.3 mm long, dentate; corolla yellow to yellow-green, funnellform, glabrous, tube 5–6 mm long, lobes ca. 2.5 mm long. *Fruits* globose, ca. 7 mm in diameter, succulent, blue-black; pyrenes planoconvex, 1.5–3.5 mm long, 5-ribbed dorsally, smooth with a deep median sulcus ventrally. At La Selva collected in flower July–August, in fruit November. Costa Rica to Brazil in wet forest at 100–900 m.

FIGURE 3b.

This species is rare in primary forest, notably along the Quebrada Esquina. *Psychotria angustiflora* is similar to *P. brachiata*; the distinctions between them are outlined under the treatment of that species.

5. *Psychotria brachiata* Swartz

Erect glabrescent shrubs 2–3 m tall, much branched; stems quadrate. *Leaf* blades elliptic to oblong, (7–)11–16(–21) cm long, (3–)5–7(–11) cm wide, acute at apex, acute to attenuate at base, chartaceous, green on both sides; secondary veins 9–12 pairs, not looping to interconnect, prominulous below, without domatia; petioles 1–2(–4) cm long; stipules persistent, membranaceous, appressed, connate interpetiolarly, 3–5 mm long, bilobed, lobes ca. 1 mm long, acute. *Inflorescences* terminal, with cymes pyramidal or sometimes tripartite, open, (3–)7–12(–17) cm long, 3–9 cm wide, glabrous to puberulent; peduncles 4–6 cm long; bracts green, ovate, 3–4 mm long; *flowers* sessile, congested in capitulae 5–10 mm in diameter, 5-merous; calyx limb 1–1.5 mm long, truncate to slightly dentate; corolla pale yellow sometimes with blue markings in throat, funnellform, pilosulous externally, glabrous internally, tube ca. 5 mm long, lobes ca. 1.5 mm long, appendaged, appendages to 0.5 mm long. *Fruits* globose, 3–4 mm in diameter, spongy, bright blue; pyrenes concavoconvex, 3–4 mm long, 3–5-ribbed dorsally, smooth ventrally. At La Selva collected in flower most frequently May–July, in fruit July–September but occasional at most other times of the year as well. Southern Mexico and the West Indies to Peru in wet forests at 0–800 m.

FIGURES 2i, 3a.

This species is common in secondary forest, particularly near the successional plots. *Psychotria brachiata* is similar to *P. angustiflora* K. Krause, which can be separated by its larger inflorescences with the flowers not congested in heads, smaller floral bracts, smaller fruits, terete stems, and occurrence in primary forest. *Psychotria brachiata* is also similar to *P. pittieri*; the

distinctions between them are outlined in the treatment of that species.

6. ***Psychotria brachybotrya*** Mueller Argoviensis

Erect glabrescent shrubs 1–1.5 m tall, much branched; stems terete to somewhat flattened. *Leaf* blades ovate, 10–13(–15) cm long, 3.5–7 cm wide, acuminate at apex, attenuate at base, chartaceous, green on both sides; secondary veins 6–8 pairs, looping to interconnect near margins, prominulous below, without domatia; petioles 0–1 cm long; stipules persistent, membranaceous, appressed, connate interpetiolarly, sheath truncate, 0.5–1 mm long, lobes 2.5–7 mm long, acute. *Inflorescences* terminal, with cymes congested to subcapitate, narrowly pyramidal to subglobose, green, ca. 1 cm long and wide, puberulent; peduncles 0–1 cm long elongating to 2 cm long and becoming purple in fruit; bracts ovate to broadly triangular, ca. 3 mm long; *flowers* sessile, 5-merous; calyx limb ca. 0.5 mm long, dentate; corolla white, tubular, glabrous, tube 1.5–2 mm long, lobes ca. 1 mm long. *Fruits* ellipsoid, ca. 5 mm in diameter, succulent, purple-black; pyrenes planoconvex, 3–4 mm long, 5-ribbed dorsally, smooth with a median sulcus ventrally. At La Selva collected in flower July–August, in fruit December. Central Mexico to Bolivia and Brazil in wet forest at 0–1,000 m. FIGURE 2h.

This species is rare in low areas in primary and old secondary forest, notably along the north side of the swamp near the 1973 Plot. *Psychotria brachybotrya* resembles *P. officinalis*, which is a smaller plant with narrower leaves, smaller inflorescences, shorter broader floral bracts, longer stipule lobes, and a linear ventral sulcus on the pyrenes.

7. ***Psychotria camponutans*** (Dwyer & Hayden) Hammel

(=*Cephaelis camponutans* Dwyer & Hayden)

Erect, glabrous to puberulent, somewhat succulent, suffruticose herbs 0.5–1.25 m tall, unbranched; stems quadrate with rounded corners. *Leaf* blades oblong to obovoid-oblong, 18–25 cm long, 7–9 cm wide, acute at apex, acute to attenuate at base, coriaceous, dark green above, paler and dull below; secondary veins 9–11 pairs, not looping to interconnect, indistinct but midrib keeled above, prominulous below, without domatia; petioles 25–55 mm long; stipules deciduous, connate interpetiolarly, triangular, succulent, divergent, 4–5 mm long, minutely bilobed. *Inflorescences* pseudoaxillary, with cymes capitate, green, puberulent, 5–10 mm in diameter, subsessile; involucre bracts green, ovate, 10 mm long, floral bracts lanceolate, 6–8 mm long, acu-

minate; *flowers* sessile, 5-merous; calyx limb ca. 1 mm long, lobed to base; corolla white, funnelform, glabrous, tube ca. 3 mm long, lobes 1–1.5 mm long. *Fruits* obovoid to ellipsoid, 7–8 mm long, succulent, red; pyrenes planoconvex, 6–7 mm long, 4–5-angled on back, smooth with a median sulcus ventrally. At La Selva collected in flower July. Costa Rica and western Panama, in wet forests of Caribbean slopes at 100–1,000 m.

This species is rare in general, although it is locally common where it does occur, in primary forest along the Quebrada Paralela in the Western Annex. In life *P. camponutans* can be recognized quickly by its plane leaf blades with keeled midribs and small nodding inflorescences.

8. ***Psychotria capacifolia*** Dwyer

Erect, glabrous to puberulent, succulent, suffruticose herbs to 1 m tall, usually unbranched; stems terete. *Leaf* blades ovate-elliptic, 25–40 cm long, 10–20 cm wide, acute at apex, acute to cuneate at base, membranaceous, glabrous adaxially, pilose below at least when young, dark often metallic green above, pale below; secondary veins (18–)21–25 pairs, looping to interconnect near margin, prominulous below, without domatia; petioles 2–10 cm long, pilose; stipules deciduous, succulent, connate interpetiolarly, broadly triangular, 3–4 mm long with a divergent to reflexed conical appendage 3 mm long. *Inflorescences* pseudoaxillary, with cymes pyramidal, green, (5–)10–20(–50) cm long and wide, tomentose; peduncles 5–20 cm long; *flowers* sessile, 5-merous; calyx limb 0.5–1 mm long, dentate; corolla white to greenish yellow, funnelform, glabrescent, tube ca. 3 mm long, lobes ca. 1 mm long. *Fruits* ovoid, ca. 6 mm long, succulent, greenish yellow; pyrenes planoconvex, ca. 5 mm long, 5-ribbed dorsally, plane with a median sulcus ventrally. At La Selva collected in flower May–June, in fruit March. Nicaragua to western Panama in wet forests of the Caribbean slopes at 20–1,300 m. FIGURE 7e, f.

This species is known from one population in the primary forest along the Quebrada El Salto near the South Boundary.

9. ***Psychotria chagensis*** Standley

Erect, glabrous, slender shrubs 1–2.5 m tall, much-branched; stems terete. *Leaf* blades obovate, (1.5–)3.5–7(–10) cm long, (0.8–)1.5–2.5(–3.5) cm wide, acute to acuminate at apex, attenuate at base, membranaceous, green on both sides; secondary veins 8–12 pairs, looping to interconnect near margins, prominulous, without domatia; petioles 0–15 mm long; stipules deciduous, membranaceous, appressed, connate interpetio-

larly and intrapetiolarly or sometimes splitting, ovate to triangular, (3–)5–10 mm long, acute to acuminate, sometimes shortly bilobed. *Inflorescences* terminal to pseudoaxillary, with cymes capitate, green, 5–7 mm in diameter, glabrous, sessile; involucre bracts broadly ovate, 10 mm long, acute to acuminate, floral bracts narrowly triangular, 4–5 mm long; *flowers* sessile, distylous, 5-merous; calyx limb 2–4 mm long, lobed for ca. ½ its length; corolla white, funnellform, glabrous, tube 7–9 mm long, lobes ca. 2 mm long. *Fruits* globose to ovoid, 6–8 mm long, succulent, red; pyrenes planoconvex, ca. 6 mm long, 4–5-ribbed dorsally, smooth with a median sulcus ventrally. At La Selva collected in flower May–June, in fruit November–December. Southern Mexico to Guatemala and Nicaragua to Panama, in wet forests of Caribbean slopes at 0–1,300 m.

FIGURE 6c, d.

This species is locally common in forested swampy areas. The leaves are frequently clustered at the stem apices and the general aspect of the plant is flat-topped. In this respect it is similar to *Psychotria graciliflora*, but *P. chagensis* can be separated by its larger leaves and capitate inflorescences.

10. *Psychotria chiapensis* Standley

Erect glabrous to puberulent shrubs or small trees 3–5(–10) m tall, much-branched; stems terete. *Leaf* blades elliptic, 10–23 cm long, 5–9 cm wide, acute at apex, acute to attenuate at base, membranaceous, green on both sides; secondary veins 9–16 pairs, not looping to interconnect, prominulous below, without domatia; petioles 1(–2.5) cm long; stipules persistent, membranaceous, appressed, connate interpetiolarly and intrapetiolarly, 2–4 mm long, bilobed for half to all of its length. *Inflorescences* terminal, with cymes corymbiform, rounded, open, green, ca. 3.5 cm long, ca. 7.5 cm wide, puberulent, composed of 3–5 capitulae 1.5–2.5 cm in diameter; peduncles 2–7 cm long; bracts green, elliptic to obovate, 5–10 mm long; *flowers* sessile, distylous, 5-merous; calyx limb 2–3 mm long, subtruncate; corollas white, salverform, glabrous, tube 30–45 mm long, lobes 10–15 mm long. *Fruits* ellipsoid to ovoid, 15–20 mm long, succulent, purple-black; pyrenes planoconvex to triangular, 10–15 mm long, 3-ribbed or -angled dorsally, smooth ventrally. At La Selva collected in flower June–July, in fruit September, November–March. Southern Mexico to Peru in wet secondary forests at 0–1,400 m.

FIGURE 3d, e, i.

This species is locally common along the Ríos Puerto Viejo and Sarapiquí, particularly along the West River Road and on the point upriver from Rafael's House. It is notable for its rela-

tively large flowers and pyrenes compared to other species of *Psychotria*. Its breeding biology was studied by Bawa and Beach (1983).

11. *Psychotria cooperi* Standley

Erect glabrous to pilosulous shrubs or trees to 6 m tall, much-branched; stems terete. *Leaf* blades elliptic, 10–18(–21) cm long, 3.5–7 cm wide, acute to acuminate at apex, acute to attenuate at base, membranaceous, green on both sides; secondary veins 11–12(–15) pairs, not looping to interconnect, prominulous above and below, without domatia; petioles 1–2 cm long; stipules persistent, membranaceous, appressed, connate interpetiolarly, 5–7 mm long, shallowly bilobed, lobes triangular to rounded, ca. 1 mm long. *Inflorescences* terminal and sometimes also pseudoaxillary, with cymes open, subglobose, green, 1–2 cm in diameter, pilosulous, subsessile; involucre bracts ovate, 8–10 mm long, floral bracts green, rounded, setaceous, 0.5–1 mm long; pedicels to 1 mm long elongating to 2–5 mm in fruit; *flowers* 5-merous; calyx limb to 1 mm long, lobed to base; corolla white, funnellform, barbate in throat but otherwise glabrous, tube ca. 5 mm long, lobes ca. 2 mm long. *Fruits* obovoid, (3–)4–5 mm long, succulent, blue to purple-black; pyrenes planoconvex, 3–4 mm long, 4(–5)-ribbed dorsally, smooth with a median sulcus ventrally. At La Selva collected in flower and fruit February–September. Costa Rica to Colombia in wet forests at 100–1,500 m.

FIGURE 3c.

This uncommon species appears to be restricted to light gaps and stream margins in primary forest, notably along the Loop Trail at the Quebrada El Saltito.

12. *Psychotria elata* (Swartz) Hammel (=*Cephaelis elata* Swartz)

Erect glabrous shrubs or small trees to 8 m tall, much-branched; stems quadrate. *Leaf* blades elliptic, (10–)15–25 cm long, (1.5–)4–7 cm wide, acute at apex, attenuate at base, chartaceous, green on both sides; secondary veins (12–)15–24 pairs, obscurely looping to interconnect, prominulous below, without domatia; petioles (1–)2–3(–4) cm long; stipules persistent, connate interpetiolarly, membranaceous, appressed, sheath truncate, 1–2 mm long, lobes ovate, 2–5 mm long. *Inflorescences* terminal, with cymes capitate, depressed globose to shortly cylindrical, flushed with orange or red, 15–25 mm in diameter excluding involucre bracts, glabrous; peduncles 2–15 cm long; involucre bracts greenish orange to bronzed, the outermost pair ovate, 1–5 cm long, floral bracts ligulate to ovate, 8–15 mm long; *flowers* distylous, 5-merous; calyx limb 1–1.5 mm long,

subtruncate to dentate; corolla white, tubular to funnelliform, glabrous, tube ca. 1.5 mm long, lobes 2.5–3 mm long. *Fruits* ovoid to ellipsoid, 10–15 mm long, ca. 4 mm in diameter, succulent, purple-black; pyrenes planoconvex, 6–8 mm long, 5-ribbed dorsally, smooth with a median sulcus ventrally. At La Selva collected in flower throughout the year, in fruit July–September. Central Mexico and the West Indies to Colombia in primary and disturbed forests at 0–2,000 m.

FIGURE 2h.

This species is common throughout the forest, particularly in old light gaps, edges, and on ridges. Its breeding biology was studied by Bawa and Beach (1983) and its pollinators by Freeman and Stiles (1990). This species and the similar but pilose *Psychotria poeppigiana* are striking when in flower, and because of their inflorescences are often called “hot lips.”

13. *Psychotria emetica* Linnaeus filius

Erect, rhizomatous, puberulent to pilosulous, suffruticose herbs to 1 m tall, sparsely branched; stems terete. *Leaf* blades elliptic to narrowly ovate, 8–15 cm long, 3–6 cm wide, acute at apex, acute to attenuate at base, chartaceous, green on both sides; secondary veins 7–11 pairs, not looping to interconnect near margins, prominulous below, without domatia; petioles 5–15 mm long; stipules persistent, membranaceous, divergent, connate interpetiolarly, narrowly triangular, ca. 2 mm long, entire. *Inflorescences* axillary, 1 per axil, with cymes capitulate, green, pilosulous, ca. 5 mm long and wide; peduncles 2–6 mm long; *flowers* sessile, 5-merous; calyx limb ca. 1 mm long, divided to base; corolla white, funnelliform, glabrous, tube ca. 2 mm long, lobes ca. 1.5 mm long. *Fruits* ellipsoid to globose, ca. 6 mm in diameter, succulent, blue; pyrenes planoconvex, ca. 5 mm long, smooth to shallowly 5-ribbed dorsally, smooth with a median keel ventrally. At La Selva collected in flower February–July, in fruit June–July. Guatemala to Bolivia in wet forests at 0–1,000 m.

FIGURE 5a; Croat, 1978: fig. 530.

This species is known only from old secondary forest and shady stream banks in riverine forest. Its rhizomes yield an inferior ipecac, and have been gathered for export.

14. *Psychotria erecta* (Aublet) Standley & Steyermark

Erect puberulent to glabrescent shrubs 1–3(–8) m tall, sparsely branched; stems terete to somewhat quadrate. *Leaf* blades elliptic, 10–20

cm long, 3–8(–10) cm wide, acute at base and apex, stiffly chartaceous, green on both sides; secondary veins 4–7(–10) pairs, looping to interconnect near margin, slightly impressed adaxially, prominent below, without domatia; petioles 1–2 cm long; stipules persistent, membranaceous, appressed, connate interpetiolarly, narrowly triangular to subulate, 2–7 mm long, entire. *Inflorescences* axillary, (1–)2–3 per axil, with cymes capitulate, green, 5–10 mm in diameter, puberulent; peduncles 2–15 mm long, sericeous; *flowers* sessile, 5-merous; calyx limb ca. 1 mm long, subtruncate; corolla white, funnelliform, glabrous, tube 3–4 mm long, lobes ca. 1.5 mm long. *Fruits* ovoid, ca. 10 mm long, 5–6 mm in diameter, succulent, dark blue; pyrenes concavoconvex, 5–7 mm long, obscurely ribbed dorsally, smooth ventrally. At La Selva collected in flower and fruit May–September. Belize and Guatemala to Brazil and Bolivia in wet forests at 0–800 m.

FIGURE 6i, j.

This species is occasional in light gaps on ridges in primary forest.

15. *Psychotria eurycarpa* Standley

Erect glabrous shrubs or trees 2–7 m tall, much-branched; stems terete. *Leaf* blades oblong to broadly elliptic, 9–20 cm long, 3.5–9(–12) cm wide, acute to acuminate at apex, acute to attenuate at base, thinly chartaceous to membranaceous, green and shiny on both sides; secondary veins 5–9 pairs, looping to interconnect, prominulous below, without domatia; petioles 10–25 mm long; stipules persistent, membranaceous, appressed, connate interpetiolarly and intrapetiolarly, 1.5–2 mm long, rounded to truncate or shallowly bilobed. *Inflorescences* terminal, with cymes open, corymbiform, rounded, green, 3–4 cm long, 5–10 cm wide, glabrous; peduncles 1–5 cm long; pedicels 0–1 mm long; *flowers* distylous, 5-merous; calyx limb 0.3–0.5 mm long, dentate; corolla white, salverform, glabrous, tube 10–15 mm long, lobes ca. 8 mm long. *Fruits* globose, 15–25 mm in diameter, succulent, purple-black; pyrenes planoconvex, 12–17 mm long, 3–5-ribbed or angled dorsally, smooth with a median sulcus ventrally. At La Selva collected in flower March, in fruit March of the following year. Costa Rica and western Panama, in wet forests at 0–1,500 m.

FIGURE 3m.

This species is occasional on slopes and ridges in primary forest. Its breeding biology was studied by Bawa and Beach (1983) as “*Coussarea* sp. voucher JHB 1424.” *Psychotria eurycarpa* is similar to *Coussarea psychotrioides*; the distinctions between them are outlined in the treatment of that species.

16. *Psychotria glomerulata* (J. Donnell Smith)
Steyermark
(=*Cephaelis glomerulata* J. Donnell Smith)

Erect glabrous shrubs 0.5–1(–2) m tall, much-branched; stems quadrate. *Leaf* blades narrowly elliptic to oblong, (5–)10–13 cm long, (15–)25–55 mm wide, acuminate at apex, attenuate at base, chartaceous, green on both surfaces; secondary veins 12–16(–20) pairs, looping to interconnect near margins, prominulous above and below, without domatia; petioles 5–15 mm long; stipules persistent, membranaceous, appressed, connate interpetiolarly and intrapetiolarly, truncate, 1.5–3 mm long, with two groups of 6–12 caducous awns 0.5–1 mm long. *Inflorescences* terminal, with cymes capitate, ovoid, pale green to purple, 1.5–2.5 cm long, glabrous; peduncles 0–15 mm long; involucre bracts broadly ovate, 10–15 mm long, rounded, floral bracts ovate, 8–10 mm long; *flowers* distylous, 5-merous; calyx limb 0.5–1 mm long, partially lobed; corolla white, funnellform, glabrous, tube 10–15 mm long, lobes 2.5–3 mm long. *Fruits* ovoid to cylindrical, 10–15 mm long, ca. 5–6 mm in diameter, succulent, bright blue; pyrenes planoconvex, 3–5 mm long, 5-ribbed dorsally, smooth with a median sulcus ventrally. At La Selva collected in flower throughout the year, in fruit May–June. Guatemala to Panama, in wet forests at 0–1,000 m.

FIGURE 1k.

This species is common along trails, on ridges, and in edges of primary forest. The flowers reportedly last for one day.

17. *Psychotria graciliflora* Bentham in Oersted

Erect glabrous shrubs 1–2 m tall, much-branched; stems terete. *Leaf* blades elliptic to obovate, 2.5–5 cm long, 1–1.5 cm wide, acute at apex, attenuate at base, membranaceous, green on both surfaces; secondary veins 5–7 pairs, looping to interconnect near distal margins, indistinct, with two domatia per leaf; petioles 3–10 mm long; stipules deciduous, membranaceous, appressed, connate interpetiolarly, broadly triangular to ovate, 1–2 mm long, with 2 linear erose awns ca. 2 mm long. *Inflorescences* terminal, with cymes open, pyramidal to rounded, green, 10–15 mm long, 1–2 cm wide, glabrous; peduncles 1–2 cm long; *flowers* distylous, 5-merous; calyx limb to 1 mm long, truncate to dentate; corolla white, funnellform, glabrous, tube ca. 3 mm long, lobes ca. 1 mm long. *Fruits* globose, ca. 5 mm in diameter, succulent, red; pyrenes planoconvex, ca. 4 mm in diameter, 4–5-ribbed dorsally, smooth with a median keel ventrally. At La Selva collected in flower May, in fruit Au-

gust–December. Southern Mexico to Panama, in wet forests from sea level to 2,500 m.

FIGURE 2q.

This species is locally common in low areas in primary forest. It resembles *Psychotria chagrensis* in its clustered leaves and general flat-topped aspect; the distinctions between these species are outlined in the treatment of the latter species.

18. *Psychotria grandis* Swartz

Erect glabrous shrubs or trees 4–7 m tall, much-branched; stems terete. *Leaf* blades narrowly elliptic to lanceolate or obovate-oblong, (12–)15–35 cm long, 4–13 cm wide, acuminate at apex, attenuate at base, membranaceous to chartaceous, green on both surfaces or the midrib sometimes white; secondary veins 12–15 pairs, looping to interconnect near margins, prominulous above and below, without domatia; petioles 0–4 cm long; stipules usually persistent, appressed, connate interpetiolarly, broadly triangular to ovate, ca. 20 mm long, acuminate. *Inflorescences* terminal, with cymes open, pyramidal, green, 5–15 cm long, 4–8 cm wide, puberulent; peduncles 3–15 cm long; pedicels ca. 1 mm long; *flowers* distylous, 5-merous; calyx limb to 1 mm long, truncate to dentate; corolla cream to greenish white, funnellform, glabrous, tube 2–3 mm long, lobes ca. 1.5 mm long. *Fruits* globose, 5–7 mm in diameter, succulent, red or black; pyrenes planoconvex, ca. 5 mm long, obscurely 6–10-ribbed dorsally, smooth with a median sulcus ventrally. At La Selva collected in flower March, in fruit August. Guatemala and the Greater Antilles to Venezuela and Ecuador in wet forests at 0–500(–2,000) m. FIGURE 5n.

Mature individuals are known only from riparian and old alluvial forest along the West River Road; juvenile plants are common and conspicuous in old secondary growth in abandoned cacao plantings, but mature individuals are not found here. The large, acuminate, usually persistent stipules are distinctive.

19. *Psychotria guapilensis* (Standley) Hammel
(=*Cephaelis discolor* Polakowsky)

Erect, glabrous, suffruticose herbs to 0.5 m tall, unbranched; stems terete. *Leaf* blades elliptic, 13.5–22.5 cm long, 5.5–10 cm wide, acuminate at apex, acute to attenuate at base, chartaceous, green on both sides; secondary veins 10–14 pairs, not looping to interconnect, prominulous above and below, without domatia; petioles 2–6 cm long; stipules persistent, membranaceous, appressed, connate interpetiolarly, 4–8 mm long, bilobed for ca. $\frac{2}{3}$ their length, lobes recurved.

Inflorescences terminal, with cymes capitate, globose, purple, 15–50 mm in diameter; peduncles 0–2 cm long; involucre bracts ovate, ca. 10 mm long, floral bracts ligulate, 7–10 mm long, strigose to pilose with purple hairs; *flowers* 5(–6)-merous; calyx limb to 1.5 mm long, dentate; corolla pale pink to violet, funnelform, glabrous, tube ca. 2.5 mm long, lobes 1.5–2 mm long. *Fruits* ovoid, ca. 1 cm long, succulent, blue; pyrenes planoconvex, ca. 5 mm long, ca. 4 mm wide, smooth dorsally, smooth with a median sulcus ventrally. At La Selva collected in flower May–July and December, in fruit July–September and December. Nicaragua to Colombia in wet forests at 0–500 m. FIGURE 2j; Croat, 1978: fig. 515.

This rare species is found most frequently in low areas in primary forest, notably along the El Suampo Trail.

20. *Psychotria haematocarpa* Standley

Erect glabrous shrubs to 2 m tall, much-branched; stems terete. *Leaf* blades elliptic-oblong, 5–15 cm long, 2.5–5 cm wide, acute to acuminate at apex, attenuate at base, chartaceous, green on both sides; secondary veins 10–13 pairs, looping to interconnect near margins, prominent below, without domatia; petioles 3–6 mm long; stipules persistent, membranaceous, appressed, connate interpetiolarly and intrapetiolarly, broadly triangular to truncate, ca. 0.5 mm long, with two narrowly triangular deciduous awns 1.5–2(–3) mm long. *Inflorescences* terminal, with cymes capitate, green, 5–10 mm in diameter, puberulous; peduncles 3–4 mm long; floral bracts green, triangular, to 0.5 mm long; *flowers* 5-merous; calyx limb to 0.2 mm long, subtruncate; corollas green to white, funnelform, glabrous, tube ca. 2 mm long, lobes to 0.5 mm long. *Fruits* globose, ca. 5 mm in diameter, succulent, red; pyrenes planoconvex, 4–5-ribbed dorsally, smooth ventrally. At La Selva collected in flower July, in fruit October–December. Nicaragua to Colombia, in wet forests at 0–900 m.

FIGURE 2n.

This species is occasional in primary forest, most frequently on ridges.

21. *Psychotria hebeclada* de Candolle

[=*Psychotria molliramis* (K. Schumann & K. Krause) Steyermark]

Erect, puberulent, suffruticose herbs or shrubs to 1–2 m tall, much-branched; stems terete. *Leaf* blades elliptic to oblong, (3.5–)7.5–17 cm long, (1–)2.5–8 cm wide, acuminate at apex, acute to attenuate at base, membranaceous, green on both sides; secondary veins 8–15 pairs, not looping to interconnect, prominent below, without do-

matia; petioles 3–10 mm long; stipules persistent, membranaceous, appressed, connate interpetiolarly and intrapetiolarly, truncate, 0.3–1 mm long, with two triangular awns 1–3.5 mm long. *Inflorescences* terminal, with cymes congested, pyramidal to conical, green to yellow-green, 2–3 cm long and wide, pilosulous; peduncles 5–45 mm long; floral bracts green, linear, 1.5–6 mm long; pedicels 0–5 mm long; *flowers* distylous, 5-merous; calyx limb 1–3 mm long, lobed nearly to base; corolla white to cream sometimes tinged with green or pink, tubular, glabrous to pilosulous externally, glabrous internally, tube 3–4 mm long, lobes ca. 1.5 mm long. *Fruits* ellipsoid, 3–5 mm in diameter, succulent, blue-black; pyrenes planoconvex, 2.5–4.5 mm long, 3-ribbed or -angled dorsally, smooth with a median sulcus ventrally. At La Selva collected in flower April–August, in fruit May–August. Southern Mexico to Ecuador, in wet and moist secondary growth at 0–1,500 m. FIGURE 2p.

This species is locally common in open secondary habitats near rivers, notably near the end of the West River Road.

22. *Psychotria ipecacuanha* (Broteri) Stokes

[=*Cephaelis ipecacuanha* (Broteri) A. Richard]

Rhizomatous, glabrous to puberulent, suffruticose herbs to 0.3 m tall, little-branched; stems terete. *Leaf* blades broadly elliptic, 10–15 cm long, 5–8 cm wide, acute at apex and base, membranaceous, green on both sides; secondary veins 5–8 pairs, not looping to interconnect, prominent below, without domatia; petioles ca. 5 mm long; stipules persistent, membranaceous, appressed, connate interpetiolarly, triangular, 3–5 mm long, with ca. 7–10 setae 5–6 mm long. *Inflorescences* terminal, with cymes capitate, pale green, ca. 1 cm in diameter, puberulent; peduncles 1–3 cm long, deflexed; floral bracts ovate, 8–10 mm long; *flowers* distylous, 5-merous; calyx limb to 1 mm long, truncate; corolla white, tubular, glabrous, tube ca. 3 mm long, lobes ca. 1.5 mm long. *Fruits* ovoid to globose, ca. 8 mm in diameter, succulent, red then black; pyrenes planoconvex, twisted, 6–7 mm long, smooth dorsally and ventrally. At La Selva collected in flower July, in fruit March. Central and South America, in wet forests at 0–600 m.

FIGURE 1b; Croat, 1978: fig. 516.

This species was reportedly planted by L. Holdridge in the cacao grove just west of the laboratory clearing, and it may now be spreading naturally. It is used locally in folk remedies, and sometimes cultivated and harvested for the pharmaceutical trade as a source of ipecac. The local name is “raicilla.”

23. *Psychotria laselvensis* C. Hamilton

Erect glabrous shrubs 1.5–2.5(–4) m tall, much-branched; stems terete. *Leaf* blades elliptic to oblanceolate, 7–15 cm long, (2–)3–6 cm wide, acute to acuminate at apex, attenuate to truncate or cordate or rarely acute at base, membranaceous, green on both sides; secondary veins 7–12 pairs, obscurely looping to interconnect near margins, prominulous on both sides, with domatia, midrib frequently white on juvenile leaves; petioles 0–2(–5) mm long; stipules deciduous, membranaceous, appressed, connate interpetiolarly, broadly triangular, 2–4 mm long. *Inflorescences* terminal, with cymes open, globose, green, 3–5 cm long and wide, puberulent; peduncles 3–10 cm long; pedicels 0–1 mm long; *flowers* distylous, 5-merous; calyx limb ca. 0.3 mm long, denticulate; corolla white, funnellform, glabrous, tube 1.5–2 mm long, lobes ca. 2 mm long. Mature *fruits* not known. At La Selva collected in flower February–May, in immature fruit July. Known only from the La Selva Biological Station.

FIGURE 4a.

This species is known from one population in the vicinity of the Southwest Corner of the original property and another along the Quebrada Sabalo.

24. *Psychotria luxurians* Rusby

Erect scaberulous shrubs or trees 4–7 m tall, much-branched; stems terete. *Leaf* blades elliptic to oblong, (13–)22–28 cm long, (5–)9–12 cm wide, acute to acuminate at apex, acute or rarely attenuate at base, membranaceous, bright green above, dull pale yellow-green below; secondary veins (8–)12–15 pairs, not looping to interconnect, prominulous below, without domatia; petioles 1–3.5 cm long; stipules usually persistent, membranaceous, appressed, connate interpetiolarly and intrapetiolarly, broadly ovate, 4–9 mm long, entire or minutely bilobed, sometimes splitting to base. *Inflorescences* terminal, with cymes open, pyramidal, green, 10–25 cm long, 9–15 cm wide, puberulous; peduncles 5–10 cm long; *flowers* 5-merous; calyx limb ca. 0.5 mm long, dentate; corolla white to greenish white, tubular, glabrous, tube 1.5–3 mm long, lobes ca. 1 mm long. *Fruits* globose, 5–8 mm in diameter, succulent, blue-black; pyrenes concavoconvex, ca. 3 mm long, 5-ribbed dorsally, smooth with a median sulcus ventrally. At La Selva collected in flower March–July, in fruit July–October. Nicaragua to Bolivia in wet secondary vegetation at 0–1,000 m.

FIGURE 3n.

This species is common in open secondary growth and uncommon in light gaps. *Psychotria luxurians* is similar to *P. berteriana* de Candolle,

which is common elsewhere in secondary vegetation and may be expected here; *Psychotria berteriana* can be separated by its truncate stipules with two deltoid lobes, its lack of bracteoles, and its longer corolla tubes.

25. *Psychotria macrophylla* Ruiz López & Pavón

Erect, glabrous, succulent shrubs or usually suffruticose herbs 0.5–1.5(–2) m tall, usually unbranched; stems terete. *Leaf* blades elliptic to oblong, (9–)20–30(–45) cm long, (3–)6–14 cm wide, acute at apex with a deltoid tip, acute to attenuate at base, membranaceous, dark green above, pale below; secondary veins 10–13 pairs, not looping to interconnect, indistinct, without domatia; petioles 1–7 cm long; stipules usually persistent, connate interpetiolarly, succulent, divergent, triangular, 3–4 mm long, very shortly bilobed. *Inflorescences* pseudoaxillary, with cymes open, pyramidal, green, 3–10 cm long, 4–6 cm wide, puberulous; peduncles 1.5–10(–14) cm long; *flowers* 5-merous; calyx limb to 0.5 mm long, truncate; corolla white, funnellform, glabrous, tube 2–3 mm long, lobes to 1 mm long. *Fruits* ellipsoid to globose, 6–9 mm in diameter, spongy, white; pyrenes planoconvex, ca. 6 mm long, 5-ribbed dorsally, smooth with a median keel ventrally. At La Selva collected in flower and fruit throughout the year. Southern Mexico to Bolivia in wet forest at 0–2,500 m.

FIGURE 6p, q.

This species is rare in shady sandy soil along rivers and streams and also in secondary growth along the West River Road.

26. *Psychotria marginata* Swartz

Erect glabrous shrubs 1.5–2.5(–3) m tall, much-branched; stems terete. *Leaf* blades oblanceolate to elliptic, 10–15(–20) cm long, 3–6 cm wide, acute to acuminate at apex, acute to attenuate at base, membranaceous to somewhat chartaceous, green on both surfaces; secondary veins (9–)12–17 pairs, looping to interconnect near margins, prominulous above and below, with domatia; margins ciliate; petioles 1–2 cm long; stipules deciduous, membranaceous, appressed, connate interpetiolarly, narrowly ovate to lanceolate, 5–12(–16) mm long, acute. *Inflorescences* terminal, with cymes open, pyramidal to rounded, green, 5–15 cm long, 8–10 cm wide; peduncles 3–8 cm long; bracts scarious, narrowly triangular, to 0.3 mm long or frequently lacking; pedicels 1–3 mm long; *flowers* distylous, 5-merous; calyx limb to 0.5 mm long, dentate; corolla white drying yellow, funnellform, glabrous, tube 2–3 mm long, lobes ca. 1 mm long. *Fruits* globose, ca. 5 mm

in diameter, succulent, yellow-orange then red; pyrenes planoconvex, ca. 3 mm long, 5-ribbed dorsally, smooth with a median keel and sulcus ventrally. At La Selva collected in flower July–November, in fruit February–March. Central Mexico and the West Indies to Bolivia in wet secondary growth at 0–600 m. FIGURE 3r.

This species is common in old secondary forest, particularly near the Successional Plots and the end of the West River Road. The prominent domatia and ciliate leaf margins are distinctive. This is one of the few species of *Psychotria* that flowers in the rainiest part of the year. Long-styled Panamanian plants produced significantly more fruit than short-styled plants (Hamilton, 1989).

27. *Psychotria microbotrys* Ruiz López ex Standley

Erect glabrous shrubs 1–2(–3.5) m tall, much-branched; stems quadrate. *Leaf* blades broadly elliptic, 15–25 cm long, 7–12 cm wide, acute to abruptly acuminate at apex with a deltoid tip, acute to cuneate at base, chartaceous, satiny green above, duller green often mottled with dull purple below; secondary veins 8–13 pairs, not looping to interconnect, prominulous above and below, without domatia; petioles 5–20 mm long; stipules persistent, membranaceous to foliaceous, appressed, connate interpetiolarly, 10–20 mm long, bilobed for $\frac{2}{3}$ to all of its length, lobes broadly acuminate. *Inflorescences* terminal, with cymes open, pyramidal, green becoming purple in fruit, 4–7 cm long, 5–8 cm wide, glabrous; peduncles 3–6 cm long; floral bracts green, narrowly triangular, to 1 mm long or frequently lacking; pedicels 0–1 mm long; *flowers* 5-merous; calyx limb to 0.2 mm long, dentate; corolla cream to yellow, funnellform, glabrous, tube 1.5–2(–3) mm long, lobes ca. 1 mm long. *Fruits* globose, ca. 8 mm in diameter, spongy, white; pyrenes planoconvex, 2.5 mm long, 5-ribbed dorsally with rugose cross-ribbing, smooth with a deep median sulcus ventrally. At La Selva collected in flower May–July, in fruit July–November. Costa Rica to Peru in wet forests at 0–1,500 m. FIGURE 2c.

This species is common in forest edges and light gaps and in old secondary forest.

28. *Psychotria officinalis* (Aublet) Raeuschel ex Sandwith

Erect glabrous shrubs or small trees 1.5–4 m tall, much-branched; stems terete. *Leaf* blades elliptic, 10–25 cm long, 4–8(–12) cm wide, acuminate at apex with tip often curved, acute to cuneate at base, chartaceous, green on both sur-

faces; secondary veins (6–)8–11 pairs, not looping to interconnect, prominulous below, without domatia; petioles 5–15 mm long; stipules persistent, membranaceous, appressed, connate interpetiolarly and intrapetiolarly, truncate, 1–2 mm long, with two lobes 1–2.5 mm long, acute. *Inflorescences* terminal, with cymes congested, pyramidal, green, 1.5–4 cm long, 2.5–6 cm wide, pilosulous; peduncles 1–3.5(–5) cm long; floral bracts green becoming purple in fruit, ligulate, 3–5 mm long; *flowers* distylous, 5-merous; calyx limb to 0.3 mm long, dentate; corollas white, funnellform, glabrous, tube 2–3 mm long, lobes ca. 1 mm long. *Fruits* globose, ca. 6 mm in diameter, succulent, purple-black; pyrenes planoconvex, 2–3 mm long, 5-ribbed dorsally, smooth with a T-shaped median sulcus ventrally. At La Selva collected in flower June–March, in fruit March–May, frequently concurrently. Central Mexico and the West Indies to Colombia and the Guianas in wet forests and edges at 0–300 m. FIGURE 3g, h.

This species is common throughout the forest but most frequently found on slopes, ridges, light gaps, and edges in primary forest. Its breeding biology was studied by Bawa and Beach (1983). *Psychotria officinalis* is similar to *P. brachybotrya*; the distinctions between them are outlined under the treatment of that species.

29. *Psychotria orchidearum* Standley

Decumbent, epiphytic, succulent, glabrous shrubs or suffruticose herbs to 1 m tall, much-branched; stems terete. *Leaf* blades oblong-lanceolate, 3–12 cm long, 1.5–4 cm wide, acute to acuminate at apex, rounded to acute at base, coriaceous; secondary veins 4–7 pairs, not looping to interconnect, indistinct, without domatia; petioles 2–6 mm long; stipules persistent, scarious, appressed, connate interpetiolarly and intrapetiolarly, truncate, (1–)2–4 mm long. *Inflorescences* terminal, with cymes open, rounded, green, 2–5 cm long, 4–6 cm wide, glabrous; peduncles 1–2 cm long; pedicels 0–2 mm long; *flowers* 5-merous; calyx limb ca. 0.3 mm long, dentate; corollas white or flushed with pink, tubular, glabrous, tube 1.5–2 mm long, lobes to 1 mm long. *Fruit* subglobose, ca. 5 mm in diameter, succulent, becoming red then purple-black; pyrenes (4–)5(–6), planoconvex, ca. 3 mm long, smooth dorsally and ventrally. At La Selva collected in fruit June–December. Nicaragua to Panama in wet forests at 100–2,200 m. FIGURE 3f.

This species is an epiphyte in the primary forest canopy. The leaf margins are sometimes hyaline. Two other epiphytic species of Rubiaceae occur at La Selva, one in *Cosmibuena* and one in *Hillia*.

30. *Psychotria panamensis* Standley var. **compressicaulis** (K. Krause) C. Hamilton
(=*Psychotria grandistipula* Standley)

Erect puberulent shrubs or trees 3–10 m tall, much-branched; stems terete. *Leaf* blades broadly elliptic to obovate, (6–)12–25 cm long, (2.5–)6–16 cm wide, acute to acuminate at apex with broad tip to 1.5 cm long, acute to obtuse or sometimes cordate in juvenile leaves at base, thickly membranaceous, green on both sides; secondary veins 10–20 pairs, looping to interconnect near margins, prominulous above and below, without domatia; petioles 5–50 mm long; stipules caducous, membranaceous, appressed, connate interpetiolarly and intrapetiolarly into a conical cap 30–45 mm long. *Inflorescences* terminal, with cymes open, rounded to pyramidal, green, ca. 6 cm long and wide increasing to twice as large in fruit, puberulent; peduncles 0–15 mm long; floral bracts scarious, deltoid, to 0.5 mm long, deciduous or lacking; pedicels ca. 1 mm long; *flowers* sessile, congested in small capitulae, monomorphic, short-styled, 5-merous; calyx limb to 0.3 mm long, truncate to sinuous; corolla white, tubular, glabrous, tube ca. 2 mm long, lobes ca. 1 mm long. *Fruits* globose, 7–9 mm in diameter, succulent, red; pyrenes planoconvex, ca. 7 mm long, 4–5-ribbed dorsally, smooth with a faint median keel ventrally. At La Selva collected in flower July–August, in fruit January. *Psychotria panamensis* is found from southern Mexico through Panama at 0–1,200 m; var. *compressicaulis* is known from wet forests in Nicaragua and Costa Rica at 0–200 m. FIGURE 5e, f.

This species is common and widespread in primary forest. It has the largest stature of the species of *Psychotria* found here.

Psychotria panamensis var. *compressicaulis* is somewhat similar to *P. limonensis*, which might be expected; that species is a small understory shrub or suffruticose herb that can be separated by its ovate interpetiolar stipules about 6 mm long.

31. *Psychotria pilosa* Ruiz López & Pavón
(=*Psychotria costaricensis* Polakowsky)

Erect pilose shrubs (0.5–)1–2.5 m tall, much-branched; stems terete. *Leaf* blades elliptic to oblong, 15–26 cm long, (5–)7–11 cm wide, acute to acuminate at apex, truncate to attenuate at base, membranaceous, green on both sides; secondary veins 16–22 pairs, looping to interconnect near margins, prominulous below, without domatia; petioles (1–)2–3(–4.5) cm long; stipules persistent, connate interpetiolarly, membranaceous or lobes scarious, appressed, broadly triangular, 15–20 mm long, bilobed for $\frac{1}{3}$ – $\frac{1}{2}$ their

length. *Inflorescences* terminal often becoming pseudoaxillary in fruit, with cymes narrowly pyramidal to cylindrical, congested, green, 5–10 cm long, 3–5 cm wide, pilose; peduncles 2–9 cm long, frequently deflexed; floral bracts green, ovate to triangular, 4–5 mm long; *flowers* monomorphic, 5-merous; calyx green, ca. 1 mm long, divided to base; corolla greenish white, funnelform, glabrous, tube 2.5–3 mm long, lobes ca. 1 mm long. *Fruits* ellipsoid to globose, ca. 5 mm in diameter, spongy, bright blue; pyrenes narrowly ovate, ca. 2.5 mm long, 5-ribbed dorsally, smooth with a deep median sulcus ventrally. At La Selva collected in flower June–August, in fruit August–December. Nicaragua to Peru in wet forests at 0–1,200 m. FIGURE 2a.

This species is occasional in old secondary forest and forest edges. *Psychotria pilosa* is similar to *P. pittieri*; the distinctions between them are outlined in the treatment of that species.

32. *Psychotria pittieri* Standley

Erect shrubs or suffruticose herbs 0.5–2 m tall, much-branched; stems terete, tomentose to glabrate. *Leaf* blades elliptic to oblong, (8–)10–12(–15) cm long, 2.5–4(–5.5) cm wide, acuminate at apex, acute to attenuate at base, membranaceous, somewhat bullate, green on both sides, glabrescent above, pilose below on veins; secondary veins 12–17 pairs, usually looping to interconnect near margins, prominulous below, without domatia; petioles 5–10(–20) mm long; stipules persistent, membranaceous, appressed, connate interpetiolarly and intrapetiolarly, truncate, ca. 2 mm long, with two acuminate awns 2–4 mm long. *Inflorescences* terminal, with cymes open, pyramidal, green, 1.5–4 cm long, 2–4 cm wide, pilose to tomentose; peduncles 1–2.5 cm long, frequently deflexed; *flowers* 5-merous; calyx green, to 0.5 mm long, dentate; corolla white to cream, glabrous, funnelform, tube ca. 1.5 mm long, lobes ca. 0.5 mm long. *Fruits* ellipsoid to globose, ca. 6 mm in diameter, spongy, bright blue; pyrenes planoconvex, 2–3 mm long, obscurely 4-ribbed dorsally, smooth with a median sulcus ventrally. At La Selva collected in flower May–July, in fruit December–April. Guatemala to Panama in wet forests at 0–1,000 m.

FIGURE 2k.

This species is common in secondary forest edges, notably along the walk between the bunkhouse and the laboratory clearing. *Psychotria pittieri* is similar to *P. pilosa* and *P. brachiata*; these species both differ in their larger leaves and more congested inflorescences and additionally *P. brachiata* has glabrous stems, *P. pilosa* more numerous secondary leaf veins.

33. *Psychotria poeppigiana* Mueller Argoviensis
[=*Cephalis tomentosa* (Aublet) Vahl]

Erect pilose to hirsute shrubs 1–2.5 m tall, much-branched; stems terete. *Leaf* blades elliptic, 12–23 cm long, 4–9 cm wide, acuminate at apex, acute to attenuate at base, membranaceous, green on both sides; secondary veins 9–14 pairs, not looping to interconnect, impressed above, prominent below, without domatia; petioles 5–20(–40) mm long; stipules persistent, membranaceous, appressed, connate interpetiolarly and intrapetiolarly, truncate, 2–6 mm long, with two narrowly triangular awns 10–11 mm long. *Inflorescences* terminal, with cymes capitate, 3–6 cm in diameter excluding involucre bracts; peduncles (2.5–)4–6(–12) cm long; involucre bracts bright red, broadly ovate, 20–30(–60) mm long, floral bracts ovate, 10–15 mm long; *flowers* distylous, 5-merous; calyx to 0.5 mm long, dentate; corolla yellow, funnellform, pilose externally, glabrous internally, tube ca. 10 mm long, lobes 1–2 mm long. *Fruits* ovoid to cylindrical, 1–1.5 cm long, 7–8 mm in diameter, succulent, bright blue; pyrenes planoconvex to concavoconvex, 5–7 mm long, 5-ribbed dorsally, sometimes with a median sulcus ventrally. At La Selva collected in flower throughout the year, in fruit August–October. Central Mexico to Bolivia and Brazil, common in wet primary and secondary forests at 0–900 m.

FIGURE 2e; Croat, 1978: fig. 517.

This species is common, particularly along trails, near open swamps, and in old secondary forest. Its pollinators were studied by Freeman and Stiles (1990). This species, and the similar but glabrous *Psychotria elata*, are striking when in flower and because of their inflorescences are often called “hot lips.”

34. *Psychotria polyphlebia* J. Donnell Smith

Erect, rhizomatous, glabrous, suffruticose herbs 30–50 cm tall, unbranched; stems terete. *Leaf* blades oblong to obovate, 10–17 cm long, 4–7.5(–8) cm wide, acute to rounded or shortly acuminate at apex, acute to attenuate at base, stiffly chartaceous, strongly bullate, green on both sides or paler below, sparsely pilose below; secondary veins 20–30 pairs, looping to interconnect near margins, prominent above and below, without domatia; petioles 1.5–6(–8) cm long, pilose; stipules deciduous, succulent, divergent, connate interpetiolarly, triangular, 2–3 mm long. *Inflorescences* pseudoaxillary, with cymes congested, globose, green, 1–2(–2.5) cm in diameter, puberulous to pilosulous; peduncles 1–4.5 cm long; floral bracts ovate to ligulate, green, 5–7 mm long, acute; *flowers* 5-merous; calyx ca. 1 mm long, dentate; corolla white, glabrous, funnel-

form, tube 4–5 mm long, lobes ca. 1 mm long. *Fruits* globose to ellipsoid, ca. 8 mm in diameter, succulent, orange then black; pyrenes planoconvex, 5–7 mm long, 5-ribbed dorsally, smooth with a median keel ventrally. At La Selva collected in flower May–August, in fruit September–November. Nicaragua to Colombia in wet forests at 0–1,200 m.

FIGURE 6l, m.

This species is rare in general although common locally in the primary forest, probably due to its rhizomatous habit. It is found along the Quebrada El Salto near the South Boundary. The leaves are usually clustered near the base of the plant.

35. *Psychotria psychotriifolia* (Seemann) Standley

Erect glabrescent to puberulent shrubs 0.5–1.5 m tall, much-branched; stems terete, distal internodes ferruginous-tomentose. *Leaf* blades oblanceolate to spatulate or elliptic, 9–15 cm long, 2–5 cm wide, acute at apex, attenuate at base, membranaceous, green on both sides; secondary veins 12–18 pairs, looping to interconnect in a marked submarginal vein, prominulous, without domatia; petioles 0–5 mm long; stipules deciduous, scarious, appressed, connate interpetiolarly and intrapetiolarly but splitting along one side, triangular to truncate, 10 mm long, with a single awn 5 mm long. *Inflorescences* terminal, with cymes rounded, paniculate to umbellate or fasciculate, green, 1–3 cm long and wide, capitulae in groups of three, 3–8 mm in diameter; peduncles 5–10 mm long; floral bracts and bracteoles green, 3–5 mm long; *flowers* distylous, 5-merous; calyx limb ca. 1.5 mm long, deeply lobed; corolla white, glabrous, tubular, tube 1–2 mm long, lobes ca. 1 mm long. *Fruits* ovoid, 5–7 mm in diameter, succulent, red; pyrenes planoconvex, ca. 4.5 mm long, 4–5-ribbed dorsally, smooth and sometimes with a faint median sulcus ventrally. At La Selva collected in flower February–July, in fruit June–October, frequently concurrently. Southern Nicaragua to northern South America in wet forests at 0–800 m.

FIGURE 6a, b; Croat, 1978: fig. 533.

This species is common on shady banks along the Ríos Puerto Viejo and Sarapiquí.

36. *Psychotria racemosa* (Aublet) Raechel

Erect puberulent shrubs 0.5–2 m tall, much-branched; stems terete. *Leaf* blades elliptic, 10–18(–24) cm long, 3–6(–7.5) cm wide, acute to acuminate at apex, acute to cuneate at base, membranaceous to somewhat chartaceous, green on both sides; secondary veins 12–14 pairs, not looping to interconnect, prominulous below,

without domatia; petioles 5–10(–20) mm long; stipules persistent, membranaceous, appressed, connate interpetiolarly and intrapetiolarly, truncate, 1–4 mm long, with two linear awns 7–15 mm long. *Inflorescences* terminal, with cymes narrowly pyramidal to cylindrical, open to somewhat congested, green, 1–4 cm long and wide, puberulent; peduncles 1–2 cm long; floral bracts linear, to 2 mm long; *flowers* 5-merous; calyx limb to 0.2 mm long, dentate; corolla white or lobes frequently green, glabrous, tubular, tube 1.5–3 mm long, lobes to 0.5 mm long. *Fruits* globose, ca. 7 mm in diameter, succulent, orange then red then black; pyrenes 5, triangular, ca. 4 mm long, 3-ribbed dorsally, smooth on sides with a sulcus on the ventral corner. At La Selva collected in flower March–June, in fruit June–February. Central Mexico to Brazil and Bolivia in wet forest at 0–1,000 m.

FIGURE 2d; Croat, 1978: fig. 534.

This species is common, particularly in old secondary forest and occasionally also in primary forest.

37. *Psychotria siggersiana* Standley

Erect, glabrescent to puberulent, succulent, suffruticose herbs ca. 0.6 m tall, unbranched; stems terete. *Leaf* blades elliptic, 12–20 cm long, 6–9.5 cm wide, acute to acuminate at apex, acute to cuneate at base, membranaceous, green on both sides or paler below, tomentose to pilose on young leaves; secondary veins 10–12 pairs, looping to interconnect near apex, prominulous below, without domatia; petioles 3–5.5 cm long; stipules deciduous, succulent, divergent, connate interpetiolarly and intrapetiolarly, truncate, 3–6 mm long, with bifid conical appendage 2–4 mm long. *Inflorescences* pseudoaxillary, with cymes congested, pyramidal, green, 2(–8) cm long and wide; peduncles 1–2(–4) cm long; floral bracts lanceolate, green, ca. 5 mm long, ciliate; *flowers* in glomerules, 5-merous; calyx limb to 0.5 mm long, dentate; corolla white, glabrous, funnelform, tube ca. 3 mm long, lobes ca. 1 mm long. *Fruits* globose, ca. 6 mm in diameter, succulent, red; pyrenes 1–2, concavoconvex, ca. 4 mm long, smooth dorsally, smooth with a median sulcus ventrally. At La Selva collected in fruit November. Costa Rica and western Panama in wet forests of Caribbean slopes at 100–1,200 m. FIGURE 7c, d.

This species is known from only one plant on the banks of the Quebrada El Salto along the South Boundary.

38. *Psychotria suerrensii* J. Donnell Smith

Erect glabrous shrubs 1–4 m tall, much-branched; stems terete. *Leaf* blades elliptic to

oblong, 12–20(–27) cm long, 5–9(–12) cm wide, acute to acuminate at apex, acute to attenuate at base, chartaceous, somewhat bullate, green above, green or sometimes flushed with purple below; secondary veins 8–13 pairs, looping to interconnect near margins, prominulous above and below, without domatia; petioles 1–7 mm; stipules persistent, membranaceous, appressed, connate interpetiolarly and intrapetiolarly, truncate, 1–2 mm long, with two subulate to lanceolate awns 3–5 mm long. *Inflorescences* terminal, with cymes congested, subglobose, green or flushed with purple, 2–6 cm in diameter, puberulent; peduncles 1–2.5 cm long; bracts foliaceous, pale green becoming purple, oblong to elliptic, 10–15 mm long; *flowers* distylous, 5-merous; calyx limb to 0.3 mm long, dentate; corolla white, funnelform, puberulent, tube ca. 10 mm long, lobes ca. 3 mm long. *Fruits* globose, ca. 8 mm in diameter, succulent, blue; pyrenes concavoconvex, 3–3.5 mm long, 5-ribbed with rugose cross-ribbing dorsally, smooth with a median sulcus ventrally. At La Selva collected in flower February–March, in fruit July–February. Nicaragua to Panama in wet forests at 0–300 m. FIGURE 2l.

This species is common on slopes and ridges in primary forest. The pith frequently turns red-purple when exposed to air and dried specimens frequently have a purple cast. Its breeding biology was studied by Bawa and Beach (1983).

39. *Psychotria uliginosa* Swartz

Erect, glabrous, suffruticose herbs 0.5–1 m tall, unbranched; stems terete. *Leaf* blades oblong-obovate, 20–31 cm long, 6–12 cm wide, acute to acuminate at apex, acute to attenuate at base, coriaceous to succulent, dark glossy green above, pale below; secondary veins 15–20 pairs, not looping to interconnect, prominulous below, without domatia; petioles 2–7 cm long; stipules persistent, succulent, divergent, connate interpetiolarly, truncate to triangular, 3–5 mm long, with a bifid conical appendage 5–6 mm long. *Inflorescences* pseudoaxillary, with cymes broadly pyramidal, open, green, 2–3 cm long and wide, glabrous; peduncles 2–6 cm long, elongating in fruit; *flowers* in small glomerules, 5-merous; calyx limb to 0.5 mm long, truncate; corolla white, glabrous, funnelform, tube ca. 1.5 mm long, lobes ca. 1 mm long. *Fruits* globose to ellipsoid, ca. 1 cm in diameter, succulent, red or black; pyrenes planoconvex, ca. 8 mm long, flattened, with marginal and median keel thickened dorsally, smooth with median keel ventrally. At La Selva collected in flower and fruit February–October. Southern Mexico and the West Indies to northwestern South America in wet forests at 0–1,000 m.

FIGURE 7a, b.

This species is rare in low areas in primary forest along shady stream banks.

31. *RANDIA* Linnaeus

Erect monoecious or dioecious or rarely hermaphroditic shrubs, trees, or lianas, often armed with thorns. *Leaves* opposite or verticillate, without domatia; stipules interpetiolarly and sometimes also intrapetiolarly connate, deciduous or rarely persistent, triangular. *Inflorescences* terminal or axillary, open to contracted cymose or reduced to a solitary flower; flowers unisexual or rarely hermaphroditic and monomorphic, 5(–7)-merous; corollas funnelform to salverform, white, aestivation convolute; ovary unilocular; ovules numerous and horizontal on parietal placentas. *Fruits* baccate, fleshy; seeds flattened, smooth, pulp mucilaginous and usually brown.

Randia includes about 60–70 species found throughout the neotropics; about 25 occur in Costa Rica. The white flowers are strongly fragrant at night but become odorless and yellowed when old. The pollen is arranged in permanent tetrads. Several species are cultivated as ornamentals. The fruits of some species are edible.

KEY TO THE SPECIES

1. Lianas climbing by recurved thorns; calyx limb divided to base, lobes 11–30 mm long; fruit cylindrical to ellipsoid, 7–9 cm long. 3. *R. pepoformis*.
 1. Erect trees or shrubs, sometimes armed with ascending to spreading straight thorns; calyx limb with well developed tube 3–35 mm long, lobes 2–20 mm long; fruit globose to ellipsoid, 3–7 cm long.
 2. Internodes developed, the leaves distributed along stems; bark red-brown; plants unarmed, cauliflorous; leaves pale beneath. 2. *R. mira*.
 2. Internodes not all developed, the leaves frequently clustered at stem apices; bark grey to dull brown; plants armed; flowers terminal on young stems; leaves not pale beneath.
 3. Leaves 12–25 cm long, subcoriaceous; stipules 5–8 mm long; young stems glabrescent; calyx tube 3–5 mm long, lobes 2–3 mm long; corolla tube 15–18 mm long, lobes 12–15 mm long; fruit 3–3.5 cm long. 1. *R. grandifolia*.
 3. Leaves 15–35 cm long, chartaceous; stipules 15–25 mm long; young stems pilosulous; calyx tube 18–35 mm long, lobes 8–20 mm long; corolla tube 70–95 mm long, lobes 5–6 cm long; fruit 6–7 cm long. 4. *R. sp. A*.
1. ***Randia grandifolia*** (J. Donnell Smith) Standley
(=*Randia diversifolia* Standley)
- Glabrescent dioecious shrubs or trees to 5 m tall, armed with ascending straight thorns 3–10

mm long. *Leaves* opposite, clustered near ends of branches; blades elliptic to lanceolate, 12–25 cm long, 5–12 cm wide, acute at apex, cuneate to attenuate at base, subcoriaceous; secondary veins 9–12 pairs; petioles 0–12 mm long; stipules connate interpetiolarly, 5–8 mm long, acute. *Inflorescences* terminal; staminate flowers 1–5, fascicled, pistillate flowers solitary; bracts lacking; *flowers* 5-merous, subsessile; calyx glabrescent, limb green, partially divided, tube 3–5 mm long, truncate, lobes narrowly triangular to lanceolate, 2–3 mm long, acute; corolla salverform, glabrous, tube 15–18 mm long, lobes broadly ovate, 12–15 mm long, acute to acuminate. *Fruits* globose to ellipsoid, 3–3.5 cm in diameter, yellow to orange; seeds orbicular to elliptic, ca. 8 mm in diameter, pulp yellow or orange. At La Selva collected in flower February–March and August, in fruit June. Nicaragua to Panama in wet forest at 100–1,200 m. FIGURE 4k.

This species is occasional in forest along streams.

2. *Randia mira* Dwyer

Glabrescent dioecious shrubs or trees to 8 m tall, unarmed. *Leaves* opposite, distributed along stems; blades elliptic to obovate, 30–42 cm long, 8–14 cm wide, acute at apex, cuneate at base, subcoriaceous; secondary veins 10–16 pairs; petioles 5–15 mm long; stipules connate interpetiolarly, 6–7 mm long, acute to acuminate. *Flowers* cauliflorous, solitary, subsessile, 6–7-merous; calyx puberulent, limb green, partially divided, tube 12–15 mm long, truncate, lobes linear, 3–4 mm long, acute; corolla salverform, puberulent externally, barbate in throat, tube 55–70 mm long, lobes lanceolate, 50–65 mm long, acute. *Fruits* globose to ellipsoid, 6–7 cm in diameter, yellow to yellow-orange; seeds elliptic, 8–10 mm in diameter. At La Selva collected in flower May–June, in fruit January and October–November. Costa Rica and Panama in wet forests of Caribbean slopes at 100–750 m. FIGURE 4c.

This species is uncommon near streams in the southern part of the property. This is the first description of the fruit of this species.

3. *Randia pepoformis* Dwyer

Glabrescent dioecious lianas climbing to 22 m by curved thorns 10–15 mm long. *Leaves* opposite, clustered near ends of branches; blades elliptic to obovate, 10–18 cm long, 4–8 cm wide, acute to acuminate at apex, cuneate to attenuate at base, chartaceous to subcoriaceous; secondary veins 7–8 pairs; petioles 5–10 mm long; stipules interpetiolarly and shortly intrapetiolarly connate, 2–5 mm long, rounded to acute. *Inflores-*

cences terminal; peduncles 0–1 cm long; *flowers* subsessile, 5(–6)-merous; staminate flowers 1–3, fasciculate, pistillate flowers solitary; calyx glabrous, limb green, divided to base, lobes narrowly elliptic to oblanceolate, 11–30 mm long, acute; corolla salverform, glabrous externally, barbate in throat, tube 30–45 mm long, lobes broadly obovate to orbicular, 18–25 mm long, rounded. *Fruit* ovoid to cylindrical, 5–9 cm long, 3–4.5 cm in diameter, yellow; seeds oblong to elliptic, ca. 10 mm long, ca. 8 mm wide. At La Selva collected in flower March and May–October. Costa Rica and Panama in wet forests of Caribbean slopes and Osa Peninsula at 100–800 m.

FIGURE 3v.

This species is known only from scattered individuals on ridges in primary forest along the Hartshorn, Near Loop, and Central Trails. This is the first description of the flowers of this species.

4. *Randia* sp. A

Pilosulous to glabrescent dioecious shrubs or trees to 8 m tall, armed with ascending straight thorns 5–15 mm long. *Leaves* opposite, clustered near ends of branches; blades elliptic to obovate, 15–35 cm long, 7–15 cm wide, acute to acuminate at apex, cuneate at base, chartaceous to subcoriaceous; secondary veins 14–15 pairs; petioles 5–8 mm long; stipules interpetiolarly connate, persistent, 15–25 mm long, acute. *Inflorescences* terminal; bracts triangular, 20–35 mm long; *flowers* subsessile, 5-merous, staminate flowers 2–8, fascicled, pistillate flowers solitary; calyx sericeous to pilosulous, limb green, partially divided, tube 18–35 mm long, truncate, lobes linear to narrowly elliptic, 8–20 mm long, acute; corolla salverform, densely sericeous externally, pilosulous in throat, tube 70–95 mm long, lobes lanceolate, 5–6 cm long, acute to acuminate. *Fruits* globose to ellipsoid, 6–7 cm in diameter, yellow; seeds elliptic, ca. 1 cm long. At La Selva collected in flower May and July, in fruit July–August. Costa Rica in wet forests of Caribbean slopes at 100–450 m.

FIGURE 4m.

This species is known only from a few individuals along streams in the northeastern part of the property. It will be formally described and named by Dr. John Dwyer using an epithet that means “similar to *Genipa*.”

32. *RICHARDIA* Linnaeus

LEWIS, W. H. AND R. L. OLIVER. 1974. Revision of *Richardia* (Rubiaceae). *Brittonia* 26: 271–301.

Erect to decumbent herbs. *Leaves* without domatia; stipules connate interpetiolarly and ad-

nate to petioles, persistent, truncate and lacinate to setaceous. *Inflorescences* terminal, capitate, sessile, subtended by 1–2 pairs of foliaceous bracts; flowers monomorphic, sometimes cleistogamous, 3–6-merous; corollas funnelform to rotate or salverform, aestivation valvate; ovary 2–6-locular; ovules solitary, axile, attached near base. *Fruits* schizocarpous, mericarps dry, indehiscent, 1-seeded; seeds ellipsoid, smooth.

Richardia includes about 15 species found in warm temperate and tropical North and South America and adventive in Africa and Asia. Most of the species occur in Brazil; one is known from Costa Rica.

1. *Richardia scabra* Linnaeus

Pilose to strigose herbs to 30 cm tall. *Leaf* blades subsessile, elliptic to oblanceolate, 2–7 cm long, 5–15 mm wide, acute at apex, acute and usually attenuate at base, membranaceous; secondary veins 2–3 pairs; stipule sheath 1–2 mm long, setae ca. 3–7, 2–4 mm long. *Inflorescences* hemispherical, 1–1.5 cm in diameter; involucre bracts ovate, 1–3 cm long, strigose, with palmate venation; *flowers* (5–)6-merous; calyx glabrescent, limb green, divided to base, lobes narrowly triangular, 2–3 mm long, acute; corolla white to pink, glabrous or pilose at apices of lobes, tube 3–4 mm long, lobes triangular, 1–2 mm long, acute; ovary 3-locular. *Mericarps* planoconvex, papillose, 2–3.5 mm long, 1.5–2 mm wide, inner face with one narrow attachment scar; seeds ca. 2 mm long. At La Selva collected in flower April–June, in fruit May–June. Weedy in warm temperate and tropical North and South America and naturalized in Africa, most frequently found in sandy soils at 0–1,500 m.

FIGURE 1c.

This species is occasional in open areas.

The pantropical weed *Richardia brasiliensis* Gómez Maza is similar and may also be expected; it can be recognized by its hirsute mericarps with two broad attachment scars on the inner face.

33. *RUDGEA* Salisbury

Erect shrubs or small trees. *Leaves* opposite or verticillate, sometimes with domatia; stipules interpetiolarly and sometimes also intrapetiolarly connate, persistent or deciduous, triangular to truncate, usually with several caducous cartilaginous appendages at apex. *Inflorescences* terminal, open cymose to capitate or reduced to a solitary flower, white; *flowers* monomorphic or distylous, 4–5(–8)-merous; corollas funnelform to salverform, white, aestivation valvate; ovules

solitary, erect, basal. *Fruits* drupaceous, fleshy; pyrenes 2, 1-seeded, planoconvex, smooth; seeds ellipsoid, smooth.

Rudgea includes about 150 species found throughout tropical America, most in South America; at least three species occur in Costa Rica. This genus is similar in aspect to some members of *Coussarea* and *Psychotria*, but can be separated by its pectinate stipules with deciduous cartilaginous appendages.

1. ***Rudgea cornifolia*** (Humboldt, Bonpland & Kunth) Standley

Glabrescent, to 6 m tall. *Leaves* opposite; blades elliptic to ovate, 5–15 cm long, 2–9 cm wide, acuminate at apex, truncate to slightly cordate at base, chartaceous; secondary veins 5–9 pairs, with domatia in axils; petioles 1–3 mm long; stipules connate interpetiolarly and intrapetiolarly, 1.5–3 mm long, truncate to rounded, with 5–8 appendages to 1 mm long. *Inflorescences* with cymes open, pyramidal, 1–2.5 cm long, 2–4 cm wide; peduncles 1–4.5 cm long; pedicels 0–5 mm long; *flowers* distylous, 5-merous; calyx glabrous, limb green, 1.5–2.5 mm long, shallowly lobed, lobes triangular, to 0.5 mm long, acute; corolla salverform, glabrous, tube ca. 4 mm long, lobes ligulate, 3.5–4.5 mm long, acute. *Fruits* globose to ellipsoid, 5–6 mm in diameter, white. At La Selva collected in flower May–July, in fruit July–August. Mexico to northern South America, frequent in wet forest at 0–800 m. FIGURE 11.

This species is occasional throughout but most common in low primary forest in the northeastern corner. Shape and size of the leaves and length of the petioles vary widely in this species. Its breeding biology was studied by Bawa and Beach (1983).

34. **SABICEA** Aublet

Frequently suffrutescent vines. *Leaves* opposite or verticillate, without domatia; stipules interpetiolarly connate, persistent, ovate to ligulate. *Inflorescences* axillary, open cymose to glomerulate; *flowers* monomorphic or distylous, 4–6-merous; corollas funnelform to salverform, aestivation valvate; ovary 2–5-locular; ovules numerous and horizontal on axile placentas. *Fruits* baccate, fleshy; seeds angled, reticulate to foveolate.

Sabicea includes about 120–135 species found in tropical America, Africa, and Madagascar; two are known from Costa Rica. Some individuals are difficult to assign to a species and may represent hybrids.

KEY TO THE SPECIES

1. Flowers pedicellate in pedunculate congested cymes, pedicels 2–8 mm long, peduncles 2–8 mm long; pubescence usually appressed; stipules 7–10 mm long. 1. *S. panamensis*.
1. Flowers subsessile in sessile glomerules; pubescence spreading or lacking; stipules 4–6 mm long. 2. *S. villosa*.

1. ***Sabicea panamensis*** Wernham
(=*Sabicea costaricensis* Wernham)

Strigose vines to 4 m high. *Leaves* opposite; blades elliptic to ovate, 6–16 cm long, 2.5–7 cm wide, acute at apex, acute to obtuse at base, chartaceous; secondary veins 7–11 pairs; petioles 5–15 mm long; stipules 7–10 mm long, acute to obtuse. *Inflorescences* with cymes open, 1–2 cm long, 1.5–3 cm wide; peduncles 2–8 mm long; bracts lanceolate to ovate, 2–5 mm long, acute; pedicels 2–8 mm long; *flowers* 5-merous, monomorphic; calyx strigose to pilose, limb green, divided to base, lobes triangular, 2–3 mm long, acute; corollas white, appressed-pilose externally, barbate in throat, tube 6–8 mm long, lobes narrowly triangular, 2–4 mm long, acute. *Fruits* globose, 8–10 mm in diameter, becoming red-pink then blue-purple; seeds ca. 0.5 mm long. At La Selva collected in flower May–August and October–November, in fruit May–June and October. Guatemala to Colombia in wet secondary vegetation at 0–1,200 m. FIGURE 3t, u.

This species is common in thickets and secondary growth.

2. ***Sabicea villosa*** Roemer & Schultes
(=*Sabicea hirsuta* Humboldt, Bonpland & Kunth)

Spreading-pilose vines to 4 m high. *Leaves* opposite; blades elliptic to lanceolate, 3.5–15 cm long, 2–6 cm wide, acute to acuminate at apex, acute and often attenuate at base, chartaceous; secondary veins 7–11 pairs; petioles 2–10 mm long; stipules 4–6 mm long, acute to obtuse. *Inflorescences* glomerulate, sessile, 5–10 mm in diameter; *flowers* sessile, monomorphic, 5-merous; calyx pilose, limb green, divided to base, lobes triangular, 3–5 mm long, acute; corolla white, pilose externally, barbate in throat, tube 4–5 mm long, lobes triangular, 1–1.5 mm long, acute. *Fruits* globose, 5–10 mm in diameter, becoming red then purple-black; seeds ca. 0.3 mm long. At La Selva collected in flower and fruit concurrently March and May–November. Guatemala and the Greater Antilles to northern South America in wet secondary vegetation and open forests at 0–1,200 m. FIGURE 3s.

This species is common in thickets and secondary growth.

35. **SIMIRA** Aublet*Sickingia* Willdenow

Erect shrubs or trees. *Leaves* sometimes pinnatifid, sometimes with domatia; stipules interpetiolarly connate, persistent or caducous, triangular. *Inflorescences* terminal and axillary, open to contracted, paniculate; flowers monomorphic, 4–6-merous; corollas funnelliform to campanulate, aestivation imbricate or open; ovules numerous and horizontal on axile placentas. *Fruits* capsular, loculicidally and basipetally dehiscent, subglobose, woody; seeds angled or flattened, with a membranaceous marginal wing.

Simira includes about 30 species found from Mexico to central South America; one is known from Costa Rica. In some members of this genus, including this, the internal tissues oxidize to a distinctive purple-red color when exposed to air.

1. **Simira maxonii** (Standley) Steyermark
[=*Sickingia maxonii* (Standley) Standley]

Puberulent to glabrescent trees to 18 m tall. *Leaf* blades entire or occasionally pinnatifid with lobes to 1 cm long, broadly elliptic to rhombic, 20–50 cm long, 12–28 cm wide, acute to acuminate at apex, cuneate to usually truncate or rounded at base, chartaceous; secondary veins 12–18 pairs, barbate in axils; petioles 5–10 mm long; stipules caducous, 25–40 mm long. *Inflorescences* with cymes open, pyramidal, 12–22 cm long, 7–18 cm wide; peduncles (0)1–5 cm long; pedicels 1–2 mm long; *flowers* 5-merous; calyx puberulent, limb green, 1.8–2 mm long, about half divided, lobes rounded; corolla pale green to cream, puberulent externally, glabrous internally, tube ca. 4 mm long, lobes ca. 2 mm long, rounded. *Fruits* 4–6 cm long, smooth, pericarp 4–5 mm thick; seeds narrowly rhombic, flattened, 12–20 mm long. At La Selva collected in flower June–July, the fruit maturing over two years. Southern Nicaragua to central Panama in wet forests at 0–200 m. FIGURE 5d.

This species is occasional in the northeastern corner, particularly along streams. The flowers reportedly have a strong odor of chocolate, and the hollow stems sometimes harbor ants.

36. **SOMMERA** Schlechtendal

WILLIAMS, L. O. 1973. *Sommerera* (Rubiaceae) in North America. *Phytologia* 26: 121–126.

Erect shrubs or small trees. *Leaves* with fine venation lineolate, sometimes with domatia; stipules connate interpetiolarly, deciduous, tri-

angular. *Inflorescences* axillary, open cymose; flowers monomorphic, 5-merous; corollas funnelliform to campanulate, aestivation valvate; ovules numerous on axile placentas. *Fruits* baccate, fleshy; seeds angled.

Sommerera includes about 15 species found throughout the neotropics; one is known from Costa Rica.

1. **Sommerera donnell-smithii** Standley
(=*Sommerera grandis* auctt.)

Appressed-sericeous to strigose, to 8 (15) m tall. *Leaf* blades elliptic to obovate, 10–28(34) cm long, 5–12(14) cm wide, acuminate at apex, obtuse to attenuate at base, chartaceous; secondary veins 11–15 pairs, barbate in axils, fine venation lineolate; petioles 12–44 mm long; stipules 14–35 mm long. *Inflorescences* with cymes 3–7 cm long, 3–5 cm wide; peduncles 1–3 cm long; bracts triangular, 1–10 mm long; pedicels 0–4 mm long; calyx limb green, divided to base, lobes triangular, (1)2–4(5) mm long, frequently unequal, acute; corolla funnelliform, pale green to white, pilosulous externally, glabrous internally, tube 3–4 mm long, lobes 2–3 mm long, acute to rounded. *Fruits* globose to ellipsoid, 6–10 mm in diameter, becoming deep red; seeds ca. 0.5 mm long. At La Selva collected in flower and fruit July. Costa Rica and Panama, frequent on wet banks at 100–1,600 m.

This species has been collected once, along the Río Puerto Viejo. It is also known from the ridge along the Río Peje.

37. **SPERMACOCE** Linnaeus

VERDCOURT, B. 1980. Studies in the Rubiaceae-Rubioideae for the "Flora of Tropical East Africa." I. *Kew Bull.* 30: 247–326.

Erect to creeping sometimes suffrutescent herbs. *Leaves* opposite or verticillate, without domatia; stipules interpetiolarly connate and adnate to petioles, persistent, truncate with 3–15 subulate lobes or setae. *Inflorescences* terminal or axillary, glomerulate, subsessile, sometimes subtended by 1–2 pairs of involucreal leaves ("foliaceous bracts"); *flowers* monomorphic or distylous, 4(–5)-merous; calyx lobes 2–4; corollas funnelliform to rotate, aestivation valvate; ovules solitary, basal. *Fruits* capsular, papery to woody, septicidally and basipetally dehiscent, one or both valves then dehiscent basipetally from apex along adaxial face; seeds ellipsoid.

Spermacoce includes about 150 species, some widespread in the New World and adventive elsewhere but many restricted to Brazil.

KEY TO THE SPECIES

1. Corollas 3–3.5 mm long, exceeding calyx lobes; calyx lobes 4, sometimes unequal; inflorescences 5–15 mm in diameter, subtended by one pair of vegetative leaves.
 2. Flowering stems determinate; flowers 5–40 or more in terminal and sometimes also a few axillary glomerules 5–15 mm in diameter; plants drying green or grey. 1. *S. assurgens*.
 2. Flowering stems indeterminate; flowers 3–8 in axillary and rarely terminal glomerules ca. 5 mm in diameter; plants frequently drying blue-green or yellow-green. 3. *S. latifolia*.
1. Corollas to 1.5 mm long, about equal to calyx lobes; calyx lobes 4, sometimes unequal, or 2; inflorescences 3–10 mm in diameter, usually subtended by 1–2 pairs of reduced involucrel leaves.
 3. Leaves 3–10 mm wide, lanceolate to narrowly elliptic, acute at apex, chartaceous. 2. *S. gracilis*.
 3. Leaves 5–20 mm wide, elliptic to ovate or somewhat oblong, obtusely angled to rounded at apex, membranaceous. 4. *B. prostrata*.

1. **Spermacoce assurgens** Ruiz López & Pavón
(=*Borreria laevis* auctt.)

Erect to somewhat decumbent, glabrescent, sometimes suffrutescent herbs to 1 m tall. *Leaves* opposite, subsessile; blades elliptic to lanceolate, 15–65 mm long, 8–25 mm wide, acute at apex, acute and usually attenuate at base, chartaceous; secondary veins 4–6 pairs; stipule sheath 1–2.5 mm long, lobes and setae ca. 5–8, 1–4 mm long. *Inflorescences* terminal and sometimes axillary, 5–15 mm in diameter, usually subtended by 1 pair of vegetative leaves; bracts to 2 mm long; *flowers* subsessile, monomorphic; calyx sparsely pilosulous, limb green, divided to base, lobes triangular, 0.5–1 mm long, usually in unequal pairs, acute; corolla white, funnellform, membranaceous, glabrous externally, barbate in throat, tube slender, 3–3.5 mm long, lobes triangular, ca. 1.5 mm long, acute. *Fruits* ellipsoid, papery, 1.5–2 mm long; seeds planoconvex to ellipsoid with a longitudinal furrow on the adaxial face. At La Selva collected in flower and fruit March, May–August, and October. Weedy and common throughout tropical America. FIGURE 1h.

This species is common in open weedy areas.

2. **Spermacoce gracilis** Ruiz López & Pavón
(=*Borreria ocymoides* auctt., in part, *Borreria repens* de Candolle, *Spermacoce mauritiana* Gideon)

Weakly to strongly erect, hispidulous to glabrate herbs to 0.4 m tall. *Leaves* opposite, subsessile; blades lanceolate to narrowly elliptic, 10–25 mm long, 3–10 mm wide, acute at apex and

base, chartaceous; secondary veins 3–4 pairs; stipule sheath ca. 1 mm long, lobes and setae 6–8, ca. 2 mm long. *Inflorescences* axillary and also terminal, 3–10 mm in diameter, usually subtended by 1–2 pairs of involucrel leaves, these lanceolate to narrowly elliptic, 5–10 mm long; *flowers* subsessile, monomorphic; calyx limb green, divided to base, lobes triangular, 0.8–1.2 mm long in unequal pairs, acute; corolla white, glabrous, rotate, 1–1.5 mm long, lobes triangular, about half this length. *Fruits* ellipsoid to obconic, laterally compressed, papery, ca. 1 mm long; seeds planoconvex to ellipsoid with a longitudinal furrow on the adaxial face. At La Selva collected in flower and fruit May. Weedy and widespread throughout the tropics. FIGURE 1j.

This species shows considerable morphological variation over its range; the description presented here applies to the plants found at the La Selva station.

3. **Spermacoce latifolia** Aublet
(=*Borreria latifolia* (Aublet) K. Schumann)

Erect, glabrescent, sometimes suffrutescent herbs to 1 m tall. *Leaves* opposite, subsessile; blades elliptic to lanceolate, 35–70 mm long, 10–30 mm wide, acute at apex and base, membranaceous to chartaceous; secondary veins 3–5 pairs; stipule sheath 1–2 mm long, lobes and setae ca. 5, 2–4 mm long. *Inflorescences* axillary and sometimes also terminal, 4–6 mm in diameter, usually subtended by 1 pair of vegetative leaves; bracts to 2 mm long; *flowers* subsessile, monomorphic; calyx limb green, divided to base, lobes triangular, 1–2 mm long, acute; corolla pale blue to white, funnellform, glabrous externally, barbate in throat, tube slender, 1.5–2 mm long, lobes triangular, 1.5–2 mm long, acute. *Fruit* ellipsoid, papery, ca. 1 mm long; seeds planoconvex to ellipsoid with a longitudinal furrow on adaxial face. At La Selva collected in flower and fruit January, March, July, and September–December. Weedy and occasional throughout tropical America.

This species is most frequently found in sunny muddy areas. It is frequently confused with the similar and more common *S. assurgens*. Dried specimens and mature plants of *S. latifolia* can be recognized quickly by their blue-green or yellow-green cast.

4. **Spermacoce prostrata** Aublet
(=*Borreria ocymoides* auctt., in part)

Weakly erect to decumbent, hispidulous to glabrate herbs to 0.3 m tall. *Leaves* opposite, subsessile; blades ovate to elliptic or somewhat oblong, 1–4 cm long, 5–20 mm wide, obtusely angled

to rounded at apex, cuneate to attenuate at base, membranaceous; secondary veins 4–6 pairs; stipule sheath ca. 1 mm long, lobes and setae ca. 6–8, ca. 2 mm long. *Inflorescences* axillary and terminal, 2–8 mm in diameter, usually subtended by 1–2 pairs of involucre leaves, these lanceolate to narrowly elliptic, 5–10 mm long; *flowers* subsessile, monomorphic; calyx limb green, divided to base, lobes 2, triangular, 0.5–0.8 mm long, acute; corolla white, glabrous, rotate, 0.5–0.8 mm long, lobes 4, triangular, about half this length. *Fruits* ellipsoid to obconic, laterally compressed, papery, ca. 1 mm long; seeds planoconvex to ellipsoid with a longitudinal furrow on adaxial face. At La Selva collected in flower and fruit February and May–June. Weedy in shaded sites in wet forest throughout the neotropics.

FIGURE 1i.

This species is occasional in shaded sites. It will key to *S. gracilis* in most keys, and is frequently misidentified. True *S. gracilis* is a stiff, usually erect, sharp-leaved plant of sunny dry sites.

38. UNCARIA Schreber

RIDSDALE, C. E. 1978. A revision of *Mitragyna* and *Uncaria* (Rubiaceae). *Blumea* 24: 43–100.

Woody lianas or clambering shrubs, climbing by recurved thorns. *Leaves* sometimes with domatia; stipules interpetiolarly connate, persistent or caducous, triangular to ovate or bilobed. *Inflorescences* axillary and terminal, capitate, heads globose, sometimes paniced; *flowers* monomorphic, 5-merous; corollas funnelform to salverform, aestivation valvate; ovules numerous and vertical on axile placentas. *Fruits* capsular, septicidally and basipetally dehiscent, fusiform, papery; seeds fusiform, flattened, with a membranaceous wing at each end.

Uncaria includes 34 species, two of them in the neotropics and the rest in the Old World tropics, most in Asia. One species is known from Costa Rica. The thorns are modified peduncles.

1. *Uncaria tomentosa* (Willdenow) de Candolle

Glabrous lianas to 30 m high, thorns 1–2 cm long. *Leaf* blades ovate to oblong, 9–15 cm long, 6–9 cm wide, acute to acuminate at apex, truncate to subcordate at base, chartaceous; secondary veins 9–10 pairs, barbate in axils; petioles 8–15 mm long; stipules persistent, ovate, ca. 8 mm long, acute, reflexed. *Inflorescences* with panicles 6–15 cm long, 4–15 cm wide; peduncles 3–7 cm long; heads 15–20 mm in diameter; bracts lacking or sometimes subtending primary branches or panicles, ovate, 4–6 mm long; calyx pilose to

sericeous, limb green, to 0.5 mm long, truncate to shallowly lobed; corolla cream to pale yellow, pilosulous externally, glabrous internally, tube 5–6 mm long, lobes ca. 1.5 cm long, obtuse to rounded. *Fruits* 7–9 mm long, ca. 4 mm wide; seeds 3–5 mm long. At La Selva collected in flower April. Belize and Guatemala through northern South America; in Costa Rica in wet forests of Caribbean slopes at 0–300 m.

FIGURE 3x; Croat, 1978: fig. 537.

This species is occasional, particularly along the Río Sarapiquí, the Southwest Trail, and in the Research Swamp. The leaves are frequently strongly whitened below.

39. WARSZEWICZIA Klotzsch

Erect shrubs or trees. *Leaves* opposite or verticillate, without domatia; stipules interpetiolarly connate, persistent, triangular. *Inflorescences* terminal and axillary, racemiform, with a central axis bearing contracted lateral cymes, in some species the calyx of the terminal flowers of each cyme bearing one expanded calyx lobe; *flowers* monomorphic, 5-merous; corollas funnelform to salverform, aestivation imbricate; ovules numerous and horizontal on axile placentas. *Fruits* capsular, septicidally and basipetally dehiscent, elliptic to turbinate, woody; seeds angled, reticulate.

Warszewiczia includes about six species found from Mexico through tropical South America; one widespread species is found in Costa Rica. *Warszewiczia coccinea* is the national tree of Trinidad and Tobago.

1. *Warszewiczia coccinea* (Vahl) Klotzsch

Strigillose to pilosulous shrubs or trees to 15 m tall. *Leaves* opposite or verticillate; blades elliptic, 16–36 cm long, 7–15 cm wide, acute at apex, cuneate at base, chartaceous; secondary veins 13–20 pairs; petioles 15–50 mm long; stipules 16–25 mm long, acute, often strongly costate. *Inflorescences* with racemes 20–60 cm long, 3–6 cm wide excluding expanded calyx lobes; peduncles 1–10 cm long; bracts triangular, 2–15 mm long, acute; *flowers* subsessile; calyx pilose, limb green, 0.5–0.8 mm long, divided nearly to base, lobes broadly rounded, expanded lobe elliptic to rhombic, 4–10 cm long, 1–4 cm wide, acute to rounded at apex, cuneate at base, glabrescent, bright pink to red, with stipe 1.5–3 cm long; corolla yellow-orange to orange, glabrous or often pilose externally in lines, barbate in throat, tube 3–3.5 mm long, lobes 2–2.5 mm long, rounded. *Fruits* 2–2.5 mm long, 3–4 mm wide; seeds 0.5–0.8 mm long. At La Selva collected in flower and fruit February–March, May–

September, and November. Nicaragua to central South America in moist forests and secondary vegetation at 0–300 m. **FIGURE 4n.**

This species is common in gaps, along edges of primary forest, and in secondary growth. Its breeding biology was studied by Bawa and Beach (1983).

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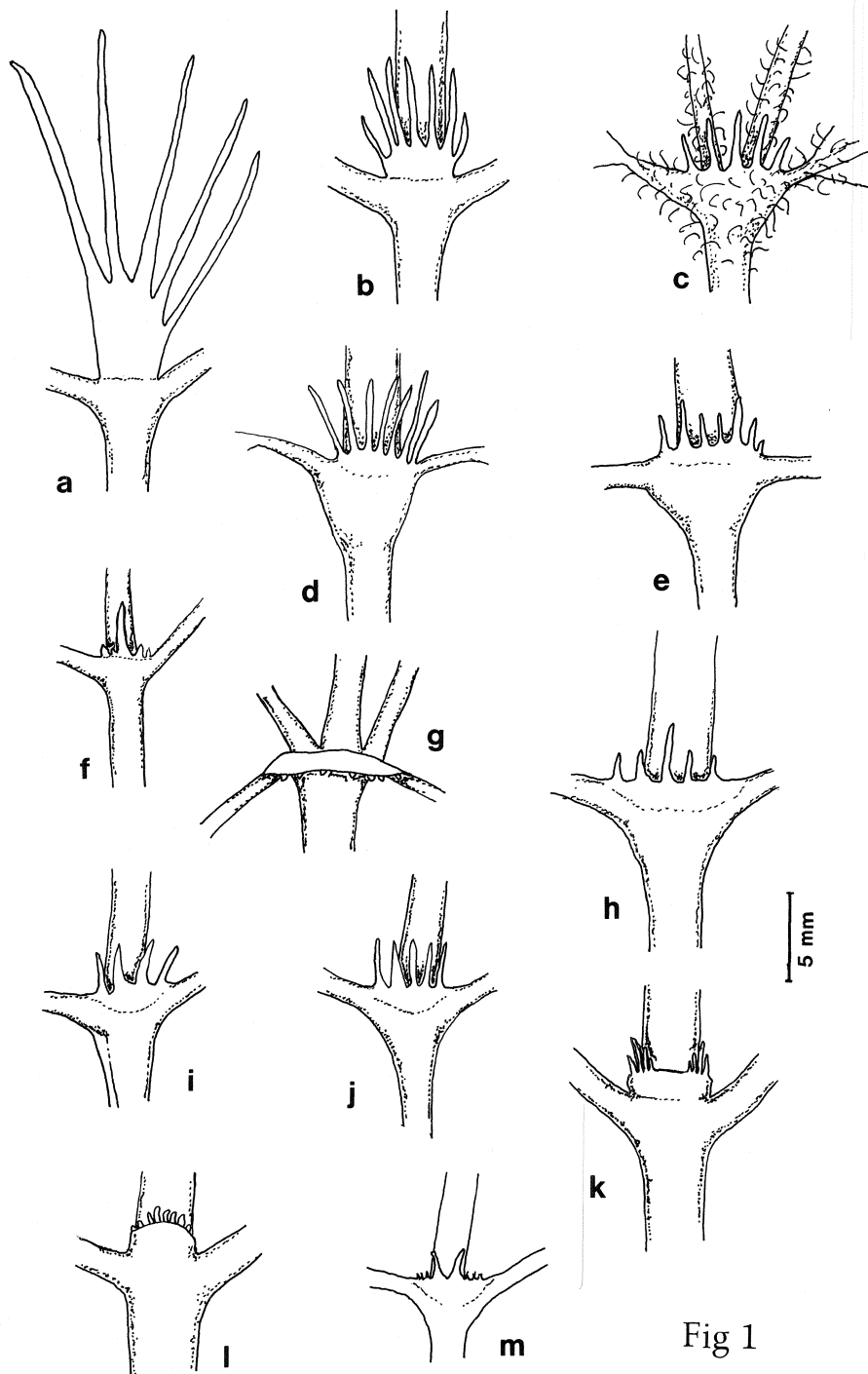


Fig 1

FIGURE 1. Stipules with several teeth. a, *Amphidasya ambigua*, node. b, *Psychotria ipecacuanha*, node. c, *Richardia scabra*, node. d, *Hemidiodia ocimifolia*, node. e, *Mitracarpus villosus*, node. f, *Coccocypselum herbaceum*, node. g, *Manettia reclinata*, node. h, *Spermacoce assurgens*, node. i, *Spermacoce prostrata*, node. j, *Spermacoce gracilis*, node. k, *Psychotria glomerulata*, node. l, *Rudgea cornifolia*, node. m, *Oldenlandia lancifolia*, node. All to same scale.

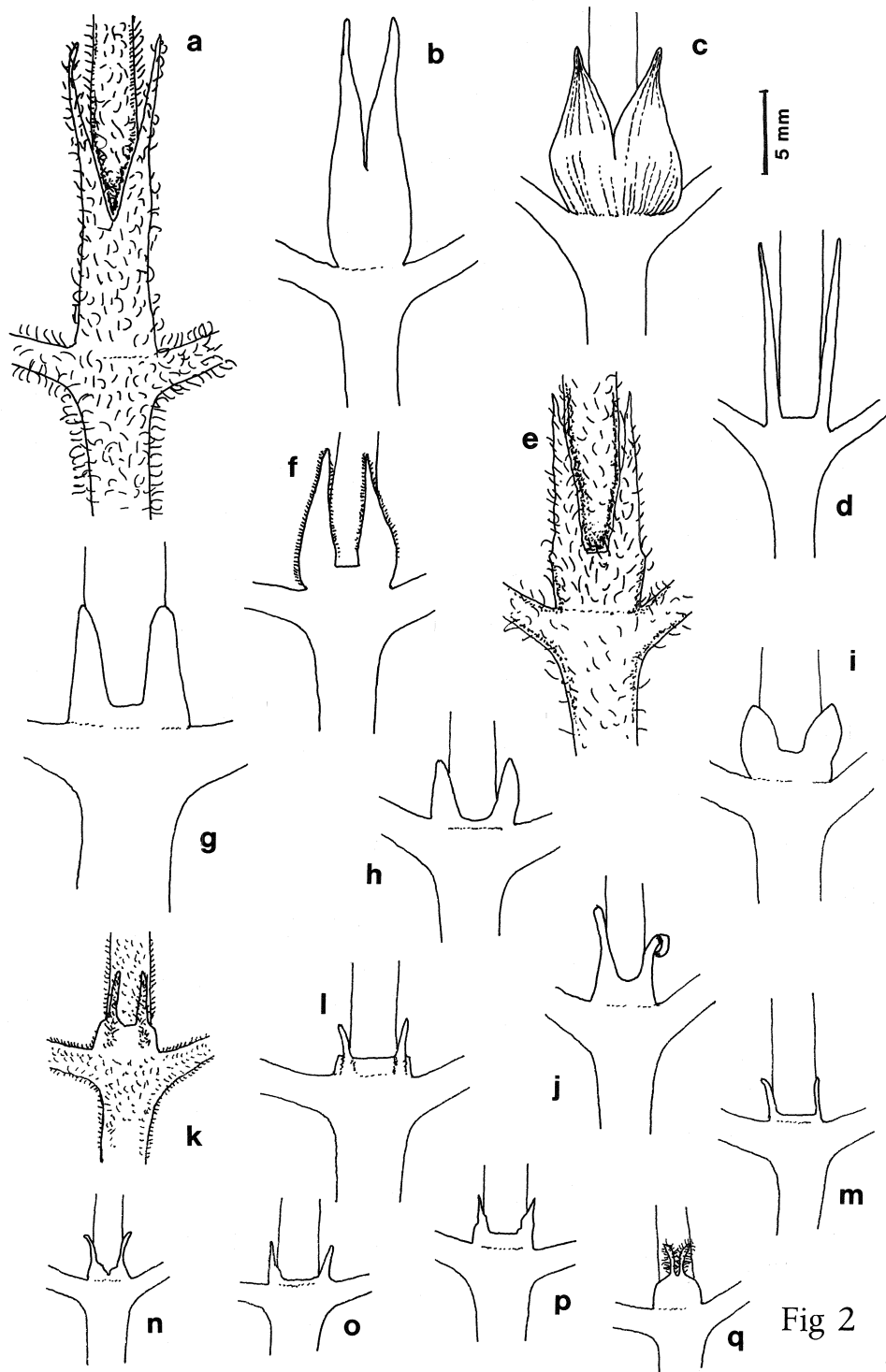


FIGURE 2. Bidentate stipules. a, *Psychotria pilosa*, node. b, *Psychotria alfaroana*, node. c, *Psychotria microbotrys*, node. d, *Psychotria racemosa*, node. e, *Psychotria poeppigiana*, node. f, *Palicourea triphylla*, node. g, *Palicourea guianensis*, node. h, *Psychotria brachybotria*, node. i, *Psychotria elata*, node. j, *Psychotria guapilensis*, node. k, *Psychotria pittieri*, node. l, *Psychotria suerrensii*, node. m, *Palicourea crocea*, node. n, *Psychotria haematocarpa*, node. o, *Psychotria acuminata*, node. p, *Psychotria hebeclada*, node. q, *Psychotria graciliflora*, node. All to same scale.

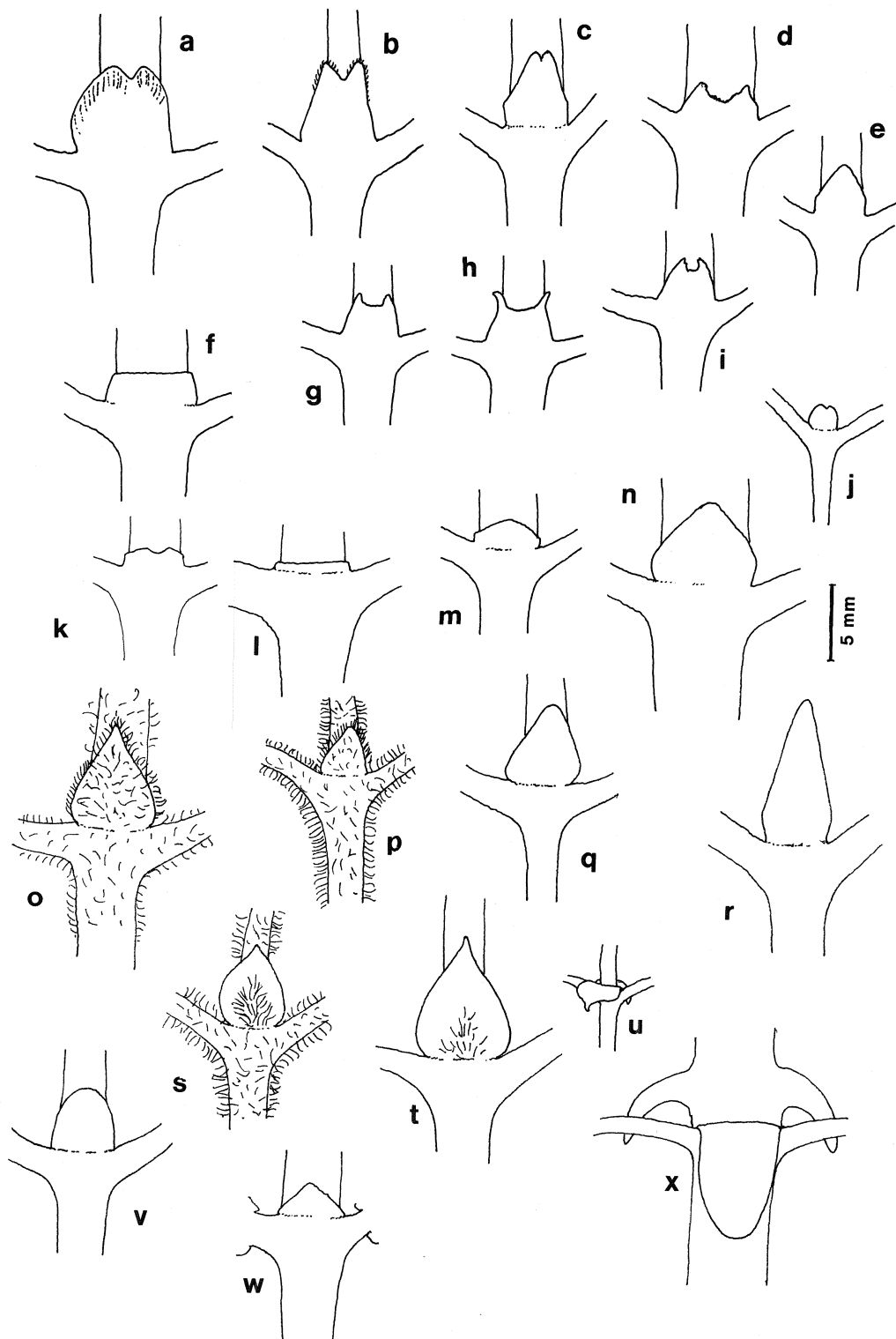


FIGURE 3. Bilobed, truncate, ovate, and lingulate stipules. a, *Psychotria brachiata*, node. b, *Psychotria angustiflora*, node. c, *Psychotria cooperi*, node. d, e, *Psychotria chiapensis*, node. f, *Psychotria orchidearum*, node. g, h, *Psychotria officinalis*, node. i, *Psychotria chiapensis*, node. j, *Geophila repens*, stem apex. k, *Coussarea nigrescens*, node. l, *Coussarea psychotrioides*, node. m, *Psychotria eurycarpa*, node. n, *Psychotria luxurians*, node. o, *Lasianthus panamensis*, node. p, *Geophila cordifolia*, node. q, *Geophila macropoda*, node. r, *Psychotria marginata*, stem apex. s, *Sabicea villosa*, node. t, u, *Sabicea panamensis*, node. v, *Randia pepoformis*, node. w, *Coussarea impatiolaris*, node. x, *Uncaria tomentosa*, node. All to same scale.

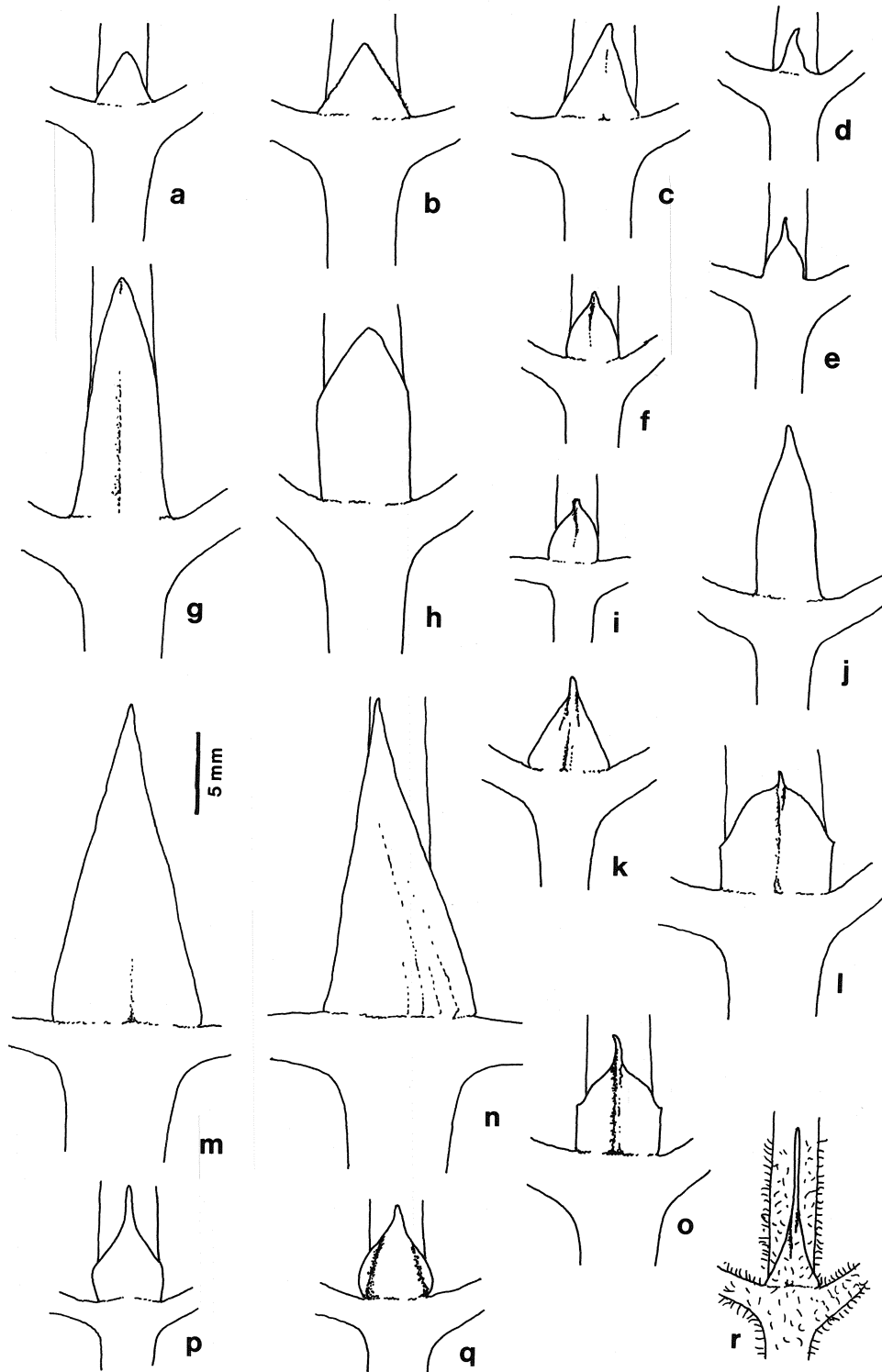


FIGURE 4. Triangular stipules. a, *Psychotria laselvensis*, node. b, *Coffea liberica*, node. c, *Randia mira*, node. d, *Hamelia patens*, node. e, *Coutarea hexandra*, node. f, *Chione sylvicola*, node. g, *Posoqueria latifolia*, node. h, *Posoqueria grandiflora*, node (*Posoqueria coriacea* is similar). i, *Ixora nicaraguensis*, node. j, *Faramea parvibractea*, stem apex. k, *Randia grandifolia*, stem apex. l, *Faramea suerrensensis*, node. m, *Randia* sp. A, stem apex. n, *Warszewiczia coccinea*, node. o, *Faramea multiflora*, node. p, *Bertiera guianensis*, node. q, *Chimarrhis parviflora*, node. r, *Hamelia xerocarpa*, node. All to same scale.

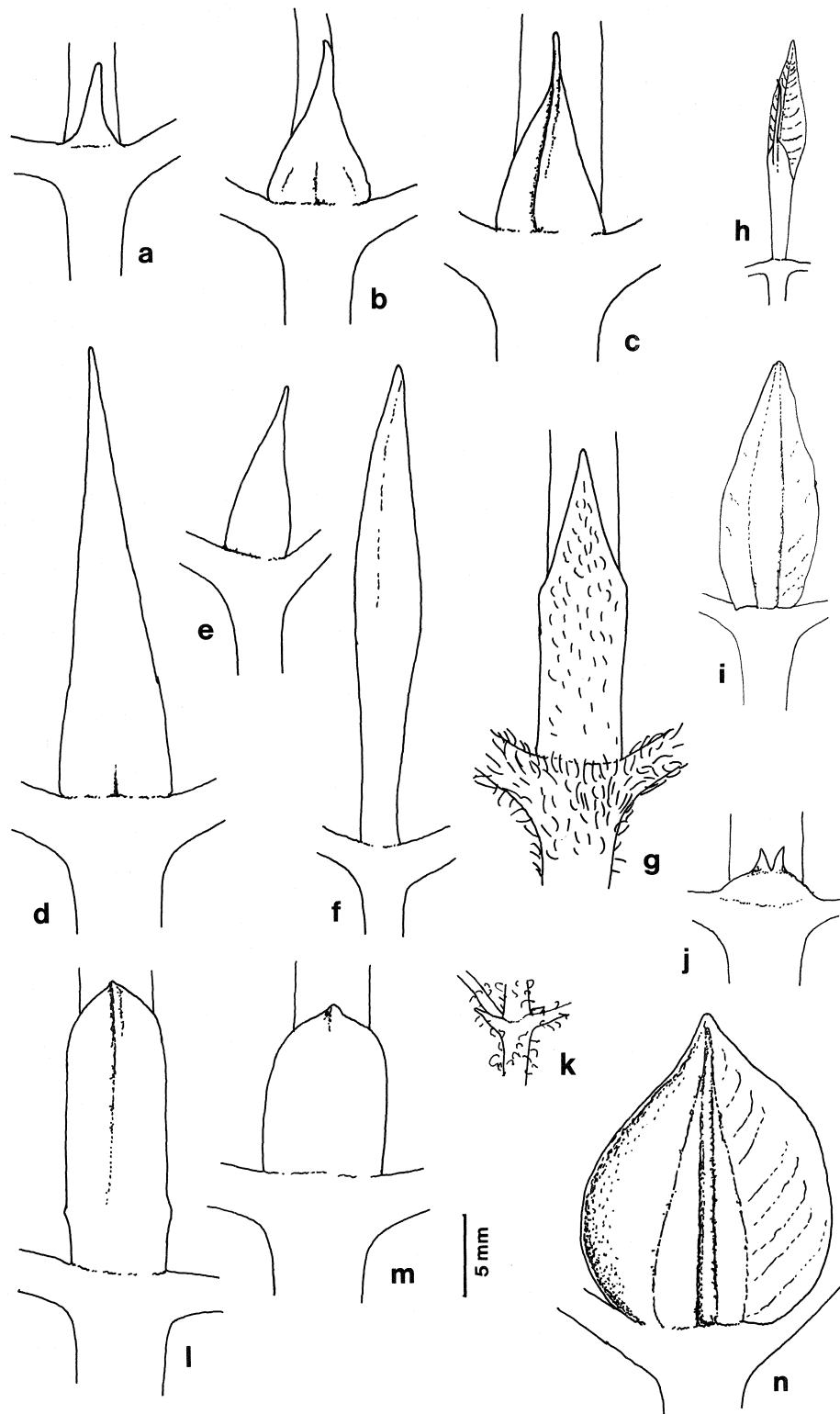


FIGURE 5. Triangular and unusual stipules. a, *Psychotria erecta*, node. b, *Coussarea hondensis*, node. c, *Genipa americana*, node. d, *Simira maxonii*, stem apex. e, f, *Psychotria panamensis*, stem apex. g, *Gonzalagunia bracteosa*, node. h, *Faremea stenura*, stem apex. i, *Ferdinandusa panamensis*, stem apex with stipule unrolled. j, *Hoffmannia liesneriana*, node. k, *Hoffmannia* sp. A, node. l, *Borojoa panamensis*, node. m, *Coussarea talamancana*, node. n, *Psychotria grandis*, node. All to same scale.

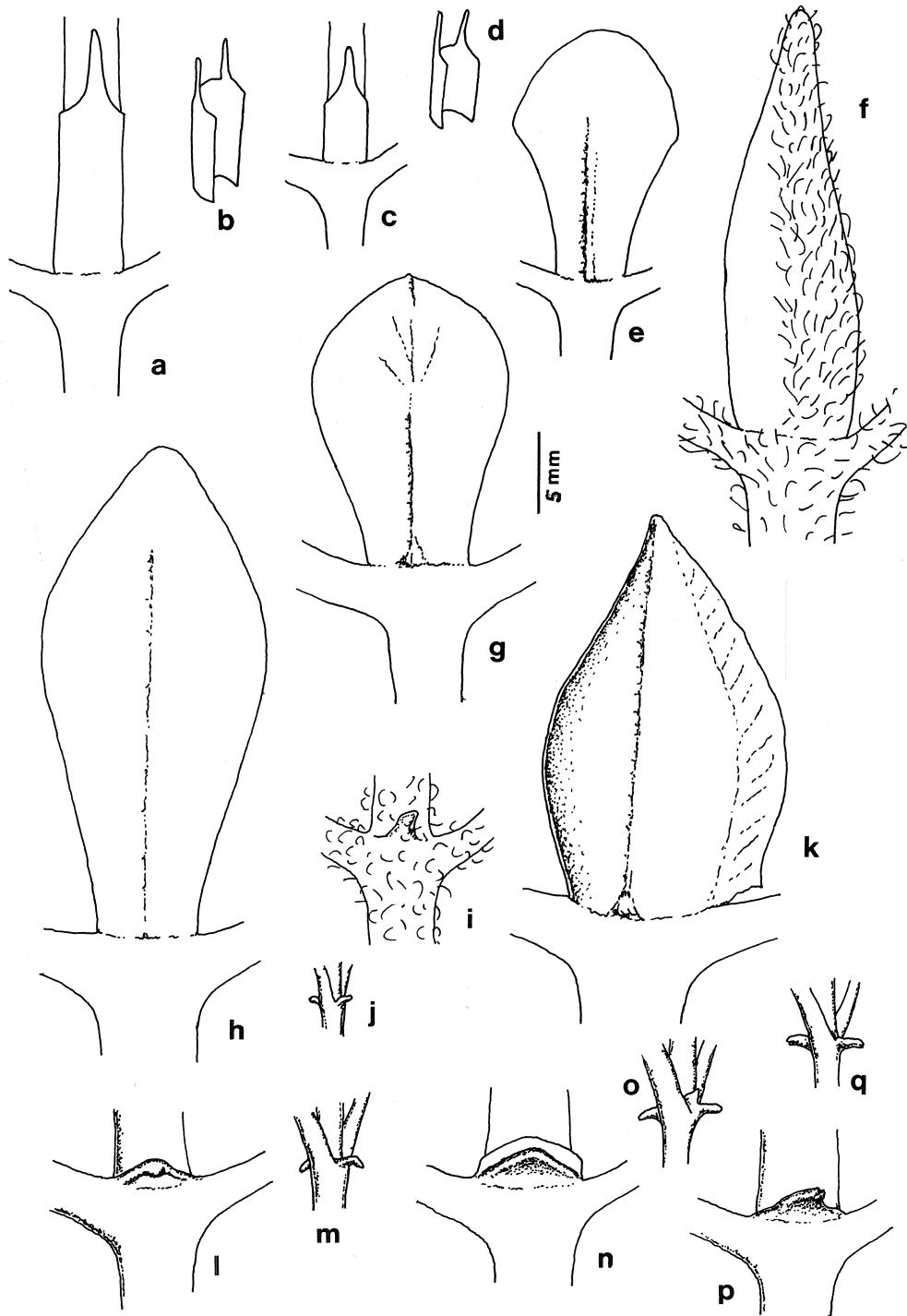


FIGURE 6. Unusual and succulent divergent stipules. a, *Psychotria psychotriifolia*, node. b, *Psychotria psychotriifolia*, stipule. c, *Psychotria chagensis*, node. d, *Psychotria chagensis*, stipules. e, *Cosmibuena macrocarpa*, stem apex. f, *Hippotis albiflora*, stem apex. g, *Ladenbergia sericophylla*, stem apex. h, *Hillia grayumii*, stem apex. i, j, *Psychotria erecta*, node. k, *Pentagonia donnell-smithii*, stem apex. l, m, *Psychotria polyphlebia*, node. n, o, *Psychotria aggregata*, node. p, q, *Psychotria macrophylla*, node. All to same scale except *Pentagonia*, which is to half this scale, i.e., bar = 10 mm.

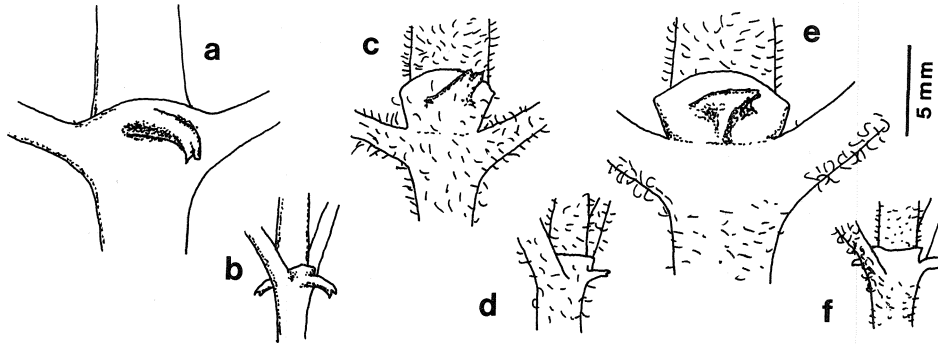


FIGURE 7. Succulent, divergent stipules. a, b, *Psychotria uliginosa*, node. c, d, *Psychotria siggersiana*, node. e, f, *Psychotria capacifolia*, node. All to same scale.