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FIELDIANA

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NEW SERIES, NO. 33

FLORA COSTARICENSIS

William Burger, Editor

Family #202 Rubiaceae

William Burger

Charlotte M. Taylor

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Families of seed plants known or expected to occur in Costa Rica and adjacent areas, listed alphabetically and numbered according to the sequence of Engler's *Syllabus der Pflanzenfamilien*, edition 11, reworked by L. Diels (1936).

200	Acanthaceae	130	Elaocarpaceae	137	Ochnaceae
136	Actinidiaceae	143	Elatinaceae	56	Oleaceae
67	Aizoaceae	172	Ericaceae	181	Oleaceae
11	Alismataceae	23	Eriocaulaceae	164	Onagraceae
64	Amaranthaceae	102	Erythroxylaceae	57	Opiliaceae
30	Amoryllidaceae	113	Euphorbiaceae	39	Orchidaceae
117	Anacardiaceae	96	Fabaceae,	197	Orobanchaceae
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184	Apocynaceae	50	Fagaceae	17	Palmae
119	Aquifoliaceae	148	Flacourtiaceae	82	Papaveraceae
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Introduction

This is the eighth issue in the *Flora Costaricensis* series. The first dealt with the Piperaceae (Fieldiana, Bot. 35, 1971). The second included families numbered 42 through 53, Chloranthaceae through Urticaceae (Fieldiana, Bot. 40, 1977). The third issue covered the Gramineae and was authored by Richard Phol (Fieldiana, Bot., new series, No. 4, 1980). The fourth issue included families numbered 54 through 70, Podostemaceae through Caryophyllaceae (Fieldiana, Bot., new series, No. 13, 1983). The fifth issue covered families 200 and 201, the Acanthaceae authored by L. H. Durkee, and the Plantaginaceae (Fieldiana, Bot., new series, No. 18, 1986). The sixth issue included fam-

ilies 80 and 81, Lauraceae and Hernandiaceae (Fieldiana, Bot., new series, No. 23, 1990). The seventh issue included families numbered 97 through 103, Krameriaceae through Zygophyllaceae (Fieldiana, Bot., new series, No. 28, 1991).

In the figures, leaves and leafy stems are drawn to the same scale throughout. Enlarged flowers and fruits are drawn to the same scale on an individual plate unless otherwise noted. The closed scales represent centimeters and the open scales represent millimeters. The figures are somewhat diagrammatic and represent the senior author's concept of a common or characteristic morphology.

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We wish to thank the staff, and especially Pablo Sánchez, of the Museo Nacional de Costa Rica for their assistance over many years. A grant from the Museo Nacional allowed the senior author to work at the Herbario Nacional for several weeks in November 1990. Charlotte Taylor received support for travel from the National Science Foundation (BSR 83-10702 and BSR 87-00068), the Fondos Institucionales Para Investigacion of the University of Puerto Rico, and the Dee Scholarship Fund of Field Museum. Collecting programs by the Missouri Botanical Garden (MO), Instituto Nacional de Biodiversidad and the Museo Nacional (CR), supported in part by grants from the National Science Foundation and the National Geographic Society, have added significantly to our knowledge of Costa Rica's Rubiaceae. The recent collections of Jorge Gómez-Laurito, Michael Grayum, William Haber, Barry Hammel, Gerardo Herrera, Quirico Jiménez, and Nelson Zamora have been

especially significant. Loans from the U.S. National Herbarium (US) and the Duke University Herbarium (DUKE) were important for our work on this family.

A number of our colleagues have been especially helpful in preparing this treatment. The annotations and advice of C. Dennis Adams, John Dwyer, Barry Hammel, and David Lorence were especially important. In addition, John Dwyer and David Lorence have provided descriptions of new species, and Roy Gereau corrected all the Latin descriptions. The Flora Mesoamericana project under the leadership of Geritt Davidse (MO) has provided information and assistance on many occasions. We are also indebted to the Missouri Botanical Garden for allowing Charlotte Taylor to contribute her time and effort to this treatment. Finally, we thank three anonymous reviewers who made many corrections and suggested useful improvements for the text.

FLORA COSTARICENSIS

Family #202 Rubiaceae

RUBIACEAE

By William Burger and Charlotte M. Taylor

Herbs, **shrubs**, or small- to medium-sized trees (rarely vines or tall canopy trees), stems glabrous to pubescent with simple hairs, terete or angular; **stipules** of opposing leaves usually united across the stem (interpetiolar), sometimes united to the petioles and forming a broad sheath (Spermacoceae), rarely separate and paired at the leaf base, stipules of the same leaf sometimes also united above the petioles (intrapetiolar) and forming a short tube, often with hair-like or tooth-like colleters at the adaxial base or along the edge, persistent to caducous and leaving a scar across the stem (stipules transformed into small leaves in *Galium* and *Sherardia*). **Leaves** opposite or sometimes whorled (very rarely alternate), always simple, petiolate or occasionally sessile, glabrous or pubescent, nearly always entire and without lobes (pinnatifid in *Pentagonia* spp., with small lobes in *Simira* spp., minutely serrate or crenate in some Spermacoceae), nearly always pinnately veined (palmately veined in some weedy Spermacoceae), domatia of pits or tufted hairs present in the vein axils on the lower surfaces of leaves in some genera. **Inflorescences** terminal or axillary, solitary to several at each node, very variable in form (open paniculate to cymose, racemose, spicate or capitate), branches of the inflorescence often opposite, bracts and bracteoles often present, the flowers often borne in distal cymes or dichasia, sometimes cincinnoid and 1-sided (rarely solitary, fasciculate, or united), sessile or pedicellate. **Flowers** usually bisexual and radially symmetrical (rarely unisexual and dioecious), most often 4- or 5-parted, epigynous, the hypanthium narrowly tubular (rarely subglobose, calyx tube usually present, calyx lobes usually present and equal or subequal (rarely with 1 lobe greatly expanded and colorful); **corolla** often salverform with a narrow tube (funnelform to rotate or tubular), corolla lobes valvate, imbricate or contorted in bud; **stamens** usually as many as the corolla lobes and alternating with them, nearly always borne on the corolla tube, filaments long to short, anthers usually narrowly oblong and basifixed to dorsifixed, dehiscing longitudinally (with terminal pores in *Rustia*); **ovary** inferior (rarely half-inferior), usually with a ring-like disc on the upper surface, with 2 (1–8) locules, placentation apical, basal or from the median septum (parietal in some Gardineae), style solitary from the center of the apex of the ovary, stigmas usually 2 or solitary (clavate to capitate). **Fruits** capsular, baccate or drupaceous and often with 2 (4–5) pyrenes (a syncarp in *Morinda* and *Schradera*, a samara in *Allenanthus*), berries sometimes large with the seeds imbedded in a fleshy pulp, capsules opening along the locules (loculicidal) or along the septum (septicidal); **seeds** sometimes with wings or tufted hairs.

The Rubiaceae are one of the largest families of flowering plants, with an estimated 10,700 species (Mabberley, 1987). The family is best represented in the evergreen tropics and is often an important component of the lower strata of such forests.

In most cases the family is easily recognized. The simple opposite leaves are nearly always entire and pinnately veined. Only a few weedy species have subpalmate venation, and a few of our woody species have lobed leaves (*Pentagonia* spp. and *Simira maxonii*). The trichomes are never branched or stellate. Some species have domatia in the form of pits or tufted hairs in the vein axils on the undersides of leaves. Though variable in presence, domatia can be helpful in identifying species. Too small to be useful to ants, these leaf domatia probably offer shelter for predatory and fungivorous mites (Pemberton & Turner, 1989). The nodes are nearly always marked by interpetiolar stipules or interpetiolar lines if the stipules have fallen. The stipules can be important in identifying species but may be apparent only on young shoots; they may be greatly enlarged when subtending inflorescences. Persisting stipules may be distorted or torn apart as the stem expands. Hair-like or tooth-like structures between the base of the stipule and the stem are called colleters. These are usually finger-like with elongate axial cells and a palisade epidermis (Lersten, 1974). They are believed to secrete mucilage, gums, or resins.

Inflorescences vary greatly in some genera. In some species the bracts subtending the first pair of opposite branches of the inflorescence may be replaced by smaller leaves. In this case an inflorescence that is solitary and terminal can be interpreted as being a group of three inflorescences: a terminal one and two axillary to the distal leaves (bract homologs). The flowers are often borne in distal cymes on opposite branches of the inflorescences. Many species are distylous with long-styled (pin) or short-styled (thrum) flowers on different plants. The corolla is nearly always radially symmetrical and with a conspicuous tube. Curvature of the tube or asymmetry of the corolla lobes is rare. The inferior ovary is usually two-locular, and the number of ovules per locule has been used as

a primary criterion for distinguishing the subfamilies.

While a very distinctive family, there are a few genera of other families that can be mistaken for Rubiaceae. Collections of *Cassipourea* (Rhizophoraceae), *Hedyosmum* (Chloranthaceae), and *Neea* (Nyctaginaceae) are often found among specimens of Rubiaceae. There are also look-alikes in Acanthaceae, Loganiaceae, and Onagraceae.

The Rubiaceae of Central America are relatively well understood, and their taxonomy is in good order. This is the result of intensive study by many workers, past and present. Among these, the work of Paul Carpenter Standley provided a solid foundation. His publications and many annotations have been particularly useful in preparing the present account. The treatments of the family for the Flora of Guatemala (Standley & Williams, 1975), Flora of Panama (Dwyer, 1980), and Flora of Venezuela (Steyermark, 1974) have also been very useful. The recent studies by Dennis Adams, John Dwyer, Clement Hamilton, Joseph Kirkbride, David Lorence, and others have clarified many difficult species groups and are cited in the text. Many collectors have contributed substantially to our knowledge of this family in Costa Rica (an index to exsiccatae is available on request).

tation, ovule orientation, and characteristics of seeds and fruits. This key follows those presented in the Flora of Guatemala (Standley & Williams, 1975) and the Flora of Panama (Dwyer, 1980). While often very difficult to implement, this key has wide application and places the genera into the traditional tribes. More modern keys can be found in Robbrecht (1988).

As Verdcourt (1976, p. 5) has stated, "[T]he family Rubiaceae contains so many genera and species, many of which resemble each other even when not closely related, that it is impossible to make a useable key which does not involve looking at small and difficult characters." To provide an alternative, we give an additional artificial key that is much simpler and attempts to make the illustrations more readily accessible. Scanning the illustrations with the help of the second key will, hopefully, allow determination of many species without having to ascertain all the morphological details required by the technical key. Commentary under the genera and species gives characteristics that can be helpful in distinguishing the taxa; the detailed descriptions are useful in confirming a determination. Nevertheless, there is no substitute for careful comparisons with annotated herbarium collections to verify a determination.

Keys to the Rubiaceae of Costa Rica

We provide a technical key to the genera that requires ascertaining corolla aestivation, placen-

Key 1: Technical Keys to the Traditional Tribes and Genera of Rubiaceae
(see Robbrecht, 1988, for a more modern system)

- 1a. Ovules more than 1 in each locule of the ovary (subfamily Cinchonoideae) 2
- 1b. Ovules solitary in the locules of the ovary (subfamily Rubioideae, except Naucleaeae) 9
- 2a. Fruits fleshy and indehiscent (baccate or berry-like) 3
- 2b. Fruits dry and dehiscent (capsule-like) 5
- 3a. Corolla lobes valvate in bud 1. Isertieae
- 3b. Corolla lobes imbricate or contorted in bud 4
- 4a. Corolla lobes imbricate in bud 2. Hamelieae
- 4b. Corolla lobes contorted in bud 3. Gardenieae
- 5a. Flowers in compact spherical heads 8. Naucleaeae
- 5b. Flowers not in compact spherical heads 6
- 6a. Seeds with wings, tufted hairs or appendages, arranged vertically imbricate on the placenta 4. Cinchoneae
- 6b. Seeds angled but not winged, or if winged then arranged horizontally on the placenta ... 7
- 7a. Corolla lobes imbricate or contorted in bud 6. Rondeletieae
- 7b. Corolla lobes valvate in bud 8
- 8a. Seeds horizontal, usually many (> 25); stipules entire or bifid; trees and shrubs

.....	5. Condamineae
8b. Seeds vertical and imbricate, usually few; stipules usually setose; herbs and subshrubs	7. Oldenlandieae
9a. (from 1b) Seeds pendulous, the radicle superior; trees, shrubs, or woody lianas	10
9b. Seeds ascending, the radicle inferior; trees, shrubs, or herbs	12
10a. Flowers in spherical/globose heads	8. Naucleae
10b. Flowers never in globose heads	11
11a. Stamens usually borne at apex of corolla tube (the rarely encountered <i>Vangueria</i> of the Vanguerieae will key out here; see text)	9. Guettardeae
11b. Stamens borne at base of the corolla tube or from the disc	10. Chiococceae
12a. Corolla lobes contorted in bud; trees and shrubs	11. Ixoreae
12b. Corolla lobes valvate in bud; trees, shrubs, and herbs	13
13a. Ovules borne on base of the locule; mostly woody plants	14
13b. Ovules borne from the septum in the center of the ovary; herbs, shrubs, or trees	17
14a. Ovary with 7–8 locules; inflorescences globose; fruits multiple, of 4–50 united flowers	14. Morindeae
14b. Ovary with 1–5 locules; inflorescences various; fruits simple or with 2 united flowers if multiple	15
15a. Ovary 1- or 2-locular and with a thin partial septum; fruits with 1 seed ..	12. Coussareae
15b. Ovary 2-locular (5-locular) and with thick well-developed septum; fruits with 2(–5) seeds	16
16a. Stamens usually inserted near the apex of the corolla tube; flowers bisexual	13. Psychotrieae
16b. Stamens usually inserted near the base of the corolla tube; flowers often unisexual	15. Anthospermeae
17a. (from 13b) Stipules not leaf-like nor setose; trees and large shrubs; flowers united near the base; fruits united or partly united into a syncarp	14. Morindeae
17b. Stipules either setose with awn-like appendages or leaf-like (and the small leaves apparently whorled and lacking stipules); herbs or small shrubs; flowers often congested but not united at the base; fruits never united into a syncarp	18
18a. Stipules usually bearing 3–30 narrow setae or awns; leaves usually opposite ..	16. Spermacoeae
18b. Stipules leaf-like; leaves and leaf-like stipules appearing as whorls of 4 or more leaves per node	17. Rubieae

1. ISERTIEAE (MUSSAENDEAE)

1a. Leaves apparently alternate (a minute opposing leaflet often present, not known from Costa Rica)	<i>Didymochlamys</i>
1b. Leaves opposite, both leaves of the node developed	2
2a. Leaves with the minor venation parallel (lineolate)	3
2b. Leaves with the minor venation not parallel	5
3a. Leaves large, to over 1 m long, with pinnatifid lobes in some species; rows of glands (colleters) present on the interior of the calyx cup; plants often monopodial	<i>Pentagonia</i>
3b. Leaves up to 35 cm long, never with pinnatifid lobes; calyx cup without glands on the interior; plants often much-branched	4
4a. Calyx 5-lobed	<i>Sommeria</i>
4b. Calyx 2-lobed or spathe-like	<i>Hippotis</i>
5a. Inflorescences axillary	6
5b. Inflorescences terminal	8
6a. Erect unbranched plants to 50 cm tall, with long closely clustered leaves; ovary 2-locular; corolla more than 30 mm long	<i>Amphidasya</i>
6b. Plants with leaves well spaced along the twining or creeping stems; ovary 2–5-locular; corolla less than 12 mm long	7

- 7a. Plants prostrate, herbaceous; ovary 2-locular; fruit bright blue *Coccocypselum*
- 7b. Plants erect or climbing, herbs or subshrubs; ovary 3–5-locular; fruits reddish becoming purple or bluish black *Sabicea*
- 8a. Flowers and inflorescences drying black; inflorescence capitate; leaves and flowers semisucculent *Schraderea*
- 8b. Flowers and inflorescences not drying black; inflorescences subcapitate only in *Amphidasya*; leaves and flowers not semisucculent 9
- 9a. Stipules fimbriate distally; herbaceous with erect unbranched stems to 0.8 m tall .. *Amphidasya*
- 9b. Stipules not fimbriate distally; woody plants with branched stems to 3 m tall 10
- 10a. Inflorescences spike-like; shrubs *Gonzalagunia*
- 10b. Inflorescences cymose to paniculate; shrubs or trees 11
- 11a. Anthers not transversely locellate (not divided by transverse walls); corollas less than 2 cm long; ovary 2-locular *Raritebe*
- 11b. Anthers transversely locellate; corollas 3 or more cm long; ovary (2–)5–6-locular *Isertia*

2. HAMELIEAE

- 1a. Inflorescences always axillary; ovary with 2 or 3 locules; stamens with connective, rarely prolonged distally [corolla lobes imbricate or subvalvate] *Hoffmannia*
- 1b. Inflorescences usually terminal; ovary with 4 or 5 locules; stamens with the connective often prolonged distally 2
- 2a. Corolla lobes imbricate in bud; raphides present in leaves; inflorescences often with few cincinnoid branches *Hamelia*
- 2b. Corolla lobes contorted in bud; raphides absent in the leaves; inflorescences with many branches, not cinnoid *Bertiera*

3. GARDENIEAE

- 1a. Ovary with a single locule and intruding parietal placentas (but often difficult to see and the abutting placentas appearing as a septum); pollen grains in tetrads 2
- 1b. Ovary with usually 2 locules (the septum often thin or obliterated as the seeds develop); pollen separate 3
 - 2a. Plants native and wild, usually armed with spines on branches, frequently with short-shoots *Randia*
 - 2b. Plants grown in gardens for ornament, usually lacking short-shoots *Gardenia*
- 3a. Flowers bisexual 4
- 3b. Flowers unisexual 6
 - 4a. Inflorescences with 1–few flowers, flowers not in a candelabra-like arrangement; leaves drying black *Genipa*
 - 4b. Inflorescences with several to many flowers; flowers usually in a candelabra-like arrangement; leaves drying black or not 5
 - 5a. Flower buds curved at the apex, corolla white and becoming yellowish in age; seeds with testa cells more than twice as long as wide *Posoqueria*
 - 5b. Flower buds straight at the apex, corolla bright yellow at anthesis; seeds with testa cells less than twice as long as wide *Tocoyena*
- 6a. Fruits rounded or globose; terminal stipules not forming a conical cap, triangular and persisting 7
- 6b. Fruits oblong; terminal stipules forming a conical cap, caducous 8
 - 7a. Fruits subtended by several whorls of persisting bracts (stipules), fruits more than 5 cm diam., pericarp thick, carnos, surfaces rough *Borojoa*
 - 7b. Fruits not subtended by several persisting bracts; fruits to 3 cm diam., pericarp thin and hard, smooth *Alibertia*

- 8a. Female flowers usually solitary; fruits hirsute *Duroioia*
- 8b. Female flowers capitate or cymose; fruits not densely hirsute *Amaioua*

4. CINCHONEAE

- 1a. Vining or clambering with slender herbaceous stems (genus placed in the Hedyotideae in modern systems) *Manettia* 2
- 1b. Shrubs or trees, stems not slender and clambering *Ferdinandusa* 2
- 2a. Anthers dimorphic or trimorphic *Ferdinandusa* 3
- 2b. Anthers monomorphic (all alike within the flower) 3
- 3a. Calyx with 1 expanded (2–5 cm) white lobe in 1 or 2 flowers of the inflorescence *Calycophyllum*
- 3b. Calyx lobes equal or subequal, inflorescences without expanded large white calyx lobes 4
- 4a. Plants epiphytic; leaves semisucculent, lateral veins often obscure when dried 5
- 4b. Plants terrestrial; leaves not semisucculent, lateral veins clearly evident 6
 - 5a. Seeds winged at either end *Cosmibuena*
 - 5b. Seeds with tufted hairs at one end *Hillia*
- 6a. Inflorescences spike-like; stamens attached at the base of the corolla tube [filaments hirsutulous] *Alseis*
- 6b. Inflorescences not spike-like, various; stamens attached above the base of the corolla tube (except in *Coutarea* and *Exostema*) 7
- 7a. Corolla lobes imbricate or contorted in bud 8
- 7b. Corolla lobes valvate in bud 9
 - 8a. Stamens conspicuously exerted; corolla not inflated in bud; fruits not compressed or lenticellate *Exostema*
 - 8b. Stamens not conspicuously exerted (may become exerted as corolla ages); corolla buds inflated in late stages (before anthesis); fruits strongly flattened, surfaces often lenticellate *Coutarea*
- 9a. Flowers 4-parted; capsules rounded *Bouvardia*
- 9b. Flowers 5-parted; capsules oblong 10
- 10a. Capsule splitting from below to the apex [a ring of hairs present within the mouth of the corolla] *Cinchona*
- 10b. Capsule splitting from above to the base 11
- 11a. Corolla lobes split at the apex; dehiscent capsules forming 4 coiled valves (not known from Costa Rica) *Joosia*
- 11b. Corolla lobes not split at the apex; capsules valves not becoming coiled 12
- 12a. Capsules opening into the locules *Macrocnemum*
- 12b. Capsules opening along the septum *Ladenbergia*

5. CONDAMINEEAE

- 1a. Anthers opening by terminal pores; leaves with pellucid glandular dots *Rustia*
- 1b. Anthers opening by longitudinal slits; leaves without pellucid glandular dots 2
- 2a. Inflorescences axillary 3
- 2b. Inflorescences terminal 4
 - 3a. Flowers solitary or few, ca. 25 cm long *Osa*
 - 3b. Flowers many, ca. 3 mm long *Chimarrhis*
- 4a. Calyx lobes equal or subequal, small; stipules large and bifid [leaves large and subsessile] *Condaminea*
- 4b. Calyx with 1 lobe enlarged (2–6 cm) and colored in 1 or a few flowers of each inflorescence; stipules small, not bifid *Pogonopus*

6. RONDELETIEAE

1a. Corolla lobes contorted in bud 2

1b. Corolla lobes imbricate in bud 5

2a. Corolla tube becoming very long (+ 10 cm), much longer than the corolla lobes; capsule valves becoming coiled; shrubs of stream sides *Lindenia*

2b. Corolla never exceeding 5 cm, tube shorter than the corolla lobes; capsule valves not becoming coiled; if woody not restricted to river edges and wet sites 3

3a. Small herbs of wet sites *Sipanaea*

3b. Trees and shrubs 4

4a. Corolla 4-parted, yellowish, glabrous within *Deppea*

4b. Corolla 5-parted, greenish white, villous within *Elaeagia*

5a. Calyx lobes unequal, often expanded into a broad lobe 6

5b. Calyx lobes equal or subequal, small and unexpanded 7

6a. Expanded calyx lobe bright red *Warszewiczia*

6b. Expanded calyx lobes whitish (in some spp.) *Rondeletia*

7a. Capsules ca. 1 cm diam., opening into the septum; seeds winged or flat and enlarged; wood turning reddish when cut and exposed (in ours) *Simira*

7b. Fruits to 5 mm diam., opening at the septum or locule; seeds lacking wings, not flattened; wood not turning reddish when cut and exposed 8

8a. Corolla tubes usually more than 8 mm long, stamens included; capsule valves usually not woody and bifid at apex; common plants in Central America *Rondeletia*

8b. Corolla tubes to 5 mm long, stamens usually exserted; capsule valves woody, bifid at the apex; rarely collected in southern Central America *Bathysa*

7. OLDENLANDIEAE

1a. Plants subshrubs, leaves usually small and stiff (ericoid); seeds plano-convex or carinate; plants of high montane formations 2800–3400 m elevation *Arcytophyllum*

1b. Plants herbs or subshrubs, leaves not stiff and ericoid; seeds angular or winged; 0–2000 m elevation 2

2a. Garden ornamentals; flowers red, pink, or white *Pentas*

2b. Weedy plants of wet or moist sites; flowers white 3

3a. Flowers 4-parted, common introduced weeds *Oldenlandia*

3b. Flowers 5-parted, rare introduced weeds *Pentodon*

8. NAUCLEEAE

1a. Woody vines with recurved spines; inflorescences axillary, pedunculate, each with 2–5 globose heads (some modern treatments place this genus in Cinchonieae) *Uncaria*

1b. Trees planted for wood, without spines; inflorescences terminal, each with 1 globose head *Neolamarckia*

9. GUETTARDEAE

1a. Woody lianas with vining branches [leaves with subparallel 3° veins; fruits fleshy; rare in Costa Rica] *Malanea*

1b. Trees or shrubs, not lianas with vining branches (except in some species of *Chomelia*) 2

2a. Corolla lobes valvate in bud; some species with subparallel (lineolate) minor venation [spines/thorns sometimes present on stems and twigs] *Chomelia*

2b. Corolla lobes imbricate in bud; minor venation of the leaves not subparallel nor lineolate 3

- 3a. Fruits dry, separating into 2 indehiscent mericarps (cocci); flowers not secund on inflorescence branches; spines sometimes present on stems and branches *Machaonia*
- 3b. Fruits fleshy; flowers often in secund arrangements; spines absent on stems and branches 4
- 4a. Fruits covered with a fine dense pubescence *Guettarda*
- 4b. Fruits glabrate (formerly *Antirhea* spp.) *Chomelia*

10. CHIOCOCCEAE

- 1a. Flowers 4-parted; fruits dry, flat and broadly winged *Allenanthus*
- 1b. Flowers 5-parted; fruits fleshy, not winged 2
- 2a. Fruits compressed laterally (oblong in cross-section); corolla lobes valvate in bud *Chiococca*
- 2b. Fruits rounded (terete in cross-section); corolla lobes imbricate in bud *Chione*

11. IXOREAE

- 1a. Inflorescences axillary; floral bracts connate and calyx-like or involucrate beneath the flowers; cultivated *Coffea*
- 1b. Inflorescences terminal; floral bracts separate, not calyx-like; wild or cultivated for ornament
..... *Ixora*

12. COUSSAREEAE

- 1a. Ovules separate in a 1-locular ovary; seeds horizontal and fruits often broader than long, exocarp usually leathery; flowers blue or white *Faramea*
- 1b. Ovules connate from a basal column, ovary 1- or 2-locular; seeds longitudinal, fruits longer than broad, exocarp spongy or carnose; flowers white *Coussarea*

13. PSYCHOTRIEAE

- 1a. Plants with creeping prostrate stems and long internodes; leaves often cordate *Geophila*
- 1b. Plants erect, herbaceous subshrubs to small trees; leaves various (rarely subcordate) 2
- 2a. Herbaceous subshrubs; fruits laterally compressed *Declieuxia*
- 2b. Shrubs, trees, or rarely subshrubs; fruits terete 3
- 3a. Stipules with a group of small digitate teeth at the apex; seeds with an incurved adaxial (ventral) surface *Rudgea*
- 3b. Stipules without digitate teeth at the apex, simple to bifid; seeds with a flat but sulcate adaxial surface 4
- 4a. Corollas usually yellow, orange, reddish, purple, or blue (rarely white), often swollen at the base, corolla tube often long (+ 1 cm) and slender, with a ring of pubescence below the middle internally; stipules usually persisting; most often found at higher elevations *Palicourea*
- 4b. Corollas usually white or green to yellowish, not gibbous near the base, corolla tubes generally short (– 1 cm), with a ring of pubescence at or above the middle internally or glabrous within; stipules persisting or deciduous; widespread with many species *Psychotria*

14. MORINDEAE

- 1a. Base of hypanthium free, not united to adjacent flowers, not forming a syncarp in fruit; ovary and fruits with 7–8 locules *Lasianthus*

- 1b. Base of hypanthium united to adjacent flowers, forming a syncarp in fruit; ovary and fruits with 1 or 2 locules 2
- 2a. Flowers and fruits drying black; syncarps fleshy, more than 1 cm diam., calyx not elevated on fruits *Morinda*
- 2b. Flowers and fruits drying dark brown; syncarps dry, less than 1 cm diam., calyx tube prominent on fruits *Appunia*

15. ANTHOSPERMEAE

- 1a. Wild plants forming prostrate mats at high elevations; leaves very small and rounded; fruits orange *Nertera*
- 1b. Cultivated ornamental small (< 1 m) erect shrubs with small narrow acute leaves; fruits brownish *Serissa*

16. SPERMACOCEAE

- 1a. Fruits with circumscissile dehiscence *Mitracarpus*
- 1b. Fruits indehiscent or opening by slits, pores or valves 2
- 2a. Fruits breaking with 3–6 separate indehiscent cocci (note that cocci are borne on the exterior of the fruiting axis and may resemble seeds; compare *Crusea*) *Richardia*
- 2b. Fruits usually with 2 separate or united cocci, cocci dehiscent or indehiscent 3
- 3a. Cocci opening distally or longitudinally (sometimes 1 of the 2 cocci not opening in a fruit) *Spermacoce*
- 3b. Cocci not opening or opening only at the base 4
- 4a. Cocci borne on and separating from a central persisting axis, indehiscent; calyx usually with rounded lobes *Crusea*
- 4b. Cocci not borne on a central axis, indehiscent or dehiscent from the base; calyx usually with acute lobes *Diodia*

17. RUBIEAE

- 1a. Leaves opposite (interpetiolar stipules connate and small) *Didymaea*
- 1b. Leaves whorled (stipules leaf-like) 2
- 2a. Native herbs; flowers on separate pedicels or solitary and involucre *Galium*
- 2b. Rare introduced procumbent herbs; flowers 4–10 and subsessile in distal involucre heads *Sherardia*

Key 2: Artificial Key to Genera and Illustrations

Note that small plants, leafy twigs, and large leaves are all drawn to the same scale throughout the 67 figures. Closed scales represent centimeters; open scales are millimeters. Unless otherwise indicated, enlarged flowers or fruits are to the same scale on the same figure. The illustrations represent typical or common morphologies; they cannot show the range of variation.

- 1a. Herbaceous plants or slender few-branched subshrubs, usually less than 1.5 m tall 2
- 1b. Trees, shrubs, vines, or lianas 23
- 2a. Creeping plants with slender flexible stems, often rooting at the nodes [flowers usually axillary] 3
- 2b. Erect or prostrate plants, lacking slender consistently creeping stems, stems slightly woody if vining 8

3a.	Leaf blades less than 1 cm broad	4
3b.	Leaf blades usually more than 1 cm broad	7
4a.	Leaves in whorls, often linear or narrow; flowers separate (<i>Galium</i>) or in terminal heads (<i>Sherardia</i> , not illustrated)	Fig. 3
4b.	Leaves opposite, linear to ovate	5
5a.	Leaves often linear; fruits dry capsules with few seeds; weeds below 1500 m elevation (<i>Oldenlandia</i>)	Fig. 3
5b.	Leaves not linear; fruits fleshy, 1–2-seeded, rarely found below 1500 m elevation	6
6a.	Fruits orange to red, globose (<i>Nertera</i>)	Fig. 3
6b.	Fruits blue to black, usually bilobed (<i>Didymaea</i>)	Fig. 3
7a.	Fruits with many seeds, blue (<i>Coccocypselum</i>)	Fig. 2
7b.	Fruits with 1–2 seeds, red, blue-black, or black (<i>Geophila</i>)	Fig. 2
8a.	(from 2b) Leaves usually less than 4 cm broad and lanceolate, often sessile	9
8b.	Leaves usually more than 4 cm broad and petiolate	17
9a.	Vining plants often climbing over other plants, with axillary flowers; fruits capsular with many seeds (<i>Manettia</i>)	Fig. 1
9b.	Plants erect or if vining then close to the ground and not usually climbing over other plants; flowers various	10
10a.	Leaves usually less than 15 mm long, stiff or coriaceous	11
10b.	Leaves more than 15 mm long, or thin and herbaceous when less than 15 mm long	12
11a.	Plants of high elevation often in exposed sites; leaves thick and blunt at the apex, usually closely spaced (<i>Arcytophyllum</i>)	Fig. 1
11b.	Plants of mid-elevations; leaves stiff and sharp at the apex (<i>Diodia brasiliensis</i> and the cultivated <i>Serissa</i> , not illustrated)	Fig. 1
12a.	Ovules more than 2 in each locule; fruits with more than 2 seeds; rarely collected plants usually found in wet or partly submerged sites (not illustrated)	13
12b.	Ovules 1 in each locule; fruits with no more than 2(–3) seeds or mericarps; commonly collected plants in many open weedy habitats, dry or wet	14
13a.	Plants with sparse small hairs; corolla pink, tube 5–14 mm long	<i>Sipanea</i>
13b.	Plants glabrous, slightly succulent; corolla white, tube 1.5–4 mm long	<i>Pentodon</i>
14a.	Stipules not clearly united to petioles, awns only 1–2 on each side of the node; stiff erect plants from a woody base (<i>Declieuxia</i>)	Fig. 1
14b.	Stipules united with the petioles forming a truncated sheath, the sheath usually with more than 3 thin erect awns on each side; fruits dry and usually 2-seeded (genera of <i>Spermacoceae</i> ; see the technical keys and the figures below)	15
15a.	Leaves usually less than 2 cm long	Figs. 1, 5–6
15b.	Leaves usually more than 2 cm long	16
16a.	Terminal capitula of flowers consistently present, often subtended by bract-like leaves (<i>Crusea</i> , <i>Mitracarpus</i> , <i>Richardia</i> , <i>Spermacoce</i>)	Figs. 4–5
16b.	Terminal capitula rarely present (<i>Diodia</i> , <i>Spermacoce</i>)	Figs. 1, 5–6
17a.	(from 8b) Inflorescences terminal on short woody stems (compare also <i>Psychotria</i> spp. in figs. 54–66)	Fig. 7
17b.	Inflorescences axillary on semisucculent or woody stems to 2 m tall	18
18a.	Locules with 2 or more ovules; fruits with many seeds (<i>Hoffmannia</i> spp.)	19
18b.	Locules with 1 ovule; fruits usually 2-seeded	22
19a.	Leaves 3/node or petioles with vesicles	Fig. 8
19b.	Leaves 2/node, petioles without vesicles	20
20a.	Species conspicuously pubescent	Figs. 7, 9
20b.	Species mostly glabrescent	21
21a.	Leaves larger and decurrent	Figs. 9–10
21b.	Leaves various, inflorescences smaller	Fig. 11

22a. Ovary usually with 8 locules (<i>Lasianthus</i>)	Fig. 9
22b. Ovary with 2 locules (<i>Psychotria</i> spp., but note that <i>Psychotria aubletiana</i> with sessile involucrate axillary capitulae is not illustrated)	Figs. 12-13
23a. (from 1b) Plants vines or lianas	24
23b. Plants shrubs, trees, or subshrubs	26
24a. Slender-stemmed vines (<i>Manettia</i> and <i>Sabicea</i>)	Figs. 1, 35
24b. Woody climbers or lianas	25
25a. Inflorescences pedunculate globose capitula; stems with sharp recurved spines; leaf blades without parallel or lineolate 3° venation (<i>Uncaria</i>)	Fig. 37
25b. Inflorescences never globose capitula, with many small flowers in panicles (and leaves with parallel 3° venation in <i>Malanea</i> , not illustrated) or with larger (> 2 cm) flowers in few-flowered inflorescences in species of <i>Hillia</i> and <i>Randia</i> ; spines sometimes present in <i>Randia</i> .	
26a. Epiphytic shrubs and small trees	27
26b. Terrestrial shrubs or trees	29
27a. Flowers small (< 15 mm), ovary with 4 locules; fruits baccate with 4 pyrenes (<i>Psychotria</i> spp.)	Fig. 60
27b. Flowers large (> 15 mm), ovary with 2-4 locules; fruits elongate capsules with many seeds or united at the base into a partial syncarp	28
28a. Corolla tube less than 2 cm long; fruits united at the base, fleshy (<i>Schradera</i>)	Fig. 19
28b. Corolla tubes more than 2 cm long; fruits free at the base, elongate capsules (<i>Cosmibuena</i> with winged seeds and <i>Hillia</i> with a tuft of hairs at 1 end of the seed)	Figs. 27-28
29a. Larger leaves usually becoming 40-50 cm long, entire or lobed in a few species; fruits many-seeded	30
29b. Larger leaves not usually becoming 40-50 cm long, never lobed; fruits 1-many-seeded	33
30a. Minor venation of the leaves subparallel (lineolate), some species with deeply lobed leaves; fruits baccate or hard, seeds angular (<i>Pentagonia</i>)	Fig. 14
30b. Minor venation reticulate, leaves entire or with small lobes; fruits capsular, seeds mostly flat	30
31a. Stipules almost separate, 4/node; inflorescences with few 1° branches and no bracteoles (<i>Condaminea</i>)	Fig. 29
31b. Stipules united, 1-2/node; inflorescences with many 1° lateral branches and small bracteoles	32
32a. Fruits small, ca. 4 mm long (<i>Elaeagia</i>)	Fig. 39
32b. Fruits large, ca. 5 cm long (<i>Simira</i>)	Fig. 38
33a. Flowers with corolla tubes more than 10 cm long, white (native species not found in gardens)	34
33b. Flowers with corolla tubes less than 10 cm long (or, if close to 10 cm, red and planted for ornament)	36
34a. Flowers funnelform distally, with a gradually expanded tube, corolla lobes broadly triangular (<i>Osa</i>)	Fig. 15
34b. Flowers salverform distally and with a narrow tube throughout, corolla lobes narrowly ovate to oblong	35
35a. Leaves narrowly elliptic, to 14 cm long, low shrubs of streamsides (<i>Lindenia</i>)	Fig. 15
35b. Leaves not narrowly elliptic, usually more than 14 cm long, shrubs and trees of forests (<i>Posoqueria</i>)	Fig. 15
36a. Inflorescences with some calyx lobes greatly expanded to form large leaf-like red or white "petals"	37
36b. Inflorescences without calyx lobes greatly expanded (slightly expanded in some spp. of <i>Rondeletia</i>)	40
37a. Inflorescences racemose, to 60 cm long, expanded calyx lobes brilliant red (<i>Warszewiczia</i>)	Fig. 16
37b. Inflorescences not racemose, to 15 cm long, expanded calyx lobes white to pinkish red or dull red	38

38a.	Expanded calyx lobes densely pubescent, dull red (white in some forms); cultivated (<i>Mussaenda</i>)	Fig. 16
38b.	Expanded sepals glabrous to glabrescent; calyx lobes white or red; native and also planted for ornament	39
39a.	Corolla tube 3 mm long, white (<i>Calycophyllum</i>)	Fig. 16
39b.	Corolla tube 25 mm long, red (<i>Pogonopus</i>)	Fig. 16
40a.	Inflorescences dense heads of closely packed flowers	41
40b.	Inflorescences lacking dense heads, if subcapitate the flowers becoming separate in fruit	43
41a.	Flowers united or connivent at the base, an involucre of bracts absent (<i>Appunia</i> , <i>Morinda</i> , <i>Schradera</i>)	Fig. 19
41b.	Flowers not united or connivent at the base, an involucre present or absent	42
42a.	Inflorescences subtended by an involucre of colorful large bracts; native trees and shrubs (<i>Psychotria</i> spp.)	Figs. 7, 17-18, 56
42b.	Inflorescences spherical, without an involucre; introduced trees (<i>Neolamarckia</i> , not illustrated).	
43a.	Inflorescences long and narrow (racemiform to spiciform)	44
43b.	Inflorescences not long and narrow	46
44a.	Flowers arising separately and sessile, inflorescences spicate; rare in Costa Rica (<i>Alseis</i> sp.)	Fig. 40
44b.	Flowers usually in small cymose groups, these often on short secondary peduncles, inflorescences racemose	45
45a.	Fruits fleshy (<i>Gonzalagunia</i>)	Figs. 20-21
45b.	Fruits dry dehiscent capsules (<i>Rondeletia</i>)	Fig. 21
46a.	Flowers solitary or few at the ends of branches or short shoots, with short inconspicuous peduncles when few; fruits usually solitary at the tips of branches, usually large (+ 2 cm) and rounded; seeds many, often imbedded in pulp or horizontal (note: <i>Faramea luteovirens</i> and <i>Rudgea monofructus</i> , with few-seeded fruits and flowers resembling those in fig. 46, and <i>Serissa</i> , a small ornamental shrub with short stiff leaves, are not illustrated)	47
46b.	Flowers not solitary at the ends of branchlets, on well-developed peduncles when few; fruits rarely solitary and terminal	48
47a.	Ovaries unilocular with parietal placentation (but difficult to see, with placentas often fusing in the center), seeds variously oriented in white pulp turning black; spines present in some species (<i>Randia</i> spp.)	Figs. 22-24
47b.	Ovaries usually 2-8-locular (but the septa often difficult to see), seeds mostly horizontal; spines absent in all species (other genera of Gardenieae; see the technical key)	Figs. 25-26
48a.	Corollas 3-10 cm long	49
48b.	Corollas less than 3 cm long	58
49a.	Fruits elongate and flattened or cigar-like capsules, seeds many and winged	50
49b.	Fruits not elongated capsules, seeds not winged	52
50a.	Flowers sericeous on the exterior (<i>Ladenbergia</i> and <i>Cinchona</i>)	Figs. 29, 37
50b.	Flowers glabrous on the exterior	51
51a.	Seed with a tuft of hairs (<i>Hillia</i>)	Figs. 27-28
51b.	Seed without hairs (<i>Cosmibuena</i>)	Figs. 27-28
52a.	Flowers usually axillary and solitary (<i>Exostema caribaeum</i>)	Fig. 31
52b.	Flowers neither axillary nor solitary	53
53a.	Corollas inflated in bud; capsules flattened and opening on the broad side (<i>Coutarea</i>)	Fig. 31
53b.	Corollas not inflated in bud; capsules not flattened or with fleshy fruits	54
54a.	Flowers red to purplish; garden ornamentals	Fig. 31
54b.	Flowers white or yellowish; native species	55
55a.	Ovule 1 in each locule (<i>Guetarda turrialbana</i>)	Fig. 30
55b.	Ovules many in each locule	56
56a.	Corolla densely sericeous (<i>Duroia</i> and <i>Amaioua</i>)	Figs. 25, 30

56b.	Corolla glabrous on the exterior	57
57a.	Corolla lobes convolute; ovary 2-locular; fruits ca. 9 cm diam. (<i>Tocoyena</i>)	Fig. 30
57b.	Corolla lobes valvate; ovary 2-6-locular; fruits ca. 1 cm diam. (<i>Isertia</i>)	Fig. 30
58a.	(from 48b) Inflorescences axillary; fruits from axillary peduncles; corollas mostly pubescent on the exterior (glabrous in <i>Chimarrhis</i> and some species of <i>Hoffmannia</i>)	59
58b.	Inflorescences terminal; fruits from terminal peduncles (or from pseudoaxillary peduncles when lateral shoots continue growth); corollas glabrous or puberulent	69
59a.	Ovule 1/locule; seeds 1/chamber in a bony endocarp, fruits drupaceous; flowers often along 1 side of the inflorescence branches; minor leaf venation parallel in some <i>Chomelia</i> and <i>Guettarda</i> spp.	60
59b.	Ovules 3-many/locule; fruits many-seeded berries and capsules; flowers mostly cymose; minor leaf venation parallel in <i>Sommeria</i>	65
60a.	Fruits small woody capsules with many seeds	61
60b.	Fruits fleshy, drupes or berries with 1-2 pyrenes or with a single stony endocarp	62
61a.	Capsules ca. 5 mm long, rounded; corollas 3-5 mm long (<i>Chimarrhis</i>)	Fig. 37
61b.	Capsules 9-20 mm long, elongate; corollas 7-14 mm long (<i>Macrocnemum</i>)	Fig. 40
62a.	Fruits usually with 2 pyrenes	63
62b.	Fruits with a single hard endocarp with 2-5 locules [fruits not flattened or economically useful]	64
63a.	Fruits usually flattened laterally and with a lustrous white surface [corolla tubes < 9 mm long; native plants] (<i>Chiococca</i>)	Fig. 36
63b.	Fruits rounded, becoming red	64
64a.	Corolla tubes > 10 mm long; widely cultivated (<i>Coffea</i> , not illustrated).	
64b.	Corolla tubes < 15 mm long; wild or rarely cultivated (species of <i>Psychotria</i>)	Figs. 12-13
65a.	Corolla lobes valvate or slightly imbricate in bud, often with a distal appendage (<i>Chomelia</i>)	Figs. 33-34
65b.	Corolla lobes broadly imbricate with 1-2 exterior lobes, lacking distal appendages (<i>Guettarda</i>)	Figs. 32-34
66a.	(from 59b) Plants generally with few lateral branches, weak subshrubs to 3 m tall (<i>Hoffmannia</i>)	Figs. 7-11
66b.	Plants trees, shrubs, or clambering	67
67a.	Fruits capsular (<i>Chimarrhis</i>)	Fig. 37
67b.	Fruits berry-like	68
68a.	Stems clambering; locules 3-5 (<i>Sabicea</i>)	Fig. 35
68b.	Trees and shrubs; locules 2 (<i>Sommeria</i>)	Fig. 35
69a.	(from 58b) Fruits dry and mostly capsules; ovaries with usually more than 1 ovule per locule	70
69b.	Fruits fleshy or with arechymatous tissue; ovaries with 1-many ovules per locule	76
70a.	Fruits dry samaras with rounded circumferential wings, red and making a colorful display; rarely collected trees (<i>Allenanthus</i> , not illustrated).	
70b.	Fruits not flattened samaras with a winged margin	71
71a.	Flowers small (- 1 cm) and often closely congested in dense inflorescences or in small groups on open branched inflorescences	72
71b.	Flowers usually more than 1 cm long, not usually closely congested in the inflorescence	75
72a.	Spines often present; capsules opening from the base (<i>Machaonia</i>)	Fig. 37
72b.	Spines absent; capsules opening from the top	73
73a.	Anthers opening by terminal pores; leaves with pellucid dots (<i>Rustia</i>)	Fig. 38
73b.	Anthers opening by lateral slits; leaves lacking pellucid dots	74
74a.	Corolla yellow; shrubs or small trees of higher elevations (<i>Deppea</i>)	Fig. 38
74b.	Corolla white; medium to large trees of low and high elevations (<i>Elaeagia</i>)	Fig. 39

- 75a. Capsules usually small (2–5 mm) and rounded; corollas often pubescent (*Rondeletia* spp.) **Figs. 41–41A**
- 75b. Capsules usually more than 9 mm long and elongated, rounded or flattened; corollas puberulent (*Cinchona* and *Exostema*) or glabrous (*Ferdinandusa* and *Macrocnemum*) **Figs. 37, 40**
- 76a. (from 69b) Ovaries with 3–many ovules per locule; fruits usually many-seeded 77
- 76b. Ovaries with 1 ovule per locule; fruits with 1–2 seeds (usually 5 in *Psychotria racemosa*) ... 80
- 77a. Anthers with the thecae divided into small sections [ovaries 2–6-locular] (*Isertia*) **Figs. 30, 49**
- 77b. Anthers with the thecae not divided into sections 78
- 78a. Ovaries and fruits 5-locular (*Hamelia*) **Figs. 34, 42**
- 78b. Ovaries and fruits 2-locular 79
- 79a. Corolla lobes valvate in bud; inflorescences with cymose branches (*Raritebe*) **Fig. 43**
- 79b. Corolla lobes contorted in bud; inflorescences with flowers along 1 side of branches (*Bertiera*) **Fig. 43**
- 80a. (from 76b) Fruits usually with only 1 pyrene (seed), rounded in cross-section; the ovary 2-locular in early stages, with a thin septum or with only 1 locule; flowers white to brilliant blue or lavender (rarely yellowish) 81
- 80b. Fruits usually with 2 pyrenes or seeds, the pyrene plano-convex in cross-section; the ovary 2-locular and with a well-developed septum in early stages; flowers white to yellow, orange, red, purple, or bluish purple (rarely blue) 84
- 81a. Flowers brilliant blue, blue-lavender, or white; fruits usually broader than long to globose; stipules acute to long-awned at the apex 82
- 81b. Flowers white to yellowish white; fruits usually longer than broad; stipules obtuse to acute, not awned 83
- 82a. Larger-leaved species of *Faramea* **Fig. 44**
- 82b. Smaller-leaved species of *Faramea* **Fig. 45**
- 83a. Smaller-leaved species of *Coussarea* **Figs. 46–47**
- 83b. Larger-leaved species of *Coussarea* **Figs. 48**
- 84a. Corolla lobes contorted in bud, corollas white to red; wild plants and cultivated ornamentals (*Ixora*) **Fig. 43**
- 84b. Corolla lobes valvate in bud, corollas white to red, yellow, or purple; plants not cultivated ornamentals 85
- 85a. Stipules usually rounded distally and with several short indurated tooth-like appendages at the apex; inflorescences often few-flowered (*Rudgea*) **Fig. 46**
- 85b. Stipules not rounded distally and with thickened tooth-like structures at the apex; inflorescences with few to many flowers 86
- 86a. Flowers usually brightly colorful, yellow to orange, purple, or bluish purple (rarely white), corolla tubes often slightly enlarged on 1 side at the base, a ring of hairs present on the interior of the swollen lower half of the corolla tube (*Palicourea* spp., see also fig. 54) 87
- 86b. Flowers usually white or slightly yellowish, corolla tubes not expanded on 1 side at the base, a ring of hairs not present in the cylindrical lower half of the interior of the corolla tube (*Psychotria* spp.) 88
- 87a. *Palicourea* spp.: inflorescences with conspicuous bracts and a species with spathaceous calyx **Fig. 49**
- 87b. *Palicourea* spp.: lowland species **Fig. 50**
- 87c. *Palicourea* spp.: flowers mostly yellow-orange **Fig. 51**
- 87d. *Palicourea* spp.: flowers mostly purple-violet **Fig. 52**
- 87e. *Palicourea* spp.: smaller-leaved species **Fig. 53**
- 88a. Fruits becoming blue, purple, or black (orange in *P. racemosa* with 5 pyrenes, red in *P. haematocarpa* with very small inflorescences); leaves drying greenish to brown (except when treated with isopropyl alcohol), domatia usually absent (except *P. acuminata*); stipules often persisting and not subtending a ring of reddish colleters (subgenus *Heteropsychotria* and other species) 89

88b. Fruits becoming red at maturity; leaves drying grayish, grayish pink, or reddish brown to black, domatia present in a few species; stipules usually caducous and enclosing a ring of reddish colleters at their base (subgenus *Psychotria*) 90

89a. *Heteropsychotria*: large-leaved and pubescent Fig. 54

89b. *Heteropsychotria*: smaller-leaved species Fig. 55

89c. *Heteropsychotria*: smaller inflorescences Fig. 56

89d. *Heteropsychotria*: large open inflorescences Fig. 57

89e. *Heteropsychotria*: conspicuous inflorescences Fig. 58

89f. *Heteropsychotria*: deciduous and other species Fig. 59

90a. Subg. *Psychotria*: species with very small leaves Fig. 60

90b. Subg. *Psychotria*: species with small leaves Fig. 61

90c. Subg. *Psychotria*: species with *Ficus*-like stipules Fig. 62

90d. Subg. *Psychotria*: species with dense pubescence Fig. 63

90e. Subg. *Psychotria*: species with larger leaves Fig. 64

90f. Subg. *Psychotria*: deciduous and unusual species Fig. 65

90g. Subg. *Psychotria*: miscellaneous unusual species Fig. 66

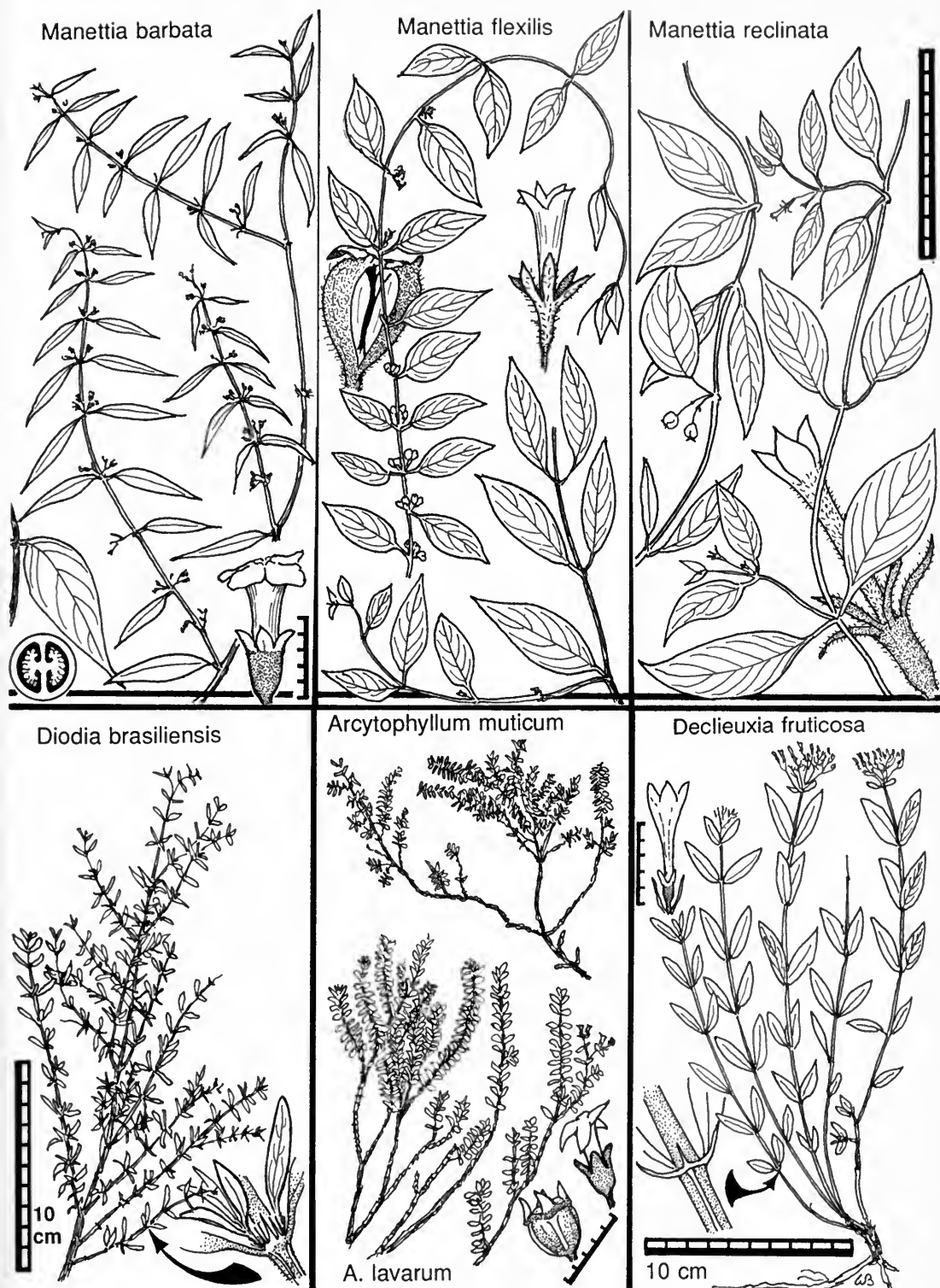
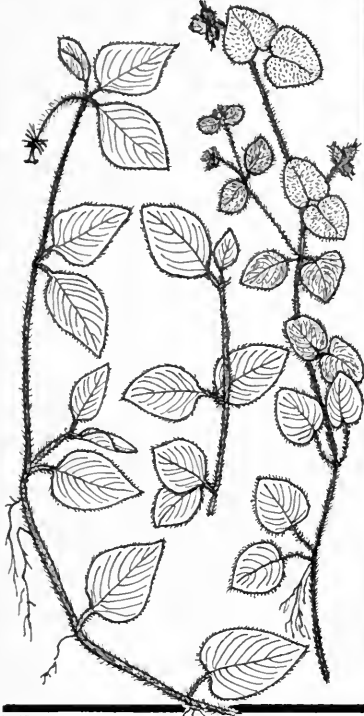
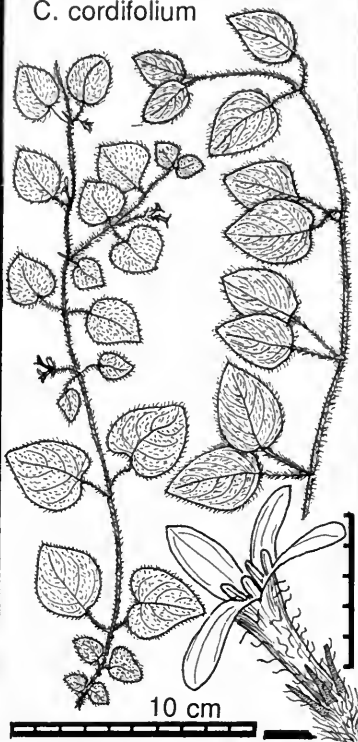


FIG. 1. Twining shrubs (*Manettia* spp.) and subshrubs with small stiff leaves (species of *Arcytophyllum*, *Declieuxia*, and *Diodia*).

Coccocypselum hirsutum



C. cordifolium



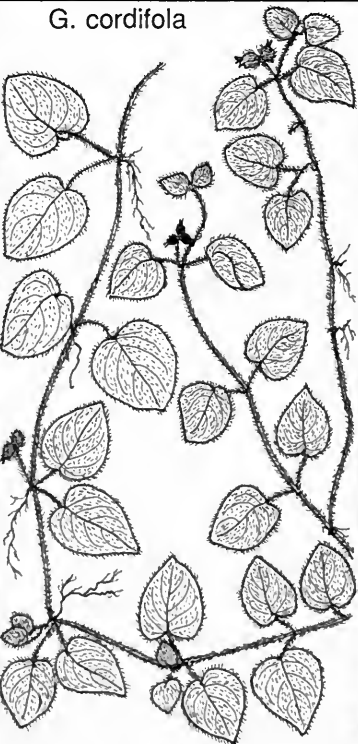
Coccocypselum lanceolatum



Geophila repens



G. cordifolia



Geophila macropoda

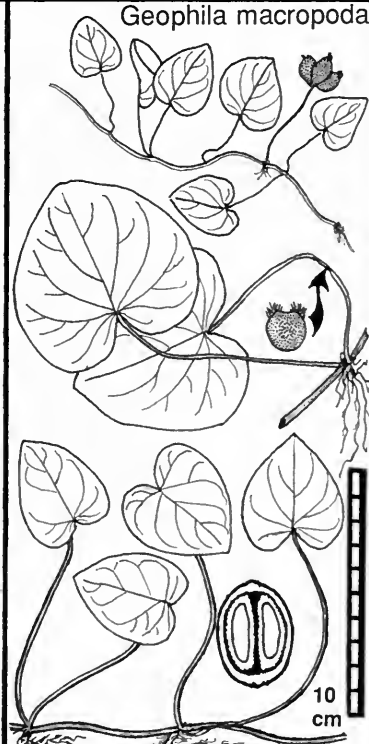


FIG. 2. Twining herbs: species of *Coccocypselum* and *Geophila*.

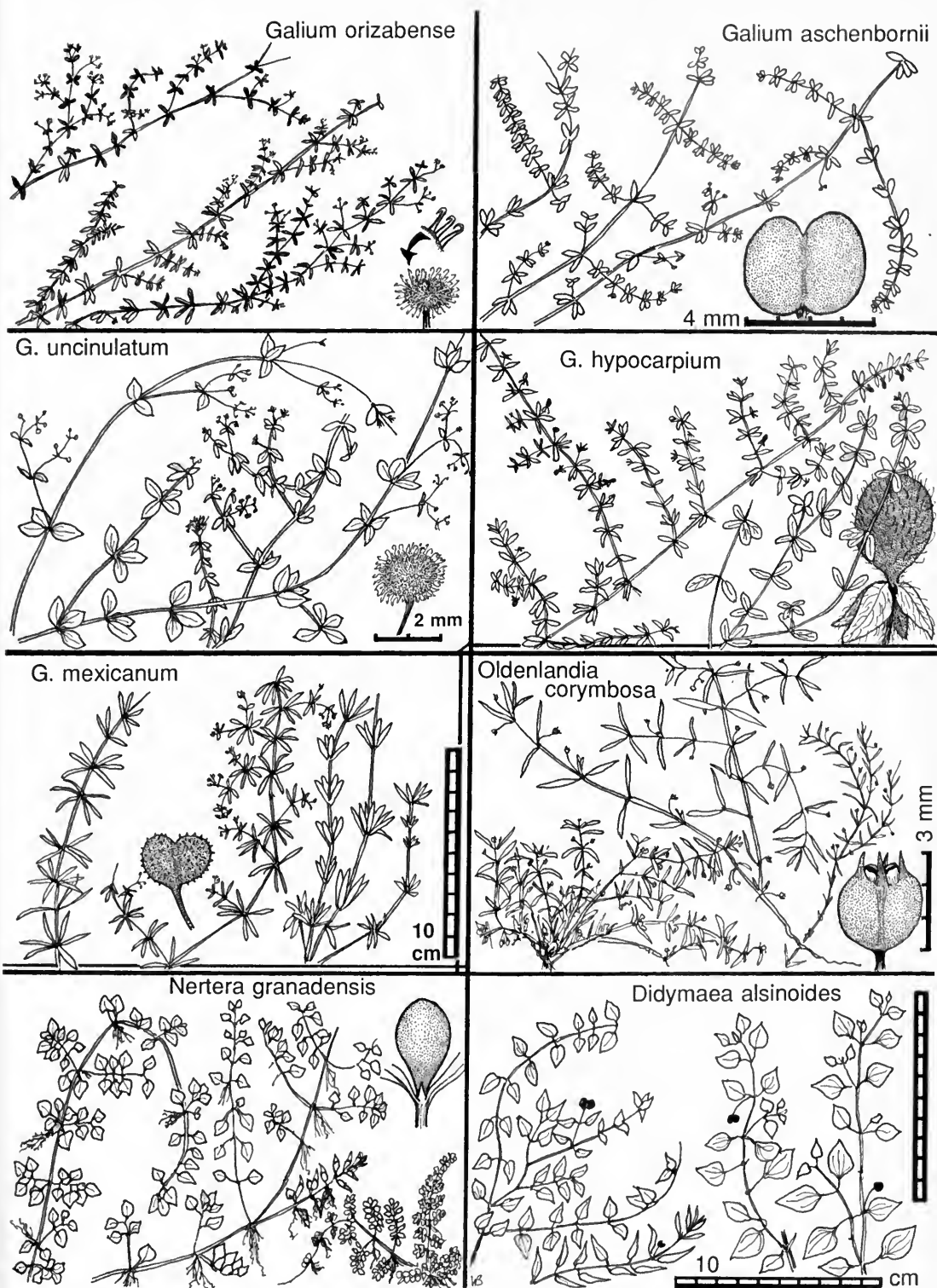


FIG. 3. Herbs with small leaves and slender stems: species of *Didymaea*, *Galium*, *Nertera*, and *Oldenlandia*.

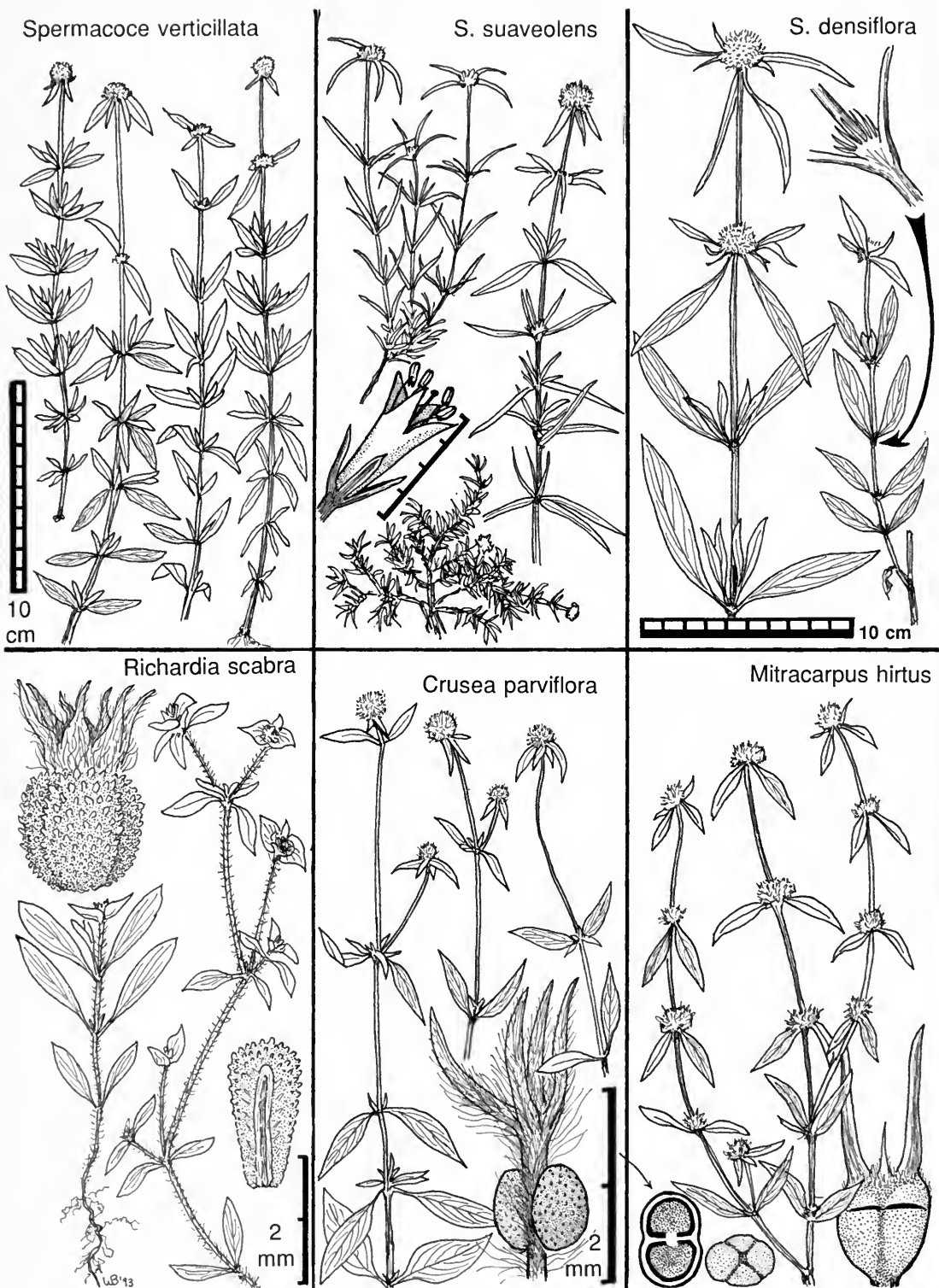


FIG. 4. Erect herbs with narrow lanceolate leaves and capitate or verticillate flowers: species of *Crusea*, *Mitracarpus*, *Richardia*, and *Spermacoce*.

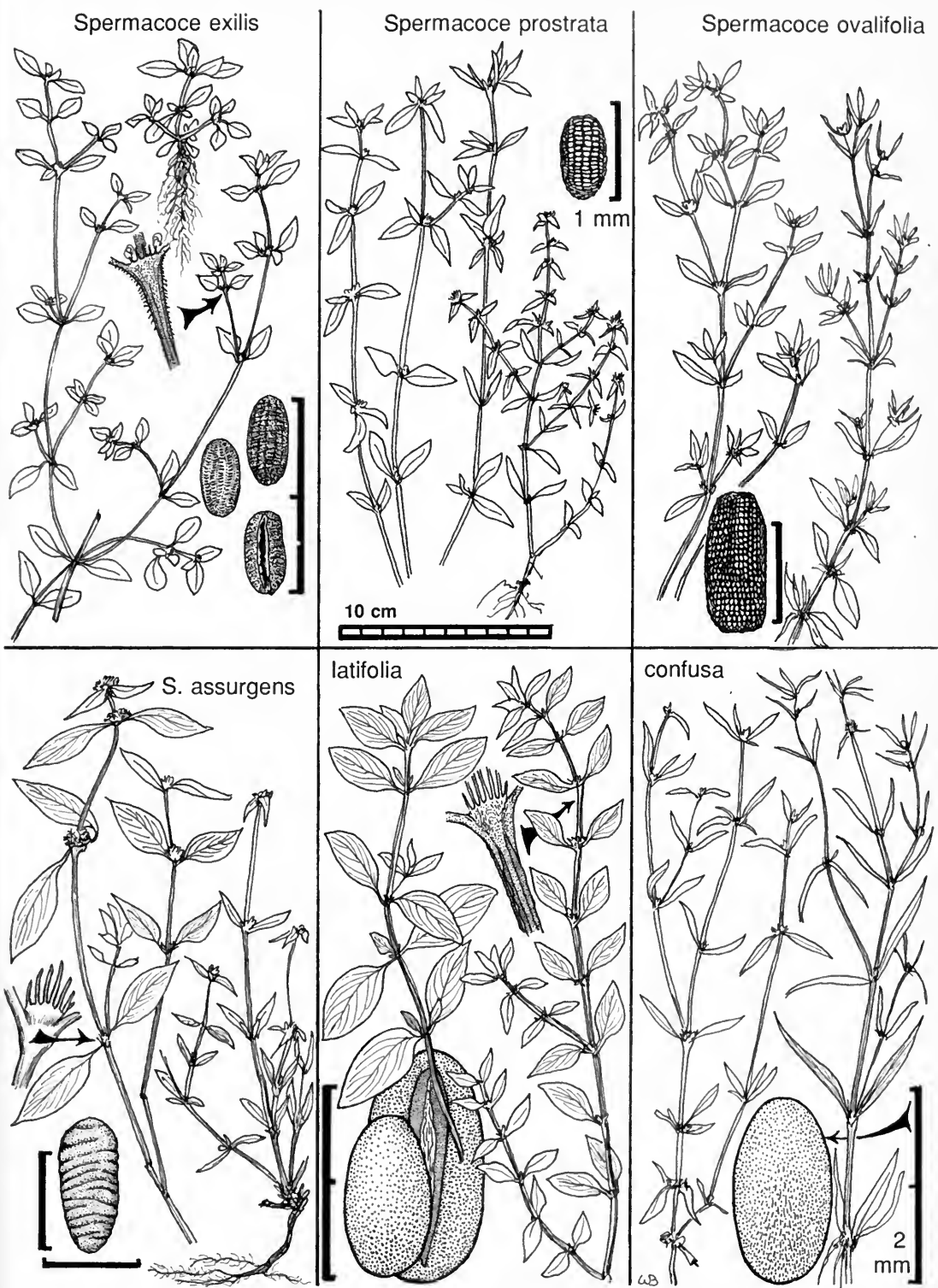


FIG. 5. Erect herbs with narrow lanceolate leaves: *Spermacoce* spp.

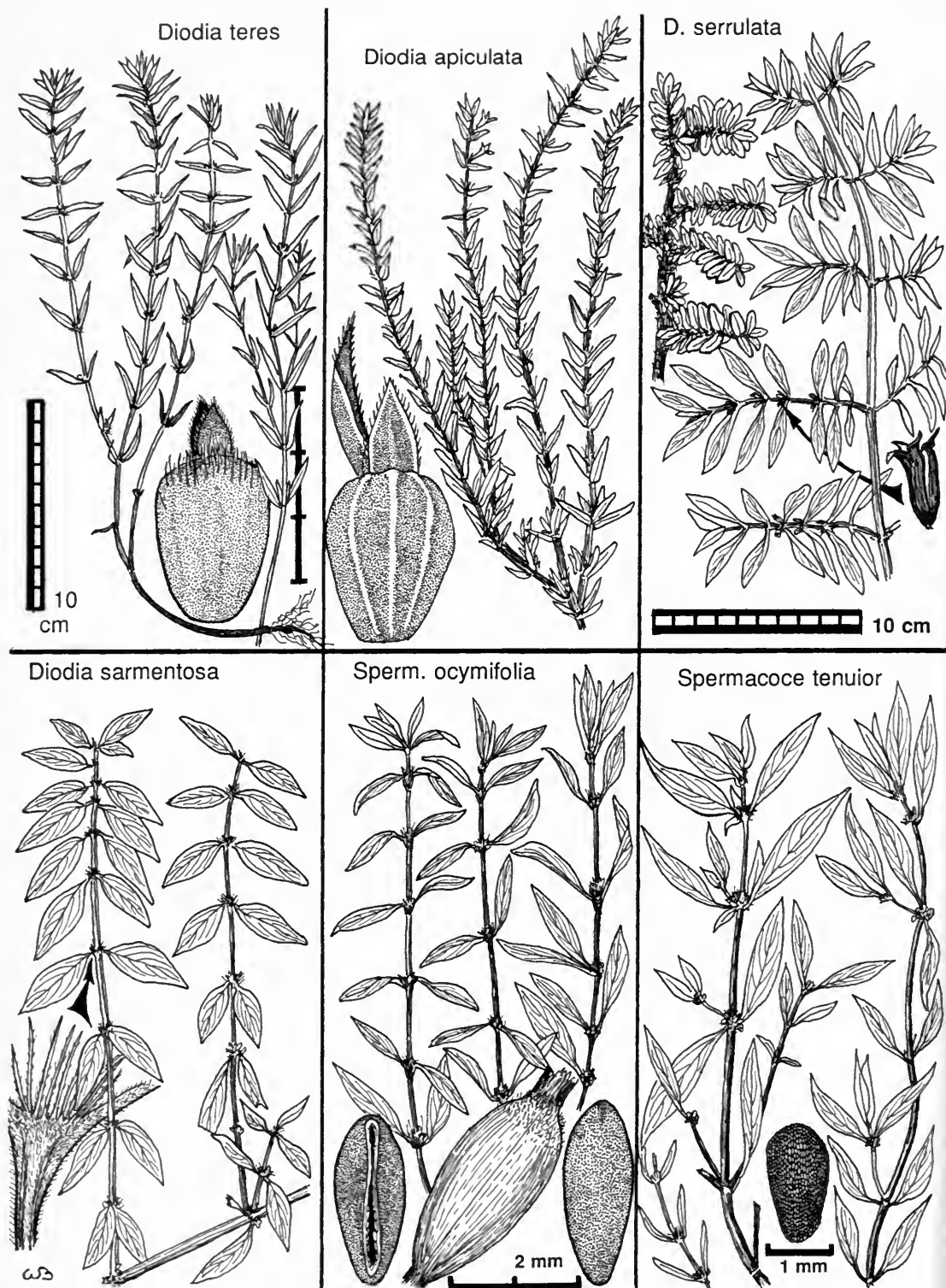
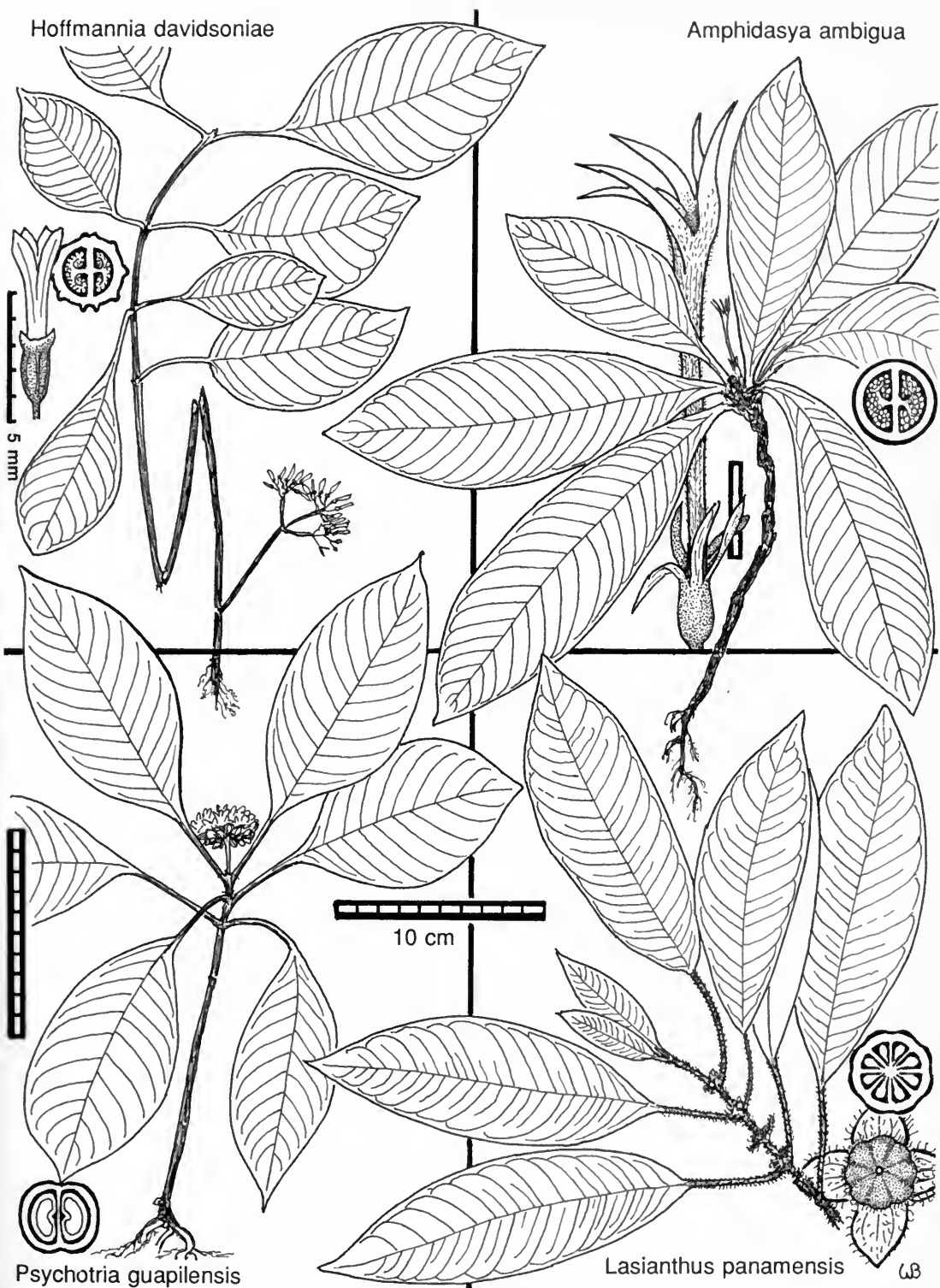


FIG. 6. Erect herbs with narrow lanceolate leaves: *Diodia* spp. and two species of *Spermatocoe*.

Hoffmannia davidsoniae

Amphidasya ambigua



Psychotria guapilensis

Lasianthus panamensis

WB

FIG. 7. Herbs or subshrubs with larger leaves: species of *Amphidasya*, *Hoffmannia*, *Lasianthus*, and *Psychotria*.

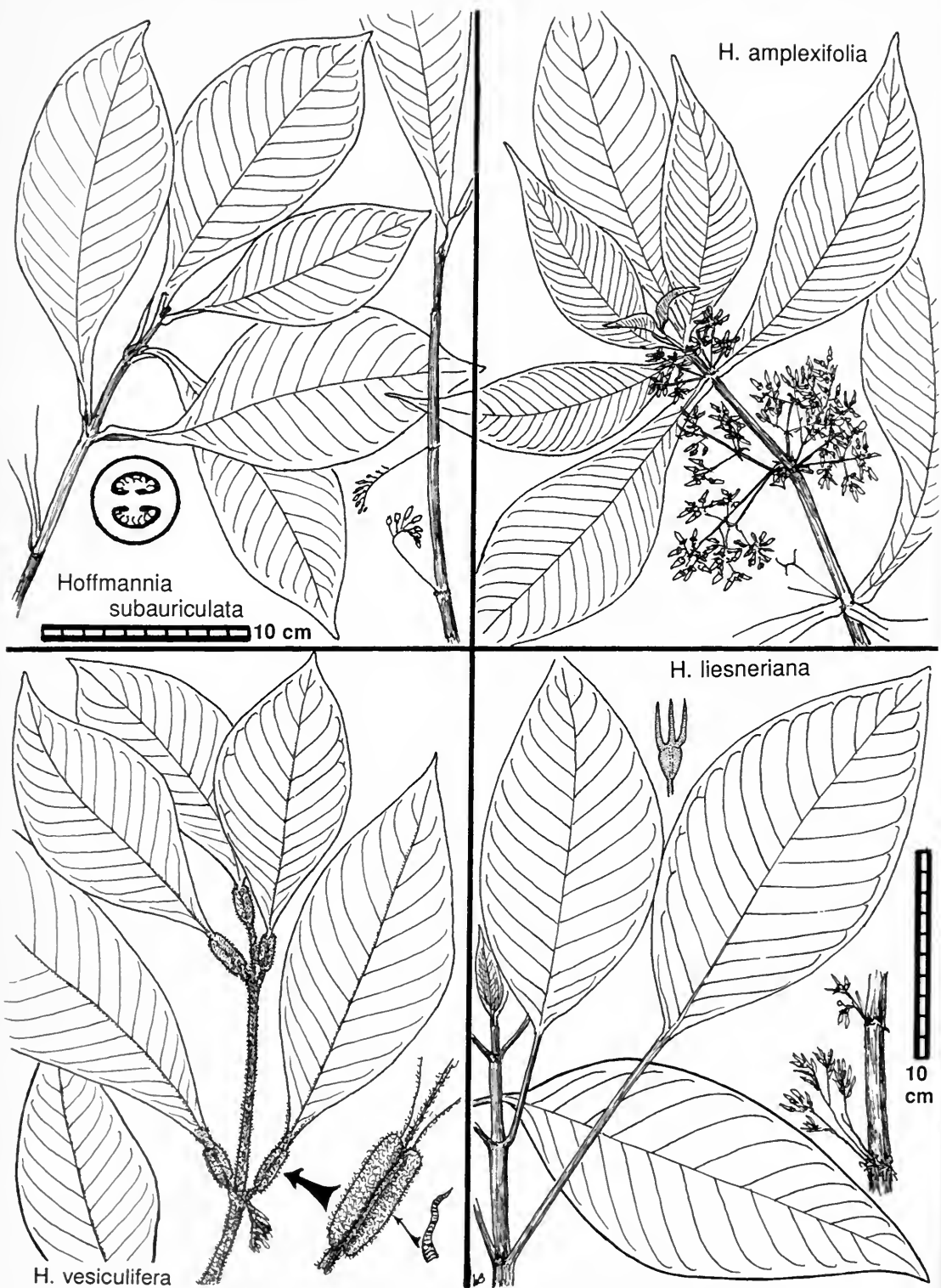


FIG. 8. Herbs or subshrubs with axillary flowers: unusual species of *Hoffmannia*.

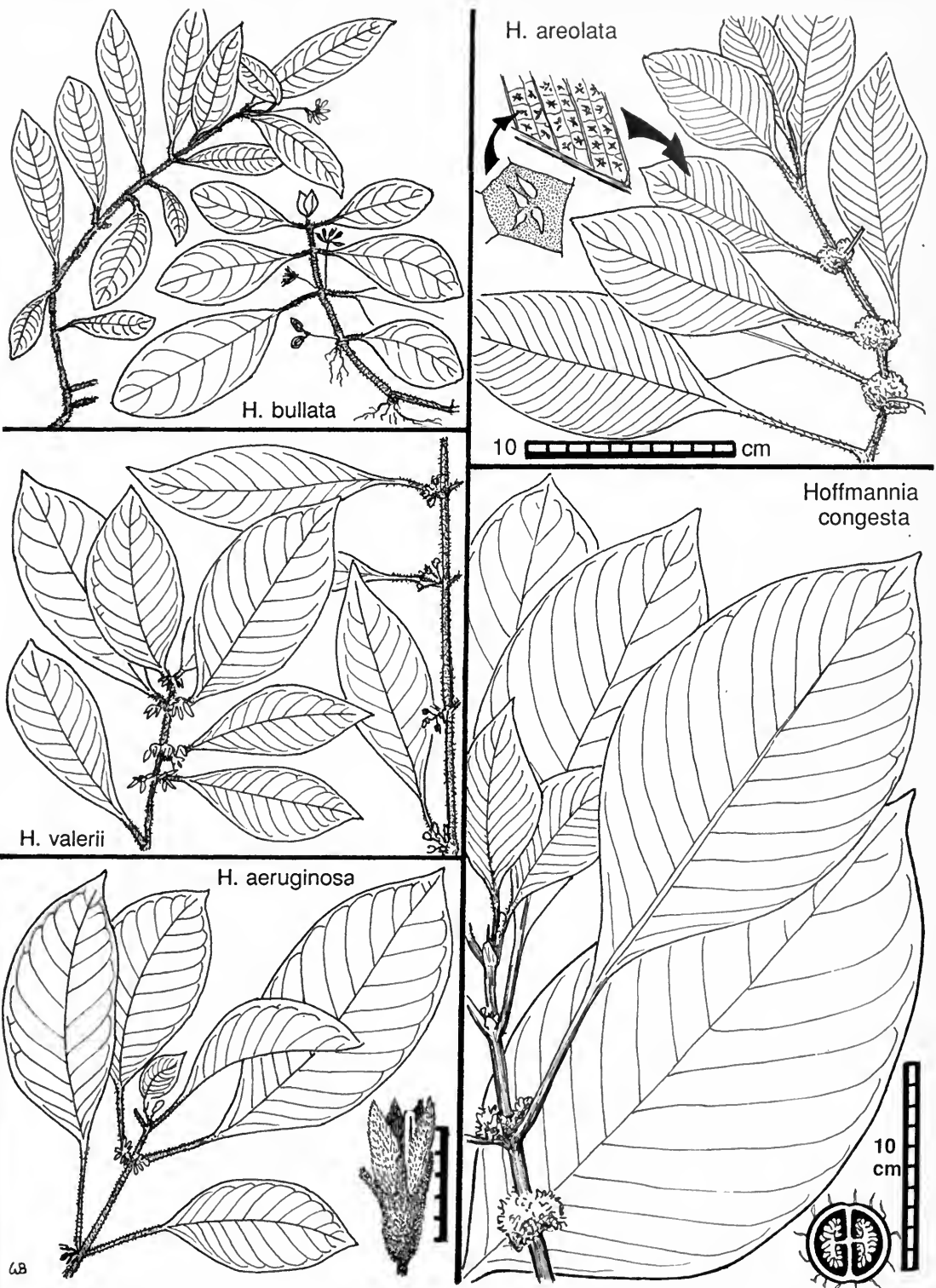


FIG. 9. Herbs or subshrubs with axillary flowers: pubescent species of *Hoffmannia* and *H. congesta*.

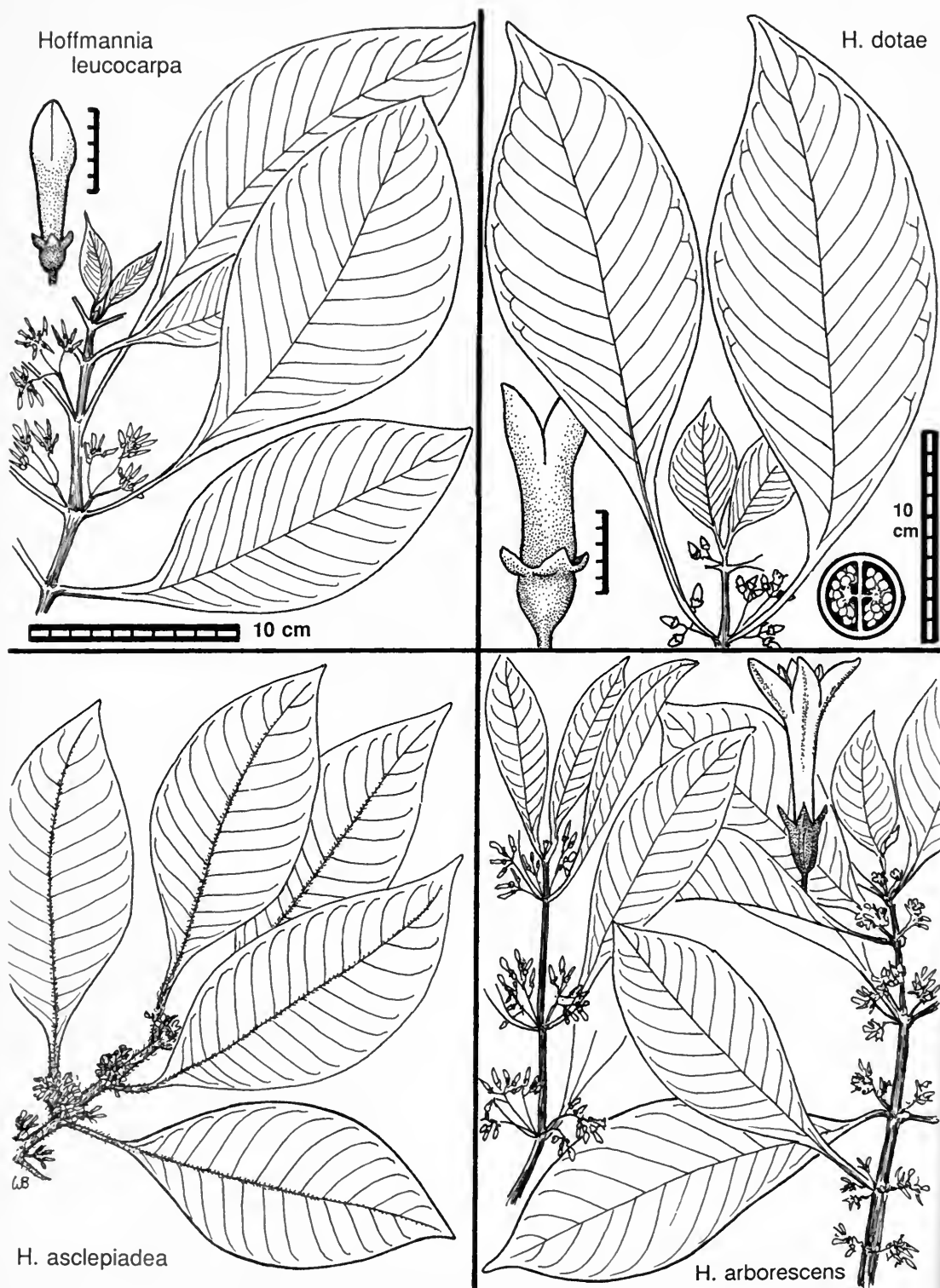


FIG. 10. Subshrubs with axillary flowers: species of *Hoffmannia* with larger leaves.

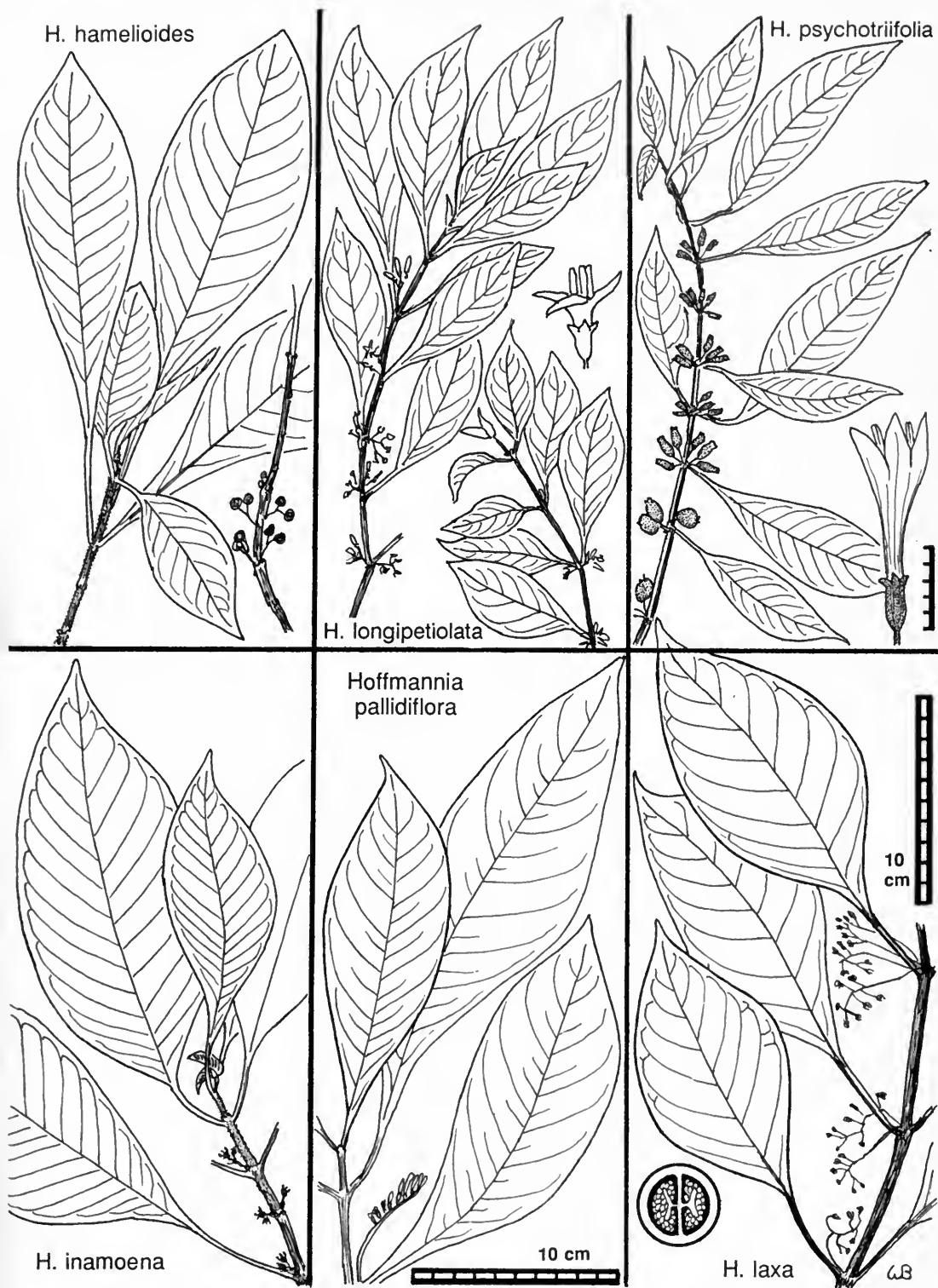


FIG. 11. Subshrubs with axillary flowers: species of *Hoffmannia* with leaves tapering gradually to the base.

P. macrophylla

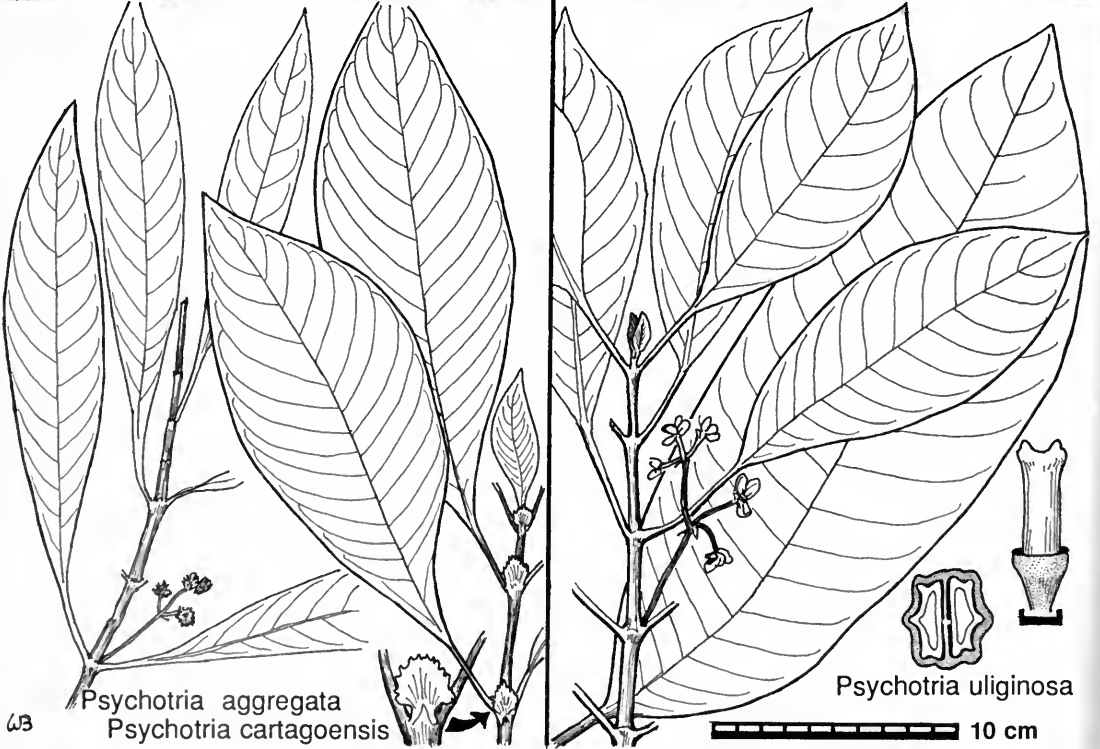
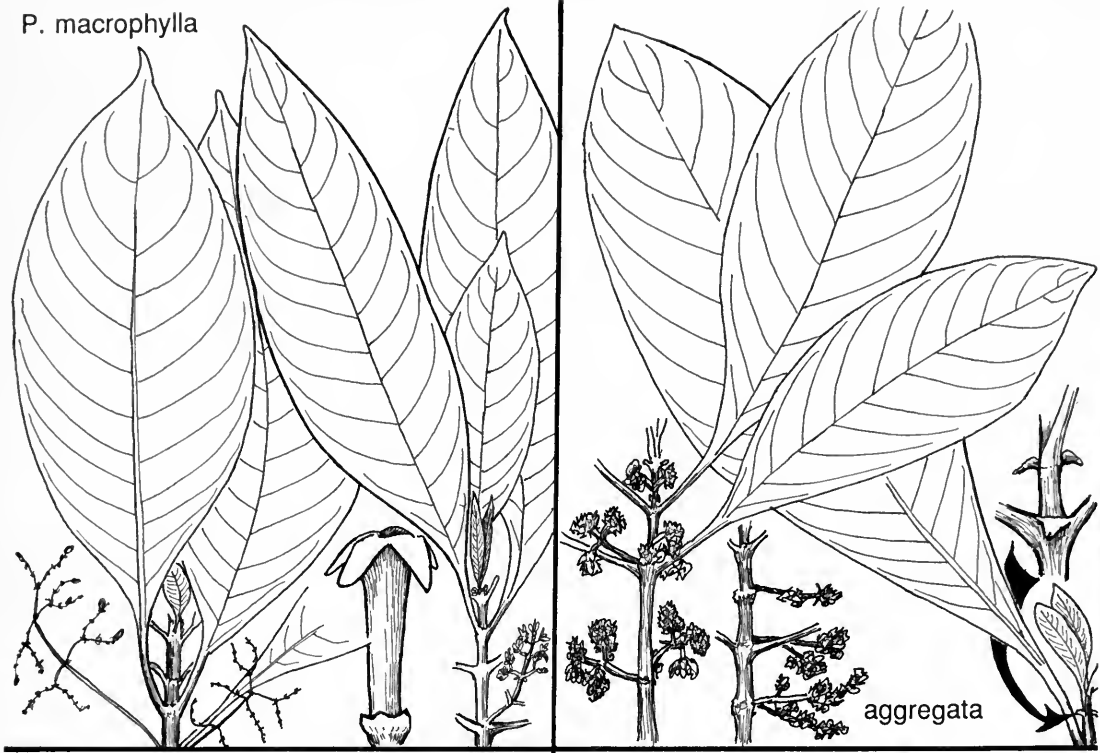


FIG. 12. Subshrubs with axillary flowers: species of *Psychotria*.

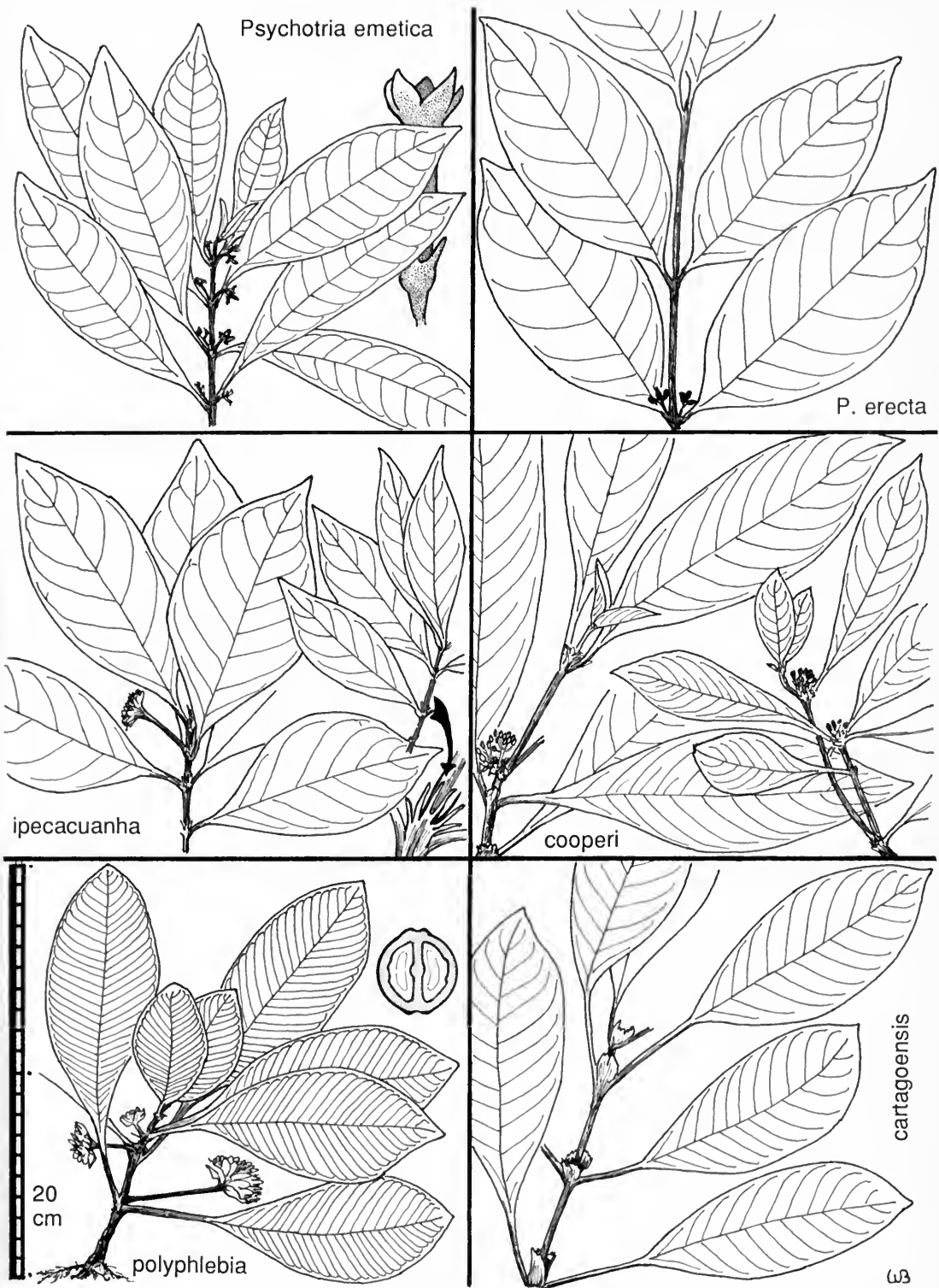


FIG. 13. Subshrubs with axillary flowers: species of *Psychotria*.



FIG. 14. Trees with very large or lobed leaves: three species of *Pentagonia*.



FIG. 15. Flowers with very long corolla tubes: species of *Lindenia*, *Osa*, and *Posoqueria*.



FIG. 16. Inflorescences with greatly expanded petal-like calyx lobes: species of *Calycophyllum*, *Mussaenda*, *Pogonopus*, and *Warszewiczia*.

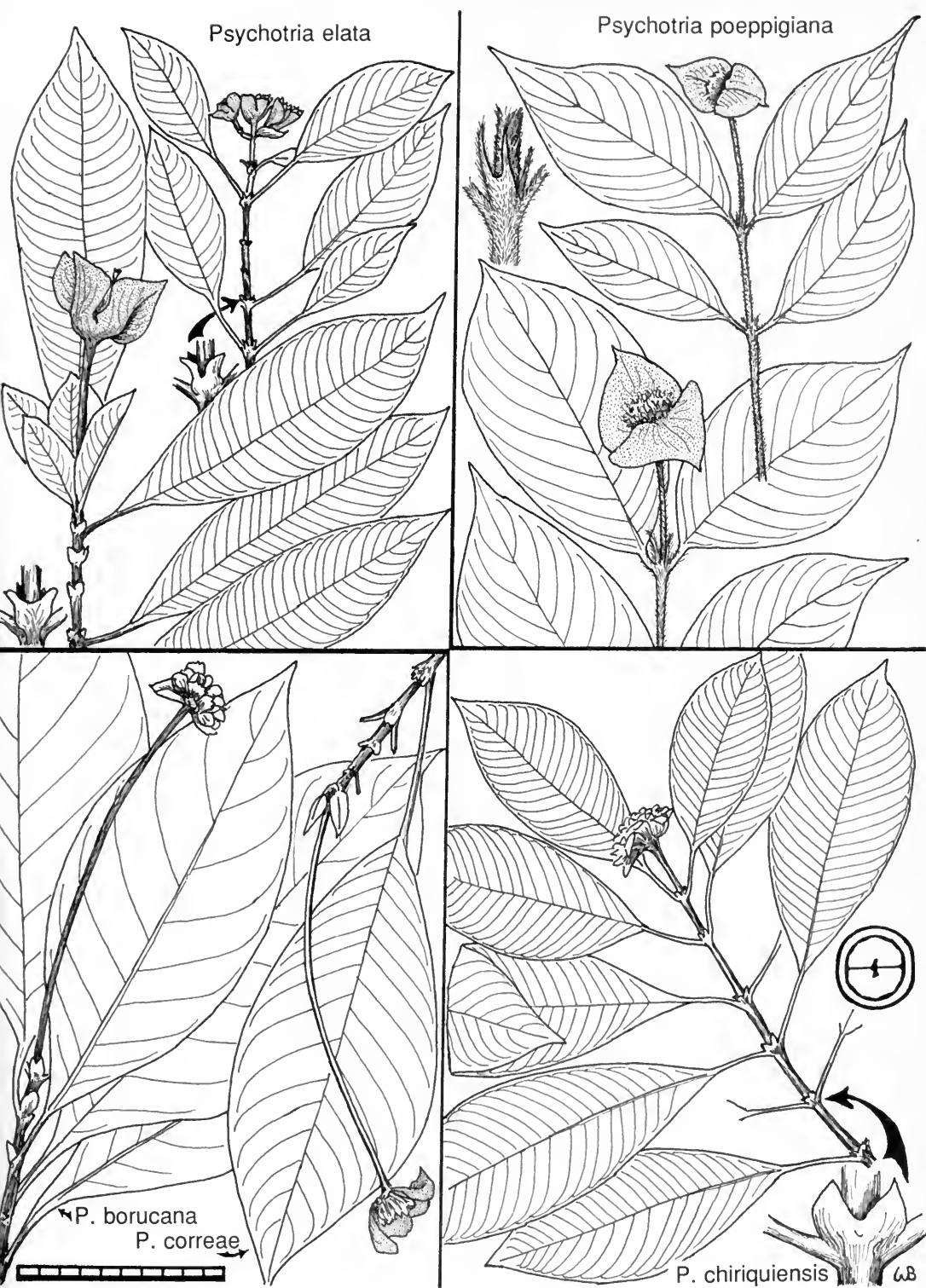


FIG. 17. Inflorescences of involucrate heads: species of *Psychotria* (formerly *Cephaelis* spp.).

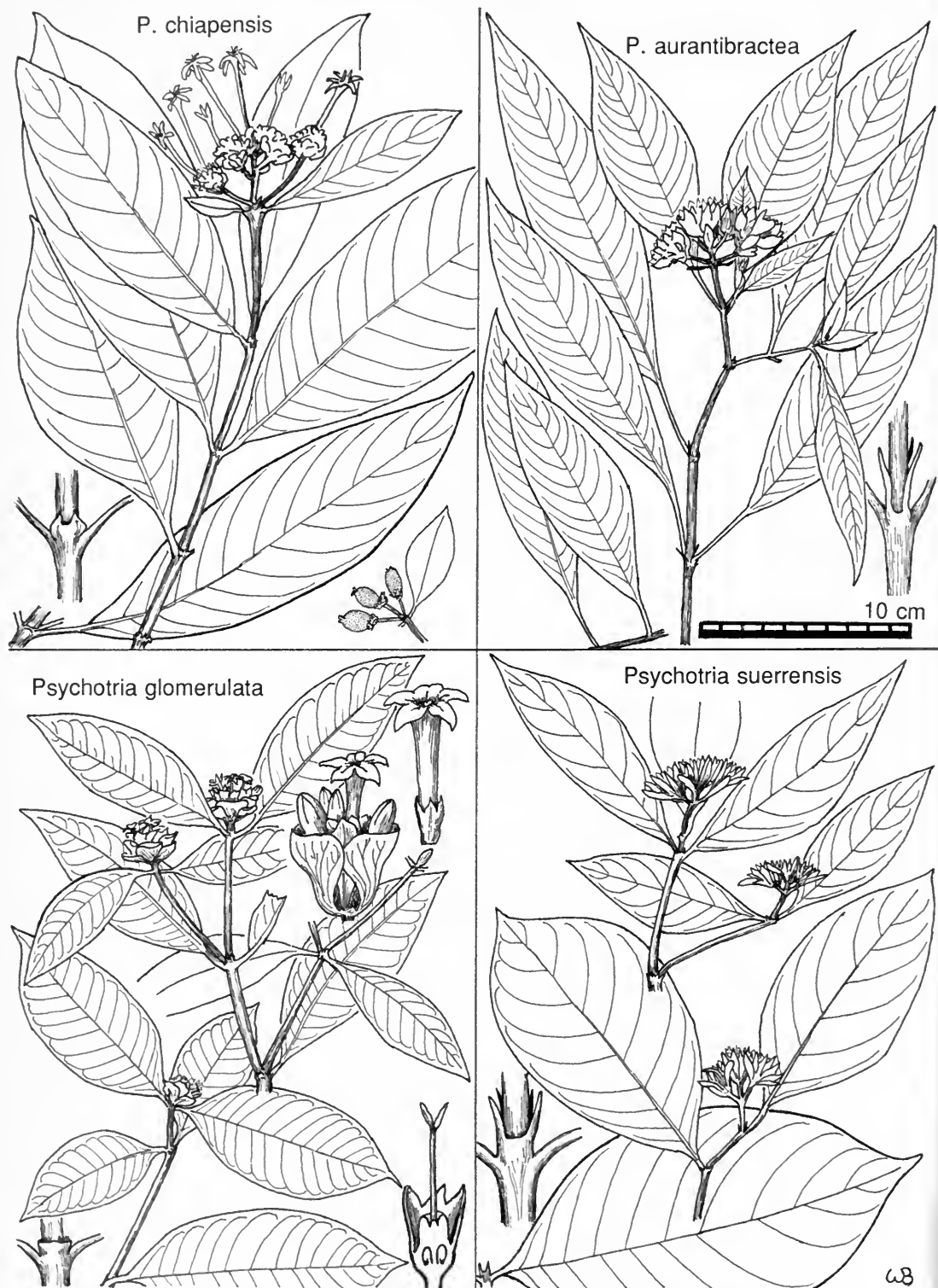
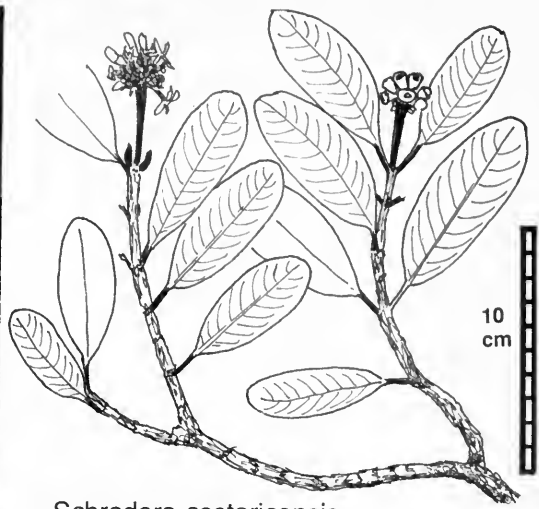


FIG. 18. Inflorescences of involucrate or conspicuously bracteate heads: species of *Psychotria*.

Appunia guatemalensis



Schradera costaricensis



M. royoc



Morinda citrifolia

Morinda panamensis



FIG. 19. Inflorescences of compact heads with flowers connivent at the base: species of *Appunia*, *Morinda*, and *Schradera*.



FIG. 20. Inflorescences long and narrow: species of *Gonzalagunia*.

Rondeletia brenesii



Rondeletia buddleoides



Rondeletia urophylla



Gonzalagunia bracteosa



FIG. 21. Inflorescences long and narrow: species of *Gonzalagunia* and *Rondeletia*.

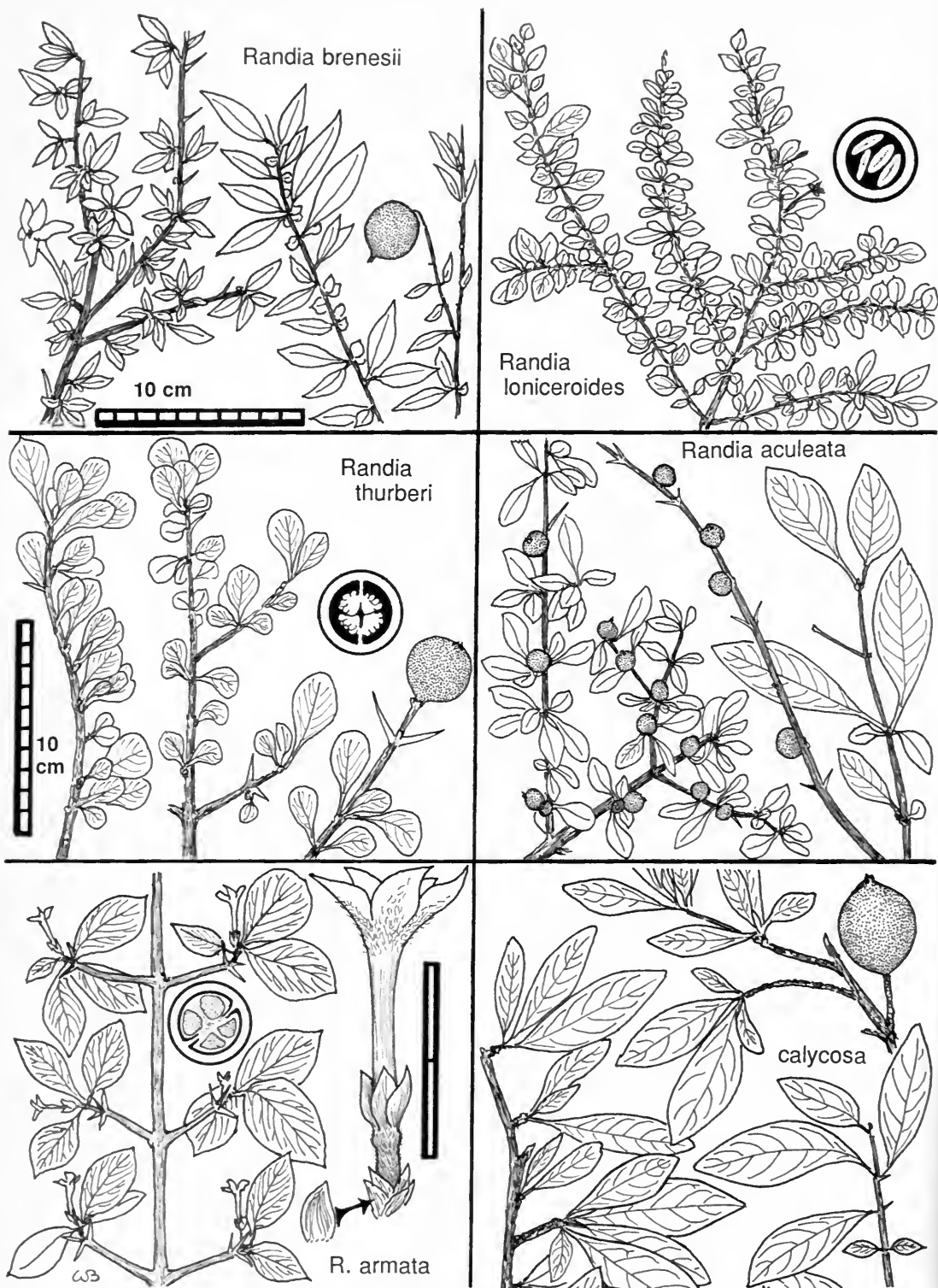


FIG. 22. Fruits usually terminal and solitary: species of *Randia* with small leaves.

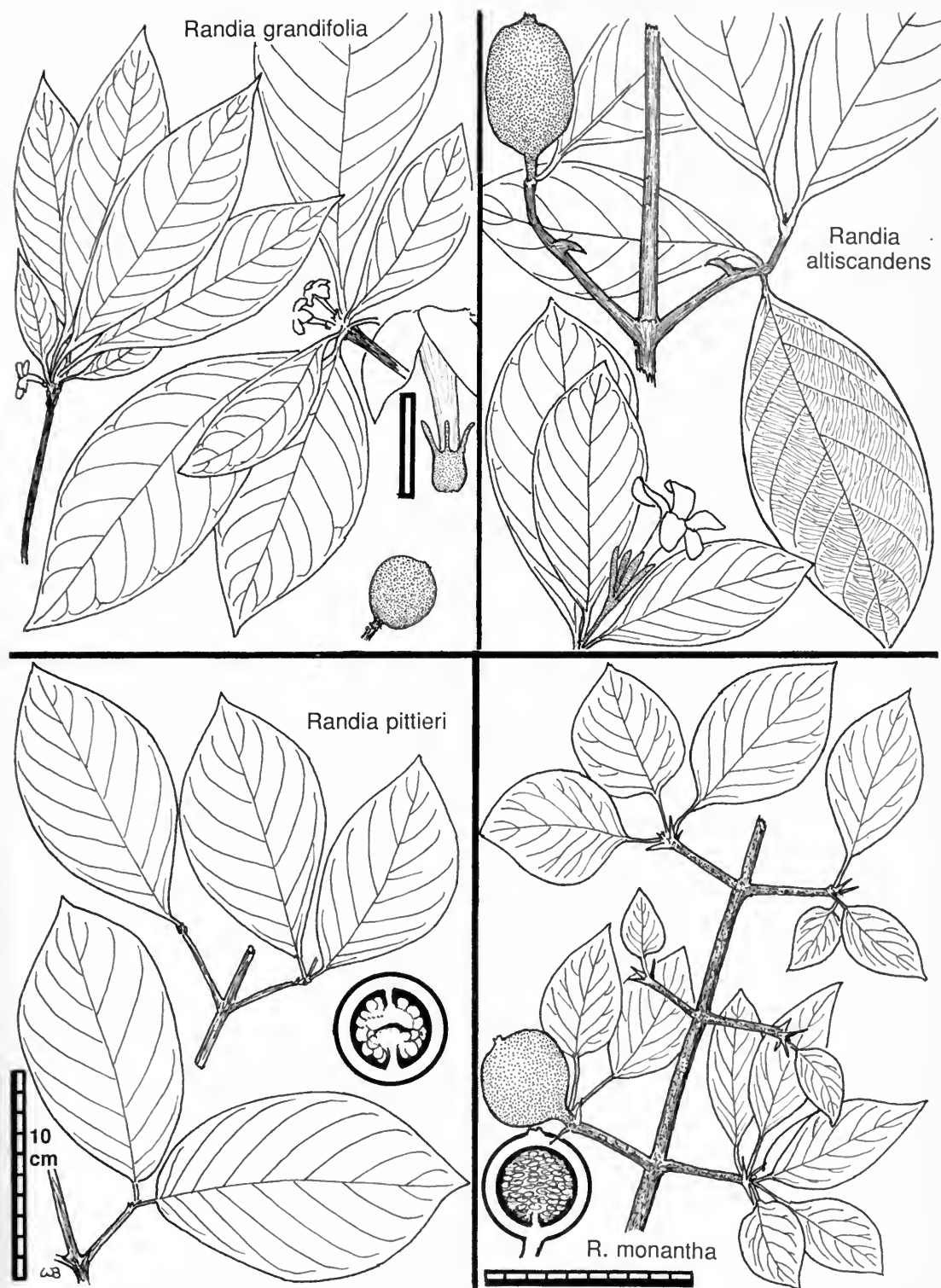


FIG. 23. Fruits usually terminal and solitary: species of *Randia* with medium-sized leaves.

R. genipoides



Randia grayumii

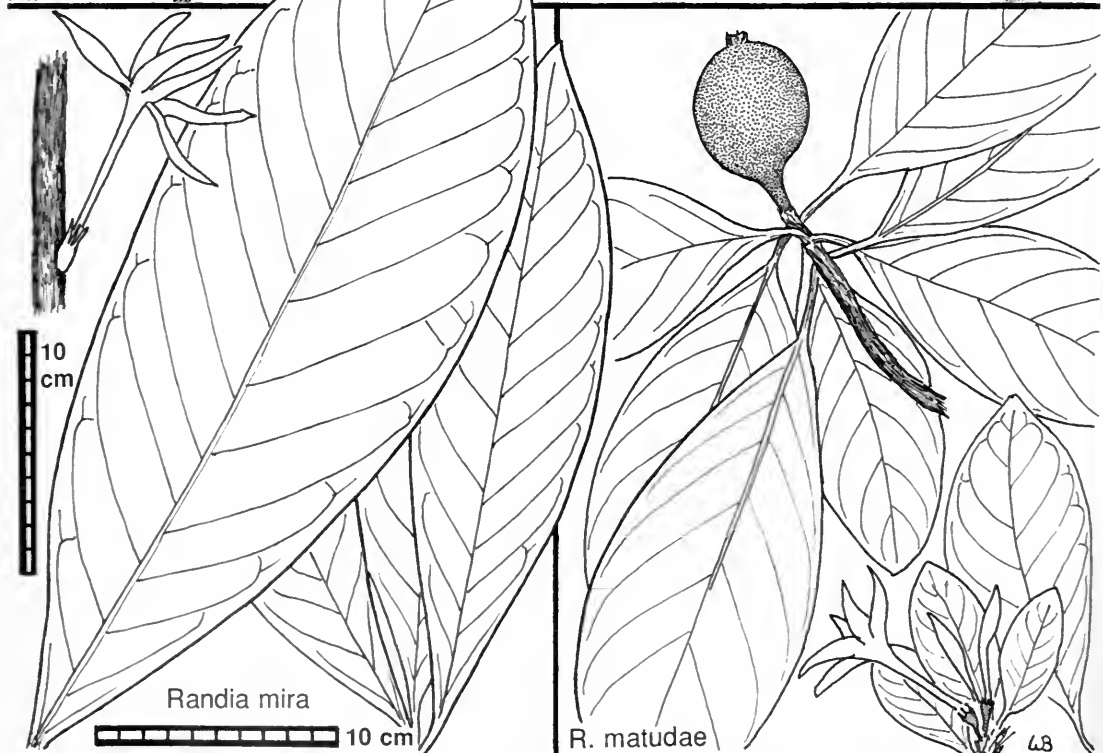


FIG. 24. Fruits usually terminal and solitary; species of *Randia* with larger leaves.

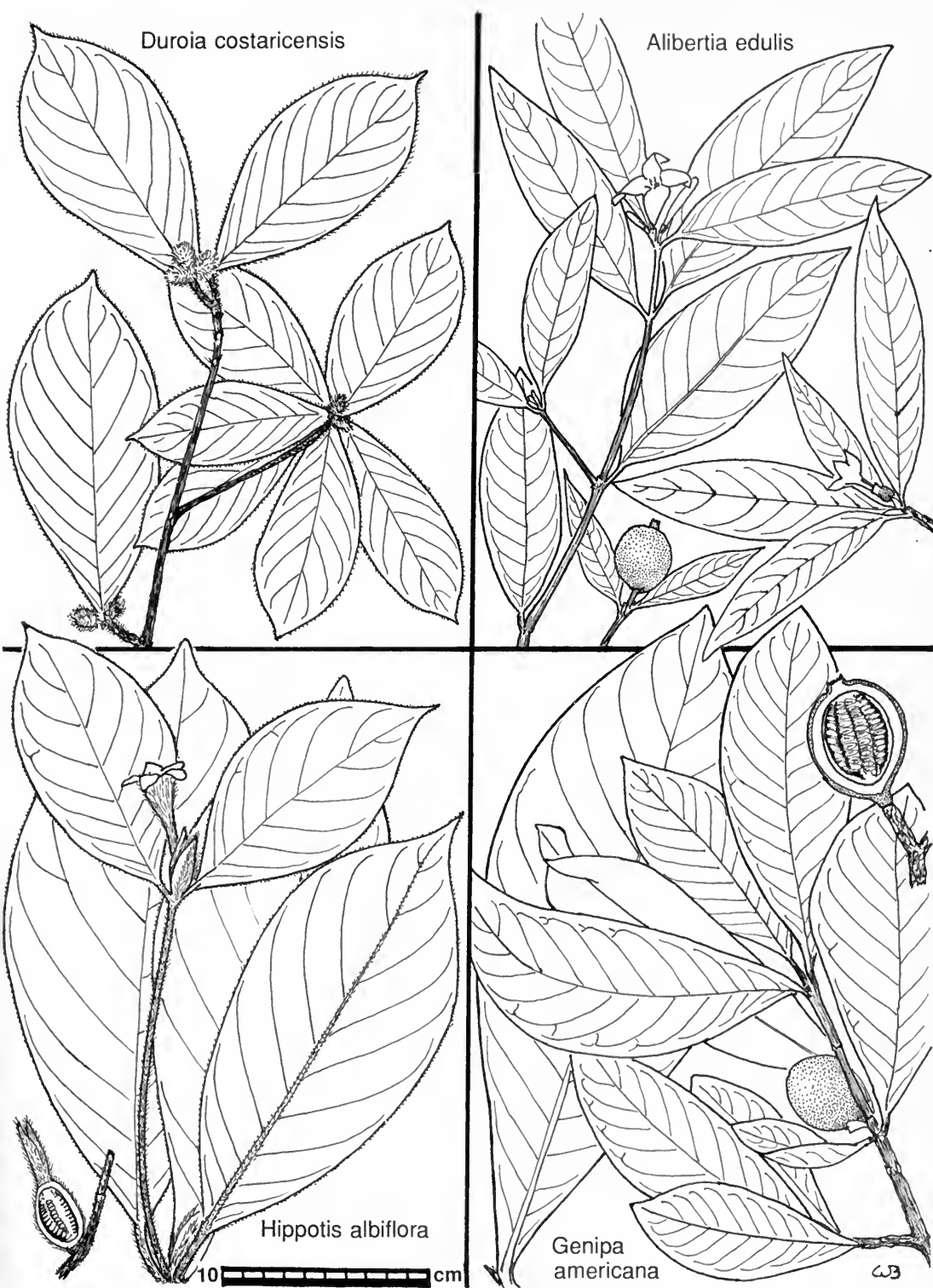


FIG. 25. Fruits usually terminal and solitary: species of *Alibertia*, *Duroia*, *Genipa*, and *Hippotis*.

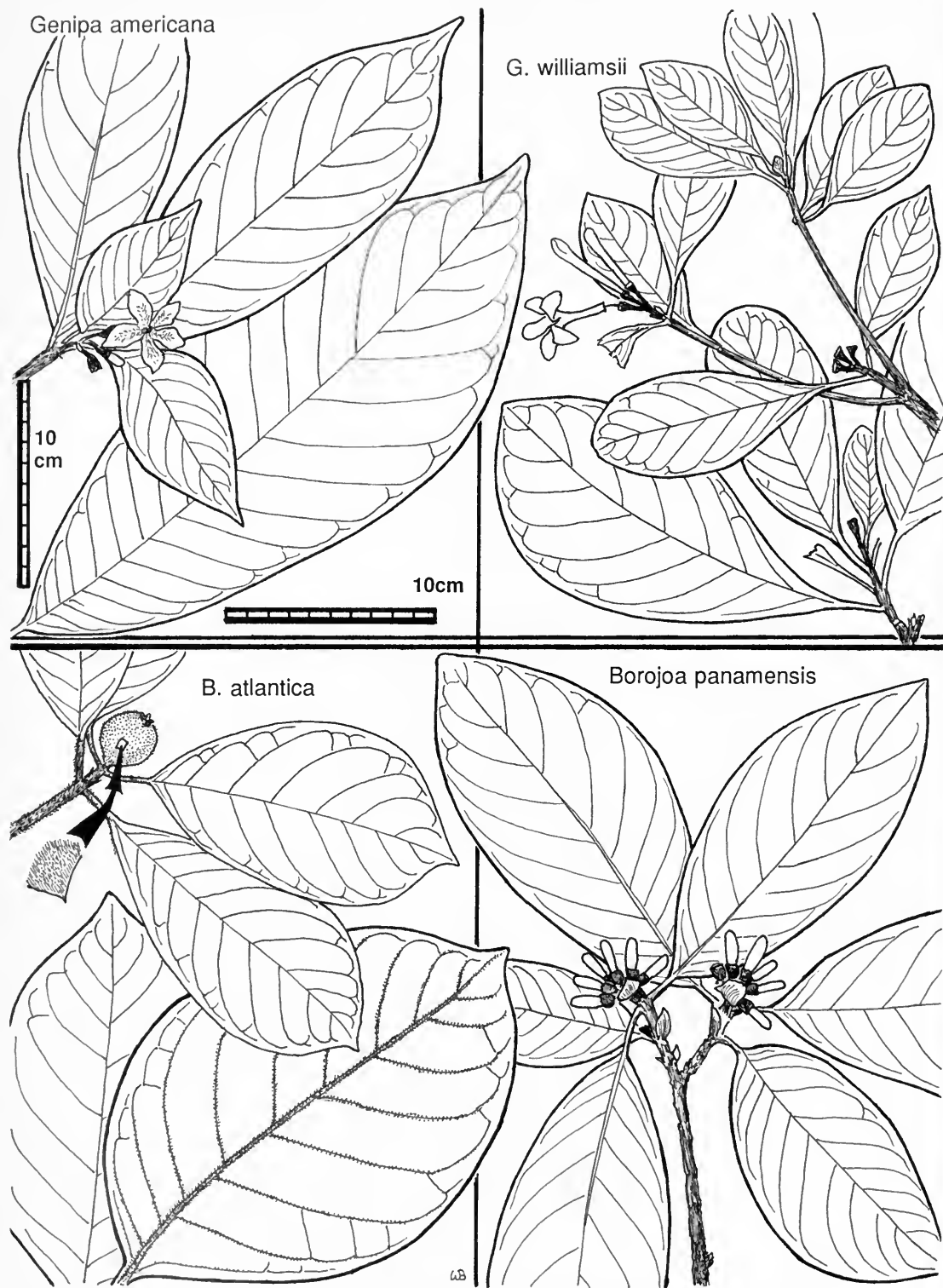


FIG. 26. Fruits usually terminal and solitary: species of *Borjoa* and *Genipa*.

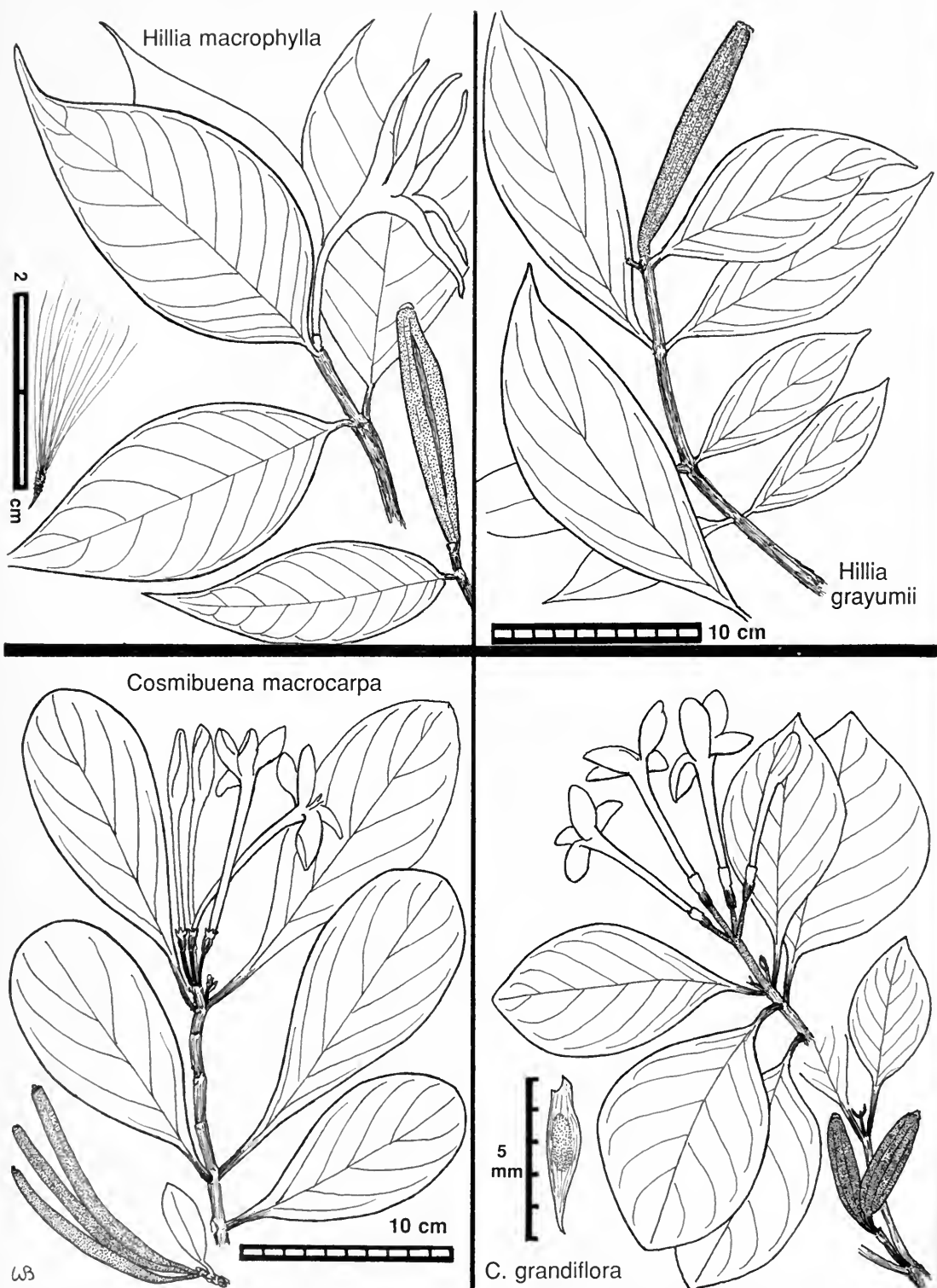


FIG. 28. Plants usually epiphytic: species of *Cosmibuena* and *Hillia* with larger leaves.



FIG. 29. Trees with large open inflorescences: species of *Ladenbergia* and *Condaminea corymbosa*.

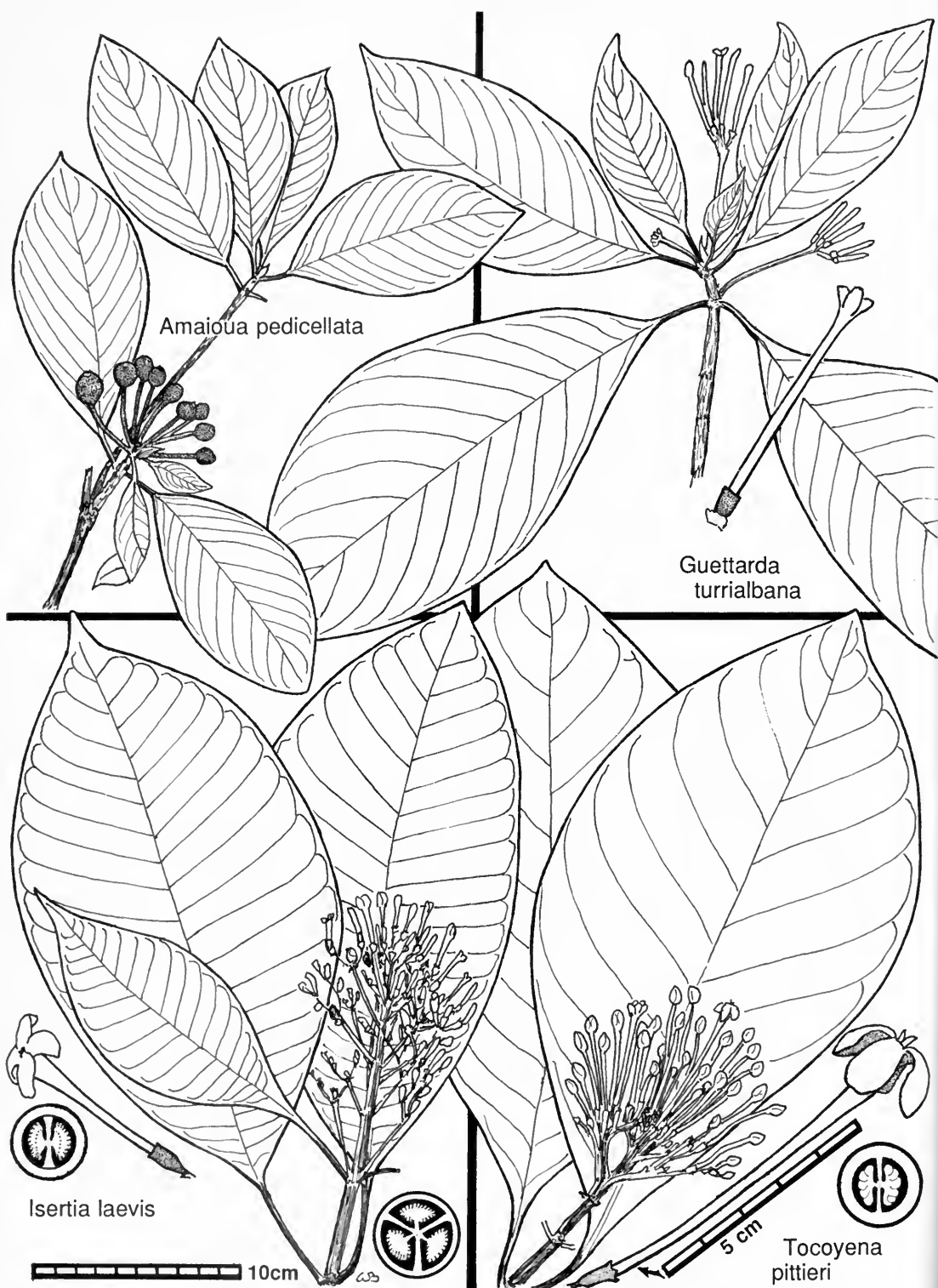


FIG. 30. Inflorescences with clusters of long-tubular flowers: species of *Amaioua*, *Guettarda*, *Isertia*, and *Tocoyena*.

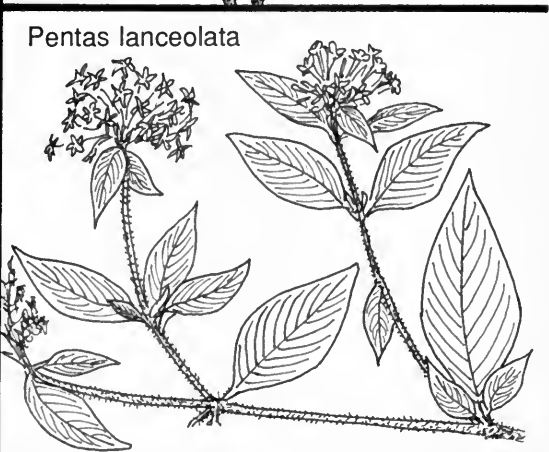
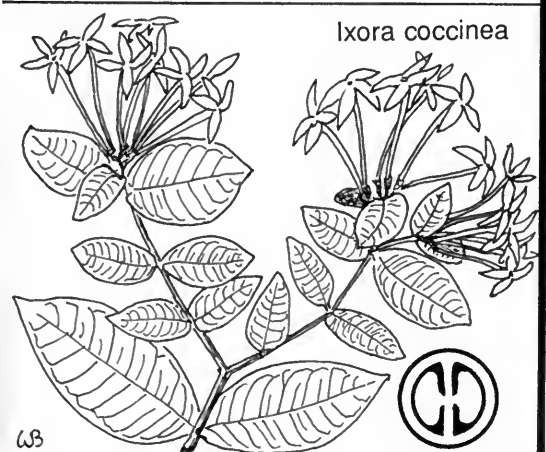
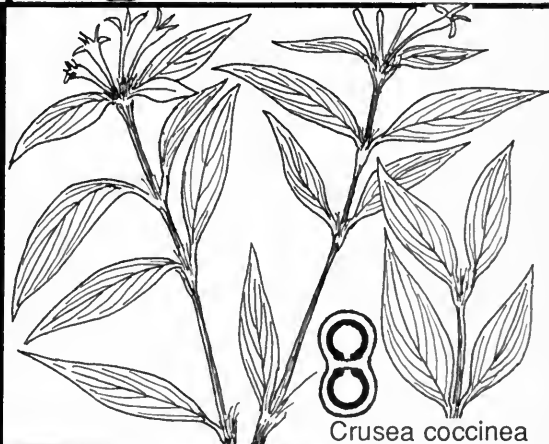
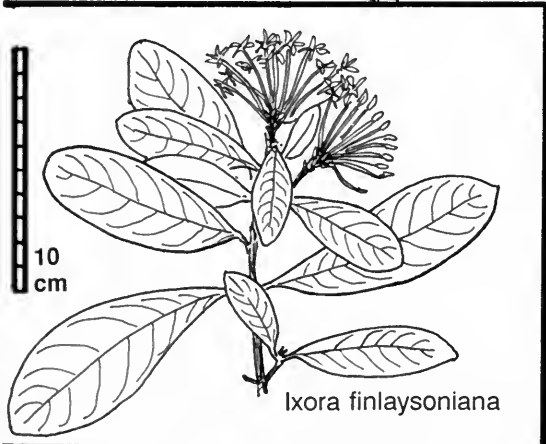
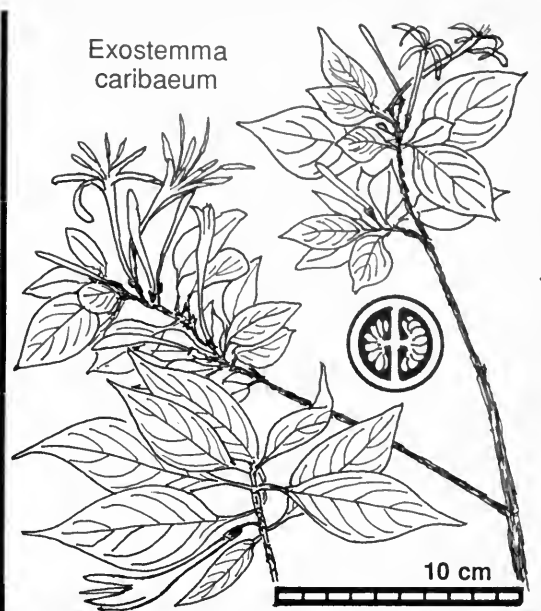
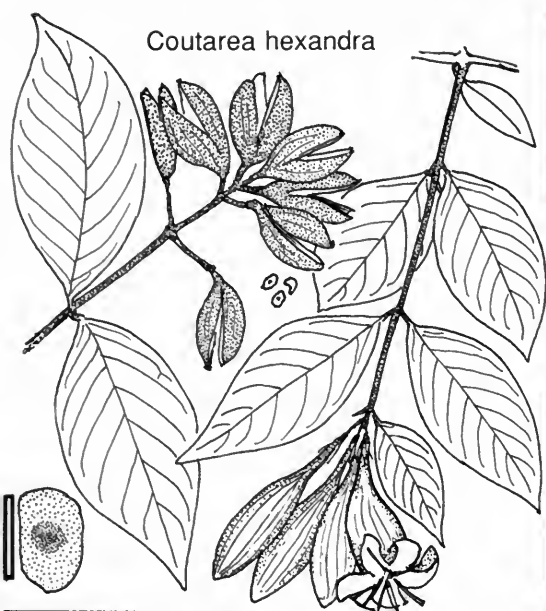
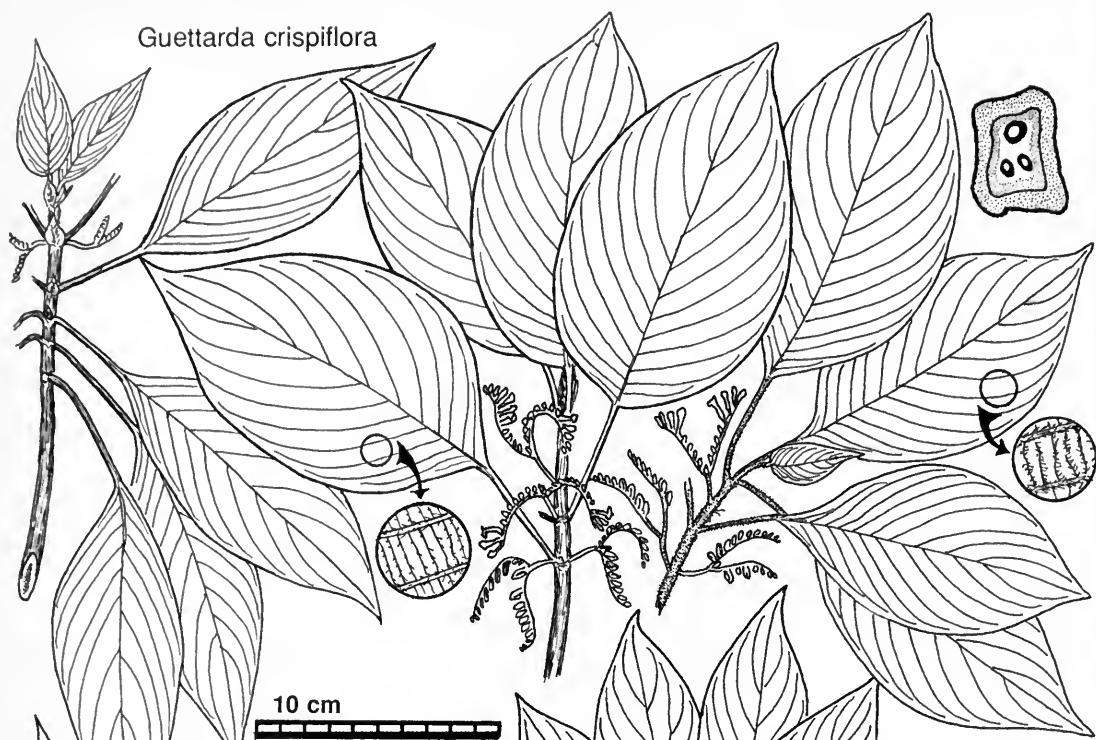
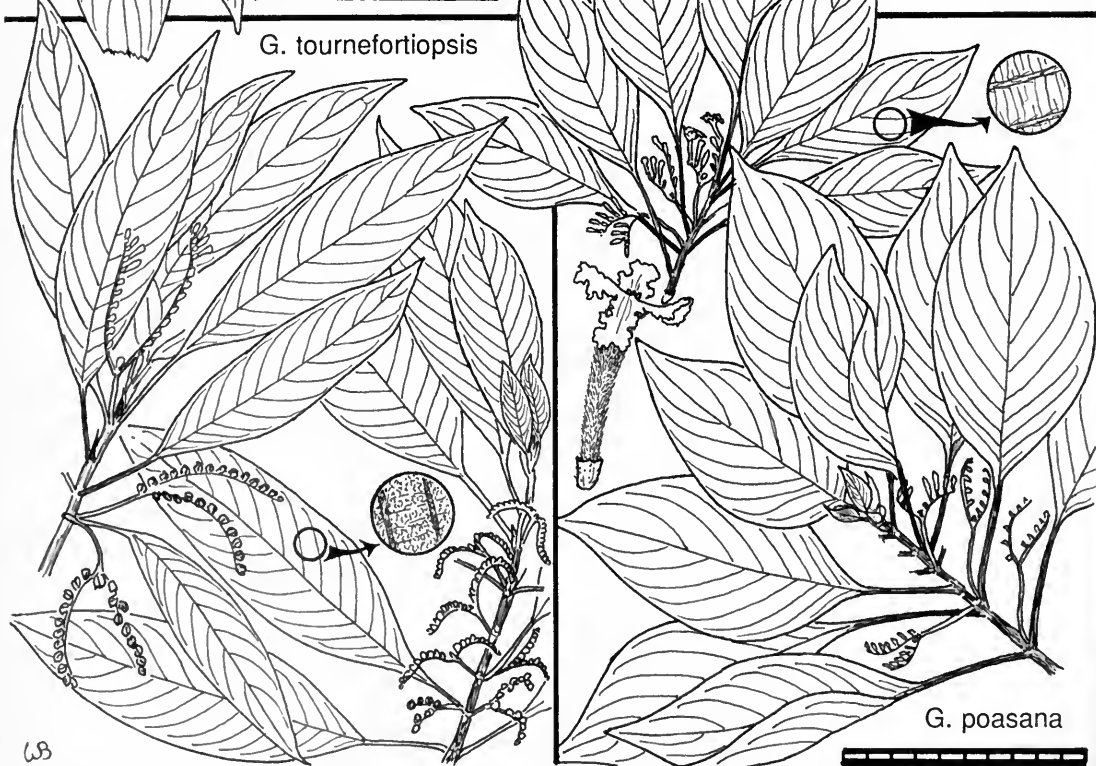


FIG. 31. Showy flowers: species of *Coutarea*, *Crusea*, *Exostemma*, *Ixora*, and *Pentas*.

Guettarda crispiflora



G. tournefortiopsis



G. poasana

FIG. 32. Inflorescences with scorpioid or helicoid branches: species of *Guettarda*.



FIG. 33. Flowers with narrow corolla tubes: species of *Guettarda* and a species of *Chomelia*.

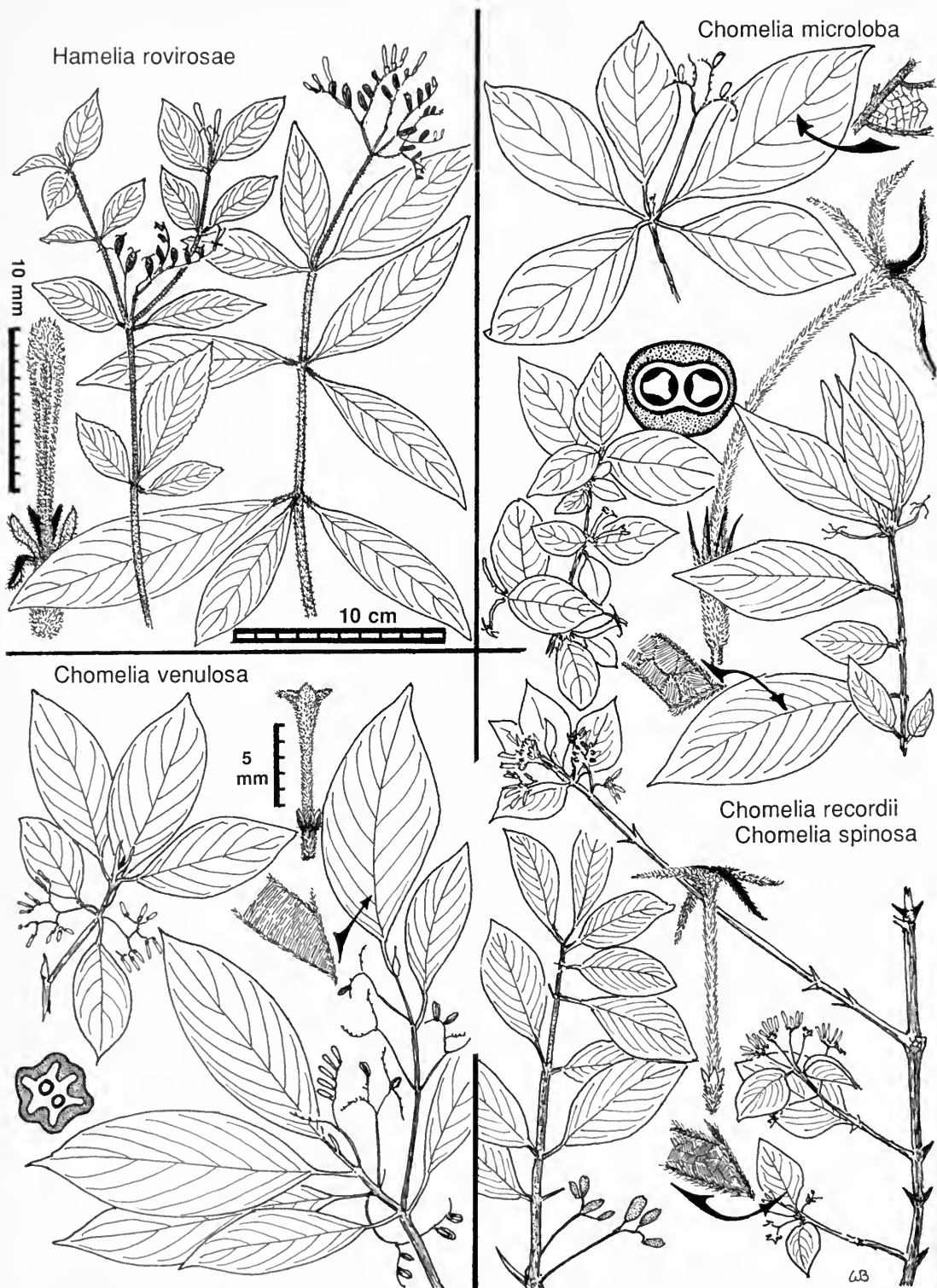


FIG. 34. Flowers with narrow corolla tubes: species of *Chomelia*, *Guettarda*, and *Hamelia*.

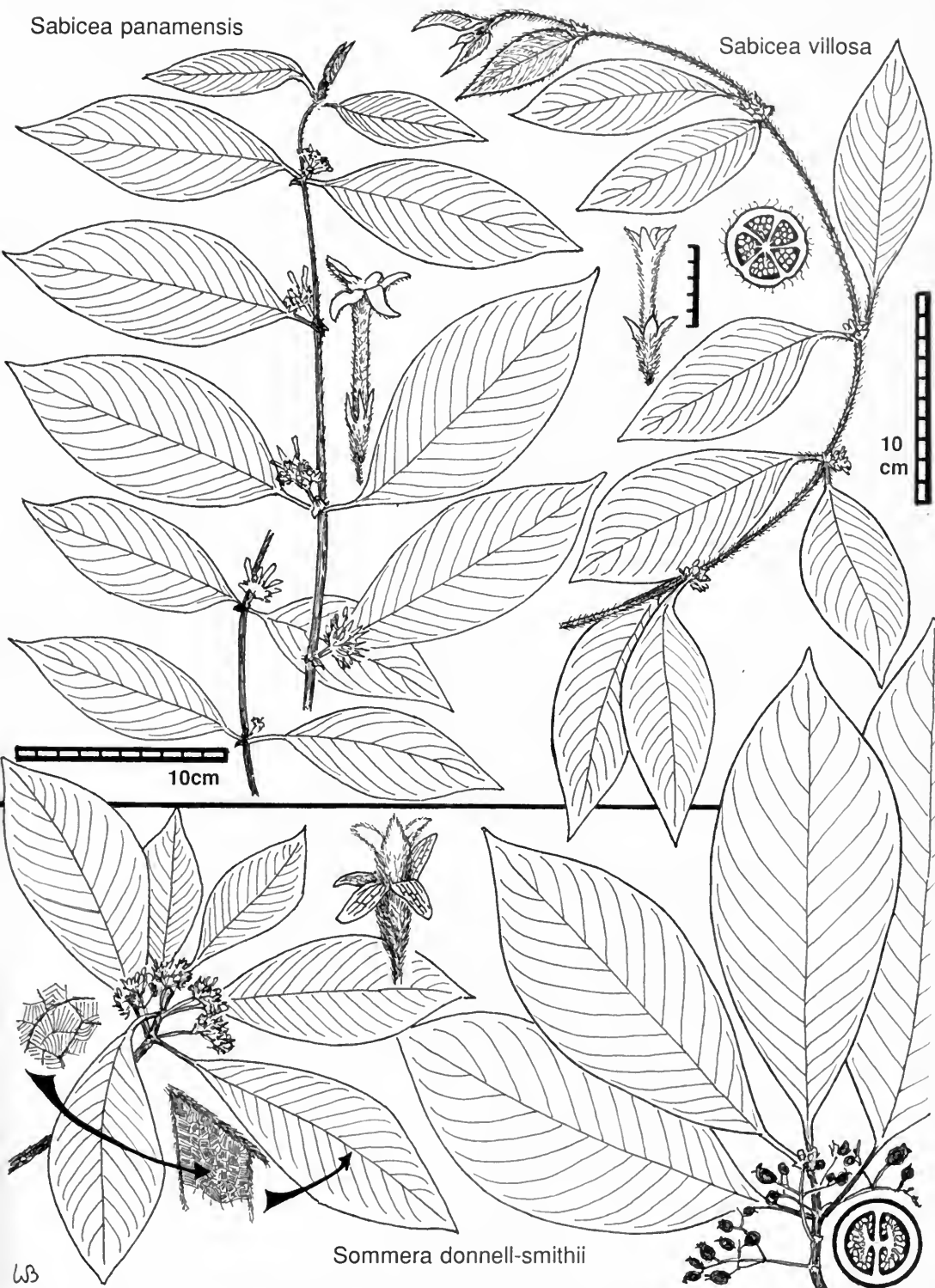


FIG. 35. Inflorescences mostly axillary: species of *Sabicea* (vines) and *Sommera* (trees).

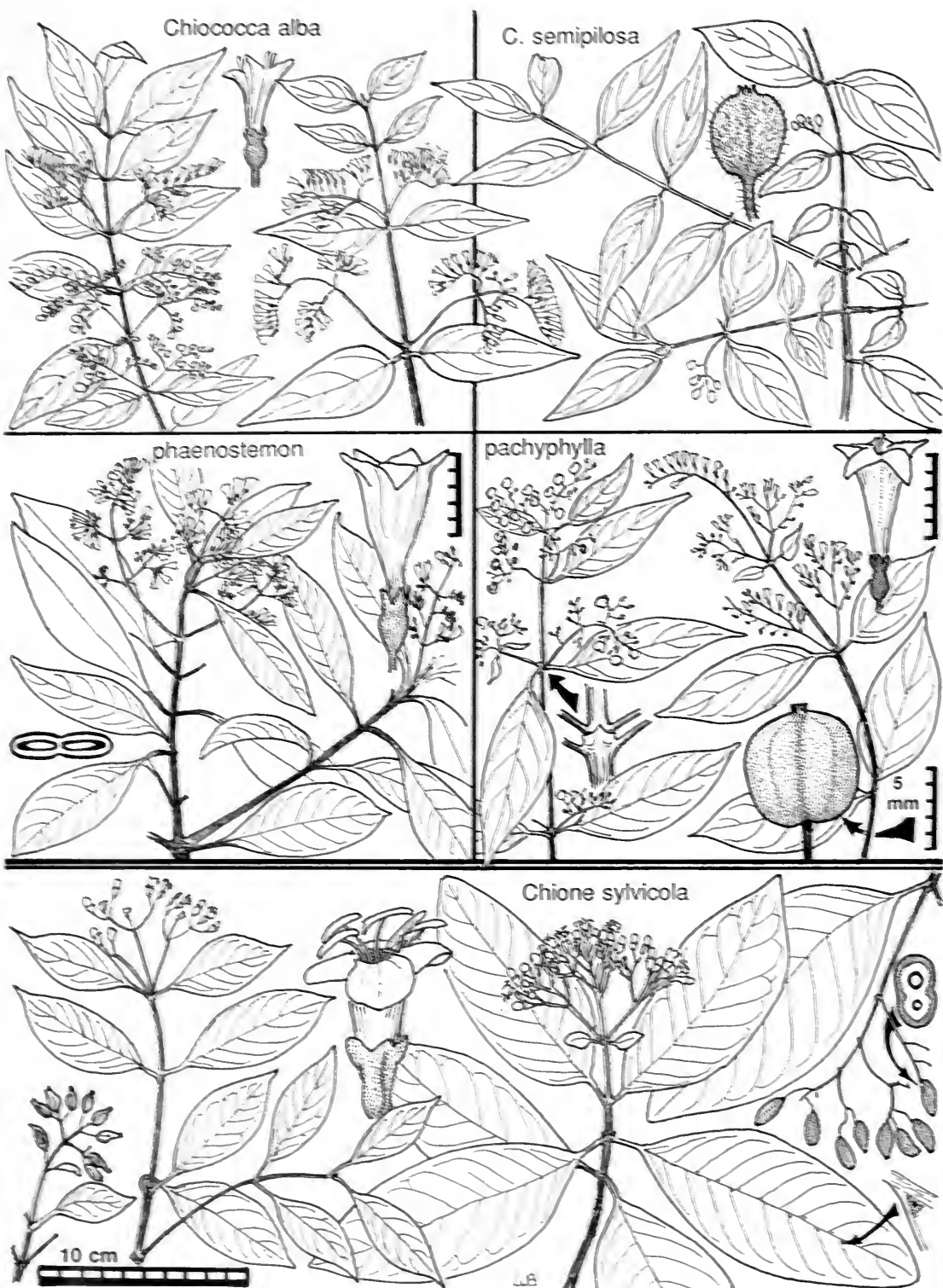


FIG. 36. Inflorescences axillary or terminal: species of *Chiococca* and a species of *Chione*.

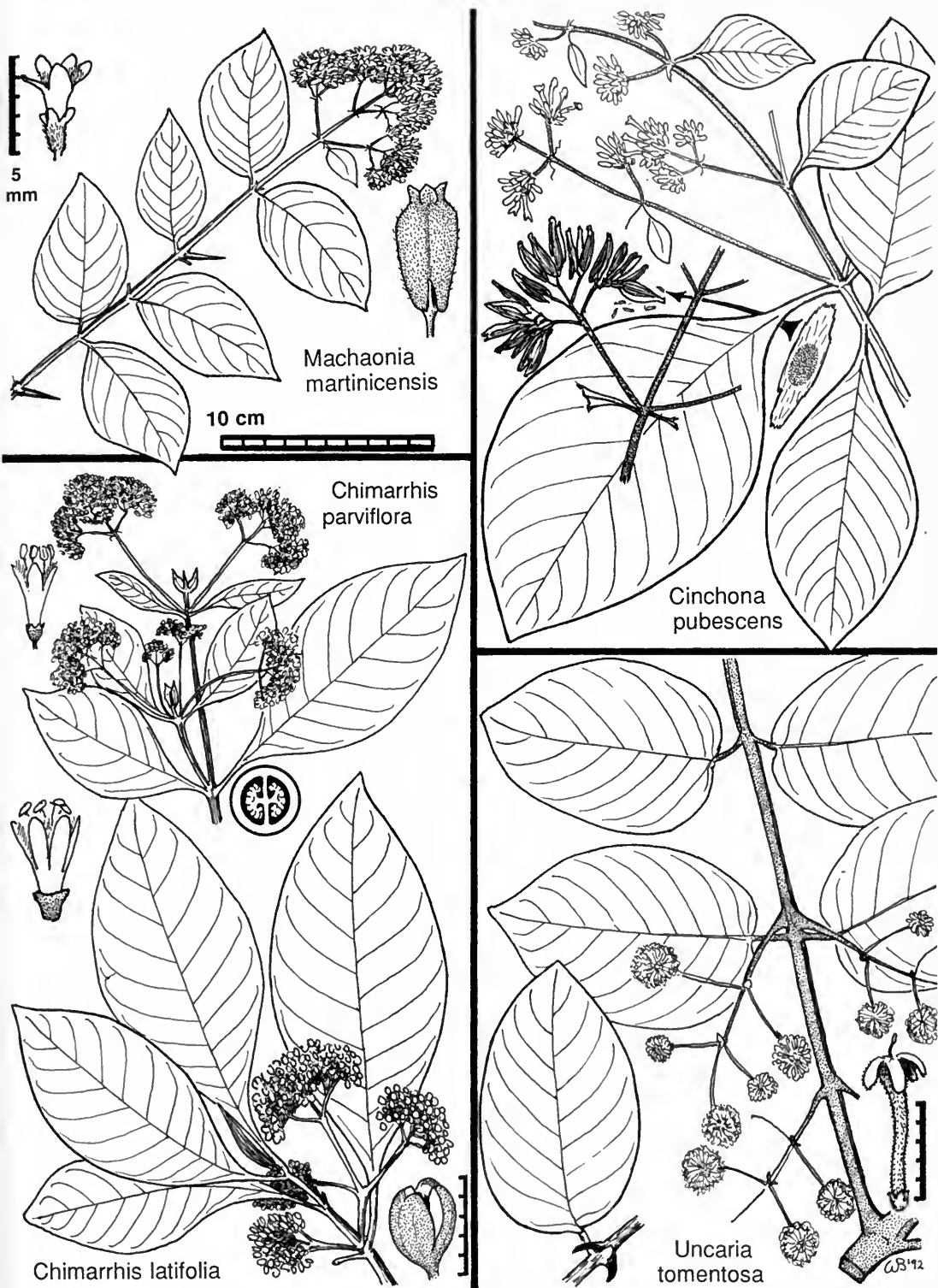


FIG. 37. Many small flowers in dense inflorescences: species of *Chimarrhis*, *Cinchona*, *Machaonia*, and *Uncaria*.



FIG. 38. Flowers in much-branched open inflorescences: species of *Deppea*, *Rustia*, and *Simira*.

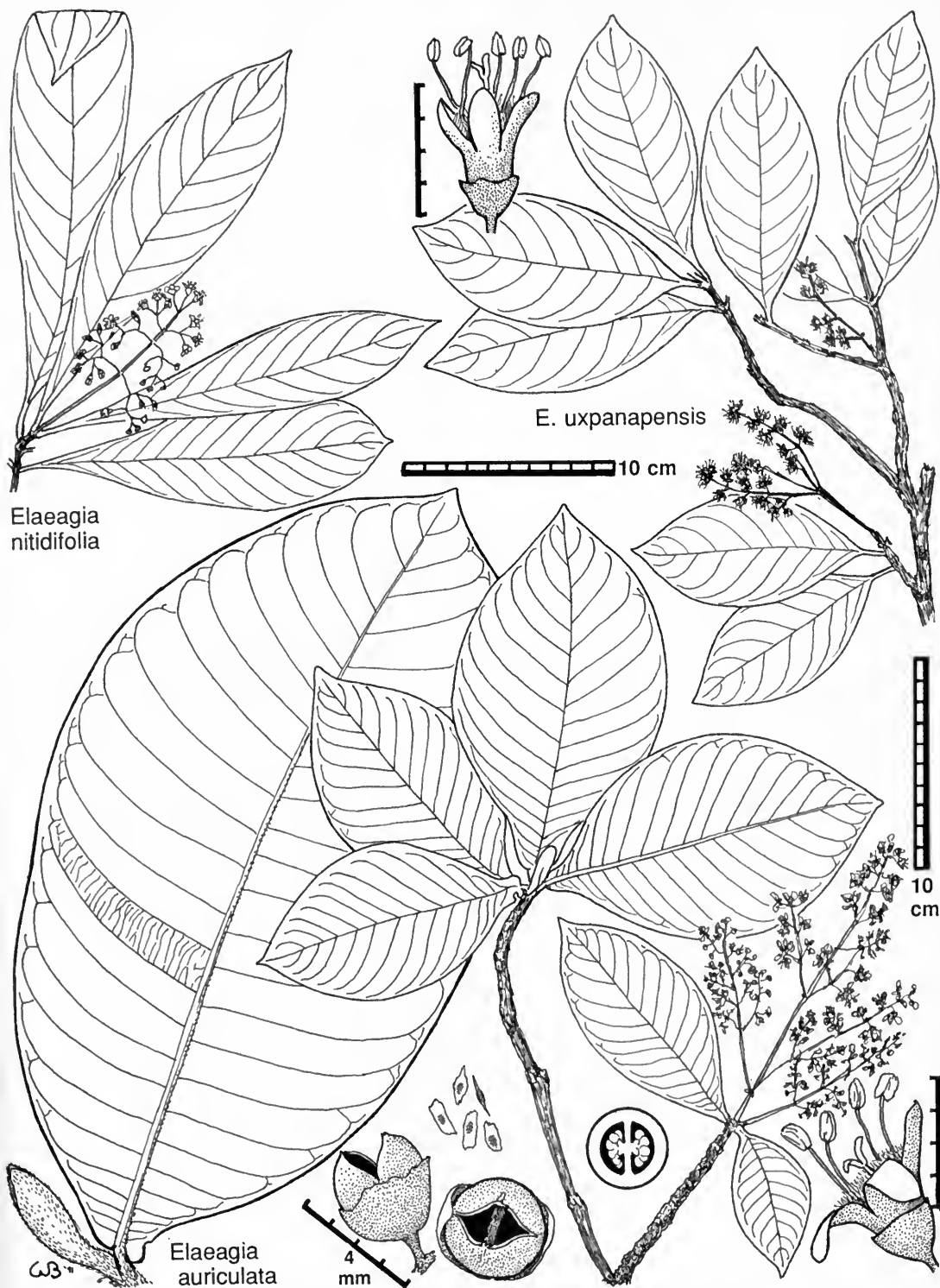


FIG. 39. Small flowers in dense or open panicles: species of *Elaeagia*.

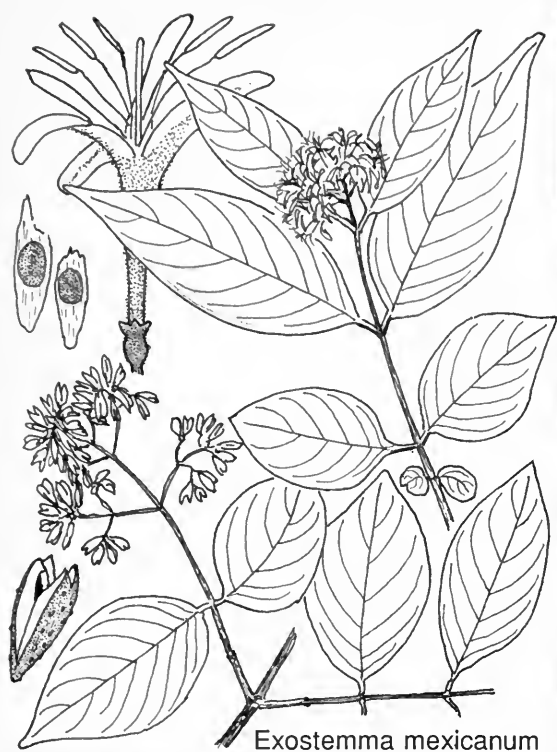


FIG. 40. Small flowers and capsular fruits: species of *Alseis*, *Exostema*, *Ferdinandusa*, and *Macrocnemum*.

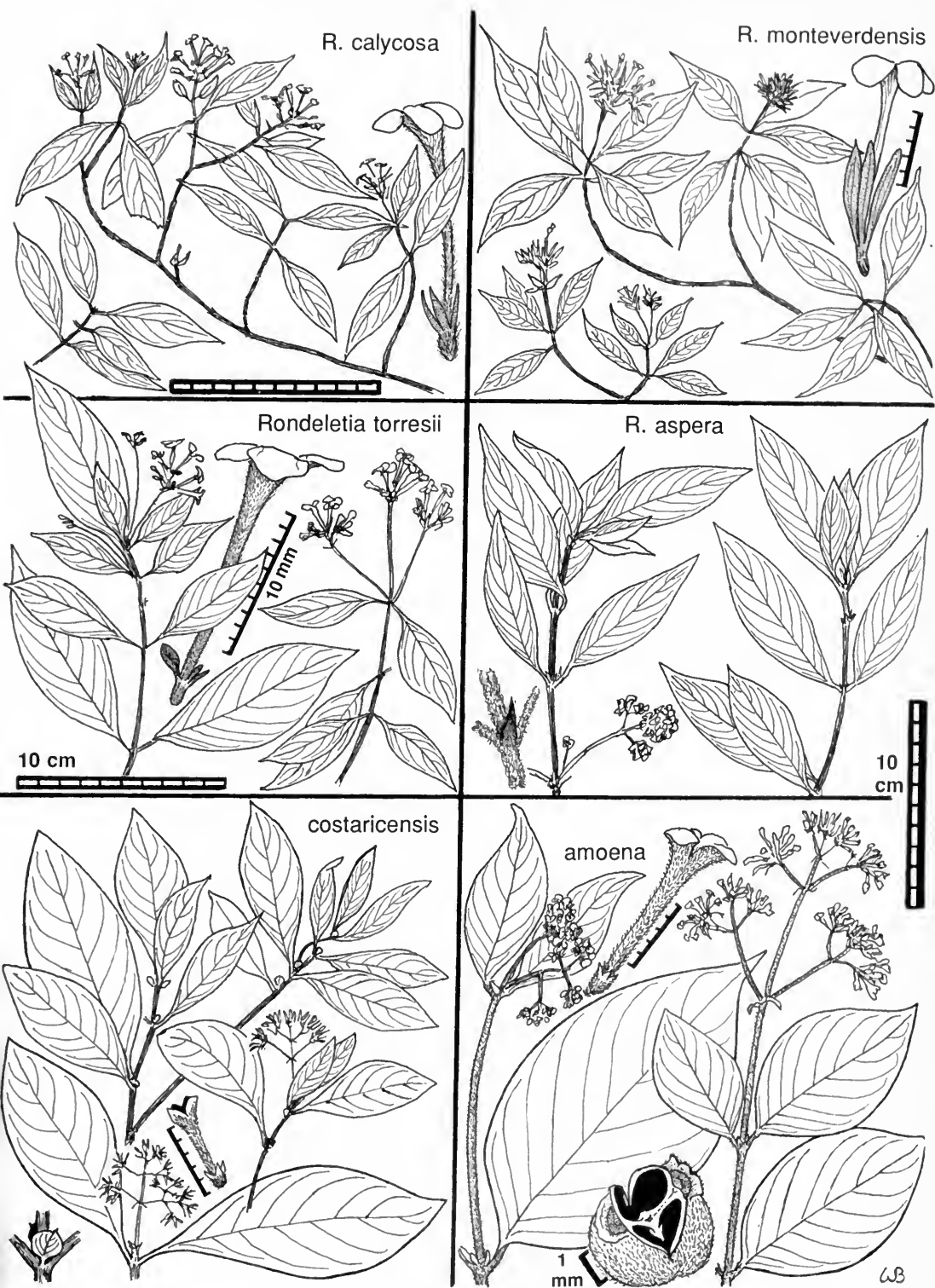


FIG. 41. *Rondeletia* spp.



FIG. 41A. *Rondeletia* spp.



FIG. 42. *Hamelia* spp.

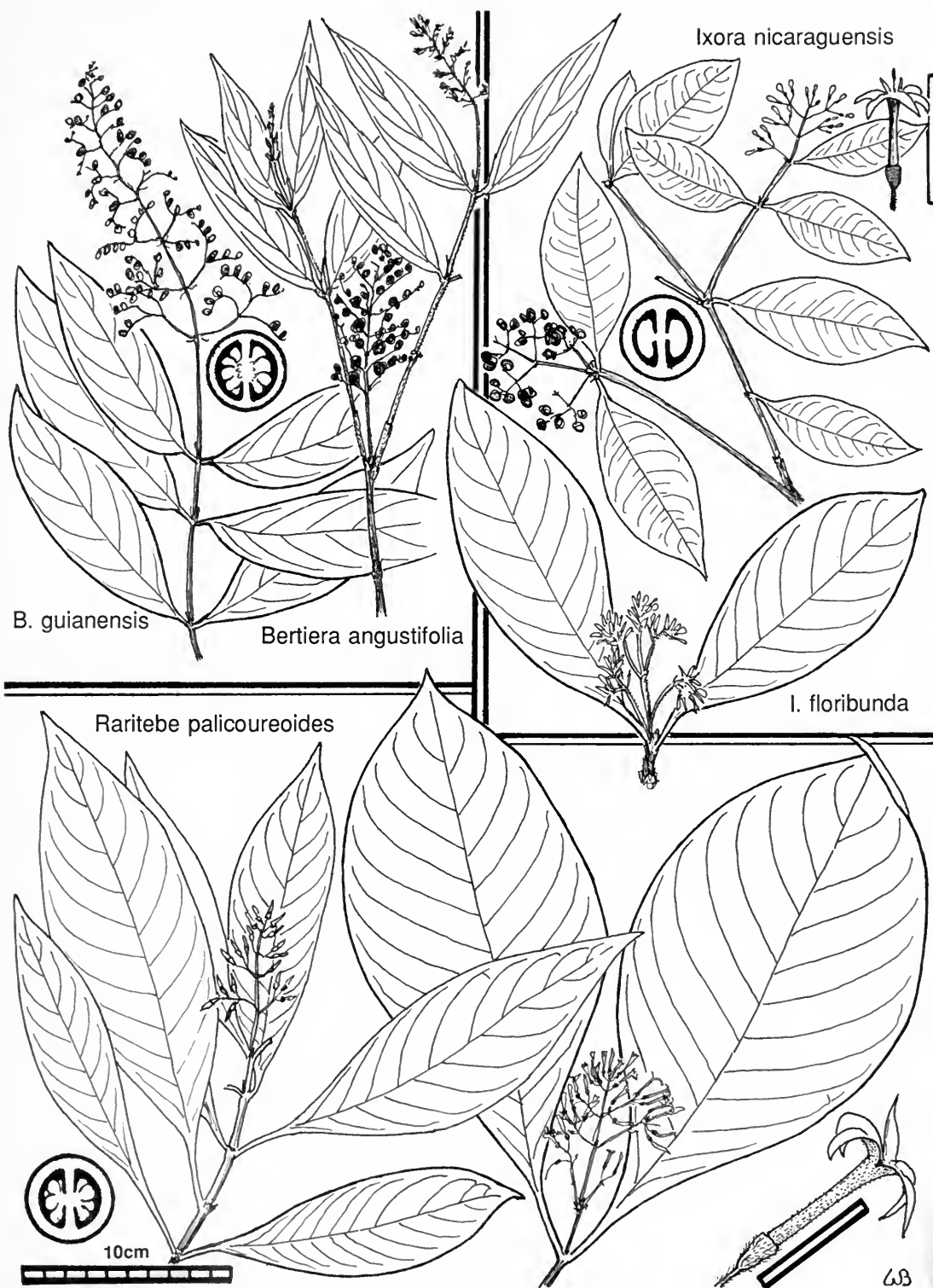


FIG. 43. *Bertiera*, *Ixora*, and *Raritebe* spp.

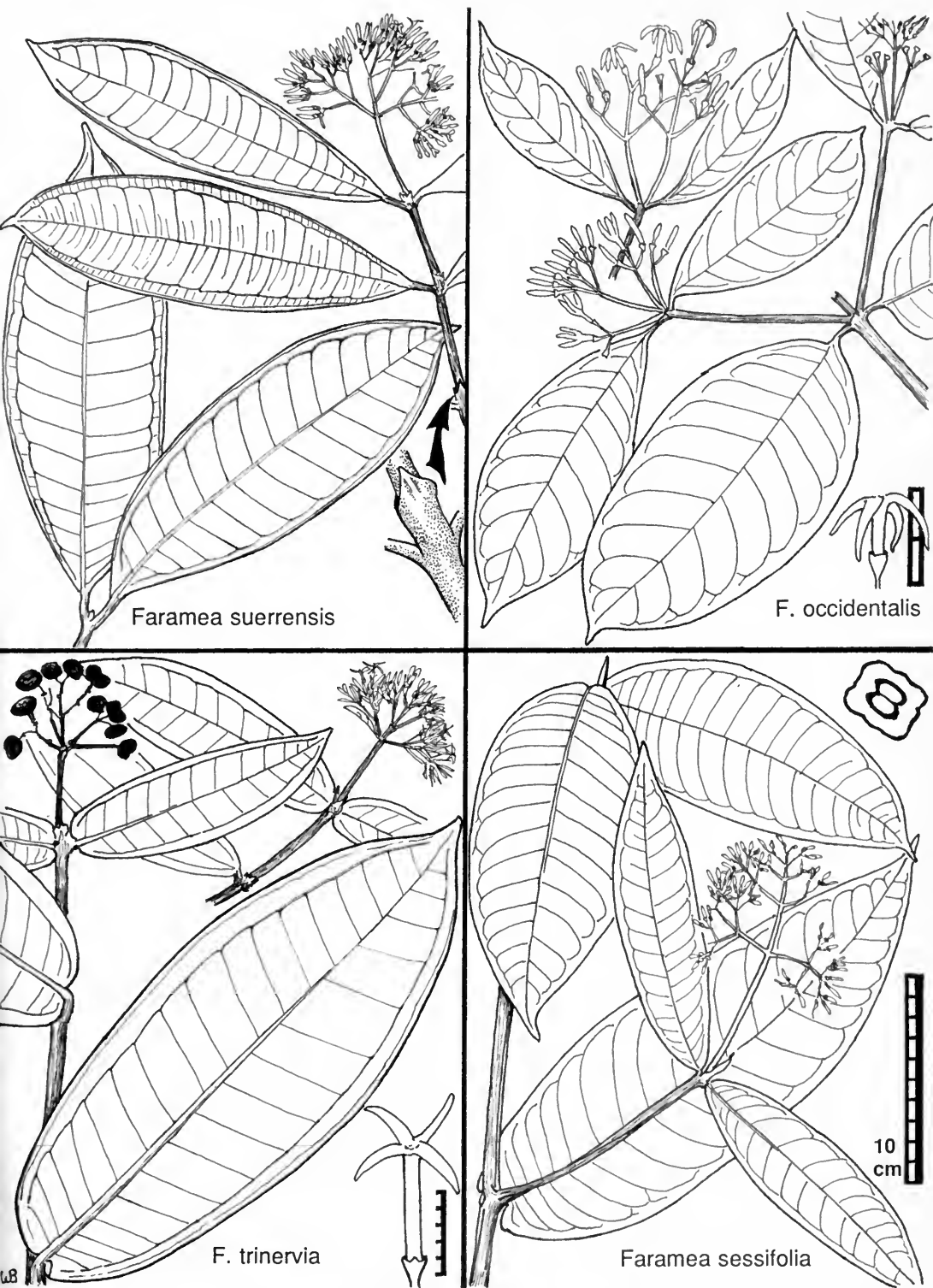


FIG. 44. *Faramaea*: species with larger leaves.

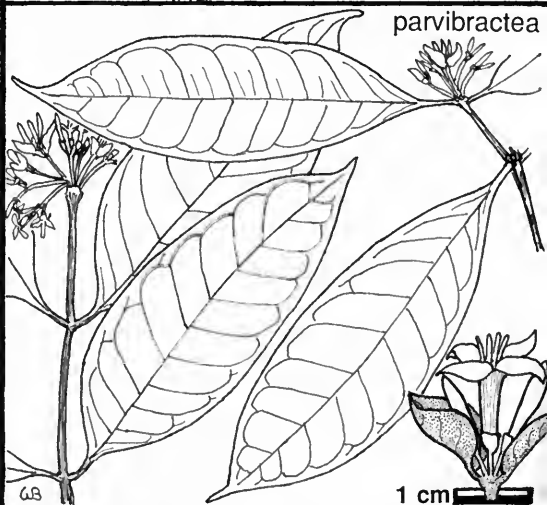
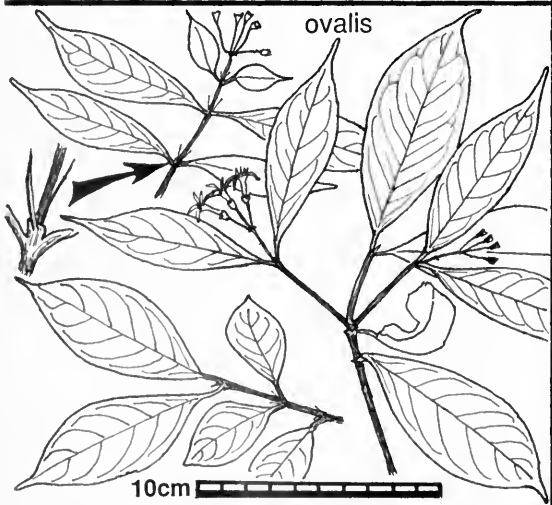
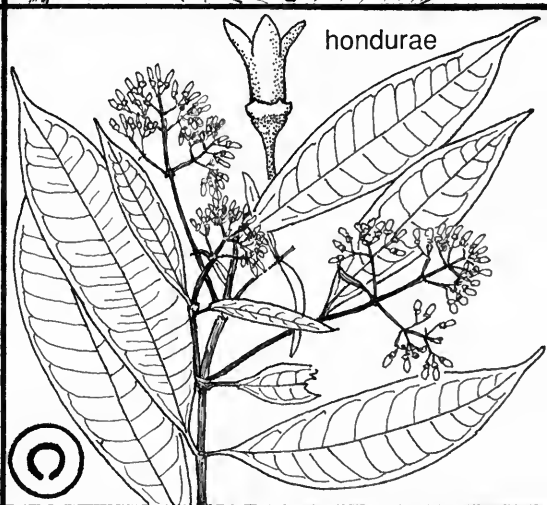
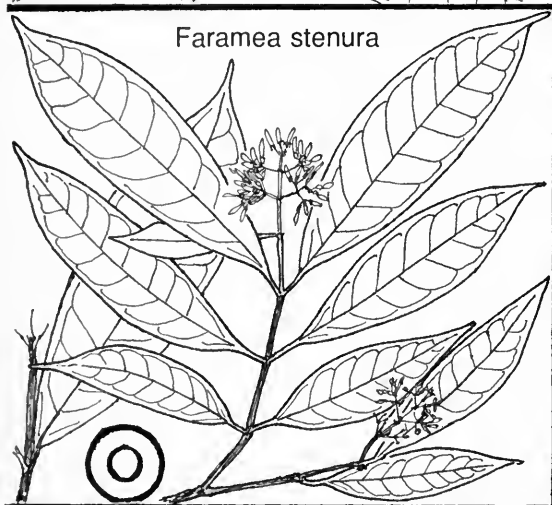
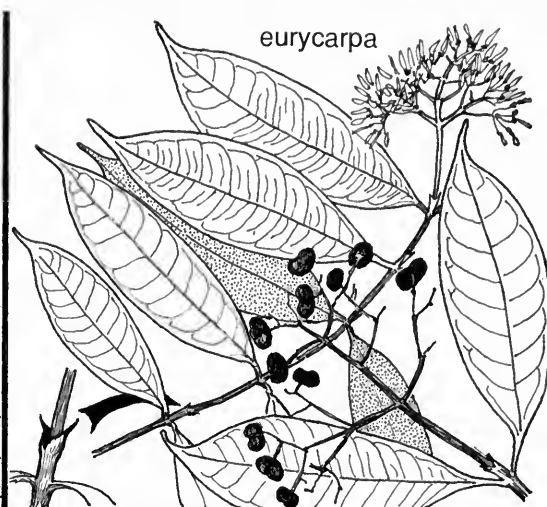
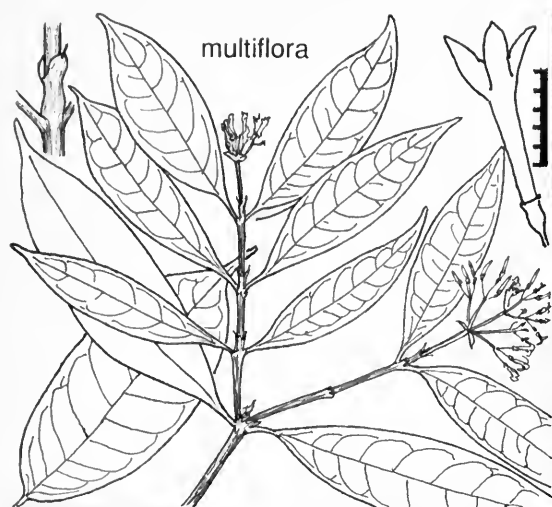


FIG. 45. *Faramaea*: species with smaller leaves.

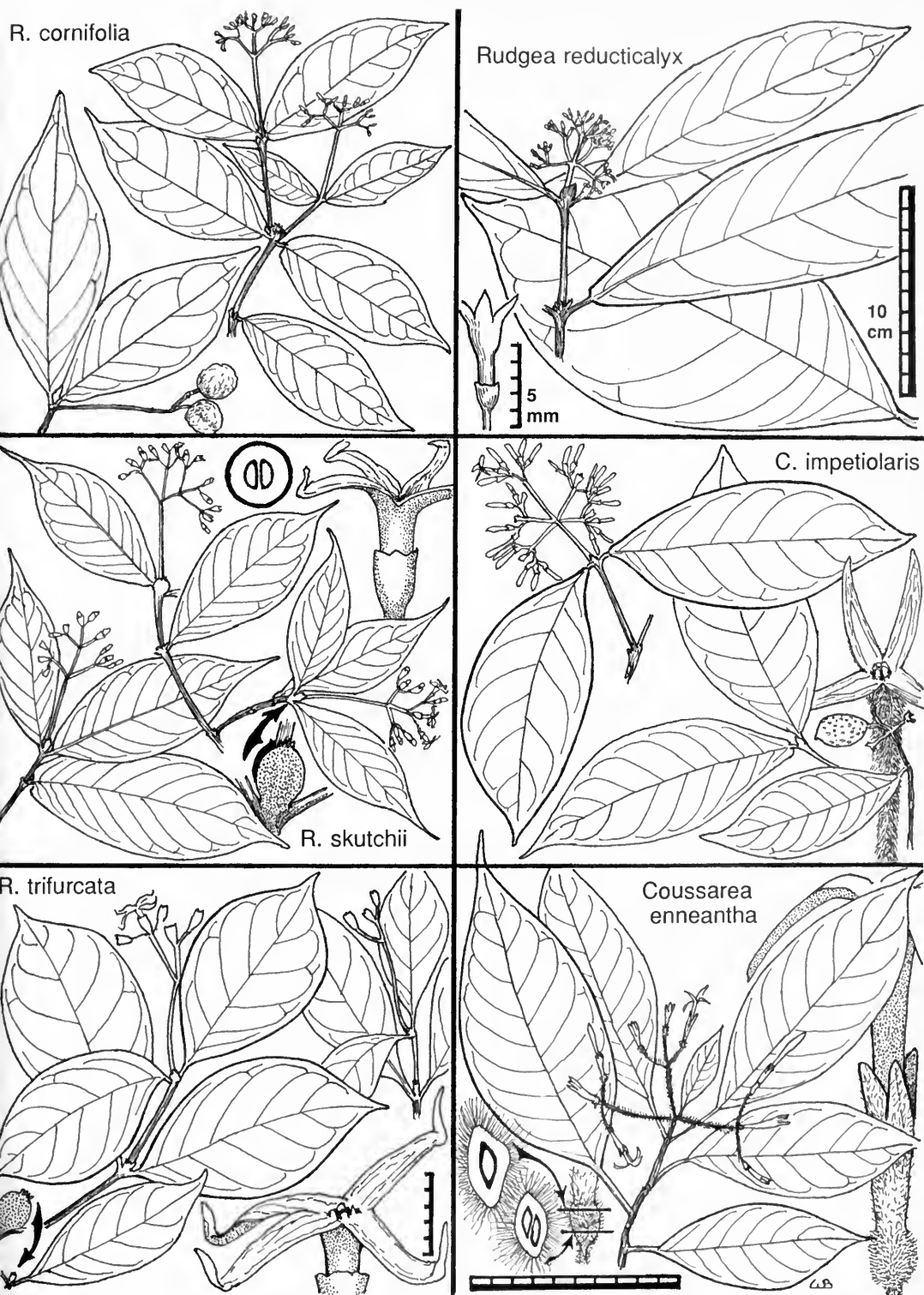


FIG. 46. *Coussarea* and *Rudgea* spp.

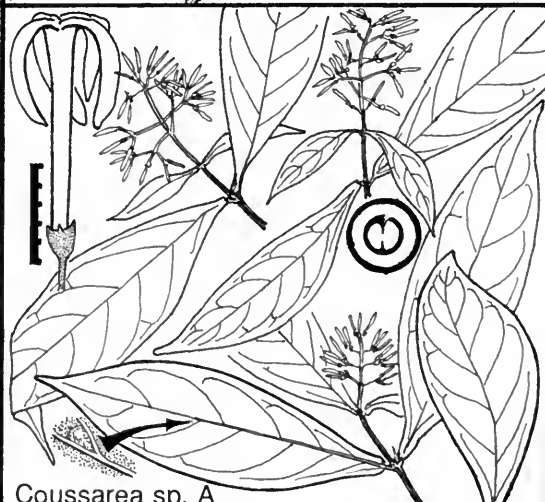
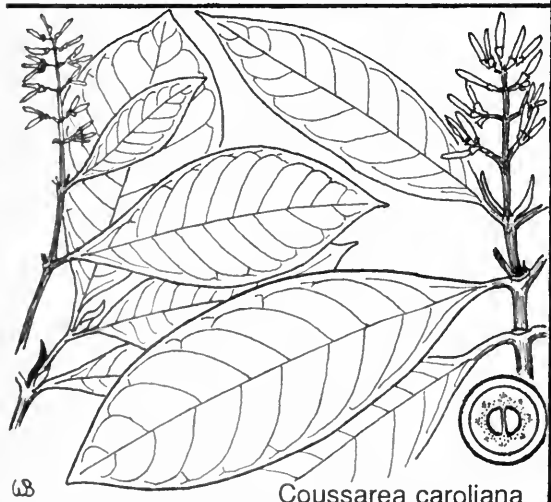
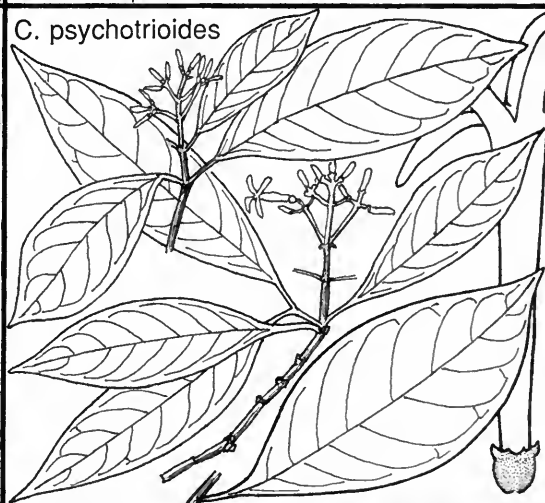
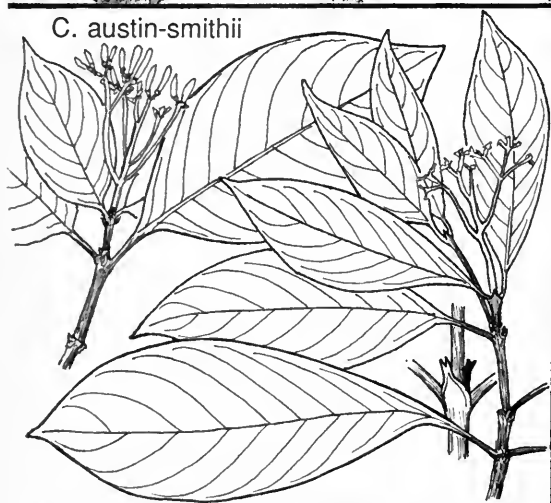
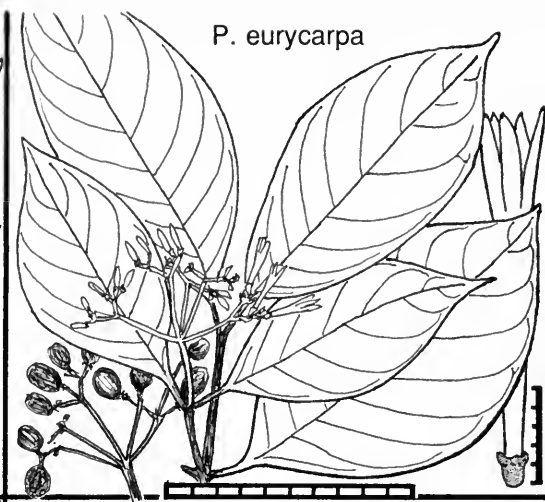
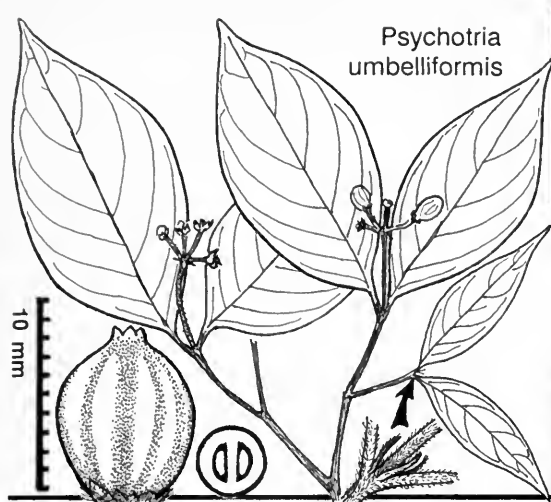


FIG. 47. *Coussarea* spp. and two similar *Psychotria* spp.

Coussarea talamancana

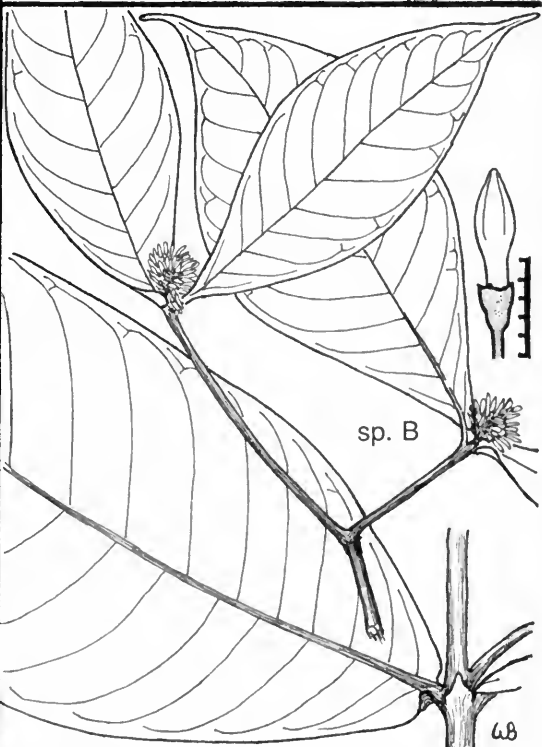
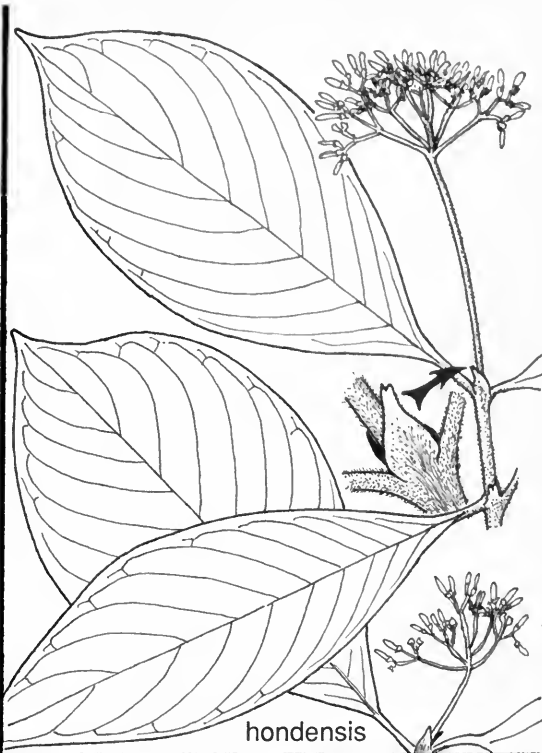
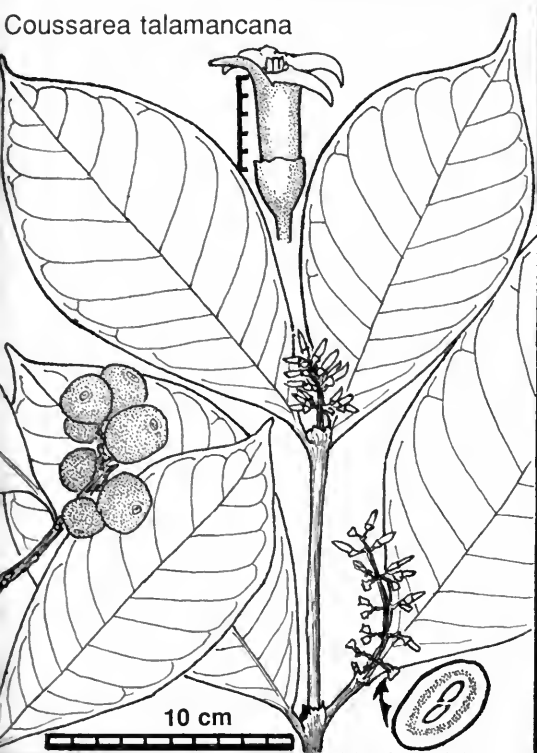


FIG. 48. *Coussarea*: species with larger leaves.

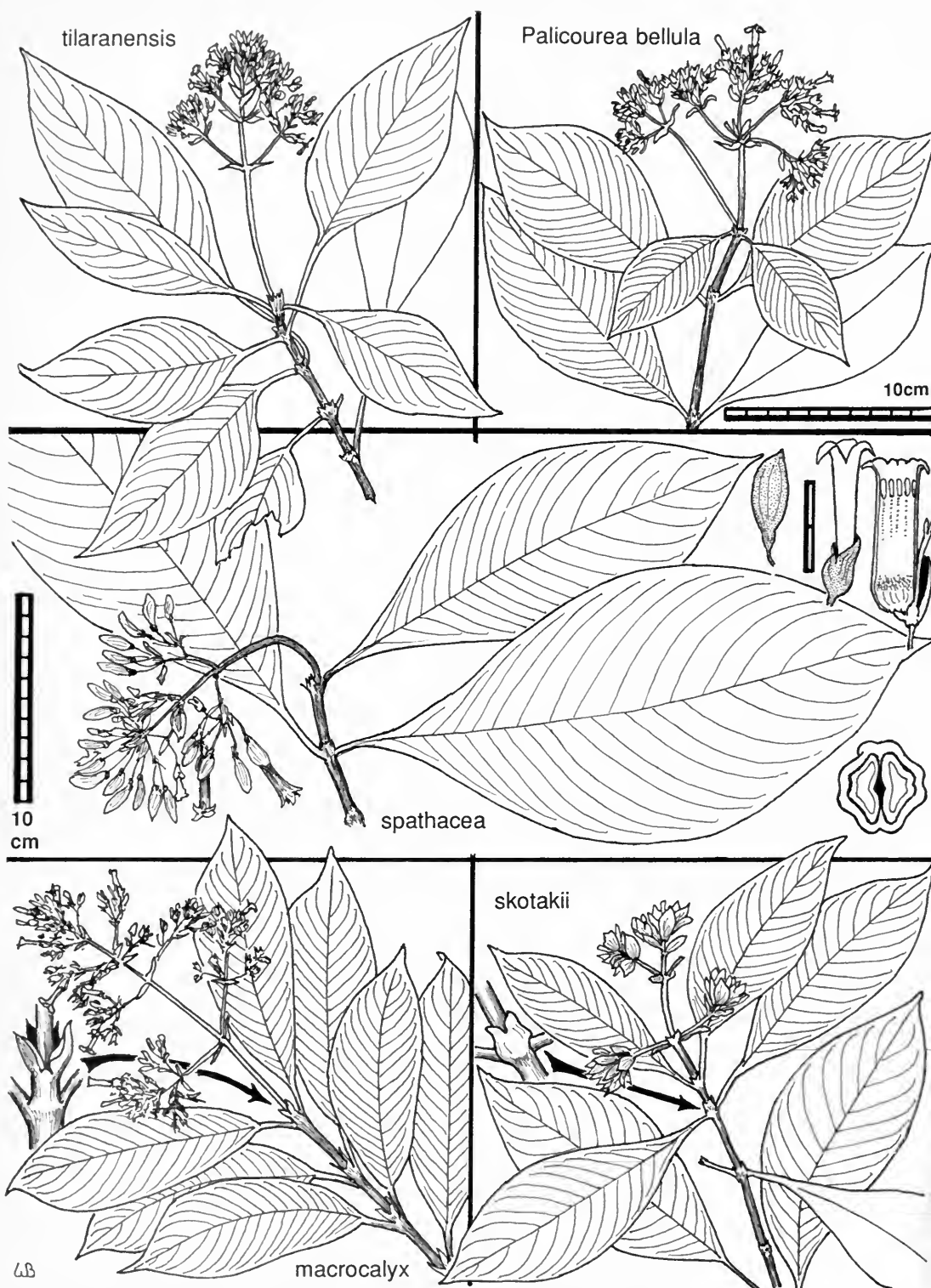


FIG. 49. *Palicourea*: species with conspicuous bracts.

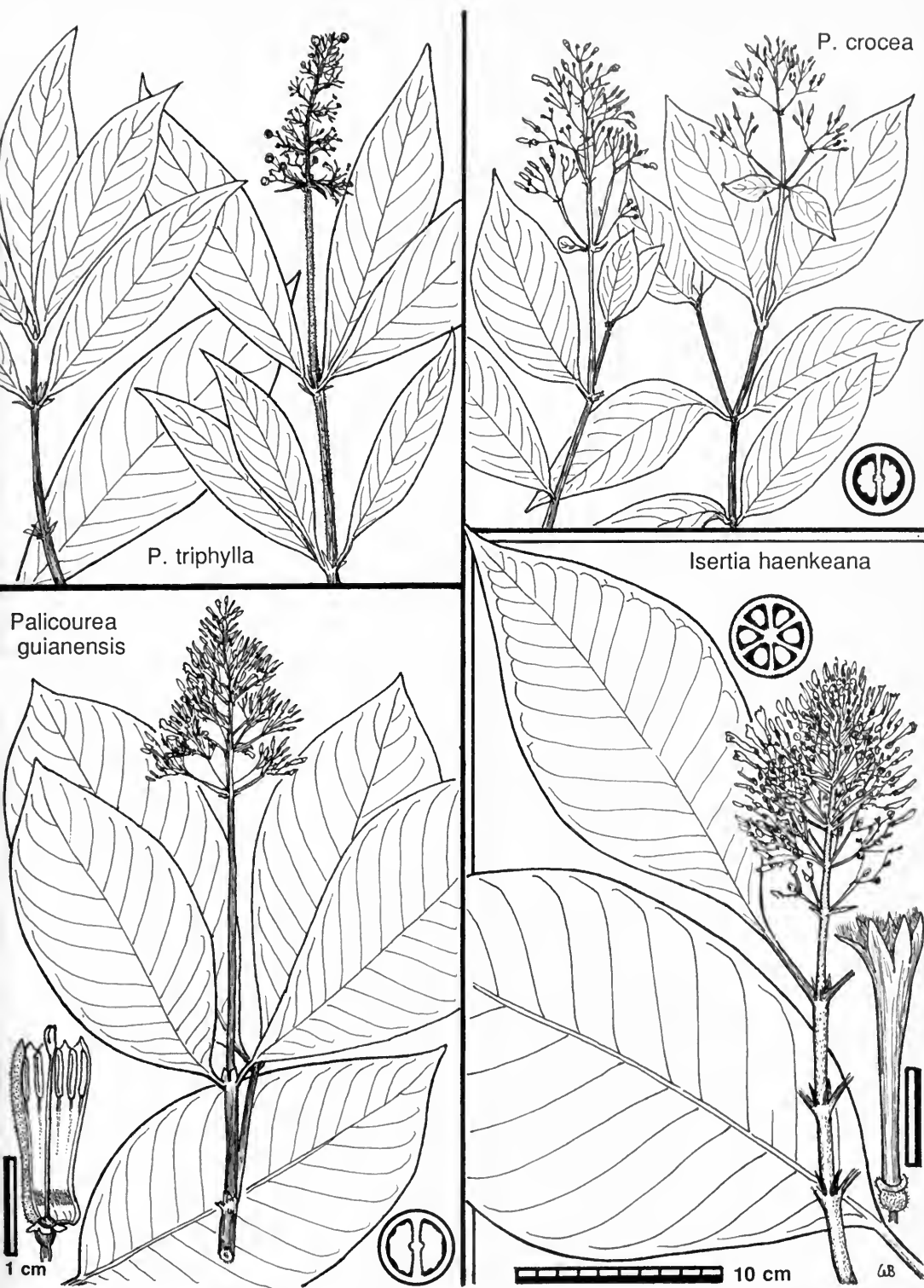
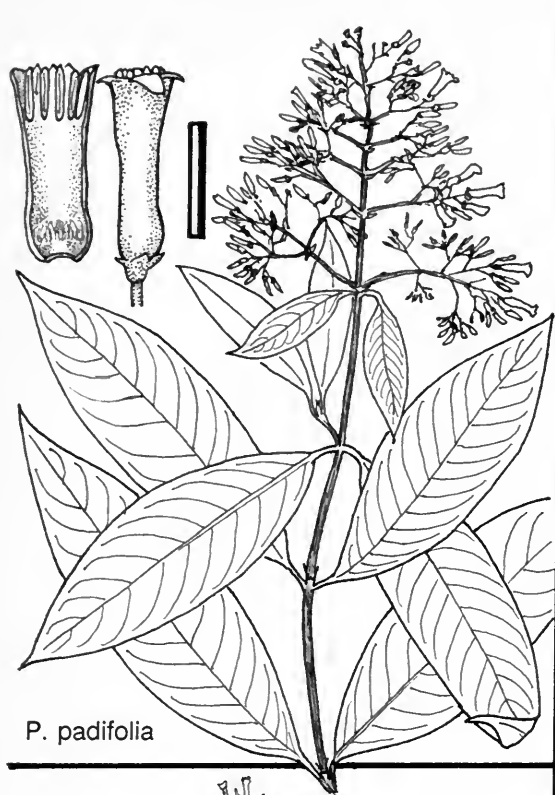


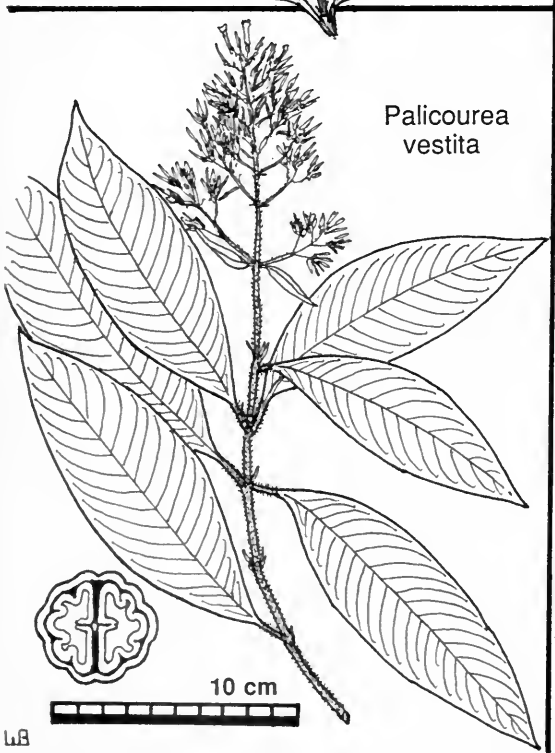
FIG. 50. *Palicourea*: species of lower elevations and a species of *Isertia*.



P. padifolia



P. orosiana



Palicourea vestita



P. lasiorrhachis

FIG. 51. *Palicourea*: species with larger leaves and yellow or orange flowers.

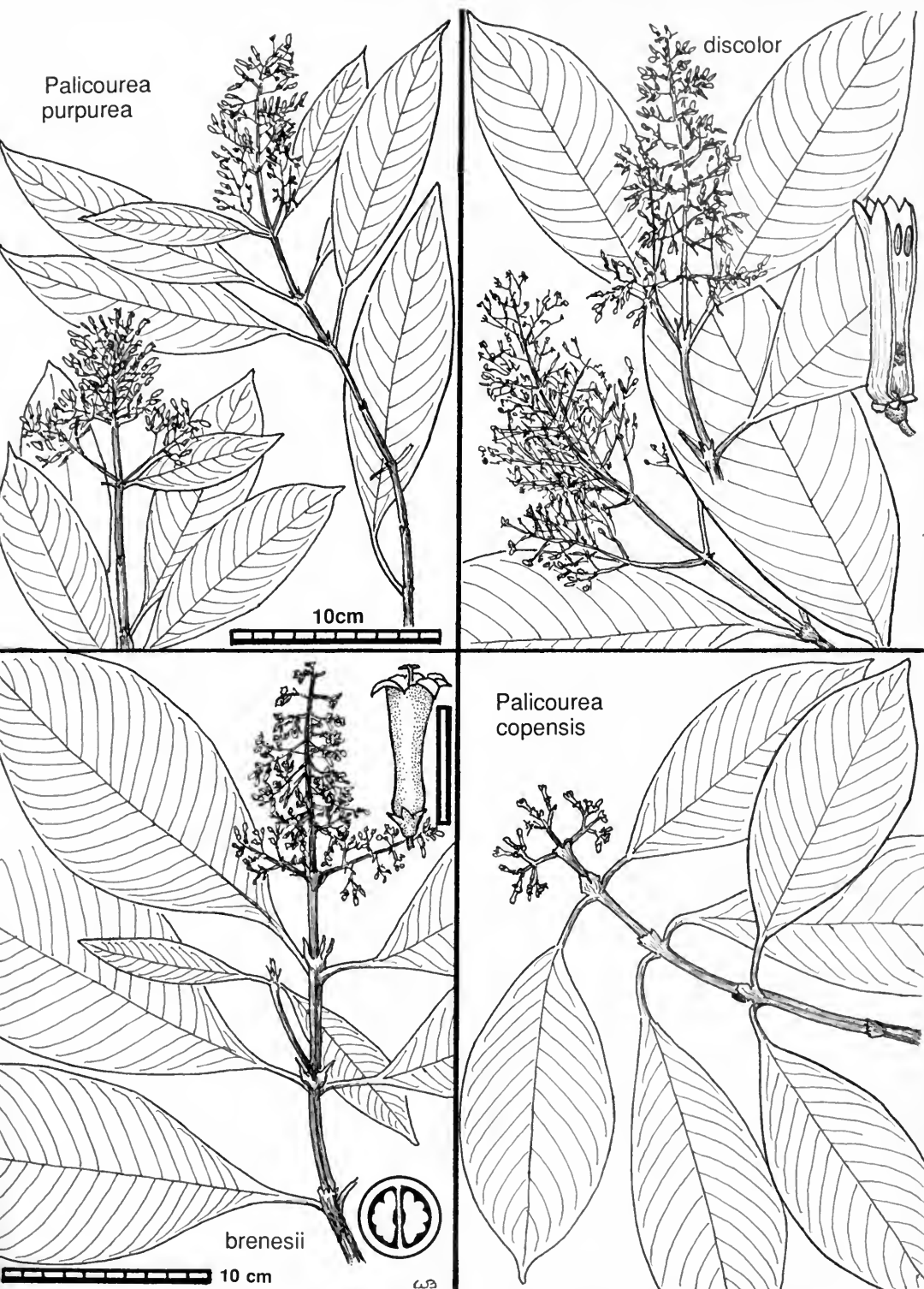
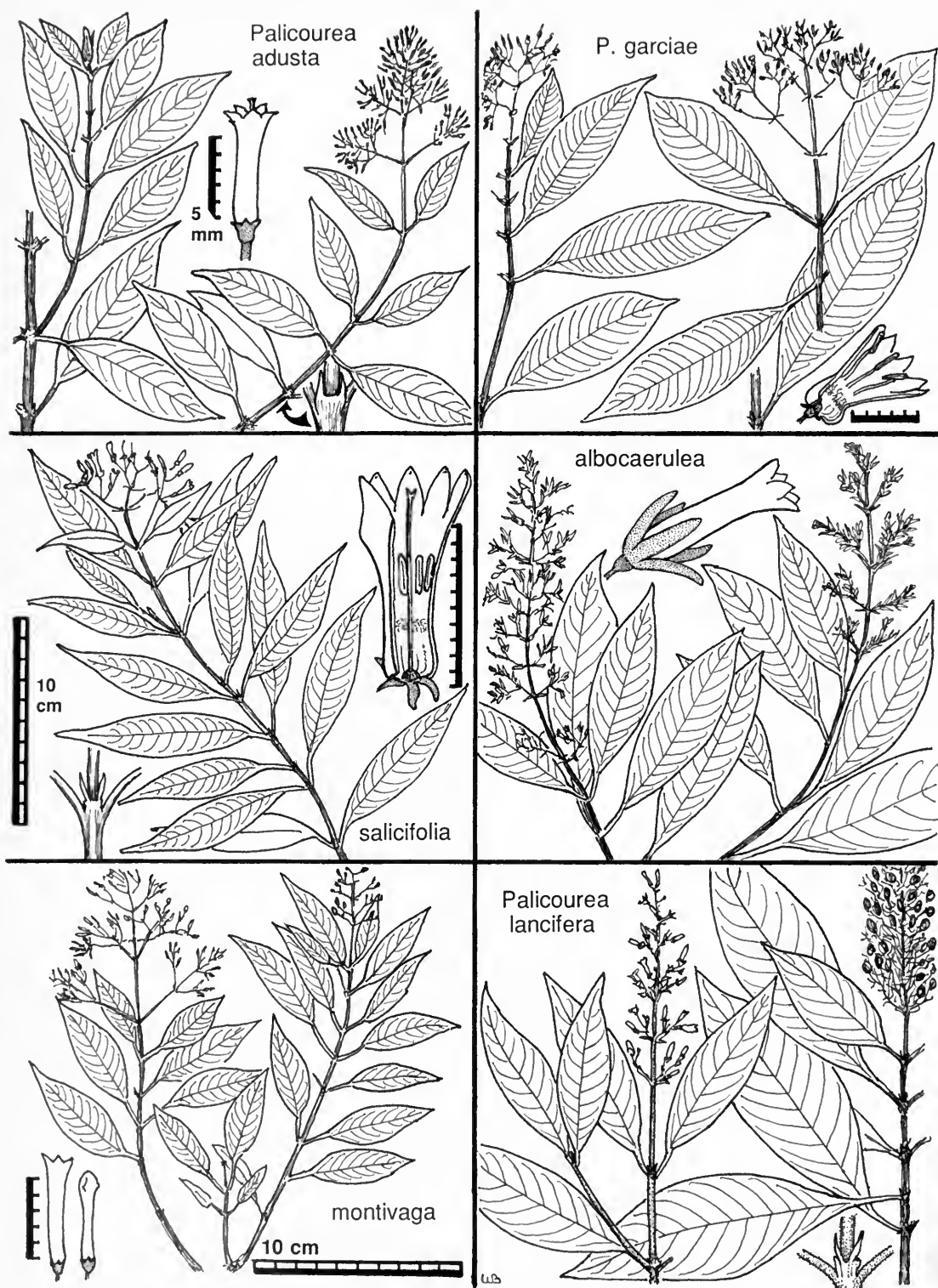


FIG. 52. *Palicourea*: species with larger leaves and blue, lavender, purple, or white flowers.



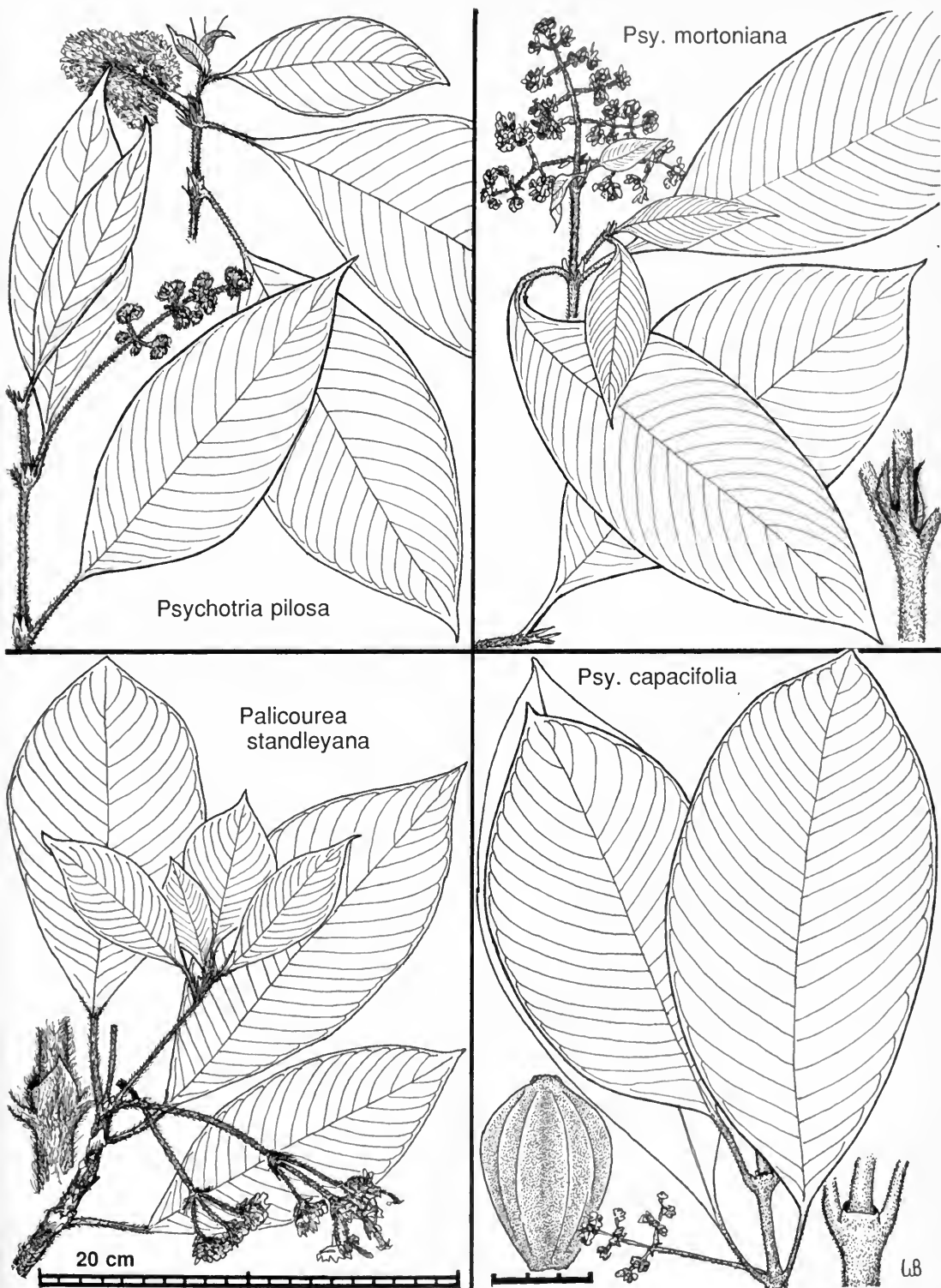


FIG. 54. *Psychotria* subg. *Heteropsychotria*: larger-leaved pubescent species, and a species of *Palicourea*.

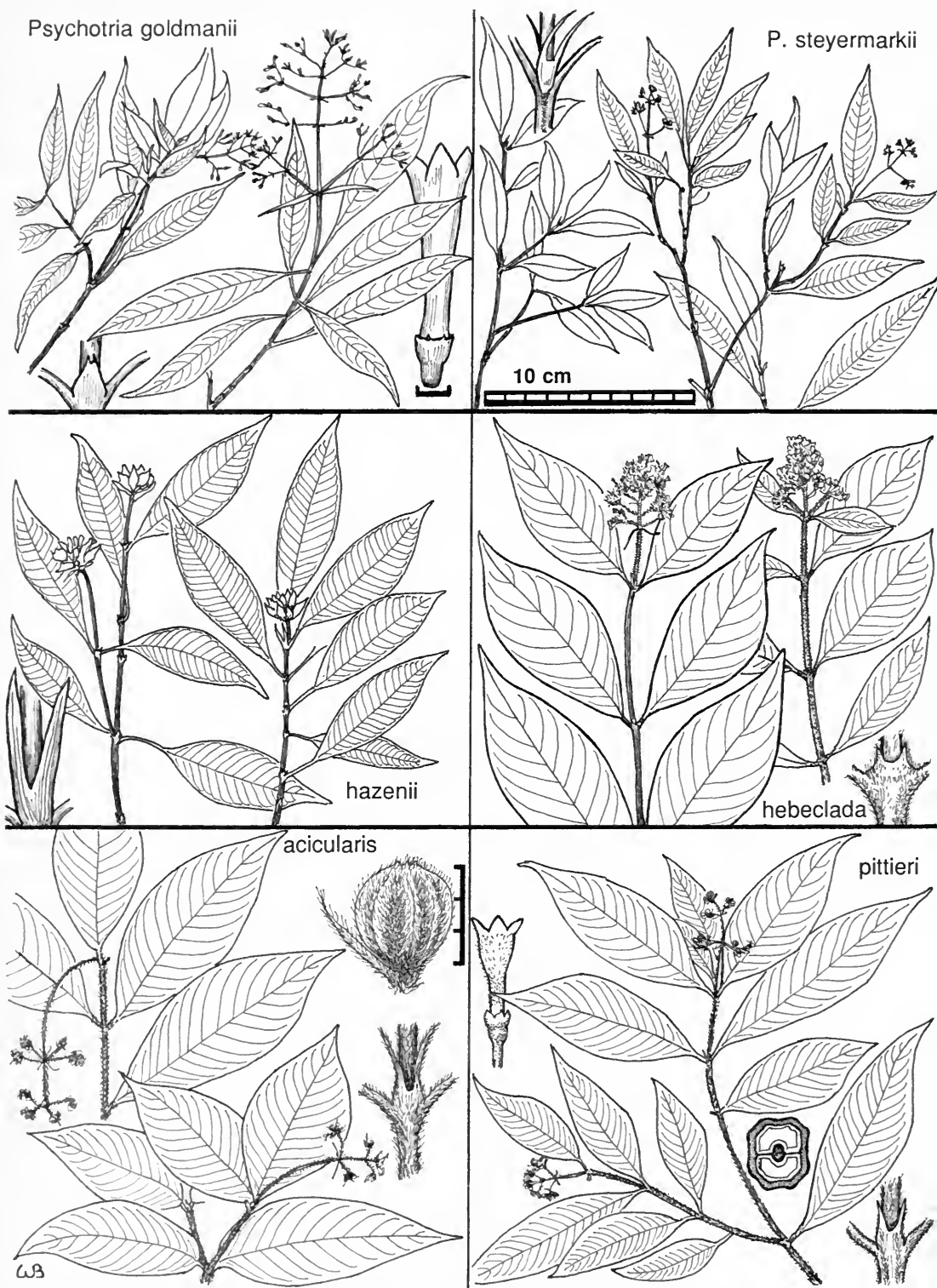


FIG. 55. *Psychotria* subg. *Heteropsychotria*: species with smaller leaves.

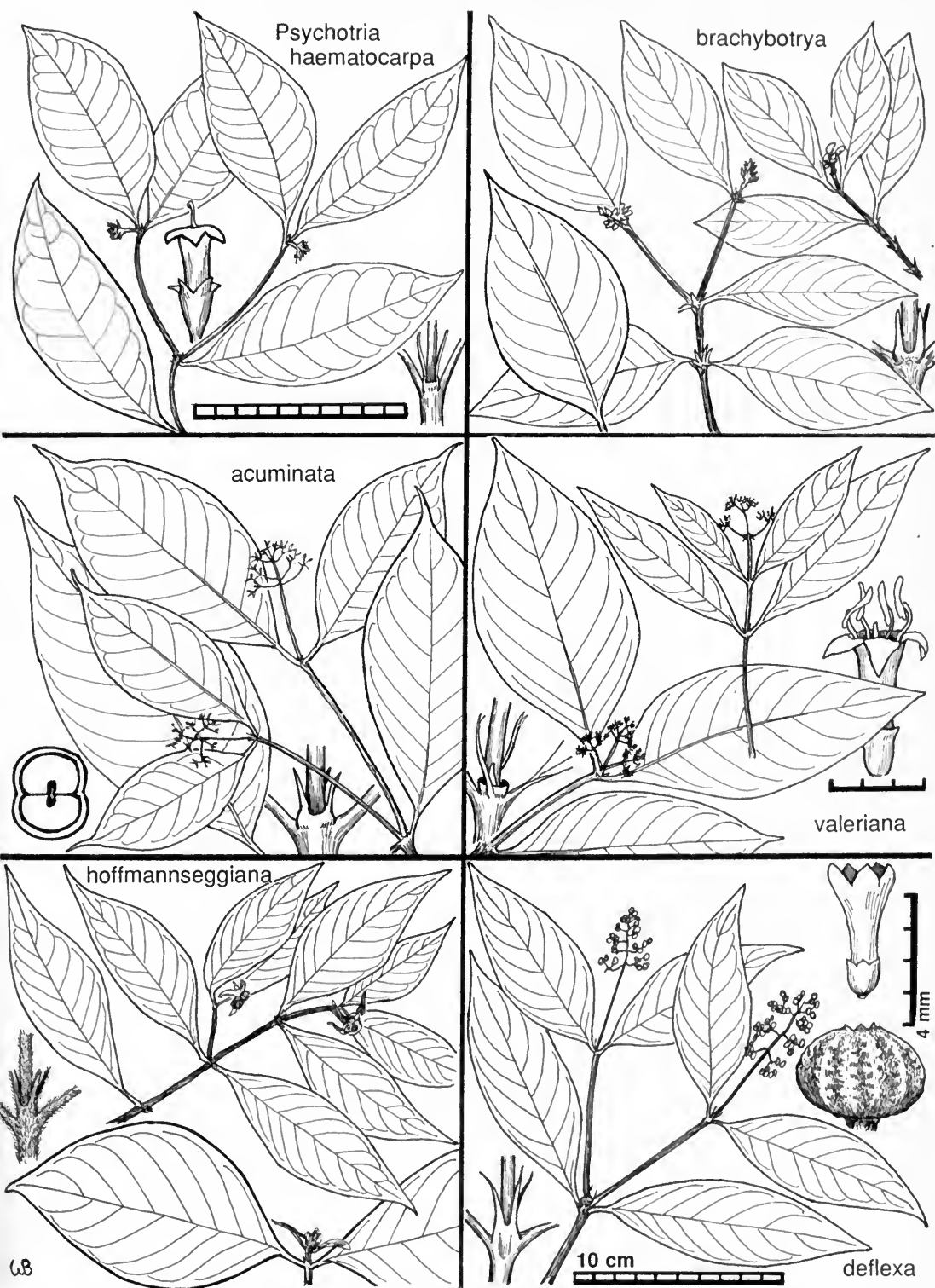


FIG. 56. *Psychotria* subg. *Heteropsychotria*: species with very small inflorescences.

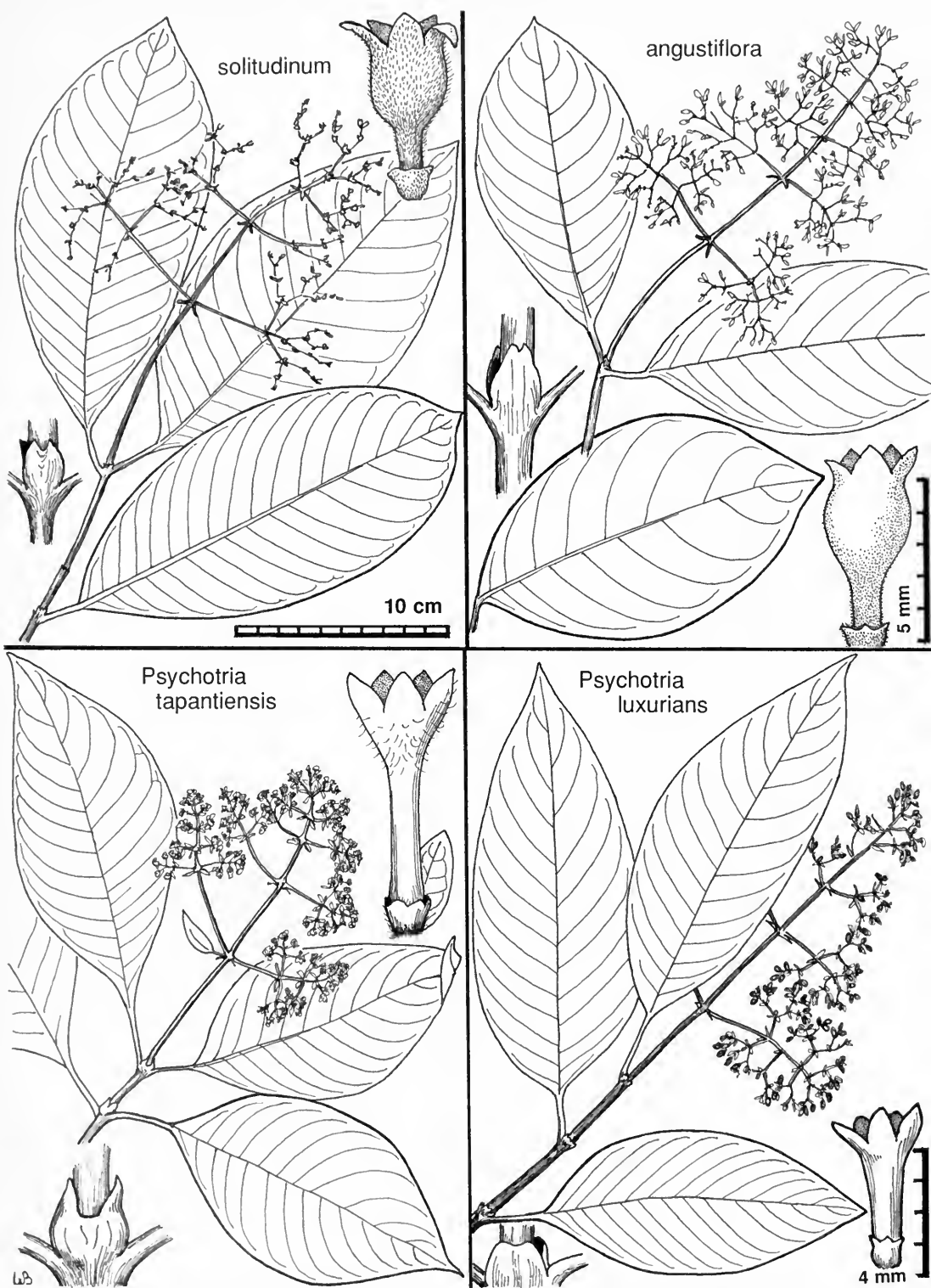


FIG. 57. *Psychotria* subg. *Heteropsychotria*: species with larger open inflorescences.

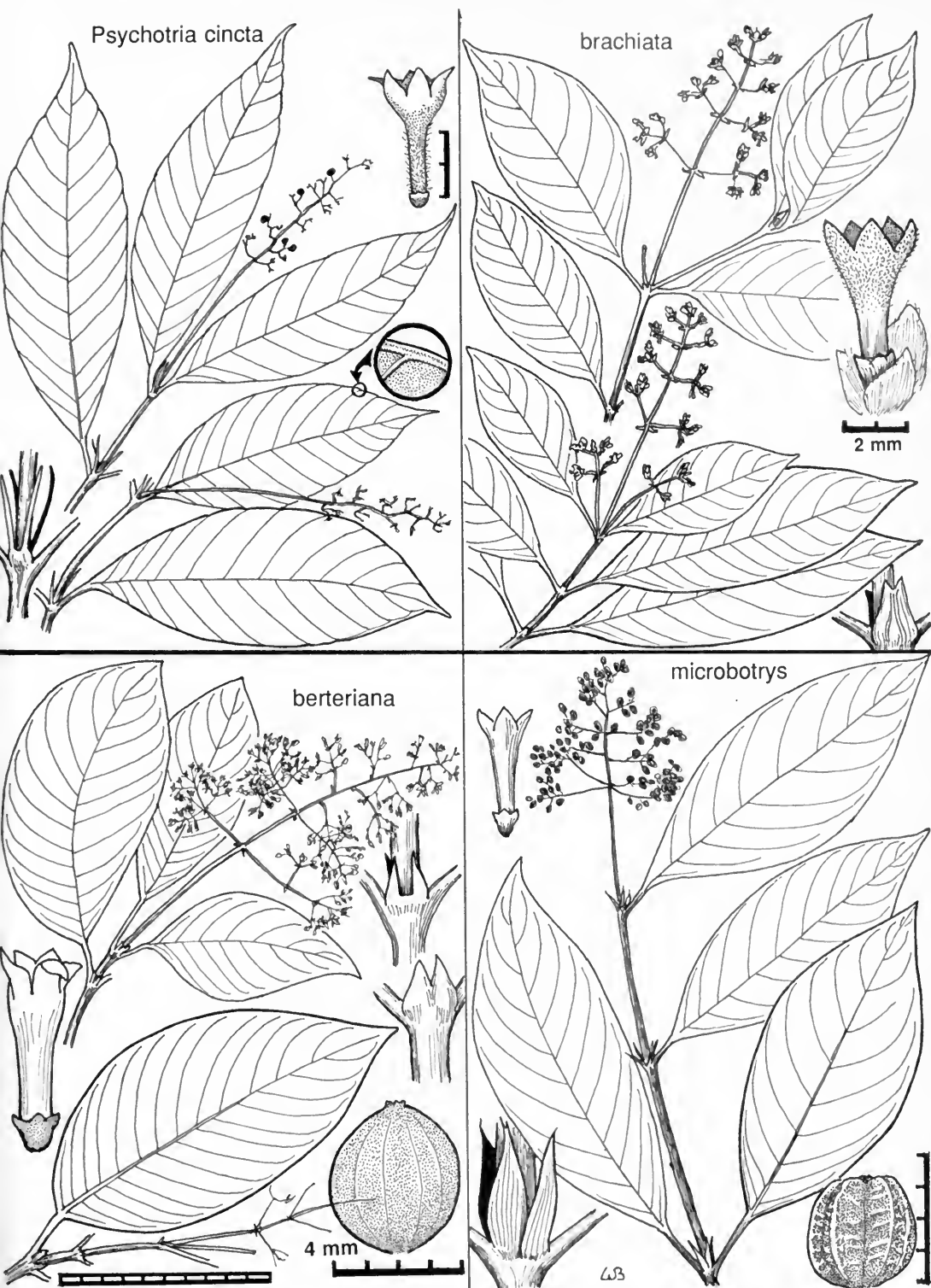


FIG. 58. *Psychotria* subg. *Heteropsychotria*: species with conspicuous open inflorescences.



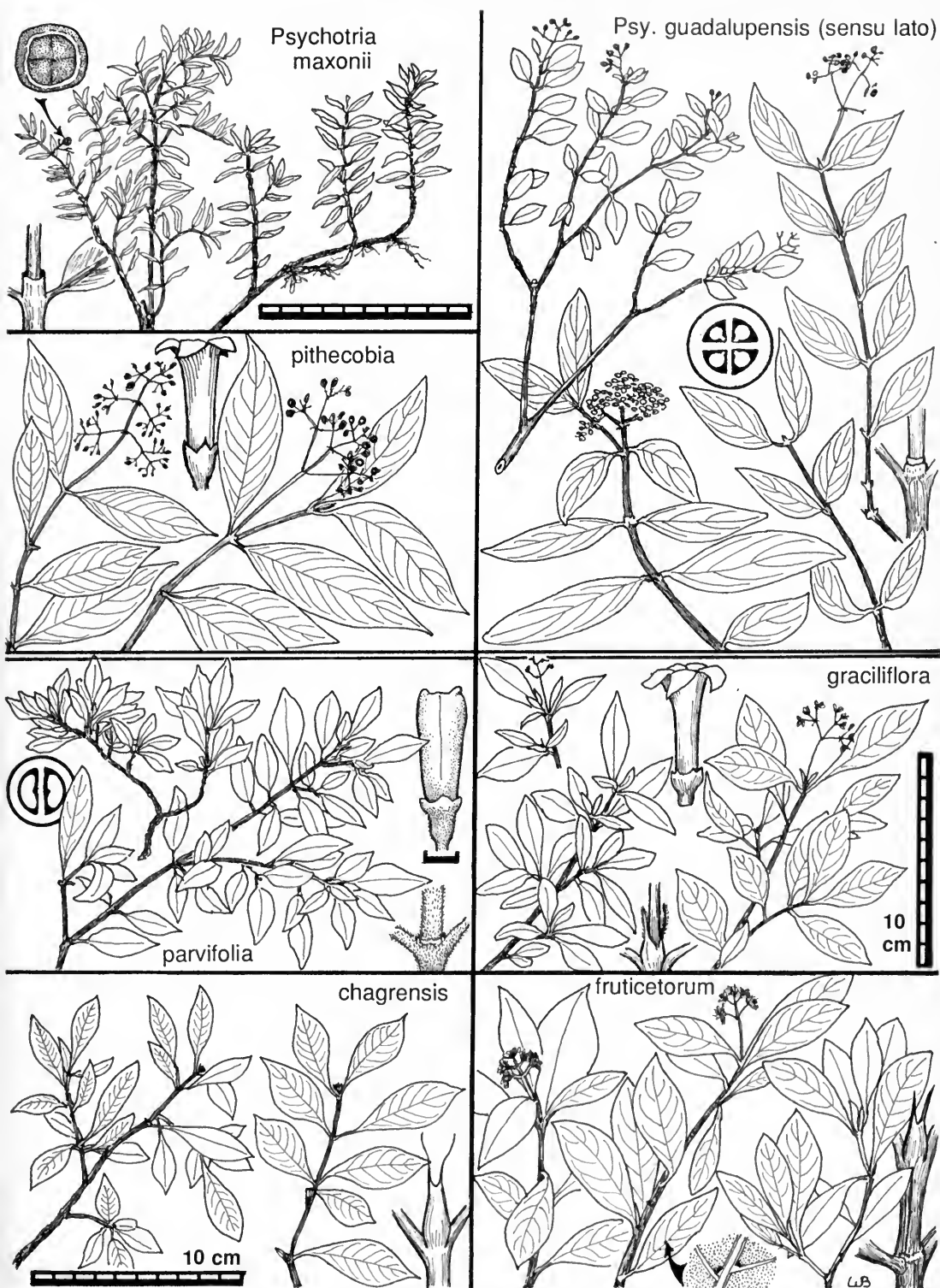


FIG. 60. *Psychotria* subg. *Psychotria*: species with very small leaves and a complex of epiphytic species.

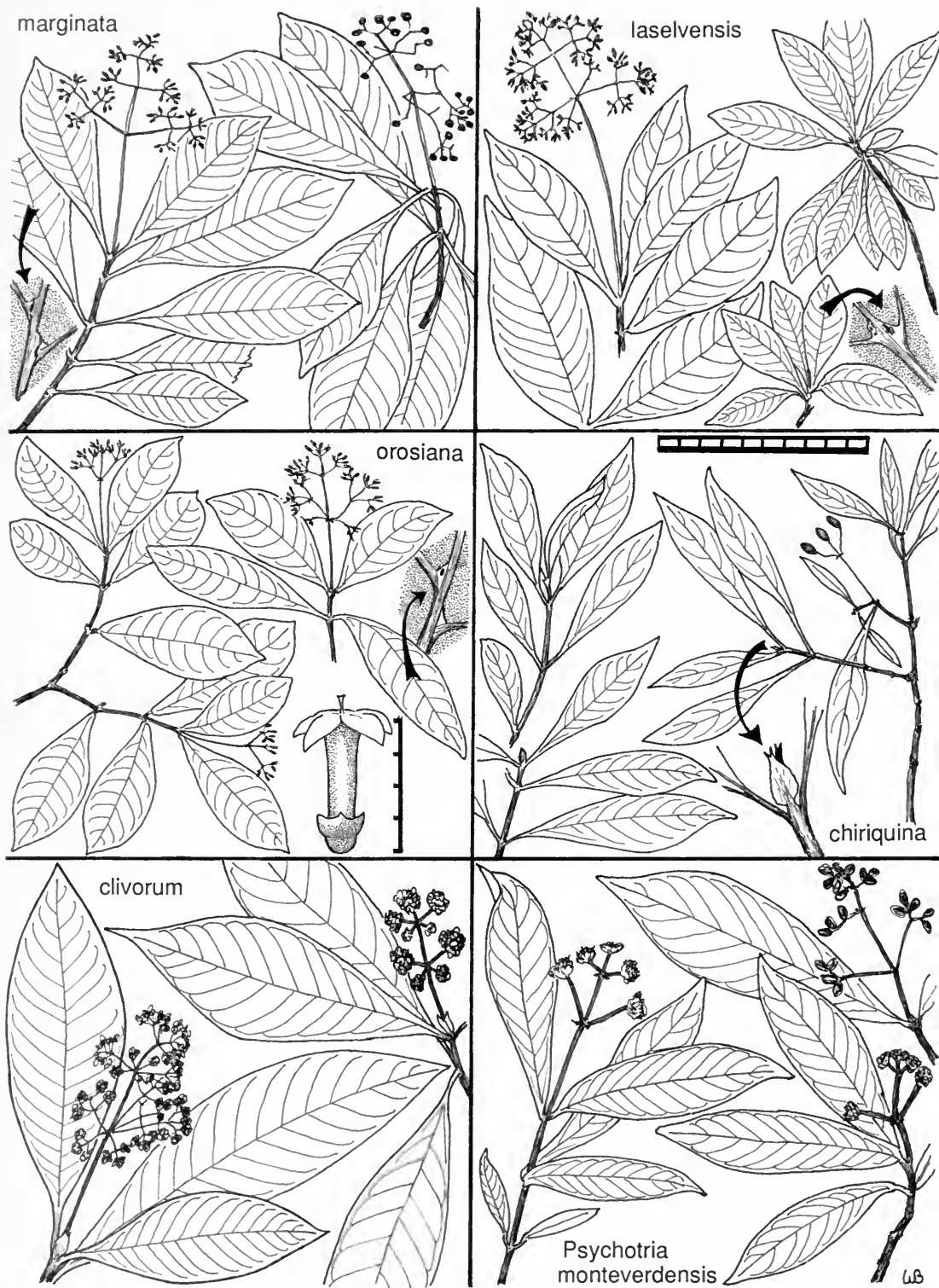


FIG. 61. *Psychotria* subg. *Psychotria*: species with smaller narrow leaves.

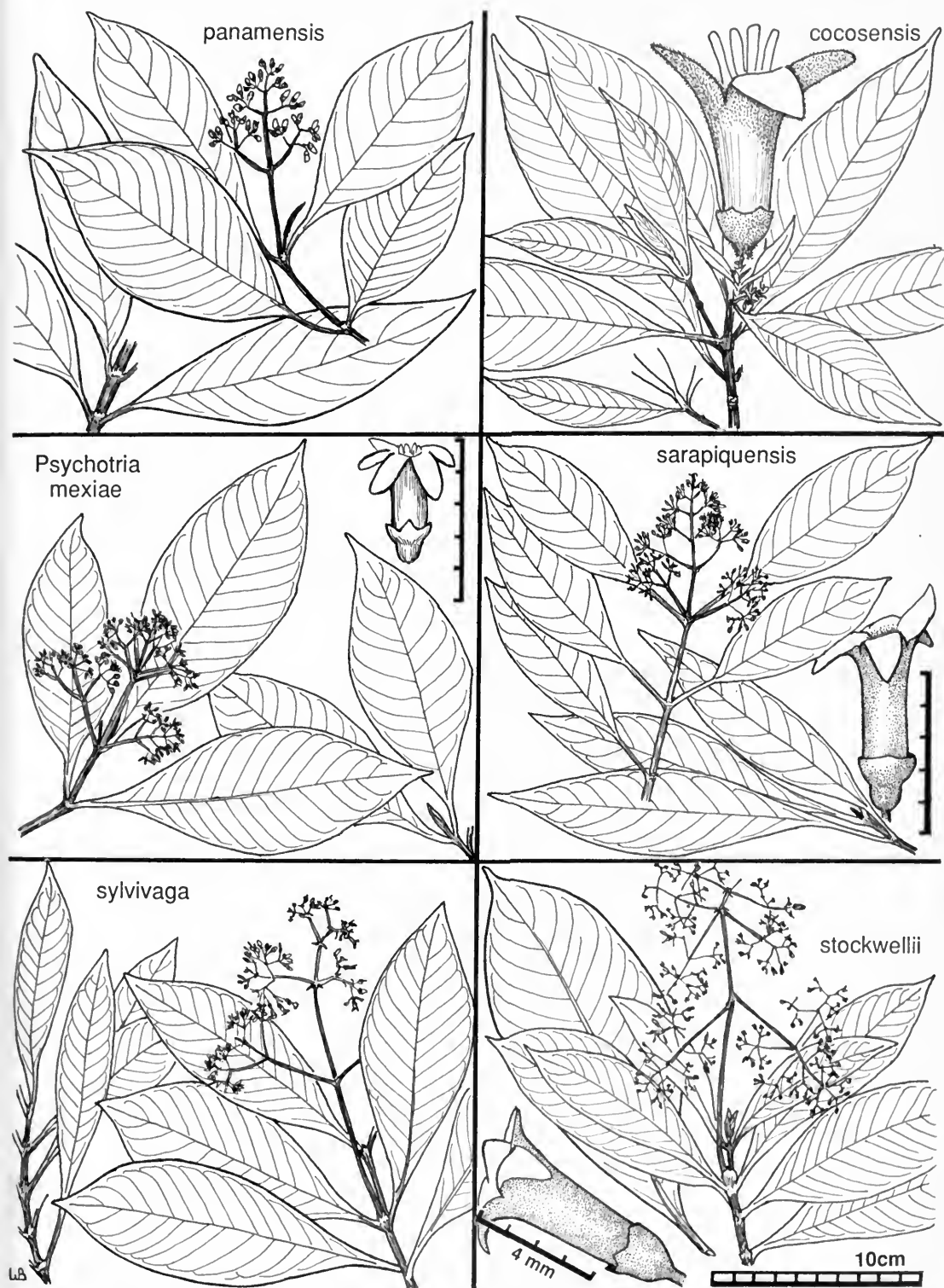


FIG. 62. *Psychotria* subg. *Psychotria*: high-elevation species and those with *Ficus*-like stipules.

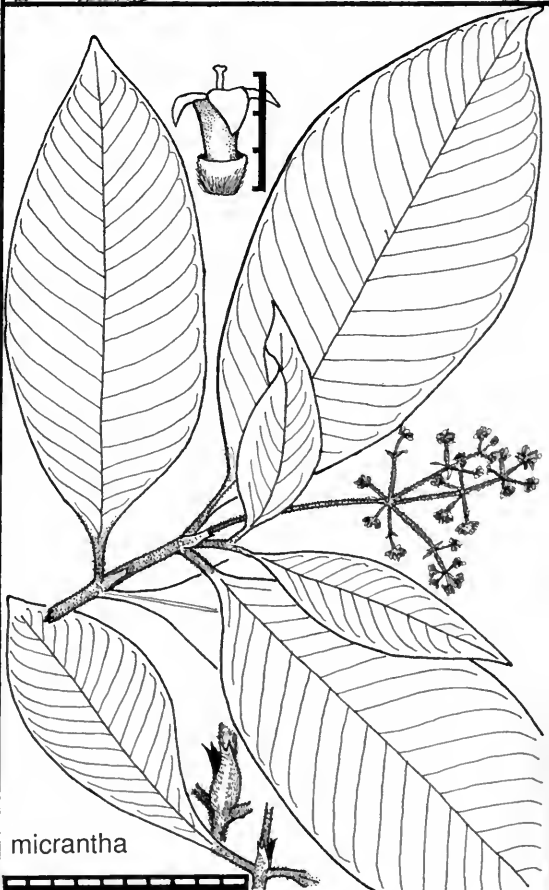
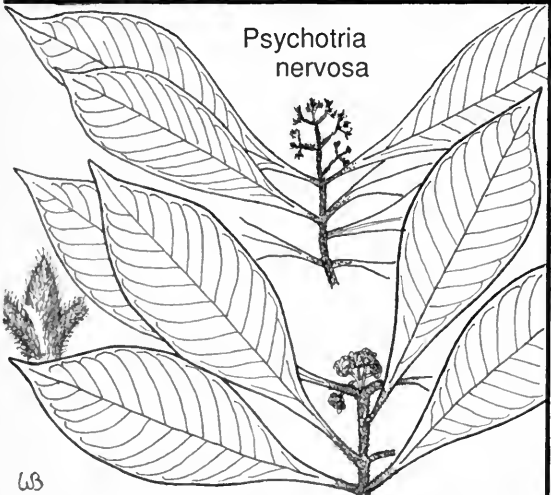
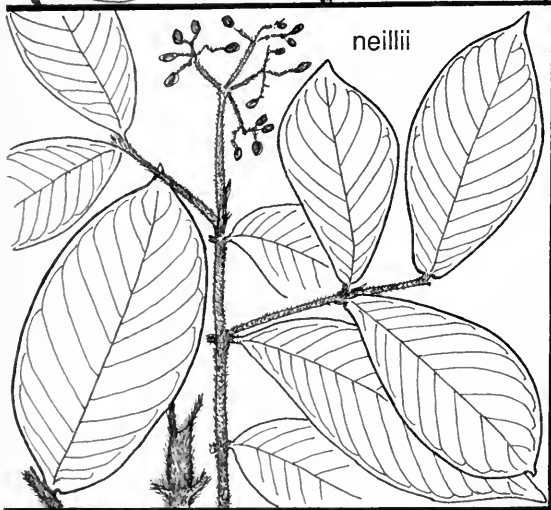
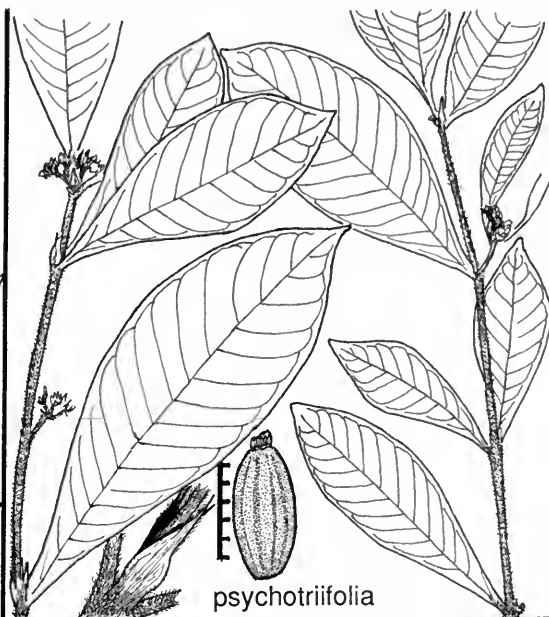
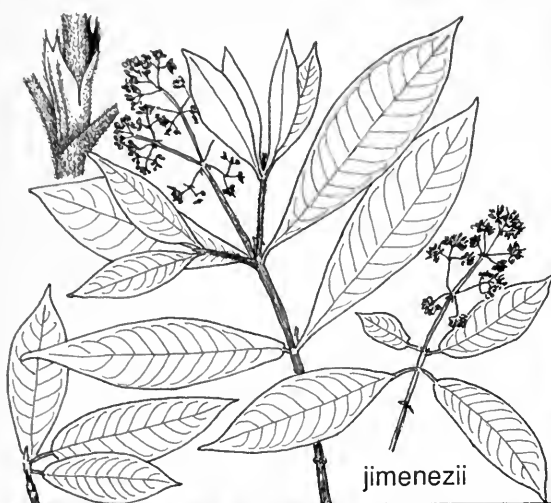


FIG. 63. *Psychotria* subg. *Psychotria*: densely pubescent species.

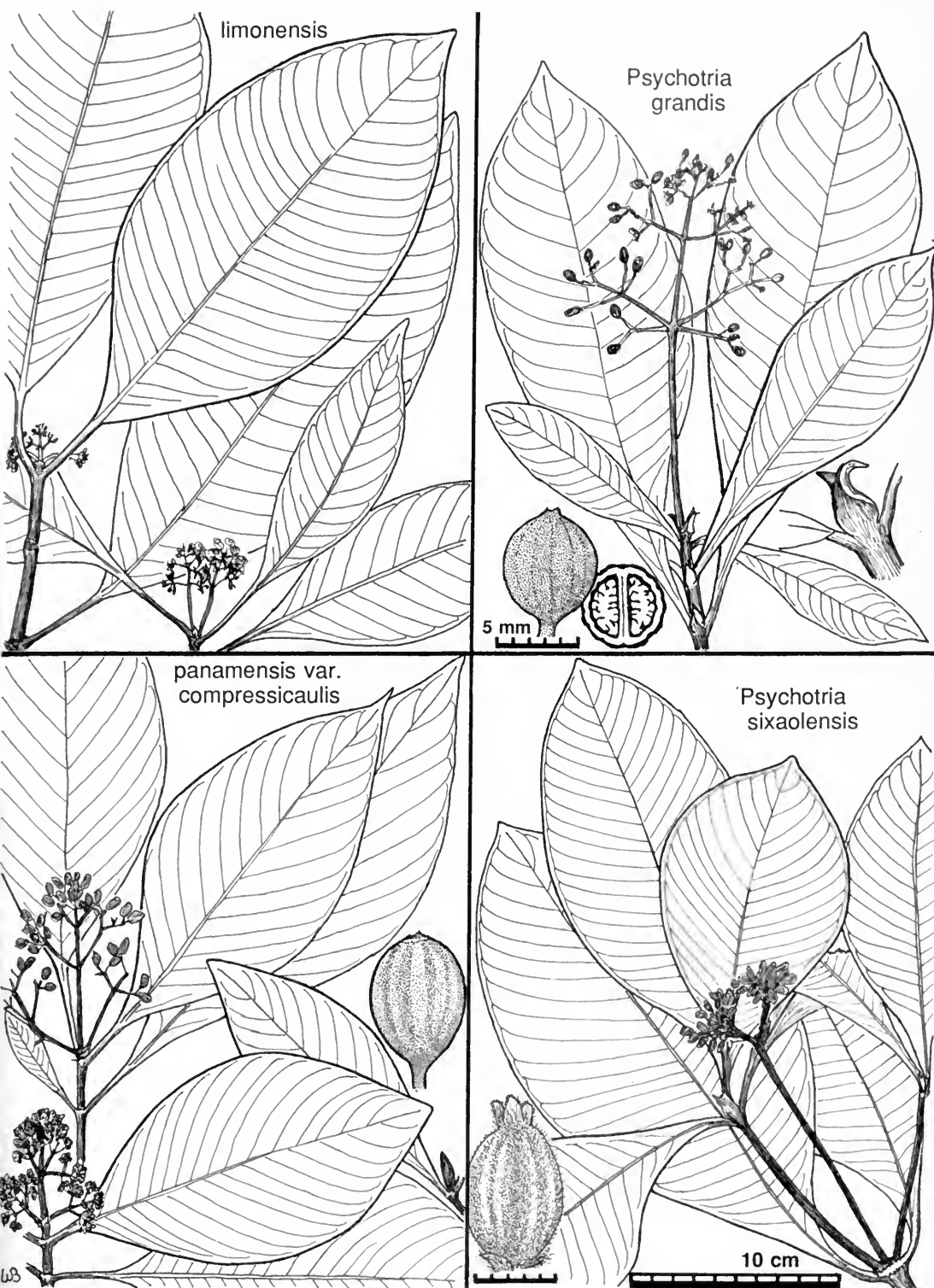


FIG. 64. *Psychotria* subg. *Psychotria*: large-leaved species.

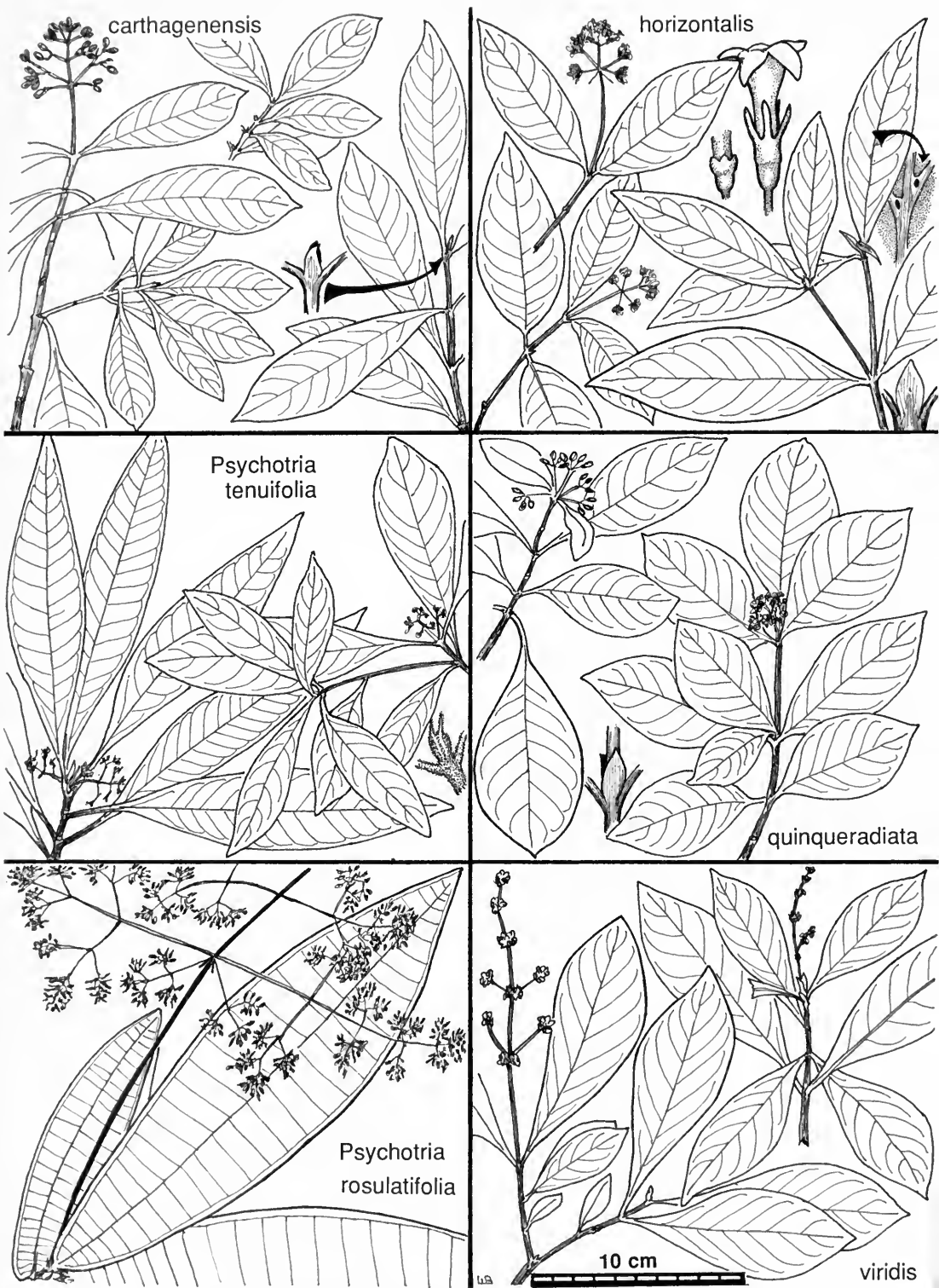


FIG. 65. *Psychotria* subg. *Psychotria*: deciduous and unusual species.

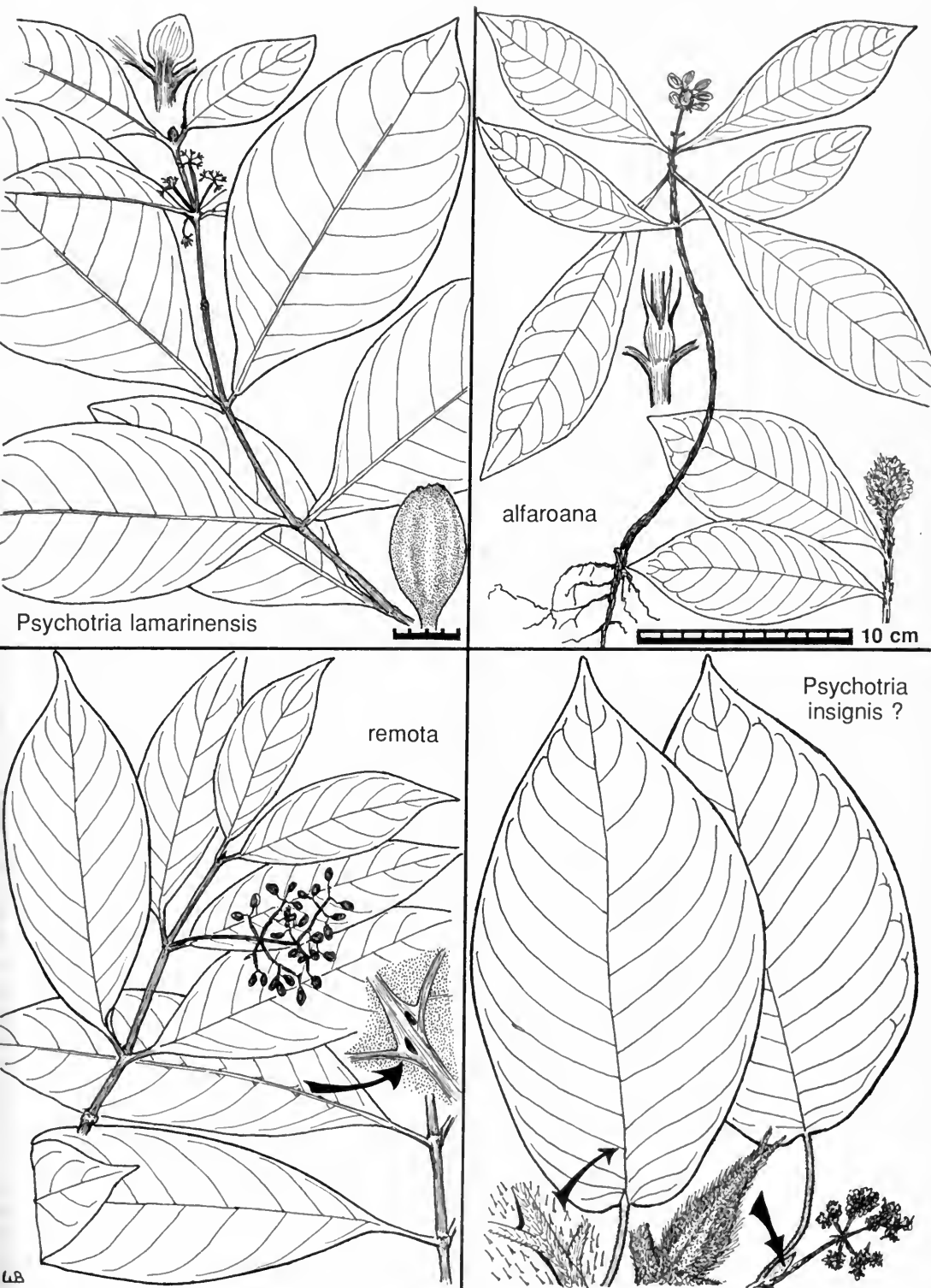


FIG. 66. *Psychotria* subg. *Psychotria*: several unusual species.

Trees or **shrubs**, dioecious, lacking spines, glabrous or sparsely puberulent; **stipules** interpetiolar (and intrapetiolar in a few spp.), acute, usually persisting. **Leaves** opposite, petiolate; **leaf blades** entire, often with domatia. **Inflorescences** terminal, ♂ flowers fasciculate or capitate, ♀ flowers solitary or 2, flowers of both sexes sessile or subsessile, subtended by persisting stipule-like bracts. **Flowers** unisexual, (3-)4-5(-8)-parted, hypanthium hemispheric (in ♀ flowers) to tubular (in ♂ flowers), calyx tube truncate or dentate; **corolla** salverform, fleshy or subcoriaceous, corolla tube cylindrical, glabrous or villous within, 3-8-lobed, lobes short to long, obtuse to acute, convolute in bud; **stamens** 3-8, filaments short or absent, anthers linear, dorsifixed, included within the

tube; **ovary** 2-8-locular, ovules 3-many on axile placentas within each locule, few-seriate to multi-seriate, often imbedded in a pulpy placenta. **Fruits** terminal and solitary, baccate, fleshy, sessile or subsessile, globose, usually over 2 cm diam., 2-8-locular with thin septa, pericarp firm and coriaceous, placentas becoming pulpy; **seeds** usually many, compressed to rounded.

A genus of about 35 species, ranging from Mexico, the West Indies, and Central America into South America. *Alibertia* is recognized by its dioecy, sessile or subsessile terminal flowers, and the large terminal subglobose fruit with a persisting terminal calyx tube. This genus is similar to *Amaioua* and *Borojoa*.

Key to the Species of *Alibertia*

- 1a. Stipules 7-20 mm long; flowers 16-34 mm long; leaves elliptic-oblong; usually tapering gradually to the apex *A. edulis*
- 1b. Stipules to 4 mm long; flowers 7-10 mm long; leaves usually somewhat obovate, abruptly narrowed to an acuminate or rounded apex *A. garapatica*

Alibertia edulis (L. C. Rich.) A. Rich. ex DC., Prodr. 4: 443. 1830. *Genipa edulis* L. C. Rich., Actes Soc. Hist. Nat. Paris 1: 107. 1792. *Gardenia edulis* (L. C. Rich.) Poir. in Lam., Encyc. Méth. Bot. Suppl. 2: 708. 1812. Figure 25.

Shrubs or rarely small trees, 1-4(-6) m tall, sometimes forming thickets, bark often peeling in longitudinal strips, leafy branchlets (1.5-)2-4.5 mm thick, glabrous or sparsely puberulent, reddish brown and becoming grayish; **stipules** 7-15(-20) mm long, 2-4(-5) mm broad at base, triangular to deltoid, acute or acuminate, longitudinally striate, acute or acuminate, brownish and glabrous, subcoriaceous, persisting with older leaves. **Leaves** with petioles 2-5(-10) mm long, 0.5-1.8 mm thick, glabrous; **leaf blades** 5-14(-20) cm long, 1.5-5(-8) cm broad, narrowly elliptic-oblong to broadly ovate-oblong, apex acute to long-acuminate, base gradually narrowed and attenuate (in narrow leaves) to rounded and subtruncate (in broader leaves from Caribbean lowlands), drying stiffly chartaceous to subcoriaceous and often grayish green, lustrous above in life, glabrous on both surfaces (or puberulent beneath in material from Caribbean lowlands), 2° veins 6-12/side, small domatia of pits and tufted hairs often present in vein axils beneath. **Inflorescences** of subsessile ♂ or ♀ flowers, subtended by stipule-like bracts 7-15 mm long. **Flowers** 4- (rarely 5-) parted, 16-34 mm long, hypanthium 4-8 mm long, 3-5 mm diam., calyx tube truncated except for the short (0.3-1.7 mm) narrow (0.3 mm) lobes; **corolla** white, tube 2-3 cm long, lobes to 2 cm long and 12 mm broad, triangular, minutely puberulent; **stamens** usually 4, subsessile, anthers ca. 13 mm long in ♂ flowers; staminodes 5 mm long in ♀ flowers. **Fruits** 2-3 cm diam., obovoid to subglobose, yellowish brown, slightly truncated distally, persisting calyx tube

4-6 mm long and 4-6 mm diam.; **seeds** 3-8 mm long, oblong, slightly flattened longitudinally, striate.

Shrubs of both deciduous and evergreen forest formations, from near sea level to 500(-1000) m elevation. Probably flowering and fruiting throughout the year, with the main flowering season April-July. The species ranges from Mexico to northern South America.

Alibertia edulis is recognized by its solitary terminal rounded fruit with persisting calyx tube, generally narrow oblong-elliptic leaves, stiff striate interpetiolar stipules, and generally shrubby habit. In Central America the species is most common in deciduous or partially deciduous woodland. Common names for this species in Central America are *lagartillo*, *trompillo*, *trompo*, *trompito*, and "wild guava." The fruit is occasionally eaten by local people and sporadically cultivated. This species may intergrade with material currently placed under other names in South America; compare *A. acuminata* (Benth.) Sandwith and *A. latifolia* (Benth.) Schum. Specimens may resemble some species of *Randia*.

Material from the Caribbean lowlands placed under this name differs in having broader leaves that dry dark and have short straight hairs on their undersurfaces. This material, while quite different from that found on the Pacific slope, appears to intergrade with the more typical forms in Guate-

mala and Belize; it is not often collected in Costa Rica.

Alibertia garapatica K. Schum. in Mart., Fl. Bras. 6(6): 384. 1889.

Shrubs or small trees to 5 m tall, leafy branchlets slender (1–2 mm thick) with slightly thickened nodes, terete, brownish, minutely (0.1 mm) puberulent and glabrescent; **stipules** 2–4 mm long, ca. 2 mm broad at the base, persisting or deciduous. **Leaves** with petioles 2–7(–10) mm long, 0.7–1.2 mm thick, minutely puberulent; **leaf blades** 5–12(–15) cm long, 2–5(–7) cm broad, broadly elliptic-obovate to broadly oblong-obovate or elliptic-oblong, apex abruptly narrowed and acuminate, caudate-acuminate or rounded, tip 5–15(–20) mm long, base obtuse to cuneate, drying stiffly chartaceous and usually grayish in color, glabrous above and below, 2° veins 5–7/side, domatia of tufted hairs in the vein axils beneath (in Colombian material). **Inflorescences** terminal and capitate, sessile or subsessile, with 4–8(–16) ♂ flowers, the ♀ flowers solitary or paired, flowers subtended by 2 triangular stipules (bracts). **Flowers** aromatic, 6–10 mm long, hypanthium 1–2 mm long, ca. 1.3 mm broad, obconic, distal margin entire, calyx cup and teeth minute (0.5 mm) or absent; **corolla** tube 3–7 mm long, greenish, lobes white, 1.5–3 mm long, ca. 1.5 mm broad near the base; **stamens** 4. **Fruits** solitary, sessile or subsessile, globose or subglobose to obovoid, ca. 25 mm long and 30 mm diam., drying black.

Trees of evergreen and partly deciduous formations on both the Caribbean and Pacific slopes in central Panama, from near sea level to 500 m elevation. In Costa Rica it is known only from near Punta Mala on the Pacific coast (*A. Jiménez 3912*, flowering in March) and the Reserva Biol. Carara (*Zuñiga 232*, fruiting in May), both in southern Puntarenas Province. The species ranges from Costa Rica to Colombia and occurs in southern Mexico.

Alibertia garapatica is recognized by its terminal subsessile flowers and solitary fruit, small interpetiolar stipules, relatively broad and slightly obovate leaves that dry chartaceous, and smaller flowers. A short tube may be present on some stipules. This species is poorly known; it may be mistaken for some species of *Randia*.

Allenanthus Standley

Small to medium size **trees**, branchlets glabrous or sparsely puberulent; **stipules** interpetiolar, persistent or deciduous. **Leaves** opposite, short-petiolate, leaf blades acuminate, entire, often with minute domatia. **Inflorescences** panicles with opposite branching, broadly corymbose in form, terminal or axillary to distal leaves,

bracteate, flowers pedicellate. **Flowers** bisexual, small (3–6 mm), hypanthium obovoid to urceolate, truncated distally, laterally compressed, calyx lobes 4, small; **corolla** whitish, tubular and with 4 spreading lobes, valvate to somewhat imbricate; **stamens** 4, borne in the throat of the corolla tube, filaments slender, anthers oblong; **ovary** 2-locular, with 1 ovule in each locule, style distally bifid. **Fruits** becoming dry and samara-like, flattened with broad lateral wings surrounding the 2 central narrow longitudinally parallel seed chambers, material of the wings slightly spongy, calyx lobes persisting; **seeds** laterally compressed, pendulous.

A small genus with two species, ranging from central Mexico to western Panama. *Allenanthus hondurensis* Standley is found in central and southern Mexico and in Honduras; our species also appears to have a disjunct distribution in Costa Rica and Panama. The flattened fruit, resembling that of *Ulmus* or some *Terminalia* species, is unique among Central American Rubiaceae.

Allenanthus erythrocarpa Standl., Ann. Missouri Bot. Gard. 27: 344. 1940. *Chimarrhis decurrens* Steyerl., Ceiba 3: 18. 1952.

Trees, 6–20 m tall, leafy branchlets 1.5–5 mm thick, internodes 4–8 cm long, usually glabrous, subterete; **stipules** 3–6 mm long, 2–3 mm broad at the base, apex acute, puberulent within, deciduous. **Leaves** with petioles 6–15 mm long, 1–1.5 mm thick, sulcate with adaxial margins with punctate (gland-like) projections along the edge; **leaf blades** 6–11 cm long, 3–5 cm broad, ovate-elliptic to ovate-oblong, apex tapering gradually and acuminate, tip to 1.5 cm long, base obtuse and slightly decurrent on petiole, drying thin chartaceous and sometimes dark in color, 2° veins 5–7/side, glabrous above or puberulent only along the major veins, with small (0.2 mm) ascending hairs on the major veins beneath, usually with small tufted domatia in slight depressions in the vein axils beneath (with 2-lipped structures ca. 1 mm long at the vein axils in *Zamora & Poveda 825*). **Inflorescences** both terminal and sometimes also axillary to distal leaves and together forming a single conspicuous panicle (thyse) to 15 cm long and 10 cm broad, becoming 20 cm long and 18 cm broad in fruit, primary peduncles 3–7 cm long, terete, shorter toward apex of the inflorescence, peduncles and rachis with opposite lateral branching, with 1 or 2 longitudinal lines of dense short (0.2–0.4 mm long) ascending hairs, bracts 1–2 mm long, pedicels 1–2 mm long. **Flowers** with the hypanthium 1–2 mm long, somewhat flattened (compressed), calyx lobes 4, 0.5–1 mm long; **corolla** becoming 4 mm long, tube ca. 3 mm long, lobes 4, rounded; **stamens** 4, exserted on slender filaments ca. 1.5 mm long, anthers ca. 0.8 mm long. **Fruits** flat and samara-like, pink to red, 5–7(–8) mm long, 3–4(–6) mm broad, oblong-elliptic in outline, the base of the fruit decurrent on pedicel, body of the fruit ca. 0.7 mm thick, fruiting pedicels ca. 4 mm long; **seeds** forming an oblong area in the center of the fruit ca. 2 mm long and 1 mm broad.

Trees of evergreen or partly deciduous forest formations of the Pacific slope, at around 500–700 m elevation. The species is known from near Parque Nacional Rincón de la Vieja in Guanacaste Province (Herrera & Rivera 843 CR, MO, Zamora & Poveda 825 CR, F). Flowers were collected in June (Panama); fruiting in August–September (Panama) and October (Costa Rica). The species is known only from Costa Rica and western Panama.

Allenanthus erythrocarpa is recognized by its flattened reddish samara-like fruit with small distal calyx lobes, conspicuous infructescences, and unusual lines of hairs along branches of the inflorescences. With their broad terminal inflorescences and bright red or pink fruits, these trees are very conspicuous when fruiting (Zamora & Poveda 825 CR, F).

Allenanthus hondurensis Standl. of northern Central America is a smaller tree found in deciduous forest, with the leaves more puberulent beneath and smaller (5 × 3 mm) yellowish fruit.

Alseis Schott

Trees or large shrubs, branchlets terete, glabrous or more often puberulent; **stipules** interpetiolar, triangular to subulate, caducous or persisting. **Leaves** opposite, often clustered at the ends of branchlets, petiolate; **leaf blades** often narrowly obovate, drying thin-chartaceous, sometimes with domatia. **Inflorescences** terminal or axillary, solitary in each axil, usually spike-like or racemose and cylindrical in form, simple or with lateral branches (paniculate and racemiform), flowers lacking pedicels or the pedicels merging gradually into the base of the ovary. **Flowers** bisexual, small, white to yellow, protogynous; hypanthium obconical to subcylindrical, calyx lobes 5, deciduous; **corolla** tube cylindrical to campanulate or urceolate, villous within, corolla lobes 5, valvate (?rarely open) in bud; **stamens** 5, filaments attached near the base of the corolla tube, anthers exserted, oblong and sagittate, dorsifixed; **ovary** 2-locular, septum thin, placentas apical with numerous ovules in each locule, style long, distally bifid with recurved stigmas. **Fruits** capsular, cylindrical, 2-locular and bivalvate, dehiscing septicidally from apex to base; **seeds** numerous, linear-fusiform, the testa reticulate and prolonged at apex and base.

A genus of about 20 species found in Mexico and Central America and southward to Peru and Brazil. The often long (ca. 20 cm) obovate leaves clustered at the ends of twigs, long (15–30 cm) spicate or racemiform inflorescences with many flowers, and narrow capsular fruit splitting into two parts distinguish members of this genus. Superficially, these plants may resemble some species

of *Gonzalagunia* and *Rondeletia*. *Alseis blackiana* Hemsl., with leaves to 30 cm long, is found in central and eastern Panama. *Alseis hondurensis* Standl. occurs in northern Honduras, Guatemala, and Belize, while *A. yucatanensis* Standl. occurs in southern Mexico, Belize, and Guatemala.

Alseis sp. aff. *A. hondurensis* Standl., Trop. Woods 16: 48. 1928. Figure 40.

Small trees, ca. 15 m tall, trunk ca. 30 cm dbh with soft bark, leafy branchlets 1.5–7 mm thick, glabrous, pale brownish, smooth; **stipules** 3–8 mm long, 1–2 mm broad at the base, triangular-subulate, apex acute, caducous. **Leaves** clustered at the ends of twigs, petioles 10–55 mm long, 0.8–2 m thick, glabrous and drying dark; **leaf blades** (7–)9–19 cm long, (2–)3–8 cm broad, elliptic-obovate to obovate or ovate-elliptic, apex short-acuminate, tip 4–7 mm long, base acute (obtus) and occasionally slightly decurrent on petiole, glabrous above, glabrous below except for some thin hairs ca. 0.7 mm long near the vein axils (domatia?), 2° veins 6–10/side. **Inflorescences** terminal or axillary, solitary or 3, 11–18 cm long, ca. 2 cm diam., spicate with flowers sessile on the rachis or with opposite basal spicate lateral branches, peduncles to 4 cm long, ca. 1 mm thick, minutely grayish puberulent, bracts and pedicels not apparent. **Flowers** with minute (0.1–0.2 mm) tomentulous grayish hairs, hypanthium ca. 1.5 mm long and 0.6 mm thick, cylindric to obconic, calyx lobes ca. 0.5 mm high and 0.6 mm broad at the base, triangular, brownish and mostly glabrous; **corolla** white, short-tubular campanulate, 2–3 m long, corolla lobes little differentiated; **stamens** exserted, anthers ca. 0.8 mm long, style branches recurved. **Fruit** apparently narrowly obovoid and splitting into 2 valves, each valve ca. 8 mm long and 2.5 mm broad, with a notch 1 mm deep at apex, yellowish and smooth-lustrous within.

This species is presently known from only two collections. Flowering material was collected in February 1989 east of Bahía de Drake on the Osa Peninsula (*Q. Jiménez et al.* 670 CR, F, MO). Old fruit were collected in July (*Hammel et al.* 17120 CR, F, MO) at the Reserva Forestal El Cangrejo (near the road from Puriscal to Quepos) at ca. 400 m elevation in San José Province.

Alseis sp. aff. *A. hondurensis* is distinguished by its sessile flowers on spicate inflorescences (rarely paniculate with one or two lateral spicate branches near the base), longer petioles drying dark, and narrowly obovoid capsule splitting into two separate valves. The type of *A. hondurensis* differs in the shorter petioles, minute puberulence on the lower leaf surfaces, the leaf blades more often oblanceolate with a gradually tapering base, and much larger minutely puberulent inflorescences. In addition, *A. hondurensis* is a species of the Caribbean lowlands, whereas our species is found on the Pa-

cific slope. *Alseis blackiana* Hemsl. of Panama differs in the much larger leaves with more secondary veins. Both those species have clearly pedicellate flowers, while the Costa Rican collections have sessile flowers. However, species of *Alseis* appear to be very variable, and it is possible that the Costa Rican material will prove to be conspecific with one of those other species.

Amaioua Aublet

Trees or shrubs, dioecious, branchlets usually puberulent; stipules united, both interpetiolar and intrapetiolar, forming a conic cap over the shoot-apex and tearing irregularly, caducous. Leaves opposite (rarely 3/node), often crowded at the distal ends of stems, petiolate; leaf blades entire, often with minute domatia in vein axils beneath. Inflorescences terminal on the main stem or on short lateral branches, usually fasciculate, with or without primary peduncles, often 3-branched, flowers in ul-

timate cymose or capitate groups or solitary. Flowers unisexual, hypanthium hemispheric to cupulate or tubular, calyx tube truncate distally or dentate, calyx lobes 6 (5) or none; corolla usually salverform, corolla tube terete, sericeous externally and minutely puberulent within, corolla lobes 6 (rarely 5), spreading, oblong, contorted in bud, cream white to greenish; stamens 6 (5), borne on the middle or lower part of the corolla tube, filaments very short, anthers narrow, dorsifixed, included; ovary 2-locular, placentas borne on the septa, ovules many and biseriate in 2 horizontal rows in each locule, style short with coherent(?) style branches. Fruits baccate, oblong, areolate at apex (calyx scar), 2-locular; seeds many, imbedded in a pulp, horizontal, suborbicular and laterally compressed.

A small genus of about seven species, mostly in South America; two species reach our area. The compact terminal inflorescences with unisexual sericeous flowers and many-seeded baccate fruit help to distinguish this genus.

Key to the Species of *Amaioua*

- 1a. Fruit in clusters on short peduncles, sessile or subsessile; ring of colleters or hairs above the new stipule scars ca. 0.5 mm long and usually obscure *A. corymbosa*
- 1b. Fruit usually borne individually on long pedicels in an umbel-like group at apex of stems; ring of colleters above the new stipule scars ca. 1 mm long, visible and drying dark reddish
..... *A. pedicellata*

***Amaioua corymbosa* H.B.K., Nov. gen. sp. 3: 419, pl. 294. 1820.**

Shrubs or small trees, 1–8(–15) m tall, leafy branchlets 2–5 mm thick, at first angular but becoming terete, appressed sericeous and glabrescent, with conspicuous leaf scars, a very short (0.5 mm) ring of colleters present just above the stipule scar on young stems; stipules 8–20 mm long and 5–8(–10) mm broad at the base, sericeous externally. Leaves with petioles 3–18(–30) mm long, to 3 mm thick, with stiff ascending sericeous hairs; leaf blades 5–14(–23) cm long, 3–8(–13) cm broad, elliptic-ovate, ovate-oblong, broadly obovate, or broadly oblong-elliptic, apex abruptly rounded or obtuse and short-acuminate, base obtuse to acute and slightly decurrent on petiole, drying stiffly chartaceous or subcoriaceous, glabrous above, glabrous to sparsely appressed puberulent on the veins beneath, 2° veins 5–8(–10)/side, some of the 3° veins subparallel and at right angles to the secondaries, usually with small tufts of hairs in the vein axils beneath. Inflorescences of ♂ flowers to 10 cm long, corymbose, primary peduncles 0.5–5 cm long, simple or with 3 primary branches and the flowers in cymose groupings, pedicels 1–8 mm long, sericeous; ♀ inflorescences to 6 cm long, subtrichotomous to capitate, secondary branches 0–3 mm long, pedicels usually absent. Male flowers with hypanthium 3–5(–6) mm long and 3–4 mm diam., sericeous, calyx teeth 0.5–1.5 mm long, linear, corolla

10–18 mm long, white or grayish green, corolla tube 5–7(–9) mm long, 1.5–3.5 mm diam., retrorse sericeous, corolla lobes usually 5 or 6, 5–7(–9) mm long, lanceolate, papillate-puberulent on the exterior; stamens 6 (5), anthers 4–6 mm long, filaments inserted in the middle of the tube. Female flowers with hypanthium 3–5 mm long, 1–2 mm diam., calyx tube 2–4 mm long, 2.2–3 mm diam., densely ascending sericeous, calyx teeth 0.5–1 mm long, subulate; corolla 8–12 mm long, tube 6–7 mm long, 2–3 mm diam., densely retrorse sericeous externally, lobes 6 (5), 4–6 mm long, 1.5–2 mm broad, lanceolate, papillate-puberulent within. Fruits 10–15(–17) mm long, 4–9(–11) mm thick (dried), usually in dense clusters of 3–10, red or reddish purple becoming black, drying dark with a pale annular ring distally (scar of the deciduous calyx tube); seeds irregular, 3–5 mm long to 4 mm broad, flattened, testa striate.

Trees of partly deciduous drier forests of the Pacific slope but also found in evergreen forest formations, from near sea level to ca. 300 m elevation. Flowering in July and fruiting in September. This species ranges from southern Mexico through Central America and southward to Colombia, Venezuela, the Guianas, and Bolivia.

Amaioua corymbosa is recognized by its sub-

sessile clusters of fruit often on three terminal branches, densely sericeous flowers with lustrous retrorse hairs on the corolla, and leaves often with minute domatia. The ring of colleters just above the encircling stipule scar are often hidden by the pubescence. Though often collected in central Panama and in Nicaragua, we have seen only a few collections of this species from northern Costa Rica: *Q. Jiménez* 376 CR from near Liberia and *Zamora & Chacón* 1355 CR from Refugio Caño Negro.

Amaioua pedicellata Dwyer, Ann. Missouri Bot. Gard. 67: 30. 1980. Figure 30.

Trees 5–10(–15) m tall, trunks to 22 cm dbh, leafy branchlets 1.6–6 mm thick, with appressed-ascending sericeous hairs 0.5–1 mm long, glabrescent, with a ring of linear colleters ca. 1 mm long encircling the node just above the stipule scar but breaking off early; **stipules** 8–16(–30) mm long, cap-like and caducous, with dense ascending lustrous sericeous hairs. **Leaves** with petioles, 8–18 mm long, 1–1.8 mm thick, appressed puberulent; **leaf blades** 6–13(–19) cm long, 3–6(–10) cm broad, broadly elliptic to broadly elliptic-oblong or elliptic-obovate, apex usually short-acuminate, tip 5–10 mm long, base obtuse (occasionally acute) and somewhat decurrent on petiole, drying stiffly chartaceous and dark brown above, upper surface of the young leaves with scattered slender whitish appressed hairs to 2 mm long but these quickly falling and the mature upper surfaces glabrous, lower surfaces with thin ascending hairs 0.3–0.5 mm long on the major and minor veins, 2° veins 7–11/side, occasionally with domatia in vein axils beneath. **Inflorescences** terminal fascicles of 6–12 pedicellate flowers, the flowers usually on unbranched pedicels (rarely on peduncles bearing 2–3 pedicellate flowers), later forming a sessile or umbellate cluster of long-pedicellate fruit, pedicels 3–8 mm long, with dense lustrous ascending sericeous hairs. **Flowers** with hypanthium and calyx tube ca. 4 mm long and 3 mm diam., calyx lobes 3–5, 0.5–1.5 mm long, subulate or linear; **corolla** rose with pale greenish tube 7–9 mm long, 1–3 mm diam., densely whitish sericeous, lobes 7–9 mm long, 3 mm broad at base, narrowly triangular. **Fruits** subglobose to oblong, 12–17 mm long, 10–14 mm diam., red to dark reddish purple (but drying black), sparsely and minutely puberulent near the distal end, annular calyx scar 3–4 mm diam., fruiting pedicels 20–35 mm long, 1–1.5 mm thick.

Trees of wet evergreen forest formations of the Caribbean slope in Costa Rica, and both the Caribbean and Pacific slopes in Panama, from 600 to 900 m elevation. Flowering in June–July; fruiting in February, September, and December (in Panama). The species is known only from central and southern Costa Rica and Coclé and Veraguas provinces in Panama.

Amaioua pedicellata is recognized by its long-

pedicellate fruit in terminal umbel-like groups, flowers coming directly from the apex of the shoot on usually unbranched stalks (pedicels), and broadly elliptic leaves with long thin hairs on the upper surface in early stages. The unusual glandular teeth (colleters) above the stipule scar near the apex of the stem are also distinctive. At present, this species appears to be limited to a rather narrow altitudinal range on the Caribbean slope in Costa Rica.

***Amphidasya* Standley**

Small **shrubs** or herbaceous subshrubs, woody at the base, stems unbranched; **stipules** connate/interpetiolar, large, lobed distally or deeply laciniate with filiform segments, persisting. **Leaves** often closely clustered near the ends of stems, often long-petiolate; **leaf blades** large, margins entire, domatia absent. **Inflorescences** terminal or axillary, cymose to capitate, short, flowers usually closely crowded, pedicels short. **Flowers** bisexual, hypanthium oblong to turbinate, calyx lobes 4–6, often unequal, persisting; **corolla** tubular-salverform, corolla lobes 4–6, valvate in bud; **stamens** 4–6, borne on the middle or upper part of the corolla tube, filaments short, anthers linear, dorsifixed; **ovary** 2-locular, with axile bilobed placentas, many ovules in each locule. **Fruits** fleshy, indehiscent, crowned by the persistent calyx lobes; **seeds** many, angular, testa reticulate.

Amphidasya is a genus of about seven species, ranging from Costa Rica through Panama to Colombia, Venezuela, and northern Brazil. Our representative is distinguished among Costa Rican Rubiaceae by the short herbaceous habit, large and long-petiolate leaves, densely clustered flowers with long calyx lobes, and long corolla tube.

***Amphidasya ambigua* (Standl.) Standl., Field Mus. Nat. Hist., Bot. Ser. 11: 181. 1931. *Sabicea ambigua* Standl., Publ. Field Columb. Mus., Bot. Ser. 7: 49. 1930. Figure 7.**

Herbs, 10–40(–90) cm tall, erect or decumbent, stems woody at the base, leafy stems 3–7 mm thick, terete, minutely puberulent, glabrescent, brownish; **stipules** 12–20(–40) mm long, ca. 4 mm broad at the base, united basal sheath 3–5 mm long, with long linear acute lobes, minutely and inconspicuously puberulent. **Leaves** clustered at the distal part of the stem, opposite or subopposite, often rosette-like, petioles 1.5–5 cm long, 1.9–2.8 mm thick, with few minute appressed hairs or glabrescent; **leaf blades** 12–28 cm long, 5–10 cm broad, narrowly elliptic-obovate to narrowly oblong-obovate or oblanceolate, apex abruptly narrowed and short-acuminate, base gradually narrowed and cuneate-attenuate,

long-decurrent on petiole, drying stiffly chartaceous, essentially glabrous above, sparsely puberulent with minute (0.1–0.2 mm) ascending hairs on the veins beneath or glabrous, 2° veins 15–25/side. **Inflorescences** densely crowded in the axils of distal leaves, to 5 cm long, base of the inflorescence not usually visible, with 4–20 closely crowded sessile or subsessile flowers, floral bracts 1–5 mm long, acute. **Flowers** 5- or 6-parted, the hypanthium 5–8 mm long, glabrous or minutely and sparsely papillate-puberulent in later stages, calyx lobes 8–18 mm long, ca. 1.5 mm broad at the base, often unequal, glabrous on the surfaces and with minute (0.1 mm) hairs along the edge; **corolla** narrowly salverform, white, puberulent on the exterior, corolla tube 32–50 mm long, 1–2.5 mm broad (dried), corolla lobes 6–18 mm long, triangular, acute. **Fruits** 8–12 mm long, 4–6 mm diam., cylindrical-oblong, with persisting calyx lobes, surface of the dried fruit bullate from pressure of the seeds within; **seeds** 0.3–0.4 mm diam., foveolate.

Plants of steep slopes in the shade of evergreen rain forests on both the Caribbean and Pacific lowlands, collected at elevations of 10–800 m (to 1500 m in Panama). Flowering in August and November–December; fruiting in March–July, September, and November. The species ranges from Costa Rica to Colombia.

Amphidasya ambigua is recognized by its short stature, distally fimbriate stipules, crowded long-petiolate leaves, crowded flowers with relatively long calyx lobes, and relatively long corolla tube. These plants resemble species of *Paradrymonia* in the Gesneriaceae (but the latter have superior ovaries). Costa Rican material was earlier thought to be a separate species, distinguished in the following key. However, recent collections from Panama and Colombia have produced many intermediate variants and resulted in a broader interpretation of *A. ambigua*. Note, however, that the preceding description is based on Costa Rican material and does not represent all the variation found within the more widely defined taxon. The following key outlines the differences between the western and eastern collections.

Amphidasya ambigua is recognized by its short stature, distally fimbriate stipules, crowded long-petiolate leaves, crowded flowers with relatively long calyx lobes, and relatively long corolla tube. These plants resemble species of *Paradrymonia* in the Gesneriaceae (but the latter have superior ovaries). Costa Rican material was earlier thought to be a separate species, distinguished in the following key. However, recent collections from Panama and Colombia have produced many intermediate variants and resulted in a broader interpretation of *A. ambigua*. Note, however, that the preceding description is based on Costa Rican material and does not represent all the variation found within the more widely defined taxon. The following key outlines the differences between the western and eastern collections.

- 1a. Leaves often elliptic-oblong, petioles 2–7 cm long and densely appressed-puberulent, major secondary veins 12–18 on each side; calyx lobes densely puberulent, corolla tube 2–3 cm long; central Panama to Colombia.
- 1b. Leaves usually slightly obovate, petioles 1.5–5 cm long and glabrescent, major secondary veins 15–25 on each side; broad surfaces of the calyx lobes glabrous, corolla tube ca. 4 cm long; Costa Rica and western Panama.

Appunia Hooker f.

Shrubs or small trees, glabrous or puberulent; **stipules** interpetiolar and united at the base with the petioles, subulate-acuminate, persisting. **Leaves** opposite, short petiolate, leaf blades often lanceolate and acuminate, entire, mostly drying thin-chartaceous, domatia absent. **Inflorescences** terminal or axillary, capitate with a few flowers congested at apex of a short to long peduncle, flowers free and subtended by bracteoles but without pedicels. **Flowers** bisexual, small, white; hypanthium hemispheric or oblong, calyx tube short-cylindrical, usually truncate, lobes absent or minute (5); **corolla** funnelform to urceolate, corolla lobes usually 5, valvate in bud; **stamens** 5, filaments short, anthers dorsifixed and included; **ovary** 4-locular, each locule with 1 ascending ovule, style slender, stigma capitate. **Fruits** fleshy and baccate, sessile and loosely aggregated on apex of the peduncle, each fruit with 4 (or fewer) nutlets, each nutlet with 2 unequal locules (a seed-bearing locule and an empty locule).

A genus of about 10 species in Central and South America. Most authors have placed this genus into synonymy under *Morinda*, but that genus has the

basally united flowers developing into a fleshy syncarp and two stigmas.

Appunia guatemalensis J. D. Smith, Bot. Gaz. 48: 294. 1909. *Morinda guatemalensis* (J. D. Smith) Steyerl., Mem. New York Bot. Gard. 23: 385. 1972. Figure 19.

Low or slender-branched **shrubs**, (0.5–)1–3(–4) m tall, leafy stems 1.2–4 mm thick, terete, glabrous or rarely minutely (0.01 mm) puberulent; **stipules** 1.5–3 mm long, 2–4 mm broad at the base, with a narrowed simple or bifid tip ca. 0.5 mm long, glabrous. **Leaves** opposite, petioles 2–5 mm long, 0.8–1.6 mm thick, glabrous or sparsely and minutely (0.05 mm) puberulent; **leaf blades** 7–16 cm long, 3–7 cm broad, elliptic-oblong to narrowly obovate, apex acuminate to acute, base acute, drying grayish green to dark olive green and often lustrous above, glabrous above and below, 2° veins 4–6/side. **Inflorescences** solitary in leaf axils (2/node), borne on glabrous peduncles 3–27 mm long and 0.5–1 mm thick (dried), capitula with 3–12 sessile and congested flowers subtended by triangular bracts ca. 1.5 mm long. **Flowers**

glabrous, hypanthium and calyx tube ca. 2 mm long, 1.7 mm diam. distally, calyx lobes not developed; **corolla** ca. 1.5 mm long, white or greenish, corolla lobes 5–6 mm long, 1.5 mm broad at the base, becoming recurved, greenish within. **Fruits** 6–8 mm long, 4–6 mm diam., subglobose, sessile, purple to brownish or black.

Plants of low elevation in open grassy sites or thickets, 0–300 m elevation. Flowering in January–September in northern Central America. The species ranges from central Mexico along the Caribbean coast to southern Nicaragua and has been only rarely collected in the Pacific lowlands of northern Costa Rica.

Appunia guatemalensis is distinguished by its small capitate inflorescences on slender peduncles in the axils of leaves, sessile flowers and fruits, and usual lack of pubescence. The inflorescences are at first borne on very short peduncles, but these elongate during anthesis and fruiting. This species resembles *Morinda royoc* (flowers fused at the base), *Psychotria erecta* (blue fruits), and *Alibertia garapatica* (terminal sessile inflorescences). *Appunia seibertii* Standley of Panama has cuneate-decurrent leaf bases. It is possible that the few collections from near Liberia represent disjunct individuals and not well-established populations.

Arctophyllum Willdenow ex Schultes

REFERENCE—P. Mena V., Revision of the genus

Key to the Species of *Arctophyllum*

- 1a. Plants shrub-like, rooting only at the base, with many erect branching stems to 70 cm tall; leaves 4–8 mm long; flowers in cymose groups on short peduncles *A. lavarum*
- 1b. Plants prostrate with main stems rooting at the nodes, short erect stems less than 20 cm tall; leaves 3–6 mm long; flowers solitary on short leafy stems *A. muticum*

Arctophyllum lavarum K. Schum. ex Standl., Contr. U.S. Natl. Herb. 18: 127. 1916. *Mallosotoma lavarum* (K. Schum.) J. D. Smith, Enum. Pl. Guatem. 5: 36. 1899, nom. nud. (based on *A. lavarum* K. Schum. in herb.). *A. chirropoëns* Suesseng., Bot. Jahrb. Syst. 72: 285. 1942. Figure 1.

Subshrubs with creeping and erect woody stems, 10–40(–70) cm tall, sometimes forming mats, with many erect branches, nodes thickened with the bases of persisting stipules and leaf bases, internodes 2–7(–18) mm long, leafy branchlets 0.5–1.5 mm thick, glabrous, with 4 longitudinal ridges, becoming silvery gray to black;

Arctophyllum (Rubiaceae, Hedyotideae). Mem. New York Bot. Gard. 60: 1–26. 1990.

Shrubs or small subshrubs, stems woody, erect or prostrate, usually with short internodes and congested leaves, nodes thickened; **stipules** united and interpetiolar, entire to bifid or setose distally, persisting. **Leaves** opposite, small, often closely crowded and imbricate, sessile or subsessile; **leaf blades** entire, thick-coriaceous, glabrous, venation often obscure, domatia absent. **Inflorescences** terminal (sometimes apparently axillary to distal leaf-like bracts), with cymose or clustered flowers on short peduncles, or of solitary flowers, pedicels short. **Flowers** bisexual, glabrous externally; hypanthium hemispheric to obovoid, calyx lobes 4(–5), often with glands between the lobes; **corolla** campanulate to funnelform, corolla lobes 4, often papillate-puberulent within, valvate in bud; **stamens** 4, free portion of the filament emerging from between the corolla lobes; anthers dorsifixed, exerted or partly included; **ovary** 2-locular, placentas borne on the septum, ovules 4–12/locule, style slender, stigmas 2. **Fruits** capsular, turbinate to subglobose, usually dehiscent septically and basipetally, 2-locular; **seeds** few, oblong and plano-convex to concave-convex, punctate.

A genus of 15 species, ranging from Costa Rica through Panama into the Andes as far south as Bolivia. These plants are distinguished by their small stiff ericoid leaves, short internodes, and small stature in paramo or similar open high-altitude vegetation types. Standley (1938, p. 1273) suggested that the genus might be congeneric with *Houstonia*.

stipules 1–2.5 mm long, distal margin entire to erose or spiny, thickened at the base. **Leaves** sessile or with petioles ca. 1 mm long, glabrous throughout, articulate at the base; **leaf blades** 4–8 mm long, 2–4 mm broad, ovate-elliptic to ovate-oblong or oblong, apex obtuse or rounded, base obtuse to subtruncate, drying thick and coriaceous, darker and lustrous above, with a rim of lustrous tissue along the edge beneath, midvein impressed above, other veins not visible above or below. **Inflorescences** to 2 cm long, usually with peduncles to 1.5 cm long, branches of the inflorescence sometimes subtended by leaf-like bracts, glabrous, flowers usually in cymose groupings (fasciculate), pedicels 0.5–2 mm long. **Flowers** ca. 7 mm long, hypanthium 1–1.5 mm long, obconic (turbinate) to hemispheric, calyx lobes 4, 1–1.5 mm long, ovate-oblong to triangular and persistent, often with 1–

3 setae between each pair; **corolla** tinged with blue, purple, or pink in bud, campanulate, corolla tube 2–3 mm long, corolla lobes 2–3 mm long, white and minutely puberulent on the inner surfaces; **stamens** 4, filaments ca. 1.5 mm long, attached near the mouth of the tube, anthers 0.8–1 mm long, purple; **ovary** with ovules borne together on a stipe from the base of the septum, style ca. 4 mm long, stigmas 2 and often connate. **Fruits** short-pedicellate, 1.5–2 mm long, subglobose, with a ring of tissue and the persistent sepals distally; **seeds** 4–8/locule, ca. 1 mm diam.

Small shrubby or mat-forming plants of open or partly shaded sites in Paramo formations and open high elevation sites, from (1800–)2500 to 3500 m elevation. They have also been found as pioneers on volcanic substrates at 800–900 m elevation in the Cordillera de Guanacaste. Flowering throughout the year (mostly in January–March and July–August). The species ranges eastward from Volcán Rincón de la Vieja to the Chiriquí highlands of Panama.

Arcytophyllum lavarum is distinguished by its short shrubby habit, short internodes with thickened nodes, small stiff opposite ericoid leaves, and four-parted campanulate flowers with corolla lobes bluish or purple on the outer (abaxial) surfaces and white on the inner (adaxial) surfaces. This species and its congener differ from all our other Rubiaceae in habit and appearance with their small thick leaves, miniature shrubby form, and exposed high-elevation habitat. These plants often grow among similar-looking species of *Hypericum* (Guttiferae, yellow flowers with many stamens), *Ugni myricoides* (H.B.K.) Berg (Myrtaceae, lacking interpetiolar stipules), and Ericaceae (alternate leaves). References to a published description by Schumann are incorrect.

***Arcytophyllum muticum* (Wedd.) Standl., J. Wash. Acad. Sci. 18: 163. 1928. *Hedyotis mutica* Wedd., Chloris Andina 2: 43, pl. 50. 1857. *A. recurvatum* Suesseng., Bot. Jahrb. Syst. 72: 286. 1942. Figure 1.**

Small prostrate **subshrubs**, 3–10(–20) cm tall, often forming short dense mats 5–10 cm thick, usually rooting from the nodes on thicker horizontal stems, much-branched, the erect leafy flowering stems without roots, internodes 0.2–6 mm long; **stipules** ca. 0.5 mm long, glabrous or with a few hairs distally, near the base and on lines beneath the stipule. **Leaves** sessile, usually closely spaced, glabrous throughout; **leaf blades** 3–5(–6) mm long, 0.5–2 mm broad, lanceolate to linear-lanceolate or narrowly oblong, apex acute to obtuse, base cuneate, drying thick-coriaceous and with similar color above and below, venation obscure. **Inflorescences** of solitary flow-

ers terminal on short leafy branchlets, borne on slender peduncles (pedicels) 2–4 mm long or sessile. **Flowers** to 12 mm long and 7 mm broad, hypanthium ca. 1 mm long, calyx lobes 1–2 mm long, narrow, **corolla** campanulate-funnelform, 5–8 mm long, white with purple or lilac on the outer surfaces, corolla tube 3–4.5 mm long, corolla lobes 2–4 mm long and 1–2 mm broad, papillate-puberulent on the lower half within (adaxially); anthers borne just beneath the sinuses of the corolla lobes, 0.7–0.8 mm long. **Fruits** 1–1.5 mm diam., subglobose, with 4–6 seeds per locule.

Small moss-like plants of paramo vegetation and in bogs and along open slopes in high montane formations, from 2700 to 3400 m elevation. Flowering in January, March, and July–August in Costa Rica. The species is found in the Cordillera de Talamanca of Costa Rica and adjacent highlands of Panama, to Colombia, Ecuador, and Venezuela.

Arcytophyllum muticum is distinguished by its short moss-like habit, very small stiff narrow opposite leaves, and woody stems with short internodes and interpetiolar stipules. The four-parted flowers and inferior ovary help distinguish these plants from similar species of Ericaceae and *Hypericum*. We have only seen six collections from Costa Rica. The diminutive size may cause many collectors to overlook this species.

Bathysa Presl

Trees or shrubs, often puberulent; **stipules** interpetiolar, entire, acute to bifid at apex, deciduous or persisting. **Leaves** opposite, petiolate; **leaf blades** entire and pinnately veined, domatia absent. **Inflorescences** terminal and solitary, paniculate with opposite branching, often much-branched with many small flowers. **Flowers** bisexual, often small, calyx cupular and truncated distally or with 4–5 calyx lobes; **corolla** funnelform to subrotate, corolla lobes 4–5; **stamens** 4–5, inserted on the throat of the tube, anthers dorsifixed and exserted; **ovary** 2-locular, ovules many in each locule. **Fruits** capsular, 2-locular with septicidal dehiscence, splitting from apex into 2 valves; **seeds** horizontal, compressed or angular, with or without marginal wings.

A genus of about 12 species, nearly all from eastern Brazil or Amazonia. The lack of intrapetiolar stipules distinguishes these plants from *Elaeagia*, while the short corolla tubes and slightly exserted stamens separate it from *Rondeletia*.

***Bathysa veraguensis* Dwyer, Ann. Missouri Bot. Gard. 67: 40. 1980.**

Small **trees** to 5 m tall, leafy branchlets 2.5–6 mm thick, minutely appressed-puberulent with yellowish hairs

0.2–0.4 mm long, terete; **stipules** 22–32 mm long, 2–6 mm broad, narrowly oblong to falcate, densely sericeous with lustrous ascending yellowish hairs. **Leaves** with petioles 4–16 mm long, 2–2.8 mm thick, densely puberulent; **leaf blades** 12–36 cm long, 9–18 cm broad, obovate to broadly oblanceolate or oblong, apex short- or long-acuminate, tip to 18 mm long, base gradually narrowed to obtuse but often abruptly rounded at the petiole, drying chartaceous and brown or reddish brown, minutely (0.1–0.3 mm) puberulent above and below, 2° veins 12–20/side. **Inflorescences** 15–30 cm long, 12–22(–30) cm broad, open panicle with a larger pair of lateral branches and much smaller distal branching, peduncles 5–9 cm long, 2–3.5 mm thick, densely sericeous with ascending hairs, pedicels 6–12 mm long, usually with bracteoles 3–4 mm long in the middle, flowers 1–3 in distal cymes. **Flowers** with hypanthium ca. 3 mm long and 3 mm diam. distally, conical, densely sericeous together with the calyx, calyx lobes 5 (4), 3–5 mm long, 3–4 mm broad at the base; **corolla** white, glabrous on the exterior, tube 3–5 mm long, to 5 mm diam.; anthers 5, 3–4 mm long. **Fruits** 8–15 mm long to 8 mm broad (including the large persisting calyx lobes), ellipsoid-cupulate from a narrow (0.7 mm) pedicel, densely sericeous.

Plants of the evergreen Pacific lowlands of the Osa Peninsula, collected at 400 m elevation. Flowering material was collected in February in Panama; old fruits were collected in June in Costa Rica (*Hammel et al. 17029 CR, MO*). This species is known only from southern Costa Rica and Coclé and Veraguas provinces in Panama.

Bathysa veraguensis is recognized by its often larger puberulent leaves with many secondary veins, large open terminal panicles with frequent distal dichotomous branching, larger distant flowers, white corollas glabrous on the exterior, and sericeous capsules with broad persisting calyx lobes. Leaf shape and pubescence appear to vary considerably, making it likely that the single Costa Rican

collection (cited above) and the Panamanian type (*Lao & Gentry 531 MO*) are conspecific.

Bertiera Aublet

Shrubs or small trees, branchlets terete, glabrous or puberulent; **stipules** connate both interpetiolar and intrapetiolar and forming a short sheath above the node (often difficult to see or interpret), interpetiolar portion triangular and acute, persistent. **Leaves** opposite, distichous, petiolate or rarely sessile; **leaf blades** entire, drying chartaceous, domatia present or absent. **Inflorescences** solitary and terminal, pedunculate panicles with a prominent central rachis and opposite or alternate lateral branches bearing flowers in cymose or helicoid (cincinus-like) arrangements, bracts narrow, flowers often sessile. **Flowers** bisexual, small, white or greenish white, hypanthium turbinate to subglobose, entire distally or with 5–6 small persisting calyx lobes; **corolla** funnelform, corolla tube narrow, usually strigillose externally, glabrous or puberulent on the throat within, corolla lobes 5 (4, 6), short, convolute in bud; **stamens** 5 (4, 6), inserted on the distal part of the corolla tube, filaments very short, anthers dorsifixed, often with the connective slightly prolonged, included in the throat; an ovarian disc or annular ring present; **ovary** 2-locular, placentas borne on the septum, with many ovules in each locule, style slender and glabrous, stigma simple or 2-lobed. **Fruits** berries, globose to ellipsoid, purple or black; **seeds** many, small, angular, foveolate or granular.

A genus of perhaps 30 species, found in the American tropics and in Africa. The genus is distinguished by its unusual stipules, thyrses-like inflorescences, and many-seeded fleshy fruit. These plants resemble some species of *Psychotria* (but those have two-seeded fruit) and some species of *Gonzalagunia* and *Rondeletia* with cymose-helicoid branching.

Key to the Species of Bertiera

- 1a. Leaves with petioles 1–4 mm long, with 5–8 strongly ascending major secondary veins on each side; stipules 7–14 mm long; Cocos Island and Panama *B. angustifolia*
- 1b. Leaves with petioles 3–9 mm long, with 4–6 major secondary veins on each side; stipules 5–8 mm long; wide ranging continental *B. guianensis*

Bertiera angustifolia Benth., Bot. voy. Sulph. 103. 1845. Figure 43.

Shrubs or small trees, 3–6 m tall, leafy branchlets 1.2–4 mm thick, with appressed-ascending sericeous hairs 0.7–1.8 mm long, internodes often uniform (ca. 2–3 cm) in length; **stipules** 7–20 mm long, 1.5–2.7 mm broad at

the base, with a narrow tip, persisting or deciduous. **Leaves** with petioles 1–3.5 mm long, sericeous with appressed-ascending hairs; **leaf blades** 9–17 cm long, 2–3.5(–5) cm broad, lanceolate to very narrowly ovate-elliptic, apex gradually narrowed and acute or acuminate, base acute to obtuse or slightly rounded, drying dark, glabrous on the upper surface except for the midvein, sericeous on the veins beneath, 2° veins 5–7/side and strongly as-

ending, with minute tufted domatia in the leaf axils beneath. **Inflorescences** 10–18 cm long, 3–6 cm broad, peduncles 4–10 cm long and often pendulous, lateral branches 1.5–3 cm long and alternate, with straight ascending hairs ca. 0.6 mm long, bracts 5–13 mm long, linear, distal bracteoles ca. 1 mm long, flowers usually sessile. **Flowers** 6–7 mm long, hypanthium 1–1.5 mm long, sericeous, calyx lobes 4 or 5, 0.2–0.5 mm long, acute; **corolla** white, sparsely pubescent, tube 2–3 mm long, 0.7 mm diam., lobes 5 (rarely 4), 1.3–2 mm long; **stamens** 5, anthers 1–1.5 mm long. **Fruits** ca. 10 mm diam., mostly sessile, drying black and with 10 longitudinal ribs (not always apparent at maturity), glabrescent.

Plants of moist evergreen lowland forest formations, from near sea level to 500 m elevation. Flowering in February and April on Cocos Island; fruiting in February. This species is known only from Cocos Island and Panama.

Bertiera angustifolia is recognized by its narrow leaves, terminal panicles with mostly sessile flowers on helicoid lateral branches, and unusual stipules. This species may be no more than a variant of *B. guianensis*, but the narrower leaves with more strongly ascending veins do give the Cocos Island plants a rather distinctive appearance.

Bertiera guianensis Aubl., Hist. pl. Guiane 1: 180, pl. 69. 1775. Figure 43.

Shrubs or small trees, 1–6(–10?) m tall, leafy branchlets 0.9–4.5 mm thick, with appressed-ascending hairs ca. 0.4 mm long, stems becoming glabrescent, internodes often quite uniform (4–5 cm) in length; **stipules** 5–15 mm long, 3–4 mm wide at the base, basal sheath 3–4(–6) mm long (above the node), acuminate (rarely slightly bifid). **Leaves** often distichous, petioles 3–10 mm long, 0.8–1.8 mm thick, strigulose; **leaf blades** 8–18(–21) cm long, 2–6(–8) cm broad, narrowly oblong to narrowly elliptic-oblong or lanceolate, apex gradually narrowed and acute or acuminate, base gradually cuneate to obtuse, drying chartaceous and dark olive green to grayish, glabrous above or with a few hairs on the midvein, sparsely strigillose with hairs 0.4–0.8 mm long beneath (the hairs on the veins longer), 2° veins 4–6 (3–8)/side, arcuate-ascending. **Inflorescences** 8–24 cm long, often pendant, lateral branches 1–5 cm long, lower branches longer and with more secondary branching (pyramidal), peduncles 2–10 cm long, 0.7–1.5 mm thick, densely strigulose with stiff whitish ascending hairs 0.5–1 mm long, bracts 3–9(–15) mm long, triangular to linear, flowers sessile or subsessile. **Flowers** ca. 8 mm long, hypanthium 0.7–1.8 mm long, pubescent, calyx lobes 5–6, 0.3–1 mm long; **corolla** white, tube 3–5 mm long, 1–2 mm wide with short stiff ascending hairs or glabrescent, corolla lobes 5, 1.5–3 mm long, ovate-oblong and acute, puberulent within; **stamens** 5–6, anthers 0.8–1.8 mm long, the connective prolonged 0.3–0.6 mm long, sagittate at the base; **ovary** with resinous dots, style ca. 2.5 mm long,

stigmas bifid and oblong, ca. 2 mm long. **Fruits** sessile, subglobose, 3–8 mm diam., with 6–10 longitudinal ribs, blue drying black; **seeds** 1–2 mm long, muricate.

Shrubs and small trees of wet evergreen lowland forest formations, from near sea level to ca. 1000 m elevation. Probably flowering and fruiting throughout the year (most flowering collections from January to August). The species ranges from Mexico, Central America, and the western Greater Antilles to Bolivia and the Guianas.

Bertiera guianensis is characterized by its narrow leaves, unusual stipules, characteristic pubescence, thyrselike inflorescences with sessile flowers often on helicoid distal branches, and 10-ribbed immature fruit. This species is usually found on ridges in primary forest at La Selva.

Borojoa Cuatrecasas

REFERENCE—J. Cuatrecasas, *Borojoa*, Nuevo género Rubiácea. Revista Acad. Colomb. Ci.-Exact. 7: 474–477. 1950.

Small trees, dioecious, glabrous; **stipules** interpetiolar and sometimes intrapetiolar with a short sheath above the node and with 2 large free interpetiolar lobes produced above the basal sheath, usually persisting. **Leaves** opposite and decussate, often large, petiolate; **leaf blades** entire, domatia sometimes present. **Inflorescences** solitary and terminal, subtended by 1–3 pairs of bracts resembling the stipules, ♂ flowers cymose or sessile in a congested head of few to many flowers, ♀ flowers usually solitary. **Flowers** unisexual and differing in form, ♂ flowers 4- or 5- (to 8-) parted, **corolla** usually funnellform, puberulent on both inner and outer surfaces, corolla lobes convolute in bud, **stamens** 5, anthers linear; ♀ **flowers** 6–8-parted, **ovary** 6–8-locular, placentation axile, ovules many in each locule, stigmas 6–8. **Fruits** berry-like, large, subglobose, pericarp usually thick-walled and fleshy, indehiscent; **seeds** imbedded in a mucilaginous pulp, attached horizontally in longitudinal rows, flattened.

Borojoa is a genus of about 10 species occurring in Costa Rica, Panama, Colombia, and Venezuela. The genus is distinguished by the solitary and terminal female flowers and fruit, and the male flowers terminal and sessile or in solitary heads. The larger leaves, unusual stipules, larger than average flowers, and fruits with thick pericarp are also distinctive. These rarely collected trees of evergreen lowland rain forests are not well understood. It is not clear at this time whether our species are peripheral elements of other species or distinct species deserving recognition (see below). The fruits are used in Chocó, Colombia, to make a refreshing drink.

Key to Two Putative Species of *Borojoa*

- 1a. Leaves essentially glabrous, drying chartaceous to subcoriaceous, often elliptic-ovate, major secondary veins 8–12 pairs; fruits 6–10 cm diam., glabrous *B. panamensis*
- 1b. Leaves glabrous to pubescent beneath, drying thin-chartaceous, usually broadly elliptic, major secondary veins 6–9 pairs; fruit 3–6 cm diam., densely velutinous or glabrescent on the outer surface *B. atlantica*

Borojoa atlantica Dwyer, Ann. Missouri Bot. Gard. 67: 46. 1980. Figure 26.

Trees to 10 m tall, leafy stems 3–5, thick, glabrescent or densely pubescent with soft erect hairs ca. 0.5 mm long, terete; stipules ca. 10 mm long, 5 mm diam., with a basal sheath 2–5 mm long and a free distal portion triangular with acuminate apex, persisting with the leaves. Leaves with petioles 10–26 mm long, 1.5–2.5 mm thick, densely pubescent to glabrescent; leaf blades 12–26 cm long, 7–16 cm wide, broadly elliptic to broadly elliptic-obovate, apex short-acuminate, base obtuse, drying thin-chartaceous to chartaceous and usually dark brown or dark greenish brown, glabrous to sparsely pubescent above, minutely puberulent to velutinous on the veins beneath with hairs ca. 0.5 mm long, 2° veins 7–11/side, with tufts of hairs in the vein axils. Inflorescences not seen. Fruits 27–60 mm long, globose to slightly obovoid, minutely velutinous, subtended by bracts ca. 5 mm long and 6 mm broad.

Plants of the wet Caribbean lowlands, 0–300 m elevation. The Costa Rican material was collected in fruit in June. The species is known from Costa Rica and Panama, but its circumscription is not yet certain. The broad leaves velutinous on the veins beneath (in our material) are distinctive, but the original description states that these plants may be almost glabrous.

Borojoa panamensis Dwyer, Phytologia 17: 446. 1968. Figure 26.

Trees 4–13 m tall, trunks to 25 cm dbh, leafy internodes 3–8 mm thick, essentially glabrous, drying brown; stipules 12–28 mm long, 5–16 mm broad, united above the node for 2–8 mm, stiff and longitudinally striate, acuminate. Leaves with petioles 13–30 mm long, 2–4 mm thick, with 2 lateral adaxial ridges, glabrous; leaf blades 13–27(–38) cm long, 7–14(–17) cm broad, elliptic-oblong, to elliptic-obovate or broadly elliptic, apex usually acuminate, base obtuse to acute (sometimes slightly decurrent on petiole), drying stiffly chartaceous to subcoriaceous and grayish green, glabrous above and below but with small tufted domatia in vein axils beneath, 2° veins (5–)7–12/side, 3° veins weakly subparallel. Inflorescences of 2–9 terminal sessile ♂ flowers (♀ flowers probably solitary), subtended by a pair of stipules ca. 10 mm long. Flowers with hypanthium and calyx tube not differentiated, ca. 8 mm long and 6 mm diam. at apex,

subglabrous and drying dark, calyx lobes 0.4–1 mm long; corolla white, sericeous with downward-pointing lustrous hairs, corolla tube ca. 12 mm long, 4 mm diam. near apex, corolla lobes 5–6, ca. 10 mm long, triangular and acute. Fruits 5–11 cm long, 6–10 cm diam., subglobose, the surface smooth, glabrous and yellowish brown, umbonate at apex, persisting calyx tube ca. 4 mm high, outer wall 8–15 mm thick; seeds 4–8 mm broad, 2–3 mm thick, angular or rounded.

Trees of evergreen forest formation, from near sea level to 600(–1500) m elevation. Flowering in March and May; fruiting in January–August and November. The species ranges from northern Costa Rica (in the Caribbean lowlands) to Panama.

Borojoa panamensis is distinguished by its glabrous (except for the domatia) stiff leaves, distinctive stipules, sessile terminal flowers with glabrescent calyx, sericeous corolla, and the large solitary terminal globose fruit. A specimen from 1500 m on Cerro Turrubares (*Q. Jiménez 836 CR*) is disjunct as regards both elevation and coming from the Pacific slope. New collections are providing a better overview of variation within this species but more material is needed. Herbarium specimens can be very similar to *Genipa americana*, but the latter have pedunculate inflorescences and short corolla tubes and the stipules lack prominent parallel venation.

Borreria G. F. W. Meyer

Borreria G. F. W. Meyer is here considered part of *Spermacoce*.

Bouvardia Salisbury

REFERENCE—W. H. Blackwell, Jr., Revision of *Bouvardia*. Ann. Missouri Bot. Gard. 55: 1–30. 1968.

Shrubs, subshrubs or perennial herbs; stipules interpetiolar, with a very short sheath united to the petioles, entire or with 1–several slender teeth or awns. Leaves opposite or in whorls of 3–4(–6), usually short-petiolate

and puberulent, entire, domatia absent. **Inflorescences** terminal, usually solitary, cymose to corymbose or subcapitate (rarely of solitary flowers). **Flowers** bisexual, dimorphic, glabrous or puberulent on the exterior, calyx lobes 4(–5), usually lanceolate, persisting; **corolla** long-tubular to salverform, usually more than 20 mm long, white to yellow, red, pink, or purple, corolla lobes 4, valvate in bud; **stamens** 4, borne above the middle of the corolla tube, anthers linear or oblong, sessile and included in pin flowers, with filaments and exserted in thrum flowers; **ovary** 2-locular, ovules many on a peltate placenta borne from the lower part of the septum, style 1, slender, exserted in pin flowers and included in thrum flowers. **Fruits** capsular, globose or obovate, didymous-globose, dehiscing at first loculicidally, then septicidally; **seeds** many and vertically imbricate, with entire wings.

Bouvardia contains about 35 species, primarily Mexican and Guatemalan but ranging to Nicaragua. It seems probable that the few specimens collected in Costa Rica and Panama over the last 100 years represent escaped cultivated material.

***Bouvardia glabra* Polak., Linnaea 41: 565. 1877.**

Ornamental **shrubs**, usually 1–1.5 m tall, leafy stems 0.6–3 mm thick, terete, pubescent or glabrescent; **stipules** 2–4 mm long, with a short (0.5 mm) base and slender awn, minutely puberulent. **Leaves** opposite, petioles 1–5 mm long; **leaf blades** 2.5–5(–10) cm long, 0.7–1.8(–3) cm broad, narrowly ovate-elliptic to lanceolate, apex tapering gradually and acute, base obtuse, drying dark brown above and much paler beneath, minutely pubescent beneath, 2° veins 4–6/side, ascending. **Inflorescence** 4–8 cm long, terminal or axillary to distal leaves, with (1)–3–9(–18) flowers, pedicels 3–7 mm long. **Flowers** with hypanthium ca. 1.5 mm long, calyx with unequal lobes 3–8 mm long, 0.4–2 mm broad, glabrous or sparsely puberulent; **corolla** glabrous, white, tube 1.5–3 cm long, 1.5–3 mm diam., lobes 4, ca. 5 mm long.

Ornamental plants not known to grow wild in Costa Rica. The type (*Polakowsky* 337 photo B & fragment F) was collected in Costa Rica. Blackwell recognized *B. glabra*, but Williams (Standley & Williams, 1975, p. 26) considered it to be a synonym of *B. longiflora* (Cav.) H.B.K. We have seen only two collections, both from gardens: *Brenes* 24418 (16) CR and *M. Valerio* 33 F. Note: The latter has more than 18 flowers in the inflorescence. Common names are *jazmín* and *jazmín de la virgen*.

***Calycophyllum* DeCandolle**

Trees, often attaining a large size, branchlets terete; **stipules** united and interpetiolar, caducous. **Leaves** opposite, petiolate; **leaf blades** entire, pinnately veined. In-

florescences terminal (lateral branches apparently axillary when subtended by distal leaves), corymbiform panicles, often many-flowered, pedunculate, flowers sessile or short-pedicellate, at first completely enclosed within close-fitting membranous (perianth-like) bracts. **Flowers** bisexual, radially symmetrical except when the calyx develops a single large petaloid structure; hypanthium oblong to obconic, terete, calyx lobes minute, absent, or 1 developed into a large petiolate and petal-like blade; **corolla** short funnelliform to campanulate, radially symmetrical, corolla tube short, villose within the upper part, corolla lobes 4–8, broad, imbricate or contorted in bud, with 1 lobe exterior; **stamens** 4–8, borne on the corolla tube, filaments slender, anthers oblong, versatile, exserted; **ovary** 2-locular, placentas borne on the septum, with few or many ovules in each locule, ovules imbricate and ascending, style slender and glabrous, stigmas 2, linear-oblong. **Fruits** a capsule, oblong-cylindrical, truncated apically, septicidally 2-valved, coriaceous or slightly woody; **seeds** few to many, the testa expanded and wing-like at both ends.

A genus of seven or eight species in the West Indies and northern South America, with one species ranging through Central America to Mexico. The development of a large whitish petal-like structure from the distal edge of an otherwise truncated calyx in some flowers distinguishes this genus, but not all flowers have this structure. The hard wood, height of the trees, and bivalvate capsule are also distinctive.

***Calycophyllum candidissimum* (Vahl) DC., Prodr. 4: 367. 1830. *Macrocnemum candidissimum* Vahl, Symb. 2: 38, pl. 30. 1791. Figure 16.**

Trees (rarely shrubs), (2)–5–18(–28) m tall, bark reddish brown and often stripping off in longitudinal strips, leafy branchlets 1–4 mm thick, glabrous or puberulent; **stipules** 5–10 mm long, 2–3 mm broad, ovate-lanceolate, caducous and exposing a ring of stiff collectors ca. 1 mm long at the node. **Leaves** with petioles (4)–8–22(–30) mm long, glabrous or puberulent; **leaf blades** 4–10(–13) cm long, 1.5–7(–8) cm broad, broadly elliptic-ovate to broadly elliptic or broadly obovate, apex abruptly narrowed and short-acuminate (obtuse), base cuneate and decurrent on petiole, drying chartaceous and brown, glabrous above and glabrous between the major veins beneath, 2° veins 4–7/side, often with minute pits and tufts of hairs (domatia) in vein axils beneath. **Inflorescences** corymbose to broadly cymose in form, often flat to broadly rounded distally, (2)–5–12(–20) cm long, often with 3 major peduncles from the end of the stems, the lateral peduncles sometimes subtended by smaller leaves (and appearing to be axillary), minutely puberulent or glabrescent, flowers in small compound dichasia with a central sessile flower, young flowers enclosed in glabrous calyptrate bracts 5–10 mm long. **Flowers** 5–9 mm long, hypanthium obconical, 2–3.5 mm long, 1.5 mm diam., glabrous or puberulent, often with glandular dots, calyx lobes usually absent, some flowers with a petiolate (clawed) petal-

like blade 2–4 cm long and 1.5–3.5 cm broad, the blade suborbicular or reniform to broadly obovate, rounded distally, obtuse to truncate or subcordate at the base, white or pale greenish white, palmately veined, the petiole-like base 1–2.5 cm long; **corolla** 5–7 mm long, white, campanulate to funnelform, corolla tube 2–3.5 mm long, ca. 1.5 mm broad at the base and 3 mm broad distally, often densely villous at apex of the throat with erect hairs ca. 1 mm long, lobes 4, 3–4.5 mm long, 2–2.5 mm broad, becoming reflexed; **stamens** 4, filaments 1.5–2.5(–3.5) mm long, anthers 1.2–1.5 mm long; style 3–5 mm long, stigmas 1.3–2 mm long. **Fruits** (6–)8–12 mm long, 3–4 mm diam., oblong-cylindrical, sessile or subsessile, glabrous or sparsely puberulent, with 8 longitudinal ribs; **seeds** 3–5 mm long, fusiform with wings at 2 ends, body of the seed ellipsoid, 1–1.5 mm long.

Conspicuous trees of deciduous and partly deciduous forest formations in the Pacific lowlands, from near sea level to about 450 m elevation (to 700 m elsewhere). Flowering in November–February and May; fruiting in January–August. The species ranges from central Mexico, Belize, and Guatemala, along the Pacific slope of central and southern Central America to Colombia and Venezuela; it also occurs in the West Indies.

Calycophyllum candidissimum is recognized by the bright whitish petaloid structures developed from the calyx of some flowers. The trees bear many inflorescences over their crowns, and the bright petal-like sepal lobes make a striking visual display when in full flower. The large size of these trees in deciduous woodland also contributes to the effect. The species has been called *madroño*, *salamo*, and *surrá* in Costa Rica. The wood is hard and highly elastic and fine textured and finishes smoothly; it has been used for tool handles, archery bows, and many other purposes (Standley, 1938).

Cephaelis Swartz

A poorly defined genus of about 100 species in the American tropics and southern Asia. The ge-

nus was distinguished by the involucrate heads of flowers, two-locular ovary with solitary basal ovules, and drupaceous fruits with two nutlets. Most authors now agree that the species of *Cephaelis* are polyphyletic and cannot be clearly segregated from *Psychotria* (Taylor et al., 1991, p. 139). See the treatment of *Psychotria* (key 3) for species formerly placed in *Cephaelis*, and Figures 17 and 18.

Chimarrhis Jacquin

Trees, often growing to large size and with buttressed trunks; **stipules** interpetiolar and intrapetiolar, leaving a scar encircling the stem above the node (and above the petiole attachment), caudate to acuminate, persistent or caducous. **Leaves** opposite, often clustered at the ends of twigs, short-petiolate; **leaf blades** large- to medium-sized, sometimes with domatia (absent in our spp.). **Inflorescences** solitary or paired in leaf axils (rarely pseudoterminal), paniculate and often corymb-like in form, flowers in open cymose groupings, bracts present. **Flowers** bisexual and radially symmetrical, monomorphic, protogynous in Costa Rica, hypanthium cupulate to tubular, truncated to dentate distally, calyx lobes 5 (4) and very small or none; **corolla** funnelform, white, corolla tube short and broad, villous within, corolla lobes 5 (4), valvate in bud; **stamens** 5 (4), borne on the throat of the corolla tube between the corolla lobes, filaments slender and villous at the base, anthers dorsifixed, often exerted; **ovary** 2-locular, placentation peltate on the septum, ovules many in each locule, style short, stigmas 2, obtuse. **Fruits** capsular, small and woody, oblong, dehiscent septically from apex and 2-valved; **seeds** many, compressed or angulate, horizontal, testa reticulate.

A genus of about 14 species ranging from Costa Rica into South America and in the West Indies. *Chimarrhis* is recognized by the axillary inflorescences, small flowers with poorly developed calyx lobes, corolla tube villous within, and small rounded bivalved capsules with many horizontal seeds. The buttressed trunks, great height of some individuals, and the stipular scar encircling the stem above the nodes are also distinctive.

Key to the Species of *Chimarrhis*

- 1a. Fruit 4–5 mm long; leaf blades 11–24 cm long and 6–11 cm broad; evergreen forests of the Pacific lowlands *C. latifolia*
- 1b. Fruit 1.5–2.5 mm long; leaf blades 5–15 cm long and 3–7.5 cm broad; Caribbean lowlands *C. parviflora*

Chimarrhis latifolia Standl., Publ. Field Columb. Mus., Bot. Ser. 4: 265. 1929. Figure 37.

Trees to 30 m tall, with high buttresses and yellow wood, leafy branchlets 4–9 mm thick, glabrous, leaf scars prominent (ca. 5 mm broad); **stipules** 2–3(–7) cm long, 4–10 mm broad at the base, acute, glabrous and reddish brown, subcoriaceous and caducous, stipular scars often turning dark. **Leaves** with petioles 18–45 mm long, 1.2–1.8 mm thick, glabrous; **leaf blades** 11–24 cm long, 6–11 cm broad, broadly elliptic to elliptic-oblong, apex obtuse or rounded with a bluntly triangular tip 4–8 mm long (or short-acuminate), base obtuse to cuneate, drying chartaceous to stiffly chartaceous, dark brown above and much paler beneath, glabrous above and below except for small groups of hairs (domatia) in the vein axils beneath, 2° veins 7–10/side, 3° veins often subperpendicular to the 2°. **Inflorescences** axillary to distal leaves (2/node), 8–16 cm long, 8–12 cm broad, corymbose with a broadly rounded distal aggregation of many flowers, primary peduncle 3–8 cm long, 2–3 mm thick, reddish brown and glabrous, branches of the inflorescence opposite or subopposite, distal flowers in cymose groups of 3, flowers sessile or short-pedicellate, pedicels and distal branches of the inflorescences minutely puberulent. **Flowers** ca. 8 mm long, protogynous, hypanthium 1.5–3 mm long, turbinate, glabrous and reddish brown when dry, calyx tube very short (ca. 0.5 mm), entire or with 5 broad 0–2 mm long lobes; **corolla** 4–5 mm long, white, glabrous externally, tube 1–2 mm long, 1.5 mm broad, lobes rounded; **stamens** 5, filaments to 4 mm long, with whitish hairs on the lower half, anthers 0.8–1 mm long; pistil with a style to 3.5 mm long, stigmas 2, thick, ca. 0.7 mm long. **Fruits** 4–5 mm long, 3 mm broad, obovoid-oblong with truncated apex, glabrous on the sides, minutely puberulent on the distal (apical) surface; **seeds** ca. 1 mm long.

Trees of evergreen lowland rain forest formations of the Pacific slope of southern Costa Rica, below 400 m elevation. Flowering in July–August (*Cooper & Slater 260 F*, us the type) and October–December; fruiting in December–January. The species is known only from the Pacific slope of southern Costa Rica (Reserva Biológica Carara to Golfo Dulce) and adjacent Panama.

Chimarrhis latifolia is recognized by the taller height of the trees, the generally glabrous parts, large leaves, corymbose inflorescences, closely clustered small flowers with short corolla tubes, and small woody bivalved fruit. *Yema de huevo* and *jagua amarillo* are common names reported for this species. A sterile specimen collected and determined by Paul Allen (5613) with large (to 44 cm) leaves, short (1–2 cm) petioles, and minute puberulence on the lower leaf surfaces and on the long (7 cm) stipules is tentatively placed here. It may represent a juvenile shoot, though said to

come from a tree 27 m tall. Allen (1956, pp. 170–172) stated that it is an important timber tree, and he provided an illustration. Note: This species may be synonymous with *C. cymosa* Jacq.

Chimarrhis parviflora Standl., Trop. Woods 11: 26. 1927. Figure 37.

Shrubs or trees to 25 m tall, to 60 cm dbh, with soft bark and low buttresses, wood yellow, leafy branchlets 1.5–4 mm thick, minutely (0.1–0.3 mm) appressed-puberulent and quickly glabrescent, internodes often short (1–2 cm); **stipules** 5–18(–30) mm long, 2–4 mm broad at the base, narrowly triangular to lanceolate, puberulent at the base and on the outer surface, caducous. **Leaves** with petioles 11–22 mm long, 1–2 mm thick, minutely appressed-puberulent and glabrescent; **leaf blades** 5–15(–18) cm long, 3–7.5 cm broad, elliptic to elliptic-oblong or elliptic-obovate, apex tapering abruptly and short-acuminate, gradually narrowed to the cuneate-attenuate base and slightly decurrent on petiole, drying chartaceous to stiffly chartaceous, usually dark above, glabrous above, minutely (0.1–0.4 mm) puberulent beneath, often densely puberulent on the major veins beneath, 2° veins 5–10/side. **Inflorescences** axillary or pseudoterminal, 2–4 at a node, 5–12(–15) cm long, 3.5–8 cm broad, densely many-flowered, peduncles 2–5(–9) cm long, minutely puberulent, branches opposite or subopposite, pedicels 0–2 mm long, bracts absent or minute (0.5 mm). **Flowers** 4–6 mm long, with sweet odor, glabrous externally, hypanthium 1–1.5 mm long, turbinate, calyx tube very short, calyx lobes 4–5, ca. 0.3 mm long, obtuse and ciliate distally; **corolla** 2–4 mm long, white, tubular-funnelform, corolla tube 1.5–2 mm long, villous within near apex, corolla lobes 4, 1–2 mm long, bluntly rounded; **stamens** 4, anthers 0.6–0.7 mm long, exserted; style 2.5 mm long, stigmas 2, broader than long. **Fruits** numerous and tightly grouped at the ends of the infructescence, 1.5–2.5 mm long, obovoid or turbinate, exocarp yellow-brown and woody, with longitudinal ribs, glabrous on the disc-like apex; **seeds** 0.8–1.2 mm long.

Trees of evergreen rain forest formations of the Caribbean slope often found in swampy areas and along stream edges, from 30 to 900 m elevation. Flowering in March–June; fruiting in May and July–September. This species is known only from Costa Rica and Panama.

Chimarrhis parviflora is recognized by its axillary corymbose inflorescences often four at a node with many small flowers congested distally, and the small woody bivalve capsules. The ability to grow to considerable height and buttressed trunks are additional distinctions. Galls are sometimes present in the infructescences and may be mistaken for young capsules.

Chiococca P. Browne

Shrubs, woody climbers or small trees, the branches often pendant or clambering, branchlets terete, glabrous or puberulent; **stipules** interpetiolar and slightly intrapetiolar (to form a very short tube or cup), usually cuspidate, persistent. **Leaves** opposite, petiolate, entire, membranaceous to coriaceous, pinnately veined, without domatia. **Inflorescences** axillary or less often terminal, racemose or panicle, flowers opposite or along only 1 side of the rachis, pedicels present or absent. **Flowers** bisexual and radially symmetrical, usually 5-parted, hypanthium ovoid to turbinate, calyx lobes 4–6, short and persisting, **corolla** campanulate to funnel-form, white to yellow, lavender or purple, corolla tube cylindrical to urceolate, often with longitudinal ribs in line with the sinuses between the lobes, glabrous within at the mouth, corolla lobes 4–5, valvate in bud, spreading or reflexed; **stamens** 4–5, inserted near the base of the tube, filaments pilose at the base, anthers linear, exserted or included; **ovary** 2-locular, with 1 ovule pendulous from apex of each locule, stigmas 1 or 2. **Fruits** drupaceous, fleshy to leathery, usually white at maturity, laterally compressed and rounded in outline (in Central America) or oblong-cylindrical when dried, with 2 pyrenes; **seeds** pendulous and laterally compressed.

Key to the Species of *Chiococca*

- 1a. Stamens usually well exserted at anthesis (with the filaments sometimes visible); corolla often campanulate-urceolate in Costa Rica; inflorescences usually with opposite branching, flowers sessile or with pedicels to 3 mm long; secondary veins obscure on the undersides of the leaves, petioles 10–30 mm long; (2700–)1600–2200 m elevation *C. phaenostemon*
- 1b. Stamens included within the corolla tube or only the tips exserted; corolla usually funnel-form; inflorescences with few alternate or opposite lateral branches, pedicels 1–6 mm long; secondary veins visible on the lower leaf surfaces, petioles 3–17 mm long; 0–1200(–1500) m elevation ... 2
- 2a. Hypanthium/ovary with thin erect hairs 0.1–0.3 mm long (rarely glabrous); leaves densely to sparsely puberulent beneath with thin straight hairs 0.2–0.3 mm long; inflorescences 2–4 cm long [petioles 1–4 mm long] *C. semipilosa*
- 2b. Hypanthium/ovary glabrous or with a minute (0.05 mm) papillate-puberulence; leaves glabrous or sparsely papillate-puberulent beneath; inflorescences (2–)4–10 cm long 3
- 3a. Leaves usually ovate-elliptic and drying grayish or greenish, rarely more than 4 cm broad, petioles 3–8 mm long; corolla 4–8 mm broad distally when open, calyx lobes narrow; fruit strongly compressed *C. alba*
- 3b. Leaves usually oblong-elliptic and drying dark brown, often more than 5 cm broad, petioles 5–17 mm long; corolla 7–10 mm broad distally when open, calyx lobes broadly rounded or obscure; fruit only slightly compressed laterally *C. pachyphylla*

***Chiococca alba* (L.) Hitchcock**, Ann. Rept. Missouri Bot. Gard. 4: 94. 1893. *Lonicra alba* L., Sp. Pl. 175. 1753. Figure 36.

Woody climbers, shrubs or less often small trees to 8 m tall and 10 cm trunk diam., distal branches often pendulous or clambering, distal twigs often opposite and held perpendicular to the main stems, leafy branchlets 0.7–4 mm thick, glabrous and terete, dark when dried;

A genus of about 20 species, ranging from the southern United States through Mexico, Central America, and the West Indies to southern South America.

Chiococca is recognized by its often pendant clambering branches, the very short stipules slightly united above the petioles (and usually with an awn), and the unusual white fruit flattened on opposite sides and rounded in outline (in Central American species). The ribbed and valvate corolla, the filaments free to the base of the corolla tube, the two-locular ovary with solitary pendulous ovules, and the white drupaceous fruits are also important distinguishing characters.

All our species are wide-ranging and quite variable; this may make them difficult to separate in the absence of flowers, since the fruit differ little among the species. In fact, the patterns of variation are so broad as to suggest that there may be hybridization between the species.

stipules 1–5 mm long, the broad basal part 0.5–2 mm long and slightly (0.5 mm) united above the petioles (intrapetiolar), with an acuminate or caudate tip 0.5–3 mm long. **Leaves** distant along the stems, petioles 3–8 mm long, 0.5–1 mm broad, glabrous; **leaf blades** (2.5–)3–9(–13) cm long, (1–)1.5–3.8(–6) cm broad, ovate-elliptic, narrowly ovate, oblong or lanceolate, apex long-acuminate (sometimes bluntly acute to short-acuminate), base obtuse to rounded and slightly decurrent on petiole, leaves drying stiffly chartaceous to membranaceous, gla-

brous above and below or with a few thin hairs ca. 0.2 mm long beneath, 2° veins 3–5/side and weakly loop-connected distally. **Inflorescences** mostly axillary, (2–)4–11 cm long, unbranched and racemiform or with few lateral branches and panicate, peduncles (0.5–)1–3.5(–7) cm long, ca. 0.5 mm thick, usually glabrous, bracts 1–1.5 mm long, narrow, the flowers usually borne along 1 side of the rachis, solitary and separate or in groups of 3, pedicels 1–8 mm long, slender, usually glabrous. **Flowers** with hypanthium 1–1.8 mm long, flattened laterally on opposing sides, ellipsoid in outline, glabrous or very minutely (0.05 mm) papillate-puberulent, calyx tube 0.5–1 mm long, calyx lobes 0.2–0.6 mm long; **corolla** funnelform, white to yellowish or rose, usually glabrous externally, tube 3–8 mm long, 2–5 mm wide at apex, lobes 5 (4), 3–4 mm long, triangular; **stamens** 5, included or slightly exerted, anthers ca. 3 mm long; styles 5–8 mm long, exerted. **Fruits** 4–7 mm long, 4–7 mm broad, rounded-oblong (abruptly rounded at top and bottom) in outline and flattened laterally on the 2 opposite surfaces, white at maturity, persisting calyx ca. 1 mm long and 1.5 mm diam.

Common clambering shrubby plants along open forest edges and disturbed areas, in both evergreen rain forest areas and in seasonally deciduous forests, from sea level to 1300(–1500) m elevation. Flowering in March–October (mostly June–August); fruiting in June–March. The species ranges from the southernmost United States (Texas and Florida), through Mexico, Central America, and the West Indies into tropical South America.

Chiococca alba is recognized by the clambering stems, the smaller often ovate to lanceolate leaves, the usually few-branched axillary inflorescences, funnelform usually yellowish white flowers, and white flattened fruit with round outline and persisting calyx. Most collections are glabrous, but a few have minute puberulence on the young stems, inflorescence, and hypanthium. The disc-like whitish seeds may have inspired two names used in Central America for the species: *lágrimas de María* and *lágrimas de San Pedro*.

Chiococca pachyphylla Wernham, J. Bot. 51: 323. 1913. Figure 36.

Lianas and woody climbers (rarely shrubs?), 1–5(–7) m tall, leafy branchlets 1–5 mm thick, glabrous, terete and drying dark or grayish; **stipules** 1–3 mm long, subacuminate to caudate at apex, slightly (0.2–0.5 mm) united above the petioles. **Leaves** well spaced along the stem, petioles 5–17 mm long, 0.6–1.2 mm broad, glabrous; **leaf blades** 6–12 cm long, 3–6 cm broad, oblong-elliptic to elliptic or ovate-elliptic, apex bluntly acute to short-acuminate, base acute to obtuse and slightly decurrent on petiole, drying stiffly chartaceous to subcoriaceous, glabrous above and below, 2° veins 3–5/side, the secondaries usually darker than the lower surface and easily

seen. **Inflorescences** 4–8 cm long, mostly axillary and with few lateral branches, the distal axes racemose, bracts 1–2 mm long, linear, pedicels 1.5–4.5 mm long, glabrous. **Flowers** glabrous externally, hypanthium 1.5–2 mm long, calyx tube 0.5–1 mm long, calyx lobes 0.1–0.4 mm long, rounded or bluntly triangular, glabrous; **corolla** funnelform, yellowish, corolla tube 5–7 mm long, gradually expanded to apex and 1–3 mm broad, lobes 2–3.5 mm long, 1.5–2 mm broad at the base, bluntly acute; **stamens** included. **Fruits** 6–8 mm long, 6–8 mm broad, broadly ellipsoid-circular to circular in outline, ca. 2 mm thick, green becoming white, glabrous, persisting calyx ca. 1 mm high and 1.5 mm diam.

Shrubs and climbers of evergreen and deciduous forest formations, from near sea level to 1500 m elevation. Flowering primarily in May–September; fruiting in August–December. The species ranges from northeastern Mexico to Costa Rica.

Chiococca pachyphylla is recognized by its more consistently vining habit, stiff usually oblong-elliptic leaves, lack of pubescence, racemose inflorescence branches, and flattened white fruit. The secondary veins on the lower leaf surfaces are much easier to see than in *C. phaenostemon*, and the flowers and fruit appear to be a bit larger than those of *C. alba*. In addition, *C. pachyphylla* has a number of characteristics that appear to be intermediate between *C. alba* and *C. phaenostemon*. Considerable variation in inflorescence and flower morphology adds to the difficulty.

Chiococca phaenostemon Schlectend., Linnaea 9: 594. 1834. Figure 36.

Shrubs or small trees (lianas), 3–14 m tall, often with separate trunks from the base, leafy stems 1.5–6 mm thick, glabrous, slightly quadrangular at first but becoming terete, older nodes conspicuously thicker than the internodes; **stipules** 2–4 mm long, the broad base 1–2 mm long, united around the stem for ca. 0.5 mm, with a narrow awn 0–2 mm long, the awn often breaking off to leave a shallow persisting cup at the older node. **Leaves** somewhat clustered at the ends of stems, petioles 7–30 mm long, 0.7–1.5 mm broad, glabrous; **leaf blades** (4–)6–13 cm long, (1.2–)1.5–4.8 cm broad, elliptic to elliptic-oblong, narrowly oblong (rarely elliptic-obovate), apex gradually tapering and cuneate or acuminate, base tapering gradually and obtuse or acute, decurrent on petiole, leaves drying stiffly chartaceous to subcoriaceous, glabrous above and below, 2° veins 5–8/side and usually obscure on the lower surface, weakly loop-connected distally. **Inflorescences** axillary or terminal, 3–12 cm long, panicate with 3–4 primary branches (and 2–3 of these with secondary branches) peduncles to 4 cm long, ca. 1 mm thick and sparsely papillate-puberulent, bracts 1–2 mm long, flowers often in cymes, pedicels 0.3–3 mm long. **Flowers** with hypanthium 1.2–2 mm long, 0.7–1.3 mm wide, glabrous, calyx tube ca. 0.5 mm long, calyx lobes 0.5 mm long; **corolla** usually campanulate to ur-

ceolate in Costa Rica (less often funnellform), white to yellowish, glabrous, tube 3–5(–6) mm long, 4–6 mm diam. at the mouth, lobes 5, 2–4 mm long, 1.5–3 mm broad at the base; anthers ca. 3 mm long, half to fully exerted. **Fruits** 5–6 mm long, 5–6 mm broad, broadly oblong or broadly obovate in outline, flattened on 2 sides (said to be thicker and rounded in northern Central America), persistent calyx 1–1.5 mm long and 1.5 mm diam., pedicels to 3 mm long.

Trees of evergreen montane forest formations, from (?700–)1600 to 2100 elevation (to 2500 m in Guatemala). Flowering in July–September; fruiting in July–August and January–February. The species ranges from northeastern Mexico to the Chiriquí Highlands of Panama.

Chiococca phaenostemon is characterized by its highland habitat, larger and campanulate corollas (in Costa Rica), and the often exerted anthers. The glabrous often long-petiolate leaves with decurrent base and the secondary veins usually obscure beneath also help to distinguish this species. While a very distinctive plant in the wild, some specimens of this species may be difficult to separate from *C. pachyphylla* and *C. alba*. The common name is *chiraquilla*.

Chiococca semipilosa Standl. & Steyerl., Publ. Field Mus. Nat. Hist., Bot. Ser. 22: 279. 1940. Figure 36.

Shrubs, 1–3(–4) m tall, leafy branchlets 1–3 mm thick, minutely puberulent with thin erect whitish hairs 0.1–0.2 mm long, soon glabrescent, terete; **stipules** 2–4 mm long, broad basal part 0.5–1 mm long, little (0.2–0.5 mm) united above the petiole, the narrow awn 1–3 mm long, minutely puberulent. **Leaves** with petioles 1–4 mm long, 0.5–1 mm broad, with lateral margins continuous with the lamina margins, minutely puberulent; **leaf blades** (1–)3–7.5(–12) cm long, (0.5–)1–2.5(–3) cm broad, narrowly ovate, ovate-lanceolate or ovate-elliptic, tapering gradually to the acute or acuminate tip, base acute to obtuse and decurrent on petiole, leaves drying stiffly chartaceous, glabrous to sparsely puberulent above with thin whitish hairs 0.2–0.3 mm long, sparsely to densely soft pubescent beneath with hairs 0.1–0.4 mm long, 2° veins 2–4/side, weakly loop-connected near the distal margin. **Inflorescences** axillary, 2–4 cm long, cymose or racemose with 3–9 flowers (rarely umbellate), peduncles 4–10 mm long, pedicels (0–)1–3(–5) mm long, puberulent. **Flowers** 5-parted, hypanthium 1–1.5 mm long, 0.7–1 mm broad, little differentiated from the pedicel, densely puberulent, calyx tube obscure, calyx lobes 0.5–1 mm long, acute and drying with little puberulence distally; **corolla** cream white to yellowish, broadly funnellform, usually minutely puberulent externally, tube 4–5 mm long, 1.5 mm diam. at the base to 3 mm near apex, lobes 1.5–2.8 mm long, 1.5–2 mm broad at the base; **stamens** included. **Fruits** 5–6 mm long, 4–5 mm broad, rounded in outline and flattened longitudinally, with thin erect

hairs ca. 0.2 mm long, persisting calyx 0.7–1.5 mm long, 1.8 mm broad, drying dark in contrast to the pale fruit.

Shrubs of evergreen and deciduous forest formations, from 200 to 1600 m elevation. Flowering in June–July; fruiting in September–January. The species ranges from Belize and Guatemala to northwestern Costa Rica.

Chiococca semipilosa is distinguished by the short thin hairs on the hypanthium/ovary, the pubescence on the lower leaf surfaces, the short few-flowered inflorescences, and the prominent calyx lobes that often dry dark. There is the possibility that material placed here is no more than an unusual form of *C. alba*. The figure is based on the Guatemalan holotype (Steyerl 31406 F).

Chione DeCandolle

Trees or shrubs, glabrous or glabrescent; **stipules** united (interpetiolar and intrapetiolar) and forming a cap over the shoot apex, leaving a scar across the stem and on the adaxial base of the petioles, small, caducous. **Leaves** petiolate; **leaf blades** often coriaceous, entire and pinnately veined, domatia present or absent. **Inflorescences** terminal, solitary or 3 at a distal node, paniculate with opposite branching and cymose or corymbose in form, pedunculate, bracteolate, flowers pedicellate. **Flowers** bisexual and radially symmetrical, apparently monomorphic, hypanthium turbinate, calyx lobes 5 or 6 or undeveloped and the distal margin undulate; **corolla** funnellform, white or yellowish, corolla tube short, glabrous within, corolla lobes 5(–6), broadly imbricate in bud with 2 exterior; **stamens** 5(–6), inserted above the base of the tube, filaments thick, anthers dorsifixed, exerted; **ovary** 2-locular, ovules solitary in each locule, pendulous from apex, style stout, stigmas 2, oblong, exerted. **Fruits** drupaceous, ovoid to ellipsoid, pyrene solitary and 2-locular; **seeds** elongate, the testa membranous.

A genus of about 15 species; fewer than 6 species are found in southern Mexico and Central America; the others occur in the West Indies. The genus is distinguished by its glabrous parts, cap-like stipules (in some species), terminal inflorescences, short corolla tubes with broadly imbricate corolla lobes (in bud), and the fleshy fruits with two-locular pyrene (stone). The genus *Oregandra* is a synonym; Standley misinterpreted the ovules when he described that genus.

Chione sylvicola (Standl.) W. Burger, Selbyana 12: 138. 1991. *Chomelia sylvicola* Standl., J. Wash. Acad. Sci. 18: 182. 1928. *Oregandra panamensis* Standl., Publ. Field Columb. Mus., Bot. Ser.

4: 265. 1929. *Anisomeris sylvicola* (Standl.) Standl., N. Amer. Fl. 32: 225. 1934. *Chione costaricensis* Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 22: 111. 1940. *Chione panamensis* Steyerl., Ceiba 3: 19. 1952. *Chione allenii* L. O. Williams, Phytologia 25: 462. 1973. Figure 36.

Shrubs or trees, (2)–6–15(–23) m tall, leafy branchlets 1–5 mm thick, glabrous, drying reddish brown to gray; stipules 3–8 mm long, obtuse, glabrous, drying dark, stipule scar crossing the stem between the leaf bases and 1–2 mm high on the adaxial side of the petioles, caducous. Leaves with petioles (5)–9–24 mm long, 0.7–1.8 mm thick, glabrous, usually sulcate above; leaf blades 6–17(–21) cm long, 2–7(–10) cm broad, elliptic-oblong, to ovate-elliptic or ovate-oblong, apex bluntly obtuse to acuminate, tip to 1 cm long, base abruptly rounded to obtuse or acute, often decurrent on petiole when acute, drying stiffly chartaceous and pale yellowish green to dark brown, glabrous above and below or with slender hairs or pits (domatia) in the vein axils beneath, 2° veins (3)–4–9/side. Inflorescences, solitary and terminal (but sometimes the lower branches subtended by smaller leaves and appearing to be axillary), 5–12 cm long, 3–8 cm broad, glabrous, peduncles 1.5–4 cm long, bracts ca. 1 mm long, subulate, pedicels 2–10 mm long and not clearly distinguished from the hypanthium. Flowers 10–12 mm long, glabrous externally, aromatic, hypanthium 3–4 mm broad at apex, calyx lobes 0–0.5 mm high, ca. 1.5 mm broad, carinose, broadly rounded; corolla white, glabrous, somewhat fleshy, tube 3–6 mm long, 2–4 mm diam., lobes 5, 2–3 mm long, 3–5 mm broad, broadly imbricate in bud, rounded distally; anthers 3–4 mm long and 0.7 mm thick, exserted. Fruits 14–22 mm long, 7–11 mm diam., ellipsoid or curved, often narrowed below the persisting calyx, red to purple (black) at maturity, persisting calyx 1–2 mm long.

Trees, less often shrubs, of evergreen rain forest formations on both the Caribbean and Pacific slopes, from near sea level to 2000 m elevation. Probably flowering and fruiting throughout the year (flowering mostly in February–June). The species ranges from southeastern Nicaragua to central Panama (but see below).

Chione sylvicola is recognized by the lack of pubescence on both vegetative and reproductive parts (except for the pubescent domatia in vein axils), unusual glabrous stipules, terminal inflorescences, versatile exserted stamens and narrowly ellipsoid fleshy red to black fruits. Specimens of this species are occasionally mistaken for species of *Neea* (Nyctaginaceae). The species concept adopted here is a broad one. The type of *C. costaricensis* (A. Smith 1778 F) came from 825 m on the Caribbean slope and has leaves intermediate between the smaller-leaved collections from the highlands and the larger-leaved lowland collec-

tions. The specimens of *Oregandra panamensis* (Cooper & Slater 144 the type, F, and 149 F) have unusually large leaves, and they may represent the same individual. The type of *C. allenii* (Allen 5321 F) has the larger leaves with greater number of secondary veins and pubescent domatia characteristic of other collections from the Golfo Dulce area. The type of *C. panamensis* (Hagen & Hagen 2137 F) is from 2000 m elevation in the Province of Chiriquí, and the leaves have minute pit domatia beneath. It may be that the species should be divided into subspecific elements or that we are mistaken in placing all this material under a single name (see Dwyer, 1980, p. 92). The type of *Chomelia sylvicola* (Standley & Valerio 49196 US) is a smaller-leaved high-elevation (2000 m) specimen with only a few leaves and fruits.

Chomelia Jacquin

Shrubs or small trees, axillary spines present in some species, branchlets terete; stipules interpetiolar, acuminate, persistent or deciduous. Leaves opposite, petiolate, entire, venation pinnate, domatia present in some species. Inflorescences solitary, axillary, pedunculate or sessile, with few to many flowers, cymose or congested and subcapitate, bracts present, bracteoles free or united. Flowers bisexual and radially symmetrical, white or yellowish white, hypanthium turbinate to oblong, calyx lobes 4(–5?), narrow and elongate, equal or unequal; corolla salverform to funnelform, with a narrow elongate tube, usually sericeous externally, usually glabrous within, corolla lobes 4(–5?), valvate or imbricate in bud, lobes with or without appendages at apex externally (abaxially); stamens 4, sessile on the throat of the corolla tube, anthers linear to sagittate, dorsifixed, included or slightly exserted, basal lobes acute to obtuse; ovary 2(–3)-locular, with 1 ovule pendulous from apex of each locule, style filiform with 2(–3) short stigmas. Fruits drupaceous, small, ellipsoid, the pyrene bony, solitary and 2-locular, with persisting calyx lobes; seeds usually 2, cylindrical, pendulous.

A genus of ca. 50 species in Central and South America, and with more than 300 species in the Old World tropics (but these are sometimes placed under *Tarenna*). Species without appendages on the corolla lobes and obtuse basal anther lobes formerly placed in the genus *Anisomeris* are here considered as part of *Chomelia*, following prevailing opinion. Some species of *Guettarda* (without spines), *Rondeletia* (capsular fruits), and *Sabicea* (vines with baccate fruits) resemble our species of *Chomelia*; the axillary flower and inflorescences, long slender sericeous corolla tubes, and narrow corolla lobes help to distinguish *Chomelia*.

Key to the Species of *Chomelia*

- 1a. Leaf blades with the smallest (4°) veins subparallel within areoles defined by the tertiary (3°) veins, or the 3° and 4° veins parallel between the secondaries 2
- 1b. Leaf blades with the smallest (4°) veins not parallel within areoles defined by the tertiary (3°) veins, 3° and 4° veins usually reticulate 4
 - 2a. Leaf blades with both the 3° and 4° veins subparallel and at right angles to the secondary veins; corolla tubes 6–8 mm long; spines absent; plants of the wet evergreen Caribbean slopes, 600–900 m elevation *C. venulosa*
 - 2b. Leaf blades with the 4° veins subparallel within areoles defined by the 3° veins; corolla tubes 12–40 mm long; spines often present; 0–1200 m elevation 3
 - 3a. Flowers borne in pedunculate cymose inflorescences; trees of deciduous and semideciduous forest formations *C. spinosa*
 - 3b. Flowers solitary or several in leaf axils, sessile or pedicellate, never cymose; trees of evergreen forest formations 0–900 m elevation *C. recordii*
- 4a. Flowers subsessile in leaf axils and at the apex of short shoots; petioles 2–5 mm long, leaf blades to 9 cm long *C. recordii*
- 4b. Flowers borne on pedunculate inflorescences in the axils of leaves; petioles 2–10 mm long, leaf blades to 15 cm long *C. microloba*

Chomelia microloba J. D. Smith, Bot. Gaz. 31: 114. 1901. *Anisomeris microloba* (J. D. Smith) Standl., Publ. Field Columb. Mus., Bot. Ser. 4: 293. 1929. *Antirhea panamensis* Standl., N. Amer. Fl. 32: 264. 1934. *Chomelia panamensis* (Standl.) Dwyer, Ann. Missouri Bot. Gard. 67: 100. 1980. *Chione chambersii* Dwyer & Hayden, Ann. Missouri Bot. Gard. 54: 138. 1967. *Chomelia peninsularis* Dwyer, Ann. Missouri Bot. Gard. 67: 101. 1980. Figures 33–34.

Shrubs or small trees, 1.8–15 m tall, leafy branchlets 1.3–3 mm thick, with thin straight ascending hairs 0.5–2 mm long, glabrescent, spines absent; stipules 2–8 mm long, ca. 2 mm broad at the base, triangular-cuspidate, with thin straight hairs, persisting with the leaves. Leaves often closely clustered distally, petioles 2–18(–50?) mm long, 0.5–1.3 mm thick, with curved hairs along the adaxial margins and glabrescent; leaf blades 4–12(–18) cm long, 2–6(–8) cm broad, narrowly to broadly ovate-elliptic, to elliptic, oblong or slightly obovate, apex usually acuminate or with a bluntly triangular tip ca. 1 cm long, base acute to obtuse, drying stiffly chartaceous, dark brown or dark green above, glabrous or sparsely pubescent above and below, usually with small (0.5–1 mm) pubescent domatia in the vein axils beneath, 2° veins 4–7/side, tissue between the secondary veins smooth when dry (the minor venation not prominent). Inflorescences 3–10 cm long, to 7 cm broad, with 12–70 flowers, peduncles 2–6 cm long, 0.3–1 mm thick, appressed-pubescent or glabrous, with a terminal flower and 2 lateral branches or with 3 1° branches and dichotomous 2° branches, pedicels 0–1 mm long. Flowers appressed-pubescent or occasionally glabrous externally, 8–12 mm long, hypanthium 1.2–2 mm long, 0.5–0.9 mm diam., cylindric or turbinate, glabrous, calyx lobes 0.2–0.5 mm long, obtuse; corolla 7–10 mm long, white, tubular-funnel-form, sparsely to densely appressed-pubescent exter-

nally, tube 7–10 mm long, 0.3–1 mm diam. in the middle, lobes ca. 3 mm long, narrowly ovate and obtuse; anthers 1.2–2 mm long; stigma ca. 1 mm long. Fruit 10–17 mm long, 4–8 mm diam., oblong to oblong-obovoid, fleshy, glabrous and drying black, rounded or truncated at apex, calyx deciduous, longitudinal ribs absent or weakly developed.

An uncommon species in evergreen lowland rain forest formations of the Pacific lowlands in Costa Rica, to ca. 500 m elevation. Flowering in February–May; fruiting in July–August. The species ranges from southwestern Costa Rica to Colombia.

Chomelia microloba is recognized by the small axillary inflorescences with dichotomous branching and subsessile flowers along one side, the minute calyx lobes, narrow corolla tube, and leaves with pubescent domatia. The leaves of the type (*Tonduz 9874* F, from Sto. Domingo de Golfo Dulce) are quite small, and they appear to be atypical for the material placed here. The much longer (to 15 cm) and broader (to 8 cm) leaves of the type of *C. peninsularis* (*Croat 22440* F, MO, from the Burica peninsula) are probably more characteristic of the species. The pubescence can differ greatly in different collections, with some flowers being quite glabrous and others appressed sericeous.

Chomelia recordii Standl., Trop. Woods 7: 9. 1926. *C. englesingii* Standl., Trop. Woods 16: 45. 1928. *Anisomeris recordii* (Standl.) Standl., N. Amer. Fl. 32: 227. 1934. *A. englesingii* (Standl.) Standl., N. Amer. Fl. 32: 227. 1934. Figure 34.

Shrubs or trees to 10 m tall, leafy branchlets 0.7–3 mm thick, with straight or crooked strigulose hairs 0.2–0.5 mm long, becoming gray and glabrescent, spines present or absent, 7–27 mm long; **stipules** 3–5 mm long, triangular and acute, pubescent, usually persisting. **Leaves** with petioles 2–5 mm long, 0.5–1 mm thick, with straight or crooked ascending hairs ca. 0.5 mm long; **leaf blades** (2–)3–9 cm long, 2–4.5 cm broad, ovate to ovate-elliptic or ovate-orbicular, apex acute to obtuse or slightly acuminate, base obtuse to rounded and subtruncate, drying thin-chartaceous, dark brown above, glabrous above or with hairs above the midvein, puberulent beneath with straight thin hairs 0.4–0.8 mm long, 2° veins 4–7/side, vein axils with dense clusters of hairs (domatia) beneath. **Inflorescences** of subsessile flowers in the leaf axils or terminal on short lateral shoots, usually 2 flowers per node (1–6), with stipule-like bracts and narrow villose bracteoles. **Flowers** ca. 30 mm long, white, hypanthium 1–2 mm long, densely villous with straight yellowish white hairs, calyx lobes 3–6 mm long, narrowly acute; **corolla** cream white to greenish white, tube 15–20(–24) mm long and 0.5–1 mm diam., with thin whitish ascending hairs 1–1.5 mm long, lobes 5–7(–15) mm long and 1–1.5 mm broad; anthers sessile, ca. 2.8 mm long, attached ca. 2 mm below apex of the tube; style linear, ca. 17 mm long, stigmas ca. 1.5 mm long, narrowly oblong. **Fruits** to 14 mm long (including calyx), 3–4 mm diam., oblong or oblong-obovoid, body of the fruit 8–9 mm long, dull red and often turning blue-black, with thin whitish ascending hairs, the persistent calyx 4–5 mm long.

Trees and shrubs of evergreen rain forest formations on both the Caribbean and Pacific slopes, from near sea level to 1200 m elevation. Flowering in April–June and August; fruiting in February, April, and November. Collections have been made in the Caribbean slope and lowlands, the General valley, and the Golfo Dulce area in Costa Rica. The species ranges from Guatemala to Colombia.

Chomelia recordii is recognized by the few sessile flowers and fruit, the narrow calyx lobes, the long slender corolla tube, and the relatively short broad leaves. The 4° veins are usually parallel within the areolae defined by the 3° veins, but this cannot be seen in some specimens.

Chomelia spinosa Jacq., Enum. Pl. Carib. 12. 1760.

Ixora spinosa (Jacq.) Lam., Encyc. Méth. Bot. 3: 344. 1789. *C. filipes* Benth. in Oerst., Vidensk. Meddel. Dansk. Naturhist. Foren. Kjobenhavn 1852: 41. 1852. *Guettarda costaricensis* K. Schum. ex Tonduz, Bull. Herb. Boissier 2: 7. 1895 (nomen). Figure 34.

Shrubs or small trees, 1.5–6(–9) m tall, straight woody spines often present on older stems, axillary and 1–4 cm long, ca. 2.5 mm wide near the base, terete, leafy branchlets 1–4 mm thick, densely puberulent with thin whitish

hairs 0.4–1 mm long, terete, becoming gray; **stipules** 4–8 mm long, ca. 2 mm broad at the base, triangular-subulate, puberulent, scarious, usually persisting. **Leaves** often crowded at the ends of branchlets, petioles 5–20 mm long, ca. 0.5 mm thick, densely puberulent; **leaf blades** 3.7–9 cm long, 2–5 cm broad, ovate-elliptic, to broadly elliptic-oblong, ovate-orbicular or slightly obovate, apex acute to short-acuminate, base acute to obtuse or slightly rounded and subtruncate, often decurrent on petiole, drying chartaceous and dark brown above, sparsely puberulent above with hairs ca. 0.4–0.6 mm long, sericeous beneath with thin whitish hairs (especially dense on the major veins), 2° veins (3–)4–7(–8)/side, strongly ascending, the minor (4°) veins subparallel with in areolae defined by the 3° veins. **Inflorescences** (1.2–)3–7 cm long, axillary, peduncles 12–45 mm long, ca. 0.5 mm thick, densely puberulent, flowers in small distal clusters of 3–7(–15) near apex of the peduncle. **Flowers** sweetly aromatic, hypanthium 2–3 mm long, ca. 1 mm diam., densely sericeous with whitish ascending hairs, calyx lobes 0.5–1 mm long, slightly unequal; **corolla** yellowish white, sericeous externally, tube 12–18(–24) mm long, 0.5–1 mm diam., lobes 4–7 mm long, 1–3 mm broad, glabrous along the edges and within (adaxially), with a short appendage near apex; filaments very short, anthers ca. 3.5 mm long, sagittate at the base, disc about 0.6 mm long; styles 14–17 mm long, stigmas ca. 1 mm long, exserted. **Fruits** sessile, 6–9(–12) mm long, 3–6 mm diam., sparsely puberulent or glabrous, becoming black.

Common shrubs and trees of deciduous and partly deciduous forest formations on the Pacific slope of Costa Rica, from near sea level to about 500 m elevation. Flowering in late June–August in Costa Rica; fruiting in June–December in Central America, with a peak of fruiting in November in Costa Rica. The species ranges from southern Mexico and Guatemala, along the Pacific coast of Central America to Colombia, Venezuela, and northern Brazil.

Chomelia spinosa is recognized by its restriction to deciduous and partly deciduous vegetation, the straight woody spines (not usually present on distal flowering branches), small cymose inflorescences on slender axillary peduncles, flowers with long slender corolla tube, and short flowering season. The minor venation is quite distinctive with the 4° veins parallel only within small areoles defined by the 3° veins, with the result that the 4° veins of adjacent areoles often are not parallel with each other. The species has been called *limoncillo*, *malacaguité*, and *malacahuité*.

Chomelia venulosa W. Burger & C. M. Taylor, sp. nov. Figure 34.

Arbores 10–25 m altae, ramulis juvenibus sericeis; stipulis 11–18 mm longis. Foliae lamina elliptica vel

oblongo-elliptica, 6–15 cm longa, 3–7 cm lata, venis lateralibus 5–7, venulis parallelis. Inflorescentiae axillares, ad 9 cm longae, pedunculo ca. 22 mm longo, ramis saepe dichotomis, floribus secundis. Flores puberuli, hypanthio 1–2 mm longo; corolla alba vel crema, tubo 6–9 mm longo, lobis 4. Fructus 13–15 mm longi.

TYPUS—*E. Bello 414* (holotypus CR, isotypi F, MO), from Reserva Biológica Monteverde, Alajuela, Costa Rica.

Trees, 10–25 m tall, to ca. 35 cm dbh, leafy stems 1–4 mm thick, sericeous or strigulose with ascending pale grayish hairs ca. 0.4 mm long; **stipules** 11–18 mm long, to 4 mm broad, lanceolate with an acute apex, sericeous at the base and along the midrib. **Leaves** with petioles (6–)12–23 mm long, 0.8–2 mm thick, sericeous with pale grayish hairs; **leaf blades** 5–15 cm long, 3–7 cm broad, elliptic to elliptic-oblong, apex short-acuminate with tip 5–8 mm long, base obtuse to acute, drying stiffly chartaceous, dark brown above, much paler beneath, glabrous or very sparsely pubescent above with thin whitish hairs to 1 mm long, appressed-pubescent beneath with thin hairs ca. 0.3 mm long and densely sericeous along the major veins, 2° veins 4–7/side, both the 3° and 4° veins at right angles to the secondaries, depressions (domatia?) sometimes present in the vein axils. **Inflorescences** solitary and axillary (2/node), ca. 5 cm long, to 9 cm in fruit, cymose with 2 lateral simple or bifid secund branches, peduncles 22–45 mm long and 1 mm thick, ascending sericeous, distal flowers along 1 side of the branch, bracts absent, flowers sessile. **Flowers** pubescent externally, hypanthium 1–2 mm long, 1 mm diam., calyx tube minute, 1.4–2 mm diam., calyx lobes 0.2–0.8 mm high; **corolla** tubular, yellow or yellowish white, fluted distally, tube 6–9 mm long, 0.8–1.5 mm diam., densely sericeous, lobes 4, 1–2 mm long, 1–2 mm broad; **stamens** 4, anthers ca. 3.5 mm long; style ca. 5 mm long, stigmas 1.2 mm long. **Fruits** 13–15 mm long, 8–9 mm thick, obovoid-oblong, with 6–8 longitudinal ribs, becoming dark brown, glabrous, persistent calyx ca. 1 mm long, pyrenes ca. 14 × 8 mm; **seeds** ca. 10 × 1 mm.

Plants of the wet evergreen forests of the Caribbean slope of Costa Rica, at 600–900 m elevation. Flowers were collected in May; fruits were collected in October–November. The species is known from below Monteverde, Alajuela (84°43'W), and the southern Cordillera de Talamanca, Limón (82°59'W). Collections in addition to the type are *Bello 172 & 872*, *Bello & Cruz 457*, *Herrera 3310*, and *Poveda 24*.

Chomelia venulosa is recognized by its parallel minor venation, sericeous flowers on short inflorescences with two simple or bifid lateral branches, and restricted altitudinal range on the Caribbean slope. The two-celled deeply ridged pyrenes, the subimbricate to valvate corolla aestivation, and the parallel minor venation suggest that this species is best placed in *Chomelia*, as opposed to *Guettarda*. It may be allied to the “*Anisomeris*” group of *Chomelia* species with appendages on the

corollas. The overall appearance of the leaves is similar to that of *Chomelia panamensis*, but the minor venation is quite unusual. The 3° and 4° veins are little differentiated, parallel to each other, and usually perpendicular to the 2° veins.

Cinchona Linnaeus

Trees of medium height or occasionally shrubs, branchlets terete or tetragonal; **stipules** interpetiolar, triangular, often large, collectors present within at the base, caducous or rarely persisting. **Leaves** opposite, often large, petiolate; **leaf blades** with entire margins, coriaceous to chartaceous, domatia absent. **Inflorescences** terminal and solitary (apparently axillary when lateral branches are subtended by reduced leaves), open-paniculate, usually large and many-flowered, branching mostly opposite. **Flowers** bisexual, small in most species, aromatic, often puberulent externally, hypanthium turbinate, calyx tube with small calyx lobes (rarely with the calyx tube entire distally); **corolla** salverform to funnellform, white to pink or purplish, corolla tube terete or slightly 5-angled, glabrous or pilose in the throat; corolla lobes 5 (4, 6), spreading, valvate in bud; **stamens** 5, inserted in the corolla tube, filaments short or long, anthers linear dorsifixed, included or their apices exerted; **ovary** 2-locular, placentas attached to the septum and spongy, ovules many in each locule, peltately attached and imbricated, style narrow, stigmas short and obtuse, included or slightly exerted. **Fruits** woody capsules, 2-locular, subcylindrical to ovoid or oblong, dehiscing septicidally from bottom to top; **seeds** many, peltate, thin and flat, testa with a broad thin peripheral wing.

A genus of 20–40 poorly defined species, ranging from Costa Rica southward to Bolivia, mostly along the Andes mountains. The capsules opening upward from the base helps separate *Cinchona* from closely related genera, such as *Ladenbergia* and *Joosia*. This genus has played an important role in the history of medicine as the source of the antimalarial drug quinine. The major commercial sources of quinine are cultivars of *Cinchona calisaya* Wedd. grown in Indonesia, which originated from the eastern slopes of the Andes. Species of the genus were introduced and have become naturalized in Guatemala (see the discussion in Standley & Williams, 1975, p. 38).

Cinchona pubescens Vahl, Skr. Naturhist. Selsk. Kjobenhavn 1: 19. 1790. Figure 37.

Small or medium-sized **trees**, (3–)5–20 m tall, trunks 8–30 cm dbh, bark pale brown and roughened, leafy branchlets 3–8 mm thick, distinctly 4-angled, minutely puberulent or glabrous; **stipules** 4–12(–20) mm long, 3–8(–12) mm broad at the base, glabrous or minutely ap-

pressed-puberulent, deciduous. **Leaves** with petioles (9–)12–35(–60) mm long, 1.3–2.5 mm thick, sparsely and minutely (0.2 mm) puberulent; **leaf blades** 10–32(–40) cm long, 7–17(–26) cm wide, broadly ovate to broadly elliptic-oblong or suborbicular, apex broadly obtuse to subacuminate, base abruptly cuneate to rounded and subtruncate, usually slightly decurrent on petiole, drying stiffly chartaceous or chartaceous, glabrous or very sparsely puberulent above, sparsely pubescent beneath with slender hairs ca. 0.3 mm long, 2° veins 7–12/side. **Inflorescences** terminal or axillary to distal leaves, 9–40 cm long, 8–24 cm broad, open paniculate with few opposite widely spaced (3–11 cm) branches, distal branches minutely tomentulose, the flowers in congested distal clusters, pedicels 0.5–3 mm long. **Flowers** white, cream, or pale pink, densely tomentulose externally, hypanthium 2–3 mm long, 1.3–2 mm diam., calyx tube 1–2(–3) mm long and 2–3 mm diam., calyx lobes 0.2–1 mm long, acute; **corolla** 15–16 mm long and funnellform, tube 10–13 mm long, 1.4–2 mm diam., glabrous within, lobes 5, lanceolate to oblong, 3–5 mm long and 1.5–2.5 mm wide, tomentulose externally and villous on the interior margins; **stamens** 5, filaments ca. 2 mm long, anthers 2.5–3 mm long; style 6–13 mm long, glabrous. **Fruits** subcylindrical to narrowly oblong, 12–35(–50) mm long, 6–9 mm diam., glabrescent or minutely (0.1 mm) puberulent, brown, lustrous yellowish brown within; **seeds** 5–12 mm long, 1.5–3 mm broad, flat and oblong-elliptic in outline, with a thin membranaceous winged margin, surfaces reticulate and the margin erose, dark center of the seed 1.8–3 mm long.

Trees of evergreen forest formation on both the Caribbean and Pacific slopes of Costa Rica, ranging from (500–)800 to 1700 m elevation. Flowering mostly in June–September, with solitary collections in November, February, and March; fruiting in February and November–December in Costa Rica. The species is apparently rarely encountered in southern Central America. Our collections come mostly from the Caribbean slopes of the Cordillera de Tilarán and the Central Highlands in the Provinces of Alajuela and Heredia. In Panama the species is known only from the Chiriquí Highlands. This species ranges southward to Venezuela, Peru, and Bolivia.

Cinchona pubescens is recognized by the larger often broadly rounded leaves, large terminal in-

florescences with small puberulent flowers in distal clusters, the narrow woody two-locular capsules, and the seed with a thin elongated membranous wing. The flowers are said to have the aroma of *Gardenia* or *Cananga odorata* (Annonaceae). The rarity of this species in southern Central America suggests that it is not native, and collections may represent relicts of native pre-Columbian introduction.

Coccocypselum P. Browne,
nomen conservandum

Herbs, annual or perennial, prostrate and creeping to erect-ascending, usually pubescent with multicellular hairs; **stipules** interpetiolar, sometimes reduced to a very short (0.2 mm) rim, small and simple with a single subulate lobe (2/node) and with 0 or 2–8 smaller lateral awns, persisting. **Leaves** petiolate, entire, domatia absent. **Inflorescences** terminal or pseudoaxillary, usually solitary, capitate with (1–)3–20 flowers, sessile or pedunculate, bracts and bracteoles small, flowers sessile. **Flowers** bisexual, monomorphic or distylous, small, calyx lobes 4, narrow and persistent; **corolla** blue to purple or white, funnellform, corolla lobes 4, valvate in bud; **stamens** 4, filaments borne on the tube of the corolla, anthers dorsifixed below the middle or near the base; **ovary** 2-locular, the placentas borne on the center of the septum, ovules many and horizontal, style with 2 short branches. **Fruits** baccate and arenchymatous, often mealy and hollow, globose to obovoid, bright blue; **seeds** many and small, angled or flattened.

A Neotropical genus of 10–20 species, ranging from Mexico and the West Indies into South America. The genus is recognized by its herbaceous habit, usually broad puberulent leaves, small capitula with few flowers, four-parted flowers, two-locular ovaries, and blue fruit with many small seeds. These plants are often confused with species of *Geophila*. *Coccocypselum lanceolatum* is our most distinctive species; the others may be difficult to distinguish.

Key to the Species of *Coccocypselum*

- 1a. Leaf blades with 8–13 pairs of secondary veins, narrower than long, ovate-triangular to lanceolate and usually acute at the apex; with 8–10 flowers in each inflorescence [1000–2000 m elevation] *C. lanceolatum*
- 1b. Leaf blades with 5–6 pairs of secondary veins, usually about as broad as long, ovate to ovate-lanceolate, acute to rounded at the apex; with 2–6 flowers in each inflorescence 2
- 2a. Inflorescences sessile in the axils of leaves; plants of evergreen lowlands, 0–1000 m elevation *C. herbaceum*

- 2b. Inflorescences pedunculate; plants of evergreen lowland and highlands, 0–2000 m elevation ... 3
 3a. Leaf blades rounded and cordate or subcordate at the base, often wider than long [1400–2000 m elevation] *C. cordifolium*
 3b. Leaf blades acute to obtuse or truncated at the base, usually as wide as long and ovate to broadly elliptic 4
 4a. Stems and leaves with hairs 0.5–1 mm long (or occasionally glabrous); calyx lobes 3–4 mm long; stipules ca. 5 mm long; common in Central America *C. hirsutum*
 4b. Stems and leaves with hairs 0.1–0.3 mm long; calyx lobes 1.5–2.7 mm long; stipules 2–4 mm long; not known from Costa Rica (key based on Steyermark, 1972) *C. guianensis*

Coccocypselum cordifolium Nees & Mart., Nova Acta Phys.-Med. Acad. Caes. Leop.-Carol. Nat. Cur. 12: 14. 1824. *Geophila pleuropoda* J. D. Smith, Bot. Gaz. 52: 50. 1911. *Geocardia pleuropoda* (J. D. Smith) Standl., Contr. U.S. Natl. Herb. 17: 445. 1914. *Tontanea pleuropoda* (J. D. Smith) Standl., N. Amer. Fl. 32: 148. 1921. *C. pleuropodum* (J. D. Smith) Standl., Publ. Field Columb. Mus., Bot. Ser. 4: 281. 1929. *C. rothschuhii* Loessner, Bot. Jahrb. Syst. 60: 370. 1926. Figure 2.

Herbs, prostrate or creeping, leafy stems 0.4–1.6 mm thick, hirsute or villous with thin straight or crooked hairs 0.5–1.5 mm long; **stipules** 1.5–3 mm long, united only at the base (ca. 0.2 mm) and with 2 narrowly linear awns on each side (4/node). **Leaves** with slender petioles 4–28(–55) mm long, villous or pilose with thin hairs; **leaf blades** 11–35 mm long, 12–42 mm broad, ovate to ovate-orbicular or ovate-reniform, apex rounded and bluntly obtuse (and usually minutely apiculate), base rounded at the cordate to subtruncate base, drying membranaceous or thin-chartaceous, sparsely to densely pubescent, the hairs 1–1.7 mm long on the upper surface and ca. 0.7 mm long beneath, 2° veins 3–5/side. **Inflorescences** axillary, usually only 1/node, 1.4–5 cm long, the capitulum less than 1 cm long and with 3 (2, 4) flowers, peduncles 4–38 mm long, villous, bracts ca. 4 mm long, linear, flowers sessile. **Flowers** with hypanthium ca. 1 mm long, with thin whitish hairs, calyx lobes 1.5–2.5 mm long, linear-lanceolate, sparsely villous; **corolla** lavender, lilac, pale blue, or whitish, tube 4–6 mm long, 2–3 mm diam. at apex, sparsely puberulent externally, lobes 3.3–5 mm long, 1.2–2 mm broad at the base, narrowly triangular to oblong. **Fruits** 5–6 mm long, 4–5 mm diam., ovoid, blue, densely villous and with the persisting calyx 2–3 mm long; **seeds** 0.2–0.5 mm diam.

Plants of evergreen lower montane rain forest formations, from 1000 to 1600 m elevation (to 2000 m in Guatemala). Rarely collected in Costa Rica's major highlands. Probably flowering and fruiting throughout the year. The species ranges from Mexico to Panama, and it is also found in eastern and southern Brazil.

Coccocypselum cordifolium is recognized by the usually subcordate or truncated leaf bases, the small

pedunculate heads with only two to four blue flowers, and the long hairs on the upper leaf surface. This species appears to be rare or overlooked in Costa Rica and Panama. This species is easy to confuse with *Geophila cordifolia*, which has one- or two-seeded red fruits.

Coccocypselum guianense (Aubl.) K. Schum. in Mart., Fl. Bras. 6(6): 315. 1889. *Tontanea guianensis* Aubl., Hist. pl. Guiane 1: 108, pl. 42. 1775.

According to Steyermark (1972), this species is distinguished from similar species by its short (1.5–2.7 mm) calyx lobes, short (0.2–0.5 mm) dense indumentum on stems and inflorescences, smaller (3–4 mm) stipules, and slightly longer (5.5–9 mm) corolla tubes. The species is said to range from Florida and the West Indies to Venezuela and the Guianas (Steyermark, 1972; Hortus Third, 1976). These plants have been used in ornamental horticulture as a ground cover and in hanging baskets. Because of these uses, it is likely that escaped populations have become established in some areas. We have not seen material that can be definitively ascribed to *C. guianense* from Costa Rica.

Coccocypselum herbaceum P. Browne, Civ. Nat. Hist. Jam. 144, pl. 6. 1756; also cited as Aublet, Hist. pl. Guiane 1: 68. 1775 (fide Adams, 1972); Lam., Encycl. 2: 56. 1786 (fide Standley & Williams, 1975). *C. repens* Sw., Prodr. 31. 1788 (not *C. repens* H.B.K. 1819, not *Condalia repens* Ruiz & Pav. 1798). *Tontanea herbacea* (P. Browne) Standl., N. Amer. Fl. 32: 147. 1921. *T. hispidula* Standl., loc. cit. 147. 1921. *C. hispidulum* (Standl.) Standl., Publ. Field Columb. Mus., Bot. Ser. 4: 281. 1929.

Herbs, procumbent or trailing, leafy stems 0.7–2 mm thick, sparsely to densely pilosulous with erect or ap-

pressed hairs 0.2–1.2 mm long; **stipules** with linear awns 3–4 mm long, ca. 0.5 mm broad at the base (2 larger awns per node), lateral lobes none or 2–4 and 0.5–1 mm long, puberulent. **Leaves** with petioles 6–27 mm long, 0.4–1 mm thick, sparsely to densely pubescent; **leaf blades** 2–5.5 cm long, 1–3.5 cm broad, ovate to ovate-oblong or ovate-triangular, apex obtuse and sometimes with a small (0.5 mm) apiculate tip, drying membranaceous to thin-chartaceous, with short (0.3 mm) or long (1–2 mm) hairs on the upper surface, glabrous or pilose beneath with hairs to 1.2 mm long, 2° veins 5–8/side. **Inflorescences** sessile or subsessile in the leaf axils (rarely with peduncles to 6 mm long), to 1 cm long, usually with 3–(6) sessile or subsessile flowers, bracts 2–3 mm long, linear. **Flowers** monomorphic, hypanthium densely hirtellous, calyx lobes 2.5–4.5 mm long, linear-lanceolate, sparsely pubescent; **corolla** dark blue to purple or with a white tube, tube 5–8 mm long, corolla 1–2 mm long, acute. **Fruits** becoming 11 mm long (not including the calyx) and 8–10 mm diam., globose or ovoid, deep blue, persisting calyx ca. 3 mm long; **seeds** 0.5–1.3 mm long, smooth or rugose, flattened and angular or lenticular.

Plants of evergreen or partly evergreen forest formations in the central highlands and in the Caribbean lowlands, from near sea level to 900 m elevation. Probably flowering throughout the year. The species ranges throughout the American tropics.

Coccocypselum herbaceum is recognized by the small sessile groups of blue flowers, creeping habit, bright blue fruit, and thin ovate leaves. This species is very similar to *C. hirsutum*, which has pedunculate inflorescences, but *C. herbaceum* is not as common in Central America. It seems possible that the two may prove to be conspecific, with *C. herbaceum* having priority.

Coccocypselum hirsutum Bartling ex DC., Prodr. 4: 396. 1830. *Tontanea hirsuta* (Bartling ex DC.) Standl., N. Amer. Fl. 32: 147. 1921. *C. glabrum* Bartl. ex DC., Prodr. 4: 397. 1830. *Tontanea glabra* (DC.) Standl., J. Wash. Acad. Sci. 15: 104. 1925. *C. hirsutum* var. *glabrum* (Bartl. ex DC.) L. O. Williams, Phytologia 25: 462. 1973. Figure 2.

Herbs, prostrate or creeping, leafy stems 0.5–2 mm thick (not including the pubescence), usually densely villous or hirsute with pale yellowish hairs 0.5–1.5 mm long; **stipules** with narrow linear awns 3–5 mm long, ca. 0.3 mm broad at the base, sparsely to densely puberulent. **Leaves** with petioles 4–16(–20) mm long, 0.4–0.8 mm thick, usually densely pubescent; **leaf blades** 2–4 cm long, 1.4–2.6 cm broad (to 6 × 4 cm in northern Central America), ovate to ovate-triangular or ovate-oblong, apex obtuse and often with a slightly (0.4 mm) apiculate tip, base obtuse to rounded and truncate, drying membranaceous to thin chartaceous and often dark green or dark

brown above, with thin straight or crooked hairs 1–1.5 mm long on the upper surface, the hairs somewhat shorter beneath except along the midvein, 2° veins 6–8/side. **Inflorescences** 1–2.5 cm long, capitula 1–1.5 cm broad, usually 3-flowered (rarely with 1–5 flowers), peduncles 3–24 mm long, bracts ca. 5 mm long and 0.5 mm broad, with slender hairs. **Flowers** with hypanthium ca. 1.5 mm long, densely villous, calyx lobes 3–4 mm long, 0.5–1 mm broad, sparsely pubescent; **corolla** blue, white, or white with purple markings, tube 5–7 mm long, 1.5–2 mm diam. near the mouth, corolla lobes 2–4 mm long and 1.5 mm broad, triangular; anthers ca. 1.5 mm long. **Fruits** 9–20 mm long, 7–12 mm diam., ovoid to broadly ellipsoid, blue or purplish blue, with spongy exocarp; **seeds** lenticular, 1–1.5 mm broad, rugose, brown.

Plants of evergreen forest formations, from 500 to 2500 m elevation. Probably flowering and fruiting throughout the year. It ranges from Mexico to South America (but see below).

Coccocypselum hirsutum is distinguished by its low creeping habit, hirsute (less often glabrous) rounded leaves, pedunculate heads of few flowers, and blue fruits. The plants placed here may not be specifically distinct from *C. herbaceum*, which is the earlier name. Peduncle length seems to vary greatly on the same plant, with subsessile and long-pedunculate capitula nearby. We agree with Williams (in Standley & Williams, 1975) that the glabrous elements of this complex do not deserve specific recognition (see synonymy above).

Coccocypselum lanceolatum (Ruiz & Pav.) Pers., Syn. Pl. 1: 32. 1805. *Condalia lanceolata* Ruiz & Pav., Pl. Fl. Peruv. 1: 54. 1798. *Coccocypselum repens* H.B.K., Nov. gen. sp. 3: 316. 1819 (not *C. repens* Sw. 1788). *Coccocypselum canescens* Willd. ex Cham. & Schlechtend., Linnaea 4: 139. 1829. *Tontanea canescens* (Cham. & Schlechtend.) Standl., N. Amer. Fl. 32: 146. 1921. Figure 2.

Herbs, prostrate to erect, 10–40 cm tall, leafy branches 1–3 mm thick, densely pubescent with whitish or pale grayish hairs 0.2–0.8 mm long; **stipules** with central awns 3–6 mm long, 0.5–1 mm broad at the base, narrowly linear for most of their length, pubescent. **Leaves** with petioles 7–22 mm long, 0.5–1 mm thick, densely pubescent; **leaf blades** 3–9 cm long, 1.5–4 cm broad, ovate-triangular to ovate-oblong or triangular-oblong, apex gradually tapering and acute (rarely obtuse), usually shortly (0.3 mm) apiculate at the tip, base obtuse to subcordate, drying membranaceous or thin-chartaceous, with thin appressed hairs ca. 0.5 mm long and parallel with the secondary veins, 2° veins 7–11/side. **Inflorescences** 2–5 cm long, capitula ca. 1 cm diam., globose, usually with more than 8 flowers and the flowers tightly congested, peduncles (6–)10–55 mm long, 0.5–1 mm

thick, densely pubescent, bracts 1–3 mm long (often difficult to see). **Flowers** with the hypanthium ca. 3 mm long, densely pubescent with hairs ca. 1 mm long, calyx lobes unequal, 2–4 mm long and 0.7–2 mm broad; **corolla** blue to bluish purple, lilac, or white marked with blue, tube ca. 2 mm long, lobes ca. 3 mm long and 1–2 mm broad; anthers ca. 1 mm long. **Fruits** 8–15 mm long, 6–10 mm diam., ovoid to ellipsoid, bright blue, pilose, persisting calyx ca. 3 mm long; **seeds** angular to tetrahedral, 0.8–1.3 mm broad, with minutely rugose surface.

Plants of partly deciduous or evergreen (but seasonally dry) forest formations, 1000–2000 m elevation. Probably flowering throughout the year (mostly in January–July). The species ranges from Guatemala through Central America to Bolivia and Brazil.

Coccocypselum lanceolatum is recognized by its narrower leaves with more numerous secondary veins, somewhat taller erect stems, dense whitish or grayish pubescence, globose heads with more than eight densely packed flowers, bluish corollas, and bright blue fruits. This is our most distinctive species of *Coccocypselum*.

Coffea Linnaeus

Shrubs or small trees, branchlets subterete, often held horizontally, usually glabrous; **stipules** interpetiolar, triangular, often persisting. **Leaves** opposite or verticillate, decussate or somewhat distichous, petiolate or subsessile; **leaf blades** entire, chartaceous to coriaceous, mostly glabrous, domatia often present. **Inflorescences** of clustered subsessile or short-pedicellate flowers in leaf axils, bracts present and united to form a short cup at the base of the pedicel. **Flowers** bisexual, monomorphic, usually radially symmetrical, white to pink, hypanthium subcylindrical to turbinate, calyx tube short, truncate to dentate or lobed, calyx lobes usually 5, small; **corolla** salverform or funnelform, corolla tube short or long, glabrous or villous at the throat, corolla lobes 4–8, oblong or obtuse, convolute in bud; **stamens** usually 5 (4–8), inserted in the throat of the tube, filaments short or none,

anthers linear, included or exserted; **ovary** 2-locular, with 1 ovule in each locule attached to the middle of the septum, style slender and glabrous, with 2 narrow stigmas (= style branches). **Fruits** drupaceous, oblong to subglobose or ovoid, exocarp fleshy or dry, with 2 woody nutlets (pyrenes) covered by a chartaceous or coriaceous endocarp (the “parchment”); pyrenes 2 (the “nutlets” or “beans”), convex abaxially and flattened and deeply grooved on the inner (adaxial) face, oblong in outline; **seeds** ellipsoid.

A tropical Old World genus of about 40 species, mostly African. This genus is the source of coffee, one of the most important agricultural commodities in world trade. *Coffea arabica* is the primary and the preferred source of coffee beans; see the discussion in the Flora of Guatemala (Standley & Williams, 1975, pp. 44–48). The quality of the coffee beans is dependent on the environment in which the plants grow, the ripeness of the fruit, methods of gathering and drying, and the final roasting of the beans (cf. J. W. Purseglove, Tropical crops: Dicotyledons, vol. 2: 458–482. 1984). Only two species are likely to be encountered in Costa Rica, and they are keyed and described below. In addition, *Coffea canephora* Pierre ex Froehner, Notizbl. Königl. Bot. Gart. Berlin 1: 237. 1897 (*C. robusta* Linden, Cat. pl. nouv. hort. colon. 11. 1900), which grows well at lower elevation and is rust-resistant, may be encountered. It produces a quality of bean intermediate between *C. arabica* and *C. liberica*. “Robusta” plants can be distinguished from “arabica” by their larger (12–40 cm) leaves, rounded at the base, 8–17 pairs of secondary veins, and more corrugated surface. It is an important source of coffee in India and Indonesia. This and many other important *Coffea* cultivars have been grown for many years at the Centro Agronómico Tropical de Investigación y Enseñanza (CATIE) near Turrialba.

Key to the Common Species of Coffea

- 1a. Flowers with 5 corolla lobes; leaf blades to 15(–18) cm long, pit domatia 0.1–0.3 mm broad, usually circular *C. arabica*
- 1b. Flowers with 6–8 corolla lobes; leaf blades to 24(–30) cm long, pit domatia 0.2–0.7 mm broad, circular to elongate *C. liberica*

Coffea arabica L., Sp. Pl. 172. 1753.

Shrubs or small trees to 8 m tall, branches often held horizontally or slightly drooping, leafy branchlets 1–4 mm thick, glabrous, nodes usually well spaced (4–7 cm)

and thickened (dried); **stipules** 3–7(–12) mm long, 2–5 mm broad, triangular to subulate, glabrous, deciduous. **Leaves** with petioles 6–12(–15) mm long, 1–1.6 mm thick, glabrous; **leaf blades** 8–15(–18) cm long, 2.5–6(–7.5) cm broad, elliptic-oblong to elliptic-obovate, apex acuminate to caudate-acuminate, tip 1–2 cm long, base obtuse

to acute, drying chartaceous to subcoriaceous, glabrous above and below, 2° veins 7–10/side, minute (0.2–0.3 mm) domatia often present at the vein axils beneath. **Inflorescences** axillary, subcapitate or appearing verticillate, ca. 5 cm long (including the corollas), with 1–9 flowers per axil, flowers subsessile. **Flowers** 12–20 mm long, white, calyx lobes 5, minute, **corolla** white, tube 10–14 mm long, lobes 14–20 mm long; anthers exserted, 8–12 mm long. **Fruits** 10–16 mm long, 8–13 mm diam., oblong and abruptly rounded at apex and base, green becoming red (drying dark), glabrous, calyx scar 2–3 mm broad; pyrenes ca. 10 × 7 × 3 mm, planoconvex.

Cultivated or rarely persisting in evergreen and partly deciduous formations, 800–2000 m elevation. The flowering season is primarily in February, with fruiting in November–December. This species, probably native to western Ethiopia, is now cultivated throughout the tropics.

Coffea arabica is recognized by its glossy dark green leaves (in life), lack of pubescence, axillary clusters of aromatic white flowers, and distinctive two-seeded fruit. This species is only occasionally found outside of cultivation; birds and bats have been described as dispersal agents. In addition to the stimulant caffeine, coffee beans contain glucose, dextrin, proteins, and the flavor-enhancing volatile oil caffeol. Cultivation in cooler temperatures at higher elevations (ca. 1000–2000 m) is an important factor in producing high-quality coffee (*café*), and this may account for the excellent reputation of Costa Rica's most valuable export crop.

Coffea liberica Bull ex Hiern., Trans. Linn. Soc., Ser. 2, 1: 171, t. 24. 1876. *C. excelsa* A. Chev., Rev. cult. colon. 12: 258. 1903.

Shrubs or small trees to 5(–15) m tall, leafy branchlets 1.8–8 mm thick, glabrous; **stipules** 3–6 mm long, 4–8 mm broad. **Leaves** with petioles (4–)8–24 mm long, 1.5–4 mm thick, glabrous; **leaf blades** (8–)12–24(–30) cm long, (4–)5–12 cm broad, elliptic-oblong to elliptic-obovate, apex bluntly obtuse to bluntly short-acuminate, base obtuse to acute, drying subcoriaceous, glabrous above and below, 2° veins 7–10/side, pit domatia 0.2–0.8 mm long at the vein axils beneath and often with a few short hairs. **Inflorescences** 2–5 cm broad, with ca. 5–10 flowers, bracts 3–8 mm long, narrowly elliptic to lanceolate. **Flowers** 6–8-parted, 25–35 mm long, corolla tube 10–14 mm long and ca. 1.5 mm diam., lobes 8–12 mm long, 2–3 mm broad; anthers to 6 mm long. **Fruits** 1.2–2.5 cm long, oblong-rotund, yellowish red.

Cultivated or escaped trees of evergreen forest formations, from near sea level to 1200 m elevation. This species is native to coastal West Africa and is now found cultivated around the world.

Coffea liberica is recognized by its larger leaves, glabrous parts, white axillary flowers, and distinctive fruit. Unlike *C. arabica*, which is essentially a highland species, *C. liberica* grows well at lower elevations. While *C. liberica* is more disease-resistant and can do well at lower altitudes, the seeds (beans) produce coffee of inferior flavor, and the species is not an important crop in Central America.

Condaminea DeCandolle

Shrubs or small trees, usually with few branches and large leaves; **stipules** interpetiolar and intrapetiolar, united above the leaf base to form a short sheath and with a broad distal 2-parted blade (sometimes appearing as 4 free stipules at each node), persisting. **Leaves** opposite and large, sessile or short-petiolate; **leaf blades** entire, lacking domatia. **Inflorescences** terminal and solitary, open panicle with cymose or corymbose distal branching, usually with 3 branches at apex of the peduncle (lateral branches equaling the continuing rachis), bracts small, bracteoles absent, pedicels short or none. **Flowers** bisexual, large, hypanthium turbinate to campanulate, calyx lobes 3–5 or none and the calyx tube entire, **corolla** funnellform to salverform, thick-fleshy, corolla tube barbate in the throat, corolla lobes 4–5, valvate in bud, glabrous; **stamens** 5, filaments inserted in the upper half of the tube, puberulent at the base, anthers narrow, sagittate at the base, exserted; **ovary** 2-locular, ovules many in each locule from axile placentas, style narrow, stigmas oblong, exserted. **Fruits** woody capsules, pyriform to turbinate, truncated at apex with a circular calyx scar, with loculicidal basipetal dehiscence forming 2 valves; **seeds** minute, attached horizontally, testa reticulate.

A genus of four or five species ranging from Costa Rica to Venezuela, Peru, and Bolivia. The large, often subsessile leaves, deeply two-parted stipules, lack of pubescence, very large terminal open-branched inflorescences, greenish flowers, and woody bivalved capsules with hundreds of minute seeds make this a distinctive genus.

Condaminea corymbosa (Ruiz & Pav.) DC., Prodr. 4: 402. 1830. *Macrocnemum corymbosum* Ruiz & Pav., Fl. Peruv. 2: 48, pl. 189. 1799. Figure 29.

Shrubs or small trees, 2–5(–7) m tall, leafy branchlets 4–12 mm thick, essentially glabrous; **stipules** apparently free and 4/node, united above the leaf base to form a short (1–4 mm) sheath adnate to the stem (but difficult to see), the free distal parts equal and 2–6(–9) cm long, 6–9(–12) mm broad, lanceolate, reddish brown, glabrous or rarely minutely puberulent, with many parallel strong-

ly ascending secondary veins, persisting. **Leaves** with petioles 0–8 mm long, usually hidden by the auriculate leaf base, glabrous; **leaf blades** 15–35(–50) cm long, 6–14(–21) cm broad, obovate-oblong to oblanceolate-oblong or oblong, apex abruptly narrowed and short-acuminate, base gradually narrowed and slightly auriculate or subcordate, drying subcoriaceous, glabrous, 2° veins 15–19/side, the minor (4°) venation raised beneath and forming a subreticulate (“wrinkled”) surface. **Inflorescences** open panicles with opposite primary branching, 20–45 cm long and 15–28 cm broad, to 60 cm long in fruit, primary peduncle 15–23 cm long, 4–12 mm thick, primary branches 7–15(–25) cm long, secondary branches 1–6 cm long, distal branches minutely puberulent, bracts 1–3 mm long, pedicels 0–4 mm long. **Flowers** 2–3 cm long, hypanthium 3–9 mm long, 3–5 mm diam., not differentiated from the pedicel, calyx tube 3–6 mm long and 4–6 mm broad, lobes 4, 5, or none, usually minute (0–0.5 mm); **corolla** salverform, white with purplish tube, slightly fleshy, tube 10–15 mm long, 3–5 mm diam., greenish white within, lobes 4–5, 6–10 mm long, 3–4 mm broad, oblong and rounded distally, becoming reflexed, glabrous; **stamens** 5, anthers 4–7 mm long, ca. 1.3 mm broad; **ovary** 2-locular, style 15–25 mm long, stigmas 2, 3–5 mm long and 0.7 mm thick, ellipsoid. **Fruits** 10–18 mm long, 6–10 mm wide, obovoid to oblong-turbinate, drying brown with longitudinal veins slightly raised, with a pale circular distal calyx scar 0.6 mm broad and 7–8 mm diam., glabrous or minutely puberulent; **seeds** 0.5–1 mm long, 0.2–0.4 mm thick.

Small (?short-lived) treelets or large shrubs of evergreen forest formations, between 10–500 and 1800 m elevation. This species has not been collected below 300 m in Costa Rica. Flowering in January–April and October; fruiting in January–April. In Costa Rica this species has been collected only near Turrialba, around the General Valley–Coto Brus region. The species ranges to Venezuela, Peru, and Bolivia.

Condaminea corymbosa is recognized by the very large subsessile leaves usually auriculate at the base, the lack of pubescence on most parts, the large terminal inflorescences (often with three equal branches from apex of the peduncle), the woody two-valved capsules with minute seeds, and characters of the genus (see above). What appear to be four large and distinct stipules at each distal node also help to distinguish this species and genus.

Key to the Species of *Cosmibuena*

- 1a. Leaf blades mostly 1.5–3.5(–4) cm wide, narrowly obovate or oblanceolate, apex obtuse, drying coriaceous and reddish brown to cinnamon brown; corolla tube and exterior of lobes white marked with pink [capsules 40–100 mm long; 700–2300 m elevation] *C. valerii*
- 1b. Leaf blades 2.5–10 cm broad, elliptic to oblong, apex obtuse to acute, drying coriaceous or subcoriaceous and grayish green; exterior of corolla tube and lobes pale green to white 2

Cosmibuena Ruiz & Pav.,
nomen conservandum

REFERENCE—C. M. Taylor, Revision of *Cosmibuena* (Rubiaceae: Cinchoneae). Ann. Missouri Bot. Gard. 79: 886–900. 1992.

Small **trees** or shrubs, epiphytic or less often terrestrial, stems glabrous and often succulent, becoming terete; **stipules** interpetiolar and partly intrapetiolar, forming a cap over the shoot apex in early stages, obovate to oblanceolate and with many parallel veins, caducous. **Leaves** decussate, petioles short and thick; **leaf blades** entire, often coriaceous (semisucculent in life), domatia absent. **Inflorescences** terminal, solitary, with few (3–11) cymose flowers or the flowers solitary, bracts resembling the stipules, flowers pedicellate. **Flowers** bisexual, usually large and fragrant at night, monomorphic, glabrous externally, hypanthium turbinate to cylindrical, calyx tube deciduous (circumscissile) or persistent (often varying within a species), calyx lobes 5–6(–7) and subequal to strongly unequal; **corolla** salverform and carnos, white or tinged with pink (turning yellow or brown when old), corolla tube long and slender, corolla lobes 5–6(–7), convolute or imbricate in bud, rounded distally; **stamens** 5–6, filaments short and attached near apex of tube, anthers basifixed and sagittate, included; **ovary** 2-locular, ovules many in each locule and borne on axile placentas, vertical and imbricated, style long and slender, often puberulent distally, stigmas 2 and papillate within. **Fruits** cylindrical capsules, woody and often with conspicuous white lenticels, dehiscent septically from apex into 2 valves, pericarp often separating from the papery endocarp; **seeds** many, elliptic and flattened, surrounded by a papery or membranaceous marginal wing, arose to fimbriate along the edge.

A genus of four species ranging from southern Mexico to Peru. The large somewhat fleshy flowers with long tubes, the glabrous coriaceous leaves, the unusual stipules, the long narrow capsules with many winged seeds, and the epiphytic habit distinguish this genus. These plants may be difficult to distinguish from species of *Hillia* (seeds with hairs), *Ladenbergia* (terrestrial, valvate corolla lobes), and *Posoqueria* (fleshy globose fruits).

- 2a. Capsules 40–65 mm long; leaf blades subcoriaceous to coriaceous, acute to obtuse at apex, secondary veins straight to curved; 200–1000 m elevation *C. grandiflora*
- 2b. Capsules 62–115 mm long; leaf blades coriaceous, obtuse to broadly rounded at apex, secondary veins straight; 0–500 m elevation *C. macrocarpa*

Cosmibuena grandiflora (Ruiz & Pav.) Rusby, Bull. New York Bot. Gard. 4: 368. 1907. *Cinchona grandiflora* Ruiz & Pav., Fl. peruv. prodr. 2: 54, pl. 198. 1799. *Cosmibuena skinneri* (Oerst.) Hemsley, Biol. centr. amer. Bot. 2: 12. 1881. *Buena skinneri* Oerst., Vidensk. Meddel. Dansk. Naturhist. Foren. Kjobenhavn 1852: 48. 1853. *Cosmibuena ovalis* Standl., Contr. U.S. Natl. Herb. 18: 137. 1916. Figure 28.

Trees or shrubs to 12 m tall, terrestrial or epiphytic, leafy branchlets 3–6 mm thick, glabrous, quickly becoming pale gray; **stipules** 8–30 mm long, to 12 mm broad, obovate to oblanceolate, the intrapetiolar tube forming $\frac{1}{4}$ – $\frac{2}{3}$ of the length (reduced below inflorescences), rounded apically, glabrous. **Leaves** with petioles (5–)10–40 mm long, 1.2–2 mm thick, drying dark; **leaf blades** 7–19 cm long, 4–12(–16) cm broad, broadly elliptic to broadly oblong or obovate, apex bluntly acute to obtuse or short-acuminate, base cuneate and slightly decurrent on petiole, drying stiffly chartaceous to subcoriaceous, dark brown or greenish brown above, glabrous above and below, 2° veins 3–7/side (in Costa Rica). **Inflorescences** with 3–5(–9) flowers, cymose to subumbellate, primary peduncle 5–30(–40) mm long, 2–3 mm diam., glabrous, pedicels (5–)10–20(–30) mm long and often merging imperceptibly into the calyx. **Flowers** 7–10 cm long, hypanthium 7–11 mm long, 4–6 mm diam., drying dark, calyx tube 3–9(–11) mm long, entire or with lobes 0–8 mm long; **corolla** white, tubular-salverform, tube 4–9(–10) cm long, 2.5–5 mm diam., lobes 5–6, (10–)20–35(–40) mm long, (6–)10–14(–20) mm broad, obovate; **stamens** 5–6, anthers 10–18 mm long; upper part of style densely puberulent, stigmas 4–7 mm long, greenish. **Fruits** (3–)4–6.5 cm long, 6–13 mm diam., oblong-cylindrical to oblong-ellipsoid; **seeds** 5–8 mm long, 0.5–1 mm broad, linear fusiform, with thin narrow wing, body of the seed 1–2 mm long.

Trees of evergreen forest formations, 50–1000 m elevation. Flowering in April and July–December; fruits were collected in March. This species ranges from southern Mexico to Peru.

Cosmibuena grandiflora is recognized by the general lack of pubescence, large fleshy flowers with long tubes, and unusual stipules. The thinner leaves drying dark above and with the secondary veins readily visible help to distinguish these plants from material placed under *C. macrocarpa*. This species is not often collected in southern Central America. The flowers are aromatic in the morning and late afternoon (Herrera 1072 CR).

Cosmibuena macrocarpa (Benth.) Klotzsch ex Walpers, Repert. bot. syst. 6: 69. 1846. *Buena macrocarpa* Benth., Bot. voy. Sulph. 104, t. 38. 1844. *C. paludicola* Standl., Contr. U.S. Natl. Herb. 18: 137. 1916. Figure 28.

Shrubs or small **trees** to 12 m tall, trunks to 25 cm dbh, epiphytic or terrestrial, leafy branchlets 3–7 mm thick, smooth and glabrous, becoming pale gray; **stipules** 12–24 mm long, 6–12 mm broad, forming a tube ca. $\frac{2}{3}$ of the length but later splitting, obovate to rounded-oblong, apex rounded to obtuse, glabrous and pale green drying reddish brown. **Leaves** with petioles 8–20(–25) mm long, 1.8–2.8 mm thick, glabrous; **leaf blades** 6–18 cm long, 2.5–8(–11) cm broad, obovate to obovate-oblong or subrotund-obovate, apex bluntly obtuse to rounded, base cuneate and slightly decurrent on petiole, drying coriaceous, often grayish, glabrous above and below (or puberulous along the midvein beneath in young leaves), 2° vein 4–5/side but difficult to see. **Inflorescence** terminal, subumbellate with 3–8 flowers, peduncles 6–15(–30) mm long, 2–4 mm diam. (peduncle and inflorescence rachis to 3 cm long), pedicels 7–20 mm long. **Flowers** 10–14 cm long, glabrous, hypanthium 6–15 mm long but not clearly differentiated from the pedicel, 2.5–4 mm diam., calyx tube 2–8 mm long, calyx teeth 0.5–4 mm long, triangular to minute; **corolla** salverform and fleshy, white or pale greenish, tube 5–9 cm long, 2.5–4.5 mm diam., lobes 5, 18–30 mm long, 9–12 mm diam., oblong; **stamens** 5, anthers 12–15 mm long, 1.5 mm wide, included; style exserted, stigmas 6–9 mm long, 1.8 mm broad. **Fruits** (4–)6–8(–12) cm long, 6–8 mm broad, linear-cylindrical to linear-oblongoid, brown, borne on pedicels 1–2 cm long, disc forming an elevated (2 × 2.5 mm) projection on the truncated apex of the capsule, surface glabrous and drying dark, often with elongate (3 mm) lenticels; **seeds** 5–9(–13) mm long and ca. 1 mm wide, thin, narrowly winged.

Trees of mangrove and evergreen lowland forest formations on the Caribbean slope, from near sea level to about 400 m elevation. In Costa Rica the species probably flowers April–November; fruiting in February–March and July–September. The species ranges from Costa Rica to Peru.

Cosmibuena macrocarpa is recognized by the large fleshy glabrous flowers with long tubes, coriaceous obovate leaves with rounded apices and obscure venation, long woody capsules with small winged seeds, and usually epiphytic habit. The name *Cosmibuena skinneri* (Oersted) Hemsley has been misapplied to this species in the past (cf. Croat, 1978; Dwyer, 1980).

Cosmibuena valerii (Standl.) C. M. Taylor, Ann. Missouri Bot. Gard. 79: 897. 1992. *Hillia valerii* Standl., J. Wash. Acad. Sci. 16: 164. 1928. *H. ligulifolia* Dwyer, Ann. Missouri Bot. Gard. 67: 218. 1980. *H. chiriquiensis* Dwyer, loc. cit. 216. 1980. Figure 27.

Shrubs or small trees, 2–15 m tall, usually epiphytic, leafy stems 2.5–7 mm thick, semisucculent, glabrous, drying reddish brown, older stems grayish; **stipules** 14–42 mm long, 6–15 mm broad, enlarged beneath the flowers, intrapetiolar and splitting along the sides, oblong to obovate, bluntly obtuse to rounded distally, becoming reddish, caducous. **Leaves** often closely clustered distally, petioles 3–12(–20) mm long, 1.5–3 mm thick, poorly defined because of the decurrent leaf margins, glabrous; **leaf blades** 3–8(–10) cm long, 1–3(–4) cm broad, narrowly obovate to narrowly obovate-oblong or oblanceolate, apex rounded to bluntly obtuse, base cuneate and decurrent on petiole, drying coriaceous and reddish brown to grayish green, glabrous above and below, 2° veins 3–6/side, strongly ascending but obscure. **Inflorescences** terminal, the flowers solitary, sessile or on peduncles to 3 mm long (and difficult to distinguish from the ovary base), bracts short (2–11 mm) and triangular or long (20–40 mm) and spatulate (enlarged stipules), caducous or persisting. **Flowers** to 12 cm long, glabrous externally, hypanthium 6–14 mm long, calyx lobes 4–18 mm long, 2–3 mm broad, triangular (when short) to narrowly lingulate (when long), obtuse or rounded distally; **corolla** salverform with a long tube, carinose, pale green to white, pink or reddish where exposed in bud, tube 4.7–9 cm long, 4–7 mm diam., lobes 5, 17–31 mm long, 10–18 mm broad, rounded distally; **stamens** 5, anthers 12–15 mm long; stigmas ca. 6 mm long. **Fruits** 4–10 cm long, 6–10(–14) mm thick, narrowly oblong or tubular, dark brown with scattered lenticels; **seeds** 5–6 mm long and ca. 0.5 mm broad, body of the seed 1.4–2 mm long, margins erose.

Plants of evergreen montane forest formations, from 700 to 2300 m elevation. Probably flowering and fruiting throughout the year. This species ranges from northwestern Costa Rica to central Panama.

Cosmibuena valerii is distinguished by its epiphytic habit, smaller narrowly obovate stiff leaves, long fleshy solitary flowers often marked with pink, and montane habitats. The foliage often dries a reddish brown. There are unusual variations in the development of both the calyx lobes and the floral bracts in this species, but neither seem important taxonomically. This species may be confused with *Cosmibuena macrocarpa* of lower el-

evations and with *Hillia tetrandra* with smaller flowers, more greenish leaves (when dried), and tufts of hairs at one end of the seed.

Coussarea Aublet

Shrubs or small trees, rarely dioecious, glabrous or less often puberulent, stems usually quadrangular in early stages but becoming terete; **stipules** interpetiolar (intrapetiolar and sometimes forming a cap over the shoot apex in a few species), obtuse to acute (never with aristate or subulate appendages), deciduous or persistent. **Leaves** opposite (rarely 3/node), petiolate or subsessile; **leaf blades** entire, domatia present in a few species. **Inflorescences** terminal, solitary, usually open panicate with opposite branching to elongate thyrsiform, racemiform, umbelliform or glomerulate, usually glabrous, flowers often in distal cymes, bracts absent or minute (< 1 mm), flowers sessile or pedicellate. **Flowers** bisexual (rarely unisexual), hypanthium turbinate or obconic or ovoid, calyx tube short and usually distally truncated (calyx lobes not clearly developed or with 3–5 small lobes); **corolla** salverform to tubular, white, corolla tube with glabrous throat, corolla lobes 4(–5), valvate in bud, oblong to elongate or triangular, often carinose; **stamens** 4(–5), borne near the mouth or near the base of the tube, anthers subsessile, linear, included or exserted; **ovary** 2-locular or incompletely 1-locular, ovules 2 and sometimes partly united, erect from a short basal column. **Fruits** fleshy, coriaceous or spongy drupes, usually longer than wide (ellipsoid to globose), usually with only 1 ovule developing, becoming blue-black or white; pyrene solitary (2), erect, without or with longitudinal ribs dorsally.

A Neotropical genus of about 100 species, with the largest number of species in South America. The genus is characterized by its usually single-seeded fruit, four-parted (less often five-parted) white flowers, often bright white inflorescences with minute bracts and bracteoles or lacking bracts entirely, and whitish infructescences. The inflorescences are rarely more than 15 cm long. The stipules are triangular to truncated and rarely bilobed. Many of our species have spongy tissues in the corolla and fruit; a number flower at night. Species of this genus can be very difficult to distinguish from some species of *Psychotria*, *Rudgea*, and *Faramea*. The pyrenes of *Psychotria* have hard walls with ridges, in contrast to the thin smooth walls of *Coussarea*. Closely similar species in these other genera are referred to under individual species below.

Key to the Species of *Coussarea*

- 1a. Leaf blades conspicuously pubescent beneath, at least along the major veins 2
- 1b. Leaf blades glabrous beneath, pubescent only in the vein axils beneath when domatia are present 4

- 2a. Calyx tube 7–12 mm long with lobes to 3 mm long; inflorescences with 3–15 distantly spaced flowers, ovary and fruit pilose *C. enneantha*
- 2b. Calyx tube 0.5–2 mm long with lobes to 1 mm long; inflorescences with 15–50 proximate flowers, ovary and fruit glabrous 3
- 3a. Leaf blades 11–28 × 5–15 cm; corolla tube 10–13 mm long, distinctly pubescent; in the Caribbean lowlands, 0–300 m elevation *C. hondensis*
- 3b. Leaf blades 6–19 × 3–8 cm; corolla tube ca. 9 mm long, glabrous or minutely puberulent; cloud forests, (600–)1200–2000 m elevation *C. austin-smithii*
- 4a. Leaves sessile, domatia of tufted hairs or pits often present along the midvein 5
- 4b. Leaves with petioles usually more than 4 mm long, domatia absent along veins beneath (rarely present in *C. chiriquiensis*) 7
- 5a. Corolla usually minutely sericeous, calyx tube 2–3 mm long; domatia usually narrow depressions along the midvein above the vein axils [leaf blades 7–18 × 3–9 cm; Caribbean lowlands of northern Costa Rica] *C. impetiolearis*
- 5b. Corolla glabrous or minutely papillate puberulent; calyx tube 1–2 mm long; domatia of shallow puberulent depressions in the vein axils or absent 6
- 6a. Inflorescences 3–10 cm long, paniculate with distinct lateral branches; leaf blades 7–16 cm long, domatia of puberulent pits in the vein axils; Caribbean lowlands of southernmost Costa Rica *C. sp. A aff. curvigemma*
- 6b. Inflorescences ca. 3 cm long, subcapitate (paniculate but with short, closely spaced, lateral branches); leaf blades more than 15 cm long, domatia present or absent; lowland rain forest *C. sp. B aff. curvigemma*
- 7a. Flowering portion of the inflorescences elongate-racemiform, distinctly longer than broad 8
- 7b. Flowering portion of the inflorescences open paniculate, corymbiform to umbelliform or pyramidal, usually with length equaling breadth 10
- 8a. Stipules narrowly oblong to linear, to 2 cm long and 4 mm thick, acute at the apex and *Ficus*-like, enclosing apices of stems or lateral branches in early stages; leaves usually less than 7 cm broad [corolla 15 mm long] *C. caroliniana*
- 8b. Stipules not linear or narrowly oblong, not resembling the stipules of *Ficus*, flattened and enclosing the shoot apex but quickly caducous; leaves usually more than 8 cm broad ... 9
- 9a. Calyx tube (limb) ca. 2 mm long; fruit 9–17 mm diam., ellipsoid to obovoid; leaf blades chartaceous, short- to long-acuminate, petioles to 15 mm long; stipules usually bluntly obtuse at apex *C. talamancana*
- 9b. Calyx tube 5–7 mm long; fruits 10–28 mm diam., ellipsoid-oblong; leaf blades subcoriaceous, short-acuminate or rounded at apex, petioles to 40 mm long; stipules usually broadly rounded distally *C. latifolia*
- 10a. Plants of montane cloud forest formations (600–)1200–2000 m elevation; stipules often persisting 11
- 10b. Plants of lowland evergreen formations, 0–600 m elevation; stipules usually caducous 13
- 11a. Corolla tube ca. 6 mm long [leaf blades 3–5 m broad, 5–7 major 2° veins] *C. chiriquiensis*
- 11b. Corolla tube 9–18 mm long 12
- 12a. Leaf blades 2–4 cm broad and 4–6 major 2° veins; Chiriquí Highlands, Panama *C. nebulosa*
- 12b. Leaves usually 3–8 cm broad and with 6–9 major 2° veins; Costa Rica . *C. austin-smithii*
- 13a. Leaves usually drying very dark or black, membranaceous to thin-chartaceous; flowers usually 4-parted; stipules often with 2 minute (0.3 mm) lobes on each side *C. nigrescens*
- 13b. Leaves usually drying greenish or brownish, usually stiffly chartaceous; flowers 5-parted; stipules various 14
- 14a. First node of the inflorescence usually with 4 lateral branches; fruits with 2 seeds, dorsal surface of seed with longitudinal ridges; corolla lobes 3–7 mm long; calyx lobes 0.3–1 mm long *Psychotria eurycarpa*
- 14b. First node of the inflorescence usually with 2 lateral branches; fruits usually single seeded (rarely 2-seeded), seed smooth on the dorsal surface; corolla lobes 6–20 mm long; stipules without lobes; calyx lobes present or absent *C. psychotrioides*

Coussarea austin-smithii Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 1286. 1938. *Psychotria tutensis* Dwyer, Ann. Missouri Bot. Gard. 67: 434. 1980. Figure 47.

Shrubs or small trees 3–6(–10) m tall, leafy stems 1.5–6 mm thick, glabrous or very minutely (0.05 mm) papillate in early stages, with thickened nodes and longitudinally striate (dried); **stipules** 4–8 mm long, 4–7 mm broad, triangular with an acuminate or narrowed apex, rarely with a small (0.5 mm) U-shaped sinus at the tip, glabrous, persisting or deciduous. **Leaves** opposite, petioles 8–30 mm long, 0.6–2 mm thick, glabrous or minutely puberulent; **leaf blades** (5)–7–19 cm long, (2)–3–8.5 cm broad, elliptic to narrowly elliptic-oblong, elliptic-obovate or narrowly ovate, apex acute to short-acuminate, base acute to obtuse and often slightly decurrent on petiole, drying chartaceous, dark green or dark brown above, glabrous above, glabrous or minutely (0.1–0.2 mm) puberulent on the veins beneath, 2° veins 6–9/side, without domatia. **Inflorescences** 5–10 cm long, equally broad, open panicle or umbelliform (3-branched, rarely with 4 branches from the first node), peduncles 12–20 mm long, 1–2 mm thick, glabrous or very minutely papillate-puberulent, primary branches 1–3 cm long and opposite or alternate, flowers cymose or in distal groups of (1) 2 or 3, bracts absent or minute (sometimes borne 3–7 mm up along the lateral branches), pedicels 0–8 mm long, purplish. **Flowers** fragrant, hypanthium 1–1.5 mm long, ca. 1.5 mm diam., obconic-tubular, glabrous, calyx tube 0.5–1 mm long and ca. 3 mm broad, broadly cupulate, calyx lobes to 0.5 mm high (and broadly triangular) or not developed and the calyx entire; **corolla** salverform, white, glabrous or minutely papillate-puberulent externally, tube 9–10 mm long (to 15 mm in life?), 1.2–2.2 mm diam., lobes 4(–5), ca. 7 mm long, 2 mm broad and fleshy, narrowly oblong; style branches 1.8 mm long. **Fruits** 10–12 mm diam., globose, greenish white with pale longitudinal lines and becoming red, purple, or black, persisting calyx less than 0.5 mm high.

Plants of evergreen montane cloud forest formations of the Caribbean slopes and continental divide, from (600–)1200 to 2000 m elevation. Flowering in June–November (peaking in August); fruiting in July and November–February. This species is known only from the Cordilleras de Guanacaste and Tilarán, the northern slopes of the Meseta Central (San Ramón–Zarcero), and above the Río Reventazón, in northern and central Costa Rica.

Coussarea austin-smithii is recognized by its usually open-corymbiform or umbelliform inflorescences without bracts, flowers with short broadly cupulate calyx with poorly developed lobes, long narrow corolla lobes, and its cloud forest habitat. This is our only *Coussarea* species growing above 1800 m elevation.

Coussarea caroliniana Standl., Field Mus. Nat. Hist., Bot. Ser. 22: 178. 1940. *C. veraguensis* Dwyer, Ann. Missouri Bot. Gard. 67: 134. 1980. Figure 47.

Shrubs or small treelets, 1.5–4(–6) m tall, leafy branchlets 1.2–5 mm thick, glabrous; **stipules** 12–20 mm long, 2–4 mm diam., united and forming a slender cap over the shoot apex, glabrous, acute at apex, usually splitting down one side and caducous. **Leaves** opposite, petioles 4–14(–18) mm long, 1–3 mm thick, glabrous, slightly sulcate above; **leaf blades** 8–14(–17) cm long, 3–7(–9.5) cm broad, elliptic-oblong, narrowly elliptic-oblong, elliptic to ovate-elliptic or elliptic-obovate, apex short-acuminate, base acute, drying chartaceous and usually grayish green, glabrous above and small linear cystoliths often visible, glabrous beneath, 2° veins 7–10/side and weakly loop-connected near the margin. **Inflorescences** 3–10 cm long, 3–5 cm broad, racemiform or spiciform, peduncles 1–3 cm long, glabrous, the proximal 2 lateral branches opposite or subopposite, to 6 mm long, distal flowers or flower clusters sessile or subsessile, bracts absent or minute (0.3 mm), pedicels 0–3 mm long. **Flowers** glabrous, hypanthium 1–2 mm long (not clearly differentiated from the pedicel or calyx tube), calyx tube 1–1.5 mm long, 1.8–2.5 mm broad at apex, entire; **corolla** white, tube 6–10 mm long, 0.7–2 mm diam., lobes 4, 4–8 mm long. **Fruits** 12–15 mm long, 7–10 mm diam., ellipsoid-oblong to oblong-obovoid, drying yellowish and minutely white-lenticellate, the persisting calyx 0.5–1 mm high.

Plants of evergreen rain forest formations on the Caribbean slope and central Cordilleras, from 350 to 1500(–1800) m elevation. Flowering in January–April; probably fruiting throughout the year. The species ranges from the Cordillera de Guanacaste eastward to the western part of the Cordillera de Talamanca and western and central Panama.

Coussarea caroliniana is recognized by its lower montane habitat, lack of puberulence, racemiform inflorescence without bracts, entire calyx tube, and distinctive fruit. The elongate *Ficus*-like stipules forming a cap over the shoot apices are distinctive; they are often seen at the base of an inflorescence enclosing the apices of new lateral shoots. None of our other species of *Coussarea* have such stipules. The dried leaves are often a characteristic grayish green beneath. Specimens with smaller leaves and immature fruits may resemble *Rudgea cornifolia*.

Several specimens with larger (18–26 × 6.5–12 cm) leaf blades and larger (30 × 13 mm) fruits on long (14 cm) infructescences are tentatively placed here. All are from the Caribbean lowlands: *Grayum et al.* 8754 CR, *Gómez-Laurito* 8785 (sterile) CR, and *Opler* 340 CR, F. They may represent an

unrecognized species or merely an extreme form of *C. caroliniana*.

Coussarea chiriquiensis (Dwyer) C. M. Taylor, comb. nov. *Rudgea chiriquiensis* Dwyer, Ann. Missouri Bot. Gard. 67: 476. 1980.

Shrubs ca. 4 m tall, leafy stems 0.7–4 mm thick, glabrous; **stipules** 2–4 mm long, broadly triangular or rounded, entire distally or with 2–4 short stiff lobes, usually with thickened teeth within, the base persisting. **Leaves** with petioles 5–16 mm long, 0.5–1.3 mm thick, glabrous; **leaf blades** (5–)6–12 cm long, (2–)3–5 cm broad, ovate-elliptic to elliptic or lanceolate, apex acute to acuminate, base obtuse to acute, drying chartaceous, dark above, glabrous, 2° veins 5–7/side. **Inflorescences** solitary and terminal, (3–)5–7 cm long, (2–)4–9 cm broad, peduncles 9–33 mm long, lateral branches of the first node opposite, often longer than the peduncle and equaling the rachis, glabrous, flowers sessile. **Flowers** glabrous, hypanthium ca. 1 mm long and 0.9 mm diam., tubular, calyx 0.5–1 mm long, broadly cupulate, calyx lobes minute or broadly triangular; **corolla** 6 mm long and 1.5 mm diam. in bud. **Fruits** not seen.

The original description of *Coussarea chiriquiensis* was based on a single collection (Croat 37071 MO) from about 1500 m elevation, above San Felix, Chiriquí, Panama. The collectors or teeth within the stipule may have been mistaken for the distal stipular teeth that distinguish *Rudgea*. We tentatively place *Burger et al. 10702* (CR, F, MO) here, which is similar but has pit-domatia and an entire stipule sheath. It was collected on the Pacific slope beneath Monteverde, Puntarenas, at ca. 1400 m elevation. All this material is very similar in overall appearance to *Coussarea nebulosa* and *Faramea ovalis*.

Coussarea enneantha Standl., J. Wash. Acad. Sci. 18: 282. 1928. Figure 46.

Shrubs or small trees, 1.5–7 m tall, leafy stems 2–4 mm thick, glabrous or with thin pale brownish hairs 0.3–0.7 mm long; **stipules** united and forming a short (2–3 mm) sheath with rounded to truncated distal margin. **Leaves** opposite, petioles 14–36 mm long, 0.6–1.4 mm thick, sparsely to densely pilose, **leaf blades** 9–17 cm long, 3–8 cm wide, elliptic to elliptic-oblong, apex acute to long-acuminate with tip 7–14 mm long, base obtuse or acute, drying thin- to stiffly chartaceous and concolorous, glabrescent above, pubescent on the veins beneath, 2° veins 8–10/side and weakly loop-connected near the margin. **Inflorescences** 2.5–8 cm long, to 8 cm broad, peduncles to 6 cm long, ca. 0.7 mm thick and with thin erect hairs 0.3–0.7 mm long, with 3–5 distant

flowers, peduncle often bearing 3 sessile or long-pedicellate flowers (or with 2 lateral flowers and a slender rachis bearing 3 remote flowers), bracts absent, pedicels to 2 cm long, pilose. **Flowers** with hypanthium 1–3 mm long and densely hirsute with erect or ascending yellowish brown hairs 0.3–0.7 mm long, calyx tube 4–8 mm long and 1.5–2.5 mm diam., sparsely pubescent, calyx lobes 4, (3–)4–8 mm long, ea. 2 mm broad, narrowly oblong; **corolla** salverform, white, tube 20–30 mm long and 3–4 mm diam., with ascending hairs ea. 0.7 mm long, corolla lobes 4, 12–15 mm long and 2 mm wide, glabrous. **Fruit** to 3 cm long and 15 mm diam., ellipsoid, densely hirsute, the persisting calyx 10–17 mm long.

Plants of evergreen rain forest formations, from near sea level to 1000 m elevation. This species is only known from Panama, but a collection from the Fish Creek Mountains in Bocas del Toro Province suggests that this species may be found in the Talamanca Valley of Costa Rica. The pubescent hypanthium, elongate calyx tube, and few-flowered inflorescences with long slender pedicels are very distinctive, but the flowers appear to vary greatly in size. The open few-flowered inflorescences resemble those of *Faramea occidentalis* and *F. pauciflora*.

Coussarea hondensis (Standl.) C. M. Taylor & W. Burger, Selbyana 12: 138. 1991. *Psychotria hondensis* Standl., J. Wash. Acad. Sci. 18: 183. 1928. *P. ostaurea* Dwyer & Hayden, Ann. Missouri Bot. Gard. 54: 143. 1967. Figure 48.

Shrubs or small trees, 2–10(–15) m tall, trunks to 20 cm dbh, leafy stems 3–9 mm thick, with fine soft hairs 0.1–0.4 mm long or minutely papillate-puberulent; **stipules** 7–15 mm long and 4–8 mm broad at the base, triangular to narrowly oblong, puberulent, acute or bidentate with teeth to 2 mm long, often persisting. **Leaves** with petioles 10–35(–70) mm long, 1–3 mm thick, pubescent; **leaf blades** 11–29 cm long, 5–16 cm broad, broadly elliptic to broadly elliptic-obovate or ovate-oblong, apex acute or short acuminate apex, tip to 10(–14) mm long, base acute to broadly obtuse, drying stiffly chartaceous and brownish or greenish, glabrous above, with short (ca. 0.2 mm) soft hairs on the veins and surfaces beneath, 2° veins 7–10/side. **Inflorescences** 6–15 cm long, to 10(–15) cm broad, panicle or eorymbiform with opposite, alternate or clustered lateral branches, peduncles 4–10 cm long, 1.5–2.5 mm thick, minutely puberulent, bracts 0.5–1 mm long or caducous, flowers in distal groups of 1–3, pedicels 0–3 mm long. **Flowers** distylous and nocturnal, hypanthium 1–2 mm long, 1.3–1.7 mm diam., turbinate, minutely puberulent, calyx tube 0.7–2 mm long, cupulate or spreading and 3 mm broad, lobes minute or absent; **corolla** salverform, white, minutely puberulent externally, tube 10–18 mm long, 0.8–3 mm diam., glabrous within, lobes 4–5, (4–)7–12

mm long, 1.5–2 mm broad, narrowly oblong, acute; anthers ca. 5 mm long. **Fruits** 12–24(–20?) mm long, ca. 10(–15?) mm diam., ellipsoid-oblong, becoming red-purple, persisting calyx less than 0.5 mm high.

Plants of evergreen rain forest formations in the Caribbean lowlands, from near sea level to 500 m elevation (to 900 m in Panama). Flowering in May–September; fruiting in June–August and October–January. The species ranges from Tortuguero in northern Costa Rica and the Osa Peninsula, southward to Coclé Province in Panama.

Coussarea hondensis is recognized by the minute soft puberulence on vegetative and flowering parts, the large long-petiolate and broadly elliptic leaves, the few- or many-branched and umbelliform inflorescences, broad and usually entire calyx, and the oblong fruit. An atypical collection (*Burger & Matta 4729 CR*, F) with almost glabrous leaves from above Golfito is tentatively placed here.

Coussarea impetiolearis J. D. Smith, Bot. Gaz. 37: 418. 1904. Figure 46.

Small trees to 17 m tall, leafy branchlets 1–3 mm thick, glabrous and drying greenish; stipules 2–4 mm long, triangular, glabrous and coriaceous, deciduous. **Leaves** subsessile, petioles 1–4 mm long, 0.7–1.8 mm thick, glabrous; leaf blades 7–18 cm long, 3–9 cm broad, narrowly to broadly elliptic, elliptic-oblong or oblanceolate, apex acuminate with tip 5–15 mm long, gradually narrowed to an acute base and slightly auriculate on the petiole, leaves drying chartaceous and greenish or grayish, glabrous above and below, but with hairs along the edges of pit domatia in or near the vein axils beneath, 2° veins 4–7/side. **Inflorescences** 3–5 cm long, to 7 cm broad, paniculate and often with 1 or 2(–3) pairs of opposite branches and 9–15 or more flowers, peduncles 10–26(–40) mm long, ca. 1.2 mm thick, glabrous, lateral branches to 12(–15) mm long, flowers sessile, bracteoles 0.3–1 mm long. **Flowers** with hypanthium ca. 2 mm long, calyx tube little differentiated from the hypanthium, 2–3 mm long, 2–3 mm diam. distally, glabrous or minutely papillate-puberulent, calyx lobes 0.2–0.3 mm high; corolla white, minutely sericeous externally, tube (8–)11–16(–20) mm long, lobes 4, 6–9 mm long, 2 mm broad at the base; anthers ca. 8 mm long. **Fruits** 15–20 mm long and 14–15 mm diam., broadly ellipsoid and slightly flattened laterally, surface smooth and pale yellowish white with distinctive white (becoming brown) tuberculate lenticels 0.5–1.4 mm long, persisting calyx ca. 2 mm high.

Plants of the lowland Caribbean rain forest formations, from 15 to 500 m elevation. Flowering in March–July; fruiting in January, March, and June–November. The species is found in the Caribbean lowlands, the Osa Peninsula, and Panama.

Coussarea impetiolearis is recognized by the sessile leaves with slightly auriculate leaf bases, the few-branched glabrous inflorescences, puberulent corolla tubes, and the unusual fruit drying pale in color and with round or oblong wart-like lenticels. The longitudinally elongate domatia with hairs along the sides or hairs along the midvein are a distinctive feature when present. This species was misinterpreted in the past to include material from Guatemala (now segregated as *C. imitans* L. O. Williams with more puberulent hypanthium-calyx and dark green fruit). *Coussarea curvigemma* Dwyer of central Panama with smaller flowers is also closely related; see the discussions under *Coussarea* spp. A & B aff. *C. curvigemma*. Material from the Osa Peninsula shows considerable variation and may indicate that the material placed under *Coussaria* sp. B is only an extreme form of *C. impetiolearis*; see the discussion under *Coussarea* sp. B. This species may be mistaken for a *Rudgea*.

Coussarea jimenezii J. D. Smith is a species of *Viburnum* (Caprifoliaceae).

Coussarea latifolia Standl., J. Wash. Acad. Sci. 18: 281. 1928. Figure 48.

Small trees, 6–15 m tall, perhaps dioecious, leafy stems 4–12 mm thick, glabrous, quadrangular; stipules ca. 5 mm long, rounded distally, glabrous, deciduous. **Leaves** opposite, petioles 9–30 mm long, 2–4 mm thick, terete, glabrous; leaf blades 17–30 cm long, 9–19 cm broad, broadly elliptic to broadly elliptic-obovate or ovate-elliptic, apex abruptly narrowed to the short-acuminate, tip 4–10 mm long, base obtuse, drying stiffly chartaceous or subcoriaceous, grayish green, glabrous above and below, 2° veins 7–9/side, domatia absent. **Inflorescences** 2–6 cm long, 3–6 cm broad, racemose in form with cymose flower clusters on short (6–15 mm) lateral branches or with pedicellate flowers from the central rachis, peduncles 2–30 mm long, 2–3.5 mm thick and glabrous, bracts minute, pedicels 1–5 mm long. **Flowers** glabrous, hypanthium 3–4 mm long, obovoid, poorly differentiated from the calyx tube, calyx tube 5–7 mm long, 4–5 mm diam., calyx lobes not developed; corolla salverform, yellowish white, tube ca. 10 mm long (perhaps not fully expanded), lobes 4, 13–15 mm long; anthers 4–5 mm long. **Fruits** 25–45 mm long (including persisting calyx 2–6 mm long), 10–28 mm diam., ellipsoid-oblong, green with white spots and becoming yellow.

Plants of evergreen rain forest formations of the Caribbean lowlands, from 5 to 300 m elevation (to 1000 m in the central highlands of Panama). Flowering in April–May; fruiting in July, September–October, and December. The species ranges

from central Costa Rica (Reventazón valley) to Colombia.

Coussarea latifolia is recognized by its large broadly elliptic leaves on prominent thick petioles and with relatively few secondary veins, the lack of pubescence, the racemose inflorescences, and long calyx tube. We have seen only the following collections from Costa Rica: *Grayum et al.* 8754 MO, *Shank & Molina* 4422 F, and *Tonduz* 9574 US holotype. This species is difficult to separate from the much more often collected *C. talamancanum* in the absence of flowers or mature fruit.

Coussarea nebulosa Dwyer, Ann. Missouri Bot. Gard. 67: 131. 1980.

Shrubs, ca. 3 m tall, leafy stems 1–5 mm thick, glabrous, becoming grayish, terete and smooth; **stipules** 1–3 mm long, 2–3 mm broad, with a broad U-shaped sinus and 2 small (0.7 mm) lobes, deciduous. **Leaves** with petioles 4–16 mm long, 0.5–1 mm thick, glabrous; **leaf blades** 6–13 cm long, 2–4 cm broad, elliptic-lanceolate to narrowly elliptic-oblong, apex tapering gradually to the acuminate, base acute, drying stiffly chartaceous and dark olive green above, glabrous above and below, 2° veins 4–6/side. **Inflorescences** solitary and terminal, 2.5–7 cm long, 1.5–6 cm broad, paniculate with opposite lateral branches, peduncle 6–46 mm long, 0.7–1.3 mm thick, glabrous, bracts ca. 2 mm long, subulate, flowers mostly sessile in distal triads. **Flowers** glabrous externally, hypanthium 0.8–1.3 mm long, ca. 1 mm diam., calyx tube 0.5–0.8 mm high, lobes 0.2–0.5 mm long; **corolla** white, tube 10–18 mm long, lobes ca. 6 mm long. **Fruits** unknown.

Coussarea nebulosa is a species of the Chiriquí Highlands known only from near Boquete at about 1200–1600 m elevation. The smaller leaves, unusual stipules (for the genus), glabrous parts, and small inflorescences are distinctive. There are two other similar small-leaved species in the Chiriquí Highlands: *Coussarea chiriquensis* and *Faramea ovalis*.

Coussarea nigrescens C. M. Taylor & Hammel, Selbyana 12: 134. 1991.

Shrubs or small treelets, 2–7 m tall, leafy stems 1.2–4 mm thick, glabrous or minutely (0.05 mm) papillate-puberulent, drying dark; **stipules** united to form a short sheath 0.8–2 mm long, at first broadly triangular but becoming truncated or with 2 minute lobes ca. 0.3 mm long, glabrous, the base persisting as a short collar above the node. **Leaves** with petioles 6–35 mm long, 0.7–1.7 mm thick, glabrous or minutely papillate-puberulent,

drying black; **leaf blades** 8–21 cm long, 3–9 cm broad, elliptic to elliptic-oblong or slightly ovate-elliptic, apex abruptly narrowed and short-acuminate with tip 2–8 mm long, base cuneate to obtuse, drying membranaceous to thin-chartaceous and blackish above, glabrous and lustrous above, glabrous or minutely puberulent along the midvein beneath, 2° veins 6–10/side, weakly loop-connected near the margin in the distal half of the leaf. **Inflorescences** solitary and terminal, 4–11 cm long, 3–11 cm broad, open umbelliform panicles with 2 or 4 branches at the first node, peduncle 15–50 mm long, 0.7–2.2 mm thick, glabrous or papillate-puberulent, drying black, bracts subtending the 1° branches 2–6 mm long, flowers sessile in distal cymes or glomerules of 3–7, distal bracts ca. 1 mm long. **Flowers** minutely (0.05 mm) papillate-puberulent externally, hypanthium 0.6–1 mm long, calyx cup only 0.5 mm long, becoming rotate, lobes minute; **corolla** tubular, white, tube 14–24 mm long and 1.2–2 mm diam., lobes 4 or 5, 6–10 mm long, lanceolate; **ovary** with well-developed septum and 2 locules. **Fruits** 9–26 mm long, 6–18 mm diam., purple-black, glabrous; pyrenes 1 or 2, globose to ellipsoid.

Plants of evergreen rain forest formations of the Caribbean lowlands and southern Pacific lowlands, from 20 to 800 m elevation. Flowering in July and October–November; fruiting in February. This species has been collected in the department of Zelaya, Nicaragua, near La Selva and Puerto Viejo de Sarapiquí, Cerro Nara east of Quepos, and Corcovado National Park in Costa Rica. This species is known only from Costa Rica and Nicaragua.

Coussarea nigrescens is recognized by the many parts drying dark or blackish, the very thin leaves, short collar-forming stipules, and slender corolla tubes that are minutely papillate-puberulent. This species may be related to *C. nebulosa* of the Chiriquí Highlands with smaller stiffer leaves that do not dry so dark, larger calyx lobes, lack of puberulence, and higher-elevation habitat.

Coussarea psychotrioides Taylor & Hammel, Selbyana 12: 135. 1991. Figure 47.

Shrubs or small **trees**, 2.5–7(–12) m tall, trunks to 20 cm dbh, leafy stems 1.5–4 mm thick, glabrous, nodes often conspicuously thickened; **stipules** 0.3–2 mm long, truncate or slightly bilobed, quickly caducous and leaving a short cupulate ring around the stem just above the distal nodes, glabrous. **Leaves** with petioles 6–20 mm long, 0.6–1.7 mm thick, glabrous, sulcate above; **leaf blades** 8–18 cm long, (2.5–)3–8.5 cm broad, narrowly elliptic to elliptic-oblong or elliptic-ovate, apex short-acuminate (rarely acute or obtuse), tip 5–12 mm long, base obtuse to acute, drying chartaceous and often yellowish green or greenish brown above, glabrous above and below, 2° veins 6–9/side and loop-connected near

the margin in the distal half of the lamina. **Inflorescences** 3–10 cm long and 4–10 cm broad, broadly paniculate to umbelliform, peduncles 1–3 cm long, 1–2 mm thick, glabrous, first branching node usually with 2 branches and these often coequal with the continuing rachis (= umbelliform), bracts 0.4–3 mm long or absent, flowers usually subsessile in distal 3–7-flowered cymes or glomerules, pedicels 0–3.5 mm long. **Flowers** glabrous, nocturnal and distylous, hypanthium 0.7–2 mm long, 0.5–1.5 mm diam., obconic or turbinate, calyx tube 0.2–1 mm long, calyx lobes not clearly developed; **corolla** white or tinged with pink, salverform or slightly funnelliform, tube 12–18 mm long, 1–2 mm diam. near the base and 2–3 mm near the mouth, often curved, lobes 5(–6), 6–12(–20) mm long, 0.8–2 mm broad. **Fruits** 14–20 mm long, 10–15 mm diam., ooblong or ovoid and abruptly rounded at apex and base, blue-black in life, persistent calyx not elevated or less than 0.5 mm high and 4 mm diam.; pyrenes 1 or 2, smooth or sulcate adaxially.

Plants of poorly drained areas in lowland rain forest formations, 50–600(–900) m elevation. Flowering in February–July; fruiting in September–February. The species is known only from the Caribbean lowlands of northern Costa Rica and the Osa Peninsula.

Coussarea psychotrioides is recognized by its restricted lowland habitat, glabrous parts, somewhat umbelliform inflorescences, and slightly pink flowers with long corolla lobes. The leaves are quite variable in shape but tend to dry greenish. This species is common at La Selva, where crushed leaves are said to have a slight odor of wintergreen. This species resembles *Psychotria eurycarpa*, which has larger stipules and calyx lobes, shorter corolla lobes, and an earlier flowering period (at La Selva). This species was studied by Bawa and Beach (1983) and referred to as *Coussarea* sp. (voucher *JHB 1467*); that Beach collection is also the type (holotype DUKE). Specimens from the Osa Peninsula often have longer (16–20 mm) corolla lobes.

***Coussarea talamancana* Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 1288. 1938. Figure 48.**

Shrubs or small trees, 2–5 m tall, dioecious, leafy stems 2–8 mm thick, glabrous, often drying pale yellowish green; **stipules** 6–16 mm long (to 22 mm below the inflorescences), to 12 mm broad, united to form a sheath around the shoot apex, broadly obtuse to rounded distally, glabrous, coriaceous, caducous. **Leaves** opposite, petioles 4–13 mm long, 1–2.5 mm thick, glabrous; **leaf blades** 12–28(–34) cm long, 4–18(–22) cm broad, broadly elliptic to elliptic-obovate or elliptic-suborbicular, apex abruptly narrowed to the acuminate, tip 6–18(–25) mm long, base broadly obtuse to acute, drying chartaceous, grayish green, glabrous above and below, 2° veins 7–10/ side, domatia absent. **Inflorescences** 3–7(–10) cm long, 3–5 cm broad, racemose panicles with short opposite

lateral branches, peduncles 5–13 mm long, 1.2–3.5 mm thick, glabrous, bracts minute or absent, pedicels 0–3 mm long. **Flowers** functionally unisexual, glabrous externally, hypanthium ca. 1–2 mm long (not clearly distinguished from the calyx tube), calyx tube ca. 2 mm long, becoming 3–5 mm broad, cupulate, calyx lobes minute or not developed; **corolla** salverform, white, tube 4–6 mm long, 1.5–2 mm diam., lobes 4, 4–6 mm long and 1.2 mm broad, narrowly oblong. **Fruits** 14–22 mm long, 9–17(–24) mm diam., ellipsoid to obovoid, becoming white with spongy exocarp in final stages; pyrene solitary.

Plants of evergreen formations of the Caribbean lowlands and the southern Pacific slope, from near sea level to 700 m elevation. Flowering in January–July; fruiting in every month but May. The species ranges along the Caribbean lowlands from northern Costa Rica to Bocas del Toro Province in Panama and in southern Puntarenas province.

Coussarea talamancana is recognized by the large broad leaves on short petioles, glabrous parts, united ovate-elliptic stipules, short racemiform inflorescences, smaller unisexual flowers, and larger spongy-white fruit. The type material (*Cooper 10466* F) has long (to 25 mm) narrow drip tips, whereas some other Costa Rican material has shorter (to 10 mm) tips, but other characteristics are very similar and suggest that the material placed here is conspecific.

***Coussarea* sp. A aff. *C. curvigemmia* Dwyer, Phytologia 38: 215. 1978. Figure 47.**

Shrubs or small trees, 2–8 m tall, leafy stems 1.5–3.5 mm thick, glabrous, grayish or yellowish green when dry; **stipules** 0.5–3 mm long, ovate and rounded distally or reduced to an entire ridge, glabrous. **Leaves** subsessile or with petioles 1–3 mm long, 0.5–1.5 mm thick, glabrous; **leaf blades** 7–16 cm long, 2.5–5 cm broad, narrowly elliptic-oblong to elliptic-obovate, apex acuminate, tip ca. 16 mm long, gradually narrowed to the acute or cuneate base and usually slightly auriculate at the petiole, drying thin-chartaceous and grayish green, glabrous above and below, with tufts of hairs in depressions (domatia) in the vein axils, 2° veins 4–7/ side. **Inflorescences** 4–7 cm long, 2–6 cm broad, paniculate with a single main rachis and short (3–12 mm) opposite or subopposite lateral branches, peduncles 1–2.2 cm long, glabrous and drying pale yellowish, flowers in distal pairs or triads, bracts subtending the flowers absent or less than 0.5 mm long. **Flowers** glabrous externally except for short (0.1 mm) erect whitish hairs on the ovary, hypanthium ca. 1 mm long, calyx tube 1–2 mm long, lobes 0.2–0.5 mm long, narrowly dentate; **corolla** narrowly tubular-salverform, white, tube 6–10 mm long, 0.7–1.5 mm diam., lobes 4, ca. 6–7 mm long; anthers 4–5 mm long, linear. **Fruits** not known (probably similar to those of *C. curvigemmia*: 10–13 × 5–8 mm, oblong and slightly flattened, whitish).

Plants of evergreen rain forest of the Caribbean lowlands, from near sea level to 300 m elevation. Flowering in April and June (*Barringer et al.* 2642 & 3615 CR, F, *Gómez-Laurito* 8388 CR). This species is known only from near Suretka in the Talamanca Valley in southern Limón Province.

Coussarea sp. A aff. *C. curvigemmia* is recognized by the thin subsessile leaves often slightly auriculate at the base and with weakly defined domatia, delicate whitish inflorescences, and small flowers with puberulent ovary and slender glabrous corolla tubes. *Coussarea curvigemmia*, of central Panama, differs from the material placed here in having clearly outlined ellipsoid pit-domatia with few or no hairs, glabrous ovaries, and minutely papillate-puberulent corollas that dry dark. Both taxa have distinctive thin, slightly curved corolla tubes, and it may be that they are conspecific. This material also resembles *Coussarea impetiolaris* with more robust inflorescences and some species of *Famea*.

Coussarea sp. B aff. *C. curvigemmia*. Figure 48.

Another species with very similar flowers may be represented by *Burger & Gentry* 8960 F from the Osa Peninsula and *Bunting & Licht* 793 F from the lower Río San Juan, Nicaragua. Both of these collections have smaller (4 cm) compact capitate inflorescences and larger (20 cm) subsessile obovate leaves with long (20 mm) narrow drip tips and with slightly auriculate leaf bases. However, the Nicaraguan collection has a pedunculate inflorescence and the Osa collection has a subsessile inflorescence, which may be immature. In contrast, *Liesner* 3225 and *Hammel et al.* 18604 (all at CR) are intermediate with typical *C. impetiolaris* and indicate that the unusual specimens may be bridged by intermediates, in which case the description given for *C. impetiolaris* needs to be expanded to include the collections placed here.

Coutarea Aublet

REFERENCE—A. Aiello, A reexamination of *Portlandia* (Rubiaceae) and associated taxa. *J. Arnold Arbor.* 60: 38–124. 1979.

Shrubs or small trees, branchlets terete, glabrous or puberulent, often with conspicuous elongate lenticels; stipules interpetiolar, short and acute, persisting. Leaves decussate or somewhat distichous, petiolate; leaf blades chartaceous, entire, some species with domatia. Inflo-

rescences terminal or apparently axillary (terminal on short axillary shoots with poorly developed leaves), flowers usually in open cymose groups of 3 or solitary, peduncles short, pedicels subtended by narrow bracts. Flowers bisexual, monomorphic, large and showy, bilaterally symmetrical due to curvature of the corolla tube and asymmetric stamens, hypanthium turbinate, calyx lobes 5–6(–8), narrow, often unequal; deciduous; corolla funnelform to campanulate and often inflated on the lower side, white to rose or purple, corolla tube slightly curved, with a glabrous throat, corolla lobes 5–6(–8), imbricate in bud; stamens 5 or 6, inserted near the base of the corolla tube, filaments long and often twisted in bud, anthers basifixed, linear, exserted or included; ovary 2-locular, placentas borne on the septum, ovules many in each locule. Fruits capsules, ovoid to obovoid or oblong, flattened, coriaceous or woody, 2-locular, dehiscing loculicidally from the apex (down the center of the broad face of the capsule) to form 2 valves; seeds many, imbricate and ascending, flattened and broadly winged with a thin margin around the circumference.

A genus of 6–10 species ranging from southern Mexico to Argentina; only 1 species is found in Mexico and Central America. The large curved corolla tubes, long free filaments, and the capsules splitting down the middle of their flattened sides make the genus distinctive. Only a few species of Rubiaceae in our flora have similarly large flowers (cf. figs. 15 and 31).

Coutarea hexandra (Jacq.) K. Schum. in Mart., Fl. Bras. 6, pt. 6: 196. 1889. *Portlandia hexandra* Jacq., Enum. Pl. Carib. 16. 1760; Sel. Stirp. 63, pl. 182, f. 20. 1763. *C. speciosa* Aubl., Pl. Guian. 1: 314, pl. 122. 1775. Figure 31.

Shrubs or small trees, 2–8(–18) m tall, leaf branchlets 1.7–4 mm thick, glabrous or sparsely puberulent, becoming dark brown with elongate whitish lenticels; stipules 1.5–4(–5) mm long, ea. 2 mm broad at the base, intrapetiolar and forming a short (0.5–1.5 mm) tube above the petioles, distally triangular and acute, glabrous in Central America. Leaves with petioles 2–10(–15) mm long, 0.7–1.5 mm wide, glabrous or minutely puberulent; leaf blades 5–15 cm long, 2–9 cm broad, ovate to broadly elliptic or ovate-oblong, apex acute, short-acuminate or caudate-acuminate, base obtuse to rounded and subtruncate (acute), drying thin-chartaceous or membranaceous, glabrous or minutely puberulent on the veins above, glabrous or minutely (0.2–0.4 mm) puberulent beneath, 2° veins (4–)6–10/side, with tufts of minute hairs (domatia) in vein axils beneath. Inflorescences few-branched and with (1–)3–9 flowers, peduncles 3–30 mm long, bracts 3–5 mm long, pedicels 2–15 mm long, merging gradually with the base of the flower, glabrous or sparsely and minutely puberulent. Flowers to 10 cm long and 4 cm broad, mostly glabrous (in Central America), hypanthium 4–7 mm long, 2–3 mm diam., calyx tube

1.5–2.5 mm long, 4–5 mm broad, calyx lobes 4–6, 4–9(–12) mm long, lanceolate to linear, deciduous; **corolla** funnellform-campanulate, white or tinged with pink, glabrous externally, tube 45–80 mm long, 10–20 mm diam. distally, slightly curved, inflated before anthesis, lobes 4–6, 1–2 cm long, 7–10 mm broad, apex ovate-triangular and obtuse to acute; **stamens** 6, filaments to 8 cm long, anthers 14–19 mm long, 0.5–1 mm thick, yellow, exserted; style to 85 mm long. **Fruits** 25–45 mm long, 15–28 mm broad, ca. 8 mm thick, oblong-obovate, woody when mature, surfaces dark brown and glabrous, with or without small white punctate lenticels, the valves slightly split in 2 at apex; **seeds** 7–14(–20) mm long, 6–9 mm broad, oblong to suborbicular, body of the seeds 3–4 mm diam., wing pale brown.

Trees and shrubs of both deciduous and evergreen forest formations, from near sea level to 900 m elevation. Flowering in late June–October; fruiting in November–April in southern Central America. This species appears to be much more common in seasonally deciduous forests than in evergreen forests in Costa Rica. The species ranges from southern Mexico and Belize to Argentina.

Coutarea hexandra is recognized by its thin short-petiolate leaves, few-flowered inflorescences with large flowers, the curved corolla tube, and the large flattened capsules with winged seeds. The fruits are unusual in that they split down the center of the broadly flattened halves (fig. 31). The flowers appear to be filled with gas before anthesis, and they are often pendulous at anthesis. The floral biology has been discussed by Haber and Frankie (1989). In northern Central America, bitter principles in the bark have been used medicinally, especially for malaria (Mabberley, 1987).

Crusea Schlechtendal & Chamisso

REFERENCE—W. R. Anderson, A monograph of

the genus *Crusea* (Rubiaceae). Mem. New York Bot. Gard. 22: 1–128. 1972.

Annual or perennial **herbs**, sometimes woody at the base, decumbent or erect, stems terete or 4-angled with longitudinal ribs, pubescent; **stipules** interpetiolar and united to adjacent petioles to form a thin sheath, with a distal cross-vein and 2–12 setae, persisting. **Leaves** opposite and decussate, sessile or petiolate, petioles adnate to the stipular sheath; **leaf blades** mostly ovate to lanceolate with strongly ascending pinnate venation, entire, domatia absent. **Inflorescences** terminal or axillary, capitate, verticillate or of congested dichasial cymes, sessile to long-pedunculate, subtended by 2, 4, or 8 (more) leaf-like bracts, pedicels short (to 2 mm) or absent. **Flowers** bisexual and radially symmetrical, homostylous, usually 4-parted, calyx lobes 4 or reduced to 2–3, with minute glands in the base of the sinuses between the lobes; **corolla** funnellform to campanulate, white to pink, red, or purple, corolla lobes 4, valvate in bud; **stamens** 4, filaments adnate to the upper half of the tube and free beneath apex of the tube, anthers dorsifixed, exserted; **ovary** 2-locular, placenta elongate from the center of the septum, with 1 ovule in each locule, stigma 2-lobed or subcapitate. **Fruits** of 2 dry 1-seeded mericarps (cocci) borne on the sides of and separating from a persisting bifid or fenestrated carpophore, mericarps indehiscent and ecostate, calyx dehiscing circumscissily or persisting; **seeds** with the persisting placenta on the adaxial face.

A genus of 13 species ranging from Arizona, U.S.A., through Mexico and Central America to western Panama. The herbaceous habit, congested subsessile flowers, often lanceolate leaves with strongly ascending secondary veins, narrow corolla tube (in our species) and unusual fruit help distinguish this genus. The mericarps are easily mistaken for seeds because of their smooth rounded brownish surfaces and longitudinal adaxial sulci. The genus reaches its southern limit in Costa Rica and western Panama and is represented by only a few collections from Costa Rica. This treatment is based on Anderson's detailed monograph.

Key to the Species of *Crusea*

- 1a. Flowers bright pink to magenta; leaf blades 1–5 cm broad, to 13 cm long 2
- 1b. Flowers white or white-tipped with pink; leaf blades 0.5–3.5 cm broad, to 8 cm long 3
 - 2a. Corolla tube 20–38 mm long, stigma lobes 1–4 mm long; secondary veins arising from the proximal half of the midvein; 1800–3000 m elevation *C. coccinea*
 - 2b. Corolla tube 5–18 mm long, stigma lobes 0–0.5 mm long; secondary veins arising from the proximal ½ or ⅔ of the midvein; 0–200 m elevation *C. hispida*
- 3a. Corolla tube 5–11 mm long, stigma lobes 0.2–0.6 mm long; plants usually found around 2000 m elevation in Costa Rica *C. longiflora*
- 3b. Corolla tube 1.8–4 mm long, stigma lobes 0.1–0.3 mm long; plants found in deciduous and partly deciduous areas below 1200 m elevation *C. parviflora*

***Crusea coccinea* DC.**, Prodr. 4: 567. 1830. *C. coccinea* var. *chiriquiensis* W. R. Anderson, Mem. New York Bot. Gard. 22: 45. 1972. Figure 31.

Decumbent or low perennial **herbs** to 1 m tall, often rooting at the nodes, leafy stems 1–3.5 mm thick, glabrous or sparsely puberulent, quadrangular or terete; **stipule** sheath 4–14 mm long (including the setae), 1–6 mm wide, glabrous or puberulent, setae 3–12 and to 12 mm long and linear, evenly spaced or in a central group with fused bases. **Leaves** with petioles 4–20(–25) mm long, glabrous or puberulent; **leaf blades** 2.2–10(–13) cm long, 1–4(–5) cm broad, narrowly elliptic to elliptic or ovate, apex acute to short- or long-acuminate, base acute and decurrent on petiole, drying stiffly chartaceous and dark, often slightly scabrous with the major veins impressed above, glabrous or sparsely puberulent above, sparsely hispidulous with short (0.3 mm) hairs along the veins beneath, 2° veins 3–6/side, strongly ascending, subparallel and arising from the proximal half of the midvein, minutely punctate on both surfaces. **Inflorescences** bracteate/involucrate heads or with verticillate flowers in the node below the terminal head, 10–15 mm diam., with 15–100 flowers in the head but few–10 flowering at the same time, involucral bracts 2 or 4, 2–4 cm long, leaf-like and often sessile within the expanded petioles and stipular sheath of the subtending node, often with additional smaller bracts. **Flowers** with hypanthium 1.4–3 mm long, glabrous or puberulent distally, calyx lobes to 8 mm long, narrowly triangular, **corolla** deep red to pink, purple, or lavender, funnelform, tube (8–)20–38 mm long, gradually expanded from a narrow (3 mm) base, lobes (3.5–)5–11 mm long; **stamens** with free portion of the filaments ca. 4–10 mm long, filiform, anthers (2–)2.5–3.8 mm long; style as long as the corolla tube. **Fruits** with a broad flat carpophore, 4–7 mm long with lobes 0.7–2 mm long, cocci (1.7–)3–6 mm long, 2–2.7 mm broad, rounded-turbinate to turbinate, brown, calyx often coming off as a complete whorl (circumscissile).

Herbs of montane evergreen forest formations of the Pacific slope and central highlands, from 1800 to 3000 m elevation. Probably flowering and fruiting mostly in the wet season and beginning of the dry season: May–January. The species ranges from western Mexico to western Panama.

Crusea coccinea is recognized by the herbaceous habit, short stipular sheath with long narrow setae, narrow leaves with subparallel secondary veins, and large pink to lavender flowers. Plants of Costa Rica and Chiriquí, Panama, belong to variety *chiriquiensis* W. R. Anderson. This variety is similar to variety *coccinea* in having larger corollas, anthers, and mericarps, but variety *chiriquiensis* differs in having leaves with major veins deeply impressed above, a greater number of stipular setae, and pink to magenta flowers. While often collected in the Chiriquí Highlands, these plants have rarely been collected in Costa Rica.

***Crusea hispida* (Miller) Robinson**, Proc. Amer. Acad. Sci. 45: 409. 1910. *Crucianella hispida* Miller, Gard. Dict. ed. 8, no. 4. 1768.

Erect annual **herbs** to 0.6 m tall, many-branched, leafy stems 0.5–4 mm thick, terete with stiff unicellular transparent or whitish hairs 1.5–3 mm long, spreading or retrorse from a thickened base, smaller (0.2 mm) hairs sometimes also present; **stipule** sheath 2–5 mm long, 4–10 mm broad, with 3–7 setae, conspicuously hispid. **Leaves** opposite, often with smaller axillary leaves from the same node, petioles 5–25 mm long, hispid; **leaf blades** 4–9(–11) cm long, 1–3.6(–4.8) cm broad, narrowly ovate-elliptic to lanceolate or narrowly ovate, apex tapering gradually and acuminate, base acute to obtuse, drying thin-chartaceous, both surfaces with thin whitish hairs ca. 1.3 mm long, 2° vein 5–6/side, strongly ascending. **Inflorescences** solitary terminal bracteate capitulae with 40–100 closely crowded sessile flowers, subtended by 8 (4) leaf-like bracts and many linear hispid bracteoles. **Flowers** with glabrous hypanthium, calyx tube 0.3–1 mm long, lobes 2–6 mm long, subulate, margins with stiff hispid hairs; **corolla** salverform, light pink to dark red or purple, tube 5.5–12(–18) mm long, ca. 0.3 mm diam. (dried), lobes 2–5 mm long; anthers 1–1.5 mm long, exserted. **Fruits** with cocci 2–3.5 mm long, 1.1–2.3 mm broad, yellowish to dark brown.

A species of open grassy sites, ranging from Mexico to El Salvador and collected only recently in Costa Rica at a single locality: Costa de Pajaros, Bahia de Nicoya, Puntarenas (*C. M. Taylor* 249 and *Wilbur* 31715, both at DUKE). This population was in flower in July; it is variety *hispida* (with shorter corolla tubes). The broader petiolate leaves, colorful flowers, and unusual pubescence distinguish this species.

***Crusea longiflora* (Willd. ex Roem. & Schult.) W. R. Anderson**, Mem. New York Bot. Gard. 22: 89. 1972. *Spermacoce longiflora* Willd. ex Roem. & Schult., Syst. Veg. 3: 531. 1818. *C. brachyphylla* Schlechtend. & Cham., Linnaea 5: 165. 1830.

Erect annual **herbs** to 50 cm tall, stems terete or less often quadrangular, pubescent to pilose with hairs 1–2 mm long; **stipule** sheath 1.4–6.5 mm long, 2–7 mm broad, with 3–7 distal setae, and 0–2 inconspicuous sessile lateral collectors, longest setae 0.5–3(–5) mm long, equaling or shorter than the sheath, with thin hairs 0.5–2 mm long. **Leaves** sessile or subsessile with petioles to 5 mm long; **leaf blades** 8–50 mm long, 3–21 mm wide, narrowly to broadly elliptic, or ovate, apex acute to obtuse, base abruptly narrowed, drying chartaceous and scabrous, sparsely hispidulous, 2° veins 2–3/side, strongly ascending. **Inflorescences** 1–2 cm diam., small terminal bracteate heads (or with lateral heads reduced to an axillary cluster of 1 or a few flowers), with up to 75(–100) flowers

in a head, involucre bracts 4 or 8. **Flowers** sometimes cleistogamous and resembling small unopened flower buds, hypanthium 0.7–1.1 mm long, glabrous, calyx tube 0.5–1 mm long, lobes 1–3.5 mm long and 0.2–0.8 mm wide, broadly to narrowly triangular, often ciliate along the edge; **corolla** white (rarely pink or lavender), tube 5–11 mm long, narrow at the base and only 0.8 mm broad at apex, papillose externally, with long straight hairs within distally, lobes 1.6–3.6 mm long, 0.8–1.5 mm broad, narrowly elliptic, becoming strongly reflexed, with few long hairs at the base within; **stamens** with filaments 1.5–3.8 mm long, anthers 0.6–1.3 mm long; style 5–16 mm long, glabrous, stigmatic lobes 0.2–0.6 mm long. **Fruits** with a bifid carpophore to 1.5 mm long, the mericarps (cocci) 1.1–2.3 mm long, ellipsoid-cylindrical, whitish to yellow-brown or dark brown, calyx often coming off as a whorl.

Herbaceous plants of montane evergreen formations, from ca. 1000 to 2700 m elevation. Flowering in July–December; fruiting in September–December (over the entire range). This species ranges from northern Mexico through Guatemala, with isolated occurrences in the highlands of Honduras and Costa Rica.

Crusea longiflora is distinguished by its erect annual habit, short stipular sheath with setae, small and narrow (often subsessile) leaves, the narrow corolla tube, and the small rounded mericarps. The long (1–2 mm) slender unicellular hairs also help distinguish this species. It has been collected infrequently in the Central Highlands at about 2200 m elevation. This species is common in Mexico.

***Crusea parviflora* Hook. & Arnott, Bot. Beechey Voy. 430, pl. 99. 1840. Figure 4.**

Erect, trailing or decumbent **herbs** to about 50 cm high and 1 m long, annual or perennial, leafy stems 0.5–3.5 mm thick, with 4 longitudinal ridges or wings in early stages, with thin whitish hairs 0.3–1.2 mm long but often glabrescent; **stipule** sheath 1–3 m long, 1.5–4 mm wide, often with minute spots, with 3–5 setae 1–7 mm long and with hairs to 1 mm long. **Leaves** with petioles 3–9 (–15) mm long, with lateral wings continuous with the lamina margin, with thin hairs on both surfaces; **leaf blades** 2.4–7 (–9) cm long, 1–3.6 cm broad, narrowly to broadly elliptic or lanceolate, apex bluntly to sharply acute, base gradually (abruptly) narrowed and decurrent on petiole, drying thin-chartaceous and often grayish green, pilose on both surfaces with thin whitish hairs 0.3–1 mm long, 2° veins 3–5/side. **Inflorescences** bracteate heads, with 10–many flowers per head and a majority of the flowers in bloom at one time, the heads terminal or axillary to distal leaves, subglobose and 1–2 cm broad, often on long (to 15 cm) peduncles, involucre bracts to 3 cm long and leaf-like, pedicels short. **Flowers** with small (0.5–1 mm) glabrous hypanthium, calyx tube 0.5–1.3 mm long, lobes 0.6–2.5 mm long, 0.2–0.5 mm broad and linear-triangular, with thin hairs

on the outer surface, calyx persisting on the fruit; **corolla** white or the lobes tipped with pink, funnelform, tube 1.8–4 mm long, 0.7–1.4 mm broad at the throat, usually glabrous externally and with longer hairs on the distal portion inside, lobes 1.3–2.8 mm long, 0.5–1 mm broad, narrowly triangular, erect to spreading (not reflexed), usually with small hairs externally at the tips; **stamens** with filaments 1.3–4.5 mm long, glabrous and becoming retracted into the corolla after anthesis; style 2.7–8 mm long, glabrous, stigmatic lobes 0.1–0.3 mm long. **Fruits** with mericarps 0.8–1.2 mm long, 0.6–0.9 mm broad, oblong-cylindrical or subglobose, surface slightly pitted.

Weedy plants of deciduous and evergreen formations, from 50 to 1600 (–2000) m elevation in Central America. Flowering in October–April; mature fruits in November–April. The species ranges from western Mexico along the Pacific slope to isolated localities in Honduras, Nicaragua, and Costa Rica.

Crusea parviflora is recognized by its short weedy habit, quadrangular or slightly winged young stems, short stipular sheath with few setae, capitate inflorescences with usually only 4 broad bracts, and unusual carpophore and seed-like mericarps. The short-pedicellate flowers contrast with the sessile flowers of similar-looking species of *Mitracarpus* and *Spermacoce*. In our area it has only been found in Guanacaste Province below 500 m elevation.

***Declieuxia* Humboldt, Bonpland & Kunth**

REFERENCE—J. H. Kirkbride, Jr., A revision of the genus *Declieuxia* (Rubiaceae). Mem. New York Bot. Gard. 28: 1–87. 1976.

Herbs or shrubs, perennial and often woody at the base, branches terete or angular, glabrous or puberulent; **stipules** interpetiolar, subulate or reduced to a line bearing 1–3 linear lobes. **Leaves** opposite or whorled, sessile or short-petiolate, leaf blades entire and usually small, linear to elliptic, deltoid or orbicular, usually coriaceous, domatia absent. **Inflorescences** of terminal or axillary panicles (compound cymes), often spike-like or racemiform, solitary to 3 at the end of the stem, pedunculate, branching often dichotomous, flowers in distal cymose groups, bracts and bracteoles present or absent. **Flowers** bisexual and radially symmetrical, small, mostly glabrous, hypanthium turbinate to subglobose or obovoid, slightly compressed laterally, calyx lobes 4 (2), equal or unequal, small and persisting; **corolla** funnelform to tubular, white to blue or purple, tube pilose-villose in the throat, corolla lobes 4, short, spreading or reflexed, valvate in bud; **stamens** 4, inserted in the corolla throat or between the lobes, filaments slender, anthers dorsifixed and versatile, partly or completely exserted; **ovary** 2-locular, ovule solitary in each locule, erect from a near-basal placenta, style slender, stigmas 2. **Fruits** drupaceous, dry or fleshy, laterally compressed and 2-parted or with 2 prominent rounded lobes, black at maturity.

A genus of about 40 species in tropical America, with the largest number of species in Brazil. Our representative of this genus is recognized by the very short woody stems, stiff subsessile leaves, cymose branching of the short inflorescences, two-lobed fleshy fruits, and restriction to open grassy habitats in deciduous or partly deciduous formations.

Declieuxia fruticosa (Willd. ex Roem. & Schult.)

Kuntze, Rev. gen. pl. 1: 279. 1891. *Houstonia fruticosa* Willd. ex Roem. & Schult., Syst. Veg. 3: 527. 1818. *D. mexicana* DC., Prodr. 4: 479. 1830. *D. fruticosa* var. *mexicana* (DC.) Standl., Field Mus. Nat. Hist., Bot. Ser. 12: 378. 1936. Figure 1.

Erect **subshrubs** or herbaceous 20–70 cm tall, often from a hard woody rootstock, with vertical simple or few-branched stems, leafy stems 0.7–3 mm thick, glabrous (in variety *mexicana*) to pubescent, with 2 or 4 longitudinal ridges or wings (0.5 mm high), becoming terete; **stipules** 2–5 mm long, linear to linear-subulate, glabrous (in variety *mexicana*) or pubescent, deciduous. **Leaves** 2 or 3/node, sessile or subsessile (petiole to 1 mm long); **leaf blades** 20–40(–50) mm long, 4–15(–22) mm broad, narrowly elliptic-oblong to linear-oblong or oblong, apex acute or obtuse, base cuneate, drying stiffly chartaceous to subcoriaceous, glabrous and often lustrous above, glabrous (in variety *mexicana*) or puberulent beneath, 2° veins (2–)3–6/side. **Inflorescences** terminal or axillary, 1–4 cm long, 1.5–5 cm broad, solitary or 3 at the ends of branchlets, open cymose panicle with dichotomous nodes (and a sessile flower at the dichotomy), primary peduncle 5–15(–40) mm long, bracts 1.5–3 mm long, linear, pedicels 0–1 mm long. **Flowers** heterostylous, hypanthium 0.3–1 mm long, calyx lobes 0.3–0.8 mm long, linear-oblong, glabrous (in variety *mexicana*) to villous, **corolla** white to blue or purple, 4.5–6 mm long, tube 3–4.5 mm long, cylindrical, lobes 4, ca. 2 mm long; anthers ca. 1 mm long, linear; style 3–4.5 mm long, stigmas 0.3 mm long. **Fruits** slightly fleshy and prominently 2-lobed (when both ovules develop), ca. 2 mm long and 3 mm broad, sessile, the lobes suborbicular, the fruit subglobose when only 1 ovule develops and ca. 2 mm diam., drying black, glabrous.

Small subshrubs of open grassy savanna-like sites in deciduous and semideciduous forest formations, from ca. 20 to 1200(–1800?) m elevation. In Costa Rica the species is restricted to the Pacific slope and is common in Guanacaste and the Buenos Aires area of the General Valley. Flowering throughout the year (primarily in July–September). The species ranges from southern Mexico to Brazil.

Declieuxia fruticosa is recognized by the short stature from a woody base, restriction to open

rocky or savanna-like habitats, the stiff narrow sessile leaves often three at a node, the short dichotomously branched panicles, the small flowers, and the sessile fleshy deeply two-lobed or rounded fruit (laterally compressed when dry). Chacón (2258 CR, MO) stated that the flowers are white with blue-lavender stamens. Our material belongs to variety *mexicana*, which is distinguished by its narrow leaves and lack of pubescence.

Deppea Chamisso & Schlechtendal

REFERENCE—D. H. Lorence and J. D. Dwyer, A revision of *Deppea* (Rubiaceae). Allertonia 4: 389–436. 1988.

Slender **shrubs** and small trees, stems sparsely to densely puberulent; **stipules** interpetiolar, small, triangular, persistent. **Leaves** opposite (rarely in whorls of 3), opposing leaves of the same node often unequal, petiolate, leaf blades entire and pinnately veined, drying thin-chartaceous, domatia sometimes present. **Inflorescences** axillary or terminal, scorpioid, umbellate or corymbiform to thyrsoid, the flowers in cymose groups (or rarely of solitary flowers), pedunculate, flowers pedicellate, bracteolate. **Flowers** bisexual and radially symmetrical, hypanthium hemispheric to turbinate or cylindrical, calyx lobes 4, minute or large, equal or unequal, usually with a small gland in each sinus; **corolla** short-funnelform to salverform, yellow (less often white, orange, or purple), corolla tube glabrous within, usually shorter than the lobes, corolla lobes 4, spreading or erect at anthesis, convolute in bud; **stamens** 4, inserted near the base of the tube, filaments short and linear, anthers dorsifixed, oblong to narrowly ellipsoid, exserted or partly included, a nectariferous disc present; **ovary** 2-locular, placentas elongate and peltate on the septum, ovules many in each locule and longitudinally imbricate, style slender, stigma entire or bilobed. **Fruits** a small dry capsule, turbinate to obovoid, coriaceous to chartaceous, usually with (6–)8 longitudinal costae, bisulcate and dehiscent loculicidally from apex, valves cleft, calyx persisting; **seeds** many and minute, angulate, testa foveolate and reticulate.

A genus of about 25 species, centered in Mexico and ranging through Central America (1 species) to southeastern Brazil (1 species). This account is based on the recent revision by Lorence and Dwyer (see reference above). *Deppea* can be confused with *Hamelia* and *Hoffmannia*, which have fleshy fruits.

Deppea grandiflora Schlechtend., Linnaea 19: 748.

1847. *D. costaricensis* Polak., Linnaea 41: 566.

1877. *D. floribunda* Hemsl., Diagn. Pl. Nov.

Mexic. 31. 1879. *D. longipes* Standl., Contr. U.S.

Natl. Herb. 18: 138. 1916. Figure 38.

Shrubs or small trees, 1–4 m tall, leafy branchlets 1–4 mm thick, hirtellous with short (0.3 mm) brownish hairs, at first with longitudinal ridges but becoming terete and glabrescent; **stipules** 0.5–1 mm long, 2–6 mm wide, broadly deltoid, glabrate to densely hirtellous, the inner surface or margin with 4–8 dark brown digitate colleters. **Leaves** opposite and subequal or unequal at the same node (with 1 up to 2 times as long as the other), petioles 6–35(–50) mm long, 0.5–2 mm thick, glabrate or densely hirtellous on the adaxial side; **leaf blades** (3–)5–17(–21) cm long, (1.5–)2–7(–8.5) cm broad, elliptic to narrowly elliptic, narrowly ovate or lanceolate, apex tapering gradually and acuminate, base attenuate to acute (obtuse), drying chartaceous, glabrous to sparsely puberulent with minute (0.2 mm) thin whitish hairs above, minutely strigillose along the veins beneath, occasionally with tufted domatia in the vein axils beneath, 2° veins 6–11/side and weakly loop-connected near the margin. **Inflorescence** terminal (rarely axillary), 3–12 cm long and 3–15 cm broad, dichasial and corymbiform, with 15–100 flowers, peduncles 1.2–7 cm long, densely and minutely strigillose-hirtellous, primary branches 1–3 cm long and with up to 3 additional orders of branching, distal cymes of 2–6 flowers, pedicels 1–4 mm long, bracteoles present or absent. **Flowers** with hypanthium 1–2 mm long, 0.5–1 mm diam., obconic or turbinate, with longitudinal costae, calyx cup 0.1–0.2 mm deep, lobes 0.3–1 mm long, deltoid; **corollas** funnelform or rotate, yellow, glabrous, tube 1–2 mm long, corolla lobes 4, 4–7 mm long, 3–4 mm wide, obtuse; **stamens** 4, filaments 2 mm long, anthers 3–4 mm long, exerted, basally sagittate; style 3.5–4.5 mm long, stigmas 1.5–2 mm long, entire. **Fruits** 2–5 mm long, 2–4 mm diam., obconical to subglobose, with 6–8 prominent longitudinal costae, opening at the top; **seeds** 0.5–0.7 mm long, discoid and often angulate, testa foveolate.

Shrubs of evergreen montane forest formations, from 1600 to 2700 m elevation. Flowering in January–July, with a peak in April. Fruiting in January–September. The species has been collected around Monteverde, Volcán Barva, and in the western Cordillera de Talamanca (to above San Isidro del General) in Costa Rica. The species ranges from central and eastern Mexico through the highlands of Guatemala and Honduras to the Chiriquí Highlands of Panama.

Deppea grandiflora is recognized by its restriction to higher montane forest formations, small shrubby habit, thin leaves unequal at a node and gradually tapering at both ends, bright yellow glabrous corollas with very short tube and broad lobes, and small costate capsules opening at the top. Plants with pseudoaxillary inflorescences and unopened flowers may resemble species of *Hoffmannia*. Material of *Chiococca* is also similar.

Didymaea Hooker f.

Perennial **herbs**, scandent or procumbent, stems brittle, usually much-branched and with long slender inter-

nodes, glabrous or rarely puberulent; **stipules** interpetiolar and 2-lobed or apparently free (with 4/node), deciduous or persisting and becoming recurved. **Leaves** petiolate; **leaf blades** entire and pinnately or subpalmately veined, membranaceous to thin chartaceous, domatia absent. **Inflorescences** of solitary flowers in the axils of leaves, the pedicels long but not articulate, becoming recurved in fruit. **Flowers** bisexual and radially symmetrical, hypanthium turbinate-globose, calyx entire; **corolla** campanulate to rotate, yellowish to greenish brown or purple, glabrous, corolla lobes 4, triangular and subacute, valvate in bud; **stamens** 4, inserted between the corolla lobes, filaments short and subulate, anthers dorsifixed; **ovary** 2-locular, ovules solitary in each locule and attached on the lower half of the septum. **Fruits** 2-parted or 2-lobed, somewhat fleshy, becoming dark blue or black and lustrous, the lobes rounded, 1 lobe usually smaller and lacking a fully developed seed; pyrenes rounded.

A small genus of two to five species, ranging from Mexico to Panama. The plants are recognized by their herbaceous climbing *Galium*-like habit, small thin leaves, minute flowers solitary in the leaf axils, and fleshy, often 2-parted rounded fruit. The circumscription of species in Central America is not resolved (see below).

Didymaea alsinoides (Cham. & Schlechtend.)

Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 1291. 1938. *Nertera alsinoides* Cham. & Schlechtend., Linnaea 6: 413. 1831. *D. alsinoides* var. *australis* Standl., loc. cit. 1292. 1938. *D. alsinoides* var. *mollis* Standl., loc. cit. 1292. 1938. *D. australis* (Standl.) L. O. Williams, Fieldiana Bot. 24, pt. 11: 61. 1972. Figure 3.

Herbs or weak-stemmed climbers, leafy stems 0.3–2 mm thick when dry, quadrangular or with 2 or 4 longitudinal ridges or wings ca. 0.5 mm high, sparsely and minutely (ca. 0.3 mm) puberulent or glabrescent; **stipules** 0.5–2.5 mm long, narrowly triangular or linear, deciduous. **Leaves** with petioles (1–)2–8 mm long, 0.2–0.5 mm broad; **leaf blades** (5–)7–30 mm long, (3–)4–14 mm broad, ovate to ovate-elliptic or narrowly ovate (rarely lanceolate), apex gradually narrowed and acute with sharp tip, base abruptly narrowed or rounded and obtuse to truncate, decurrent on petiole, drying membranaceous (translucent), glabrous or minutely puberulent above the midvein on the upper surface, sparsely pubescent beneath with thin hairs ca. 0.3 mm long, 2° veins 1–3/side, often with subpalmate venation in broadly ovate leaves. **Inflorescence** of solitary flowers in leaf axils, usually only 1 flower per node, pedicels 1–5 mm long, glabrous. **Flowers** ca. 3–4 mm long, hypanthium ca. 0.7 mm long, calyx to 0.2 mm long, truncate; corolla ca. 3 mm long, greenish purple, tube ca. 1.5 mm long. **Fruits** 4–6 mm long, subglobose when 1-seeded, deeply 2-parted and 6–8 mm broad when 2-seeded, becoming fleshy and blue at maturity, lustrous, drying black, usually glabrous; **seeds** often curved and reticulate.

Climbing plants of the shaded understory in montane evergreen wet forest formations, from 1500 to 2800(–3100) m elevation. Flowering and fruiting in September–June. The species (in a wide sense) ranges from Mexico to the Chiriquí Highlands of Panama.

Didymaea alsinoides is recognized in Costa Rica by its slender-stemmed clambering habit, thin, usually ovate leaves, minute flowers usually solitary at each node, and small fleshy blue-black fruit that are subglobose or deeply two-lobed. The preceding description is based on Costa Rican and Panamanian collections referred to as *Didymaea australis* by Williams. They differ from the more northerly collections in having more ovate leaves often truncate at the base. Recognizing the various morphological and geographic forms of *D. alsinoides* as separate species seems unwise, insofar as nearly all live in the same kind of montane habitats and there is considerable morphological variation in any one area; compare Williams' treatment (in Standley & Williams, 1975, pp. 60–63). Compare *Nertera granadensis* with smaller leaves and orange fruit.

Diodia Linnaeus

Annual or perennial **herbs** or small shrubs, erect or scandent, usually woody at the base, stems often much-branched near the base, terete or 4-angled, glabrous or pubescent; **stipules** interpetiolar and united with the leaf bases to form a broad sheath, usually bearing 2–12 slender

awn from the truncated or rounded distal edge of the sheath, persisting. **Leaves** opposite or pseudoverticillate (with smaller axillary leaves), sessile or short-petiolate; **leaf blades** mostly narrow and often scabrous, entire or serrulate with minute scabrous hairs along the margin. **Inflorescences** axillary and sessile, capitate or fasciculate (rarely of solitary axillary flowers) and often verticillate, long-spicate when the distal subtending leaves are reduced, subtended by the leaves and stipular sheaths, flowers usually subsessile. **Flowers** bisexual and radially symmetrical, small or minute, hypanthium obovoid to turbinate, calyx lobes 2–4; **corolla** funnelliform to campanulate, white to pink or purplish, corolla tube short or long, throat glabrous to villous, corolla lobes 4(3, 5–6), valvate in bud; **stamens** 4 (3, 5–6), inserted in the corolla throat, filaments filiform, anthers dorsifixed, linear-oblong; **ovary** 2-locular (rarely 3- or 4-locular), ovule solitary and ascending in each locule, affixed to the center of the septum, style filiform and exserted, bilobed or with 2 short branches. **Fruits** splitting into 2 mericarps (cocci), crustaceous to slightly woody, septicidal from apex (rarely splitting at the base), without a central axis, each mericarp indehiscent or opening slightly at the base; **seeds** ellipsoid, longitudinally sulcate on the inner face, rounded abaxially.

A genus of about 35 species in the tropical and subtropical Americas and with a few species in Africa. The weedy growth habit, awned stipular sheaths, narrow leaves, small sessile flowers, and fruit of two one-seeded indehiscent mericarps help to distinguish this genus. Species of this genus may resemble species of *Crusea* and *Spermacoce*, but the leaves do not become pseudoverticillate. This treatment has benefited from the annotations and advice of C. D. Adams (pers. comm., 1991).

Key to the Species of Diodia

- 1a. Plants essentially glabrous, often prostrate and restricted to the Caribbean seashore; leaves often closely clustered on short lateral branches (1–4.5 cm long); rarely collected *D. serrulata*
- 1b. Plants minutely to conspicuously pubescent, rarely prostrate and not restricted to the Caribbean shore; leaves not closely clustered on short lateral branches 2
- 2a. Largest leaves usually less than 3 cm long, stems erect, stipular sheaths with usually glabrous awns 3
- 2b. Largest leaves more than 3 cm long, stems erect or clambering, stipular sheaths with awns with thin whitish hairs distally or glabrous 5
- 3a. Leaves usually petiolate, to 2 cm long, thin-chartaceous and drying dark, often verticillate; evergreen formations, 600–1200 m elevation *D. brasiliensis*
- 3b. Leaves sessile, to 3(–4) cm long, subcoriaceous and drying grayish, opposite; savannas in seasonally very dry deciduous forest areas, 0–300 m elevation 4
- 4a. Top of the fruit with erect stiff hairs 0.2–0.5 mm long, back of the fruit smooth; plants annual (collections often with slender fibrous roots); corolla 3–4 mm long; a common species *D. teres*
- 4b. Top of the fruit glabrous or with few minute white hairs, back of the fruit with 3 longitudinal ribs; plants mostly perennial (collections with thick taproots); corolla 8–10 mm long; rare ... *D. apiculata*

- 5a. Fruits dehiscent, rounded and indehiscent at the apex or opening slightly at the apex but mericarps then often separating from the base and opening slightly at the base; stipular awns mostly glabrous; leaves usually chartaceous; commonly collected *Spermacoce ocymifolia*
- 5b. Fruits (mericarps) indehiscent or opening slightly near the top; stipular awns with thin hairs; leaves usually drying stiffly chartaceous; rarely collected *D. sarmentosa*

Diodia apiculata (Willd. ex Roem. & Schult.) K. Schum. in Engler, Bot. Jahrb. 10: 313. 1889. *Spermacoce apiculata* Willd. ex Roem. & Schult., Syst. Veg. 3: 531. 1818. *D. rigida* (Willd. ex Roem. & Schult.) Schlechtend. & Cham., Linnaea 3: 301. 1828. *Spermacoce rigida* Willd. ex Roem. & Schult., Syst. Veg. 3: 531. 1818, not *S. rigida* Salisb. 1796. Figure 6.

Herbs or subshrubs 9–40 cm tall, stems erect or procumbent, perennial and usually woody and branched at the base, leafy stems 0.5–3 mm thick, hirsutulous to hispidulous with whitish hairs ca. 0.3 mm long or with sparse longer hairs to 1 mm long (rarely glabrous); **stipule** sheath 1–2 mm long, with 6–9 setae 3–10 mm long. **Leaves** opposite, often closely spaced, sessile; **leaf blades** 10–30 mm long, 1.5–7 mm broad, linear-lanceolate to narrowly linear-oblong, broadest near the base, apex gradually narrowed and acute with slender tip, base obtuse to subtruncate, margins usually revolute, drying subcoriaceous, hispidulous or hirsute above and below, 2° veins 2–3/side or obscure. **Inflorescences** fasciculate, ca. 5 mm broad, with 2–8 flowers at a node, flowers sessile. **Flowers** ca. 10 mm long, hypanthium 2–2.5 mm long, 1–1.5 mm diam. (3–4 mm at the mouth), calyx lobes 1.8–2.2 mm long, unequal, subulate-lanceolate, erect, green; **corolla** funnelform to campanulate, white to rose, glabrous on the exterior, tube 4–8 mm long and 1–1.5 mm diam., lobes 2–5 mm long, broadly ovate to triangular, 1.5–3 mm broad at the base; **stamens** with filaments 0.5–0.8 mm long, anthers 0.7–1.7 mm long; style 5–8 mm long. **Fruits** 2.5–3(–4) mm long, glabrous or puberulent, mericarps with 3 longitudinal costae (ribs) on the curved dorsal (abaxial) side, obovoid, flat on the inner (adaxial) side, 1.5–2.2 mm broad, calyx lobes to 2 mm long.

Plants of seasonally very dry deciduous formations, from near sea level to 300 m (to 1600 m elevation in Honduras and to 2000 m in Guatemala). Probably flowering throughout the year in northern Central America. It is primarily found in the region around Liberia, Guanacaste, and is collected in the wet season in Costa Rica. The species ranges from Mexico and the West Indies through Central America to Brazil.

Diodia apiculata is distinguished by the setose stipular sheaths, narrow sessile stiff scabrous leaves, the small axillary flowers, and the mericarps with three longitudinal ribs. The mericarps are often sparsely puberulent, in contrast to the very similar *D. teres*.

Diodia brasiliensis Spreng., Syst. Veg. 1: 406. 1824. *D. polymorpha* Cham. & Schlechtend., Linnaea 3: 344. 1828. *D. brasiliensis* var. *angulata* (Benth.) Standl., Carnegie Inst. Wash. Publ. 461: 90. 1935. *Triodon angulatum* Benth., Pl. Hartw. 70. 1840. Figure 1.

Small **shrubs** to 1 m tall, much-branched, leafy stems 0.3–2(–5) mm thick, glabrous (minutely puberulent), with 4 longitudinal ribs and 4-angled; **stipule** sheath small (0.5 mm), setae to 2 mm long. **Leaves** opposite or pseudovercillate with 4, 6, or 8 small leaves at a node on reduced axillary shoots (sometimes appearing to be anisomorphic with pairs of leaves differing in size), petioles 0–4 mm long; **leaf blades** 4–15(–20) mm long, 1–4(–5) mm broad, oblong to elliptic, apex bluntly acute, base acute and decurrent on petiole, drying chartaceous and dark, scabrous along the margin, 2° veins 2/side or obscure. **Inflorescences** often spiciform with flowers verticillate in the axils of greatly reduced distal leaves, capitulae 3–5 mm broad, flowers sessile. **Flowers** 3–4 mm long, hypanthium 0.3–0.5 mm long, calyx lobes 4, ca. 0.5 mm long; **corolla** white, tube 1–2 mm long, lobes 4(–5), ca. 1 mm long. **Fruits** broadly turbinate, 2 mm long (including the calyx lobes), 2 mm diam., glabrous, the persistent calyx lobes ca. 0.7 mm long, the mericarps usually remaining attached to each other at the base, smooth on their abaxial surfaces.

Small plants of open or forested sites in evergreen formations, from 600 to 1000 m elevation in most of Central America (near sea level in Belize). Probably flowering and fruiting throughout the year. The species ranges from Mexico to Brazil.

Diodia brasiliensis is recognized by its many-branched erect stems and the small leaves often pseudovercillate and drying black. This species is only known from collections by Brenes near San Ramón and it may not be native to Costa Rica. Some of this material had been annotated as *C. polymorpha*, now considered to be a synonym of *D. brasiliensis*.

Diodia sarmentosa Sw., Prodr. Veg. Ind. Occ. 30. 1788.

Herbs, stems procumbent to scandent, to 4 m long, sometimes forming tangles, leafy stems 0.7–4 mm thick, with 4 longitudinal ridges, hispidulous with hairs 0.3–0.6 mm long; **stipule** sheaths 1–3 mm long, bearing more

than 6 brown setae 4–8 mm long on each side, setae with minute thin hairs distally. **Leaves** opposite, petioles 0–3 mm long; **leaf blades** 3–6 cm long, 0.8–2.5 cm broad, lanceolate to oblong-lanceolate, narrowly oblong-elliptic or narrowly ovate, apex acuminate, base obtuse, margins minutely aculeate-serrulate, drying subcoriaceous, scabrous and hispidulous above and below, with short (0.1–0.2) scabrous hairs and longer 0.2–0.5 mm hairs, 2° veins 3–5/side, deeply impressed above and prominent below, strongly arcuate-ascending. **Inflorescences** glomerules of 1–5 flowers in each axil, 5–15 mm broad, often becoming verticillate in fruit, bracts linear-lanceolate. **Flowers** with hypanthium ca. 2 mm long and 1 mm diam., calyx lobes usually 2 large and 2 small, to 2.5 mm long, persistent; **corolla** white, tube 1–1.5 mm long, lobes 1–1.5 mm long. **Fruits** splitting into 2 mericarps, 3.5–5 mm long, 2–2.8 mm broad, obovoid, persisting sepals 1–2 mm long, sparsely puberulent with short (0.2 mm) straight hairs, abaxial surface without ribs; **seeds** ca. 3×1.6 mm, dark brown, smooth.

Scandent plants of evergreen or partly deciduous forest formations, from near sea level to 900 m elevation (to 1500 m in Guatemala). Flowering and fruiting in December–May. The species is rarely encountered in southern Central America, though it occurs on Cocos Island. The species ranges from Mexico and the West Indies into northern South America, and it occurs in Africa.

Diodia sarmentosa is recognized by the thin stipular setae, stiff subsessile leaves with deeply impressed and strongly ascending secondary veins, very small axillary flowers, and small two-parted fruit.

Diodia serrulata (P. Beauv.) G. Taylor in Exell, Cat. S. Tomé 220. 1940. *Spermacoce serrulata* P. Beauv., Fl. Oware 1: 39, t. 23. 1805. *D. maritima* Thonning ex Schumacher, Beskr. Guin. Pl. 75. 1827.

Prostrate or clambering **herbs**, sometimes forming mats, stems to 1.5 m long, leafy stems 1.2–4 mm thick, glabrous and brownish, at first with prominent wings but becoming quadrangular or terete; **stipule** sheath 1.5–2.5 mm long, to 3 mm broad, with 3–5 linear awns 0.5–3 mm long, glabrous or with a few minute hairs. **Leaves** opposite or sometimes appearing verticillate (4), often crowded on short lateral branches, subsessile or with short (2 mm) winged petioles; **leaf blades** 10–45 mm long, 4–13 mm broad, narrowly elliptic to lanceolate, oblong-lanceolate or narrowly elliptic-oblong, apex acute, gradually narrowed to the cuneate base and decurrent on petiole, drying stiffly chartaceous and grayish brown above, glabrous above, slightly scabrous beneath, 2° veins 3–4/side. **Inflorescences** of solitary axillary flowers (2/ node), subsessile on pedicels ca. 1 mm long. **Flowers** glabrous externally, calyx lobes 4; **corolla** white, 6–7 mm long, lobes 4, 2 mm long; anthers 0.9 mm long. **Fruits**

5–6 mm long, ca. 3 mm wide, splitting into 2 indehiscent mericarps, glabrous and persisting calyx lobes to 2 mm long; **seeds** 2.1–2.3 mm long, 1.4–1.6 mm broad, dark reddish brown and smooth.

Rarely collected plants restricted to areas close to the Caribbean seashore. Probably flowering and fruiting throughout the year. The species ranges from British Honduras and the West Indies to Colombia; it also occurs on the west coast of Africa.

Diodia serrulata is distinguished by its ocean-side habitat, often prostrate habit, glabrous parts, awned stipular sheath, and solitary flowers. The leaf edges are entire and quite scabrous but not serrulate. We have seen only the following from Costa Rica: *Gómez-Laurito 12109* CR, Playa Cacles near Pto. Viejo, and *Shank & Molina 4336* F, Playa del Parismina, Limón.

Diodia teres Walt., Fl. Carol. 87. 1788. *D. prostrata* Sw., Prodr. Veg. Ind. Occ. 30. 1788. Figure 6.

Annual **herbs** to 40 cm tall, usually stiffly erect, stems simple or branched near the base, leafy stems 0.7–2.3 mm thick, with 4 longitudinal ribs, hispidulous and scabrous with short (0.1–0.3 mm) and longer (1–2 mm) hairs, internodes usually 0.5–3 cm long; **stipule** sheaths 1–2 mm long, with 6–9 conspicuous glabrous awns 2–8 mm long. **Leaves** sessile, **leaf blades** (4–)10–30(–45) mm long, 1–6(–8) mm broad, linear to linear-elliptic or linear-oblong, broadest near the base, apex acute, tip 0.5–1.8 mm long, usually revolute along the thickened margin, scabrous-hispid along the margin, drying subcoriaceous, scabrous or hirsute above, scabrous and hispidulous beneath with thin white hairs 0.7–1.7 mm long, 2° veins usually obscure. **Inflorescences** of sessile solitary or clustered flowers in leaf axils, the glomerules 3–6 mm broad and with 2–4 flowers at each node. **Flowers** with hypanthium 1.5–2 mm long, calyx lobes often unequal, 0.5–3 mm long and 0.1–0.8 mm broad, green; **corolla** pink to purplish (white), tube 3–4.5 mm long, 0.5–0.7 mm diam. near the base, glabrous to sparsely puberulent, lobes 1.5–2.5 mm long, 0.5–1.5 mm broad; **stamens** with filaments 0.5 mm long, anthers 0.5–0.7 mm long, style 3–5 mm long. **Fruits** 2–5 mm long, with erect thin hairs at apex and persisting calyx ca. 1 mm long, mericarps (cocci) 1.8–2.5 mm broad, abaxial surface without longitudinal ribs (in Central America), minutely pubescent.

Plants of seasonally very dry deciduous formations (especially sandy grass savannas) on the northern Pacific slope, 0–300 m elevation (to 1400 m in Guatemala). Flowering and fruiting in June–January. The species ranges from the eastern United States to South America.

Diodia teres is recognized by its short height,

stipular setae, stiff narrow sessile scabrous leaves (drying grayish), very small axillary pink flowers, and distinctive mericarps (cocci).

Duroia Linnaeus f.

Small **trees** or shrubs, dioecious, branchlets tetragynous or terete, with expanded areas housing ants in a few species, glabrous or puberulent; **stipules** interpetiolar and intrapetiolar, forming a cap over the shoot apex, circumsessile and deciduous. **Leaves** opposite or verticillate with 3–5 leaves at a node, sessile or petiolate, entire and pinnately veined, drying thin-chartaceous to coriaceous. **Inflorescences** terminal, ♂ flowers subcapitate, umbellate, to corymbose or cymose, sessile or pedunculate, ♀ flowers 1–3 at the tip of the stem, sessile or pedunculate, the flowers usually short-pedicellate. **Flowers** unisexual, radially symmetrical, usually large, hypanthium oblong to hemispheric, calyx cupular to tubular, truncated and entire or with 5–9 lobes, **corolla** salverform, white to yellowish white, often thick or fleshy,

sericeous on the outer surfaces, glabrous or pilose in the tube within, corolla lobes 5–9(–12), convolute in bud; **stamens** 5–9, inserted in the corolla tube, subsessile or sessile, anthers dorsifixed, linear, acute, included; **ovary** 1–5-locular, with 5–6 parietal placentas sometimes joined in the center, ovules many and biseriate, stigmas 2. **Fruits** baccate, globose to oblong, large with a thick fleshy cortex, with 1–4 locules; **seeds** large and horizontal, flattened and suborbicular, immersed in pulp, testa thin.

A tropical American genus of about 25 species, with 2 or 3 species in Central America. *Duroia hirsuta* (Poepp. & Endl.) Schumann and *D. petiolaris* Hook. f. have swollen elongated areas of the stem with longitudinal slits, and *D. saccifera* Hook. f. has saccate ant domatia at the base of its leaf blades. Our species have no such structures and are not known to have an association with ants. Specimens may resemble species of *Amaioua*, *Hippotis*, and *Randia*.

Key to the Species of Duroia

- 1a. Leaves subsessile, obovate, with hairs ca. 2 mm long, minor venation lineolate; calyx ca. 4 mm long, male corolla lobes 5–8 mm long *D. costaricensis*
- 1b. Leaves petiolate, broadly oblong to elliptic-obovate, with hairs ca. 0.5 mm long, minor venation not lineolate; calyx ca. 8 mm long, male corolla lobes ca. 10 mm long *D. utleyorum*

Duroia costaricensis Standl., Contr. U.S. Natl. Herb. 20: 208. 1919. Figure 25.

diam., oblong to ovoid, covered with long hairs but with the surface visible beneath the hairs.

Shrubs or small **trees**, 5–10 m tall, leafy branchlets 2–6 mm thick, hirsutulous with straight thin ascending hairs ca. 2 mm long, becoming reddish brown and glabrescent; **stipules** 15–45 mm long, caducous, densely hirsute-sericeous on the outer surfaces. **Leaves** closely crowded at the tips of branchlets, subsessile with petioles 2–6(–10) mm long and ca. 2 mm thick, densely hirsute; **leaf blades** (7–)9–19 cm long, (3–)4–7.5 cm broad, oblong-obovate to narrowly obovate, widest at or above the middle, apex abruptly narrowed and slender acuminate or caudate-acuminate, the narrow (ca. 2 mm) tip 5–13 mm long, gradually narrowed to the cuneate base, drying thin-chartaceous, often brown, with long (1.5–2.5 mm) thin straight or slightly crooked hairs on upper and lower surfaces, 2° veins 5–8/side, 3° veins subparallel between the secondaries. **Male flowers** 8–15 and subcapitate or fasciculate-cymose (tightly clustered at the tips of stems), 15–20 mm long, outer surfaces of calyx and corolla densely sericeous with ascending hairs, calyx 4–5 mm long, calyx lobes 6–7 and equalling the tube; **corolla** 11–15 mm long, white, corolla lobes 6–8, 5–8 mm long, equalling or longer than the tube. **Female flowers** 1(–3) subsessile at apex of branchlets, hypanthium ca. 8 mm long, densely sericeous, with hairs 2–3 mm long, calyx lobes ca. 4 mm long, linear. **Fruits** 1–3 at the tips of branchlets, subsessile, ca. 22 mm long, 12 mm

Small trees of lowland rain forest formations of the Golfo Dulce region, from 10 to 200 m elevation. Flowering in March and May–June; fruiting in July–August and October. This species is known only from southernmost Costa Rica.

Duroia costaricensis is recognized by the subsessile thin hirsute obovate leaves clustered at the ends of stems, the terminal clusters of subsessile sericeous flowers, and the hirsute subsessile fruits at the tips of branches. The type collection (Pittier 6803 us) came from Sierpe, but most of the other collections come from near Rincón de Osa. *Duroia hirsuta* (Poepp. & Endl.) Schumann of South America has inflated stems, longer petioles, generally longer leaves, pedunculate male flowers, and larger fruit. *Duroia genipifolia*, now *Randia genipifolia* (Standl. & Steyererm.) Lorence, of Guatemala has less hirsute leaves with better defined petioles and more elliptic blades. All three species are similar in appearance. This species also resembles Costa Rican material of *Hippotis*.

Duroia utleyorum Dwyer, sp. nov.

Frutices vel arbores 1.5–7 m altae. Foliae lamina oblonga vel oblongo-elliptica, 10–23 cm longa, 6–14 cm lata; nervi laterales 7–11, hirsutulis; petiolis 6–23 mm longis. Flores lobis calycinis ca. 1 mm longis; corollae tubo ca. 12 mm longo, lobis ca. 10 mm longis. Fructus immaturi solitarii terminales.

TYPE—*Liesner 1774* (holotypus CR, isotypus MO), from Rincón de Osa, Costa Rica.

Shrubs or small trees, (1.5–)4–7 m tall, leafy stems 2–5 mm thick, densely pubescent with thin straight yellowish hairs 0.3–0.7 mm long; stipules ca. 9 mm long and 4 mm broad, ovate-lanceolate with a sharp acuminate apex, united (intrapetiolar) to form a short (1 mm) basal tube, with thin brown margins and hirsute. Leaves with petioles 6–23 mm long, 1–3 mm thick, hirsutulous with yellowish hairs; leaf blades 10–23 cm long, 6–14 cm broad, broadly oblong to broadly obovate or elliptic-oblong, apex short-acuminate with tip 5–15 mm long, base obtuse to rounded and subtruncate, drying chartaceous, brown, pubescent on the major veins above, densely hirsute on the veins beneath with yellowish hairs ca. 0.7 mm long, sparsely hirsutulous between the veins, 2° veins 7–11/side. Inflorescences of solitary terminal female flowers, on pedicels ca. 8 mm long; male inflorescences of 3–7 terminal sessile flowers. Flowers whitish pilosulous to sericeous; ♂ flowers with calyx tube 5–6 mm long, calyx teeth ca. 1 mm long, remote; corolla (preanthesis) white and probably salverform, tube 12 mm long, lobes 10 mm long, convolute and apparently lanceolate. Fruits solitary and terminal, the immature fruit ca. 15 mm diam. and globose with persisting calyx 10 mm high and 8 mm diam., densely hirsutulous with hairs ca. 0.5 mm long.

A species of lowland (10–300 m) rain forest formations on both the Caribbean and Pacific slopes of Costa Rica. Young flowers were collected in February on the Osa Peninsula (*Jiménez et al. 650* CR, *Liesner 1774 & 1853* CR, MO); young fruits were collected along the Río Sarapiquí in May (*Hartshorn 1486* CR).

Duroia utleyorum is recognized by its larger broad leaves, sessile terminal flowers, and lowland

evergreen forest habitat. This poorly known species is more likely to be confused with species of *Randia* than with its local cogener. Many important collections have been made in Costa Rica by Kathleen and John Utley.

Elaeagia Weddel

Trees or large shrubs, branchlets terete and puberulent; stipules interpetiolar (also intrapetiolar in some species), often covering the shoot apex, caducous or deciduous. Leaves opposite, petiolate or subsessile; leaf blades entire and pinnately veined, usually puberulent, thin-chartaceous to coriaceous, domatia present or absent. Inflorescences terminal, paniculate (rarely racemose), many-flowered, pedunculate. Flowers bisexual, radially symmetrical, usually small, hypanthium hemispheric to turbinate, often sulcate on opposite sides, calyx tube cupular and spreading or inflated, calyx lobes 5 or none, short or inconspicuous; corolla campanulate to funnel-form, corolla white to yellow-white, tube usually short and broad, corolla lobes 5, oblong, rotate to reflexed, convolute to slightly imbricate in bud; stamens 5, inserted between the corolla lobes, filament densely puberulent at the base, anthers dorsifixed, oblong, exerted; ovary 2-locular, placentas peltate and attached to the septum, ovules many in each locule, crowded and vertical, style short, stigmas 2 with obtuse tips. Fruits small woody capsules, crowned or encircled by the persistent calyx, loculicidally and basipetally dehiscent into 2 valves, the valves splitting at the top; seeds many, minute, elongate with membranous or winged testa.

A genus of about 12 species in Mexico, Central America, Cuba, and tropical South America. *Elaeagia utilis* Weddel of Colombia is the source of a protective lacquer. The genus was misspelled as *Elaeagnia* in the Flora of Panama (1980). Three mesoamerican species of *Elaeagia* were compared by Lorence (in Bol. Soc. Bot. Mexico 45: 65–69. 1983). The small rounded capsules resemble those of *Chimarrhis*.

Key to the Species of *Elaeagia* in Costa Rica

- 1a. Leaf blades usually 9–25 cm wide, often subsessile and sometimes auriculate at the base, with 11–19 pairs of secondary veins; inflorescences usually much-branched panicles *E. auriculata*
- 1b. Leaf blades usually 3–9 cm wide, clearly petiolate and gradually narrowed to the base, with 6–12 pairs of secondary veins; inflorescences with few lateral branches (paniculate with many branches in *E. myriantha*) 2
- 2a. Calyx cup entire distally; flowers separate and borne on long (4 mm) slender pedicels *E. nitidifolia*
- 2b. Calyx cup with undulate or minutely lobed margin; flowers crowded and subsessile in small groups of 2–5 3

- 3a. Corolla tubes 1–1.5 mm long, lobes ca. 1.7 mm long; leaf blades with 7–9 major 2° veins per side, without tufted domatia along the 2° veins; Cordillera de Tilarán *E. uxpanapensis*
- 3b. Corolla tubes 2.2–3.4 mm long, lobes 0.4–1 mm long; leaf blades with 9–12 major 2° veins per side, often with tufted domatia along the 2° veins; General Valley *E. myriantha*

***Elaeagia auriculata* Hemsl., Diagn. Pl. Nov. Mexic. 32. 1879. Figure 39.**

Shrubs or small trees, 3–10 m tall, leafy branchlets 3–8 mm thick, puberulent or glabrescent; **stipules** 20–50 mm long, to 20 mm broad, oblong and rounded at apex, reddish brown and with subparallel venation. **Leaves** with petioles 0–10 mm long, 1.5–3 mm thick, often difficult to see on auriculate leaves; **leaf blades** (12–)15–40 cm long, (6–)9–25 cm broad, elliptic-obovate to broadly elliptic or obovate, apex abruptly narrowed or rounded and obtuse to short-acuminate, gradually narrowed to the cuneate or auriculate base, drying chartaceous to subcoriaceous, dark brown above, upper surface glabrous to short (0.2–0.5 mm) pubescent, lower surfaces sparsely to densely pubescent with short stiff hairs, 2° veins 11–16(–19)/side, 3° veins usually subparallel and the 4° veins raised beneath. **Inflorescences** 12–20 cm long, to ca. 20 cm broad, many flowered and much-branched panicles, solitary or 3 from the terminal leaf-bearing node, primary peduncles 3–5 cm long, with 3–4 pairs of 1° opposite lateral branches, puberulent, flowers in racemose or cymose distal branches, pedicels 1–5 mm long. **Flowers** 5–7 mm long, hypanthium ca. 1 mm long, calyx cup ca. 1 mm long (including the lobes), calyx lobes 0.5–1 mm long and 1.5 mm broad, glabrous; **corolla** white, tube 1–2 mm long, lobes 1–2 mm long and becoming reflexed; **stamens** with filaments 2 mm long, glabrous distally, anthers ca. 1.5 mm long. **Fruits** 3–5 mm long and 3–4.5 mm broad, short-ovoid and broadly rounded, calyx persistent and visible on the lower part of the capsule, opening at the top (but not splitting to the base), becoming dark brown or black; **seeds** 0.6–1 mm long, body of the seed 0.2–0.4 mm long, with a thin membranous wing at opposite ends.

Trees of evergreen lower montane cloud forest and rain forest formations, along the central highlands, from Volcán Tenorio in the Cordillera de Guanacaste to San Vito de Coto Brus, and on the Caribbean slope, ranging from 350 to 1700 m elevation. Flowering in November–March; fruiting in February–June. The species ranges from Guatemala and Honduras to eastern Panama.

Elaeagia auriculata is recognized by the large oblong stipules, short petioles, large broad leaves often auriculate at the base, large terminal panicles, small flowers with truncated calyx lobes and very short corolla tubes, and short rounded capsules opening only at the top. The very large leaves with an auriculate base obscuring the petiole are very distinctive, but not all specimens have this kind of leaf base (see below). The small capsules make this species look like species of *Chimmarhis*.

Elaeagia karstenii Standley was recorded for Costa Rica's flora (Standley, 1938) on the basis of a single sterile collection: *Valerio 1665* f, from Tapantí at 1300 m. The longer (10–14 mm) and slender (1.5–2 mm) petioles and the smaller sparsely puberulent leaves do resemble some examples of *E. karstenii* from South America. However, longer petioles with cuneate (not auriculate) lamina bases do occur in specimens that otherwise appear to be typical of *E. auriculata*: *Lent 3734* and *Molina et al. 17346* (note: both of the latter collections come from below 1000 m elevation). Thus, it is possible that *Valerio 1665* is an aberrant juvenile shoot of an *E. auriculata* plant. Alternatively, expanding the concept of *E. auriculata* to include material with longer petioles, cuneate leaf bases, and smaller more glabrous leaves may require the inclusion of South American specimens and synonymizing *E. karstenii*.

***Elaeagia myriantha* (Standl.) C. M. Taylor & Hammel, Novon (in press). *Sickingia myriantha* Standl., Publ. Field Columb. Mus., Bot. Ser. 7: 27. 1930. *Holtonia myriantha* (Standl.) Standl., Trop. Woods 30: 37. 1932. *Simira myriantha* (Standl.) Steyerem., Mem. New York Bot. Gard. 23: 306. 1972. *Deppea panamensis* Dwyer, Ann. Missouri Bot. Gard. 67: 145. 1980.**

Trees, 8–25 m tall, leafy stems 2–7 mm thick, glabrous, drying brownish or grayish; **stipules** 3–5 mm long, short-tubular with rounded lobes, often splitting between the leaf bases and remaining entire above the petioles (ligulate), translucent, persisting. **Leaves** with petioles 5–20(–30) mm long, 0.8–2 mm thick, glabrous, drying reddish brown to dark brown; **leaf blades** (5–)9–20 cm long, (2–)3.5–7(–8) cm broad, elliptic-oblong to elliptic or elliptic-obovate, apex acuminate with tip 10–15 mm long, base gradually narrowed and acute or cuneate and decurrent on petiole, drying chartaceous, greenish to dark brown, glabrous above, glabrous or minutely (0.05 mm) papillate-puberulent on the veins beneath, 2° veins 9–12/side, domatia with short hairs present in the vein axils. **Inflorescences** 10–22 cm long, 12–18 cm broad, pyramidal with usually opposite 1° branches, peduncles 8–40 mm long, 1.5–2.5 mm thick, minutely puberulent, larger (2 cm) narrow leaf-like bracts present or absent, with smaller (0.5–3 mm) bracts and bracteoles subtending branches and flowers, flowers usually subsessile in groups of 2–5. **Flowers** glabrous externally, hypanthium 1–1.5 mm long, obconic, calyx cup 0.1–0.3 mm long,

1.3 mm diam., calyx lobes 0.2–0.4 mm long, broadly triangular; **corolla** tubular-campanulate, cream white, tube 2.2–3.4 mm long, ca. 2 mm diam., lobes 5, 0.4–1 mm long, triangular, slightly imbricate in bud; filaments exerted 0.5–2 mm, anthers ca. 1.5 mm long; stigmas 1–2 mm long. **Fruits** ca. 3 mm long, 3 mm broad at the top when opened, dark brown; **seeds** 0.3–0.5 mm long, broad, reticulate.

Collected with flowers in January in the General Valley at 975 m elevation (*Skutch 2387* US, the only Costa Rican collection). This species is also known from the Andes of Colombia and Venezuela.

Elaeagia myriantha is distinguished by the large pyramidal terminal panicles of small white flowers with broad cylindrical corolla tube and minute lobes and the almost glabrous leaves with pubescent domatia in the vein axils. These are unusual in that they are found in the axils of some 3° veins as well as along the midvein. The Colombian type (*H. H. Smith 1810* F) has smaller leaves than most other collections.

Elaeagia nitidifolia Dwyer, Ann. Missouri Bot. Gard. 67: 157. 1980. *Chiococca jefensis* Dwyer, loc. cit. 67: 88, f. 19. 1980. Figure 39.

Trees to 12 m tall, leafy stems 2–4 m thick, glabrous, becoming terete; **stipules** 3–5 mm long, to 4 mm broad, cylindrical at first but splitting, rounded above the petiole and deeply split between the petioles (becoming ligulate), glabrous. **Leaves** closely clustered distally, petioles 6–17(–25) mm long, 1–2 mm thick, glabrous; **leaf blades** 10–23 cm long, 3.5–8 cm broad, oblanceolate to narrowly oblong-obovate or elliptic-oblong, apex short-acuminate, tip 5–8 mm long, gradually narrowed to the cuneate base and decurrent on petiole, drying chartaceous, subglabrous above, minutely (0.05–0.1 mm) papillate-puberulent on the veins beneath, 2° veins 8–12/ side. **Inflorescences** solitary or 3, terminal, 8–16 cm long, open panicate with distant cymose flower groups, peduncles 3–5 cm long, glabrous, pedicels 3–10 mm long, slender. **Flowers** with hypanthium and calyx continuous, ca. 3 mm long and 3–4 mm broad distally, calyx cup entire distally; **corolla** white, tube 1–2 mm long, lobes 5, 3–4 mm long, 1.3–2 mm broad, oblong; anthers 1.5–2 mm long; stigma lobes 2–2.5 mm long. **Fruits** to 6 mm long and 10 mm broad, turbinate, truncated distally.

Trees of wet evergreen forest formations of the Caribbean slope at 400–800 m elevation. The species is only known from the Rara Avis site in Heredia and was collected flowering in September (*O. Vargas 128* CR, MO). The species is also known from central and eastern Panama.

Elaeagia nitidifolia is distinguished by its unusual ligulate stipules, the open few-flowered in-

florescences, long pedicels, and cupulate calyx with entire margin. Specimens may resemble *Rustia occidentalis* (with porate anthers) and *Simira myriantha* (with smaller corolla lobes and domatia).

Elaeagia uxpanapensis D. Lorence, Bol. Soc. Bot. Méx. 45: 66. 1983 (1984). Figure 39.

Trees, 15–40 m tall, 55–80 cm dbh, leafy stems 3–9 mm thick, flattened in early stages, glabrous and becoming terete; **stipules** 8–16 mm long, 3–7 mm broad, ovate lanceolate with overlapping margins, acute at the apex, glabrous and drying dark, deciduous. **Leaves** with petioles 3–12 mm long, ca. 1.5 mm thick, glabrous, drying dark; **leaf blades** 6–15(–20) cm long, 3–7(–9) cm broad, broadly elliptic to broadly oblong or slightly elliptic-obovate, apex abruptly narrowed and bluntly obtuse, base cuneate and slightly decurrent on petiole, drying stiffly chartaceous to subcoriaceous, dark grayish brown above, glabrous above, with a few thin yellowish hairs 0.3–1 mm long along the side of the midvein beneath and in leaf axils (= domatia?), 2° veins 7–9/ side. **Inflorescences** solitary and terminal or axillary to distal leaves, 6–14 cm long (perhaps enlarging in fruit), narrowly panicate, peduncles 2.5–5 cm long, glabrous, proximal lateral branches 1–6 cm long, usually minutely appressed-puberulent, flowers sessile in opposite or terminal glomerules of 2–5 flowers, bracts 0.5–3 mm long. **Flowers** ca. 4 mm long, yellowish green, hypanthium 1–1.8 mm long, minutely puberulent at the base, calyx lobes 0.5–1 mm long; **corolla** white, salverform to short-funnelform, glabrous externally, tube 1–1.5 mm long, scarcely exceeding the calyx lobes, lobes 4–5, ca. 1.7 mm long and 1 mm wide, bluntly rounded distally, with long hairs at the mouth of the tube and base of lobes within; **stamens** 4–5, filaments 2–4 mm long, anthers 0.6–0.7 mm long, oblong; style and stigma 3–4 mm long, stigmatic lobes 1 mm long. **Fruits** not seen (probably ca. 2 mm long and 2.5 mm broad).

Only known from the wet Caribbean slopes of the Cordillera de Tilarán at ca. 900 m elevation. Immature flowers were collected in July (*Haber & Bello 1928* CR, MO) and mature flowers in May (*Herrera 600* CR, MO). This species is known only from the Río Peñas Blancas valley below Monteverde and the Reserva Forestal de San Ramón (*Gómez-Laurito 12065* CR), in Alajuela Province. The species is also known from southern Mexico.

Elaeagia uxpanapensis is recognized by the opposite subsessile flower clusters along the branches of the inflorescence, the very small flowers, and the two-locular ovule with placentas borne on the septum. The large size of the trees, flattened young leafy stems, and occasional domatia along the midvein are additional distinctive characteristics. When first discovered in Costa Rica, specimens were thought to be a species related to *Warszewiczia schwackei* Schum. of South America.

Exostema L. Richard

Shrubs or trees, branchlets usually terete, glabrous or puberulent; **stipules** interpetiolar, small, entire or bifid, deciduous or persisting. **Leaves** petiolate or subsessile; **leaf blades** entire, drying membranaceous to subcoriaceous, domatia sometimes present. **Inflorescences** terminal or axillary panicles with the distal flowers usually in groups of 3, or of solitary axillary flowers, with or without bracts, pedicels present. **Flowers** bisexual, radially symmetrical (or somewhat bilaterally symmetrical by curvature of the corolla tube), small to large, hypanthium cylindrical or obovoid, calyx with (4–)5(–6) lobes, lobes broad or narrow; **corolla** short or long, salverform, tube often long and narrow, throat glabrous or barbate, corolla lobes (4–)5, oblong or linear, imbricate in bud with 2 exterior; **stamens** 5 inserted at the base of the corolla tube, filaments essentially free, elongate and fi-

liform, anthers basifixed, linear, usually exserted; **ovary** 2-locular, placentas peltate on the septum with many ascending ovules, style filiform, usually exserted, stigma capitate or bilobed. **Fruits** capsular, woody, 2-locular, ellipsoid to cylindrical, septicidal from apex, bivalved, valves entire or bipartite from the apex; **seeds** many, imbricate, flattened and oblong, testa forming a thin marginal wing around the body of the seed.

A genus of ca. 35 species of the American tropics, especially abundant in drier vegetation of the West Indies. The flowers with narrow corolla lobes almost equalling the length of the slender corolla tube and the long linear exserted anthers make the flowers quite distinctive. Our species are confined to deciduous or partly deciduous vegetation.

Key to the Species of *Exostema*

- 1a. Flowers solitary in the axils of leaves, 6–8 cm long, corolla lobes 4–5; fruit ca. 1 cm broad, erect; leaf blades usually clearly decurrent on the petiole, domatia absent *E. caribaeum*
- 1b. Flowers more than 1, borne in small panicles axillary to distal leaves or terminal, 2–3 cm long; corolla lobes 6; fruit 3–4 mm broad, pendulous; leaf blades very slightly decurrent on the petiole, domatia often present *E. mexicanum*

Exostema caribaeum (Jacq.) Roem. & Schult., Syst. Veg. 5: 19. 1819. *Cinchona caribaeum* Jacq., Enum. Pl. Carib. 16. 1760. *E. longicuspe* Oerst., Vidensk. Meddel. Dansk. Naturhist. Foren. Kjobenhaven 1852: 48. 1853. Figure 31.

Shrubs or small trees to 8 m tall, leafy branchlets 1.2–3.5 mm thick, glabrous; **stipules** 1–3(–5) mm long, 2–3 mm broad at the base, triangular to subulate, glabrous on the abaxial surface but slightly ciliate along the distal edge, persistent. **Leaves** evenly spaced along the stems, petioles 6–12(–16) mm long, 0.4–0.8 mm thick; **leaf blades** 4–11 cm long, 1.5–5 cm broad, elliptic-ovate to ovate, apex gradually narrowed and acuminate, tip 1–2 cm long, base obtuse to acute and decurrent on petiole, drying thin-chartaceous and dark, glabrous above, glabrous or pubescent with thin curved whitish hairs ca. 0.4 mm long beneath, often with short (0.5 mm) hairs (domatia) in the vein axils beneath, 2° veins 4–5/side. **Inflorescences** absent, the flowers solitary in distal leaf axils, bracts ca. 1 mm long, pedicels 4–10 mm long, ca. 0.5 mm thick (dry), glabrous. **Flowers** 6–8 cm long, hypanthium 3–5 mm long, 2–3 mm diam., glabrous, calyx lobes 0.5–1 mm long, broadly triangular; **corolla** white, glabrous, tube 23–45 mm long, 2–3 mm diam., often curved, lobes 25–40 mm long, ca. 2 broad and linear, becoming recurved; **stamens** 5, long-exserted, anthers 16–26 mm long, 0.2–0.3 mm broad (dry); stigma 2 mm long. **Fruits** 7–15 mm long, 6–14 mm broad, oblong-ellipsoid, smooth and dark brown externally; **seeds** 3–6 mm long and 3–4 mm broad, with a thin brownish wing on all sides and slightly longer at the 2 ends, body of the seed ca. 5 mm long and 3 mm broad.

Trees of deciduous and partly deciduous forests of the Pacific slope, from near sea level to 300 m elevation (to 1300 m in Guatemala). Rarely collected in Costa Rica (Guanacaste and adjacent Puntarenas provinces). In Central America flowering in June–August; fruiting in October–January and April. The species ranges from central Mexico to northern Costa Rica and the West Indies.

Exostema caribaeum is recognized by its restriction to seasonally very dry vegetation, the long flowers solitary in leaf axils, the long narrow corolla tube, long corolla lobes, and long slender exserted anthers. The woody bivalved fruit splitting down the broader side and the seeds surrounded by a short thin wing are also distinctive. We have not seen Oersted's type of *E. longicuspe* from Puntarenas (cf. Standley, 1938, p. 1295). This species is called "caribee bark tree" and "princewood" in the Caribbean, where the wood is used for making handles. The bark is used for treating fevers and malaria in Mexico.

Exostema mexicanum A. Gray, Proc. Amer. Acad. Sci. 5: 180. 1861. Figure 40.

Small to medium-sized trees to 20 m tall with trunks to 40 cm dbh, leafy branchlets 1.3–4 mm thick, glabrous

to sparsely puberulent, lenticels conspicuous, stems becoming grayish; **stipules** 1–3(–4) mm long, triangular and acuminate to short-tubular and cuspidate, deciduous. **Leaves** well spaced along the stems, petioles 4–10(–15) mm long; **leaf blades** (5–)6–15(–18) cm long, (2–)3–7.5(–10) cm broad, ovate-oblong to elliptic-oblong, apex long-acuminate, base obtuse to rounded and subtruncate, usually glabrous above and below except for the minute (0.2 mm) hairs (domatia) in the vein axils beneath, 2° veins 6–9/side. **Inflorescences** 3–6(–12) cm long, 4–7(–10) cm broad, terminal or axillary to distal leaves, primary peduncles 1.5–4 cm long, glabrous or minutely puberulent, trichotomous, lenticellate, bracts 1–2 mm long, distal flowers in groups of 3, often crowded, pedicels 2–4 mm long, minutely (0.1 mm) puberulent. **Flowers** ca. 2 cm long, hypanthium 1.5–2.4 mm long, glabrous or sparsely and minutely puberulent, calyx lobes 5–6, very small (0.5 mm) and deltoid/acute; **corolla** white to yellowish white or yellow, subglabrous or with thin curved whitish hairs, tube 7–10 mm long, 0.7–1.3 mm diam., lobes 6, ca. 9–12 mm long, 1.5 mm broad, oblanceolate-linear; **stamens** 6, filaments to 16 mm long, anther 3–4 mm long, 0.2–0.3 mm broad; style to 2 cm long, stigmas clavate, 0.6 mm long. **Fruits** 10–14 mm long, 3–4 mm broad, obovoid-clavate to narrowly oblong-obovoid, surface glabrous and dark brown with whitish lenticels, the 2 valves each splitting in 2 at the top; **seeds** 6–9 mm long, 2–3 mm broad, body of the seed ca. 2.5 × 1.5 mm, oblong, wing often lobed on 1 end.

Trees of deciduous and partly deciduous forests of the Pacific slope, from near sea level to 900 m elevation (to 1300 m in Guatemala). Flowering in July–September; fruiting in July and September–February. The species ranges from Tamaulipas, Mexico, to central Panama.

Exostema mexicanum is distinguished by its deciduous habitat and thin leaves, close clusters of narrow-tubed flowers in short axillary or terminal panicles, the long narrow corolla lobes, exserted linear anthers, and woody bivalved capsules with winged seeds. The bark has been boiled to make a treatment for malaria and fevers. This species is rarely collected in Costa Rica.

Faramea Aublet

Shrubs or small trees, branchlets terete, 4-angled or flattened, usually glabrous; **stipules** interpetiolar and in-

trapetiolar, often forming a tubular sheath above the leaf base, short-triangular to long-aristate at apex (with 2 awns per node), persistent or deciduous. **Leaves** often held in a single plane, petiolate (rarely sessile); **leaf blades** entire, usually oblong to lanceolate, usually glabrous, lacking domatia, pinnately veined. **Inflorescences** terminal (rarely axillary), 1–many-flowered, corymbose to umbellate (rarely capitate), pedunculate, peduncle and branches often with a pale blue or purple color like the flowers, pedicels usually present. **Flowers** bisexual and radially symmetrical, monomorphic or distylous, hypanthium small, ovoid to turbinate, terete or angular, calyx cupular to short-tubular, truncate and entire to 4-lobed, persistent; **corolla** usually salverform, white to blue or lavender, tube short or long, usually narrow, glabrous, corolla lobes 4(–5), linear to lanceolate, valvate in bud, spreading or reflexed; **stamens** 4 (5, 6), inserted on the tube or at the throat, anthers linear, dorsifixed, linear, included or exserted; **ovary** 1-locular (rarely 2-locular in early stages), ovules 2 (less often 1), erect from a basal placenta, style filiform, with 2 short branches. **Fruit** baccate or drupaceous, transversely oblate (reniform) to subglobose, often broader than long, smooth or costate, deep blue to blue-black, 1-locular and 1- (rarely 2-) seeded; **seed** (pyrene) horizontal, transversely indented (excavated) and somewhat reniform, with thin testa.

A large genus of about 130 species, ranging from Mexico, Central America, and the West Indies through tropical South America. The unusual fruit (usually broader than long) and single seed help to distinguish this genus. A striking sky blue to lavender color of both the flowers and inflorescences characterizes a number of our species. The usually four-parted flowers, short-tubular stipules with only a single apex on each side, and a well-developed submarginal vein are additional characters found in many species. The fruits tend to have a leathery exocarp in *Faramea*, in contrast to the succulent exocarps of *Coussarea* and *Psychotria*. Despite these unusual traits, specimens of some species may look very similar to some species of *Psychotria*, *Coussarea*, and *Rudgea*.

Key to the Species of *Faramea*

- 1a. Flowers solitary or the inflorescence with 2–3 flowers (1–4 flowers per node); rarely collected 2
- 1b. Flowers few to many in pedunculate open inflorescences; commonly collected species 4
 - 2a. Leaf blades 12–20 cm long; peduncles 2–5 cm long, calyx and hypanthium ca. 12 mm long [Caribbean slope at 20–1100 m elevation in Costa Rica] *F. pauciflora*
 - 2b. Leaf blades 1–4 cm long; peduncles less than 2 cm long, calyx and hypanthium less than 5 mm long 3

- 3a. Inflorescences terminal; shrubs 3–4 m tall; Pacific slope, 1200–1700 m elevation *F. capulifolia*
- 3b. Inflorescences axillary; herbaceous subshrubs ca. 1 m tall; Caribbean slope, ca. 300 m elevation *F. myrticifolia*
- 4a. Leaves sessile or subsessile and the leaf blade usually rounded at the petiole, petioles 0–5 mm long 5
- 4b. Leaves definitely petiolate or if subsessile the leaf blades not rounded at the petiole, petioles 4–20 mm long 7
- 5a. Leaf blades narrowly oblanceolate, 10–16 cm long and 1.5–3.5 cm broad; Chiriquí Highlands at ca. 2000 m elevation *F. scalaris*
- 5b. Leaf blades usually oblong, 15–27 cm long and 6–17 cm broad; 0–500 m elevation 6
- 6a. Leaves strongly tripliveined, secondary veins united by a linear (melastome-like) lateral submarginal vein; southern Caribbean lowlands *F. trinervia*
- 6b. Leaves not strongly tripliveined, secondary veins loop-connected near margin; Golfo Dulce area *F. sessifolia*
- 7a. Leaves strongly tripliveined (like that of Melastomaceae); flowers and fruit bright blue; 0–800(–1000) m elevation *F. suerrensii*
- 7b. Leaves not strongly tripliveined and lacking strong lateral veins near the margin (sometimes present in *F. eurycarpa*), the 2° veins often loop-connected near the margin with the submarginal vein arcuate; flowers blue or white 8
- 8a. Inflorescences umbellate or fasciculate in the leaf axils, without lateral branches; flowers usually white 9
- 8b. Inflorescences paniculate, corymbose or cymose, with conspicuous lateral branches from the primary peduncle or central rachis; flowers blue or white 10
- 9a. Inflorescences fasciculate, some flowers subtended by ovate bracts 5–11 mm long; flowers not drying black; leaf blades to 17 cm long, usually oblong; 0–300 m elevation *F. parvibracteata*
- 9b. Inflorescences umbellate, lacking conspicuous bracts; flowers drying black; leaf blades to 11 cm long, elliptic; 1000–2300 m elevation *F. ovalis*
- 10a. Flowers with the corolla tube 12–22 mm long and corolla lobes 8–18 mm long, white and usually drying black; fruit slightly broader than long, often with persisting calyx tube; stipular awns 4–18 mm long [0–800 m elevation] *F. occidentalis*
- 10b. Flowers with corolla tubes 4–13 mm long, corolla lobes 3–7(–10) mm long, blue or white and rarely drying black; fruit distinctly broader than long, a persisting calyx tube rarely present; stipular awns 1–6 mm long 11
- 11a. Leaf blades usually drying yellowish green beneath, with a prominent submarginal vein; inflorescences robust with branches ca. 1 mm thick when dry; stipules early deciduous; corolla tube 6–10 mm long; 500–1700 m elevation *F. eurycarpa*
- 11b. Leaf blades usually drying grayish or pale green beneath; inflorescences delicate with primary branches ca. 0.5 mm thick when dry; 0–1600 m elevation 13
- 12a. Stipules clearly tubular and persisting on the leafy stems; corolla tubes 6–12 mm long, calyx lobes 0.2–0.4 mm long *F. multiflora*
- 12b. Stipules quickly deciduous, tubes short and inconspicuous; corolla tubes 2–6 mm long, calyx lobes 0–0.7 mm long 13
- 13a. Corolla tube slender, 0.7–1.5 mm diam., blue; 0–400 m elevation *F. stenura*
- 13b. Corolla tube broad, 1.5–2 mm diam., white; 1300–1400 m elevation *F. honduræ*

***Faramea capulifolia* Dwyer, sp. nov.**

Frutices ad 4 m alti. Foliae lamina lanceolata, 2–6 cm longa, 0.5–1.6 cm lata, acumine ad 10 mm longo, venis lateralibus 10–16; petiolis 2–4 mm longis; stipulis 2–8 mm longis, vagina 1–5 mm longa. Inflorescentiae terminales, pedunculo nullo vel 15–20 mm longo, glabro,

fructum solitarium gerenti. Flores non visi. Fructus globosus, 6–9 mm longus, glaber, niger.

TYPUS—*Folsom 4262* (holotypus MO, isotypus ?PMA), from Cerro Pirre, ridgetop at 1200 m elevation, Darien, Panama.

Shrubs, 1–4 m tall, leafy stems 0.5–4 mm thick, glabrous with 2 or 4 barely distinct longitudinal ridges;

stipules 2–8 mm long, sheathing tube 1–5 mm long, truncated distally with 1 small narrow lobe (2/node), glabrous, deciduous. **Leaves** with petioles 2–4 mm long, ca. 0.5 mm thick, glabrous, sulcate above; **leaf blades** 2–6 cm long, 0.5–1.6 cm broad, lanceolate to narrowly ovate-elliptic, apex acuminate, base acute and slightly decurrent on petioles, drying chartaceous, olive green above, glabrous above and below, 2° veins 5–9/side and loop-connected ca. 1 mm from the leaf margin (major and intermediate secondaries often difficult to distinguish). **Inflorescences** terminal and solitary, sessile or with peduncles to 2 cm long in fruit (after the loss of the distal leaf pair), peduncles ca. 0.4 mm thick and glabrous, pedicels 0–2 mm long, fruit solitary. **Flowers** solitary, ca. 10 mm long, glabrous, corolla ca. 8 mm long, rose-colored, tube ca. 5 mm long, ca. 0.9 mm diam. **Fruits** 6–9 mm diam., glabrous, persisting calyx 0.5–1 mm high, surfaces smooth, brilliant blue or becoming black.

Understory plants in wet cloud forests from 1000 to 1700 m elevation. Flowering in May; fruiting in June–July and December. This species is known only from the Cordillera de Tilarán area in Costa Rica and eastern Panama.

Faramea capulifolia is recognized by its small leaves, glabrous parts, and solitary terminal flowers and fruits. The Costa Rican material has somewhat smaller leaves (to 4.5 cm long) and blue fruits, whereas the type has leaves to 6 cm long and fruits becoming black. The fruits are subtended by a node where the leaves have fallen, with the distal internode appearing to be a peduncle. Flowering data was added in proof, based on Gómez-Laurito 12431 F. Also placed here are Barringer et al. 4194 CR, F; Dyer 1711 F, and Zamora et al. 647 CR, F.

Faramea eurycarpa J. D. Smith, Bot. Gaz. 44: 113. 1907. *F. bocaturensis* Dwyer, Ann. Missouri Bot. Gard. 67: 163. 1980. Figure 45.

Shrubs or small trees to 4(–8) m tall, leafy branchlets 1.5–5 mm thick, glabrous and drying yellowish green; **stipules** to 16 mm long, united to form a tubular sheath 3–8 mm long, 2–4 mm broad, with awns 1–3 mm long, deciduous. **Leaves** with petioles 3–7(–10) mm long, 1–1.5 mm thick, glabrous; **leaf blades** (5)–9–16(–19) cm long, (2)–3–5.5 cm broad, narrowly oblong to elliptic-oblong, apex obtuse or rounded and acuminate to caudate-acuminate, tip 10–14(–20) mm long and ca. 2 mm broad, base cuneate (or slightly rounded at the petiole), drying chartaceous, usually yellowish green below with the midvein yellow, glabrous above and below, 2° veins 9–14/side and loop-connected near the margin to form an arcuate submarginal vein 2–4 mm from the edge, with less distinct secondary veins paralleling the major secondaries. **Inflorescences** terminal and solitary, to 14 cm long and 12 cm broad, pyramidal panicles with opposite bracteolate branches, glabrous, peduncles 2–5 cm long, stout and 1.3–3 mm thick (dried), the slender pedicels

4–10 mm long. **Flowers** with hypanthium 0.7–1.5 mm long, calyx cup 0.5–1.5 mm long, calyx teeth 4 or 5, 0.3–1 mm long, narrow distally; **corolla** salverform, blue, purple, or white with purple apex, tube 6–10 mm long, 1–1.5 mm diam., lobes 2–4 mm long, narrowly ovate; **stamens** 4, attached near the middle of the tube and subsessile, anthers 3–4 mm long; style 4–8 mm long, stigmas ca. 0.7 mm long. **Fruits** 6–8 mm long and 9–13 mm broad, transverse-reniform to subglobose, blue, purple, or black, drying dark, smooth or slightly rugose when dried, persisting calyx less than 1 mm high.

Plants of the very wet evergreen cloud forests of the Caribbean slope, from (300–)500 to 1200(–1700) m elevation. Flowering in March–June, September, and December; probably fruiting throughout the year. The species ranges from Costa Rica and Panama to Colombia and Ecuador.

Faramea eurycarpa is recognized by the oblong leaves with slender “drip tips,” greenish yellow color of the veins beneath when dried, deciduous stipules, arcuate submarginal vein, and small blue flowers with small corolla lobes. The inflorescence branches and deciduous tubular stipules are much thicker in texture than those of *F. multiflora*, which shares many of the same habitats as *F. eurycarpa*. Collections from the Chiriquí Highlands have a greater range of variation than those found in Costa Rica, but they do not appear to be specifically distinct. The name *F. bocaturensis* Dwyer applies to the distinctive Chiriquí Highland material.

Faramea hondurae Standl., J. Wash. Acad. Sci. 18: 169. 1928. Figure 45.

Shrubs, 3–4.5 m tall, leafy branchlets 1.3–3 mm thick, glabrous; **stipules** forming a short (3–4 mm) tube, caducous and leaving a transverse whitish scar. **Leaves** with petioles 6–16 mm long, 0.8–1.4 mm broad, glabrous; **leaf blades** (6)–10–19 cm long, (1.5)–3–5 cm broad, narrowly oblong to narrowly elliptic-oblong, apex long-acuminate to caudate-acuminate, tip 12–20 mm long, base acute, drying chartaceous and dark green above, glabrous above and below, 2° veins ca. 14/side (but with less prominent 2° veins between the major), an arcuate submarginal vein present near (ca. 2 mm) the margin and connecting the secondaries. **Inflorescences** terminal or axillary to distal leaves, solitary or 3, 5–8 cm long, to 6 cm broad, panicle with 2 or 3 pairs of opposite branches, primary peduncles 20–30 mm long, bracts 2–6 mm long and mucronate, distal bracteoles 0.5–3 mm long, pedicels 2–5 mm long, slender, glabrous. **Flowers** glabrous, hypanthium ca. 1 mm long, turbinate, calyx tube 0.5–1.5 mm long, campanulate, with 4 minute lobes; **corolla** salverform, white, tube 2–4 mm long, 1.5–2 mm diam., lobes 1–2 mm long, obtuse; anthers ca. 1.5 mm long, style and stigma ca. 2.3 mm long. **Fruits** unknown.

A problematic species known only from two collections (*Standley 36534* us, *37890* us the type) collected between 1300 and 1700 m elevation near Bajo La Hondura, San José, in March 1924. The short, relatively broad white corolla tubes make this species unique among our species of *Faramea* and make the generic placement doubtful. However, a dissection of an ovary (*Standley 36534*) showed two ovules in a single locule, consistent with Standley's placement of this species in *Faramea*.

Faramea multiflora A. Rich., ex DC., Prodr. 4: 497. 1830. *F. talamancarum* Standl., Publ. Field Columb. Mus., Bot. Ser. 4: 332. 1929. Figure 45.

Shrubs or small trees, (1)2–5(–6) m tall, leafy branchlets 1–3.5 mm thick, terete and glabrous; **stipules** 4–8(–13) mm long, 2–3 mm broad but broader beneath the inflorescence, the tubular basal sheath 2–5 mm long, awns 1–5(–8) mm long, persisting. **Leaves** with petioles 3–7(–11) mm long, 0.7–1.8 mm thick; **leaf blades** (6)–8–13(–17) cm long, 1.5–4(–7) cm wide, oblong to oblong-obovate or narrowly elliptic-oblong, apex gradually or abruptly narrowed and caudate-acuminate or acuminate, tip 7–15 mm long and straight or falcate, base acute or obtuse, leaves drying thin-chartaceous to chartaceous and dark greenish above, 2° veins 6–12/side (and lesser parallel 2° veins between the major), united near the margin by a slender arcuate submarginal vein 2–4 mm from the leaf edge. **Inflorescences** terminal, solitary (or 3), 5–14 cm long, to 9 cm broad, panicle with opposite branches 1–2 cm long, bright blue, glabrous, primary peduncles 2–3(–6) cm long, basal branches subtended by small leaves or broad bracts 8–22 mm long, distal bracts absent, pedicels 3–7(–10) mm long, slender. **Flowers** glabrous externally, hypanthium 0.5–1 mm long, calyx tube 0.2–0.4 mm long, calyx lobes 4, 0.1–0.4 mm long; **corolla** bright sky blue, salverform, tube 6–12 mm long, 1.2–2 mm diam., lobes 4, 4–9 mm long, 1.3–2.5 mm broad, ovate-oblong; anthers 2–3 mm long. **Fruits** 6–8 mm long, (8)–10–13 mm broad, oblate or transversely reniform, laterally compressed (oblong in cross-section), surface smooth and without costae, blue-black at maturity; pyrenes solitary.

Understory shrubs of wet evergreen forest interiors and forest edges, from 20 to 1600 m elevation. Flowering in every month but October (flowering is mainly in May–June at La Selva); fruiting throughout the year. The species ranges from northern Costa Rica to Brazil and Bolivia.

Faramea multiflora is recognized by the thin smaller leaves (often drying grayish green beneath), narrow acuminate apices, persisting tubular stipule sheaths, and bright blue flowers and inflorescences. This species is very similar in ap-

pearance to *F. stenura* but the tubular stipules of *F. multiflora* are persisting, the calyx lobes are less well developed, and distal inflorescence branches lack the small bracts characteristic of *F. stenura*. Central American collections differ in minor ways (generally smaller thinner leaves and inflorescences) from South American collections, but all appear to be part of the same wide-ranging species.

Faramea myrticifolia Dwyer, sp. nov.

Suffrutes 0.3–0.4 m alti; ramulis multis glabris. Foliae lamina elliptica 2–4 cm longa, 8–15 mm lata, glabra, venis lateralibus 6–8; petiolis 3–6 mm longis; stipulis 4–5 mm longis. Inflorescentiae axillares, flores 2–5 gerentes, pedunculis 2–4 mm longis; pedicellis 1–2 mm longis. Flores glabri; calycis cupula ca. 0.5 mm longa, lobis ca. 0.5 mm longis, lilacinis; corolla viridi-alba, ca. 4 mm longa. Fructus ca. 8 mm lati, globosus, azureus, glaber.

TYPUS—*L. D. Gómez et al. 23401* (holotypus CR, isotypus MO), from Las Brisas de Pacuarito, Limón, Costa Rica.

Herbaceous **subshrubs**, ca. 40 cm tall, main stem unbranched for 20 cm and with many slender distal opposite horizontal branches, leafy stems 0.5–1.3 mm thick, glabrous, prominently 2- or 4-ridged; **stipules** 4–5 mm long, with a short (0.5–1 mm) truncated tube and single filiform central awn 3–5 mm long, persisting. **Leaves** with petioles 3–6 mm long, 0.3–0.9 mm thick, glabrous; **leaf blades** 2–4 cm long, 8–15 mm broad, elliptic to elliptic-oblong, apex acute or short-acuminate, base acute and decurrent on petiole, drying chartaceous, dark green above, glabrous above and below, 2° veins 6–8/side and loop-connected 1–1.5 mm from the margin. **Inflorescences** axillary to leaves, 1 or 2/node, cymose umbellate with 2–5 flowers on a short (2–4 mm) glabrous peduncle drying dark, glabrous, bracts ca. 2 mm long and linear, pedicels 1–2 mm long. **Flowers** glabrous and drying blackish, hypanthium 0.5–1 mm long, calyx tube ca. 0.5 mm long and truncated with linear lobes 0.5 mm long; **corolla** greenish white, ca. 4 mm long and 0.7 mm diam. in bud. **Fruit** globose, ca. 8 mm diam., intense blue but drying black, usually 1/node.

Distinctive little plants with many (ca. 12) distal lateral horizontal branches, small leaves, unusual stipules, and minute flowers. Presently known only from the type, collected near Siquerres, Limón, 18 April 1985, at about 300 m elevation. It appears to be related to *F. cobana* J. D. Smith of Honduras, but that species has larger (8–10 cm) leaves, longer peduncles (to 15 mm), and a higher-elevation habitat.

Faramea occidentalis (L.) A. Rich., Mém. Fam. Rubiac. 96. 1830. *Ixora occidentalis* L., Syst. Nat. ed. 2: 893. 1759. *F. zeteki* Standl., Contr.

Arnold Arbor. 5: 147. 1933. *F. belizensis* Standl., Carnegie Inst. Wash. Publ. 461: 90. 1935. *F. standleyana* L. O. Williams, Phytologia 26: 490. 1973. Figure 44.

Shrubs or small trees, 2–6(–10) m tall, to 20 cm dbh, leafy branchlets 1.5–5 mm thick, glabrous, terete, often dichotomously or trichotomously branched; **stipule** sheath 2–8 mm long, 5–8 mm wide at the base, with awns 4–12(–18) mm long, deciduous. **Leaves** with petioles 6–15 mm long, 1–2 mm thick, glabrate; **leaf blades** 8–18(–21) cm long, (2.5–)3.5–9.5(–11) cm broad, oblong or elliptic to narrowly elliptic-obovate (less often ovate-oblong), apex rounded to obtuse and acuminate to caudate-acuminate, the narrow (2 mm) tip 4–17 mm long, base acute to obtuse or rounded and subtruncate, drying chartaceous to stiffly chartaceous, glabrous above, glabrous or minutely puberulent beneath, 2° veins 6–10/ side and only loosely loop-connected near the margin (a definite submarginal vein absent), with 1–3 more weakly defined secondaries between the major secondary veins. **Inflorescences** terminal or less often axillary, solitary or several, 5–12 cm long, equally broad, umbelliform or trichotomous, few-branched and with 3–9 flowers, often drying black, peduncles 1.5–6 cm long, lateral branches opposite and few, distal flowers usually in groups of 3, bracts 4 mm long, linear, pedicels 3–12(–20) mm long. **Flowers** white but drying black, sweet scented in life, probably nocturnal, hypanthium ca. 2 mm long, oblong, calyx cup 1.5–3 mm long, teeth absent or minute; **corolla** salverform, tube 10–19(–22) mm long, 2–3 m diam., narrowly cylindrical, lobes 4, 8–16(–25) mm long, 1.3–3 mm wide near the base, lanceolate to narrowly ovate; **stamens** 4, filaments 0.5 mm long, anthers ca. 8 mm long, slightly exserted; style as long as the corolla tube or ¼th as long, stigma 2.5–5.5 mm long. **Fruits** 6–9 mm long, 9–14 mm diam., globose to subglobose-oblate, persisting calyx 1–2 mm long and 2–3 mm diam., drying black.

Trees and shrubs of evergreen forest formations, from near sea level to 1000 m elevation. Flowering in February–July and October in southern Central America (primarily in June in Costa Rica); probably fruiting throughout the year. The species ranges from southern Mexico, Central America, and the West Indies through tropical South America.

Faramea occidentalis is recognized by the large slender flowers drying black, relatively few-branched and few-flowered inflorescences also drying black, and rounded fruit slightly shorter than broad. This species varies greatly in leaf form and it does not have a well-developed submarginal vein. Though wide-ranging, it has not been collected very often in Costa Rica. This species is closely related to *F. luteovirens* with larger flowers. Fruiting and sterile material may be difficult to separate from *F. eurycarpa*.

Faramea ovalis Standl., Contr. U.S. Natl. Herb. 18: 138. 1916. *F. quercetorum* Standl., J. Wash. Acad. Sci. 18: 168. 1928. Figure 45.

Small trees or shrubs, 2–6(–13) m tall, to 20 cm dbh, leafy branchlets 1–4 mm thick, glabrous, becoming grayish; **stipules** 3–13 mm long, the basal cupulate tube 1–2 mm high, with a single slender awn 3–10 mm long, often persisting. **Leaves** not closely congested, petioles 3–10 mm long, 0.7–1.8 mm thick, glabrous; **leaf blades** 3–11 cm long, 1.5–4.8 cm broad, elliptic-oblong to oblong or narrowly elliptic, apex abruptly narrowed and acuminate or caudate-acuminate, the tip 6–13 mm long, base acute to obtuse, drying stiffly chartaceous and grayish green to dark green above (slightly paler beneath), glabrous above and below, 2° veins (3–)5–8/ side and loop-connected distally, with a vein-like edge along the leaf margin. **Inflorescences** terminal (axillary), 3–7 cm long, to 4 cm broad, umbellate with 3–5(–9) flowers, peduncles 8–24 mm long, 0.5 mm diam., glabrous and drying dark, pedicels 4–18 mm long, ca. 0.5 mm thick. **Flowers** glabrous externally, drying dark, hypanthium 1–2 mm long, calyx tube 0.5–2 mm high, teeth to 0.5 mm long; **corolla** salverform to somewhat funnellform, white or tinted with pink-purple, tube (7–)9–14 mm long, 1.2–3 mm diam., lobes 4–6 mm long; **stamens** 4. **Fruit** 6–10 mm diam., globose, blue drying black and smooth, persisting calyx tube 1–2.5 mm long and ca. 2 mm diam.

Plants of moist evergreen cloud forests, 1000–2300 m elevation (400–600 m on Volcán Orosí). Flowering in March–June and December; probably fruiting throughout the year. The species is found in the northwestern cordilleras, eastern parts of the Cordillera de Talamanca, and the Chiriquí Highlands.

Faramea ovalis is recognized by its cloud forest habitat, lack of pubescence, smaller often caudate-acuminate leaves, umbellate inflorescences with relatively few large flowers, and globose black fruits. The species resembles smaller-leaved specimens of *F. occidentalis* and some species of *Coussarea*.

Faramea parvibractea Steyerf., Mem. New York Bot. Gard. 17: 376. 1967. Figure 45.

Shrubs or small trees 2–8 m tall, leafy branchlets 1–4 mm thick, glabrous and drying greenish, strongly quadrangular; **stipules** 6–15 mm long, 0.5–1 mm broad, encircling the shoot apex, quickly caducous. **Leaves** with petioles 5–14(–20) mm long, ca. 1 mm thick, glabrous; **leaf blades** 7–17 cm long, 1.5–6(–7.5) cm broad, elliptic-oblong, ovate-oblong, to oblong-lanceolate, apex acuminate to caudate-acuminate, tip 6–12 mm long, base acute to obtuse, drying chartaceous, glabrous above and below, 2° veins 6–10/ side, weakly loop-connected 3–5 mm from the margin. **Inflorescences** fasciculate or pseudumbellate from distal nodes, to 6(–10) cm long and equally broad, with 6–11(–19) primary peduncles 11–

20(–30) mm long, flowers usually borne in distal groups of (1)–2, 3, or 5 at apex of the primary peduncles, a few peduncles with broadly ovate leaf-like bracts 5.5–16 mm long and 3–12 mm broad at their apex, bracts subcordate and with petiole-like base ca. 1 mm long, white in life, pedicels 1–3 mm long. **Flowers** with hypanthium 0.5–1.5 mm long, calyx tube 0.5–1 mm long, calyx lobes small and usually unequal (ca. 0.1 mm and 0.5 mm), **corolla** funnellform, white, 7–12(–16) mm long, tube 5–8 mm long, 1.5–3 mm diam., lobes 4, 5–10 mm long, 2–3.5 mm broad, lanceolate to narrowly oblong, obtuse; **stamens** exserted, filaments 3–3.5 mm long, inserted at or below the middle of the tube, anthers 3.5–4 mm long, linear, bluntly rounded; style 4–6 mm long. **Fruits** 5–7 mm long, 8–12 mm broad, oblate and rounded in cross-section, smooth, the ribs obscure or prominent when dried; pyrene solitary.

Plants of wet lowland rain forest formations of the Caribbean slope, from 4 to 600 m elevation. Flowering in January–June and October; fruiting in February and May–August. The Costa Rican collections are mostly from between Tortugero and Limón, with a few from the Osa Peninsula. This species is also known from Panama and Venezuela.

Fareamea parvibractea is recognized by the clusters of few-flowered peduncles at distal nodes, the ovate-subcordate bracts subtending some flower groups, the elliptic-oblong leaves with “drip tips,” the narrow stipules enclosing the shoot apices, the glabrous white flowers, and the fruit often in umbellate groups at the ends of leafy stems. The unusual bracts do not appear to be developed beneath all the flower groups, but they are large and contradict the specific name.

Fareamea pauciflora Dwyer, Ann. Missouri Bot. Gard. 67: 172. 1980.

Understory **shrubs** or small trees, 2–5(–10) m tall, branches at right angles to main stem, leafy stems 1.5–4 mm thick, glabrous; **stipules** 8–15 mm long and 4 mm broad, triangular to tubular with 2 slender awns 3–5 mm long, covering the terminal bud, glabrous, drying black, caducous. **Leaves** held in a single plane, petioles 4–7(–12) mm long, 0.9–1.5 mm thick, glabrous, drying dark; **leaf blades** 11–22 cm long, 4–11 cm broad, elliptic-oblong to narrowly oblong or elliptic-obovate, apex acuminate or caudate-acuminate, tip 7–17 mm long, base acute, drying stiffly chartaceous, dark brown or blackish above, glabrous above, glabrous or sparsely and minutely papillate-puberulent beneath, 2° veins 8–12/side. **Inflorescences** ca. 10 cm long with 1–3 flowers, terminal or axillary, usually 1/node, peduncles 2–5 cm long, 0.7–1.5 mm thick, often with 1–2 pairs of stipule-like bracts near the base and terminated by several minute bracts, pedicels 15–55 mm long, 0.5 mm thick, glabrous and drying

black, merging with the hypanthium. **Flowers** glabrous externally and drying black, hypanthium and calyx 10–15 mm long, 2.5–4 mm diam., tube ca. 4 mm long, lobes few or unequal, 1–8 mm long; **corolla** salverform, white, tube 10–22 mm long, lobes 4, 13–30 mm long, rotate and with a narrow tip 4–9 mm long often held at 90°. **Fruits** 12–14 mm long, 10–14 mm diam., with a persisting calyx tube 7–9 mm long and 3–4 mm diam., dark blue drying black, pendulous.

Plants of the wet Caribbean slope at elevations from 20 to 1100 m. Flowering in March–April; fruiting in March–April and August–September in Panama. The species ranges from near Nuevo Arenal southward to Colombia.

Fareamea pauciflora is unusual because of its glabrous parts, usually axillary inflorescences with one to three long white flowers and long pedicels. Two Costa Rican collections have been seen: *Herzera* 2556 and *A. Smith* 1644. This species is closely related to *F. luteovirens* Dwyer of Panama with thicker leaves, fewer 2° veins, and shorter calyx. Compare *F. occidentalis* and the pubescent but similarly few-flowered *Coussarea enneantha* (fig. 46).

Fareamea scalaris Standl., Contr. U.S. Natl. Herb. 13: 139. 1916.

Shrubs or small trees, 1.5–6 m tall, leafy branchlets 1.5–4 mm thick, terete or quadrangular, drying brownish, leaves distant (3–6 cm) along the stems; **stipules** 4–8 mm long, with a short-tubular sheath, truncated or deltoid at apex, with or without a short (1–2 mm) awn, persistent. **Leaves** subsessile with petioles 1–3(–5) mm long; **leaf blades** (5)–7–15 cm long, (1)–1.3–4 cm broad, narrowly elliptic-oblong to narrowly oblanceolate, apex acuminate, tip 7–15 mm long and straight or falcate, base gradually narrowed but often slightly rounded and subauriculate at the petiole, drying chartaceous and greenish, glabrous above and below, 2° veins 9–13/side, these arising at almost 90° angles and united by a linear or slightly arcuate lateral vein 2–5 mm from the leaf edge, a slender submarginal vein also present 0.3–1 mm from the margin in fully developed leaves. **Inflorescences** terminal and solitary, 3–6 cm long, paniculate with short opposite branches, primary peduncles 15–20 mm long, glabrous, bracts caducous, pedicels 2–4 mm long. **Flowers** glabrous, hypanthium ca. 1.5 mm long, calyx tube ca. 0.5 mm long, lobes 0.1–0.3 mm; **corolla** salverform, blue becoming white, tube 7–10 mm long, 1–1.5 mm diam., lobes 3–4 mm long, ca. 3 mm broad, ovate, disc 1 mm long; style ca. 7 mm long. **Fruits** unknown.

Plants of montane wet forest formations, from 1800 to 2300 m elevation. Flowering in January and March. The species is known only from the Chiriquí Highlands in western Panama.

Faramaea scalaris is distinguished by its narrow subsessile leaves with prominent lateral (melastome-like) venation, the small inflorescences, and the restricted high-elevation habitat. The unusual leaf venation suggests that this species is closely related to *F. trinervia* and *F. suerrensii* of lowland formations.

***Faramaea sessifolia* P. Allen, Rain Forests of Golfo Dulce 409. 1956. Figure 44.**

Shrubs or small trees, 3–7 m tall, leafy branchlets 2–7 mm thick, the nodes to 10 mm thick, rectangular in cross-section (flattened and 4-angular), glabrous, drying yellowish; **stipules** 10–25 mm long, 3–5 mm broad at the base, triangular-subulate with a narrow distal tip, caducous. **Leaves** somewhat dimorphic with smaller and narrower leaves often subtending the inflorescences, sessile or subsessile, petioles 0–4(–6) mm long, ca. 2 mm thick; larger **leaf blades** 17–27 cm long, 6–17 cm broad, narrowly oblong to ovate-oblong, smaller leaf blades 8–17(–19) cm long and 2–4(–6) cm broad, narrowly oblong-lanceolate to narrowly oblong, apex abruptly narrowed (in larger leaves) or gradually narrowed (in smaller leaves) and acuminate, tips 8–17 mm long, base rounded and subtruncate, drying chartaceous and yellowish green, glabrous above and below, 2° veins 12–16/side and loop-connected 2–5 mm from the margin. **Inflorescences** terminal, solitary or 3, 10–15 cm long and 10–12 cm broad, paniculate with opposite many-flowered branches, primary peduncles (2)–6–7 cm long, 0.7–2 mm thick, glabrous, whitish in life and yellowish when dried, bracts 0.5–1 mm long, pedicels 1–2 mm long above small (0.5 mm) bracteoles. **Flowers** glabrous, hypanthium 0.5–1 mm long, calyx tube 0.2–0.5 mm long, lobes 0.2–0.4 mm long; **corolla** salverform, bright blue or bluish purple, tube ca. 6–7 mm long and 1 mm diam., lobes 3–4 mm long, to 2 mm broad at base. **Fruits** 4–5 mm high, 7–9 mm broad, oblate, circular or oblong in cross-section, with 8 longitudinal costae, pale grayish brown becoming black.

Plants of the lowland rain forests of the Osa Peninsula region, 20–400 m elevation. Flowering in April–May (Allen 5539 F, US type); fruiting in March, August–September, and November. The species is known only from southwestern Costa Rica.

Faramaea sessifolia is recognized by its large subsessile leaves with many secondary veins and arcuate submarginal vein, leafy stems rectangular in cross-section, lack of pubescence, blue flowers, and restricted distribution. The veins on the lower leaf surface and inflorescences dry yellowish. This name should not be confused with *F. sessilifolia* (H.B.K.) A. DC. of South America.

***Faramaea stenura* Standl., Publ. Field Columb. Mus., Bot. Ser. 4: 331. 1929. Figure 45.**

Small trees to 7 m tall, leafy branchlets 1.7–4 mm thick, glabrous, drying greenish; **stipules** 6–10 mm long, 3–4 mm broad at the base, triangular to ovate, acute or mucronate at apex, caducous. **Leaves** with petioles 5–10 mm long, 0.6–1.5 mm thick; **leaf blades** 9–19 cm long, 2.5–5.5 cm wide, narrowly oblong to narrowly oblong-obovate, apex acuminate, tip 5–23 mm long, base acute to cuneate, drying chartaceous, dark grayish green above, glabrous above and below, 2° veins 9–12/side, arising at almost 90° and weakly loop-connected near the margin, with thinner secondaries present and parallel with the larger. **Inflorescences** usually terminal and solitary, paniculate pyramidal, 3–5.5 cm long, 4–7 cm broad, blue, primary peduncles 1.5–5(–8) cm long and 1–1.5 mm thick, bracts 3–5 mm long, linear or triangular, purplish, pedicels 2–4 mm long. **Flowers** glabrous externally, hypanthium ca. 0.6 mm long, calyx tube 0.2–0.3 mm long, lobes 4, 0.3–0.7 mm long; **corolla** salverform, pale to deep blue, glabrous, tube 5–8 mm long, lobes 4, 3–5 mm long, 1.2–1.5 mm broad, elliptic to ovate, acute at apex. **Fruits** 4–8 mm long, 12–15 mm broad, transversely reniform (oblong in cross-section), rounded basally and flattened or depressed above, smooth and usually drying green.

Plants of lowland rain forest formations, 30–600 m elevation (but see below). Flowering in January–September; probably fruiting throughout the year. It ranges along the Caribbean coast, from Veracruz, Mexico, to western Panama, and in the Golfo Dulce area.

Faramaea stenura is distinguished by its small blue corollas, caducous stipules, oblate fruit, and narrowly oblong leaves with long “drip tips.” This species is very similar to *F. multiflora*, but their stipules help differentiate most collections. At La Selva *F. stenura* grows in low swales, whereas *F. multiflora* grows on the ridgetops. There are very similar plants growing at higher elevations (ca. 1200 m) in Chiriquí with larger (10 × 14 mm) ribbed fruit that dry whitish. It is not clear whether they are a high-elevation subspecies or an undescribed closely related species.

***Faramaea suerrensii* (J. D. Smith) J. D. Smith, Bot. Gaz. 44: 112. 1907. *Faramaea trinervia* K. Schum. & J. D. Smith var. *suerrensii* J. D. Smith, Bot. Gaz. 31: 115. 1901. Figure 44.**

Shrubs or small treelets, 2–6 m tall, leafy branchlets 2–6 mm thick (to 12 mm broad at the node), usually quadrangular in cross-section, glabrous; **stipules** 5–10 mm long, 3–8(–12) mm wide at the base, often united to form a short tube, entire or rounded with a small (1

mm) mucronate tip. **Leaves** with petioles 4–18 mm long, 1–2 mm thick; **leaf blades** 9–20(–28) cm long, 3–8(–12) cm broad, narrowly elliptic-oblong to oblong or narrowly oblong-oblancoate, apex short-acuminate to long-cuspidate, tip to 18 mm long in some specimens, base acute to rounded and subtruncate, drying chartaceous to subcoriaceous, pale grayish green to yellowish green, glabrous above and below, the major veins often becoming impressed above, 2° veins 8–16(–25)/side and with less prominent parallel 2° veins, 2° veins arising at nearly 90° from the midvein and joined near the margin by a prominent linear lateral vein (2)–5–7(–14) mm from the leaf edge, with a smaller submarginal vein 0.5–2 mm from the leaf edge. **Inflorescences** terminal and solitary (or 3), corymbose panicles with opposite branching, 9–12(–20) cm long, to 16 cm broad, bright blue, many-flowered, peduncles 2–5(–9) cm long, 2–3 mm thick, glabrous, pedicels 2.5–9 mm long. **Flowers** distylous, glabrous, hypanthium ca. 1.2 mm long, calyx tube a small (0.3 mm) rim, lobes minute or 0.5 mm long and triangular; **corolla** salverform, brilliant pale blue to deep blue, tube 6–10 mm long, 0.8–1.5 mm diam., lobes 4, 3–5 mm long, ca. 1.7 mm broad; **stamens** 4, filaments attached near the middle of the tube, anthers 2.2 mm long, included. **Fruits** 6–11 mm long, 12–16 mm broad, transversely reniform and rounded-oblong in cross-section (somewhat flattened laterally and flat or slightly depressed distally), longitudinal ribs slightly developed or obscure, exocarp spongy and deep blue in life; pyrenes solitary.

Plants of lowland rain forest formations on both the Pacific and Caribbean slopes, from near sea level to 800(–1000) m elevation. Flowering in January–August and November; fruiting in every month except December. The species ranges from southern Nicaragua through Costa Rica and Panama to northwestern Colombia.

Faramea suerrensii is distinguished by its larger leaves with prominent melastome-like venation, brilliant bluish inflorescences and flowers, lack of pubescence, and lowland rain forest habitat. The unusual quality of the blue coloring of the inflorescence and the leaf venation make this one of our most distinctive species of Rubiaceae. This species is very closely related to *F. trinervia* (q.v.); it is possible that the two may be conspecific as Schumann and Smith originally thought. The breeding system was studied by Bawa and Beach (1983).

Faramea trinervia K. Schum. & J. D. Smith, Bot. Gaz. 31: 115. 1901. *F. bullata* Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 4: 294. 1929. Figure 44.

Shrubs or small trees, leafy stems 2–6 mm thick, glabrous; **stipules** 6–10 mm long, the basal tube 2–4 mm long with rounded or acute apex and narrow awn 3–5 mm long. **Leaves** sessile or subsessile with petioles 2–4

mm long; **leaf blades** 14–31 cm long, 4–12 cm broad, narrowly oblong to narrowly oblong-obovate, apex acuminate or caudate-acuminate, somewhat narrowed below the middle, base abruptly rounded and subcordate, drying stiffly chartaceous to subcoriaceous, grayish green, glabrous above and below, 2° veins 10–17(–22)/side (difficult to separate from the less prominent secondaries), united near the margin by a linear lateral vein 5–10 mm from the leaf edge, a smaller submarginal vein also present 1–3 mm from the edge. **Inflorescence** solitary and terminal (or 3 with 2 axillary), 4–7 cm long, to 12 cm broad, paniculate with opposite or trichotomous branching at the apex of the peduncle, basal bracts (small leaves) to 2 cm long, peduncles 3–6 cm long, 2.2–3.4 mm thick. **Flowers** glabrous externally, hypanthium ca. 1 mm long, obconic, calyx limb ca. 0.3 mm long with minute (0.2 mm) lobes; **corolla** color not known, salverform, tube 6–7 mm long, 0.5–0.9 mm diam., lobes 4, ca. 4 mm long and 1 mm broad. **Fruits** 7–8 mm long and 12–16 mm broad, oblate-reniform, flat or depressed centrally above, drying smooth and black.

A species of lowland Caribbean rain forest formations, 10–600 m elevation. Flowering in March (*Tonduz 8690* us) and April (*Tonduz 9583* us the type); fruiting in April (*Barringer et al. 2632* CR, F) and July (*J. Chacón 209* CR). This species is known only from the Talamanca valley region, southeastern Costa Rica, and Bocas del Toro Province in Panama.

Faramea trinervia is recognized by the stiff narrowly oblong leaves with melastome-like venation, coupled with the short petioles and rounded auriculate leaf bases. This species is very similar to and may prove to be conspecific with material placed under *F. suerrensii* (a later name). The thicker subsessile leaves rounded at the base are a unique character combination within the more common and more widely ranging *F. suerrensii*, and we treat the two as distinct species, although they appear identical in most other respects. The type of *F. bullata* (*Cooper 507* F from Panama) has short petioles but with a rounded lamina base, and we interpret it as an aberrant form of *F. trinervia*.

Ferdinandusa Pohl

Trees or shrubs, stems glabrous or puberulent; **stipules** interpetiolar, triangular, deciduous or caducous. **Leaves** opposite or verticillate, decussate or distichous, petiolate, glabrous or puberulent, entire, pinnately veined, without domatia. **Inflorescences** terminal or axillary to the distal leaf pair, paniculate with opposite branching and cymose to corymbose in form (rarely fasciculate or umbellate), bracteate, flowers pedicellate. **Flowers** bisexual and usually radially symmetrical (corolla tube sometimes curved), monomorphic, calyx cupular, calyx teeth

short, deciduous or persistent; **corolla** salverform to funnelform, white to reddish or greenish, corolla lobes 4(–5), convolute or broadly imbricate in bud, rounded distally; **stamens** 4(–5), filaments attached in the upper part of the tube, anthers versatile, exserted or included; **ovary** 2-locular with few to many ovules vertical on the axile placentas, stigmas subcapitate. **Fruits** a cylindrical to oblong (subglobose) woody capsule with septicidal dehiscence from apex; **seeds** few to many, elliptic and flattened, with entire to lacerate marginal wings.

A genus of 20–25 species with 1 species in Costa Rica and Panama and the others in South America. The elongate capsular fruit with small winged seeds and broadly overlapping corolla lobes distinguish this genus. Compare this genus with material placed in *Ladenbergia* (with valvate corolla lobes) and *Macrocnemum*.

Ferdinandusa panamensis Standl. & L. O. Williams, *Ceiba* 3: 34. 1952. Figure 40.

Trees to 20 m tall, major branches held at 90° angles or drooping, leafy stems 2–5 mm thick, terete or slightly quadrangular, glabrous or with erect hairs 0.5–1 mm long, stems slightly resinous where the hairs are broken off; **stipules** 5–20 mm long, narrowly triangular, acuminate, glabrous, caducous. **Leaves** opposite or 3/node, smaller in size beneath the inflorescence, petioles 4–10 mm long, 1.5–3 mm thick, glabrous or pubescent; **leaf blades** (6–)10–18(–22) cm long, (4–)6–10 cm broad, oblong to elliptic-oblong or ovate-oblong, apex abruptly short-acuminate, tip 3–10 mm long, base obtuse to rounded or truncate (subcordate), leaves drying stiffly chartaceous, glabrous above and below or with erect brownish hairs 0.5–1 mm long on the veins beneath and more sparsely on the surfaces beneath, 2° veins 6–9/side, arcuate-ascending near the margin but loop-connected only near apex, domatia absent. **Inflorescences** terminal (apparently axillary when leaves develop at the first branching node of the panicle), solitary or 3, 6–15 cm long, 6–22 cm broad, primary peduncles 2–5 cm long, bracteolate, bracts ca. 1 mm long, pedicels 5–12 mm long and merging with the flower base. **Flowers** glabrous, hypanthium ca. 2 mm long, calyx cup 0.5–1 mm long, 2–4 mm diam., calyx teeth 4 or 5, ca. 0.5 mm long; **corolla** funnelform, yellowish green or white, fleshy, tube (4–)6–18(–25) mm long, 2–3 mm diam., slightly expanded at the base, and much expanded distally, lobes 5, 4–6 mm long, 3–6 mm broad at the base; **stamens** 5, filaments linear, attached near the middle of the tube, anthers sometimes dimorphic (long and short); style to 11 mm long, stigmas ca. 1.5 mm long. **Fruits** (2–)3–6 cm long, 6–12 mm thick, narrowly oblong or cylindrical, abruptly rounded at the base and apex, with a short (0.5–1 mm) persistent calyx, surface smooth and with obscure longitudinal ribs, brown; **seeds** 1–2 cm long, elliptic.

Trees of lowland Caribbean rain forest formations, from near sea level to 200 m elevation. Flowers have been collected in January–May and

November–December; fruits were collected in February–July. The species is known only from Costa Rica and near Chiriquí Lagoon in Panama (von Wedel 2232 F the type).

Ferdinandusa panamensis is recognized by the elongate woody capsules with small winged seeds, fleshy flowers with broadly overlapping corolla lobes, broad leaves often rounded at the base, and the occasional presence of stiff brownish hairs. The names *café macho* and *cafecillo* have been used for this species in Costa Rica. The wood is very hard and young trees are used for boat poles.

Galium Linnaeus

REFERENCES—L. Dempster, The genus *Galium* (Rubiaceae) in Mexico and Central America. Univ. Calif. Publ. Bot. 73: 1–33. 1978. The genus *Galium* (Rubiaceae) in South America, IV. Allertonia 5: 283–345. 1990. F. Ehrendorfer, Revision of the genus *Relbunium* (Endl.) Benth. & Hook. (Rubiaceae–Galieae). Bot. Jahrb. Syst. 76: 516–553. 1955.

Herbs or slender vines, annual or perennial, often woody at the base (rarely shrubs), erect, decumbent or climbing, monoecious or dioecious, stems usually slender and with 4 prominent longitudinal ridges (square in cross section), glabrous or puberulent with thin hairs; **stipules** apparently absent but represented by leaf-like parts, indistinguishable from the true leaves (except that they lack axillary buds). **Leaves** in whorls of (3–)4–8(–10 to many) at each node, comprising the true leaves and the transformed stipules, sessile or subsessile, often narrowly oblong, entire or with sharp retrorse trichomes along the edge (serrulate), with 1 or 3 major veins, without domatia. **Inflorescences** terminal or axillary, often paniculate with dichasial or trichotomous branching, or with 3 terminal flowers from the distal node, inflorescences often with bract-like reduced leaves and thin-divaricate branching (with a 4-parted involucre in species formerly placed in *Relbunium*), pedicels articulate beneath the flower. **Flowers** bisexual or unisexual, radially symmetrical, usually very small, calyx tube minute or lacking; **corolla** rotate to campanulate or urceolate, white to yellow, green, pink, or red, corolla lobes (3–)4(–5), valvate in bud; **stamens** (2–)3–4(–5), filaments attached to the short tube of the corolla, anthers versatile and exserted; **ovary** 2-locular with 1 ovule borne on the septum in each locule, styles 2 (sometimes united at the base), stigmas capitate. **Fruits** usually 2-lobed or 2-parted (singular when 1 ovule fails to develop), dry or fleshy, smooth and glabrous to tuberculate or densely hispidulous, small, finally separating into 2 1-seeded mericarps, the mericarps rounded and indehiscent; **seeds** convex dorsally, attached to the pericarp, testa membranous.

A large genus of some 300–400 species, especially well represented in the North Temperate

zone and at higher elevations in the tropics. Dempster listed 41 species in Mexico and Central America (3 of which are probably early introductions); the genus is especially well represented in Baja California and the central highlands of Mexico. *Galium*, as a genus, is easy to recognize with its small whorled leaves on slender herbaceous

clambering 4-angled stems, minute flowers on slender pedicles, and 2-lobed little fruit. Material of *Galium* may be mistaken for species of *Didymaea* and *Nertera*. This treatment is based in large part on the annotations and publications of Laura-May Dempster.

Key to the Species of *Galium*

- 1a. Leaves in whorls of 6 or 8(–10); fruit covered with ascending curved hairs *G. mexicanum*
- 1b. Leaves in whorl of 4 at each node; fruit glabrous or with uncinata (hooked at the tip) hairs ... 2
- 2a. Flowers solitary in the leaf axils and subtended by a whorl of 4 leaf-like or calyx-like bracts *G. hypocarpium*
- 2b. Flowers rarely solitary in leaf axils, rarely subtended by 4 bracts 3
- 3a. Fruits glabrous, leaves with 1 primary vein and no lateral veins [usually glabrous; stems with minute (0.1–0.2 mm) hairs] *G. aschenbornii*
- 3b. Fruits covered with ascending uncinata hairs; leaves with 1 primary vein and 2 lateral veins usually visible 4
- 4a. Leaf blades usually ovate to elliptic; stems and leaves with few to many longer (0.4 mm) hairs; inflorescences usually with few (ca. 5) flowers; corollas often hispidulous *G. uncinatum*
- 4b. Leaf blades usually oblong-lanceolate to elliptic, stems and leaves sparsely short-puberulent (ca. 0.2 mm); inflorescences usually with more than 5 flowers; corollas glabrous *G. orizabense*

Galium aschenbornii Schauer, Linnaea 20: 701. 1847. *Relbunium aschenbornii* (Schauer) Hemsl., Biol. centr. amer. Bot. 2: 62. 1881. Figure 3.

Creeping or climbing **herbs** to 1.2 m long, with slender woody or herbaceous stems arising from a small root-stock, sometimes rooting from distal nodes, with both long (5 cm) and short (4 mm) internodes, leafy stems 0.3–1 mm thick, glabrous or with short retrorse hairs 0.1–0.2 mm long; **stipules** leaf-like. **Leaves** usually 4/node, petioles 0.1–0.5 mm long; **leaf blades** 4–8(–14) mm long, 1.2–3(–4) mm broad, narrowly oblong or elliptic-oblong (to lanceolate or ovate-oblong), apex obtuse to acute with a short (0.3 mm) tip, base acute to obtuse (rarely rounded), margin entire or with a few retrorse aculeolate trichomes, midvein prominent, secondary and lateral veins obscure or weakly developed. **Inflorescences** often of 3 terminal flowers subtended by a whorl of 4 reduced leaves, or of several flowers in compound dichasia, pedicels 1–5 mm long, filiform. **Flowers** ca. 1.5 mm long, greenish yellow, said to be ♂, ♀, and bisexual on the same plant or on different plants, hypanthium 0.5–0.7 mm long, calyx ca. 0.3 mm long; **corolla** rotate, lobes 0.5–1 mm long, white to yellowish or red. **Fruits** 3–4 mm long, 4–7 mm broad when dry, 2-lobed distally, orange becoming black, glabrous and wrinkled when dried, borne on slender pedicels 2–5 mm long.

Plants of evergreen montane forest formations, from 1200 to 2900(–3400) m in Central America. Probably flowering and fruiting throughout the

year. The species ranges from the states of Jalisco and San Luis Potosí in Mexico to western Panama.

Galium aschenbornii is recognized by the usually narrow leaves in whorls of four, short petioles, and glabrous fruit. It is infrequently collected in Costa Rica.

Galium hypocarpium (L.) Clos in Gay, Fl. Chil. 3: 186. 1847. *Vaillantia hypocarpia* L., Syst. Nat. ed. 10: 1307. 1759. *Relbunium hypocarpium* (L.) Hemsl., Biol. centr. amer. Bot. 2: 63. 1881. *G. hypocarpium* (L.) Fosberg, Sida 2: 386. 1966. Figure 3.

Herbs to 60 cm high, prostrate to procumbent or climbing over low objects, leafy stems 0.4–1.3 mm thick, with 4 prominent longitudinal ridges, nodes usually well spaced, puberulent with thin whitish hairs 0.3–1 mm long; **stipules** leaf-like. **Leaves** 4/node, sessile; **leaf blades** 3–13(–22) mm long, 2–4(–8) mm broad, oblong to ovate-oblong or broadly oblong-obovate, apex obtuse to rounded, with a minutely apiculate tip, base obtuse, drying chartaceous to subcoriaceous, both surfaces with stiff ascending hairs to 0.7 mm long or the surfaces glabrous and the margins hirsutulous, 2° veins 2–3/side (or the venation obscure). **Inflorescences** of solitary flowers in the leaf axils, usually with 2 flowers per node, peduncles 5–15 mm long, with an involucre of 4 bracteoles subtending each flower, bracteoles subequal, 2–4 mm long,

ovate to oblong or lanceolate, hirsutulous. **Flowers** small, hypanthium rounded, calyx tube and teeth undeveloped; **corolla** campanulate, white, 1.5–2.5 mm long, tube cylindrical, lobes 4, shorter than the bracteoles and alternating with them, surfaces glabrous and with marginal hairs; **stamens** 4, filaments short, anthers small. **Fruits** 2–3 mm long, to 3.5 mm broad, broadly 2- or 3-lobed, or with only 1 seed and globose, orange or reddish orange, glabrous to puberulent.

Plants of moist evergreen montane forest formations and high elevation paramos, from 1800 to 3400 m elevation. Probably flowering and fruiting throughout the year. The species ranges from Veracruz, Mexico, southward through the higher elevations of Central America into the Andes mountains of South America as far south as northern Chile and Argentina.

Galium hypocarpium is recognized by its slender stems with four leaves at each node, creeping or clambering habit, the solitary axillary flowers subtended by an involucre of four leaf-like bracteoles. These plants closely resemble our other species of *Galium*, but the other species rarely have single flowers subtended by a four-parted involucre.

***Galium mexicanum* H.B.K., Nov. gen. sp. 3: 337 (quarto). 1818. Figure 3.**

Trailing or climbing **herbs** to 1(–2.4?) m long, leafy internodes 0.3–2.8 mm thick, with minute (0.1–0.3 mm) retrorse aculeolate hairs, often with dense longer (0.5 mm) whitish hairs at the node; **stipules** leaf-like. **Leaves** usually 6 or 8(–12)/node, essentially sessile; **leaf blades** (4–)8–20(–25) mm long, 1–3 mm broad, narrowly oblanceolate to narrowly oblong, apex obtuse (rounded), usually with an apiculate tip ca. 0.5 mm long, base gradually narrowed, with curved aculeolate retrorse hairs (ca. 0.2 mm long) along the margin and midvein beneath, mostly glabrous above and on the flat surfaces beneath, primary vein prominent, 2 weakly defined lateral veins often present. **Inflorescences** usually terminal, paniculate arrangements of small cymose groups of 3–7 flowers subtended by reduced leaf-like bracts, with divaricate branching and slender pedicels 1–3 mm long. **Flowers** 1.5–2 mm long, bisexual, hypanthium 0.5–0.7 mm long, turbinate, densely hirsutulous with minute (0.1 mm) ascending hairs, calyx reduced; **corolla** 1–1.5 mm long, white to pink or red, campanulate or rotate, glabrous externally, puberulent within. **Fruits** dry, ca. 3 mm broad, covered with ascending slightly curved hairs or with a few uncinete hairs at the tip (in Costa Rica).

Plants of evergreen montane forest formations, from (1200–)1600 to 3100 m elevation. Flowering in April–July and December–January in southern Central America. Rarely collected in Costa Rica but apparently common in the Chiriquí High-

lands. The species ranges from the southwestern United States to Panama.

Galium mexicanum is recognized by the slender clambering stems with whorls of six or eight narrowly oblong or oblanceolate leaves and the small fruit with dense pubescence of curved hairs. The aculeolate trichomes on stems and leaves help the plants to climb and makes them adhesive and very difficult to disentangle from shrubbery or clothing.

***Galium orizabense* Hemsley, Diagn. Pl. Nov. Mexic. 3: 54. 1878. Figure 3.**

Erect or spreading **herbs**, 20–75 cm long, with several to many stems from a small root stock, leafy stems 0.3–1 mm thick, with thin white curves hairs 0.1–0.3 mm long; **stipules** leaf-like. **Leaves** 4/node, subsessile or short-petiolate, petioles to 2 mm long; **leaf blades** 6–18(–25) mm long, 2–4(–5) mm broad, narrowly oblong to narrowly elliptic-oblong or lanceolate, apex obtuse or short-apiculate, drying thin-chartaceous or membranaceous, with thin hairs ca. 0.3 mm long, on the upper surface, margin and major veins beneath, with a prominent 1° vein and 2 straight lateral veins (usually readily apparent). **Inflorescences** paniculate, with divaricate branches subtended by slightly reduced leaves, often with 5–15 flowers on open lateral branches, pedicels 1–10 mm long. **Flowers** 1–1.5 mm long, hypanthium ca. 0.5 mm long, covered with minute hairs; **corolla** rotate, lobes ca. 0.4 mm long and equally broad, white or greenish yellow. **Fruits** dry, 1–2 mm broad, covered with minute uncinete hairs, borne on thin (to 0.5 mm) pedicels.

Plants of evergreen montane forest formations, from 1500 to 2500 m in southern Central America. Flowering in March, July–August, and December–January in southern Central America. The species ranges from eastern and central Mexico to Panama.

Galium orizabense is recognized by the uncinete hairs on the fruit and the narrow verticillate leaves. This species is very similar to *G. uncinatum* and the two may be conspecific. However, most specimens can be differentiated by the key, and we follow Dempster's treatment.

***Galium uncinatum* DC., Prodr. 4: 600. 1830. Figure 3.**

Prostrate or procumbent **herbs** 15–90 cm long, leafy stems 0.3–1.5 mm thick, with thin whitish hairs 0.3–0.6 mm long, slightly scabrous; **stipules** leaf-like. **Leaves** 4/node, sessile or subsessile with petioles to 1(–2) mm long; **leaf blades** (4–)6–12(–22) mm long, (2–)2.5–6(–13) mm broad, ovate to narrowly ovate or narrowly oblong, apex obtuse (rounded) with a short (0.5 mm) tip, base obtuse,

drying membranaceous or chartaceous, margin and surfaces with thin ascending or spreading hairs 0.2–0.4 mm long, with 1° vein and 2 well-defined lateral veins, the lateral veins 0.5–1 mm from the margin in larger leaves. **Inflorescences** terminal or axillary, with opposite or cymose branching, to 3 cm long, flowers usually few (3–5) on the slender peduncles, often subtended by whorls of reduced leaves, pedicels 1–10 mm long, 0.1–0.2 mm thick when dried. **Flowers** 1–1.5 mm long, hypanthium/ovary ca. 0.5 mm long, covered by minute hairs that will expand in fruit, calyx reduced; **corolla** campanulate to rotate, white to greenish or yellow, usually puberulent externally. **Fruits** ca. 1.5 mm long and (1–)2–3 mm broad, usually 2-lobed and rounded, dry and covered by pale yellowish or whitish hooked (uncinate) hairs ca. 0.3–0.4 mm long.

Plants of evergreen montane forest formations from 1000 to 2800(–3300) m elevation. Flowering collections have been made in all months of the year except May and October–November in Central America. The species has been little collected in Costa Rica. The species ranges from southern Arizona and Texas (U.S.A.) through Mexico and highland Central America to Panama.

Galium uncinatum is recognized by having four, often broad, little leaves at each node, small few-flowered inflorescences with thin peduncles and pedicels, and fruits densely covered with thin uncinata hairs. This species is very similar to *G. orizabense* (q.v.), which appears to live in the same habitats but tends to have narrower leaves and shorter puberulence. Specimens referred to as *Galium obovatum* H.B.K. by Standley, both in the herbarium and in his flora (1938), are *G. uncinatum*.

Gardenia Linnaeus

Trees or shrubs, branches terete, glabrous or puberulent; **stipules** interpetiolar and intrapetiolar, triangular, apex acute to acuminate, often forming a short sheath at the base. **Leaves** opposite or in whorls of 3, subsessile to short-petiolate, coriaceous to chartaceous, entire, pinately veined, domatia often present. **Inflorescences** terminal or axillary, of 1 or 3 flowers (rarely more and corymbose), sessile or short-pedicellate. **Flowers** radially symmetrical, bisexual, usually large, hypanthium ovoid to ellipsoid or obconic, calyx tube short (sometimes spathe-like), calyx lobes 5–8 when present; **corolla** salverform to campanulate or funnelform, white or yellow, corolla tube glabrous or puberulent, corolla lobes 5–11, convolute in bud, spreading or recurved; **stamens** 5–9, inserted on the upper half of the tube, filaments short or absent, anthers dorsifixed, linear to linear-oblong, included or partly exserted, disc annular to crenate; **ovary** 1-locular (rarely 2- or 6-locular at apex), ovules many and horizontal on parietal placentas, style linear and

terete, stigma linear to clavate, 1- or 2-lobed. **Fruits** oblong to ovoid, pyriform or globose, terete or costate, the outer wall fleshy to leathery or woody, rupturing irregularly or the endocarp breaking into 2–5 valves; **seeds** very many, imbedded in a fleshy pulp, horizontal, angulate, embryo small.

A genus of about 200 species in the tropics and subtropics of the Old World. A few species are important as ornamental trees in warm climates; they are also grown under glass in cold climates for their large aromatic flowers, which are often used for corsages. The genus is similar to *Genipa*. The genus has not become naturalized in Central America, where one species is commonly seen in gardens.

Gardenia augusta (L.) Merr., Interpr. Herb. Amboin. 485. 1917. *Varneria augusta* L., Amoen. Acad. 4: 136. 1759. *G. jasminoides* Ellis, Phil. Trans. 51, pt. 2: 935. 1761. *G. florida* L., Sp. Pl. ed. 2: 305. 1762.

Shrubs or many-branched small **trees** to 5 m tall, leafy branchlets 1.5–5 mm thick, sparsely and minutely (0.2 mm) puberulent, glabrescent; **stipules** 5–10 mm long, at first enclosing the apex and splitting down one side to become spathe-like, with a short tube 2–4 mm long at the base, persisting. **Leaves** 2(–3)/node, petioles 1–4 mm long and little differentiated from the leaf base; **leaf blades** 3–12 cm long, 1.5–5 cm broad, elliptic-obovate to elliptic-oblong or broadly elliptic (in smaller leaves), apex acuminate, base acute and decurrent on petiole, glabrous above and below (but sometimes with pit domatia and a few hairs in the leaf axils), 2° veins 6–9/side. **Inflorescences** often of 3 terminal flowers, or solitary flowers in the axils of near-terminal leaves, pedicels ca. 10 mm long. **Flowers** large (6–10 cm long), apparently differing in size in different cultivars, sweetly aromatic, hypanthium ca. 10 mm long, calyx lobes 8–30 mm long, narrowly oblong, spur-like; **corolla** white, tube 2–5 cm long, corolla lobes usually 6 (some cultivars with 2 series), ca. 25 mm long and 18 mm broad, obovate; anthers ca. 18 mm long.

Plants of parks and gardens cultivated for their large white sweetly aromatic flowers. These plants, native to Asia, are called *jazmín*, *jazmín del cabo*, and “gardenia.”

Genipa Linnaeus

Trees, branchlets usually thick, terete, glabrous or puberulent; **stipules** interpetiolar and intrapetiolar, connate to form a short tube, caducous or deciduous with the leaves. **Leaves** opposite and decussate, subsessile or pet-

iolate, often large, pinnately veined, chartaceous to coriaceous, without domatia. **Inflorescences** terminal or axillary, flowers solitary or in few-flowered cymes or subcapitate, pedicels present and continuous with the hypanthium base. **Flowers** radially symmetrical, bisexual (rarely unisexual and dioecious), 5- or 6-parted, hypanthium turbinate to campanulate, calyx tube truncated and entire or with 5-6 short lobes; **corolla** salverform to funnellform, carnos, white to yellowish white, tube short to long, glabrous or puberulent externally, barbate in the throat within and at the base of the lobes, corolla lobes 5-6, convolute in bud, spreading; **stamens** 5-6, inserted in the upper part of the tube, anthers subsessile, dorsifixed, linear, partly exserted; **ovary** 1-locular or becoming 2-locular, style thick, stigmas fusiform, placentation parietal, ovules many and horizontal in vertical files. **Fruits** baccate, large, ovoid to subglobose or ob-ovoid, calyx tube persistent at apex of the fruit, pericarp thick, fleshy to coriaceous; **seeds** many, large, com-

pressed (with two parallel flattened sides), the testa slightly fibrous.

A genus of 5-10 species, ranging from southern Florida (U.S.A.) and Mexico through Central America into tropical South America. The genus is distinguished by its few-flowered terminal and subterminal inflorescences, large flowers with thick corolla lobes, parietal placentation, and many large horizontal seeds in vertical files within the large, often solitary fruit. *Genipa vulcanicola* Standl. of Mexico and Guatemala has been transferred to *Glossostipula concinna* (Standl.) Lorence; it has axile placentation.

Key to the Species of *Genipa*

- 1a. Corolla densely sericeous distally, peduncles to 25 mm long; stipules acute at apex, persisting with the leaves; leaves glabrous or pubescent, with 7-18 major secondary veins on each side; widespread *G. americana*
- 1b. Corolla glabrous on the outer surfaces, peduncles to 10 mm long; stipules broadly ellipsoid and rounded at apex, usually caducous; leaves glabrous above and with appressed hairs on the veins beneath, with 6-9 major secondary veins on each side; not recorded north of southern Costa Rica *G. williamsii*

Genipa americana L., Syst. Nat. ed. 10. 2: 931. 1759. *G. oblongifolia* Ruiz & Pav., Fl. Peruv. Chil. 2: 67, pl. 220. 1798. *G. caruto* H.B.K., Nov. gen. sp. 3: 407 (quarto). 1820. *G. americana* var. *caruto* (H.B.K.) Schum. in Mart., Fl. Bras. 6(6): 352. 1889. *G. codonocalyx* Standl., Contr. U.S. Natl. Herb. 17: 446. 1914. *G. venosa* Standl., J. Wash. Acad. Sci. 18: 168. 1928. Figure 26.

Small to large trees 4-27 m tall, often with a spreading hemispheric crown, trunk to 50 cm thick, bark smooth and lenticellate, leafy branchlets 4-9 mm thick, densely pubescent in early stages or glabrous; **stipules** 10-25 mm long, triangular, the basal sheathing tube 1-3 mm long, acute, deciduous with the leaves. **Leaves** with petioles 2-13 mm long, 2-3 mm thick, glabrous or pubescent; **leaf blades** 12-42 cm long, (4-)6-19 cm broad, obovate to elliptic-obovate or broadly oblanceolate, apex acuminate to obtuse or rounded, gradually narrowed to a cuneate or slightly decurrent base, drying chartaceous and often very dark above, glabrous and lustrous above, glabrous to densely pubescent beneath with thin soft hairs ca. 0.5 mm long, 2° veins 9-18/side. **Inflorescences** terminal or subterminal, 4-10 cm long and with 1-9 flowers, cymose, peduncles to 25 mm long, glabrous, pedicels 4-12 mm long. **Flowers** 2.5-4 cm long, appar-

ently bisexual but perhaps functionally unisexual, hypanthium difficult to distinguish from the calyx tube and together 7-17 mm long, calyx tube to 10 mm diam. distally, truncate or with broad short lobes, glabrous on the exterior and puberulent within; **corolla** ca. 4 cm broad, salverform, carnos, densely descending-sericeous externally (except at the base of the tube), white or yellowish white, darkening with age, tube 5-15 mm long, 4-7 mm diam. (to 10 mm at the lobes), lobes 5-6, 11-28 mm long, 5-12 mm broad, obovate and rounded at apex; anthers 6-14 mm long, becoming recurved between the lobes; stigmas ca. 5 mm long. **Fruits** 4-11 cm long, 3-11 cm diam., obovoid to subglobose, smooth and grayish brown or yellowish brown, the persisting calyx 3-6 mm long, crateriform on apex of the fruit and 8-10 mm diam., pedicels up to 5 cm long in fruit; **seeds** 6-12 mm long, 4-7 mm broad, ca. 2.3 mm thick.

Trees of both wet evergreen rain forests and seasonally very dry deciduous forest formations in the Caribbean and Pacific lowlands, from near sea level to 900 m elevation. Flowering occurs primarily in March-August; fruiting throughout the year. This species ranges from southern Florida and the West Indies, through Mexico and Central America through tropical South America to Paraguay.

Genipa americana is recognized by the larger leaves with short petioles clustered at the ends of stems, usually solitary large fruit with many horizontal seeds in vertical files, and large sericeous flowers with short corolla tubes and large lobes. This is a common and distinctive tree, especially conspicuous in deciduous forest formations in the dry season because of its large terminal fruit (but compare *Alibertia edulis*). This species may be confused with species of *Borojoa*, but those tend to have sessile terminal flowers and stipules with parallel venation. *Guaitil*, *caruto*, *jagua*, and *jagua negro* are common names for this species. The juice of the young pulpy fruit turns black or dark blue and is used by Native Americans as a dye or body paint. The species is sometimes cultivated, and the fruit is eaten. The wood is easy to work but strong and resistant; it is used for making furniture and carts and in building construction.

Genipa americana is here interpreted to be a very variable species, following Dwyer (1980) and Steyermark (1974). The types of Standley's *G. codonocalyx* (Pittier 12085 US) and *G. venosa* (Standley & Valerio 45269 US) appear to represent no more than unusual forms of *G. americana* and were described when the full pattern of variation in *G. americana* was not apparent. The type of *G. venosa* has prominent petioles (3.5–4 cm long) and unusually long fruit, but it seems better to treat it as a variant of *G. americana* rather than as a distinct species. Collections with the leaves densely pilose beneath have been referred to variety *caruto* (H.B.K.) K. Schum.

Genipa williamsii Standl., J. Wash. Acad. Sci. 8: 642. 1918. Figure 26.

Small to medium-sized trees, 4–20 m tall, with boles ca. 25 cm dbh, leafy stems 3–7 mm thick, glabrescent, becoming pale brown; stipules 10–32 mm long, 6–18 mm broad, ovate from a narrowed base, flattened, appressed-sericeous. Leaves with petioles 7–22(–60) mm long, 1.5–2.7(–4) mm thick, glabrous, often drying blackish and lustrous; leaf blades 8–17(–33) cm long, 5–10(–16) cm broad, obovate-oblong, to broadly elliptic or elliptic-oblong, apex rounded and lacking a narrowed tip, base obtuse to acute and slightly decurrent on petiole, drying stiffly chartaceous to subcoriaceous and dark reddish brown above, glabrous above, appressed-sericeous on the major veins beneath with hairs ca. 0.3 mm long, 2° veins 7–9/side and weakly loop-connected distally, 3° venation obscure. Inflorescences of ca. 3 (4–7) terminal flowers subtended by 2 ovate-lanceolate bracts (stipules) ca. 12 mm long with glabrous surfaces but ciliolate along the edge, peduncles 5–10 mm long, pedicels 8–10 mm long and continuous with the hypanthium, drying black,

bracteoles 3 mm long or reduced to ridges. Flowers glabrous externally, drying black, hypanthium 3–4 mm long, 4–5 mm broad at apex, obconic, calyx tube 0.5–1 mm high, entire or slightly undulate; corolla salverform, white and carnos, corolla tube 1.8–3 cm long, 4–5 mm diam., lobes 5, 18 mm long, 8–12 mm broad distally, obovate-oblong and rounded distally; anthers sessile, stigmas 4, to 4 mm long, unequal. Fruits subglobose, ca. 7 cm diam., drying black; seeds ca. 10 mm long, 5–6 mm broad, imbedded in white pulp.

This species has been collected only in southernmost Limón Province at 450–650 m elevation (Hammel et al. 17597 CR, MO, Herrera 3208 CR, MO) in Costa Rica. Flowering in July; fruiting in April–June and October in Panama. The species ranges to Colombia.

Genipa williamsii is recognized by the leaves rounded distally, clavate flower buds, and both the fleshy flowers and the large fruits that dry black. It is similar to species of *Ladenbergia*, but those have domatia and valvate corolla lobes.

Geophila D. Don

REFERENCE—L. O. Williams, *Geophila* (Rubiaceae) in North America. Phytologia 26: 263–264. 1973.

Creeping perennial herbs, stems slender and puberulent or glabrous, rooting at the nodes; stipules interpetiolar, small, rounded-ovate to triangular, entire to shallowly bilobed, persisting. Leaves usually with long petioles; leaf blades rounded and often cordate at the base, membranaceous to thin-chartaceous, venation pinnate, domatia absent. Inflorescences terminal or pseudoaxillary, few-flowered heads or cymes, peduncles short or long, flowers subtended by an involucre of small bracts, pedicels short or absent. Flowers radially symmetrical and bisexual, usually 5-parted (less often 4–7-parted), calyx tube with 4–7 narrow lobes, persistent; corolla funnelform to salverform, white, corolla tube narrow, pilose in the throat, corolla lobes 4–7, valvate in bud, spreading or recurved; stamens 4–7, filaments filiform and inserted in the floral tube, anthers dorsifixed, linear, half exserted; ovary 2-locular, ovules solitary in each locule and basal, style slender with 2 stigmas. Fruits a juicy berry, usually containing 2 1-seeded pyrenes (nutlets); pyrenes planoconvex and smooth or costate on the dorsal surface, with a ventral sulcus.

A genus of 20–30 species native to the American tropics, Africa, and Asia. The slender creeping stems, long-petiolate leaves with rounded blades, few-flowered inflorescences, and fleshy, two-seeded fruits characterize this genus. These plants may be mistaken for species of *Coccocypselum*, but that genus has many-seeded fruit.

Key to the Species of *Geophila*

- 1a. Fruit black at maturity, pyrenes weakly costate; peduncles 2–10 cm long; basal lobes of the leaf blades separated by a sinus (cordate with non-overlapping lobes) *G. macropoda*
- 1b. Fruit red at maturity (if fruit are blue go to the genus *Coccocypselum*), pyrenes strongly costate; peduncles 0.2–10 cm long; basal lobes of the leaf blades separate to overlapping 2
- 2a. Ovary, fruit and leaves conspicuously pilose with thin hairs 0.5–2 mm long [leaf blades subcordate with a small basal sinus; peduncles to 7 cm long in fruit] *G. cordifolia*
- 2b. Ovary and fruit glabrous, leaves glabrous or puberulent with short (0.1–0.3 mm) hairs; peduncles to ca. 2 cm long 3a
- 3a. Leaf blades ovate and slightly longer than broad, often narrowed at apex, cordate but usually without a visible basal sinus (because the lobes overlap slightly) *G. repens*
- 3b. Leaf blades ovate-triangular and distinctly longer than broad, usually acute at apex, cordate to subcordate at the base and with a small sinus *G. gracilis*

Geophila cordifolia Miq., Stirp. Surin. Sel. 176. 1850. *Mapouria trichogyne* Muell.-Arg. in Mart., Fl. Bras. 6(5): 426. 1881. *Geophila trichogyne* (Muell.-Arg.) Standl., Publ. Field Columb. Mus., Bot. Ser. 7: 423. 1931. Figure 2.

Creeping **herbs**, leafy stems 0.7–1.5 mm thick, densely pubescent with slender pale straight or crooked hairs 0.5–2 mm long; **stipules** 2–4(–6) mm long, 1.5–4 mm broad (broadest beneath the inflorescences), usually glabrous, persisting. **Leaves** with petioles 3–7(–13) cm long (shorter on leaves subtending the inflorescences), conspicuously pubescent with slender crooked or straight multicellular hairs 0.7–1.5 mm long; **leaf blades** 3–7(–11) cm long, 2–6(–8.5) cm broad, broadly ovate to oblong-ovate or narrowly ovate (triangular-ovate), apex obtuse to short-acuminate, base cordate with rounded lobes 8–35 mm broad, basal sinus 3–15 mm deep, drying thin-chartaceous and brownish, both surfaces covered with thin usually crooked hairs 0.7–2 mm long, 2° veins 3–5/side, not usually loop-connected near the margin. **Inflorescences** terminal, capitate, 1–3 cm long (to 6 cm in fruit), with 5–17 flowers, peduncles 5–15 mm long, elongating in fruit, densely pubescent, bracts 3–10 mm long, lanceolate and pubescent, pedicels 0.5–3 mm long. **Flowers** with an urceolate hypanthium, calyx tube 0.5 mm long and 1.5 mm diam., lobes ca. 3 mm long, with slender hairs ca. 1 mm long; **corolla** 5–6 mm long, white often tinged with pink distally, tube 2–4.5 mm long, glabrous externally, with a short collar of hairs at the point of filament attachment within, lobes 5, 1.5–2.5 mm long; **stamens** with anthers 0.8–1 mm long, included. **Fruits** ca. 8 mm long, ovoid-globose, orange to red, with scattered slender hairs, pyrenes ca. 4 mm long and 3 mm broad, with 3–5 prominent longitudinal dorsal ribs.

Plants of evergreen forest formations, from near sea level to 500(–1100) m elevation. Probably flowering and fruiting primarily in the wet season (May–December). The species ranges from Belize along the Atlantic slope of Central America to Colombia, Venezuela, and the Amazon basin in Brazil and Peru.

Geophila cordifolia is recognized by the long, often crooked, thin multicellular hairs that cover almost all parts of the plants. The long-petiolate leaves with cordate bases, short inflorescences elongating in fruit, and glabrous stipules are addition distinctions. In Costa Rica the species is known only from the La Selva area and from Volcán Rincón de la Vieja.

Geophila gracilis (Ruiz & Pav.) DC., Prodr. 4: 537. 1830. *Psychotria gracilis* Ruiz & Pav., Fl. Peruv. 2: 63, pl. 211, f. C. 1799. *G. croatii* Steyerm., Phytologia 35: 401. 1977.

Creeping **herbs** to 20 cm tall or slender-stemmed vines to 1.5 m long, leafy stems 0.3–1.3 mm thick, glabrous, horizontal internodes 3–7 cm long, with adventitious roots near the nodes; **stipules** 2–4 mm long, 1–2 mm broad, usually rounded at apex, curving outward in age and persisting. **Leaves** with petioles 2–8 cm long (but shorter below the inflorescences), 0.3–1 mm thick, glabrous abaxially and with 2 rows of short (0.2–0.5 mm) stiff retrorse or erect hairs along either side of the adaxial sulcus; **leaf blades** 1.8–5 cm long, 1–3.5 cm broad, triangular-ovate to ovate, apex gradually narrowed and acute (or obtuse), base cordate to subcordate, sinus 3–8 mm deep, the basal lobes usually separate but occasionally overlapping and the sinus obscured, drying thin-chartaceous, glabrous above or with few thin hairs 0.3–0.8 mm long, usually glabrous beneath, 2° veins 3–4/side, usually loop-connected near the margin. **Inflorescences** terminal, 12–15 mm long, capitate with ca. 3–7 flowers, peduncles 2–8 mm long (apparently longer when the leaves of the subtending node are reduced and bract-like, bracts 4–7 mm long, 1–1.5 mm broad, united at the base and persisting, pedicels 0–1 mm long. **Flowers** with hypanthium ca. 2 mm long, calyx lobes ca. 3 mm long and 0.5 mm broad, narrowly oblong, persistent and enlarging in fruit; corolla white. **Fruits** red at maturity, 3–5 mm long, subglobose, pyrenes ca. 3.5 mm long, with 3 prominent longitudinal dorsal ridges.

Plants of evergreen forest formations, from near sea level to ca. 500 m elevation. Flowering in May–December (primarily in June and July in central Panama; Croat, 1978). The species is known from southeastern Nicaragua, the Canal area of Panama, and the upper Amazon basin of Brazil, Peru, and Bolivia.

Geophila gracilis is recognized by its slender stems rooting at most nodes, triangular-ovate leaf blades with little or no puberulence, and short terminal capitate inflorescences subtended by bracts fused at the base. Variation in specimens from South America clearly encompass the distinctions used to separate *G. croatii*. This species is apparently common on Barro Colorado Island, Panama, and has been collected in Nicaragua, but it has yet to be collected in Costa Rica.

Geophila macropoda (Ruiz & Pav.) DC., Prodr. 4: 537. 1830. *Psychotria macropoda* Ruiz & Pav., Fl. Peruv. 2: 63, pl. 211, f.6. 1799. Figure 2.

Creeping herbs, leafy stems 0.8–2 mm thick, glabrous or very minutely (0.1 mm) puberulent, often with 2 prominent longitudinal ridges; **stipules** 2–6 mm long, ovate-oblong, glabrous, deciduous or obscured by the adventitious roots. **Leaves** with petioles (2–)3–14 cm long (shorter below the inflorescences), 0.7–1.2 mm thick, glabrous abaxially but with 2 adaxial ridges with short (0.1–0.4 mm) dense hairs; **leaf blades** 3–9 cm long, 2.5–8 cm broad, broadly ovate to ovate-orbicular, apex rounded to broadly obtuse, base cordate with lobes 1–4 cm broad, basal sinus 2–15 mm deep, drying membranaceous or thin-chartaceous and often grayish green, glabrous above, glabrous beneath except for the minute puberulence on the major veins near the base, 2° veins 3–5/side and weakly loop-connected near the margin. **Inflorescences** usually axillary, 2–4 cm long and elongating in fruit, capitate with 3–7 flowers, peduncle 1.5–5(–7) cm long, minutely puberulent with whitish hairs ca. 0.1 mm long, bracts 3–6 mm long, united at the base, pedicels to 2 mm long. **Flowers** with hypanthium ca. 1.5 mm long, essentially glabrous, calyx lobes 2–3 mm long; **corolla** 3–7 mm long, tube 3–4 mm long, corolla lobes 5, 2–3 mm long. **Fruits** black or blue, sessile, 5–10 mm long, 3–7 mm diam., ellipsoid to ovoid; pyrenes 4–7 mm long, 2–3 mm broad, without raised longitudinal ribs (costae) on the convex surface.

Plants of the lowland Caribbean rain forest formations, from near sea level to 600 m. Flowering in April–November. The species ranges from southern Mexico through Central America to Bolivia and Paraguay.

Geophila macropoda is recognized by the axillary and long-pedunculate inflorescences, closely clustered flowers, black fruit, and pyrenes without prominent longitudinal costae.

Geophila repens (L.) I. M. Johnston, Sargentia 8: 281. 1949. *Rondeletia repens* L., Syst. ed. 10: 928. 1759. *Psychotria herbacea* Jacq., Enum. Pl. Carib. 16. 1760. *Geophila herbacea* (Jacq.) Schumann in Engl. & Prantl., Nat. Pflanzenfam. 4, 4: 119. 1891. Figure 2.

Creeping herbs to ca. 10 cm high, leafy stems 0.5–1 mm thick, glabrous or very sparsely and minutely puberulent; **stipules** 0.5–2 mm long, 1–2 mm broad, broadly ovate, glabrous, persisting or deciduous. **Leaves** with petioles 1–6(–8.5) cm long (sometimes shorter in leaves subtending the inflorescences), 0.4–1.3 mm thick, glabrous on the abaxial surface but with short (0.2–0.5 mm) retrorse or crooked hairs along the adaxial (upper) side; **leaf blades** 1.2–5.5 cm long, 1–5 cm broad, broadly ovate to ovate-suborbicular, apex bluntly obtuse or rounded-obtuse, base cordate with lobes 5–25 mm broad, basal sinus 1–7 mm deep and usually obscured by the overlapping basal lobes, drying membranaceous, upper surface glabrous or with a few short hairs near the margins, glabrous beneath or with a few short (0.1–0.3 mm) hairs on the veins near the petiole, 2° veins 3–5/side, cystoliths visible (as short whitish lines) or obscure on the lower surface. **Inflorescences** solitary and terminal on short leafy shoots (apparently 2–3 and axillary when directly subtended by small leaves), with (1–)2–5 flowers, peduncles 5–35 mm long, puberulent with short retrorse hairs, subtending bracts 3–6 mm long, united at the base and lanceolate distally, pedicels 0–2 mm long. **Flowers** white or becoming pink in age, hypanthium ca. 1 mm long, calyx tube 1–1.5 mm long, glabrous, calyx lobes 1–3 mm long, 0.3–0.7 mm broad, glabrous; **corolla** 8–14 mm long, glabrous or puberulent, funnelform, tube 6–9 mm long and 1–1.5 mm diam., lobes 5, 3–5 mm long, 1.5–2.5 mm broad, ovate and obtuse to acute; **stamens** with filaments ca. 0.5 mm long, attached near the middle of the tube, anthers ca. 2 mm long; style 5–7 mm long. **Fruits** 8–10 mm long, ovoid or globose, bright red at maturity, subsessile or short (1–2.5 mm) pedicellate; pyrenes 3.5–5 mm long, 2.5–3 mm broad, with 3 slightly raised longitudinal ribs (costae) on the convex face.

Plants of the shaded forest floor in evergreen or partly deciduous forest formations of both the Caribbean and Pacific lowlands of Costa Rica, from near sea level to 800 m elevation. Flowering in June–October; fruiting in July–November. The species ranges from Mexico and the West Indies to Peru and Bolivia in the New World; it is also found in West Africa, the Philippines, and the western Pacific.

Geophila repens is recognized by its creeping habit and short stature, small cordate leaves with the sinus obscured, petioles with puberulence along one side, bright red fruit, and pyrenes with weakly developed costae. This is our most commonly encountered species of *Geophila*; it has been collected at La Selva and from near Cañas in Guanacaste Province to the Golfo Dulce area along the

Pacific. *Lechuga* is a name used for this species in the Golfo Dulce region. Breeding biology was studied by Bawa and Beach (1983).

Gonzalagunia Ruiz Lopez & Pavón

Shrubs or small trees, distal branches often curved, pendant or scandent, leafy stems usually slender and pubescent, terete, nodes usually thickened; **stipules** interpetiolar, usually broad at the base and triangular with a narrow distal awn (rarely intrapetiolar and tubular). **Leaves** distichous, petiolate or sessile; **leaf blades** often thin-chartaceous, usually narrow and with ascending secondary veins, domatia absent or obscure. **Inflorescences** solitary, usually terminal and narrowly long-racemiform, spiciform or thyrsiform, the flowers solitary, cymose or fasciculate on short lateral branches of the central axis, bracteoles present, flowers sessile or pedicellate. **Flowers** radially symmetrical, bisexual, monomorphic or distylous, small, 4- (less often 5-) parted, hypanthium urceolate to rounded, calyx tube very short, calyx lobes 4 or 5, small, equal or unequal, persisting in fruit; **corolla** salverform to funnellform, white or pink, corolla tube narrow, villose in the throat, corolla lobes

4(–5), imbricate or valvate; **stamens** 4(–5), filaments short or absent, anthers dorsifixed, 2-lobed at the base, exerted or partly exerted; **ovary** 2-or 4-locular, ovules numerous, placentation peltate on the septum, style with 2 or 4 stigmatic lobes. **Fruits** baccate, fleshy or spongy, subglobose, 2- or 4-locular and usually with 2 or 4 lobes or sulci, with 2 or 4 hard cocci; **seeds** 4—many within the cocci, minute.

A genus of 25–35 species, ranging from Mexico, Central America, and the West Indies through tropical South America. The long narrow spike-like distal inflorescences, slender drooping distal stems, small narrow-tubed flowers and baccate fruits with 2–4 pyrenes make this a very distinctive genus. Some species of *Rondeletia* with long-narrow inflorescences may be confused with species of *Gonzalagunia* in the absence of fruit; *Rondeletia* has capsular fruit. Several of our species are weedy shrubs of open secondary growth and closely related; they can be difficult to distinguish in the absence of mature flowers or fruit. A few species resemble species of *Buddleia* (Loganiaceae).

Key to the Species of *Gonzalagunia*

- 1a. Stipules united or overlapping above the petioles to form a short tubular sheath or broad tube-like base 4–12 mm long 2
- 1b. Stipules not forming a tube above the node, or the broad margins not overlapping at the base, stipule only 1–3 mm long before being narrowed into the awn-like apex 3
 - 2a. Stipular sheath to 1 cm long; flower clusters and lateral branches of the inflorescences subtended by caducous bracts 4–12 mm long and 1–2 mm broad, corolla 3–4 mm long; leaf blades with 5–8 pairs of major secondary veins; small treelets of wet forest understory *G. bracteosa*
 - 2b. Stipular sheath 0–5 mm long or the stipule margins slightly overlapping; bracts less than 2 mm long, corolla 4–6 mm long; with 10–14 pairs of secondary veins; trees to 18 m tall *Rondeletia brenesii*
- 3a. Petioles usually less than 4 mm long; corolla tube usually less than 7 mm long 4
- 3b. Petioles usually more than 4 mm long; corolla tube usually more than 7 mm long 7
 - 4a. Leaf blades with 4–7 pairs of major secondary veins, laminae thin-textured; flowers thin-textured and often solitary, corolla glabrous externally *G. rudis*
 - 4b. Leaf blades with 7–13 pairs of major secondary veins; thinly to stiff-chartaceous; flowers thick-textured, corolla densely sericeous externally 5
 - 5a. Leaf blades sessile, narrowly lanceolate, 9–26 cm long, with 9–15 pairs of secondary veins arising at angles of about 30–40° [only known from the Golfo Dulce area] *G. brenesii*
 - 5b. Leaf blades sessile or short petiolate, ovate to elliptic and rarely lanceolate, to 16(–30?) cm long, with 4–12 pairs of secondary veins arising at angles of 40–60° 5
 - 6a. Corolla lobes ca. 1.5 mm long; leaf blades with 4–11 pairs of major secondary veins, ovate to ovate-elliptic, thinly chartaceous; Caribbean and Pacific slope, 0–1200 m elevation *G. ovatifolia*
 - 6b. Corolla lobes 3–4 mm long; leaf blades with 7–12 pairs of major secondary veins, ovate-elliptic to lanceolate, stiffly chartaceous; wet Caribbean slope 300–1200 m elevation *G. stenostachya*
- 7a. Mature fruit becoming blue-black; corollas white or white tinged with pink, corolla tubes 8–13 mm long; inflorescences with the flower clusters sessile; 0–1200(–1500) m elevation .. *G. panamensis*

- 7b. Mature fruit white; corollas reddish to pink, corolla tubes 6–10 mm long; inflorescences with the flower clusters on short (1–3 mm) peduncles (but note that some inflorescences may only have solitary flowers and no apparent secondary peduncles); 900–2200 m elevation *G. rosea*

Gonzalagunia bracteosa (J. D. Smith) B. L. Robinson, Proc. Amer. Acad. Arts 45: 405. 1910.
Gonzalea bracteosa J. D. Smith, Bot. Gaz. 33: 252. 1902. Figure 21.

Shrubs or small treelets, 1.5–4 m tall, leafy branchlets 2–4(–6) mm thick, terete, with many ascending strigose hairs 1–1.5 mm long; **stipules** 8–18(–24) mm long, 3–6 mm broad, with a tubular sheath to 12 mm long, dark brown and pubescent along the midvein, acute to acuminate and with a slender tip 1–7 mm long. **Leaves** with petioles 2–10 mm long, 1–2 mm thick, broad, pubescent; **leaf blades** 6–19(–22) cm long, 2.5–7.5(–8.5) cm broad, narrowly elliptic-obovate to obovate-oblong, oblong or elliptic, usually broadest above the middle, apex acuminate (acute), tip to 15 mm long, gradually narrowed to the acute or obtuse base, leaves usually drying chartaceous and dark brown above (rarely subcoriaceous), sparsely pubescent above with thin appressed hairs 0.5–1 mm long (densely strigulose on the midvein), more densely appressed-pubescent beneath with brownish hairs 0.5–1.3 mm long, 2° veins 5–7/side. **Inflorescences** solitary, axillary or terminal, 6–25 cm long, spike-like or thyriform panicles with small (5–15 mm) alternate or opposite flower clusters 2–14 mm distant along the rachis (rarely with lateral branches to 4 cm long), primary peduncles 2–8 cm long, with ascending hairs to 2 mm long, several bracts 5–12 mm long and 1–2 mm broad subtending the flower clusters, flowers sessile. **Flowers** with hypanthium ca. 1 mm long, densely hirtellous, calyx tube minute, calyx lobes ca. 0.5 mm long, difficult to see among the hairs, glabrous on the inner surface; **corolla** funnelform, greenish white to white, with few straight hairs 0.5 mm long externally, tube 2–3 mm long, corolla lobes 5, 1–2 mm long; **stamens** 5, anthers ca. 1 mm long; style ca. 2.5 mm long, stigma 0.4 mm long. **Fruits** 3–5 mm long, 3–5 mm broad, depressed globose, becoming blue or blue-black, pubescent, sessile; pyrenes 2–4.

Plants of lowland rain forest formations on the Caribbean and Pacific slopes in Costa Rica, from 10 to 850 m elevation. Flowering in January–September; fruiting throughout the year. The species ranges from northeastern Costa Rica to Colombia.

Gonzalagunia bracteosa is characterized by the hirsutulous pubescence on many parts, obovate-oblong leaves drying dark above, narrow inflorescences with short flower clusters subtended by conspicuous bracts, small sessile flowers, and tubular stipules. Two collections are noteworthy because the inflorescences have lateral branches 2–4 cm long and with many bracts along their length: *Folsom 9778* (DUKE, F) and *Zamora & Sánchez 469* (CR, F). Specimens exhibiting such unusual variation in bract development and inflo-

rescences appear to be restricted to northeastern Costa Rica. This species differs greatly from our other members of the genus; it resembles *Psychotria pilosa*.

Gonzalagunia brenesii Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 1302. 1938. Figure 20.

Shrubs, 1.5–3 m tall, leaf branchlets 1.5–6(–8) mm thick, rounded-quadrangular in cross-section, sparsely pubescent with appressed hairs ca. 0.5 mm long or glabrous, drying reddish brown; **stipules** 4–8 mm long, 2.5–7 mm broad at the base, with a very short (1–2 mm) broadly triangular base and a slender awn 4–6 mm long. **Leaves** subsessile, petioles 0–3(–5) mm long; **leaf blades** 9–26 cm long, 2.7–6 cm broad, narrowly lanceolate to narrowly elliptic-oblong or elliptic-oblong, apex tapering gradually and long-acuminate, base obtuse, drying chartaceous and dark brown above, lustrous above in life, glabrous or sparsely pubescent above, with thin whitish ascending hairs beneath, the hairs longer (ca. 0.4 mm) on the major veins beneath, 2° veins 9–13/side and weakly loop-connected distally, 3° veins subparallel. **Inflorescences** solitary and terminal, 20–50 cm long, spiciform with short (1–5 mm) lateral branches bearing 2–6 flowers, peduncles 0–6 cm long, 1.5–3 mm thick, with ascending appressed hairs, bracts 1–3 mm long, linear, pedicels 1–2 mm long. **Flowers** 6–12 mm long, hypanthium 0.5–1 mm long, sericeous at the base, calyx tube ca. 0.5 mm long, calyx lobes 0.2–0.3 mm long, glabrous; **corolla** white or pink, tube 7–10 mm long and 0.7–1 mm diam., pubescent, lobes 3 mm long and 1.8 mm broad, obtuse; **ovary** 4-locular. **Fruits** 3–5 mm long, 3–6 mm broad, usually 4-lobed, becoming white, minutely and sparsely puberulent.

Plants of rain forest formations in Costa Rica's southern Pacific lowlands, from near sea level to 500 m elevation. Flowering in April–December; fruiting in January and August–September. This species is endemic to Costa Rica, ranging from the forests of the Pacific slope above Quepos eastward to the Osa Peninsula.

Gonzalagunia brenesii is distinguished by its restricted range, long narrow subsessile leaves, long spicate inflorescences, and short narrowly tubular white or pink flowers. This species appears to be related to the *G. panamensis*–*G. rosea* complex.

Gonzalagunia ovatifolia (J. D. Smith) B. L. Robinson, Proc. Amer. Acad. Arts 45: 405. 1910.

Gonzalea ovatifolium J. D. Smith, Bot. Gaz. 27: 336. 1899. Figure 20.

Shrubs to 3(–4) m tall, leafy branchlets 1.3–4 mm thick, with thin ascending brownish hairs ca. 0.5 mm long, terete, glabrescent; **stipules** 6–10 mm long, subulate with a short (1–2 mm) base and long (4–7 mm) awn-like apex. **Leaves** subsessile with petioles 1–4(–5) mm long, ca. 1.3 mm thick, pubescent; **leaf blades** 5–12(–16) cm long, 2–6(–7) cm broad, ovate to ovate-elliptic, apex short- or long-acuminate, tip 3–20 mm long, abruptly narrowed to rounded at the obtuse base, unequal at the base, the leaves drying thin-chartaceous and dark above, pale grayish to pale greenish beneath, essentially glabrous above, appressed-pubescent on the veins beneath with thin short (ca. 0.5 mm) hairs, 2° veins 6–11/side. **Inflorescence** solitary and terminal, 12–45 cm long, narrowly spike-like with flowers in distant (3–10 mm) clusters, rachis slender 0.5–1 mm thick, with thin whitish ascending hairs ca. 0.5 mm long, flowers in sessile or subsessile groups of 1–3, subtended by linear bracts 2–4 mm long, flowers usually solitary in the distal half of the inflorescence, pedicels to 1 mm long. **Flowers** with hypanthium ca. 1 mm long, densely sericeous, calyx lobes 1–2 mm long, glabrous; **corolla** white, tube 4–5 mm long, lobes 1–2 mm long; anthers ca. 1 mm long. **Fruits** 2–3 mm long and 3–4 mm broad (dried), white, usually 4-lobed, pubescent with thin hairs ca. 0.3 mm long.

Shrubs of wet evergreen forest formations of both the Caribbean and Pacific slopes in Costa Rica, from near sea level to 1200 m elevation. Flowering in January–April and July–August; fruiting in the same months and in October and December. The species ranges from Nicaragua to Colombia.

Gonzalagunia ovatifolia is recognized by its subsessile ovate acuminate leaves, the long inflorescences with few-flowered cymes or solitary flowers along its length, and the small corollas. This species may be difficult to separate from some specimens of *G. rosea* (q.v.).

Gonzalagunia panamensis (Cav.) K. Schum. In Mart., Fl. Bras. 6(6): 292. 1889. *Buena panamensis* Cav., Anales Hist. Nat. 2: 279. 1800. *Gonzalea panamensis* (Cav.) Spreng., Syst. Veg. 1: 417. 1825. Figure 20.

Shrubs to 3(–5) m tall, erect or scandent, leafy branchlets 0.8–4 mm thick, terete or slightly quadrangular, sparsely to densely sericeous with thin whitish ascending hairs ca. 0.5 mm long; **stipules** 4–7 mm long, the broad base 0.5–2 mm long, subulate with a narrow awn-like tip, pubescent on the midrib and edges. **Leaves** with petioles 6–27 mm long (shorter on young axillary shoots), ca. 1 mm thick, pubescent, with lateral margins continuous with the decurrent leaf margin; **leaf blades** 5–15 cm long, 1–6 cm broad, narrowly lanceolate to lanceo-

late-elliptic or ovate-lanceolate, apex tapering gradually and acute or acuminate, base acute and often decurrent on petiole, drying thin-chartaceous, densely pubescent on the veins and more sparsely between the veins with appressed hairs ca. 0.3 mm long above and below, 2° veins 5–7/side, ascending. **Inflorescences** solitary and terminal (or axillary by later lateral growth of side shoots), 6–22(–40) cm long, peduncles 1–5 cm long, 1–2 mm thick, pubescent, the flower clusters ca. 5 mm diam., essentially sessile (but solitary flowers pedicellate), bracts to 4 mm long and linear, pedicels 0–2 mm long. **Flowers** 4-parted, hypanthium 0.7–1 mm long, sparsely pubescent, calyx ca. 1 mm long, calyx lobes 0.5–1 mm long and 0.5 mm broad at the base; **corolla** white or white tinged with pink, tube (8–)10–13 mm long, 0.7–1 mm diam., sparsely pubescent, lobes 2–3 mm long, ca. 2 mm broad at the base, puberulent within; **stamens** 4, anthers 2–2.2 mm long; style 7–10 mm long, stigma ca. 0.7 mm long. **Fruits** 2.5–4 mm long, 3–8 mm broad, depressed globose to 4-lobed, glabrous or sparsely puberulent, red becoming purple black or black.

Shrubs of evergreen or partly deciduous forest formations of the Pacific slope in Costa Rica, from near sea level to 1200 m elevation. Flowering in all months except March–April and November; fruiting in January, February, September–October, and December. The species ranges from Mexico to Colombia and in the West Indies.

Gonzalagunia panamensis is recognized by the usually lanceolate leaves on slender well-developed petioles, the flower clusters sessile on the inflorescence rachis (or the flowers solitary and pedicellate), the long narrow white corolla tube, and the fruit turning red or black. Collections from higher elevations have broader leaves and may represent introgression from another species; compare *G. ovatifolia* and *G. rosea*.

Gonzalagunia rosea Standl., Ann. Missouri Bot. Gard. 25: 836. 1938. *G. longithyrsa* Fosberg, Sida 2: 387. 1966. Figure 20.

Shrubs or small trees, 2–4(–6) m tall, branches erect or scandent, leafy branchlets 1–4 mm thick, terete, with stiff appressed-ascending pale yellowish or grayish hairs 0.2–0.5 mm long; **stipules** 3–7 mm long, ca. 3–4 mm wide at base, broadly triangular with a short (1–4 mm) narrow tip, pubescent on the edge and midrib. **Leaves** with petioles 4–20 mm long, ca. 1 mm thick, densely pubescent; **leaf blades** 7–18(–22) cm long, 2–6(–8) cm broad, narrowly ovate-elliptic to lanceolate, lanceolate-oblong or narrowly elliptic-oblong, apex gradually or abruptly acuminate (acute) with tip 5–15 mm long, base acute to obtuse, drying thin-chartaceous to chartaceous, dark grayish brown above, puberulent on the upper surface (denser on the major veins) with short (0.2–0.3 mm) straight hairs, more densely puberulent beneath with hairs to 0.5 mm beneath, 2° veins 5–9(–11)/side, strongly ascending (and not loop-connected near the margin). In-

florescences solitary, terminal (axillary by further growth of lateral branches), 12–35 cm long, flowering part ca. 2.5 cm broad, peduncles 5–35 mm long, 1–2.5 mm thick, densely short hirsute, flowers in groups of 1–3(–5) and borne on secondary peduncles 1–5 mm long, alternate or opposite on the rachis and 2–10 mm distant, bracts 1–3 mm long and linear, pedicels 1–3(–4) mm long. **Flowers** with hypanthium 0.5–1.5 mm long, ca. 1 mm diam., densely pubescent, calyx tube ca. 0.5 mm long, calyx lobes 4 or 5, 0.5 mm high, triangular; **corolla** red in early bud, becoming rose red or pink, tube (6–)8–10 mm long, 0.7–1.6 mm diam., slender and widening below the lobes, sparsely to densely puberulent, lobes 2–3 mm long, ca. 2 mm wide at the base, glabrous distally on the inner surface and villous near the mouth; **stamens** 4, anthers 2–2.5 mm long, anthers partly exerted; style 9–11 mm long, stigma 0.3–0.7 mm long. **Fruits** 3–5 mm long, 3–6 mm broad, white, usually 4-lobed, glabrous or sparsely puberulent.

Common shrubby plants of lower montane evergreen forest formations, from (900–)1100–2200 m elevation. Probably flowering and fruiting throughout the year, but flowering primarily in February–September and fruiting primarily in June–September. The species ranges from the Cordillera de Tilarán in Costa Rica to eastern Panama.

Gonzalagunia rosea is recognized by the thin-petiolate narrowly ovate to lanceolate leaves, the long inflorescences with pedunculate flower clusters, the pink corollas, and the spongy white fruit. This is a common weedy shrub of open habitats. Some specimens of this species may be difficult to distinguish from *G. panamensis* and *G. ovatifolia*, and it is possible that hybridization occurs.

Gonzalagunia rudis (Standl.) Standl., J. Wash. Acad. Sci. 17: 170. 1927. *Duggenia rudis* Standl., Contr. U.S. Natl. Herb. 18: 125. 1916.

Shrubs, 1.5–4 m tall, leafy stems 0.7–3 mm thick, with minute (0.2 mm) thin appressed-ascending whitish hairs, terete and glabrescent; **stipules** 4–7 mm long, with a short (1–2 mm) broad base and long narrow awn. **Leaves** with petioles 1–3 mm long, ca. 1 mm thick, hertellous; **leaf blades** 2.5–10 cm long, 1–4 cm broad, narrowly ovate to ovate-oblong or lanceolate, apex tapering gradually and acute to long-acuminate, base acute to obtuse, drying thin-chartaceous, with scattered thin appressed hairs ca. 0.5 mm long on both surfaces, with denser pubescence on the veins beneath, 2° veins 4–7/side. **Inflorescences** terminal or axillary, solitary, 4–14 cm long, spicate, peduncles 1–3 cm long, 0.3–0.7 mm thick, densely pubescent with ascending hairs, flowers usually solitary or in groups of 2–3 ca. 5 mm diam., subtended by linear bracts 2–3(–5) mm long, pedicels 1–2 mm long. **Flowers** 5-parted, hypanthium ca. 1 mm long, urceolate, densely puberulent, calyx lobes 1–2 mm long, linear; **corolla** white, tube ca. 6 mm long and 0.7 mm diam., lobes ca. 5 mm long and 1 mm broad, glabrous externally, puberulent

within; **stamens** included. **Fruits** 2–4 mm long, 2.5–5 mm broad, white, depressed globose, 4-lobed, with thin erect hairs 0.5 mm long.

Plants of evergreen forest formation on the Pacific slope of southern Costa Rica, from near sea level to 500 m elevation (to 1000 m in Panama). Flowering primarily in the wet season (June–September). This species ranges from about 84°W in Costa Rica to eastern Panama.

Gonzalagunia rudis is recognized by its smaller thin lanceolate leaves, the slender spike-like inflorescences with mostly solitary subsessile flowers, and the unusual calyx and corolla with long narrow lobes. Costa Rican collections differ somewhat in their narrower more lanceolate leaves, but collections with such leaves are also found in Panama.

Gonzalagunia stenostachya (Standl.) W. Burger, comb. nov. *Rondeletia stenostachya* Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 1372. 1938. *Arachnothryx stenostachya* (Standl.) Borhidi, Acta Bot. Hung. 33: 303. 1987.

Shrubs to 3 m tall, leafy stems 2.3–6 mm thick, with short dense yellowish or reddish brown hairs ca. 0.5 mm long; **stipules** 4–15 mm long, triangular, acute, with yellowish hairs along the midrib. **Leaves** with petioles 2–4 mm long, ca. 1.5 mm thick; **leaf blades** 7–16 cm long, 2–6 cm broad, elliptic, elliptic-oblong to lanceolate or oblanceolate, apex acute or short-acuminate, base gradually narrowed and cuneate base (rounded in *Dryer 1274*), drying stiffly chartaceous and dark reddish brown above (grayish green beneath), with thin hairs 0.4 mm long or glabrescent above, densely puberulent on the midvein beneath, 2° veins 7–12/side, ascending. **Inflorescences** (7–)15–25 cm long, 1.3–2.5 cm broad, spiciform thyrsoid panicles, peduncles 1.3–6 cm long, 1.2–2 mm thick, strigose, lateral cymules sessile and separate along the rachis, of (1–)2–5 flowers, bracts ca. 3 mm long, linear, pedicels 0–4 mm long. **Flowers** 4-parted, hypanthium ca. 1.5 mm long and 1.5 mm diam., densely sericeous, calyx lobes 1–2 mm long, narrowly triangular; **corolla** white, densely sericeous with hairs 0.5–0.9 mm long, tube 4–9 mm long, slender, lobes 3–4.5 mm long, oblong. **Fruits** ca. 3 mm long and 4 mm broad (?immature) with sericeous hairs ca. 0.5 mm long.

Plants of wet evergreen forest formations of the Caribbean slope, 300–1200 m elevation. Flowering in February–March, July, and October; fruiting in October. This endemic species is known from near Monteverde and the La Selva–Braulio Carillo area.

Gonzalagunia stenostachya is recognized by its subsessile leaves with many ascending secondary veins, the long slender spikes with sessile and well-

separated cymules, and the sericeous flowers. The Panamanian *G. kallunkii* Dwyer (?= *G. veraguen-sis* Dwyer) has rather similar inflorescences but the petioles of that species are well developed and the leaves have fewer secondary veins.

Guettarda Linnaeus

Trees or shrubs, branchlets terete, puberulent or gla-brous, occasionally with spines; **stipules** interpetiolar, simple or slightly connate above the petioles (intrapetiolar), often slightly overlapping above the node, triangular and acuminate to rounded distally, persisting or decid-uous. **Leaves** opposite (rarely 3 or 4/node), petioles short to long; **leaf blades** entire, with pinnate venation, the distal secondaries often strongly ascending and the 3° veins often subparallel, domatia sometimes present. **In-florescences** solitary and axillary (1 or 2/node), usually pedunculate and with cymose branching, branches of the inflorescences often dichotomous (bifurcate) and with sessile flowers along 1 side, bracts and bracteoles present or reduced. **Flowers** bisexual (rarely unisexual), radially symmetrical, 4–9-parted (usually 5- or 6-parted), hy-panthium ovoid to globose or tubular, calyx tube cu-pulate to campanulate or short-tubular, calyx entire or with 2–9 poorly developed lobes/teeth; **corolla** funnel-form or salverform, white, yellowish, purple or bluish,

corolla lobes 4–9, imbricate or subvalvate, the margins often undulate; **stamens** 4–9, anthers narrow, sessile or subsessile, dorsifixed, included; **ovary** 2–9-locular, with 1 pendulous ovule from apex of each elongate-tubular locule, stigma capitate or lobed. **Fruits** drupaceous, glo-bose to elongate, rounded or angulate in cross-section, the exocarp fleshy but thin, endocarp woody to stony, 2–9-locular.

A genus of 60–80 species in the New World tropics, with a few species in the southwest Pacific and a species widespread on tropical coasts (*G. speciosa* L.). Some species of *Guettarda* have in-florescences with two equal cincinnoid branches; these are scorpioid cymes (cincinnati) in which the sessile flowers are all in a close line along a single side of the rachis. The leaves of *Guettarda* are generally thin, often clustered at the ends of branchlets, and with the distal secondaries strong-ly ascending. Domatia are often present, and the 3° veins are usually subparallel. The inflorescences are always axillary, and the flowers are all salver-form in Costa Rican species. This treatment ben-efited from the annotations made by Alfredo Gri-jalva in 1982.

Key to the Species of *Guettarda*

- 1a. Inflorescences subsessile; plants of Cocos Island and the evergreen Pacific lowlands ... *G. conferta*
- 1b. Inflorescences short-to long-pedunculate; plants of mainland Central America 2
- 2a. Bracts subtending the flowers 3–6 mm long, thin-brownish, narrowly ovate-oblong; Pacific slope and lowlands 3
- 2b. Bracts subtending the flower absent or less than 3 mm long and caducous 4
- 3a. Inflorescences with peduncles 2.5–6 cm long; leaf blades usually rounded at the base; Gulf of Nicoya *G. brenesii*
- 3b. Inflorescences with peduncles 1–3 cm long; leaf blades acute at the base; western Costa Rica *G. foliacea*
- 4a. Inflorescences with short (to 1 cm) branches, the branches not cincinnoid (scorpioid-cymose) in appearance 5
- 4b. Inflorescences with conspicuous lateral cincinnoid (scorpioid) branches more than 1 cm long (with the flowers all along 1 side 6
- 5a. Corolla tubes 8–12 mm long, peduncles less than 3 cm long; petioles 4–30(–40) mm long; fruit ca. 12 mm long, subglobose; Pacific and Caribbean lowlands *G. macrosperma*
- 5b. Corolla tubes 13–18 mm long, peduncles more than 3 cm long; petioles 20–70 mm long; fruit ca. 20 mm long, oblong, truncated distally; Golfo Dulce and Panama *G. sanblasensis*
- 6a. Trees to 30 m tall; leaves and twigs glabrous; flowers becoming 2–4 mm distant on the rachis [corolla tubes 20–30 mm long] *G. turrialbana*
- 6b. Trees to 10(–25) m tall; leaves and stems densely to sparsely puberulent; flowers 0–2 mm distant on the rachis 7
- 7a. Stipules glabrous, often broadly overlapping; midvein sparsely appressed strigose along the sides beneath [corolla tube 16–20 mm long; 1500–2500 m elevation] *G. poasana*
- 7b. Stipules pubescent (at least along the midrib); midvein densely pubescent over the entire surface on the lower side of the leaf blade 8

- 8a. Leaf blades narrowly oblong and coriaceous, densely tomentulose beneath; corolla tube 4–7 mm long [1200–1900 m elevation] *G. tornefortiopsis*
- 8b. Leaf blades elliptic to broadly ovate, drying chartaceous, lacking a densely matted tomentum beneath; corolla tubes 6–18 mm long 9
- 9a. Leaf blades rounded and often truncate at the base, to 30 cm long; peduncles to 10 cm long [corolla tubes 15–18 mm long]; northern Caribbean lowlands *G. combsii*
- 9b. Leaf blades usually acute to obtuse at the base, to 22 cm long; peduncles to 4 cm long; evergreen formations 300–1700 m elevation 10
- 10a. Leaf blades with 6–10 pairs of major secondary veins, 3° veins clearly differentiated from the smaller 4° veins; corolla tubes 13–18 mm long; Central Highlands and evergreen Pacific lowlands *G. crispiflora*
- 10b. Leaf blades with 3–5 pairs of major secondary veins, 3° and 4° veins little differentiated and parallel with each other; corolla tubes 6–9 mm long; Caribbean slope *Chomelia venulosa*

Guettarda brenesii Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 1303. 1938. Figure 33.

Trees to 10 m tall, leafy branchlets 2–4 mm thick, at first with straight ascending hairs 0.5–1 mm long, terete, soon glabrescent and becoming very dark with numerous narrow lenticels ca. 0.5 mm long; **stipules** 7–12 mm long, narrowly ovate-triangular, acute, sericeous along the midrib and base, deciduous. **Leaves** clustered at the end of branchlets, petioles 5–12 mm long, ca. 1 mm thick, with thin ascending hairs 0.5–1.3 mm long; **leaf blades** (4–)6.5–21 cm long, (3–)4.5–12 cm broad, broadly ovate to broadly elliptic, apex obtuse or subrotund, base obtuse (and rounded at the petiole) to broadly rounded and subcordate, drying chartaceous and dark above, sparsely hispidulous above with hairs ca. 0.5 mm long, more densely pubescent beneath with thin whitish hairs to 1 mm long, 2° veins 6–8/side, with denser tufts of hairs (domatia) in the vein axils, 3° veins subparallel basally and joining with the opposing tertiary veins at an angle. **Inflorescences** 3–10 cm long, equally wide, axillary, peduncle 2–6.5 cm long, ca. 0.8 mm thick, pubescent, usually bifurcate with 2 main branches and further cymose branching, bracts and bracteoles 4–8 mm long, lanceolate, pubescent along the midrib, distal axes to 4 mm long often bearing single flowers and resembling pedicels (but with bracteoles at their apex beneath the flowers). **Flowers** with hypanthium ca. 1 mm long and 1 mm broad, short-tubular and sericeous, calyx tube ca. 1 mm long, entire and more sparsely pubescent distally; **corolla** white, tube (9–)14–18 mm long, 0.5–0.8 mm diam., with minute appressed-ascending whitish hairs externally, lobes 5, ca. 3 mm long and 1.7 mm broad, margin broadly rounded and subentire. **Fruits** unknown.

Trees of lowland deciduous forest formations near the Bay of Nicoya. Immature inflorescences were collected in June (*Brenes 15694* the type), and inflorescences with falling corollas were collected in July. Fruiting in July–August and October–November. The species is known only from along the Pacific coast of central Costa Rica.

Guettarda brenesii is recognized by the bracteate inflorescences, the long narrow corollas, the broadly ovate leaves, and the rocky, seasonally very dry

seaside habitat. This species is probably related to *G. foliacea*, which shares characters of the inflorescence. The type appears to have immature leaves and inflorescences; hence, Standley's description represents minimal measurements. A highly restricted range and short flowering season may explain the paucity of collections.

Guettarda combsii Urban, Symb. Ant. 6: 48. 1909.

Small to large trees (shrubs), 5–30 m tall, trunks to 60 cm dbh, leafy branchlets 2–6 mm thick, with soft whitish erect or ascending hairs 0.5–1 mm long but soon glabrescent, terete; **stipules** 6–14 mm long, ovate to lanceolate, acuminate, pubescent along the midrib. **Leaves** often clustered at the ends of branchlets, petioles 2–9 cm long, 1.3–2 mm thick, minutely pubescent; **leaf blades** 7–20(–28) cm long, 5–13(–20) cm broad, very variable in shape, from broadly ovate to ovate-oblong or suborbicular, apex abruptly narrowed and obtuse or short acuminate, base broadly obtuse to rounded and truncate to subcordate, drying thin-chartaceous, subglabrous or sparsely pubescent above with thin hairs ca. 1 mm long, more densely pubescent beneath with thin whitish hairs 0.5–1 mm long, 2° veins 8–11/side, 3° veins parallel and prominent. **Inflorescences** 12–18 cm long, with long (5–15 cm) peduncles and 2 or 4 distal cincinnoid branches 2–5 cm long, minutely (0.1–0.4 mm) pubescent, bracts 2–4 mm long and ca. 1 mm broad, flowers sessile and closely spaced. **Flowers** with hypanthium ca. 1 mm long and 1.3 mm diam., with a dense greenish white or pale grayish white tomentum, calyx tube 1.5–2.5 mm long, entire or 2-lobed; **corolla** greenish white to cream white, tube 15–18 mm long, 1–1.5 mm diam., with dense retrorse sericeous hairs, corolla lobes 5–7, ca. 3–4 mm long; **ovary** 4- or 5-locular. **Fruits** 6–8 mm long, subglobose, covered with a dense minute (0.05 mm) tomentum, grayish green, the surface becoming wrinkled.

Trees of evergreen Caribbean rain forest formations, from near sea level to 900 m elevation. Flowering in May; fruiting in September in Belize. The species ranges from Belize to southeastern Nicaragua.

Guettarda combsii is recognized by the broad pubescent leaf blades usually rounded and truncate to subcordate at the base, the long-pendunculate inflorescences with four short cincinnoid branches, and the subglobose fruit. The fact that these plants become very tall trees may account for the paucity of collections in southern Central America. A sterile collection from a tall tree at Bluefields, Nicaragua (Proctor *et al.* 27130 F), suggests that this species is also likely to occur in northern Costa Rica.

***Guettarda conferta* Benth., Bot. voy. Sulph. 106. 1845.**

Trees to 10 m tall, with dense, ferruginous hairs on the branchlets, petioles, peduncles, and nerves of the leaves; **stipules** broadly obovate, 12 mm long, hirsute externally at base, otherwise glabrous, about equaling the petioles, deciduous. **Leaves** with blades 10–20 cm long, 6–9 cm broad, ovate, apex acuminate, base acute, hirsute on both sides. **Inflorescences** 2.5–3 cm long, cymose, subsessile, the branches recurved and 2.5 cm long or less. **Flowers** ca. 8 mm long, calyx tube 1–2 mm long, shallowly 3- or 4-dentate; **corolla** white, sericeous-hirtellous, tube ca. 10 mm long, corolla lobes 4, ca. 4 mm long, obtuse crispate. **Fruits** ovoid-tetragonous, 4 mm long, 3 mm diam., hirsute, 4-locular.

Plants of Cocos Island and the Pacific slope of southern Costa Rica and the Osa Peninsula, 0–300 m elevation. Flowering in August and December; fruiting in January.

Guettarda conferta is distinguished by its short sessile inflorescences. In general aspect this species resembles *G. crispiflora*.

***Guettarda crispiflora* Vahl, Ecolog. Amer. 36: pl. 6. 1797. *G. chiriquiensis* Standl., Ann. Missouri Bot. Gard. 25: 838. 1938. Figure 32.**

Small to medium-sized trees 4–20 m tall, leafy branchlets 1.5–6 mm thick, at first quadrangular but soon becoming terete, with short (0.3 mm) thin appressed-ascending hairs but glabrescent; **stipules** 8–18(–22) mm long, to 1 cm broad, ovate-elliptic to slightly obovate, apex acute to acuminate, with thin ascending sericeous hairs along the midrib and at the base. **Leaves** clustered distally, petioles 2–7 cm long, 1.3–2 mm thick, minutely puberulent and with longer hairs along the adaxial side; **leaf blades** (6–)8–22 cm long, (3–)5–11 cm broad, ovate-elliptic or ovate-oblong to ovate-lanceolate or broadly ovate, apex tapering gradually and acuminate or acute, base obtuse to slightly rounded or attenuate and acute, drying stiffly chartaceous, glabrous or minutely (0.2 mm) puberulent above, pubescent beneath with larger (0.4–1 mm) hairs on the major veins and smaller (0.3 mm) thin

whitish hairs on the 3° veins, tufts of hairs (domatia) sometimes present in the vein axils beneath, 2° veins 6–10/side, distal 2° veins strongly ascending, 3° veins often parallel. **Inflorescences** 2–6(–8) cm long, equally wide, with a short (4–25 mm) peduncle and 2 diverging cincinnoid branches 15–30(–60) mm long and enlarging in fruit, the rachis minutely grayish white tomentulose, the flowers sessile and closely (0–4 mm) spaced. **Flowers** sweet-scented, hypanthium 1.5–2.5 mm long, 1.5–2 mm diam., densely grayish white tomentulous, calyx tube ca. 0.5 mm long, calyx lobes 4, ca. 0.5 mm high; **corolla** white or pinkish, tube 13–18 mm long, 1–1.5 mm diam., narrowly tubular, densely short-sericeous with retrorse or spreading hairs, lobes 5–6 mm long, the lobes with smaller undulate marginal lobes. **Fruits** ca. 8 mm long and 6 mm diam., oblong and with 4 prominent longitudinal ribs, becoming purple and with a white pulp.

Trees of the Caribbean slope cloud forest formations and southern Pacific wet forest formations, from 300 to 1700 m elevation. Flowering in January, April, and June–September, with January and August collections being most frequent; fruiting in March and June–January. In our area the species is known from the Caribbean slope of the Central Highlands (from near Monteverde eastward to Tapanti, Cartago, and San Joaquin de Dota, San José), on the Osa Peninsula, near San Vito, and in the Chiriquí Highlands. The species also occurs in the Lesser Antilles and Trinidad.

Guettarda crispiflora is recognized by the short-pedunculate inflorescences with bifurcate cincinnoid branching, the white corollas with crisped and undulate corolla lobes, the four-angled fruit, longer petioles, and the subparallel (almost lineolate) minor venation. *Guettarda poasana* is closely related to *G. crispiflora*, and material of the two species should be compared when making identifications. *Guettarda chiriquiensis* was distinguished by its more densely pubescent vegetative parts, but there are a few intermediate collections in Costa Rica. Nevertheless, the distinctive populations of the Chiriquí Highlands and adjacent Costa Rica may be worthy of subspecific rank.

***Guettarda foliacea* Standley, Contr. U.S. Natl. Herb. 18: 139. 1916. Figure 33.**

Shrubs or small trees, 3–6(–10) m tall, often branching from the base and with clambering branches, leafy stems 0.9–4 mm thick, at first strigose with thin ascending hairs 0.3–1 mm long, glabrescent, becoming brown and terete, spines often present; **stipules** 3–5(–12) mm long, triangular to lanceolate, strigulose, caducous. **Leaves** opposite, petioles 3–25 mm long, 0.4–1.2 mm thick, appressed strigose to sericeous; **leaf blades** 3–16 cm long, 2–7 cm broad, elliptic to ovate or obovate, apex acute to short-acuminate, base cuneate to slightly rounded or

subtruncate, drying thin-chartaceous and greenish, with thin whitish hairs 0.2–0.9 mm long on both surfaces (dense only on the major veins), 2° veins 4–8/side, 4° veins often parallel, domatia of dense hairs present in the vein axils beneath. **Inflorescences** 2–7 cm long, to 5 cm broad, peduncles 5–30 mm long, 0.5–1.1 mm thick, with thin ascending hairs, usually with a single pair of dichotomous distal branches (each with 3–7 flowers), subtended by lanceolate ciliate bracts 3–8 mm long, flowers sessile and crowded in cymes. **Flowers** densely minutely sericeous externally, hypanthium ca. 1 mm long, calyx tube 1–1.5 mm long, ca. 1.3 mm diam., entire; **corolla** white, tube 12–20 mm long, lobes 4(–5), 2–5 mm long, rounded distally. **Fruits** 1–3 cm diam., globose, with a dense minutely velutinous surface, becoming red.

Plants of evergreen or partly deciduous forests, 0–300(–1000) m elevation. In central Panama flowering occurs primarily in late June–early July (Croat, 1978) and fruiting in September–November. This species ranges from the Cordillera de Tilarán to Colombia.

Guettarda foliacea is recognized by its small inflorescences, lack of calyx lobes, thin variable leaves on slender petioles, and minor venation, often with a small group of parallel veins (sublineolate). The spines are rarely seen on herbarium collections. The westernmost collection (84°53'W, *Haber et al.* 4775 CR, MO) came from the edge of cloud forest at 1000 m elevation with immature flowers in May.

Guettarda macrosperma J. D. Smith, Bot. Gaz. 18: 204. 1893. Figure 33.

Shrubs or more often trees, 4–12(–30) m tall, trunks often fluted or with deep depressions, with dark bark exfoliating in patches, leafy branchlets 1.2–4 mm thick, sparsely puberulent with thin ascending hairs 0.5–1.5 mm long, soon glabrescent and becoming dark brown or blackish with short (0.3–1.2 mm) grayish lenticels; **stipules** 3–8(–12) mm long, triangular-lanceolate, densely sericeous on the back with longer hairs, caducous. **Leaves** often crowded at the ends of branchlets, petioles (4–)10–45 mm long, 0.8–1.7 mm thick, with straight ascending hairs; **leaf blades** (4–)6–18 cm long, (2–)3–11 cm broad, broadly elliptic, broadly ovate-elliptic, obovate-elliptic, or elliptic-oblong, apex abruptly narrowed and short-acuminate to acute or obtuse, base obtuse to rounded and subtruncate, drying chartaceous to stiffly chartaceous, sparsely pubescent with thin short (0.3–0.7 mm) hairs and glabrescent, with thin short (ca. 0.3 mm) ascending hairs along the 3° veins beneath and with longer and denser hairs along the major veins, 2° veins 4–8/side, 3° veins rarely subparallel, often with tufts of hairs (domatia) in the vein axils. **Inflorescences** 2–6 cm long, primary peduncles 4–38 mm long, usually with 2 short distal branches, densely ascending sericeous, bracts 2–3 mm long, flowers sessile and closely crowded (not clearly cincinnoid in arrangement). **Flowers** with hypanthium 1–1.5 mm long and ca. 1 mm diam., densely whitish

tomentulose, calyx tube 0.5–1 mm long, entire; **corolla** white or yellowish, tube 8–13 mm long, 0.5–1.3 mm diam., narrowly tubular, lobes 3–4 mm long, rounded distally. **Fruits** 10–18 mm long, globose to oblong, yellowish brown or grayish with a dense covering of minute (0.1–0.2 mm) velvet-like or matted hairs.

Trees and shrubs of both evergreen and deciduous forest formations, from near sea level to 1000 m elevation on the Pacific slope and from near sea level to ca. 500 m on the Caribbean slope. Flowering in March–November, with the majority collected in May; fruiting in July–January. The species ranges from southern Mexico to Panama.

Guettarda macrosperma is recognized by its small cymose inflorescences, rounded fleshy fruit usually over 1 cm diam., and often smaller leaves with the subparallel 3° veins usually meeting at angles between the 2° veins (>-shaped). Trees in the Caribbean lowlands may reach 30 m in height; the same trunk and bark characteristics are found in trees of both seasonally dry forest and evergreen rain forests (N. Zamora, pers. comm.). Some specimens may resemble *Chomelia panamensis*. It appears that *Guettarda divaricata* (Roem. & Schult.) Standl. of Mexico is closely related, and the two may be part of a more broadly defined taxon. *Malacahuite* is a common name.

Guettarda poasana Standl., J. Wash. Acad. Sci. 18: 182. 1928. Figure 32.

Small trees, 3–10(–15) m tall, trunk to 40 cm thick, bark shredding off in oblong patches, leafy branchlets 2–5 mm diam., somewhat flattened in early stages and glabrous, drying dark but becoming grayish in age, lenticels difficult to see; **stipules** 12–20 mm long, 8–10 mm broad, ovate and long-acuminate at apex, the stipules overlapping on the sides, glabrous. **Leaves** clustered near the ends of branches, petioles (2–)3–7(–10) cm long, 0.8–1.6 mm thick, glabrous and drying dark; **leaf blades** 7–14(–16) cm long, 2.5–6(–9) cm broad, broadly elliptic-ovate to broadly elliptic or elliptic, apex gradually tapering and short-acuminate, base obtuse to acute and slightly decurrent on petiole, drying stiffly chartaceous, glabrous and lustrous above, minor venation with thin whitish ascending hairs ca. 0.3 mm long beneath, with longer (0.5–1 mm) straight hairs on the midvein and secondaries beneath, 2° veins 5–8/side, the distal strongly ascending, 3° veins often subparallel but not prominent beneath, small tufts of hairs (domatia) often present in the vein axils beneath. **Inflorescences** axillary, 3–6 cm long and equally wide, peduncles 1–3 cm long, glabrous or sparsely puberulent, with 2 cincinnoid branches 2–3.5 cm long, the flowers 5–11 on each branch and sessile, ca. 1–4 mm distant. **Flowers** sweet-scented, hypanthium 1.5–2 mm long, 1.3 mm diam., glabrous or sparsely puberulent, calyx tube 0.5–1 mm long, lobes ca. 0.3 mm long; **corolla** white, reddish, or lavender, tube 16–20 mm

long 1–1.4 mm diam., densely tomentulose externally, lobes 4–5, 4–6 mm long, usually white with fringed-undulate smaller lobes; tips of the anthers exerted 1–2 mm from the mouth of the tube. **Fruits** becoming 8 mm long and 6 mm diam., oblong and with 4 prominent longitudinal ridges, reddish purple.

Trees of evergreen cloud forest formations, 1300–2200(–2700?) m elevation (down to 1100 m on the northern volcanoes). Flowering in March and May–November (mostly in June); fruiting probably throughout the year. This species is endemic to Costa Rica and ranges from the Cordillera de Guanacaste in the west to the eastern slopes of Volcán Barva.

Guettarda poasana is recognized by its glabrous stipules and stems, long-petiolate leaves, narrowly tubular flowers with whitish fringed lobes, four-angled fruit, and restricted cloud forest range. The petioles dry dark and are sometimes pink in life. This species is closely related to *G. crispiflora* and might be considered a subspecific element of that species. However, though their ranges overlap slightly, *G. crispiflora* and *G. poasana* do not grow in the same locality; *G. poasana* is generally found at higher altitudes.

Guettarda sanblasensis Dwyer, Ann. Missouri Bot. Gard. 67: 204. 1980. Figure 33.

Trees, 12–20 m tall, leafy branchlets 1.5–4 mm thick, with short (0.3 mm) appressed-ascending hairs, quickly glabrescent, terete; **stipules** 3–6 mm long, densely sericeous with pale yellowish ascending hairs 0.5–1 mm long, early caducous. **Leaves** 1–5 cm distant at the ends of branchlets, petioles 2–7 cm long, 0.7–1.3 mm thick, with slender appressed-ascending hairs; **leaf blades** 11–22 cm long, (4–)6–12 cm broad, broadly elliptic to broadly ovate-elliptic, apex abruptly narrowed and short-acuminate (or acute), base obtuse to slightly rounded, drying chartaceous and dark brown above, lustrous above and with scattered thin appressed hairs 0.2–0.3 mm long, the hairs more numerous and longer (0.3–0.5 mm) beneath, 2° veins 5–9/side, the distal arcuate-ascending, 3° veins prominent above and below and paler in color beneath, subparallel or >-shaped between the secondaries, with minute tufts of hair (domatia) in the vein axils beneath. **Inflorescences** 6–10 cm long, primary peduncles to 6 cm long, ca. 1.2 mm thick and minutely appressed-puberulent, bifid but the 2 branches with additional dichotomous branches (not scorpioid/cinclinoid), pedicels 0–2 mm long, bracts minute (0.5 mm) and caducous. **Flowers** with hypanthium ca. 1.5 mm long and 1.2 mm diam., with longitudinal ribs, calyx tube 2–3 mm long and ca. 2 mm diam., minutely velutinous, subentire distally; **corolla** white or pink, tube 13–18 mm long, 1–1.3 mm diam., minutely (0.2 mm) ascending-sericeous, lobes 5–6, 4–5 mm long and 1–1.5 mm broad, oblong and entire, stigma 0.5 mm long, subglobose. **Fruits** 2–2.2 cm long

and 8–12 mm thick, oblong-obovoid, abruptly rounded (truncated) at apex, persisting calyx 1–3 mm long, 1.5–2 mm diam., surface minutely velutinous and yellowish or grayish brown.

Trees of evergreen forest formations of the Pacific lowlands, from near sea level to 600 m elevation and usually on limestone. Flowering in July–September; fruiting in September–November. This species is known only from a few collections in the Golfo Dulce region of Costa Rica; it ranges to eastern Panama.

Guettarda sanblasensis is recognized by the broadly elliptic leaves on long slender petioles, the long-pedunculate inflorescences with dichotomous or cymose distal branching, long-tubular corollas with five or six entire oblong perianth lobes, and oblong fruit with truncated apex and usually persisting calyx tube.

Guettarda tournefortiopsis Standl., Publ. Field Columb. Mus., Bot. Ser. 7: 293. 1931. *Tournefortiopsis reticulata* Rusby, Bull. New York Bot. Gard. 4: 369. 1907, non *G. reticulata* Griseb., 1863. Figure 32.

Small trees, 4–10 m tall, leafy branchlets 1.5–6 mm thick, at first densely tomentose with soft wooly hairs to 2 mm long, 4-angular, soon glabrescent and dark with lenticels 0.3–0.7 long, becoming terete and pale grayish; **stipules** 12–20 mm long, narrowly ovate-triangular and acuminate, tomentose, usually early deciduous. **Leaves** with petioles 13–35 mm long, 1.5–2.2 mm thick, glabrescent and drying dark; **leaf blades** 9–16 cm long, 2–5 cm broad, lanceolate to narrowly oblong-lanceolate or narrowly elliptic-oblong, apex acute to short acuminate, base obtuse to acute and usually with the margin revolute, drying subcoriaceous, dark brown above, glabrous and usually lustrous above, with the major and minor veins slightly impressed above and the surface slightly rugose, densely tomentulous between the veins beneath and whitish to pale brown in color, 2° veins 9–11/side, domatia present. **Inflorescences** 2–5 cm long and equally wide, becoming 8 cm long in fruit, peduncles 12–20 mm long (to 30 mm in fruit), 1.5 mm thick and tomentulous, with 2 cinclinoid branches 2–6 cm long and each branch bearing up to 20 flowers in 2 rows along 1 side, flowers sessile and closely crowded, bracts absent. **Flowers** with hypanthium 1.5–2 mm long, covered by a dense tomentum, calyx lobes ca. 1 mm broad, broadly obtuse and difficult to see; **corolla** reddish to coral pink, white within, tube 4–7 mm long, ca. 1.5 mm diam., densely puberulent with retrorse hairs externally, lobes 5, 1–2 mm long. **Fruits** 5–8 mm long, 4–6 mm diam., globose to rounded-oblong, 5-angled during development, sessile, becoming purple or black.

Trees of wet montane cloud forest formations, from 800 to 1900 m elevation. Collections with

flowers (or flower buds) and fruits have been made in January–March and August–October. Known only from the Cordillera de Tilarán and the western parts of the Cordillera de Talamanca, provinces of Cartago and San José, in Costa Rica. The species is also known from the Chiriquí Highlands and was originally described from Bolivia.

Guettarda tournefortiopsis is easily recognized because of its stiff narrow leaves densely tomentulose beneath (when young), the two-branched scorpioid inflorescences (resembling those found in the Boraginaceae), small tomentulose red flowers, and small sessile fruits.

***Guettarda turrialbana* Zamora & Poveda, Ann. Missouri Bot. Gard. 75: 1157. 1988. Figure 30.**

Trees to 30 m tall and with trunks 40 cm dbh, bark exfoliating, leafy branchlets 1.5–6 mm thick, glabrous and dark in early stages, terete, becoming pale grayish and with few broadly ellipsoid lenticels 0.8–1.5 mm long; **stipules** ca. 12–25 mm long, triangular and acuminate, overlapping, glabrous, deciduous. **Leaves** clustered at the ends of branchlets, petioles 2–3.5 cm long, 1–2 mm thick, glabrous and drying dark; **leaf blades** 9–26 cm long, 4–12 cm broad, oblong to broadly elliptic-oblong or ovate-oblong, apex abruptly narrowed and short-acuminate, base abruptly narrowed or rounded and obtuse, drying stiffly chartaceous, dark brown above, glabrous and lustrous above, subglabrous beneath with tufts of hairs (domatia) in the vein axils, 2° veins 8–10/side, 3° veins slightly raised above but not clearly subparallel. **Inflorescences** 5–11 cm long, primary peduncles 3–5 cm long, 1–1.3 mm thick, glabrous and drying dark, cymose with 2 primary branches, the branches 2–3 cm long and with 3–5 flowers 2–5 mm distant on the rachis (or the branches very short and all the flowers close together in *Hammel et al. 16848 CR, MO*), pedicels short (1 mm) or absent, flower subtended by short (0.5 mm) broad bracts. **Flowers** glabrous externally, with the sweet odor of *Coffea* flowers, hypanthium ca. 2 mm long and 1.2 mm diam., calyx cup ca. 2 mm long, ca. 3 mm diam. distally and entire; **corolla** white, tube 20–40 mm long, 2–2.8 mm diam., puberulent within, lobes 5, ca. 5 mm long and 2 mm broad, oblong and entire, distally rounded. **Fruits** 24–28 mm long, 6–12 mm diam., oblong, glabrous.

Trees of lowland rain forest formations; collected at 600 m elevation, below the CATIE site near Turrialba on the Caribbean slope, and on the Osa Peninsula at 200–300 m elevation. Flowering in May (*Hammel et al. 16848 CR, F, MO*) and June (*Herrera 4246 MO, Zamora et al. 1263 CR* holotype, F); fruiting in August and September. Endemic.

Guettarda turrialbana is recognized by its tall stature, mostly glabrous parts, oblong leaves, few-flowered bifurcate inflorescences, entire calyx cup,

and long corolla tubes. The tall size of this distinctive species may explain why it had not been collected before 1986. The collections from the Osa Peninsula differ in a number of ways from the type; more material is needed to assess the pattern of variation.

Hamelia Jacquin

REFERENCE—T. S. Elias, A monograph of the genus *Hamelia* (Rubiaceae). Mem. New York Bot. Gard. 26: 81–144. 1976.

Shrubs or small trees, branchlets usually slender, terete or 4-angled in cross-section, glabrous to densely puberulent; **stipules** interpetiolar, usually small, entire or with an awn (or trilobate), caducous or less often persistent. **Leaves** opposite and decussate or in whorls of 3–5/node, usually regularly spaced by well-developed internodes, often long-petiolate, usually thin in texture, glabrous or puberulent, pinnately veined, domatia present in some species, conspicuous raphides visible on the dried leaf surfaces in a few species. **Inflorescences** terminal or less often axillary, 3–many-flowered, often thyrselike with cymose branches or with helicoid branches, pedunculate, the flowers often all along 1 side of the distal branches, sessile or short-pedicellate. **Flowers** bisexual and radially symmetrical, monomorphic, hypanthium urceolate to tubular, calyx tube minute or absent, calyx lobes 5, small, rounded to elongate, usually persisting; **corolla** narrowly tubular to funnelform or campanulate-urceolate (with a short narrow base), bright yellow to orange, orange-red, or deep red, with 5 longitudinal ribs alternating with the lobes, corolla lobes 5, erect to recurved, slightly imbricate in bud; **stamens** 5, filaments inserted at the base of the corolla tube, flattened, anthers long-linear, sagittate at the base and usually with the connective prolonged distally, included or partly exerted; **ovary** (4–)5-locular, with axile placentation and many ovules in each locule, style narrowly cylindrical, stigmas 1–5. **Fruit** a fleshy berry, oblong to ovoid or subglobose, with 5 longitudinal ribs, terminated by the circular calyx scar and a conical disc; **seeds** numerous, plano-convex or angled, foveolate.

Hamelia ranges from southern Florida, U.S.A., through Mexico, Central America, and the West Indies into tropical South America. Elias recognized 16 species in his fine monograph. The narrowly tubular or funnelform yellow to orange or red flowers are usually all aligned on the uppermost sides of the inflorescence branches. In some, the inflorescences have longer cincinnus-like branches. Many of our species have three to four leaves at distal nodes and a number have long-petiolate leaves; most have small tufts of hairs (domatia) in the vein axils beneath. Individual plants may vary greatly within many species, and this makes identification difficult. In addition, there

may be intermediates or hybrids between some of our species.

The genus is divided into two subgenera. Subgenus *Hamelia* has narrowly tubular flowers that do not enlarge distally at anthesis and are red, orange, or yellow in color. Subgenus *Amphituba* has the yellow corolla tube slightly to conspicuously expanded distally at anthesis. However, the

flowers of subgenus *Amphituba* remain narrowly tubular until just before anthesis and may be difficult to distinguish from those of subgenus *Hamelia* on this account. Species of *Hoffmannia* may be similar, but they have consistently axillary inflorescences; compare *Deppea*, with papery capsules.

Key to the Species of *Hamelia*

- 1a. Young stems and undersides of leaves conspicuously pubescent with hairs 0.2–0.5 mm long . . . 2
- 1b. Young stems and undersides of leaves glabrous or with minute (0.1–0.2 mm) inconspicuous hairs 4
 - 2a. Stipules 7–17 mm long; leaf blades with 8–18 major 2° veins on each side, with hairs to 1 mm long; corolla expanded distally at anthesis, corolla lobes 2–6 mm long [calyx lobes 0.5–2 mm long] *H. xerocarpa*
 - 2b. Stipules 2–5(–8) mm long; leaf blades with 4–9 major 2° veins on each side, with hairs to 0.5 mm long; corolla narrowly tubular, corolla lobes 1–2 mm long 3
 - 3a. Calyx lobes 0–0.7 mm long; seeds 0.6–0.9 mm long; petioles 10–80 mm long; common widespread plants, 0–1500 m elevation *H. patens*
 - 3b. Calyx lobes 2–4 mm long; seeds 1–1.2 mm long; petioles 3–20 mm long; uncommon plants of the Caribbean lowlands, 0–300 m elevation *H. rovirosae*
- 4a. Corolla tube 8–13 mm long at anthesis; fruits 5–10 mm long 5
- 4b. Corolla tube 13–35 mm long at anthesis; fruits 7–16 mm long 6
 - 5a. Inflorescences 3–9 cm long, corolla tube becoming expanded distally at anthesis; leaf blades with 5–9 major 2° veins on each side, 5–17(–23) cm long, usually drying greenish to pale grayish; fruits 4–7 mm long; Caribbean and evergreen Pacific lowlands *H. axillaris*
 - 5b. Inflorescences 8–18 cm long, corolla tube narrowly tubular at anthesis; leaf blades with 7–12 major 2° veins on each side, 10–27(–32) cm long, usually drying reddish brown to pinkish gray; fruits 6–10 mm long; evergreen Pacific slope *H. magnifolia*
- 6a. Leaf blades with 8–13 major 2° veins on each side; corolla tube distally widened (4–7 mm) at anthesis; corolla lobes 2–4 mm long 7
- 6b. Leaf blades with 3–9 major 2° veins on each side; corolla tube narrowly (2–4 mm) tubular at anthesis (in *H. patens*, often broader in *H. calycosa*) 8
 - 7a. Leaf blades 3–6 cm broad; corolla tube 13–22 mm long; 0–800 m elevation . . . *H. xerocarpa*
 - 7b. Leaf blades 4–12 cm broad; corolla tube 25–35 mm long; 700–1600 m elevation *H. macrantha*
- 8a. Leaf blades with 6–9 pairs of 2° veins, petioles 10–80 mm long; sepal lobes 0–0.8 mm long, corolla lobes 1–2 mm long; common, 0–1500 m elevation *H. patens*
- 8b. Leaf blades with 3–7 pairs of 2° veins, petioles 8–20 mm long; sepal lobes 1–2.5 mm long, corolla lobes 3–6 mm long; not reported from Costa Rica *H. calycosa*

Hamelia axillaris Sw., Prodr. 46. 1788. *H. lutea* Rohr ex Smith in Rees, Cyclop. 17. 1811. Figure 42.

Shrubs, 1–5 m tall or small treelets to 5 m tall, leafy branchlets 1.2–4 mm thick, glabrous, with 4 longitudinal ribs and 4-angular in cross-section but becoming terete; **stipules** 2–6(–8) mm long, ca. 1 mm broad, triangular to narrow with folded margins. **Leaves** opposite (rarely 4/node), petioles 1–4(–7) cm long, ca. 1 mm wide, gla-

brous to sparsely and minutely papillate-puberulent; **leaf blades** 5–17(–23) cm long, 2–8 cm broad, narrowly elliptic, elliptic-oblong or obovate to narrowly obovate-oblong, apex acuminate with tip ca. 1 cm long, base attenuate and decurrent on petiole, drying chartaceous or membranaceous, glabrous above, glabrous or minutely (0.1 mm) papillate-puberulent beneath, with tufts of hairs (domatia) in the vein axils, 2° veins 5–9/side and loop-connected near the margin, short (0.1–0.3 mm) linear cystoliths visible on the lower surface when dry. **Inflorescences** axillary or terminal, 3–8 cm long, 3–8 cm

broad, compound dichasia with lateral branches 1–4.5 cm long, often scorpioid with 3–15 secund flowers on the uppermost side, peduncles 5–15 mm long, glabrous or minutely and sparsely puberulent, bracts 0.5–1 mm long, narrow, flowers sessile or with pedicels. **Flowers** with hypanthium 1.5–3 mm long, ca. 1.2 mm diam., glabrous, lobes 0.5–1.5 mm long, 1 mm wide at the base, glabrous to puberulent; **corollas** yellow, narrowly urceolate to funnellform, tube 8–13 mm long, ca. 1 mm diam. near the base and 3–5 mm wide distally, glabrous, lobes 1–2 mm long, broadly triangular; **stamens** with filaments 4–5 mm long, anthers 5–8 mm long with apical connective 0.5 mm long, style 8–10 mm long, stigmas 3–4 mm long. **Fruits** 4.5–7 mm long, 3–4 mm diam., ovoid-oblong to subglobose, disc 0.5 mm high and 0.7 mm broad; **seeds** ca. 1 mm long.

Plants of the evergreen Caribbean slope and the Osa Peninsula, from near sea level to 600(–1000) m elevation. Flowering primarily in late June–October; fruiting in February and June–December. The species is known from southern Mexico, Belize, Guatemala, the larger West Indian islands, and from Nicaragua southward to Venezuela and Bolivia.

Hamelia axillaris is recognized by its short yellow corollas funnellform at anthesis, short rounded fruit, general lack of pubescence, and usually compact inflorescences with flowers along one side of the distal branches. There may be intermediates between this species and *H. magnifolia* on the Osa Peninsula; compare the extreme upper-right figure in Figure 42 (based on *Utley & Utley 1208 f*).

Hamelia calycosa J. D. Smith, Bot. Gaz. 12: 132. 1887.

Shrubs or small trees to 12 m tall, leafy branchlets 1–3 mm thick, glabrous or glabrescent; **stipules** 1–2.5(–4) mm long, ca. 1 mm broad at the base, subulate or with a narrow awn, minutely puberulent. **Leaves** opposite or 3–4/node on distal branches, petioles 6–20 mm long, 0.4–0.8 mm broad, glabrate; **leaf blades** 3–11(–15) cm long, 1–3.5(–5) cm broad, lanceolate to narrowly elliptic-oblong or elliptic-oblong, apex tapering gradually and acuminate, tip ca. 7 mm long, base acute to cuneate and decurrent on petiole, drying membranaceous to chartaceous, glabrous above, glabrous or minutely (0.1–0.2 mm) pubescent beneath or rarely with longer (0.7 mm) thin hairs, with tufts of hairs (domatia) in the vein axils beneath, 2° veins 3–7/side. **Inflorescences** terminal or rarely axillary, 3–10 cm long, with 4–24 flowers, peduncles to 2 cm long and often with 2 dichotomous branches distally, usually minutely puberulent, bracts 1–2 mm long, subulate or triangular, flowers secund and with pedicels 1–5(–8) mm long. **Flowers** with hypanthium 2–4 mm long, oblong, glabrous or sparsely pubescent, calyx lobes 1–3 mm long, ca. 0.5 mm wide, narrowly oblong, caducous; **corolla** funnellform, yellow or pale orange (striped with maroon), tube 15–24(–32) mm long,

constricted (1.5 mm) near the base and 8–10 mm diam. distally, pubescent externally, lobes 3–6 mm long, ovate; **stamens** 5, filaments 4–6 mm long, anthers 15–18 mm long, 1 mm wide, distal rounded connective ca. 1 mm long, style to 14 mm long, stigmas 5 and connate, ca. 1.2 mm long. **Fruits** 7–16 mm long, 4–8 mm thick, cylindrical, disc conical and 1–3 mm long; **seeds** 1–1.2 mm long.

Trees and shrubs of Caribbean rain forest formations, from near sea level to 1500 m elevation. Flowering is in April–September in northern Central America. The species ranges from southern Mexico, Belize, Guatemala, Honduras, Panama, and Colombia to Peru.

Hamelia calycosa is recognized by the larger sepal lobes, longer corollas expanded distally, pedicellate fruit, and smaller leaves with short petioles. Although not yet collected in Costa Rica, this species is likely to be present.

Hamelia macrantha Little, Carib. Forester 9: 274. 1948.

Shrubs or small trees to 8(–12) m tall and 13 cm dbh, leafy branchlets 2–6 mm thick, 4-angular in cross-section, glabrous or minutely puberulent; **stipules** 3–7 mm long, 1–2.5 mm broad at the base, triangular to awl-shaped, glabrous or rarely puberulent. **Leaves** opposite but 3–4 at distal nodes, petioles (1.5)–6–11 cm long, 1.3–2.7 mm broad, glabrous or puberulent; **leaf blades** (7)–12–23(–27) cm long, (3)–4–12(–15) cm broad, broadly oblong or elliptic-oblong to ovate or obovate, apex obtuse to abruptly short-acuminate, base rounded and subtruncate to obtuse (cuneate), drying membranaceous to chartaceous, glabrous above, glabrous to minutely (0.1 mm) papillate puberulent beneath in Costa Rica, domatia sometimes present, 2° veins 8–12/side and loop-connected near the margin. **Inflorescences** terminal or axillary, 6–17 cm long and wide, to 15 cm broad, paniculate, 20–many-flowered, peduncles 2–8 cm long, 1–3 mm thick, lateral branches to 6 cm long, bracts 0.4–0.7 mm long, ovate and acute, glabrate or puberulent, flowers sessile to short (2 mm) pedicellate. **Flowers** with hypanthium 3–5 mm long, 1.5–2 mm diam., glabrous, calyx lobes 0.7–1.5(–2) mm long, 1–1.5 mm broad at the base, triangular-subulate; **corolla** yellow, tubular-funnelform, tube 23–35 mm long, constricted near the base and 5–7 mm diam. distally, glabrous, lobes 3–5 mm long, ovate, glabrous; **stamens** with filaments 6–8 mm long, anthers 16–20 mm long, included, connective prolonged ca. 1 mm beyond the thecae; style to 20 mm long, stigmas 5–8 mm long. **Fruits** 11–15 mm long, 3.5–5 mm diam., ellipsoid, red becoming black and lustrous, ovarian disc conical; **seeds** 0.8–1 mm long.

Trees and shrubs of evergreen cloud forest and lower montane forest formations on both the Caribbean and Pacific slopes, from 700 to 1500 m elevation in Costa Rica. Flowering in June–Sep-

tember in Costa Rica and Panama; fruiting in August–September. The species ranges from Costa Rica and Panama to Colombia and Ecuador.

Hamelia macrantha is recognized by the large yellow corolla tube slightly widened distally at anthesis, larger leaves with many secondary veins and often with long narrow petioles, and the montane habitat (in Costa Rica). Note that the widened corolla tube is only seen at anthesis. The foliage of this species resembles that of some specimens of *H. xerocarpa* variety *costaricensis*, and the two species may be difficult to separate.

***Hamelia magnifolia* Wernham, J. Bot. 49: 210. 1911. Figure 42.**

Shrubs or small trees to 5(–6) m tall, trunks to 12 cm dbh, leafy branchlets 2–7 mm thick, with 4 longitudinal ridges and quadrangular in cross-section, glabrous or minutely (0.1 mm) papillate-puberulent; **stipules** 4–9 mm long, to 2 mm wide at the base, narrowly triangular (rarely bifid), glabrate. **Leaves** opposite (rarely 4/node), petioles 1.5(–7) cm long, 1.7–2.3 mm broad; **leaf blades** 10–27(–32) cm long, 4–11(–15) cm broad, broadly oblong to ovate-oblong, elliptic-oblong or ovate-elliptic, apex short-to long-acuminate with tip to 2 cm long, base rounded and truncate to obtuse, drying stiffly chartaceous, glabrous above, glabrous beneath, 2° veins 7–12(–15)/side, some 3° veins subparallel, domatia absent. **Inflorescences** terminal, 8–12(–18) cm long, to 15 cm wide, panicle with opposite branching, with more than 60 flowers, peduncles 1–3 cm long, distal branches to 7 cm long and with secund flowers, minutely papillate-puberulent or glabrous, bracts 0.5–1 mm long, narrow pedicels 0–1 mm long. **Flowers** with hypanthium 2–3 mm long, 0.8–1.5 mm diam., minutely puberulent, calyx lobes 0.3–0.6 mm long, 1 mm broad at the base, deltoid or broadly rounded, puberulent along the margin; **corolla** narrowly tubular at anthesis (also somewhat narrowed above the base and below the middle), yellow, tube 10–13 mm long, 2–3 mm diam., lobes 1.2–3 mm long; **stamens** with filaments 2–3 mm long, anthers 6–8 mm long, apical connective ovate and ca. 1 mm long. **Fruits** 6–10 mm long, 3–4 mm diam., oblong to broadly ellipsoid, glabrous, ovarian disc ca. 1 mm long, red; **seeds** 0.4–0.5 mm diam.

Plants of evergreen forest formations on the Pacific slope, from 100 to 900 m elevation in Costa Rica. Flowering in January–August; fruiting in June–September and December–January. The species is restricted to the evergreen formations of the Pacific slopes of southern Costa Rica and adjacent areas in Chiriquí Province, Panama.

Hamelia magnifolia is recognized by the small narrowly tubular flowers in large inflorescences, the large leaves often rounded at the base and with many secondary veins, the smaller fruits, and the

restricted geographic range. Standley (1938) listed *zorillo colorado* as a common name.

***Hamelia patens* Jacq., Enum. Pl. Carib. 16. 1760.**
H. patens var. *glabra* Oersted, Vidensk. Meddel. Naturhist. Foren. Kjobenhavn 1852: 42. 1853.
H. viridifolia Wernham, J. Bot. 49: 213. 1911. Figure 42.

Shrubs or small trees, 2–7 m tall, leafy branchlets 1–7 mm thick, glabrous or pubescent with crooked translucent or yellowish hairs to 0.6 mm long (in variety *patens*), 4-angled in early stages but becoming terete; **stipules** 2–6 mm long, narrowly oblong to linear, pubescent, as many as the leaves at each node. **Leaves** usually 3(–4) at distal nodes (less often opposite or rarely 5/node), often unequal at the same node, separated by well-developed internodes, petioles (8–)20–55(–80) mm long, 0.6–1.6 mm wide, glabrous to densely pubescent; **leaf blades** 5–17(–23) cm long, 1–7(–10) cm broad, elliptic-oblong, ovate-elliptic, ovate-oblong, or elliptic-obovate-elliptic, apex usually short-acuminate, base acute to attenuate (obtuse in larger leaves) and decurrent on petiole, drying membranaceous to thin-chartaceous, glabrous (or sparsely pubescent in variety *patens*) above, glabrous to densely villous beneath with thin straight or curved whitish hairs 0.2–0.5 mm long (rarely with scurfy yellowish hairs), tufts of hairs (domatia) often present in vein axils beneath, 2° veins 6–9/side, small (0.2 mm) linear raphides (cystoliths) resembling appressed hairs often visible on the dark upper surface of dried leaves. **Inflorescences** terminal, solitary or 2–4, 4–9(–15) cm long, to 12(–20) cm broad, an open panicle with 2–3 nodes on the rachis and 2–4 branches at each node, peduncles 1–3 cm long (to 5 cm in fruit), minutely papillate-puberulent (less often with conspicuous hairs), often orange to coral red, primary branches often ending in a flower and 2 long distal secondary branches bearing a row of sessile or subsessile flowers along the upper side, bracts 0.3–1 mm long, triangular, distal flowers with pedicels 1–5 mm long. **Flowers** with hypanthium 1.5–3 mm long, 1–2 mm diam., longitudinally ribbed, deep red, glabrate to densely short-villous, calyx lobes 0.5–1 mm high, rounded or broadly triangular, persisting; **corolla** narrowly tubular at anthesis, orange to reddish-orange, tube (12–)14–18(–23) mm long, 1.5–3 mm diam., lobes 1–2.5 mm long, 1–2 mm broad at the base, triangular; **stamens** with filaments 5–7 mm long, anthers 8–12 mm long, included or slightly (3 mm) exerted, the apiculate connective 0.5 mm long; stigmas 3–5 mm long. **Fruits** 6–13 mm long, 4–10 mm diam., oblong to ovoid-oblong (subglobose), red becoming black or bluish, glabrous or with hairs ca. 0.2 mm long, raphides often visible on the surface, with a ring around the top formed by the calyx scar ca. 3 mm diam., disc to 1 mm high and inconspicuous; **seeds** 0.5–1 mm long.

Common shrubs and treelets of open early secondary growth in evergreen and partly deciduous forest formations, from near sea level to 1600 m elevation. Flowering and fruiting in all months of

the year in Costa Rica. The species ranges from southern Florida, Mexico, the West Indies, and Central America southward to northern Argentina and Paraguay (the species is not found in the Guianas, northeastern Brazil, the central Amazon basin, or central Brazil).

Hamelia patens is recognized by its bright orange or red-orange flowers with narrowly tubular corollas with small lobes and included anthers and the usually three- or four-leaved distal nodes. The open inflorescences with dichotomous or dichasial branching and with secund flowers often in a row along the upper side of distal inflorescence branches are also distinctive. These shrubs and little tree-lets of open evergreen lowland secondary sites are among the most common and conspicuous of Costa Rica's woody flora. They appear to germinate only in open sunny sites. The breeding biology of this species was studied by Bawa and Beach (1983). Standley (1938) listed the common names *añileto*, *azulillo*, *coralillo*, *palo camarón*, *pissi*, *zorillo*, and *zorillo real*, and he cited Pittier for the Indian names *pili-tso* (Guatuso) and *tsus-krá* (Brunka).

Hamelia patens variety *patens* has the leaves sparsely to densely villous (especially on the lower surface), and the flowers are sparsely to densely villous externally. Variety *glabra* Oersted has the leaves glabrous above and sparsely villous or puberulent on the veins beneath, and the flowers are usually glabrous externally. There seem to be no ecological or geographic distinctions between the varieties, and they may be no more than glabrous and puberulent forms found within the same populations.

***Hamelia rovirosae* Wernham, J. Bot. 49: 211. 1911.**

Figure 34.

Shrubs or slender treelets to 5(–10) m tall, leafy branchlets 0.8–3.5 mm diam., with curved or crooked multicellular hairs 0.3–1 mm long and often in longitudinal rows, with 4 longitudinal ribs and quadrangular in early stages but becoming terete and glabrescent; **stipules** 2–6(–8) mm long, with a very short (1 mm) broad base and long narrow linear awn, puberulent, caducous or persisting with the leaves. **Leaves** usually 3/node (rarely opposite), petioles 3–14(–20) mm long, 0.5–1 mm thick, pubescent with short crooked hairs; **leaf blades** (2.5–)5–15 cm long, (1.5–)2–6 cm wide, elliptic-oblong to elliptic-ovate, elliptic or elliptic-obovate, apex acute to short-acuminate, base acute to attenuate and slightly decurrent on petiole, drying thin-chartaceous, glabrous to sparsely pubescent above, sparsely to densely villous beneath with thin straight or crooked hairs 0.2–0.5 mm long, with denser tufts of hairs (domatia) in the vein axils, 2° veins 3–7/side and weakly loop-connected near

margin. **Inflorescences** 4–12 cm long, equally broad, peduncles to 3 cm long, villous, floral rachis with dichotomous distal branches bearing 2–8 flowers, bracts to 0.5 mm long, caducous, flowers sessile or short (1–2 mm) pedicellate. **Flowers** with hypanthium 2–4.5 mm long, villous with curly hairs ca. 0.5 mm long, calyx lobes 2–4 mm long and enlarging in fruit, 1 mm wide and oblong, villous; **corolla** narrowly tubular at anthesis, reddish orange to bright red or dark red, tube 16–22 mm long, 2–3 mm diam., minutely villous with hairs ca. 0.5 mm long (often in longitudinal rows), lobes 1–2 mm long, 1–1.5 mm broad at the base, ovate; **stamens** with filaments 7–9 mm long, anthers 10–12 mm long, slightly exerted, connective appendage ca. 0.5 mm long; stigmas connate, 2–3 mm long. **Fruit** 8–14 mm long, 4–8 mm diam., cylindrical to oblong-ellipsoid, red becoming black, covered with small (ca 0.5 mm) crooked hairs, persisting sepals to 6 mm long and 2 mm broad; **seeds** ca. 1 mm long.

Shrubs of Caribbean lowland evergreen forest formations, from near sea level to 200 m elevation. Flowering in February, April, and July–October in Central America. The species ranges along the Caribbean lowlands, from Tabasco, Mexico, to Bocas del Toro, Panama.

Hamelia rovirosae is recognized by the unusual crooked multicellular hairs, corollas narrowly tubular at anthesis, puberulent fruit with prominent calyx lobes, and restriction to the Caribbean lowlands. This species is frequently confused with *H. patens*.

***Hamelia xerocarpa* Kuntze, Rev. gen. pl. 1: 284.**

1891. *H. costaricensis* Standl., Contr. U.S. Natl. Mus. 20: 207. 1919. *H. panamensis* Standl., loc. cit. 208. 1919. *H. rowlei* Standl., J. Wash. Acad. Sci. 15: 7. 1925. *H. storkii* Standl., loc. cit. 7. 1925. Figure 42.

Shrubs or small trees to 5 m tall, leafy branchlets 1.5–5 mm thick, with 4 longitudinal ridges and quadrangular in cross-section, glabrous to sparsely pilose with stiff erect hairs to 0.9 mm long; **stipules** 6–13(–17) mm long, cuspidate and often with 2 small lateral teeth, glabrate or pubescent along the edge, drying black. **Leaves** usually 3 or 4/node, petioles (10–15)–85 mm long, about 1 mm broad, glabrous to densely pubescent; **leaf blades** 8.5–17(–37?) cm long, 3.5–9(–14?) cm broad, ovate to broadly elliptic-oblong or ovate-rotund, apex acute to acuminate, base obtuse to cuneate and decurrent on petiole, leaves drying thin-chartaceous, glabrate above, usually minutely papillate-puberulent or with straight or curved hairs 0.2–0.9 mm long beneath, 2° veins (7–)9–13(–18)/side and loop-connected near the margin, 3° veins often subparallel, domatia present or absent. **Inflorescences** terminal on short lateral branches (and apparently axillary), 5–15 cm long and equally wide, peduncles 1–2.5(–5) cm long, the dichasia to 6(–15) cm long and with 3–9(–26) flowers along 1 side, glabrous or with yellowish

hairs to 1 mm long, bracts 0.6–0.8 mm long, the second flowers sessile or subsessile. **Flowers** with hypanthium 2–3 mm long, glabrous to pilose, calyx lobes 0.5–2 mm long, ovate, glabrous to pilose; **corolla** funnellform (but narrowly tubular until anthesis), yellow, tube 18–36 mm long, 4–7 mm diam., glabrous to densely puberulent with hairs 0.2–0.4 mm long, lobes 2–5(–8) mm long, 2–5 mm broad at the base, ovate and acute; **stamens** with filaments 8–16 mm long, anthers 10–16 mm long, connective little (1 mm) extended distally; style ca. 20 mm long, stigmas 5, to 5 mm long. **Fruits** 11–14 mm long and 3–5 mm diam., oblong to ovoid-oblong; **seeds** 0.5–1 mm long.

Plants of evergreen lowland formations and gallery forests in deciduous areas, from near sea level to 800 m elevation. Flowering in May–December (throughout the year in Panama). The species ranges from Nicaragua to northern Colombia.

Hamelia xerocarpa is recognized by the broader corolla tube (at anthesis) with longer corolla lobes, the unusual yellowish puberulence (when present), the lowland evergreen habitat, and the leaves usually with many secondary veins and often with long petioles. Unfortunately, few herbarium collections exhibit the broader funnellform corollas in anthesis, and it is easy to misidentify this species. This species may be difficult to separate from *H. macrantha*. The breeding biology was studied by Bawa and Beach (1983).

Hamelia xerocarpa variety *xerocarpa* is distinguished by the conspicuous hairs on many parts of the plant and the leaves with 11–18 pairs of secondary veins. Variety *costaricensis* (Standl.) Elias is recognized by the lack of pubescence and leaves with 9–12 pairs of secondary veins.

Hillia Jacquin

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

Key to the Species of *Hillia*

- 1a. Corolla pinkish to red or orange, funnellform or tubular with the central part of the tube inflated and narrowed at both ends, flowers not scented; subgenus *Ravnia* 2
- 1b. Corolla greenish or white, long-tubular with rotate lobes or salverform, corolla tube expanded only at the corolla lobes, flowers often sweet-scented; subgenus *Hillia* 4
 - 2a. Corolla tube rose red and inflated in the middle, 3–5 cm long, flowers often in groups of 3; a commonly collected species *H. triflora*
 - 2b. Corolla tube yellow-orange to peach or rose, funnellform and widest at the mouth, 4–6.5 cm long, flowers solitary; rarely collected species 3
 - 3a. Corolla lobes 6–12 mm long; free portion of the filaments ca. 1 mm long *H. allenii*

Shrubs, small trees, or lianas, epiphytic or less often terrestrial, branchlets thick and terete, glabrous; **stipules** interpetiolar and intrapetiolar but splitting apart along the edges, lingulate and blunt at apex, caducous. **Leaves** opposite, equal or unequal at each node, subsessile to short-petiolate; **leaf blades** elliptic to obovate, entire, decurrent on the petiole, semisucculent and drying coriaceous, without domatia. **Inflorescences** of solitary terminal flowers (or 3-flowered dichasia in *H. triflora*), bracts reduced or absent (the flowers at first enclosed within the large untied stipules), pedicels short or absent. **Flowers** bisexual, monomorphic, often large, glabrous externally, hypanthium continuous with the pedicel, calyx tube often absent, calyx lobes 2–5 and distant (or none), sometimes with a secondary smaller set of calyx lobes alternate with the larger lobes; **corolla** salverform to funnellform or tubular, white to yellowish, pinkish, orange, or red, semisucculent, corolla lobes (3–)5–7(–9), convolute in bud, becoming reflexed; **stamens** (4–)5–7, filaments very short and inserted below the throat, anthers basifixed, elongate-linear, obtuse at each end, included (except in *H. longifilamentosa*); **ovary** 2-locular, ovules many and ascending in each locule on septal placentas, style as long as the corolla tubes, stigmas subcapitate or 2. **Fruits** woody capsules, narrowly cylindrical to very narrowly oblong, truncated distally, dark brown and smooth, dehiscing septicidally and basipetally into 2 flattened valves; **seeds** many and imbricated, rhombic and flattened, with a minute circumferential wing, appendaged at the base and with a tuft of hairs at the distal apex.

Hillia is a genus of about 20 species, ranging from southern Mexico to Brazil and Peru. The genus is recognized by the larger flowers with long tubes, many ascending imbricated ovules, long tubular (“cigar-shaped”) capsules, and flattened winged seeds with a tuft of hairs at one end. The more colorful flowers of subgenus *Ravnia* (see following key) appear to be an adaptation to bird pollination. Specimens lacking flowers or fruit can be very difficult to identify to species. In addition, one group of our species may be part of a polymorphic complex; see the discussion under *H. maxonii*. Some of our species of *Hillia* are very similar to *Cosmibuena*, but that genus has seeds lacking the tufted hairs at one end.

- 3b. Corolla lobes 13–17 mm long; free portion of the filaments 9–10 mm long *H. longifilamentosa*
- 4a. Plants of lower elevation forest, not known from above 300 m in Costa Rica; larger leaf blades more than 10 cm long and 5 cm broad 5
- 4b. Plants of higher elevations, rarely collected below 600 m; larger leaf blades rarely more than 10 cm long or 5 cm broad 6
- 5a. Leaf blades with thin texture, the 5–6 pairs of 2° veins arising at ca. 60° angles from the midvein; corolla tubes 8–10 cm long *H. macrophylla*
- 5b. Leaf blades thick-textured, the 4–5 pairs of 2° veins arising at ca. 30° angles from the midvein; corolla tubes 4–5 cm long *H. grayumii*
- 6a. Leaf blades 4–10 cm long, usually tapering gradually to a bluntly acute apex, broadest at the middle or below; corolla tubes 4–5 cm long; seed hairs ca. 17 mm long *H. loranthoides*
- 6b. Leaf blades 0.7–3.7 cm long, usually bluntly obtuse to rounded at the apex; corolla tubes rarely exceeding 4 cm in length; seed hairs ca. 10 mm long 7
- 7a. Leaf blades 12–37 mm long, stipules 6–16 mm long; corolla lobes suborbicular, corolla tubes 24–42 mm long; seeds ca. 3 mm long; 1400–2400 m elevation *H. maxonii*
- 7b. Leaf blades 7–14 mm long, stipules 3–7 mm long; corolla lobes broadly to narrowly ovate, corolla tubes 15–35 mm long; seeds ca. 2 mm long; 600–1600 m elevation *H. panamensis*

Hillia allenii C. M. Taylor, Selbyana 11: 32. 1989.
Ravnia panamensis Steyerl., Ceiba 3: 22. 1952,
 not *Hillia panamensis* Standl.

Epiphytic shrubs to 1.5 m tall, leafy stems 2.5–7 mm thick, glabrous, terete; **stipules** 10–12 mm long, lingulate, quickly caducous. **Leaves** with short (1–4 mm), thick (2–3 mm) petioles, glabrous and drying dark; **leaf blades** 4–11 cm long, 1.5–5 cm broad, elliptic to narrowly elliptic-oblong, apex slender acuminate, base cuneate or slightly rounded, drying subcoriaceous, dark brown above, glabrous above and below, 2° veins 5–9/side, usually obscure. **Inflorescences** of solitary terminal flowers borne on short (3–4 mm) thick (2 mm) glabrous pedicels drying black. **Flowers** glabrous externally, hypanthium 4–7 mm long and 3.5 mm thick, calyx tube not developed, calyx lobes 6, 6–14 mm long, 2–3 mm broad, narrowly spatulate-oblong; **corolla** funnellform, pale red and pale yellow to salmon-pink, tube 25–40 mm long, lobes 6, 6–12 mm long and 10 mm broad at the base, bluntly acute; anthers 5–7 mm long on filaments ca. 1 mm long. **Fruits** not seen.

Plants of montane cloud forest formations at ca. 1000 m elevation. Flowering in June and September. This species known only from the Cordillera de Tilarán and in western Panama.

Hillia allenii is recognized by the brightly colored funnellform corolla and the short filaments. Fruiting material may be very difficult to distinguish from that of *H. longifilamentosa*.

Hillia grayumii C. M. Taylor, Selbyana 12: 137. 1991. Figure 28.

Epiphytic shrubs, ca. 1 m tall, leafy stems 4–7 mm thick, slightly quadrangular, glabrous, brownish, mi-

nutely grooved; **stipules** ca. 40 mm long, 6–8 mm broad, lanceolate, caducous. **Leaves** isophyllous, usually decussate, petioles 6–20 mm long, 2–3 mm thick, articulated at the stem; **leaf blades** 9–19 cm long, 3–6.5 cm broad, elliptic to elliptic-oblong, apex acuminate with tip 1–2 cm long, base obtuse or acute, drying stiffly chartaceous or subcoriaceous and dark brown above, glabrous above and below, 2° veins 4–6/side and strongly ascending (ca. 30°), obscure beneath. **Inflorescences** of solitary terminal flowers, subtending stipules caducous, peduncles 2–3 mm long, bracts 1–3 mm long, triangular, acute. **Flowers** glabrous, hypanthium 7–8 mm long, cylindrical, calyx limb to 0.5 mm long, truncate or slightly lobed; **corolla** tubular-funnelform, bright pale green to yellow, tube 43–50 mm long, lobes 6, 8–9 mm long, triangular, obtuse to rounded; filaments ca. 10 mm long, anthers 6, ca. 9 mm long. **Fruits** 10–12 cm long and 8–14 mm broad, drying dark brown, stipe ca. 3 mm long; **seeds** 3 mm long, 0.5 mm broad.

Plants of lowland rain forest and swamp forest formations, collected from near sea level to 600 m elevation. Flowering in May–June; fruiting in March and May–June. The species is known only from the Caribbean lowlands of northern and central Costa Rica.

Hillia grayumii is distinguished from its congeners by the lowland habitat, yellowish funnellform flowers, and large fruit. Among Costa Rican species, it is similar to *H. macrophylla*, but that species grows in cloud forests and has thin-textured leaves and tubular flowers.

Hillia longifilamentosa (Steyerl.) C. M. Taylor, Selbyana 11: 32. 1989. *Ravnia longifilamentosa* Steyerl., Ceiba 3: 21. 1952.

Epiphytic or clambering **shrubs** to 6 m tall, leafy stems 2–7 mm thick, glabrous, smooth, brown to gray; **stipules** 22–37 mm long, elliptic to oblanceolate, caducous. **Leaves** with petioles 2–8 mm long, thick, glabrous; **leaf blades** 6–16 cm long, 2–7 cm broad, elliptic or elliptic-oblong, apex acute or slightly acuminate, base obtuse to cuneate, drying subcoriaceous, grayish green, glabrous above and below, 2° veins 4–6/side, strongly ascending. **Inflorescences** of solitary terminal flowers, pedicels ca. 1 mm long, bracts 2–3 mm long, triangular, acute. **Flowers** with hypanthium 4–10 mm long, obconic to ellipsoid, calyx lobes 6, 6–14 mm long, narrowly triangular to lingulate or oblanceolate; **corolla** tubular-rotate, orange-red to salmon-pink, or white marked with pink, tube 32–43 mm long, ca. 3 mm diam., lobes 6, 13–17 mm long, triangular to lingulate; **stamens** 4–6, anthers ca. 5 mm long, well exerted, dark green. **Fruits** 10 cm long.

Plants of montane cloud forest formations, 1100–1700 m elevation. Flowering in April, July–August, and November. This species is known only from a few collections, ranging from Zarcero, Alajuela, to Chiriquí, Panama.

Hillia longifilamentosa is distinguished by its solitary terminal flowers with anthers extended 8–10 mm beyond the throat of the tube. Compare *H. allenii*.

***Hillia loranthoides* Standl., J. Wash. Acad. Sci. 18: 165. 1928. Figure 27.**

Epiphytic **shrubs**, 0.4–1.5 m tall but with vining branches, leafy stems 3–8 mm thick, glabrous, grayish, terete or quadrangular; **stipules** 18–22 mm long (to 35 mm beneath the flowers), 6–10 mm broad, oblong-obovate, obtuse or rounded distally. **Leaves** closely clustered or distant, decussate, petioles 4–8(–15) mm long, 1.5–2.8 mm thick; **leaf blades** (3–)4–10 cm long, (1.3–)2–4.5 cm broad, elliptic to elliptic-oblong, ovate or ovate-lanceolate, apex bluntly acute or obtuse, base obtuse to cuneate, drying coriaceous, dark grayish, 2° veins 4–5/side, strongly ascending or obscure. **Inflorescences** of solitary terminal sessile flowers, subtended by a pair of enlarged (8–25 mm) oblong-obovate bract-like reddish stipules, 1–2 smaller (1–4 mm) pairs of triangular or lingulate bracteoles often present at the base of the short pedicel. **Flowers** 6–7 cm long, hypanthium ca. 4 mm long, calyx tube minute, calyx lobes 4, 8–10 mm long, 1–2 mm broad, linear-lingulate; **corolla** tubular with rotate lobes, white or cream, carnosae, tube 40–60 mm long, 2–5 mm diam., lobes 4, 10–25 mm long, 8–16 mm broad, rounded distally. **Fruits** 3–8 cm long, 7–10 mm diam.; **seeds** ca. 2.5 mm long and 0.7 mm thick, distal hairs 6–17 mm long.

Plants of evergreen montane forests, from (300–)700 to 1400 m elevation. Flowering in February–May; fruiting in January and May. In Costa Rica, this species is known only from the Cordillera de Tilarán, near San Ramón, and El Retiro

(Cartago) and from a single lower elevation collection on the Osa Peninsula. The species is also known from southern Mexico.

Hillia loranthoides is distinguished by its thick leaves, usually tapering gradually to the apex, larger flowers with slender tubes, and seeds with longer bristles. Its distribution is unusual and may be an artifact of the difficulty of collecting epiphytes.

***Hillia macrophylla* Standl., Publ. Field Columb. Mus., Bot. Ser. 7: 201. 1931. Figure 28.**

Epiphytic **shrubs** or vines, 3–7 m tall, leafy branchlets 3–7 mm thick, glabrous, pale brown and lenticellate; **stipules** 10–35 mm long, 12–25 mm broad, narrowly lanceolate (in Costa Rica) to oval-oblong, the basal sheath 1–2 mm long, caducous. **Leaves** decussate, petioles 6–20 mm long, 2–3.5 mm thick, terete, clearly differentiated from the lamina base; **leaf blades** 9–21 cm long, 6–10 cm broad, ovate-elliptic to elliptic-oblong or elliptic, apex acuminate (acute), base obtuse, drying membranaceous to chartaceous, dark brown above, glabrous above and below, major veins with a rugose texture, 2° veins 6–9/side arising at ca. 60° angles and loop-connected near the margin. **Inflorescences** of large solitary sessile terminal flowers, subtended by elongated (20–50 × 5–24 mm) caducous stipules, bracteoles usually absent. **Flowers** with hypanthium 6–7 mm long, 3–3.5 mm diam., cylindrical, calyx tube 0–0.5 mm long, subentire; **corolla** tubular-salverform, white, tube 5.5–11 cm long, 2–4.5 mm diam., lobes 5 or 6, 2.5–5 cm long, ca. 8 mm broad at the base and narrow (4 mm) distally, linear-lanceolate to narrowly triangular. **Fruits** 7–12 cm long, the opened valves becoming 14–20 mm broad, rounded at the base, acute at apex, sessile; **seeds** 1.5–4 mm long with distal hairs 14–18 mm long.

Plants of moist cloud forests from 800 to 1800 m elevation. Flowering in March–June; a single fruiting collection was made in December. This species is known only from near Monteverde, Cataratas de San Ramón, and above the Río Gato, Cartago, in Costa Rica. It is also found in Colombia, Ecuador, and Peru.

Hillia macrophylla is unique among our species of *Hillia* because of the larger thin-textured leaves, more numerous ascending secondary veins, and long-tubular flowers with corolla lobes that have long (3–4 cm), narrow tips. It is a rarely collected species. South American collections appear to have larger (3–4 mm) seeds and larger stipules subtending the flowers.

***Hillia maxonii* Standl., J. Wash. Acad. Sci. 18: 163. 1928. *H. palmana* Standl., loc. cit. 18: 164. 1928. *H. hathewayi* Fosberg, Sida 2: 387. 1966. Figure 27.**

Epiphytic **shrubs**, 0.7–2.5(–5) m tall, often pendant to 5 mm long, leafy stems 1–5 mm thick, dark or pale grayish, glabrous, older nodes articulate with transverse ridges; **stipules** 6–16(–32) mm long, 2–6 mm broad, oblong-obovate to obovate, rounded, larger and bract-like beneath the flowers. **Leaves** decussate and often crowded on short (3–15 mm) internodes, petioles 2–6(–15) mm long; **leaf blades** (12–)18–37(–60) mm long, 6–20(–30) mm broad, obovate to oblong-obovate or ovate-elliptic, apex bluntly obtuse to rounded, base obtuse to cuneate, decurrent on the petiole, drying subcoriaceous and dark grayish or brownish, glabrous above and below, 2° veins 3–4/side, strongly ascending or obscure. **Inflorescences** of solitary, terminal, sessile flowers subtended by a pair of enlarged bract-like stipules rounded at apex. **Flowers** glabrous externally, fragrant, hypanthium ca. 2.5 mm long and 1.8 mm thick, calyx tube very short, calyx lobes absent or 4–6 mm long, 0.5–1.8 mm broad; **corolla** tubular with rotate lobes, slightly fleshy, tube 24–42 mm long, 1.4–4 mm diam., greenish or white, lobes 4, 10–14(–22) mm long and usually equally broad or broader than long, suborbicular and rounded distally, bright white or yellowish white. **Fruits** (22–)30–60 mm long, 5–9 mm thick, the valves to 8 mm broad when opened and expanded; **seeds** 3–4 mm long, 0.5–1 mm diam., distal hairs 6–13 mm long.

Plants of evergreen montane forest formations from 500 to 2400 m elevation. Flowering in April–September and December; fruiting in September and November–March. This species has been collected near Managua, Nicaragua, in the Cordillera de Tilarán, Cordillera Central, in the western part of the Cordillera de Talamanca, and in Chiriquí and Veraguas, Panama.

Hillia maxonii is recognized by its usually epiphytic habit, smaller stiff leaves, bract-like stipules subtending the flowers, and tubular corollas with broadly rounded lobes. Smaller-leaved specimens of this species may represent intermediates with *H. panamensis*. Larger-leaved specimens resemble *H. tetrandra* Sw. of the West Indies and northern Central America. However, *H. tetrandra* has larger (5–11 × 2.5–6 cm) leaves that are more often obovate, quite unlike those of southern Central America. All three taxa exhibit a wide range of variation, and it is possible that they are elements of a single polymorphic species. (A similar problem is found in the epiphytic species of *Psychotria*; see the discussion under *P. guadalupensis*.)

Hillia panamensis Standl., N. Amer. Fl. 32: 117. 1921. *H. chiapensis* Standl., J. Wash. Acad. Sci. 16: 16. 1926. Figure 27.

Epiphytic **shrubs** or small treelets to 4 m tall, leafy stems 1–2.7 mm thick, glabrous and grayish, often de-

veloping opposite longitudinal sulci and expanded nodes; **stipules** 3–7 mm long, 1–2 mm broad, oblong to narrowly obovate and rounded distally, translucent. **Leaves** decussate and usually closely crowded on short (0.5–5 mm) internodes, petioles 1–4 mm long; **leaf blades** 7–12(–14) mm long, 4–8(–10) mm broad, elliptic to elliptic-oblong or obovate, apex acute to bluntly obtuse or rounded, base cuneate to obtuse, drying stiffly chartaceous to subcoriaceous, grayish to very dark, margins often becoming slightly revolute, glabrous above and below, 2° veins 2–3/side, strongly ascending or obscure. **Inflorescences** of solitary terminal flowers, the distal stipule pair slightly expanded (6 × 2.5 mm) and bract-like smaller (1–2 mm) rounded bracts sometimes present at the base of the sessile flowers. **Flowers** glabrous externally, hypanthium ca. 1.5 mm long, 1 mm thick, tubular, calyx lobes to 11 mm long, 0.3–0.6 mm broad, linear, caducous; **corolla** tubular with rotate lobes, white, slightly succulent, tube 15–30(–38) mm long, 0.9–1.5 mm diam., lobes 4, 5–7 mm long, 3.5–6 mm broad, ovate to lanceolate, bluntly obtuse. **Fruits** 20–42 mm long, opened expanded valves 3–4 mm wide; **seeds** ca. 2 mm long and 0.6 mm thick, distal hairs 10 mm long.

Plants of evergreen montane forest formations from 600 to 1600 m elevation. Flowering in May–August; fruiting in December. This species is found in southern Mexico–Guatemala, in the Cordilleras de Guanacaste and Tilarán in Costa Rica, and in western and central Panama.

Hillia panamensis is distinguished by its epiphytic habit, very small stiff closely crowded leaves, fragrant flowers with long slender corolla tubes, and rotate lobes usually narrower than long. It has been called *jasmin del volcán*. This species may not be specifically distinct from the very similar, and partly sympatric, *H. maxonii*. But the differences used in the keys do seem to separate a great majority of specimens. See the discussion under *H. maxonii*.

Hillia triflora (Oersted) C. M. Taylor, Selbyana 11: 30. 1989. *Ravnia triflora* Oersted, Vidensk. Meddel. Dansk Naturhist. Foren. Kjobenhavn 1852: 49. 1853. *Ravnia pittieri* Standl., N. Amer. Fl. 32: 114. 1921. *Lagenanthus parviflorus* Ewan, Mutisia 4: 5. 1952. *H. triflora* var. *pittieri* (Standl.) C. M. Taylor, Selbyana 11: 31. 1989. Figure 27.

Epiphytic (rarely terrestrial) **shrubs**, 0.5–1.5(–3) m tall (branches to 2 m long and pendulous), leafy stems 1.8–5 mm thick, glabrous; **stipules** 15–43 mm long, 4–10 mm broad, largest beneath the inflorescences, elliptic and acute, glabrous and caducous. **Leaves** usually decussate, isophyllous or anisophyllous at a node, petioles 3–7(–12) mm long, 1.5–2 mm thick, poorly differentiated from the base; **leaf blades** 5–13(–19) cm long, 1.5–4.5 cm broad, narrowly elliptic-oblong to oblanceolate, elliptic-oblong

or oblong (linear-lanceolate in variety *pittieri*), apex tapering gradually and narrowly acuminate, tapering gradually to the acute or cuneate base, drying coriaceous, dark green or grayish green above, 2° veins 3–5/side. **Inflorescences** of 1 or 3 terminal flowers borne on a very short (0.5–2 mm) thick peduncle, bracts ca. 3 mm long or absent, pedicels 1–6 mm long but difficult to distinguish from the hypanthium. **Flowers** glabrous externally, hypanthium ca. 5 mm long, 1.2–1.8 mm diam. calyx lobes 6 (5, 7), 4–14 mm long, 0.5–1 mm broad, linear-oblong; **corolla** red, tubular with relatively small lobes, tube 40–65 mm long, 1.5–10 mm broad, lobes 6 (5, 7), 3–4 mm long, to 5 mm broad at the base; **stamens** 5–6, anthers 3–5 mm long, partially exserted. **Fruits** 5–10 cm long, ca. 8 mm diam., valves becoming up to 12 mm broad; **seeds** 0.8–2.5 mm long, distal hairs 15–30 mm long.

Plants of montane and premontane evergreen forest formations from (100–)800 to 2400 m ele-

vation. The lowest elevation collections are from La Selva; this species has not been collected from below 1000 m on the Pacific slope. Flowering in all months, but most commonly February–August; fruiting in October–February. The species ranges from southern Mexico to northwestern Colombia.

Hillia triflora is distinguish by its epiphytic habit, the tubular reddish flowers usually in terminal triads, long narrow capsules, and seeds with a distal tuft of hairs. There are few fruiting collections. There may be some local differentiation between the two varieties; at Monteverde, variety *pittieri* is found at slightly lower elevations than is variety *triflora*. The following key distinguishes the two varieties.

- 1a. Leaves at each node approximately equal in size at the same node on flowering shoots; mature corolla tube not or only slightly inflated, up to 1.6 times broader in the broadest portion as at the apex *H. triflora* var. *triflora*
- 1b. Leaves at each node strongly differing in size on flowering shoots, larger leaves ca. 1.5 times longer than the other leaf of the same node; mature corolla tube strongly inflated, ca. 1.8 times broader in center than at the apex *H. triflora* var. *pittieri*

Hippotis Ruiz Lopez & Pavón

Trees or shrubs, puberulent (in ours) or glabrous; **stipules** interpetiolar, triangular to obovate, large and caducous. **Leaves** opposite, decussate, petiolate; **leaf blades** usually thin, pinnately veined, without domatia, with the minor venation parallel (lineolate) within the areolae formed by the 3° and 4° veins. **Inflorescences** axillary to leaves or undeveloped leaves and axillary in fruit, short cymose and 2–3-flowered, capitate or of solitary flowers. **Flowers** bisexual, monomorphic, radially symmetrical or bilaterally symmetrical by curvature of the corolla, usually large, sericeous externally, calyx bilobate or spathaceous; **corolla** tubular or funnelform, white, rose, red, or pale orange, corolla tube straight or curved, corolla lobes 5, short and truncated or emarginate, plicate-valvate in bud; **stamens** 5, filaments usually unequal, borne at the middle or lower half of the tube, anthers included; **ovary** 2-locular, placentas peltate from the center of the septum, with many horizontal ovules in each locule, stigmas 2, subcapitate. **Fruits** baccate, ovoid to ellipsoid or globose; **seeds** many, small, angular.

A genus of around 12 species in northern South America, Ecuador, and Peru; 1 species reaches northernmost Costa Rica. The larger thin hairy leaves, unusual lineolate minor venation, few larger pseudoterminal flowers, spathaceous calyx, and hairy fleshy fruit with many small seeds help to distinguish our species.

Hippotis albiflora Karst., Fl. Colomb. 1: 33, pl. 17. 1858. *Duroia panamensis* Dwyer, Ann. Missouri Bot. Gard. 55: 38. 1968. Figure 25.

Small **trees**, 3–17 m tall, leafy stems 2.5–8 mm thick, densely pilose with yellowish hairs 1–3 mm long, terete or slightly quadrangular, older stems glabrescent and pale grayish; **stipules** 15–30 mm long, 5–12 mm broad, narrowly ovate or lanceolate, with long yellowish hairs externally. **leaves** with petioles 10–28(–35) mm long, 1.5–2.5 mm thick, densely pilose with erect or ascending hairs 1–2 mm long; **leaf blades** 14–30(–35) cm long, 6–14(–18) cm broad, obovate to oblong-obovate, apex tapering gradually or abruptly and acuminate or caudate-acuminate, tip 1–2 cm long, base obtuse to rounded and subtruncate, drying thin-chartaceous to chartaceous, densely pilose on both surfaces with thin straight or curved hairs 0.7–2 mm long, 2° veins 7–10/side, 3° veins often subparallel, the smallest veins distinctly parallel (lineolate) in small groups. **Inflorescences** of 1–3 flowers in the axils of the distal leaves but often appearing terminal, peduncles absent or very short, bracts 3–5 mm long, ovate, pedicels 3–8 mm long, 1–2 mm thick and densely yellowish velutinous. **Flowers** 5–6 cm long, hypanthium and calyx 3.3–3.8 cm long, ca. 8 mm broad, densely pilose, spathe-like and split ca. 10 mm down 1 side; **corolla** ca. 5 cm long and 2 cm broad distally, funnel-form, white to cream, pilose externally, tube 35–45 mm long, greenish white, straight or slightly curved, lobes 5–8 mm long and 10 mm broad, obtuse. **Fruits** 3–4 cm long (not including the persisting calyx), 1–2 cm diam.,

ellipsoid and hirsute, becoming purple; **seeds** 2 mm long, foveolate.

Plants of rain forest formations in the Caribbean lowlands, from 10 to 400 m elevation (to 1600 m in Venezuela). Flowering in February, April, and July–October; fruiting in May–September. This species has been collected near Río Colorado in northern Costa Rica, from La Selva and the Hitoy Cerere reserve. It is also known from the province of Bocas del Toro, in Panama, and from Colombia and Venezuela.

Hippotis albiflora is recognized by the conspicuous pubescence, larger thin leaves with lineolate minor venation, few large pseudoterminal flowers, spathaceous calyx, and larger, hirsute, many-seeded fruit. Our material may differ in some details from that described from Venezuela; it could be that Costa Rican populations are worthy of subspecific recognition. Compare this species with *Duroia costaricensis*.

Hoffmannia Swartz

Herbs, herbaceous **subshrubs**, or slender shrubs, main vertical stems usually with few or no lateral branches, glabrous or pubescent, terete or quadrangular, internodes often hollow when dried; **stipules** interpetiolar, usually small and triangular, often succulent and divergent, caducous. **Leaves** opposite and decussate or rarely verticillate, equal at the node or sometimes slightly unequal, petiolate or occasionally sessile, petioles with inflated chambers (ant vesicles) in a few species; **leaf blades** usually drying membranaceous to chartaceous (rarely subcoriaceous), entire, often decurrent on the petiole, pinately veined, often with conspicuous raphides on the dried leaf surfaces, domatia rarely present. **Inflorescences** axillary, sessile or pedunculate, with few to many flowers, usually cymose or dichasial and often with helioid branches, fasciculate to capitate in a few species, flowers usually pedicellate, bracts and bracteoles rarely

present. **Flowers** bisexual and monomorphic, glabrous or pubescent externally, hypanthium often with longitudinal ribs, calyx tube usually very short, calyx lobes 4(–5), usually short and often triangular, persisting; **corolla** salverform to funnellform or rotate, white, yellow, orange, or rose to deep red or purple, corolla tube short and usually narrow, glabrous on the interior, corolla lobes 4(–5), imbricate along the edges or apparently valvate, apex usually acute; **stamens** 4 (3–5), borne within the tube of the corolla, filaments very short, anthers linear to narrowly oblong, usually white; **ovary** 2- (3, 4) locular, each locule with many ovules borne longitudinally on bilamellate axile placentas, style slender, stigmas bilobate or clavate. **Fruits** baccate, usually small, 2- (3, 4) locular, often becoming enlarged and spongy at maturity, with many minute multiseriate horizontal seeds; **seeds** angulate, their surfaces often reticulate to foveolate.

A genus of about 100 species, ranging from Mexico and the West Indies to South America. A majority of the species are found in Mexico and northern Central America. The usually single-stemmed habit, presence of raphides in many parts, small triangular stipules (often caducous), axillary inflorescences, four-parted flowers, and many-seeded fleshy fruits help to distinguish the species of *Hoffmannia* from other Rubiaceae in Costa Rica. Most of the Costa Rican species are restricted to areas with very high rainfall (none are found in deciduous vegetation), and relatively few species grow below 800 m elevation.

Hoffmannia is probably Costa Rica’s taxonomically most difficult genus of Rubiaceae. These semisucculent subshrubs do not dry well, and the flowers, often in small dense clusters, are also not well preserved. In addition, there appears to be great variation from plant to plant within many species. The genus is related to *Hamelia* and *Deppea*; it is currently being studied by Dr. John Dwyer (MO), and the review presented here should be considered no more than tentative.

Key to the Species of *Hoffmannia*

- 1a. Petioles with lateral longitudinal inflated vesicles; plants to 1.2 m tall, surfaces with longer (1.5 mm) multicellular hairs *H. vesiculifera*
- 1b. Petioles without lateral inflated structures; plants 0.5–3 m tall, glabrous to villous with multicellular hairs 2
- 2a. Inflorescences sessile and capitate in the leaf axils in early stages (rarely becoming pedunculate or branched in later stages), often verticillate at the nodes 3
- 2b. Inflorescences sessile and fasciculate to pedunculate and paniculate or cymose, neither densely capitate nor verticillate 4
- 3a. Leaf blades neither bullate nor areolate, to 30(–40) cm long, glabrous or pubescent; corolla ca. 7 mm long; commonly collected plants *H. congesta*

- 3b. Leaf blades bullate or areolate, to 20(–25) cm long, pubescent; corolla ca. 4.5 mm long; rare
..... *H. areolata*
- 4a. Leaves usually 3/node, leaf blades cuneate at the base with long-decurrent lateral margins on the petiole and these slightly expanded near the stem, lateral margins of the petiole 2–4 mm broad [leaf blades with 11–18 pairs of 2° veins]; Vara Blanca to the upper Río Grande de Orosi, 1400–1600 m elevation *H. amplexifolia*
- 4b. Leaves opposite (rarely with 3 leaves per node), leaf blades obtuse to cuneate at the base, if long-decurrent on the petiole never forming a lateral margin 2–4 mm wide along the petiole and not expanded near the base; species widely distributed, 10–2300 m elevation 5
- 5a. Plants of Cocos Island 6
- 5b. Plants of mainland Central America 7
- 6a. Petioles 2–5 cm long; corolla glabrous on the exterior *H. piratarum*
- 6b. Petioles 6–8 cm long; corolla puberulent on the exterior *H. nesiota*
- 7a. Young stems glabrous or subglabrous, or with very small (0.2 mm) hairs in longitudinal lines along the young stem 8
- 7b. Young stems densely pubescent with crooked multicellular hairs, the hairs varying 0.3–2 mm long, older stems pubescent or glabrescent 19
- 8a. Inflorescences short, the 1° peduncle and rachis usually less than 3 cm long (if plants grow below 600 m elevation and have petioles 2–6 cm long and leaves 4–15 cm broad, go to dichotomy 12) 9
- 8b. Inflorescences small to large, peduncle and rachis of some inflorescences usually exceeding 4 cm in length 12
- 9a. Corolla tubes 3–4 mm diam. and 3–4 mm long; leaf blades 15–35 cm long with 9–15 pairs of 2° veins, cuneate basally and long-decurrent on the petiole *H. dotae*
- 9b. Corolla tubes 1–3 mm diam. (dried) and 1–6 mm long; leaf blades 5–15 cm long with 5–9 pairs of 2° veins, abruptly narrowed at the base (but leaves to 23 cm long, with 7–12 pairs of 2° veins, and cuneate long-decurrent bases in *H. hamelioides*) 10
- 10a. Corolla 9–14 mm long, corolla lobes 3–6 mm long; calyx lobes ca. 1.5 mm long, ovary 2–3 mm long; flowers fasciculate (inflorescences rarely pedunculate), usually more than 15/node; fruit elongate when dried *H. psychotriifolia*
- 10b. Corolla less than 9 mm long, corolla lobes 1.5–4 mm long; calyx lobes 0.5–1 mm long, ovary 1–2 mm long; flowers fasciculate or borne on slender pedunculate; fruit rounded when dried 11
- 11a. Inflorescences compact, fasciculate or with short stiff peduncles, often less than 2 cm long; leaf blades to 15 cm long, rarely tapering gradually at the base and decurrent on the petiole; a commonly collected species *H. longipetiolata*
- 11b. Inflorescences open with thin peduncles and pedicels, usually more than 2 cm long; leaf blades to 23 cm long, usually tapering gradually at the base and decurrent on the petiole; uncommon plants *H. hamelioides*
- 12a. Sepal lobes 2–4 mm long; corolla tube 1–3 mm long, corolla lobes 3–7 mm long; plants not collected from about 700 m elevation [leaf blades usually with an arcuate submarginal vein and abruptly narrowed at the base] *H. liesneriana*
- 12b. Sepal lobes rarely more than 1.8 mm long; corolla tube usually more than 2 mm long (except in *H. laxa*), corolla lobes 2–6 mm long; plants rarely found below 800 m elevation (except *H. pallidiflora*) 13
- 13a. Secondary veins loop-connected near the margin to form an arcuate submarginal vein; inflorescences with a prominent erect peduncle 4–10 cm long and usually terminated by 3 branches; 1200–1500 m elevation *H. davidsoniae*
- 13b. Secondary veins loop-connected only in the distal part of the lamina, not forming an arcuate submarginal vein; inflorescences often pendant, with shorter slender peduncles (400–)800–2300 m elevation 14
- 14a. Corolla tubes 4–8 mm long; inflorescences short to long and with many lateral branches; leaf blades drying stiffly chartaceous and often large, 12–37 cm long with 9–15 pairs of 2° veins; 1000–2200 m elevation 15

14b.	Corolla tubes 1.5–4 mm long; inflorescences short (to 6 cm) with few lateral branches [corolla tube 1.5–4 mm long]; leaf blades drying membranaceous to thin-chartaceous, 7–20(–25) cm long with 7–10 pairs of 2° veins; (400–)800–1500 m elevation	17
15a.	Leaves usually drying grayish and stiffly chartaceous, petioles 2–10 cm long; leaf blades cuneate and slightly decurrent on the petiole; (corolla tubes 4–8 mm long); fruit rose-red to white; central Costa Rica	<i>H. leucocarpa</i>
15b.	Leaves usually drying dark brown and chartaceous, petioles 2–5 cm long; leaf blades usually cuneate and long-decurrent at the base; fruit red; central Costa Rica to the Chiriquí Highlands (note: the following 2 species may intergrade)	16
16a.	Corolla tubes 6–10 mm long; calyx lobes 1.2–3 mm long; leaf blades often narrowly obovate and long attenuate at the base; central Costa Rica to Panama, 1000–2500 m elevation	<i>H. arborescens</i>
16b.	Corolla tubes 3–7 mm long; calyx lobes 0.5–1.5 mm long; leaf blades not usually narrowly obovate and long attenuate at the base; westernmost Costa Rica and the Chiriquí Highlands, 1100–1700 m elevation	<i>H. pittieri</i>
17a.	Inflorescences usually unbranched (sometimes bifurcate) [drying yellowish and not very slender, probably erect; pedicels 0–3 mm long and ca. 0.5 mm thick (dried); corolla tube 2.5–4 mm long; 400–1300 m elevation on the Caribbean slope]	<i>H. pallidiflora</i>
17b.	Inflorescences usually branched	18
18a.	Inflorescences with very thin (0.2–0.3 mm) branches that usually dry black, pendulous, flowering portion 2–4 cm long, pedicels 4–9 mm long and 0.2–0.3 mm thick (dried); 1000–1500 m elevation	<i>H. laxa</i>
18b.	Inflorescences with thicker branches that do not dry black, flowering portion 1–2 cm long, pedicels 2–6 mm long, not thin and black; 0–200 m elevation, Osa Peninsula	<i>H. hammelii</i>
19a.	(from 7b) Leaf blades rounded to bluntly obtuse at the apex, often bullate, many 4° veins parallel (sublineolate but difficult to see); inflorescences with few (3–7) subsessile flowers on long (3–7 cm) peduncles; plants to 40 cm tall [200–1200 m elevation]	<i>H. bullata</i>
19b.	Leaf blades acute to acuminate (rarely obtuse) at the apex, never bullate, 4° veins partly parallel only in <i>H. aeruginosa</i> ; inflorescences with short (0–2 cm) peduncles or with more than 7 flowers if peduncles are long, pedicels 0–2 cm long; plants usually more than 40 cm tall	20
20a.	Secondary veins loop-connected near the margin to form an arcuate submarginal vein [inflorescences subsessile and usually less than 2 cm long]	21
20b.	Secondary veins loop-connected only in the distal part of the blade, a submarginal vein absent (except in the distal third)	22
21a.	Leaf blades cuneate and slightly decurrent at the base, with 9–15 pairs of 2° veins; 400–1000 m elevation	<i>H. inamoena</i>
21b.	Leaf blades acute to obtuse at the base, not usually decurrent on the petiole, with 7–12 pairs of 2° veins; 1000–1500 m elevation in north-central Costa Rica	<i>H. aeruginosa</i>
22a.	Plants not found above 900 m elevation; leaf blades usually less than 15 cm long, rarely cuneate and long-decurrent at the base, with 6–10 pairs of 2° veins	<i>H. valerii</i>
22b.	Plants not found below 1000 m elevation; leaf blades often exceeding 15 cm in length, usually gradually cuneate and long-decurrent on the petioles, with 7–12 pairs of 2° veins	23
23a.	Inflorescences with thick densely villous peduncles and pedicels; calyx lobes 1.5–3 mm long; corolla tube 6–8 mm long (lobes 3–4.5 mm long)	<i>H. asclepiadea</i>
23b.	Inflorescences with slender glabrescent or sparsely puberulent peduncles and pedicels; calyx lobes 0.3–1.5 mm long; corolla tubes 1.5–4 mm long (note: the following 2 species may be synonymous)	24
24a.	Inflorescences short but open and few-flowered; corolla lobes mostly 2–4 mm long	<i>H. hamelioides</i>
24b.	Inflorescences short but crowded and the flowers clustered around the node; corolla lobes 3–7 mm long	<i>H. decurrens</i>

Hoffmannia aeruginosa Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 1313. 1938. Figure 9.

Herbaceous **subshrubs** or slender shrubs, 0.5–2.5(–4) m tall, with few branches, leafy stems 2–6 mm thick, quadrangular or rounded, densely pilose with reddish brown crooked hairs 0.2–0.7 mm long; **stipules** 1–2 mm long, 2–3 mm broad at the base, broadly triangular, villous, persisting. **Leaves** with petioles (10–)20–70 mm long, 0.8–2 mm thick, densely villous, often with petioles of the same node differing in length; **leaf blades** (6–)9–20 cm long, (3–)4–10 cm broad, elliptic-oblong to ovate-elliptic or broadly elliptic, apex acuminate or short-acuminate to acute, base obtuse to acute (not or only slightly decurrent on the petiole); drying thin-chartaceous, grayish or grayish brown above, glabrous above, puberulent beneath with short (0.1–0.2 mm) hairs on 2° veins and longer (0.5–2 mm) hairs on the midvein, 2° veins 7–12/ side and evenly loop-connected 2–4 mm from the margin, many 4° veins parallel (forming rectangular areolae). **Inflorescences** solitary and axillary (2/node), 1–2 cm long with 2–10 flowers, glomerulate, sessile or on short (3 mm) peduncles, unbranched, flowers sessile or subsessile. **Flowers** densely covered with curly-crooked hairs 0.3–0.5 mm long, dark reddish brown when dried, hypanthium 2.5–3 mm long, 2 mm diam. distally, obconic, calyx lobes 1.3–2.5 mm long, ca. 0.6 mm wide, narrowly oblong; **corolla** rotate, reddish, tube 1–2 mm long, lobes 4–6 mm long, 2–3 mm broad; anthers ca. 2.5 mm long; style and stigma white. **Fruits** not seen.

Plants of wet cloud forest formations on the Caribbean slope from (?100–)800 to 1600 m elevation. Flowering in April–August. The species is known from north-central Costa Rica, near Ciudad Quesada and Zarcero, and from western Panama.

Hoffmannia aeruginosa is recognized by the dense reddish (in life) multicellular hairs on all parts, long-petiolate leaves (with blades scarcely decurrent), small dense inflorescences, and restricted range. The petioles often unequal at a node, the subparallel minor venation and arcuate submarginal vein are also distinctive features. Compare this species with material placed under *H. inamoena* with less dense pubescence, especially on the petioles.

Hoffmannia affinis Hemsley, Diagn. Pl. Nov. 31. 1879.

TYPE—*Endres 150*, without locality.

Branches terete, puberulent when young. Leaves with petioles ca. 6 mm long; leaf blades 10–12.5 cm long, ovate-oblong, obtusely acuminate, attenuate at the base, minutely puberulent beneath. In-

florescences umbellate-cymose, fasciculate, with ca. 6 flowers, peduncles 8–16 mm long, slender, pedicels 2–4 mm long. Flowers 6–8 mm long, puberulent. Based on Standley (1938), who had only seen the description.

Hoffmannia amplexifolia Standl., J. Wash. Acad. Sci. 15: 8. 1925. Figure 8.

Herbs or subshrubs, 1.2–(3) m tall, leafy stems 3–10 mm thick, glabrous or minutely puberulent on the ridges in early stages, with 3 longitudinal ridges; **stipules** 1–2 mm long and 2 mm broad at the base, triangular, puberulent along the edge. **Leaves** 3 (4)/node, petioles absent or short (3 mm) when the decurrent leaf base is reduced to a lateral ridge, minutely puberulent beneath; **leaf blades** (11–)16–37 cm long, 3–13 cm broad, narrowly elliptic to oblanceolate or very narrowly elliptic, gradually narrowed to the long-acuminate apex, gradually narrowed to the cuneate and long-decurrent base with a margin 2–4 mm wide along the petiole, often expanded (to 6 mm) and auriculate at the base, leaves drying chartaceous and dark brown to grayish above, glabrescent above, minutely (0.1–0.2 mm) puberulent below, 2° veins 11–18(–22)/side, usually loop-connected 1–4 mm from the leaf edge. **Inflorescences** axillary to leaves, 2–12/node, to 10 cm long, with short (3–15 mm) or long (to 60 mm), thick (1.5–2 mm) peduncles and long (to 7 cm) slender lateral branches from the apex of the peduncle, minutely puberulent, pedicels 0.5 mm long with hairs 0.1–0.4 mm long. **Flowers** sparsely to densely puberulent with minute crooked hairs that dry reddish, hypanthium 2–3 mm long, 1.5–2 mm diam. distally, turbinate to obconic, calyx reddish, calyx cup ca. 0.7 mm deep, calyx lobes 1–2.5 mm long and 0.5–1 mm broad, triangular to oblong; **corolla** rotate, greenish white to pale yellow, tube 1–4 mm long, 1–2 mm diam., lobes 4–9 mm long, 1.5–3 mm broad; anthers 3–5 mm long and 0.7–1.5 mm broad, connivent, yellow. **Fruits** becoming pink or red, to 8 mm diam. in life (4–5 mm long dried), ellipsoid to subglobose.

Plants of the very wet forests of the Caribbean slope, 800–2000 m elevation. Flowering in March–July; fruiting in October–December and March. The species is known only from central Costa Rica (Vara Blanca de Sarapiquí to Tapantí).

Hoffmannia amplexifolia is recognized by the nodes with three leaves, long-decurrent leaf base forming a leafy lateral margin along the petiole and often slightly expanded (auriculate) at the base (appearing to be amplexicaul), distinctive puberulence (but not on the stems), much-branched inflorescences, and broad connivent anthers. *Almeda et al. 6665* (CAS, F) from near Las Alturas, Puntarenas, is tentatively placed here; it has very pubescent inflorescences with corolla tubes 5–6

mm long. Pressed specimens can be similar to *H. subauriculata* with two leaves per node.

Hoffmannia arborescens J. D. Smith, Bot. Gaz. 37: 417. 1904. *H. josefina* Standl., J. Wash. Acad. Sci. 15: 8. 1925. (?*H. steinworthii* Fosberg, Sida 2: 388. 1966.) Figure 10.

Herbaceous **subshrubs**, 1.5–2 m tall, leafy stems 2–6 mm thick when dried, glabrescent; **stipules** ca. 2 mm long. **Leaves** with petioles 3–8(–25) mm long; **leaf blades** 7–18 cm long, 2.5–7 cm broad, oblanceolate to narrowly obovate, base acute to attenuate and long-decurrent on petiole, glabrous above and below, drying stiffly chartaceous, often dark reddish brown above, 2° veins 6–12/side. **Inflorescences** 1–3 in each leaf axil (2–6/node), 3–5 cm long, to 4 cm broad, open cymose with many branches, peduncles 3–20 mm long, puberulent with stiff hairs, flowers crowded distally, pedicels 2–6 mm long. **Flowers** with hypanthium 2–3 mm long, ca. 2 mm diam., calyx lobes 1–3 mm long, 1 mm broad at the base, blunt at apex; **corolla** funnellform, white to yellow or flushed with red, glabrous or puberulent, tube 6–8(–10) mm long, 1–2 mm diam., lobes 3–6 mm long. **Fruits** ca. 8 × 4.5 mm, red.

In evergreen montane forests from 1600 to 2500 m elevation. Flowering in February, April–August, and November–December; fruits were collected in February (immature fruits in August). This species ranges from Costa Rica to western Panama.

Hoffmannia arborescens is recognized by the usually narrowly obovate leaves gradually long-attenuate at the base, flowers on short inflorescences in leaf axils (or below), larger flowers with prominent calyx lobes, long corollas, and the higher altitude range. Occasional individual plants may be puberulent (*Q. Jiménez* 231 CR). This species may resemble *H. hamelioides*, while large-leaved specimens may be confused with the more common and closely related *H. leucocarpa*. The differences between *H. arborescens* and *H. pittieri* are minor, and the two species may intergrade in the highlands of western Panama, where *H. pittieri* is common and distinctive.

This species was described from material originating from Sta. Rosa del Copey at ca. 1800 m elevation (*Tonduz* 12230 = *J. D. Smith* n. 8121 US holotype). An isotype labeled as *H. arborescens* at CR lacks any indication of having the leaf-like floral bracts 1 cm long mentioned in the original description. This may have been an error on the part of J. D. Smith, as no such bracts have been seen in any Costa Rican material of *Hoffmannia*. The type bears the same Herb. Nat. C.R. number

(12230) as does the type of *H. decurrens* Standl. (q.v.), and they probably represent a mixed collection of two different species.

Hoffmannia areolata Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 22: 52. 1940. Figure 9.

Herbaceous **subshrubs** or slender stemmed shrublets, 0.6–1.5(–2) m tall, leafy stems 2–9 mm thick, glabrescent or sparsely pilose with crooked hairs 0.3–0.7 mm long; **stipules** 3–6 mm long and 2–4 mm broad at the base, glabrous, ligulate, caducous. **Leaves** with petioles 3–40(–90) mm long, difficult to distinguish from the decurrent lamina base; **leaf blades** (6–)8–20(–30) cm long, 3–8(–12) cm broad, elliptic to ovate-elliptic or oblanceolate, apex tapering gradually and acute or short-acuminate, more abruptly narrowed to an obtuse or cuneate base and long-decurrent on petiole, drying membranaceous to stiffly chartaceous, dark greenish above, the surface distinctly bullate and with short (0.2–0.5 mm) scabrous hairs above, with thinner hairs ca. 0.3 mm long beneath, 2° veins 11–16/side. **Inflorescences** verticillate in leaf axils, glomerulate, to 2 cm long and 8–15 mm broad, sessile, often obscuring the node, with pink hairs, the flowers sessile or subsessile. **Flowers** closely congested within the inflorescence, reddish tomentulous, calyx lobes 3–5 mm long and 0.5 mm broad, greenish to magenta; **corolla** funnellform, white, rose or translucent, ca. 4.5 mm long; tube ca. 2.5 mm long with lobes ca. 2 mm long; anthers ca. 1.5 mm long. **Fruits** 4–8 mm long, 3–6 mm diam. (to 10 mm in life), ellipsoid to subglobose, rose to deep red, spongy.

A little-collected species of montane cloud forest formation, 900–2100 m elevation. Flowering in March–December; fruiting in April, July–September, and January. The species ranges from the Cordillera de Tilarán eastward to the Chiriquí Highlands of Panama.

Hoffmannia areolata is recognized by its rugose-bullate leaves (areolate beneath), densely flowered axillary sessile glomerulate (usually verticillate) inflorescences, very small flowers, and hairs with thickened bases. The leaves are very dark green above in life. In general aspect, these plants resemble *H. congesta* and some *Psychotria* spp. with axillary inflorescences.

Hoffmannia asclepiadea Standl., J. Wash. Acad. Sci. 15: 7. 1925. Figure 10.

Slender herbaceous **shrubs**, 1.5–2(–3) m tall, usually unbranched, leafy stems 2.5–7 mm thick, sparsely to densely pilose with crooked hairs 0.3–0.5 mm long (?rarely glabrous as in *Williams et al.* 28096 CR, F); **stipules** 2–4 mm long and 3 mm broad at the base, triangular, puberulent, caducous. **Leaves** with petioles 1.5–5 cm long,

1–3 mm thick, densely to sparsely puberulent; **leaf blades** 6–21 cm long, 4–9(–11) cm broad, elliptic to elliptic-oblong or ovate-elliptic, apex acuminate with tip 1–2 cm long, base rounded to obtuse to cuneate-decurrent, drying chartaceous, dark brown above (much paler beneath), glabrous or sparsely pubescent above with hairs to 0.7 mm long, more densely pubescent beneath with crooked reddish hairs, 2° veins 9–12/side, often loop-connected near the margin. **Inflorescences** 2/node, open cymose, 2–4 cm long, with many closely spaced flowers on pubescent peduncles 3–10 mm long and ca. 0.7 mm thick, usually with 3 major branches and small (0.6 mm) bracteoles, pedicels 1–3 mm long, short villous. **Flowers** pubescent, with 5 distal longitudinal lines of hairs on the unopened buds, hypanthium 1–1.5 mm long, calyx lobes 0.5–1 mm long, narrowly triangular; **corolla** funnellform, pale yellow, tube 6–8 mm long, ca. 1.5 mm diam., lobes 2–3(–4.5?) mm long, to 2 mm broad. **Fruits** said to be subglobose and red.

Plants of wet cloud forest formations from 1900 to 2300 m elevation. Flowering in April–July. The species is known only from along the Cordillera Central and western portion of the Cordillera de Talamanca in central Costa Rica.

Hoffmannia asclepiadea is recognized by the dense puberulence on leaves and inflorescences, compact many-flowered inflorescences on very short peduncles, longer corolla tubes, and restriction to higher-elevation cloud forests. This species may be no more than a very puberulent form of another species, such as *H. arborescens*.

***Hoffmannia bullata* L. O. Williams, Fieldiana Bot.** 36: 52. 1973. Figure 9.

Herbs or herbaceous subshrubs, 10–60 cm tall, erect or decumbent, stems unbranched, lower nodes with roots, leafy stems 1–4(–7) mm thick, densely pilosulous with curved hairs 0.1–0.3 mm long drying reddish brown, terete; **stipules** 2–3 mm long, triangular, deciduous. **Leaves** opposite, petioles 4–45(–55) mm long, 1–2.5 mm thick, pilosulous with curved or crooked multicellular hairs; **leaf blades** 4–22 cm long, 2–9(–12) cm broad, obovate to oblong-obovate, apex rounded to bluntly obtuse, base obtuse to cuneate (not or only slightly decurrent on petiole), drying chartaceous, grayish or grayish brown above, glabrous above, minutely puberulent on the veins beneath with curved reddish hairs ca. 0.2 mm long, 2° veins 5–12/side, many 4° veins subparallel (sublineolate) and demarking narrow rectangular areas on the upper dried surface (but often difficult to see). **Inflorescences** usually solitary in leaf axils (1–2/node), 3–8 cm long, glomerulate or subumbellate, peduncles 2–7 cm long, 0.5–1 mm thick, glabrous or sparsely pilose, with 3–9 flowers along the same side of bifurcate branches, pedicels 1–5 mm long. **Flowers** sparsely puberulent or subglabrous, hypanthium 2–3 mm long, 1.5–2 mm broad distally, urceolate or turbinate, red, calyx lobes 1–2.5 mm long, 0.4 mm broad and acute; **corolla** rotate, pale red or rose, 7–10 mm long in bud, tube 3–4 mm long and 0.8 mm diam., lobes 3–

6 mm long and 2 mm broad; anthers ca. 3.2 mm long. **Fruits** becoming red or orange-red, 6–10 mm long and 4–9 mm diam., subglobose but with a truncated apex and persisting calyx.

Plants of wet evergreen forest formations from 50 to 1200 m elevation in Costa Rica. Sometimes forming a ground cover under the deep shade of the forest. Flowering in April–August; fruiting January–July in Costa Rica. This species ranges from Veracruz, Mexico, to central Panama.

Hoffmannia bullata is recognized by its small stature with roots at lower nodes, prominently bullate leaves that are obtuse or rounded apically, few-flowered inflorescences with long peduncles, and puberulence on many parts. The sublineolate 4° venation is distinctive but difficult to see in some collections. The midvein is often white on the dark green upper surface in living material. This species displays much variation within its range and within Costa Rica. Collections from the Pacific slope and near the Panama border tend to have smaller stature and narrowly elliptic-oblong leaves with more deeply impressed venation and acute apices (fig. 9, uppermost left). These differences are worthy of more detailed study. In addition, *H. discolor* (Lemaire) Hemsl. of Veracruz, Mexico, is closely related, but the leaves dry darker, the flowers have longer (2–4 mm) linear calyx lobes, and the fruits are larger.

***Hoffmannia congesta* (Oerst.) Dwyer, comb. nov.**
Xerococcus congestus Oerst., Vidensk. Meddel. Dansk Naturhist. Foren. Kjobenhavn 1852: 52. 1853. Figure 9.

Herbs or subshrubs, 0.5–2(–3) m tall, stem erect and usually unbranched, terete, leafy stems 3–15 mm thick, glabrous or with a few large (1 mm) crooked hairs; **stipules** 6–14(–20) mm long, 4–6 mm broad at the base, triangular-ovate, with or without an awn, glabrous, coriaceous, deciduous. **Leaves** with petioles 2–8(–15) cm long, 1.2–3 mm broad, glabrous or with crooked multicellular hairs to 2 mm long; **leaf blades** 15–30(–40) cm long, 8–15(–25) cm broad, broadly elliptic to broadly ovate-elliptic or elliptic-obovate, apex short-acuminate, somewhat rounded to abruptly narrowed at the obtuse to acute base and slightly decurrent on petiole (rarely long-decurrent or sometimes rounded to a truncated base in large leaves), drying stiffly chartaceous, dark brown or dark grayish above, glabrous or with scattered crooked hairs, 2° veins 7–14(–17)/side. **Inflorescences** solitary in leaf axils (2/node), sessile and usually glomerulate, many-flowered, 1–2 cm long and to 6 cm broad (across the node), subglobose to verticillate, reddish, pedicels 0–2.5 mm long. **Flowers** tightly congested, sparsely and minutely puberulent, hypanthium 3 mm long and 1–2 mm

diam., calyx red, calyx lobes 3–6 mm long, 1–1.5 mm broad, obtuse at the tip, with parallel venation; **corolla** salverform, white, tube 2–3.5 mm long, lobes 2–3.5 mm long and 1 mm broad. **Fruit** becoming white and spongy, ca. 5 × 3 mm when dried, oblong.

Understory plants of the wet Caribbean slopes from 700 to 1800 (–2400?) m elevation. Flowering in January–October; fruiting in October–March. The species ranges from the Cordillera de Tilarán eastward to Veraguas, Panama.

Hoffmannia congesta is characterized by its sessile (often verticillate) glomerulate reddish inflorescences, long calyx lobes, white fruit, unbranched stems, large leaves, and prominent stipules. This is one of our most commonly collected and most distinctive species of *Hoffmannia*. In the past it was assigned to its own genus (*Xerococcus*); specimens are often found in the unidentified section of Rubiaceae collections.

***Hoffmannia davidsoniae* Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 22: 53. 1946. (?= *H. lancistigma* Dwyer, Ann. Missouri Bot. Gard. 56: 279. 1969). Figure 7.**

Herbs or slender subshrubs, 0.5–1.7 m tall, stems usually unbranched, leafy stems 1.5–5 mm thick, glabrescent (rarely densely puberulent, cf. *Davidse et al.* 29175 CR); **stipules** 1.5–3 mm long, ca. 1 mm broad at the base, narrowly triangular, caducous. **Leaves** with petioles 1–7 cm long, 0.8–2 mm thick, glabrous; **leaf blades** 8–17 cm long, 3–9 (–12) cm broad, broadly oblong to elliptic-oblong or ovate-oblong (rarely lanceolate), apex narrowed abruptly and short-acuminate, base obtuse to acute and slightly decurrent on petiole, drying grayish to dark brown or dark grayish green above, glabrous above and below or minutely puberulent, 2° veins 10–14/side, sometimes arising from the midvein at nearly 90°, loop-connected distally and forming an arcuate submarginal vein 1–4 mm from the edge. **Inflorescences** borne on lower leafless nodes, 1–2/node, 5–15 cm long, paniculate and with a prominent peduncle 4–6 (–12) cm long and 1–2.3 mm thick, glabrous, with 3 (–4) distal branches and each branch with 7–17 flowers, pedicels 2–4 (–6) mm long. **Flowers** glabrous, hypanthium 2–3 mm long, ca. 1 mm diam. distally, turbinate, calyx lobes 0.3–1 mm long, triangular; **corolla** rotate to funnelliform, yellow or flushed with purple, tube 1–4 mm long, lobes 2–4 (–6) mm long; anthers to 3.8 mm long. **Fruit** ca. 8 mm long and 4 mm diam., ellipsoid to subglobose, becoming red.

Plants of wet cloud forest formations at 700–2300 m elevation. Flowering in January, April, July, and September; fruiting in September and December–January. The species ranges from central Costa Rica eastward to the Chiriquí Highlands.

Hoffmannia davidsoniae is a little-collected species characterized by the long stiff peduncles usually terminated by three branches and the long-petiolate leaves with an arcuate submarginal vein. This species is poorly known in Costa Rica, and there appears to be great variation from collection to collection. The secondary veins often arise at nearly 90° from the midvein, but there are collections in which this is not the case. This species is closely related to *H. liesneriana*.

***Hoffmannia decurrens* Standl., Contr. U.S. Natl. Herb. 20: 205. 1919.**

Slender **shrubs** or subshrubs, 1.5–3 m tall, leafy stems 1.5–4 mm thick, densely puberulent with crooked yellowish brown or reddish brown hairs 0.1–0.3 mm long; **stipules** 1.5–3 mm long, ca. 2 mm broad at the base, triangular, hirsutulous, deciduous. **Leaves** with petioles 5–40 mm long, ca. 1 mm thick, difficult to distinguish from the lamina base, densely hirsutulous with hairs 0.3–0.5 mm long; **leaf blades** 7–21 cm long, 2–7 cm broad, elliptic-obovate to oblanceolate or elliptic, apex acuminate, gradually narrowed to a narrowly cuneate base and long-decurrent on petiole, drying membranaceous or thin-chartaceous and dark greenish brown or grayish green above, glabrous on the upper surface, pubescent on the veins beneath with hairs 0.2–0.7 mm long, 2° veins 7–10/side. **Inflorescences** 1–3/axil, 1–2 (–3) cm long, cymose or fasciculate with few (1–5) flowers or rarely 2-branched and scorpioid with 5–10 flowers, peduncles 5–10 (–24) mm long, 0.2–0.3 mm thick, puberulent, pedicels 2–6 mm long, slender. **Flowers** sparsely to conspicuously pubescent, hypanthium 0.7–1.3 (–2) mm long, 0.6–1 (–1.7) mm diam. distally, turbinate, calyx lobes 0.7–1.5 mm long, triangular; **corolla** yellow or whitish, tube 2–4 mm long, lobes 3–7 mm long, ca. 2 mm wide at the base. **Fruits** becoming 8–9 mm long, 5–6 mm diam. (dried), ovoid to globose, red, borne on slender peduncles and pedicels.

Plants of montane evergreen forest formations, 1100–2000 m elevation. Flowering in April–June and December; fruiting in December–February. This poorly characterized species is endemic to Costa Rica and presently known to range from Monteverde to Sta. Maria de Dota.

Hoffmannia decurrens is recognized by the puberulent young stems, narrowly obovate leaves with cuneate long-decurrent base, and very short inflorescences with very slender peduncle and pedicels. This species is poorly characterized at present, with a diverse array of specimens placed here. This species may include material presently assigned to *H. hamelioides*. The type, *Tonduz 12230* us, bears the same collection number as the type of *H. arborescens*; these types (not seen) probably represent a mixed collection.

Hoffmannia dotae Standl., J. Wash. Acad. Sci. 18: 181. 1928. *H. ramonensis* Standl., loc. cit. 180. 1928. Figure 10.

Single-stemmed **shrubs** or herbaceous subshrubs, (0.5–)1–3(–6?) m tall, leafy stems 2–10 mm thick, glabrous to pilosulous, older stems terete and hollow, woody; **stipules** 3–4 mm long and 4 mm broad at the base, glabrous, deciduous. **Leaves** 2 (rarely 3) at a node, petioles 4–20 mm long (to 5 cm if including the decurrent lamina base), ca. 1.5 mm broad, glabrous; **leaf blades** 15–30(–35) cm long, (4–)7–12 cm broad, elliptic-obovate to obovate-oblong or oblanceolate, apex short-acuminate, tapering gradually or abruptly to the cuneate and long-decurrent base, the narrowed basal part of the lamina to 6 cm long, drying membranaceous to thin-chartaceous, usually dark brown or gray above, glabrous above, pubescent in very early stages beneath and becoming glabrous or with reddish brown hairs 0.1–0.4 mm long along the major veins, 2° veins 9–15/side and often loop-connected near the edge. **Inflorescences** axillary or at older leafless nodes, 1–3/axil (2–6/node), 1.5–3(–5) cm long, ca. 15 mm broad, usually paniculate with 3 primary branches and 4–9 flowers, peduncles 0–5 mm long (to 35 mm when the primary peduncle is reduced and the 1° branches function as peduncles), minutely puberulent, pedicels 3–6 mm long. **Flowers** conspicuously (0.1–0.3 mm) puberulent or glabrous, hypanthium 3–4 mm long, 2–3 mm diam. distally, obconic and reddish, calyx tube ca. 0.5 mm long and rotate, lobes (1–)2–4 mm long, 1–2 mm broad at the base, bluntly triangular to oblong, often held horizontally; **corolla** rotate, usually red or orange at the base and orange or yellowish distally, fleshy and glabrous, buds ca. 10 mm long, tube 2–5 mm long, 2.5–4 mm diam., lobes 4–9 mm long, 2–3 mm broad, yellowish within. **Fruits** 6–8 mm long and 4–6 mm diam. (dried), ca. 8 mm diam. in life, orange or reddish.

Plants of wet montane cloud forest formations, from 850 to 2100 m elevation. Flowering in February–September; fruiting in September–January. It is uncommon in Costa Rica, except for the San Vito area. This species ranges from the Cordillera de Tilarán to the Chiriqui Highlands of Panama.

Hoffmannia dotae is recognized by its larger leaf blades with long-decurrent base forming narrowly winged margins along the sides of the petiole (but not auriculate at the base), the often cauliflorous few-flowered inflorescences, and the short thick corolla tube with larger stiff yellow petals. The flower buds with their short conical corolla tubes and broad (3–4 mm) base distinguish this species from all other Costa Rican species, none of which have such thick corolla tubes. Compare *H. leucocarpa* with more numerous slender flowers and leaves acute to cuneate at the base.

Hoffmannia gesnerioides (Oerst.) Kuntze, Rev. gen. pl. 285. 1891. *Ophryococcus gesnerioides* Oerst.,

Vidensk. Meddel. Dansk. Naturhist. Foren. Kjobenhavn 1852: 53. 1852.

This species ranges from Guatemala to central Nicaragua at elevations of 1000–1500 m. The small stature (to 60 cm), long reddish hairs, and few-flowered cymes on peduncles that elongate to 3 cm in fruit help to distinguish this species, which is not known from Costa Rica.

Hoffmannia hamelioides Standl., J. Wash. Acad. Sci. 15: 8. 1925. Figure 11.

Herbs or shrubs, (0.5–)1.5–3 m tall, stems often branched, leafy stems 1.2–3 mm thick, usually densely covered with crooked reddish brown multicellular hairs 0.3–1 mm long (sometimes glabrescent); **stipules** 2–3 mm long, triangular, drying reddish brown. **Leaves** with petioles 6–25 mm long, 0.7–1.5 mm thick, usually densely puberulent; **leaf blades** 8–23 cm long, 3–8 cm broad, oblanceolate-elliptic to narrowly obovate or elliptic-oblong, apex acuminate, base gradually narrowed and acute or long-cuneate, decurrent on petiole, drying membranaceous to thin-chartaceous, dark brown to blackish brown above, glabrous or pubescent beneath with crooked hairs 0.2–0.7(–1) mm long, 2° veins 7–12/side. **Inflorescences** axillary or at older nodes, solitary (1–2/node), 1–3 cm long, usually on short (1–10 mm) slender peduncles, with 3–7 flowers, pedicels 0.7–1.5 mm long, 0.2–0.4 mm thick, minutely (0.1–0.2 mm) puberulent. **Flowers** with short (0.2–0.7 mm) crooked hairs, buds ca. 8 mm long, hypanthium ca. 2 mm long and 1.5–2 mm diam., calyx lobes 0.7–1.5 mm long, 0.3–0.6 mm broad, narrowly oblong to linear; **corolla** yellowish white or yellow, tube 1.5–2 mm long, 1.5–2 mm diam., lobes 2–4 mm long, 1.5–2 mm broad, apex acute, becoming reflexed. **Fruits** 4–8 mm long, 3–6 mm diam. (dried) reddish at maturity, with persisting calyx lobes.

Plants of evergreen forests in the central highlands, from 450 to 2200 m elevation. Flowering in February and May–July; fruiting in July and December. This species is known only from the Central Volcanic highlands and the Cordillera de Talamanca in Costa Rica.

Hoffmannia hamelioides is recognized by the usually puberulent young stems, narrowly oblanceolate leaves gradually tapering to the long-attenuate base on slender petioles, small inflorescences with filamentous peduncles and pedicels, and short corolla tubes. Compare this species with *H. decurrens* (perhaps synonymous) and *H. valerii* with cuneate to truncated leaf bases and lower elevation habitat. Glabrous individuals resemble a number of species, especially *H. longepetiolata*.

Hoffmannia hammelii C. M. Taylor, sp. nov.

Species *Hoffmanniae laxae* similis, sed ab ea stipulis brevioribus (0.7–1.5 mm longis) ac cymis secundis differt; etiam *H. pallidiflorae* similis, sed foliis basi acutis ac lobulis corollinis brevioribus (3–4 mm longis) differt.

TYPE—*Liesner 2907* (holotypus CR, isotypus MO), from near Sirena, Corocovado National Park, 0–200 m alt., 5 July 1977, Puntarenas, Costa Rica.

Herbaceous **subshrubs**, 0.3–0.5(–1) m tall, stems branched only near the ground, leafy stems 1.3–3 mm thick, glabrous and terete, often drying dark; **stipules** 0.7–1.5 mm long, ca. 1 mm broad at the base, glabrous, deciduous. **Leaves** with petioles 6–27 mm long, 0.7–1.4 mm broad, glabrous; **leaf blades** (4–)7–18 cm long, (1.5–)4–7 cm broad, elliptic to elliptic-obovate or elliptic-oblong, apex acuminate, base acute (not decurrent), drying stiffly chartaceous, grayish above, usually paler or yellowish beneath, glabrous above and below, 2° veins 7–13/side. **Inflorescences** solitary and axillary to leaves (1–2/node), 2–7 cm long but the flowering portion only 1–2 cm long, with a single rachis or cymose with a terminal flower and 2 lateral branches with 5–12 flowers each, peduncles 15–50 mm long, rachis with 2–7(–11) flowers along 1 side, glabrous, pedicels 2–6 mm long. **Flowers** with ovary/hypanthium 2 mm long and 1.5 mm diam., calyx tube 0.5 mm long, calyx lobes 0.5–0.8 mm long, ca. 1 mm broad at the base, triangular; **corolla** rotate, white to yellow-green, tube 2–3 mm long, lobes 3–4 mm long. **Fruits** ca. 5 mm diam., ellipsoid to subglobose, red, glabrous.

Plants of the evergreen Pacific lowlands, from near sea level to 200 m elevation. Flowering in July–September and November; fruiting in January. This species is endemic to the Golfo Dulce area and the Osa Peninsula.

Hoffmannia hammelii is recognized by its small stature, leaves tapering equally to apex and base, small flower groups on long slender peduncles, leaves often drying grayish or reddish brown, and restricted geographic range. This species appears to be part of a species group including *H. laxa*, *H. pallidiflora*, *H. bullata*, and *H. discolor* (Lemaire) Hemsl. of Mexico. The species is named in honor of Barry Hammel, who has made many important contributions to our knowledge of Costa Rica's Rubiaceae. Other collections seen were *M. Chavarría et al. 254* CR, *Kernan 813 & 1249* CR, MO, and *Knapp 2184* CR, MO.

Hoffmannia inamoena Standl., J. Wash. Acad. Sci. 18: 179. 1928. *H. fimbriantha* Dwyer, Ann. Missouri Bot. Gard. 56: 277. 1969. Figure 11.

Herbaceous **subshrubs**, 1–2 m tall, with few branches, leafy stems 2.5–5 mm thick, sparsely to densely minutely (0.1–0.2 mm) puberulent in early stages but soon gla-

brous and drying grayish, quadrangular; **stipules** 2–3 mm long. **Leaves** with petioles 10–60 mm long, 0.8–2 mm thick, minutely and sparsely puberulent or glabrous; **leaf blades** 8–22 cm long, 3.5–10 cm broad, elliptic-oblong to oblong or obovate, apex acuminate with tip 3–15 mm long, base obtuse to acute and usually slightly decurrent on petiole, drying membranaceous or thin-chartaceous and grayish green above, glabrous above, very minutely (0.05 mm) puberulent on the veins beneath or glabrous, 2° veins 9–14/side and loop-connected near the margin. **Inflorescences** axillary or on older leafless nodes (1–2/node), ca. 1 cm long and 1–5 flowers, glomerulate, sessile or with peduncles 1–3 mm long, pedicels 1–3 mm long, pubescent with hairs 0.1–0.4 mm long or glabrous. **Flowers** with crooked reddish hairs to 0.3 mm long (rarely glabrous), hypanthium ca. 2 mm long and 1.7 mm diam. distally, urceolate, calyx lobes 1.3–2.3 mm long, narrowly oblong to narrowly triangular, apex obtuse; **corolla** rotate, deep red, puberulent, tube ca. 1.5 mm long, lobes ca. 4 mm long. **Fruits** 5–7 mm long, subglobose, becoming white, puberulent.

Plants of evergreen forest formations from 400 to 1000 m elevation. Flowering in January and May–July; fruiting in June and November–December. The species ranges from Bijagua, Alajuela, eastward along the Caribbean slope to Río Reventazon, and in the General Valley of the Pacific slope.

Hoffmannia inamoena is recognized by the minute puberulence on many parts, secondary veins clearly loop-connected near the margin of the leaf, very small sessile inflorescences, and relatively large narrow calyx lobes. The material placed here is rather poor and may not represent a single species. Holm and Iltis (58 F) noted that both flowers and fruit fall easily from the stems.

Hoffmannia laxa Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 22: 116. 1940. Figure 11.

Herbaceous **subshrubs** or slender shrublets 1–2 m tall, branched only near the base, leafy stems 1–6 mm thick, glabrous; **stipules** 1–3 mm long, triangular, glabrous, deciduous. **Leaves** with petioles 1.5–6(–9) cm long, 0.8–2.2 mm broad, glabrous; **leaf blades** 7–18(–21) cm long, 4–9.5(–11) cm broad, elliptic to elliptic-ovate or ovate, apex acuminate, tapering gradually or abruptly to the cuneate or acute base and slightly decurrent on petiole, drying thin-chartaceous, grayish green to dark brownish green above, glabrous above and below, 2° veins 7–11/side. **Inflorescences** 1–3 in each leaf axil (2–6/node), 3–8 cm long, ca. 2 cm broad, pendant, open panicle or racemose with few (8–15) distant flowers, reddish in life, peduncles 10–45 mm long, 0.2–0.8 mm thick, glabrous, rachis often elongate with alternate flowers and minute (0.5 mm) bracteoles, pedicels 4–9 mm long (to 16 mm in fruit), 0.2–0.3 mm thick (dried). **Flowers** glabrous, hypanthium ca. 2 mm long and 1.8 mm diam., subglobose, calyx lobes 0.2–0.7 mm long, triangular; **corolla**

funneliform, white to pale green, tube 1–2(–3) mm long, lobes 3–5 mm long and 1 mm broad at the base; anthers ca. 2 mm long. **Fruits** to 8 mm long, 4–5 mm diam., globose to ellipsoid, greenish white when immature, whitish purple or red to bluish black or purple-black at maturity, with a small persisting calyx tube; **seeds** black.

Plants of evergreen lower montane forest formation on both the Caribbean and Pacific slopes, 200–1600 m elevation. Flowering in February–June and August–October; fruiting in January and March–October. This species is known only from Monteverde eastward to the slopes of Volcán Poas and in western Panama.

Hoffmannia laxa is recognized by the often long-petiolate somewhat larger leaves, the lack of pubescence, the open few-flowered inflorescences with long thin filamentous (when dried) peduncles and pedicels, and the small flowers with very short corolla tubes. The name *H. capillacea* Dwyer has been applied incorrectly to material of this species.

Hoffmannia leucocarpa Standl., J. Wash. Acad. Sci. 15: 9. 1925. *H. carpinterae* Standl., N. Amer. Fl. 32: 199. 1934, nom. nov. for *H. macrophylla* Standl., J. Wash. Acad. Sci. 15: 9. 1925, non *H. macrophylla* Hemsl. (?= *H. trichocalyx* Standl., J. Wash. Acad. Sci. 18: 181. 1928.) Figure 10.

Slender **shrubs** or small treelets, 1–2.5(–4) m tall, with few or no lateral branches, leafy stems 2.5–8 mm thick, glabrous (rarely ferruginous-villous), usually hollow; **stipules** 1.5–4 mm long, 2–4 mm broad at the base, triangular, glabrous, deciduous. **Leaves** with petioles 1.5–7(–10) cm long, 1.3–3.8 mm broad, glabrous; **leaf blades** 14–24(–35) cm long, 5–12(–15) cm broad, elliptic to broadly elliptic, apex tapering abruptly and acuminate, tapering more gradually to the cuneate base and slightly decurrent on petiole, drying chartaceous to stiffly chartaceous, pale greenish brown to dark grayish green above, glabrous above and below, 2° veins 11–14/side. **Inflorescences** 1–3/axil below the leaves (2–6/node), 4–8(–15) cm long, with 1 or 2 orders of branching (rarely with a single rachis), often pendant, peduncles 2–5(–8) cm long, 0.5–2 mm thick, usually terminated by 3 subequal 1° branches, glabrous or less often minutely puberulent, pedicels 2–8(–10) mm long, sparsely to densely puberulent or villose. **Flowers** with hypanthium ca. 2 mm long and 1.5 mm diam., obconic, puberulent with thin hairs ca. 0.2 mm long, calyx green to pink, orange or red, calyx tube 1–2 mm long, lobes 0.5–2 mm long, bluntly triangular; **corolla** rotate to funneliform, pale pink to yellow marked with orange or red, glabrous to villousulose, tube 4–8 mm long, 1.5–2 mm diam., lobes (2–)3–7 mm long, 2 mm broad at the base; anthers ca. 4 mm long. **Fruits** 8–10 mm long and 7–8 mm diam., globose to obovoid (ca. 1 cm diam. in life), often bisulcate in development, white to pink or red.

Plants of the wet Caribbean cloud forests and nearby areas, from 1000 to 2300 m elevation. Flowering in February–July; fruiting in February, April, June–July, and October–December. The species ranges from the eastern part of the Cordillera de Tilarán (Monteverde) to the western slopes of Volcán Irazu in central Costa Rica (but see below).

Hoffmannia leucocarpa is recognized by the larger firm-textured leaves on long petioles, pedunculate and branched (usually pendant) inflorescences, and the larger flowers with corolla tubes and lobes usually equal in length. The fruit can be white or pink to red. This species differs from larger-leaved specimens of *H. longepetiolata* by the more rigid leaf blades with short-acuminate apices, larger inflorescences, and larger corollas. This species may intergrade with *H. arborescens*, forming a complex that includes *H. pittieri*. Dried specimens can be similar to *H. dotae*, but that species has smaller inflorescences and much broader and more succulent corolla tubes and the leaves have winged petioles. Most material placed here has branched inflorescences, but a few have monopodial circinnate inflorescences; this is another example of the great variability within *Hoffmannia* species and why determining species in the genus is so difficult.

The preceding circumscription excludes a number of specimens from the San Vito area formerly placed here. These are treated as unusual elements of *H. pittieri* or *H. arborescens*. *Hoffmannia trichocalyx* probably represents an unusually pubescent representative of this species; it is based on *Standley & Torres* 47690 (holotype), 47480, 47819, & 47924, all us.

Hoffmannia liesneriana L. O. Williams, Fieldiana Bot. 36: 54. 1973. Figure 8.

Herbs or slender subshrubs, 0.3–1(–1.5) m tall, stems usually unbranched, quadrangular with opposing flat and sulcate surfaces, leafy stems 4–12 mm thick, glabrous (strigillose); **stipules** 1–3 mm long, 3 mm broad at the base, triangular, glabrous. **Leaves** with petioles (2–)6–13 cm long, 1.5–3 mm thick, glabrous; **leaf blades** (11–)13–24 cm long, (6–)7–13 cm broad, broadly ovate-elliptic to broadly elliptic-oblong, apex abruptly narrowed and short acuminate, abruptly narrowed to an obtuse or rounded base, drying chartaceous, dark grayish or grayish brown above, glabrous above, sparsely to densely minutely (0.1–0.2 mm) puberulent on the veins beneath, 2° veins (7–)10–14(–17)/side, usually loop-connected near the margin. **Inflorescences** borne at older leafless nodes or near the ground, 1–4/node, 2–11 cm long, with many flowers in 1–several dense clusters or on helicoid branch-

es but rarely expanded, reddish to reddish purple, peduncles 4–50 mm long, glabrous or sparsely puberulent, pedicels 0–4 mm long, slender. **Flowers** subglabrous or puberulent with hairs ca. 0.2 mm long, reddish, hypanthium 3–4 mm long, 2–2.6 mm diam., calyx lobes 2–5 mm long, ca. 0.4 mm broad; **corolla** salverform, rose or pinkish red to red-brown, tube 1–3 mm long, lobes 3–7 mm long, ca. 1.3 mm broad; anthers ca. 4 mm long, white. **Fruits** 4–6 mm long, 2–3 mm diam. (dried), red; **seeds** ca. 0.2 mm long.

Plants of lowland rain forest formations on the Caribbean slope, 50–600(–1100) m elevation. Flowering in March and May–November; fruiting in the same months and in January. This species apparently ranges from Río San Lorenzo, Alajuela, eastward to Guapiles, Limón, in Costa Rica.

Hoffmannia liesneriana is recognized by the large leaves with long petioles, the short unbranched stems, flowers in close clusters on cauliflorous inflorescences, long calyx lobes, and lower-elevation habitat. Unlike so many of our other *Hoffmannia* species, this species has leaves that are often abruptly narrowed at the base (but some collections do have long-decurrent leaf blades). This species resembles *Psychotria capacifolia* with white flowers. Compare *H. davidsoniae* and *H. eliasii* Dwyer of Panama.

Hoffmannia longipetiolata Polak., *Linnaea* 41: 567. 1877. *H. tonduzii* Standl., *Contr. U.S. Natl. Herb.* 20: 205. 1919. *H. woodsonii* Standl., *Ann. Missouri Bot. Gard.* 28: 471. 1941. Figure 11.

Small **shrubs** or herbaceous subshrubs, 1–2 m tall, usually few-branched and slender-stemmed, leafy stems 0.8–5 mm thick, glabrous or minutely puberulent along narrow longitudinal ridges or with crooked hairs 0.5 mm long in early stages; **stipules** 0.7–3 mm long, 2–3 mm broad at the base, triangular, glabrous, deciduous. **Leaves** with petioles 3–15(–40) mm long, 0.5–1 mm broad, glabrous or puberulent; **leaf blades** 4–12(–15) cm long, 1.5–4(–6) cm broad, elliptic-obovate to elliptic or ovate-elliptic, apex short- to long-acuminate, tip to 15 mm long, base acute to cuneate and somewhat decurrent, drying membranaceous to thin-chartaceous, brownish green to grayish green above, glabrous above, glabrous or minutely puberulent on the veins beneath, 2° veins 4–7(–9)/side. **Inflorescences** 1–3/axil (2–6/node), 1–2 cm long, cymes or fascicles with (1–)3–6(–12) flowers, peduncles 2–5 mm long, pedicels 2–8(–10) mm long, ca. 0.3 mm thick, glabrous or rarely sparsely and minutely (0.1 mm) puberulent. **Flowers** greenish yellow, glabrous, hypanthium 1.5–2 mm long, 1.3 mm diam. distally, obconic, calyx lobes 0.5–1(–2) mm long, ca. 1 mm broad at the base, triangular and acute; **corolla** rostrate, yellow, pink or cream white, tube 1.5–3 mm long, 1.3–1.5 mm diam., lobes 2–4 mm long, 1.5–2 mm broad at the base, reflexed; anthers 3–3.5 mm long. **Fruits** 5–6 mm diam., subglobose, red to pink.

Plants of wet evergreen forest formations on both the Caribbean and Pacific slopes, 600–1800(–2000) m elevation. Flowering in January–October, with the majority in May–July; fruiting in April and September–February. The species ranges from the Cordillera de Guanacaste eastward to central Panama.

Hoffmannia longipetiolata is recognized by the smaller or medium-sized leaves that taper gradually to apex and base, little or no pubescence, terete stems, very small few-flowered inflorescences, and small glabrous yellow flowers. The thin peduncles and pedicels, short corolla tubes, and larger corolla lobes are also helpful in recognizing this species. This is one of the most commonly collected species of *Hoffmannia* in Costa Rica. Originally it was thought that the smaller-leaved specimens determined as *H. tonduzii* were distinct, but there are too many intermediate collections to be able to segregate the larger-leaved specimens (some of which have long petioles). Collections from lower (600–900 m) elevations and from western Panama often have larger leaves than collections from central highland Costa Rica. Two species that are very similar to *H. longipetiolata* are *H. decurrens* (with densely puberulent young stems) and *H. psychotriifolia* (with larger fasciculate flowers and narrowly ellipsoid fruits).

Hoffmannia nesiota J. D. Smith, *Bot. Gaz.* 61: 374. 1916.

Shrublets, branchlets subterete, glabrous; **stipules** not seen. **Leaves** with petioles 7–8 cm long, 2–3 mm thick, pubescent; mature **leaf blades** 18–26 cm long, 10–13 cm broad, elliptic to broadly elliptic-oblong, acuminate, base obtuse and slightly decurrent, stiffly chartaceous and pubescent or glabrescent, 2° veins 12–16/side. **Inflorescences** cymose with peduncles 1–5 cm long, pubescent or glabrescent, lacking bracts and bracteoles, pedicels 6–10 mm, slender. **Flowers** 15–16 mm long, with calyx lobes 1.5–2 mm long, triangular; **corolla** 11 mm long, rotate, puberulent, tube 5–6 mm long, lobes 5–6 mm long, linear; **ovary** trilocular, style 12 mm long. **Fruits** ca. 1 cm diam.; **seeds** ellipsoid ca. 0.5 mm long.

A poorly known species endemic to Cocos Island. The species is only known from the type collection: *Pittier 12387* us, collected at Wafer Bay, June 1898, and *Barclay 2178* us, April 1838. The Barclay collection is much more pubescent than the type but appears to represent the same species. Fruits of the Barclay collection are two-locular, not three-locular as described for the type.

Hoffmannia nicotianifolia (Mart. & Gal.) L. O.

Williams is a species of Mexico and northern Central America; the name has been incorrectly applied to Costa Rican collections.

Hoffmannia pallidiflora Standl., J. Wash. Acad. Sci. 15: 9. 1925. *H. rexmontis* Dwyer, Ann. Missouri Bot. Gard. 67: 241. 1980. Figure 11.

Herbs or subshrubs, 0.5–1.5 m tall, erect or leaning on others, usually unbranched, leafy stems 2–6 mm thick, glabrous, apparently succulent in life and distorted on drying; **stipules** 2–3 mm long, 2 mm broad at the base, glabrous, caducous. **Leaves** with petioles (1.2–)2–6 cm long, 0.8–1.8 mm broad, petioles of the same node often unequal in length, glabrous; **leaf blades** 10–25 cm long, 4–10 cm broad, broadly elliptic to elliptic-oblong or elliptic-obovate, apex acuminate with a narrowed tip 5–15 mm long, tapering gradually to a cuneate base (or abruptly obtuse) and decurrent on petiole, drying membranaceous, dark yellowish green or grayish green, glabrous above and below, 2° veins 8–11/side. **Inflorescences** solitary and axillary to basal leaves or cauliflorous (2/node), 3–8 cm long, with a single unbranched rachis or with 2 lateral helicoid branches 1–3 cm long, peduncles 15–35 mm long, 0.3–1 mm thick, flowers 3–30, pedicels 0–3 (–6) mm long, ca. 0.5 mm thick. **Flowers** glabrous, hypanthium 2–3 mm long and 1 mm diam. at apex, narrowly obconic, calyx lobes 1–2 mm long, triangular to ligulate, acute; **corolla** funnelform, white or pale yellowish green, tube 2–4 mm long, ca. 1.3 mm diam., lobes 4.5–8 mm long, 0.8–1.7 broad. **Fruits** white becoming red or dark reddish purple, 4–6 mm diam. (to 1 cm in life), globose or ellipsoid-oblong during development.

Plants of the wet cloud forests along the Caribbean escarpment, (400–)700–1400 m elevation. Flowering in January–June; fruit in February–June, August, and November–December. Collections have been made from Bijagua, Alajuela, south-eastward to the upper Río Grande de Orosí, Cartago, and in western Panama.

Hoffmannia pallidiflora is recognized by the glabrous, slender, usually simple unbranched or two-branched pedunculate inflorescences, very thin leaves usually decurrent at the base and often long-petiolate, narrowly obconic hypanthium, and restriction to the middle elevations of the Caribbean slope. The thin foliage dries yellowish to very dark green. The slender unbranched inflorescences have flowers along only one side and usually dry yellowish.

Hoffmannia piratarum Standl., J. Wash. Acad. Sci. 18: 180. 1928.

Shrublets, branchlets obtusely tetragonal, glabrous;

stipules caducous. **Leaves** with petioles 25–45 mm long; **leaf blades** 10–20 cm long, 5–6 cm broad, elliptic-lanceolate, long-acuminate, the tip often falcate, drying membranaceous, dark green and glabrous above, sparsely short villous and glabrescent beneath, with 8–9 2° veins on each side. **Inflorescences** in leaf axils, 1–3/node, to 3 cm long, peduncles 1–2.5 cm long, short villous, pedicels 2–5 mm long. **Flowers** puberulent proximally, hypanthium 3 mm long, calyx lobes 2–3 mm long, triangular or rounded; **corolla** glabrous, tube ca. 4 mm long, 2 mm diam. at base and 5 mm at apex, corolla lobes ca. 6 mm long. **Fruits** ca. 6 mm long.

Plants of Wafer Bay, Cocos Island. Flowering in January. Standley knew it only from the type collection *Pittier 16259* us, and the preceding description is based on his description.

Hoffmannia pittieri Standl., Contr. U.S. Natl. Herb. 18: 140. 1916. *H. panamensis* Standl., Contr. U.S. Natl. Herb. 20: 204. 1919.

Shrubs or subshrubs, 1.5–3(–4) m tall, usually with unbranched main stems, leafy stems 2–9 mm thick, becoming woody and 12 mm thick, glabrous or densely pubescent on the young stems; **stipules** ca. 1.5 mm long, ca. 2.5 mm broad at the base, broadly triangular, glabrous. **Leaves** with petioles 1.5–7 cm long, 1.5–5 mm broad, glabrous or rarely puberulent in early stages, with narrow lateral margins continuous with the lamina margins; **leaf blades** 12–26(–35) cm long, 4–12(–16) cm broad, elliptic-obovate to elliptic-oblong or oblanceolate, apex acuminate with tip 8–18 mm long, gradually narrowed to the cuneate base and long-decurrent on the petiole, drying chartaceous and dark brown or dark grayish green above, glabrous above and below (rarely puberulent in early stages), 2° veins 9–14/side and weakly loop-connected near the margin. **Inflorescences** 1–5/axil from thickened reduced peduncles, 2–5(–9) cm long, with (5–)10–15 flowers, peduncles 4–40 mm long, with 1° branches 3–30 mm long (often 2-branched with alternate flowers along 1 side), glabrous to densely reddish puberulent, pedicels to 9 mm long. **Flowers** glabrous to reddish puberulent, hypanthium 2–3 mm long, 1.5–2 mm diam., oblong-obconic, calyx orange-red, calyx lobes 0.5–1 mm long; **corolla** yellowish tipped with red or orange, tube 3–6 mm long, 0.7–1.6 mm thick, lobes 3–5 mm long, 1.7 mm broad at the base. **Fruits** ca. 5 mm diam., deep green becoming deep red.

Plants of evergreen montane forest formations, 1100–1700(–2200) m elevation. Flowering in February–August; fruiting in January–February and August. The species (as here interpreted, see below) ranges from the San Vito de Coto Brus area into the adjacent Chiriquí Highlands of Panama.

Hoffmannia pittieri is recognized by the taller, more woody stems, larger leaves with cuneate long-decurrent leaf bases, inflorescences with slender-pedicellate flowers, short corolla lobes, and re-

stricted latitudinal range. The inflorescences vary from short to moderately long with few to many branches. The interpretation presented here assumes that the very similar *H. leucocarpa* does not range eastward of Volcán Irazú. There is probably intergradation with *H. arborescens* (which usually has larger more branched inflorescences), and it may be necessary to place all this material under a more broadly defined *H. arborescens*.

Hoffmannia psychotriifolia (Benth. in Oerst.) Gri-seb., Fl. Brit. W. Ind. 321. 1861. *Higginsia psychotriaefolia* Benth. in Oerst., Vidensk. Meddel. Dansk. Naturhist. Foren. Kjobenhavn 1852: 50. 1853. Figure 11.

Slender **shrubs** or herbaceous subshrubs, 1–2.5(–4) m tall, with few lateral branches, leafy stems 0.8–4.5 mm thick, glabrous, terete; **stipules** 1–1.5 mm long or reduced to a ridge, 1–2 mm broad at the base, triangular, glabrous. **Leaves** with petioles 8–35(–50) mm long, 0.7–1.5 mm thick, glabrous; **leaf blades** 5–14(–20) cm long, 1.5–4.5(–6) cm broad, narrowly elliptic to oblanceolate or narrowly elliptic-obovate, apex acuminate with tip 1–2 cm long, gradually narrowed to the acute or cuneate and decurrent base, drying membranaceous to thin-chartaceous, dark green or dark grayish brown above, distinctly paler beneath, glabrous above and below, 2° veins 5–9/side. **Inflorescences** usually fasciculate from a thickened solitary short-shoot (brachyblasts) in the leaf axils, with 5–30 flowers per node, peduncles rarely present or 0–3(–8) mm long, pedicels 2–8 mm long, ca. 0.3 mm thick, glabrous or minutely puberulent. **Flowers** glabrous, to 18 mm long, hypanthium 2–3 mm long, 0.7–1.7 mm diam. distally, oblong-obconic, with longitudinal ridges, calyx lobes 0.6–2(–3) mm long, triangular to ligulate; **corolla** funnelform, pale yellow to white or pink, tube 4–9 mm long, 1–3 mm diam., lobes 3–6 mm long, 1.4–2 mm broad at the base. **Fruits** 6–12 mm long, 5–8 mm diam., oblong-ellipsoid, becoming red and translucent.

Plants of evergreen montane forest formations, (900–)1100–2100(–2400) m elevation. Flowering in January–July and September–November; fruiting in February–September and November. The species ranges from southern Mexico and Guatemala to Panama and occurs in the West Indies.

Hoffmannia psychotriifolia is recognized by the thin-glabrous leaves tapering gradually to both apex and base, stems rounded and slender, small, usually fasciculate inflorescences, slender pedicels, larger flowers with well-developed calyx lobes, longer ridged ovary, and oblong fruit. This species may be difficult to separate from *H. longipetiolata* (including *H. tonduzii*), but that species has smaller flowers, few-flowered, often pedunculate inflorescences, and young stems that may have puberulent longitudinal ridges.

Hoffmannia refulgens (Hooker) Hemsley was based on cultivated material thought to have been collected in South America but most probably from northern Central America or southern Mexico (D. Lorence, pers. comm.). This name has been used for Costa Rican collections now placed under *H. bullata*.

Hoffmannia subauriculata Standl., J. Wash. Acad. Sci. 18: 179. 1928. *H. haydenii* Dwyer, Ann. Missouri Bot. Gard. 56: 277. 1969. Figure 8.

Herbaceous **subshrubs**, 1–2 m tall few-branched, leafy stems 1.5–5(–7) mm thick, subglabrous; **stipules** 2–3 mm long. **Leaves** subsessile with poorly defined petioles because of the long-attenuate lamina base and winged lateral margins 2–4 mm broad (short petioles 1–3 mm long sometimes present below the auricles); **leaf blades** 8–25(–40?) cm long, 3–10(–13) cm broad, obovate to oblanceolate or broadly elliptic, apex short-acuminate, tapering very gradually to the cuneate or long-attenuate base (5–7 × 1 cm) and usually slightly auriculate near the stem, drying dark, glabrous above, subglabrous or minutely puberulent on the veins below, 2° veins 9–13/side. **Inflorescences** 2–4 on lower leafless nodes, 3–9 cm long, usually with few or no lateral branches (cymose to cincinnoid), with ca. 6–12 flowers, peduncles 2–4 cm long, glabrous or with reddish curved hairs to 0.2 mm long, pedicels 2–6(–12) mm long. **Flowers** with minute curved hairs or glabrous, with calyx lobes ca. 1.5 mm long, triangular; **corolla** not seen at anthesis. **Fruits** ca. 8 × 6 mm, ellipsoid, bright red.

Plants of wet evergreen forests in the central mountains and on the Caribbean slope, from 100 to 1800 m elevation. Flowering in June–July and November; fruiting in December–January. The species ranges from near Monteverde to central Panama.

Hoffmannia subauriculata is distinguished by the long-decurrent leaves with broad (ca. 5 mm) lateral margins (along what would otherwise be a petiole) and their slight auriculate expansion near the base. The inflorescences appear to develop only at leafless nodes. This species is similar to *H. amplexifolia*, which has three leaves per node.

Hoffmannia valerii Standl., J. Wash. Acad. Sci. 18: 178. 1928. Figure 9.

Weak-stemmed **shrubs** or subshrubs, 0.5–1.5(–3?) m tall, usually without lateral branches, leafy stems 1–4 mm thick, with thin crooked multicellular hairs 0.3–1.5 mm long; **stipules** 1–4 mm long, rounded distally or with an awn, caducous. **Leaves** with petioles 8–60 mm long, 0.8–1.6 mm thick, villous with hairs 0.3–1 mm long; **leaf blades** 4–14(–19) cm long, 1.8–7(–9) cm broad,

broadly elliptic to narrowly elliptic-oblong or ovate-elliptic, apex acuminate, base obtuse to acute and somewhat decurrent on petiole, drying membranaceous to thin-chartaceous, dark brown or grayish green above, glabrous or with few scattered hairs above, with more numerous crooked hairs 0.3–1.5 mm long beneath, 2° veins 6–10/side. **Inflorescences** axillary or at leafless nodes, 2–4/node, 1–2(–3) cm long, fasciculate or contracted cymes with 3–9 flowers, peduncles 1–4 mm long, pedicels 2–8(–12) mm long, filiform, villous or subglabrous. **Flowers** puberulent with crooked hairs that dry reddish, hypanthium 2–3 mm long, 1.5–2 mm diam. distally, calyx lobes 1–3(–4) mm long, narrowly triangular; **corolla** rotate, pale yellow, tube 1–3 mm long, lobes 3–5(–7) mm long; anthers 2–3 mm long. **Fruits** 4–6 mm long, 4–5 mm diam., ellipsoid, becoming orange or bright red.

Plants of the wet evergreen Caribbean slope and lowlands, often along streams and in wet areas, 50–950 m elevation. Flowering in February–August and November; fruiting in January, July, and November. The species ranges from near Arenal, Alajuela, to western Panama.

Hoffmannia valerii is recognized by the long hairs on many younger parts, slender unbranched stems, small short-pedunculate or fasciculate inflorescences, short corolla tubes, and lower-elevation habitats. The type (*Valerio 57* US) was collected at 600 m elevation near Arenal, Guanacaste Province. This species resembles *H. gesnerioides* (Oerst.) Kuntze of Nicaragua at 800–1500 m elevation, but that species has longer (2–4 cm) peduncles, attenuate leaf bases, and dense spreading villose pubescence on all parts. Costa Rican material identified as *H. boraginoides* Dwyer ined. appear to be plants of *H. valerii* that have unusually long (2.5–3 mm) calyx lobes. The excellent DUKE collections from La Selva display considerable variation in sepal lobe length, and it seems best to consider these plants all part of *H. valerii*.

Hoffmannia vesiculifera Standl., Publ. Field Columb. Mus., Bot. Ser. 4: 285. 1929. *H. kirkbridei* Dwyer, Ann. Missouri Bot. Gard. 56: 278. 1969. *H. morii* Dwyer, loc. cit. 67: 236. 1980. Figure 8.

Herbs or subshrubs, 0.3–1.5 m tall, main stems usually unbranched, leafy stems 2.5–10 mm thick, usually densely villous with multicellular crooked reddish brown hairs to 1.5(–3) mm long; **stipules** to 2–5 mm long, little developed and difficult to see among the pubescence, caducous. **Leaves** with petioles 14–45 mm long, with a lateral longitudinal inflated chamber (vesicle or pouch) 12–20 mm long and 4–9 mm broad on each side (2/ petiole), with conspicuous reddish brown hairs; **leaf blades** 12–27(–40) cm long, 7–15(–20) cm broad, elliptic to elliptic-obovate (less often obovate-oblong or oblanceolate), apex acuminate to short-acuminate, base obtuse to

cuneate and decurrent (to the inflated vesicles), drying thin-chartaceous, dark brown or grayish above, paler grayish or reddish brown beneath, with few scattered crooked multicellular hairs above and below, more densely hirsutulous on the midveins above and below, the crooked reddish hairs 0.4–1.3(–3) mm long, 2° veins 8–17/side. **Inflorescences** axillary or terminal on short lateral axillary shoots and subtended by leaf-like bracts ca. 2 cm long, solitary (2/node), sessile or with peduncles (= lateral branches?) to 3 cm long, flowers 10–many, in dense sessile capitulae or on condensed helicoid cymes (with the inflorescences occasionally expanding to 7 cm and becoming branched in fruit, as in the type: *Cooper 231* F), pedicels to 4 mm long. **Flowers** yellowish but drying reddish brown, with conspicuous hairs 1–2 mm long, hypanthium ca. 2.5 mm long, and 1.5 mm diam., calyx lobes 2.5–7 mm long, linear, with few to many reddish hairs; **corolla** rotate, glabrous, cream yellow to reddish, tube 2–4(–8) mm long, corolla lobes 4–17 mm long, to 3 mm broad at the base, lanceolate; anthers 3.5–4 mm long. **Fruits** 4–6 mm long, 3–5 mm diam., becoming bright red or white, thin-walled with longitudinal ribs, often with long (1 mm) crooked hairs.

Plants of wet evergreen forests of the Caribbean slope and lowlands, (20–)300–1500 m elevation. (Note: All Costa Rican collections came from above 300 m elevation.) Flowering in February–June and September; fruiting in April and October–February. The species ranges from central Costa Rica to central Panama.

Hoffmannia vesiculifera is our most distinctive species of *Hoffmannia*. The unusual inflated structures of the petiole are found in no other Costa Rican species of Rubiaceae and resemble those found on some Melastomaceae. The long crooked multicellular hairs, condensed inflorescences, and long-linear calyx lobes are additional distinctions. The variation in leaf size and form and inflorescences (dense heads to helicoid cymes or, rarely, branching infructescences) is considerable but does not warrant segregation of species or subspecies. The inflorescences may all be borne on lateral axillary branches that are variously reduced, as evidenced by the paired leaf-like bracts subtending the inflorescences. Only one of our collections, *Lent 911* F, cited small ants in the petiole chambers.

Holtonia Standley

Holtonia Standley is now considered part of *Elaeagia*.

Isertia Schreber

REFERENCE—B. Boom, A revision of the genus

Isertia (Isertieae: Rubiaceae). Brittonia 36: 425–454. 1984.

Shrubs or trees, branchlets slender and subterete or thick and quadrangular, glabrous or puberulent; **stipules** interpetiolar or intrapetiolar, sometimes deeply divided and apparently 2/node, persisting. **Leaves** opposite, petiolate, often large; **leaf blades** drying thin-chartaceous to coriaceous, venation pinnate, domatia absent. **Inflorescences** terminal and solitary, paniculate-thyriform or racemose-thyriform, often large, the secondary branches terminating in dichasia or scorpioid cymes, flowers sessile or pedicellate. **Flowers** bisexual, radially symmetrical, hypanthium ovoid to subglobose, calyx lobes 4–6, small, equal or unequal, persisting; **corolla** tubular-funnelform to salverform, corolla tube short or elongate, villous in the throat, corolla lobes 4–6(7), short and spreading, valvate or imbricate in bud; **stamens** 4–7, filaments inserted near the mouth of the tube, anthers dorsifixed, loculate with the interior of the thecae divided into small chambers, included or exerted; **ovary** 2–6(–7)-

locular, ovules numerous on axile placentas, style linear, stigma with 2–6(7) oblong lobes. **Fruits** berry-like with fleshy exocarp and 2–6 pyrenes, each pyrene (nutlet) with a bony endocarp and 2–many seeds, globose; **seeds** minute, angular, brownish, the testa deeply foveolate.

A genus of 14 species, ranging from Central America through northern South America and occurring naturally only in western Cuba and Guadeloupe in the Caribbean. Boom has divided the genus into two sections: section *Cassupa* with 2–3(–4) locules and stigmas and fleshy fruit and section *Isertia* with (4)–5–7 locules and stigmas and hard fruit. Our two species represent both sections of the genus. The large leaves, large many-branched solitary terminal inflorescences, flowers with long narrow corolla tubes, and loculate anthers distinguish this genus.

Key to the Species of *Isertia*

- 1a. Leaf blades usually dull greenish or grayish beneath, usually acute at the base and decurrent on the petiole; corolla yellow to orange or red, corolla tubes to 28 mm long; fruit oblate, ca. 7 mm diam. *I. haenkeana*
- 1b. Leaf blades usually whitish gray beneath, subtruncate to obtuse at the base and not conspicuously decurrent on the petiole; corolla white, corolla tubes to 55 mm long; fruit ellipsoid, ca. 10 mm diam. *I. laevis*

Isertia haenkeana DC., Prodr. 4: 437. 1830. *I. deamii* Bartlett, Proc. Amer. Acad. Sci. 33: 59. 1907. *I. deamii* var. *stenophylla* J. D. Smith, Bot. Gaz. 61: 374. 1916. Figure 50.

Shrubs or small trees, 2–6(–20) m tall, branches thick and often slightly narrower at the node, leafy branchlets 3–10 mm thick, quadrangular with rounded edges, becoming terete, densely puberulent with short (0.2–0.6 mm) grayish hairs; **stipules** 4/node (or interpreted as 2 with 2 almost separate lobes), 7–14(–45) mm long, 2–8 mm broad at base, narrowly triangular with long-acute apex, glabrous abaxially or sericeous along the midvein (strigulose), drying dark. **Leaves** often smaller beneath the inflorescence, petioles 5–50 mm long, 1.8–4 mm thick, with adaxial margins continuous with the lamina margins, densely puberulent; **leaf blades** (7–)14–45(–64) cm long, (4)–7–16(–28) cm broad, elliptic to elliptic-oblong or elliptic-obovate, apex short- or long-acuminate, base gradually narrowed and acute to attenuate, decurrent on petiole, drying chartaceous, dark brown above, glabrous and often lustrous above, with thin erect or appressed whitish hairs 0.2–0.5 mm long on the veins beneath, 2° veins 14–22/side and loop-connected near the margin. **Inflorescences** 8–22 cm long, 6–12 cm broad, peduncle a thick extension of the stem, to 5 cm long, with a thick central rachis and many lateral branches, strigulose, the lateral branches (dichasia) with a short (1–2 cm) reddish orange peduncle and a terminal flower at the dichotomy

of 2 longer scorpioid branches with 4–9 flowers, the secondary branches subtended by narrow bracts 3–11 mm long, pedicles 0–2 mm long, bracteoles 1–2 mm long. **Flowers** with hypanthium and calyx tube 2–3 mm long and equally broad, cupulate, subentire with 4 minute lobes, sparsely strigulose externally; **corolla** bright yellow turning orange or reddish, tube 17–25(–28) mm long, ca. 1.5 mm diam. at base and 2–3 mm distally, lobes 5–6, 5–7 mm long, with prominent dense yellowish hairs ca. 2 mm long on the inner face basally; **stamens** 5 or 6, filaments and anthers 3.5–6 mm long; **ovary** 4–6(–7) locular. **Fruits** berry-like, 4–5 mm long and 6–8 mm diam., oblate, smooth and strigulose, usually with 5 or 6 cartilaginous lobes and 5–6 multiseeded pyrenes; **seeds** 0.6–0.9 mm long.

Plants of evergreen lowland wet forest formations, from near sea level to 600 m elevation in southern Central America. Probably flowering throughout the year; in central Panama flowering is primarily in the early rainy season (May–July), with fruit maturing in the late wet season and early dry season (Croat, 1978). This species ranges from Mexico to Panama, Columbia, and Venezuela and is found in westernmost Cuba.

Isertia haenkeana is recognized by its large opposite leaves with many secondary veins and de-

current lamina base, four persisting stipules at each node, cupular calyx with minute lobes, narrow yellow to red corolla tubes, short corolla lobes with bearded hairs within, and rounded berry-like fruit with hardened pyrenes within. This species resembles *Palicourea guianensis*.

Isertia laevis (Triana) B. M. Boom, Brittonia 36: 433. 1984. *Cassupa laevis* Triana, Ann. Sci. Nat. Paris, Sér. IV 9: 44. 1858. *C. panamensis* Standl., Contr. U.S. Natl. Herb. 18: 135. 1916. *I. panamensis* (Standl.) Standl., Publ. Field Columb. Mus., Bot. Ser. 8: 346. 1931. Figure 30.

Small trees to 10(–15) m tall, often with several trunks ca. 10 cm diam., leafy branchlets 4–12 mm thick, quadrangular with rounded edges, densely appressed-puberulent or strigulose with short (ca. 0.3 mm) yellowish or brownish hairs; **stipules** apparently 4/node but united at the base (for 1–2 mm) and leaving a scar around the stem above the leaf bases, 6–12 (20–40) mm long, 3–6 mm broad, triangular-subulate, coriaceous, glabrous or sparsely puberulent on the abaxial surface. **Leaves** opposite, petioles 1.6–7.5(–12) cm long, 2–5 mm thick, minutely (0.1–0.2 mm) puberulent; **leaf blades** smaller beneath the inflorescences, 15–60 cm long, 7–22 cm broad, oblong to ovate-oblong or elliptic-oblong, apex acuminate or acute apex, tip to 2 cm long, base obtuse to rounded and truncate (rarely slightly decurrent on petiole), drying chartaceous to subcoriaceous, usually dark brown above, glabrous or subglabrous above and with the minor venation often impressed, minutely puberulent on the veins beneath, whitish canescent between the veins and the major and minor venation clearly outlined, 2° veins 15–22/side and loop-connected near the margin, proximal 2° veins arising at 90° to the midvein, 3° veins subparallel. **Inflorescences** (7–)14–35 cm long, (4–)6–15 cm broad, ovoid to ellipsoid in outline and with many short (4 cm) lateral branches, peduncle 2–6 cm long, to 6 mm thick, lateral branches usually a 5-flowered dichasium (the distal branches with 2 flowers on the upper side), with short (1–3.5 cm) secondary peduncles, sparsely and minutely puberulent, flowers sessile or short (2–4 mm) pedicellate, bracteoles 1–3 mm long, broadly ovate. **Flowers** sweet smelling and apparently opening in the evening, hypanthium and calyx tube 5–7 mm long, 3–5 mm diam., an elongate cup glabrous externally, the calyx lobes minute and 3–6 or obscure; **corolla** salverform, white, tube 32–55 mm long, 2–5 mm diam., sparsely and minutely puberulent externally, corolla lobes 6–7, 10–14 mm long, with long (1 mm) yellowish hairs inside near the mouth; **stamens** 6–7, filaments ca. 3 mm long and laminar, anthers 7–9 mm long, included; **ovary** 2–3-locular, style 32–55 mm long, stigma with 2 oblong lobes 3–5 mm long. **Fruits** berries to 12 mm long, 8–11 mm diam., ellipsoid to subglobose, smooth and usually glabrous, becoming black; **seeds** 0.7–1 mm long.

Trees of open secondary vegetation in evergreen rain forest formations in both the Caribbean and southern Pacific lowlands, from near sea level to

about 800 m elevation in Costa Rica. Probably flowering throughout the year but with flowers and fruit collected mostly in May–September. This species ranges from Costa Rica and Panama along the Andes to Bolivia and in the adjacent Amazon Basin.

Isertia laevis is recognized by its large opposite leaves with whitish surfaces beneath, four persisting stipules at each node, solitary terminal inflorescences with long-tubed white flowers, subentire calyx tube, and subglobose berries. Panamanian material of this species was called *Isertia hypoleuca* by Croat (1978) and Dwyer (1980), but *I. hypoleuca* Benthham is a different species occurring in Venezuela, the Guianas, and the Amazon basin.

***Ixora* Linnaeus**

Shrubs or small trees, branchlets terete or angular, mostly glabrous; **stipules** interpetiolar (also slightly united above the petioles to form a very short intrapetiolar ridge), simple, usually broad at the base and acuminate, persisting. **Leaves** opposite and decussate or in whorls of 3, sessile or petiolate, laminae often coriaceous, venation pinnate, domatia absent. **Inflorescences** terminal or less often axillary, cymose, thyrsoid or paniculate, branching often trichotomous, often with a rounded or flattened top (corymbose), flowers pedicellate and subtended by 2 bracteoles. **Flowers** bisexual and monomorphic, hypanthium ovoid, calyx tube short, calyx lobes 4 (5), short or extended, **corolla** salverform, white to pinkish, red, scarlet, or yellow, corolla tube narrow, glabrous or puberulent at the throat, corolla lobes 4 (5–8), linear-lanceolate to ovate, imbricate or convolute in bud and rotate at anthesis; **stamens** 4 (5–8), inserted in the throat or mouth of the tube, filaments short or none, anthers oblong to linear, dorsifixed, exserted or partly exserted; **ovary** 2-locular with 1 ovule in each locule, peltately attached to the middle of the septum, style filiform, stigmas 2. **Fruits** baccate, red becoming black, the pericarp fleshy or leathery, with 1–2 pyrenes; **seeds** concave-convex or plano-convex to subglobose.

A pantropical genus of ca. 400 species with the largest number of species in Africa and the Indo-Pacific area. The colorful inflorescences, narrow corolla tubes, stamens borne near the apex of the corolla tube, and two-seeded fruit help to characterize the genus. The flowers are protandrous in a distinctive manner: pollen is transferred from the clustered anthers into a concave area of the stigmatic head; elongation of the stigma disperses the pollen. Later, the stigma lobes open to expose their receptive surfaces for pollination. Four species are known to occur in Central America; two are native and two are widely cultivated as ornamentals.

Key to the Species of *Ixora*

- 1a. Flowers closely crowded together in capitate inflorescences; corolla tubes 25–45 mm long; plants cultivated for ornament 2
- 1b. Flowers crowded in distal cymose groups in an open paniculate inflorescence; corolla tubes 3–8 mm long; native wild species 3
 - 2a. Flowers red or orange; leaves sessile or subsessile *I. coccinea*
 - 2b. Flowers white; leaves petiolate *I. finlaysoniana*
- 3a. Fruits ca. 10 mm diam.; flowers sessile in small glomerules, peduncles 0.7–3 mm thick; leaf blades 12–26 cm long *I. floribunda*
- 3b. Fruits ca. 4 mm diam.; flowers in panicles and pedicellate, peduncles 0.3–1 mm thick; leaf blades 7–16 cm long *I. nicaraguensis*

***Ixora coccinea* L., Sp. Pl. 110. 1753. Figure 31.**

Shrubs 0.5–3(–5) m tall, much branched, leafy branchlets 1–4 mm thick, glabrous, terete; **stipules** 0.5–1.5 mm long at the broad base and with a narrow tip 2–14 mm long, glabrous. **Leaves** opposite, sessile or subsessile with petioles to 2 mm long; **leaf blades** (2–)3–10(–16) cm long, (1–)1.5–4.5(–6) cm broad, oblong to elliptic-oblong, ovate-oblong or oblong-obovate, apex rounded to obtuse or acute and often with minute (0.5–1 mm) slender tip, base rounded and subtruncate or subcordate to obtuse, drying stiffly chartaceous or subcoriaceous, glabrous above and below. **Inflorescences** terminal, to 10 cm long, flowers closely clustered (subcapitate), peduncles 1–3 cm long, flowers usually sessile at the apex of short-stipitate triads (cymes). **Flowers** with hypanthium 1–1.5 mm long, turbinate, calyx lobes 4, ca. 1 mm long; **corolla** red or orange-red, tube 25–45 mm long, only 0.5–1 mm diam., glabrous or subglabrous, corolla lobes 4, 10–15 mm long, 4–8 mm broad; **stamens** 4, anthers exserted and soon deciduous; style usually exserted. **Fruits** 8–15 mm diam. (rarely developed in cultivars).

Ixora coccinea is a widely cultivated species throughout Central America, from near sea level to about 1500 m elevation. The rounded clusters of brilliant reddish flowers with long slender tubes and the evergreen leaves make it an attractive ornamental. The species originated in India and is now grown throughout the tropics and subtropics. Several varieties and forms have been recognized; see F. R. Fosberg and H.-H. Sachet, Three cultivated *Ixoras*. *Baileya* 23: 74–85. 1989. This species is called *cruz de Malta*, *flor de fuego*, *jazmín*, *jazmín rojo*, and *jazmín de coral*.

***Ixora finlaysoniana* Wallich ex G. Don, Gen. hist. 3: 572. 1834. Figure 31.**

Shrubs or small trees to 5 m tall, leafy branchlets 2–6 mm thick, glabrous, becoming terete with age; **stipules** 2–7 mm long, triangular and acuminate or broad with 1 or 2 awns. **Leaves** opposite, petioles 4–20 mm long,

1–2 mm thick, glabrous; **leaf blades** 6–18 cm long, 2–6.5 cm broad, narrowly oblong to narrowly oblong-obovate, apex bluntly obtuse or rounded (acute), base gradually narrowed and obtuse or acute, drying subcoriaceous, glabrous above and below. **Inflorescences** terminal, 5–10 cm long, to 10 cm broad and rounded, of densely congested cymose branches forming a capitate cluster, peduncles 0–3 cm long. **Flowers** glabrous, hypanthium 1–2 mm long, calyx lobes 3–4 mm long 1.5–2 mm broad, petaloid in texture; **corolla** white, tube 20–30 mm long, 0.3–1 mm diam., lobes 4–6(–8) mm long, 1–2(–3) mm wide; **stamens** 5, exserted, anthers narrow; stigma ca. 2.2 mm long, slender and narrowly 2-lobed.

Ixora finlaysoniana is widely cultivated in the tropics and planted at lower (0–1000 m) elevations in Central America. The rounded inflorescences of many white flowers with long slender tubes, the lack of pubescence, the foliaceous sepal lobes, and the short-petiolate coriaceous oblong leaves characterize this species. Native of southeast Asia; this species is referred to as *corona de la reina* and *mono de reina*.

***Ixora floribunda* (A. Rich.) Griseb., Cat. Pl. Cub. 134. 1866. *Siderodendron floribundum* A. Rich. in Sagra, Hist. Cuba 11: 24. 1850. Figure 43.**

Small trees to 15 m tall, short-shoots frequently present, leafy branchlets 2.2–6 mm thick, smooth and glabrous, terete; **stipules** 4–10 mm long, united above the leaf bases to form a short (1–4 mm) sheath, triangular-subulate and often shifted to the side above the petiole (not strictly interpetiolar), glabrous abaxially. **Leaves** opposite, petioles 10–25 mm long, 1.5–2.5 mm thick, glabrous; **leaf blades** 12–26 cm long, 4–10 cm broad, oblong to elliptic-oblong, or obovate, apex obtuse to short-acuminate, base obtuse to attenuate and decurrent on petiole, drying stiff-chartaceous to subcoriaceous, concolorous, glabrous above and below, 2° veins 6–10/side, not loop-connected distally. **Inflorescences** terminal, 1–3, 5–12 cm long, panicles with 2–3 pairs of opposite branches, primary peduncles 1–3 cm long, secondary peduncles equally long and densely puberulent with short (0.2–0.3

mm) grayish hairs, flowers sessile and 3–12 in distal cymose clusters. **Flowers** with hypanthium ca. 1.5 mm long and 1.2 mm diam., turbinate, covered with short (0.2 mm) thin erect whitish hairs (and with some smaller glandular hairs); calyx tube 0.5–1 mm long, calyx lobes minute; **corolla** white, tube ca. 4 mm long, 0.3–0.6 mm diam. in proximal half, glabrous externally, white-villous within, lobes 4, 3–4 mm long, ca. 1.5 mm wide, glabrous; filaments 0.6–1.5 mm long, anthers ca. 3.3 mm long, ca. 1.5 mm broad; stigma lobes ca. 1.5 mm long and unequal. **Fruits** 6–10 mm long, subglobose, sessile, sparsely puberulent, drying red and smooth, persistent calyx tube 0.4–0.7 mm high and ca. 1.2 mm broad.

Trees of both lowland rain forest formations and seasonally deciduous formations, from 10 to 800 m elevation in Central America. Flowering in January–February; fruiting in March–May in Central America. This species, apparently uncommon in Central America, ranges from Honduras and El Salvador to Colombia and some of the West Indies.

Ixora floribunda is recognized by its stiff-glabrous elliptic-oblong leaves, terminal inflorescences of white salverform flowers, puberulent calyx, and sessile red berries. Our collections come from the area between Cañas and Bagaces and Monte Aguacate on the seasonally deciduous Pacific slope of central Costa Rica. The species has also been collected in the Caribbean rain forest formations of Honduras and Nicaragua. It has been called *palo de María*.

Ixora nicaraguensis Wernham, J. Bot. 50: 243. 1912. *I. rauwolfioides* Standl., Trop. Woods 11: 25. 1927. Figure 43.

Shrubs or small trees to 10 m tall, often with many branches, leafy branchlets 1.5–3 mm thick, glabrous, terete, grayish; **stipules** 3–6(–8) mm long, 2–3 mm broad at the base, broadly triangular and acuminate to cuspidate with a short awn to 3 mm long. **Leaves** opposite, petioles 3–9 mm long, 0.7–2 mm broad, glabrous, with lateral (or adaxial) ridges; **leaf blades** 6–13(–16) cm long, 2–5(–7) cm broad, elliptic-oblong, oblong or ovate-oblong, apex abruptly narrowed and acute or short-acuminate, base obtuse to somewhat attenuate and slightly decurrent on petiole, drying chartaceous, glabrous on both surfaces, 2° veins 6–12/side, often obscure and weakly loop-connected distally. **Inflorescences** 1–3 and terminal, 3–9 cm long and equally broad, open pyramidal panicles with 2–3 pairs of opposite branches, peduncles 1–25 mm long, 0.3–1 mm thick, minutely (0.1–0.2 mm) puberulent, flowers on slender pedicels 0–10 mm long in distal triads, distal bracts ca. 0.5 mm long. **Flowers** with hypanthium and calyx tube 1–1.7 mm long, minutely puberulent or glabrous, calyx lobes obsolete or minute (0.1–0.5 mm); **corolla** white, glabrous externally, tube 3–6 mm long, ca. 1 mm diam., lobes 4, 3–4 mm

long, 1–2 mm broad, oblong and rounded distally; filaments 0.5–1 mm long, anthers 2–3 mm long, 0.3 mm thick; stigma ca. 1.5 mm long, exserted. **Fruits** 5–6 mm long, 4–5 mm diam., subglobose to ovoid, glabrous and red; pyrcnes 5 mm long.

Plants of evergreen rain forest formations on both the Caribbean and southern Pacific slope of Costa Rica, from near sea level to 300 m elevation. Flowering in February–March and June–October; fruiting in March and July–November. This species ranges from Belize to eastern Panama.

Ixora nicaraguensis is recognized by its small white flowers on open thin-branched inflorescences, slender corolla tubes, and small globose two-seeded fruit, borne on thin-branched infructescences. This species may be mistaken for a *Psychotria*, but the corolla lobes are valvate in bud in *Psychotria* (and related genera).

Ladenbergia Klotzsch

Small to large trees, the bark with bitter substances; **stipules** usually large, interpetiolar or also united distally (intrapetiolar) and forming a ring around the stem above the leaf bases after falling, triangular to obovate, with colleters at the adaxial base, caducous. **Leaves** opposite (occasionally whorled), petiolate, often subcoriaceous, pinnately veined, some species with domatia. **Inflorescences** terminal, panicate with opposite branching or cymose, ebracteolate. **Flowers** bisexual, monomorphic, medium to large, fragrant, hypanthium turbinate to cylindrical, calyx tube cupular, calyx lobes short or long; **corolla** funnelform or salverform, sericeous externally, corolla lobes 5–6, valvate in bud, minutely papillose within and on the margins; **stamens** 5–6, filaments very short, inserted near the center of the tube, anthers linear, dorsifixed, included; **ovary** 2-locular, placentas elongate, spongy and borne on the septum, ovules numerous in each locule and vertically imbricate, style slender, stigmatic lobes 2. **Fruits** elongated capsules, cylindrical or flattened, with septicidal dehiscence (but the septum very thin and dehiscence often appearing to be loculicidal), splitting from the top into 2 woody or coriaceous valves; **seeds** numerous, longitudinally imbricate and peltate, flattened and elongate, body oblong and surrounded with a thin flattened dentate or laciniate wing.

A genus of about 30 species ranging from Costa Rica to Bolivia; most of the species are Andean. The genus is similar to *Cinchona* and *Condaminia*. The large salverform and sericeous flowers with long valvate corolla lobes, large stiff usually broad leaves, large broad stipules, and 2-valved capsules with winged seeds help to characterize the genus.

Paul Standley's original separation of Costa Ri-

can material into three species appears to represent three valid morphological entities that are not sympatric, and intermediate collections are not

apparent. Nevertheless, the species are very similar, and they might prove to be three subspecies of a single species.

Key to the Species of *Ladenbergia*

- 1a. Tufts of stiff hairs (0.5–1 mm long) usually present at the base of the petiole in young leaves; leaf blades often acute at the base [corolla tubes 10–23 mm long, corolla lobes 11–17 mm long]; (1200–)1500–2100 m elevation *L. valerii*
- 1b. Base of the petiole glabrous or with minute (0.2 mm) appressed hairs; leaf blades rarely acute at the base; 0–1500 m elevation 2
- 2a. Corolla tubes 15–20 mm long, corolla lobes 8–12 mm long; fruit 2–5.5 cm long; central highlands 1000–1400 m elevation *L. brenesii*
- 2b. Corolla tubes 25–50 mm long, corolla lobes 16–20 mm long; fruit 6–9 cm long; evergreen lowlands, 0–1000 m elevation *L. sericophylla*

Ladenbergia brenesii Standl., Pub. Field Mus. Nat. Hist., Bot. Ser. 18: 1323. 1938. Figure 29.

Trees, 5–25 m tall, leafy branchlets 4–12 mm thick, glabrous or sparsely puberulent at the nodes with short (0.1–0.3 mm) hairs, quadrangular, becoming terete and pale grayish; **stipules** 16–35 mm long, 4–16 mm broad, ovate to obovate, obtuse to acute at the apex, glabrous or with few slender ascending hairs ca. 0.5 mm long. **Leaves** with petioles 10–35 mm long, 1.8–3.5 mm thick, glabrous and drying dark; **leaf blades** 12–25 cm long, 5–13 cm broad, broadly elliptic to elliptic-oblong or elliptic-obovate, apex abruptly narrowed and obtuse or bluntly acute, base obtuse or slightly rounded, drying subcoriaceous, glabrous above, glabrous or with a few scattered hairs below, 2° veins (6–)7–10/side. **Inflorescences** 6–18 cm long, pyramidal, peduncles 2–7 cm long, glabrous, with opposite branches and bracts to 5 mm long, pedicels 0–3 mm long. **Flowers** with hypanthium 3–6 mm long, 2.5–5 mm diam., clavate-tubular, densely sericeous with yellowish brown ascending hairs, calyx tube ca. 1 mm long, calyx lobes 1–2(–4) mm long, ca. 2 mm broad, broadly rounded, glabrous or sparsely puberulent distally and with a minutely ciliate edge; **corolla** white, tube 15–20 mm long, 5–6 mm diam., densely sericeous, lobes 8–12 mm long, 2–3.5 mm broad. **Fruits** (2–)3–6 cm long, 5–10 mm broad (to 16 mm when fully flattened), subterete and narrowly oblong before dehiscent, valves puberulent externally and lustrous within; **seeds** 12–15 mm long, 3–4 mm broad, surrounded by a thin translucent erose wing, body of the seed 3–4 mm long and ca. 2 mm broad.

Trees of wet evergreen cloud forest formations of the central highlands, 1000–1400 m elevation. Flowering in March–July; fruiting in July–November. The species is endemic and ranges from the Cordillera de Tilarán to the western parts of the Cordillera de Talamanca.

Ladenbergia brenesii is recognized by its cloud forest habitat, large puberulent flowers, long nar-

row capsules splitting into valves that become flat, and broad glabrous leaves. Compare this species to *L. valerii* with which it can easily be confused. Also known as *aquijilla* and *quina*.

Ladenbergia sericophylla Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 1324. 1938. Figure 29.

Trees, 8–35 m tall, trunks to 60 cm. dbh, leafy internodes 5–12 mm thick, young stems quadrangular and drying dark, quickly becoming pale gray and terete; **stipules** 15–45 mm long, 10–22 mm broad, oblong or obovate-oblong, rounded at the apex, minutely puberulent with thin appressed-ascending hairs 0.1–0.3 mm long. **Leaves** opposite, petioles 15–45(–60) mm long, 2–3.5 mm thick, glabrous and drying very dark, reddish in life; **leaf blades** 14–24(–30) cm long, 8–16(–18) cm broad, very broadly elliptic to broadly elliptic-oblong or slightly obovate, apex abruptly narrowed and rounded or bluntly obtuse, base abruptly narrowed and obtuse or slightly attenuate, decurrent, drying stiffly chartaceous to subcoriaceous, usually dark brown above, glabrous above, minutely (0.1–0.3 mm) appressed-puberulent on the veins beneath and with larger (1 mm) hairs in the vein axils (domatia), 2° veins 5–8/side. **Inflorescences** 10–20 cm long, to 18 cm broad, pyramidal, peduncles 1–5 cm long, 4–8 mm thick, glabrous or minutely appressed-puberulent, lateral branches opposite and subtended by bracts 3–6 mm long, bracteoles subtending the flowers 1–2 mm long, rounded apically, pedicels 1–6 mm long. **Flowers** with hypanthium 5–7 mm long, 2–3 mm diam., tubular, densely sericeous with ascending yellowish hairs, calyx tube 2–4 mm long, cupulate, sparsely puberulent or glabrous, calyx lobes 2–3 mm long, 2.5–3 mm broad, rounded at the apex, glabrous and drying dark; **corolla** white or yellowish white, tube 25–50 mm long, 3–5 mm diam., densely sericeous, lobes 16–30 mm long, ca. 4 mm wide and narrowly oblong to lanceolate. **Fruits** 6–11 cm long, 10–14 mm broad, oblong-cylindrical and rounded-rectangular in cross-section, straight or curved (falcate), mi-

nutely appressed-puberulent, persisting calyx 3–6 mm long and 6–8 mm broad, narrowed at the base to form a pedicel 5–15 mm long; **seeds** 11–20 mm long, 4–5 mm broad with thin wing, body of the seed ca. 3×1.5 mm.

Tall trees of evergreen rain forest formations of the Caribbean lowlands and on the southern Pacific slope, 20–1000 m elevation. Flowering in January–February, July, and September; fruiting in January–May. This species is only known from La Selva, the western parts of the General Valley, the mountains bordering the Pacific near Cañas Gordas, and the Osa Peninsula. While endemic to Costa Rica, it may also occur in westernmost Panama.

Ladenbergia sericophylla is characterized by its large broad leaves with appressed hairs on the veins beneath, large broad stipules, long salverform sericeous corollas, and large capsular fruit. The taller height of these trees may explain why our collections of this species are so few.

***Ladenbergia valerii* Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 1324. 1938. Figure 29.**

Small trees, 3–20 m tall, leafy branchlets 2–10 mm thick, quadrangular or terete in early stages, essentially glabrous but with stiff retrorse or erect hairs ca. 0.5 mm long at the base of the petiole attachment; **stipules** 8–16 mm long, 5–8 mm broad, broadly elliptic or ovate, apex rounded, sparsely puberulent with appressed hairs or glabrous and with a few hairs at the base and along the midrib abaxially. **Leaves** opposite, petioles 6–25 mm long, 1.5–2.5 mm thick, glabrous or very sparsely appressed-puberulent (except for tufts of longer hairs below the base), drying dark; **leaf blades** 6–17(–28) cm long, 3–8(–13) cm broad, broadly elliptic to elliptic-obovate or narrowly elliptic, apex abruptly narrowed and short-acuminate or bluntly acute, base obtuse to acute, drying stiffly chartaceous to subcoriaceous, glabrous or with a few thin hairs above, with thin straight hairs 0.3–0.7 mm long on the major veins beneath, 2° veins 5–9/side. **Inflorescences** 7–20 cm long, pyramidal with opposite branching, peduncles 2–7 cm long, sparsely puberulent or glabrous, bracts ca. 3 mm long, distal flowers in triads and subtended by bracteoles 0.5–1 mm long, pedicels 0–3 mm long and merging with the hypanthium. **Flowers** with hypanthium and calyx tube 5–8 mm long, 2–3 mm diam., densely appressed yellowish sericeous, calyx lobes 3–6 mm long, 2.5–3.5 mm broad at the base, broadly rounded to obtuse distally and becoming reflexed, glabrous; **corolla** white or white with longitudinal pink stripes, salverform, tube 10–23 mm long, 1.5–4.5 mm diam., densely sericeous with ascending hairs, lobes 5, (11–)12–17 mm long, 2.5–4.5 mm broad, lanceolate to narrowly oblong, papillate-puberulent within, becoming recurved. **Fruits** 3–8(–11) cm long, 8–14 mm broad; **seeds** 10–14 mm long, 2–4 mm wide, body of the seed 3 mm long and 1.5 mm wide.

Trees of montane cloud forest formations from

(1200–)1600 to 2100 m elevation. Flowering in January–September and November; fruiting in May–August. The species ranges from the Cordillera de Tilarán to the Cordillera de Talamanca (as far east as 83°04'W) and will probably be found in nearby Panama.

Ladenbergia valerii is recognized by its higher-elevation habitat, unusual tufts of stiff short hairs beneath the petioles on otherwise glabrous or glabrescent stems, sericeous corolla with relatively long corolla lobes, and capsular fruit. This species is very closely related to *L. brenesii* of similar forests at somewhat lower elevations.

Lasianthus Jack

Herbaceous **subshrubs** (in Central America), shrubs or rarely small trees, glabrous or pubescent; **stipules** interpetiolar, broadly triangular to lanceolate, persisting or deciduous. **Leaves** opposite and decussate, petiolate, usually acuminate at the apex, pinnately veined and often with many arching secondary veins, without domatia. **Inflorescences** axillary, mostly sessile fascicles or cymose glomerules, (sometimes pedunculate and simple or branched), flowers sessile or subsessile, bracts small. **Flowers** bisexual (rarely unisexual and monoecious), radially symmetrical, mostly small, sometimes heterostylous, hypanthium urceolate to ovoid or subglobose, calyx lobes 3–6, acute or rounded, persisting; **corolla** salverform to funnelform, white, corolla tube densely hairy in the throat, corolla lobes 4–6, spreading or erect; **stamens** 4–6, filaments very short and borne in the throat, corolla lobes 4–6, anthers dorsifixed near the base, included or slightly exerted; **ovary** 4–12-locular, ovules solitary in each locule, erect from the base of the locule or septum, style short or long, stigmas 4–10, linear or lobed. **Fruits** usually succulent, blue to purple, black, or red, with 4–12 pyrenes, the pyrenes 1-sceded and 3-angled with flat sides, the dorsal side grooved, keeled or winged; **seeds** narrowly oblong.

A genus of about 150 species, of southeastern Asia, Malaysia, tropical Australia, and Africa. Two species are found in the West Indies, and one species in our area and South America. Our species with eight-locular ovary and style with eight stigmas is unique among Central American Rubiaceae. Our species was originally described as a new genus, *Dressleriopsis* Dwyer.

***Lasianthus panamensis* (Dwyer) Robbrecht, Ann. Missouri Bot. Gard. 69: 427. 1982. *Dressleriopsis panamensis* Dwyer, Ann. Missouri Bot. Gard. 67: 154. 1980. Figure 7.**

Herbaceous rhizomatous **subshrubs** to 0.6(–1) m tall, leafy stems 2–6 mm thick, hirsute with slender erect hairs

to 2 mm long; **stipules** 4–7 mm long, 3–6 mm broad at the base, broadly triangular and hirsute along the midrib. **Leaves** with petioles 3–9 cm long, 1.5–2.5 mm thick, hirsute; **leaf blades** 10–19 cm long, 5–9 cm broad, oblong to elliptic-oblong, apex narrowed abruptly and short-acuminate, tip 0–8 mm long, base obtuse and rounded to subcordate-auriculate, often unequal at the petiole, drying thin-chartaceous, dark grayish brown, with scattered thin straight or crooked hairs 0.5–2 mm long on upper and lower surfaces, 2° veins 9–14/side and loop-connected near the margin to form an arcuate submarginal vein, often with a shorter (parallel) minor 2° vein between the major. **Inflorescences** axillary, dense fascicles of sessile flowers 1–2 cm broad, glomerulate or verticillate, bracts ca. 2 mm long and difficult to see among the long hairs. **Flowers** monomorphic, with hypanthium ca. 2 mm long, subglobose, hirsute, calyx lobes 4, 3–4 mm long, 2–3 mm broad, with hairs to 1 mm long; **corolla** white, tube 3–4 mm long, lobes 5 (4, 6), 1.5–4 mm long, oblong; **stamens** 5 (4, 6), anthers ca. 1 mm long; **ovary** with 8 locules, style to 5 mm long, stigmas 8, oblong and radiate. **Fruits** berry-like, to 11 mm diam., globose, purple-black, pyrenes 8 or fewer, 3 mm long, with an oblique scar on the concave side.

Plants of wet evergreen forest formations on the Caribbean slope (at ca. 100 m elevation) and in the central highlands of Panama (to 1000 m elevation). Flowering and fruiting in July. This species is known from the La Selva area, Heredia, and in Panama and Colombia.

Lasianthus panamensis is recognized by its slender hirsute stems to 1 m tall, long-petiolate oblong leaves with many secondary veins forming an arcuate submarginal vein, sessile fasciculate inflorescences, and fleshy berries with up to eight pyrenes. No other Central American species of Rubiaceae has ovaries with eight locules. Superficially, these plants resemble some species of *Hoffmannia* and a few species of *Psychotria* with axillary inflorescences.

Lindenia Benth

REFERENCE—S. Darwin, The genus *Lindenia* (Rubiaceae). J. Arnold Arbor. 57: 426–449. 1976.

Small shrubs growing along rivers and streams, branchlets terete, glabrous or puberulent; **stipules** interpetiolar, borne above the petiole bases, short, usually persisting. **Leaves** opposite short-petiolate; **leaf blades** narrow, often drying dark, chartaceous, pinnately veined, domatia absent. **Inflorescences** terminal, short and few-flowered, flowers often in triads or solitary, bracts and bracteoles present, pedicels short. **Flowers** bisexual, radially symmetrical, large and showy, hypanthium elongate-turbinate, with 5 longitudinal ribs or angles, calyx with 5 elongate lobes, lobes equal or unequal, persisting in fruit; **corolla** narrowly salverform with a narrow elon-

gate tube, glabrous within, corolla lobes 5, convolute in bud and spreading at anthesis; **stamens** 5, sessile on the mouth of the tube, linear and exserted; **ovary** 2-locular, ovules very many, vertical, placentas longitudinally adnate to the septum, style slender and bifid. **Fruits** woody capsules, clavate to pyriform or obovoid, with persisting calyx lobes distally, 2-locular, splitting septicidally into 2 valves from the top; **seeds** numerous, angulate/rhomboidal.

A genus of three species, with the other two species endemic in the western Pacific islands of Fiji and New Caledonia, respectively. The stream-side habitat, narrow leaves on thick stems, few terminal flowers, and very long corolla tubes make this genus quite distinctive.

Lindenia rivalis Benth., Pl. Hartw. 84. 1841. Figure 15.

Small shrubs, 0.4–1.2(–2) m tall, leafy branchlets 1.5–6 mm thick, glabrous or minutely puberulent with thin ascending hairs ca. 0.2 mm long, older stems drying black; **stipules** 3–5(–10) mm long, 1.5–4 mm broad, the broad basal portion 2–3 mm high and with a narrow awn to 2(–5) mm long, glabrous, thin and brown. **Leaves** clustered near the ends of branchlets, petioles 2–10(–16) mm long, 0.4–1.5(–2) mm broad, little differentiated from the leaf base; **leaf blades** 3–12(–17) cm long, 0.8–3(–4) cm broad, oblanceolate to very narrowly elliptic-oblong or narrowly elliptic, apex tapering gradually and acute, sometimes with a short (0.5–1 mm) spine-like tip, base tapering gradually and acute, decurrent on petiole, drying chartaceous to coriaceous, the margin often revolute, glabrous above, glabrous or puberulent beneath with thin erect hairs 0.2–0.3 mm long, 2° veins 6–8/side, not loop-connected. **Inflorescences** of solitary flowers or short (2–10 mm) pedunculate triads (or clusters of up to 7 flowers), bracts difficult to see among the distal leaves 4–9 mm long, pedicels to 10 mm long, poorly differentiated from the flower base. **Flowers** nocturnal, hypanthium 5–9 mm long, 2–3.5 mm diam., puberulent, calyx tube minute, calyx lobes 10–17(–22) mm long, 0.7–2(–2.8) mm broad, narrowly oblong and acute, green; **corolla** white or white tinged with pink, tube 10–17 cm long, 2–3.5 mm diam., puberulent externally with hairs 0.2–0.5 mm long, lobes 15–27(–35) mm long, 5–14(–16) mm broad, narrowly to broadly elliptic, acute at the apex; **stamens** sessile, anthers ca. 10 mm long, 1–1.4 mm broad; style slender equalling or slightly exceeding the tube, stigmatic area ca. 10 m long. **Fruits** to 4 cm long, body of the fruit 15–25 mm long, 9–14 mm broad, with long persisting calyx lobes before dehiscence, broadly obovoid or pyriform, the woody valves twisting; **seeds** 1.5–2 mm long.

Small woody shrubs of stream sides and often growing on rocks next to the water, in deciduous forest areas of Guanacaste Province, 0–700 m elevation (to 1300 m in Honduras). Flowering in February–October in southern Central America (primarily April–July); probably fruiting through-

out the year (mostly August–March). The species ranges from northeastern Mexico and along the Pacific slope of Central America to central Panama.

Lindenia rivalis is recognized by its small stiff narrow leaves on thick dark branches, short stature and riverside habitat in seasonally deciduous areas, few terminal flowers, and extremely long narrow corolla tube. Opler's observation (Opler 1945 F) that the flower is nocturnal would be consistent with the long narrow tube being an adaptation for Sphingid moth pollination. Our only other Rubiaceae with such long/narrow corolla tubes have much larger leaves. Also known as *jazmincillo* and *lirio de agua*.

Machaonia Humboldt & Bonpland

Shrubs or small trees, stems often armed with spines (leafless short-shoots), glabrous or puberulent, terete; stipules interpetiolar, triangular or subulate and often with a distal awn, persisting. Leaves opposite (rarely ternate or verticillate), sessile or petiolate, thin-textured, pinnately veined. Inflorescences terminal, solitary, pa-

niculate with opposite branching (or rarely umbeliform), bracteate, flowers in cymose or crowded distal clusters. Flowers bisexual and radially symmetrical, small, 4–5-parted, hypanthium turbinate or obovoid, slightly compressed laterally, calyx tube minute or cupulate, calyx lobes 4–5(–6), equal or unequal, persisting; corolla short-funnelform or short-salverform, white, corolla tube with long hairs in the throat, lobes imbricate in bud, rounded distally; stamens 4–5, filaments short or long, borne in the throat of the tube, anthers oblong, dorsifixed and versatile, included or exerted; ovary 2-locular, with 1 ovule pendulous from the apex of each locule, style slender, with 2 stigmas. Fruits small and dry, capsule-like and splitting from the bottom into 2 elongate cocci (mericarps), pendulous for a short period from the apex to the persisting stipe-like central axis; seeds elongate and cylindrical.

A tropical American genus of about 30 species, found in Mexico, Central America, the West Indies, and tropical South America. The genus is recognized by its small flowers with short corolla tubes, two-locular ovary with solitary pendulous ovules, and unusual capsule-like fruit. The subcapitate clusters of distal flowers on an openly branching panicle, small thin leaves, and occasional presence of spines are also distinctive.

Key to the Species of Machaonia

- 1a. Hypanthium/ovary of the flower with few small hairs; fruit 5–7 mm long (including calyx lobes), brownish and with few hairs often in rows; lowland evergreen Costa Rica *M. martinicensis*
- 1b. Hypanthium/ovary of the flower whitish with a dense covering of short whitish hairs; fruit 4–5 mm long, yellow or whitish with many hairs; Belize and central Panama *M. acuminata*

Machaonia acuminata Humb. & Bonpl., Pl. Aequin. 1: 101. 1806.

Shrubs or small trees, occasionally with spines to 4 cm long at the nodes, leafy branchlets 1.2–6 mm thick, glabrous to densely villose with hairs to 1 mm long, terete; stipules 2–4 mm long, triangular-subulate with a narrow awn apically, puberulent. Leaves often distichous, petioles 3–10 mm long, 0.6–1 mm broad, puberulent and often with the hairs restricted to adaxial side; leaf blades (3–)4–7(–10) cm long, 1.5–4(–6) cm long, ovate to ovate-elliptic or broadly ovate, apex acute (obtuse) to short-acuminate and often slightly curved, base obtuse to rounded and subtruncate, drying thin-chartaceous, glabrate above, with thin whitish hairs 0.3–0.7 mm long on the lower surfaces, 2° veins 3–6/size, tufted hairs rarely present in the leaf axils. Inflorescences 4–20 cm long, 3–10 cm broad, open panicles, peduncles 2–4 cm long and 1.5–3 mm thick, puberulent, bracts to 7 mm long and linear, peduncles of the lateral branches 5–40 mm long, flowers closely crowded in subcapitate distal groups of 7 or more, flowers sessile or subsessile, bracteoles ca. 1 mm long. Flowers with hypanthium ca. 2 mm long, turbinate or oblong, minutely puberulent

with thin ascending whitish hairs, calyx lobes 0.5–1 mm long, erect, rounded distally, puberulent; corolla white, 4–5 mm long, tube 1.5–3 mm long, sparsely puberulent or glabrous, lobes 1.5–2.5 mm long, ca. 1.1 mm broad, rounded at the tip; stamens exerted, anthers 0.3–0.6 mm long; styles 1–3.5 mm long, stigmas 0.3–0.6 mm long. Fruits 4–5 mm long (including the persisting calyx), 1.5–2 mm broad, narrowly obovoid or turbinate, minutely (0.1–0.2 mm) puberulent with ascending whitish hairs, splitting at the top into 2 valve-like parts and later separating at the base, persisting central axis 2.5–3.2 mm long.

Plants of lowland evergreen and partly deciduous forest formations. Flowering in May–November; fruiting in August–September and November. This species is known from southern Mexico, northeastern Guatemala, Belize, and central Panama southward to Ecuador and Brazil.

Machaonia acuminata is recognized by its occasional spines, thin small ovate leaves, small flowers with whitish puberulent ovary, and small

fruit. This species has not been found in Honduras, El Salvador, Nicaragua, or Costa Rica. Its close similarity to *M. martinicensis* and peculiar distribution makes one wonder if the two are really different species.

***Machaonia martinicensis* (DC.) Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 22: 193. 1940. *Tertrea martinicensis* DC., Prodr. 4: 481. 1830. *M. rotundata* Griseb., Fl. Brit. W. Ind. 348. 1861. *M. rotundata* var. *dodgei* Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 1326. 1938. Figure 37.**

Shrubs or (rarely small trees or vines), 1–4(–8) m tall, branches occasionally with spines to 35 mm long, leafy branchlets 1.6–5 mm thick, smooth glabrate; **stipules** 2.5–4 mm long, rounded or triangular at the apex and with a short narrow awn. **Leaves** opposite (rarely alternate), petioles 4–12 mm long, 0.5–1.2 mm broad, glabrous or puberulent on the adaxial side; **leaf blades** 4–9 cm long, 1.8–5 cm wide, ovate to ovate-oblong (elliptic-oblong), apex obtuse to acute or short-acuminate, base broadly obtuse or rounded and sometimes decurrent on petiole, drying thin-chartaceous, glabrous above, glabrous below or with few short (0.2 mm) hairs beneath or with tufts of hairs (domatia) in the vein axils, 2° veins 5–7/side. **Inflorescences** 6–11(–15) cm long, to 14 cm broad in fruit, peduncles 2–6 cm long, ca. 2 mm thick, with whitish hairs 0.2 mm long, bracts 3–5 mm long and linear (or sometimes leaf-like), secondary branches with (secondary) peduncles 10–20 mm long, with soft whitish hairs 0.2–0.3 mm long, flowers sessile or subsessile in distal subcapitate clusters of 5–15. **Flowers** with buds 5–6 mm long, hypanthium 1.5–2.5 mm long, sparsely puberulent, calyx lobes 0.7–1.2 mm long, broadly rounded distally; **corolla** white or pale greenish, tube 1.5–3 mm long, stiff, densely villous at the mouth within, sparsely puberulent externally, lobes 1–2 mm long; **stamens** 5, anthers ca. 0.6 mm long; style 3.5 mm long, stigmas 0.5–1.2 mm long. **Fruits** 5–7 mm long, 2–3 mm broad, narrowly turbinate-oblong, with 2 longitudinal sulci and separating at the base, surface reddish brown or brown, with few hairs (often in lines), persisting axis 4–5 mm long.

Shrubs usually growing near the ocean shore, in mangroves, or along rivers near the ocean in evergreen forest areas of both the Caribbean and Pacific coasts. Flowering in March–April and June–August; fruiting in July–September. The species ranges from southeastern Nicaragua southward to Colombia and also in Jamaica.

Machaonia martinicensis is recognized by its restriction to near-shore environments, small thin-ovate leaves, occasional spines, small flowers in close clusters in an open panicle, and the unusual capsule-like fruit splitting from the bottom. The species has been collected along the Caribbean shore and on the Osa Peninsula in Costa Rica.

Macrocnemum P. Browne

Trees or shrubs, branchlets terete, glabrous or puberulent; **stipules** interpetiolar, oblong to obovate, caducous or persisting with the leaves. **Leaves** opposite, petiolate; **leaf blades** with pinnate venation, domatia often present. **Inflorescences** terminal or axillary, paniculate with opposite branches, bracteate, flowers in distal cymose groupings, sessile or pedicellate. **Flowers** bisexual and radially symmetrical, calyx tube very short and cupulate, calyx lobes 5, small, persisting; **corolla** funnellform or salverform, corolla lobes 5, broadly imbricate in bud and spreading at anthesis, often wider than long, minutely puberulent within; **stamens** 5, filaments short and villous, anthers oblong; **ovary** 2-locular, ovules many, peltate and vertically imbricate on the central placenta. **Fruits** capsular, bisulcate and dehiscing loculicidally into 2 valves; **seeds** flattened, narrowly elongate with thin wings.

A small genus of about 20 species, ranging from Central America to Colombia and in the West Indies. The broad rounded stipules, broadly overlapping corolla lobes (in bud), bilocular capsules, and many small imbricate winged seeds help to distinguish this genus.

Macrocnemum glabrescens (Benth.) Wedd., Ann. Sci. Nat. Paris, ser. 4, 1: 76. 1854. *Lasionema glabrescens* Benth., Bot. voy. Sulph. 105. 1845. Figure 40.

Trees (rarely shrubs) (4–)8–25 m tall, bark brown and the trunk deeply fluted, leafy branchlets 2–7 mm thick, glabrous or minutely (0.1 mm) appressed-puberulent, angular in early stages but becoming terete; **stipules** (8–)10–20 mm long, 5–10 mm broad, apex oblong-obovate and rounded, with thin appressed hairs 0.1–0.2 mm long, leaving a scar around the stem above the node. **Leaves** often with the petioles unequal at the same node, petioles 5–20 mm long, 0.7–1.8 mm broad, sulcate adaxially; **leaf blades** 7–17(–21) cm long, 4–9 cm broad, obovate to obovate-oblong, or ovate-oblong, apex abruptly narrowed and obtuse or short-acuminate apex, tip to 1 cm long, base gradually narrowed and obtuse or acute, drying thin- to stiff-chartaceous, very dark above, glabrous above, glabrous or minutely appressed-puberulent on the veins beneath, usually with tufts of hairs ca. 1 mm long in the vein axils beneath (= domatia), 2° veins 5–9/side. **Inflorescences** terminal or axillary, solitary or 3 when the first branching node is subtended by a pair of leaves, 8–28 cm long, to 20 cm broad, paniculate with few opposite lateral branches to 12 cm long, peduncles to 18 cm long, bracts 3–6 mm long or leaf-like, lanceolate, flowers in distal cymes or clusters of more than 10, sessile or with pedicels to 3 mm long, bracteoles 0.5–1.5 mm long. **Flowers** with a hypanthium 3–4 mm long and ca. 2.4 mm diam., glabrous or minutely puberulent, calyx tube minute, calyx lobes 0.3–1 mm long, broadly triangular; **corolla** bright rose pink, magenta or the tube becoming maroon, salverform, tube 6–10 mm long, 1.3–

2 mm diam., with 5 longitudinal ribs, glabrous or rarely sparsely and minutely puberulent, villous at the stamen attachment within, lobes 3–4 mm long, 4–5 mm broad, broadly ovate and rounded distally; **stamens** 5, filaments 2–4 mm long, villous below the middle, anthers 0.8–1 mm long; style 6–8 mm long, stigma lobes ca. 0.5 mm long, green. **Fruits** 9–16(–20) mm long, 2–4 mm broad (to 4 mm when split open), narrowly oblong-tubular, with obscure longitudinal ribs, valves opening but remaining attached at both apex and base, persisting calyx ca. 2 mm broad and 1 mm high (together with disc); **seeds** 2–3 mm long, 0.5–1 mm broad, with a membranaceous wing at opposite ends, body of the seed ca. 0.6 mm long.

Trees of evergreen or partly deciduous forest formations from near sea level to 400(–1000) m elevation. Flowering in December–April; fruiting in March–July in Costa Rica and Panama. The species ranges from the evergreen lowlands of southern Costa Rica, through Panama, to Colombia.

Macrocnemum glabrescens is recognized by its broadly rounded stipules, usually thin-obovate leaves (often on petioles differing in length at the same node), large open panicles with small bright pink flowers, broadly overlapping corolla lobes, and narrow capsules with opened valves remaining attached at the base and apex. This species is only known from near the Hitoy Cerere reserve, Dominical, and the Golfo Dulce region in Costa Rica, but the original description mentions Nicoya and it is possible that it grows in moist forest on the southern part of the Nicoya Peninsula. This species appears to be common in central Panama; see flower description in Croat (1978, p. 811). This species resembles *Ferdinandusa panamensis*. Standley (1938) listed *palo cuadrado* as a common name.

Malanea Aublet

Shrubs, woody **lianas**, or trees, stems glabrous or puberulent, terete; **stipules** interpetiolar, simple, caducous. **Leaves** opposite, petiolate, entire, pinnately veined, with domatia. **Inflorescences** axillary, paniculate with short opposite or subopposite lateral branches resembling spikes (or with fasciculate flowers on the central rachis or lateral branches), flowers sessile or subsessile, bracteolate. **Flowers** bisexual and radially symmetrical, small, hypanthium turbinate to campanulate, calyx lobes 4, short; **corolla** funnelform to rotate, pale green to white, tube short, throat villous within, corolla lobes valvate or slightly imbricate, villous on the adaxial surface; **stamens** 4, filament borne on the throat of the corolla, anthers dorsifixed and partly exserted; **ovary** 2-locular, ovules solitary in each locule and pendulous from the apex of the

locule. **Fruits** fleshy, oblong or ovoid, 2-locular, exocarp thin-fleshy, endocarp woody or hard; **seeds** ellipsoid.

A genus of 20–30 species in tropical South America and the West Indies. *Malanea colombiana* has been discovered along the Caribbean coast in Belize, in northern Nicaragua, and in southeastern Costa Rica. *Malanea erecta* Seem. (photo F), said to have been collected by Seemann in Panama, was not treated in the Flora of Panama.

Malanea colombiana Standl., Publ. Field Columb. Mus., Bot. Ser. 7: 66, 1930. *Chomelia coclensis* Dwyer, Ann. Missouri Bot. Gard. 67: 97. 1980.

Lianas or clambering shrubs with vining branches, leafy stems 1.7–8 mm thick, with closely appressed-ascending straight hairs 0.4–0.8 mm long, glabrescent and lenticellate; **stipules** 6–18 mm long, 2.5–8 mm broad, oblong or obovate, with many ascending veins, appressed-puberulent at the base and midrib, deciduous. **Leaves** with petioles (4–)7–22 mm long, 0.6–2 mm thick, appressed-puberulent; **leaf blades** 5–13 cm long, 2.5–7 cm broad, ovate-elliptic to ovate or oblong-elliptic, apex obtuse to short-acuminate or acute, base obtuse to slightly rounded and subtruncate, drying stiffly chartaceous, dark brown above, glabrous above or with appressed hairs along the midvein and widely scattered elsewhere, with appressed thin whitish hairs 0.3–1 mm long beneath, often with tufts of hairs in the vein axils beneath, 2° veins 5–7/side, distal secondaries to arcuate-ascending, 3° veins numerous and closely parallel to form a straight or sinuous pattern between the secondaries. **Inflorescences** 4–13 cm long, 3–8 cm broad, pyramidal with progressively shorter opposite branches, peduncles 2–6 cm long, 0.6–1.8 mm thick, sciraceous, lateral branches 1–3(–4) cm long, bracts 1.5–4 mm long and linear, bracteoles ca. 1 mm long, flowers sessile or with pedicels to 1.5 mm long. **Flowers** 3–4 mm long, hypanthium 0.5–1 mm long, turbinate, calyx lobes 0.1–0.4 mm long, broadly triangular or poorly developed; **corolla** white or yellowish white, tube 1.5–2.5 mm long, ca. 1 mm diam. at mouth, lobes 4, 1–2 mm long, 1 mm broad at the base, villous within; anthers 0.5–0.8 mm long; style exserted, stigma lobes ca. 0.4 mm long. **Fruits** 5–6 mm long, 3–4 mm diam., oblong-cylindrical, becoming purplish red and drying black, persisting calyx very short (0.5 mm) and not elevated.

Plants of evergreen or partly deciduous vegetation, 2–200 m elevation. Flowering in June in Costa Rica (*Herrera 3081* CR, MO); fruiting in August in northern Nicaragua (*Molina 14926* & *151125* EAP, F). The species ranges from Belize to Colombia.

Malanea colombiana is recognized by its very small flowers with four-lobed perianth, corolla lobes conspicuously villous within, fleshy oblong

fruit, unusual tertiary venation, and climbing habit. The tertiary veins of the leaf are many and parallel with inconspicuous transverse connections. The Costa Rican collection has minor venation that differs by having a more reticulate arrangement of 3° veins with sublineolate 4° veins. More material is necessary to confirm its placement under this name. The flowers resemble those of *Elaeagia*, Figure 39.

Manettia Mutis ex Linnaeus

Herbs or climbers, stems herbaceous or slightly woody, glabrous or puberulent; **stipules** interpetiolar, small, sometimes adnate to the petiole, triangular to laciniate, persistent. **Leaves** opposite and decussate, petiolate or sessile; **leaf blades** often narrow, pinnately veined, domatia absent. **Inflorescences** axillary (rarely terminal), cymose to paniculate, fasciculate, umbellate or the flowers occasionally solitary, bracts and bracteoles present, flowers pedicellate. **Flowers** bisexual, monomorphic or distylous, radially symmetrical, small (in Central America) to large, hypanthium turbinate, calyx lobes usually

4 (5, 8), short or long, with glands or teeth in the sinuses; **corolla** funnellform or tubular, white, pink, red, lavender, blue, or yellow, corolla lobes 4(–5), valvate in bud; **stamens** 4, filaments attached in the throat or at the mouth, anthers versatile, exerted or included; **ovary** 2-locular, ovules numerous and imbricate, vertical on axile placentas, style filiform, stigmas 2 clavate or bifid. **Fruits** thin-walled capsules, obovoid or turbinate to subglobose, biloculate and bisulcate, splitting septicidally from the apex into 2 valves; **seeds** compressed-discoid, usually with a thin wing surrounding the central seed.

A tropical American genus of about 100 species. The slender twining stems, smaller narrow leaves, small inflorescences, small flowers (in Central American species), small obovoid capsules breaking into two valves, and winged or flattened seeds with erose margin help to distinguish these plants. This study has benefited from the herbarium annotations of In-Cho Chung and David Lorence. *Manettia luteo-rubra* variety *paraguariensis* (Chodat) Chung (= *M. inflata* Sprague) is an ornamental grown for its bright red flowers tipped with yellow.

Key to the Species of *Manettia*

- 1a. Leaf blades narrowly lanceolate and often sessile; seeds ca. 1 mm diam., orbicular with an erose margin (the wing minute or absent); flowers white, corolla tube 3–5 mm long *M. barbata*
- 1b. Leaf blades rarely consistently lanceolate, petioles usually well developed; seeds 2–3 mm long, oblong or orbicular with a thin expanded marginal wing; flowers white, pink, red, or magenta, corolla tubes 4–13 mm long 2
- 2a. Corollas white; capsules 4–6 mm long; leaf blades usually puberulent beneath; 1000–1600 m elevation *M. flexilis*
- 2b. Corolla brilliant red to magenta or pink; capsules 6–10 mm long; leaf blades usually glabrous beneath; 30–1100 m elevation *M. reclinata*

Manettia barbata Oersted, Vidensk. Meddel. Kjobenhavn 1852: 47. 1853. *M. stenophylla* J. D. Smith, Bot. Gaz. 56: 58. 1913. Figure 1.

Slender vines to 3 m high, leafy internodes 0.7–2.5 mm thick, glabrous or subglabrous; **stipules** 0.5–3 mm, long, broadly triangular, glabrous. **Leaves** with petioles 1–5 mm long, 0.3–1.5 mm broad, glabrous; **leaf blades** 3–10 cm long, 0.4–3 cm broad, lanceolate to narrowly elliptic-lanceolate or linear-lanceolate, apex tapering gradually and long-acuminate or acute, base obtuse or slightly rounded, drying chartaceous, pale grayish green or grayish brown, glabrous above and below, 2° veins 4–7/side. **Inflorescences** 10–15 mm long, axillary cymes of usually 3 flowers, peduncles only 1–4 mm long, bracts to 3 mm long, lanceolate, pedicels 2–5 mm long, bracteoles 0.5–1(–2) mm long. **Flowers** with hypanthium 2–3 mm long, 1.2–2 mm diam., calyx lobes 1.2–2 mm long, 0.7–1.2 mm broad, ovate; **corolla** white, tube 3–6 mm long, 2 mm diam., lobes 2–3 mm long, glabrous exter-

nally and villous within; anthers ca. 1 mm long; stigma ca. 0.5 mm long, oblong to lanceolate. **Fruits** 4–8 mm long, 3–7 mm broad, persisting calyx to 1.5 mm long and usually recurved; **seeds** 0.7–1 mm diam., orbicular, wing reduced to a dentate rim around the seed, body of seed ca. 0.6 mm diam., discoid.

Uncommon plants of evergreen forest formations, from 500 to 1300(–2400?) m elevation. Flowering in November–January; fruiting in January and March. This species is known only from central and southern Costa Rica.

Manettia barbata is recognized by its narrowly lanceolate leaves, twining habit, few-flowered and short-pedunculate inflorescences, short corolla tubes, smaller capsules, and circular-discoid seeds with little evidence of a wing.

Manettia flexilis Brandegee, Univ. Calif. Publ. Bot. 6: 196. 1915. *M. estrellae* Standl., J. Wash. Acad. Sci. 15: 6. 1925. Figure 1.

Vines to 4 m high, leafy stems 0.7–2 mm long, puberulent with curled whitish hairs ca. 0.2 mm long; **stipules** 1–2 mm long, adnate to the petiole base, rounded distally or with short (0.3 mm) thick spike-like projections. **Leaves** with petioles 2–10 mm long, 0.3–0.7 mm thick, puberulent; **leaf blades** (2.5–)3–7 cm long, 1–3 cm broad, oblong to ovate or lanceolate, apex acute to long-attenuate, base obtuse to acute, drying membranaceous or thin-chartaceous, dark green above, pale grayish green beneath, glabrous or puberulent above, short pilose beneath with thin whitish hairs ca. 0.3 mm long, 2° veins 4–6/side, the upper secondaries strongly arcuate-ascending. **Inflorescences** axillary, cymose or umbelliform flowers few (rarely 1), peduncles 1–7 mm long, bracts ca. 2 mm long, flowers closely crowded, pedicels 1–5 mm long. **Flowers** with hypanthium 2–3 mm long, densely puberulent with straight or curved multicellular hairs 0.2–0.5 mm long, calyx cup to 0.4 mm long, calyx lobes (2–)3–4 mm long, 0.8–1.5 mm broad, lanceolate, with erect glands ca. 0.3 mm long in the sinus; **corolla** white or rose red, tube 4–10 mm long, ca. 1.3 mm diam., short villose externally, glabrous within, lobes 4, 2–5 mm long, ca. 0.7 mm broad, ovate to triangular, densely villous externally; **stamens** 4, anthers ca. 0.7 mm long. **Fruits** 5–7 mm long, 4–6 mm broad, broadly obovoid to subglobose, rounded and truncated at the apex, with few scattered hairs; **seeds** 2–3 mm long, oblong and with a thin translucent wing, body of the seed ca. 1 mm long and oblong.

Plants of evergreen and partly deciduous forest formations in the central cordilleras, from ca. 1000 to 1600 m elevation. Probably flowering and fruiting throughout the year. The species ranges from southern Mexico to western Panama.

Manettia flexilis is recognized by its smaller capsules, winged seeds, puberulent stems and leaves, and mid-elevation habitats. This species is infrequently collected.

Manettia reclinata Mutis in L., Mant. Pl. 2: 558. 1771. *Nacibea coccinea* Aubl., Hist. pl. Guiane 96, t. 37, f. 1. 1775. *M. coccinea* (Aubl.) Willd. in L., Sp. Pl. ed. 4, 1: 624. 1797. *M. cuspidata* Bertero in Spreng., Syst. Veg. 1: 415. 1825. *M. panamensis* Duchass. & Walp., Linnaea 23: 753. 1850. *M. costaricensis* Wernham, J. Bot. 56, suppl. 1: 38. 1919. *M. orbifera* Wernham, loc. cit. 41. 1919. *M. seleriana* Loes., Verhand. Bot. Vereins Brandenb. 65: 107. 1923. Figure 1.

Vines to 4 m high, stems often with 4 narrow longitudinal ridges, leafy stems 0.7–2.5 mm thick, sparsely puberulent (rarely glabrous), often with a row of minute (0.1–0.2 mm) hairs along the longitudinal ridges; **stipules**

1–2 mm long, broadly triangular, minutely puberulent. **Leaves** with petioles 2–14(–20) mm long, 0.6–1.2 mm broad, sparsely puberulent; **leaf blades** (2–)3–10 cm long, 1–3(–5) cm broad, narrowly ovate to ovate-elliptic or lanceolate, acute or acuminate at the apex, obtuse to acute at the base, leaves drying thinly chartaceous and dark green above, paler greenish gray beneath, usually glabrous above and below, with 4–6 major secondary veins strongly ascending on each side. **Inflorescences** axillary or terminal, usually solitary with 2–4 flowers per node, peduncles 0.5–2.5 cm long, puberulent, pedicels 10–25 mm long (to 35 mm in fruit). **Flowers** with hypanthium 3–5 mm long, oblong, calyx tube to 1 mm long, calyx lobes 4–8, unequal, 4–7 mm long, 0.3–1.3 mm broad, linear to lanceolate; **corolla** red, rose red, deep pink, scarlet, or magenta, tube 6–13 mm long, 2–2.5 mm diam., glabrate to densely minutely puberulent externally, with yellowish hairs in throat, corolla lobes 4 (5, 6), 2–4 mm long, 2.5–4.5 mm wide, ovate, puberulent externally and glabrous within; **stamens** 4 (5, 6), filaments ca. 1 mm long, anthers ca. 3 mm long; style ca. 11 mm long. **Fruits** 6–10 mm long, 6–9 mm broad, obovoid or subglobose, glabrous or pubescent with thin curled hairs to 0.5 mm long, with 8 longitudinal ribs (2 in the sulci), calyx lobes persisting and recurved; **seeds** 2–2.5 mm diam., thin-discoid and orbicular, with an erose translucent wing around the margin, body of the fruit 0.7–1 mm diam.

Plants of wet evergreen forest formations, 0–1300 m elevation. Flowering in October–May; fruiting in December–May. The species ranges from southern Mexico and the West Indies into northern South America.

Manettia reclinata is recognized by its larger red or pink flowers, few flowers per node, usually glabrous leaves, larger rounded capsules borne on long pedicels, flat orbicular seeds with thin winged margin, and vining habit. This species appears to be much more common than its congeners in Costa Rica.

Mitracarpus Zuccarini

Annual or perennial **herbs**, erect or decumbent, stems tetragonus in cross-section, glabrous or puberulent; **stipules** adnate to the petiole base to form a sheath with 3–15 slender distal setae (awns), persistent. **Leaves** opposite and decussate, subsessile to short-petiolate, leaf blades usually narrow (linear to ovate), chartaceous, domatia absent. **Inflorescences** axillary or terminal, capitate or glomerulate with densely crowded flowers, the heads sometimes subtended by 4 leaf-like bracts, flowers sessile or subsessile. **Flowers** bisexual and monomorphic, very small, hypanthium turbinate to subglobose, calyx tube short, calyx lobes 4(–5), unequal, persistent; **corolla** white, salverform or funnelform, tube usually with a ring of hairs within, glabrous or villous in the throat, corolla lobes 4 (3), valvate in bud; **stamens** 4, inserted on the throat, anthers oblong to linear, dorsifixed, included or exserted; **ovary** 2–3-locular, with 1

ovule in each locule attached to a peltate placenta in the center of the septum, style short or long, with 2 short linear stigmas. **Fruits** thin-walled capsules, 2- or 3-locular with circumscissile or transverse dehiscence from below the middle (the upper portion breaking away with the persisting calyx and exposing the seeds), septum persisting with the basal part of the capsule; **seeds** ellipsoid to oblate or globose, ventral (adaxial) surface with 4 sulci radiating from a central area to give an X-like pattern demarking 4 broadly rounded areas, abaxial surface smooth.

A Neotropical genus of 30–45 species, with most in Brazil. The genus is very similar to *Crusea*, *Diodia*, and *Spermacoce* with its weedy-herbaceous habit, broad stipules with distal awns, narrowly elliptic leaves, small flowers in verticillate heads, and two-locular capsules with two seeds. *Mitracarpus* is unusual in the circumscissile dehiscence of the capsule and the X-like (cruciform) sulcus on the inner face of the seed.

Mitracarpus hirtus (L.) DC., Prodr. 4: 572. 1830. *Spermacoce hirta* L., Sp. Pl. ed. 2: 148. 1762. *S. villosa* Sw., Prodr. 29. 1788. *M. villosus* (Sw.) Cham. & Schlend., Linnaea 3: 363. 1828. *M. breviflorus* Gray, Pl. Wright. 2, 68. 1853. Figure 4.

Herbs to 0.6(–1) m tall, erect or spreading, stems usually simple distally and with few branches mostly near the base, often slightly woody at the base, leafy stems 0.7–2.5 mm thick, with 4 longitudinal ridges and somewhat quadrangular in cross-section, usually with curved thin hairs 0.2–1.5 mm long and longer (1.5–2 mm) translucent hairs at the nodes; **stipules** united to the petiole base to form a broad sheath 1–3(–4) mm long, the straight distal margin of the sheath with 6–9(–13) linear setae 1–5 mm long. **Leaves** subsessile, petioles 0–3 mm long, not clearly differentiated from the base of the blade; **leaf blades** 2–5(–8) cm long, 0.5–1.5(–2) cm broad, narrowly elliptic to lanceolate, or narrowly elliptic-oblong, apex tapering gradually and acute, base cuneate, drying stiffly chartaceous, glabrescent or sparsely hispidulous above, sparsely hispidulous beneath with hairs ca. 0.3 mm long and along the margin, 2° veins 2–3/ide, strongly ascending. **Inflorescences** axillary or terminal, flowers densely crowded in capitulae or verticils 4–10 mm high and 8–15(–20) mm broad, bracts 2–4 mm long but difficult to distinguish among the sepal lobes in the tightly congested heads, flowers sessile or subsessile. **Flowers** with hypanthium 1–2 mm long, glabrous beneath and hispidulous distally, calyx lobes 4, unequal, the 2 larger 1.5–2.5 mm long, lanceolate, thick centrally and with a hyaline margin; **corolla** white, glabrous or minutely hairy externally, tube 1.5–2 mm long, 0.3–0.9 mm diam., lobes 4, 0.6–1.1 mm long, 0.4–1 mm broad at the base, ovate or triangular; **stamens** 4, filaments very short or absent, anthers 0.4–0.7 mm long, usually exserted; style 1–1.6 mm long, stigma 0.3–0.5 mm long. **Fruits** with the top part coming off to expose the 2 locules and 2 seeds,

persisting calyx and top of fruit 2–3.5 mm long, body of the yellowish brown capsule ca. 1 mm long, 0.6–1 mm broad; **seeds** 0.5–0.8 long and ca. 0.6 mm wide, oblong-oblate, yellowish brown, with 4 sulci forming an impressed X on the adaxial face, smooth or pitted on the abaxial face.

Common weedy plants of open disturbed sites in both deciduous and evergreen formations, 0–1200(–1400) m elevation. Flowering primarily in June–December in Costa Rica. The species is found in the southwestern United States and throughout tropical America; it has become established through much of tropical Africa and has been found in India, Burma, and the western Pacific.

Mitracarpus hirtus is recognized by its herbaceous weedy habit, setose sheathing stipules, narrow hispidulous leaves with few secondary veins, axillary heads of small congested flowers, and unusual fruit and seed. It is found in both the Caribbean and Pacific lowlands and the central uplands. There has been considerable confusion regarding the nomenclature of this species and especially the applicability of the names; we follow the recent annotations of C. Dennis Adams. These plants can be mistaken for species of *Spermacoce*, *Diodia*, and *Hyptis* (Labiatae).

Morinda Linnaeus

Small to large **trees** or shrubs (lianas), stems terete or quadrangular in cross-section, glabrous or puberulent; **stipules** interpetiolar and sometimes slightly connate to form a short sheath above the petioles (intrapetiolar), entire to cuspidate or bifid, glabrous. **Leaves** opposite or 3/node (sometimes only 1 at a flowering node), petiolate, pinnately veined, often slightly succulent in life, usually with tufts of hairs (domatia) in the vein axils beneath. **Inflorescences** terminal or axillary, with 1 or 2 (rarely more) capitate heads on a common peduncle (the heads rarely sessile), large or small bracts sometimes present, flowers sessile in the capitulum with the basal parts usually united. **Flowers** bisexual (rarely unisexual), radially symmetrical, usually distylous, hypanthium free or united with other flowers, calyx tube urceolate or hemispheric, often entire distally, calyx lobes usually minute or absent; **corolla** funnelform or salverform, corolla tube glabrous or puberulent in the throat, puberulent at the base within, corolla lobes 4–7, narrow and valvate in bud; **stamens** 4–7, filaments short and inserted in the throat of the corolla, anthers dorsifixed and versatile, included or exserted, connective often prolonged distally; **ovary** 2- or 4-locular 1 ovule in each locule, ovules erect and attached below the middle or at the base of the septum, style slender, with 2 short or long style branches. **Fruits** fused into a fleshy syncarp made up of the united ovaries (or their bases), often large and turning white, pyrenes 1-seeded or part of a 2–4-locular woody structure; **seeds** obovoid or reniform.

A pantropical genus of 50–80 species; most of the species are native to the Old World. The flowering capitula with the basal parts of the flowers united, and the latter forming a fleshy largely syncarpous fruiting capitulum, make this genus very distinctive among our Rubiaceae. Three species have been recorded from southern Central Amer-

ica; two additional native species (*M. asperula* Standl. and *M. yucatanensis* Greenm.) are found in northern Central America. There is considerable variation within our species, and this can make their identification difficult. Current holdings of this genus are very limited; all the Costa Rican material is from near the seashore.

Key to the Species of *Morinda*

- 1a. Leaf blades usually less than 5 cm broad, usually drying grayish or yellowish; branches often scandent *M. royoc*
- 1b. Leaf blades more than 5 cm broad, usually drying very dark in color; branches never clambering or scandent 2
- 2a. Inflorescences usually solitary, with only 1 capitulum per peduncle, fruiting syncarps 3–12 cm diam.; largest leaf blades usually more than 20 cm long and 14 cm broad; only found near the ocean shore *M. citrifolia*
- 2b. Inflorescences 1–3/node, with 1–3 capitula per primary peduncle, fruiting syncarp 0.5–3 cm diam.; largest leaf blades usually less than 20 cm long and 14 cm broad; lowland rain forests *M. panamensis*

Morinda citrifolia L., Sp. Pl. 176. 1753. Figure 19.

Shrubs or small trees, (1)–2–8(–12) m tall, trunks to 15 cm thick, wood yellow, branchlets quadrangular or terete, leafy stems 2.5–12 mm thick, glabrous; **stipules** 6–20 mm long, 5–14 mm broad, oblong to suborbicular-triangular and rounded distally, glabrous. **Leaves** well spaced along the stem, petioles 12–20 mm long, ca. 2 mm broad, glabrous, with slightly winged adaxial margins; **leaf blades** 12–28(–40) cm long, 7–16(–24) cm broad, oblong to broadly elliptic-oblong or ovate-oblong, apex obtuse to acute (very short acuminate), base broadly obtuse to cuneate, drying chartaceous or thin-chartaceous, often dark in color, glabrous above and below but with tufts of hairs in the vein axils beneath, 2° veins 6–8/side. **Inflorescences** axillary and drying black, solitary or 2–3/node, capitulae 9–20 mm long, to 20 mm diam., oblong to subglobose, peduncles 10–22(–30) mm long, 1.2–2 mm thick, glabrous, flowers sessile and united at the base. **Flowers** united basally (hypanthia connate), calyx tube minute and truncated with a scarios margin; **corolla** white, slightly thickened, glabrous externally, tube 6–10 mm long, cylindrical, corolla lobes usually 5, 3–8 mm long, ca. 1.5 mm wide, obtuse, thick-fleshy; **stamens** 4–6, filaments slightly unequal, anthers to 5 mm long, becoming twisted; stigma to 5 mm long and 0.8 mm wide, erose. **Fruits** united into a syncarp, 4–12 cm diam., fleshy succulent and irregularly globose to oblate, white with green “eyes” ca. 8 mm diam. formed by the calyx and disc of individual flowers, pyrenes to 10 mm diam.; **seeds** 3.5 mm long.

Plants usually found near ocean beaches and lagoons along the Caribbean shore from Honduras to Panama, 0–20 m elevation. Flowering and fruiting throughout the year (Sánchez 1983). The orig-

inal range of this species was from India to the East Indies and northern Australia. It has become naturalized in a number of areas around the Caribbean.

Morinda citrifolia is recognized by its large white *Annona*-like syncarps, large opposite leaves on thick stems, and seaside Caribbean habitat. Herbarium specimens can be difficult to distinguish from *M. panamensis*. *Yema de huevo* is a common name; the fruits are edible.

Morinda panamensis Seem., Bot. voy. Herald 136. 1854. Figure 19.

Shrubs or trees, 3–25 m tall, branchlets quadrangular in cross-section, leafy stems 1.5–6 mm thick, minutely (0.1 mm) farinose puberulent, glabrescent; **stipules** apparently with the distal part tearing off to leave a cupulate base 1–3 mm long forming a shallow cup around the stem, at first broadly oblong (to 10 mm long and 9 mm broad) and covering the shoot apex. **Leaves** with petioles 5–25 mm long, 1–2 m thick, glabrous or minutely (0.1 mm) puberulent; **leaf blades** 9–21 cm long, 4–13 cm broad, broadly elliptic to elliptic-oblong or ovate-oblong, apex bluntly short-acuminate with tip to 10 mm long, base obtuse or cuneate, drying thin-chartaceous, dark, glabrous above, glabrous or minutely (0.2–0.3 mm) puberulent beneath and with dense tufts of hairs (domatia) in the vein axils, 2° veins 4–7/side, central 2° veins 1–4 cm distant. **Inflorescences** 1–3/node, capitate, peduncles 4–35(–55) mm long, 0.7–1.5 mm thick, the primary peduncle simple or with 3–4 equal or unequal branches to 3 cm long, usually glabrous, each capitulum 4–10 mm

long and 5–10 mm wide, oblong to globose, with 9 flowers or more, flowers sessile and united. **Flowers** united below, glabrous externally (rarely minutely puberulent) and drying black, hypanthium partly free distally for 1–2 mm, calyx tube ca. 0.3 mm long and subentire; **corolla** white, tube 5–10 mm long, lobes 4, 3–6 mm long, 1–2 mm broad, narrowly oblong; **stamens** 4, anthers 2.5–3.5 mm long; stigmas 3.5–5 mm long. **Fruit** a syncarp, 15–30 mm diam., subglobose, the calyx tube little (0–0.5 mm) elevated above the surface of the fruit and 2.5–4 mm diam.

Plants of wet evergreen lowland rain forest formations, 0–600 m elevation. Flowering in March–May in Central America; fruiting in July–September. This species ranges around the Gulf of Mexico and the Caribbean from Florida (U.S.A.), Mexico, Central America, and the West Indies to Panama.

Morinda panamensis is recognized by its unusual capitula of flowers with united ovaries, seeds imbedded within a globose syncarp, thin leaves drying very dark, and rain forest habitat. Some herbarium specimens can be very similar to specimens of *M. citrifolia*, and it is possible that there are intermediates in nature. An unusual collection from near Upala (Herrera 1783 CR, MO) is minutely puberulent on all parts.

Morinda royoc L., Sp. Pl. 176. 1753. Figure 19.

Shrubs, vines, or small trees, 1–3(–7) m tall, often with scandent branches, leafy branchlets 1–5 mm thick, young stems with obscure longitudinal ridges and quadrangular or terete, minutely puberulent with thin hairs 0.1 mm long; **stipules** 1–2(–4) mm long, 3–5 mm wide at the base, triangular or with an awn 1–2 mm long, glabrous and drying yellowish brown. **Leaves** with petioles 4–14 mm long, 0.5–1 mm broad, with adaxial margins, glabrous or minutely puberulent; **leaf blades** 4–11(–13) cm long, 1–4.5 cm broad, narrowly elliptic-oblong to oblanceolate or linear-oblancheolate, usually 4 times longer than broad, apex acute to short-acuminate, base gradually narrowed and acute or attenuate, drying stiffly chartaceous, grayish or yellowish, with the margin often involute, glabrous above and below but often with barbate hairs in the leaf axils and along the midvein, 2° veins 3–6/side, arcuate and weakly loop-connected near the margin. **Inflorescences** solitary and axillary, the capitulae 4–12 mm diam., usually oblong, sessile or with peduncles 0–7(–10) mm long, minutely puberulent, flowers sessile and united. **Flowers** united together in the lower half of their ovary, free portion of the hypanthium and calyx 1–3 mm long, calyx entire distally (or obscurely 5-lobed), minutely puberulent; **corolla** white, 6–8 mm long, tube ca. 5 mm long and 2 mm diam., cylindrical, minutely (0.1 mm) puberulent externally, lobes 1–2 mm long; **stamens** 5–6, anthers ca. 2 mm long; style 3–5 mm long, stigmas ca. 1.5 mm long. **Fruit** a syncarp, 8–25 mm diam., irregularly globose, pyrenes 5 mm long.

Plants of the Caribbean lowlands (from pine savannas to evergreen forest formations) in Central America. Flowering in January–August. The species ranges from Florida (U.S.A.), Mexico, Central America, and the West Indies to northern South America.

Morinda royoc is recognized by its vining branches, smaller narrow leaves that rarely dry very dark, small syncarpous capitulae, and small stipules. We have seen no specimens from Costa Rica, but the species has been collected near Bluefields, Nicaragua, and in central Panama. Most Central American collections are described as vines. *Appunia guatemalensis* can appear quite similar, but the branches are not vining and the fruit develop separately.

Mussaenda Linnaeus

Shrubs, erect or climbing; **stipules** interpetiolar, united and solitary or separate and paired (4/node). **Leaves** opposite, petiolate, pinnately veined and often acuminate at the apex, domatia absent. **Inflorescences** terminal, cymose, bracts and bracteoles deciduous; a few flowers of the inflorescence with a single greatly expanded colorful and leaf-like expanded sepal lobe. **Flowers** bisexual and radially symmetrical (except for those flowers where 1 sepal lobe is greatly enlarged), calyx tube turbinate or ovoid, calyx lobes 5, 1 lobe greatly expanded in a few flowers of most species; **corolla** narrowly funnellform or salverform, glabrous or puberulent on the outer surface, corolla tube puberulent in the throat, corolla lobes 5; **stamens** 5, filaments very short, borne near the base or the upper part of the tube, anthers sagittate at the base; **ovary** 2-locular with many ovules, style 2-branched. **Fruits** usually fleshy and indehiscent (rarely dry and loculicidally dehiscent); **seeds** small and ellipsoid.

A tropical Old World genus of about 200 species. The greatly enlarged and colorful sepal lobes on a few flowers of each inflorescence are found in most species of the genus and account for the ornamental appeal of the following species.

Mussaenda erythrophylla Schumach. & Thonn., Beskr. Guin. Pl. 116. 1827. Figure 16.

Shrubs or woody climbers, 1.5–3(–8) m tall, leafy branchlets 2–6 mm thick, densely velutinous with yellowish hairs ca. 1 mm long, terete; **stipules** 4/node, 6–11 mm long, ovate-triangular, glabrous on the inner face. **Leaves** with petioles 4–18 mm long, with hairs to 1.5 mm long; **leaf blades** 4–12(–15) cm long, 3–7 cm long, ovate to broadly ovate-elliptic or ovate-orbicular, apex short-acuminate, base obtuse or rounded and subtruncate, densely puberulent on both surfaces with slender

hairs 0.5–2 mm long, 2° veins 5–7/side, arcuate-ascending. **Inflorescences** ca. 10 cm long and 20 cm broad, at the ends of distal unbranched leafy stems, with opposite or trichotomous branches, densely velutinous. **Flowers** densely puberulent externally, calyx lobes 6–12 mm long, 1–3 mm broad, red; the enlarged sepal lobe leaf-like, 4.5–6.5 cm long, 3–6.5 cm broad, on petioles 2–8 mm long, with ca. 7 palmate veins, bright red; **corolla** yellow to pink, tube 15–30 mm long, lobes 3–9 mm long, 4–7 mm broad, broadly ovate, whitish and papillate puberulent within.

Popular small shrubs or climbers grown for ornament in parks and gardens. The enlarged leaf-like sepal lobes are bright crimson to deep red and give a very colorful effect. They flower throughout the year but usually do not produce fruits.

Neolamarckia Bosser

Trees; stipules interpetiolar, triangular, deciduous. **Leaves** opposite, petiolate, entire, domatia absent. **Inflorescences** terminal, usually solitary, capitate and pedunculate, flowers densely congested. **Flowers** bisexual and radially symmetrical, calyx lobes small; **corolla** funnelform, corolla lobes 4–5, imbricate in bud; **ovary** 2-locular at the base, placentation axile with many vertical ovules; stigma fusiform. **Fruits** capsules, loculicidally dehiscent from the apex, thin-walled; **seeds** 1–5 in each locule, small and angular.

A genus of two species of southeast Asia. One species is occasionally planted in Costa Rica.

Neolamarckia cadamba (Roxb.) Bosser, Bull. Mus. Hist. Nat. Paris 4 ser. sect. B. Adansonia 6: 247. 1984. *Nauclea cadamba* Roxb., Fl. Ind., ed. 1, 2: 121. 1824. *Anthocephalus cadamba* (Roxb.) Miq., Fl. Ind. Bat. 2: 135. 1856. *A. morindae-folius* Korth., Verh. Nat. Gesch. 154, t. 48. 1842. *A. indicus* A. Rich., Mem. Soc. Hist. Nat. Paris 5: 238. 1834, nom. illeg. *Cephalanthus chinensis* auctt., non Lamarck; *A. chinensis* auctt.

Trees, 5–15(–30) m tall, fast-growing in early stages, leafy stems 2.3–10 mm thick, glabrous, quadrangular; **stipules** oblong, covering the buds, caducous. **Leaves** usually somewhat pendant, deciduous, petioles 22–55 mm long, 1–4 mm thick, glabrous or minutely puberulent, drying dark; **leaf blades** (7–)13–34 cm long, (5–)6.5–18 cm broad, ovate to ovate-oblong or oblong, apex abruptly narrowed and blunt or short-acuminate, base obtuse to rounded and truncate or subcordate, drying brownish, glabrous above, glabrous or minutely (0.05 mm) puberulent beneath, 2° veins (4–)8–16/side, 3° veins subparallel. **Inflorescences** solitary, terminal on short lateral branchlets, each with a single globose capitulum 3–

4 cm diam., peduncles 2–4 cm long, flowers many and closely congested. **Flowers** not convicent basally; **corolla** 7–8 mm long, narrowly funnelform, lobes 5, ca. 1.5 mm long; style long-exserted. **Fruits** tightly congested in the spherical heads, splitting into 4 parts; **seeds** minute.

The solitary pedunculate globose heads and larger drooping leaves distinguish this introduced species. It is fast-growing in open sites until it reaches about 10 m in height. Common names used in southeast Asia are *kadam*, *kedam*, and *laran*. The literature of this tree is to be found under *Anthocephalus*, now a synonym of *Breonia*. See J. D. E. Fox, *Anthocephalus chinensis*, the Laran Tree of Sabah. Econ. Bot. 25: 221–233. 1971.

Nertera Banks & Solander Nomen conservandum

Perennial **herbs**, creeping and repent, glabrous or sparsely puberulent, much-branched and often rooting at the nodes (often forming mats); **stipules** interpetiolar, small, partly united to the petiole bases, entire or with 2 teeth, persistent. **Leaves** opposite, very small, petiolate or sessile; **leaf blades** ovate to rounded, glabrous or puberulent, venation pinnate or subpalmate; domatia absent. **Inflorescences** of solitary flowers, axillary or terminal, the flowers sessile or subsessile. **Flowers** bisexual, radially symmetrical, hypanthium ovoid to turbinate, calyx tube truncated and entire or slightly lobed; **corolla** broadly funnelform to tubular, corolla lobes 4–5, valvate in bud; **stamens** with thin filaments attached to the base of the tube, anthers basifixed, the connective apiculate, exserted; **ovary** 2-locular, with 1 ovule borne from the base of each locule, style deeply 2-branched and slender. **Fruits** fleshy drupes (rarely dry), rounded, with 2 plano-convex pyrenes.

A genus of 6–12 species found in Australia, New Zealand, Malaya, Indonesia, South China, and some Pacific islands; in addition, a single species ranges from Mexico through the higher moist mountains of Central and South America to Chile.

Nertera granadensis (Mutis ex L.f.) Druce, Bot. Soc. Exch. Club Brit. Isles 1916: 637. 1917. *Gomozia granadensis* Mutis ex L.f., Suppl. Pl. 129. 1781. *Nertera depressa* Banks & Solander ex Gaert., Fruct. et Sem. Pl. 1: 124. 1788. Figure 3.

Creeping prostrate or pendant **herbs** to 5 cm tall and up to ca. 1 m long, terrestrial or low epiphytic, often forming mats, stems 0.3–1 mm thick and rooting at many nodes, often tetragonous in cross-section in life, glabrous or with a few scattered hairs; **stipules** 0.3–1 mm long, triangular, united at the base with the bases of the pet-

ioles, persisting. **Leaves** quite variable on different plants, petioles 0.7–6(–9) mm long, 0.2–0.4 mm broad, glabrous, sometimes sulcate above; **leaf blades** (1.5–)2.5–8(–13) mm long, (1.2–)2–7(–12) mm broad, ovate-triangular to ovate-orbicular or ovate-deltoid, apex obtuse to rounded, sometimes with a minutely apiculate tip, base rounded and truncate to obtuse, often decurrent on petiole in larger leaves, drying thin-chartaceous but semisucculent in life, glabrous above and below (rarely puberulent), 2° veins 2–4/side, strongly ascending. **Inflorescences** absent, the solitary sessile flowers axillary to distal leaves, the flowers covered by surrounding leaves and very difficult to see in pressed herbarium material. **Flowers** minute (ca. 4 mm long), usually glabrous externally, hypanthium 0.5–1 mm long, calyx lobes absent; **corolla** 1–3 mm long, greenish to yellow or white, tube 0.6–1 mm long, widely funnelliform (subcampanulate), lobes ca. 0.5 mm long, glabrous; anthers 0.3–0.5 mm long. **Fruits** sessile, 4–7 mm diam., globose, bright orange, orange-red, or deep red, fleshy part often translucent, pyrenes 2–2.5 mm long and 1.2–2 mm wide, oblong.

Plants of wet evergreen montane forest formations, from (1000–)1500 to 3400 m elevation in Central America. Fruiting throughout the year in Costa Rica. This species ranges from Mexico, through the high mountains of Central America and South America, as far south as Chile. This species, when interpreted in a broad sense, is said to be found throughout the range of the genus.

Nertera granadensis is a very distinctive species with its low-creeping and mat-forming habit, very small paired leaves, lack of pubescence, solitary little flowers, bright orange-red berries, and restriction to higher-elevation wet forest habitats. Collections with larger (10 mm) leaves can look very different from those with smaller (4 mm) leaves. It is common in some montane rain forests, covering mossy banks and old logs. In Costa Rica it seems to be restricted to the central Volcanic Highlands and the Cordillera de Talamanca. The brightly colored berries and mat-forming ability have made this species valuable as a greenhouse or moist-area ornamental. These plants resemble small collections of *Didymaea*.

Oldenlandia Linnaeus

REFERENCES—E. E. Terrell, Synopsis of *Oldenlandia* (Rubiaceae) in the United States. *Phytologia* 68: 125–133. 1990. E. E. Terrell and W. H.

Lewis, Overview and annotated list of North American species of *Hedyotis*, *Houstonia*, *Oldenlandia* (Rubiaceae) and related genera. *Phytologia* 71: 221–243. 1991. D. A. Halford, Review of the genus *Oldenlandia* L. (Rubiaceae) and related genera in Australia. *Austrobaileya* 3: 683–722. 1992.

Annual or perennial **herbs** (rarely subshrubs), stems erect or decumbent, simple or branched, glabrous or puberulent; **stipules** interpetiolar, small, acute to acuminate, often united to the base of the petioles to form a short sheath, with 1–several awns. **Leaves** opposite and decussate, sessile or short-petiolate; **leaf blades** usually narrow, often with a stiff mucronate tip, domatia absent. **Inflorescences** axillary or terminal, open and branched panicles and cymes or the flowers solitary or fasciculate in the leaf axils, flowers sessile to long-pedicellate. **Flowers** bisexual, monomorphic or distylous, usually small, hypanthium turbinate to hemispheric, calyx lobes (3–)4(–5–8), equal, narrowly to broadly triangular; **corolla** rotate or salverform to funnelliform, white to lavender, pink, or purple, tube cylindrical, the throat often puberulent, corolla lobes (3–)4(–5), valvate in bud; **stamens** (3–)4(–5), anthers dorsifixed and sessile or on short filaments inserted on the throat, included or exerted; **ovary** 2-locular, usually with many horizontal ovules on peltate placentas attached near the base of the septum, style filiform, stigmas 2, linear to subglobose. **Fruits** capsular, often papery, globose to oblong, usually with a loculicidally dehiscent apex (beak), later also septicidally dehiscent; **seeds** usually many (50–100), angular to subglobose, smooth to reticulate or alveolate, often becoming viscid when moistened.

A pantropical and subtropical genus with probably ca. 100 species but with problems regarding generic circumscription. Some authors have suggested placing this genus under *Hedyotis* or *Houstonia*, while others divide it into smaller genera; see the references cited above. Our plants of this genus are recognized by their delicate herbaceous habit, the very small or linear-lanceolate leaves, the axillary flowers or small few-flowered inflorescences, the minute flowers on filiform pedicels, and the broadly rounded thin-walled capsules with small seeds.

Many Costa Rican collections formerly identified as *O. corymbosa*, *O. herbacea*, and *O. lancifolia* are probably the same species: *O. corymbosa*. This conclusion is based on an overview of the material and following the keys and descriptions of Verdcourt in the *Flora of Tropical East Africa* (1976).

Key to the Species of *Oldenlandia*

- 1a. Leaf blades less than 5 mm long, usually broadly ovate; plants often forming small mats (not yet collected in Costa Rica) *O. callitrichoides*

- 1b. Leaf blades more than 5 mm long, narrowly elliptic-ovate to lanceolate or linear; plants diffuse or forming loose mats 2
- 2a. Corolla 2–11 mm long; fruit with a beak 0.8–1 mm long (not yet known to occur in Costa Rica) *O. herbacea*
- 2b. Corolla 0.5–2 mm long; fruit with a small or well-developed beak 3
- 3a. Flowers pink or white marked with lavender, flowers often 2–3/peduncle; fruit globose to globose-oblate, rounded at the base but not saccate, with a beak 0.1–0.6 mm high *O. corymbosa*
- 3b. Flowers white, flowers usually solitary; fruit broader than long and distinctly rounded (saccate) at the base, with a beak ca. 1 mm long *O. lancifolia*

Oldenlandia callitrichoides Griseb., Mem. Am. Acad. 2, 8: 506. 1863. *Oldenlandiopsis callitrichoides* (Griseb.) Terrell & W. H. Lewis, Brittonia 42: 185. 1990.

Prostrate **herbs** to 10 cm tall, much-branched and often forming mats, leafy stems 0.1–0.5 mm thick (when dried), glabrous; **stipules** adnate to petiole base and forming a short sheath to 0.5 mm long, sheath entire distally or with a small appendage, glabrous. **Leaves** very small, petiole 0.5–2 mm long; **leaf blades** 1–3.5 mm long, 1–3 mm broad, rounded-triangular to ovate, apex bluntly obtuse or rounded, base broadly obtuse to rounded and subtruncate, somewhat decurrent on petiole, drying membranaceous, greenish, glabrous above and below (or with a few broad-based hairs ca. 0.2 mm long), 2° veins 3–4/side, strongly ascending. **Inflorescences** of solitary flowers in distal leaf axils, usually only 1 flower per node, pedicels 1–9 mm long, filiform, glabrous. **Flowers** 2–3 mm long, hypanthium 1–1.5 mm long, calyx lobes 0.2–0.6 mm long. **Fruits** 2–3 mm long (including the calyx lobes), ca. 1 mm diam., distally truncated, with a few whitish raphides on the greenish surface, calyx lobes ca. 0.5 mm long.

Distinctive little plants usually found on sandy soil in open sunny situations, in tropical lowland sites. This species has the smallest leaves found among Central American Rubiaceae. In general aspect, these plants resemble *Pilea hernariarioides* (Sw.) Weddell and *P. microphylla* (L.) Liebm. This species is known from the Yucatan peninsula and from central Panama, but it has not been collected elsewhere in Central America. Terrell and Lewis based a new genus on this distinctive species (see synonymy).

Oldenlandia corymbosa L., Sp. Pl. 119. 1753. Figure 3.

Herbs to 15(–30) cm tall, prostrate or erect, with few to many branches, leafy stems 0.2–1.3 mm thick, glabrous or with a few hairs at the nodes; **stipules** with a sheath 0.3–2 mm long, with 2–5 slender unequal awns to 1.5 mm long. **Leaves** sessile or with petioles to 1 mm long; **leaf blades** (7–)15–30(–45) mm long, 0.5–3.5(–6) mm broad, linear to linear-oblong or very narrowly el-

liptic-oblong, apex abruptly obtuse to acute and with a minute (0.2 mm) apiculate tip, narrowed to the base, drying chartaceous and with the margins usually revolute, dark above, glabrous or minutely scabrid above and below (or with the cystoliths appearing like minute tri-chomes), 2° veins usually obscure. **Inflorescences** axillary, with single flowers on slender pedicels or cymose-umbellate with 3 (2–5) flowers on a common filiform peduncle 2–8 mm long, both singular and umbellate inflorescences often present on the same stem or node, pedicels 2–6(–12) mm long, filiform and glabrous. **Flowers** very small, hypanthium 0.5–1 mm long, obconical to cupular, glabrous, calyx lobes 4, 0.7–1.5 mm long, narrowly triangular; **corolla** rotate, white or white marked with lavender, blue, or purple, tube 0.6–1 mm long, lobes 0.5–1.2 mm long; **stamens** 4, sessile on the distal half of the tube, anthers ca. 0.4 mm long. **Fruits** 1.7–2.7 mm diam., body of the fruit 1.2–2 mm long and truncated at the apex, raphides prominent, calyx lobes ca. 0.5 mm long, borne on slender pedicels 4–11 mm long; **seeds** ca. 0.3 mm long, ellipsoid to depressed conic, reticulate.

Plants of open weedy sites on sandy soils in evergreen and in seasonally deciduous formations, from near sea level to 1500 m. Probably flowering and fruiting throughout the year. The species has been found in both the Caribbean and Pacific lowlands and in the Meseta Central. The species appears to have originated in Africa but is now widespread in the tropics.

Oldenlandia corymbosa is recognized by its short weedy habit, almost linear subsessile leaves, minute flowers, and rounded capsules. The senior author believes that this is probably the correct name for all the Central American material formerly called *O. corymbosa*, *O. herbacea*, and *O. lancifolia*. Separation of species on the basis of inflorescence differences or whether or not the stipules are bifid appears to be trivial.

Oldenlandia herbacea (L.) Roxb., Hort. Bengal. 11. 1814. *Hedyotis herbacea* L., Sp. Pl. 102. 1753.

Annual or perennial **herbs**, 5–60 cm tall, erect to spreading and decumbent, stems glabrous, with 4 lon-

gitudinal ridges; **stipules** forming a very short (0.1–0.5 mm) sheath, truncate and with a few awns to 0.3 mm long. **Leaves** sessile; **leaf blades** 6–55 mm long, 1–4 mm wide, linear to linear-lanceolate, apex acute, base cuneate, drying chartaceous, glabrous or with a few short hairs along the margins. **Inflorescences** axillary, flowers 1 or 2/node, pedicels 3–30 mm long, filiform, glabrous. **Flowers** usually isostylous, hypanthium 0.5–1 mm long, ovoid, glabrous to papillate or puberulent, calyx lobes 0.5–2.5 mm long, narrowly triangular, scabridulous on the margins; **corolla** white or lavender, or the tube green and the lobes with purple marks, corolla tube 2–11 mm long, cylindrical, lobes 1–3 mm long, ovate. **Fruits** 2.2–5 mm long, 1.5–2 mm diam., subglobose to ovoid, drying pale yellowish, glabrous to puberulent, crowned by the dark calyx lobes, beak 0.8–1 mm long; **seeds** 0.2–0.4 mm long, ovoid to ellipsoid, reticulate, brown.

Weeds of open sunny sites. Originally from Africa but now naturalized in Asia and parts of the Americas. The above description is based on Verdcourt (1976). This species has not yet been recorded from Costa Rica. Central American material earlier placed under this name is likely to be *Oldenlandia corymbosa* or *O. lancifolia*.

Oldenlandia lancifolia (Schumach.) DC., Prodr. 4: 425. 1830. *Hedyotis lancifolia* Schumach. in Schumach. & Thonn., Beskr. Guin. Pl. 72. 1827. *Manettia bocaturensis* Dwyer, Ann. Missouri Bot. Gard. 67: 278. 1980.

Perennial (rarely annual) **herbs** to 90 cm long, prostrate or creeping, usually much-branched near the base and with simple distal stems, leafy stems glabrous or rarely minutely scabridulous; **stipules** forming a sheath to 1 mm long, with 2–5 slender awns 0.5–1.5 mm long. **Leaves** sessile or subsessile; **leaf blades** 10–60 mm long, 2–12 mm broad, linear or linear-lanceolate to narrowly elliptic, apex acute, base cuneate, drying chartaceous, dark green above, glabrous on both surfaces but often minutely scabrid along the revolute margins, 2° veins 3–5/side, strongly ascending but thin and difficult to see. **Inflorescences** axillary, of solitary flowers or several flowers on very short peduncles (or reduced lateral shoots), pedicels 5–30 mm long, filiform, glabrous or scabridulous. **Flowers** monomorphic, ca. 3 mm long, hypanthium ca. 0.8 mm long and 1.5 mm diam., cupulate, glabrous or with scattered short hairs, calyx lobes 1–1.8 mm long, triangular, glabrous or scabridulous; **corolla** white (sometimes tinged with pink or purple), tube ca. 1 mm long, lobes 1–2 mm long; stigma lobes 0.7–1.4 mm long. **Fruits** 2–3 mm long (including the 1 mm tall beak), 3.2–5 mm in diam., depressed subglobose; **seeds** 0.3–0.4 mm long.

Herbs of both seasonally deciduous formations and lowland rain forest areas. The species is widespread in tropical Africa and has been introduced to parts of the South America and the West Indies. The preceding description follows that of Verdcourt (1976).

Central American material earlier ascribed to this species is probably *O. corymbosa*. Likewise, Steyermark's use of this name in the Flora de Venezuela (1974, pp. 408–411), may be incorrect.

Osa Aiello

REFERENCE—A. Aiello, A re-examination of *Portlandia* and associated taxa. J. Arnold Arbor. 60: 38–126. 1979.

Small **trees**, stems slightly expanded at the nodes; **stipules** united (interpetiolar), small, with an acute central lobe. **Leaves** opposite, petiolate, attenuate at the apex, drying thin-chartaceous and grayish green, entire, pinately veined, domatia absent. **Inflorescence** of single axillary flowers, borne on pedicels continuous with the base of the hypanthium/ovary. **Flowers** large, radially symmetrical, glabrous, calyx with 6 long narrow lobes; **corolla** with a long tube and distally funnelform, corolla lobes 5, broadly triangular; **stamens** 5, anthers linear; **ovary** 2-locular, placentas borne on the septum, with ca. 10 ovules in each locule, style filiform. **Fruits** thin-walled capsules, ellipsoid, with 6 longitudinal ribs, apparently opening septicidally, the calyx lobes persisting distally; **seeds** biseriate, slightly compressed, lacking wings, not imbricate, with persisting funicle.

A monotypic genus known only from the Osa Peninsula of Costa Rica. No other species of Costa Rican Rubiaceae has such large flowers. This genus is related to *Portlandia* and to a lesser extent to *Hintonia*.

Osa pulchra (D. Simpson) Aiello, J. Arnold Arbor. 60: 116. 1979. *Hintonia pulchra* D. Simpson, Phytologia 29: 277. 1974. Figure 15.

A small **tree** or slender treelet, 2.5–15 m tall, leafy stem 1.5–6 mm thick, glabrous, slightly expanded below the node; **stipules** 1–3 mm long, the broad base 1–2 mm high with a narrowed acute tip 0.5–1.5 mm long, persisting. **Leaves** with petioles 4–12 mm long, 0.7–1.5 mm thick, glabrous, poorly differentiated from the lamina base; **leaf blades** 12–19 cm long, 3–6 cm broad, elliptic-oblong or narrowly oblong, apex gradually narrowed and acuminate, base acute to attenuate, drying thin-chartaceous and grayish green, glabrous above and below, 2° veins 6–8/side, 3° veins obscure, domatia lacking. **Inflorescences** of solitary flowers in the axils of distal leaves, pedicels ca. 15 mm long but merging imperceptibly into the flower base, ca. 1 mm diam., glabrous, drying black. **Flowers** glabrous externally, probably slightly pendulous, apparently homostylous, hypanthium ca. 6 mm long, obconic, calyx lobes 18–40 mm long, 0.5–2.5 mm broad; **corolla** long-tubular and funnelform distally (trumpet-shaped), white, tube 17–27 cm long, 4–5 mm

diam. and gradually flaring to 80 mm diam. at the mouth, lobes ca. 15 mm long and 30–40 mm broad at the base, broadly obtuse; anthers more than 20 mm long, 0.7 mm thick. **Fruits** ca. 3 cm long and 1.5 cm broad, oblong-ellipsoid, dark brown, the sepal lobes persisting but breaking off; **seeds** ca. 6 mm long, testa tuberculate.

This species is known from only a few collections in lowland rain forest near Rincón de Osa at ca. 50 m elevation on the Osa Peninsula. Flowering in January–February, with immature fruits in June and mature fruits in January.

Osa pulchra is distinguished by its very large trumpet-shaped flowers that are thin in texture. No other Costa Rican member of the Rubiaceae has so long a flower. The long narrow basal tube suggests pollination by a long-tongued sphingid moth. The flowers are reminiscent of those of ornamental species of *Brugmansia* (formerly included in *Datura*, Solanaceae).

Palicourea Aublet

REFERENCE—C. M. Taylor, Revision of *Palicourea* in Mexico and Central America. Syst. Bot. Monogr. 26: 1–102. 1989.

Shrubs or small trees, glabrous or pubescent, stems terete, trigonous or quadrangular; **stipules** interpetiolar and often also intrapetiolar to form a sheathing tube with 2 triangular lobes or awns on each side (4/node) or sometimes elongated interpetiolarly into emarginate or bilobed apices with the intrapetiolar sheath poorly developed, colleters present within at the base. **Leaves** opposite and decussate or rarely 3–4/node, petiolate or rarely sessile; **leaf blades** entire and often elliptic, apex acute to acuminate, base rounded to acute, drying chartaceous to subcoriaceous, pinnately veined, domatia present or absent. **Inflorescences** terminal, paniculate with opposite or alternate branching, variable in form (from elongate and racemose to thyrsoid or broadly corymbose) with flowers usually in distal cymose groups, peduncles and branches of the inflorescences often colored red, orange, yellow, purple, or blue (rarely green), glabrous or pubescent, bracts and bracteoles usually present (in Costa Rica), flowers usually pedicellate. **Flowers** bisexual and usually distylous, radially symmetric or slightly bilat-

erally symmetric when the corolla is curved or gibbous on 1 side, glabrous or pubescent externally, hypanthium usually turbinate, calyx tube with 5 calyx lobes (rarely truncated or spathaceous); **corolla** yellow, orange, red, purple, or blue (rarely white or cream), tubular to funnelform or salverform, membranaceous to carnos, the corolla tube straight or curved, usually expanded (gibbous) near the base, glabrous or puberulent externally, usually with a ring of hairs within the lower half of the tube (more rarely with the hairs in the upper half), corolla lobes 5, valvate in bud; **stamens** 5, inserted in the middle or on the throat of the tube, anthers dorsifixed and bifid at the base, included or exserted; **ovary** 2(–6)-locular, with 1 erect ovule from a basal placenta in each cell, stigmas 2-branched. **Fruits** fleshy, exocarp bluish to bluish black or purplish black; pyrenes usually 2, hemispheric with ca. 5 longitudinal ribs on the rounded back, usually with a longitudinal sulcus on the flattened inner face.

A Neotropical genus of about 200 species, ranging throughout moist tropical vegetation from Mexico and the West Indies to southern Brazil and Paraguay. Most species are South American; there are 31 in Costa Rica. As in *Hoffmannia*, this genus has speciated profusely at middle and higher (1000–2800 m) elevations. These plants are recognized by their colorful terminal inflorescences, corolla tubes often slightly bent or expanded at the base, ovaries with a single erect ovule in each locule, and the fleshy fruit usually with longitudinal ribs when dried. The infructescences usually become purple regardless of their color during anthesis. The stipules forming a short tube above the node and with two distal awns or lobes, and the leaves with many secondary veins are additional characteristics distinguishing many Costa Rican species.

Palicourea is separated from the closely related genus *Psychotria* by the ring of hairs in the interior of the lower half of the corolla tube, a tendency for the corolla tube to be inflated or gibbous near the base, the more colorful inflorescences, and the generally larger more colorful corollas. Despite these differences, dried fruiting material may be very difficult to separate.

Key to the Species of *Palicourea*

- 1a. Plants of lowland formations, rarely found from as high as 1000 m elevation 2a
- 1b. Plants of montane forest formations, from (900–)1000 to 3200 m elevation 5a
- 2a. Flowers lavender or white marked with purple; stipule forming a sheath to 8 mm long [leaves with 9–15 pairs of secondary veins; from wet Caribbean slopes at 500–1000 m elevation] *P. copensis*
- 2b. Flowers red, orange, or yellow; stipular sheath 0–2 mm long; wide-ranging species 3a

- 3a. Leaves 3/node, stipular teeth 6/node, 8–12 mm long and persisting, leaf blades to 8 cm broad *P. triphylla*
- 3b. Leaves 2/node, stipular teeth or lobes 4, 2–9 mm long, often deciduous, leaf blades to 16 cm broad 4a
- 4a. Stipular lobes rounded; leaf blades 15–28 cm long, to 16 cm broad *P. guianensis*
- 4b. Stipular teeth acute; leaf blades 7–14 cm long, to 7 cm broad *P. crocea*
- 5a. Plants pilose with hairs 1.5–2 mm long; stipules united and bifid or emarginate on each side; flowers yellow and pilose *P. standleyana*
- 5b. Plants glabrous to puberulent, the hairs not exceeding 1 mm in length; stipules 4-lobed, bifid or emarginate; flowers white, yellow, blue, or purplish 6a
- 6a. Calyx teeth or calyx lobes regularly more than 1.5 mm long [often persisting in fruit and with slightly smaller dimensions; flowers usually blue, purple, or white (red to yellowish only in *P. macrocalyx* and *P. orosiana*)] 7a
- 6b. Calyx teeth or calyx lobes 0.2–1.5 mm long 17a
- 7a. Calyx lobes more than 3.5 mm long 8a
- 7b. Calyx lobes less than 3.5 mm long 15a
- 8a. Calyx spathe-like and splitting down 1 side (to 20 mm long); corolla tube 3–4 cm long; leaves with 12–22 pairs of 2° veins *P. spathaceae*
- 8b. Calyx 5-lobed (not spathe-like); corolla tubes 8–26 mm long; leaves with up to 19 pairs of 2° veins 9a
- 9a. Corolla 20–26 mm long, ca. 4 mm diam. [calyx lobes 4–14 mm long, lanceolate; bracts of the inflorescence to 25 mm long and lanceolate; secondary veins 12–18 pairs; 1400–2200 m elevation] *P. hammelii*
- 9b. Corolla tubes less than 20 mm long and 4 mm diam. 10a
- 10a. Young stems minutely puberulent 11a
- 10b. Young stems glabrous 12a
- 11a. Calyx lobes 10–14 mm long, corolla white; stipule lobes 7–20 mm long; leaves with 15–19 pairs of 2° veins; western Panama *P. bella*
- 11b. Calyx lobes 6–11 mm long, corolla yellow; stipule lobes 6–17 mm long; leaves with 8–12 pairs of 2° veins; central Costa Rica *P. orosiana*
- 12a. Leaves with 17–20 pairs of 2° veins; stipule lobes 2–9 mm long [corolla white]; floral bracts 12–16 mm long; central Costa Rica *P. bellula*
- 12b. Leaves with 7–14 pairs of 2° veins; stipule lobes 2–10 mm long 12a
- 13a. Floral bracts 10–20 mm long, persisting and enclosing the flowers; corollas white; 2600–2800 m elevation in the Talamanca mountains *P. skotackii*
- 13b. Floral bracts 6–10 mm long, deciduous; corollas white with yellow or blue; Cordillera de Tilarán and central volcanic highlands, 1400–2200 m elevation .. 14a
- 14a. Corolla white and blue; stipule lobes 2–4 mm long; inflorescence to 22 cm long and narrowly thyriform *P. albocaerulea*
- 14b. Corolla white and yellow; stipule lobes 4–10 mm long; inflorescences to 15 cm long and paniculate *P. macrocalyx*
- 15a. Young stems usually puberulent [flowers white; inflorescences narrowly thyriform; leaves 2–7 cm broad; 800–1600 m elevation] *P. lancifera*
- 15b. Young stems glabrous 16a
- 16a. Leaves 1–2(–3) cm broad, blades to 8(–10) cm long; corolla blue and white (compare also 17a below) *P. salicifolia*
- 16b. Leaves becoming larger and broader; flowers variously colored 17a
- 17a. Flowers purple to violet, blue, or white (if reddish then reddish purple or lavender) 18a
- 17b. Flowers yellow to orange or red-orange 24a
- 18a. Leaf blades not more than 9 cm long [0.7–3.5 cm broad]; young stems often slightly puberulent 19a
- 18b. Leaf blades usually becoming more than 9 cm long; young stems glabrous or puberulent beneath the inflorescence 20a

- 19a. Inflorescences blue, corolla white to violet or blue; leaves thick, petioles thick; 1800–3200 m elevation *P. adusta*
- 19b. Inflorescences yellowish green, corolla white to yellow; leaves thin, petioles slender; 1300–2300 m elevation *P. montivaga*
- 20a. Leaf blades 1–3(–4) cm broad, to ca. 14 cm long 21a
- 20b. Leaf blades usually becoming more than 4 cm broad, to 24 cm long 22a
- 21a. Inflorescences thyriform and purple, to 16 cm long; calyx lobes ca. 0.4 mm long *P. angustifolia*
- 21b. Inflorescences paniculate and purple, to 8 cm long; calyx lobes ca. 1 mm long *P. purpurea*
- 22a. Corolla white, tube 3–6 mm long; calyx lobes ca. 0.3 mm long; leaves with 9–11 pairs of 2° veins *P. tilaranensis*
- 22b. Corolla blue to purple, tube 5–10 mm long; calyx lobes 1–3 mm long; leaves with 11–21 pairs of 2° veins 23a
- 23a. Inflorescence purple, paniculate; leaf blades to 26 × 13 cm, with 11–19 pairs of 2° veins *P. discolor*
- 23b. Inflorescence blue, thyriform; leaf blades to 18 × 8 cm, with 15–21 pairs of 2° veins *P. brenesii*
- 24a. Stems and veins on the lower leaf surfaces densely puberulent with short stiff scurfy or slender hairs; flowers puberulent *P. vestita*
- 24b. Stems glabrous to sparsely puberulent; flowers glabrous or puberulent 25a
- 25a. Stipule lobes/teeth 0.5–2 mm long; leaf blades 3–12 cm long and 1–3.5 cm broad 26a
- 25b. Stipule lobes/teeth 2–8 mm long; leaf blades usually more than 7 cm long and 3 cm broad .. 27a
- 26a. Flowers yellow or white with yellow and purple; leaves with 12–18 pairs of 2° veins; 1200–1600 m elevation *P. garciae*
- 26b. Flowers white and yellow; leaves with 6–9 pairs of 2° veins; wide ranging in Costa Rica; 1100–2000 m elevation *P. montivaga*
- 27a. Inflorescence branches red to orange (to purple in fruit); corolla tube 6–10 mm long, orange; (800–)1200–1700 m elevation *P. padifolia*
- 27b. Inflorescence branches yellow to greenish yellow; corolla tube 7–13 mm long, yellow; (800–)1000–2300 m elevation 28a
- 28a. Corolla tube 7–11 mm long; stems glabrous; leaves with 8–13 pairs of 2° veins *P. padifolia*
- 28b. Corolla tube 11–13 mm long; stems puberulent or glabrous; leaves with 11–19 pairs of 2° veins *P. lasiorhachis*

Palicourea adusta Standl., J. Wash. Acad. Sci. 18: 279. 1928. Figure 53.

Small **shrubs** or rarely little treelets, 0.5–3(–6) m tall, leafy branchlets 0.7–6 mm thick, glabrous or with minute (0.1–0.5 mm) appressed hairs, becoming terete; **stipules** 2–6 mm long, united above the petiole and forming a very short (1–3 mm) tubular sheath, with 2 distal teeth 1–3 mm long. **Leaves** opposite, petioles 4–12(–22) mm long, 0.5–1 mm thick, glabrous (rarely minutely puberulent); **leaf blades** 3–7(–10) cm long, 1–3.5 cm broad, narrowly to broadly elliptic, elliptic-oblong, apex acuminate with tip 5–10(–15) mm long, base broadly obtuse to acute and slightly decurrent on the petiole, drying thin-chartaceous to stiffly chartaceous, brown to greenish, glabrous above and usually with linear cystoliths visible, glabrous or with a few minute appressed hairs on the veins beneath, 2° veins 6–11/side and usually joining a vein at the edge of the leaf, intersecondaries present. **Inflorescences** 6–12 cm long, 4–9 cm broad, open py-

ramidal with opposite branching, yellowish to blue-gray, peduncles 1.5–5 cm long, 0.7–1.4 mm thick, puberulent with ascending hairs 0.2–0.4 mm long, bracts 1–4 mm long, linear-lanceolate, bracteoles 1–2.5 mm long, pedicels 1–5 mm long. **Flowers** usually glabrous externally, hypanthium 1–1.5 mm long, turbinate, glabrous or sparsely puberulent (hairs to 1 mm long), calyx lobes 0.5–0.8(–1.5) mm long, ca. 1 mm broad at the base; **corolla** tubular, bluish purple, violet, or white marked with purple or violet, usually glabrous, tube 6–10.5 mm long, 1–2 mm diam. and slightly expanded at the base, corolla lobes 5, 1.5–3 mm long, minutely whitish papillate along the inner margin; anthers 1.5–2 mm long. **Fruits** 3–4.5(–6) mm long and 4 mm diam., obovoid, becoming dark purple to deep blue and translucent, with longitudinal ridges when dry, persisting calyx ca. 0.7 mm high.

Plants of ridges and wet open areas in evergreen montane rain forest formations, (1800–)2200–3100

m elevation. Probably flowering and fruiting throughout the year. These plants appear to prefer ridges and wet open areas. The species ranges from the Cordillera de Tilarán to western Panama.

Palicourea adusta is recognized by its high-altitude habitat, small leaves, small calyx lobes, usually bluish flowers (less often yellowish or purple). This species is similar to *P. montivaga* with white flowers and *P. salicifolia* with yellowish inflorescences.

***Palicourea albocaerulea* C. M. Taylor, Syst. Bot. Monogr. 26: 15. 1989. Figure 53.**

Shrubs or small trees, 2–7 m tall, leafy stems 1.2–4 mm thick, glabrous, quadrangular or rounded; **stipules** to 8 mm long, united at the base to form a sheath 1–4 mm long, apex truncated with 2 teeth 2–4 mm long. **Leaves** opposite, petioles 8–22 mm long, 0.6–1.2 mm thick, glabrous, often drying reddish brown; **leaf blades** 5–15 cm long, 2–5 cm broad, narrowly elliptic to narrowly oblong or elliptic-oblong, apex acuminate with tip 6–15 mm long, base acute (obtus) to attenuate and slightly decurrent on petiole, drying chartaceous, glabrous above, glabrous beneath or with a few short (0.1–0.3 mm) hairs along the midvein beneath, linear cystoliths sometimes visible on the lower surface, 2° veins 7–11/side and merging with a marginal vein at the leaf edge. **Inflorescences** 11–22 cm long, 3–8 cm broad, narrowly pyramidal (thyrsoid) with opposite or alternate lateral branches, peduncles 1.5–5 cm long, 1.6–2.2 mm thick, glabrous and drying dark brown, bracts 6–10 mm long, linear and acute, pedicels 3.5–10 mm long, bracteoles 2–6(–8) mm long, glabrous. **Flowers** glabrous externally, hypanthium ca. 1.5 mm long, ca. 0.5 mm diam. and funnellform, calyx lobes 5, 3.5–9 mm long, 1–1.2 mm broad, narrowly oblong, often unequal; **corolla** tubular, white or white with blue, tube 8–11 mm long, 2–3 mm diam., slightly expanded near the base, corolla lobes 1–2 mm long and 1.5 mm broad at the base; anthers ca. 2 mm long. **Fruits** 5–8 mm long (not including the calyx lobes) and 5–10 mm diam., ovoid or globose, bluish black, persisting calyx lobes ca. 7 mm long.

Plants of lower montane cloud forest formations, from 1450 to 1650 m elevation. Flowering in September–December; fruiting in June. This species is only known from the Cordillera de Tilarán and adjacent areas in Costa Rica.

Palicourea albocaerulea is recognized by its restricted range, generally glabrous parts, long inflorescences, long calyx lobes, and white corollas that turn blue with age. The narrow leaves and long slender petioles are also distinctive. This is our only species in which the flowers change from white to blue. Compare this species with *P. lancifera* with shorter calyx lobes and flowers that do not turn blue.

***Palicourea angustifolia* H.B.K., Nov. gen. sp. 3: 367. 1819. *P. lanceolata* Oersted ex Polakowsky., Vidensk. Meddel. Dansk. Naturhist. Foren. Kjobenhavn 17. 1852.**

Shrubs or small trees, 2–5(–10) m tall, leafy branchlets 1.3–4 mm thick, glabrous or rarely sparsely puberulent, terete; **stipules** to 10 mm long, the tubular sheath 2–4 mm long and truncate but with slender awns 3–6(–8) mm long, glabrous, persisting. **Leaves** opposite, petioles 2–9(–13) mm long, 0.6–1.2 mm thick, glabrous; **leaf blades** 5–15(–23) cm long, 1–4(–5) cm broad, lanceolate to narrowly elliptic or very narrowly oblong, apex gradually narrowed and acute or acuminate, tip 4–14(–25) mm long, base acute and slightly decurrent on petiole, drying chartaceous, glabrous above, glabrous beneath or with short (0.4 mm) thin whitish hairs along the veins, 2° veins 10–14/side. **Inflorescences** 3–14(–16) cm long, 3–6(–8) cm broad, a narrowly pyramidal (thyrsoid) panicle, peduncles 1.5–3(–6) cm long, 1–2 mm, thick, glabrous or minutely appressed-puberulent, lateral branches opposite, subopposite or alternate, purple to magenta, bracts 2–5 mm long, pedicels 0–3 mm long, bracteoles ca. 1 mm long. **Flowers** glabrous or minutely (0.1 mm) papillate puberulent externally, hypanthium ca. 1 mm long, calyx lobes ca. 0.4 mm long, triangular; **corolla** slender funnellform, rose red to purple or fuchsia, tube 9–14 mm long, 1.5–2.5 mm diam., expanded near the base, corolla lobes 5, 1.2–2.5 mm long; anthers 1.7–2.5 mm long, included. **Fruits** 4–6 mm long and 5 mm diam., globose to ovoid, becoming purple and drying black, puberulent or glabrate, persisting calyx ca. 0.5 mm long.

Plants of evergreen montane forest formations on both the Caribbean and Pacific slopes, from (1400–)1600 to 2000(–2300) m elevation. Flowering and fruiting throughout the year but with most flowering collections made in January–September. The species ranges from central Costa Rica to Peru.

Palicourea angustifolia is recognized by the narrow leaves, truncated stipule sheath with long awns, narrow inflorescences, and slender funnellform purple corollas with relatively short lobes. This species resembles *P. padifolia* and *P. purpurea* but differs in the relatively narrower inflorescences, shorter pedicels, and thinner, more funnellform corollas that are usually minutely puberulent at the base. In addition, *P. padifolia* has yellow corollas and red or orange inflorescence branches.

***Palicourea bella* (Standl.) Dwyer, Ann. Missouri Bot. Gard. 67: 299. 1980. *Psychotria bella* Standl., J. Wash. Acad. Sci. 18: 185. 1928.**

Shrubs or small trees to 5 m tall, leafy stems ca. 4 mm thick and quadrangular, glabrous or with small (0.1–0.3 mm) hairs; **stipules** 10–20 mm long, to 15 mm broad,

with thin leaf-like texture, united above the petioles, oblong, rounded and bilobed to emarginate. **Leaves** clustered distally, petioles 8–20 mm long, 1.2–2 mm thick, puberulent; **leaf blades** 9–22 cm long, 3–8.5 cm broad, elliptic to elliptic-obovate or oblong-elliptic, apex acuminate, base gradually narrowed and acute, drying chartaceous, dark greenish brown, glabrous or with short (0.3 mm) hairs on the veins and smaller hairs between the veins on both surfaces, 2° veins 12–19/side. **Inflorescences** solitary, 8–20 cm long, 7–10 cm broad, broadly corymbiform, peduncles 5–13 cm long, to 2 mm thick and sparsely strigulose, bracts 10–26 mm long, ovate-oblong, translucent brown and sparsely hirtellous, secondary peduncles 15–25 mm long, bright pink to purple, pedicels 2–8 mm long, obscured by the large bracts and bracteoles to 8 mm long. **Flowers** with hypanthium ca. 2 mm long, glabrous or with conspicuous thin yellowish hairs ca. 0.7 mm long, the calyx lobes 6–14 mm long, 3–6 mm broad, ovate to ovate-elliptic, drying thin translucent with scattered short (0.2 mm) hairs; **corolla** tubular, white to pink, cariose, tube 14–20 mm long and 2–3 mm diam., dilated at the base, corolla lobes 4–5 mm long, ovate; anthers ca. 3.5 mm long. **Fruits** ca. 6 mm long and 6 mm diam., ellipsoid, glabrous or sparsely puberulent.

Plants of evergreen montane forest formations at (1500–)2000–2700 m elevation. Flowering in April. This species is only known from Chiriquí Province in Panama and a collection from the Caribbean slope of central Costa Rica at 1500 m.

Palicourea bella is recognized by the broadly two-lobed stipules, corymbiform inflorescences with broad thin bracts, and the large thin calyx lobes. In life, both inflorescences and calyx are red-violet to bright pink in color. The similarity in morphology, texture, and vestiture of bracts and calyx lobes is an interesting example of heterotopy. This species is similar to *P. bellula* (q.v.) as well as to *P. hammelii* C. M. Taylor and *P. ochnoides* Dwyer of western Panama. *Grayum* 7046 (CR, MO) from Volcán Barva is tentatively placed here.

Palicourea bellula C. M. Taylor, Syst. Bot. Monogr. 26: 24. 1989. Figure 49.

Shrubs or slender treelets, to 2.5 m tall, leafy stems 2.5–5 mm thick, glabrous, quadrangular and drying dark, grayish in age; **stipules** 5–11 mm long, 7–10 mm broad, united above the petioles for 2–3 mm to form a broad tube, with 2 rounded lobes 2–4 mm high, thin in texture and glabrous. **Leaves** opposite, petioles 4–18 mm long, 1.5–2.5 mm thick, glabrous, sulcate adaxially near the base; **leaf blades** 7.5–14 cm long, 3.5–7 cm broad, broadly elliptic to slightly elliptic-obovate, apex acuminate, tip ca. 5–10(–15) mm long, base obtuse (acute) and slightly decurrent on petiole, drying stiffly chartaceous, greenish, glabrous above, with thin whitish hairs 0.3–1 mm long along the sides of the midvein and on some 2° veins beneath, 2° veins (10–)17–20/side. **Inflorescences** 1 or 3,

9–14 cm long, 9–11 cm broad, rounded panicles, red-violet to fuchsia, peduncles 3–8 cm long, 1–3 mm thick, glabrous, bracts 12–16 mm long, 3–4 mm broad, lanceolate, bracteoles 5–12 mm long and 3–5 mm broad, narrowly ovate, pedicels 4–12 mm long. **Flowers** glabrous externally, hypanthium ca. 1 mm long and 1.2 mm diam., drying dark and glabrous, calyx tube 2–3 mm long and broadly cupulate, calyx lobes 5, 4–7 mm long, 2–3 mm broad, ovate, red-violet to fuchsia; **corolla** white, tubular, cariose, tube 12–15 mm long and 2.5 mm diam., corolla lobes 2–3 mm long; anthers ca. 3 mm long. **Fruits** not seen at maturity.

Plants of open sites in montane rain forest formations near the continental divide at 1900–2200 m elevation. Flowering in January–February, May, and November. This species is only known from between Volcán Viejo (Alajuela) and the southeastern slope of Volcán Barva near the upper part of Río Patria (Heredia Province) Costa Rica.

Palicourea bellula is distinguished by its colorful glabrous inflorescences with conspicuous pink to purple bracts and calyx lobes, tubular white corollas, leaves with many closely parallel secondary veins, broadly rounded stipule lobes, and restricted cloud forest habitat. This species is similar to *P. bella*, but the calyx and corolla are usually smaller and stiffer than in *P. bella*. *Palicourea hammelii* and *P. ochnoides* are similar but lack the broad imbricate calyx lobes.

Palicourea brenesii Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 1333. 1938. *P. talamancana* Standl. & L. O. Williams, Ceiba 1: 250. 1951. Figure 52.

Shrubs, 1–4 m tall, erect or clambering, often with only a few distal branches 2.5–5 mm thick, glabrous or sparsely strigillose with hairs 0.5–1 mm long, drying dark, quadrangular; **stipules** united to form a tubular sheath 3–6 mm long, truncated distally and with 2 prominent teeth (on each side) 4–7(–10) mm long and 1–2 mm broad at the base, usually glabrous, persisting. **Leaves** opposite, petioles 1.5–3 cm long, 1.2–2.2 mm thick, glabrous; **leaf blades** 9–18 cm long, 3.5–8 cm broad, broadly elliptic to elliptic-obovate or elliptic-oblong, apex abruptly narrowed and short-acuminate, base obtuse to acute, drying stiffly chartaceous, brownish or yellowish, glabrous above, glabrous or sparsely puberulent beneath, 2° veins 15–21/side. **Inflorescences** 8–15 cm long, 4–9 cm broad (at broadest part), pyramidal or elongate thyrsoid panicles, often blue throughout, peduncles 2–5 cm long, 1.5–3 mm thick, sparsely to densely puberulent with thin hairs ca. 0.2 mm long, bracts 5–8 mm long, ca. 2 mm broad, lanceolate, pedicels 0–6(–8) mm long, bracteoles 1–5 mm long. **Flowers** minutely puberulent and glabrescent distally, hypanthium ca. 1 mm long and 0.8 mm diam., calyx tube broadly cupulate, calyx lobes 1–2.5 mm long, broadly triangular and obtuse; **corolla**

blue, tubular, glabrous near the base and densely appressed-puberulent distally or glabrous throughout, tube 8–11 mm long, ca. 2 mm diam., narrowed near the middle, corolla lobes 5, 3–5 mm long; anthers ca. 2.5 mm long. **Fruits** 4–6 mm long, 4–6 mm diam., globose, glabrate.

Plants of evergreen montane rain forest formations, from 1800 to 2600(–3200) m elevation. Flowering and fruiting in February–June. The species has only been collected in the northern part of the Meseta Central (near Zarcero and Palmira) and along the Interamerican Highway in the western part of the Cordillera de Talamanca in Costa Rica.

Palicourea brenesii is distinguished by the larger leaves with many secondary veins, bright “china blue” thyrsoid panicles, and small blue to violet flowers with conspicuous calyx lobes. The usually glabrous stems contrast with the puberulent peduncle and inflorescence branches. The striking bright blue color of the inflorescence is similar to that found in species of *Faramea*. The disjunct collections from the Cordillera de Talamanca have smaller corollas and stipule lobes to 10 mm long. This species is very similar to *P. discolor* after the flowers have faded.

Palicourea copensis (Dwyer) C. M. Taylor, comb. nov. *Psychotria copensis* Dwyer, Ann. Missouri Bot. Gard. 67: 365. 1980. Figure 52.

Shrubs or small treelets, 2–5 m tall, leafy stems 2–5 mm thick, with curved yellowish or whitish hairs 0.4–0.9 mm long, glabrescent; **stipules** 6–12 mm long, united to form a broad tube to 10 mm long, 4–8 mm broad (to 14 mm broad below the inflorescences), bilobed with a distal sinus 1–6 mm deep, glabrous but with a ciliate margin, persisting. **Leaves** with petioles 10–55 mm long, 1.3–2.3 mm thick, glabrous or sparsely puberulent beneath; **leaf blades** 9–23 cm long, 3.5–9 cm broad, elliptic-obovate to elliptic-oblong, apex narrowly acuminate and 5–13 mm long, base cuneate and slightly decurrent on petiole, drying chartaceous, dark green above (pale green beneath), glabrous above or with a few hairs along the major veins, sparsely pubescent beneath with crooked whitish hairs 0.4–1.5 mm long, 2° veins 9–14/side and arcuate-ascending distally. **Inflorescences** terminal or pseudoaxillary, 1 or several per node, 2–7(–11) cm long, 3–6(–12) cm broad, pyramidal with few opposite branches, peduncles 8–26 mm long, ca. 1.5 mm thick, pubescent or glabrous, bracts 3–7 mm long, flowers in distal cymose or irregular clusters. **Flowers** with hypanthium ca. 1 mm long, obconic, glabrous or pubescent, calyx yellowish, calyx lobes quite variable, 1–3 mm long, oblong and obtuse; **corollas** lavender or white marked with purple, salverform with a distinctly gibbous base, tube 7–12 mm long, 2–4 mm diam., puberulent, corolla lobes 3–5 mm

long; anthers ca. 3 mm long. **Fruits** 6–7 mm long, 4–5 mm diam., obovoid, becoming blue or violet.

Plants of the very wet Caribbean escarpment, between 400 and 1000 m elevation. Flowering and fruiting in March–May and November. The species is known from the Caribbean slopes of Volcán Barva and the P. N. Braulio Carrillo area in central Costa Rica. It was originally described from El Copé in Coclé Province, Panama.

Palicourea copensis is recognized by its white or lavender flowers, variable sepal lobes, smaller thick-branched inflorescences, large persisting stipules, puberulence of usually curved hairs, and lower montane habitat. This is a rarely collected species that appears to prefer creek margins.

Palicourea crocea (Sw.) Roem. & Schult., Syst. Veg. 5: 193. 1819. *Psychotria crocea* Sw., Prodr. 44. 1788. Figure 50.

Shrubs or small trees, 1–5 m tall, leafy stems 1–4 mm thick, glabrous or minutely puberulent, terete; **stipules** united to form a short (0.5–2 mm) truncated tube with narrow distal teeth 1–4 mm long, glabrous, deciduous. **Leaves** opposite, petioles 6–12(–20) mm long, 1–1.5 mm thick, usually glabrous; **leaf blades** 7–14(–19) cm long, 2.5–6(–7) cm broad, elliptic, narrowly elliptic, lanceolate, to elliptic-ovate or elliptic-oblong, apex acute to acuminate, base obtuse to acute and slightly decurrent on the petiole, drying membranaceous to thin-chartaceous, greenish, usually glabrous above, with short (0.3 mm) thin hairs along the sides of the midvein beneath, 2° veins 8–12/side. **Inflorescences** 6–15 cm long, 2.5–7 cm broad, narrow pyramidal to rounded with opposite or subopposite (alternate distally) branching, reddish to orange or pink, peduncles 1.5–11 cm long, 1–2 mm thick, glabrous or sparsely and minutely puberulent, bracts 1–10 mm long, linear-lanceolate and deciduous, pedicels 4–8(–12) mm long, slender, bracteoles ca. 1 mm long and deciduous. **Flowers** distylous, glabrous or minutely puberulent externally, hypanthium ca. 1 mm long and 0.7 mm diam., calyx lobes 0.3–0.5 mm long, broadly ovate; **corolla** tubular, dark red to yellow-orange or pink (rarely bluish green), tube 5–9 mm long, 1.5–3 mm diam., inflated near the base, corolla lobes 1–2.5 mm long; anthers ca. 2.7 mm long. **Fruits** 4–6 mm long and 4 mm diam., subglobose or ovoid, becoming dark blue or black, longitudinally ribbed when dry, persisting calyx minute.

Plants of secondary growth in evergreen rain forest areas often along streams and paths in the Caribbean lowlands, from near sea level to 600 m elevation. Flowering and fruiting throughout the year (flowering mostly in April–August in Central America). The species ranges from central Mexico and the West Indies to Paraguay.

Palicourea crocea is recognized by its smaller

stature and lowland habitat, short stipular tube, colorful thyrsoid inflorescences, minute calyx lobes, and orange or red corolla tubes. This species is often found in swampy areas and other sites with poor drainage. This species is sometimes confused with *P. padifolia*, of higher elevations and with longer stipule sheaths, with *P. guianensis*, with longer stipule lobes, and with species of *Hamelia*.

Palicourea discolor K. Krause, Bot. Jahrb. Syst. 54: Beibl. 119: 40. 1916. *P. macrosepala* K. Krause, loc. cit. 41. 1916. *P. panamaensis* Standl., Ann. Missouri Bot. Gard. 25: 839. 1938. Figure 52.

Shrubs or small trees, 1–4(1–6) m tall, leafy stems 3–6 mm thick, glabrous and quadrangular; **stipules** united to form a broadly tubular sheath 2–6 mm long, truncated apically and with 2 narrow teeth 4–7 mm long, glabrous and persisting. **Leaves** opposite, petioles 1–3(–5) cm long, 1.7–2.7 mm thick, glabrous; **leaf blades** 10–26 cm long, 5–13 cm broad, elliptic to broadly elliptic-oblong, acute to short-acuminate, the tip 5–10(–15) mm long, obtuse or acute at the base, drying stiffly chartaceous, dark brown or greenish above, glabrous above, sparsely puberulent with inconspicuous (0.05–0.2 mm) thin whitish hairs on the veins beneath, 2° veins 11–19/side, united distally with a vein at the leaf edge. **Inflorescences** solitary or the basal branches subtended by leaves and apparently 3, 12–22(–30) cm long, 10–15(–24) cm broad, pyramidal with opposite or subopposite branches, bright purple in life, peduncles 2–14 cm long, 2.5–4 mm thick, glabrous, bracts 5–8 mm long, 1 mm wide, linear-lanceolate, pedicels 1–8 long, glabrous, bracteoles absent. **Flowers** glabrous externally, hypanthium 0.5–1.3 mm long and 0.3–1 mm diam., calyx lobes 1.5–5 mm long, acute to linguulate, very variable in some collections; **corolla** purple or white flushed with purple, carose, tube 7–13 mm long, 1–2 mm diam., corolla lobes 1–3.5 mm long. **Fruits** 4–5 mm long and 4–5 mm diam., globose to globose-ellipsoid, with longitudinal ribs (dried), calyx persisting or deciduous.

Plants of forest interiors and shaded thickets in evergreen montane forest formations, from 1100 to 1900(–2600) m elevation. Flowering and fruiting in February–August. The species ranges from the upper Río Grande de Orosí and Moravia de Chirripó in the Cordillera de Talamanca of Costa Rica southward into the Chiriquí Highlands of western Panama.

Palicourea discolor is recognized by its relatively large leaves and inflorescences, purple flowers and inflorescence branches, and variable calyx lobes to 5 mm long. This species is similar to *P. brenesii* with bright blue inflorescences and smaller corollas and *P. purpurea* with smaller calyx lobes and smaller leaves.

Palicourea garciae Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 22: 195. 1940, non *P. garciae* Steryerm. 1971. *Psychotria copeyana* Standl. & L. O. Williams, Ceiba 1: 251. 1940. Figure 53.

Shrubs or small trees, 1.5–5 m tall, leafy branchlets 1.5–3.5 mm thick, glabrous or with short (0.3 mm) ascending yellowish hairs, quickly becoming glabrescent and terete, drying dark; **stipules** united to form a tubular sheath 2–4 mm long, each side with 2 short (1 mm) distal lobes and a small (1 mm) central sinus, glabrous or minutely appressed-puberulent. **Leaves** opposite, petioles 5–15 mm long, 0.6–1.2 mm thick, glabrous; **leaf blades** 5–12(–15) cm long, 2–4(–4.5) cm broad, narrowly elliptic, narrowly elliptic-ovate to narrowly oblong or lanceolate, apex acuminate with tip 7–15 mm long, base acute to obtuse and slightly decurrent on petiole, drying stiffly chartaceous, much darker above than beneath, glabrous above or with hairs along the midvein, with few or many minute (0.05–0.2 mm) hairs along the major veins beneath and usually glabrescent, 2° veins 12–18/side, arising from the midvein at near 90°. **Inflorescences** solitary, 4–12 cm long, 6–12 cm broad, open pyramidal or rounded corymbiform with opposite (subopposite) branching, green or flushed with purple, peduncles (1–)2.5–4 cm long, very sparsely to densely puberulent with short (0.2 mm) thin hairs, bracts 2–5 mm long, linear-subulate, pedicels 1–5 mm long, bracteoles ca. 1 mm long. **Flowers** glabrous externally, hypanthium 1–1.5 mm long, 0.8–1 mm diam., calyx lobes 5, 0.7–1.5 mm long, acute; **corolla** funnellform and gibbous near the base, white or flushed with yellow or purple distally (grayish to purple near the base), tube 6–8 mm long, constricted in the middle (1–1.5 mm diam.) and gibbous near the base, corolla lobes 2–3 mm long and 1 mm broad at the base; anthers 2–2.5 mm long. **Fruits** 4–5 mm long, 3–4 mm diam., globose to ellipsoid, becoming pale blue at maturity, with longitudinal ribs, persisting calyx ca. 1 mm long.

Plants of montane rain forest formations, from 1200 to 1600(–2000) m elevation. Flowering in March and May–August; fruiting in May–June and August. The species ranges from central Costa Rica to Colombia.

Palicourea garciae is recognized by the small narrow leaves with many secondary veins, the small corolla tubes strongly bent below the middle and inflated at the base, and the small pale blue fruit. The very short tubular sheath and bifid interpetiolar part of the stipule is noteworthy. *Psychotria copeyana* was based on a specimen (Williams & Allen 16482 ♀) with immature inflorescences from El Copey. Vegetatively this species resembles several smaller-leaved species of *Psychotria*, but the strongly gibbous flowers are very different.

Palicourea guianensis Aubl., Hist. pl. Guiane 1: 173, t. 66. 1775. *Psychotria palicourea* Sw., Fl. Ind. Occ. 1797. Figure 50.

Shrubs or small trees, 2–6(–10) m tall, leafy stems 1.5–8 mm thick, glabrous or minutely puberulent, quadrangular, often drying dark and contracted beneath the node; **stipules** free or united for 1–2 mm at the base, lobes, 5–8(–12) mm long, lobes 2–4 mm broad, blunt, glabrous and drying dark. **Leaves** opposite, petioles 8–24(–38) mm long, 1.3–3 mm thick, glabrous; **leaf blades** (12–)15–28 cm long, (5–)7–18 cm broad, broadly ovate-elliptic to ovate-oblong, elliptic-oblong or ovate, apex acute or acuminate, base obtuse to rounded and subtruncate, drying thin-chartaceous, concolorous, glabrous or minutely (0.1 mm) papillate-puberulent above and below, 2° veins 10–15/side. **Inflorescences** usually solitary, 7–18 cm long, 4–12 cm broad, pyramidal or thyriform with many closely crowded alternate or subopposite branches, red-orange when flowering and later turning purple, peduncles 3–12 cm long, 1.8–3.2 mm thick, minutely puberulent with thin hairs ca. 0.1 mm long, bracts absent or 0.5–7 mm long and often adnate to the primary branches, pedicels 2–5(–8) mm long, minutely puberulent. **Flowers** monomorphic, minutely puberulent externally, hypanthium ca. 1.5 mm long and 0.8 mm diam., tubular, calyx lobes 0.2–0.6 mm long, broadly obtuse; **corolla** yellow or orange, tube 8–25 mm long and 2–3 mm diam. at base, contracted in the middle and a slightly inflated distally, corolla lobes 1–2 mm long, triangular; **ovary** 2–6-locular. **Fruits** 4–7 mm long, 4–5 mm diam., ovoid to ellipsoid, becoming purple violet and drying black with prominent longitudinal ribs, persisting calyx and disc ca. 1 mm high.

Plants of open secondary formations in evergreen and partly deciduous forest areas, from near sea level to 900 m elevation. Flowering and fruiting occur throughout the year; flowering mostly in March–July in Costa Rica. The species ranges from southern Mexico and the West Indies southward to southern Brazil and Bolivia.

Palicourea guianensis is recognized by its lowland habitat, the wide glabrous or very minutely puberulent thin-textured leaves, the large rounded stipule lobes, the conspicuous densely flowered yellow or orange inflorescences, and yellow or orange puberulent corollas. Most of our collections come from the Caribbean lowlands and from the Golfo Dulce area. Central American material has two-locular ovaries, but specimens from eastern South American may have three- or four-locular ovaries. *Palicourea guianensis* resembles *P. padifolia* (q.v.).

Palicourea hammelii Taylor, Syst. Bot. Monogr. 26: 43. 1989.

Small **trees** to 5 m tall, leafy stems 3–7 mm thick, glabrous or minutely (0.1 mm) appressed-puberulent, drying dark; **stipules** 6–12 mm long, with a sheathing base 3–5 mm long with 2 lobes (4/node) 3–7 mm long, persisting. **Leaves** with petioles 13–35 mm long, 1.3–2

mm thick, glabrous or minutely puberulent, drying dark; **leaf blades** 8.5–20 cm long, 2.5–8.5 cm broad, elliptic to elliptic-obovate, apex acuminate with tip 5–15 mm long, base gradually narrowed and acute or cuneate, slightly decurrent on petiole, drying stiffly chartaceous, dark olive green above, glabrous above or puberulent on the midvein, puberulent beneath with crooked hairs 0.05–0.3 mm long, 2° veins 12–18/side. **Inflorescences** 4–14 cm long, to 13 cm broad, open pyramidal, pink to purple but drying dark, peduncle 15–35 mm long, 1.5–3 mm thick, glabrous or very sparsely minutely puberulent, proximal bracts 18–35 mm long, ca. 5 mm broad, lanceolate, distal bracteoles 6–20 mm long, pedicels 4–15 mm long. **Flowers** glabrous externally, hypanthium ca. 2 mm long and 1 mm diam., calyx 13–20 mm long, pink to purple, calyx lobes 4–12 mm long, lanceolate, unequal; **corolla** white, tubular, tube 20–27 mm long, ca. 4 mm diam., corolla lobes 3–6 mm long, triangular. **Fruits** 8–10 mm long, 7–8 diam., ellipsoid.

Palicourea hammelii was originally described from collections made between 1400 and 2200 m elevation in Chiriquí, Panama. It has been recently collected on the Fila Matama at 1600 m elevation on the Caribbean slope of the Cordillera de Talamanca (*Herrera & Chacón 2781* CR, MO). This species resembles *P. bella* with ovate calyx lobes and *P. bellula* with a shorter corolla tube.

Palicourea lancifera Standl. & L. O. Williams, Ceiba 1: 249. 1951. Figure 53.

Shrubs, 1.5–3(–5) m tall, leafy stems 1.3–4 mm thick, glabrous to (less often) densely puberulent with crooked yellowish hairs 0.1–0.3 mm long, quadrangular at first, glabrescent; **stipules** united to form a tubular sheath 3–5 mm long, apex truncated with 2 narrow teeth 2–5 mm long on each side. **Leaves** opposite, petioles 7–25(–30) mm long, 0.4–1.2 mm thick, glabrous or minutely puberulent; **leaf blades** 5–15(–18) cm long, 2–5(–7) cm broad, elliptic to narrowly elliptic-oblong, apex acuminate with tip 6–20 mm long, base acute and decurrent on petiole, drying thin-chartaceous or chartaceous, dark greenish or brownish above, glabrous above, minutely (0.1–0.4 mm) strigulose on the veins beneath, 2° veins 8–12/side and connecting with a vein along the leaf edge. **Inflorescences** solitary, 7–17(–21) cm long, 2–6(–9) cm broad, narrowly pyramidal with many short branches, green or marked with yellow, peduncles 1–4 cm long, 1–2 mm thick, glabrous to densely puberulent, bracts 5–8 mm long, narrowly lanceolate, flowers often alternate along the lateral branches, bracteoles 1.5–4 mm long, pedicels 2–7(–17) mm long. **Flowers** glabrous or sparsely puberulent externally, hypanthium 1–1.5 mm long, ca. 1 mm diam., calyx lobes 1.5–3 mm long, often unequal, acute or rounded distally; **corolla** white or flushed with green or yellow, tubular, tube 7–11 mm long, ca. 2 mm diam. and expanded at the base, corolla lobes 1–2 mm long; anthers 2–2.5 mm long. **Fruits** 4–5 mm long and 4–5 mm diam., ovoid or globose-oblate, persisting calyx ca. 1.5 mm high.

Plants of very wet lower montane cloud forest formations, from 800 to 1700 m elevation. Flowering June–November; apparently fruiting throughout the year. This species ranges from the Reserva Forestal de San Ramón and Zapote de San Carlos (Alajuela) eastward to Moravia de Chirripó (Limon) and the western part of the General Valley (San José).

Palicourea lancifera is recognized by its narrow long-petiolate leaves, narrowly thyrsoid greenish inflorescences, slightly larger calyx lobes rounded distally, and white or pale yellow corolla tubes. This species resembles *P. albocaerulea* with longer calyx lobes and *P. leucantha* J. D. Smith of Mexico and northern Central America.

Palicourea lasiorrhachis Oersted, Vidensk. Meddel. Dansk. Naturhist. Foren. Kjobenhavn 39. 1852. *P. veraguensis* Dwyer, Ann. Missouri Bot. Gard. 67: 318. 1980. Figure 51.

Shrubs or small treelets, 1–5(–7) m tall, leafy stems 1.8–5 mm thick, glabrous to pubescent with stiff yellowish curved hairs to 0.5 mm long; **stipules** united and forming a broad tube 2–9 mm long, truncated and with narrow teeth 2–5(–8) mm long, glabrous or minutely puberulent, persisting. **Leaves** opposite, petioles 7–24(–32) mm long, 1–2 mm thick, glabrous or puberulent; **leaf blades** 6–17(–26) cm long, 2–8(–10) cm broad, elliptic to narrowly ovate-elliptic or elliptic-oblong, apex tapering gradually and acuminate, tip 4–13(–20) mm long, base acute to obtuse, drying chartaceous, dark grayish green to brownish above, glabrous above, sparsely to densely puberulent along the major veins beneath with short (0.3 mm) yellowish or longer (1 mm) whitish ascending hairs (rarely glabrous), 2° veins (8–)11–14(–18)/side and joining a vein along the leaf edge distally. **Inflorescences** 5–15(–20) cm long, 4–13 cm broad, narrowly pyramidal with 4–8 pairs of opposite or subopposite lateral branches from the central rachis, greenish to bright yellow, peduncles 1.5–7(–10) cm long, 0.7–2.8 mm thick, sparsely to densely puberulent with stiff multicellular hairs 0.3–1 mm long, bracts 2–9 mm long, linear-subulate, pedicels 1–6 mm long, minutely puberulent, yellow to bright green, bracteoles 0.5–2 mm long. **Flowers** sparsely to densely pubescent externally (often glabrescent), hypanthium 0.5–1.5 mm long, ca. 1 mm diam. distally, obconic, calyx lobes 0.3–1.2 mm long, obtuse; **corolla** yellow to greenish, tubular-funnelform, tube 6–15 mm long, narrowed in the middle, ca. 2 mm diam. at the base and 3 mm diam. distally, corolla lobes 1–2.5 mm long, ca. 1.5 mm broad at the base, triangular; anthers 1.5–2 mm long or 2.5–3 mm long in short-styled form. **Fruits** 4–5 mm long and 3–4 mm diam., obovoid, with prominent longitudinal ribs, puberulent or glabrescent, blue or black.

Understory plants of very wet montane rain forest formations, from (1000–)1300 to 2600 m el-

elevation. Flowering throughout the year (mostly in May–June); probably fruiting throughout the year. This species ranges from the Cordillera de Tilarán along the continental divide and Cordillera de Talamanca to western Panama.

Palicourea lasiorrhachis is recognized by the often narrow leaves, usually puberulent beneath, the minutely puberulent inflorescences (rarely glabrous) with yellow pedicels, the small calyx lobes, narrowly funnelform yellow corolla tubes, and small obovoid fruit. This common species is quite variable and includes individual collections that differ greatly from each other in regard to leaf size, leaf shape, puberulence, and aspects of flowers and inflorescences. A group of collections from near El Empalme have thicker stems; stiffer, more oblong leaves; secondary veins arising at almost 90° angles; and dense puberulence. This species may be difficult to distinguish from *P. vestita* (q.v.). It is often confused with *P. padifolia*, which has red-orange inflorescence branches and more tubular corollas. Also compare *P. montivaga* (smaller plants with white flowers) and *P. adusta* (with blue flowers).

Palicourea macrocalyx Standl., J. Wash. Acad. Sci. 18: 278. 1928. Figure 49.

Small **shrub**, subshrubs, or little treelets, 0.5–2(–6) m tall, leafy branchlets 1.5–4(–10) mm thick, glabrous, flattened or quadrangular but quickly becoming terete; **stipules** with a broad thick sheath 2–6 mm long, truncated and with narrow acute teeth 4–10 mm long and 1–3 mm broad, glabrous and persisting. **Leaves** opposite, petioles 7–30(–45) mm long, 0.9–2.2 mm thick, glabrous; **leaf blades** 5–15(–18) cm long, 2–6(–9.5) cm broad, elliptic-obovate to obovate-oblong or elliptic (rarely broadly oblong), apex acuminate with tip 4–13 mm long, base obtuse to acute (subtruncate), drying stiffly chartaceous to subcoriaceous, olive green or brownish above, glabrous above and below or with small (0.3–0.5 mm) hairs along the midvein, 2° veins 9–13/side. **Inflorescences** 3–8(–15) cm long, 2–10 cm broad, pyramidal, yellow or marked with purple, peduncles 1–8.5 cm long, 1–1.8 mm thick, glabrous, bracts ca. 6 mm long, pedicels 1–8 mm long, glabrous, bracteoles 1–4 mm long. **Flowers** glabrous externally, hypanthium ca. 1 mm long, narrowly obconic, calyx lobes 3–6 mm long, 1–2 mm broad, narrowly triangular to ovate, green or yellow and sometimes marked with purple; **corolla** tubular, yellow or greenish yellow, tube 8–13 mm long, ca. 2 mm diam., slightly narrower in the center, corolla lobes 2–3 mm long, obtuse; anthers 1–2 mm long. **Fruits** 5–6 mm long, 4–5 mm diam., ellipsoid, becoming blue, longitudinally ribbed (when dried), with persisting calyx to 6 mm long.

Plants of the very wet cloud forests along the continental divide, from 1300 to 2200 m eleva-

tion. Probably flowering throughout the year; fruiting in April–May and August–October. Endemic to Costa Rica, and collected primarily in the Cordillera de Tilarán, but ranging to near San Isidro de Heredia on the western slopes of Volcán Irazu.

Palicourea macrocalyx is distinguished by the stiff slightly obovate leaves with many secondary veins, lack of pubescence, yellow inflorescences sometimes marked with purple, the larger imbricate greenish yellow calyx lobes, and yellow corollas. The name of this species should not be confused with *P. macrosepala* Krause, a synonym of *P. discolor*. This species is very similar to *P. bellula*, which has longer corolla tubes.

Palicourea montivaga Standl., J. Wash. Acad. Sci. 18: 279. 1928. Figure 53.

Shrubs, 1–3 m tall (rarely slender treelets to 6 m), leafy stems 0.9–6 mm thick, glabrous or with a few thin hairs ca. 0.3 m long distally, terete; **stipules** with a tubular sheath 0.5–4 mm long, truncated distally and with triangular or linear teeth 0.5–2.5 mm long, glabrous and persisting. **Leaves** opposite, petioles 6–14(–25) mm long, 0.4–1.1 mm thick, glabrous, slightly sulcate above; **leaf blades** 3–7(–9) cm long, 1–2.5(–3) cm broad, lanceolate or elliptic-lanceolate to narrowly elliptic-oblong, apex tapering gradually and acute or acuminate, tip to 15 mm long, base acute (obtuse), drying chartaceous, dark green or brown above, glabrous above, glabrous or with a few thin hairs 0.1–0.5 mm long on the veins beneath, 2° veins 6–9/side. **Inflorescences** 2–10 cm long, 2–8 cm broad, pyramidal with open opposite branching, peduncles 8–45 mm long, 0.3–1.2 mm thick, glabrous or minutely puberulent, inflorescence branches usually bright yellow (green), bracts 2–3.5 mm long, linear, pedicels 1–6 mm long. **Flowers** usually glabrous externally, hypanthium 0.5–1 mm long, ca. 1 mm diam. distally, obconic, calyx lobes 0.4–1 mm long, acute or obtuse; **corolla** white or yellow, tube 5–9 mm long, 1–1.3 mm diam., corolla lobes 1–2 mm long; anthers ca. 1.5 mm long. **Fruits** 4–5 mm long, 3–4 mm diam., obovoid, becoming longitudinally ribbed.

Plants of montane rain forest formations, from (1100–)1300 to 2300(–2900?) m elevation. Probably flowering throughout the year, but mostly in April–August; fruiting April–November. The species is endemic and ranges from Volcán Tenorio southward along the continental divide to the western slopes of Volcán Irazu.

Palicourea montivaga is recognized by its small narrow leaves with long tips, glabrous parts, small yellowish inflorescences, small white or yellowish corollas, and montane habitat. This species is closely related to *P. adusta* with smaller bluish flowers and *P. lasiorrhachis* with relatively larger

yellowish floral parts and shorter leaf tips. The plant attributed to this species from Panama (Dwyer, 1980) is *P. lasiorrhachis*. Material of *P. padifolia* can also be confused with this species.

Palicourea orosiana C. M. Taylor, Syst. Bot. Monogr. 26: 61. 1989. Figure 51.

Shrubs, 2–8 m tall, leafy stems 1.8–4 mm thick, strigulose with stiff straight hairs to 1 mm long; **stipules** with a short (1.5–3 mm) sheath (difficult to see under the strigulose hairs) and narrow distal teeth 6–17 mm long, covered with long (1–2 mm) thin hairs. **Leaves** opposite, petioles 4–12 mm long, 1–1.9 mm thick, puberulent in early stages with straight or curved ascending hairs; **leaf blades** 7–14 cm long, 2.5–4.5 cm broad, elliptic-oblong to narrowly elliptic, apex acuminate with tip 6–10(–13) mm long, base acute, drying stiffly chartaceous, yellowish, upper surface glabrous, glabrous on 2° veins and interveinal areas beneath but with straight stiff hairs 0.5–1.5 mm long on the sides of the midvein, 2° veins 8–13/side. **Inflorescences** solitary, 7–11 cm long, 7–8 cm broad, pyramidal, yellowish, peduncles 3.5–6.5 cm long and 1.5 mm thick, strigulose, bracts and bracteoles 3–7(–13) mm long, ca. 1 mm broad, yellowish and resembling the calyx lobes, pedicels 2–6 mm long. **Flowers** greenish yellow, hypanthium ca. 1.3 mm long and 1 mm diam., densely pubescent, calyx lobes 5–11 mm long, 0.8–1.1 mm broad near the base, narrowly triangular, acute, sparsely pubescent with thin whitish hairs ca. 0.5 mm long, drying yellow; **corolla** tubular, yellow, tube ca. 10 mm long, with whitish ascending hairs, corolla lobes ca. 2 mm long; anthers ca. 2.5 mm long. **Fruits** not seen.

Plants of the wet cloud forests of the Caribbean slopes and continental divide, at 1200–2100 m elevation. Flowering in May–June. This species has only been collected above the upper Río Grande de Orosí near Tapantí, Cartago, in Costa Rica; it is also known from western Panama.

Palicourea orosiana is distinguished by its puberulent yellowish inflorescence and flowers, larger yellowish bracts and calyx lobes, and the long stipule lobes. The pubescence along the midvein on the underside of the leaf is also unusual. This species is similar to *P. lasiorrhachis*, which has much smaller calyx lobes, and to *P. macrocalyx*, which has glabrous inflorescences and broadly imbricate calyx lobes.

Palicourea padifolia (Willd. ex Roem. & Schult.) C. M. Taylor & Lorence, Taxon 34: 669. 1985. *Psychotria padifolia* Willd. ex Roem. & Schult., Syst. Veg. 5: 189. 1819. *Psychotria mexicana* Willd. ex Roem. & Schult., loc. cit. 192. 1819. *Palicourea costaricensis* Benth. ex Oerst., Vidensk. Meddel. Dansk. Naturhist. Foren. Kjo-

benhavn 1852: 38. 1853. *Palicourea subrubra* Polak., *Linnaea* 41: 571. 1877. *P. galeottiana* sensu Standley, not M. Martens (see Taylor & Lorence, 1985, cited above). Figure 51.

Shrubs or small trees, (1)2–7(–10) m tall, leafy stems 1.5–5 mm thick, glabrous (rarely hirsutulous), quadrangular but becoming terete; **stipules** with a tubular sheath 1–4 mm long, truncated distally and with narrow awns 2–10 mm long, glabrous. **Leaves** opposite (rarely 4/node), petioles 4–16(–22) mm long, 0.6–1.8 mm thick, glabrous; **leaf blades** 6–16(–24) cm long, 2–6(–8.5) cm broad, narrowly elliptic-oblong to narrowly oblong, elliptic-ovate or lanceolate (rarely elliptic-obovate), apex acute to acuminate with tip 4–12(–20) mm long, base acute to obtuse, drying stiffly chartaceous, glabrous and with short (0.2 mm) cystoliths often visible above, glabrous beneath except for thin whitish hairs 0.3–0.9 mm long on the major veins beneath or only along the midvein, 2° veins 8–14/side. **Inflorescences** (5)–7–18 cm long, 4–14 cm broad, broadly pyramidal, reddish purple to salmon red or orange (yellow), peduncle 1.5–5 cm long, 1.2–2 mm thick, glabrous or sparsely puberulent, bracts (1)2–6(–8) mm long and linear-subulate, bracteoles 0.5–2 mm long, pedicels 1–6(–10) mm long. **Flowers** glabrous or sparsely puberulent externally, hypanthium 0.7–1 mm long, 0.5–1 mm diam., calyx lobes 0.5–1 mm long, triangular, obtuse; **corolla** tubular to slightly funnelform, carnose, orange or yellow, tube 8–15(–18) mm long and 1.5–2.5 mm diam., narrower in the middle, corolla lobes 2–3 mm long, ca. 1.5 mm broad at the base, obtuse; anthers 2.5–4 mm long. **Fruits** 4–6(–10) mm long, 4–6(–10) mm diam., ovoid to ellipsoid or globose, longitudinally ribbed, persisting calyx ca. 1 mm high.

Plants of evergreen lower montane forest formations and in moist sites in deciduous forest formations, (800)–1000–2000(–2400) m elevation. Flowering and fruiting throughout the year (mostly flowering in December–August and fruiting in January–August). The species is quite common in Costa Rica and ranges from the Cordilleras de Guanacaste and Tilarán, around the Caribbean side of the central volcanic chain, through the Cordillera de Talamanca. The species ranges from eastern Mexico to Panama.

Palicourea padifolia is recognized by its usually narrow leaves, short-tubular stipule sheaths, colorful inflorescences with (usually) reddish pedicels, minute calyx lobes, narrow yellowish (or orange) corolla tubes, and montane habitats with high rainfall. This is the most commonly collected species of *Palicourea* in Central America. This species is easily mistaken for *P. angustifolia*, *P. crocea*, and *P. purpurea*, but those species have purplish flowers. *Palicourea lasiorrhachis* is similar but has yellow inflorescence branches and corollas. *Palicourea padifolia* is very closely related to *P. thyrsiflora* (Ruiz & Pavón) Roem. & Schult. of Ecuador

and Peru and may be conspecific, but neither of the two species has been collected in Colombia or the eastern half of Panama. Fruiting plants of this species may be confused with species of *Psychotria*, but the inflorescences are more colorful in *P. padifolia*.

***Palicourea purpurea* C. M. Taylor, Syst. Bot. Monogr. 26: 71. 1989. Figure 52.**

Shrubs or small trees, (1)–3–6(–10) m tall, leafy stems 1–4 mm thick, glabrous, **stipules** with sheaths 1–4 mm long, truncated distally and with slender teeth 2–5 mm long, glabrous and persisting. **Leaves** opposite, petioles 6–25(–35) mm long, 0.6–1.3 mm thick, glabrous; **leaf blades** 7–19 cm long, 2–7 cm broad, narrowly elliptic to elliptic-oblong, apex acuminate with tip 5–15 mm long, base acute and slightly decurrent on petiole, drying chartaceous, dark brown above, glabrous above and below or with a few thin white hairs along the side of the midvein beneath, 2° veins 6–10/side. **Inflorescences** 5–12 cm long, 4–11 cm broad, pyramidal, purplish to deep lavender in color, peduncles 2–6 cm long, 1.2–1.8 mm thick, glabrous, bracts 2–7(–10) mm long, linear-subulate, bracteoles 1–3 mm long, pedicels 0–11 mm long. **Flowers** glabrous externally, hypanthium 0.6–1 mm long and 1 mm diam. at apex, obconic, calyx lobes 0.3–1 long and 1 mm broad at the base, triangular; **corolla** tubular and carnose, purple to lavender, pink, or white, tube 11–18 mm long and 2–4 mm diam., slightly expanded at the base, corolla lobes 2–4 mm long; anthers 3.5–4 mm long. **Fruits** 4–6 mm long and 4–5 mm diam., globose, drying black and with longitudinal ridges.

Plants of montane evergreen forest formations, (750)–1200–2800 m elevation. Flowering in March, May–July, and December; fruiting in January–September and December. The species is found on the Caribbean slope and continental divide of the Central Volcanic chain and in the area above Río Grande de Orosí and in western and central Panama.

Palicourea purpurea is distinguished by its longer purplish corollas, purple inflorescence branches, and globose fruit. It is very similar to *P. padifolia*, but that species has yellow or orange corollas and red or orange inflorescence branches, and ovoid or slightly flattened fruit. *Palicourea discolor* is also similar but has larger leaves, inflorescences, and calyx lobes. Compare *P. angustifolia* also.

***Palicourea salicifolia* Standl., J. Wash. Acad. Sci. 18: 280. 1928. *P. austinsmithii* Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 1333. 1938. *P. caerulescens* Suesseng., Bot. Jahrb. Syst. 72: 286. 1942. Figure 53.**

Shrubs, 0.5–4 tall, leafy stems 1–4 mm thick, glabrous and quadrangular, young stems drying black, pale gray in age; **stipules** with short (1–2 mm) tubes truncated and with narrow teeth 1–2 mm long, glabrous. **Leaves** opposite, petioles 3–9(–15) mm long, 0.4–0.8 mm thick, glabrous; **leaf blades** 4–8(–10) cm long, 1–2(–3) cm broad, narrowly elliptic to lanceolate or lanceolate-oblong, apex usually tapering gradually and acute or acuminate, base acute and slightly decurrent on petiole, drying stiffly chartaceous, glabrous above and below (rarely minutely puberulent along the midvein), 2° veins 9–13/side. **Inflorescences** 2–6 cm long, 3–6(–8) cm broad, pyramidal, green or marked with blue or purple, peduncles 3–18 mm long, glabrous and usually drying black, bracts 4–7 mm long, 1 mm broad at the base, pedicels 0–8 mm long, bracteoles ca. 3 mm long. **Flowers** glabrous externally, hypanthium ca. 1.3 mm long and 1 mm diam. distally, calyx lobes 2–3(–4) mm long, ca. 1 mm broad, oblong and rounded distally; **corolla** funnelform, carinose, white and often flushed with blue or purple, tube 6–13 mm long, ca. 2 mm diam., narrowed in the middle, corolla lobes 3–6 mm long, to 2 mm broad at the base; anthers 2–4 mm long. **Fruits** 6–8 mm long and 5–7 mm diam., obovoid or ellipsoid, flattened, becoming deep blue (pedicels also blue), with strong longitudinal ribs (dried).

Plants of evergreen montane forest formations, from 1500 to 2700 m elevation. Flowering in January–September; fruiting in December–March and May–August. The species is known from Monteverde and the northern part of the Meseta Central (near Zarcero), from the Cerro de Carpintera, and in the Cordillera de Talamanca.

Palicourea salicifolia is recognized by the small narrow leaves tapering at both apex and base, small inflorescences that often dry black, slightly enlarged calyx lobes, and funnelform white corollas marked with blue or purple. The fruit have sharply defined longitudinal ribs. Two collections from below 2000 m (*Dryer 768 & 965* from Monteverde and *Stork 1175* from Carpintera) have dried pale greenish and the inflorescences are little-branched. Because of its small leaves, this species resembles *P. adusta* and *P. montivaga* with shorter corolla tubes and calyx lobes.

Palicourea skotakii C. M. Taylor, Syst. Bot. Monogr. 26: 76. 1989. Figure 49.

Shrubs, 1.5–2 m tall, leafy stems 1.5–5 mm thick, glabrous, quadrangular or flattened; **stipules** 6–8 mm long, tubular sheath 3–8 mm long, broadly bilobed distally with obtuse lobes ca. 2 mm long and 3 mm broad, glabrous, becoming coriaceous. **Leaves** opposite, petioles 10–24 mm long, 1–1.6 mm thick, glabrous; **leaf blades** 7–13(–17) cm long, 3–5–5.5(–6.5) cm broad, elliptic to elliptic-oblong or elliptic-obovate, apex abruptly nar-

rowed and acuminate, base acute and slightly decurrent on petiole, drying stiffly chartaceous to subcoriaceous, dark greenish above, glabrous above and below, 2° veins 9–14/side and joining a vein along the leaf edge distally, parallel minor 2° veins usually present. **Inflorescences** 4–10 cm long, 5–11 cm broad, usually 3-branched, rounded to pyramidal, peduncle 2.5–4 cm long and 3 mm thick, glabrous, bracts 15–30 mm long, pale green (dried), bracteoles to 15 mm long, ovate and imbricate around the flowers, persisting. **Flowers** glabrous externally, calyx lobes 2–6 mm long, lanceolate to ligulate, usually unequal; **corolla** funnelform, carinose, white, tube ca. 10 mm long, corolla lobes ca. 6 mm long; anthers ca. 2.5 mm long. **Fruits** 6–7 mm long, 5 mm diam., ellipsoid to slightly obovoid.

Plants of high montane rain forest formations at 2700–2800 m elevation. Flowering in March and June. Endemic; like the type (*Taylor & Skotak 4756 DUKE*), all collections are from along the Interamerican Highway in the western part of the Cordillera de Talamanca.

Palicourea skotakii is distinguished by its high-altitude habitat, stipules with broad lobes, lack of pubescence, large greenish ovate persisting bracts and bracteoles, and white corollas. This species resembles *P. bella*; it also resembles *Psychotria chlorochlamys* and its allies.

Palicourea spathacea C. M. Taylor, Syst. Bot. 9: 226. 1984. Figure 49.

Shrubs or small trees, 2–8 m tall, leafy stems 2–8 mm thick, quadrangular, with thin brownish hairs to 0.5 mm long but soon glabrescent; **stipules** 5–12 mm long, 4–8 mm broad, bilobed, puberulent near the base and along the midrib abaxially. **Leaves** opposite, petioles 8–20 mm long, 1–2.2 mm thick, appressed pubescent with thin ascending hairs or glabrescent; **leaf blades** 12–28 cm long, 4.5–14 cm broad, elliptic-obovate to broadly elliptic, obovate or elliptic-oblong, apex short-acuminate with tip 8–15 mm long, base narrowed gradually and acute or cuneate, slightly decurrent on petiole, drying stiffly chartaceous, dark green or brown above (much paler beneath), glabrous above, with thin brownish ascending hairs to 1 mm long on the midvein beneath and shorter (0.1–0.3 mm) hairs on the minor venation and surfaces, 2° veins 12–22/side (and usually with a weaker 2° between them). **Inflorescences** solitary, drooping, 10–23 cm long, 8–16(–20) cm broad, open broadly pyramidal or hemispheric, peduncles 3–9 cm long, 1.5–3.5 mm thick, puberulent near the base, bracts 15–20 mm long and 5 mm broad, bracteoles 8–15 mm long, ca. 4 mm broad, pink to purple (white), glabrous pedicels 12–26 mm long, ca. 0.5 mm thick and black when dried. **Flowers** glabrous externally, hypanthium ca. 1.5 mm long and 1.2 mm diam., cylindrical and drying black, calyx tube spathe-like and 15–20 mm long by 5–8 mm diam., splitting open along 1 side, pink to purple; **corolla** tubular, carinose, white, tube 3–4 cm long, 4–5 mm diam., straight

or slightly curved, corolla lobes 4–7 mm long; anthers 4.5–5 mm long. **Fruits** ca. 8 mm long (not including the persisting calyx), ca. 7 mm in diam., dark purple but drying black and with longitudinal ribs.

Plants of the very wet lower montane rain forest formations on the Caribbean slope of the Cordillera de Talamanca, at 1300–1700 m elevation. Flowering in March, April, and November–December; fruiting in April–May, July–August, and December. This species is only known from the upper drainage area of Río Grande de Orosí near Tapantí, Cartago Province.

Palicourea spathacea is a striking species; the bright pink or purplish bracts, bracteoles, and large spathaceous calyx make the inflorescences especially conspicuous. The long white corollas, large leaves with many secondary veins and cuneate bases, and stipules with a single obtuse apex on each side are further distinctions. The calyx is inflated before anthesis and splits for half to three-quarters of its length as the corolla emerges; there are no calyx lobes.

Palicourea standleyana C. M. Taylor, Syst. Bot. Monogr. 26: 81. 1989. *Psychotria brenesii* Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 1347. 1938, not *Palicourea brenesii* Standl., 1938. Figure 54.

Shrubs or small trees, 2–7 m tall, leafy branchlets 3–6 mm thick, densely pilose with thin yellowish hairs 1–3 mm long; **stipules** (6–)8–18 mm long, 3–8 mm broad, with a tubular sheath 4–8 mm long, acute or with 2 short (1–2 mm) lobes, sparsely pilose. **Leaves** with petioles 1–4 cm long, 0.7–1.7 mm thick, pilose with straight or slightly curved hairs to 2 mm long; **leaf blades** 9–23 cm long, 3–9 cm broad, broadly elliptic, elliptic-ovate or elliptic-obovate, apex acuminate to caudate-acuminate with 8–15(–20) mm long, base obtuse to acute, drying stiffly chartaceous, dark brown above, densely pilose above and below with hairs 1–1.5 mm long, 2° veins (8–)10–17/side, connected distally to make a slightly arcuate submarginal vein. **Inflorescences** terminal, 3 or 1 with 3 main branches from a short (0–15 mm) common peduncle, 7–12 cm long, to 14 cm broad, open trichotomous panicles, primary (basal) lateral branches 3–7 cm long, pilose, bracts 4–11 mm long, ca. 1.5 mm broad, lanceolate, flowers in close distal clusters subtended by ovate pilose bracts, pedicels 0–5 long. **Flowers** puberulent externally, hypanthium ca. 2 mm long, calyx lobes 2–4 mm long but difficult to see among the hairs; **corolla** tubular-funnelform, carnos, deep lemon yellow to greenish yellow, tube 10–12 mm long, 1.5–2 mm diam., expanded at the base and with hairs to 2 mm long, corolla lobes 3–5 mm long; anthers 2.5–3 mm long. **Fruits** 6–8 mm long (not including the 3-mm-long calyx), 5 mm diam., ellipsoid, pilose, becoming blue.

Plants of very wet cloud forest formations along the Caribbean slope and continental divide, 1100–1600 m elevation. Flowering in December–July; fruiting in January–June. The species has been collected in the Cordilleras de Guanacaste and Tilarán, north of San Ramón (Alajuela), near Tapantí (Cartago), in Chiriquí, Panama, and Nariño Province, Colombia.

Palicourea standleyana is recognized by the prominent pubescence on all parts, the large tubular stipules, stiff leaves with many secondary veins and submarginal veins, open three-branched inflorescences, and bright yellow corollas. This species is easily confused with *Psychotria pilosa*, but that species has much smaller corollas and smaller fruit and the corolla tubes lack the internal ring of the hairs that define *Palicourea*.

Palicourea tilaranensis C. M. Taylor, Syst. Bot. Monogr. 26: 84. 1989. Figure 49.

Small shrubs, ca. 1.5 m tall, leafy stems ca. 3 mm thick, quadrangular and glabrous, young stems drying black; **stipules** 5–8 mm long, with a very short (0.5–1.2 mm) tubular sheath, stipule lobes to 4 mm long, broadly obtuse to deeply bilobed, persisting. **Leaves** opposite, petioles 13–40(–65) mm long, 0.7–1.7 mm thick, glabrous; **leaf blades** 8–16 cm long, 3.5–6 cm thick, ovate to ovate-elliptic or ovate-oblong, apex acuminate with tip 7–14 mm long, base obtuse, drying stiffly chartaceous, dark greenish brown, glabrous above and below, 2° veins 8–11/side. **Inflorescences** 12–15 cm long, 6–9 cm broad, pyramidal panicles with opposite branching, peduncles 4–6 cm long, 1.5–2 mm thick, glabrous, bracts 8–13 mm long, 2–4 mm broad, lanceolate, bracteoles ca. 5 mm long and 2 mm broad, flowers sessile or on pedicels to 4 mm long within the persisting bracteoles. **Flowers** glabrous externally, hypanthium 0.5–1 mm long, calyx lobes 0.3–1.5 mm long, triangular; **corolla** tubular, carnos, white, tube 3–7 mm long, ca. 1.8 mm diam., slightly narrowed in the middle, corolla lobes ca. 2 mm long. **Fruits** not seen.

Plants of evergreen lower montane rain forest formations, at about 1550–1800 m elevation. Flowering in February and June. This species is known only from the Monteverde Nature Reserve, in the Cordillera de Tilarán.

Palicourea tilaranensis is recognized by its restricted range, large and persisting bracts and bracteoles, small calyx lobes, and white corollas. It resembles *Psychotria palicouroides* and its allies.

Palicourea triphylla DC., Prodr. 4: 526. 1830. *Psychotria triphylla* (DC.) Muell.-Arg. in Mart., Fl.

Bras. 6(5): 233. 1881. *Palicourea longibracteata* Bartling ex DC., Prodr. 4: 527. 1830. *Palicourea parviflora* Benth., Bot. voy. Sulph. 107. 1844. Figure 50.

Shrubs or herbaceous subshrubs, 1–3(–5) m tall, erect and usually unbranched (rarely clambering), leafy internodes 2.3–7 mm thick, glabrous or sparsely pubescent on the new growth and nodes with short (0.1–0.3 mm) thin hairs, terete; **stipules** united for only 1–2 mm at the base or free, stipule lobes 6/node, 6–12(–15) mm long and ca. 2 mm broad at the base, narrowly triangular and acute, glabrous abaxially and ciliolate along the edge. **Leaves** 3/node (rarely 2 or 4), petioles 3–7(–15) mm long, 1.4–2 mm broad, minutely pubescent but glabrescent; **leaf blades** 7–20 cm long, 3–8 cm broad, narrowly elliptic-oblong to lanceolate, narrowly elliptic or oblanceolate, apex tapering gradually and acuminate with tip 5–15 mm long, base cuneate to acute (obtuse) and slightly decurrent on petiole, drying thinly to stiffly chartaceous, minute (0.05–0.2 mm) thin hairs along the major veins above, with thin whitish hairs 0.1–0.3 mm long on the veins and surfaces beneath, 2° veins 7–11(–15)/side. **Inflorescences** 6–20 cm long (to 26 cm in fruit), 5–10 cm broad near the base, pyramidal to narrowly thyrsoide-cylindrical, red to orange or orange-yellow, peduncles 5–12(–18) cm long, 1.5–3 mm thick, puberulent with thin whitish hairs, bracts 5–20(–30) mm long linear-subulate, pedicels 1–5 mm long, puberulent. **Flowers** distylous, minutely puberulent, hypanthium ca. 1 mm long and 0.5 mm diam., tubular, calyx lobes 0.2–1 mm long, broadly triangular; **corolla** tubular or slightly funnelform, yellow or reddish distally, tube 8–14 mm long, 1.5–3 mm diam., inflated at the base, corolla lobes 1–2 mm long; anthers 2.5–3.5 mm long. **Fruits** 4–5 mm long, 3–5 mm diam., ovoid to globose with prominent longitudinal ridges (dried), becoming blue, purple, or black at maturity, glabrous or puberulent, calyx ca. 0.7 mm high.

Plants of open wet or poorly drained sties in evergreen or partly deciduous forest formations in the Caribbean lowlands and on the Pacific slope of central and southern Costa Rica and in Panama, from near sea level to 700 m elevation, but to 1300 m on the semideciduous Pacific slope. Flowering and fruiting throughout the year (but flowering mostly in April–July). The species ranges from the Caribbean side of central Mexico and Cuba to Brazil and Bolivia.

Palicourea triphylla is recognized by its ternate leaves, puberulence of short thin hairs, long persisting stipules with six teeth per node, orange-yellow inflorescences with persisting bracts, small corolla lobes, and gibbous corollas with multicellular hairs. The species is often found in open swampy sites.

Palicourea vestita Standl., J. Wash. Acad. Sci. 18: 277. 1928. Figure 51.

Shrubs or small treelets, 1–4 m tall, leafy stems 1.5–5 mm thick, densely hirsutulous with yellowish hairs 0.3–0.9 mm long; **stipules** with a tube 3–6 mm long, with narrow teeth 3–8 mm long, puberulent, persisting. **Leaves** opposite, petioles 6–18(–30) mm long, 0.8–1.6(–2.2) thick, densely puberulent with yellowish hairs; **leaf blades** (6–)8.5–19 cm long, (1.7–)2.5–7 cm broad, elliptic to elliptic-oblong, elliptic-obovate or lanceolate, apex acuminate (acute) with tip to 1 cm long, base acute to cuneate (obtuse), drying stiffly chartaceous, often yellowish green, glabrous above or with thin hairs along the midvein, pubescent along the major veins beneath with thin yellowish hairs 0.4–1.2 mm long, 2° veins 12–20/side and with minor short parallel 2° veins between them. **Inflorescences** 5–12 cm long, 5–8 cm broad near the base, thyrsoform pyramidal, yellowish, peduncles 2–8 cm long, 1–3 mm thick, densely pubescent, bracts 4–10 mm long and 1.5 mm broad, bracteoles 1–4 mm long and persisting, pedicels 2–5 mm long. **Flowers** sparsely and minutely puberulent externally, hypanthium 1–1.5 mm long, obconic, calyx lobes 0.7–1.5 mm long, acute; **corolla** bright yellow, tube 7–13 mm long, ca. 2 mm diam., slightly inflated at the base, corolla lobes 1.5–3 mm long; anthers 2.1–2.5 mm long. **Fruits** 5–8 mm long, 3.5–6 mm diam., obovoid, persisting calyx ca. 0.7 mm high.

Plants of evergreen montane wet forest formations of the Cordillera de Talamanca, from 1200 to 2600 m elevation. Flowering in April–August; fruiting in June–August, October, and December. The species is known only from Costa Rica and western Panama.

Palicourea vestita is recognized by the short yellowish hairs on most plant parts, the leaves with many secondary veins, the elongate thyrsoform inflorescences, and the bright yellow corolla tube. This species is distinguished from the very similar but more common *P. lasiorrhachis* by the more numerous secondary veins and longer calyx lobes.

Pentagonia Bentham Nomen conservandum

Shrubs or small **trees** (rarely large trees), main stems often unbranched or with few lateral branches, stems thick, flattened, quadrangular or terete in early stages, glabrous or puberulent, often with conspicuous rounded lenticles; **stipules** interpetiolar, free, large, triangular, usually early deciduous. **Leaves** opposite and decussate, usually very large, sessile or petiolate, the petioles sometimes with auriculate (leafy) developments at the base; **leaf blades** entire or pinnatifid, usually drying coriaceous, the minor venation lineolate-parallel and often with 2 distinct orientations in the same leaf area (parallel with the tertiary veins and at right angles to the tertiary veins),

domatia absent. **Inflorescences** axillary to distal leaves, usually short-pedunculate, cymose or corymbose to glomerulate, generally with fewer than 25 flowers, bracts developed or minute, flowers subsessile or pedicellate. **Flowers** bisexual and monomorphic, radially symmetrical, often large, usually densely pubescent externally, hypanthium conical to turbinate or campanulate, calyx tube well developed, calyx lobes 5–6 or spathaceous, lobes equal or unequal, often with glands inside at the base; **corolla** tubular to funnelform, carinose, white to yellow or red, glabrous within the throat, villous at the stamen attachment, corolla lobes 5–6, valvate in bud, short; **stamens** 5–6, filaments borne on the middle of the tube, equal or unequal, usually villous at the base, anthers dorsifixed, included; **ovary** 2-locular, ovules many on expanded elongate placentas borne on the septum, stigmas subcapitate or branched. **Fruits** baccate, fleshy or becoming hard and nut-like when dry, usually globose and the surface often lenticellate-muricate, 2-locular, the large calyx often persisting on the mature fruit; **seeds** many, angular.

A genus of about 20 species, ranging from Guatemala into northern and western South America. The very large leaves with distinctive minor venation, the small axillary inflorescences with larger crowded flowers, the stiff pubescent tubular corollas, and the globose indehiscent fruit with large persisting calyx distinguish this genus. The very large leaves are correlated with a lack of lateral branches on a solitary vertical trunk in many species. The leaves are often reddish or purplish beneath, making the plants even more striking. The genus is seriously in need of revision. The large leaves often very variable in form and size, the compact inflorescences resulting in crushed or hidden flowers, and a paucity of collections account for the fact that the species are still poorly understood.

Key to the Species of *Pentagonia*

- 1a. Leaf blades entire, never lobed distally; Caribbean lowlands and central cordilleras 2a
- 1b. Leaf blades conspicuously pinnatifid or pinnately lobed; Pacific evergreen lowlands 6a
- 2a. Leaves and stems with hairs ca. 1.4 mm long, leaves sessile, the leaf blade slightly auriculate near the stem *P. hirsuta*
- 2b. Leaves and stems with hairs less than 0.5 mm long, leaf blades petiolate and never with expanded auriculate tissue near the base 3a
- 3a. Calyx lobes usually less than 3 mm long; inflorescences usually open and branched, with the branches easily seen at anthesis *P. costaricensis*
- 3b. Calyx lobes usually more than 4 mm long; inflorescences compact, the branches of the inflorescence short and usually difficult to see (except in fruit) 4a
- 4a. Bracts of the inflorescence minute or undeveloped; calyx often absent at the apex of the mature fruit; leaves obtuse to rounded/subtruncate at the base; Guatemala to Costa Rica *P. donnell-smithii*
- 4b. Bracts of the inflorescence conspicuous in early stages, more than 10 mm long and 4 mm broad; calyx persistent on the mature fruit; leaves rarely rounded or subtruncate at the base; southernmost Costa Rica and Panama 5a
- 5a. Leaves subsessile with a thick petiole less than 2 cm long, lamina long-cuneate at the base; floral bracts 5–10 mm long *P. wendlandii*
- 5b. Leaves with well-developed petioles more than 3 cm long, lamina obtuse to cuneate at the base; bracts 10–18 mm long *P. macrophylla*
- 6a. Leaf blade long-decurrent (at its base) on the petiole *P. tinajita*
- 6b. Leaf blade not at all decurrent on the petiole *P. gymnopoda*

Pentagonia costaricensis (Standley) W. Burger & C. M. Taylor, comb. nov. *Nothophlebia costaricensis* Standl., Contr. U.S. Natl. Herb. 17: 438. 1914. Figure 14.

Trees, 5–18 m tall, leaf stems 6–12(–22) mm thick, glabrous or subglabrous, flattened-quadrangular in early stages, often with dark round lenticels ca. 1 mm diam.;

stipules 2–6(–8) cm long, lanceolate, glabrous or minutely appressed-sericeous. **Leaves** with petioles (2.5–)4–7 cm long, 2.5–7 mm thick, glabrous or subglabrous and drying brown; **leaf blades** (21–)27–100 cm long, (12–)16–50 cm broad, broadly elliptic-obovate to very broadly obovate, apex abruptly narrowed and broadly obtuse, base obtuse and only slightly decurrent (rarely slightly auriculate at the petiole as in *Gomez-Laurito* 9321 CR, f), margin entire, drying coriaceous, glabrous above and

below or with minute sericeous hairs on the veins beneath, 2° veins 8–11/side, the minor venation closely parallel in 2 different directions (but both systems not always apparent). **Inflorescences** 3–12 cm long, 3–15 cm broad, often dichotomously branched, the primary peduncle 5–20 mm long, secondary branches 5–20 mm long, major branches lacking subtending bracts, ultimate branches usually with 3-flowered cymes, striate and glabrous with elongate (0.4–2 mm) lenticels, pedicels 0–7 mm long. **Flowers** with hypanthium 2–4 mm long and 2–3 mm diam., obconic, minutely puberulent or glabrous externally, calyx tube 4–7(–12) mm long, 4.5–6 mm diam., cupular to short-tubular, with parallel venation, rose-colored, calyx lobes 0.5–2 mm high, 2–4 mm broad, broadly rounded to obtuse or obscure, variable and often unequal; **corolla** cream white or yellow, tube 12–20 mm long, 3–5 mm diam., minutely yellowish puberulent externally, corolla lobes 3–6 mm long; anthers white. **Fruits** (based on *Hammel & Grayum 14292*) 10–20 mm diam., globose with a persistent calyx tube 4–5 mm high and 4 mm diam. at the top, calyx lobes often obscure.

Trees of evergreen lowland rain forest formations, 5–600(–900) m elevation. Flowering in April–May and November; fruiting in May, July–September, and November. The species is known only from the Caribbean lowlands, from northern Costa Rica to western Panama.

Pentagonia costaricensis is recognized by the very large leaves, unusual minor venation, branched inflorescences, short calyx lobes, and smaller fruit. Standley erected the genus *Nothophlebia* for this unusual species but admitted (Standley 1938, p. 1329) that it might be referred to *Pentagonia*. A collection from 1300–1400 m near Las Alturas (*Almeda et al. 6699 F*) with larger calyx lobes and glabrous corolla tube is tentatively placed here.

Pentagonia donnell-smithii (Standl.) Standl., J. Wash. Acad. Sci. 17: 170. 1927. *Watsonamra donnell-smithii* Standl., Contr. U.S. Natl. Herb. 17: 442. 1914. Figure 14.

Small trees or treelets, 2–7(–12) m tall, often with a single stem, leafy stems 5–22 mm thick, at first appressed-sericeous but quickly becoming glabrous; **stipules** 2.5–9 cm long, 6–25 mm broad, lanceolate to narrowly ovate, with appressed-ascending sericeous hairs 0.2–0.5 mm long externally. **Leaves** often reddish beneath when young, petioles (2–)3–12 cm long, 1.5–6 mm thick, appressed-puberulent with thin ascending hairs ca. 0.2 mm long; **leaf blades** (15–)26–90 cm long, (9–)13–50 cm broad, broadly elliptic to broadly elliptic-oblong or broadly ovate, apex bluntly obtuse or rounded, base rounded and subtruncate to cuneate-obtuse, margin entire and without lobes, drying chartaceous to subcoriaceous, pale to dark grayish green, glabrous above, sparsely to moderately puberulent with thin ascending hairs on the veins beneath, 2° veins 10–14/side, minor ve-

nation closely parallel. **Inflorescences** 2.5–5 cm long, to 8 cm broad (including both inflorescences of the node), primary peduncle 1–2 cm long and 2–3 mm thick branches of the inflorescence usually short and obscured by the flowers, bracts 0–2 mm long, pedicels 0–6 mm long. **Flowers** with hypanthium 3–7 mm long, ca. 3 mm diam. distally, calyx tube 6–10 mm long, ca. 6 mm diam., minutely ascending sericeous, calyx lobes 4–8 mm long, 3–4 mm broad, broadly rounded distally, **corolla** yellow or white, corolla tube 15–30 mm long, 3–5(–6) mm diam. and broadest near the base, with short thin hairs ca. 0.2 mm long, corolla lobes 5, 5–10 mm long, acute. **Fruits** 16–40 mm diam., globose or globose-ovoid, outer wall hard and 2–3 mm thick, with small (0.5 mm) tuberculate lenticels, calyx deciduous or less often persisting on the mature fruit; **seeds** 3–5 mm long, ellipsoid, orange.

Trees of evergreen rain forest formations on the Caribbean slope and lowlands of Costa Rica, from near sea level to 900 m elevation. Flowering in March–July and October–November in Costa Rica; probably fruiting throughout the year. The species ranges from Guatemala southward along the Caribbean to central Costa Rica.

Pentagonia donnell-smithii is recognized by the very large leaves with unusual minor venation, the small compact inflorescences lacking developed bracts, the prominent calyx lobes, stiff corolla tubes, and usually globose fruit. The mature fruit in most Costa Rican collections are lacking the calyx, but the calyx persists regularly in Guatemala and Honduras. Standley (1938) suggested that this species be submerged in *P. macrophylla*. But while the two species appear to be closely related, *P. macrophylla* has a red calyx, white corolla, and large distinctive bracts subtending the branches of the inflorescence in early stages. No such bracts are seen in *P. donnell-smithii*. Also, this species does not appear to occur in eastern Costa Rica, where intergradation might be expected.

Sterile material of these species, and of *P. costaricensis* and *P. wendlandii*, may not be separable, since there is considerable variation within each species. For example, a dwarf treelet 1 m tall with very short (2 cm) petioles and slightly obovate leaves resembling the leaves of *P. wendlandii* was collected near Puerto Viejo de Sarapiquí (*A. Jiménez 3424 CR*). This collection lacks the bracts that are found in both *P. macrophylla* and *P. wendlandii* and is therefore placed here under *P. donnell-smithii*.

Pentagonia gymnopoda (Standl.) Standl., J. Wash. Acad. Sci. 17: 171. 1927. *Watsonamra gymnopoda* Standl., Contr. U.S. Natl. Herb. 17: 444. 1914.

Small **treelets**, 1–6 m tall, usually with a vertical unbranched stem, leafy stems 6–16 mm thick, somewhat flattened in early stages but becoming terete, glabrous, grayish; **stipules** 4–6 cm long, 2–3.5 cm broad, broadly triangular to lanceolate, apparently glabrous or minutely appressed-puberulent. **Leaves** with petioles 5–12 cm long, 2.7–5 mm thick, glabrous or minutely (0.1 mm) puberulent; **leaf blades** 28–70(–100) cm long, 30–45(–70) cm broad, ovate to oblong in general outline but deeply pinnatifid to the distal part of the blade, with 5–7 major oblong lobes, the lobes 5–25(–35) cm long and 2–7(–8) cm broad, apex acute to acuminate, base truncate to acute, drying chartaceous, dull grayish green above, glabrous above, minutely (0.1–0.2 mm) papillate-puberulent on the veins beneath, 2° veins 5–9/side. **Inflorescences** closely crowded in the leaf axils, 2–5 cm long, subsessile and partly covered by the broad stipules or with a peduncle up to 1 cm long, bracts to 3 cm long, flowers closely crowded and apparently sessile. **Flowers** with hypanthium ca. 10 mm long, densely appressed-puberulent, calyx tube 6–10 mm long and ca. 6 mm diam., calyx lobes 5, 18–15 mm long, 5–8 mm broad, stiff and parallel veined; **corolla** white to yellow or pale green, tube ca. 20 mm long, puberulent externally, corolla lobes ca. 10 mm long; **stamens** 5, filaments 8–10 mm long and unequal, anthers ca. 3 mm long; style ca. 9 mm long. **Fruits** 15–20 mm diam., globose to ovate or pyriform, the persisting calyx to 22 mm long and 6 mm diam.

Poorly known plants of evergreen lowland rain forest formations. Flowering in January–February; fruiting in January–February. The species ranges from the Carara Biological Reserve (84°35'W) southeastward along the Pacific lowlands to central Panama.

Pentagonia gymnopoda is recognized by the very large deeply pinnatifid leaves, small axillary inflorescences, congested flowers, and sessile fruit. The broad stipules often cover part of the inflorescence. Currently known from only about four collections in Costa Rica. Compare the closely similar *P. tinajita*.

***Pentagonia hirsuta* Standl., J. Wash. Acad. Sci. 17: 170. 1927.**

Probably small **treelets**, young branches ca. 10 mm thick, hirsute; **stipules** not seen. **Leaves** sessile and entire; **leaf blades** ca. 60 cm long and 27 cm broad, broadly obovate or broadly elliptic-obovate, apex short-acuminate, lamina gradually narrowed below the middle and cuneate but merging with a 3-cm-broad basal region that is slightly expanded (auriculate) and cordate-clasping at the stem, the auricles ca. 2 cm wide on each side, drying chartaceous, the upper and lower surfaces with numerous thin straight hairs 0.7–1.8 mm long, 2° veins 14–17/side, with 1–3 branches distally and obscurely loop-connected near the margin. **Inflorescences** poorly known, small, with crowded sessile flowers in the leaf axils. **Flowers**

poorly known, hypanthium densely hirsute, calyx ca. 24 mm long (including both tube and lobes), membranous, hirsute with whitish hairs. **Fruits** unknown.

Pentagonia hirsuta is a poorly known species from about 500 m elevation near Tsakí in the Talamanca valley, Limón Province, on the Caribbean slope of easternmost Costa Rica. The type and only collection (*Tonduz 9415* F, US) was made in March 1895. The long hairs on stems and leaves are very unusual within *Pentagonia*. The leaf shape resembles that of *P. wendlandii* in the long base but not in its shape; *P. wendlandii* seems to have more narrowly obovate leaves not as auriculate at the base (and without the long hairs).

***Pentagonia macrophylla* Benth., Bot. voy. Sulph. 105, t. 39. 1845. *Watsonamra macrophylla* (Benth.) Kuntze, Rev. gen. pl. 302. 1891. *W. pubescens* Standl., Contr. U.S. Natl. Herb. 17: 441. 1914.**

Trees or shrubs to 5(–10) m tall, often unbranched, leafy twigs 6–12 mm thick, minutely (0.1–0.3 mm) puberulent, quadrangular or becoming terete; **stipules** 3–7 cm long, 12–15 mm broad at the base, triangular and acuminate, glabrous or puberulent. **Leaves** with petioles 3–9(–12) cm long, 2.5–5 mm thick, minutely puberulent or glabrescent; **leaf blades** 22–45(–65) cm long 11–28(–37) cm broad, elliptic to elliptic-obovate or very broadly elliptic, apex gradually narrowed and acute, base gradually narrowed and obtuse or acute, drying subcoriaceous, grayish, glabrous above, minutely puberulent beneath, 2° veins 9–13/side, minor venation parallel. **Inflorescences** axillary, ca. 5 cm long (including the flowers), dense corymbs of 3–7 flowers, sessile or with short (ca. 1 cm) peduncles, bracts 10–18 mm long, 6–9 mm broad, oblong-ovate, apex obtuse, red, with many parallel veins, minutely sericeous or glabrous with a ciliate margin, pedicels 0–4 mm long. **Flowers** ca. 3 cm long, hypanthium 6–8 mm long, glabrous or minutely sericeous, calyx lobes 5, 6–12 mm long (becoming 20 mm long in fruit), to 7 mm broad, usually red; **corollas** yellow, sparsely to densely sericeous externally, tube 14–40 mm long, 3–10 mm diam., corolla lobes 5, 4–7 mm long, ovate with acute apices; **stamens** differing in size, anthers 3.5–8 mm long; style 20–25 mm long. **Fruits** 15–28 mm diam., globose beneath the persisting calyx, red or orange; **seeds** ca. 4 mm long.

Plants of lowland evergreen forest vegetation, at 10–900 m elevation in Panama. Flowering mostly in late April–September in central Panama (Croat, 1978). The species ranges from near the Panama border in Limón Province to Colombia.

Pentagonia macrophylla is distinguished from its congeners by the larger bright red bracts and red calyx lobes. We have not seen material of this

species collected in Costa Rica, but the species was studied near BriBri (Limón) by Lucinda McDade (see *Oecologia* 68: 218–223. 1986).

Pentagonia tinajita Seem., Bot. voy. Herald. 134. 1854. *P. alfaroana* Standl., J. Wash. Acad. Sci. 17: 171. 1927. Figure 14.

Small unbranched **treelets**, 1–3(–4) m tall, stems at first with 4 prominent ridges or flattened soon becoming terete, leafy stems 5–12 mm thick, glabrous; **stipules** 3–5.5 long, 1.2–2 cm broad, ovate-oblong, obtuse or bifid with striate parallel venation, puberulent along the midrib. **Leaves** with petioles 0–11(–20) cm long (variable in length due to the decurrent lamina base), 2.5–4.5 mm thick; **leaf blades** 30–80(–100) cm long, 22–40 cm broad, pinnately lobed and ovate in general outline (from a cuneate base), the sinuses 5–15 cm deep near the base and becoming more shallow distally, pinnatifid in the lower 2/3 of the lamina, sinuses usually rounded, usually obtuse at the apices, abruptly narrowed and cuneate at the base with long-decurrent lamina margins running down to the petiole or to the leaf base, leaves drying thin-chartaceous and dark green above (paler green beneath), with few short (0.2 mm) hairs on the upper surfaces, with more frequent short (0.3–0.4 mm) thin hairs on the lower surfaces, 2° veins 6–12/side, minor veins 0.2–0.4 mm apart. **Inflorescences** sessile or subsessile, densely fasciculate, bracts to 2 cm long and 3–4 mm broad, with parallel longitudinal veins and difficult to distinguish from the calyx lobes. **Flowers** with hypanthium ca. 5 mm long, calyx tube 10–15 mm long, calyx lobes 4–8 mm long, 3–4 mm broad, with the same stiff texture brown color and parallel venation as the bracts; **corolla** tube 2–2.5 cm long, 4 mm diam. at the base and 8 mm distally, stiff, corolla lobes 6–8 mm long. **Fruits** 10–20 mm long and 12–15 mm diam., globose or ovoid, the persisting calyx 10–20 mm long (tube and lobes).

Poorly known plants of lowland rain forest formations, 0–200 m elevation. Flowering in January; fruiting in February and April. The species ranges along the Pacific lowlands of central Costa Rica to western Panama.

Pentagonia tinajita is recognized by the large thin pinnatifid leaves with decurrent lamina base, congested axillary inflorescences, and smaller fruit. *Pentagonia alfaroana* (based on *Standley 40194* F, US) was said to differ because the larger leaf lobes are also pinnatifid, but leaf lobing appears to vary greatly and does not appear to be a sound basis for separating a species. Compare *P. gymnopoda*, which may be conspecific.

Pentagonia wendlandii Hook., Bot. Mag. pl. 5230. 1861. *Watsonamra wendlandii* (Hook.) Kuntze, Rev. gen. pl. 320. 1891.

Shrubs or small **treelets** to 3 m tall, main stems usually unbranched and with a cluster of leaves at the top, leafy stems 8–20 mm thick, with 4 prominent ridges, minutely appressed-puberulent or glabrous; **stipules** 2.5–6.5 cm long, lanceolate to ovate-oblong, minutely appressed-puberulent. **Leaves** entire and subsessile, petioles 5–15 mm long, 6–10 m thick; **leaf blades** 50–100 cm long, 25–50 cm broad, narrowly obovate to obovate-oblong, apex broadly obtuse or rounded, gradually narrowed below the middle, base cuneate and slightly auriculate, leaves drying stiffly chartaceous or subcoriaceous and brown, glabrous above, minutely (0.1 mm) puberulent on the veins beneath or glabrescent, 2° veins 14–16/side. **Inflorescences** to 5 cm long, with ca. 6–15 flowers, peduncles ca. 5 mm long, bracts 6–10 mm long, ca. 5 mm broad, oblong and brown, with whitish sericeous hairs along the midrib, flowers subsessile (or with pedicels to 10 mm long, fide Dwyer). **Flowers** (from Dwyer, 1980) with a calyx tube ca. 10 mm long, campanulate, purplish red, stiff, puberulent, with numerous glands at the base within, calyx lobes 5, slightly unequal, 5–10 mm long, 1 calyx lobe usually short and acute; **corolla** yellow, tube ca. 25 mm long, narrowly cylindrical, glabrous to puberulent externally, corolla lobes 4–7 mm long, 2.2–2.6 mm wide, oblong to triangular; **stamens** 5, filaments to 16 mm long, unequal, anthers ca. 4 mm long, oblong; style ca. 18 mm long, stigmas 3.5 mm long. **Fruits** to 45 mm long, oblong rotund, drying black, the persisting calyx to 15 mm long.

Pentagonia wendlandii occurs in Caribbean lowland rain forest formations, from near sea level to ca. 500 m elevation. The species ranges from Bocas del Toro Province to central Panama, but we have seen no flowering or fruiting material from Costa Rica. (A leaf associated with *Gómez-Laurito 9321* and collected near BriBri may be this species, but the flowering sheet appears to be *P. costariensis*.) The species appears to be closely related to *P. macrophylla* Benth. of central Panama but differs in the long-cuneate leaf base with a very short petiole. See the discussion under *P. donnell-smithii*.

Pentas Benth

Herbs or **shrubs**, stems erect or clambering, puberulent in most species, from a fibrous or woody rootstock; **stipules** interpetiolar with 2–many awns or narrow lobes. **Leaves** opposite or in whorls of 3–5, petiolate; **leaf blades** entire and usually narrowly ovate to lanceolate, pinnately veined, without domatia. **Inflorescences** terminal or axillary to the distal leaf pair, usually much-branched and cymose. **Flowers** bisexual, radially symmetrical, monomorphic, dimorphic, or trimorphic, calyx lobes 5, equal or unequal with 1–3 longer than the others; **corolla** usually salverform with a narrow tube, throat pilose within, corolla lobes 5, ovate to oblong or lanceolate; stamens usually included, anthers usually linear and with short filaments; **ovary** 2- or 3-locular, with many ovules in each locule. **Fruits** capsules, usually ovoid and longitudinally ribbed, beaked, splitting open at apex into 2

or 4 valves; **seeds** minute, tetrahedral or subglobose, with reticulate testa.

A genus of ca. 40 species of Africa, Arabia, and Madagascar. The following species is a popular garden ornamental with bright red, rose, lilac, or white flowers.

Pentas lanceolata (Forssk.) Deflers, Voy. Yemen, 142. 1889. *Ophiorhiza lanceolata* Forssk., F. Aegypt.-Arab. 42. 1775. Figure 31.

Herbs or **subshrubs** with erect or clambering stems, 0.5–2 m tall, stems 1.5–5 mm thick, puberulent with crooked whitish hairs ca. 0.5 mm long; **stipules** 2–9 mm long, with a short base and 3–9 slender setae, persisting. **Leaves** opposite, petioles 0–5(–15) mm long, puberulent; **leaf blades** (3–)4–13(–18) cm long, (1–)2–6 cm broad, ovate-lanceolate to lanceolate or elliptic, apex acute, base acute and slightly decurrent on petiole, drying stiffly chartaceous, sparsely to densely puberulent above and below, 2° veins 6–9/side and strongly ascending. **Inflorescences** terminal or with the distal leaf pair subtending the lateral branches, 3–9 cm long and equally broad, subcapitate or corymbose and hemispheric, puberulent. **Flowers** often trimorphic (style exserted and anthers included, anthers exserted and style included, both anthers and style included), calyx tube 1–3 mm long, calyx lobes 5, usually unequal with the longer 4–12 mm long; **corolla** brilliant rose red to lilac or white, tube 14–25(–40) mm long, ca. 0.5 mm diam. but enlarged in the distal 2–6 mm and 3–6 mm diam., throat filled with erect whitish hairs, corolla lobes 3–10 mm long, acute, ovate-lanceolate to ovate-oblong, acute.

A popular ornamental grown in gardens around the world. In Central America plants with deep red or pinkish red corollas are most common. It has become naturalized in Colombia. Compare *Ixora coccinea*, another garden favorite.

Pentodon Hochsteter

Annual or short-lived **herbs**, glabrous; **stipules** united to the petiole bases and forming a short truncated sheath with minute distal lobes. **Leaves** opposite, sessile or short-petiolate, entire with obscure pinnate venation, domatia absent. **Inflorescences** terminal or axillary and 1/node, racemose with 1–4 distal nodes and 1–4 long-pedicellate flowers at each node or few flowered and irregular (as in ours). **Flowers** bisexual, distylous, glabrous externally, calyx with 5 small equal lobes; **corolla** funnelform, tube glabrous or with hairs at the throat within, corolla lobes 5; **stamens** 5, included or exserted, subsessile from near the base of the tube or between the petal lobes; **ovary** 2-locular, with many ovules in each locule borne on peltate placentas from the septum. **Fruits** capsules, loculicidally dehiscent; **seeds** many, small, black.

A genus of probably two African species, with one now introduced into parts of the Americas. These plants are distinguished from the closely related *Oldenlandia* by the five-parted flowers.

Pentodon pentandrus (Schumach. & Thonn.) Vatke, Oest. Bot. Zeitschr. 25: 231. 1875. *Hedyotis pentandra* Schumach. & Thonn., Kongel. Dansk. Vidensk. Selsk. Naturvidenske, Math. Afh. 3: 71. 1827. *Oldenlandia pentandra* (Schumach. & Thonn.) DC., Prodr. 4: 427. 1830. *H. halei* Torr. & Gray, Fl. N. Amer. 2: 42. 1841. *P. halei* (Torr. & Gray) Gray, Syn. Fl. N. Amer. 1, pt. 2: 28. 1884.

Herbs with weakly erect or decumbent stems 10–30 cm high, stems 0.8–1.8 mm thick, glabrous and slightly succulent; **stipule** sheath 0.5–1.5(–3) mm long, entire or with 1–3 short (0.3–2 mm) subulate lobes. **Leaves** with poorly defined petioles 0.5–10 mm long (in ours); **leaf blades** 1.5–4(–8) cm long, 0.4–2.5 cm broad, narrowly ovate-elliptic to elliptic (elliptic-lanceolate to linear-lanceolate), apex obtuse to acute, base obtuse to cuneate and decurrent on the petiole, drying membranaceous or thin-chartaceous (often translucent), greenish and glabrous on both surfaces, 2° veins 3–4/side but difficult to see. **Inflorescences** 2–5 cm long, of (1–)3–5 irregularly arranged flowers in leaf axils or at apex (elongate racemose inflorescences not seen in North American material), peduncles 0–8 mm long, pedicels 2–5 mm long. **Flowers** glabrous externally, hypanthium 2–3 mm long, calyx tube 0.3–1 mm long, calyx lobes 0.5–1.5 mm long, acute; **corolla** white in ours, tube 1.5–4 mm long, 2–3 mm diam., corolla lobes 5, 1–3 mm long, 0.7–2 mm broad, ovate-triangular. **Fruits** 2.5–4 mm long, 2–3 mm diam., obconic to oblong; **seeds** 0.3 mm long.

Plants of moist depressions in open sunny sites, often along streams. Collected in central Nicaragua as early as 1869 and recently found along Rio San Juan, and in Belize. Originally in tropical Africa, Texas to Florida, and Cuba.

Pentodon pentandrus is recognized by its delicate habit with small thin ovate-elliptic leaves, small few-flowered and irregularly arranged inflorescences, small five-parted flowers, and small capsules with many seeds. The North American material (as represented by *P. halei* from the southern U.S.A. and illustrated in Correll & Correll, 1982, fig. 615) differs greatly from typical African collections (Verdcourt, 1976, p. 264, fig. 38). Measurements in parenthesis in the description represent African material. Nevertheless, the species varies greatly in Africa, and the North American material probably represents an early atypical introduction (Verdcourt, 1976, p. 263). Compare *Sipanea biflora*.

Pogonopus Klotzsch

Trees or shrubs; **stipules** interpetiolar, free, small, deltoid to narrow, deciduous with the leaves. **Leaves** opposite, petiolate; **leaf blades** usually thin, entire, pinnately veined, domatia absent. **Inflorescences** terminal, paniculate and subcorymbose-cymose, pedunculate, bracteolate, 1 or 2 flowers of the inflorescence usually with a greatly enlarged sepal lobe forming a broad petiole leaf-like and colorful "petal." **Flowers** bisexual, radially symmetrical (except for those with a single greatly enlarged sepal lobe or where the tube is curved), hypanthium turbinate, calyx tube short, calyx lobes 5, dentate and deciduous (each inflorescence usually with 1 or 2 flowers with a greatly expanded calyx lobe); **corolla** cylindrical, straight or curved, barbate in the throat, corolla lobes 5, short, valvate in bud; **stamens** 5, inserted near the base of the corolla tube, filaments slender and glabrous, anthers versatile dorsifixed above the middle, exerted; **ovary** 2-locular, ovules many on placentas longitudinally adnate to the placenta, style slender with 2 linear or oblong branches. **Fruits** capsular, subglobose to oblong-ovoid, 2-locular, areolate at apex, loculicidally bivalvate; **seeds** many, horizontal, crowded.

A neotropical genus of three species; one species ranges from Mexico to South America and is grown as an ornamental. The greatly enlarged and brightly colored laminar sepal lobe of one or two flowers in each inflorescence is distinctive (but compare *Mussaenda erythrophylla*).

Pogonopus speciosus (Jacq.) Schum. in Mart. Fl. Bras. 6, pt. 6: 265. 1889. *Macrocnemum speciosum* Jacq., Hort. Schoenbr. 1: 19, t. 43. 1797. *Macrocnemum exsertum* Oersted, Vidensk. Meddel. Kjöbenhavn 45. 1852. *P. exsertum* Oersted, Amer. Centr. 17. 1863. Figure 16.

Shrubs or small trees, 2–6(–12) m tall, leafy stems 1.5–5 mm thick, minutely (0.2–0.4 mm) appressed-pubescent and glabrescent in age, the older stems with conspicuous rounded to linear whitish lenticels 0.5–1(–2.3) mm long; **stipules** 1–3.5 mm long, 3–4 mm broad and with a rounded or cuspidate tip to 1 m long. **Leaves** with petioles 2–15 mm long, 1–2 mm broad, appressed-pubescent, often with lateral wings continuous with the lamina margins; **leaf blades** 7–18(–25) cm long, 3–7.5(–9.5) cm broad, elliptic-obovate or elliptic-oblong (smaller leaves near the inflorescence usually ovate), apex acuminate with tip 5–15 mm long, base tapering gradually and cuneate-acute, decurrent on the petiole, drying thin-chartaceous, glabrous above, sparsely pubescent on the veins beneath with thin whitish hairs 0.2–0.4 mm long, 2° veins 4–10/side, the minor venation forming a small reticulum on both surfaces. **Inflorescences** terminal or axillary, 4–18 cm long, peduncles to 5 cm long, main axis usually with opposite branches, minutely appressed-pubescent, flowers usually in compact distal cymose groups, bracteoles 2–4 mm long, lanceolate to linear, pedicels 0–3(–5) mm long. **Flowers** with hypan-

thium 3 mm long, 2–3 mm diam., conical-turbinate, sparsely and minutely puberulent, drying dark, calyx lobes 0.6–2 mm long, 0.2–0.3 mm broad, **expanded calyx lobe** with a petiole 8–20 mm long and lamina 2–4(–6) cm long and 1.5–3.5(–5) cm broad, broadly ovate or ovate-orbicular, bluntly obtuse to rounded, dark red to bright red or rose red, palmately veined; **corolla** tubular, rose red to dark red, tube 12–28 mm long, straight or curved, 3–6 mm diam. distally, densely and minutely pubescent with ascending hairs, corolla lobes 3–5 mm long, 2–3 mm broad at the base; **stamens** with filaments 20–23 mm long, anthers ca. 2.5 mm long; style 30–35 mm long, stigmas 2–2.5 mm long. **Fruits** 6–9 mm long, 5–7 mm diam., oblong-urceolate, minutely (0.1 mm) puberulent, with 2 longitudinal sulci, abruptly truncated at apex, the linear calyx lobes often persisting.

Ornamental plants grown in both evergreen and deciduous environments in Central America, from near sea level to about 500 m elevation. Probably flowering principally in the rainy season: August–December. The species grows wild in southern Mexico, the Guanacaste lowlands, and central Panama and in Colombia and Venezuela.

Pogonopus speciosus is recognized by the bright red or rose petaloid expansions of the calyx in a few flowers of each inflorescence. This species is not known from the wild in Nicaragua, El Salvador, or Honduras; it is possible that it was brought to Mexico as an ornamental in pre-Columbian times. Compare *Mussaenda erythrophylla*, another ornamental with bright red petaloid sepal lobes.

Posoqueria Aublet

Trees, treelets, or shrubs, branches soon becoming terete, glabrous or pubescent, usually thick; **stipules** interpetiolar, free, large, triangular, usually early deciduous. **Leaves** opposite and decussate, petiolate; **leaf blades** usually large, entire, often coriaceous, usually with domatia. **Inflorescences** terminal, usually few-flowered and short (but the flowers very long), corymbose to cymose or umbellate, pedunculate, bracts absent or minute, flowers pedicellate. **Flowers** bisexual and monomorphic, (4–)5(–6)-parted, radially symmetrical or bilaterally symmetrical because of the curved corolla tube, hypanthium little differentiated from the pedicel, calyx tube short, calyx lobes short-dentate, usually persisting, often auriculate at the base, with glands within; **corolla** long-salverform or long-tubular, white, corolla tube long and narrow, glabrous externally, glabrous or glandular-papillate within, corolla lobes imbricate or contorted in bud, rotate or reflexed; **stamens** unequal or subequal, short and inserted on the mouth of the tube, glabrous or pilose, anthers basifixed and sagitate, linear-oblong, exerted, (the pollen is said to be released explosively in some spp.); **ovary** 2-locular or incompletely 1-locular, ovules many in each locule and erect on stipitate bilamellar placentas borne on the septum, style filiform, as

long as the tube, stigmas short and bifid. **Fruits** baccate or drying hard and indehiscent, globose to ovoid, 1- or 2-locular, often large; **seeds** large, hard, rounded and obtusely angled to flattened, imbedded in a gelatinous pulp.

A Neotropical genus of 12–16 species, with most of the species in South America; a single species ranges as far north as southern Mexico. The genus is distinctive because of the larger stiff leaves, large stipules, the long white flowers, and the globose

indehiscent fruit with large seeds imbedded in a fleshy pulp. The corolla tubes are usually more than 10 cm long and less than 1 cm diam. The flowers are strongly fragrant at night when they open but yellowish and odorless by morning; these are probably pollinated by long-tongued moths. In some species the stamens are held asymmetrically and under tension over the mouth of the corolla tube until they are disturbed, when they snap forward. Compare *Borojoa* and *Tocoyena*.

Key to the Species of *Posoqueria*

- 1a. Corolla tubes (20–)30–38 cm long; leaf blades (10–)18–46 cm long leaf blades usually puberulent with very thin hairs beneath (but difficult to see, except along the larger veins), usually slightly rough and minor venation obscure beneath (uncommon) *P. grandiflora*
- 1b. Corolla tubes 8–20 cm long; leaf blades 10–20(–24) cm long, essentially glabrous beneath 2a
- 2a. Leaf blades drying dull above with the tertiary veins not easily seen, the minor venation not raised; fruit dull yellow to orange, ellipsoid to ovoid, with pericarp leathery and 4–10 mm thick *P. coriacea*
- 2b. Leaf blades lustrous above with tertiary veins easily seen and sometimes slightly elevated; fruit orange and globose, with pericarp hard and brittle, 1–3 mm thick *P. latifolia*

Posoqueria coriacea M. Martens & Galeotti, Bull. Acad. Brux. 11: 240. 1844.

Small **trees** or shrubs, 3–8(–20) m tall, branchlets 2–7 mm thick, glabrous; **stipules** 8–12(–28) mm long, ovate, ovate-oblong to ovate-lanceolate or suborbicular, acute, glabrous. **Leaves** with petioles 6–22 mm long, glabrous; **leaf blades** (6–)10–22(–27) cm long, (3–)5–12(–18) cm broad, narrowly elliptic to ovate or narrowly obovate, apex obtuse to abruptly acute, base cuneate to rounded and subtruncate, drying coriaceous, 2° veins 4–8/side. **Inflorescences** 2–4 cm long and 2–3 cm broad (not including the corolla lengths), cymose-corymbose, with 7–25 flowers, peduncles 1–2 cm long, glabrous or minutely puberulent, pedicels 5–10(–23) mm long, glabrate. **Flowers** with hypanthium + calyx 6–8 mm long, subulate glands present within the calyx, calyx lobes 5, unequal, 0.5–1.2 mm long, rounded; **corolla** greenish white, glabrous externally, long-tubular, tube 9–20 cm long, 1.5–3 mm diam. in the lower half, pilose within the throat and at the base of the lobes, corolla lobes 5, 15–25 mm long, unequal, rounded distally; anthers 7–10 mm long. **Fruits** 7–10 cm diam., ellipsoid to ovoid, brown, pericarp leathery, 4–10 mm thick; **seeds** 10–12 mm diam., angular, aril white.

Plants of lowland rain forest formations, from near sea level to 1100 m elevation (to 1500 m in South America). Flowering January–March; fruiting in March–April, June–August, and October–November. The species ranges from Mexico to Brazil.

Posoqueria coriacea is characterized by the long-

tubular flowers, dull leaf surfaces, and fruit with thick leathery rind. The 2° veins are often somewhat impressed in thick mature leaves when dried. The larger leaf dimensions noted above in parentheses are from Steyermark’s Flora of Venezuela treatment (1974) and may not occur in Costa Rica. The breeding system of this species was studied by Bawa and Beach (1983).

Posoqueria grandiflora Standl., J. Wash. Acad. Sci. 18: 166. 1928. *P. maxima* Standl., Publ. Field Columb. Mus., Bot. Ser. 7: 57. 1930. Figure 15.

Small **trees**, treelets, or shrubs, 2–7(–17) m tall, trunk to 18 cm dbh, leafy stems 2.5–12 mm thick, glabrous or minutely puberulent with thin erect hairs 0.1–0.2 mm long; **stipules** 8–18 mm long, 4–11 mm broad, triangular, glabrescent, deciduous. **Leaves** well spaced along the stem, petioles 7–20 mm long, 2–4 mm thick, glabrous or minutely puberulent; **leaf blades** (13–)18–34(–46) cm long, 6–17(–23) cm broad, elliptic to elliptic-obovate or elliptic-oblong, apex acuminate to short-acuminate or bluntly rounded, base tapering gradually to slightly rounded and obtuse or acute, drying subcoriaceous to coriaceous, pale grayish green beneath, glabrous above, with thin erect hairs 0.1–0.5 mm beneath or the hairs difficult to see and apparently glabrous, slightly rough to the touch beneath, 2° veins 4–8/side and prominent on both surfaces, minor venation obscure on both surfaces. **Inflorescences** only 3–6 cm long (not including the corolla tubes), corymbose with ca. 10–20 flowers, peduncles 1–

2 cm long and 3–8 mm thick, pedicels 2–12 mm long, ca. 2 mm thick, glabrous or minutely puberulent. **Flowers** glabrous, hypanthium 3–6 mm long, little differentiated from the pedicel, calyx tube 3–6 mm long, 3–6 mm diam., calyx lobes 5, 0.5–1.5 mm long, broadly rounded distally; **corolla** long-tubular with rotate lobes, white, tube (12.5–)15–36 cm long 2.5–4 mm diam., lobes 5, 20–38 mm long, 7–13 mm broad, oblong-obovate and rounded; **stamens** with unequal filaments to 15 mm long, 0.5–1 mm thick, anthers 9–12 mm long, to 2 mm broad, linear-lanceolate. **Fruits** 7–12 cm long, 4–7 cm diam., ovoid to ellipsoid, with a slightly roughened bark-like (minutely lenticellate) brownish surface, pericarp 5–12 mm thick; **seeds** 6–10 mm long, orange to white.

Trees and treelets of evergreen lowland Caribbean rain forest formations, from 40 to 300 m elevation. Flowering in February, April, July, and September–October; probably fruiting throughout the year. The species ranges from northeastern Costa Rica to Colombia.

Posoqueria grandiflora is recognized by its very long flowers on small terminal inflorescences, the relatively large corolla lobes, and the large leaves with obscure minor venation and pubescence (when present), which makes the lower leaf surfaces slightly rough to the touch. This species appears to be less common than its congeners in Costa Rica. The species has been called “wild coffee” in the Caribbean lowlands. An unusual collection (*Wilbur 20711* DUKE, F) from southern Costa Rica has large leaves with conspicuous long hairs, and flowers with very long corolla tubes, but is probably no more than an extreme form of this species. The Colombian material ascribed to *P. maxima* appears to be conspecific; Steyermark erred in making it a subspecies of *P. coriacea* Mart. & Gal.

***Posoqueria latifolia* (Rudge) Roem. & Schult., Syst. Veg. 5: 227. 1819. *Solena latifolia* Rudge, Pl. Guian. 1: 26, t. 40. 1806. *Stannia panamensis* Walp. & Duchass., Linnaea 23: 755. 1850. *P. panamensis* (Walp. & Duchass.) Walp., Ann. Bot. Syst. 2: 797. 1852. Figure 15.**

Small trees to 9(–20) m tall, trunks to 25(–40) cm dbh, wood hard and reddish, leafy stems 2–6 mm thick, glabrous; **stipules** 7–18 mm long, 3–8 mm broad at the base, triangular to ovate-oblong, sometimes slightly (1 mm) united above the petioles, apex obtuse to acuminate, stiff, glabrous. **Leaves** distant along the stem, petioles (4–)7–20 mm long, 1.5–4 mm thick, glabrous; **leaf blades** (7–)10–20(–24) cm long, (3–)4–10(–14) cm broad, elliptic-oblong to elliptic-ovate or ovate, apex obtuse or short-acuminate, base abruptly narrowed and obtuse or rounded, drying stiffly chartaceous to subcoriaceous, glabrous

above and below, 2° veins 5–7/side, the minor venation visible on both surfaces. **Inflorescences** 2–5 cm long (not measuring the corolla tubes), corymbose with 7–18 flowers, peduncles 1–2 cm long, 2–3 mm thick, bracteoles ca. 0.5 mm long, pedicels 3–9 mm long, glabrous. **Flowers** glabrous externally, sweet aromatic, hypanthium 3–6 mm long, calyx lobes poorly developed, 0–0.5 mm long; **corolla** long-tubular with usually reflexed lobes, white, tube 8–14(–16) cm long, 2–3.3 mm diam., lobes 5 (4), 12–20(–26) mm long, 4.5–5.5 mm broad, narrowly oblong, rounded; **stamens** 5 (4), filaments to 6 mm long, ca. 0.4 mm thick, anthers 6–7.5 mm long, ca. 1 mm broad, linear-oblong, with basal lobes ca. 1 mm long; style ca. 9 cm long. **Fruits** 4–6 cm diam., globose to ovoid, yellow or orange at maturity, the pericarp only 1–3 mm thick, surface becoming wrinkled; **seeds** 6–12 mm long, often triangular, translucent in life, arils white to yellow-orange, in a fleshy sweet pulp.

Trees and treelets found in rain forests, partly deciduous forests, and moist sites in deciduous forests, from 2 to 700(–1200) m elevation. Probably flowering and fruiting throughout the year (but mostly flowering in March–October and fruiting in October–April). This common species occurs in all the lowland evergreen areas of Costa Rica. The species ranges from southern Mexico to the Amazon basin of Brazil and Bolivia.

Posoqueria latifolia is recognized by the larger stiff glabrous leaves, the small terminal inflorescences with very long tubular flowers, and the globose fruit. The barely visible minor (3° and 4°) venation appears to be a consistent way of differentiating the leaves of *P. latifolia* from those of *P. coriacea*. Croat (1978, p. 814) remarks that the anthers are united at anthesis along one side of the tube and burst apart when contacted. He also notes that the flowers open late in the day and do not persist on the following day. Common names recorded in Costa Rica are *boca de vieja*, *carica*, *fruta de mono*, *guayaba de mono*, *guayaba mica*, *manzana de mico*, *picarito*, and *querica*. The names *jicarillo* and *querica* are used in southeastern Nicaragua. The fruit’s pulp is edible and sweet.

***Psychotria* Linnaeus**
Nomen conservandum

REFERENCES—C. Hamilton, A revision of Mesoamerican *Psychotria* subgenus *Psychotria* (Rubiaceae), part I: Introduction and species 1–16. Ann. Missouri Bot. Gard. 76: 67–111. Part II: Species 17–47. Ann. Missouri Bot. Gard. 76: 386–429. Part III: Species 48–61 and appendices. Ann. Missouri Bot. Gard. 76: 886–916. 1989. A. Mo-

lina, Revisión de las Especies de *Cephaelis* en México, Centro America y las Antillas. Ceiba 4: 1–38. 1953. (Other references are listed under specific species below, under the family description, and at the end of the text.)

Shrubs or small treelets, less often medium-sized trees or herbaceous subshrubs (rarely lianas), terrestrial or rarely epiphytic, stems often slightly thickened at the nodes, glabrous or puberulent; **stipules** usually united and interpetiolar with 1 or 2(–5) apices or lobes on each side, sometimes also united around the stem above the petioles (intrapetiolar) and forming a short tube or sheath, rarely separate to the base and appearing free, deciduous or persisting, colleters often present on the stems at the adaxial base of the stipules (and drying reddish in subgenus *Psychotria*). **Leaves** opposite and decussate (rarely 3 or 4/node), petiolate or rarely sessile, usually acuminate at the apex; **leaf blades** entire and pinnately veined, raphides (cystoliths) present and obscure or conspicuous, some species with domatia in the vein axils beneath (some African species with bacterial nodules in the leaves). **Inflorescences** mostly terminal and occasionally becoming pseudoaxillary by further growth of an axillary branch, less often consistently axillary, usually solitary at a node, usually pedunculate and paniculate with opposite branching, bracts large to small or rarely undeveloped, bracts forming an involucre in some species formerly placed in *Cephaelis*, flowers often borne in distal bracteolate cymes, sessile or pedicellate. **Flowers** bisexual (in Central America), radially symmetrical, usually small, often distylous with long-styled (pin) and short-styled (thrum) forms within the same species, calyx tube usually short and cupulate, with 4 or 5(–6) short calyx lobes or without lobes and entire; **corolla** tubular to funnelliform or campanulate, white to pink or yellowish, corolla tube usually short or narrow, often with tufted hairs at the throat within, glabrous or puberulent externally, corolla lobes 4–5(–6), always valvate in bud, often thickened at the tips; **stamens** 4–5(–6), borne from the middle or upper part of the tube, filaments slender, anthers narrow, included or exserted, disc ring-shaped and encircling the base of the style; **ovary** usually 2-locular (rarely with 4–6 locules), 1 erect ovule borne from the base of each locule or from the base of the thick septum, style long or short, with 2 (rarely 4–6) linear stigmas. **Fruits** fleshy drupes, red, yellow, blue, purple, black, or white when ripe, often with spongy arenchymatous tissue, usually with 2 (4–6) hard pyrenes, pyrenes plano-convex with a flattened interior (adaxial) face and a rounded exterior (abaxial) surface, often with longitudinal ridges on the exterior surface (rarely with transverse ribs or projections), usually with a median longitudinal sulcus on the inner face.

Psychotria is the largest genus of Rubiaceae and one of the largest genera of Angiosperms, with an estimated 1,500–1,600 species in the tropics and subtropics of both hemispheres. Together with *Piper* (Piperaceae) and *Miconia* (Melastomaceae),

Psychotria is one of Costa Rica's three most speciose woody genera, especially common in the understory of evergreen forests and forest edges. Some species are difficult to separate from similar species in *Coussarea*, *Faramea*, and *Palicourea* (q.v.). While *Cephaelis* appeared to be a very distinctive genus in Central America, a great number of intermediate species have necessitated the inclusion of its species in *Psychotria*. Our treatment has benefited greatly from Hammel's work on *Psychotria* at La Selva (in Taylor, 1991). Likewise, Hamilton's recent revision (see references above) of the species in subgenus *Psychotria* has been especially helpful, as these species are often difficult to differentiate; we have not deviated from his species concepts in this treatment.

Psychotria is generally characterized by the solitary terminal inflorescences with opposite branching (in most species), the 1- or 2-lobed interpetiolar stipules, entire and pinnately veined opposite leaves, smaller flowers with minute calyx lobes, short corolla tubes, valvate corolla lobes, basal solitary ovules, and fleshy fruit usually with 2 hard seed-like pyrenes. The short shrubby habit, preferences for areas of high rainfall, fruit often with longitudinal ridges, and white or yellowish flowers are additional characteristics. Those species with axillary inflorescences tend to have unbranched succulent stems or few-branched woody stems (see below). All the fruits appear to be bird-dispersed; they are fleshy and bright red, blue to purplish and black, or arenchymatous and whitish. Two species of *Psychotria* found in Costa Rica, *P. emetica* and *P. ipecacuanha*, are used medicinally.

Most species of *Psychotria* in Costa Rica are readily recognizable but the differences between closely related species can be subtle. There appear to be real problems of intergradation in the epiphytic species, and the succulent-stemmed herbaceous species with axillary inflorescences present problems of species delimitation. Except for the groups just mentioned, the majority of species stand well apart and give little evidence of hybridization or intergradation. The difficulty in identifying a specimen to species often is due to the large number of species in the genus, and the wide range of variation found within some species. Below we provide keys to four groups within the genus; groups 2 and 3 appear to be largely monophyletic. The illustrations are an additional avenue for identification and are grouped by inflorescence position, subgeneric placement, and general similarity.

Key to Four Species Groups of *Psychotria* in Costa Rica

- 1a. Plants nearly always epiphytic and with subcoriaceous leaves drying grayish; ovary usually with 4 locules; fruits red and often with 4 seeds; *or* plants of Cocos Island Group 1
- 1b. Plants not epiphytic, leaves various; ovary with 2 (rarely 5) locules; fruit usually with 2 (rarely 5) seeds; *and* plants not known from Cocos Island 3
- 2a. Inflorescences regularly axillary; main stems usually short (ca. 1 m) and succulent in a majority of species, both succulent and woody stems often with hollow sections within when dried ... Group 2
- 2b. Inflorescences terminal, only occasionally axillary where lateral shoots have continued to develop; main stems usually woody and rarely with hollow sections when dried 3
- 3a. Leaves drying greenish, gray-green, yellow-green, yellowish brown, or brown (note that leaves treated with isopropyl alcohol may turn reddish brown and that some species have pinkish venation in life), domatia rarely present; stipules often persisting, the stipules not subtending and enclosing a ring of reddish hairs (colleters) in early stages; fruit usually becoming blue, purple, or black (red only in *P. haematocarpa* with very small inflorescences, or orange in later stages in *P. racemosa* with 5 locules and 5-seeded fruit); subgenus *Heteropsychotria* Group 3
- 3b. Leaves drying grayish to black, pinkish brown or dark reddish brown, domatia present in a few species; stipules usually falling off as the leaves expand (caducous), and usually enclosing a short ring of reddish hairs (these often persisting just above the stipule scar); fruit always red at maturity (never with more than 2 seeds); subgenus *Psychotria* Group 4

Key to Group 1: Epiphytic Species of *Psychotria* in Costa Rica and Three Species of Cocos Island

The epiphytic species appear to represent a very natural (probably monophyletic) group. However, there is the strong likelihood that a large number of our collections belong to a single polymorphic entity, for which *P. guadalupensis* is the earliest name. *Psychotria maxonii* appears to be quite distinct, but there are a significant percentage of collections that appear to be intermediate between *P. guadalupensis* and *P. pithecolobium*. See the discussion under *P. guadalupensis*.

- 1a. Epiphytic plants of continental Costa Rica 2
- 1b. Trees and shrubs of Cocos Island 4
- 2a. Leaves to 5(–7) mm wide, 10–28 mm long, narrowly lanceolate to narrowly oblong; inflorescences to 3 cm long *P. maxonii*
- 2b. Leaves 8–40 mm wide, 20–120 mm long, more than 40 mm long if lanceolate or narrowly oblong; inflorescences 3–14 cm long 3
- 3a. Leaves with 6 or more pairs of secondary veins, the veins clearly elevated and visible on the dried leaf surfaces, leaves more than 4 cm long and 2 cm broad; inflorescences with peduncles 2–7 cm long *P. pithecolobium*
- 3b. Leaves with fewer than 6 pairs of major secondary veins, the veins often obscure on the surfaces of the dried leaves, leaves 3–10 cm long and 1–5 cm broad, very variable (on different plants) as regards size, shape, and texture; peduncles 0.5–3 (rarely to 5) cm long ... *P. guadalupensis*
- 4a. Leaves to 25 cm long, drying subcoriaceous and dark reddish brown; stipules forming an acute *Ficus*-like cap over the shoot apex and early deciduous *P. cocosensis*
- 4b. Leaves to 15 cm long, drying thin-chartaceous and greenish or grayish; stipules with 2 acute lobes on each side and persisting 5a
- 5a. Inflorescences less than 3 cm long, with thick (1 mm) lateral branches less than 5 mm long; stipule lobes 2–4 mm long *P. brachybotrya*
- 5b. Inflorescences usually becoming more than 3 cm long, with slender (0.3 mm) lateral branches 5–10 mm long; stipule lobes ca. 1 mm long *Psychotria* sp. A

Key to Group 2: Species of *Psychotria* with Axillary Inflorescences

- 1a. Inflorescences axillary to both leaves of the node, usually with 2 or more inflorescences at distal nodes, inflorescences usually less than 5 cm long; fruits becoming blue, black, or purple 2

- 1b. Inflorescences axillary to only 1 leaf at each node, usually with 1 inflorescence at distal nodes, inflorescences often more than 5 cm long; fruits white to yellow or red 8
- 2a. Inflorescences sessile and forming a dense verticillate cluster at the node 3
- 2b. Inflorescences short-pedunculate, not forming dense verticillate clusters around the node 5
 - 3a. Inflorescences lacking an involucre of bracts, calyx lobes to 3 mm long (not *Psychotria* spp.) *Hoffmannia* spp.
 - 3b. Inflorescences subtended by an involucre of broad bracts, calyx lobes to 2 mm long 4
 - 4a. Bracts subtending the inflorescences pale green; stipules to 10 mm long and 5 mm broad; widely distributed at 1200–2800 m elevation *P. aubletiana*
 - 4b. Bracts reddish; stipules 12–22 mm long and almost as broad; 700–1500 m near Orosí and Muñeco *P. cartagoensis*
- 5a. Leaves drying greenish to greenish brown, shrubs or small trees with many branches, young stems glabrous; stipules forming a short sheath; inflorescences with many branches, often with more than 10 fruits *P. cooperi*
- 5b. Leaves drying grayish or dark brown, subshrubs or few-branched shrubs, young stems minutely puberulent; stipules not forming a sheath; inflorescences few-branched, rarely with more than 5 fruits 6
- 6a. Inflorescences usually 4/node; plants growing to 2(–5) m tall, with lateral branches; leaf blades drying stiffly chartaceous [often obtuse at the base; peduncles to 15 mm long] ... *P. erecta*
- 6b. Inflorescences 2/node; plants growing to 1 m tall, unbranched; leaf blades drying thin-chartaceous 7
- 7a. Leaf blades drying brownish, often cuneate basally; peduncle to 5 mm long, inflorescence less than 2.5 cm long *P. emetica*
- 7b. Leaf blades drying greenish, often decurrent basally; peduncle to 70 mm long, inflorescences more than 3 cm long *P. aggregata*
- 8a. (from 1b) Stipules lobed or fimbriate distally, to 3 cm long, translucent to opaque 9
- 8b. Stipules entire distally, bluntly obtuse to rounded, to 1 cm long, thick and opaque 11
 - 9a. Stipules to 20 mm broad, drying yellowish and translucent, fimbriate to bluntly lobed [inflorescences neither capitate nor hirsute; fruit becoming white] *P. cartagoensis*
 - 9b. Stipules to 7 mm broad, drying dark and opaque, with stiff narrow or filiform teeth; fruit becoming red, purple, or blue 10
 - 10a. Leaves pilose with hairs to 2 mm long; inflorescences to 15 cm long, much-branched and lacking an involucre; fruit becoming purple or blue *P. pilosa*
 - 10b. Leaves glabrous or with short (0.5 mm) hairs; inflorescences to 5 cm long, capitate and involucre; fruit red *P. ipecacuanha*
- 11a. Leaves with more than 18 pairs of closely parallel secondary veins, veins becoming prominently raised and the leaf corrugated in age, bluntly obtuse to rounded distally; plants rarely exceeding 40 cm in height [fruits red] *P. polyphlebia*
- 11b. Leaves with fewer than 18 pairs of secondary veins, not becoming corrugated, usually acuminate at apex; plants usually more than 50 cm tall 12
- 12a. Fruits becoming orange or red 13
- 12b. Fruits becoming white or yellowish green 14
 - 13a. Leaf blades drying dark above and much paler beneath, young leaves glabrous; pyrenes with a longitudinal costa on the back; commonly collected *P. uliginosa*
 - 13b. Leaf blades drying greenish to dark brown above and only slightly paler beneath; young leaves densely hirsute beneath with hairs to 1 mm long; pyrenes lacking dorsal costae; rare *P. siggersiana*
- 14a. Young leaves villose beneath with hairs to 1 mm long, a definite arcuate submarginal vein present 2–3 mm from the leaf edge, with 16–22 pairs of major secondary veins; fruit becoming greenish yellow *P. capacifolia*
- 14b. Young leaves minutely puberulent or glabrous, a definite submarginal vein absent, with 10–16 pairs of secondary veins (and often loop-connected in the distal part of the leaf); fruit becoming white and spongy. (Note: This is a variable group of plants that may intergrade.) 15

- 15a. Inflorescences with thin widely spreading distal branches, bracts subtending the major branches less than 4 mm long, flowers borne separately along the distal branches *P. macrophylla*
- 15b. Inflorescences with thick (1 mm) distal branches or the inflorescences compact and short (5 cm), bracts subtending the basal branches or basal flowers more than 4 mm long 16
- 16a. Peduncles 0–3 cm long, flowers loosely clustered to capitate; leaves usually elliptic (rarely consistently narrow); widespread in Costa Rica *P. aggregata*
- 16b. Peduncles to 15 cm long, flowers usually capitate on the peduncle or on 3 short branches on the peduncle; leaves usually elliptic-lanceolate; eastern part of the Cordillera de Talamanca
..... *P. aggregata* (*sensu stricto*)

Key to Group 3: Species of Subgenus *Heteropsychotria* and Similar Species in Costa Rica
(Including Species Formerly in *Cephaelis*)

- 1a. Flowers borne in dense capitate or subcapitate inflorescences with closely clustered flowers, bracts usually conspicuous and enclosing the flowers; inflorescences terminal and solitary or 3 closely grouped together (species formerly placed in *Cephaelis* and others) 2
- 1b. Flowers in open or congested inflorescences but not capitate or subcapitate (flowers sometimes in small distal capitula or glomerules on secondary branches within branched inflorescences); bracts small to conspicuous or absent, bracts rarely enclosing and obscuring the flowers 16
 - 2a. Inflorescences subtended by 2(–3) large bracts forming a basal cupulate involucre, capitulum solitary, 3–10 cm broad 3
 - 2b. Inflorescences usually with more than 4 basal bracts, lacking a single cupulate involucre at the apex of the peduncle; inflorescence of 1 or 3 capitula, 1–5 cm broad 6
 - 3a. Bracts reddish (rarely yellow), inflorescences erect; very common shrubs in lowland evergreen formations 4
 - 3b. Bracts purple to lilac, inflorescences erect or pendant; rarely collected species 5
 - 4a. Stems and leaves glabrous; stipules with 2 rounded lobes on each side .. *P. elata*
 - 4b. Stems and leaves densely tomentulose; stipules with 2 sharp teeth on each side
..... *P. poeppigiana*
 - 5a. Montane (800–1200 m) plants; bracts purple, inflorescences pendant; leaf blades with ca. 14 pairs of 2° veins *P. correae*
 - 5b. Lowland (0–500 m) plants; bracts lilac, inflorescences erect; leaf blades with ca. 7 pairs of 2° veins *P. borucana*
 - 6a. Stipules with more than 2 slender teeth on each side (more than 6 teeth per node); unbranched subshrubs less than 1 m tall; fruit red [medicinal plants rarely collected in Costa Rica] ...
..... *P. ipecacuanha*
 - 6b. Stipules with 2 slender teeth on each side, or with 2 rounded lobes or unlobed (with 4 or fewer stipule lobes per node); plants mostly shrubby and more than 1 m tall (except *P. guapilensis*); fruit blue or purple 7
 - 7a. Corollas more than 4 cm long; fruit becoming more than 12 mm long; bracts usually bluntly obtuse and green *P. chiapensis*
 - 7b. Corollas less than 3 cm long; fruit less than 12 mm long; bracts acute to rounded and green to purple 8
 - 8a. Basal bracts of the inflorescences rounded to bluntly obtuse at the apex 9
 - 8b. Basal bracts acute to acuminate 14
 - 9a. Bracts white to pale green or bluish, glabrous, broadly rounded distally forming a tight cupulate involucre beneath the congested capitulum [0–600 m elevation]
..... *P. glomerulata*
 - 9b. Bracts green to deep purple, glabrous to puberulent, bluntly obtuse distally (rounded in *P. platypoda*), not forming a definite cup at the base of the inflorescence 10
 - 10a. Bracts deep purple or reddish purple, inflorescences often densely compacted and spherical; plants usually less than 1 m tall *P. guapilensis*
 - 10b. Bracts greenish to purple, inflorescences never spherical, often loosely compacted; plants usually more than 1 m tall 11

- 11a. Inflorescences usually of 3 pedunculate capitula; bracts white to pink (purple in fruit); stipular tube 2–5 mm long; 2° veins 8–12/side [1000–2500 m elevation] ... *P. dichroa*
- 11b. Inflorescences usually of a single pedunculate capitulum; bracts whitish to green or purple; stipular tube ca. 1 mm long; 2° veins 11–22/side 12
- 12a. Bracts broadly ovate and rounded at the base, purple; stipule lobes short and bluntly rounded; 1200–2300 m elevation *P. molinianum*
- 12b. Bracts usually narrowed at the base, whitish to green or purple; stipules lobes short to long, acute; 0–800 m elevation 13
- 13a. Bracts elliptic-obovate to oblanceolate; flowers usually puberulent, corolla tube 9–13 mm long; commonly collected *P. suerrensii*
- 13b. Bracts broadly rounded; flowers glabrous, corolla tube 3–6 mm long; rare in Costa Rica *P. platypoda*
- 14a. (from 8b) Bracts orange or reddish orange, ovate and broadly overlapping; plants confined to the southern Pacific slope, 600–1300 m elevation *P. aurantibractea*
- 14b. Bracts green or greenish with white, blue, or purple, linear lanceolate to ovate but not broadly overlapping; plants wide ranging 15
- 15a. Bracts narrowly ovate, often marked with blue; inflorescences ca. 3 cm long and 2 cm broad with erect bracts; stipule lobes thin and translucent, to 6 mm long; Caribbean slope, 900–1600 m elevation *P. hazenii*
- 15b. Bracts often linear-lanceolate, usually marked with white or purple; inflorescences short (1 cm) with broadly spreading bracts; stipule lobes stiff and opaque, to 4 mm long; widely ranging in moist evergreen formations, 0–800 m elevation *P. hoffmannseggiana*
- 16a. (from 1b) Young stems densely and conspicuously puberulent with hairs 0.3–2 mm long; peduncles and branches of the inflorescence usually densely puberulent 17
- 16b. Young stems glabrous or sparsely puberulent with inconspicuous hairs less than 0.3 mm long; peduncles and branches of the inflorescences glabrous or puberulent 25
- 17a. Hairs usually becoming more than 0.8 mm long, leaf blades drying dark above and 12–30 cm long, often with more than 14 pairs of major 2° veins; flowers in dense distal clusters, subtended by conspicuous bracts 18
- 17b. Hairs rarely exceeding 0.8 mm in length; leaf blades usually drying greenish (rarely dark brownish above), usually less than 20 cm long, with less than 14 pairs of major 2° veins; flowers in open or small distal clusters, bracts various 19
- 18a. Leaf blades with 9–18 pairs of major 2° veins; flowers subtended by densely puberulent lanceolate bracts ca. 2 mm broad; wide-ranging *P. pilosa*
- 18b. Leaf blades with (14–)17–23 pairs of major 2° veins; flowers subtended by sparsely puberulent ovate bracts 2–3 mm broad; southwestern Costa Rica *P. mortoniana*
- 19a. Ovary with 5 locules, fruits often with 5 seeds; stipules with 2 long (6–14 mm) stiff persisting awns on each side; leaf blades with conspicuous subparallel 3° veins [9–21(–26) cm long] *P. racemosa*
- 19b. Ovary with 2 locules, fruits never with more than 2 seeds; stipules rarely with 2 long stiff awns (*P. umbelliformis*); leaf blades rarely with conspicuous 3° veins 20
- 20a. Inflorescence umbelliform, flowers in 3 small glomerules on equal primary branches at the apex of a long peduncle; leaves glabrous above [rare] *P. umbelliformis*
- 20b. Inflorescences not as above; leaves puberulent or glabrescent above 21
- 21a. Leaf blades cuneate at the base and long-decurrent on the petiole, thin in texture; flowering portion of the inflorescences often broader than long; deciduous and evergreen formations of the Pacific slope *P. pubescens*
- 21b. Leaf blades not cuneate and long-decurrent at the base (sometimes decurrent in *P. steyermarkii*), mostly stiff-chartaceous when dried; flowering portion of the inflorescence rarely broader than long; plants of evergreen formations 22
- 22a. Pubescence of young stems usually in narrow longitudinal lines; leaf blades 3–12 cm long and 1–3 cm broad; stipules with narrow awns 2–5 mm long [plants of lower montane (800–1800 m) cloud forests; inflorescences few-branched and racemose] *P. steyermarkii*
- 22b. Pubescence not in narrow longitudinal lines; leaf blades 6–20 cm long, 2–5 cm broad; lines; plants rarely collected above 800 m elevation 23

- 23a. Plants of the Osa Peninsula; inflorescences with hairs to 1.5 mm long, branches and flower clusters distant and subtended by linear bracts to 8 mm long [leaf blades 5–12 cm long and with 10–12 pairs of major 2° veins] *P. acicularis*
- 23b. Plants not known from the Osa Peninsula or from the Pacific slope below 400 m elevation; inflorescences with hairs usually less than 1 mm long, flower clusters congested or distant, subtended by linear bracts usually less than 4 mm long 24
- 24a. Inflorescences with crowded flowers and branches, usually less than 4 cm broad, narrowly pyramidal, erect, calyx lobes 0.3–1.5 mm long; leaf blades 7–20 cm long, with 8–14 pairs of major 2° veins; awns of the stipules to 3 mm long *P. hebeclada*
- 24b. Inflorescences usually with open branching and separate flower clusters, usually more than 3 cm broad, broadly pyramidal, often pendant; calyx lobes 0.2–0.5 mm long; leaf blades 6–15 cm long and with 8–11 pairs of major secondary veins; awns of the stipules to 7 mm long *P. pittieri*
- 25a. (from 16b) Inflorescences large and many-branched, usually becoming more than 12 cm long and 10 cm broad, broadly paniculate; leaf blades usually large (often to more than 18 cm long); fruit rarely more than 4 mm diam. when dried (to 5 mm in *P. solitudinum*) 26
- 25b. Inflorescences smaller, rarely more than 12 cm long (and if so narrowly racemiform) and usually less than 10 cm broad, paniculate to subcapitate or racemiform; leaf blades often less than 15 cm long; fruit 3–12 mm diam. when dried 31
- 26a. Stipule lobes to 15 mm long and 5 mm broad at the base, conspicuous; flowers distant in small (1–2) alternate sessile groups along the slender distal branches of the inflorescence; fruits grayish blue to white *P. microbotrys*
- 26b. Stipule lobes rarely more than 5 mm long, usually less than 2 mm broad at the base; flowers distant in small sessile groups only in *P. solitudinum*; fruit blue to black 27
- 27a. Stipules at first acute distally but splitting and developing 2 acute teeth or awns separated by a broad U-shaped sinus; leaf blades often drying dark brown above; rarely collected below 400 m elevation *P. berteriana*
- 27b. Stipules at first rounded or obtuse at the apex, splitting into 2 broad lobes separated by a narrow V-shaped sinus; leaf blades drying dark greenish brown to yellowish green or grayish green; plants growing from 0 to 1700 m elevation 28
- 28a. Flowers in small (1–2) separate groups along the (usually dichotomous) slender distal branches of the inflorescence [corolla tube 4–5 mm long, narrowed at the base and urceolate distally]; southwest Pacific slope of Costa Rica *P. solitudinum*
- 28b. Flowers in distal small cymes on multiple-branched inflorescences with opposite and cymose branching; corolla various; plants not collected from the southwest Pacific area of Costa Rica 29
- 29a. Plants only known from the upper Río Grande de Orosí and Tapantí above 1300 m elevation; floral bracts ca. 3 mm long, often persisting with the flowers and obtuse distally; corolla tube ca. 6 mm long and tubular *P. tapantiensis*
- 29b. Plants not collected above 1200 m elevation; floral bracts to 3 mm long, early deciduous; corolla tube 2–7 mm long 30
- 30a. Corolla tube 2–3 mm long, funnellform or tubular; floral bracts usually rounded at the apex; leaf blades with 8–14 pairs of major 2° veins; fruit blue *P. luxurians*
- 30b. Corolla tube 6–7 mm long, narrowed at the base and expanded distally; floral bracts usually acute at the apex; leaf blades with ca. 8–10 pairs of major 2° veins; fruit becoming blue or black *P. angustiflora*
- 31a. (from 25b) Inflorescences 12–20 cm long and only 2–5 cm broad, racemiform or thyrses-like, peduncles 6–12 cm long; leaf blades with a distinct marginal vein within ca. 0.3 mm of the leaf edge and connecting the distal ends of the major secondary veins; stipules narrowly 2-lobed ... *P. cincta*
- 31b. Inflorescences rarely over 14 cm long, usually more than 4 cm broad when over 10 cm long, not racemiform or narrowly thyrses-like; leaf blades lacking a distinct marginal vein along the leaf edge; stipules various 32
- 32a. Inflorescences with conspicuous bracts and bracteoles to 14 mm long and 3 mm broad, the bracts persisting with the flowers 33

- 32b. Inflorescences without conspicuous bracts, bracts rarely more than 3 mm long or more than 1 mm broad, bracts often deciduous before the flowers mature 37
- 33a. Inflorescence small and compact, less than 3 cm long but expanding in fruit; stipules with narrow awns 2–6 mm long [0–900 m elevation] *P. brachybotrya*
- 33b. Inflorescences larger and more open, to 10 cm long; stipule lobes less than 2 mm long or triangular (not narrowly awned) 34
- 34a. Stipules very shortly (1–3 mm) bilobed with a U-shaped sinus between them [lateral branches of the inflorescences not subtended by bracts; stipules 2–5 mm long] *P. officinalis*
- 34b. Stipules bilobed distally with a short or long V-shaped sinus between the lobes 35
- 35a. Flowers subtended by ovate bracteoles 2–3 mm long, lateral branches of the inflorescences subtended by adnate bracts to 8 mm long; stipules 3–7 mm long *P. brachiata*
- 35b. Flowers subtended by lanceolate to oblanceolate bracts 4–14 mm long, lateral branches of the inflorescence usually without subtending bracts; stipules 8–20 mm long 36
- 36a. Flowers subtended by lanceolate bracts 4–9 mm long; inflorescences with 4 or more nodes with lateral branches; corolla tube 3–7 mm long *P. capitata*
- 36b. Flowers subtended by oblanceolate bracts 5–14 mm long; inflorescences with 1–3 nodes with lateral branches; corolla tube 7–10 mm long *P. calochlamys*
- 37a. (from 32b) Stipules with 1 narrow lobe (usually 2/node), the awn-like lobe acute (rarely bifid) distally and with an inner (adaxial) tooth; 500–1600 m elevation *P. valeriana*
- 37b. Stipules with 2 lobes on each side (4/node), the lobes separate laterally and without a tooth-like adaxial (inner) appendage, or the lobes/teeth not developed; 0–2000 m elevation 38
- 38a. Inflorescences less than 1.5 cm long, less than 12 mm wide; fruit becoming red at maturity *P. haematocarpa*
- 38b. Inflorescences becoming more than 2 cm long and more than 2 cm broad; fruit blue to purple or black at maturity (orange during development in *P. racemosa*) 39
- 39a. Leaf blades linear-lanceolate to narrowly elliptic-oblong, largest blades less than 3 cm broad; 1000–2000 m elevation *P. goldmanii*
- 39b. Leaf blades rarely linear-lanceolate, larger leaves over 3 cm broad; 0–1500 m elevation 40
- 40a. Inflorescence branches 0.7–1.5 mm thick when dried, flowering part of the inflorescence (beyond the peduncle) broader than long 41
- 40b. Inflorescence branches slender (ca. 0.4 mm thick) when dried, flowering portion of the inflorescences usually longer than broad [fruit less than 8 mm long and 7 mm diam. when dried] 43
- 41a. Corolla tubes less than 3 mm long; inflorescences consistently with 4 lateral branches at the first node; rare in Costa Rica at 1500 m elevation *P. allenii*
- 41b. Corolla tubes 10–15 mm long; inflorescences with 2 or 4 opposite lateral branches at the first node; from below 1200 m elevation in Costa Rica 42
- 42a. Fruit 8–12 mm long and 7–10 mm diam., without transverse projections; leaf blades stiffly chartaceous; calyx lobes ca. 0.2 mm long *P. eurycarpa*
- 42b. Fruit 4–5 mm long and ca. 6 mm diam., with transverse projections when dried; leaf blades thinly chartaceous; calyx lobes 0.2–1 mm long *P. domingensis*
- 43a. Leaf blades drying membranaceous or thin-chartaceous, usually cuneate at the base and decurrent on the petiole; plants often found in deciduous forest formations 44
- 43b. Leaf blades usually drying chartaceous, rarely cuneate and conspicuously decurrent on the petiole; never collected in deciduous areas 45
- 44a. Leaf blades with 3–7 pairs of major 2° veins, often obovate; corolla tube 6–10 mm long; fruit 7–10 mm long *P. microdon*
- 44b. Leaf blades with 9–15 pairs of major 2° veins, elliptic to ovate; corolla tube 2.5–4 mm long; fruit 5–6 mm long *P. pubescens*
- 45a. Fruits often with 5 seeds, ovary with 5 locules; stipules with stiff sharp awns 6–14 mm long and persisting; leaf blades with 3° veins subparallel [with 7–12 pairs of major 2° veins] .. *P. racemosa*
- 45b. Fruit never with more than 2 seeds, ovary with 2 locules; stipules with awns or lobes 2–8 mm long; 3° veins not subparallel 46
- 46a. Stipules with lobes or teeth absent or rarely 1 mm long, corolla tube 5–8 mm long (rare in Costa Rica) *P. phanerandra*
- 46b. Stipules with lobes or teeth 2–8 mm long; corolla tubes 0.7–5 mm long 47

- 47a. Stipules with narrow lobes 2–3 mm long; fruits ca. 4 mm long and 6 mm with smooth rounded surfaces (dried); leaf blades with long (1–3 cm) drip tips; inflorescences often small (to 6 cm long) *P. acuminata*
- 47b. Stipules with narrow awns 3–8 mm long; fruits ca. 3 mm long and 4 mm diam. with longitudinal ribs and transverse depressions; leaf blades with narrowed tips 1–2 cm long; inflorescences to 12 cm long *P. deflexa*

Key to Group 4: Species of Subgenus *Psychotria* and Similar Species in Costa Rica

- 1a. Leaf blades 3–9 cm long, very rarely more than 7 cm long; small shrubs of evergreen forests ... 2
- 1b. Leaf blades 5–30 cm long, the largest leaf blades usually more than 9 cm long; plants of evergreen and deciduous habitats 6
- 2a. Young stems densely puberulent with short (0.1–0.2 mm) reddish brown hairs; stipules acute at the apex and caducous; inflorescences less than 16 mm long [1200–2200 m elevation] *P. parvifolia*
- 2b. Young stems glabrous (except for a ring of reddish hairs above the stipular scar); stipules bilobed or bifurcate distally; inflorescences usually more than 20 mm long (except in *P. chagrensis*) 3
- 3a. Inflorescences capitate and sessile, less than 17 mm long and subtended by large bracts to 1 cm long, corolla tube 4–8 mm long; stipules bifurcate distally with a V-shaped sinus [wet lowlands, 0–300 m elevation] *P. chagrensis*
- 3b. Inflorescences paniculate and pedunculate usually more than 20 mm long and subtended by inconspicuous bracts, corolla tubes 2–4 mm long; stipules with 2 distal lobes separated by a broad U-shaped sinus 4
- 4a. Stipule lobes glabrous or minutely (< 0.05 mm) papillate puberulent; inflorescence branches ca. 0.4 mm thick when dried [0–500 m elevation in Nicaragua and Panama] *P. fruticetorum*
- 4b. Stipule lobes minutely (ca. 0.1 mm) ciliolate; inflorescence branches 0.2–0.3 mm thick when dried; plants known to occur in Costa Rica 5
- 5a. Leaf blades rarely more than 5 cm long; petioles 2–10 mm long (the leaves not sessile); inflorescences not exceeding 5 cm in length [0–1800 m elevation] *P. graciliflora*
- 5b. Leaf blades (at least the larger blades) usually exceeding 10 cm in length, petioles 0–50 mm long (leaves sessile in some spp.); inflorescences usually exceeding 5 cm in length 21
- 6a. (from 1b) Young stems conspicuously puberulent with reddish hairs 0.2–2 mm long, internodes puberulent above the ring of reddish hairs (colleters) at the stipule scar 7
- 6b. Young stems glabrous or inconspicuously puberulent with minute (0.03–0.1 mm) hairs, but a ring of reddish hairs (colleters) often present just above the stipule scars 14
- 7a. Inflorescences small (1–5 cm), flowers usually congested distally; peduncles to 2 cm long 8
- 7b. Inflorescences larger (4–15 cm long), flowers separate or congested, peduncles 1.5–15 cm long 10
- 8a. Leaf blades with an arcuate submarginal vein; stipules with a tube 4–14 mm long and narrow awns; fruits 5–6 mm long [0–200(–800) m elevation] *P. psychotriifolia*
- 8b. Leaf blades usually lacking an arcuate submarginal vein but the distal veins often loop-connected; stipules with a tube 0–5 mm long, usually lacking narrow awns; fruits 6–14 mm long 9
- 9a. Leaf blades usually elliptic-obovate or elliptic; stipules 3–11 mm long; fruits 6–8 mm long; widespread at 20–800(–1200) m elevation *P. nervosa*
- 9b. Leaf blades usually oblanceolate to narrowly elliptic-oblong; stipules 8–14 mm long; fruits unknown; Chiriquí Highlands ca. 1200 m elevation *P. boquetensis*
- 10a. Leaf blades with 14–33 pairs of major 2° veins, leaf blades 12–30 cm long; peduncles 4–14 cm long 11
- 10b. Leaf blades with 8–13 pairs of major 2° veins, leaf blades 6–30 cm long; peduncles 1.5–8 cm long 12

- 11a. Leaf blades with 14–22 pairs of major 2° veins; lacking a definite submarginal vein, 3° veins subparallel; floral bracts ca. 3 mm long, narrowly triangular *P. micrantha*
- 11b. Leaf blades with 20–34 pairs of major 2° veins, with definite submarginal veins and subparallel 3° veins; floral bracts ca. 7 mm long and ovate *P. sixaolensis*
- 12a. Leaf blades rounded at the base and subcordate at the petiole, to 30 cm long, petioles 6–12 cm long; stipules ca. 2 cm long; rarely collected plants of the Caribbean escarpment [200–500 m elevation] *P. insignis*
- 12b. Leaf blades not rounded and subcordate at the base (or if so not regularly exceeding 18 cm in length), petioles usually less than 6 cm long; widespread 13
- 13a. Corolla tubes 2–2.5 mm long; fruit 4–6 mm long; peduncles 1.5–5 cm long; leaf blades usually drying reddish brown or brown, major veins not impressed on the upper surfaces; (200–)400–1600 m elevation *P. jimenezii*
- 13b. Corolla tubes 1.5–2 mm long; fruit 5–7 mm long; peduncles 3–8 cm long; leaf blades usually drying grayish, major veins impressed on the upper leaf surfaces; 20–400 m elevation *P. neillii*
- 14a. (from 6b) Larger leaf blades usually more than 10 cm broad and usually more than 20 cm long 15
- 14b. largest leaf blades less than 10 cm broad, rarely more than 20 cm long 21
- 15a. Inflorescences short (3–11 cm long) and compact (2–5 cm broad), with lateral branches to 1 cm long and often difficult to see; plants 0.5–2 m tall 16
- 15b. Inflorescences to 30 cm long and 4–15 cm broad, with lateral branches more than 1 cm long and clearly visible; plants 1–10 m tall 18
- 16a. Leaf blades with 16–19 pairs of major 2° veins, usually more than 25 cm long, rounded to obtuse at the apex; bracts ca. 5 mm long *P. chitarriana*
- 16b. Leaf blades with 8–14 pairs of major 2° veins, usually less than 25 cm long, short-acuminate to acute at the apex; bracts 0.2–2 mm long 17
- 17a. Stipules with a basal tubular sheath and 2 narrow distal lobes; leaf blades with 10–14 major 2° veins on each side, usually obovate; inflorescences to 7 cm long, compact panicles of cymes *P. alfaroana*
- 17b. Stipules not tubular at base, broadly ovate and bluntly obtuse at the apex; leaf blades with 8–11 pairs of major 2° veins, usually broadly elliptic; inflorescences to 3 cm long, with short lateral branches and appearing subumbellate *P. lamarinensis*
- 18a. Stipules united over the shoot apex (as in *Ficus*) and tearing off as the leaves begin to grow, narrowly conical in early stages; fruit 5–9 mm long (var. *compressicaulis* of) *P. panamensis*
- 18b. Stipules united only at their base, open distally and often with the base persisting, ovate-triangular in form; fruit 4–6 mm long 19
- 19a. Leaf blades sessile and subcordate at base, usually 3–4 times longer than wide, 2° veins arising from the midvein at angles of 80–100° *P. rosulatifolia*
- 19b. Leaf blades with prominent petioles, never rounded at the base, blades 2–3 times longer than wide, 2° veins usually arising at angles of 60–70° 20
- 20a. Secondary veins not usually loop-connected; stipules 8–30 mm long and acute to acuminate at the apex; inflorescences to 30 cm long *P. grandis*
- 20b. Secondary veins loop-connected distally to form an arcuate submarginal vein; stipules 5–12 mm long and rounded to acute; inflorescences to 10 cm long *P. limonensis*
- 21a. (from 5b and 14b) Flowers in dense sessile verticils on a single elongated (4–9 cm) rachis or in dense clusters in a compact often globose arrangement, inflorescences solitary and apical, spiciform or capitate/subcapitate, primary branches short (< 1.5 cm) or absent 22
- 21b. Flowers usually in open cymes, or on open spreading branches of the inflorescences when closely clustered, never spiciform or globose-capitate, primary branches of inflorescences usually more than 1 cm long 23
- 22a. Flowers in dense sessile verticillate clusters along the slender elongated (3–9 cm) rachis, inflorescences spiciform with a single pair of proximal opposite branches or none; leaf blades usually with domatia in the distal vein axils *P. viridis*

- 22b. Flowers in dense subcapitate globose or ellipsoid inflorescences with a rachis less than 4 cm long; leaf blades lacking large domatia *P. alfaroana*
- 23a. Stipules united over the shoot apex and forming a cap with a single acute apex as in *Ficus* (usually not split or open distally during development), narrowly conical to cylindrical and elongate, usually becoming more than 5 mm long before splitting, caducous as the leaves begin to expand (note that new lateral branches beneath the inflorescences often are enclosed within *Ficus*-like stipules after other stipules have fallen); inflorescences with opposite branches; leaves lacking a submarginal vein 24
- 23b. Stipules united over the shoot apex only in very early stages (if present the united cap usually splitting before reaching 5 mm in length and open distally in later development), caducous or tardily deciduous, larger *Ficus*-like stipules not present; inflorescences with opposite or whorled branches; leaves with or without a submarginal vein 27
- 24a. Leaf blades usually with pit domatia or tufted hairs in the vein axils beneath, drying grayish or pinkish gray above, with 10–13 pairs of major 2° veins; ca. 600 m elevation in the Cordillera de Tilarán *P. mexiae*
- 24b. Leaf blades lacking pit domatia or tufted hairs in the vein axils, drying grayish to dark reddish brown, with 5–16 pairs of major 2° veins; 400–2100 m elevation 25
- 25a. Stipules 2–6 mm long, central 2° veins arising at angles of 60–90°, leaf blades 4–12 × 1.5–5 cm [drying dark grayish above, with 5–7 pairs of major 2° veins; fruits 4–7 mm long] ..
..... *P. orosiana*
- 25b. Stipules usually becoming more than 6 mm long; central 2° veins arising at angles of 50–70°, leaf blades 6–22 × 2–10 cm 26
- 26a. Leaf blades usually drying grayish above, with 6–8 pairs of major 2°, usually narrowly elliptic and with long petioles; stipules becoming 5–45 mm long; dried fruits 7–10 mm long
..... *P. sarapiquensis*
- 26b. Leaf blades usually drying reddish brown to dark brown (less often dark grayish), with 6–16 pairs of major 2° veins, very variable in shape and texture; stipules becoming 8–80 mm long; fruits 5–9 mm long *P. panamensis*
- 27a. (from 23b) Inflorescences only 2–4 cm broad, with short (< 2 cm) lateral branches (sometimes becoming larger as the fruit develop) [flowers often closely congested distally]; leaf blades with 2° veins often weakly loop-connected near the margin; plants usually found in deciduous and partly deciduous formations 28
- 27b. Inflorescences usually 4–8 cm broad, the lateral branches usually more than 2 cm long; leaf blades with or without loop-connected 2° veins; plants not found in deciduous formations 31
- 28a. Corolla tube 4–5 mm long; fruit 6–9 mm long; inflorescences 1–3 cm long, with opposite branches or the flowers subsessile at the end of the peduncle [broad ovate stipules with an obtuse apex often subtending the young inflorescence] *P. quinquerradiata*
- 28b. Corolla tube 1–3.5 mm long; fruit 4–8 mm long; inflorescences 1.5–10 cm long, with opposite or whorled branches 29
- 29a. Inflorescences with only 2 branches at each node, often umbelliform; corolla tube 1.5–2 mm long; stipules 6–14 mm long, acute and becoming narrowly 2-lobed at the apex; leaf blades narrowly elliptic, to 20 cm long *P. tenuifolia*
- 29b. Inflorescences usually with 4 branches at the first node (2 longer and 2 shorter), rarely umbelliform; corolla tube 2.2–3.5 mm long; stipules 2–8 mm long and bluntly obtuse; leaf blades usually obovate to elliptic, to 15 cm long 30
- 30a. Pit domatia rarely present in distal vein axils beneath; leaves usually drying gray to pinkish gray; calyx not usually persisting on the fruit; deciduous formations (in Costa Rica)
..... *P. carthagenensis*
- 30b. Domatia or tufts of hairs often present along the midvein beneath; leaf blades usually drying gray to greenish gray [calyx often persisting on the fruit with lobes 0.5–3 mm long]; in both evergreen and deciduous areas *P. horizontalis*
- 31a. (from 27b) Inflorescences usually with 4 lateral branches at the first node (2 smaller descending and 2 larger ascending); leaf blades usually narrowly elliptic to oblanceolate and with an arcuate submarginal vein formed by the loop-connected secondaries (compare dichotomy 28 also) .. 32
- 31b. Inflorescences with 2 opposite lateral branches at the first node; leaf blades various 33

- 32a. Corolla tube 2–2.5 mm long; leaves usually drying grayish; wet lowlands (0–800 m elevation) *P. clivorum*
- 32b. Corolla tube 3–5 mm long; leaves usually drying reddish or grayish brown; montane (2000–2600 m elevation) forests *P. sylvivaga*
- 33a. Leaf blades usually with large (1–3 mm) domatia in the vein axils beneath, often opening by ellipsoid slits [blades 11–24 cm long, usually elliptic-oblong and drying dark reddish brown; inflorescence axes winged; peduncles ca. 2 mm thick; fruit 7–9 mm long; rarely collected in Costa Rica] *P. remota*
- 33b. Leaf blades without large webbed domatia in the vein axils, smaller domatia present or absent 34
- 34a. Calyx lobes well developed (0.5–1 mm long); peduncles 1.5–2.5 mm thick when dried, primary branches of the flowering inflorescences 1–1.5 mm thick when dried; leaf blades lacking domatia, often oblanceolate, to 22 cm long; montane (1300–2600 m elevation) forest species 35
- 34b. Calyx lobes minute (0.3 mm) or absent; peduncles 0.5–1.5 mm thick when dried, primary branches of the flowering inflorescences usually less than 1 mm thick when dried; leaf blades often with domatia on the lower surfaces, not usually oblanceolate or more than 15 cm long (except in *P. sarapiquensis*); 0–2500 m elevation 37
- 35a. Primary branches of the inflorescence usually diverging at more than 100° from the more distal rachis (\pm reflexed); leaf blades with 10–15 pairs of major 2° veins, with or without an arcuate submarginal vein [flowers on open cymes on tertiary branches of a much-branched inflorescence, peduncles 5–9 cm long; 1700–2000 m elevation] *P. stockwellii*
- 35b. Primary branches of the inflorescence usually diverging at 90° or less from the rachis, perpendicular or ascending; leaf blades with 8–11 pairs of major 2° veins; usually with a definite submarginal vein 36
- 36a. Flowers in dense glomerules at the ends of the few (ca. 5) 1° or (ca. 9) 1° and 2° branches; peduncles 1.5–5.5 cm long; 900–1500 m elevation *P. monteverdensis*
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Psychotria acicularis C. M. Taylor, sp. nov. Figure 55.

Species *Psychotriae pittieri* Standley affinis, sed ab ea bracteis majoribus (3–10 mm longis) et angustioribus dif-
fert.

TYPUS—*J. Utley & K. Utley 1036* (holotypus CR, isotypi F, MO!), from region to southwest of airstrip, 20–60 m alt., 20 July 1974, Rincón de Osa, Puntarenas, Costa Rica.

Small shrubs, 0.5–2 m tall, leafy stems 0.7–2 mm thick, densely hirsutulous with thin hairs 0.4–1.5 mm

long, older stems glabrescent; **stipules** 3–8 mm long, with a short (1–3 mm) tube and 2 slender teeth 3–7 mm long on each side, densely hirsutulous in early stages, persisting or deciduous. **Leaves** with petioles 2–9(–13) mm long, ca. 0.7 mm thick, densely hirsutulous, often somewhat unequal at the same node; **leaf blades** 5–12 cm long, 2–4.5 cm broad, narrowly ovate-elliptic to elliptic or elliptic-oblong, apex acuminate with a tip 4–12 mm long, base usually obtuse, drying thinly chartaceous or membranaceous, dark green above, with slender hairs 0.5–1.2 mm long on the upper surface, especially along midvein, becoming glabrescent, more densely hirsutulous beneath with slightly shorter more persistent hairs, 2° 10–15/side. **Inflorescences** terminal and solitary, 5–12 cm long, open or elongate panicles with usually 4 branches at apex of the peduncle and 2 additional pairs of opposite or alternate branches, peduncles 3–8 cm long, ca. 0.7 mm thick (dried), hirsutulous with hairs to 1.5 mm long, bracts 3–10 mm long and linear, flowers subsessile in condensed distal cymes, bracteoles 2–4 mm long, linear. **Flowers** densely puberulent externally, hypanthium ca. 1 mm long, sericeous with ascending thin whitish hairs ca. 0.5 mm long, calyx lobes 0.5–1 mm long, lanceolate; **corolla** white, narrowly salverform, tube ca. 3 mm long and 0.5 mm diam., corolla lobes ca. 1.2 mm long; anthers ca. 1 mm long. **Fruits** 3–3.5 mm long, 2.5–3 mm diam., broadly ellipsoid, bluish with thin ascending hairs ca. 0.5 mm long, persisting calyx lobes ca. 0.5 mm long.

Plants of the rain forest interior on the Osa Peninsula, at elevations of 20–80 m. Flowering in May and July; fruiting in May–August. This species is only known from near Rincón de Osa on the Osa Peninsula in southwestern Costa Rica.

Psychotria acicularis is recognized by its hirsutulous indumentum on all parts, small stature, small leaves, open inflorescences with conspicuous linear bracts, sessile flowers borne in distal clusters, small blue fruit, and limited geographic range. This species, a member of subgenus *Heteropsychotria*, resembles *P. pittieri* vegetatively but differs in its linear bracts and inflorescences with four branches at the first (basal) node. Additional specimens seen were Aguilar 6423 (CR), Burch 4413 (DUKE, MO), Burger & Stolze 5449 (CR, F, MO), Duke 16111 (MO), Kennedy 1934 (MO), Raven 21532 (CR, F), and Utley & Utley 1174 (CR, F).

***Psychotria acuminata* Benth., Bot. voy. Sulph. 107. 1845. *P. cuspidata* sensu Standl. et auctores, non Bredem. ex Roem. & Schult. fide Steyermark 1974. Figure 56.**

Shrubs or subshrubs, 1–2(–3) m tall, much-branched, leafy stems 1.5–5 mm thick, glabrous, quadrate to terete; **stipules** with a short (0.5–2 mm) truncated tube with 2 narrow awns 1.5–3 mm long on each side, these deciduous. **Leaves** with petioles 5–15(–18) mm long, 0.7–1.4

mm thick, minutely (0.05 mm) papillate-puberulent; **leaf blades** 7–15(–19) cm long, 3–8(–10) cm broad, elliptic to oblong-elliptic or ovate-elliptic, apex short- to long-acuminate or caudate-acuminate with tip 1–3 cm long, base acute to obtuse, drying thin-chartaceous and greenish or brownish, glabrous above and below, or with tufted domatia in the vein axils beneath, 2° veins 7–12/side, midveins sometimes reddish beneath. **Inflorescences** solitary and terminal, 2–6 cm long (to 7 cm in fruit); 2–4(–5) cm broad, paniculate, peduncles 1–4 cm long, 0.5–1 mm thick, minutely papillate-puberulent (or apparently glabrous), primary branches opposite or alternate, bracts subtending the inflorescence branches absent or small (1 mm) and adnate to branches, floral bracts absent, pedicels 0–2 mm long. **Flowers** distylous, minutely (0.05 mm) papillate-puberulent externally, hypanthium ca. 0.5 mm long and 0.5 mm diam., calyx 0.3–0.7 mm long with weakly defined lobes; **corolla** white or pale yellow, tube 2–4(1–5) mm long and 0.5–1 mm diam., lobes 5, 1.5–2.5 mm long, rounded; anthers 1–1.2 mm long, linear. **Fruits** 4 mm long, 5–7 mm diam., 2-lobed and rounded, smooth, becoming blue, bluish gray, or purple; pyrenes 2.5 mm long and 3 mm broad, hemispheric with a longitudinal sulcus on the inner face.

Plants of evergreen lowland rain forest formations on both the Caribbean and Pacific slopes, from near sea level to 900(–1100) m elevation in Costa Rica. Flowering in January–August in southern Central America (usually May–June at La Selva). Fruiting is primarily in June–December. The species ranges from Mexico and the West Indies to Venezuela and Peru.

Psychotria acuminata is characterized by its glabrous or minutely papillate-puberulent parts, lustrous acuminate leaves with pronounced narrow drip tips, small flowers and inflorescences, 2-awned stipules, and smooth rounded bilobed blue fruit. In some specimens, the stipules appear to be undeveloped. The small stature, leaf size, and foliage drying greenish are similar to many other species, but the small yellowish papillate-puberulent inflorescences and smooth bilobed fruit are distinctive. Also, the veins on the undersides of the leaves are sometimes pink. The presence of domatia-like tufts of hairs in the vein axils is uncommon among our species of *Psychotria* subgenus *Heteropsychotria*. The breeding biology was studied by Bawa and Beach (1983). *Psychotria valeriana* of higher elevations is similar but has a single stipular awn with an adaxial tooth on each side of the stem. [The name *P. cuspidata* deserves more careful review; it may be that Steyermark failed to recognize a specific distinction between the Caribbean material and his Venezuelan specimens.—C.M.T.]

***Psychotria aggregata* Standl., Contr. U.S. Natl. Herb. 18: 128. 1916. *P. tonduzii* Standl., J. Wash.**

Acad. Sci. 15: 287. 1925. *Montamans panamensis* Dwyer, Ann. Missouri Bot. Gard. 67: 286. 1980. Figure 12.

Herbaceous **subshrubs** with succulent stems, 0.5–1.5(–2) m tall, leafy stems 1.6–6 mm thick (dried), quadrangular, glabrous; **stipules** 2–9(–12) mm long, to 7 mm broad, triangular with a short (2–3 mm) cupular base and bifid conical appendages 4–7 mm long, base persisting. **Leaves** with petioles 3–10(–13) cm long, 1–2 mm thick, glabrous; **leaf blades** 12–30(–38) cm long, (3–)5–17 cm broad, elliptic-oblong to elliptic-obovate or elliptic-oblancoolate, apex tapering gradually and acute or acuminate, tip 5–15(–22) mm long, base obtuse to cuneate or acute and decurrent on petiole, drying chartaceous and dark to pale grayish green, glabrous above, glabrous or minutely papillate-puberulent beneath, 2° veins 10–19/side. **Inflorescences** axillary, solitary, 4–15 cm long, 2–4 cm broad, congested to capitate or with 1–2 pairs of lateral branches, peduncles 1–5(–8) cm long, 1–2 mm thick, glabrous or minutely and sparsely puberulent, bracts at the lateral branches 2–8 mm long, flowers subsessile in closely crowded distal glomerules on the 1° or 2° branches, bracteoles 1–4 mm long. **Flowers** with hypanthium 1–2 mm long, glabrous or sparsely and minutely puberulent, calyx 0.5–2 mm long, lobes 5, 0.5–4 mm long, obtuse to linear; **corolla** white, funnellform glabrous or minutely puberulent externally, tube 2–4 mm long, ca. 1 mm diam., corolla lobes 5, ca. 1 mm long, obtuse and galeate; anthers ca. 1.2 mm long. **Fruits** 5–7 mm long (dried), 4–6 mm diam. (to 10 mm in life), ovoid to subglobose, spongy, white; pyrenes ca. 6 mm long, with margin and median keel thickened dorsally.

Plants of evergreen montane rain forest and cloud forest formations, from 10 to 2300 m elevation (but most common in the 400–1700-m range). Apparently flowering and fruiting throughout the year. The species ranges from northern Costa Rica into western Panama.

Psychotria aggregata is recognized by its short succulent unbranched main stems, large essentially glabrous leaves, axillary inflorescences with flowers in dense bracteolate clusters, and spongy white fruits. This species is quite similar to *P. macrophylla* but differs in the more condensed inflorescences and the pyrenes. (This and related species have recently been studied by Molly Nepokroeff, wis, 1992.) The type of *P. aggregata* (Pittier 3264 us from Horqueta, Chiriquí, Panama) is a very poor specimen, but it is an early name for this variable taxon, commonly called *P. tonduzii* by previous authors.

Psychotria alfaroana Standl., J. Wash. Acad. Sci. 18: 273. 1928. Figure 66.

Herbaceous erect **subshrubs**, 0.2–0.6(–1) m tall, usually with a single erect unbranched stem, rhizomatous,

leafy stems 2–4 mm thick, glabrous, terete; **stipules** to 20 mm long, basal sheath 5–8 mm long and 4 mm broad, with 2 narrow distal lobes 3–12 mm long, glabrous or sparsely puberulent, caducous. **Leaves** with petioles (2–)6–25(–30) mm long, 1.5–2 mm thick, sulcate above, glabrous; **leaf blades** 11–22(–30) cm long, 4–11 cm broad, obovate to elliptic-obovate or elliptic-oblancoolate, apex short-acuminate or subacute, base gradually narrowed and cuneate, decurrent on petiole, drying thin- to stiffly chartaceous, grayish or grayish green, glabrous above, with minute (0.1–0.3 mm) thin hairs along major veins beneath, 2° veins 10–14/side, weakly connected by an arcuate submarginal vein. **Inflorescences** terminal, solitary, 3–8 cm long, 2–4 cm broad, compact globose or elongate dense panicles of cymes, peduncle 1–4 cm long, 1.2–2 mm thick, glabrous, bracts 0.5–1 mm long, pedicels 1–2 mm long. **Flowers** glabrous externally, hypanthium ca. 1.5 mm long, calyx tube ca. 1 mm long, cupulate, calyx lobes 5, 0.5–2 mm long, narrowly oblong; **corolla** white, tube 2.5–4 mm long, ca. 2 mm diam., lobes 5, 1.5–3 mm long, ca. 1 mm broad at base; **stamens** 5, anthers 0.8–1.3 mm long. **Fruits** 8–12 mm long, 4–6 mm diam., ellipsoid, red at maturity, becoming black when dried, persisting calyx to 3 mm long; pyrenes ca. 7 mm long, usually with 5 dorsal ribs.

Plants of wet rain forest formations of the Caribbean slope and continental divide, 20–900(–1100) m elevation. Flowering in January–September; fruiting in January–February and June–August. The species ranges from the Cordillera de Guanacaste in Costa Rica to Bocas del Toro Province in Panama.

Psychotria alfaroana is recognized by its very short stature, usually obovate leaves, compact subglobose inflorescences, and larger fruit. The bright red fruit and leaves drying grayish are characteristics of subg. *Psychotria*. Standley and Velez made a number of collections of this species near Tilarán, including the holotype (41579 us). A collection from along Río Corobici (Opler 138 F) is provisionally placed here; this is the only collection from the Pacific lowlands. Several collections with exceptionally large (35 × 15 cm) leaves attenuate almost to the base and then abruptly subauriculate are tentatively placed here: Gómez-Laurito 11570, Hammel et al. 16895, and Herrera & Chacón 2355 (all at CR).

Psychotria allenii Standl., Ann. Missouri Bot. Gard. 27: 342. 1940.

Small trees or shrubs, (2–)4–10 m tall, leafy stems 1–4 mm thick, glabrous or minutely and sparsely puberulent; **stipules** united around the stem for 0.5–3 mm, with 2 acute lobes 1–5 mm long, separated by a V- or U-shaped sinus, persisting. **Leaves** with petioles 6–18 mm long, 0.8–1.3 mm thick, glabrous; **leaf blades** 5–16 cm long, 3–7(–8) cm broad, ovate-elliptic or ovate-ob-

long to narrowly elliptic-oblong, apex acuminate with tip ca. 5 mm long, base obtuse to slightly rounded, drying dark olive green or grayish green and chartaceous, glabrous above, glabrous or minutely puberulent beneath, 2° veins 5–7/side, distal veins strongly arcuate-ascending. **Inflorescences** 8–10 cm long, 5–7 cm broad, pyramidal panicle with distal branches progressively shorter, peduncles 3.5–6.5 cm long, 0.9–2.3 mm thick, glabrous or puberulent, the first node with 4 lateral branches 2–3.5 cm long subtended by linear bracts 1–3 mm long, flowers mostly sessile and crowded in distal cymes. **Flowers** with hypanthium 0.4–0.8 mm long, glabrous or sparsely papillate-puberulent, calyx ca. 0.7 mm long with glabrous lobes ca. 0.3 mm long; **corolla** white, tube 0.7–2 mm long and 1 mm diam., lobes 5, ca. 1.7 mm long; stamens 5. **Fruits** 6–15 mm long and ca. 6 mm diam. when dried, bright blue; pyrenes smooth, subglobose.

Plants of moist evergreen lower montane forests, 50–900(–1500) m elevation. Flowering and fruiting in February–August in Panama. The species is known only from Monteverde in Costa Rica (*Koptur* 74 MO with flowers and early fruits in October). The species ranges to central Panama.

Psychotria allenii is recognized by its distinctive pyramidal inflorescences with relatively thick peduncles, four stout lateral branches at the first few nodes, and small sessile flowers. This species is quite similar to *P. officinalis*, but that species has floral bracts and larger flowers and lacks the robust lateral branches of the inflorescence. The Costa Rican collection has narrower elliptic-oblong leaves than Panamanian material, and it was a 2-m shrub rather than a tree.

Psychotria angustiflora K. Krause, Bot. Jahrb. 54, Beibl. 119: 43. 1916. *P. mima* Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 22: 386. 31 Oct. 1940 (holotype: *Skutch* 4589 F from Costa Rica), not *P. mima* Standl., loc. cit. 22: 204. 10 Sept. 1940 (holotype: *L. B. Smith* 1878 F from Brazil). Figure 57.

Shrubs or small trees to 5 m tall, leafy stems 1.5–5 mm thick, glabrous, terete; **stipules** 3–8 mm long, 2–6 mm broad, triangular to ovate and rounded at the narrowed tip, with a short (1–3 mm) tube, obtuse or bilobed with a small (1 mm) sinus, glabrous, persisting. **Leaves** with petioles 15–35(–60) mm long, 1.2–3 mm thick, glabrous, with 2 adaxial ridges; **leaf blades** (9–)15–24(–30) cm long, (4–)7–14(–16) cm broad, oblong to ovate-oblong, broadly elliptic or broadly elliptic-obovate, apex short-acuminate with a tip 5–10 mm long, base broadly obtuse (rarely acute), drying thin-chartaceous and greenish gray or greenish brown above, glabrous above and below, 2° veins 8–11/side, central 2° veins ca. 2 cm distant in larger leaves. **Inflorescences** terminal, solitary (3–)17–45 cm long, (8–)15–25 cm broad, pyramidal pa-

niculate with distant opposite lateral branches, peduncles 6–15 cm long, 1.5–2 mm thick, glabrous or minutely puberulent, bracts to 7 mm long and 1.5 mm broad, flowers subsessile in distal cymes or along slender distal branches, subtended by bracteoles ca. 1 mm long. **Flowers** minutely papillate-puberulent externally, hypanthium ca. 0.7 mm long, calyx ca. 0.4 mm long, calyx lobes ca. 0.2 mm long, acute; **corolla** pale yellow or greenish yellow (rarely white), tubular-obovoid or funnelliform, tube 5–7.5 mm long, 0.9–1.3 mm diam. in the lower half and 2–3 mm distally, lobes 5, 1–2.5 mm long, triangular and acute, erect. **Fruits** 4–5 mm long and 3–5 mm diam. (to 8 mm in life), subglobose with ca. 6 longitudinal ribs, becoming blue or black; pyrenes 1.5–3.5 mm long.

Plants of evergreen rain forest formations, from near sea level to 900 m elevation on the Caribbean slope. Flowering in January–August; fruiting in June and October–November. The species ranges from near La Selva, Heredia, to Brazil.

Psychotria angustiflora is recognized by its large open inflorescences with small distal bracteoles, narrowly obovoid yellowish corolla, larger leaves, and ovate stipules that are obtuse or minutely two-lobed at apex. The stipules may become two-parted as the expanding stem breaks them apart. The flower buds are quite narrow before the corolla is fully expanded. The isotype of *P. angustiflora* (*Tonduz* 12996 US) fits in well with the material placed here. This species should be compared to *P. berteriana* (smaller flowers, different stipules, narrower leaves) and *P. luxurians* (smaller flowers, larger bracteoles).

Psychotria aubletiana Steyererm., Mem. New York Bot. Gard. 23: 694. 1972. *Cephaelis axillaris* Sw., Prodr. 45. 1788, not *P. axillaris* Willd. *P. aubletiana* var. *centro-americana* Steyererm., loc. cit. 698. 1972.

Herbs or subshrubs, 0.5–1.5(–4) m tall, erect and few-branched, stems slightly succulent, leafy stems 1–5 mm thick, glabrous or rarely densely puberulent with soft yellowish hairs ca. 0.2 mm long, quadrangular, drying dark; **stipules** 5–10 mm long, to 6 mm broad, basal sheath 3–5 mm long, ovate with a short (2–4 mm) sinus and 2 irregular rounded lobes per side. **Leaves** with petioles 6–20(–40) mm long, 0.7–1.8 mm thick, glabrous or minutely puberulent; **leaf blades** 4–15(–18) cm long, 1–4(–6.5) cm broad, elliptic-oblong, narrowly oblong-obovate to narrowly elliptic-obovate, oblong-lanceolate or narrowly elliptic, apex acuminate (rarely acute) with tip 4–12 mm long, acute at the base (obtuse in larger leaves), drying stiffly chartaceous, dark greenish above, much paler beneath, glabrous above, glabrous beneath or with short (0.1–0.2 mm) hairs on major veins, 2° veins 6–8/side (with lesser parallel intermediate 2° veins). **Inflorescences** axillary and sessile, 1.3–2 cm diam., densely compact, subglobose, with distal 2-lobed stipules resem-

bling bracts, bracts obovate, purple or green, 2–7 mm long, flower 5–15/head, sessile. **Flowers** with 5 calyx lobes 1–2 mm long; **corolla** white, glabrous, tube ca. 10 mm long, lobes 5, 3–3.5 mm long, triangular; **stamens** 5, anthers 1–2 mm long. **Fruits** 5–7 mm diam., ellipsoid, bright blue; pyrenes 3–5 mm long and 2–4 mm broad.

Understory plants of evergreen montane rain forest formations, from (600–)1200 to 2300(–2800) m elevation in Costa Rica. Probably flowering and fruiting throughout the year. The species ranges from Guatemala through Central America to Colombia, Venezuela, and the lesser Antilles.

Psychotria aubletiana is recognized by its small stature, sessile rounded inflorescences often encircling distal nodes and subtended by an involucre of broad bracts, short white corolla tubes, and bright blue fruit. This species is not easily confused with other species of *Psychotria*.

***Psychotria aurantibractea* C. M. Taylor, nom. nov.**

Cephaelis pittieri K. Krause, Bot. Jahrb. Syst. 54, Beibl. 119: 45. 1916, not *Psychotria pittieri* Standl. Figure 18.

Shrubs, 1–3 m tall, leafy stems 1.3–4.5 mm thick, glabrous, often narrowed below the node when dried; **stipules** united for only 0.5–2 mm around stem, with 2 narrowly triangular or linear teeth 2–8 mm long, separated by 2–3 mm, persisting. **Leaves** with petioles 5–40 mm long, 0.8–1.5 mm thick, glabrous; **leaf blades** 8–21(–28) cm long, 2–6 cm broad, narrowly oblong to narrowly elliptic-oblong or lanceolate, apex gradually tapering and acute or acuminate, tip to 15 mm long, base cuneate to acute, drying membranaceous or thin-chartaceous and dark brown, glabrous above, glabrous or sparsely and minutely (0.1 mm) puberulent on the veins beneath, 2° veins 10–16/side. **Inflorescences** terminal, 1 or 3, 2.5–6 cm long, 4–6 cm broad (to 8 cm when tripartite), usually with 3 capitate or cymose clusters of flowers on short (1–4 mm) primary branches, peduncles 5–25 mm long, 1.3–2.2 mm thick, minutely puberulent, bracts 8–15 mm long, 4–9 mm broad, ovate to lanceolate, acuminate, orange (rarely red), sparsely puberulent and ciliolate along margins, flowers sessile. **Flowers** enclosed by bracts and bracteoles, hypanthium ca. 1.5 mm long, densely pubescent with straight ascending hairs, calyx lobes 5, ca. 1.3 mm long, dentate with narrow lobes; **corolla** yellow or yellow-rose, tube ca. 5 mm long, lobes ca. 2 mm long. **Fruits** 5–7 mm long, 2.5–5 mm diam., ovoid-ellipsoid, with prominent longitudinal costae and short thin hairs, color unknown, persisting calyx 1.3–2 mm long, conical; pyrenes ridged.

Plants of continually wet or seasonally dry evergreen forest formations, from 200 to 1200 m elevation. Flowering in May–July; fruiting in August–September and January. This species is endemic to southern Costa Rica, from San Isidro del

General to San Vito and the Osa Peninsula, and on the adjacent Caribbean slope (at 83°W).

Psychotria aurantibractea is recognized by its terminal inflorescences composed of large ovate, orange or reddish bracts, narrow leaves, and restricted geographical range. The colorful bracteate inflorescences made this and other species formerly placed in *Cephaelis* so distinctive in Central America.

***Psychotria berteriana* DC., Prodr. 4: 515. 1830.**
Figure 58.

Shrubs or small trees, 1.5–6(–8) m tall, leafy stems (1.5–)3–5 mm thick, glabrous or minutely puberulent with hairs 0.1–0.2 mm long; **stipules** at first triangular and acute with a small distal cleft, becoming 2-lobed or 2-awned (on each side), basal sheath 0.5–2 mm long with acute lobes 1–3.5 mm long. **Leaves** with petioles 10–30(–52) mm long, 0.6–1.8 mm thick, glabrous or minutely puberulent; **leaf blades** 8–20(–26) cm long, 3–9(–11) cm broad, narrowly ovate-elliptic to elliptic or elliptic-oblong, apex acuminate with 5–15 mm long, base acute and cuneate to obtuse (rarely rounded and subtruncate in large leaves), drying membranaceous to thin-chartaceous, dark green or brown, glabrous or with minute (0.1–0.2 mm) hairs along the veins above, glabrous or with thin whitish hairs ca. 0.2 mm long beneath, 2° veins 7–15/side. **Inflorescences** terminal and solitary, 5–16(–22) cm long, 5–15 cm broad, oblong but becoming broadly pyramidal panicle with opposite or alternate branches, yellowish in life, peduncles 5–10 cm long, 1.3–2.2 mm thick, sparsely puberulent with thin hairs ca. 0.2 mm long, bracts 3–8 mm long, ca. 0.6 mm broad, flowers sessile in distal cymes, bracteoles 1–2 mm long. **Flowers** minutely puberulent externally (rarely glabrous), hypanthium ca. 0.5 mm long, calyx lobes ca. 0.2 mm long; **corolla** tubular-salverform, yellow to white, tube 1.5–4 mm long, 1–2 mm diam., glabrous proximally, lobes 5, 1–1.5 mm long; anthers 1–1.4 mm long. **Fruits** 3–4 mm long (5 mm including the persisting calyx), 3–4 mm diam., subglobose, fleshy, lustrous black; pyrenes with 3–5 dorsal ridges.

Plants of evergreen rain forest formations, from near sea level to 1700 m elevation (to 1200 m on the Pacific slope of southern Costa Rica). Flowering throughout the year; probably fruiting throughout the year. The species ranges from Mexico to South America.

Psychotria berteriana is characterized by its large, many-branched, pyramidal inflorescences, thin leaves often with long slender petioles and drying dark, two-lobed stipules, small flowers, and small rounded fruit. Compare *P. luxurians* and *P. angustiflora* (with longer thinner corolla tubes). A broader interpretation of *P. berteriana* might require the inclusion of *P. luxurians*. The greenish

yellow inflorescences resemble those found in *Palicourea tilarensis*.

Psychotria boquetensis Dwyer, Ann. Missouri Bot. Gard. 67: 349. 1980.

Shrubs, 0.5–2 m tall, leafy stems 1.2–3.5 mm thick, tomentulous with reddish hairs 0.4–1 mm long; **stipules** 8–14 mm long, 2–6 mm broad, oblanceolate to ovate, obtuse to acuminate at apex (not bilobed in the type as described by Hamilton, 1989), caducous. **Leaves** with petioles 1–6 mm long, 0.7–1.2 mm broad, with curved thin reddish hairs ca. 0.3 mm long; **leaf blades** 4–16 cm long, 1–4 cm broad, narrowly elliptic-oblong to oblanceolate, apex acuminate with tip 4–15 mm long, base gradually narrowed and acute or cuneate, decurrent on petiole, drying thinly chartaceous and dark reddish brown, puberulent along the primary and secondary veins above and below, with hairs 0.2–0.7 mm long along the margin, 2° veins 10–13/side, with minute tufted domatia in the axils beneath. **Inflorescences** terminal or pseudoaxillary, several at a node, 2–4 cm long, small panicles, peduncles ca. 20 mm long and 0.6 mm thick, bracts represented by dense whitish hairs 0.5–1 mm long, flowers sessile or subsessile in compact cymes. **Flowers** glabrous on the distal surfaces, hypanthium ca. 1 mm long and puberulent, calyx lobes 1–1.5 mm long, narrowly triangular; **corolla** white, urceolate, tube 1.5–2.5 mm long and 1 mm diam., lobes 5, 1–1.5 mm long; **stamens** 5, anthers 0.5–0.7 mm long. **Fruits** unknown.

Plants of the Boquete region of the Chiriquí Highlands at about 1200 m elevation. Flowering material was collected in May–June. The species is only known from western Panama.

Psychotria boquetensis is recognized by the narrow leaves with conspicuous reddish hairs, membranaceous broad caducous stipules, small inflorescences, and narrow calyx lobes to 1.5 mm long. The species is closely related to *P. nervosa* but differs in the large calyx lobes, narrower leaves, and smaller inflorescences. This distinctive species is a member of subgenus *Psychotria*.

Psychotria borucana (A. Molina) C. M. Taylor & W. Burger, comb. nov., Cat. fl. Peru (in press). *Cephaelis affinis* Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 8: 184. 1930, not *P. affinis* Baker. *C. borucana* A. Molina, Ceiba 4: 31. 1951. Figure 17.

Shrubs or woody herbs, 1.5–4 m tall, leafy stems 2.5–8 mm thick, glabrous and drying dark, quadrangular or flattened; **stipules** 9–20 mm long and 5–10(–15) mm broad, basal sheath 1–2 mm long, ovate-triangular, obtuse, with parallel venation, glabrous or minutely brownish puberulent. **Leaves** with petioles 12–50 mm long,

1.7–3(–5) mm thick, glabrous (as in the type) or minutely papillate-puberulent with erect brownish hairs 0.1 mm long; **leaf blades** 15–28(–32) cm long, 7–14(–16) cm broad, obovate to elliptic obovate (as in the type) to broadly elliptic, apex short-acuminate (acute) with tip 5–15 mm long, base gradually narrowed and cuneate to obtuse, drying stiffly chartaceous, dark grayish above and markedly paler beneath, glabrous above, glabrous beneath (as in the type) or with minute hairs 0.1–0.2 mm long throughout, 2° veins 6–10/side. **Inflorescences** terminal, capitulae solitary, 2–4 cm broad, peduncle 5–20 cm long, 2.5–4 mm diam., glabrous or minutely puberulent, basal bracts mostly 2, 4–15 mm long, broadly ovate to reniform, interior bracteoles 4–8 mm long, spatulate, pale purple, lavender, or green marked with purple, flowers enclosed by bracts. **Flowers** with hypanthium ca. 2 mm long, calyx 1–3 mm long and 3 mm broad; **corolla** funnelform, white, glabrous, 20–22 mm long, tube 14–19 mm long and 2–4 mm diam., lobes 5(–6), 2.5–3 mm long 1.5–2 mm broad at the base, acute; **stamens** 5(–6), anthers subsessile, ca. 2.8 mm long; style ca. 16 mm long. **Fruits** ca. 8 mm long and 8 mm diam., rounded-oblong, becoming blue or purple, 10-ribbed when dried; pyrenes with 4–6 ribs.

Plants of evergreen forest formations of the Pacific slope, from around 50 to 500 m elevation in southern and south-central Costa Rica. Flowering in May–July; fruiting in late August and November. The species is also known from Peru.

Psychotria borucana is recognized by its large leaves, long-pedunculate purple heads, two broad inflorescence bracts with reticulate venation, long corolla tube with short lobes, unusual stipules, and restricted range (in Costa Rica). The leaves are quite variable in shape. Compare *P. correae* with pendant heads and more secondary veins.

Psychotria brachiata Sw., Prodr. 45. 1788. Figure 58.

Shrubs or small trees, (0.5–)1.5–3(–5) m tall, leafy branchlets 1.2–5 mm thick, glabrous, quadrangular becoming terete; **stipules** 3–7 mm long, 2–5 mm broad, rounded and bilobed with a sinus 0.5–2 mm deep and 2 rounded lobes, glabrous and persisting. **Leaves** with petioles (1–)1.5–3.5 cm long, 1–1.5 mm thick, glabrous; **leaf blades** 9–17(–21) cm long, 3–7(–11) cm broad, elliptic to elliptic-oblong or elliptic-obovate, apex usually short-acuminate with tip 5–10(–15) mm long, base acute to attenuate (obtuse), drying thin-chartaceous or chartaceous and greenish or brownish, glabrous above, glabrous beneath except for a line of short (0.5 mm) hairs along sides of midvein, 2° veins 7–10/side. **Inflorescences** terminal and solitary or 3 (4, 5), 10–20 cm long, 3–10 cm broad, open pyramidal panicles with opposite separated (6–30 mm) lateral branches mostly arising at 90° angles, peduncles 1.5–6 cm long, with thin hairs ca. 0.4 mm long (mostly in 2 longitudinal rows), often with 3 2° branches bearing the distal flower clusters, bracts 3–8 mm long and 1.5–3 mm broad, lanceolate, floral bracts

2–3 mm long, broadly ovate, ciliolate along the margins, pedicels 0–2 mm long, flowers borne in capitulae 5–10 mm broad. **Flowers** with hypanthium 1–1.5 mm long, calyx 1–1.5 mm long, yellowish, calyx truncate or slightly dentate; **corolla** yellow or white (often with bluish tips and yellow throat), funnelliform, tube 3–5 mm long and 0.7–2 mm diam., usually glabrous externally on the lower half, lobes 5, 1–1.5 mm long. **Fruits** 4–5 mm long (including calyx) and 3–6 mm diam., obovoid to ellipsoid but becoming subglobose and spongy in life (to 10 mm diam.), bright blue to dark blue or purple, with prominent longitudinal ribs, persisting calyx ca. 1 mm long; pyrenes 3–4 mm long, with 3–5 ribs.

Plants of secondary vegetation in evergreen tropical and premontane wet forest formations on the Caribbean slope and in the General Valley, from 5 to 800 m elevation in Costa Rica. This species appears to flower and fruit throughout the year in Central America. At La Selva flowering is primarily in May–July and fruiting is mostly in July–September. The species ranges from the West Indies and Mexico through Central America to Peru.

Psychotria brachiata is recognized by its open inflorescences with well separated short opposite branches bearing closely clustered yellowish flowers in distal groups subtended by prominent persisting bracts. The small stature, nearly glabrous leaves usually drying greenish, spongy bright blue fruit with longitudinal ribs, and persisting stipules are additional features. Immature inflorescences of *P. brachiata* are racemose with the congested flowers in unexpanded capitula at the ends of the opposite lateral branches.

Steyermark (1972, pp. 585–586) distinguishes *P. caerulea* Ruiz & Pavón from *P. brachiata* by its larger corollas (11–12 mm long), external corolla surface that is densely puberulent throughout, more prominent calyx lobes, larger clusters of flowers, and larger floral bracts forming a more definite involucre. Specimens that fit Steyermark's definition of *P. caerulea* appear to occur in Bocas del Toro, Panama (D. Simpson in herb. 1977), and it is possible that they also occur in nearby Costa Rica. The question of whether or not these two species intergrade and are conspecific might make a worthwhile study.

***Psychotria brachybotrya* Muell.-Arg.** in Mart., Fl. Bras. 6(5): 327. 1881. *P. iquitosensis* Standl., Publ. Field Columb. Mus., Bot. Ser. 8: 195. 1930. Figure 56.

Shrubs or subshrubs, 1–2(–3) m tall, leafy branchlets 0.8–4 mm thick, glabrous; **stipules** separate or with a

short (0.5–1 mm) sheath, lobes 2/side, 2–7 mm long, 0.5–1 mm broad at base, linear to narrowly triangular, usually separated by a U-shaped sinus, glabrous, persisting. **Leaves** with petioles 3–10 mm long (poorly differentiated from the decurrent leaf base), glabrous; **leaf blades** 9–16(–18) cm long, 3–7(–8) cm broad, ovate-elliptic to ovate or elliptic, apex usually tapering gradually and short-acuminate or acute, tip 5–10 mm long, tapering gradually or abruptly to the attenuate base (acute to broadly obtuse above the narrowed base), drying thinly chartaceous and greenish, glabrous above and below, 2° veins 4–8/side and arcuate ascending, distal 3° veins often subparallel. **Inflorescences** terminal and solitary, 1.2–3 cm long but enlarging in fruit, 1–2 cm wide, narrowly paniculate with short opposite lateral branches or sometimes subcapitate, peduncle 3–18 mm long, ca. 1 mm thick, with thin whitish hairs to 0.5 mm long, 2° branches 0–5 mm long, cymes congested, usually subtended by 3 involucre narrowly ovate to lanceolate bracts, median bracts 3–6 mm long and 2–3 mm broad, with 2 shorter lateral bracts, all 3 united at base, flowers sessile. **Flowers** with hypanthium ca. 0.5 mm long, puberulent, calyx lobes 5, 0.2–0.3 mm long; **corolla** white, salverform, tube 1.5–4 mm long, ca. 1 mm diam. distally, glabrous or puberulent, lobes 5, 0.8–1.5 mm long. **Fruits** ca. 4 mm long and 4 mm diam., globose to oblong, becoming purple-black at maturity (blue-black on Cocos Island), with prominent longitudinal ribs (transverse ridges sometimes visible when dried), calyx minute (0.3 mm high) or obscure; pyrenes 3–4 mm long, with 4–5 prominent ridges.

Plants of the lowland rain forest formations on both the Caribbean and Pacific slopes, from near sea level to 400(–900) m elevation and usually found in shaded, poorly drained sites. Flowering in July–August; fruiting in August–October and December. In addition to the mainland plants, a distinctive population of this species is found on Cocos Island (see below). The species ranges from Costa Rica and Panama to Brazil and Bolivia.

Psychotria brachybotrya is distinguished by its well-separated stipule lobes, glabrous leaves drying green, small compact inflorescences, flowers subtended by an involucre of bracts, small white flowers, and purplish black fruit. Inflorescences change in shape as they grow and expand. Collections from Cocos Island placed under this name differ from the mainland material in having smaller leaves with blades (4–)6–9 cm long and 1.5–3.5 cm broad; the stipules, flowers, and fruit are very similar. Compare this species to *P. hoffmannsegiana*, *P. platypoda*, and *P. officinalis*. Hammel (in Taylor, 1991) noted that *P. brachybotrya* is usually a larger plant than *P. officinalis* and the latter has a linear ventral sulcus on the pyrene.

***Psychotria calochlamys* Standl., Publ. Field Columb. Mus., Bot. Ser. 8: 199. 1930.**

Small shrubs or treelets, 1.5–4.5 m tall, leafy stems 2.5–4.5 mm thick, glabrous or sparsely and minutely puberulent; **stipules** 13–28 mm long and 5–9 mm broad at the base, ovate-triangular with 2 attenuate-acute lobes 6–10 mm long, greenish to wine red or violet, with fine parallel venation, chartaceous. **Leaves** with petioles 3–16(–25) mm long, 0.9–2 mm thick, glabrous; **leaf blades** 8–23 cm long, 2–8.5 cm broad, elliptic-ovate to oblong-lanceolate or lanceolate, apex gradually tapering and acuminate, tip 5–10 mm long, base acute to obtuse, drying chartaceous and greenish, glabrous above and below, 2° veins 11–17/side, often with lesser 2° veins between the major. **Inflorescences** solitary and terminal, 12–14 cm long and 6–7 cm broad, hemispheric panicles with 2–3(–4) branches at the first and second nodes, peduncles 3–8 cm long and 1.5–2 mm thick, white, minutely (0.1 mm) puberulent, bracts subtending the first whorl of branches 1.5–2 cm long, 3–4 mm wide, narrowly elliptic, resembling the stipules in texture, distal bracteoles 5–14 mm long, 2–4 mm broad, lanceolate, persisting, white to violet, enclosing the sessile flowers. **Flowers** ca. 15 mm long, hypanthium 0.6–1 mm long, calyx 0.6–0.8 mm long, lobes 5, triangular; **corolla** white to purple or pale violet, yellow in throat, tubular-salverform, tube 7–10 mm long, lobes 5, 2–3 mm long; anthers ca. 1.5 mm long and curved. **Fruits** ca. 6 mm long and 4 mm diam., oblong, dark purple or black; pyrenes with 4–5 ribs.

In Costa Rica this disjunct species is only known from the hills near Golfito, Puntarenas, at about 100 m elevation, flowering in December–January. The species also occurs in Chocó, Colombia, and Amazonian Peru.

Psychotria calochlamys is distinguished by its large deciduous stipules, long and persisting white or lilac bracts and bracteoles, and large flowers. The unusual form and size of the stipules is similar in *P. capitata*, a close relative. The inflorescence with large white (or purplish) bracts and flowers is unlike any other Costa Rican species of *Psychotria* and reminiscent of some species of *Paliourea*. The disjunct occurrence in Costa Rica is similar to that of some other species in the Golfo Dulce region. This species may prove to be conspecific with *P. stipulosa* Muell. Arg. of Amazonian South America, but that species (interpreted in a broad sense) includes variation not seen in our material.

Psychotria calophylla Standl., Contr. U.S. Natl. Herb. 18: 129. 1916.

Small trees, 3–18 m tall, with larger (13–26 × 5–12 cm) elliptic to obovate leaves usually reddish tomentulose beneath, with an arcuate submarginal vein; the inflorescences paniculate with usually 3 ranks of branching, the flowers in distal glomerules, and larger (10–14 × 6–9 mm) ellipsoid fruit.

The leaves drying grayish and the bright red fruit are characteristics of the subgenus *Psychotria*. This species has a disjunct distribution and is not known from Costa Rica. It is found in southern Mexico and Guatemala and again in Colón and Coclé provinces in Panama.

Psychotria camponutans (Dwyer & Hayden) Hammel, Selbyana 12: 139. 1991. *Cephaelis camponutans* Dwyer & Hayden, Ann. Missouri Bot. Gard. 55: 35. 1968.

Semisucculent herbs or subshrubs 0.5–1.2 m tall, rhizomatous, stems unbranched, leafy stems 2–4 mm thick, quadrangular or terete, glabrous, drying black and contracted below the nodes; **stipules** 6–8(–15) mm long, 5–6(–10) mm broad, broadly ovate with a serrated margin and 2 long lobes, glabrous and thin, distal parts deciduous but with a persisting truncated sheath 1–1.5 mm long. **Leaves** with petioles 18–55 mm long, 1.2–2 mm thick, glabrous, drying black; **leaf blades** (11–)18–25 cm long, (4–)7–9 cm broad, narrowly elliptic-oblong to oblong or oblong-obovate, apex acuminate with tip 6–13 mm long, acute at base and slightly decurrent on petiole, drying thinly chartaceous, dark or grayish above, glabrous above and below, 2° veins 8–15/side but these difficult to see. **Inflorescences** axillary and 1/node, 1–2 cm long, to 2 cm diam., capitate, peduncle 4–10 mm long, with involucre bracts 8–15 mm long, 5 mm broad, ovate and acuminate, glabrous and green, flowers sessile and congested, each enclosed by 2 lanceolate bracteoles 6–8 mm long. **Flowers** glabrous, calyx lobes 5–6, ca. 1 mm long; **corolla** white, funnelform, tube ca. 3 mm long, corolla lobes 1–1.5 mm long. **Fruits** 7–8 mm long, 4–5 mm diam., ellipsoid to obovoid, crowned by a persisting calyx, deep maroon red or pale rose red, bracts red to purple; pyrenes 6–7 mm long, ribbed.

Plants of the wet evergreen forests of the Caribbean slope, from 300 to 900 m elevation. Flowering in April and July; immature fruit were collected in September. Costa Rica to central Panama.

Psychotria camponutans is distinguished by its short semisucculent erect stems with small axillary capitate inflorescences, reddish fruit, and restriction to the Caribbean slope. Compare *P. uliginosa* and *P. cartagoensis*.

Psychotria capacifolia Dwyer, Ann. Missouri Bot. Gard. 67: 353. 1980. Figure 54.

Herbs or subshrubs, 0.4–1(–2?) m tall, usually succulent and unbranched, leafy stems 3–12 mm thick, glabrous or with hairs to 1 mm long at nodes, terete, drying dark; **stipules** 3–6 mm long, to 8 mm broad, broadly obtuse to truncate and entire, with a conical caducous lateral appendage to 3 mm long, densely hirtellous. **Leaves** densely hirtellous in early stages but usually glabrescent

in age, petioles 3–10 cm long, 2–4 mm thick, with hairs ca. 1 mm long in early stages; **leaf blades** 20–40 cm long, 9–16(–20) cm broad, oblong to elliptic-oblong or elliptic-obovate, apex abruptly narrowed and short-acuminate, base cuneate to obtuse, drying thinly chartaceous and grayish green, usually glabrous above, glabrescent or with thin hairs to 1.4 mm long beneath, 2° veins 17–22/side, connected by a distinct slightly arcuate submarginal vein 2–3 mm from the margin. **Inflorescences** axillary, 1/node, (8–)15–35 cm long, 5–12 cm wide, open panicles with opposite branching, peduncles 7–22 cm long, 1.5–2.2 thick, with thin yellowish to reddish brown hairs 0.2–0.7 mm long, bracts 1–2 mm long, flowers sessile on distal dichotomous branches or distal clusters, bracteoles ca. 0.5 mm long. **Flowers** puberulent externally, hypanthium ca. 0.7 mm long, calyx to 1 mm long, calyx lobes 5, 0.3–0.5 mm long, triangular; **corolla** white or pale yellow, funnellform, tube 2.5–4 mm long, 0.5–1 mm diam. basally and 2 mm distally, lobes 5, ca. 1 mm long. **Fruits** 5–6 mm long, 3–4 mm broad, ovoid, yellow-green or whitish, with ca. 10 longitudinal ribs; pyrenes ca. 5 mm long.

Plants of evergreen rain forest formations on the Caribbean slope, ranging from 5 to 1300 m elevation. Flowering in January–September; fruiting in March–November. The species ranges from southern Nicaragua to western Panama.

Psychotria capacifolia is recognized by its short succulent stems, pubescence on younger parts, large leaves, axillary often large puberulent inflorescences, well-developed (only slightly arcuate) submarginal vein, and the yellowish green fruit. The corolla interior is said to have a “ball” of hairs within (Dwyer, 1980, p. 354). This species closely resembles some material placed under *P. macrophylla*, *P. siggersiana*, and *P. aggregate*, but the differences used in the keys appear to reflect a real discontinuity of gene flow.

***Psychotria capitata* Ruiz & Pav., Fl. Peruv. 2: 59, pl. 206. 1799.**

Shrubs or small treelets 1–3(–4) m tall, leafy stems 2–4 mm thick, glabrous; **stipules** 8–18 mm long, 4–7 mm broad, ovate-lanceolate, acute at apex, with 2 triangular lobes 1–10 mm long, glabrous, deciduous. **Leaves** with petioles 4–20 mm long, 1–2 mm thick, glabrous, often drying yellowish green; **leaf blades** 6–16(–22) cm long, 2.5–6(–8) cm broad, elliptic-oblong to elliptic, ovate-elliptic or elliptic-lanceolate, apex short-acuminate with tip 5–12 mm long, base acute or obtuse and slightly decurrent on petiole, drying stiffly chartaceous, greenish, glabrous above and below (except for short hairs along the sides of the midvein beneath), 2° veins 9–14/side, arising at almost 90° from midvein. **Inflorescences** terminal and solitary, 5–13 cm long, 3–6 cm broad, an open racemose or congested panicle, white at anthesis, peduncles (1–)2.5–7 cm long, ca. 1.5 mm thick, glabrous (rarely puberulent), branches opposite or ternate (alter-

nate) and usually without subtending bracts, flowers sessile in distal cymose groupings of 2–4 subtended by white lanceolate bracteoles 4–9 mm long and 1–2 mm broad. **Flowers** glabrous externally, hypanthium ca. 1 mm long, calyx ca. 0.5 mm long, calyx lobes 4–5, ca. 0.3 mm long, triangular; **corolla** white or cream (yellow in throat), tube 3–7 mm long, 1 mm diam. near base, lobes 4–5, 1.5–4 mm long; **stamens** 4 or 5 anthers 1–2 mm long. **Fruits** 5–7 mm long, ca. 5 mm diam., subglobose, dark blue-black to purple-black or black; pyrenes ribbed.

Plants of lowland evergreen forest formations, 0–200 m elevation. Flowering and fruiting throughout the year (mostly in December–July). The species ranges from Belize (Croat, 1978), the Caribbean lowlands of Nicaragua and Panama to Peru and Brazil; it is not known from Costa Rica.

Psychotria capitata is recognized by its white flowers and inflorescences, conspicuous bracts on the distal parts of the inflorescences, leaves usually glabrous and drying greenish, and the large bilobed stipules. This species is similar to *P. calochlamys*, which has larger bracts and stipules and less prominent secondary venation. Compare also *Psychotria officinalis* and *Palicourea tilaranensis*. This species appears to be less variable in Central America than in South America (cf. Steyermark, 1974).

***Psychotria cartagoensis* Nepokroeff, nom. nov.**
Cephaelis latistipula Standl., J. Wash. Acad. Sci. 18: 281. 1928, not *Psychotria latistipula* Benth. Figure 13.

Herbaceous **subshrubs**, 0.3–1 m tall, stems erect and usually unbranched, leafy stems 2–6 mm thick, glabrous, quadrangular or terete; **stipules** (5–)12–22 mm long, 12–18 mm broad, ovate in general outline, bilobed with a narrow sinus 2–7 mm deep, glabrous, stiff and persisting. **Leaves** well separated along the stem, petioles 2–6(–7) cm long, 1.2–3.7 mm thick, glabrous, drying dark; **leaf blades** 13–27 cm long, 5–9 cm broad, elliptic-oblong, oblong-lanceolate, elliptic-obovate, or ovate-elliptic, apex abruptly narrowed or rounded and shortly acute or short-acuminate, base acute to cuneate, drying stiffly chartaceous, dark gray-green above, much paler beneath, 2° veins 9–13/side, arising at 60–80° and arcuate distally. **Inflorescences** axillary and sessile or subsessile, broadly capitate, 1–2 cm long and 2–4 cm broad, becoming dark magenta or purplish, bracts 7–8 mm long and 2–4 mm broad, innermost bracteoles lanceolate, flowers enclosed by many bracteoles. **Flowers** glabrous externally, hypanthium ca. 2 mm long, turbinate, calyx cup 0.3–1 mm long, calyx lobes 4–5(–6), 1–4 mm long, lanceolate; **corolla** 4–5 mm long, funnellform, white, lobes 5, 1.2–3 mm long, acute; anthers 2.5 mm long. **Fruits** ca. 6 mm long and 4 mm broad (not including the 2 mm long persisting calyx), reddish purple.

Understory plants of evergreen wet forests of the Caribbean slope, from 800 to 1500 m elevation. Flowering in March (*Standley 39695* is the type of *C. latistipula*) and May–June; fruiting in June and November. The species has only been collected in the valley of Río Sarapiquí (Heredia Province) and near Orosí and Muñeco (Cartago) in central Costa Rica.

Psychotria cartagoensis is recognized by its short unbranched habit, broad bilobed stipules, axillary and subsessile heads, and absence of pubescence. Among our species, *Hoffmannia congesta* is most likely to be confused with this species, but that species lacks the involucre bracts and has many-seeded fruits. This species and its allies have been studied by Molly Nepokroeff (wis, 1992); *P. wilburiana* Dwyer and *P. dukei* Dwyer of Panama are closely related.

***Psychotria carthagenensis* Jacq., Enum. Pl. Carib. 16. 1760. Figure 65.**

Shrubs, subshrubs, or small treelets, 0.3–3(–4) m tall, leafy branches 1.5–4 mm thick, glabrous and terete, becoming gray; **stipules** 3–8 mm long, 1.5–5 mm broad, ovate to oblong or slightly obovate, apex rounded or bluntly acute, glabrous, drying dark reddish brown, caducous. **Leaves** with petioles 3–10 mm long, ca. 1 mm thick, with decurrent lamina base; **leaf blades** (4)–6–13(–15) cm long, (1.7)–2–5(–7) cm broad, oblanceolate to narrowly elliptic-obovate or narrowly elliptic, apex obtuse to very shortly acuminate (tip ca. 4 mm long), base gradually narrowed and cuneate or acute, decurrent on petiole, drying chartaceous, gray or reddish gray, glabrous on both surfaces, 2° veins 6–8/side, domatia rarely present in distal vein axils. **Inflorescences** terminal and solitary, 3–8(–10) cm long, 2.5–4 cm broad, a compact panicle with usually 3 nodes of opposite branches diminishing in size toward apex (also verticillate or umbellate), peduncle to 4.5(–6) cm long, 0.6–1.3 mm thick, glabrous, bracts subtending the lateral branches 0.5–1.5 mm long, subulate to broadly ovate, flowers in distal cymes, pedicels 0–2 mm long, bracteoles to 0.5 mm long. **Flowers** glabrous or minutely (0.05 mm) papillate-puberulent externally, hypanthium ca. 1 mm long, calyx ca. 0.5 mm long, subentire or with 5 short triangular lobes; **corolla** white, funnelform-salverform, tube 2.5–3 mm long, ca. 1 mm diam. near base, lobes 5, 1.2–2 mm long; anthers 1–1.5 mm long. **Fruits** ca. 5 mm long and 4 mm diam., oblong or ellipsoid, becoming red or orange, with 10 vertical ribs, glabrous; pyrenes with 2 sulci on the inner face and 5 ribs on the exterior surface.

Plants of shaded sites in seasonally dry deciduous forest formations of Guanacaste and northernmost Alajuela Province, from 5 to 200(–600) m elevation (rarely to 1400 m elsewhere). Flowering in November–August (primarily February–

July); fruiting throughout the year. The species ranges from Mexico and the West Indies to Bolivia and Argentina.

Psychotria carthagenensis is recognized by its deciduous forest habitat, smaller oblanceolate or obovate leaves, lack of conspicuous pubescence, small flowers and inflorescences drying reddish, and inflorescences often with nodes bearing two larger and two smaller lateral branches. The tendency of the leaves to dry gray or reddish and the red or orange fruit are characteristics of members of subgenus *Psychotria*. The correct spelling of this species is *carthagenensis* (not *carthaginensis*). This species is similar to *P. tenuifolia* of similar habitats but with bilobed stipules.

***Psychotria chagrensis* Standl., J. Wash. Acad. Sci. 15: 105. 1925. Figure 60.**

Shrubs, 1–3 m tall, many-branched and often flat-topped, leafy branchlets 1–3 mm thick, glabrous, reddish brown or dark; **stipules** 3–10 mm long, 1–3 mm broad near base (broader when subtending the inflorescence), narrowly tubular to narrowly ovate and acute at apex with 1 or 2 slender awns 1–3 mm long, glabrous and drying dark reddish brown, caducous. **Leaves** usually closely clustered distally, petioles 1–12(–17) mm long, ca. 0.7 mm thick, glabrous; **leaf blades** 2.5–8(–10) cm long, 0.9–3(–3.5) cm broad, obovate to oblanceolate, elliptic-obovate or elliptic, apex acuminate or caudate-acuminate to bluntly obtuse, tip ca. 5 mm long, base cuneate to acute and decurrent on petiole, drying stiffly chartaceous, gray or reddish brown, glabrous above and below, 2° veins 6–9/side (but sometimes difficult to see), joined by an arcuate submarginal vein near margin. **Inflorescences** terminal (rarely pseudoaxillary), 6–16 mm long, to 7 mm broad, sessile, subtended by broad stipule-like dark reddish brown glabrous bracts to 1 cm long, fasciculate or capitate, with few sessile flowers, bracteoles 4–5 mm long. **Flowers** distylous, glabrous externally, hypanthium ca. 1 mm long, calyx 2–4 mm long, lobes 1–2 mm long, narrowly triangular; **corolla** funnelform, white, tube 4–9 mm long and 1–1.3 m diam., lobes 5, 2–3 mm long; **stamens** 5, anthers ca. 1 mm long. **Fruits** becoming 8 mm long (not including persisting calyx), 3–6 mm diam., oblong-ellipsoid to ovoid, persisting calyx 2–3 mm long, becoming red or purple pyrenes ca. 6 mm long, weakly ribbed.

Understory plants often found in low wet depressions in evergreen rain forest formations, from near sea level to 700 m elevation on the Caribbean slope and Osa Peninsula. Probably flowering and fruiting throughout the year (flowering mostly in March–August). At La Selva flowering is most common in May–June and fruiting in November–December. The species ranges from southern Nicaragua to Colombia and Peru, but with disjunct

populations in Veracruz, Mexico, and Izabal, Guatemala.

Psychotria chagrensis is recognized by its short (often flat-topped) habit, very small obovate leaves, distinctive stipules, small sessile fasciculate or capitate inflorescences, and unusual calyx lobes. The leaves drying grayish or reddish and the red fruit are characteristic of subgenus *Psychotria*. The slender secondary veins often have point indentations on the lower surface after the leaves have been dried. The very small leaves are unusual among the woody plants of the lowland rain forest floor; compare *P. graciliflora*, *P. parvifolia*, and *Randia loniceroides*.

***Psychotria chiapensis* Standl., Contr. U.S. Natl.**

Herb. 23: 1390. 1926. *Cephaelis tetragona* J. D. Smith, Bot. Gaz. 61: 376. 1916, not *Psychotria tetragona* Seem., 1867. Figure 18.

Shrubs, treelets, or small trees, 2.5–8(–10) m tall, much-branched with rounded crown, leafy stems 2–6(–8) mm thick, terete and often conspicuously contracted for 5–10 mm below the node after drying, glabrous or with short (0.2 mm) hairs in new growth, center with white spongy pith; stipules 2–5 mm long, 2–4(–8) mm broad, broadly triangular, rounded with a small apical sinus, with 2 triangular acute lobes to 2 mm long. Leaves with petioles 7–35 mm long, 0.8–2.3 mm thick, glabrous (sometimes puberulent near inflorescences); leaf blades 9–20(–23) cm long, 3–8(–9) cm broad, elliptic-obovate to elliptic-oblong or narrowly oblong-obovate, apex short-acuminate or acute with tip 5–10 mm long, base usually gradually narrowed and cuneate base, slightly decurrent on petiole, drying thin-chartaceous and grayish green to dark brown above, distinctly paler beneath, glabrous above and below except for short (0.2 mm hairs) along sides of midvein beneath, 2° veins 9–12/side. Inflorescences terminal, 1 (or 3 when basal lateral branches are axillary to distal leaves), 4–12 cm long, 5–8 cm broad, subcapitate or corymbiform with 3–7 dense bracteate flower clusters, peduncles 1–8(–15) cm long, 1.3–3 mm thick, minutely puberulent with hairs 0.2 mm long, bracts 6–10 mm long, 4–8 mm broad, ovate to ovate-elliptic, obtuse to rounded, minutely ciliolate along margins, with 6–many flowers closely clustered and sessile. Flowers distylous, calyx resembling the bracts in texture and color, 3–5 mm long, calyx lobes 5, ca. 1.5 mm long, triangular; corolla salverform, white, glabrous externally in ours, tube 20–45 mm long, 1–3 mm diam. for most of its length, lobes 5, 9–15 mm long and 3 mm broad; anthers ca. 4 mm long. Fruits 12–16 mm long (not including the calyx) and 9–13 mm diam., ellipsoid to ovoid, purple-black, strongly 4-angled, persisting calyx 2–3 mm long; pyrenes 10–13 mm long, 7 mm broad and 3 mm thick, bony, with 3 dorsal ribs and concave areas between.

Plants of evergreen lowland rain forest formations on both the Caribbean and Pacific slopes,

from near sea level to 700 m elevation. Flowering in May–September and January; fruiting in July–March. The species ranges from southern Mexico and Belize to central Panama.

Psychotria chiapensis has the longest corolla tubes among Central American *Psychotria* species; it is pollinated by long-tongued sphingid moths (cf. Bawa & Beach, 1983). The terminal subcapitate inflorescences (often in groups of three) with broad bracts and the relatively large four-edged fruit are also distinctive. The paucity of puberulence, and leaves usually broadest at or above the middle are additional characters that make this species stand apart. It is called *cocobolito* in Panama.

***Psychotria chiriquiensis* (Standl.) C. M. Taylor, comb. nov. *Cephaelis chiriquiensis* Standl., Ann. Missouri Bot. Gard. 28: 469. 1941. Figure 17.**

Shrubs, 1–2 m tall, leafy stems 2–5 mm thick, glabrous; stipules 3–5 mm long, with a short (1 mm) tube and 4 rounded ovate lobes 2–4 mm long at each node, these separate on the internode but overlapping above petioles, persisting. Leaves well separated along stems, petioles 15–40(–57) mm long, 0.5–1.5 mm thick, glabrous; leaf blades 8–16(–20) cm long, 3–7(–9) cm broad, elliptic to elliptic-oblong, apex acuminate with tip 5–10 mm long, base obtuse to acute, drying stiffly chartaceous, dark green to yellowish brown or grayish brown, glabrous above and beneath, 2° veins 11–22/side, loop-connected distally to form an arcuate submarginal vein. Inflorescences terminal (pseudoaxillary), solitary or 3, 3–12 cm long, 3–8 cm broad, capitulum often with 3 short (2–5 mm) primary branches (especially in fruit), involucre bracts 12–20 mm long, 20–50 mm broad, broadly ovate, purple to reddish violet, peduncle 1–6(–8) cm long, 2–3.5 mm thick, glabrous, flowers subsessile within many imbricate bracteoles 8–12 × 5–10 mm, elliptic to oblong. Flowers glabrous externally, hypanthium ca. 1 mm long, 0.5 mm diam., turbinate, calyx tube ca. 1 mm long, lobes ca. 0.5 mm long; corolla tubular-funnelform, purplish, tube 9–12 mm long and 1.7 mm diam., lobes 5–6, 1.5–2 mm long; anthers to 2 mm long. Fruits elliptic, blue, enclosed within the inflorescence; pyrenes with 4–5 ridges.

Plants of lower montane rain forest formations, from 1200 to 1800 m elevation. Flowering in January–September; fruiting in October–December. This species ranges from Volcán Tenorio to southward along the Caribbean slope and continental divide to the Chiriquí Highlands.

Psychotria chiriquiensis is recognized by its involucre capitate inflorescences with broad purple bracts, long-petiolate leaves with many prominent secondary veins, lack of pubescence, and rounded stipule lobes usually overlapping above

the petiole. This species is named in honor of Antonio Molina R., who monographed the Mexican and Central American species of *Cephaelis* in 1953 and has made many important collections in Central America. This species is very similar to *P. elata*, with larger red bracts, heads not three-branched, and white corollas. It is also similar to *P. dichroa*.

***Psychotria chiriquina* Standl., Contr. U.S. Natl. Herb. 18: 129. 1916. Figure 61.**

Shrubs or small trees, 2–6 m tall, leafy stems 1–4 mm thick, glabrous, dark reddish brown; **stipules** 4–8(–10) mm long, 3–5 mm broad, ovate to elliptic, apex acute, ciliolate to erose or shortly bilobed, united around stem at base, glabrous or puberulent, caducous. **Leaves** with petioles 7–18(–35) mm long (sometimes variable on the same stem), 0.4–1.3 mm broad, glabrous; **leaf blade** 5–15 cm long, 2–6 cm broad, narrowly elliptic, elliptic-oblong to oblanceolate or oblong-obovate, apex gradually tapering and acute or acuminate, tip ca. 10 mm long, gradually narrowed to an acute base and decurrent on petiole, drying stiffly chartaceous, dark reddish brown above, glabrous above and below except for hairs along sides of midvein, occasional pit domatia in vein axils beneath, 2° veins 6–12/side. **Inflorescences** terminal, usually solitary or 3, 3–10(–17) cm long, a few-branched panicle, often trichotomous, peduncles 1.5–5 cm long, 0.5–2 mm thick, essentially glabrous, pedicels 0–3 mm long. **Flowers** glabrous externally, calyx ca. 1 mm long, truncate or with 5 small (0.6 mm) lobes; **corolla** white, salverform or funnelform, tube 3–6 mm long, 1.5–2 mm diam., glabrous or puberulent externally, lobes 5, 1.5–2 mm long; **stamens** 5, anthers ca. 1 mm long. **Fruits** 5–8 mm long, 4–6 mm diam., oblong to subglobose, becoming red, persisting calyx 0.5–1 mm long; pyrenes with 4–5 rounded ribs.

Plants of evergreen montane cloud forest formations, from (900–)1500 to 2500 m elevation. Flowering in January–May (July–August in Nicaragua); fruiting in August–April (November–May in Nicaragua). The species is known from northern and central Nicaragua and from the easternmost part of the Cordillera de Talamanca in Costa Rica and the Chiriquí Highlands in Panama.

Psychotria chiriquina is recognized by its higher elevation habitats, stipules often with two small distal lobes, narrow leaves tapering gradually to apex and base, pit domatia, small flowers, and poorly developed calyx lobes. The red fruit and leaves/branchlets drying dark reddish brown are characters of subgenus *Psychotria*. Compare *P. sarapiquensis*, with a shorter calyx, and *P. sylvivaga*. This species is also similar to *P. panamensis* and with very different stipules.

***Psychotria chitariana* Dwyer & C. Hamilton, Phytologia 64: 221. 1988.**

Subshrubs, 30–100 cm tall, leafy stems 4–9 mm thick, glabrous, drying dark; **stipules** 15–18 mm long, ovate, with 2 awns ca. 3 mm long, caducous. **Leaves** with petioles 0–27 mm long, ca. 3 mm thick, glabrous, with lateral margins and flattened above; **leaf blades** 25–40 cm long, 10–17 cm broad, elliptic-obovate to obovate-oblong or oblanceolate, apex obtuse to acute, base gradually narrowed and cuneate or expanded and auriculate at the petiole, drying thinly chartaceous, grayish brown to reddish brown, glabrous above and below, 2° veins 12–17/side, loop-connected 2–3 mm from the margin. **Inflorescences** terminal and solitary, dense panicles of congested cymes, globose or hemispheric, 3–11 cm long, 3–5 cm broad, peduncles 1–2.5(–4.5?) cm long, bracts ca. 5–6 × 1–3 mm, glabrous, flowers closely congested, pedicels 3–5 mm long, bracteoles to 0.5 mm long. **Flowers** glabrous externally, calyx ca. 1 mm long, cupulate, lobes 5, short; **corolla** funnelform, greenish white, tube 4.5–5 mm long, 1–1.5 mm diam., lobes 1.5–2.3 mm long, triangular or oblong; anthers ca. 1.5 mm long. **Fruits** not seen.

Known only from the Caribbean slope of the Cordillera de Talamanca in Costa Rica, from 200 to 800 m elevation. Flowering in April–May; immature fruits were collected in September. The species ranges from the valley of Río Chitaría east of Turrialba (*Liesner et al. 15400 CR*, MO holotype) to the valley of Río Estrella.

Psychotria chitariana is distinguished by its short stature, large obovate leaves with rounded and obtuse apex, and unusual inflorescence. The leaves drying dark grayish (or reddish brown) is a characteristic of subgenus *Psychotria*. Compare *P. alfaroana* with more open inflorescences and acute leaf bases.

***Psychotria cincta* Standl., Publ. Field Columb. Mus., Bot. Ser. 7: 90. 1930. Figure 58.**

Shrubs, 1–2.5(–4) m tall, leafy branches 1.5–4 mm thick, glabrous and drying greenish or dark; **stipules** forming a small basal (1–3 mm) sheath, with 2 awns (4/ node), awns 6–14 mm long, ca. 0.5 mm broad, glabrous, persisting. **Leaves** with petioles 8–20 mm long, 1–1.5 mm thick, glabrous; **leaf blades** 12.5–21(–28) cm long, 3.5–7(–9) cm broad, elliptic-oblong to oblong or ovate-oblong, apex tapering gradually and acuminate, tip 8–18 mm long, base acute to obtuse, drying stiffly chartaceous, green or grayish green, glabrous above and below, 2° veins 9–11(–14)/side, leaf margin with a distinctly thickened vein along the edge. **Inflorescences** terminal and solitary, usually pendant, 12–20 cm long, 2–4 cm broad, racemiform thyrsoid panicles with short (1–2 cm) usually alternate lateral cymose branches, peduncles 6–14 cm long, 0.6–1.2 mm thick, sparsely and minutely puberulent with short (0.1–0.2 mm) thin hairs, bracts

linear, adnate to lateral branches or absent, bracteole 0–0.5 mm long, pedicels 0–2 mm long. **Flowers** minutely puberulent externally, hypanthium 0.5 mm long, calyx 0.2–0.4 mm long, truncate or with minute lobes; **corolla** funnellform or salverform, white or greenish white, tube 2–3 mm long, ca. 0.5 mm diam., lobes 5, 1–1.5 mm long. **Fruits** 4–6 mm long, subglobose, obscurely ribbed, glabrous, red becoming black; pyrenes shallowly ribbed.

Plants of evergreen lowland Caribbean rain forest formations, from near sea level to 500 m elevation. Flowering in February–July; fruiting in August. The species ranges from Nicaragua to Colombia.

Psychotria cincta is recognized by its persisting stipules with long narrow awns, the often oblong leaves usually drying yellowish green, the long narrow pendant inflorescences with unusually short lateral branches, and the small puberulent flowers. In addition, the thickened leaf margins are notable. This distinctive species is presently known only from La Selva and nearby areas in Costa Rica. Compare *P. deflexa*, which lacks the thickened leaf margins and has pyrenes with transverse ribbing.

***Psychotria clivorum* Standl. & Steyerl., Publ. Field Mus. Nat. Hist., Bot. Ser. 23: 87. 1944, based on *P. limonensis* var. *angustifolia* Standl., loc. cit. 17: 282. 1937. Figure 61.**

Shrubs or small trees, 1.5–6 m tall, leafy stems 2–4 mm thick, glabrous; **stipules** 10–16 mm long, 2–5 mm broad (broader beneath the inflorescences), with a sheath 1–4 mm long, ovate to elliptic, usually bilobed with 2 acute lobes and a short (1–3 mm) sinus at apex, glabrous, dark reddish brown, caducous. **Leaves** variable in shape (on different plants), petioles 6–35 mm long, 1–1.7 mm thick, glabrous; **leaf blades** 10–22 cm long, 3.5–8 cm broad, narrowly elliptic-oblong to elliptic or oblanceolate, apex acuminate, tip 7–15 mm long, base acute to cuneate and often long-decurrent on petiole, drying membranaceous to thinly chartaceous, grayish or gray tinted with red, glabrous above and below (midvein rarely sparsely puberulent beneath), 2° veins 8–12/side, loop connected 1–3 mm from margin, small pit domatia usually present. **Inflorescences** terminal and solitary, 6–10 cm long, 3–7 cm broad, open panicles, usually with 4 lateral branches from 2 proximal nodes, peduncles 1–5 cm long and 2.2 mm thick, minutely puberulent or glabrous, reddish brown, bracts to 2(–3) mm long, pedicels 0–2 mm long. **Flowers** glabrous externally, hypanthium ca. 0.6 mm long, conical, calyx tube ca. 0.5 mm long with minute (0.2 mm) broadly triangular lobes; **corolla** funnellform, white, tube 2–2.5 mm long, 1.2–1.5 mm diam., lobes 1–2 mm long; anthers ca. 1 mm long. **Fruits** 5–6 mm long, 4–5 mm diam., ellipsoid or obovoid, longitudinally ribbed, red; pyrenes with 3–5 longitudinal ridges.

Plants of evergreen forest formations of the Caribbean slope; from near sea level to 800 m elevation (to 1400 m in Guatemala). Most flowering collections have been made in March–May. A little-collected species ranging from Veracruz, Mexico, to central Panama.

Psychotria clivorum is recognized by its larger narrow leaves gradually narrowed to the base with numerous pit domatia and distinct submarginal vein, stipules tubular at base and sometimes bilobed distally, inflorescences with whorled lateral branches at first two nodes (usually of two unequal pairs), small flowers, and reddish fruit. The tendency of the leaves to dry grayish and the stipules to dry reddish is characteristic of subgenus *Psychotria*. Specimens of this species may be difficult to separate from material of *P. orosiana* and *P. sarapiquensis*.

***Psychotria cocosensis* C. Hamilton, Phytologia 64: 222. 1988. Figure 62.**

Shrubs or small trees to 5 m tall, leafy stems ca. 2–7 mm thick, glabrous; **stipules** (7–)12–35 mm long, (1.5–)2–5 mm broad, lanceolate, glabrous, drying dark reddish brown, caducous. **Leaves** with petioles 5–16(–23) mm long, 1–2.5 mm thick, glabrous; **leaf blades** (8–)12–17 cm long, (3–)5–7 cm broad, narrowly elliptic to elliptic-oblong or broadly elliptic-obovate, apex acuminate or caudate-acuminate with tip 4–12 mm long, base acute to attenuate and decurrent on petiole, drying subcoriaceous, reddish brown to grayish brown, glabrous above and beneath, 2° veins 9–12/side, small pit domatia often present in the vein axils beneath. **Inflorescences** terminal or pseudoaxillary, solitary or 3-parted, 1.3–3 cm long, few-branched panicles with distal 3-flowered cymules, peduncles 0–7 mm long, ca. 1 mm thick, glabrous, bracts 0.5–1.5 mm long, triangular, glabrous, pedicels 2–3 mm long. **Flowers** puberulent externally, hypanthium ca. 0.5 mm long, glabrous, calyx tube ca. 1 mm long and 2 mm broad, cupulate, slightly denatate; **corolla** funnellform, white, tube ca. 3 mm long and 2 mm diam., lobes 5, ca. 4 mm long, 2 mm wide; **stamens** 5, anthers ca. 2 mm long. **Fruits** ca. 6 mm long, 5–6 mm diam., ellipsoid to globose, orange then red and finally purple, drying dark reddish brown, persisting calyx 0.8–1.5 mm long.

Plants known only from Cocos Island, from near sea level to 50 m elevation. We have seen four collections: *Foster 4132* f, *Holdridge 5169* us, *Pittier 12375* us (the holotype), and *Pittier 16279* GH, US. Flowering in April–June; fruiting in January, April, and June.

Psychotria cocosensis is similar to *P. panamensis* but differs in its subcoriaceous leaves and larger fruits with persisting cupulate calyx. The very small domatia, short inflorescences, and flowers with long

corolla lobes are distinctive. The red fruit and tendency of the leaves to dry reddish brown are characteristics of subgenus *Psychotria*. The Holdridge collection is unusual in having broadly elliptic-obovate leaves that have dried grayish and significantly paler beneath.

***Psychotria cooperi* Standl., Publ. Field Columb. Mus., Bot. Ser. 4: 296. 1929. Figure 13.**

Small trees or shrubs, 3–8 m tall, to 10 cm dbh, leafy stems 1.4–5 thick, glabrous, terete or slightly tetragonal; **stipules** 5–9(–11) mm long, to 8 mm broad, with a broad tube, truncate to rounded or bilobed with a small (1 mm) sinus at apex, glabrous, persisting or deciduous. **Leaves** opposite or 3 at a node, petioles 7–25 mm long, 0.7–1.7 mm thick, glabrous; **leaf blades** 8–21 cm long, 3.5–7 cm broad, elliptic-oblong to elliptic or elliptic-obovate, apex acuminate with tip 3–10 mm long, base gradually narrowed and acute or cuneate base, slightly decurrent on petiole, drying chartaceous, dark yellowish green to dark brown above, distinctly paler beneath, glabrous except for short (0.2–0.3 mm) stiff hairs along the sides of the midvein above and below (sometimes with thin hairs along the secondary veins beneath), 2° veins 7–11/side, arcuate-ascending near the margin. **Inflorescences** terminal or pseudoaxillary and becoming verticillate, sessile or subsessile, 1–3.5 cm long, to 3.5 cm broad, a compact globose irregularly branched panicle, peduncle 1–7 mm long, bracts to 10 mm long, bracteoles ca. 1 mm long and digitate-glandular, pedicels to 6 mm long in fruit. **Flowers** glabrous externally, distylous, hypanthium ca. 0.7 mm long, calyx lobes 5, ca. 1 mm long; **corolla** funnelform, white, tube 4–5 mm long, 1.3 mm diam., lobes reflexed at anthesis, ca. 2 mm long. **Fruits** 4–5(–10?) mm long, 2.5–3.5 mm diam., obovoid or turbinate and truncated distally, dark blue or purple, persisting calyx ca. 1 mm long; pyrenes 3–4 mm long, with 4–5 longitudinal ribs.

Plants of lowland rain forest formations from 20 to 300(–600) m elevation, often found in light gaps and stream sides. Flowering and fruiting throughout the year with most collections from January–March. The species ranges from north-eastern Costa Rica to Colombia.

Psychotria cooperi is recognized by its small congested axillary inflorescences (sometimes appearing verticillate), the broad short-tubular stipules, leaves often drying yellowish green, small white flowers, and blue or purple obovoid fruit. The flowers are mostly sessile in terminal inflorescences but become axillary as the stems continue to grow. These small treelets are called *cocobolito* in Bocas del Toro, Panama. Fruiting material may resemble *Palicourea copensis*.

***Psychotria correae* (Dwyer & Hayden) C. M. Taylor, comb. nov. *Cephaelis correae* Dwyer & Hayden, Ann. Missouri Bot. Gard. 55: 36. 1968. Figure 17.**

Shrubs or small trees, 2–3.5(–5) m tall, leafy stems 3–6 mm thick, glabrous, quadrangular; **stipules** with a very short (1–3 mm) sheath with 2 broadly rounded often overlapping lobes ca. 4 mm long and 4 mm broad separated by a U-shaped sinus, glabrous. **Leaves** with petioles 15–80 mm long (opposing petioles often unequal), 1.2–2.5 mm thick, glabrous; **leaf blades** 11–28 cm long, 5–13 cm broad, broadly elliptic-oblong, ovate-oblong, apex abruptly narrowed and short-acuminate with tip ca. 4 mm long, base broadly obtuse, drying chartaceous, green, glabrous above and below, 2° veins 13–17(–20)/side. **Inflorescences** solitary and terminal or pseudoaxillary, capitulae 1–2 cm long, 2–3 cm diam., involucre 5–10 cm wide, peduncles (3–)5–12(–22) cm long, ca. 2 mm thick, glabrous, erect and becoming pendant, the 2 large involucre bracts 2.5–5 cm long and 4–5 cm broad, ovate to reniform, rose red to magenta or purple, glabrous, bracteoles 8–15 mm long, obovate. **Flowers** glabrous externally, calyx lobes 5, ca. 1 mm long; **corolla** narrowly funnelform, white, tube to 10 mm long, cylindrical, lobes 5, ca. 3 mm long; anthers ca. 3 mm long. **Fruits** 10–15 mm long, ca. 6 mm diam., obovoid-oblong, blue; pyrenes with 4–5 slightly elevated ridges

Plants of evergreen cloud forest formations along the central cordilleras at 900–1100 m elevation. Flowering in March–August; fruiting in October. This species is only known from the Cordilleras de Guanacaste and Tilarán and the Province of Coclé in Panama.

Psychotria correae is recognized by the larger leaves with many secondary veins, the unusual stipules, the long-pedunculate inflorescences becoming pendant in later stages, and the large purplish bracts subtending the capitulum. Specimens of this species can be confused with *P. elata*, which has erect capitulae with smaller involucre bracts and shorter peduncles, and to *P. chiriquiensis*, which lacks involucre bracts. This attractive species was named in honor of our respected Panamanian colleague Mireya Correa.

***Psychotria deflexa* DC., Prodr. 4: 510. 1830. *P. patens* auct. non Sw. fide Steyermark 1972. Figure 56.**

Shrubs, (0.5–)1–3 m tall, leafy stems 0.5–5 mm thick, glabrous or sparsely puberulent in early stages; **stipules** united around stem for 0.5–2 mm and with 2 subulate or linear awns 3–8 long on each side, glabrous, persisting. **Leaves** with petioles 3–9(–12) mm long, 0.5–1.3 mm thick, glabrous; **leaf blades** 7–15(–18) cm long, (1.5–)2–

5(–7) cm broad, narrowly ovate-elliptic to narrowly elliptic, elliptic-lanceolate or rarely lanceolate, apex tapering gradually and acute or acuminate, tip 10–20 mm long, base broadly obtuse to acute, drying chartaceous, greenish or brown, glabrous above and below, 2° veins 4–8/side. **Inflorescences** terminal (rarely pseudoaxillary) and solitary, 4–11 cm long and 2–4 cm broad, narrowly pyramidal or thyriform panicles with slender central rachis and short (5–14 mm) opposite or subopposite lateral branches (expanding somewhat in fruit), peduncles 2.5–5 cm long, 0.4–1.1 mm thick, glabrous or minutely puberulent, lateral branches without subtending bracts, pedicels 1–2 mm long, bracteoles ca. 1 mm long. **Flowers** glabrous externally, hypanthium ca. 1 mm long, calyx ca. 0.5 mm long, dentate; **corolla** white, funnel-form, tube 1.6–3 mm long, 0.3–1 mm diam. (in Costa Rica), lobes 4–5, ca. 1 mm long; **stamens** 4, anthers ca. 1 mm long. **Fruits** 2–3 mm long and 3–4 mm diam. (8–10 mm when aerenchymatous), oblate and somewhat bilobed, longitudinally ridged, becoming purple, violet, or blue (pulpy white within); pyrenes with 3–4 ridges and transverse ribs.

Understory plants of wet evergreen or partly deciduous forest formations from ca. 500 to 1200 m elevation on the Caribbean slope of the cordilleras and near sea level on the Osa Peninsula. Flowering in June–August; fruiting in July–March. This species ranges from Mexico to Peru and Bolivia.

Psychotria deflexa is recognized by its persisting narrowly awned stipules, narrow leaves, general lack of pubescence (only the slender narrow inflorescence is minutely puberulent), small flowers, and purple or blue fruit with transverse ribs. Flowers in Costa Rican material appear to be much smaller than those described by Steyermark (1974, p. 1284). This species may resemble *P. cincta* and *P. microbotrys*. There are collections (Kernan & Phillips 661 & 789 CR) from Corcovado National Park that have unusually thin pedicels and inflorescences. However, these aberrant samples are bridged by other collections (Liesner 2842 & 3198 CR, also from the Osa Peninsula) that appear to be intermediate with the more normal inflorescences. These populations are worthy of further study.

Psychotria dichroa (Standl.) C. M. Taylor, comb. nov. *Evea dichroa* Standl., Contr. U.S. Natl. Herb. 18: 124. 1916. *Cephaelis dichroa* (Standl.) Standl. Publ. Field Columb. Mus., Bot. Ser. 4: 296. 1929.

Small **shrubs**, 0.6–2 m tall, leafy stems 1.3–4 mm thick, glabrous; **stipules** 2.5–6 mm long, with a short (2–3 mm)

sheath, with 2 short (1–2 mm) obtuse or rounded lobes separated by a U-shaped sinus, glabrous. **Leaves** with petioles 4–25 mm long, 0.7–1.2 thick, glabrous; **leaf blades** 4–11(–13) cm long, 1.8–4.3 cm broad, narrowly elliptic to lanceolate, apex tapering gradually and acuminate, tip 5–10 mm long, base acute and slightly decurrent on petiole, drying subcoriaceous, dark brownish green above, glabrous above and below, 2° veins (6–)8–12/side. **Inflorescences** 1–3 and terminal, 3–10 cm long, 3–8 cm wide, usually subtended by a pair of smaller (15 mm) leaves, capitula ca. 15–25 mm long and equally broad (enlarging in fruit), subtended by 2 involucre bracts 12–20 mm long and 8–15 mm broad, white becoming pinkish (dark purple in fruit), peduncles 3–9 cm long and 1.5–3.5 mm thick, glabrous, flowers sessile within bracteoles. **Flowers** glabrous externally, hypanthium ca. 1.5 mm long, calyx ca. 3 mm long, lobes ca. 1.5 mm long and triangular; **corolla** funnelform, white to pink, tube 5–10 mm long, ca. 2 mm diam., corolla lobes 2–3 mm long, bluntly acute. **Fruits** 8–9 mm long (including the 1 mm high calyx), 4 mm diam., narrowly obovoid, blue-black, drying dark reddish brown; pyrenes usually smooth.

Plants of evergreen montane forest formations, 1200–2600 m elevation. Flowering January–September. This species is only known from the Chiriquí Highlands of western Panama and the Caribbean slope of the Cordillera de Talamanca.

Psychotria dichroa is recognized by the leaves with prominent 2° veins, one to three terminal small involucre heads, white flowers, and highland habitat. In Costa Rica, it is rarely collected and appears to be restricted to the understory of high-elevation (2000–2500 m) *Quercus* forests. This species is similar to *P. chiriquiensis* with reddish purple capitula.

Psychotria domingensis Jacq., Enum. Pl. 16. 1760. *Psychotria pavetta* Sw., Prodr. 45. 1788. *Palicourea domingensis* (Jacq.) DC., Prodr. 4: 529. 1830. *Palicourea pavetta* (Sw.) DC., loc. cit. 525. 1830. *Psychotria mombachensis* Standl., Publ. Field Columb. Mus., Bot. Ser. 8: 188. 1930.

Shrubs, 1–2 m tall, leafy stems 2–5 mm thick, glabrous, often with a shrunken area below the node after drying; **stipules** 2–5 mm long, with 2 triangular lobes separate almost to base by a broad (1–2 mm) U-shaped sinus, acute or awned, glabrous, deciduous or persisting. **Leaves** with petioles 5–20 mm long, 0.7–1.7 mm thick, glabrous, often drying yellowish; **leaf blades** 8–19 cm long, 3–7 cm broad, elliptic-oblong to narrowly elliptic-obovate, apex acuminate or gradually tapering and acute, base acute to obtuse and slightly decurrent on petiole, drying membranaceous to thin-chartaceous, yellowish green to greenish brown or brown, glabrous above and below, 2° veins 8–11/side. **Inflorescences** solitary or 3, terminal or pseudoaxillary, 4–9 cm long, 3–6 cm broad,

a rounded open panicle with opposite branching, peduncle 3–20 mm long, ca. 1.5 mm thick and yellowish when dried, glabrous or minutely papillate-puberulent, bracts absent or 1–6 mm long and linear, flowers in distal cymes of 3, pedicels 0–3 mm long, ca. 1 mm thick, bracteoles minute or absent. **Flowers** glabrous or minutely puberulent externally, hypanthium ca. 1.2 mm long, calyx tube ca. 0.5 mm long, lobes 0.2–1 mm long, narrowly acute; **corolla** white, tubular-salverform, tube ca. 12 mm long, 0.8–1.7 mm diam., lobes ca. 4–5 mm long and 2 mm broad. **Fruits** 4–5 mm long, ca. 6 mm diam., subglobose to ellipsoid, purple-black, with 4–5 longitudinal costae and smaller transverse ribs when dried; pyrenes angled.

Plants of evergreen or seasonally deciduous formations, from 20 to 900 m elevation. Flowering in April and June (the Nicaraguan type of *P. mombachensis* (Maxon et al. 7818 F) was flowering in July); a Costa Rican collection from near Tilarán (Standley & Valerio 45222 us) was fruiting in January. The species is frequent in the West Indies and Guatemala–southern Mexico but is known from only a few collections in southern Central America.

Psychotria domingensis is recognized by the inflorescences with thick branches and relatively few flowers, larger fruit with longitudinal and transverse ridges, thin glabrous leaves that often dry yellowish green, two-lobed stipules, and dried stems often conspicuously contracted beneath the node. The few collections from Costa Rica come from both evergreen and deciduous areas. This species is rather similar to *P. eurycarpa* of wet forests, but that species has stiffer leaves lustrous above, poorly developed calyx lobes, and larger fruit without transverse ribs. It is also similar to *P. microdon* and some species of *Coussarea* (see fig. 47).

Psychotria dukei Dwyer, Ann. Missouri Bot. Gard. 67: 371. 1980.

Shrubs or herbaceous subshrubs, 0.5–1.5(–2) m tall, leafy stems succulent in life, 1.8–7 mm thick (dried), glabrous; **stipules** 7–20 mm long, 8–18 mm broad, ovate-triangular, bilobed or fimbriate, yellowish and membranaceous, lobes 1–4 mm long, deciduous. **Leaves** with petioles 1–5 cm long, 1–2.3 mm broad, glabrous; **leaf blades** (11–)13–27 cm long, 4–11 cm broad, elliptic-oblong to oblong or elliptic-ovate, apex short-acuminate with tip 5–10 mm long, base obtuse to cuneate and decurrent on petiole, drying chartaceous, dark green or greenish brown, glabrous above, minutely (0.1 mm) puberulent along the major veins beneath, 2° veins 10–18/ side. **Inflorescences** axillary, solitary at each node, 2.5–9 cm long, pyramidal, often with the flowers crowded in 3 capitula on 3 primary branches 3–20 mm long (rarely with further secondary branches), peduncles 8–35(–60)

mm long, ca. 1.2 mm thick, minutely puberulent or glabrous, bracts 2–10 mm long, triangular to lanceolate, bracteoles 2–5 mm long, often forming a small involucre beneath the sessile flowers. **Flowers** glabrous externally, hypanthium ca. 1 mm long, calyx tube ca. 0.5 mm long, entire; **corolla** tubular-funnelform, white, tube 3–4 mm long, ca. 0.5 mm diam. basally, lobes ca. 1.5 mm long. **Fruits** 5–6 mm long, 3–4 mm diam., oblong, white; pyrenes longitudinally ridged.

Plants of lower montane rain forest formations from (800–)1100 to 1800 m elevation. Flowering in March and June–August; fruiting in March–November. The species ranges from the Cordillera de Tilarán to Chocó, Colombia.

Psychotria dukei is recognized by its usually unbranched succulent stems, axillary inflorescences with flowers in capitate clusters, white fruit, and unusual stipules. This species is easily confused with *P. aggregata* or *P. macrophylla*, but the large thin stipules and inflorescence bracts are distinctive. This species is rarely collected in Costa Rica. Compare *P. dukei* with *P. wilburiana* Dwyer of Panama.

Psychotria elata (Sw.) Hammel, Selbyana 12: 139. 1991. *Cephaelis elata* Sw., Prodr. 45. 1788. *C. punicea* Vahl, Eclog. Amer. 1: 19. 1796. *C. costaricensis* Schlechtend., Linnaea 28: 546. 1856. *Evea elata* (Sw.) Standl., Contr. U.S. Natl. Herb. 18: 123. 1916. *C. elata* forma *lutea* Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 1279. 1938. Figure 17.

Shrubs, subshrubs, or small trees, 0.5–5(–8) m tall, leafy stems 1.3–5 mm thick, glabrous, terete or quadrangular; **stipules** united around stem for 1–2 mm, with 2 ovate lobes on each side, 2–5 mm long and ca. 3 mm broad, obtuse to broadly rounded and separated by a U- or V-shaped sinus, glabrous, persisting. **Leaves** with petioles 4–22(–30) mm long, 1–2 mm wide, glabrous; **leaf blades** 6–25 cm long, 2.5–7(–8.5) cm broad, oblong to elliptic-oblong, oblong-obovate, or oblanceolate, apex acute to short-acuminate, tip 4–10 mm long, base cuneate to acute or obtuse, drying thinly to stiffly chartaceous, green, glabrous above and below, 2° veins (9–)13–20(–23)/side. **Inflorescences** terminal and solitary (rarely 2–3), capitate and globose-hemispherical, capitula 1.5–4 cm long, involucre 2–7 cm broad, peduncles 2–13 cm long, 1.5–3 mm thick, erect or becoming pendant, glabrous, the 2 involucre basal bracts 15–55 mm long, 15–45 mm broad, deep red to orange-red (yellow), ovate to reniform, rounded to acuminate, glabrous, bracteoles 5–10 mm long, flowers sessile. **Flowers** glabrous externally (rarely puberulent), calyx ca. 1 mm long, dentate; **corolla** white (rarely pink or yellow), narrowly funnelform, tube ca. 16 mm long, 1.5–2.5 mm diam., lobes 5, 2.5–4 mm long, narrowly triangular; **stamens** 5, anthers 2–3 mm long. **Fruits** 5–10 mm long, 2–5 mm diam.,

ovoid, blue becoming black; pyrenes 4–7 mm long and 3–4 mm broad, 5-ribbed.

Common shrubs of evergreen forest edges and forest interiors, from 30 to 1700 m elevation. Flowering and fruiting throughout the year (primarily flowering in January–August). Fruiting at La Selva in July–September. The species ranges from Mexico and the West Indies, through Central America to Colombia.

Psychotria elata is recognized by its glabrous parts, usually narrowly oblong leaves with many secondary veins, solitary long-pedunculate heads, large brilliant red (rarely yellow) bracts subtending the capitulum, and white corollas. The yellow-bracted form appears to be most common in the General Valley and Golfo Dulce area. This is one of Central America's most distinctive species of Rubiaceae, common in light gaps and on the edges of forests. The flowers are visited by butterflies and hummingbirds (Freeman & Stiles, 1990); breeding biology was studied by Bawa and Beach (1983). This is one of the species that made *Cephaelis* so distinctive a genus in Central America. Compare *P. poeppigiana* with conspicuous pubescence, *P. chiriquiensis* with purple capitula lacking the large involucre bracts, *P. correae* with longer peduncles and larger bracts, and *P. dichroa* with several smaller heads.

***Psychotria emetica* L.f., Suppl. Pl. 144. 1781. Figure 13.**

Small herbs and subshrubs, 0.2–1 m tall, rhizomatous, stems usually unbranched, terete, leafy internodes 1–4 mm thick, appressed-puberulent with stiff crooked brownish hairs 0.2–0.4 mm long; **stipules** 2–4 mm long, 1–2 mm broad at base, narrowly triangular and appressed-puberulent, drying dark, usually caducous. **Leaves** with petioles 3–12(–20) mm long, 1–2 mm broad, appressed-puberulent with stiff brownish hairs; **leaf blades** (7–)8.5–13(–17) cm long, 2–5(–6.5) cm broad, elliptic to narrowly elliptic-oblong, elliptic-obovate or oblanceolate, apex acute or short-acuminate, tip ca. 5 mm long, base cuneate to acute and slightly decurrent on petiole, drying thinly chartaceous, dark grayish green or dark grayish brown, glabrous above, sparsely appressed-puberulent with short (0.1–0.3 mm) hairs beneath, 2° veins 5–9/side. **Inflorescences** axillary, usually solitary in each axil (2/node), 1–2 cm long, condensed cymose or subcapitate, with 3–10 flowers, peduncles 3–12 mm long, ca. 0.7 mm thick, puberulent, bracts 1–2 mm long, triangular-acute, pedicels 0–5 mm long. **Flowers** with hypanthium ca. 1 mm long, conical and appressed-puberulent, calyx lobes 1–1.5 mm long, narrowly triangular; **corolla** white, funnelform, glabrous externally, tube 2–4 mm long, 1–1.5 mm diam. at mouth, lobes 5, 1.5–2 mm long, acute. **Fruits** 8–10 mm long and 4–6 mm diam.,

oblong or ellipsoid, persisting calyx 1–1.5 mm long, becoming blue; pyrenes ca. 5 mm long, smooth.

Plants of shaded understory in lowland evergreen rain forest formations, from 10 to 300 m elevation. In Costa Rica and Panama flowering in February–August; fruiting mostly in June–November. This species ranges from Guatemala to Bolivia.

Psychotria emetica is recognized by its short, usually unbranched stems, small condensed axillary inflorescences, and bright blue fruit. These plants are occasionally cultivated and have been called *raicilla* and *raicilla macho* in Costa Rica, Nicaragua, and Panama. This species differs from the closely similar *P. erecta* by its smaller stature, puberulent stems, and floral details. The roots contain the drug ipecac but it is of inferior quality to that found in *P. ipecacuanha*.

***Psychotria erecta* (Aubl.) Standl. & Steyerl., Publ. Field Mus. Nat. Hist., Bot. Ser. 23: 24. 1943. *Ronabea erecta* Aubl., Hist. pl. Guiane 1: 156. 1775. Figure 13.**

Shrubs or treelets, (0.5–)1–3(–8) m tall, leafy stems 1.5–7 mm thick, sparsely appressed-puberulent with thin ascending hairs ca. 0.3 mm long, becoming glabrescent and drying dark; **stipules** with a persistent short (0.5 mm) base and single slender awn 2–6 mm long, ca. 0.5 mm wide, triangular to subulate, appressed-puberulent. **Leaves** with petioles 8–18(–35) mm long, 0.7–2(–2.5) mm thick, appressed-puberulent with hairs 0.2–0.3 mm long; **leaf blades** 8–20 cm long, 3–9 cm broad, elliptic-oblong to oblong or slightly obovate, apex abruptly narrowed and short-acuminate, tip 4–11 mm long, base obtuse to acute, drying chartaceous to subcoriaceous, dark olive green or brownish green, glabrous above, glabrous or sparsely puberulent beneath with thin appressed hairs, 2° veins 5–8/side. **Inflorescences** 1–3 in each axil (2–6/node), 1–3 cm long, 5–10 mm broad, subcapitate condensed cymose with 3–7 closely crowded flowers, peduncles 0–8(–18) mm long, ca. 0.7 mm thick, appressed-puberulent with ascending yellowish hairs, flowers subsessile or sessile, bracteoles to 1 mm long. **Flowers** with hypanthium 1–2 mm long, sparsely appressed puberulent near the base, calyx ca. 1 mm long, glabrous, lobes ca. 0.2 mm high; **corolla** white, tubular-salverform, glabrous, tube 3–4 mm long, 1 mm diam., glabrous externally, lobes 5(–6), 1.5–3 mm long. **Fruits** 8–10 mm long, 5–8 mm diam., ellipsoid or oblong, glabrous, becoming blue-black; pyrenes 5–7 mm long, smooth.

Plants of evergreen rain forest formations, from near sea level to 700(–1000) m elevation on both the Caribbean and Pacific coasts. At La Selva this species is usually found on ridges near light gaps. Flowering in May–October; probably fruiting

throughout the year. This species ranges from Mexico and the West Indies to Bolivia.

Psychotria erecta is recognized by its axillary small subcapitate inflorescences with few small flowers, blue fruit, and oblong leaves often drying dark. This species is similar to *P. emetica* but grows to a larger size with broader and thicker leaves and glabrescent stems. Both species have axillary, not pseudoaxillary, inflorescences. Compare *Appunia guatemalensis*.

***Psychotria eurycarpa* Standl., J. Wash. Acad. Sci. 18: 275. 1928. Figure 47.**

Shrubs or small trees, 1.5–5(–7) m tall, leafy stems 1–3 mm thick, glabrous or rarely minutely papillate-puberulent; **stipules** 1–3 mm high and 3–4 mm broad, truncate to broadly rounded with a small (0.2 mm deep) sinus, persisting or deciduous. **Leaves** with petioles 12–28(–35) mm long, 0.7–1.5 mm thick, glabrous and often drying yellowish; **leaf blades** 6–14(–21) cm long, 2.7–7(–11) cm broad, ovate-elliptic to elliptic or broadly elliptic, apex short-acuminate with a narrowed tip 3–10 mm long, base obtuse to acute, drying stiffly chartaceous, yellowish green, glabrous and lustrous above, glabrous beneath, 2° veins 4–7/side. **Inflorescences** terminal and solitary, 5–11 cm long, 5–9 cm broad, broadly pyramidal panicles with opposite branching or umbellate, the first node often with 4 lateral branches, peduncles 15–55 mm long, 1–2 mm thick, yellowish, glabrous, bracts ca. 1 mm long, flowers sessile or subsessile in glomerules of 2–5. **Flowers** nocturnal, glabrous or very minutely papillate-puberulent externally, hypanthium ca. 1 mm long and 0.6 mm diam., obconic, calyx tube 0.3–0.7 mm high with minute (0.2 mm) lobes; **corolla** narrowly funnel-form, white, tube 6–15 mm long and 0.8 mm diam. (1.7 mm distally), lobes 5 (6, 7), 3–8 mm long, 0.5–1 mm broad, narrowly oblong. **Fruits** 8–20 mm long (to 25 mm when succulent), 7–15 mm diam., oblong to subglobose, blue-black or dark purple (often drying pale yellowish brown), longitudinal ridges present but not prominent when dried; pyrenes 12–17 mm long, obscurely 3–5-angled.

Plants of lowland rain forest formations and lower montane cloud forest formations, from 20 to 900(–1100) m elevation. Flowering in February–May; fruiting in October–April and June. This species is only known from the Caribbean coastal plain, Cordillera de Guanacaste, Cordillera de Tilarán, and the Caribbean slopes of the Central Highlands as far east as Rio Reventazón, and in western Panama.

Psychotria eurycarpa is recognized by the usually glabrous parts often drying yellowish green, the short stipules (truncated or with minute apical sinus), few-branched inflorescences with thick peduncles and thick lateral branches and inconspicuous bracts, longer corolla tubes, and the large

fruit. Breeding biology was studied by Bawa and Beach (1983). A collection (*Taylor 3546*) from Las Cruces (San Vito) is tentatively placed here; it is the highest elevation (1100 m) and easternmost collection in Costa Rica. *Folsom 9188* DUKE, from La Selva with corolla tubes to 18 mm long and corolla lobes to 12 mm long, is provisionally placed here. Individuals of this species may be difficult to distinguish from *P. domingensis* (with bilobed stipules and flowers in distal triads) and *Coussarea psychotrioides* (q.v.).

***Psychotria fruticetorum* Standl., J. Arnold Arbor. 11: 42. 1930. Figure 60.**

Shrubs, subshrubs, or small treelets, 0.3–3(–5) m tall, leafy stems 0.7–3.5 mm thick, glabrous; **stipules** 2–4 mm long, 1–3.5 mm broad at base, triangular to ovate, truncate to acute, with 2 awns 1–1.5 mm long, glabrous or minutely (0.05 mm) papillate, drying reddish brown, caducous. **Leaves** with petioles 0–6(–8) mm long, 0.7–1.2 mm thick, glabrous; **leaf blades** 3–8.5(–11?) cm long, 1–4(–5?) cm broad, elliptic to obovate or oblanceolate, apex acute to subacuminate, base cuneate to acute, drying stiffly chartaceous to subcoriaceous, grayish to dark reddish brown, glabrous above and below, 2° veins 4–7/side, often with minute pit domatia or tufts of hairs in the axils of 2° veins beneath. **Inflorescences** terminal and solitary, 3–4.5 cm long, 3–4 cm wide, rounded panicles with opposite or whorled branches, peduncles 5–20 mm long, 0.5–0.8 mm thick, glabrous, bracts ca. 1 mm long, flowers subsessile in distal cymes, pedicels 0.5–1 mm long. **Flowers** glabrous externally, hypanthium ca. 0.8 mm long, obconic, calyx lobes ca. 0.5 mm long; **corolla** funnel-form to salverform, white, tube ca. 2 mm long, 1–1.2 mm diam., lobes 5, ca. 1.5 mm long and 0.7 mm broad at the base; **stamens** 5, anthers ca. 0.8 mm long. **Fruits** 4–5 mm long, 3–4 mm diam., ellipsoid with ca. 10 longitudinal ridges, bright red; pyrenes ridged.

Plants of wet evergreen lowland forest formations (and in open pine savannas in Nicaragua), from near sea level to 200 m elevation (to over 1300 m in Mexico and Guatemala). Flowering in southern Central America in March–May and September; fruiting in July–December. The species ranges from Mexico, mostly along the Caribbean, to Panama but is disjunct from Nicaragua to central Panama.

Psychotria fruticetorum is recognized by the small, often cuneate and subsessile leaves, caducous stipules with two distal awns, general lack of pubescence, small domatia, small inflorescences, and small flowers and fruit. The tendency of the leaves to dry grayish or reddish and the bright red berries are characteristics of subgenus *Psychotria*. Presently, this species is not known from Costa Rica, though it grows near Bluefields, Nicaragua,

and in central Panama. It may be restricted to limestone soils.

Psychotria glomerulata (J. D. Smith) Steyerf., Mem. New York Bot. Gard. 23: 670. 1972. *Cephaelis glomerulata* J. D. Smith, Bot. Gaz. 16: 12, pl. 1. 1891. Figure 18.

Small **shrubs** or treelets, 0.6–2(–4?) m tall, much-branched, leafy stems 1–5 mm thick, quadrangular, glabrous; **stipules** with a short (0.5–2 mm) sheath, truncated and entire at apex, glabrous, persisting. **Leaves** with petioles 3–11(–15) mm long, 0.8–1.3 mm thick, glabrous, yellowish green; **leaf blades** 5–14(–17) cm long, 1.5–5(–6.5) cm broad, narrowly oblong to narrowly elliptic-oblong, oblong or lanceolate, apex acuminate with tip 4–12 mm long, base obtuse to acute or cuneate and slightly decurrent on petiole, drying chartaceous to stiffly chartaceous, glabrous above and below, 2° veins 9–13/side and loop-connected near the the margin. **Inflorescences** terminal and solitary, capitula 1.2–2.5 cm long, 1.5–3.5 cm broad, oblate to subglobose, subtended by 4 decussate involucre bracts 10–16 mm long and 12 mm broad, oblong to broadly obovate and rounded distally, greenish yellow or whitish and sometimes edged with blue or purple, glabrous, peduncle to 5(–15) mm long, flowers tightly enclosed within the bracts and spatulate bracteoles. **Flowers** glabrous externally, hypanthium ca. 1 mm long, calyx lobes 5, 0.5–1.5 mm long; **corolla** funnelliform, white, tube 10–15 mm long, 1–2 mm diam., lobes 5, 1.5–3 mm long; **stamens** 5, anthers 2–3 mm long. **Fruits** 6–13 mm long and 5–10 mm diam., ellipsoid, bright blue; pyrenes 4–6 mm long and 3–4 mm diam., apparently smooth.

Understory shrubs of evergreen rain forest formations, from near sea level to 600 m elevation along the Caribbean slope and coastal plain. Probably flowering and fruiting throughout the year but flowering mostly in March–April and August–October. This species ranges from southern Mexico and Belize along the Caribbean lowlands to Panama.

Psychotria glomerulata is recognized by its short stature, narrow leaves, lack of pubescence, solitary sessile terminal heads with four (to eight) white or yellow-green involucre bracts, and lowland Caribbean habitat. Our figure is based on the original illustration. This species is similar to *P. guapilensis* with long stipule lobes; *P. apoda* Steyerf. of South America may be synonymous.

Psychotria goldmanii Standl., Contr. U.S. Natl. Herb. 18: 130. 1916. *P. torresiana* Standl., J. Wash. Acad. Sci. 15: 288. 1925. *P. eugenifolia* Dwyer, Ann. Missouri Bot. Gard. 67: 375. 1980. Figure 55.

Shrubs or small treelets, 1.5–3(–5) m tall, leafy stems 0.6–4 mm thick, glabrous, flattened or quadrangular at first, soon terete and with thickened nodes; **stipules** 1–3 mm long, 1.5–2.5 mm broad, with 2 acute lobes and distal sinus 0.3–2 mm deep, glabrous, deciduous or persisting. **Leaves** with petioles 3–22 mm long, 0.3–1 mm thick, glabrous; **leaf blades** (2–)3–10(–13) cm long, (0.8–)1–2.5(–3) cm broad, narrowly elliptic-oblong to lanceolate or linear-lanceolate, apex long-acuminate with tip 7–15 mm long, base gradually narrowed or abruptly acute and slightly decurrent on petiole, drying chartaceous, dark green or brown above, glabrous above and below, 2° vein 8–13/side, often with parallel intermediate 2° veins. **Inflorescences** terminal and solitary (pseudoaillary), 4–14 cm long, to 11 cm broad, open pyramidal panicles with distant slender opposite or subopposite branches, peduncles 15–52 mm long, 0.7–1.2 mm thick and glabrous, bracts 3–10 mm long and linear to triangular (or leaf-like), distal branching cymose (often minutely puberulent), flowers usually sessile in triads. **Flowers** glabrous on the exterior, hypanthium ca. 1 mm long, obconic, calyx tube ca. 1 mm long, subentire or with 5 acute lobes to 0.5 mm long; **corolla** funnelliform, greenish white, tube 4–6 mm long, 0.6–1 mm diam., lobes 5, 1–2 mm long. **Fruits** 3–5 mm long, 2.5–4 mm diam., ellipsoid-oblong, blue, purple, or white, persisting calyx 0.3–0.7 mm long; pyrenes 3–5 angled or -ridged.

Plants of evergreen montane forest formations, from 1000 to 2000 m elevation. Flowering in March, April, and October; fruiting in January and March–August. The species ranges from the Cordillera de Guanacaste eastward along the highlands to Darién, Panama.

Psychotria goldmanii is recognized by its higher-elevation habitat, smaller narrow long-acuminate glabrous leaves, calyx with minute lobes, longer corolla tube, and small blue fruit. The leaves often dry with the lower surfaces markedly paler in color and obscure 3° venation. The stipules with two small lobes are also distinctive. Few other species of *Psychotria* in southern Central America develop such narrow linear-lanceolate leaves (an extreme form of which is represented by the type of *P. torresiana*, Standley 39769 us). Compare *P. steyermarkii* with more numerous 2° veins and *P. valeriana* with one stipule appendage. Smaller-leaved specimens of this species may be difficult to distinguish from *Palicourea montivaga*, but that species has shorter leaves, very slender petioles, a tendency to develop a short stipular tube, inflorescences that dry yellowish, and corollas that are swollen at the base.

Psychotria graciliflora Benth. in Oerstr., Vidensk. Meddel. Dansk. Naturhist. Foren. Kjobenhavn 1852: 35. 1853. *P. vallensis* Dwyer, Ann. Missouri Bot. Gard. 67: 438. 1980 (fide Hamilton 1989). Figure 60.

Shrubs, 0.6–2(–3) mm tall, much-branched and often flat-topped, leafy stems 0.7–2(–3) mm thick, glabrous (except for reddish collectors at the node), usually with 2 (opposite) longitudinal ridges between nodes; **stipules** with a narrowly triangular to ovate base 1–2 mm long and 2 awns 1–2 mm long, with ascending hairs 0.1–0.2 mm long, reddish brown, deciduous. **Leaves** mostly clustered near the ends of branchlets, petioles 2–10 mm long, 0.5–1 mm broad, glabrous; **leaf blades** 1.5–6(–8) cm long, 0.7–3 cm broad, elliptic to ovate-elliptic, apex bluntly obtuse to acute or subacuminate, base cuneate to acute and decurrent on petiole, drying chartaceous, dark gray or reddish gray above, glabrous above and below, 2° veins 3–6/side, pit domatia rarely present. **Inflorescences** terminal and solitary, 2–6 cm long, 2–5 cm broad, pyramidal rounded panicles with 1–2 pairs of opposite branches or umbellate, peduncles 1–2(–3.5) cm long, ca. 0.5 mm thick, glabrous and drying dark, bracts and bracteoles to 1 mm long, flowers often sessile in distal cymes or triads. **Flowers** glabrous externally, hypanthium ca. 0.7 mm long, obconic, calyx tube ca. 0.5 mm long, lobes 0.2–1 mm high; **corolla** white, salverform, tube 2.5–3.5 mm long, 0.5–0.8 mm diam., lobes 5, 1–2 mm long; **stamens** 5, anthers ca. 0.9 mm long. **Fruits** 4–6 mm long, 3–5 mm diam., globose to ellipsoid, with ca. 10 longitudinal ridges, bright red or orange; pyrenes ca. 4 mm diam.

Understory plants of wet evergreen forest formations on both the Caribbean and Pacific slopes, from near sea level to 1700 elevation (to 2500 m elsewhere, and not found below 1000 m on the Pacific slope of Costa Rica). Flowering in February–August (mostly in March–May); fruiting throughout the year. The species ranges from southern Mexico to Colombia.

Psychotria graciliflora is recognized by its very small leaves, usually horizontal glabrous branches, caducous stipules with two slender pubescent awns, small open inflorescences with slender peduncles, and small flowers with minute calyx lobes. The bright red fruit and tendency for leaves to dry grayish or reddish are characteristics of subgenus *Psychotria*. Costa Rican material of this species has smaller leaves with fewer secondary veins than material from Honduras and Nicaragua (Hamilton, 1989, cited under the genus). This species resembles *P. carthagenensis*, *P. chagrensis*, and *P. parvifolia* (see fig. 60).

Psychotria grandis Sw., Prodr. 43. 1788. Figure 64.

Shrubs or small trees, (1.5–)4–8(–10) m tall, trunks to 20 cm diam., leafy stems 4–10 mm thick, terete, glabrous or minutely papillate-puberulent in early stages; **stipules** 8–30 mm long, 5–20 mm broad, broadly ovate-triangular with the margins often revolute, acute to acuminate

and often minutely (1 mm) 2-lobed, usually glabrous, often inflated at the base, deciduous. **Leaves** with poorly defined petioles 0.5–3.5 cm long, 1.3–3 mm broad, glabrous; **leaf blades** (11–)18–40 cm long, (3–)6–16 cm broad, obovate to elliptic-obovate or oblanceolate, apex obtuse to short-acuminate with tip ca. 5 mm long, gradually narrowed to the cuneate base and long-decurrent on petiole, drying chartaceous to subcoriaceous, grayish green to pinkish gray or dark grayish above, glabrous above and below, 2° veins 12–16/side. **Inflorescences** terminal or pseudoaxillary and solitary, 12–25(–30) cm long, 10–18 cm broad, open pyramidal panicles with opposite branching or with 4 branches (2 larger and 2 smaller) at lower nodes, peduncles 11–18 cm long, 2–4 mm thick, glabrous or minutely (0.05 mm) papillate-puberulent, flowers 2–5 in distal cymes, bracts ca. 2 mm long and triangular, pedicels 1–3 mm long, bracteoles ca. 0.5 mm long. Flowers mostly glabrous externally, hypanthium ca. 0.8 mm long, obconic, calyx tube ca. 0.6 mm long, lobes 5, 0–0.3 mm high, triangular; **corolla** white, funnelform, tube 2–4 mm long, 1.5–2 mm diam., lobes 5, 1.5–2 mm long and 1.1 mm broad at the base; **stamens** 5, anthers 0.8 mm long. **Fruits** 5–7 mm long and 5 mm diam., broadly ellipsoid or subglobose, orange or red, surfaces smooth and rounded; pyrenes ca. 5 mm long, with 4–5 rounded dorsal ribs.

Trees of wet evergreen forest formations on both the Caribbean and Pacific slopes of Costa Rica, from near the seashore to 800 m elevation. Flowering in February–July; fruiting mostly in July–February. The species ranges from southern Mexico and the Greater Antilles to northern South America.

Psychotria grandis is recognized by its often larger (tree) habit, large glabrous-obovate leaf blades decurrent on the petioles, large ovate-acuminate stipules with reflexed lateral margins, large inflorescences, and small flowers. The red fruit and vegetative parts drying grayish or reddish are characteristics of the subgenus *Psychotria*. Guatemalan material is often puberulent and with larger inflorescences; Nicaraguan collections have larger fruit. This species is closely related to *P. costavenia* Griseb., which ranges from Mexico and Cuba into southern Nicaragua and is smaller in its parts.

Psychotria guadalupensis (DC.) Howard, J. Arnold Arbor. 47: 139. 1966, *sensu lato*. *Loranthus guadalupensis* DC., Prodr. 4: 294. 1830. *Viscoides pendulum* Jacq., Select. Stirp. Amer. 73, pl. 51, f. 1. 1763. *P. parasitica* Sw., Prodr. 44. 1788, nomen illeg. *P. pendula* (Jacq.) Urb., Symb. Ant. 1: 445. 1900, non *P. pendula* Hooker f., 1880. *P. peperomia* Standl., Contr. U.S. Natl. Herb. 18: 132. 1916. *P. orchidearum* Standl., J. Wash. Acad. Sci. 18: 276. 1928. Figure 60.

Small epiphytic **shrubs**, stems 0.2–1 m long, leafy stems 1–4 mm thick, glabrous, often slightly succulent; **stipules** with a short (0.5–2.5 mm) usually membranaceous translucent sheath, breaking apart and becoming thickened and whitish at the base. **Leaves** with petioles 1–6 mm long, 0.7–1.2 mm thick, glabrous; **leaf blades** 12–40 mm long, 7–22 mm broad, ovate or ovate-elliptic to obovate, apex bluntly obtuse to rounded, base obtuse to acute and slightly decurrent on petiole, drying stiffly chartaceous to subcoriaceous, gray to dark gray above, paler beneath, glabrous above and below, with 2–5 obscure 2° veins per side arising at angles of 20–40° (veins rarely prominent). **Inflorescences** terminal and solitary, 1.5–5 cm long, equally broad, few-flowered cymes to pyramidal panicles with opposite or 3-partite branching, peduncles 3–30 mm long, 0.4–1.1 mm thick, glabrous and reddish in life but often drying black, bracts 2–6 mm long, longer bracts linear, flowers in distal cymes or triads, pedicels 0.5–5 mm long. **Flowers** glabrous externally, hypanthium 1–1.2 mm long, 0.5–0.7 mm diam., calyx tube ca. 0.3 mm long, calyx lobes 0.4–1 mm long, triangular and acute, often reddish; **corolla** white or rose, salverform, tube (4–)6–8 mm long, ca. 1 mm diam., lobes 4, 1.5–2 mm long. **Fruits** 3–6 mm long, 3–5 mm diam., globose to oblate, usually with 4 pyrenes, red or purple and finally black.

Epiphytes of lower montane cloud forest formations of the Caribbean slope and continental divide, from (200–)1000 to 2300 m elevation. Flowering in January–August; fruiting in February–September and December. The species ranges from Mexico and the West Indies to the Guianas.

Psychotria guadalupensis is recognized by its epiphytic habit, unusual stipular tube, thick leaves often with obscure venation, variable inflorescences with slender peduncles, longer-tubed flowers, and four-locular ovary. The leaves drying grayish and red fruit are characters shared with subgenus *Psychotria*. The differentiation between this species and material placed under *P. pithecolobium* may be artificial, though it does separate a large portion of the specimens effectively. Costa Rican material placed here has longer corolla tubes, and leaf secondary veins are less numerous and less prominent when dried as in *P. pithecolobium*, and they arise from the midvein at a smaller angle. But there do appear to be a few intermediates, and paucity of collections makes it difficult to tell whether or not the longer corolla tubes of *P. guadalupensis* are a consistent difference. (See Howard's discussion of variation in this species, J. Arnold Arbor. 47: 139–142. 1966.)

The preceding description refers to Costa Rican material (excluding specimens assigned to *P. pithecolobium*) and differs from that given by Steyermark (1974). For example, corolla tubes are ca. 3 mm long in Venezuela (and in *P. pithecolobium*), much

shorter than usually seen in this material. It seems probable that the length of the corolla tube varies as greatly (between different plants) as do so many other characters of inflorescences and leaves in this complex.

The type of *P. orchidearum* Standl. (Standley & Valerio 50863 us) has rather small (2 cm long) leaves and small inflorescences, but the leaves are not as narrow as those in *P. maxonii*. The type of *P. peperomiae* Standl. (Pittier 3235 us from Panama) has somewhat larger leaves and is intermediate between the larger-leaved forms of this species and the type of *P. orchidearum*. The fact that all these plants share the same habitats and altitudinal range suggests that they may be part of a single polymorphic complex.

***Psychotria guapilensis* (Standl.) Hammel, Selbyana 12: 139. 1991. *Cephaelis discolor* Polak., Linnaea 41: 572. 1877, not *P. discolor* (Griseb.) Rolfe. *C. tonduzii* Krause, Bot. Jahrb. Syst. 54, Beibl. 119: 45. 1916, not *P. tonduzii* Standl. *C. nana* Standl., J. Wash. Acad. Sci. 17: 171. 1917, not *P. nana* K. Krause. *Evea guapilensis* Standl., J. Wash. Acad. Sci. 15: 104. 1925. *C. nicaraguensis* Standl., Trop. Woods 16: 46. 1928. *C. guapilensis* (Standl.) Standl., Publ. Field Columb. Mus., Bot. Ser. 4: 295. 1929. Figure 7.**

Herbs or subshrubs, 25–90 cm tall, with only 1 or 2 unbranched terete stems 2–4 mm thick, glabrous; **stipules** with basal portion 2–4 mm long, with 2 narrow triangular lobes 3–8 mm long, glabrous, often deciduous. **Leaves** with petioles 2–9.5 cm long, 0.8–2 mm thick, glabrous; **leaf blades** 9–24 cm long 3.5–10 cm wide, elliptic-oblong to oblong or elliptic-obovate, apex abruptly narrowed and acuminate, tip 6–15 mm long, base obtuse to acute and slightly decurrent on petiole, drying thinly chartaceous, dark green or brown, glabrous above and below, 2° veins 10–14/side. **Inflorescences** terminal and solitary, ca. 5–8 cm long, the dense capitula 2–3 cm long and 2.5–5 cm broad, globose to oblate, peduncles 4–40 mm long, ca. 1.5 mm thick, glabrous, with many ovate-involute bracts 6–10 × 6–10 mm, covering the outer surface and becoming dark reddish purple in color, bracteoles spatulate and with purple hairs, flowers sessile. **Flowers** glabrous externally, hypanthium ca. 1.5 mm long, calyx short-cupulate, lobes 4–5(–6), 0.8–1.5 mm long, triangular; **corolla** pale pink to purple, funnellform, tube ca. 2.5 mm long, lobes 5(–6), 1.5–2 mm long. **Fruits** ca. 10 mm long, pyriform to ellipsoid, bright blue; pyrenes 5–6 mm long and 4 mm broad, smooth to slightly angled on the dorsal surface.

Understory plants in primary rain forest formations of the Caribbean slope in Costa Rica,

from 30 to 900 m elevation. Probably flowering and fruiting throughout the year but most collections have been made in July–September. The species ranges from southeastern Nicaragua to the Chocó region of Colombia.

Psychotria guapilensis is recognized by its small herbaceous habit, long and slender petioles, dense rounded short-pedunculate terminal heads covered by many purplish to maroon bracts, and bright blue fruit. This species resembles *P. glomerulata*.

***Psychotria haematocarpa* Standl., J. Wash. Acad. Sci. 18: 274. 1928. Figure 56.**

Shrubs, 1–2.5 m tall, leafy stems 0.8–2.5 mm thick, glabrous and terete, with 2 opposite longitudinal ridges in early stages; **stipules** with a short (ca. 1 mm) truncate sheath with 2 filiform awns per side 2–5 mm long, early deciduous or the base of the stipule becoming thickened. **Leaves** with petioles 2–8(–14) mm long, ca. 1 mm thick, glabrous, drying yellowish; **leaf blades** 6–15 cm long, 2–5.5 cm broad, elliptic to oblong-elliptic, apex acuminate with tip 5–13 mm long, base attenuate or acute and decurrent on petiole, drying membranaceous or thin-chartaceous, green or grayish green, glabrous above and below, 2° veins 6–10/side and loop-connected near (1.5–3 mm) the margin. **Inflorescences** terminal (pseudoaxillary), solitary, rounded to subcapitate 4–10 mm long, to 10 mm broad, condensed cymes with 5–9 flowers, peduncles 2–5 mm long, ca. 0.5 mm thick, glabrous (or minutely puberulent), bracts 0.5–2 mm long, green, glabrous, pedicels 0–2 mm long. **Flowers** minutely papillate-puberulent externally, hypanthium ca. 1 mm long, calyx 1–2 mm long, thin, lobes 5, 0.8–1.3 mm long, triangular; **corolla** short-salverform, pale greenish or white, tube 2–2.5 mm long, ca. 0.5 mm diam. at base, lobes 0.5–1 mm long, acute. **Fruits** 5–6 mm long, 4–5 mm diam., elliptic-oblong to globose, orange and finally bright red (dark purple?) at maturity; pyrenes with 4–5 rounded ridges.

Plants of evergreen forests on the Caribbean slope from 50 to 1000 m elevation and on the Pacific slope at 500–1000 m. Flowering in July–August near La Selva; fruiting in October–February. This species ranges from Nicaragua to Colombia.

Psychotria haematocarpa is recognized by its small stipules with deciduous filiform awns, smaller green dried leaves with loop-connected secondary veins, very small condensed inflorescences, and red fruit. The calyx resembles the corolla in size and texture. This is one of only a few species of subgenus *Heteropsychotria* with red fruit, rather than blue or black. These are the smallest inflorescences of any of our species of *Psychotria* (or any of our shrubby species of Rubiaceae), and this small size may explain the paucity of collections, as the flowers and fruit are very difficult to see

among the leaves. Compare *P. brachybotrya*, with larger bracts and purple fruits, and smaller specimens of *P. hoffmannseggiana*, with larger bracts.

***Psychotria hazenii* Standl., Publ. Field Columb. Mus., Bot. Ser. 7: 96. 1930. *P. ramonensis* Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 1360. 1938. *Cephaelis chlorochlamys* Standl., loc. cit. 1278. 1938. Figure 55.**

Small shrubs, 1–2 m tall, leafy stems 0.9–3 mm thick, glabrous, drying yellowish green; **stipules** with a tubular sheath 3–7 mm long, with 2 narrow lobes 4–11 mm long and 0.5–1.5 mm broad, linear to narrowly lanceolate, glabrous. **Leaves** with petioles 6–20(–40) mm long, 0.3–0.8(–1.3) mm broad, glabrous; **leaf blades** (3.5–)6–11(–17) cm long, (1–)1.8–3.5(–4) cm broad, narrowly elliptic to elliptic-oblong, apex tapering gradually or abruptly and acuminate, tip 5–12 mm long, base acute to obtuse and slightly decurrent on petiole, drying chartaceous, dark green or brownish, glabrous above and below (or sparsely and minutely puberulent along the midvein beneath), 2° veins 11–17/side. **Inflorescences** terminal and solitary (or 3), 2–4 cm long, 1.5–2.5 cm broad, loosely condensed bracteate heads, peduncles 10–25 mm long (to 30 mm in fruit), ca. 1 mm thick and glabrous, bracts subtending the inflorescence branches 1–2 cm long, 4–7 mm broad, ovate and acute or acuminate, glabrous externally (puberulent within), chartaceous, green with bluish tips, flowers sessile within enclosing bracts. **Flowers** with hypanthium ca. 1.8 mm long and 1.4 mm diam., obovoid-oblong, white, glabrous, calyx tube ca. 0.7 mm long, lobes 5, 1–2 mm long, ca. 1.2 mm broad at the base, triangular, bluish distally; corolla not seen. **Fruits** 4–8 mm long, oblong, becoming bright blue with a spongy texture, persisting calyx 1–2 mm long.

Plants of lower montane rain forest formations along the Caribbean slope and continental divide, from 900 to 1600 m elevation. Probably flowering in May–July; fruiting in August–November. In Costa Rica this species is only known from the Caribbean slopes of the Cordillera de Tilarán and central Volcanic Highlands; it is also found in Colombia and Ecuador.

Psychotria hazenii is recognized by the tubular stipules with two long narrow awns, the slender petioles, the condensed inflorescences with large broadly imbricate bracts, and bright blue fruit. Our inability to find material with corollas suggests that flowering is nocturnal. This species resembles *P. steyermarkii* with smaller bracts and *P. pittieri*; compare also *Palicourea skotakii*.

***Psychotria hebeclada* DC., Prodr. 4: 513. 1830.** Probably including *P. molliramis* (K. Schum. & Krarse.) Steyermark., Mem. New York Bot. Gard.

23: 529. 1972. *Palicourea molliramis* K. Schum. & Krause, Bot. Jahrb. Syst., 40: 331 1910. Figure 55.

Shrubs or subshrubs, 0.7–2(–3) m tall, leafy stems 1–4 mm thick, terete, sparsely to densely puberulent or hispidulous with curved whitish hairs 0.2–0.8 mm long, often contracted beneath the node when dried; **stipules** with a short truncate tube 0–2 mm long, with 2 distal linear lobes or spines 1–3 mm long, puberulent, persisting or breaking apart. **Leaves** with petioles 4–15(–30) mm long, 0.8–1.2 mm thick, puberulent; **leaf blades** 7–20 cm long, 3–8 cm broad, elliptic to ovate-elliptic or elliptic-obovate, apex acuminate with tip 4–14 mm long, base cuneate to acute (obtus), drying membranaceous to thin-chartaceous, dark green to brownish green above, much paler beneath, sparsely puberulent or subglabrous above, puberulent beneath (especially along the midvein) with thin straight hairs 0.1–0.4 mm long, 2° veins (6–)8–14/side. **Inflorescences** terminal and solitary (or 3), (2.5–)3–6(–12) cm long, 1.5–4(–8) cm broad, narrowly pyramidal or subcylindrical open panicles of closely spaced flowers (in early stages), expanding in fruit, primary branches opposite or alternate, peduncles to 45(–60) mm long, 1–1.8 mm thick, with curved or crooked thin hairs 0.2–0.6 mm long, bracts 2–4 mm long, linear (not apparent beneath the proximal branches), pedicels 1–2(–5) mm long, often purplish, bracteoles 1–2 mm long. **Flowers** distylous, puberulent externally, hypanthium ca. 0.7 mm long and 0.5 mm diam., obconic, calyx lobes 5, 0.3–1.5 mm long, ca. 0.3 mm broad, ligulate; **corolla** white or tinged with pink or purple near the mouth, salverform, tube 2–4 mm long, 1–2 mm diam. and often constricted in middle, lobes 5, 1.5–2 mm long; anthers 1.2–1.7 mm long. **Fruits** 4–5 long, 3–5 mm diam., subglobose, with 8 or 10 sharply defined longitudinal ridges, glabrous, purple or blue-black; pyrenes 2.5–4.5 mm long, ridged.

Plants of evergreen forest formations on the Caribbean slope (20–600 m elevation) and on the Pacific slope of southern Costa Rica from 40 to 700(–1000?) m. Flowering in March–August in Costa Rica and Panama; fruiting in May–January. The species ranges from southern Mexico to Ecuador and Venezuela.

Psychotria hebeclada is recognized by its small stature, distinctive pubescence on most parts, two-awned stipules, relatively compact pyramidal to subcylindrical conical inflorescences (in early stages), flowers with well-developed calyx lobes, and small fruit finally becoming black. These plants are often found along rivers, streams, and forest edges. This species was called *P. pubescens* in the Flora of Barro Colorado Island, but *P. pubescens* is found in deciduous forests and has smaller calyx lobes. It appears that *P. hebeclada* is synonymous with *P. molliramis* as used by Steyermark (1974). Poor material of this species may resemble *P. racemosa*. *Liesner 14126 CR* with glabrous inflores-

cences, large calyx lobes, and minutely papillate-puberulent corolla tube is tentatively placed here; it may be a closely related South American species.

Psychotria hoffmannseggiana (Willd. ex Roem. & Schult.) Muell. Arg. in Mart., Fl. Bras. 6(5): 356. 1881. *P. furcata* DC., Prodr. 4: 512. 1830. *P. involucrata* sensu Standley and others, in part, not Sw. (cf. Steyermark, 1974). Figure 56.

Shrubs, 0.7–2(–4) m tall, leafy stems 0.7–4.5 mm thick, minutely (0.1–0.2 mm) glabrous to papillate-puberulent (conspicuously pubescent with thin straight hairs in a few collections); **stipules** 2–4 mm long, basal sheath 0.3–2 mm long, with 2 awns 1–3 mm long (4/node) separated by a U-shaped sinus, glabrous (pubescent), usually persisting. **Leaves** with petioles 2–8 mm long, ca. 0.5 mm thick, glabrous or with hairs 0.1–0.2(–0.5) mm long; **leaf blades** 5–14(–17) cm long, 1.5–6(–8) cm broad, ovate-elliptic, narrowly ovate, elliptic or elliptic-oblong (lanceolate), apex tapering gradually and acuminate with tip 3–14 mm long, base cuneate to acute and often decurrent on petiole, drying thinly chartaceous and usually greenish, glabrous above or puberulent only on midvein, glabrous or puberulent beneath with thin hairs 0.1–0.3 mm long (more rarely with hairs ca. 0.5 mm long), 2° veins 5–9/side. **Inflorescences** terminal and solitary, 6–25 mm long, involucre up to 6 cm broad, capitate or condensed-cymose with (3–)7–30 congested flowers, peduncles 3–20 mm long, 0.7–1.8 mm thick, pubescent or glabrescent, bracts 3–22(–35) mm long, 1–6 mm broad, linear-lanceolate, conspicuous and persisting, green to purple, flowers sessile. **Flowers** glabrous or puberulent externally, hypanthium 1–2 mm long, calyx lobes 0.2–0.8 mm long, acute to rounded; **corolla** white, funnelform, tube 2–6 mm long, 0.8–2.5 mm diam., lobes 1.3–2 mm long; **stamens** 4 or 5, anthers ca. 1 mm long. **Fruits** 3–6 mm long, 4–5 mm diam., subglobose to slightly oblong, with 8 longitudinal ridges, becoming purple to dark maroon or black, glabrous or puberulent; pyrenes ridged.

Plants of wet evergreen lowland rain forest formations, from near sea level to 700 m elevation, both on the Caribbean slope and in the General Valley and Golfo Dulce area. Flowering primarily in May–August; fruiting in July–March. The species ranges from Veracruz, Mexico, into Venezuela and Brazilian Amazonia.

Psychotria hoffmannseggiana is recognized by its persisting two-awned stipules, small capitate inflorescences with conspicuous narrow spreading or recurved persisting bracts, small flowers, and purple fruit. The subcapitate inflorescences can expand after anthesis and become slightly branched. The leaves can vary greatly in size in different plants and, while most of our plants have little pubescence, a few are densely pubescent. Plants of southwestern Costa Rica often have con-

spicuously larger bracts than specimens from other areas. This species is very similar to *P. officinalis*, which has larger branched inflorescences. The material placed here was called *P. involucrata* Sw. by Standley (1938 and in herb.), but Steyermark (1972, p. 603) showed that the Swartz name is a synonym of *P. officinalis*. Some authors may prefer to retain *P. furcata* as a distinct species, but the South American material of *P. hoffmannseggiana* includes a wide range of variation, some of which is similar to that seen in the type of *P. furcata*.

***Psychotria horizontalis* Sw., Prodr. 44. 1788. *P. longicollis* Benth. in Oerst., Vidensk. Meddel. Dansk. Naturhist. Foren. Kjobenhavn 1852: 33. 1853. Figure 65.**

Small shrubs to little treelets, 1–3 m tall, leafy stems 1–4 mm thick, glabrous (rarely minutely puberulent), usually becoming pale grayish; stipules 2–7 mm long, 1–4 mm broad at base, triangular to narrowly ovate, obtuse to acute, usually glabrous, drying reddish brown, caducous. **Leaves** with petioles 1–7(–11) mm long, 0.5–1.3 mm thick, glabrous or minutely puberulent; **leaf blades** 3–9(–13) cm long, 1.5–4.5(–6) cm broad, elliptic to ovate-elliptic, obovate, lanceolate or oblanceolate, apex acute to short-acuminate, base obtuse or slightly auriculate, drying thin-chartaceous or chartaceous, dark gray to pinkish gray or brown, glabrous above and below (rarely with thin hairs ca. 0.2 mm long on the veins beneath), 2° veins 5–9/side, occasionally with tufted hairs or pit domatia in vein axils beneath. **Inflorescences** terminal and solitary, 2–6 cm long (to 13 cm in fruit), 1.5–4(–7) cm broad, rounded open panicles with opposite or whorled branching (often globose-umbellate), peduncles 1–3(–7) cm long, 0.5–1.3 mm thick, glabrous or puberulent, with 2–5 flowers separate or closely clustered in distal cymes, pedicels 0–2 mm long, bracteoles 0.2–1 mm long. **Flowers** glabrous externally, hypanthium 0.7–1 mm long, obconic, calyx tube ca. 0.6 mm long, lobes 5, 0.5–3 mm long, linear to ligulate; **corolla** funnelliform, white, tube 2.3–3.5 mm long and 0.7–1.4 mm diam., lobes 5, ca. 1.5 mm long; anthers 0.7–1.2 mm long. **Fruits** 4–8 mm long, 3–6 mm diam., ellipsoid to ovoid, orange becoming bright or dark red; pyrenes ca. 4 × 3 mm, with 3–5 rounded ridges.

Plants of both evergreen and seasonally deciduous forest formations, most often collected from the seasonally dry Pacific slope, 20–1600 m elevation. Flowering most often in May–August; fruiting throughout the year (June–December in Costa Rica). This species ranges from Mexico to Ecuador and Brazil; it is also found in Cuba and Hispaniola.

Psychotria horizontalis is recognized by its smaller often subsessile leaves often with domatia, unlobed stipules, often umbelliform inflores-

cences, and the small flowers often with large calyx lobes. The leaves are often undulate along the edge in life and may have an arcuate submarginal vein. The red fruits and tendency for the leaves to dry grayish are characteristics of subgenus *Psychotria*. There seems to be great variation in flowers and inflorescence, with thicker puberulent peduncles being correlated with more congested flowers. The calyx lobes also seem to vary greatly in their development. Compare *P. quinqueradiata*.

***Psychotria insignis* Standl., Contr. U.S. Natl. Herb. 18: 130. 1916. Figure 66.**

Small treelets or shrubs, 2.5–6 m tall, leafy stems 3–8 mm thick, distinctly flattened in early stages, densely dark reddish brown pubescent with hairs 0.1–0.4 mm long; stipules 12–27 mm long, 4–10 mm broad, ovate-lanceolate with an acute bifid tip, awns 2–4 mm long, reddish pubescent with longer hairs along the midrib and margins, usually caducous. **Leaves** with petioles 3–5.5 cm long, 1.5–3 mm thick, densely pubescent with dark reddish brown hairs 0.1–0.5 mm long; **leaf blades** 14–30 cm long, 7–18 cm broad, broadly elliptic to broadly elliptic-ovate or elliptic-obovate, apex abruptly narrowed and acuminate with tip 7–18 mm long, rounded at the subcordate based, basal lobes often unequal, forming a sinus 0–10 mm deep, drying chartaceous, dark grayish brown or dark reddish brown, glabrous above (except the midvein), densely pubescent beneath, 2° veins 14–18/side and loop-connected in distal part of the blade. **Inflorescences** solitary and terminal, 5–9 cm long, 4–6 cm broad, short pyramidal panicles with 4 lateral branches (2 short and 2 longer) at the first node and short dense branches at the closely congested second and third nodes, peduncles 1.8–4 cm long, 1.4–2 mm thick densely pilose, bracts of the first node 6–8 mm long, flowers sessile in dense glomerules of 3–10, bracteoles 1–3 mm long. **Flowers** reddish puberulent externally, hypanthium 0.5–1 mm long, obconic, calyx tube 0.5 mm long, lobes 5, 0.5–1 mm long, triangular; **corolla** white, tube 2–3 mm long, with prominent hairs 0.3–0.4 mm long, lobes 5, ca. 1 mm long. **Fruits** 5–6 mm long, 3–4 mm diam., ellipsoid with longitudinal sulci (dried), puberulent, calyx persisting.

Plants of the wet evergreen Caribbean slope, from 20 to 400 m elevation. Flowering in September–October; fruiting in September. We have seen only three collections: *Herrera 2248* (CR) and *Grayum et al. 8929* (CR, MO) from central Costa Rica and the type (*Pittier 4410* US holotype) from San Blas, Panama.

Psychotria insignis is recognized by the densely pubescent parts, large long-petiolate leaves often subcordate at the base, and unusual compact inflorescence. The upper surface of the leaf blade is sometimes vaginate at the juncture with the pet-

iole. This species is a member of subgenus *Psychotria*. Our material differs from the type in that the 2° veins do not arise at 90° angles from the midvein and the submarginal is not as well developed. This name is used provisionally for the Costa Rican collections.

***Psychotria ipecacuanha* (Brotero) Stokes, Bot. mat. med. 1: 365. 1812. *Callicocca ipecacuanha* Brotero, Memoria sobre a Ipecacuanha do Brasil 27. 1801, Trans. Linn. Soc. London 6: 137. 1802. *Cephaelis ipecacuanha* (Brotero) A. Rich., Bull. Fac. Med. 4: 92. 1818. Figure 13.**

Herbaceous **subshrubs**, 25–50 cm tall, usually with a single erect unbranched stem, rhizomatous, leafy stems 1.5–4 mm thick, glabrous, terete; **stipules** with a short (2 mm) sheath, truncate with 4–8 setae per side 3–6 mm long, persisting. **Leaves** crowded distally, petioles 3–8 mm long, 1–2 mm thick, glabrous; **leaf blades** 7–17 cm long, 4–9 cm broad, obovate to oblong or elliptic-obovate, apex acute or short-acuminate, base cuneate to rounded-obtuse, drying membranaceous to thin-chartaceous, glabrous or minutely puberulent above and below, 2° veins 5–7/side. **Inflorescences** terminal or axillary, solitary, capitulae to 2 cm long and 1–3 cm broad, subglobose, peduncles 1–4 cm long, deflexed, involucre bracts 5–10 mm long, ovate, acute, flowers sessile. **Flowers** distylous, glabrous externally, hypanthium ca. 2 mm long, ellipsoid, calyx teeth 5, ca. 0.5 mm long; **corolla** funnelform, white, tube 3–4 mm long, cylindrical, lobes 5, 1.5–2.5 mm long; **stamens** 5, anthers ca. 1.6 mm long. **Fruits** ca. 10 mm long, becoming red then black; pyrenes 6–7 mm long, ridged.

Plants of the lowland Caribbean rain forest formations (0–600 m elevation), and probably the result of introduction for cultivation in Central America. The species ranges from southeastern Nicaragua to the Amazon basin of Brazil.

Psychotria ipecacuanha is recognized by its short unbranched rhizomatous habit, unusual fimbriate stipules, leaves with broad blades and short petioles, small involucre heads, and red to black fruit. The roots and rhizomes are the source of the alkaloid emetin and are used in folk medicine or cultivated for pharmaceutical use as ipecac. The species is referred to as “ipecac” and *raicilla* or *ipecacuana*.

***Psychotria jimenezii* Standl., J. Wash. Acad. Sci. 15: 288. 1925. *P. wendlandiana* Oerst. ex Standl., loc. cit. 18: 9. 1928. Figure 63.**

Shrubs and small treelets, 2–5(–7) m tall, to 15 cm dbh, leafy stems 1.2–4.5 mm thick, pubescent with as-

cending reddish hairs ca. 0.3 mm long (rarely glabrous), terete; **stipules** 5–12 mm long, 2–5 mm broad at the base, triangular to ovate, acute to acuminate (or shortly bifid), puberulent, margins ciliate, drying reddish brown. **Leaves** with petioles variable among plants, 0–20(–35) mm long, 0.8–1.5 mm thick, hirsutulous to papillate-puberulent; **leaf blades** 6–16 cm long, 1.7–5 cm broad, oblanceolate to narrowly obovate or narrowly elliptic-oblong, apex acute to acuminate with tip 3–10 mm long, base gradually narrowed and cuneate or rounded-auriculate, drying membranaceous to thin-chartaceous, dark brown or almost black above, glabrous above, with short (0.1–0.2 mm) reddish hairs on the veins beneath, 2° veins 8–12/side. **Inflorescences** terminal and solitary, 4–10 cm long, 3–5 cm broad, open pyramidal panicles, peduncles 15–50 mm long, ca. 1 mm thick, yellowish green in life, densely reddish brown hirsutulous when dried, first node with 4 branches (2 long and 2 short), bracts 2–6 mm long, triangular, flowers subsessile in crowded distal clusters of 3–8, bracteoles 0.5–1 mm long. **Flowers** usually glabrous externally, hypanthium ca. 0.7 mm long, obconic, calyx ca. 0.5 mm long, calyx lobes obscure; **corolla** tubular, cream white to yellowish or greenish yellow, tube 1.5–2.5 mm long and 1.4 mm diam., lobes 5, ca. 1.2 mm long, 0.9 mm broad at base; **stamens** 5, anthers 0.7 mm long. **Fruits** 4–6 mm long, 4–5 mm diam., subglobose, bright red; pyrenes with 4–5 rounded longitudinal ridges.

Understory plants of evergreen lower montane cloud forest formations along the Caribbean slope and continental divide, from (200–)400 to 1600 m elevation. Flowering in January–June; fruiting in February–April, August–October, and December. The species is found in the Cordilleras de Guanacaste and Tilarán and on the Caribbean side of the Meseta Central in central and north-central Costa Rica.

Psychotria jimenezii is recognized by its reddish pubescence (sometimes glabrous), usually oblanceolate leaves, triangular stipules acute to acuminate, inflorescences with four branches at the first node and second node (two short basal and two longer ascending branches), and small glabrous flowers. The tendency of the leaves to dry grayish and the fruit becoming red are characteristics of the subgenus *Psychotria*. The length of petioles and shape of the leaf (especially the base) can differ greatly in different collections of this species. The narrowed lamina base is subauriculate in the type of *P. wendlandii* (Wendland 781 us). Compare *P. horizontalis*, *P. orosiana*, and *P. laselvensis*.

***Psychotria lamarinensis* C. Hamilton, Phytologia 64: 227. 1988. Figure 66.**

Shrubs, ca. 2 m tall, leafy stems 1.7–4.5 mm thick, glabrous, grayish, terete; **stipules** 8–12(–20) mm long, 6–

12 mm broad, broadly ovate, apex obtuse, reddish brown, glabrous, caducous. **Leaves** with petioles 2–8 mm long, 1.4–2.7 mm thick, glabrous, slightly sulcate above; **leaf blades** 13–22 cm long, 5–13 cm broad, elliptic to broadly elliptic or elliptic-obovate, apex acute or short-acuminate with tip ca. 5 mm long, base obtuse to cuneate or slightly truncated (rounded), drying chartaceous, grayish or reddish brown, 2° veins 8–11/side, minute pit domatia sometimes present in the vein axils. **Inflorescences** terminal or pseudoaxillary, 2–5, 1.5–3 cm long, to 2 cm broad, condensed globose panicles of cymes with short lateral branches (or appearing umbellate), peduncles 4–20 mm long, 0.8–1.2 mm thick, glabrous, dark red, usually with 4 subequal branches at first node, bracts 0.2–2 mm long, triangular, bracteoles not apparent, pedicels 0.5–1.5 mm long. **Flowers** glabrous externally, calyx tube ca. 0.5 mm long, cupulate, truncate or with very short teeth; **corolla** tubular, white, tube 2.5–3 mm long and 1 mm diam., lobes 5, 1–2 mm long and 1 mm broad, with a linear (1.5 mm) extension from near the apex; **stamens** 5, anthers ca. 0.7 mm long. **Fruits** 7–8 mm long, 4–5 mm diam., oblong-ellipsoid; pyrenes smooth.

Plants of deeply shaded sites in evergreen rain forest formations on the Caribbean slope, at 20–500 m elevation. Flowering in March–May; fruiting in November. This endemic species ranges from Canalete (Alajuela) to Cahuita (Limón).

Psychotria lamarinensis is recognized by its larger broad glabrous short-petiolate leaves (cuneate basally but slightly rounded at the petiole), small short-branched globose panicles, and broadly ovate stipules. The leaves drying grayish or reddish brown are characteristic of species in subgenus *Psychotria*. The extensions on the corolla lobes are separate in bud. This species is closely related to *P. quinquerradiata*, but *P. lamarinensis* has shorter corolla tubes and larger leaves with the veins diverging at angles of 70–80°.

Psychotria laselvensis C. Hamilton, *Phytologia* 64: 228. 1988. Figure 61.

Shrubs, 1.2–4 m tall, leafy stems 1.3–3 mm thick, erect, glabrous, bark smooth; **stipules** 2–4(–6) mm long, 1–3 mm broad, triangular to ovate, glabrous or puberulent on the midrib externally, caducous. **Leaves** sessile or with petioles 1–7 mm long, 0.4–0.8 mm thick, glabrous; **leaf blades** 5–13(–16) cm long, 1.5–4(–6) cm broad, elliptic to narrowly elliptic-oblong or elliptic-lanceolate, apex acute or short-acuminate with tip to 1 cm long, base acute to cuneate and often slightly auriculate at the petiole, drying thin-chartaceous, dark grayish above, glabrous above and below, 2° veins 7–10/side, pit domatia often present in distal vein axils beneath. **Inflorescences** terminal and solitary, 6–15 cm long, 4–7 cm broad, open pyramidal, panicles with thin opposite branches, peduncles 4–9 cm long, 0.4–0.7 mm thick, glabrous, with 2 or 4 lateral branches at the first node, bracts 0.5–1.5(–3?) mm long, flowers often in distal pairs or triads, pedicels

ca. 0.5 mm long, bracteoles ca. 0.5 mm long. **Flowers** distylous, glabrous externally, hypanthium ca. 0.7 mm long, obconic, calyx lobes poorly developed (to 0.2 mm long); **corolla** narrowly funnelform, white or pale yellow, tube 1.5–3 mm long, 1–2 mm diam., lobes 5, 1.5–2 mm long; anthers 1–1.2 mm long. **Fruits** 4–5 mm diam., globose, red; pyrenes with 4–5 rounded ridges.

Plants of lowland Caribbean rain forest understory, at 50–300 m elevation on the Caribbean slope. Flowering in February–June (mostly May); fruiting in July. The species is only known from the La Selva research station and nearby areas, Heredia, and northern Limón provinces.

Psychotria laselvensis is recognized by its smaller elliptic to oblanceolate leaves, larger inflorescences with very thin open spreading branches, and pedicellate flowers. The veins are often flattened and expanded at the vein axils and form pit domatia distally. The leaves drying grayish and the red fruit are characteristics of subgenus *Psychotria*. This species resembles *P. marginata* with more acute leaf bases and is closely related to *P. graciliflora* and *P. orosiana*.

Psychotria limonensis K. Krause, *Bot. Jahrb.* 54, Beibl. 119: 43. 1916. Figure 64.

Shrubs, subshrubs, or small trees, 0.6–2(–6) m tall, leafy stems 2–6 mm thick, glabrous or sparsely puberulent, drying reddish to pale gray or dark; **stipules** 5–12 mm long, 3–6 mm broad, triangular to ovate, rounded to acute, entire or shortly bifid, glabrous, drying reddish brown, caducous. **Leaves** with petioles 1.2–6 cm long, 0.7–3 mm thick, glabrous; **leaf blades** 11–22(–28) cm long, 5–12(–15) cm broad, ovate-elliptic to elliptic-oblong or broadly elliptic, apex acute to short- or long-acuminate with tip 5–20 mm long, base obtuse to acute (occasionally slightly decurrent on petiole), drying thin to stiffly chartaceous, gray to dark reddish brown, glabrous above and below, 2° veins (7–)10–19/side and distally loop-connected to form a submarginal vein. **Inflorescences** terminal (pseudoaxillary), solitary of 3, 3–9 cm long, 5–11 cm broad, broad panicles with opposite or whorled branches, peduncles 1–4 cm long, 1.2–2.5 mm thick, glabrous and reddish brown, bracts 0.5–1.2 mm long, triangular, flowers in congested cymes of 3–6, pedicels 0–1.5 mm long. **Flowers** glabrous externally, hypanthium ca. 0.5 mm long, obconic, calyx tube ca. 0.4 mm long, lobes 0.2–0.5 mm high, obtuse; **corolla** funnel-form to rotate, white, tube 2–2.6 mm long and 1–1.7 mm diam., lobes (4–)5(–6), 1.2–1.5 mm long, triangular; **stamens** (4–)5(–6), anthers 0.8–1 mm long. **Fruits** 4–5 mm long, 3–4 mm diam., ellipsoid, bright red; pyrenes with ca. 5 longitudinal ridges.

Plants of evergreen lowland rain forest formations on both the Caribbean and Pacific slopes, from near sea level to 200 m elevation (to 700 or

rarely 1700 m elsewhere). Probably flowering and fruiting throughout the year (fruiting primarily in June–January in Costa Rica). The species ranges from southern Mexico and Belize to Panama and Colombia.

Psychotria limonensis is recognized by its large leaves with many secondary veins and arcuate submarginal vein, usual lack of pubescence, unlobed stipules, small flowers with four to six corolla lobes, and small fruit. The red fruit and tendency for leaves to dry gray or pinkish are characteristics of subgenus *Psychotria*. The secondary veins arise at almost 90° angles from the midvein. This species can be mistaken for specimens of *P. panamensis* var. *compressicaulis* with larger leaves and calyptate stipules. It is also similar to *P. mexiae* with longer corollas and acute buds.

Psychotria longipedunculoides C. M. Taylor, nom. nov. *P. longipedunculata* Dwyer, Ann. Missouri Bot. Gard. 67: 389. 1980, non *P. longepedunculata* (Gardn.) Muell. Arg. in Mart.

Herbaceous **subshrubs**, 0.5–1.2 m tall, usually unbranched, leafy stems 1.7–6 mm thick, semisucculent, glabrous or minutely papillate-puberulent; **stipules** 6–8 mm long, 6–8 mm broad, broadly ovate, margin irregular or roughly 2-lobed, thin and translucent, deciduous or persisting. **Leaves** with petioles 14–33 mm long, 0.8–1.5 mm thick (dried), glabrous; **leaf blades** 12–18 cm long, 5–7(–9) cm broad, elliptic to elliptic-oblong or elliptic-obovate, apex acute or acuminate with tip 5–10 mm long, gradually narrowed to the acute base and slightly decurrent on petiole, drying membranaceous to thin-chartaceous, pale olive gray above, 2° veins 12–15/side, an arcuate submarginal vein present. **Inflorescences** solitary and axillary from distal nodes, 12–16 cm long, 1.5–3 cm broad, congested pyramidal panicles to subcapitate, flowering portion 1.2–3 cm long, peduncles 10–14 cm long, 0.9–1.4 mm thick, glabrous, bracts 1–6(–12) mm long, linear-subulate, flowers sessile or subsessile. **Flowers** glabrous externally, hypanthium ca. 0.5 mm long, ellipsoid, calyx lobes 5, ca. 1.5 mm long; **corolla** to 2.5 mm long, funnellform, greenish white, lobes 5, **stamens** 5; anthers ca. 0.8 mm long. **Fruits** 4–6.5 mm long, ca. 3 mm diam., oblong-obovoid; pyrenes with 4–5 rounded ridges.

Recently collected on the Caribbean slope of the Talamanca mountains at ca. 700 m elevation near the border with Panama (*Herrera 3255* CR, MO, USJ). Flowering and fruiting in July. This species is only known from eastern Costa Rica, western Panama, and Chocó, Colombia.

Psychotria longipedunculoides is recognized by the single-stemmed semisucculent habit, glabrous

parts, solitary axillary inflorescences with small flower clusters on a long peduncle, and membranaceous ovate stipules. Similar in habit to *P. macrophylla* but differing by linear bracts, congested flowers, and stipules.

Psychotria luxurians Rusby, Mem. Torrey Bot. Club 6: 50. 1896. *P. berteriana* subsp. *luxurians* (Rusby) Steyerf., Mem. New York Bot. Gard. 22: 534. 1972. Figure 57.

Small **trees** or shrubs, 2–8(–12) m tall, leafy stems 2.5–7 mm thick, glabrous or minutely (0.05 mm) papillate-puberulent, terete; **stipules** 3–6(–9) mm long, to 6 mm broad, broadly ovate rounded to obtuse, splitting in age or with a short (1 mm) sinus, usually glabrous, deciduous. **Leaves** with petioles 5–35 mm long, 1.3–3 mm thick, glabrous or minutely papillate-puberulent; **leaf blades** 12–26(–32) cm long, 5–11(–13) cm broad, elliptic-oblong to elliptic or oblong, apex acuminate with a narrowed tip 4–15 mm long, base obtuse to cuneate (acute) base, drying chartaceous, dark green or brown above (distinctly paler beneath), glabrous above and below or minutely papillate-puberulent beneath, 2° veins 8–14/side. **Inflorescences** terminal, solitary or 3, (7–)12–26 cm long, 8–20 cm broad, pyramidal open panicles with mostly opposite branching, peduncles 2–8 cm long, 1.2–6 mm thick, minutely papillate-puberulent, bracts of primary branches 1–8(–12) mm long and ca. 1 mm broad, triangular to elliptic, flowers congested in cymose clusters of 3–10, bracteoles 1.5–3 mm long, elliptic, pedicels 0–2 mm long. **Flowers** glabrous externally, hypanthium 0.7–1.3 mm long, obconic, calyx lobes 0.2–0.5(–0.8) mm long, broadly obtuse; **corolla** short-funnelform, white, greenish white or yellowish, tube 2–4 mm long and 1.5–2 mm diam., lobes 5, 1–1.7 mm long and 0.7–1 mm broad, obtuse or rounded. **Fruits** 3–5 mm long and 3–6 mm diam., oblong or globose, blue, blue-black, or purple; pyrenes 3 mm long, with 4–5 dorsal ridges.

Plants in open secondary growth and light gaps in evergreen rain forest formations of the Caribbean slopes and lowlands, 20–1000 m elevation. Flowering primarily in March–July in Costa Rica; fruiting in July–November. This species ranges from southern Nicaragua to Bolivia.

Psychotria luxurians is recognized by its large essentially glabrous leaves usually drying greenish, the short and broad stipules that are entire or with two very short rounded lobes, large minutely papillate-puberulent inflorescences with many small elliptic bracts, numerous small flowers, and small blue fruit. Ants may live within the stems of this species (*Beach 1480* CR). Note that the persisting bracts subtending the flowers can be mistaken for calyx lobes. This species can be confused with *P. angustiflora* and *P. berteriana*, but those species do not have their flowers surrounded by as many

conspicuous bracteoles, and the flowers differ. Steyermark (1972) treated this as a variety of *P. berteriana* with larger bracts, but the stipule morphology is different in the two. *Psychotria tapan-tiensis* of higher elevations is closely related with larger bracteoles, corollas, and fruits.

Psychotria macrophylla Ruiz & Pav., Fl. Peruv. 2: 56. 1799. *P. anomothyrsa* K. Schum. & J. D. Smith, Bot. Gaz. 35: 3. 1903. *P. macrophylla* var. *angustissima* Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 22: 203. 1940. *P. macrophylla* ssp. *anomothyrsa* (K. Schum. & J. D. Smith) Steyermark, Mem. New York Bot. Gard. 23: 563. 1972. Figure 12.

Herbs or subshrubs, 0.5–1.5(–2) m tall, leafy stems 3–11 mm thick, semisucculent, usually unbranched, glabrous, becoming terete; **stipules** 2–5 mm long, triangular, usually with a narrow divergent succulent slightly bilobed apex, glabrous. **Leaves** with petioles 2–8 cm long, 1.2–3 mm thick, glabrous or rarely puberulent in early stages; **leaf blades** 12–32 cm long, 4–14 cm broad, elliptic to elliptic-oblong, narrowly to broadly oblong, or lanceolate, apex acuminate with tip 8–18 mm long (rarely gradually narrowed and acute), base obtuse to acute and slightly decurrent on petiole, drying membranaceous to thin-chartaceous, dark greenish to dark brownish above, usually glabrous above and below, 2° veins 8–15/side, occasionally loop-connected near the margins. **Inflorescences** axillary, usually 1/node, 3–15 cm long (to 25 cm in fruit), 4–6 cm wide, usually open pyramidal panicles with opposite branching, peduncles 0.7–8(–12) cm long, glabrous or occasionally puberulent with hairs 0.1–0.4 mm long, bracts 0.5–2(–10) mm long, triangular, flowers solitary or in small glomerules of 2–3 along the distal axes, sessile or subsessile. **Flowers** glabrous or puberulent externally, hypanthium ca. 0.5 long, obconic, calyx ca. 0.7 mm long, lobes ca. 0.2 mm high, broadly triangular; **corolla** tubular-salverform, white, tube 2–4 mm long and 0.6–1.5 mm diam., lobes 4 or 5, 1–2 mm long; **stamens** 4–5, anthers 1.2 mm long. **Fruits** 5–7 mm long and 3–4 mm diam., oblong, white and arechymatous; pyrenes ca. 6 mm long, with 4–5 rounded ridges.

Understory plants of wet sites in evergreen forest formations, from 20 to 2200 m elevation in Costa Rica. The species appears to be more common in highland forests than in those below 500 m elevation; it is rare in sandy streamside soils at La Selva. Flowering and fruiting throughout the year (but flowering mostly in January–August). The species ranges from southern Mexico to Bolivia.

Psychotria macrophylla is recognized by its usually short stature with succulent unbranched main stems, the axillary inflorescences, small subsessile flowers on branched inflorescences, white fruit with four to five rounded ribs. This species is variable;

leaves range from narrowly lanceolate to broadly elliptic in different plants; most plants are glabrous but a few are minutely puberulent. Some dried collections have crinkled leaf margins. The arrangement of flowers on the distal branches of the inflorescence varies greatly, from open-cymose to spicate. Steyermark (1974) interpreted some of this variation in Venezuela as hybridization between *P. macrophylla* and *P. uliginosa*, but this seems doubtful and it may be simply that individual plants of *P. macrophylla* can vary greatly in the expression of a variety of morphological features. Compare *Psychotria aggregata*, with densely aggregated flowers, slightly larger calyx lobes, and pyrenes with a single dorsal ridge. See the discussions under *P. capacifolia*, *P. siggersiana*, and *P. aggregata*. This group of species was recently studied by Molly Nepokroeff (wis, 1992).

Psychotria marginata Sw., Prodr. 43. 1788. *P. nicaraguensis* Benth. in Oersted, Vidensk. Meddel. Dansk. Naturhist. Foren. Kjobenhavn 1852: 34. 1853. Figure 61.

Shrubs or treelets, (0.5–)1–3(–4) m tall, leafy stems 1.3–4 mm thick, terete, glabrous; **stipules** 5–14 mm long, to 5 mm broad, narrowly ovate and acute, glabrous, usually drying reddish brown, caducous. **Leaves** often clustered distally, petioles 4–22(–35) mm long, 1–1.8 mm thick; **leaf blades** 6–17 cm long, 2–6 cm broad, narrowly obovate to elliptic obovate, oblanceolate or elliptic-oblong, apex acute to acuminate with tip 3–10 mm long (rarely obtuse), base acute to cuneate and decurrent on petiole, drying chartaceous or stiffly chartaceous and grayish, glabrous above, glabrous beneath or minutely (0.05 mm) papillate-puberulent on the veins beneath, 2° veins 7–13/side, weakly loop-connected in the distal part of the leaf, margin thickened along the edge, usually ciliolate, midvein usually with small expanded flaps-like domatia near the vein axils beneath. **Inflorescences** terminal and solitary, 7–17 cm long, 5–12 cm broad, open pyramidal panicles with thin opposite branches diverging at 90° angles, peduncles 2–7 cm long, 0.6–1.7 mm thick, glabrous, bracts 1–3 mm long, triangular, flowers 2–6 in distal cymes, pedicels 1–3(–9) mm long. **Flowers** distylous, glabrous externally, hypanthium ca. 0.6 mm long, obconic, calyx tube ca. 0.4 mm long, lobes 0.2 mm high, broadly triangular or obscure; **corolla** short-funnelform, white or yellowish, tube 2–3 mm long, 0.7–1.3 mm diam., lobes 5, 1–1.5 mm long; anthers 0.8–1.1 mm long. **Fruits** 3.5–6 mm long, 3–6 mm diam., subglobose, red or purple; pyrene ca. 3 mm long, with 4–5 ridges.

Plants in secondary growth of evergreen forests and partly deciduous forest formations, from 10 to 800 (–1100) m elevation. Flowering and fruiting throughout the year (fruiting most often in Feb-

ruary–May in Costa Rica). At La Selva, this species flowers in the wettest part of the year: July–November. The species ranges from Mexico and the West Indies to Peru and Bolivia.

Psychotria marginata is recognized by its small stature, acute triangular stipules, usually obovate leaf blades often with pronounced domatia and ciliate margins, small flowers, and small fruit on long thin pedicels in open inflorescences. The red fruit and leaves drying grayish (less often reddish) are characteristics of subgenus *Psychotria*. Compare this species to *P. laselvensis*, which lacks ciliate leaf margins and has a shortly truncated or rounded leaf base.

***Psychotria maxonii* Standl.**, Proc. Biol. Soc. Wash. 37: 53. 1924. Figure 60.

Small epiphytic shrubs with stems 0.2–0.5(–1) m long, often pendant, leafy stems 0.6–2 mm thick, succulent, glabrous and often becoming pale grayish; stipules with united truncated membranaceous tube 1–2 mm long, glabrous, persisting and sometimes becoming thickened and pale-colored at base. Leaves subsessile or with petioles 1–3 mm long and 0.3–0.5 mm thick, glabrous; leaf blades 12–23(–28) mm long, 3–5(–6) mm broad, narrowly lanceolate to linear-lanceolate, apex tapering gradually and acute, base acute or obtuse and slightly decurrent on petiole, drying stiffly chartaceous or subcoriaceous dark gray above, glabrous above and beneath, 2° and 3° veins obscure in dried material, margins slightly revolute. Inflorescences terminal or axillary, 1/node, 2–4 cm long, 2–4 cm wide, open few-flowered 3-branched pyramidal panicles or cymes with slender opposite branches often red in color, bracts ca. 0.4 mm long, peduncles 3–12 mm long, 0.2–0.5 mm thick, glabrous, drying black, pedicels filiform, 1–5 mm long. Flowers glabrous externally, hypanthium ca. 1 mm long, obovoid to oblong, calyx ca. 0.7 mm long (including lobes), lobes 4, ca. 0.5 mm long and triangular; corolla salverform, white and often tinged with red or pink, tube 2.5–4(–6) mm long, 0.4–0.8 mm diam., lobes 4, 1–1.5 mm long, obtuse; stamens 4, anthers ca. 1 mm long. Fruits ca. 4 mm long and 4 mm diam., globose, becoming orange or red and finally black; pyrenes smooth.

Epiphytic plants in montane cloud forest formations, from 1500 to 2300 m elevation. Flowering in February–March, May, and July–August; fruiting in January–March, July, and October. The species ranges from the northern part of the Meseta Central (near San Ramón) along the Caribbean escarpment and continental divide to the highlands of western Panama.

Psychotria maxonii is recognized by the epiphytic habit, small narrow succulent leaves, small thin few-flowered inflorescences, and small flowers with slender corolla tubes. The leaves dry grayish

and the fruit become red, then black (as do species of subgenus *Psychotria*). Panamanian collections appear to have more ovate leaves than are found in Costa Rica. No other Central American species of *Psychotria* has such small and narrow leaves. This species is closely related to *P. guadalupensis* and shares the same habitats in Costa Rica with that species. It is possible that the two species are actually conspecific, with *P. maxonii* being no more than a very unusual form of *P. guadalupensis*; see the discussions under *P. guadalupensis* and *P. pithecobia*.

***Psychotria mexiae* Standl.**, Publ. Field Columb. Mus., Bot. Ser. 4: 296. 1929. *Palicourea nigrescens* M. Martens & Galeotti, Bull. Acad. Roy. Sci. Bruxelles 11(50): 136. 1844, not *Psychotria nigrescens* De Wild, 1924. *P. schippii* Standl. & Steyerl., Publ. Field Mus. Bot. Hist., Bot. Ser. 23: 24. 1943. Figure 62.

Shrubs or small trees, 2–5(–10) m tall, leafy stems 2–4 mm thick, glabrous (in Costa Rica) or sparsely puberulent; stipules 12–20(–40) mm long, 1.5–3(–5) mm broad at the base, narrowly lanceolate and sheathing the apex (as in *Ficus*), glabrous, caducous. Leaves with petioles 3–20 mm long, 1.3–2 mm broad, glabrous; leaf blades 8–16(–20) cm long, 2.5–7(–8.5) cm broad, elliptic to narrowly elliptic, apex acuminate with tip 10–17 mm long, base acute to obtuse and decurrent on petiole, drying thinly chartaceous to stiffly chartaceous, dark above, glabrous above and below (rarely with hairs along midvein beneath), 2° veins 10–13/side, domatia with small hairs often present in the vein axils beneath. Inflorescences terminal, 1–3, 3–6 cm long, 2–5 cm wide, rounded to broadly pyramidal panicles with usually 4 branches at the first node, peduncles 8–28 mm long, 1.5–2 mm thick, bracts and bracteoles not apparent, cymes of 3–8 flowers, pedicels 0.5–1 mm long. Flowers glabrous or puberulent externally, calyx tube ca. 0.3 mm long cupulate, lobes little developed; corolla funnelform, white (drying pink), tube 2.5–4.5 mm long, ca. 1 mm diam., lobes 5, 1.5–2 mm long, ca. 1 mm broad at the base; stamens 5, anthers 0.8–1 mm long. Fruits 4.5–6 mm long, 3.5–5 mm diam., ellipsoid to subglobose, becoming red; pyrenes with 4–5 ridges.

Plants of lower montane evergreen forest formations, at about 600–700 m elevation in Costa Rica. Fruiting in January (*Standley & Valerio 45770 & 46375* us). The species ranges from Mexico to the region of Tilarán in northern Costa Rica.

Psychotria mexiae is recognized by its elliptic leaves with small domatia, fused stipules forming a cap over the apex, short inflorescences, longer corolla tubes often drying pink, and spherical fruit with shallow longitudinal grooves when dried. The

leaves drying grayish and the red fruit are characteristic of subgenus *Psychotria*. This species resembles *P. tenuifolia*, *P. panamensis*, and *P. limonensis*. This species is only known in Costa Rica from the two collections cited above.

Psychotria micrantha H.B.K., Nov. gen. sp. 3: 363 (quarto), pl. 284. Nov. 1819. *P. rufescens* Roem. & Schult., Syst. Veg. 5: 192. Dec. 1819, non *P. rufescens* H.B.K. Figure 63.

Shrubs or small trees, 2–8 m tall, leafy stems 3–8 mm thick, densely hirsutulous with erect reddish brown hairs 0.3–0.7 mm long; **stipules** 9–18 mm long, 3–8 mm broad at base, triangular to narrowly ovate, with 2 narrow lanceolate acuminate lobes 1–7 mm long, reddish brown puberulent, deciduous. **Leaves** with petioles 6–26 mm long, 1.2–3 mm thick, densely hirsutulous with reddish brown hairs; **leaf blades** 12–30 cm long, 4–13 cm broad, oblong to elliptic, or narrowly elliptic-oblong, apex acute to short-acuminate with tip 5–10 mm, base obtuse to cuneate and slightly decurrent on petiole (rarely slightly auriculate), drying thin- to stiff-chartaceous, grayish to dark reddish brown, pubescent above and below with hairs 0.2–0.9 mm long, longest and most dense on the midvein beneath, 2° veins 14–22/side and loop-connected distally, 3° veins often subparallel. **Inflorescences** terminal (pseudoaxillary) and solitary (rarely 2), 5–15 cm long, to 12 cm broad, pyramidal to rounded open panicles usually with 4 closely set branches (2 longer and 2 shorter) at first node of 1° and 2° axes, peduncles 4–10 cm long, 0.8–1.5 mm thick, densely hirsutulous with reddish brown hairs 0.3–0.5 mm long, bract, 2–3 mm long, triangular, flowers sessile in distal clusters or capitulae of 3–8. **Flowers** densely puberulent externally, hypanthium and calyx 1.5–2 mm long, lobes ca. 0.2 mm long; **corolla** white, salverform, tube 1.5–2.5 mm long, 0.5–1 mm diam., lobes 5, 1.3–2 mm long; **stamens** 5, anthers 0.8–1.2 mm long. **Fruits** 3–7 mm long, 3–4 mm diam., ellipsoid to subglobose, red, hirsutulous; pyrenes with 4–5 low ridges.

Rarely collected plants of evergreen rain forest formations, from 250 to 700(–1000) m elevation in Costa Rica. Flowering in May–September in southern Central America; fruits have been collected primarily in late May–December. In Costa Rica this species has only been collected from the Zona Protectora above La Selva, the drainage area of the Río Renventazón, and the General Valley. The species ranges from Guatemala, Nicaragua, and central Costa Rica to Venezuela, Peru, and Bolivia.

Psychotria micrantha is recognized by its dense hirsutulous surfaces with reddish brown hairs, large bifid stipules, large leaves with many secondary veins, open panicle inflorescences with flowers in dense distal clusters, and small hirsutulous fruit.

The red fruit and tendency of the leaves to dry grayish or reddish brown are characteristics of the subgenus *Psychotria*. Close to *P. neilii* with leaves abruptly truncate and rounded. It may be confused with material of *P. mortoniana*.

Psychotria microbotrys Ruiz ex Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 8: 204. 1930. Figure 58.

Shrubs or small treelets, 1–3(–4) m tall, leafy stems 1.7–6 mm thick, quadrangular, glabrous; **stipules** united around the stem for 1–4 mm or apparently separate, 7–21 mm long, 2–5 mm broad at base, ovate, deeply bifid on each side with 2 prominent narrowly ovate or triangular lobes on each side (4/node), these acute and often minutely bifid, glabrous, persisting. **Leaves** with petioles 7–25(–38) mm long, 1–2.5 mm thick, glabrous, drying dark; **leaf blades** 11–27 cm long, 4–13 cm broad, ovate-elliptic, elliptic or oblong, apex short-acuminate with tip 5–13 mm long, base obtuse to acute and slightly decurrent on petiole, drying thin-chartaceous, yellowish green or brownish green, glabrous on both surfaces, 2° veins 7–12/side. **Inflorescences** terminal and solitary, 3–6 cm long, 2.5–4 cm wide (to 15 × 10 cm and purplish in fruit), pyramidal panicle with opposite or alternate branching, peduncles 2–6 cm long, 1–1.8 mm thick, glabrous, bracts 2–4 mm long, linear, branches often dichotomous or trichotomous distally, flowers alternate or in groups of 2–4, bracteoles ca. 1 mm long, pedicels 0–1 mm long. **Flowers** glabrous externally, hypanthium ca. 0.8 mm long and 0.5 mm diam., cylindrical, calyx tube 0.3–0.4 mm long, calyx lobes minute or obscure; **corolla** salverform, yellow, white, or greenish, tube 1.8–3.2 mm long, 0.4–0.8 mm diam., lobes 5, ca. 1 mm long. **Fruits** ca. 3–5 mm long and 3–5 mm broad, 8 mm diam. and spongy when fully ripe, oblate to subglobose, green to grayish blue or white, branches of the infructescence often purplish; pyrenes ca. 2.5 mm long, with 4–5 longitudinal ridges and transverse ribs.

Understory plants of evergreen forest formations; from 50 to 1000 m elevation on the Caribbean slope and lowlands, and on the Pacific slope of southern Costa Rica from 500 to 1500 m elevation. Flowering in February–March and May–July; fruiting primarily in July–January. The species ranges from Costa Rica to Peru.

Psychotria microbotrys is recognized by its larger glabrous leaves, large and deeply two-lobed (or almost separate) persisting stipules, larger inflorescences, small flowers, and small fruit becoming spongy white at maturity. The transverse ridges between the ribs on the immature dried fruit and the tendency of the distal inflorescence branches to be dichotomous with alternating flowers or flower clusters are additional distinctions. The majority of Costa Rican collections come from the

Caribbean lowlands of northern Costa Rica and from the General Valley–San Vito area of the Pacific slope. Similar to *P. deflexa*, which has much smaller stipules.

***Psychotria microdon* (DC.) Urban, Symb. Ant. 9: 539. 1928. *Rondeletia microdon* DC., Prodr. 4: 408. 1830. Figure 59.**

Shrubs, subshrubs, or small trees (sometimes clambering), 0.4–3(–5) m tall, leafy stems 1–3 mm thick, glabrous or with thin hairs ca. 0.2 mm long, greenish and becoming pale gray; **stipules** 1–2 mm long, ca. 2 mm broad, broadly triangular, obtuse or rounded, glabrous or puberulent, pale yellowish and thick in texture, often persisting. **Leaves** usually closely clustered distally, petioles 3–15(–60) mm long, 0.5–1.2 mm thick, glabrous or puberulent; **leaf blades** 4–15 cm long, 1.5–6 cm broad, obovate to elliptic-obovate, elliptic-oblancoate, elliptic, or ovate-elliptic, apex acuminate with tip 3–14 mm long, base acute to obtuse and decurrent on petiole, drying membranaceous or thin-chartaceous, green to dark brownish green above, glabrous above, glabrous or puberulent beneath with thin whitish hairs 0.2–0.4 mm long, usually with thin hairs grouped near the vein axils beneath (domatia), 2° veins 3–7/side. **Inflorescences** terminal, solitary or several, 3–10 cm long, 2–8 cm broad, open rounded panicles with opposite branching or 3 primary branches, peduncles 2–7 cm long, 0.6–1.7 mm thick, glabrous or minutely puberulent, bracts ca. 1.4 mm long, flowers in distal cymes of 2–5, pedicels 0.5–4 mm long. **Flowers** glabrous or minutely papillate-puberulent externally, hypanthium 1–1.5 mm long, obconic, calyx tube 0.8–2 mm long, 2–3 mm broad, cupulate to campanulate, lobes 5, minute; **corolla** salverform, white, tube (4–)6–10 mm long, 1–2 mm diam., lobes 5, 2–6 mm long, to 2.2 mm broad at base. **Fruits** 7–10 mm long, 5–7 mm diam., ellipsoid, becoming red-orange; pyrenes with 2–3 ridges.

Plants of forest understory and thickets in seasonally very dry and deciduous woodland formations, from near sea level to 200 m elevation (rarely to 600 m). Flowering in May–August; fruiting in July–October and January. The species ranges from Mexico and the West Indies to Venezuela and Peru.

Psychotria microdon is recognized by its deciduous forest habitat, smooth grayish stems, thin often obovate leaves clustered at the ends of branchlets, broad stiff stipules, thin but well-developed calyx tube with minute or absent lobes, and larger corollas blooming in the first half of the wet season. The leaves sometimes dry grayish green (resembling species of subgenus *Psychotria*). Specimens whose lower leaf surfaces are puberulent have been called *P. microdon* variety *meridionalis* (Steyermark, 1974), but this is a minor distinction,

not correlated with ecology or geography. This is our only species of the largely African subgenus *Tetrameræ* (Hieron) R. Petit. Compare *P. pubescens*, also of deciduous forest formations but with yellowish flowers.

***Psychotria monteverdensis* Dwyer & C. Hamilton, Phytologia 64: 230. 1988. Figure 61.**

Shrubs or small trees, 2–5 m tall, leafy stems 2.5–4 mm thick, glabrous; **stipules** with a sheath 7–15 mm long and 4–6 mm broad, triangular to ovate with 2 aristate lobes 2–4 mm long, glabrous, drying reddish brown, caducous. **Leaves** subsessile, petioles 1–5 mm long, 1.2–2.2 mm broad, glabrous, sulcate above; **leaf blades** (5–)7–16 cm long, (1–)2–4.5 cm broad, oblanceolate to narrowly elliptic, apex acute or acuminate with tip ca. 5 mm long, base cuneate and slightly rounded (auriculate) at petiole, drying stiffly chartaceous, grayish green or pinkish gray, glabrous above and below, 2° veins (5–)8–10/side and united distally by an arcuate submarginal vein. **Inflorescences** terminal and solitary, 4–10 cm long, 3–4 cm wide, open pyramidal panicles, peduncles 15–50 mm long, 2–2.5 mm thick, glabrous or pilosulous, bracts 4–8 mm long, triangular, ciliate, flowers usually in distal glomerules of 3–6, bracteoles 1–4 mm long, ovate, ciliate, pedicels 0–1.5 mm long. **Flowers** glabrous externally, hypanthium ca. 2 mm long, obconic, calyx tube ca. 1 mm long, cupular, lobes 5, 0.5–1 mm long, triangular, often ciliolate; **corolla** funnelliform, greenish yellow, tube 2–3(–5) mm long and 1–2(–3) mm diam., lobes 5, ca. 2 mm long, with keel-like appendages; **stamens** 5, anthers ca. 1.2 mm long. **Fruits** 7–8 mm long (not including the 1–2-mm-high calyx), 5–7 mm diam., ellipsoid; pyrenes 4–5-ridged.

Plants of evergreen lower montane rain forest formations, at 900–1600 m elevation. Flowering in May–July; fruiting in June–July, September, and November. This endemic species is only known from the eastern slopes of Volcán Miravalles, the Monteverde Nature Preserve, and the eastern part of the Cordillera de Talamanca.

Psychotria monteverdensis is recognized by its sheathing stipules with slender biaristate tips, subsessile and oblanceolate leaves with prominent submarginal veins (often slightly auriculate at the base), few-branched inflorescences with flowers in distal glomerules, and short thick corollas with keel-like structures on the large corolla lobes.

***Psychotria mortoniana* Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 355. 1938. Figure 54.**

Shrubs or small trees, 1.5–8(–10) m tall, leafy stems 1.3–8 mm thick, densely pubescent with straight, curved or crooked hairs 0.3–0.9(–1.5) mm long; **stipules** 6–18

mm long, to 9 mm broad near the base, narrowly ovate, bifid and often splitting into 2 acuminate lobes 2–8 mm long, pubescent, persisting. **Leaves** with petioles 10–45 mm long, 0.8–2.5 mm thick, with straight or crooked yellowish hairs 0.3–1 mm long; **leaf blades** 13–30 cm long, 5–12 cm broad, elliptic to elliptic-obovate or elliptic-oblong, apex long-acuminate with tip 11–27 mm long, obtuse to acute at the base, drying membranaceous to thin-chartaceous, dark olive green or brownish green, pubescent on the major veins above, densely pubescent beneath with pale-colored hairs (to 1.2 mm long on midvein), 2° veins (14–)17–23/side, weakly loop-connected near the margin in the distal part of the leaf. **Inflorescences** terminal and solitary, 9–16 cm long, 8–14 cm broad, open pyramidal panicles with opposite primary branching, peduncles 1–9 cm long, 1.5–3 mm thick, densely villous or hirsutulous with yellowish brown hairs, bracts subtending the proximal pair of branches 6–12 mm long and 2–3 mm broad, narrowly triangular, flowers mostly sessile in crowded distal clusters of 3–10, partly enclosed by the persisting bracteoles 6–12 × 2–3 mm. **Flowers** glabrous externally, hypanthium ca. 1 mm long, obconic, calyx ca. 0.5 mm long, lobes ovate, obtuse; **corolla** tubular, white to pale yellowish, tube 3–5 mm long and 1–1.5 mm diam., lobes 0.8–1.3 mm long and 0.5 mm broad at base, rounded. **Fruits** 3–6 mm long and 3–4 mm diam., ellipsoid, black, glabrous; pyrenes with 4–5 angles.

Plants of evergreen forest formations of the Pacific slope, from 100 to 1100 m elevation. Flowering in May and July–August; fruiting in August–September and December–January. The species is only known from southern Puntarenas province in Costa Rica and from the nearby Chiriquí Highlands in Panama.

Psychotria mortoniana is recognized by its dense pubescence, large leaves with many secondary veins large bifid stipules, larger inflorescences with flowers in dense distal clusters, and sessile fruit partly enclosed by persisting elliptic bracteoles. The rounded bracteoles and the tendency to dry dark brown are additional distinctions. This species has only been collected from the General Valley, around Golfo Dulce and near San Vito in southern Costa Rica. Specimens of this species may resemble *P. pilosa* and *P. micrantha*.

Psychotria neillii C. Hamilton & Dwyer, *Phytologia* 64: 231. 1988. Figure 63.

Shrubs, or small trees, 1–4 m tall, leafy stems 1.5–4 mm thick, hirsutulous with reddish brown hairs ca. 0.7 mm long; **stipules** 7–16 mm long, 3–5 mm broad at base, basal sheath ca. 4 mm long, apex biacuminate with narrow tips 3–5 mm long, puberulent, deciduous. **Leaves** subsessile, petioles 2–8 mm long, ca. 2 mm thick, densely puberulent, terete; **leaf blades** 8–15(–18) cm long, 3–6.5(–7.5) cm broad, obovate to elliptic-obovate or oblanceolate, apex abruptly short-acuminate with tip 3–8

mm long, base gradually narrowed and rounded-auculate or subcordate at petiole, the lamina drying thin to stiffly chartaceous, grayish or reddish brown, glabrous above, with thin reddish hairs 0.2–0.8 mm long beneath (especially along the midvein), 2° veins 8–12/side. **Inflorescences** terminal or becoming axillary, solitary, 7–13(–15) cm long, to 8 cm broad, open panicles, usually with 2 nodes bearing 2–4 lateral branches, peduncles 3–8(–10) cm long, 0.8–1.7 mm thick, with short reddish hairs, bracts ca. 4 mm long, bracteoles ca. 0.5 mm long, pedicels 0–1 mm long. **Flowers** puberulent externally, calyx tube ca. 0.3 mm long, calyx lobes ca. 0.2 mm long, triangular; **corolla** yellowish white, tube 1.5–2 mm long, ca. 1 mm diam., lobes 5, ca. 1 mm long; **stamens** 5, anthers 0.8 mm long. **Fruits** 5–7 mm long, 3.5–5 mm diam., obovoid-oblong and truncated at apex, reddish purple at maturity.

Plants of lowland Caribbean rain forest formations, from 80 to 400 m elevation. Flowering in January–February and April; fruiting in February and April–July. The species ranges from southernmost Nicaragua to southernmost Costa Rica.

Psychotria neillii is recognized by the densely hirsutulous young stems, subsessile obovate leaves rounded at the base, thin-puberulent inflorescence axes, small flowers and obovoid-oblong fruit with truncated apex. The leaves usually drying grayish and the red fruit are characteristics of subgenus *Psychotria*. This species is similar to *P. micrantha*, which has flowers and fruits in denser clusters, acute leaf bases, and larger stipules. Compare also *P. jimenezii* from higher elevations, usually glabrescent, with differing stipules and inflorescences.

Psychotria nervosa Sw., Prodr. 43. 1788. *P. undata* Jacq., Hort. Schoenbr. 3: 5, pl. 260. 1798. *P. elongata* Benth. in Oersted, Vidensk. Meddel. Dansk. Naturhist. Foren. Kjøbenhavn 1852: 32. 1853. *P. quinifolia* Dwyer, Ann. Missouri Bot. Gard. 53: 108. 1966. Figure 63.

Shrubs or rarely small treelets, 0.5–1.5(–3) m tall, leafy stems 0.9–4 mm thick, sparsely to densely pubescent with usually crooked reddish hairs 0.3–1 mm long; **stipules** 3–9(–11) mm long, 2–4(–6) mm broad, narrowly to broadly ovate (sometimes tubular near the base), rounded distally to obtuse, drying reddish brown, sparsely to densely pubescent, caducous. **Leaves** usually clustered at the tips of branchlets, petioles 2–22 mm long, 0.7–1.5 mm thick, usually pubescent, with adaxial margins continuous with the leaf margins; **leaf blades** 7–13(–19) cm long, 2–5(–7) cm broad, elliptic-obovate to elliptic or obovate, apex acute to acuminate with tip 3–10 mm long, base acute and often long-decurrent on petiole, drying thin- to stiff-chartaceous, grayish to pinkish gray or reddish brown, sparsely puberulent above, sparsely to densely pubescent beneath (especially on the midvein) with hairs

0.3–0.7 mm long, 2° veins 7–13/side and often weakly loop-connected near the margin. **Inflorescences** terminal (pseudoaxillary), solitary or several, 1–5 cm long, to 5 cm broad, cymose or trichotomous, peduncle 5–18 mm long, hirsutulous with reddish brown hairs, bracts to 0.5 mm long, flowers closely clustered and sessile or subsessile in distal cymes of 3–5. **Flowers** with hypanthium ca. 0.5 mm long, densely hirsutulous, calyx 0.5–1 mm long, calyx lobes 0.2 mm long or obscure; **corolla** funnelform, white, sparsely puberulent externally, tube 2–4 mm long, 1–2 mm diam., lobes 5(–6), 1–2 mm long; **stamens** 5, anthers 0.7–1 mm long. **Fruits** 6–8 mm long, 2.5–4 mm diam. ellipsoid to oblong sparsely hirsute with thin erect hairs, becoming red-orange or red; pyrenes with 3–5 ridges.

Plants of seasonally very dry and deciduous woodland formations, semideciduous forest, and (less often) evergreen forest formations, from 20 to 800 m elevation (to 1200 near San Vito). Flowering and fruiting throughout the year (flowering primarily in June–July, and fruiting in July–January in Costa Rica). The species ranges from Mexico and the West Indies to northern South America.

Psychotria nervosa is recognized by its deciduous woodland habitat (less often in evergreen forests in Costa Rica), reddish pubescence on most parts, rounded to globose terminal buds, thin usually ovate stipules, leaves narrowed to the base and decurrent on the petiole, and small inflorescences. The red fruit and tendency for the foliage to dry reddish brown are characteristics of subgenus *Psychotria*. This species is sometimes confused with *P. pubescens*, but that species has persisting two-lobed stipules.

***Psychotria officinalis* (Aubl.) Raeuschel ex Sandw.,** Kew Bull. 1931: 473. 1931. *Nonatelia officinalis* Aubl., Hist. pl. Guiane 1: 182, pl. 70, f. 1. 1775. *P. involucrata* Sw., Fl. Ind. Occ. 1: 413. 1797. Figure 59.

Shrubs or small treelets, 1–3(–8) m tall, trunks to ca. 2.5 cm diam., leafy stems 1.3–5 mm thick, glabrous or rarely minutely (0.2 mm) puberulent, terete; **stipules** 2–4(–6) mm long, 3–6 mm broad, often with a short (0.5–1 mm) cupular sheath, truncated distally and with 2 narrow lobes 1–3 mm long separated by a U-shaped sinus 1–2 mm wide, usually glabrous and persisting. **Leaves** with petioles 4–12(–20) mm long, 1.2–2 mm thick, usually glabrous, slightly sulcate above with 2 adaxial ridges; **leaf blades** 7–17(–25) cm long, 3–8(–12) cm broad, ovate-elliptic to ovate-oblong, lanceolate-elliptic or elliptic, apex acute to acuminate with tip 6–20 mm long, base obtuse to acute and slightly decurrent on petiole, drying thin-chartaceous, dark yellowish green to olive green, glabrous above, glabrous below or minutely (0.1

mm) puberulent along major veins, 2° veins 6–10/side and strongly ascending. **Inflorescences** terminal and solitary (rarely 2), (1.5–)2–6 cm long (to 10 cm in fruit), 2–4 cm broad, panicles with 2–4 opposing pairs of short lateral branches or sometimes subcapitate, peduncles 1–4(–5) cm long, ca. 1.4 mm thick, sparsely and minutely puberulent, flowers sessile in distal clusters of 3–8, subtended by bracts 2–8 mm long and 1–3 mm broad, lanceolate to elliptic, yellow becoming purplish in fruit. **Flowers** distylous, usually sparsely puberulent with thin whitish hairs 0.1–0.2 mm long externally, hypanthium 0.5–0.9 mm long (obscured by the bracts), calyx cup ca. 0.4 mm high, lobes 0.2 mm high or obscure; **corolla** funnelform, white or yellow, tube 2–5 mm long, 1.2–2 mm diam., lobes 5, 1–2 mm long and 1.2 mm broad at base; anthers ca. 1.5 mm long. **Fruits** 4–6 mm long, 4–5 mm diam., becoming subglobose, becoming dark purple or black, infructescence and pedicels often purplish; pyrenes 2–3 mm long, with 4–5 ridges.

Plants of shaded understory in evergreen forest formations, 50–1200 m elevation. At La Selva it is usually found on slopes and ridges in forest understory. Flowering and fruiting throughout the year (flowering primarily in March–July). The species ranges from southern Mexico and the West Indies to northeastern Brazil and the Guianas.

Psychotria officinalis is recognized by the small terminal-branched inflorescences with prominent bracts subtending the distal flower clusters, the minutely and sparsely puberulent little flowers, the short two-lobed stipules, and black or purple fruit. The primary inflorescence branches are not subtended by bracts, but the distal flower groups are sometimes subtended by a larger central bract and two lateral braces adnate near the base to form a small involucre. The conspicuous bracts and tendency of the inflorescence branches to become purplish is reminiscent of the closely related *P. hoffmannseggiana* with condensed inflorescences. Specimens in early stages of flowering may be mistaken for that species as well as *P. brachybotrya* and *P. platypoda*.

This is one of our most common species of Rubiaceae, but its range in Costa Rica appears to be restricted to the Caribbean lowlands and lower Caribbean escarpment (to 900 m), the General Valley (ca. 500–900 m), and the San Vito area (to 1200 m). Except for the San Vito area (near the Panama border), the species has not been collected above 900 m in Costa Rica. The name *P. involucrata* has been applied to material of this species and *P. hoffmannseggiana* in the past. Breeding behavior was studied by Bawa and Beach (1983).

***Psychotria orosiana* Standl.,** J. Wash. Acad. Sci. 15: 288. 1925. Figure 61.

Shrubs 1–2(–3) m tall, leafy branchlets 0.7–4 mm thick, glabrous, drying gray or blackened; **stipules** 2–5 mm long, to 3 mm broad at base, narrowly to broadly triangular and with 2 closely set minutely reddish brown puberulent awns with blunt tips, caducous. **Leaves** clustered distally, sessile or subsessile, petioles 0–5 mm long, glabrous; **leaf blades** 4–9(–13) cm long, 1.5–3(–5) cm broad, elliptic-obovate, oblong-obovate to elliptic or oblanceolate, apex obtuse to acute or short-acuminate with tip 3–10 mm long, base acute to cuneate (rarely slightly truncated) and long-decurrent on petiole, drying membranaceous to thin-chartaceous, dark gray or blackish above, glabrous above and below, 2° veins 5–7/side, pit domatia often present in the vein axils beneath. **Inflorescences** terminal and solitary, 3–7(–10) cm long, 3–6 cm broad, open panicles with few slender opposite primary and secondary branches, peduncles 1–4.5(–7) cm long, ca. 0.5 mm thick, glabrous, bracts ca. 1 mm long, triangular, flowers in distal cymes of 3–6, pedicels 0–3 mm long, bracteoles ca. 0.5 mm long. **Flowers** glabrous externally, hypanthium ca. 1 mm long, obconic, calyx ca. 0.5 mm long, lobes to 0.3 mm long, triangular or obscure; **corolla** funnelform, white or yellow-white, tube 2–5 mm long, 1–1.5 mm diam., lobes 5, 1–1.4 mm long; **stamens** 5, anthers 0.7–1 mm long. **Fruits** 4–7 mm long and 4–6 mm diam., ellipsoid, smooth, drying black; pyrenes with 4–5 ridges.

Plants of evergreen montane forest formations in the central cordilleras, from (400–)1200 to 1900 m elevation. Flowering in January–July and September; fruiting in March, June, and August–October. In Costa Rica this species has only been collected from near Monteverde, San Ramón, Carpintera, and Tablazo and the southern drainage of the upper Río Reventazón. This species is only known from Costa Rica and western Panama.

Psychotria orosiana is recognized by its smaller obovate leaf blades usually decurrent at the base and often without a well-developed petiole (and often drying blackish gray above), domatia (when present), montane habitat, glabrous parts except stipules with two puberulent awns, and open slender-branched inflorescences with small flowers. The tendency of leaves to turn grayish and the red fruit are characteristics of subgenus *Psychotria*. This species resembles *P. graciliflora* but has larger inflorescences and longer corolla tubes. It also resembles *P. laselvensis* (q.v.).

Psychotria panamensis Standl., Contr. U.S. Natl. Herb. 18: 132. 1916. *P. magna* Standl., loc. cit. 131. 1916. *P. compressicaulis* K. Krause, Bot. Jahrb. Syst. 54, Beibl. 119: 44. 1916. *P. grandistipula* Standl., J. Wash. Acad. Sci. 18: 276. 1928, non *P. grandistipula* Merrill, 1923. *P. molinae* Standl., Ceiba 1: 46. 1950. Figures 62 and 64.

Small trees or shrubs, 2–12(–20?) m tall, trunks 4–20 cm diam., leafy stems 1.5–8 mm thick, glabrous or minutely (0.1 mm) puberulent in early stages; **stipules** 5–25 mm long, to 55(–80) mm when subtending inflorescences, 2–7(–12) mm broad, lanceolate with a long narrowed apex often curved back in late stages, united to form a cap over the apex and splitting on 1 or 2 sides, glabrous (ciliolate along the interior edge), greenish white to yellowish in life but drying dark reddish brown, caducous. **Leaves** differing greatly in size in the highland and lowland varieties (see below), with petioles 5–53 mm long, 1–2.7 mm thick, glabrous or very minutely (0.05 mm) puberulent, opposing petioles often unequal; **leaf blades** 6–28 cm long, 2–16 cm broad, elliptic to ovate-elliptic or obovate-elliptic, apex acuminate (acute, obtuse) with tip 3–15 mm long, base gradually narrowed and acute or obtuse, slightly decurrent on petiole, drying chartaceous, dark grayish to dark reddish brown, glabrous above, glabrous or minutely (0.05 mm) papillate-puberulent beneath, 2° veins (5–)8–19/side (sometimes loop-connected near the margin). **Inflorescences** terminal and solitary (or 3), 5–10 cm long (to 16 cm in fruit), 5–10 cm wide, open pyramidal panicles branches, peduncles 5–35(–50) mm long, 1–2.5 mm thick, usually glabrous, bracts ca. 1 mm long and 2–3 mm broad, cymes of 2–5 flowers, pedicels 0–1(–4) mm long and puberulent. **Flowers** monomorphic and short-styled, glabrous externally, hypanthium 0.7–1.5 mm long, calyx 0.5–0.8 mm long and 2 mm diam., calyx lobes not developed or obscure; **corolla** white or greenish yellow, tube 2–3 mm long and 1.5–2 mm diam., lobes 5, 1–3 mm long and triangular, rotate or reflexed; **stamens** 5, anthers 0.7–1 mm long. **Fruits** 5–9 mm long and 4–7 mm diam., ellipsoid to subglobose, yellowish becoming red; pyrene ca. 7 mm long, with 3–5 ridges.

Plants usually found in high rainfall formations, 20–2100 m elevation. Flowering in March–October in Costa Rica and Panama (flowering primarily in July–August at La Selva); fruiting throughout the year. The species ranges from Mexico to Colombia.

Psychotria panamensis is recognized by its habit (usually a small tree), the often long and unequal petioles, large caducous stipules, that enclose the shoot apex as in *Ficus*, and the flowers with short thick perianth tube and subentire calyx. The numerous secondary veins are usually quite straight and not as arcuate as in other species. The tendency of foliage to dry grayish or dark reddish brown and the fruit turning red are characteristics of subgenus *Psychotria*. A majority of Costa Rican collections are from higher-elevation cloud forests and belong to variety *panamensis* with smaller narrower leaves than the lowland plants (see below). This species is closely related to *P. sarapiquensis*, which shares the same type of stipule but has narrower leaves with fewer secondary veins, and to *P. cocosensis*, with larger flowers. Compare also *P. nervosa* with enlarged stipules below the

inflorescences and lacking the acute terminal buds of *P. panamensis*.

Hamilton distinguished four varieties, of which three are found in southern Central America: variety *compressicaulis* (K. Krause) C. Hamilton, va-

riety *magna* (Standl.) C. Hamilton, and variety *panamensis*. The following key separates the three varieties. However, it is possible that the two varieties found in Costa Rica will prove to be two closely related but distinct species.

- 1a. Dried fruits 4.5–5 mm long, 3.5–4 mm diam.; Caribbean lowlands of eastern Panama var. *magna*
- 1b. Dried fruits 5.5–8 mm long, 4.5–9 mm diam. 2
- 2a. Leaf blades 15–28 cm long, 5.5–15 cm broad, with 12–19 secondary veins on each side; fruit 5.5–7 mm long; lowland Caribbean Nicaragua to Panama var. *compressicaulis*
- 2b. Leaf blades usually 9–15 cm long, 4–6 cm broad, with 8–16 secondary veins on each side; fruit usually 7–9 mm long; Mexico to Panama, mostly above 500 m elevation var. *panamensis*

***Psychotria parvifolia* Benth.** in Oerst., Vidensk. Meddel. Dansk Naturhist. Foren. Kjobenhavn 1852: 35. 1853. Figure 60.

Shrubs or small treelets, 0.7–3(–5?) m tall, leafy branchlets 0.5–3 mm thick, at first densely puberulent with minute (0.1–0.2 mm) reddish brown hairs, soon glabrescent; **stipules** 2–6 mm long, 1–2 mm broad at the base, united and lanceolate or oblong with acute tip, splitting down 1 side, minutely puberulent and drying reddish brown, caducous. **Leaves** clustered at the ends of branchlets, petioles 2–14 mm long, 0.3–0.6 mm thick, puberulent with minute reddish brown hairs; **leaf blades** 1–3.5(–5) cm long, 0.5–1.4(–2) cm broad, elliptic to ovate-elliptic or rhombic, apex acute or obtuse, base acute and slightly decurrent on petiole, drying membranaceous to thin-chartaceous, dark grayish green or dark brown above, glabrous above, glabrous beneath except for the minute (0.1 mm) reddish brown hairs along the midvein, 2° veins 2–5/side and obscurely loop-connected near the margin. **Inflorescences** terminal or pseudoaxillary, 1–3/ node, 5–20 mm long, to 8 mm broad, cymose or 3-branched, peduncles 2–8 mm long, 0.4–0.8 mm thick, minutely reddish brown puberulent, bracts ca. 1 mm long and glabrous, flowers often in triads, pedicels 0–3 mm long. **Flowers** with hypanthium 0.7–1 mm long, obconic or turbinate and minutely (0.05 mm) papillate-puberulent or glabrous, calyx 0.3–0.5 mm long, with minute lobes or subtire distally; **corolla** white, salverform, glabrous externally, tube 2–4 mm long and 1–1.5 mm diam., lobes 4, 1–2 mm long, triangular; **stamens** 4, anthers ca. 0.7 mm long. **Fruits** 4–6 mm long, 4–5 mm diam., ellipsoid to subglobose, becoming orange-red; pyrenes with 4–5 rounded ridges.

Understory plants of lower montane evergreen wet forest formations, from 1200 to 2200 m elevation in Costa Rica. Probably flowering throughout the year (mostly in July–August); fruiting in October–May. The species ranges from central Costa Rica to western Panama.

Psychotria parvifolia is recognized by its small

flat-topped stature, very small leaves with few secondary veins, puberulent stems, calyptrate stipules, and small few-flowered inflorescences. The tendency of the leaves to dry grayish beneath and the reddish fruit are characteristics of subgenus *Psychotria*. These plants are often conspicuous for their many horizontal branchlets and small leaves, especially in forest interiors where such small leaves are rare on woody plants. The Panamanian collections tend to have inflorescences with thinner axes, longer (3 mm) pedicels, and longer corolla tubes. Compare *P. graciliflora* with different stipules.

***Psychotria phanaerandra* (Standl. & Steyererm.) Lorence, Novon 2: 260. 1992.** *Palicourea phanaerandra* Standl. & Steyererm., Publ. Field Mus. Nat. Hist., Bot. Ser. 23: 252. 1947. *Psychotria luteotuba* Lorence, Bol. Soc. Bot. Méx. 47: 55. 1987.

Shrubs, 1–6 m tall, leafy stems 0.6–4 mm thick, glabrous and becoming grayish (rarely minutely papillate-puberulent); **stipules** with a tube and 2 linear lobes ca. 0.5 mm long, deciduous. **Leaves** with petioles 2–8 mm long, 0.4–0.9 mm thick, glabrous, drying dark; **leaf blades** 4–11 cm long, 1.3–4.5 cm broad, elliptic to narrowly elliptic-oblong or lanceolate, apex tapering gradually and long-acuminate with tip 3–18 mm long, base attenuate, drying membranaceous to firmly chartaceous, grayish green to dark brown above, glabrous above and below, 2° veins 5–8/side. **Inflorescences** solitary and terminal, 3–5 cm long, 1.5–3 cm broad, cymose-paniculate with few opposite or alternate branches, peduncle 15–22 mm long, 0.4–0.7 mm thick, usually glabrous, braces 0.5–1.4 mm long or absent, pedicels 0–2 mm long. **Flowers** glabrous externally (rarely sparsely papillate-puberulent), hypanthium 0.5–0.8 mm long, 0.6 mm diam., calyx limb

ca. 0.5 mm long with minute (0.1–0.2 mm) lobes; **corolla** white to lilac, pale purple or rose-lilac, tubular-funnel-form, tube (3–)4–8 mm long, ca. 1 mm diam., lobes 4, 2.5–5 mm long; **stamens** 4, anthers 1.8–2.5 mm long. **Fruits** 4–6 mm long, 5–6 mm diam., ovoid or globose-oblate, black; pyrenes with 3 prominent ridges.

Plants of wet evergreen forest on the Caribbean slope at 600–900 m elevation. It ranges from 20 to 2100 m elevation in Mexico and Guatemala. Flowering in March–June and December (throughout its range); fruiting in July–December and February. The species is also known from Mexico, Guatemala, and Honduras.

Psychotria phanaerandra is recognized by its small leaves, small slender few-flowered inflorescences, lilac corolla, and smooth glabrous fruit becoming black. Our material differs from northern collections by the more slender petioles, thinner translucent leaves with longer apices, lower-elevation wet forest habitat and lilac (not yellow or white) flowers. Compare with material placed in *P. deflexa*.

Psychotria pilosa Ruiz & Pav., Fl. Peruv. 2: 60. 1799. *P. costaricensis* Polak., Linnaea 41: 571. 1877. Figure 54.

Shrubs or subshrubs, 1–2(–3) m tall, leafy internodes 1.4–7 mm thick, terete, hirsute to pilose with erect or ascending thin hairs 1.3–2 mm long; **stipules** 8–25 mm long, 4–10 mm broad at the base, with 2 narrowly triangular or subulate lobes 4–12 mm long, sparsely pubescent distally, persisting. **Leaves** distant along the stem, petioles 12–40 mm long, 0.8–2.2 mm thick, densely pilose with thin straight or crooked hairs to 2 mm long; **leaf blades** (10–)12–27 cm long, (3–)4–13 cm broad, ovate-elliptic to elliptic-oblong or elliptic-obovate, apex gradually to abruptly acuminate or caudate-acuminate with tip to 2 cm long, base obtuse to cuneate and slightly decurrent on petiole, drying membranaceous to thin-chartaceous, dark olive green or brownish (rarely deeply blue-violet beneath), pilose above and below with hairs to 1.5 mm long, 2° veins 9–18/side, loop-connected distally to form an arcuate submarginal vein. **Inflorescences** terminal or pseudoaxillary, solitary, becoming pendant, 5–14 cm long, 2–8 cm broad, congested-pyramidal to subcylindrical panicles with opposite branches and densely clustered flowers (or condensed and subcapitate), peduncles 1–8 cm long, 1–2.5 mm thick, densely pilose with yellowish brown hairs, bracts to 8 mm long and 4 mm broad, bracteoles 3–6 mm long, ovate and glabrous to pilose abaxially, flowers sessile and enclosed within the persisting bracts. **Flowers** monomorphic, pilose externally, calyx ca. 1 mm long, dentate; **corolla** funnel-form, white, sparsely puberulent externally, tube 3–6 mm long and 1.5 mm diam., lobes 5, 1–3 mm long. **Fruits** ca. 4 mm long (not including the 1 mm persisting calyx) and 3–5 mm diam., to 10 mm when succulent, pilose,

bright blue or purple; pyrenes ca. 2.5 mm long with 3–4 ridges.

Understory plants in evergreen rain forest formations of the Caribbean slope, General Valley, and Golfo Dulce area, from 20 to 900 (rarely to 1500) m elevation. Flowering in March–August; fruiting in August–March. This species ranges from Nicaragua to Peru.

Psychotria pilosa is recognized by its long pilose hairs on almost all surfaces, large two-lobed persisting stipules, large leaves with arcuate submarginal vein, densely flowered inflorescences, small flowers subtended by broad persisting bracts, and bright blue fruit. There is considerable variation in the form of the inflorescences and prominence of floral bracts among different individual plants. This species is rarely collected on the Pacific slope. Individual collections with conspicuous blue-violet coloring on the leaf undersurfaces are occasionally collected but they appear to be no more than an unusual form. This species is one of our more distinctive species of *Psychotria*. Sterile collections may resemble *P. mortoniana*, *P. micrantha*, and *P. pittieri*, but they have shorter pubescence and smaller bracts. Compare the closely similar *Palicourea standleyana* with differing flowers and fruits.

Psychotria pithecobia Standl., Publ. Field Columb. Mus., Bot. Ser. 8: 187. 1930. Figure 60.

Shrubs to 1(–2) m tall, epiphytic (terrestrial), stems sometimes vine-like, leafy stems 1.5–6 mm thick, glabrous and drying pale yellowish; **stipules** with a membranaceous tubular truncated sheath 2–4 mm long, caducous or becoming indurated at base. **Leaves** with petioles 4–12 mm long, 1–1.8 mm thick, glabrous; **leaf blades** 4–12 cm long, 2–4.5 cm broad, elliptic-oblong to ovate-elliptic or elliptic, apex acute or short-acuminate with tip to 1 cm long, base acute to obtuse and slightly decurrent on petiole, drying grayish green to dark olive green, glabrous on both surfaces and with short (0.1–0.2 mm) linear cystoliths that may resemble hairs, 2° veins 5–11/side and arising at angles of 40–60° from the mid-vein. **Inflorescences** terminal (rarely axillary) and solitary, 4–14 cm long, to 8 cm broad, open panicles with distant opposite branching and flowers in distal cymose groups, often red, becoming pendant, peduncles 2–6 cm long, 0.7–1.3 mm thick, glabrous, drying black, bracts 1.5–5 mm long and subulate to linear, pedicels 1–5 mm long. **Flowers** glabrous externally, hypanthium ca. 1 mm long, calyx tube ca. 0.3 mm long, calyx lobes 0.2–0.7 mm long, triangular, obtuse or acute; **corolla** salverform, white or pink, tube 2–3.5 mm long, ca. 1 mm diam., lobes 4, 1–1.5 mm long. **Fruits** ca. 4.5 mm long and 3.5 mm diam., oblong to obovoid, orange or red at maturity.

Plants of evergreen lower montane cloud forest formations, from (500–)800 to 2200 m elevation. Flowering in December–July; fruiting in every month. This species (as presently defined) ranges from the Cordillera de Tilarán in Costa Rica to the western highlands of Panama.

Psychotria pithecolobium is recognized by its usually epiphytic habit, small tubular stipules (in early stages), succulent leaves with distinctive venation, large open reddened inflorescences, and small flowers with four-locular ovaries. The leaves drying grayish and the red fruit are characters shared with species of subgenus *Psychotria*. Specimens placed here may be no more than a distinctive variety of *P. guadalupensis* (DC.) Howard. They differ by the large leaves tapering gradually to the apex and with a greater number of ascending secondary veins clearly visible and elevated on the dried surfaces. The smaller corollas in specimens placed here are consistent with Steyermark's (1972) description of *P. guadalupensis* in Venezuela but differ from Costa Rican material being called *P. guadalupensis* (q.v.). While these differences are distinctive in many collections, there may be a few intermediate collections. Costa Rican material placed under the names *P. pithecolobium* and *P. guadalupensis* appears to have exactly the same ecological preferences and the same local distribution; this also suggests that they may represent different morphological forms of the same species.

Psychotria pittieri Standl., Contr. U.S. Natl. Herb. 18: 132. 1916. *P. dispersa* Standl., J. Wash. Acad. Sci. 18: 184. 1928. Figure 55.

Shrubs or subshrubs, 0.5–1.5(–2.5) m tall, much-branched, leafy stems 1–3 mm thick, terete, sparsely to densely pubescent with thin whitish or yellowish hairs 0.2–1 mm long; **stipules** 3–7 mm long, with a tube 0–2 mm long, broadly ovate with 2 narrow awns 1.5–7 mm long separated by a U-shaped sinus, pubescent, persisting. **Leaves** with petioles 4–12(–22) mm long, 0.5–1 mm thick, sparsely to densely pubescent to hirsutulous; **leaf blades** 6–11(–15) cm long, 2–4(–5) cm broad, elliptic to elliptic-obovate or elliptic-oblong, apex acuminate with tip 5–14 mm long, base acute to attenuate and slightly decurrent on petiole, thinly chartaceous, drying brownish or green, glabrous or with short hairs along the midvein above, sparsely to densely puberulent on the veins beneath with hairs 0.1–0.4 mm long, 2° veins 8–11/side. **Inflorescences** terminal or becoming pseudoaxillary, solitary, usually pendant, 3–10 cm long, 2–4 cm wide, pyramidal open panicles, distal branching cymose, peduncles 1–3 cm long, 0.5–1 mm thick, hispidulous, bracts 4–8 mm long, linear, flowers mostly sessile, bracteoles ca. 2 mm long. **Flowers** minutely puberulent externally, hypanthium ca. 1 mm long and 0.8 mm diam., turbinate,

calyx lobes 0.2–0.5 mm long, acute; **corolla** white to yellowish or greenish, tubular-salverform, tube 2–4 mm long, 0.8–1.5 mm diam., lobes 5, 0.5–0.7 mm long. **Fruits** 3–4 mm long, 2.5–4 mm diam. (6 mm in life), ellipsoid or globose, minutely papillate-puberulent, becoming bright blue or blue-purple; pyrenes 2–3 mm long, with 4–5 ridges.

Plants of wet evergreen forest understory on the Caribbean slope and in the central cordilleras, from near sea level to 1100 m elevation. Flowering primarily in May–July; fruiting throughout the year (mostly in October–March). The species ranges from Belize and Guatemala to central Panama.

Psychotria pittieri is recognized by its small stature, pubescent stems and peduncles, long stipular awns, smaller leaves, short inflorescences that are often pendant, small flowers, and bright blue fruit. It is one of our more common species. This species is similar to *P. acicularis* of the Osa Peninsula, with long slender bracts, and *P. steyermarkii*, which has more glabrous stems and peduncles and much larger bracts.

Psychotria platypoda DC., Prodr. 4: 510. 1830.

Shrubs or subshrubs, 1–3 m tall, leafy stems 1–3 mm thick, glabrous; **stipules** with a cupulate base 1–2 mm long and linear-lanceolate or oblong-lanceolate lobes 0.5–2.5(–4) mm long (4/node), glabrous, usually persisting. **Leaves** with petioles 5–18 mm long, 0.8–1.8 mm thick, glabrous; **leaf blades** 8–19 cm long, 4–8 cm broad, narrowly elliptic to elliptic-lanceolate or narrowly ovate, apex tapering gradually and acuminate, base tapering gradually and slightly decurrent, drying chartaceous, olive green above, glabrous or with few hairs along the midvein beneath, 2° veins 6–10/side and arcuate-ascending. **Inflorescences** solitary and terminal, 12–25 mm long, 7–20 mm broad, capitate or condensed cymose with 3–5 short branches, with 12–60 flowers, peduncles 3–12 mm long, ca. 1.5 mm thick, glabrous or minutely hirsute, conspicuous bracts 7–10 mm long, 6–14 mm broad, rounded distally, white tinged with green to purple in color, subtending the branches of the inflorescence, flowers often in groups of 10–12 subtended by 1 larger and 2 smaller bracts. **Flowers** glabrous externally, hypanthium ca. 0.8 mm long, calyx ca. 0.5 mm long, calyx teeth 0.1–0.2 mm long; **corolla** white, tubular-funnel-form, tube 3–6 mm long, lobes 5, 1.2–1.8 mm long, rounded distally. **Fruits** 3–5 mm long, 3–6 mm diam., blue to dark violet or black; pyrenes smooth with 3–5 planar ridges.

Plants of evergreen forest formations, 50–800 m elevation. Immature fruits were collected in November, mature fruits in January. The species ranges from Costa Rica to Peru and eastern Brazil.

Psychotria platypoda is recognized by the broad colorful bracts that subtend the young compact

inflorescences. The small flowers, black or bluish fruits, glabrous leaves tapering gradually at both ends, and two-toothed stipules are additional characteristics. This species is quite variable in South America, and there is the possibility that hybridization occurs with *P. officinalis* or *P. hoffmannseggiana* (q.v.). Rarely collected in Costa Rica; Chilamate de Sarapiquí, Valle del General, Rincón de Osa.

Psychotria poeppigiana Muell. Arg. in Mart., Fl. Bras. 6(5): 370. 1881. *Tapogomea tomentosa* Aubl., Hist. pl. Guiane 160, pl. 61. 1775, not *Psychotria tomentosa* Hemsl. *Cephaelis tomentosa* (Aubl.) Vahl, Ecolog. Amer. 1: 19. 1796. *C. hirsuta* Mart. & Gal., Bull. Acad. Brux. (11) 1: 135. 1844. *Evea tomentosa* (Aubl.) Standl., Contr. U.S. Natl. Herb. 18: 123. 1916. Figure 17.

Shrubs or herbaceous subshrubs, 0.7–3(–6) m tall, leafy stems 1.5–6 mm thick, terete, pilose to villose with thin ascending or erect straight hairs ca. 2 mm long; **stipules** with a tubular sheath 2–8 mm long (but this often difficult to see or becoming torn) and linear awns 4–16 mm long, hirsute, the dark interior collectors to 3 mm long. **Leaves** with petioles 4–18(–30) mm long, 0.7–1.5 mm thick, hirsute with thin yellowish hairs; **leaf blades** 8–18(–24) cm long, 3–8(–11) cm broad, narrowly ovate-elliptic to lanceolate or elliptic-oblong, apex tapering gradually and acute or acuminate with tip to 20 mm long, base obtuse to acute or cuneate and slightly decurrent on petiole, drying thin-chartaceous or chartaceous, dark green above, with thin hairs 1–1.5 mm long on the surfaces (sometimes breaking off near the base) and longer (to 2 mm) hairs along the midvein above and below, 2° veins 6–12/side. **Inflorescences** terminal and solitary, the involucre capitula ca. 2 cm long and 3–8 cm broad, peduncles 1.3–8(–13) cm long, ca. 1.5 mm thick and densely villous or hirsute, the 2 opposite basal bracts ca. 3 cm long and 3–4 cm broad, united at the base, broadly ovate and acute or mucronate, bright red or orange red, flowers sessile and closely crowded. **Flowers** distylous, puberulent externally, hypanthium 1.5–2 mm long, calyx lobes 5, 0.6–2 mm long, with a linear gland in each sinus; **corolla** tubular, yellow or yellowish white, with ascending hairs, tube 10–14 mm long, narrowly funnelliform, lobes 5, 2–3 mm long, narrowly triangular; anthers 1.8–2.5 mm long. **Fruits** 1–2 cm long, 5–10 mm diam., ob-ovoid or oblong, fleshy, bright blue; pyrenes 5–8 mm long, 1–2 mm broad, with 3–5 ridges.

Plants of forest shade and forest edges in evergreen rain forest formations, from near sea level to 800(–1100) m elevation. Flowering throughout the year; probably also fruiting throughout the year. The species ranges from Mexico and Central America to Brazil and Bolivia.

Psychotria poeppigiana (formerly *Cephaelis to-*

mentosa) is recognized by the usually shrubby habit, conspicuous pubescence, solitary terminal heads subtended by two bright red bracts, the yellowish corolla, and the blue fruit. This is a very common and conspicuous plant in the evergreen lowlands, but it is rarely collected above 1000 m elevation in Costa Rica. It is one of the species that made Central American members of *Cephaelis* seem so distinctive.

Psychotria polyphlebia J. D. Smith, Bot. Gaz. 33: 253. 1902. Figure 13.

Herbs or small subshrubs, 15–50 cm tall, rhizomatous, usually with a single unbranched stem, leafy stems 1.5–6 mm thick, glabrous or at first hirsute with hairs to 1 mm long, usually quickly glabrescent and drying black, terete; **stipules** 1–3 mm long, 4–6 mm broad, broadly triangular, obtuse, glabrous or puberulent, inconspicuous and deciduous. **Leaves** with petioles 1–4(–7) cm long, 1–2.7 mm broad, sparsely puberulent to densely hirsute with hairs 0.5–1.5 mm long; **leaf blades** 7–16 cm long, 3–7 cm broad, oblong to obovate-oblong or obovate, apex bluntly obtuse to rounded, base cuneate to acute and decurrent on petiole, drying thin- to stiffly chartaceous, grayish green to dark olive green above, glabrous or with stiff straight hairs 0.5–1.3 mm long above, hirsute beneath with thin usually straight hairs, 2° veins 15–25/side and usually loop-connected close to the leaf margin, surface of the leaf becoming transversely corrugated. **Inflorescences** solitary in leaf axils (usually 1/node), 2–8 cm long, 15–30 mm broad, capitate-hemispheric, peduncles 1–6 cm long, 1–2 mm thick, glabrous or hirsutulous, lower bracts ca. 8 mm long and 1.5 mm broad, flowers sessile or subsessile, enclosed by subequal ovate to lanceolate bracts to 6 mm long and 3 mm broad. **Flowers** 5-parted, calyx minutely denticulate; **corolla** white, thin and translucent, tubular-funnelform, tube 4–5 mm long, 1 mm diam., lobes 5, 1–1.5 mm long. **Fruits** 6–9 mm long, 4–6 mm diam., oblong, becoming orange or red and finally black, glabrous; pyrenes 5–7 mm long, with 3–5 ridges.

Plants of the deeply shaded forest floor in evergreen rain forest formations primarily on the Caribbean slope, from 20 to 1200 m elevation. Flowering in February–August; fruiting throughout the year. The species ranges from Nicaragua to Colombia.

Psychotria polyphlebia is recognized by its small size, stiff corrugated leaves held horizontally over the dark forest floor, many secondary veins, the usually long-pedunculate capitate inflorescences from the axils of leaves, and small flowers hidden by bracts. The tendency of the undersides of leaves to dry grayish and the red or orange fruits are characters usually associated with subgenus *Psychotria*. This is one of the most distinctive species

of *Psychotria* in Costa Rica; no other is so short in stature with such distinctive leaves.

***Psychotria psychotriifolia* (Seem.) Standl., Contr. U.S. Natl. Herb. 18: 133. 1916. *Cephaelis psychotriaefolia* Seem., Bot. voy. Herald 138. 1854. Figure 63.**

Shrubs or subshrubs, 0.5–2(–3) m tall, leafy stems 1.5–8 mm thick, at first densely puberulent with reddish brown or yellowish hairs ca. 0.2 mm long, glabrescent, terete; **stipules** with a truncate tube 4–14 mm long and 2–4 mm diam., awns 1–5 mm long, narrow, 2/side, minutely puberulent along the midrib and awn, drying reddish brown, usually splitting down 1 side and deciduous. **Leaves** with petioles 3–10(–20) mm long, 0.8–2 mm broad, minutely (0.05–0.2 mm) papillate-puberulent; **leaf blades** 5–15(–20) cm long, 2.5–7 cm broad, oblanceolate to narrowly obovate or elliptic-ob lanceolate, apex acute or obtuse, base gradually narrowed and cuneate, decurrent on petiole, drying chartaceous or stiffly chartaceous, grayish to pinkish or orange-brown, glabrous above, minutely papillate-puberulent along major veins and with longer (0.2 mm) hairs distally and along the leaf margin, 2° veins 8–14/side and loop-connected near the margin to form a submarginal vein. **Inflorescences** terminal or pseudoaxillary, 1–4/node, 10–30 mm long, pyramidal panicles of glomerules or with 3 capitula on a primary peduncle (rarely with heads in an umbellate configuration), peduncles 3–10 mm long (to 18 mm in fruit), 0.8–1.8 mm thick, sparsely to densely puberulent, lower bracts biaristate (resembling the stipules) and 3–5 mm long, often forming an involucre, flowers sessile or subsessile and partly enclosed by the narrowly ovate bracteoles ca. 3 mm long. **Flowers** distylous, hypanthium and calyx ca. 2 mm long, calyx lobes ca. 1 mm long; **corolla** rotate, pale green or white, tube 1–2 mm long, lobes (4–)5, 1–1.7 mm long and 0.6 mm broad at base; **stamens** 5, anthers 0.5–0.7 mm long. **Fruits** 5–6 mm long (not including the 0.5–2 mm long calyx), 3–4 mm diam., ellipsoid, longitudinally grooved, glabrous and becoming bright red; pyrenes ca. 4.5 mm long, with 3–5 ridges.

Plants of Caribbean lowland evergreen forest formations, from near sea level to 600(–800) m elevation. Flowering and fruiting throughout the year (flowering February–September in Costa Rica). The species ranges from southern Nicaragua to Colombia and Venezuela.

Psychotria psychotriifolia is recognized by the slightly oblanceolate leaves with arcuate submarginal veins, puberulent young stems, tubular biaristate stipules, small flowers in dense bracteate or involucre capitula, ellipsoid fruit with persisting calyx, and lowland habitat. The inflorescences often become pseudoaxillary. The tendency of vegetative parts to dry reddish brown or gray and the red fruit are characteristics of subgenus *Psychotria*.

***Psychotria pubescens* Sw., Prodr. 44. 1788. *P. glauca* Polak., Linnaea 41: 569. 1877. Figure 59.**

Shrubs, 1–2(–3) m tall, leafy stems 0.7–4 mm thick, minutely papillate-puberulent to hirtellous with hairs 0.2–0.8 mm long or sometimes glabrous; **stipules** 3–8 mm long, 2–4 mm broad at the base, with a truncate to triangular basal portion ca. 2 mm long and 2 narrow distal lobes 1–4 mm long (4/node). **Leaves** with petioles 4–28 mm long, 0.5–1.5 mm thick, with adaxial margins continuous with the lamina margins, usually minutely papillate-puberulent; **leaf blades** (5–)7–15(–18) cm long, (1.3–)2–5(–7) cm broad, ovate-elliptic, to elliptic-lanceolate or elliptic-oblong, apex acuminate to acute (obtusely) with a tip 3–10 mm long, base cuneate to acute (obtusely) and decurrent on petiole, drying membranaceous to thin-chartaceous and dark green, sparsely and minutely (0.1–0.2 mm) puberulent or subglabrous above and below, 2° veins 9–12(–15)/side, weakly loop-connected near the margin distally. **Inflorescences** terminal and solitary (or 3), 2–6 cm long, 1.5–5 cm broad, compact (at first) to open-corymbose panicles with opposite branching, peduncles 6–30 mm long, ca. 1 mm thick, densely puberulent to glabrous, bracts 2–6 mm long, linear, flowers 2–3(–5) in cymes or triads, pedicels 0–2 mm long. **Flowers** usually very minutely (0.05 mm) papillate-puberulent externally, hypanthium ca. 0.6 mm long and 0.5 mm diam., calyx tube ca. 0.2 mm long and 1 mm broad with lobes 0.4 mm long; **corolla** funnelform, white or yellowish, tube 2–4 mm long, 0.8–1.8 mm diam., slightly constricted in the middle, lobes 5 or 6, ca. 1.5 mm long. **Fruits** 5–6 mm long and 5–6 mm diam., oblate to globose, with prominent longitudinal ridges, purple or black.

Plants of shaded sites in deciduous or partially deciduous forest formations, from 20 to 1200(–1500) m elevation on the Pacific slope of central and northern Costa Rica. Flowering in May–August; fruiting in July–January. This species is found from Mexico to Panama and in the West Indies.

Psychotria pubescens is recognized by the usual presence of minute hairs on young stems and inflorescences, short two-awned stipules, thin leaf blades with decurrent base, small flowers, and seasonally dry habitat. Despite the specific name, some plants may be nearly completely glabrous. Likewise, there is great variation in leaf form between different plants, from small and lanceolate to larger and more obovate or oblong. The inflorescences are usually rounded distally at anthesis. This species can be confused with *P. microdon*, which also lives in deciduous vegetation but has longer perianth parts, red fruits, and a more clambering habit.

***Psychotria quinquerradiata* Polak., Linnaea 41: 570. 1877. *Mapouria obovata* Oerst., Amer. Centr.**

17, t. 14, f. 3 and 4. 1863. *P. morae* Polak., loc. cit. 570. 1877. *P. obovata* (Oerst.) Hemsl., Biol. centr. amer. Bot. 2: 50. 1881, non *P. obovata* Ruiz & Pav. 1799. Figure 65.

Shrubs, 0.5–2.5 m tall, leafy stems 1.2–4 mm thick, glabrous, older twigs becoming pale gray and often with whitish lenticels; **stipules** 4–6 mm long and 2–5 mm broad but to 15 mm long and 8 mm broad below the inflorescences, lanceolate to narrowly ovate or broadly obovate beneath the inflorescences, acute, glabrous and drying dark reddish brown, usually caducous. **Leaves** with petioles 1.5–6(–10) mm long, 1–2 mm thick, glabrous; **leaf blades** (3.5–)5–13(–15) cm long, (1.5–)2–5.5(–7) cm broad, elliptic-obovate to obovate, oblanceolate, elliptic or subpandurate, apex acute to short-acuminate with tip 3–5 mm long, base cuneate or acute and decurrent on petiole or the blade sometimes rounded and subcordate at base, drying thin-chartaceous or chartaceous, grayish or pinkish brown, glabrous above and below, 2° veins 5–7/side, often with minute pit domatia or tufts of hairs in the vein axils beneath. **Inflorescences** terminal and 1–5, 1–3 cm long and elongating to 5 cm in fruit, to 1.5 cm wide, subcapitate or densely cymose to umbellate, peduncles 2–35 mm long, 0.4–1 mm thick, glabrous, bracts and bracteoles not evident, flowers in distal triads, diads or glomerules of 5–15, pedicels 0–1 mm long. **Flowers** glabrous externally, hypanthium ca. 1 mm long, calyx tube ca. 0.4 mm long, lobes slightly dentate; **corolla** white, funnellform, tube 3.5–5 mm long, 1–2 mm diam., lobes 5, 1.5–3 mm long; **stamens** 5, anthers 1–1.5 mm long. **Fruits** 6–9 mm long, 4–6 mm diam., oblong or ellipsoid, bright red or orange; pyrenes ca. 4 mm long and 3 mm broad, with 3–5 low ridges.

Plants of forest understory in both seasonally deciduous woodland and wet evergreen rain forest formations, from near sea level to 1400 m elevation. This species is rarely collected in the Caribbean lowlands of Costa Rica; it forms a distinctive understory in parts of Parque Nacional Rincón de la Vieja. Flowering throughout the year (primarily in January–July); fruiting in August–February in Costa Rica. The species ranges from Veracruz, Mexico, southward through Central America to western Panama.

Psychotria quinquerradiata is recognized by the usually short-petiolate and obovate leaves, the broad stipules below the young inflorescences, the capitate to umbellate-fasciculate inflorescences, and sessile flowers. The tendency of the leaves to dry gray or reddish and the bright red fruit are characteristics of subgenus *Psychotria*. The stipules are often much enlarged below the young inflorescences. As in some other species of *Psychotria*, the petioles and leaf bases can vary greatly in different individuals: from sessile to longer-petiolate and from decurrent to slightly auriculate. This species resembles *P. carthaginensis* but differs

in venation and inflorescences. Compare also *P. venosa* and *P. chagrensis*.

Psychotria racemosa (Aubl.) Raeschel, Nomen. ed. 3, 56. 1797. *Nonatelia racemosa* Aubl., Hist. pl. Guiane 180, pl. 72. 1775. *P. racemosa* (Aubl.) Rich., Actes Soc. Hist. Nat. Paris 1: 107. 1792 fide Dwyer 1980. *Rudgea thyrsiflora* J. D. Smith, Bot. Gaz. 61: 375. 1916. Figure 59.

Shrubs or herbaceous subshrubs, 0.5–2(–4) m tall, leafy stems 1.5–5 mm thick, sparsely to densely puberulent with ascending hairs 0.1–0.3 mm long; **stipules** with a short (1–3 mm) sheath and 2 long (6–14 mm) narrow (0.3–0.6 mm) awns on each side (4/node), with indurated glabrous yellowish collectors ca. 1.5 mm long interior to the sheath, puberulent and persistent. **Leaves** with petioles 5–20(–35) mm long, 0.9–1.5 mm thick, densely puberulent (except for the adaxial midvein); **leaf blades** 9–21(–26) cm long, 3–7(–11) cm broad, elliptic to elliptic-oblong or ovate-oblong, apex acuminate with tip 5–15 mm long, base obtuse to acute and slightly decurrent on petiole, drying chartaceous, green to brownish green, glabrous above, minutely (0.1–0.2 mm) puberulent along the veins beneath, 2° veins 7–12/side, the 3° veins subparallel and prominent beneath. **Inflorescences** terminal or becoming axillary, 1(–2)/node, 3–7 cm long and 1.5–2.3 cm broad (to 10 × 4 cm in fruit), pyramidal or hemispheric panicles with usually short (often distinctly cymose) lateral branches, peduncles 1–2 cm long and 1.5 mm thick, densely yellowish puberulent, bracts to 6 mm long, linear, bracteoles ca. 2 mm long, pedicels 0–2 mm long. **Flowers** minutely puberulent on the exterior, hypanthium 0.8–1 mm long, obconic, calyx ca. 0.4 mm long, lobes ca. 0.3 mm long and obtuse; **corolla** tubular-salverform, white, greenish or yellow, tube 1–3 mm long, 0.6–1.2 mm diam., lobes 4 or 5, 0.5–1 mm long. **Fruits** 4–5 mm long, 5–7 mm diam., oblate to globose, glabrous, becoming orange or red and finally purple or black, fleshy; pyrenes usually 5, ca. 4 mm long, with 3 sharp dorsal ridges.

Understory plants in evergreen lowland forest formations on both the Caribbean and Pacific slopes, from near sea level to 800 m elevation (rarely found above 400 m on the Caribbean slope). Flowering in March–July; fruiting throughout the year in Costa Rica. This species is found throughout the Caribbean lowlands in Costa Rica and in evergreen forests of the Pacific slope of southern Costa Rica. The species occurs in southern Mexico and ranges from Nicaragua to Brazil and Bolivia.

Psychotria racemosa is recognized by the minute puberulence on younger stems and leaf undersides, the persisting stipules with long stiff narrow awns, subparallel tertiary veins, relatively short puberulent inflorescences, small puberulent flowers, five-locular ovaries, and fruit with usually five seeds.

The five-locular gynoecium is unique among Central American species of *Psychotria*.

Psychotria remota Benth., J. Bot. 3: 225. 1841. *Mapouria remota* (Benth.) Muell. Arg., Flora 59: 459. 1876, and in Mart., Fl. Bras. 6(5): 407. 1881. *P. alboviridula* K. Krause, Notizbl. Bot. Gart. Berlin 6: 208. 1914. Figure 66.

Shrubs or small treelets, 1.5–5(–8) m tall, leafy stems 1.5–5 mm thick, glabrous and drying dark reddish brown; stipules 3–6 mm long, 1–3 mm broad at base, triangular, tip acute or acuminate (biacuminate), glabrous, caducous. **Leaves** with petioles 5–24 mm long, 1–2 mm thick, glabrous, often with prominent adaxial margins forming a slight sulcus; **leaf blades** 10–24 cm long, 3–7.5(–9) cm broad, elliptic to elliptic-oblong or narrowly ovate-oblong, apex acuminate with tip 4–13 mm long, base acute or obtuse and slightly decurrent on petiole, drying stiffly chartaceous or subcoriaceous, dark grayish or reddish brown, glabrous above and below, 2° veins 7–10/side, axils of the veins often with pit domatia 0.3–1 mm long beneath. **Inflorescences** terminal or becoming axillary, 6–17 cm long, 4–10 cm broad, open panicles with 2–5 pairs of lateral branches, peduncles 2–7 cm long, 0.9–2 mm thick, glabrous and drying dark reddish brown, bracts 1–3 mm long, subulate to triangular, flowers sessile or subsessile in distal cymes of 3 or clusters. **Flowers** glabrous externally, hypanthium 0.8–1.5 mm long, turbinate, calyx tube ca. 0.5 mm long, subtruncate or with lobes to 0.3 mm long; **corolla** campanulate, white or yellowish green, tube 1.5–2 mm long, 1–1.5 mm diam., lobes 5, 1–1.2 mm long, triangular; **stamens** 5, anthers 0.3–0.6 mm long. **Fruits** 7–9 mm long, 4–6 mm diam., ellipsoid or oblong, becoming orange to maroon red; pyrenes with 4–5 shallow ridges.

Plants of evergreen rain forest formations along the Caribbean lowlands, from near sea level to 200 m elevation (to 1000 m in Panama). Flowering in March–April and September–October; fruiting in March–May, July, and September. The species ranges from Costa Rica to Peru and Brazil.

Psychotria remota is recognized by its glabrous parts often drying dark in color, stiff leaves usually with conspicuous pit domatia beneath, small flowers on inflorescences with slightly winged branches, and flowers and fruits usually disposed at 90° to each other. The first branch pair of the inflorescences is usually much larger than the others. The tendency of leaves to dry grayish or reddish brown and the red fruit are characteristics of subgenus *Psychotria*. This species is rare in Costa Rica. None of our other species of *Psychotria* have such large pit domatia, but these are not always present. Compare *P. panamensis* with very different stipules.

Psychotria rosulatifolia Dwyer, Ann. Missouri Bot. Gard. 67: 423. 1980. Figure 65.

Small treelets, ca. 3 m tall, leafy stems 3–6 mm thick, glabrous and grayish; stipules 8–16 mm long, 5–8 mm broad at the base, triangular to ovate, bifid and acute with a distal sinus 0–1 mm deep, glabrous, caducous. **Leaves** sessile or subsessile, petioles 0–7 mm long, ca. 3 mm thick, glabrous, drying dark; **leaf blades** 15–32 cm long, 4–11 cm broad, very narrowly elliptic to narrowly elliptic-oblong or lanceolate-elliptic, apex acute to subacuminate, base rounded and subcordate (slightly auriculate), drying stiffly chartaceous, dark grayish, glabrous above and below except for minute (0.1–0.2 mm) thin hairs along the midvein beneath, 2° veins 18–22/side and arising at angles of 90–100° from the midvein (to the apex), united by a prominent submarginal vein 1–2 mm from the leaf edge. **Inflorescences** terminal and solitary, ca. 38 cm long and 30 cm broad, an open pyramidal panicle with widely spaced opposite branches, with 2 very short and 2 long lateral branches at the first node, peduncle 5–18 cm long and 2 mm thick, sparsely and minutely puberulent, bracts ca. 3 mm long, flowers in cymes or 3–7, pedicels 1–3 mm. **Flowers** subglabrous externally, buds yellow, hypanthium 0.5 mm long and 0.3 mm diam., calyx tube 0.2–0.3 mm long, lobes 0.1–0.2 mm long; **corolla** tubular, white, tube 3–6 mm long, lobes 3–4 mm long. **Fruits** 5–6 mm long, 3–4 mm diam., ellipsoid, red; pyrenes with 4–5 long ridges.

Plants of the wet Caribbean slope of the southern Cordillera de Talamanca, collected at ca. 700 m elevation (*Herrera 3306* CR, MO) with immature flowers in July. The species is known only from this collection in Costa Rica and several collections from Darien, Panama.

Psychotria rosulatifolia is unusual because of its long narrow subsessile (sometimes auriculate) leaves, secondary veins arising at angles of 90–100°, well-developed submarginal vein, and large open inflorescences with two small and two long lateral branches at the first node. The leaves are sometimes disposed in distal rosettes.

Psychotria sarapiquensis Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 1360. 1938. Figure 62.

Shrubs or small trees, 2–7(–9) m tall, leafy stems 1–4(–6) mm thick, glabrous and often drying grayish green; stipules 5–12(–45) mm long, 2–5 mm diam., calyptrate, narrowly conical to lanceolate, acute at the apex, glabrous, drying reddish brown, caducous. **Leaves** with petioles 9–35(–45) mm long, 0.8–1.8 mm thick, glabrous; **leaf blades** 6–12(–15) cm long, 2–4(–7) cm broad, ovate-elliptic to narrowly elliptic or lanceolate, usually apex tapering gradually and acuminate or acute with tip 3–14 mm long, base acute to cuneate and decurrent on petiole, drying stiffly chartaceous, grayish green to dark green above, glabrous above and below, 2° veins 6–8/side. **Inflorescences** terminal 1 or 3 (2–) 4–13 cm long, to 10 cm

broad, open pyramidal panicles with opposite branching or 3 main branches, peduncle (1–)2–4 cm long, 0.8–1.9 mm thick, glabrous, bracts 0.5–1 mm long, broad, flowers in distal umbels or clusters of 3–5, pedicels 1–3 mm long. **Flowers** glabrous externally, hypanthium ca. 1.3 mm long, obconic, calyx 0.5–1 mm long, ca. 2 mm broad at the truncated distal margin; **corolla** funnellform greenish white, tube 1–3(–4) mm long and 2 mm diam., lobes 5, 1.5–3 mm long and 1.3 mm broad at the base, triangular; **stamens** 5, anthers 1.2–1.5 mm long. **Fruits** 7–10 mm long, 4–8 mm diam., obovoid-oblong, becoming yellow then bright red; pyrenes with 3–5 rounded ridges.

Plants of lower montane forest formations of the Caribbean slope and near the continental divide, from (600–)1200 to 1600 m elevation (400–900 m in Mexico). Flowering in January, March, July–August (*Skutch 3330* us the type), and October; fruiting in January–March and August. The species range is disjunct; it occurs in Veracruz, Mexico, and in the west-central cordilleras of Costa Rica (Cordillera de Tilarán to Vara Blanca de Sarapiquí) and the western half of Panama.

Psychotria sarapiquensis is recognized by its long-petiolate narrowly elliptic leaves, glabrous parts, calyptrate caducous stipules enclosing the shoot apices, entire calyx, short corolla tubes, longer fruit, and restricted habitat (in Costa Rica). The tendency for the leaves to dry grayish and the fruit turning bright red are characteristics of subgenus *Psychotria*. The larger leaf dimensions come from material collected in Mexico. This species is closely related to *P. panamensis*, with similar *Ficus*-like stipules, but *P. sarapiquensis* has smaller leaves with fewer secondary veins. It can also be confused with *P. chiriquina*, *P. orosiana*, and *P. tenuifolia*.

Psychotria siggersiana Standl., J. Wash. Acad. Sci. 15: 289. 1925. *P. morii* Dwyer, Ann. Missouri Bot. Gard. 67: 400. 1980.

Herbs or succulent-stemmed subshrubs, 0.5–1(–2) m tall, leafy stems 4–12 mm thick and usually unbranched, glabrous or sparsely puberulent and glabrescent, succulent and terete; **stipules** 3–7 mm long, ca. 8 mm broad, with a short collar around the stem, rounded deltoid, with a deciduous conical lateral appendage 1–2 mm long, usually glabrous, persistent. **Leaves** with petioles 4.5–10 cm long, 1.7–4 mm thick, typically with thin crooked hairs to 1 mm long (glabrous); **leaf blades** (12–)20–35 cm long, (6–)11–17 cm broad, ovate-elliptic to elliptic-oblong, apex acuminate with tip 5–10 mm long, base obtuse or cuneate, drying thin-chartaceous, dark brownish green above, with thin crooked hairs to 1.2 mm long on the upper surface, the hairs mostly shorter and denser beneath, 2° veins 8–11/side. **Inflorescences** axillary, solitary at a node, 3–15 cm long, pyramidal panicles with open opposite branching, peduncles 1–3(–4) cm long,

1.3–2 mm thick, puberulent, bracts 5–8 mm long and 3 mm broad at the base, lanceolate to elliptic, flowers 3–7 within distal glomerules and sessile, enclosed by broad bracteoles. **Flowers** with calyx 0.5–1 mm long, lobes deltoid-ovate; **corolla** funnellform, white or greenish white, tube ca. 3 mm long, sparsely short villous or glabrous externally, lobes 5, ca. 1 mm long. **Fruits** 5–6 mm long, globose, red; pyrenes ca. 4 mm long, dorsal surface smooth.

Plants of the wet lowland Caribbean rain forest formations at 100–1200 m elevation. Flowering in January, March (*Standley 37210* us the holotype), and August; fruiting in January, March, and October–November. This rarely collected species is known only from the Caribbean slope and lowlands of Costa Rica, western Panama, and Chocó, Colombia.

Psychotria siggersiana is recognized by the short usually unbranched habit, large leaves with long hairs, axillary inflorescences with larger bracts broadly sheathing the distal floral glomerules, and the red fruits. Standley distinguished *P. siggersiana* primarily by its pubescence, but the type also has unusually large floral bracts (as does *P. aggregata*, which looks quite similar). The red fruits with pyrenes that lack costae on their abaxial surface are distinctive, but specimens with young fruits can be difficult to separate from other members of the *P. aggregata*–*macrophylla* species alliance.

Psychotria sixaolensis C. Hamilton, Phytologia 64: 234. 1988. Figure 64.

Shrubs or subshrubs, 1–4 m tall, leafy internodes 4–9 mm thick, young stems pubescent with reddish brown hairs 0.2–0.8 mm long but quickly becoming completely glabrous; **stipules** 10–25 mm long and 6–12 mm broad, ovate in outline and sheathing at base, acutely lobed for $\frac{1}{4}$ – $\frac{2}{3}$, caducous. **Leaves** with petioles 10–35(–50) mm long, ca. 2 mm diam., poorly distinguished from the lamina base, puberulent; **leaf blades** (14–)16–30 cm long, (5.5–)8–14 cm broad, obovate to elliptic-obovate, elliptic or elliptic-oblong, apex abruptly narrowed and short-acuminate (obtuse) with tip ca. 5 mm long, base cuneate to acute, long-decurrent on petiole, drying chartaceous, dark reddish brown, glabrous above, with dense reddish brown hairs 0.3–0.7 mm long along the major veins, reddish brown tomentulose beneath, 2° veins 20–33/side, a well-defined slightly arcuate submarginal vein 1–2 mm from the edge. **Inflorescences** terminal and solitary, 5–17 cm long, subcapitate or with 3 capitulae on short (5 mm) secondary branches, fruiting peduncles 7–14 cm long, 3–4.5 mm thick, bracts and bracteoles ca. 7 × 6 mm, ovate, reddish brown puberulent with hairs ca. 0.3 mm long, flowers sessile and densely crowded in distal glomerules of 8–20. **Flowers** puberulent externally, calyx tube 1–2 mm long, lobes 5, 2–3 mm long and 0.8 mm wide; **corolla** tubular, white or greenish white, tube ca.

4 mm long and 2.5 mm diam., lobes 5, ca. 3 mm long and 1.5 mm broad, thickened near apex; **stamens** 5, anthers 1.3 mm long. **Fruits** 7–10 mm long (not including the calyx), 5–6 mm diam., ellipsoid with a persisting calyx 2–3 mm long, red at maturity; pyrene with 4–5 sharp ridges.

Plants of lowland Caribbean rain forest formations, from near sea level to 500 m elevation. Flowering in April and August; fruiting in August. This species is known only from southern Limón Province and Bocas del Toro Province in Panama.

Psychotria sixaolensis is recognized by its densely pubescent leaves and inflorescences, large leaves with many secondary veins and well-developed submarginal vein, long-pedunculate subcapitate panicles with large ovate bracts, and flowers in dense glomerules. The red fruit and leaves drying reddish brown are characteristics of subgenus *Psychotria*.

***Psychotria solitudinum* Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 22: 207. 1940. Figure 57.**

Shrubs or small trees, 2–6 m tall, leafy stems 2–6 mm thick, glabrous, usually drying yellowish green; **stipules** 2–6 mm long, 2–4.5 mm broad, oblong to ovate, rounded with 2 short (0.5–1 mm) lobes separated by a small sinus, glabrous, persisting. **Leaves** with petioles 7–35(–50) mm long, 1–2 mm thick, glabrous, drying yellowish; **leaf blades** (7–)10–21(–30) cm long, (2.5–)4.5–10(–14) cm broad, obovate-oblong to ovate-elliptic, elliptic-oblong or oblong, apex acuminate with tip 5–13 mm long, base acute to broadly obtuse (slightly round) and often slightly decurrent on petioles, drying chartaceous or stiffly chartaceous, grayish green above, glabrous above, glabrous or with few thin hairs 0.2–0.6 mm long along the sides of the midvein beneath, 2° veins 12–18/side, arising at nearly 90° from the midvein, distally loop-connected to form an arcuate submarginal vein. **Inflorescences** solitary and terminal, 8–26 cm long, 10–20 cm broad, open pyramidal panicles with distant opposite lateral branches and distal cymose or dichotomous branches, peduncles to 8 cm long and 2 mm thick, usually glabrous, bracts 3–5 mm long, bracteoles 2–3 mm long, flowers mostly sessile, separated or in glomerules of 2–3. **Flowers** with thin white hairs 0.2–0.5 mm long on the outer surfaces (less often glabrous), hypanthium ca. 1 mm long, calyx tube ca. 0.5 mm long, lobes poorly differentiated; **corolla** funnellform-urceolate, pale green to yellow (white), tube 4–5 mm long, 0.7–1.5 mm diam. near base and 2–3 mm distally, lobes ca. 1 mm long, with distal projections in early stages. **Fruits** ca. 4 mm long (not including calyx) and 4–5 mm broad, oblate to obovoid or subglobose, bluish, purplish, or black in final stages, usually puberulent, persisting calyx ca. 1 mm high; pyrenes with 4–5 ridges.

Plants of wet evergreen forest formations of the Pacific slope (in Costa Rica), from 30 to 800 m

elevation. Flowering in January–August; fruiting in March–September. This species ranges from south-central Costa Rica to Colombia.

Psychotria solitudinum is recognized by its larger leaves with many secondary veins and a submarginal vein, ovate stipules with a small distal sinus, large open inflorescences with sessile flowers usually borne along dichotomous distal branches, puberulent yellow flowers, and small puberulent fruit. The leaves are subglabrous and tend to dry yellowish green. This species, which is restricted to the Pacific side of southern Costa Rica, appears to be closely related to *P. angustiflora*, *P. brachiatata*, and *P. tapantiana* (q.v.). Specimens of *P. microbotrys* and *P. brachiata* with young flowers are also similar.

***Psychotria steyermarkii* Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 22: 387. 1940. Figure 55.**

Small shrubs, (0.5–)1–2 m tall, leafy stems 0.5–3.5 mm thick, with thin whitish hairs 0.1–0.3 mm long often in longitudinal ridges or rarely glabrous; **stipules** with a sheath 1–4 mm long, truncated and with 2 filiform or narrowly lanceolate awns 2–5 mm long, puberulent at the base, usually persisting. **Leaves** with petioles 4–14(–20) mm long, 0.4–0.8 mm thick, glabrous or minutely puberulent; **leaf blades** 3.5–11(–14) cm long, 1–3(–3.5) cm broad, narrowly elliptic to narrowly elliptic-oblong or elliptic-lanceolate, apex tapering gradually and acuminate, tip 3–8 mm long, base acute and decurrent on petiole, drying chartaceous, dark greenish or brownish green above, glabrous or with a few hairs along the midvein above, minutely (0.1–0.2 mm) puberulent along the major veins beneath or glabrescent, 2° veins 9–14(–17)/side, loop-connected near the margin. **Inflorescences** terminal, usually solitary, 3–9 cm long, 2–3 cm broad, open pyramidal panicles with 2–3 pairs of lateral branches, peduncles 1.4–3 cm long, ca. 0.7 mm thick, puberulent, bracts and bracteoles 3–8 mm long, to 4 mm broad, ovate-lanceolate and forming a persisting involucre, sometimes marked with blue, glabrous, flowers sessile in glomerules of 2–5. **Flowers** glabrous or minutely puberulent externally, hypanthium and calyx obscured by the bracts and bracteoles, calyx lobes 0.4–1 mm long; **corolla** salverform, white or greenish white, tube ca. 3 mm long, ca. 0.7 mm diam., lobes ca. 1.5 mm long. **Fruits** 3.5–5 mm long, 3.5–5 mm diam., subglobose, bright blue; pyrenes with 3–5 planar angles.

Plants of evergreen lower montane forest formations and cloud forests, from 800 to 1800 m elevation. Flowering in May–August; fruiting in August–September and November–February in Costa Rica. The species ranges from the Cordillera de Tilarán to the Chiriquí Highlands and is found in southern Mexico, Guatemala, and Nicaragua.

Psychotria steyermarkii is distinguished by its

small leaves, cloud forest habitat, tubular awned stipules, small racemose inflorescences, and small flowers in distal bracteate clusters. The fruits become bright blue and very attractive. This species has been mistaken for *P. graciliflora* of subgenus *Psychotria* with bright red fruits and *P. pittieri* with larger leaves and lower-elevation habitat. This species may also be mistaken for *P. goldmanii* of similar habitat with longer narrow leaves and different stipules. The Guatemalan type (*Steyermark 33700* F) has unusually large leaves, but a smaller-leaved fruiting collection from Guatemala (*Steyermark 33461* F) is very similar to Costa Rican material. Herbarium material annotated *P. cornigera* Dwyer (ined.) is this species. Compare *P. hazenii*.

Psychotria stockwellii Hamilton, *Phytologia* 64: 235. 1988. Figure 62.

Small trees or shrubs, 2–10 m tall, leafy stems 2–6 mm thick, glabrous or sometimes pilosulous, drying dark; stipules 9–15 mm long, 3.5–7(–9) mm broad, ovate, acute and usually bilobed with a short sinus (1 mm), glabrous, caducous. Leaves with petioles 5–25 mm long, 1–3 mm broad, glabrous; leaf blades 8–20 cm long, 2.5–8 cm broad, elliptic-obovate to elliptic or oblanceolate, apex acuminate with tip 5–10 mm long, base gradually narrowed and cuneate or acute, decurrent on petiole, drying chartaceous or thin-chartaceous, very dark above, glabrous on both surfaces (or the midvein minutely puberulent beneath), 2° veins 10–15/side, often with a weaker 2° between the major 2° veins and parallel with them. Inflorescences terminal (pseudoaxillary), solitary, 9–18(–24) cm long, 5–12 cm broad, open pyramidal panicles with opposite 1°, 2°, and 3° branches usually borne at angles greater than 90° from the apex, peduncles 5–9 cm long, ca. 2 mm thick and glabrous, bracts and bracteoles 0.5–2 mm long, triangular, flowers in distal cymes or triads, pedicels 0.5–2 mm long, minutely papillate-puberulent. Flowers with hypanthium 0.5–1 mm long, obconic, calyx tube 0.3–0.8 mm long, lobes 5, 0.3–0.7 mm long, minutely puberulent distally; corolla tubular-campanulate, cream white or greenish white, glabrous externally, tube 4–5 mm long, 1.5–2 mm diam., lobes 5, ca. 2 mm long and 1 mm broad at the base; stamens 5, anthers 1–1.2 mm long. Fruits 5–6 mm long, 4–6 mm diam., ellipsoid to oblate, red; pyrenes with 4–5 ridges.

Plants of montane rain forest formations, from (1000–)1700 to 2300(–2700?) m elevation. Flowering in January–October; fruiting in October and January–April. The species is known in Costa Rica only from the northwestern part of the central highlands (Monteverde to Vara Blanca). It is also found in the Chiriquí Highlands of western Panama.

Psychotria stockwellii is recognized by the nar-

rowly obovate leaves that dry dark above, many secondary veins, broadly ovate stipules, larger inflorescences with many orders of opposite branches, and higher-elevation habitat. The leaves drying pinkish gray or dark reddish gray beneath and the bright red fruit are characteristics of subgenus *Psychotria*. The type has the 1° branches of the inflorescence arising at angles of more than 100°, but this may have been a negatively geotropic response on a pendant branch. Recent collections from Panama suggest that this species may intergrade with *P. sylvivaga* (q.v.). Compare *P. chiriquina*, which has inflorescences with two unequal pairs of branches (4/node) at the first node.

Psychotria subsessilis Benth. in Oersted., *Vidensk. Meddel. Dansk. Naturhist. Foren. Kjobenhavn* 1852: 34. 1853.

A badly damaged isotype (*Oersted 11613* us) gives the impression that this may be an earlier name for *P. panamensis*. It does not appear to be *P. grandis* as annotated by Urban in 1913 and cited by Standley in 1938. It comes from an elevation in which the transition between the two subspecies of *P. panamensis* may occur. However, those subspecies are quite different and may be worthy of specific rank. Thus, there is both a nomenclatural problem and one of species delimitation here. The name and collection were not included in the monograph by Hamilton (1989).

Psychotria suerrensii J. D. Smith, *Bot. Gaz.* 27: 337. 1899. Figure 18.

Shrubs, 1–3(–4) m tall, leafy stems 1–5 mm thick, glabrous or minutely (0.1–0.2 mm) puberulent and glabrescent, often drying orange or reddish, terete; stipules with a short (1–3 mm) truncate sheath and 2 narrow lobes or awns 3–6 mm long on each side, glabrous or minutely puberulent, persisting. Leaves with petioles 3–8(–12) mm long, 1–1.8 mm thick, glabrous or very minutely (0.1 mm) puberulent; leaf blades 10–20(–25) cm long, 3–8(–11) cm broad, elliptic to ovate-elliptic or ovate-oblong, apex acuminate with tip 5–20 mm long, base obtuse or acute and slightly decurrent on petiole, drying chartaceous to stiffly chartaceous, greenish to brown above, glabrous above, sparsely and minutely puberulent on the veins beneath with thin whitish hairs 0.1–0.2 mm long, 2° veins 6–11/side, the larger veins often drying pinkish red beneath. Inflorescences terminal and solitary (or 3), 2.5–4 cm long, 3–5 cm broad, densely bracteate hemispheric (subcapitate) cymes or panicles (sometimes subumbellate), peduncles 7–28 mm long, 1.3–2 mm thick, minutely puberulent, bracts 12–20(–32) mm long, 3–6(–14) mm broad, oblanceolate to elliptic-obovate, green

to rose or dark purple in fruit, flowers sessile and hidden within bracts. **Flowers** distylous, with thin whitish hairs externally, hypanthium ca. 1 mm long, turbinate, calyx tube 0.3–0.8 mm long, lobes 0.3–0.5 mm long; **corolla** tubular-funnelform, white or white with pinkish coloring (violet), usually drying pinkish, tube 9–13 mm long, 0.8–1.2 mm diam. in lower half, 2 mm diam. distally, lobes 5, 2–4 mm long, ca. 1.5 mm broad at the base, triangular; anthers 2.5 mm long. **Fruits** 4–5 mm long (not including the 0.4–1-mm-high calyx) and 4–5 mm diam., subglobose or oblong, bright blue, purple or black, somewhat rugose when dried, glabrous or sparsely puberulent; pyrenes 3–3.5 mm long, smooth or with 3–5 ridges and slight transverse ribbing.

A common species of lowland rain forest formations, from 20 to 600 m elevation on the Caribbean slope and from 300 to 500 m on the Pacific slope (to 1000 m in Honduras). Flowering primarily in February–May; fruiting mostly in June–February. The species ranges from Honduras to central Panama.

Psychotria suerrensii is recognized by its short-petiolate leaves that often dry greenish and with veins reddish beneath, small two-lobed stipules, unusual subcapitate inflorescences with many large brightly colored persisting bracts, and longer corollas. The freshly cut pith turns red, as it does in *Simira*. While common in the Caribbean lowlands, this species is rare on the Pacific slope where it has not been collected below 300 m elevation. This species resembles *P. hoffmannseggiana* (with smaller bracts and inflorescences). Breeding biology was studied by Bawa and Beach (1983).

Psychotria suerrensii is closely related to *P. lupulina* Benth., a variable and wide-ranging species of South America (cf. Steyermark, 1974, pp. 1539–1544). If *P. lupulina* is circumscribed very broadly, it is probable that *P. suerrensii* will be included as a northern subspecies with consistently larger corollas and slightly ridged pyrenes.

***Psychotria sylvivaga* Standl., J. Wash. Acad. Sci. 18: 274. 1928. Figure 62.**

Shrubs or subshrubs, 1–4 m tall, leafy stems 1.2–4 mm thick, glabrous or sparsely puberulent (except for a ring of reddish hairs at the node); **stipules** 6–15 mm long, 3–7 mm broad, ovate, acute to obtuse, sometimes with a tubular sheath 10 mm long, glabrous and drying reddish brown, caducous. **Leaves** with petioles 6–26(–35) mm long, 0.6–1.8 mm thick, glabrous; **leaf blades** (6–)9–17 long, (2.5–)3–5.5 cm broad, elliptic-oblancoate to narrowly elliptic or elliptic-oblong, apex acute or short-acuminate, base tapering gradually and cuneate to acute, slightly decurrent on petiole, drying membranaceous to chartaceous, dark grayish or reddish brown, glabrous above, glabrous or minutely papillate-puberulent on the

veins beneath, 2° veins 8–12/side. **Inflorescences** terminal or becoming axillary, solitary, 5–16 cm long and 3–10 cm broad, usually an open panicle, peduncle 4–7(–12) cm long and 1 mm thick, to 10 cm in fruit, glabrous or sparsely puberulent, bracts 1–4 mm long, subulate, pedicels 1–2 mm long. **Flowers** glabrous on the outside, hypanthium ca. 0.7 mm long, obconic, calyx ca. 0.8 mm long, lobes ca. 0.4 mm long, obtuse; **corolla** white, tubular-salverform, tube 3–6 mm long, narrow (1.3 mm) or expanded distally to 2 mm diam., lobes 1–2 mm long, triangular. **Fruits** 5–9 mm long, not including the persisting (1–3 mm) calyx, 5–6 mm diam., subglobose, red.

Plants of montane forest formations, from 1300 to 2700 m elevation. Flowering in January–September; fruiting in November–December and March. The species ranges from the Cordillera de Tilarán to the Chiriquí Highlands of Panama.

Psychotria sylvivaga is recognized by its higher-elevation habitat, leaves usually widest above the middle and with ca. 10 pairs of secondary veins, larger narrowly ovate unlobed stipules, and longer corolla tube. The leaves drying dark grayish or reddish brown and the red fruit are characteristics of subgenus *Psychotria*. Recent collections from Panama make it appear that this species is more variable than previously thought. This includes material collected in the Cerro de la Muerte at about 2500 m elevation with more broadly elliptic leaves and somewhat larger flowers. In addition, a broader interpretation might require the inclusion of *P. stockwellii*.

***Psychotria tapantiensis* C. M. Taylor, sp. nov. Figure 57.**

Arbuscula 1–4 m alta, ubique dense pilosula. Folia laminis ellipticis, 8.5–23.5 cm longis, 4–10 cm latis, venis secundariis paribus 12–17 dispositis; petiolo 1–4 cm longo; stipulis vagina 2–3 mm longa atque lobulis deltoideis 1.5–2 mm longis munitis. Inflorescentia ex panícula terminali pyramidalis 8–12 cm longa, 5.5–12 cm lata, pedunculo 5–8 cm longo insidente constans; bracteis flores subtentibus ex ellipticis ovatis, 2–5 mm longis. Flores limbo calycino usque ad 0.5 mm longo, dentato; corolla infundibuliformi, tubo 5–7 mm longo, lobulis 1–1.5 mm longis. Fructus diametro 3–4 mm, atropurpureus.

TYPE—*R. L. Wilbur 30741* (holotypus DUKE), 10 Aug. 1980, Reserva Tapantí, 11 km above the Tapanti bridge, Cartago, Costa Rica.

Shrubs or small trees, (1–)2–4 m tall, leafy stems 2–8 mm thick, minutely puberulent to pilosulous with straight or curved hairs 0.1–0.3 mm long; **stipules** 2–6 mm long, sheath 2–3 mm long with 2 triangular lobes on each side 1.5–4 mm long, obtuse to rounded, glabrous. **Leaves** with petioles 1–4 cm long, 1.2–2 mm thick, minutely puberulent; **leaf blades** (8–)10–20(–23.5) cm long, (4–)4.5–

9(–10) cm broad, elliptic, ovate-elliptic to elliptic-oblong, apex acuminate with tip 8–15 mm long, base obtuse to acute, drying chartaceous, dark yellowish green or brownish green above, minutely (0.05–0.1 mm) puberulent above (barely visible but soft to the touch), softly puberulent beneath with yellowish hairs 0.1–0.4 mm long, 2° veins 11–17/side. **Inflorescences** terminal, pyramidal open panicles 8–25 cm long, 6–17 cm broad, peduncles 5–10(–15) cm long, 1–3 mm thick, minutely puberulent, bracts 6–8 mm long, 2–3 mm broad, lanceolate, flowers sessile in open distal cymes, bracteoles 2–5 mm long and 2–3 mm broad, often persisting in fruit. **Flowers** usually glabrous externally, hypanthium ca. 0.5 mm long, calyx lobes ca. 0.3 mm long, obtuse; **corolla** whitish to yellow, yellow-green or pink, tubular-funnelform, tube 5–7 mm long, 1.3–1.8 mm diam., lobes 1–1.5 mm long, triangular. **Fruits** 3–4 mm long, 3–4 mm diam., globose to oboate, becoming black or dark purplish; pyrenes with 4–5 sharp ridges, concave between them.

Plants of lower montane cloud forest formations on the Caribbean slope, at 1400–1600 m elevation. Flowering in March and June–August; fruiting in May–August. This species is known only from between Vara Blanca (Alajuela/Heredia) and the upper drainage area of Río Grande de Orosí, Cartago.

Psychotria tapantiensis is recognized by the large many-branched inflorescences usually with large persisting bracteoles, larger leaves softly puberulent beneath, and small blackish fruit. The species, a member of subgenus *Heteropsychotria*, is closely related to *P. luxurians* of lower elevations with narrower bracts and more rounded stipules. It may be easily confused with *P. berteriana* with stipules with two-angled lobes and smaller bracts. Early collections were mistakenly annotated as *P. palicouroides*. The species is common around the Refugio Nacional Tapantí.

***Psychotria tenuifolia* Sw.**, Prodr. 43. 1788. *P. sessilifolia* Martens & Galeotti, Bull. Acad. Roy. Sci. Bruxelles 11: 228. 1844. *P. granadensis* Benth. in Oerst., Vidensk. Meddel. Dansk. Naturhist. Foren. Kjobenhavn 1852: 34. 1853. Figure 65.

Shrubs or subshrubs, 0.3–2 m tall, leafy stems 1–5 mm thick, minutely (0.05–0.1 mm) papillate-puberulent or glabrous; **stipules** 6–14 mm long, 4–6 mm broad at base, triangular to ovate with 2 closely spaced lobes 1–6 mm long, the lobes narrowly triangular to linear, drying reddish brown, deciduous. **Leaves** often closely clustered distally, petioles 2–25(–40) mm long, 0.6–2 mm broad, glabrous; **leaf blades** (3.5–)6–20(–23) cm long, (1.5–)2–6.5(–7.7) cm broad, narrowly elliptic to oblanceolate, elliptic or lanceolate, apex usually tapering gradually and acute (obtuse or short-acuminate), base cuneate to acute

and decurrent on petiole, drying membranaceous to thin-chartaceous, grayish or dark grayish brown above, glabrous above, glabrous or sparsely to densely puberulent beneath with thin whitish hairs 0.05–0.2 mm long, 2° veins 7–13/side, loop-connected distally to form a thin-arcuate submarginal vein. **Inflorescences** terminal or becoming axillary, 1–6/node, 1.5–4 cm long, 2–3 cm broad, open paniculate, peduncles 5–20 mm long, 0.5–1.3 mm thick, minutely puberulent, bracts and bracteoles 0.5–1 mm long, subulate, flowers sessile or on short (1 mm) pedicels in dense distal clusters of 3–5. **Flowers** minutely papillate-puberulent or glabrous externally, hypanthium ca. 0.5 mm long, calyx 0.2–0.5 mm long, lobes ca. 0.3 mm long, obtuse; **corolla** salverform, white or yellowish green, tube 1.5–2 mm long, 0.8–1 mm diam., lobes 5, 1–1.8 mm long, ca. 1 mm broad at the base, triangular, barbate in throat; **stamens** 5, anthers 0.5–0.7 mm long. **Fruits** 4–5 mm long, 3–4 mm diam., usually ellipsoid, red; pyrenes with ca. 5 low rounded ridges.

Plants of both deciduous woodlands and evergreen premontane moist forest formations, from near sea level to 800(–1100) m elevation in Costa Rica (to 2000 m elsewhere). Flowering in April–August in southern Central America; fruiting throughout the year but primarily in July–December. The species ranges from Mexico to eastern Panama and occurs in southern Florida, Cuba, and Hispaniola.

Psychotria tenuifolia is recognized by its short stature, thin (often narrow) leaves with slender arcuate submarginal vein, biacuminate deciduous stipules, usual presence of thin whitish hairs, clusters of short umbelliform panicles, small ellipsoid fruit, and preference for deciduous woodlands (in Costa Rica). The tendency of leaves to dry grayish and the bright red fruit are characteristics of subgenus *Psychotria*. This is a variable species, in both morphology and ecology. It has rarely been collected outside of lowland Guanacaste in Costa Rica; it has not been collected in the eastern half of Costa Rica or the western half of Panama. Compare *P. pubescens*.

***Psychotria trichotoma* M. Mart. & Galeotti**, Bull. Acad. Roy. Sci. Bruxelles 11: 227. 1844.

This species does not appear to occur in Costa Rica. It ranges from southern Mexico to central Nicaragua and is found also in Venezuela and Ecuador. The records for Panama were misidentifications (Hamilton, 1989). This species belongs to subgenus *Psychotria* and is part of a group including *P. carthaginensis*, *P. chagrensis*, *P. limonensis*, *P. quinqueradiata*, and *P. tenuifolia*. This species is recognized by the larger (10–26 × 6–15 cm)

leaves with ca. 15 2° veins per side, larger (7–16 cm) inflorescences, and larger (6–8 mm) obovoid fruit.

***Psychotria turrubarensis* Burger & Q. Jiménez, Brenesia (in press).**

Shrubs, ca. 4 m tall, leafy stems 1.3–3.5 mm thick, glabrous, drying pale grayish; **stipules** 12–16 mm long, 3–4 mm broad at the base, lanceolate, forming a calyptrate sheath over the shoot apex and splitting along 1 side, broadly ovate (ca. 10 × 10 mm) below the young inflorescences, drying dark reddish brown, caducous. **Leaves** opposite or apparently in a whorl of 4 when an internode fails to develop, petioles 5–18 mm long, 1.1–2.3 mm broad, glabrous and drying dark; **leaf blades** 7–13 cm long, 3–5.5(–6.5) cm broad, elliptic to elliptic-oblong or narrowly elliptic-obovate, apex acute to bluntly obtuse, base acute to cuneate and slightly decurrent on petiole, drying stiffly chartaceous, grayish, glabrous above and below, 2° veins 5–9/side, deep rounded pit domatia (0.2–0.4 mm) usually present in vein axils beneath. **Inflorescences** terminal or pseudoterminal, solitary, sessile capitula, 8–16 mm long, 10–15 mm broad, at first enclosed by the broad bracteate stipules, bracteoles to 2 mm long, difficult to see among the villous-arachnoid hairs, flowers sessile or subsessile. **Flowers** with corolla appendages separate in bud, hypanthium ca. 1 mm long, calyx with villous yellowish hairs, lobes 5, ca. 1 mm long; **corolla** white, salverform, glabrous externally, corolla tube to 5 mm long, 2 mm diam. distally, with dense thin hairs within the throat, lobes ca. 3 mm long and 1 mm broad, with a thickened rounded appendage ca. 0.3 mm diam. **Fruits** 7–8 mm long, 6–9 mm thick, subglobose, red at maturity and subsessile, surface smooth; pyrene 7 × 6.5 mm, flat on the inner (adaxial) face, with 5 longitudinal sulci abaxially.

Plants of evergreen forest on the Pacific slope in central Costa Rica at about 1600 m elevation. Flowering and fruiting on 6 November 1989 (Q. Jiménez *et al.* 935 CR holotype, f). This species is known only from the Faldas del Cerro Bares in the Zona Protectora de Turrubares, San José Province.

Psychotria turrubarensis is distinguished by its small sessile capitate inflorescences, united stipules forming a calyptrate *Ficus*-like sheath over the vegetative shoot apices, lack of puberulence on vegetative parts, well-developed pit domatia, and appendage at the tips of the corolla lobes. The red fruit and leaves drying grayish are characteristics of subgenus *Psychotria*. The Cerros de Turrubares are a conspicuous feature at the southwestern perimeter of the Meseta Central, but they are isolated and have been little explored. It is surprising that so small an area should harbor such a distinctive new species.

***Psychotria uliginosa* Sw., Prodr. 43: 1788. Figure 12.**

Herbaceous **subshrubs**, 0.5–1.5 mm tall, stems usually unbranched and succulent, leafy stems 2–12 mm thick, terete and often thickened at the nodes, glabrous; **stipules** 3–6 mm long in early stages, shorter and broader (to 10 mm) in age, with a short (2–4 mm) sheath, broadly obtuse or truncate distally, glabrous and persisting. **Leaves** well spaced along the stem, petioles 2–6 cm long, 1.5–3 mm thick, glabrous; **leaf blades** (11–)15–35 cm long, (3–)5–13 cm broad, narrowly elliptic-oblong to elliptic-obovate or elliptic-oblong, apex gradually or abruptly narrowed and short-acuminate, tip 3–10 mm long, base cuneate or acute and slightly decurrent on petiole, slightly succulent in life but drying chartaceous, dark green above and pale green beneath in life but becoming dark brown above when dried and much paler beneath, glabrous above and below, 2° veins 9–15/side. **Inflorescences** axillary, usually 1/node, 2–5 cm long at anthesis, to 10 cm long in fruit, 2–8 cm broad, open pyramidal panicle with usually 3 main branches and flowers in dense distal congested clusters, peduncles 1–6 cm long, ca. 1.5 mm thick, glabrous, bracts 2–4 mm long, narrowly triangular, flowers sessile. **Flowers** glabrous or rarely sparsely and minutely puberulent externally, hypanthium and calyx 1.5–2.5 mm long, obconic or cylindrical, calyx tube truncate or with minute (0.2 mm) lobes; **corolla** white or pinkish, tube 1–2.5 mm long and ca. 0.7 mm diam., lobes 0.5–1.5 mm long. **Fruits** 7–10 mm long, 6–8 mm diam., oblong or ovoid, bright red or orange-red; pyrenes ca. 8 mm long, with 1 prominent ridge and 2 thickened margins.

Plants of shaded understory in wet evergreen rain forest formations on both the Caribbean and Pacific slopes, from near sea level to 900(–1100) m elevation. Probably flowering throughout the year; fruiting in all months. This species ranges from Mexico and the West Indies to Ecuador and the Guianas.

Psychotria uliginosa is recognized by its short usually unbranched semisucculent stems, short truncated stipules (in age), large glabrous leaves dark above and pale beneath, axillary inflorescences with congested little flowers, and bright red fruit. This distinctive species is uncommon on the Pacific slope. The general aspect of these plants is similar to *P. macrophylla* and *P. aggregata*, but those species have white fruits and the leaves drying greenish without so great a color contrast between the upper and lower surfaces.

***Psychotria umbelliformis* Dwyer & Hayden, Ann. Missouri Bot. Gard. 55: 44. 1968. Figure 47.**

Shrubs or small treelets to 2 m tall, leafy stems 2–6 mm thick, densely pubescent with stiff yellowish hairs ca. 0.5 mm long; **stipules** united around stem 1–2 mm,

with 2 slender distal awns 4–11 mm long, puberulent, deciduous. **Leaves** with slender petioles (4–)7–25 mm long, 1–2.2 mm thick, densely pubescent; **leaf blades** (6–)8–18(–26) cm long, (3–)5–8(–9) cm broad, ovate-elliptic to elliptic-oblong, apex tapering gradually and acuminate or acute with tip to 2 cm long, base acute to obtuse, drying chartaceous, dark green above, glabrous above and with small (0.1–0.2 mm) whitish cystoliths visible, pubescent beneath with thin yellowish hairs 0.3–0.6 mm long especially on major veins, 2° veins 7–9/side, distal veins arcuate-ascending. **Inflorescences** terminal and solitary, 5–8 cm long, 3–6 cm broad, umbelliform, peduncles 3–5 cm long, 1.5–2 mm thick, densely pubescent, with 3 primary branches 1–2 cm long bearing terminal capitulae 6–10 mm broad, bracts ca. 7 mm long and 3 mm broad at the base, flowers sessile in glomerules of 3–8, subtended by bracteoles ca. 4 mm long, ovate-triangular. **Flowers** puberulent externally, calyx ca. 2.5 mm long, lobes to 0.8 mm long, obtuse or acute; **corolla** salverform, yellowish white and greenish, tube ca. 12 mm long, lobes ca. 8 mm long; **stamens** 5, anthers ca. 2 mm long. **Fruits** 15–18 mm long, oblong, glabrous and smooth, black; pyrenes smooth.

Plants of evergreen lower montane forest formations and lowland rain forest formations, from near sea level to 1500 m elevation. Flowering in July–August. Rarely collected plants of the Caribbean slopes and lowlands; known only from Costa Rica and Panama.

Psychotria umbelliformis is recognized by the pilosulous hairs on nearly all surfaces (except the upper leaf surfaces), longer petioles, umbelliform inflorescences with three distal capitula or glomerules of sessile flowers, and longer corollas. This species is poorly known. We have seen only the following collections from Costa Rica: *Croat 36753* CR, MO, US, and *Standley 36775* US.

Psychotria valeriana Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 1363. 1938. Figure 56.

Shrubs, (1–)1.5–3(–4) m tall, leafy stems 0.7–3 mm thick, glabrous and smooth, internodes usually becoming elongated (4–15 cm); **stipules** with short-truncate collar-like sheath 0.3–2 mm long and 1 central distal awn 2–4 mm long that may be split (bifid) near the tip (rarely bifid to the base), often with 1 (rarely 2) thickened “teeth” ca. 1 mm long borne on the adaxial side from the base of the awn, glabrous, persisting. **Leaves** with petioles 4–9(–12) mm long, 0.5–1.3 mm thick, glabrous; **leaf blades** 7–13(–15) cm long, 2.3–4(–5.5) cm broad, narrowly ovate-elliptic to elliptic, lanceolate-oblong or narrowly elliptic-oblong, apex acuminate or narrowly acute with tip 5–12 mm long, base acute (obtuse) and slightly decurrent on petiole, drying thin-chartaceous and olive green to greenish brown above, glabrous above and below, 2° veins 5–8/side. **Inflorescences** terminal and solitary (3), 1.5–5 cm long, 1.5–3 cm broad, small open pyramidal panicles with usually 2 pairs of opposite branches, peduncles 4–

18 mm long, ca. 1 mm thick, glabrous, bracts 2–3 mm long, linear, flowers subsessile in distal cymes, pedicels 0–1 mm long. **Flowers** glabrous externally, hypanthium ca. 0.8 mm long, cylindric or obconic, calyx tube ca. 0.3 mm long, truncate; **corolla** tubular, white, tube 1.8–3.5 mm long and ca. 1 mm diam., lobes 4, 0.4–1.5 mm long; **stamens** 4, anthers 0.8–1.1 mm long. **Fruits** 4–5 mm long and 5–6 mm diam., smooth and bilobed or globose, yellow or orange and becoming black and lustrous.

Understory plants in lower montane cloud forest formations on the Caribbean slope and continental divide, from 800 to 1600(–1900) m elevation. It has been collected at about 450 m elevation on Volcán Orosí, a pattern of unusually low elevation seen in a number of other species. Flowering in May–July; fruiting in October–March. In Costa Rica nearly all our collections coming from the Cordillera de Tilarán and from north of San Ramón, Alajuela. The species ranges eastward into Panama.

Psychotria valeriana is recognized by the very unusual stipular morphology, lack of pubescence, small inflorescences with little flowers, restricted flowering period, and fruits usually without prominent longitudinal ribs. The single stipular awn is occasionally deeply bifid but always arises at one point in the center of the distal stipule margin. The tooth-like appendage on the inner (adaxial) surface of the awn is unique among our species. Unlike most of our other species of subgenus *Heteropsychotria*, the fruit is orange during later stages. This species is very similar to *P. acuminata* of lower elevations, but the stipular morphology helps to separate the two.

Psychotria viridis Ruiz & Pav., Fl. Peruv. 2: 61, pl. 210. 1799. *P. glomerata* H.B.K., Nov. gen. sp. 3: 362 (quarto). 1819. *P. microdesmia* Oerst., Vidensk. Meddel. Dansk. Naturhist. Foren. Kjobenhavn 1852: 36. 1853. Figure 65.

Shrubs, 1.5–5 m tall, leafy stems 1.5–4 mm thick, glabrous; **stipules** 7–14 mm long, 3–5 mm broad, obovate, acuminate and fimbriate along the distal edge, glabrous, membranaceous and drying reddish brown. **Leaves** often closely clustered distally, petioles 3–9 mm long, 0.5–1.3 mm thick, glabrous; **leaf blades** 5–15 cm long, 2–5.5 cm broad, elliptic-obovate to oblanceolate or obovate, apex acute or short-acuminate, base tapering gradually and acute or cuneate, decurrent on the petiole, drying thin-chartaceous, pinkish gray or light to dark gray above, glabrous above and below, 2° veins 5–7/side, large (1–2 mm) pit domatia often present in the axils of distal veins beneath. **Inflorescences** terminal and solitary, 4–10 cm long, spiciform with verticillate groups of flowers or with 1(–2) pair(s) of opposite lateral branches

above the peduncle, peduncles 10–30 mm long, ca. 1 mm thick, glabrous, flowers sessile in verticils of 4–8 separated by 5–15 mm. **Flowers** glabrous externally, hypanthium ca. 0.5 mm long, calyx ca. 0.3 mm long, subtruncate; **corolla** urceolate, white, tube ca. 1.5 mm long and 1 mm diam., lobes 5, ca. 1 mm long. **Fruits** 4–6 mm long, 4–6 mm diam., globose or ellipsoid, turning red; pyrenes with 4–5 rounded ridges.

Rarely collected plants (in Costa Rica) of evergreen Caribbean rain forest formations and in the General Valley, from near sea level to 700(–900) m elevation in Costa Rica. Flowering in March, and October–January; probably fruiting throughout the year. The species ranges from Cuba, Belize, and Guatemala to Bolivia.

Psychotria viridis is distinguished by the thin narrowly obovate leaves with large domatia, broad thin stipules often fimbriate and caudate-acuminate at the apex, and the unusual inflorescences with few or no lateral branches and the flowers in well-separated verticils. No other Costa Rican *Psychotria* has such an inflorescence. The red fruit and leaves drying grayish are characteristics of subgenus *Psychotria*. The few Costa Rican collections come from the Caribbean lowlands in central and southern Costa Rica (not known from La Selva) and the slopes of the Talamanca mountains. It is more common in South America.

Psychotria sp. A, Cocos Island, subgenus *Heteropsychotria*, not matched.

Shrubs or small trees, leafy stems 0.9–2 mm thick, glabrous, with minute longitudinal striations; **stipules** 1–2 mm long, with a small U-shaped sinus 0.7–1.2 mm deep separating the 2 acute lobes, glabrous, persisting or breaking off. **Leaves** with petioles 3–15 mm long, 0.4–1 mm thick (dried), glabrous; **leaf blades** 5.5–10 cm long, 1.7–3.7 cm broad, narrowly ovate-elliptic to elliptic-lanceolate or elliptic, apex gradually narrowed and acuminate with tip 5–10 mm long, base obtuse to acute and slightly decurrent on petiole, drying membranaceous to thin-chartaceous, greenish brown above, glabrous above or below, 2° veins 5–8/side. **Inflorescences** solitary and terminal, 5–9 cm long, open panicle with 2 lateral branches at first node, peduncles 3–5 cm long, 0.5–1 mm thick, glabrous, bracts to 9 mm long and linear, flowers in distal thin-branched dichasia of 3–5 or short helicoid cymes, pedicels 0–4 mm long. **Flowers** not seen at anthesis, hypanthium ca. 1 mm long and 0.7 mm diam., calyx cupulate, lobes 0.5–1 mm long, triangular and acute. **Fruits** ca. 4 mm long (not including the 1 mm long persisting calyx), ca. 3.5 mm diam., ovoid-ellipsoid, black; pyrenes 4–5 angled.

This species is presently known from only a single collection from Cocos Island: *Holdridge 5168*

(CR, F, US) collected in late February 1963. The species is characterized by its thin smaller elliptic-lanceolate leaves, short stipules with small distal lobes, few-flowered inflorescences with slender peduncles, and very slender elongate branches and pedicels. The well-developed calyx lobes and lack of puberulence are also noteworthy. It appears to be a species of Colombia.

Psychotria sp. B, subgenus *Psychotria* aff. *P. papantlense* (Oerst.) Hemsl.

Small trees, 1–4 m tall, leafy stems 0.9–3.5 mm thick, glabrous and pale grayish, smooth; stipules sheathing, 4–9 mm long, acute (or biaristate), reddish when dried, caducous. **Leaves** with petioles 5–35 mm long, 0.5–1.2 mm thick, glabrous; **leaf blades** 6–11 cm long, 1.8–4 cm broad, narrowly elliptic-oblong to narrowly oblong, acuminate at the apex, tapering gradually to the cuneate attenuate base and decurrent on the petiole, drying thin-chartaceous and grayish green, glabrous above and below, 2° veins 7–9/side. **Inflorescences** not seen at anthesis, 5–9 cm long, apparently with only 2 lateral branches at the first node, with few branches and few (1–4) fruits, peduncles 2–3 cm long, 1.6 mm thick, glabrous. **Flowers** not seen at anthesis. **Fruits** 6–10 mm long, 4–6 mm diam., ellipsoid, purple at maturity.

The thin long-decurrent gray-green leaves and open few-fruited infructescences are reminiscent of *P. papantlense*, but that species usually has inflorescences with four branches at the first node and is not known south of Belize and southern Mexico. This description is based on *Haber et al. 4440* (CR, MO) from 1000 m elevation near Tilarán; fruiting in April. This may be an atypical southern extension of *P. papantlense* or perhaps a new species.

Randia Linnaeus

Shrubs, trees, or lianas, bisexual or unisexual (dioecious), glabrous or puberulent, nodes often with 1–4 axillary or extraaxillary spines; **stipules** interpetiolar, small and triangular to tubular (intrapetiolar) at the base, often imbricate on the short-shoots. **Leaves** opposite or fasciculate on short-shoots, sessile or petiolate, membranaceous to coriaceous, entire, rarely with domatia of tufted hairs in the vein axils. **Inflorescences** terminal or axillary (rarely cauliflorous), of solitary flowers or with few fasciculate or rarely cymose flowers, sessile or pedicellate, often subtended by bracteate stipules. **Flowers** unisexual and dioecious or monoecious, less often bisexual, 4–7-parted, hypanthium cupulate to tubular, truncated distally and with slender or expanded (foliaceous) calyx lobes; **corolla** salverform or funnellform, white or pale yellow, glabrous or villous within, tube short to

long, lobes (4-)5-6(-7), convolute in bud; **stamens** usually 5, inserted in the distal part of the tube, filaments short or absent; **ovary** basically 1-locular, ovules many in 3-4 tiers on the 2 fleshy parietal placentas. **Fruits** baccate, 1-locular or becoming 2-locular, globose to ellipsoid with a thick coriaceous pericarp; **seeds** discoid, arranged horizontally in a gelatinous pulp.

Randia is now considered to be a Neotropical genus of 60-70 species, ranging from southern Florida and Texas through Central America and the West Indies to Bolivia. Our treatment follows the annotations and advice of David Lorence (PTBG). He distinguishes *Randia* from other genera of the Gardineae by the following combination of characters: (1) a unilocular ovary with parietal placentas that may abut in fruit and give the ap-

pearance of bilocularity, (2) many discoid seeds imbedded in sweet pulp becoming brown or black, (3) a seed coat with thick-walled testa cells having a smooth or papillose inner wall, and (4) pollen in permanent tetrads (rarely diads or monads).

Species of *Randia* are characterized by the usually terminal solitary flowers or few-flowered inflorescences, salverform white or yellowish corollas with convolute lobes in bud, and hard-surfaced baccate fruit with many horizontal discoid seeds. A number of species have conspicuous short-shoots with tightly clustered distal leaves, and many species have conspicuous sharp-tipped spines. The great variability of leaf size and form, dioecy, and spiny branches that discourage collectors make this a taxonomically difficult genus.

Key to the Species of *Randia*

- 1a. Plants lianas or vines 2
- 1b. Plants trees or shrubs 4
 - 2a. Plants glabrous, spines usually solitary and recurved *R. altiscandens*
 - 2b. Plants puberulent to pilose, spines opposite or in 4's at each node 3
 - 3a. Spines usually 4/node; ♂ corolla tubes ca. 8 cm long, ♀ corolla tubes ca. 5 cm long *R. vazquezii*
 - 3b. Spines usually opposite; ♂ corolla tubes 4-5 cm long, ♀ corolla tubes 3-3.5 cm long *R. retroflexa*
- 4a. Fruits cauliflorous and more than 4 cm diam.; flowers cauliflorous or axillary, more than 5 cm long; leaf blades often exceeding 25 cm in length and with 10-16 pairs of 2° veins; plants of wet evergreen forests [10-700 m elevation] 5
- 4b. Fruits usually borne in among the leaves, less than 3 cm diam. if cauliflorous; flowers axillary or terminal, 2-10 cm long; leaf blades rarely exceeding 25 cm in length or with more than 10 pairs of 2° veins (except *R. genipoides*); plants of wet evergreen to dry deciduous forests 6
 - 5a. Corolla tube 5-8 cm long, flowers cauliflorous; leaf blades cuneate at the base ... *R. mira*
 - 5b. Corolla tube ca. 4.5 cm long, flowers often axillary; leaf blades slightly rounded or subtruncate at the base *R. pterocarpa*
- 6a. Leaves of the same node differing greatly in size and the larger leaves more than 10 cm long [hypanthium and calyx sometimes with minute red glands] *R. gentryi*
- 6b. Leaf blades about the same size at each node or the larger blades less than 5 cm long if differing greatly in size 7
- 7a. Mature flowers present 8
- 7b. Mature fruit present 19
 - 8a. Calyx lobes laminar, nearly as broad as long, obtuse or rounded distally and with a narrowed petiole-like base [evergreen forests 800-2300 m elevation] *R. calycosa*
 - 8b. Calyx lobes not laminar, narrowly triangular or awned, lacking a narrowed petiole-like base 9
 - 9a. Corolla tube less than 2 cm long 10
 - 9b. Corolla tube more than 2 cm long 14
 - 10a. Largest leaf blades less than 6 cm long, often appearing to be very unequal at the same node or short-shoot, with 3-4 pairs of 2° veins 11
 - 10b. Larger leaf blades more than 6 cm long, usually equal or subequal at a node, with 2-11 pairs of 2° veins 12
 - 11a. Calyx lobes minute or absent; leaf blades to long, often obovate; wet forests 20-500 m elevation *R. loniceroides*

- 11b. Calyx lobes 1–2 mm long; leaf blades to 6 cm long, usually elliptic; dry deciduous forests 0–300 m elevation *R. thurberi*
- 12a. Calyx lobes 0–1 mm long; corolla tube 3–7 mm long; evergreen and deciduous formations [0–900 m elevation] *R. aculeata*
- 12b. Calyx lobes 1–9 mm long, corolla tube 8–18 mm long; wet evergreen formations 13
- 13a. Calyx lobes 1–4 mm long, corolla tube 10–18 mm long; 0–1100 m elevation *R. grandifolia*
- 13b. Calyx lobes 5–9 mm long, corolla tube 8–14 mm long; 1000–2300 m elevation *R. calycosa*
- 14a. Largest leaf blades less than 6 cm long, often very different in size at the same node [corolla tube 25–45 mm long, wet evergreen forests] *R. brenesii*
- 14b. Largest leaf blades more than 10 cm long, usually similar in size at each node 15
- 15a. Corolla tube 20–50 mm long 16
- 15b. Corolla tube 50–90 mm long 18
- 16a. Calyx lobes 1–3 mm long; cloud forests, 1300–1600 m elevation *R. matudae*
- 16b. Calyx lobes 3–6 mm long; lowland evergreen forests, 0–800 m elevation 17
- 17a. Petioles to 10 mm long, leaf blades rarely more than 6 cm broad; widespread *R. armata*
- 17b. Petioles ca. 20 mm long, leaf blades usually more than 10 cm broad; rarely collected plants of the Caribbean lowlands *R. grayumii*
- 18a. Calyx lobes ca. 4 mm long; leaf blades to 16 cm long, elliptic to ovate *R. pittieri*
- 18b. Calyx lobes 11–25 mm long; leaf blades to 35 cm long, oblanceolate *R. genipoides*
- 19a. (from 7b) Fruits 10–15 mm long, globose 20
- 19b. Fruits 15–100 mm long, globose to ovoid or ellipsoid 21
- 20a. Leaf blades 6–30 mm long, rounded to bluntly obtuse at the apex, 2° veins 3–4/side; spines usually absent; wet forests, 20–500 m elevation *R. loniceroides*
- 20b. Leaf blades 8–90 mm long, acute to bluntly obtuse at the apex, 2° veins 3–8/side; spines usually present; dry or wet forests, 0–1700 m elevation *R. aculeata*
- 21a. Fruits 15–40 mm long 22
- 21b. Fruits 40–100 mm long 28
- 22a. Leaf blades not exceeding 6 cm in length 23
- 22b. Larger blades regularly exceeding 6 cm in length 25
- 23a. Leaf blades to 4 cm long, often differing greatly in size at the same node [wet evergreen forests, 100–1600 m elevation] *R. brenesii*
- 23b. Leaf blades to 6 cm long, usually equal or subequal at the same node 24
- 24a. Persisting calyx 0–2 mm high; dry deciduous forests, 0–300 mm elevation *R. thurberi*
- 24b. Persisting calyx 6–15 mm high; evergreen montane forests, 1000–2300 m elevation .. *R. calycosa*
- 25a. Leaf blades often oblanceolate to obovate; stipules with a short awn 1–2 mm long; evergreen forests, 1000–2300 m elevation *R. calycosa*
- 25b. Leaf blades never oblanceolate, sometimes obovate; stipules acute or with a narrow tip; evergreen or partly deciduous forests, 0–1100 m elevation 26
- 26a. Spines absent; leaf blades 17–28 cm long, minutely (0.05 mm) puberulent or glabrous beneath; stipules somewhat striate; sepal lobes (on fruits) to 5 mm long and narrow; Caribbean lowlands *R. grayumii*
- 26b. Spines usually present, and without the above combination of characters; widespread species 27
- 27a. Spines often 4/node; leaf blades 3–18 cm long, usually puberulent and often with tufted domatia in the vein axils; deciduous to evergreen formations *R. armata*
- 27b. Spines 2/node; leaf blades 7–30 cm long, glabrous and without tufted domatia in vein axils; evergreen formations *R. grandifolia*
- 28a. (from 21b) Stipules 15–25 mm long; leaves closely clustered at the ends of branchlets, blades 14–35 cm long, oblanceolate to narrowly elliptic [evergreen forests, 50–500 m elevation] *R. genipoides*

- 28b. Stipules rarely exceeding 5 mm in length; leaves not more than 16 cm long if closely clustered at the ends of stems, blades to 22 cm long and never oblanceolate 29
- 29a. Plants of cloud forests, 1300–1600 m elevation; spines absent, leaves and stems glabrous, leaf blades stiffly chartaceous to subcoriaceous *R. matudae*
- 29b. Plants of lowland evergreen or partly deciduous forest formations, 0–1000 m elevation; spines often 4/node, leaves and stems puberulent, blades membranaceous to thin-chartaceous 30
- 30a. Leaf blades with 3–7 pairs of secondary veins, 4–11 cm long; deciduous forests ... *R. monantha*
- 30b. Leaf blades with 9–12 pairs of secondary veins, 7–16 cm long; evergreen and partly deciduous forests *R. pittieri*

***Randia aculeata* L., Sp. Pl. 1192. 1753. *R. mitis* L., Sp. Pl. 1192. 1753. *R. karstenii* Polak., Linnaea 41: 568. 1877, fide Lorence in herb. Figure 22.**

Shrubs or small trees, 1.5–3(–5) m tall, dioecious, bark smooth and gray, leafy stems 1.2–4 mm thick, glabrous or rarely puberulent, spines 6–20 mm long, 1.5–3 mm diam. near the base, opposite and lateral, erect or ascending, sometimes terminating the stem and Y-shaped; **stipules** 1–3 mm long, 1–3 mm broad, broadly triangular, thin, brownish, sparsely puberulent, without clear venation. **Leaves** usually closely congested on short-shoots, opposing leaves subequal, smallest leaves sessile, petioles 0.5–12 mm long, 0.5–1 mm broad; **leaf blades** (0.8–)1.2–6(–9) cm long, (0.4–)0.8–3(–4) cm broad, ovate to elliptic-ovate, obovate or obovate-orbicular, apex bluntly obtuse to rounded, base tapering gradually and cuneate, decurrent on petiole, drying stiffly chartaceous, dark or pale grayish, glabrous (rarely puberulent), 2° veins 3–8/side. **Inflorescences** terminal on the short-shoots along the stem or apparently axillary, flowers usually solitary, pedicels absent or undifferentiated from the ovary base. **Flowers** functionally unisexual, usually glabrous externally, hypanthium 0.5–1 mm long, calyx tube becoming 1–1.5 mm high, ca. 2 mm broad, calyx lobes 4–5, ca. 0.5 mm long; **corolla** salverform, white, glabrous externally, tube 3–8 mm long, 1.5–3 mm diam., lobes 4–5(–6), 3–6 mm long, 2 mm broad at the base, acute. **Fruits** terminal on small short-shoots and appearing to be axillary, (8–)10–14 mm long, (7–)8–14 mm diam., subglobose to ovoid, greenish becoming white, persisting calyx tube 1–2 mm high and 1.5–2 mm broad, pericarp ca. 1 mm thick.

Plants of partly deciduous and evergreen forest formations on both the Caribbean and Pacific slopes, from near sea level to 1700 m elevation. Flowering in May; fruiting in January, June, and November. This species ranges from Mexico, Florida, and the West Indies to Colombia and Venezuela.

Randia aculeata is recognized by the small distally rounded leaves closely clustered on short-shoots, presence of paired spines, smaller flowers, and white fruit. Our collections are essentially glabrous but *R. aculeata* variety *dasyclada* Steyerm. often has hirtellous stems; it is found along the Caribbean coast of Panama. Specimens formerly

assigned to *Randia karstenii* have thinner leaves that dry dark and have been found at higher (1000–1700 m) elevations or in evergreen forests. We follow Lorence in including this material under *R. aculeata*. More typical material of *R. aculeata* is found in the drier parts of the Meseta Central where it is called *espino blanco*. Considerable morphological variation occurs throughout the range of this species, making it a difficult species complex (D. Lorence, pers. comm.).

***Randia altiscandens* (Ducke) C. M. Taylor, comb. nov. *Basanacantha altiscandens* Ducke, Arq. Inst. Biol. Veg. Rio Janeiro 2: 172. 1935. *R. pepoformis* Dwyer, Ann. Missouri Bot. Gard. 67: 451. 1980. Figure 23.**

Lianas to over 30 m high, dioecious, leafy stems 2–6 mm thick, glabrous, terete, yellowish becoming grayish with age, with usually solitary recurved or retrorse spines 10–20 mm long, 3 mm thick at the base; **stipules** 3–5 mm long, 2–3 mm broad at the base, triangular to oblong with obtuse apex, free or united to form a short (0.5 mm) tube. **Leaves** clustered near the ends of branchlets, petioles 5–12(–20) mm long, 0.9–1.9 mm broad, glabrous; **leaf blades** 10–18(–24) cm long, 4–9(–12.5) cm broad, elliptic to elliptic-obovate or obovate, apex obtuse to acute, base obtuse to cuneate and slightly decurrent on petiole, drying chartaceous to subcoriaceous, grayish above, glabrous above and below, 2° veins 5–8/side and loop-connected at the margin in the distal half of the blade, 3° veins subparallel and raised on both surfaces. **Inflorescences** terminal, of 1–3 ♂ flowers or solitary ♀ flowers, peduncles of the flower groups 0–10 mm long, pedicels 18–22 mm long, ca. 2 mm thick, glabrous, undifferentiated from the hypanthium. **Flowers** unisexual, glabrous externally, hypanthium 2–3 mm diam., continuous with the pedicel, calyx tube ca. 1 mm long, calyx lobes 5–6, 5–30 mm long, 1–6 mm broad, narrowly elliptic-oblong to lanceolate-oblong, with a primary vein and parallel secondaries, acute at the apex, narrowed at the base, stiffly chartaceous; **corolla** salverform, white, yellow and pilose within the tube, tube 30–50 mm long, 3–5 mm diam., to 10 mm at the throat, lobes 5(–6), 18–26 mm long, 14–18 mm broad, rounded distally; anthers 6.5–8 mm long. **Fruits** 5–9 cm long, 3–5.5 cm diam., ovoid to cylindrical, glabrous and lenticellate, drying black, borne on pedicels to 3 cm long, persisting calyx

ca. 6 mm long and 8 mm diam., pericarp 3–5 mm thick; seeds ca. 11×8 mm, oblong-ellipsoid.

Plants of rain forest formations on both the Caribbean and southern Pacific slopes in Costa Rica, 0–400 m elevation, to 1300 in Panama. Flowering in January, March, and May–October; fruiting in February and August. This species is known from the La Selva research site, the Hitoy Cerere reserve in the Caribbean lowlands, and Corcovado National Park (Osa Peninsula); it ranges southward into the Amazon basin.

Randia altiscandens is distinguished by its climbing habit, usually solitary retrorse spines, prominent subparallel 3° venation, large mostly solitary unisexual flowers, and large oblong fruit. Both corollas and fruit dry black, but the leaves and calyx lobes dry pale grayish. The calyx lobes vary greatly in length in different plants.

***Randia armata* (Sw.) DC., Prodr. 4: 387. 1830.**
Gardenia armata Sw., Prodr. 51, 1788. *Mussaenda spinosa* Jacq., Stirp. Am. 70. 1763. *Randia spinosa* (Jacq.) Karst., Fl. Colomb. 2: 128. 1869, not *R. spinosa* (Thunb.) Poir., 1812. Figure 22.

Shrubs or small trees, 3–6(–10) m tall, dioecious, leafy stems 1–4 mm thick, glabrous or puberulent with minute (0.2–0.3 mm) thin whitish hairs, glabrescent, spines present or absent, usually 4/node, 6–18(–25) mm long, 1–2 mm thick at the base, ascending; **stipules** 4–9 mm long, 2–4 mm broad at the base, brownish, with many parallel veins, glabrous (longer hairs within at the base), often persisting. **Leaves** usually closely crowded at ends of stems or short-shoots, petioles 3–6(–11) mm long; **leaf blades** (2.5–)4–15(–19) cm long, (1.5–)2–6(–10) cm wide, broadly elliptic, elliptic-oblong, ovate, elliptic-obovate, or obovate, apex abruptly acute to gradually acuminate, base obtuse or acute and slightly decurrent on petiole, drying membranaceous to chartaceous and pale to dark greenish or brown above (much paler beneath), essentially glabrous above, with thin whitish hairs ca. 0.2 mm long on the veins beneath, 2° veins 5–8/side, tufted domatia present in some vein axils beneath. **Inflorescences** of terminal solitary ♀ flowers or 2–4(–8) ♂ flowers, subtended by persisting stipules, sessile or on pedicels to 9 mm long and 0.5 mm thick, sparsely to densely puberulent with whitish hairs. **Flowers** unisexual, with gardenia-like odor, hypanthium 1–2 mm long, obconic, to 10 mm long and ellipsoid in ♀ flowers, calyx tube ca. 0.5 mm long, calyx lobes 4–5, 3–6(–8) mm long, 1–2.5(–3.5) mm broad, lanceolate to obovate, striate, yellowish, minutely serrate, glabrous or rarely puberulent; **corolla** tubular-salverform, glabrous or minutely puberulent distally on the tube, tube 22–28 mm long, 0.8–2 mm diam. (5 mm at the throat), lobes 5, 9–12 mm long, ca. 6 mm broad, ovate-lanceolate to rhombic; anthers 3.5–5 mm long. **Fruits** 18–35 mm long, 20–28 mm diam., oblong-ellip-

soid to ovoid, glabrous or sparsely and minutely puberulent, surface smooth and becoming yellow or orange, persisting calyx 1–2 mm high and ca. 6 mm broad, pericarp ca. 1 mm thick; seeds 5–10 mm broad and 2 mm thick.

Plants of partly deciduous and evergreen forest formations and along stream sides in deciduous forests, from near sea level to 800 m elevation. Flowering in February–May; fruiting in all months. The species ranges from Mexico and the West Indies to Colombia and Brazil.

Randia armata is recognized by the nodes often with four spines, the stiff striate persisting stipules, closely clustered leaves, tufted domatia in some vein axils, and varied lower elevation habitats. Leaf size and shape can vary greatly in different sites. On Barro Colorado Island, Panama, the leaves are deciduous before flowering (Croat, 1978). Common names reported for Costa Rica are *crucillo*, *crucito*, *flor de cruz*, *jagua macho*, *limoncillo*, *miel quema*, *mostrenco*, and *palo de cruz*.

***Randia brenesii* Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 1365. 1938. Figure 22.**

Shrubs or small trees, 1–5 m tall, branches mostly held horizontally, dioecious, leafy stems 1.2–4 mm thick, at first with small (0.2–0.4 mm) ascending stiff brownish hairs, glabrescent, terete, spines 6–18 mm long, 0.5–2 mm thick, usually solitary; **stipules** 1–2 mm long, thin, brownish, glabrous, deciduous. **Leaves** opposite and often appearing unequal (anisophyllous), congested on short-shoots or separate along the stem, petioles 1–3(–5) mm long; **leaf blades** 4–40 mm long, (2–)4–15 mm broad, elliptic or narrowly elliptic-rhombic to ovate-lanceolate (broadly ovate in the very small leaves), apex acute, base acute to cuneate and decurrent on petiole, drying chartaceous, dark grayish green, glabrous above, with few small (0.2–0.4 mm) straight ascending hairs on the mid-vein beneath, 2° veins 3–4/side, strongly ascending. **Inflorescences** of solitary terminal flowers on axillary short-shoots, sessile and subtended by a few short (1 mm) bracteate stipules. **Flowers** unisexual, ca. 4 cm long, hypanthium 1.5–2.5 mm long, calyx tube 3–4 mm long, 0.8–2 mm diam., calyx lobes 5, 3–5 mm long, 1.5–5 mm broad, ovate and acute, with a narrow petiole-like base, ciliate; **corolla** salverform, white, glabrous externally, tube 25–45 mm long, 1–3 mm diam., lobes 5, 11–15(–22) mm long, 4–6(–15) wide, elliptic-oblong to ovate-oblong. **Fruits** 15–28 mm long, 14–25 mm diam., globose, glabrous, persisting calyx 2–5 mm high, 2–4 mm broad, pericarp 1–2 mm thick.

Plants of evergreen forest formations on the Caribbean slope, along the continental divide, and in the evergreen Pacific lowlands from 20 to 1600 m elevation. Flowering in February–June and Oc-

tober; probably fruiting throughout the year. The species ranges from Nicaragua to Panama.

Randia brenesii is recognized by the small opposite leaves that are very different in size, solitary flowers, foliaceous calyx lobes, globose fruit, and wet forest understory habitat. The leaves may be subequal but with two larger and two smaller leaves decussate and arising from the apex of the same short-shoot, giving the impression of anisophylly. The unusual calyx lobes distinguish this species from *R. loniceroides*. This species also resembles *Psychotria parvifolia*, but that species has subequal opposing leaves. Common names are *cachitos* and *horquetilla de montaña*.

***Randia calycosa* Standl., Contr. U.S. Natl. Herb. 20: 201. 1919. Figure 22.**

Shrubs or trees, 3–9 m tall, trunk to 25 cm diam., leafy stems 1.2–5 mm thick, with ascending brownish hairs 0.3–0.5 mm long, spines solitary or opposite 4–9(–15) mm long, 1.5–2 mm thick at the base; **stipules** 4–6 mm long, stipular tube ca. 2 mm long, apex obtuse and with a linear awn ca. 2 mm long, deciduous. **Leaves** opposite along the stems or sometimes clustered on short-shoots, petioles 3–8 mm long, 0.7–1.4 mm thick, glabrous or sparsely puberulent; **leaf blades** (2–)4–13 cm long, (1.3–)2–5 cm broad, elliptic-obovate to oblong-obovate or ovate, apex acute to acuminate with tip to 7 mm long, base tapering gradually and acute or cuneate, slightly decurrent on petiole, drying thin- to stiffly chartaceous and usually dark grayish above, glabrous above and below or with short (0.5 mm) thin whitish hairs on the midvein beneath, 2° veins 5–9/side. **Inflorescences** of solitary terminal flowers on short-shoots, subtended by cupulate bracteate stipules 2–3 mm long. **Flowers** with hypanthium 6 mm long and 4 mm diam., cylindrical, densely sericeous with brownish ascending hairs, calyx tube 4 mm deep, 3 mm diam., little differentiated from the hypanthium, calyx lobes 5–6, 5–9(–11) mm long, 5–8 mm broad, broadly ovate and foliaceous with a petiole-like base; **corolla** white but drying dark, corolla tube 8–24(–30) mm long, 1–3(–4) mm diam., with whitish appressed hairs ca. 0.5 mm long or glabrous, lobes 5, 10–15(–30) mm long, 5 mm broad at the base. **Fruits** 30–40 mm long, 25–35 mm diam., oblong-globose, persisting calyx 6–15 mm high.

Plants of lower montane evergreen forest formations, from 800 to 2300 m elevation. Flowering in February and April–May; fruiting in May, August, and November. This species ranges from the Cordillera de Tilarán to Veraguas, Panama.

Randia calycosa is recognized by its laminar calyx lobes, short spines, average-sized leaves, relatively large corolla lobes, and higher-elevation evergreen habitats. The flowers appear to vary greatly in size; for example, *Almeda et al.* 5078 f, from Monteverde, has corollas that are 6 cm long.

Randia formosa (Jacq.) K. Schum. is now called *Rosenbergiodendron formosum* (Jacq.) F. Gaerl. (Lorence in herb.); it ranges from central Panama to Peru. The corolla tubes are 8–10 cm long and densely whitish sericeous externally. The corolla lobes are 3–7 cm long and elliptic. The green fruits become 3 cm long and have broad white stripes down their sides and a narrow persisting calyx 5–7 mm long.

***Randia genipoides* Dwyer, sp. nov. Figure 24.**

Arbores ad 25 m altae. Folia anguste obovata vel elliptica, ad 35 cm longa et 15 cm lata, venis lateralibus ca. 28; petiolis 5–8 mm longis; stipulis 9–25 mm longis. Inflorescentia flores femineas ca. 3 vel masculas 2–8 gerens. Flores hypanthio ca. 12 mm longo, calycis dentibus 5, 17–28 mm longis; corolla alba vel flavida pilis ca. 0.5 mm longis vestita, tubo 50–90 mm longo, lobis 5, 35–50 mm longis. Fructus 6–8 cm longis, 4–7 cm crassus; seminibus ca. 10 mm latis.

Typus—*G. Herrera 1129* (holotypus CR, isotypi F, MO), from Upala, Alajuela, Costa Rica.

Small or medium-sized trees, 3–8(–25) m tall, dioecious, leafy stems 3–9 mm thick, glabrous and grayish, with prominent leaf scars, spines paired, 5–15 mm long, 1–3 mm thick, or often absent on distal twigs; **stipules** 9–25 mm long, lanceolate and acute, long (0.5–1 mm) whitish hairs present within, deciduous. **Leaves** closely clustered at the ends of stems, subsessile or with short (5–8 mm) petioles, ca. 2 mm broad; **leaf blades** 14–35 cm long, 5–12(–15) cm broad, oblanceolate to narrowly obovate or elliptic, apex abruptly narrowed and acuminate with tip 6–10 mm long, base tapering gradually and cuneate, drying chartaceous, grayish or grayish brown above, glabrate above, minutely (0.2–0.4 mm) strigillose along the veins beneath, 2° veins 12–15/side, 3° veins often subparallel. **Inflorescences** of 3 terminal ♀ flowers or 2–8 ♂ flowers at the tips of leafy branchlets, subsessile and subtended by lanceolate bracteate stipules 12–35 mm long and with thin hairs. **Flowers** unisexual, to 11 cm long, hypanthium ca. 12 mm long, not clearly differentiated from calyx, calyx tube 8–14 mm long, densely appressed-strigillose with hairs ca. 0.2 mm long, truncated distally and with 5 slender calyx lobes 17–28 mm long; **corolla** salverform, yellowish white with appressed-ascending whitish or yellowish hairs ca. 0.5 mm long, tube 50–90 mm long, 2–4 mm diam., lobes 5, 35–50 mm long and 7 mm broad near the base. **Fruits** 6–8 cm long, 4–7 cm diam., oblong-ellipsoid to subglobose, persisting calyx 5–10 mm long and 6–8 mm broad, sparsely and minutely puberulent; **seeds** ca. 10 mm broad, ellipsoid.

Plants of lowland rain forest formations, from 50 to 500 m elevation. Flowering in April–May and July; fruiting in June–September and November (the type). The species is endemic to Costa Rica.

Randia genipoides is recognized by the larger

narrowly obovate leaves closely clustered at the ends of stems, the greater number of secondary veins and subparallel tertiary veins, the large flowers sericeous or appressed-strigillose externally, long corolla lobes, and larger globose fruit. No other Costa Rican species of *Randia* has similarly clustered large oblanceolate leaves. Other collections seen are *Burger & Baker 9837 CR*, *F, Frankie 121a MO*, *Frankie 121c CR, F*, and *Zamora 998 CR*. A fruiting collection (*Herrera 4334 MO*) from the Osa Peninsula is the only collection known from the Pacific lowlands.

Randia gentryi Dwyer, Ann. Missouri Bot. Gard. 67: 447. 1980.

Small trees to 10 m tall, leafy branchlets ca. 2–3 mm thick, glabrous; **stipules** not seen, caducous. **Leaves** strongly unequal at each node, petioles of the larger leaves 2–5 mm long, ca. 1.5 mm thick, glabrous; **leaf blades** of larger leaves 8–23 cm long, 2.2–7 cm wide, elliptic to oblong or narrowly elliptic-oblong, the smaller leaves subsessile with blades 1–4 cm long and ovate, apex acuminate to acute (sometimes rounded in the small leaves), cuneate at the base, drying stiffly chartaceous, glabrous, 2° veins 8–12/side. **Inflorescences** axillary, peduncles to 5 mm long, bracts crowded and imbricate, flowers solitary, pedicels 0–3 mm long. **Flowers** glabrous externally except for minute red glands on hypanthium and calyx, hypanthium ca. 4 mm long, oblong, calyx tube 5–8 mm long, truncated, lobes 5, 2.5–3.8 mm long, ca. 1 mm wide; **corolla** white, carnos, tube 20–70 mm long, 2–4 mm diam., lobes 5, ca. 20 mm long, ovate-elliptic to oblong, strongly imbricate; **stamens** 5, anthers ca. 7.5 mm long; style ca. 12 mm long. **Fruits** 28–35 × 25–30 mm, oblong, rounded, glabrous, calyx ca. 3.5 mm long.

Plants of evergreen wet forest formations, 30–1400 m elevation. The species has only recently been collected on the Osa Peninsula, with flowers in May (*Hammel & Quintanilla 18217 MO*) and immature fruit in August (*Herrera 4133 MO*). The species ranges to northwestern Colombia.

Randia gentryi is recognized by the nodes with opposite leaves differing greatly in size, the larger leaves over 12 cm long, the larger flowers, and the minute glandular dots on the lower parts of the flower.

Randia grandifolia (J. D. Smith) Standl., J. Wash. Acad. Sci. 18: 116. 1928. *Basanacantha grandifolia* J. D. Smith, Bot. Gaz. 55: 436. 1913. Figure 23.

Shrubs or small trees, 2–6(–10) m tall, to 10 cm dbh, dioecious, leafy stems 1.5–8 mm thick, glabrous, the

outer grayish bark sometimes flaking off, spines 3–12 mm long, 1–2 mm thick, ascending, 1–2/node or often lacking; **stipules** 3–8 mm long, narrowed into a slender tip 1–2 mm long, brown, glabrous externally, with thin white hairs within. **Leaves** usually closely congested at the tips of branchlets, petioles 6–30 mm long, 0.8–2 mm broad, glabrous; **leaf blades** 7–22(–30) cm long, 3–10(–12) cm broad, elliptic, ovate, ovate-elliptic or elliptic-oblong to lanceolate, apex acute to short-acuminate, base obtuse to acute and slightly decurrent on petiole, drying thin to thick-chartaceous, grayish green to yellowish green, glabrous above and beneath, 2° veins 6–11/side. **Inflorescence** terminal on leafy branchlets, of solitary ♀ flowers or 1–5 ♂ flowers, subtended by triangular bracteate stipules ca. 3 mm long, flowers subsessile or with pedicels to 3 mm long. **Flowers** with hypanthium and calyx tube 4–10 mm long, 2–3 mm diam., calyx tube truncated distally with 5 slender (rarely expanded) calyx lobes 1–4 mm long, sparsely puberulent with thin appressed hairs; **corolla** salverform, white, glabrous externally, tube 10–18(–20) mm long, 2–3 mm diam., lobes 5, 8–12(–15) mm long, 2–9 mm broad. **Fruits** 3–4 cm long, 2.5–3.5 cm diam., globose to ellipsoid, slightly flattened on opposite sides, greenish white becoming yellow or orange, pulp white to yellow, pericarp 1–2 mm thick; **seeds** ca. 8 mm long, rounded.

Plants of evergreen wet forest habitats on both the Caribbean and Pacific slopes of Costa Rica, from near sea level to 1100 m elevation. Flowering in February–May and August; fruiting in April–January in Costa Rica. The species ranges from Mexico to Bocas del Toro, Panama.

Randia grandifolia is distinguished by its rain forest habitat, congested leaves varying greatly in size, shape, and texture, and flowers with relatively large corolla lobes. The calyx lobes may sometimes be expanded. This is a fairly common species on the Caribbean slope but has been only rarely collected in the Golfo Dulce area on the Pacific side of Costa Rica (*Tonduz 9982* us the type). It is often confused with *R. armata*.

Randia grayumii Dwyer & Lorence, sp. nov. Figure 24.

Frutex vel arbor parva usque ad 4 m alta, ramulis inermibus. Folia chartacea, lamina elliptica, oblonga vel oblongo-elliptica, 18–30 × 8–16 cm. Inflorescentia staminata capituliformis, involucreta, flores 10–12 generis. Flos lobis calycinis lineari-lanceolatis erectis, 3–4 × 0.5–0.7 mm; corolla infundibuliformi tubo gracili 22–28 mm longo, 1–1.2 mm diametro; fauce sparsim villosa, 4–6 mm diametro.

TYPUS—*Graynum & Schatz 5287* (holotypus MO, isotypus ?CR), Costa Rica.

Dioecious shrubs or small spindly trees, 2–4 m tall, unarmed, leafy twigs 3–5 mm wide, often forked, finely hirtellous or glabrate, lenticellate, longitudinally wrin-

kled, drying pale green or brown, internodes (0.5–)2–10 cm long; stipules 2.5–4.5 mm long, 2.5–3.5 mm broad, broadly ovate-triangular, the awn 0.5 mm long, brownish white, margins scarious, ciliate, externally finely puberulent, internally with basal ring of sericeous white hairs and digitate white collectors. Leaves opposite, petioles 1.5–3.5 cm long, 2–3 mm thick, often winged, finely hirtellous; leaf blades 18–30 cm long, 8–16 cm broad, elliptic, oblong or oblong-elliptic, apex deltoid with acumens 1–2 cm long, base cuneate, usually abruptly attenuate and decurrent, chartaceous and drying green, finely hirtellous above and beneath, glabrescent above, costa slender and sulcate above, to 2 mm wide and drying yellowish, 2° veins 9–12/side, festooned brochidodromous, forming an undulate submarginal vein. Male inflorescences terminal, 3–4 cm long and 4–5 cm broad (including corollas), condensed rounded capituliform 10–12 flowered cymes, subtended by an involucre of ca. 12 overlapping ascending glumaceous ovate-oblong bracts in 4 rows, 3–12 × 2–6 mm, glabrous, margins ciliate, pedicels 3–10 × 0.3–0.5 mm, finely hirtellous. Female inflorescences not seen at anthesis. Male flowers with hypanthium 0.8–1.2 long, 1.2–1.5 mm thick, calyx lobes 3–4 mm long, 0.5–0.7 mm broad, linear-lanceolate, stiff, erect, often involute, glabrous, yellowish white, margins ciliate; corolla funnellform, white, drying black, tube 22–28 mm long, 1–1.2 mm wide medially, throat abruptly flared to 4–6 mm wide, externally minutely puberulent, base of lobes and throat villous within, lobes 5, 7–10 mm long, 5–7 mm broad, obovate-oblong, recurved; stamens with tips exerted, anthers 2.5 mm long, linear; style 22–28 mm long, stigma 0.5 mm long, clavate, tip exerted, disc conical, 0.5–0.6 mm long, glabrous. Fruits solitary, 3–5 cm diam., subglobose, borne on a short pedicel 2–5 × 3–4 mm, wall glabrous, tuberculate, 1–1.5 mm thick, yellow or orange when ripe; seeds numerous, 8–10 mm diam., irregularly discoidal.

Understory plants of the Caribbean lowland evergreen forest formations, 10–800 m elevation. Flowering in April–May; fruiting in January–April and September. The species ranges from near the Nicaraguan border in Costa Rica to central Panama.

Randia grayumii is very closely related to *R. armata* and *R. grandifolia* but is distinguished by the large leaves with relatively few secondary veins and male inflorescences subtended by a small involucre of stipule-like bracts. Additional Costa Rican collections seen are *Davidse & Herrera 31470* MO, *Gómez et al. 21125* MO, *Lent 524* F, *Stevens 23659* MO, PTGB, and *Stevens et al. 24831* MO. Panamanian collections seen are *Kennedy et al. 3365* us and *von Wedel 2342* us. [Descriptions provided by D. Lorence.]

***Randia loniceroides* Dwyer & Lorence, Bol. Soc. Bot. Méx. 47: 40. 1987. Figure 22.**

Small shrubs, 0.5–1.5 m tall, dioecious, branching mostly horizontal, leafy branches 0.5–3 mm thick, with

ascending hairs ca. 0.3 mm long, glabrescent, spines to 6(–10) mm long and 0.5 mm thick, solitary, often absent; stipules 1–2 mm long, forming a short tube but splitting up and caducous. Leaves opposite along the stems or closely clustered on short-shoots, opposing leaves subequal or differing greatly in size, subsessile or with short-puberulent petioles 1–2 mm long; leaf blades 6–23(–30) mm long, 4–11(–15) mm broad, elliptic to obovate or narrowly obovate, apex bluntly obtuse or rounded, base tapering gradually and cuneate, decurrent on petiole, drying thin-chartaceous, dark grayish or grayish green, glabrous or with a few ascending hairs 0.2–0.3 mm long on the midvein above and below, 2° veins 3–4/side. Inflorescences of solitary flowers, apparently axillary (terminal on very small axillary short-shoots), flowers sessile and subtended by small (1 mm) imbricated bracteate stipules. Flowers ca. 20 mm long, hypanthium 0.5–1.5 mm long, calyx tube ca. 1 mm deep and 1 mm broad, truncate or with narrow lobes; corolla salverform, white drying black, glabrous externally, tube 15–18 mm long, 0.5–1 mm diam., lobes 4 or 5, (3–)6–9 mm long, 3–6 mm broad. Fruits 10–15 mm diam., globose, becoming pale whitish green, surface smooth, pericarp ca. 1 mm thick.

Plants of lowland rain forest formations of the Caribbean slope, 20–500 m elevation (to 1000 m in Mexico). Flowering in March–May; fruiting in January. This species is currently known only from Veracruz, Mexico, and northern Costa Rica.

Randia loniceroides is recognized by the very small leaves that may be subequal or strongly anisomorphic, small stature with horizontal branching, apparently axillary flowers and fruit, and rain forest habitat.

***Randia matudae* Lorence & Dwyer, Bol. Soc. Bot. Mexico 47: 42. 1987. *Casasia chiapensis* Miranda, Ceiba 4: 142. 1954, non *R. chiapensis* Standl. Figure 24.**

Trees to 30 m tall, dioecious, leafy stems 3–10 mm thick, glabrous except above the stipule scars with slender hairs 0.5–1.5 mm long, bark of young twigs reddish brown and exfoliating in small pieces, spines absent; stipules 4–5 mm long, 3 mm broad at the base, triangular, glabrous externally. Leaves not closely crowded on the distal branchlets, petioles 6–22(–38) mm long, 1.3–3 mm broad; leaf blades 9–22(–29) cm long, 4–8(–12) cm broad, elliptic to elliptic-obovate or elliptic-oblong, apex acute or bluntly acute, base tapering gradually and cuneate or acute, slightly decurrent on petiole, drying stiffly chartaceous to subcoriaceous, usually very dark grayish above, glabrous above and below, occasionally with hairs or pits (domatia) in the vein axils beneath, 2° veins 5–9/side. Inflorescences of a solitary ♀ flower or (11–)3–9 ♂ flowers, peduncles of the ♂ 6–10 mm long or absent, pedicels 4–8 mm long and not differentiated from the base of the hypanthium, glabrous, drying black. Flowers glabrous externally, drying black, hypanthium ca. 6 mm long, 2–4 mm diam., calyx tube 4–6 mm long, calyx

lobes 4 (or with additional smaller lobes between), 1–3 mm long, narrow; **corolla** salverform, white, tube 30–40 mm long, 3–5 mm diam., lobes 4 or 5, 22–30(–40) mm long, ca. 10 mm broad near the base, acute. **Fruits** 5–7 cm long, 4.5–6.5 cm diam., globose to oblong, outer rind 5–10 mm thick (dried), persisting calyx to 8 mm high and 10 mm broad, pericarp 2–5 mm thick; **seeds** ca. 10 × 7 mm, elliptic.

Plants of wet evergreen cloud forest formations of the Cordillera de Tilarán at around 1300–1600 m elevation in Costa Rica but ranging from 20 to 2000 m in Guatemala. Flowering in June–August and October; fruiting in February, June, and October. This species ranges from southern Mexico to northern Costa Rica.

Randia matudae is characterized by the large-sized tree habit, most plant parts turning dark on drying, larger leaves, and cloud forest habitat (in Costa Rica). Material of this species was incorrectly referred to *Genipa vulcanicola* Standl. in the Flora of Guatemala (Standley & Williams, 1975); that species is now called *Glossostipula concinna* (Standl.) Lorence.

Randia mira Dwyer, Ann. Missouri Bot. Gard. 67: 450. 1980. Figure 24.

Shrubs or small treelets, 3–6(–8) m tall, dioecious, leafy stems 4–14 mm thick, glabrous, young stems with smooth reddish brown bark exfoliating in thin longitudinal strips, spines absent; **stipules** 6–10 mm long, to 10 mm broad at the base, triangular with a distal awn 0.5–4 mm long, minutely appressed-puberulent. **Leaves** not usually closely spaced distally, petioles (5–)12–25 mm long, 2–4 mm thick, minutely appressed-puberulent and glabrescent; **leaf blades** 24–44 cm long, 8–17 cm broad, elliptic to narrowly obovate or narrowly oblong-obovate, apex acute to acuminate, base gradually narrowed and cuneate, drying stiffly chartaceous to subcoriaceous, grayish green or dark olive green above, glabrous above, with few thin appressed hairs ca. 0.3 mm long on the surfaces beneath and glabrescent, 2° veins 10–16/side. **Inflorescences** with 1–several flowers terminal on cauliflorous short-shoots, flowers sessile and subtended by a small involucre of imbricate bracteate stipules ca. 3 mm long and with short (1 mm) awns. **Flowers** 10–15 cm long, minutely puberulent externally, drying black, hypanthium 3–4 mm long, ca. 2 mm thick, not clearly distinguished from the calyx, calyx tube 10–14 mm long, 5–7 mm diam., cylindrical with a truncated apex and short (1–3 mm) linear lobes; **corolla** tubular-salverform, puberulent externally, tube 55–80 mm long, 3–5 mm diam., lobes 5–7, 45–70 mm long, 6–12 mm broad, lanceolate to narrowly elliptic-lanceolate, with narrowly acute apices; anthers 6–7. **Fruits** 4–7 cm diam., globose, yellow to yellow-orange, pericarp 5–10 mm thick; **seeds** 8–10 mm broad, ellipsoid.

Plants of lowland rain forest formations of the

Caribbean slope, 10–700 m elevation. Flowering in May–June (February–March in Panama); fruiting in October–January. The species ranges from northern Costa Rica to central Panama.

Randia mira is distinguished by the large cauliflorous flowers with six to seven narrow corolla lobes, larger succulent or subcoriaceous leaves, lack of spines, thin exfoliating reddish brown bark on young stems, and lowland rain forest habitat.

Randia monantha Benth., Pl. Hartw. 84. 1841. *Basanacantha monantha* (Benth.) Hook. f. ex Hemsl., Biol. centr. amer. Bot. 2: 39. 1881. *B. subcordata* Standl., Contr. U.S. Natl. Herb. 18: 133. 1916. *R. subcordata* (Standl.) Standl., Contr. U.S. Natl. Herb. 20: 201. 1919. Figure 23.

Shrubs or small **trees**, 3–6 m tall, dioecious, leafy stems 1–5 mm thick, with ascending whitish hairs ca. 0.5 mm long but quickly glabrescent, terete, brownish, spines 5–15(–20) mm long, 1–2 mm thick, often 4/node, ascending; **stipules** 2–5 mm long, 3–4 mm broad at the base, lanceolate with a narrowly acute apex, glabrous on the back and ciliolate along the edge. **Leaves** usually closely clustered at the ends of stems or on short-shoots, petioles 6–28(–35) mm long, 0.7–1.2 mm wide, with stiff hairs 0.3–0.9 mm long; **leaf blades** (2–)4.5–11 cm long, (1–)2–6 cm broad, ovate to ovate-elliptic, broadly elliptic or elliptic-oblong, apex obtuse to acute (short-acuminate), often with a short acute tip, base cuneate to obtuse or acute or occasionally truncated and subcordate, drying membranaceous to chartaceous, dark or pale grayish above, with thin whitish hairs on both surfaces, 2° veins 3–7/side. **Inflorescences** of solitary ♀ or few ♂ flowers, terminal on stems or short-shoots, flowers sessile and subtended by bracteate stipules. **Flowers** unisexual, the ♂ to 7 cm long, appressed-puberulent externally, hypanthium 5–15 mm long, ca. 4 mm diam., tubular, calyx tube 8–10 mm long, 3–4 mm diam., calyx lobes 5, 4–8(–12) mm long, 1–1.8 mm broad, linear; **corolla** salverform, white to cream yellow, tube 30–45 mm long (to 60 mm in ♂ flowers), 0.8–2.4 mm diam., to 4 mm broad at the mouth, with thin erect whitish hairs externally, lobes 5, 14–24 mm long (to 40 mm in ♂ flowers), 4–10 mm broad at the base, glabrous but with a ciliolate edge, ovate to ovate-lanceolate. **Fruits** 4–5(–6) cm long, 5–5.5 cm diam., globose to oblate, persisting calyx ca. 5 mm high and 6 mm broad, pericarp 3–4 mm thick (dried); **seeds** 8 × 5 mm, discoid, in a cream-colored pulp that becomes black.

Plants of seasonally very dry deciduous or partly deciduous forest formations of the Pacific slope, 20–900 m elevation (to 1400 m in Guatemala). Flowering in March–June; fruiting in all months except March and October. The species ranges from Mexico and Guatemala along the Pacific slope into central Costa Rica.

Randia monantha is recognized by its deciduous forest habitat, stems usually with four spines at distal nodes, thin-pubescent leaves, larger puberulent unisexual flowers, and long calyx lobes. *Cru-cilla* is a common name.

Randia pittieri (Standl.) Standl., Contr. U.S. Natl. Mus. 20: 201. 1919. *Basanacantha pittieri* Standl., loc. cit. 18: 134. 1916. Figure 23.

Shrubs or small treelets, 1–4 m tall, leafy stems 2–4 mm thick, glabrous, brownish to grayish, terete, spines usually 4/node, 4–15 mm long, 1–3 mm at the base; **stipules** 7–12 mm long, 3–4 mm broad at the base, narrowly triangular and acute at the apex, brown, glabrous externally, thin white hairs within. **Leaves** closely clustered at the ends of stems, petioles 5–15(–24) mm long, 0.7–1.5 mm broad, pubescent with stiff hairs; **leaf blades** 7–16 cm long, 4–10 cm broad, broadly ovate to elliptic-ovate or obovate, apex abruptly acute to gradually obtuse, often with a short (0.5–2 mm) sharp tip, base obtuse to slightly rounded, drying chartaceous, grayish above, with thin slightly curved hairs 0.2–1 mm long above and below, 2° veins 9–12/side. **Inflorescences** not seen, probably of solitary ♀ flowers and several ♂ flowers, terminal on the ends of leafy branchlets, pedicels of ♂ flowers 4–5 mm long. **Flowers** dioecious, calyx tube ca. 4 mm long, with subulate lobes 4–5 mm long, glabrous except for thin whitish hairs on the lobes and around the margin of the tube; **corolla** tubular-salverform, white, tube ca. 6 cm long, slightly expanded at the throat, lobes 25–30 mm long, lanceolate to elliptic lanceolate; anthers sessile in the throat, ca. 10 mm long. **Fruits** ca. 6 cm long and 5 cm diam., subglobose, with thin hairs or glabrescent, persisting calyx ca. 5 mm high.

Plants of evergreen rain forests and partly deciduous forests, from near sea level to 1000 m elevation. Flowering in February; fruiting in April. The species has been collected in the Caribbean lowlands (*Pittier 16036* is the type), Cordillera de Guanacaste, and around the Meseta Central in Costa Rica.

Randia pittieri is distinguished by often having four spines at a node, thinner-textured pubescent leaves, corollas with long (6 cm) tube, and larger fruit. This species is not well collected; it is very similar to *R. monantha* and *R. armata*.

Randia pterocarpa Lorence & Dwyer, Bol. Soc. Bot. Méx. 47: 43. 1987.

Shrubs or small trees, 2–5 m tall, leafy stems 3–8 mm thick, glabrous, pale yellowish brown to dark brown, smooth or exfoliating, spines absent; **stipules** 3–6 mm long, intrapetiolar and forming a short adnate tube, triangular distally, glabrous, deciduous. **Leaves** opposite,

not closely congested distally, petioles 2–9 mm long, 2.5–3.5 mm thick, drying dark, glabrous; **leaf blades** 16–37(–50) cm long, 6–14(–17) cm broad, narrowly ovate-elliptic or elliptic-oblong, apex tapering gradually and subacuminate, base gradually narrowed but abruptly rounded or truncated at the petiole, drying stiffly chartaceous, dark grayish green, glabrous above and below, 2° veins 11–15/side. **Inflorescences** axillary or cauliflorous, of 1–5 flowers subtended by scarious bracteoles 1–2 mm long, pedicels 1–4 mm long, not differentiated from the hypanthium. **Flowers** probably bisexual, glabrous externally, calyx tube 1.5–3 mm long, 1.5–2.1 mm diam., truncated distally or with 5 small (0.2–1 mm) acute lobes; **corolla** salverform, white, tube 40–55 mm long, lobes 5, 25–38 mm long, elliptic-lanceolate. **Fruits** 5–10 cm long, 5–10 cm diam., obovoid, surface with 5 (9–11) longitudinal slightly elevated (1–3 mm) costae; **seeds** 10 × 8 mm, flattened, elliptic.

Plants of the very wet lower montane cloud forests of the Caribbean slope, 400–600 m elevation. The species is found in southern Mexico and in Costa Rica.

Randia pterocarpa is recognized by its long narrow leaves, lack of pubescence, cauliflorous fruit with elevated costae, and limited altitudinal range (in Costa Rica).

Randia retroflexa Lorence & M. Nee, Brittonia 39: 371. 1987.

Lianas or shrubs with clambering branches, to over 13 m high with stems to 7 cm thick, dioecious, leafy stems 2–5 mm thick, pilose with spreading hairs 1–2 mm long, spines 5–10 mm long, 2–4 mm thick at the base, recurved (less often straight); **stipules** 6–10 mm long, 3–5 mm broad at the base, triangular to ovate, appressed-hirsute, persisting or deciduous. **Leaves** equal or subequal at each node, petioles 3–30 mm long, 1–2 mm thick, hirsute; **leaf blades** 6–23 cm long, 3–12.5 cm broad, elliptic to elliptic-obovate, apex acute to short-acuminate or obtuse, base obtuse to rounded or cuneate, drying membranaceous to chartaceous, appressed-hirsutulous on both surfaces, 2° veins 5–9/side. **Inflorescences** terminal, ♂ to 9 cm long and 20 cm wide (including corollas), candelabra-like and corymbose with 3–20 flowers, ♀ flowers 2–6 sessile and subcapitate, peduncles 0–10 mm long. **Flowers** densely hirsutulous externally, hypanthium 2–3 mm long, obconical (3–6 mm long in ♀), calyx tube 8–10 mm long, calyx lobes 5(–6), 1–12 mm long, 0.3–1 mm wide in ♂, 2–4 mm wide in ♀; **corolla** white, tube 4–5 cm long in ♂ (3–3.5 cm in ♀), lobes 5, 1.5–4 cm long; anthers 10–12 mm long. **Fruits** solitary, to 7 × 6 cm, persisting calyx to 10 mm long and 7 mm diam.; **seeds** 8–10 mm diam., 1.5–3 mm thick.

Randia retroflexa is distinguished by its climbing or clambering branches, spine-bearing stems, hirsute pubescence, large flowers, and larger fruits.

Two sterile collections (*Haber et al.* 4823 MO, *Hammel & Haber* 13921 MO) are provisionally placed here by David Lorence. He notes that they differ from Mexican collections by having spines that are straight and in groups of four but are similar in other aspects. Both collections were made in the Cordillera de Tilarán, between 600 and 1200 m elevation. One collection was flowering in May. The species ranges to Mexico.

Randia thurberi S. Watson, Proc. Amer. Acad. Sci. 24: 53. 1889. *R. crescentioides* Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 23: 88. 1944. Figure 22.

Small trees or shrubs, (2-)3-6 m tall, dioecious, branches usually held horizontally, puberulent in early stages, glabrescent and grayish, spines opposite, 6-20 mm long, 1.2-2.8 mm thick near the base, sharp-tipped; stipules less than 2 mm long. Leaves opposite or 4, on condensed (4×1.5 mm) short-shoots, 2 or 4, equal or unequal in size, petioles poorly differentiated, 0-8 mm long, puberulent or glabrous; leaf blades 6-40(-60) mm long, 4-18(-50) mm broad, obovate to obovate-suborbicular, apex rounded to bluntly obtuse, base gradually narrowed and cuneate, decurrent on petiole, drying membranaceous to stiffly chartaceous, grayish green, glabrous to densely puberulent with whitish hairs 0.2-0.4 mm long, 2° veins 3-5/side, ascending. Inflorescences of several or solitary flowers terminal on the ends of stems or short-shoots, subtended by a pair of thin brownish bracts 1-2 mm long, sessile. Flowers unisexual, hypanthium ca. 2 mm long, obconic, glabrous to densely velutinous, calyx lobes 1-2 mm long, acute; corolla funnelform, white, tube ca. 15 mm long, 0.9-2 mm diam., to 4 mm at the mouth, puberulent externally distally; lobes 7-10 long, 3-4 mm wide, broadly elliptic. Fruits 2.5-3.5 cm diam., globose, grayish green but turning black when dried, glabrous to densely puberulent, persisting calyx absent or small (1-2 mm high), 3-4 mm wide, pericarp ca. 3 mm thick.

Plants of seasonally very dry deciduous forests of the northwestern Pacific lowlands, 0-300 m elevation (to 1200 in Mexico). Fruiting in July-October. This species ranges from Mexico along the Pacific lowlands of Central America to northwestern Costa Rica.

Randia thurberi is recognized by its deciduous forest habitat, small often unequal obovate leaves usually clustered in 4's (2 pairs) at the ends of short-shoots, straight paired spines, and medium-sized flowers and fruits. Plants may differ greatly in the degree or absence of pubescence. At present the species is only known in Costa Rica from Santa Rosa National Park and Finca La Pacifica near Cañas.

Randia vazquezii Lorence & Dwyer, Bol. Soc. Bot. Méx. 47: 37-48. 1987.

Vines or lianas, to 20 m high with trunks 18 cm diam., probably dioecious, leafy stems pilose to spreading pilosulous, spines 3-4/node, 5-9(-30) mm long, ca. 2 mm diam., erect or reflexed; stipules 4-11 mm long, 3-5 mm broad at the base, thin, externally glabrous, deciduous. Leaves separated along the stem or clustered distally, petioles 7-20(-30) mm long, at first strigillose; leaf blades 8-16(-22) cm long, 4-9(-12) cm broad, elliptic to ovate-elliptic or obovate, apex acuminate with a tip 6-14 mm long, base obtuse to cuneate, drying chartaceous, grayish or brownish green, pubescent on both surfaces, 2° veins 6-10/side. Inflorescences terminal, of solitary ♀ flowers or 1-4 fasciculate ♂ flowers, pedicels 5-6 mm long. Flowers with hypanthium 3-5 mm long, calyx tube 1-18 mm long, lobes 5, 6-15 mm long and linear in ♂, 15-20 mm long and oblanceolate in ♀; corolla salverform, white or yellowish, strigose to sericeous externally, tube ca. 8 cm long in ♂, ca. 5 cm long in ♀, lobes 5, 30-35 mm long, 9-15 mm broad; anthers 8-9 mm long. Fruits ca. 9 cm long, 6-7 cm diam., ellipsoid, brown, warty, pericarp 3-5 mm thick.

In wet forests at 400-1200 m elevation. Fruiting in May and August. Known from Braulio Carillo N.P. and near San Isidro del General. The species also occurs in southern Mexico and Guatemala.

Randia vazquezii is recognized by its climbing habit, spiny stems, thin-pubescent leaves, and large flowers. Compare *R. retroflexa* with longer pubescence and shorter flowers.

Raritebe Wernham

REFERENCE—J. H. Kirkbride, Jr., *Raritebe*, an overlooked genus of the Rubiaceae. Brittonia 31: 299-312. 1979.

Small trees or shrubs, without raphides, hairs with incomplete septa; stipules interpetiolar, free, entire, persisting. Leaves opposite or 3/node, petiolate; leaf blades entire, pinnately veined, domatia absent. Inflorescences terminal, open panicate with cymose distal branches, pedunculate, the flowers pedicellate. Flowers bisexual and radially symmetrical, homostylous or heterostylous, hypanthium turbinate, calyx short-tubular, interior of the tube with 2-7 small glands near the base of each sinus, calyx lobes 4-5(-7), small or absent and the calyx entire, persisting; corolla salverform, white, lobes 5, valvate in bud, distally carinate and the proximal part flat triangular; stamens 5, filaments borne on the tube near or below the middle, anthers free or coherent, 4-theous, narrow, dorsifixed below the middle, obtuse to cordate at the base, the connective extended and acute, included, disc circular and entire; ovary 2-locular, ovules many on V-shaped to cordiform placentas, style glabrous, stigma bilobate and included. Fruits fleshy and indehiscent, green

becoming orange and finally black; **seeds** many and globular.

A genus of six species (Dwyer, 1980) or only one species (Kirkbride, 1979) ranging from Costa Rica and Panama to Colombia, Ecuador, and Peru. The genus is closely related to *Isertia* and *Amphidasya* according to Kirkbride (cited above, 1979, p. 302), but there are Costa Rican specimens placed in *Coussarea* that also seem to be close. The genus *Dukea* Dwyer is a synonym of *Raritebe*. Kirkbride's broad interpretation is followed here.

Raritebe palicouroides Wernham, J. Bot. 55: 337. 1917. *Coussarea euryphylla* Standl., Publ. Field Columb. Mus., Bot. Ser. 4: 294. 1929. *Bertiera panamensis* Standl., N. Amer. Fl. 32: 180. 1934. *C. colonis* Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 22: 179. 1940. *Dukea euryphylla* (Standl.) Dwyer, Ann. Missouri Bot. Gard. 53: 366. 1966. Figure 43.

Shrubs or small trees, 1–7 m tall, leafy stems 1.8–7 mm thick, usually flattened (compressed) on opposing sides in early stages, with thin-ascending hairs 0.2–0.3 mm long; **stipules** 7–18(–24) mm long, 2.5–7 mm broad at the base, narrowly triangular and acute to long-acuminate, puberulent on both surfaces. **Leaves** with petioles (5–)10–45 mm long, 1–2.5 mm thick, narrowly caniculate above, minutely appressed puberulent; **leaf blades** 12–37 cm long, 4–14 cm broad, elliptic-oblong to elliptic or narrowly elliptic-oblong, apex acuminate with tip 10–15 mm long, base acute to attenuate, drying thin-chartaceous, glabrous or very sparsely strigose above (the thin hairs difficult to see), with thin appressed-ascending hairs 0.2–0.5 mm long on the veins beneath or subglabrous, 2° veins 8–13/side, arcuate-ascending and weakly loop-connected in the distal third of the blade. **Inflorescences** (2–)6–18 cm long, (3–)5–20 cm broad, peduncle 1.5–7.5 cm long, appressed puberulent, branches opposite and distant, bracts 1–5 mm long and usually linear, stipule-like structures also present at the lower branching nodes, pedicels 1–8 mm long, slender and appressed strigulose. **Flowers** homostylous in subspecies *dwyeranum*, hypanthium 1.6–2.2 mm long, ca. 2 mm diam., calyx tube becoming 1–1.7 mm long, calyx lobes 0.1–0.4 mm long, broadly triangular to obscure; **corolla** tubular-salverform, white, tube (5–)6–9 mm long, 0.9–1.4 mm diam., minutely puberulent with hairs 0.1–0.2 mm long, lobes (3–)4–8 mm long, 0.5–1.2 mm broad, linear to narrowly oblong, glabrous to sparsely puberulent externally; **stamens** with filaments 0.3–1.6 mm long, anthers 2.2–4.4 mm long; styles 2–2.4 or 3.8–6.5 mm long, stigmas 0.9–2.3 mm long. **Fruit** 4–6 mm diam., globose, yellow-orange; **seeds** 0.2–0.6 mm diam.

Small trees and shrubs of evergreen rain forest and cloud forest formations of the Caribbean slope, from near sea level to 1400 m elevation. Probably

flowering and fruiting throughout the year (mostly flowering in March–August and fruiting in March–December). This species (considered in the wide sense) ranges from Costa Rica and Panama to Peru.

Raritebe palicouroides is recognized by its appressed puberulence, the terminal compact to widely branched inflorescences, the small tubular flowers with poorly developed calyx lobes, the stamens cohering together at anthesis (in our subspecies), and the small fleshy fruit with many round seeds. Only subspecies *dwyeranum* Kirkbride occurs in Costa Rica and Panama; it is distinguished from other members of this species by having homostylous flowers with anthers 2.8–4.4 mm long and styles 4.2–6.5 mm long. There is a great deal of variation in the leaves and inflorescences of different individual plants in this species. We follow Kirkbride, who interpreted this species so broadly as to include all six species recognized by Dwyer (1980, p. 452). Specimens in early stages of flowering can be easily mistaken for specimens of some species of *Coussarea*.

Richardia Linnaeus

REFERENCE—W. H. Lewis and R. L. Oliver, Revision of *Richardia* (Rubiaceae). Brittonia 26: 271–301. 1974.

Herbs, perennial or less often annual, decumbent and forming mats or erect, stems terete, usually densely pubescent; **stipules** interpetiolar, adnate to the petiole base and forming a truncated sheath with long distal setae (awns). **Leaves** opposite, sessile or short-petiolate; **leaf blades** linear to ovate, margins entire and often revolute, hirsute to scabrous or glabrous, domatia absent. **Inflorescences** terminal, capitate and sessile, subtended by an involucre of 4 decussate or 2 opposite (rarely 1) involucre bracts, the bracts similar to foliage leaves but often wider and palmately veined, the flowers closely crowded, pedicels absent or short. **Flowers** bisexual and monomorphic, radially symmetrical, with hypanthium turbinate to subglobose, calyx lobes 4–8, usually 2–3 times as long as the calyx tube, persisting; **corolla** funnelform or less often rotate to salverform, white to lavender (rarely yellow or orange), lobes 3–6, ovate to lanceolate, valvate in bud; **stamens** (3–)4 or 6, filaments short (long in a few species) and borne near the mouth of the corolla tube, anthers elongate or ovoid, dorsifixed, exerted; disc an unlobed ring or cylinder; **ovary** inferior or half-inferior, usually 3- or 4-locular (rarely 2 or 5–6), with 1 ovule affixed to the septum near the base in each locule, style simple or branched, stigmas capitate or spatulate. **Fruits** breaking up into 3 or 4 (2, 5–6) dry mericarps (cocci), thin- to thick-walled, the mericarps usually obovoid and smooth to papillose, the adaxial face narrowly to broadly sulcate; **seeds** oval or ellipsoid, smooth, brown.

A genus of 15 species in the tropics and subtropics of the Americas, from southeastern United States to northern Argentina. Most species occur in Brazil but none are found in the Amazon basin. A few species have become weeds in Africa and elsewhere. The genus is characterized by the short

weedy habit, usually narrow leaves attenuate at the base, terminal capitate heads of flowers, three- or four-locular ovaries, and small fruit breaking up into mericarps. This genus is closely related to *Crusea* and *Diodia* but differs in the usually three-carpellate ovary and the involucrate heads.

Key to the Species of *Richardia*

- 1a. Mericarps papillose-muricate, with 1 narrow sulcus on the inner face; leaf surfaces very scabrous with short stiff hairs [a common species] *R. scabra*
- 1b. Mericarps minutely hirsute, with 2 broad depressions and a median keel on the inner face; leaf surfaces smooth or only slightly scabrous above *R. brasiliensis*

Richardia brasiliensis Gomes, Mem. Ipecacuanha Bras. 31, t. 2. 1801. *Richardsonia brasiliensis* (Gomes) Hayne, Arzengew. 8: 21, t. 21. 1855.

Prostrate **herbs**, annual or perennial, often forming mats from a central taproot, stems to 50 cm long (rarely rooting from the nodes), leafy stems 0.3–4 mm thick, with thin spreading hairs 0.3–2 mm long; **stipule** sheaths 1–3.5 mm long, with 3–5 setae 1–5 mm long. **Leaves** with petioles to 15 mm long but poorly defined because of the decurrent leaf base; **leaf blades** 1–4(–7) cm long, 4–20(–27) mm broad, elliptic to ovate, apex acute, base gradually narrowed and attenuate, decurrent on the petiole, scabrous and with thin hairs on both surfaces. **Inflorescences** 7–12 mm diam., usually with more than 20 flowers, the longer bracts 15–35 mm long, 6–20 mm broad, shorter bracts 10–17 mm long and 4–10 mm broad or sometimes absent. **Flowers** with hypanthium 1–2 mm long, calyx tube to 1 mm long, calyx lobes 6 (5), 1–1.5 mm long and 0.3–1 mm broad, lanceolate to ovate-triangular, margins with conspicuous cilia; **corolla** funnellform, white (rose), corolla tube 2–8 mm long, lobes 6 (4), 1–3 mm long and 0.5–1 mm broad; **stamens** 6 (4); ovary 3-locular, style 3–4 mm long, stigmas 3, 0.2–0.4 mm long. **Fruit** breaking up into 3 (2) mericarps 2–4 mm long and 1.4–2 mm broad, oblong-obovoid, adaxial surface smooth and broadly concave with a longitudinal keel or rib; **seeds** ca. 2.5 mm long and 1.8 mm thick.

spreading hairs to 1.8 mm long; **stipule** sheaths 2–4 mm long with 3–7 setae 1–5 mm long, difficult to see among the longer hairs at the nodes. **Leaves** with petioles 3–12 mm long, poorly differentiated from the lamina base; **leaf blades** (10–)20–45(–65) mm long, (3–)5–15(–23) mm broad, narrowly elliptic to elliptic-oblong or elliptic-ob-lanceolate, apex acute to obtuse, base attenuate and decurrent on petiole, scabrous and with short (ca. 0.5 mm) stiff appressed or ascending hairs along the margins and on both surfaces, 2° veins 2–3/side and strongly ascending. **Inflorescences** terminal and solitary, 6–16 mm diam., capitate, usually with more than 10 flowers, usually subtended by an opposite pair of ovate bracts 10–27 mm long and 6–15 mm wide and shorter (4–15 × 3–9 mm) bracts. **Flowers** with hypanthium 2–3 mm long, calyx tube ca. 1 mm long, calyx lobes 6, 1.8–3 mm long, ca. 1 mm wide, hispid or with a ciliate margin; **corolla** funnel-form to salverform, white or pale pink or marked with pink, glabrous, tube (2–)4–7 mm long, lobes 6 (5), 0.8–3 mm long and 1–1.5 mm wide; **stamens** 6 (5), exserted or included, anthers 0.4–0.8 mm long; **ovary** usually 3-locular, style ca. 7.5 mm long, stigmas 3, ca. 0.7 mm long. **Fruits** usually with 3 mericarps 1.8–2.7 mm long and 1–1.8 mm broad, plano-convex and oblong to obovoid, inner face with a narrow longitudinal sulcus, muricate to papillate on the abaxial surface with the papillae larger (0.3 mm) distally; **seeds** 2–2.5 mm long and 1.3 mm thick, purplish brown.

Weedy plants of open sunny sites in both evergreen and seasonally deciduous areas, from near sea level to 2000 m elevation. Not yet collected in Central America but very likely to be present. The species, originally from Brazil, is now also found in Mexico, the southeastern United States, tropical Africa, southern Asia, and the Pacific.

Richardia scabra L., Sp. Pl. 330. 1753. Figure 4.

Annual or perennial **herbs**, stems sprawling or erect, to 70 cm long and 30 cm high, not usually rooting at the nodes, leafy stems 0.7–3.5 mm thick, with stiff thin

Common weedy plants of open sunny sites in both seasonally deciduous and evergreen forest formations, from near sea level to 1800 m elevation. Flowering throughout the year but primarily in the wet season (June–December) in deciduous formations. The species ranges from the Carolinas, in the eastern United States, southward through Mexico and Central America to northern South America, Cuba, and Jamaica. It has also become naturalized in parts of Africa, southeast Asia, and the Pacific.

Richardia scabra is recognized by the usually procumbent mat-forming pubescent stems, scabrous leaves attenuate at the base, small terminal

capitate inflorescences consistently subtended by a pair of broad leaf-like bracts, flowers with six stamens, and fruit usually with three mericarps. The mericarps, borne on the exterior of the fruit, can be mistaken for muricate-papillate seeds when they fall off. The dried plants have a slightly grayish appearance due to the thin transparent hairs on many parts.

Rondeletia Linnaeus

REFERENCES—J. H. Kirkbride, A revision of the Panamanian species of *Rondeletia* (Rubiaceae). Ann. Missouri Bot. Gard. 55: 372–391. (1968) 1969. D. H. Lorence, New species and combinations in Mexican and Central American *Rondeletia* (Rubiaceae). Novon 1: 135–157. 1991.

Shrubs or small trees, branchlets terete or angular, usually puberulent; **stipules** interpetiolar, rarely slightly united above the petioles and forming a very short sheath (intrapetiolar), variable in size and form, usually triangular (rarely bilobed). **Leaves** opposite (rarely 3/node), petiolate or rarely sessile; **leaf blades** entire, membranaceous to coriaceous, glabrous to densely puberulent, domatia often present. **Inflorescences** terminal or axillary, paniculate with opposite branching, cymose to long-thyrsoïd (rarely racemose or spike-like), pedunculate, bracts small to large, flowers sessile to pedicellate. **Flowers** bisexual and radially symmetrical, often dimorphic, hypanthium rotund to oblong, usually puberulent, calyx tube absent or very short, calyx lobes 4–5 (6, 7), equal or often unequal; **corolla** salverform, pink to rose red, reddish purple, yellow, or white, corolla tube usually narrow, the interior of the throat glabrous with an annular thickening at the mouth (in *Rondeletia sensu stricto*), yellow-bearded at the mouth (*Rogiera*) or glabrous without a callosity at the mouth (*Arachnothrix*), lobes 4–5(–6), usually spreading, imbricate in bud; **stamens** 4–5(–6), filaments usually very short and attached in the upper half of the tube, anthers dorsifixed, oblong and introrse, included (rarely exserted); **ovary** 2-locular, ovules many in each locule on placentas borne on the septum, style slender, stigmas narrowly 2-lobed. **Fruit** a thin-walled capsule, globose to ovoid, oblong or oblate, 2-locular, dehiscent loculicidally or septicidally, the valves often opening at the top and bipartite from the top; **seeds**

many, oblong and winged at both ends (in *Rondeletia sensu stricto*) or rhomboid to triangular and usually without wings or ribs (in *Arachnothrix* and *Rogiera*).

A genus of about 125 species, ranging from the West Indies and Mexico, through Central America into tropical South America. Important centers of diversity are located in Central America and the West Indies. *Rondeletia* is recognized by its relatively small flowers with narrow tubes, the calyx lobes often slightly enlarged or conspicuously unequal, the thin-walled capsules, and the narrow winged seeds (in some species). The genus is not represented in Costa Rica's Caribbean lowlands, except near the Panama border.

As observed by Williams (Standley & Williams, 1975, p. 178), Central America has an unusual number of narrowly endemic *Rondeletia* species. Among our species, *R. aspera*, *R. calycosa*, *R. chaconii*, *R. cooperi*, *R. montevertensis*, *R. povedae*, *R. stenostachya*, *R. tayloriae*, and *R. urophylla* appear to have very restricted ranges. Another unusual feature of some species is the near-identity of form between floral bracts and the expanded calyx lobes (an example of homeosis or heterotopy). Some of our species are easily mistaken for species of *Gonzalagunia* and even *Buddleja* (Loganiaceae).

The circumscription of *Rondeletia* has not been resolved. Steyermark (1974, p. 296) and Borhidi (Bot. Közlem. 62: 27. 1975) accepted *Arachnothrix* as a separate genus, and Borhidi accepted *Rogiera* and *Javorkea* as well (Acta Bot. Hung. 28: 67. 1982). Kirkbride (cited above) suggested that species in the centers of diversity need to be better understood before generic concepts are redefined, and Lorence (cited above) recently argued for a broad interpretation of the genus. We have benefited from the annotations and advice of David Lorence, who is studying this genus in Central America and Mexico; he has contributed the descriptions of three new species (see below).

Key to the Species of *Rondeletia*

- 1a. Leaves with a dense white tomentum with persisting arachnoid hairs beneath; calyx lobes small and equal or subequal 2
- 1b. Leaves not persistently whitish tomentulous beneath, lower leaf surface visible between the minor venation in mature leaves, arachnoid hairs only on young shoots if present; calyx lobes equal to very unequal 3
- 2a. Inflorescences long-thyrsoïd; weedy and widespread, 500–2000 m elevation *R. buddleoides*

- 2b. Inflorescences subcapitate; endemic, Pacific slope, 600–1200 m elevation *R. aspera*
- 3a. Inflorescences long-thyrsoïd, much longer than wide 4
- 3b. Inflorescences paniculate, usually as wide as long 7
- 4a. Some flowers or flower groups sessile and widely separated along the rachis; fruits fleshy, not forming a dehiscent capsule *Gonzalagunia stenostachys*
- 4b. Flowers and flower groups borne on short lateral branches of the inflorescence rachis; fruits becoming dehiscent capsules 5
- 5a. Flowers borne closely together on the branches of the inflorescence; calyx lobes small and subequal [corolla tube usually glabrous; usually trees] *R. brenesii*
- 5b. Flowers borne slightly distant on the lateral branches of the inflorescence; calyx lobes prominent and distinctly unequal 6
- 6a. Each flower with 1, 2, or 3 calyx lobes distinctly enlarged, corolla tube glabrous or sparsely puberulent externally; shrubs; Golfo Dulce area *R. urophylla*
- 6b. Usually with only 1 calyx lobe enlarged on each flower; corolla tube puberulent; trees of the Caribbean lowlands *R. bertierioides*
- 7a. Leaf blades subcoriaceous in texture, becoming bullate in age, minor venation raised beneath and hirsutulous, often broadly ovate; corolla yellow barbate in the throat; stipules usually becoming reflexed [to 17 mm long; widespread, 1000–2500 m elevation] *R. amoena*
- 7b. Leaf blades membranaceous to chartaceous, never bullate in age, minor venation flat beneath, glabrescent to sericeous, blades never broadly ovate; corolla not yellow barbate in the throat; stipules not becoming reflexed 8
- 8a. Stipules leaf-like in form, with a narrow petiole-like stalk and rounded distal blade [leaves 2/node, Caribbean slope, 500–1200 m elevation] *R. costaricensis*
- 8b. Stipules not leaf-like in form, broad at the base and without a petiole-like base 9
- 9a. Leaves usually 3/node 10
- 9b. Leaves usually 2/node 11
- 10a. Corolla tube glabrous on the exterior, 11–15 mm long; petioles 2–10 mm long; western cordilleras at 1200–1700 m elevation *R. monteверdensis*
- 10b. Corolla tube strigulose on the exterior, 10–11 mm long; petioles 1–2 mm long; ca. 700 m elevation on the Pacific slope *R. povedae*
- 11a. Calyx lobes subequal or equal 12
- 11b. Calyx lobes unequal 14
- 12a. Calyx lobes to 6 mm long and lanceolate; leaves to 9 cm long; corolla usually pinkish or rose red [Central Highlands at 1100–1700 m elevation] *R. calycosa*
- 12b. Calyx lobes to 2.5 mm long and triangular to ovate or elliptic; corolla white or yellowish 13
- 13a. Calyx lobes to 2.5 mm long, broadly elliptic to ovate or obovate; corolla tube 9–10 mm long; Caribbean slopes of the Talamanca range 800–1400 m elevation *R. tayloriae*
- 13b. Calyx lobes to 1.5 mm long, narrowly triangular; corolla tube 5–9 mm long; deciduous lowlands of Guanacaste *R. hamelifolia*
- 14a. Plants of the Caribbean lowlands of southern Costa Rica and western Panama [corolla tubes 9–12 mm long] 15
- 14b. Plants of the central cordilleras, 600–2000 m elevation 16
- 15a. Inflorescences with 2–3 pairs of lateral branches; enlarged calyx lobes puberulent *R. cooperi*
- 15b. Inflorescences with 4–6 pairs of lateral branches; enlarged calyx lobes glabrescent *R. bertierioides*
- 16a. Larger leaf blades lanceolate to elliptic, usually 3–4 times longer than wide, petioles to 10 mm long [small calyx lobes 0.5–2 mm long, large calyx lobes 6–12 mm long and bluntly rounded distally; 0–1000 m elevation] *R. salicifolia*
- 16b. Large leaf blades elliptic, ca. 2 times as long as wide, petioles to 40 mm long 17
- 17a. Small calyx lobes 1–3.5 mm long and linear, large calyx lobes 2–6 mm long; 900–2200 m elevation *R. torresii*
- 17b. Small calyx lobes 3–5 mm long and subulate, large calyx lobes 6–9 mm long; rarely collected plants of the wet Caribbean slope at ca. 700 m elevation *R. chaconii*

Rondeletia amoena (Planch.) Hemsl., Diagn. Pl. Nov. Mexic. 26, 1879. *Rogiera amoena* Planch., Fl. Serres 5: 442. 1849. *Rondeletia versicolor* Hooker, Bot. Mag. 77: t. 4579. 1851. *Rondeletia latifolia* Oerst., Vidensk. Meddel. Dansk. Naturhist. Foren. Kjobenhavn 1852: 43. 1853. *R. rugosa* Benth. ex Oersted, loc. cit. 43. 1853. *R. pittierii* K. Schum. & Krause, Bot. Jahrb. Syst. 40: 316. 1908 (photo from B at F). Figure 41.

Shrubs or small trees, 2–7(–10) m tall, leafy branchlets 2–6 mm thick, with soft erect or ascending yellowish hairs 0.2–0.5 mm long, becoming brown; stipules 4–13(–17) mm long, 3–10 mm broad, triangular, sericeous externally, usually glabrous within, becoming reflexed, persisting or deciduous. Leaves opposite, petioles 3–12(–18) mm long, 1.5–3 mm thick, densely yellowish puberulent; leaf blades 6–16(–22) cm long, (3)–4–9(–12) cm broad, broadly ovate, to ovate-elliptic or ovate-oblong (rarely broadly elliptic), apex acuminate (rarely abruptly acute), base broadly obtuse to rounded and subtruncate, drying subcoriaceous or stiffly chartaceous, upper surface with thin strigose hairs 0.3–0.7 mm long (dense over the midvein), lower surface with similar yellowish erect hairs, 2° veins 5–8/side, the 3° veins prominent beneath, veins often becoming impressed above in older leaves. Inflorescences usually terminal, 5–18 cm long and almost as broad, rounded and open panicleate with 2 or 3 pairs of opposite branches, peduncles 2–10 cm long, first pair of lateral branches much larger than the distal (the inflorescence often somewhat tripartite), branches sometimes subtended by small leaves, reduced leaves or small narrow bracts, densely yellowish sericeous-velutinous, pedicels 0–3 mm long. Flowers with hypanthium ca. 1.5 mm long, urceolate or subglobose, densely velutinous with ascending pale yellowish hairs, calyx lobes 4–6, 0.7–1.5 mm long, oblong and slightly unequal, glabrous within; corolla white or pink, minutely puberulent externally, tube 9–14 mm long, ca. 2 mm diam. distally, with dense erect yellowish hairs 0.5 mm long at the mouth of the tube, lobes 5–6, 1.5–3 mm long, ca. 1.2–2 mm broad, rounded distally; stamens with filaments 1.5–2.5 mm long, anthers ca. 2 mm long. Fruits 3–5 mm long, 3–6 mm broad, oblate-subglobose with 2 longitudinal sulci on opposite sides, woody, loculicidal, calyx lobes reflexed or deciduous, glabrescent in late stages.

Plants of evergreen montane forest formations, from 1000 to 2000(–2500) m elevation. Flowering is primarily in November–February in Costa Rica; fruiting throughout the year. It has been collected in the Cordillera de Tilarán (Monteverde), on the western and eastern edges of the Meseta Central, and in the Cordillera de Talamanca. The species ranges from southern Mexico to western Panama.

Rondeletia amoena is recognized by its thick broadly ovate leaves often becoming bullate in age, reflexed stipules, open panicles often with three main branches, pink flowers with yellowish hairs

in the throat, and the small rounded two-locular capsules. This common species is quite different in appearance from our other species of *Rondeletia* and explains Planchon's using this species as the basis for his genus *Rogiera*. This species has been used as a garden ornamental and is known as *quina*, *quina falsa*, and *teresa*.

Rondeletia aspera Standl., N. Amer. Fl. 32: 54. 1918. Figure 41.

Shrubs or small trees to 12 m tall, trunk to 25 cm dbh, leafy branchlets 2–3.5 mm thick, covered at first with soft white arachnoid (and sericeous) hairs but quickly becoming glabrous and reddish brown to very dark brown; stipules 2–6(–10) mm long, broadly triangular (when short) to oblong-lanceolate, erect, puberulent, deciduous. Leaves often clustered at the end of branches, petioles 3–8(–12) mm long, 0.5–1 mm thick, puberulent; leaf blades 5–10(–12) cm long, 1.5–3.5(–4) cm broad, lanceolate to lanceolate-oblong or narrowly ovate-elliptic, apex tapering gradually and acute or acuminate, base acute to obtuse, drying thin-chartaceous, usually dark green above with soft or slightly rough hairs (scabrous in the type), at first densely arachnose tomentulose beneath and covering the entire surface, the older leaf surface remaining white or becoming green with thin hairs 0.3–0.5 mm long beneath, 2° veins 5–8/side and strongly arcuate ascending. Inflorescences terminal, 2.5–7 cm long, compact subcapitate cymose panicles, peduncle 5–30 mm long, white tomentulose, the flowering portion as broad as long and the flowers closely crowded, subsessile. Flowers with hypanthium 1.5–2 mm long, ca. 1.3 mm diam., with ascending sericeous and tomentulose white hairs, calyx lobes 0.5–1.5 mm long, narrowly triangular to rounded, equal or subequal; corolla whitish to reddish brown, tube 8–11 mm long, 0.7–1.5 mm diam., with soft thin white hairs externally, lobes 4, 2.5–3 mm long, 1.5–2 mm broad, glabrous within. Fruits 3–6 mm long, 3–6 mm broad, puberulent, closely clustered, at first opening partially septicidally and then each half opening (loculicidal) at the top.

Plants of partly deciduous forest formations on the Pacific slope, from about 600 to 1200 m elevation. Flowering in December–February; fruiting in April, June, and August. The species is only known from the region between Monteverde and Ciudad Colón (San José) in central Costa Rica.

Rondeletia aspera is recognized by its smaller leaves crowded at the ends of slender branches, lamina that have a dense white arachnoid tomentum beneath and dry dark above, and the small subcapitate inflorescences. The restricted range of this species is another important distinction. This species would have to be transferred to *Arachnothrix*, if that genus were accepted.

Rondeletia bertierioides Standl., Publ. Field Columb. Mus., Bot. Ser. 4: 267. 1929.

Small trees to 6 m tall or rarely shrubs, leafy branchlets 1–3 mm thick, arachnoid-tomentulous and whitish in early stages, soon glabrescent; **stipules** 3–5(–7) mm long, triangular to subulate with a narrow tip 1–3 mm long, puberulent at the base, glabrous distally and drying dark. **Leaves** opposite and equal or unequal, petioles 4–12(–30) mm long, 0.5–1 mm thick, with thin whitish arachnoid and appressed hairs in early stages but quickly glabrescent; **leaf blades** (4–)6–15(–22) cm long, 1.5–5(–8) cm broad, narrowly elliptic to elliptic or narrowly ovate-elliptic, apex tapering gradually and acuminate (acute), base acute to obtuse and slightly decurrent on petiole, drying thin-chartaceous, dark brown above, quickly becoming glabrous above, appressed-puberulent along the veins beneath or glabrescent, 2° veins 5–7/side, 3° veins subparallel. **Inflorescences** terminal (rarely axillary), 7–20 cm long, 3–8 cm broad, narrowly pyramidal with 5–6 pairs of short helicoid-cymose lateral branches 1–3 cm long, peduncles 2.5–5 cm long, 0.7–1.4 mm thick, appressed-tomentulose, bracts 2–4(–9) mm long, linear to lanceolate, pedicels 0–2(–3) mm long. **Flowers** with a hypanthium 1–1.5 mm long, ca. 0.7 mm diam., appressed-tomentulose, calyx lobes 4, the 3 small lobes 0.3–2 mm long, triangular to oblong or linear, the long calyx lobes 1.5–4(–12) mm long, 1–3(–5) mm wide (usually 3 times longer than the small lobes), white; **corolla** white tinged with pink, tube 9–12 mm long, ca. 0.8 mm diam., puberulent externally, lobes 4, 2–2.7 mm long, broadly rounded distally; anthers 2–2.7 mm long. **Fruits** ca. 4 mm long, ellipsoid with longitudinal ribs (costae), glabrous at maturity, septicidal, calyx lobes persisting and perhaps enlarging.

Plants of the lowland Caribbean rain forest formations and premontane rain forest formations, from near sea level to 1000 m elevation. Flowering in February, April, July, and September. Two atypical Costa Rican collections are tentatively placed here (see below). Otherwise, this species is only known from the provinces of Bocas del Toro, Coclé, and Veraguas in western Panama.

Rondeletia bertierioides is recognized by the long narrow or pyramidal inflorescences with slender corolla tubes, the calyx with a single enlarged lobe, and arachnoid hairs on newly developing plant parts. Included here are *Barringer et al.* 3523 (CR, F, MO) and *Burger & Antonio* 10896 (CR, F) collected near BriBri in southern Limón Province, Costa Rica. These have more broadly (to 10 cm) paniculate inflorescences and conspicuously enlarged calyx lobes to 12 mm long and 5 mm broad. The young parts are arachnose tomentulose (in the Barringer collection) and other features conform to the measurements given by Kirkbride. The type (*Cooper* 12231 us) has narrow (3 cm) inflorescences and calyx lobes only 1–3 mm long.

Rondeletia brenesii Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 1370. 1938. *Gonzalagunia exaltata* Standl., loc. cit. 22: 385. 1940. Figure 21.

Trees, 8–18 m tall, trunks 20–30 cm diam., leafy branchlets 3–4 mm thick, with thin appressed hairs but soon glabrescent; **stipules** 7–15 mm long, united above the petioles for a short (1–4 mm) distance or overlapping to form a short tube, with a narrow attenuate tip 2–7 mm long, with thin whitish hairs or glabrescent. **Leaves** often closely clustered at the tips of branches, petioles 6–20 mm long, 1–1.7 mm thick, puberulent with lateral margins continuous with the lamina margins; **leaf blades** 11–22 cm long, 3–6.5 cm broad, narrowly elliptic-oblong to oblong-oblancoolate or elliptic, apex tapering gradually and narrowly acuminate with tip 7–25 mm long, base gradually narrowed and attenuate, decurrent on the petiole, drying thin-chartaceous, brown above, glabrescent above, with very thin soft whitish hairs 0.5–1 mm long beneath, 2° veins (8–)11–15/side, strongly ascending but not loop-connected near the margin. **Inflorescences** terminal and solitary, 15–18 cm long, thyrsoid panicles only 2–3 cm broad, peduncles 1–2 cm long and 2 mm thick, the rachis pilose with thin whitish hairs, with 5–15 closely crowded flowers on each lateral branch, secondary peduncles 1–3 mm long, pedicels 0–1 mm long. **Flowers** with hypanthium 0.5–0.9 mm long, subglobose, calyx lobes 4, 0.5–1 mm long, subequal, triangular to acuminate, sparsely puberulent; **corolla** white, tube 4–8 mm long, 0.4–0.7 mm diam., glabrous or sparsely puberulent, lobes 4, ca. 1.5 mm long and 1.5 mm broad at the base, rounded distally; anthers ca. 1.5 mm long, included. **Fruits** dicocccous, mericarps 3 mm diam., subglobose, flattened laterally.

Plants of the evergreen premontane rain forest and moist forest formations (primarily on the Caribbean slope), from 300 to 1100 m elevation. Flowering in February–April. This species is only known from the area between Volcán Arenal (Alajuela) and the western slopes of the Meseta Central, and with a single collection from near San Isidro del General (San José), in central Costa Rica.

Rondeletia brenesii is recognized by the narrowly elliptic leaves with many 2° veins, the unusual stipules, the long narrow thyrs-like inflorescences, and small almost glabrous four-lobed corollas. The larger stature attained by this species is also unusual. Compare *R. stachyoidea* J. D. Smith of northern Central America, which has narrower leaf blades, fewer secondary veins, sessile flower groups, and a lower-elevation habitat.

Rondeletia buddleoides Benth., Pl. Hartw. 69. 1840. *R. affinis* Hemsl., Diagn. Pl. Nov. Mexic. 28. 1879. *R. buddleoides* var. *aspera* Kirkbride, Ann. Missouri Bot. Gard. 55: 379. 1968. Figure 21.

Shrubs or small trees, 2–8(–12) m tall, trunks to 20 cm diam., leafy branchlets 1.2–6 mm thick, white tomentulose at first but becoming glabrous and brown; **stipules** 4–11 mm long, 1–5 mm wide, usually narrow near the base and broader distally, oblong to oblong-obovate, often with a strong keel along the back, usually glabrous. **Leaves** with the petiole 3–20 mm long, white tomentulose when young; **leaf blades** 4–22 cm long, 1–8 cm broad, narrowly elliptic to elliptic-oblong (less often somewhat ovate or obovate), apex acute or abruptly acuminate, base obtuse to acute, drying thin- to stiffly chartaceous, upper surfaces becoming very dark after the thin hairs are lost, lower surfaces whitish on all surfaces with a dense matted tomentum of arachnoid and thin straight hairs, the major veins often darkly outlined against the white tomentum beneath, 2° veins 8–12/side, 3° veins subparallel. **Inflorescences** usually terminal, solitary, 14–22(–30) cm long, 2–4 cm broad, elongate thyrsoid panicles, peduncles 3–30(–80) mm long, the lateral branches short (2–5 mm) and bearing cymes or helicoid branches of 3–12 flowers, rachis at first white tomentulose, bracteoles 1–2 mm long, pedicels 0–1 mm long. **Flowers** with hypanthium ellipsoid to subglobose, 1–1.5 mm long, 0.5–1.5 mm diam., white tomentulose, calyx lobes 0.3–1 mm long, equal; **corolla** white, rose or yellowish, tube 6–11 mm long, 0.5–1 mm diam., minutely tomentulose, lobes 4, 1.5–2.5 mm long, equally broad; anthers ca. 1.5 mm long. **Fruits** 3–4 mm long, subglobose, dehiscent septically.

Common shrubs and trees of evergreen formations on both the Pacific and Caribbean slopes, (600–)800–2000 m elevation. Flowering primarily in May–September; fruiting in January–September. In Costa Rica, the species occurs along the central highlands from the Cordillera de Guana-caste to the eastern parts of the Cordillera de Talamanca. Despite this range, the species appears to be absent in some areas, such as around the central volcanoes. The species ranges from southern Mexico to western Panama.

Rondeletia buddleoides is recognized by the usually narrow leaves with a dense white tomentum beneath, the long narrow thyrsoid inflorescence with pink, white, or yellowish flowers, the slender corolla tubes, and the small septicidal capsules. This species resembles *Buddleia americana* (Loganiaceae), in regard to both the leaves whitish beneath and the long narrow inflorescences with tubular flowers. It is not easily confused with any of our other species of *Rondeletia*.

Rondeletia calycosa J. D. Smith, Bot. Gaz. 56: 69. 1913. Figure 41.

Shrubs or small treelets to 5 m tall, leafy branchlets 1–3 mm thick, at first ascending sericeous with slender hairs ca. 0.3 mm long, quickly becoming glabrous and dark brown; **stipules** 2–3(–4) mm long, triangular to cus-

pidate with a narrow awn ca. 1 mm long, glabrous, persisting with the leaves. **Leaves** opposite, petioles (2–)3–9 mm long, 0.5–0.8 mm thick, at first with ascending sericeous hairs; **leaf blades** 4–9 cm long, 1–3 cm broad, elliptic to elliptic-oblong or narrowly elliptic-obovate, apex acuminate with tip 8–14(–18) mm long, base acute or obtuse, drying stiffly chartaceous, much darker above than below, glabrous or with very thin hairs 0.3–0.8 mm long on the upper surface, with short (0.3 mm) appressed-ascending hairs on the veins beneath, 2° veins 4–6/side, arcuate-ascending. **Inflorescences** terminal, 3–7 cm long, corymbose-rounded to pyramidal, peduncles 1–3 cm long, basal branches often subtended by reduced leaves, flowers usually in distal 3-flowered cymes, bracts 2–4(–6) mm long, linear-oblong to narrowly elliptical, pedicels 1–5 mm long, appressed-puberulent. **Flowers** with hypanthium ca. 2 mm long and 1.3 mm diam., with ascending yellowish hairs, calyx tube ca. 1 mm long, calyx lobes 4, usually unequal with 1 (2) larger lobes 3–5 mm long and 3 (2) smaller (1–2 mm) lobes, or occasionally the 4 lobes subequal and 3–6 mm long, linear-oblong; **corolla** red to dark rose or pink, tube 12–15(–17) mm long, 0.8–1 mm diam. throughout its length, appressed-puberulent, lobes 4, 2–3 mm long, ca. 2.5 mm broad, rounded and undulate distally; style ca. 9 mm long, stigmas linear, 2.5 mm long. **Fruits** ca. 5 × 4 mm, ellipsoid, laterally flattened.

Shrubs of lower montane rain forest formations along the Caribbean escarpment, from 1100 to 1700 m elevation. Flowering in August and September–October. The species is only known from near Zarcero, east of Volcán Barva, Cerros de Zurquí, and the La Palma–La Hondura area, in central Costa Rica.

Rondeletia calycosa is recognized by the small stature and small leaves on slender stems, the small open inflorescences with flowers in distal cymes, the large equal or unequal calyx lobes, and the long narrow reddish corolla tube. Development of the sepal lobes appears to differ significantly in different collections; compare material placed under *R. torresii*. A collection (Zuñiga & Jiménez 15 CR, F) from Res. Biol. Carara at 300 m is tentatively placed here; it may be an unusual population or a related species.

Rondeletia chaconii Lorence, sp. nov. Figure 41A.

Species *Rondeletia scabrae* Hemsley affinis, sed ramulis dense velutino-tomentosis, foliis majoribus (6.5–)9–20 × (3.5–)4–7.8 cm, stipulis grandioribus, 7–11 × 3.2–5.2 mm, pedunculo 5 cm longo, corolla sericea differt.

TYPUS—I. A. Chacón 177 (holotypus CR 92850), from bosque socolado, finca de Bernardo Gómez, 700 m, Magsasay, Heredia. Costa Rica, 21 Jan. 1983. Figure 41A.

Small tree, 5 m tall, leafy twigs 2–3 mm diam., at first densely velutinous, the trichomes 1–1.5 mm long, light

brown, simple straight, septate, the internodes 1.5–6 cm long; **stipules** 7–11 × 3.2–5.2 mm, ovate, interpetiolar, brown, externally strigose, internally white-sericeous, also with several dark brown collectors 0.5 mm long. **Leaves** opposite, those of a pair at a node subequal, petioles 5–30 × 1–1.5 mm, strigose-hirsute; **leaf blades** (6.5–)9–20 cm long, (3.5–)4–7.8 cm broad, elliptic, apex acuminate with tips 1.5–2 cm long, base acute or cuneate, occasionally slightly attenuate, stiffly chartaceous, discolorous, drying dark brown adaxially, abaxially paler brown, adaxially strigose-hirsute with scattered pale brownish white trichomes 0.5–1 mm long, trichomes denser along the costa, veins and margin, the pubescence slightly more dense abaxially, 2° veins 9–12/side, arcuate-ascending, brochidodromous, 3° veins forming a strong intersecondary cross-webbing pattern. **Inflorescences** terminal, becoming pseudoaxillary, cymose-corymbiform with 10–15 sessile or subsessile flowers, densely hirsute-sericeous with pale brown or white trichomes, the peduncle 5 cm long, 0.6 mm diam., with 3 1° branches, each 1.2–1.4 cm long and bearing 1–3 cymules of 1–3 flowers, the branches, cymules and flowers basally bracteolate, bracteoles hastate or lanceolate-subulate, 4–6 × 0.6–3 mm, sericeous. **Flowers** 4-merous, hypanthium ca. 1 × 1 mm, obovoid, densely sericeous, calyx cup 0.4 mm deep, calyx lobes sericeous externally, strigose within, unequal, 1 large (6–9 × 2–3 mm) and foliaceous, venose, oblan-ceolate or elliptic, the smaller 3 subulate, 3–5 × 0.4–0.8 mm, each sinus with several short brown collectors; **corolla** white, salverform, tube 13–16 long, 1.2–1.4 mm wide distally, externally sericeous, internally pilosulous in basal 1/3, lobes suborbicular, 2.5–3 × 2.5–3 mm, externally sericeous basally mixed with shorter hirtellous trichomes above and on margin, internally minutely papillose-puberulent especially around throat, the margins often crisped; **stamens** in long-styled flowers included, attached 3.5–4 mm below throat, in short-styled flowers attached 2 mm below throat, filaments 0.5 mm long, anthers 2–2.2 mm long, linear-ellipsoid; style glabrous, in short-styled flowers included, 6.5–7 mm long, the stigmatas linear-ellipsoid, 2 mm long, in long-styled flowers 13 mm long with ovoid stigmas 0.5 mm long, disc pilose. **Fruits and seeds** not seen.

Plants of the wet evergreen Caribbean slope at 700–900 m elevation. Flowering in January and known only from the type collection and *Bello 2082* CR, MO.

Rondeletia chaconii belongs to section *Calycosae* of subgenus *Arachnothryx*. It is most closely allied to the groups of large-flowered species with large, unequal calyx lobes and large white corollas including *R. macrocalyx* Standl. & Steyerl., *R. uxpanapensis* Lorence & Castillo-Campos, and especially *R. scabra* Hemsl. (synonyms: *R. mexiae* Standl. and *R. acuminata* (Oerst. ex Standl.) Lorence & Castillo-Campos). It is easily distinguished from these species by its long-pedunculate inflorescence. It is most unusual that the holotype, which consists of two twigs, has both short-styled flowers (left twig) and long-styled flowers (right twig). The collector's data state "*Arbol de 5 m de*

alto, con flores blancas," but it is unlikely that both floral morphs would occur on the same plant. [Contributed by D. Lorence.]

Rondeletia cooperi Standl., Publ. Field Columb. Mus., Bot. Ser. 4: 267. 1929.

Shrubs or small trees, 2–7 m tall, trunk ca. 5 cm diam., leafy branchlets 1–3 mm thick, puberulent with soft appressed-ascending hairs 0.2–0.5 mm long, with erect hairs ca. 1 mm long at the node (usually covered by the stipules); **stipules** 2–11 mm long, triangular (when short) or cuspidate with a narrow tip to 8 mm long, appressed-puberulent. **Leaves** with petioles 4–22(–30) mm long, 0.7–1.7 mm thick, puberulent; **leaf blades** (8–)12–22 cm long, (3.5–)5–9 cm broad, elliptic to elliptic-oblong or slightly obovate, apex acuminate with a narrow tip 5–12(–25) mm long, base obtuse to acute, drying thin-chartaceous, glabrescent above, minutely (0.1–0.3 mm) appressed puberulent on the veins beneath, 2° veins 5–8/side, arcuate ascending distally but not clearly loop-connected. **Inflorescences** terminal, 9–17(–25) cm long, to 10 cm broad, open panicles with 2–5 pairs of primary branches to 5 cm long, peduncles 4–16 cm long, ca. 1.5 mm thick, strigulose, flowers on distal cymose or scorpioid axes, pedicels 0–1(–3) mm long. **Flowers** with hypanthium ca. 2 mm long and 1.3 mm diam., oblong, densely ferruginous with ascending hairs, calyx tube ca. 0.5 mm long, calyx lobes 4, strongly unequal, the 1 large lobe 3–4 mm long and 1.5–2 mm broad, narrowly ovate to elliptic, the small lobes 0.7–1 mm long, ca. 0.4 mm wide, narrowly oblong; **corolla** white, tube 9–11 mm long, 0.6–1 mm diam., strigillose, lobes 4, 2–3 mm long. **Fruits** to 4.5 mm long and 3.5 mm diam., costate, septicidal to the middle, calyx lobes persisting.

Plants of lowland Caribbean rain forest formations, from near sea level to 400 m elevation. Flowering in the period of January–March (*Cooper 600* F holotype, MO). This species is only known from Bocas del Toro, Panama.

Rondeletia cooperi is recognized by its lowland habitat, single enlarged calyx lobe on each flower, and narrow corolla tube. This is a very poorly known species, rather similar to *R. bertieroides* but lacking the arachnoid hairs in early stages and having widely branched inflorescences. However, it may prove to be synonymous with that species.

Rondeletia costaricensis Standl., N. Amer. Fl. 32: 61. 1918. Figure 41.

Shrubs or small trees, 2–10 m tall, leafy branchlets 1–3 mm thick, glabrous from earliest stages (or with a few hairs at the nodes); **stipules** (3–)4–7 mm long, to 6 mm broad, leaf-like distally with a short (1 mm) petiole-like stalk and rounded lamina cordate at the base and emarginate or retuse at the rounded apex, glabrous or with a

few hairs at the base. **Leaves** with petioles 4–10 (–16) mm long, 0.6–1.7 mm thick, glabrous, drying dark; **leaf blades** 7–14 (–18) cm long, 2.3–5.5 (–8) cm broad, elliptic to elliptic-oblong or slightly obovate, apex usually short-acuminate (acute), base obtuse to acute and slightly decurrent on the petiole, drying membranaceous or thin-chartaceous, usually dark in color above, glabrous above and below, 2° veins 4–6/side and weakly loop-connected distally. **Inflorescences** terminal, 4–9 cm long, to 8 cm broad, open panicles with 1 or 2 pairs of major opposite lateral branches, peduncles to 5 cm long and 1 mm thick, minutely (0.1–0.2 mm) appressed-puberulent, bracts 2–4 mm long, linear, pedicels 0–3 mm long. **Flowers** with hypanthium 1–1.3 mm long, ca. 1 mm diam., obconic to urceolate, densely sericeous with yellowish hairs, calyx lobes 4, to 0.7 mm long, equal, glabrous distally; **corolla** white, tube 6–9 mm long, 0.5–1.5 mm diam., minutely appressed puberulent, lobes 4, 1–3 mm long, rounded and undulate distally. **Fruits** 4–5 mm long, 3.5–4.5 mm diam., subglobose to turbinate in forms, slightly rounded at the truncated distal surface, persisting calyx lobes ca. 0.5 mm long; **seeds** ca. 1.2 mm long, broadly ellipsoid-lenticular, with a few hairs along the edge.

Plants of premontane rain forest formations on the Caribbean slope, from 600 to 1200 m elevation. Flowering in March–May; fruiting in June–October. This species is only known from the Caribbean slope in the region between P. N. Rincón de la Vieja (85°19'W) and above Ciudad Quesada (84°27'W) in north-central Costa Rica.

Rondeletia costaricensis is distinguished by its unique stipules, thin glabrous leaves, small terminal inflorescences, small calyx lobes not differing in size, and slender corolla tubes. The stipules are slightly intrapetiolar and united above the base for about 1–2 mm before becoming narrowed to the petiole-like base of the broad distal laminar part. This broad leaf-like distal part of the stipule is glabrous and has pinnate venation.

***Rondeletia hamelifolia* Dwyer & Hayden, Ann. Missouri Bot. Gard. 54: 144. 1967. Figure 41A.**

Small trees or shrubs, 5–8 m tall, leafy stems 1.5–3 mm thick, strigulose-sericeous and later glabrescent, terete; **stipules** 2–10 mm long, 1.5–5 mm broad at the base, triangular and acute, sericeous, persistent. **Leaves** with petioles 2–15 mm long, densely strigulose; **leaf blades** 4–19 cm long, 2–6 cm broad, elliptic, apex deltoid-acuminate to acute, base cuneate, drying chartaceous, sparsely strigillose above and below (more densely on the veins), 2° veins 5–9/side. **Inflorescences** terminal, 4–13 cm long and 3–9 cm broad, open panicle with 60–180 flowers in distal cymes, peduncles (1–)2.5–4.5 cm long, densely strigose-sericeous (as are branches, bracts and pedicels), bracts 1–4 mm long, triangular to linear, pedicels 0–4 mm long. **Flowers** with subglobose hypanthium 1–1.2 mm long, calyx lobes 5, 0.5–2 mm long, linear; **corolla** salverform, white, tube 5–9 mm long, ca. 1 mm diam.,

lobes 5, 1.5–2.5 mm long, rounded. **Fruits** 3–7 mm long and ca. 5 mm wide, ellipsoid to subglobose, papery, dehiscent to half the length; **seeds** 1.2–1.9 mm long, fusiform with a wing at each end.

Plants of seasonally dry deciduous forest, 100–250 m elevation. Flowers and fruit were collected in January (*Liesner 4521 CR*). In Costa Rica this species has only been collected from along Río Guapote in the Santa Rosa National Park, Guanacaste; it also occurs in Panama.

Rondeletia hamelifolia is recognized by its deciduous forest habitat, often larger leaves that taper gradually to both apex and base, and the slender white corolla tubes. The five-parted flowers, corolla with a fleshy ring around the throat, loculicidal capsules, and seed characters place this species in subgenus *Rondeletia*.

***Rondeletia monteverdensis* Lorence, Novon 1: 147–148. 1991. Figure 41.**

Shrubs or small trees, 2–6 (–16) m tall, trunk to 15 cm dbh, leafy branchlets 1–3 mm thick, with a few thin whitish hairs in the earliest stages and quickly glabrescent or glabrous throughout (but with erect tufted hairs at the node within the stipules), becoming dark brown; **stipules** 1–3 mm long, 1–2 mm wide with a short (0.5 mm) sheath, triangular or subulate, with a few hairs along the distal margins, sericeous within. **Leaves** usually 3/node, subequal to unequal (50%) at a node, petioles 2–6 (–10) mm long, 0.5–1 mm thick, glabrescent; **leaf blades** (2–)3–8.5 cm long, 1–2.5 cm broad, elliptic to narrowly elliptic-obovate or oblanceolate, apex abruptly narrowed to a long-acuminate with tip 7–15 mm long, base gradually narrowed and acute, drying stiffly chartaceous, dark above and pale grayish green beneath, glabrous or with scattered very thin whitish hairs to 1 mm long above, with few hairs or glabrescent beneath, 2° veins 3–6/side, ascending. **Inflorescences** terminal, 3–7 (–12) cm long, 3–5 cm broad, pyramidal with 2 or 3 ternate nodes and 15–30 flowers, peduncles 5–40 (–60) mm long, 0.6–1 mm thick, glabrous or sparsely puberulent, primary bracts 5–17 mm long, 1–3 mm broad, linear to narrowly oblong, floral bracts 4–5 mm long, pale brown and resembling the enlarged calyx lobes, essentially glabrous, palmately 3-veined, deciduous, pedicels 0–3 mm long. **Flowers** with hypanthium 1.5–2 mm long, obovoid-ellipsoid, with thin white hairs, calyx lobes 4, unequal but all enlarged, (3–)5–11 mm long, 1–2.5 mm broad, lanceolate, greenish white but drying pale brown, glabrous; **corolla** salverform, white, glabrous externally, tube 11–15 mm long, 0.5–1.2 mm diam., lobes 4, 2–4 mm long, 2–2.5 mm broad, broadly rounded distally; **stamens** sessile, anthers 2.5–3 mm long. **Fruits** 4–5 mm long, 2.5–4 mm broad, obovoid-ellipsoid, bisulcate, with 8 pale longitudinal ribs, apparently at first septicidally dehiscent and the 2 valves then opening at the apex.

Plants of lower montane and premontane rain

forest formations in the northwestern cordilleras, from (1200–)1400 to 1700 m elevation. Flowering in February–August; fruiting in May and July–November. This species is only known from the Cordillera de Guanacaste and Cordillera de Tilarán in northwestern Costa Rica.

Rondeletia montevertensis is recognized by the small ternate leaves with prominent drip tips, the compact inflorescences with large bracts and nearly identical large calyx lobes, and the glabrous white corollas. The similarity in form, texture, and color of the inflorescence bracts and enlarged sepal lobes is a striking example of homeosis or heterotopy: it is also seen in the closely related *R. calycosa*, where the bracts and calyx lobes are not as large and distinctive. A collection by G. Herrera (651 CR, F, MO) from 1200 m on Volcán Santa Maria differs from the Monteverde material in having narrower leaves, smaller bracts, and smaller calyx lobes.

***Rondeletia povedae* Lorence, sp. nov. Figure 41A.**

Species *Rondeletiae montevertensis* Lorence affinis, sed inflorescentia ramulis petiolisque dense strigulosis, foliorum petiolis 1–2 mm longis, laminae pagina abaxiali tomentosa, inflorescentia subsessili, lobis calycinis minoribus ligulato-subulatis 1–2 × 0.3–0.5 mm differt.

TYPUS—*L. J. Poveda* 441 (holotypus CR 51260, isotypus MO 2211249), from Santa Rosa de Puriscal, San José, Costa Rica, 17 Jan. 1973. Figure 41A.

Shrubs, ca. 4 m tall, leafy twigs 1.2–1.5 mm thick, at first densely strigulose, the trichomes brownish white, simple, straight or curved, to 0.5 mm long, the internodes 0.3–3.5 cm long, bark brown; **stipules** 2–3.5 mm long, 1–2 mm broad, narrowly triangular, acuminate, intrapetiolar sheath 0.5 mm long, externally densely strigulose, internally densely white-villous, the margins and internal surface with several blackish digitate collectors. **Leaves** usually in whorls of 3, occasionally opposite, those at a node unequal, the smallest usually 50% the size of the largest, subsessile, petioles 1–2 mm long, 0.5–0.8 mm thick, densely strigulose; **leaf blades** (3–)4–9.5 cm long, (0.9–)1.5–2.7 cm broad, oblanceolate or narrowly elliptic-lanceolate, apex long-acuminate and often falcate, tip 5–15 mm long, base acute or usually abruptly rounded or obtuse, chartaceous, strongly discolorous, drying dark brown adaxially and pale brown abaxially, adaxially sparsely arachnoid-pubescent with scattered curling trichomes, glabrescent, abaxially moderately arachnoid-tomentose with persistent white trichomes, strigulose along the costa, 2° veins 7–8/side, camptodromous, arcuate-ascending, a distinct marginal vein present, tertiary veins forming a strong intersecondary cross-webbing pattern. **Inflorescence** terminal, often inclined, cymose-corymbiform, 12–16-flowered, densely strigulose with whitish trichomes, the slender peduncle 2–3.5 cm long, the rachis with 1(–2) whorls of 3 1° branches 8–12 mm long, each ending in a 1–3-flowered cymule, the axes

bracteolate, the bracteoles subulate, 2–3 mm long, pedicels 0.3–4 mm long, 0.2–0.3 mm thick (central flowers sessile). **Flowers** 4-merous, hypanthium 1.2–1.4 × 1.2 mm, ovoid compressed, densely strigulose, calyx cup 0.3 mm deep, lobes 4 (rarely 5), subequal to unequal, 1 usually larger than the other 3, linear-subulate to lanceolate, 1–2.5 × 0.2–0.5 mm, densely strigulose externally, recurved, each sinus with 1–3 small brown collectors; **corolla** salverform, white and pink, tube 10–11 mm long, 1.5 mm wide distally, externally strigillose, internally hirtellous in basal 1/3, lobes irregularly suborbicular, 2–3 × 2–3 mm, externally sparsely strigulose, internally glabrous, the throat glabrous, the margin undulate; **stamens** in long-styled flowers included, sessile, attached 5 mm below throat, anthers linear, 2.5 mm long; style in long-styled flowers 11 mm long, glabrous, the stigmas 2 mm long, narrowly ellipsoid, slightly exerted, the disc pilose without. **Fruits** broadly ovoid-subglobose capsules, 2–3 × 2.5–4 mm, smooth, blackish, strigulose, bisulcate, dehiscence loculicidal then septicidal; **seeds** 0.7–0.9 × 0.4–0.5 mm, ellipsoid, light brown, narrowly winged, the wing broader at each end, the testa cells elongate, shallowly reticulate.

Plants of the seasonally dry Pacific slope at ca. 400 m elevation in central Costa Rica. This species is only known from the type collection.

Rondeletia povedae is recognized by the smaller often lanceolate leaves, usually three at each node, and the Pacific slope habitat. In terms of floral and capsule morphology, *R. povedae* is referable to subgenus *Arachnothryx*, section *Calycosae*, although the elongate seeds with a wing at each end and elongate testa cells with a shallow reticulum are suggestive of subgenus *Rondeletia*. This new species is most closely allied to *R. montevertensis* Lorence, which also has ternate leaves but differs by the characters given in the diagnosis. [Contributed by D. Lorence.]

***Rondeletia salicifolia* Dwyer & Hayden, Phytologia 15: 58. 1967.**

Trees, 4–8 m tall, leafy branchlets with slender yellowish hairs; **stipules** to 4 mm long, triangular from a broad and thickened ring-like base, with a short curved awn, puberulent. **Leaves** with petioles 5–10 mm long; **leaf blades** 3–20 cm long, 2–9 cm broad, lanceolate to elliptic, the larger blades 3–4 times longer than wide, apex obtuse to slightly acuminate with narrow (1.5–2 mm) tip to 20 mm long, base obtuse to acute, drying stiffly chartaceous, dark brown, with minute yellowish hairs on the veins beneath, 2° veins 4–6/side. **Inflorescences** terminal or axillary, paniculate with 2 or 3 pairs of opposite branches, peduncles to 6 cm long, lateral branches up to 12 cm long, tomentulose, flowers sessile in cymose or scorpioid arrangements. **Flowers** with hypanthium ca. 2 mm long and tomentulose, calyx tube ca. 0.5 mm long, calyx lobes 4, strikingly unequal with

the single enlarged lobe 3–4 times longer than the short lobes, small lobes 0.7–3 mm long, the large calyx lobe 6–12 mm long and up to 7 mm broad, elliptic to ovate, bluntly rounded; **corolla** white, corolla tube 8–15 mm long, glabrate externally, lobes rounded; filaments to 2 mm long, anthers ca. 3 mm long. **Fruit** to 4 mm diam., subglobose, costate, the hairs deciduous.

Plants of premontane rain forest and cloud forest formations in Panama, from near sea level to ca. 1000 m elevation. This species is reported to occur at the Monteverde Reserve. The species ranges into central Panama.

Rondeletia salicifolia is recognized by the narrow leaves, and calyx with 1 enlarged lobe. Photographs distributed as *R. salicifolia* H.B.K. do not represent a published name; they are *R. leucophylla* H.B.K. of Mexico (fide Lorence in herb.).

***Rondeletia tayloriae* Lorence, sp. nov.** Figure 41A.

Species *Rondeletia torresii* affinis, sed lobis calycinis aequalibus vel subaequalibus foliaceis ellipticis ovatis vel obovatis 1.5–2.5 mm longis 0.8–1.5 mm latis, apicibus obtusis vel rotundatis et corolla minore 2–3 mm longa, 1.8–2.4 mm lata differt.

TYPUS—*Herrera & Chacón 2656* (holotypus CR, isotypi MO, PTGB), from Fila Matama, Valle de la Estrella, 1350 m, Cantón de Limón, Limón, Costa Rica, 19 Apr. 1989.

Small trees, 6–8 m tall, slender twigs 1.2–3 mm diam., densely strigillose when young, trichomes 0.2–0.3 mm long, stiff and acicular, the internodes 1.5–12 cm long; **stipules** erect, rigid, 2–3.5 × 2.5–5 mm, deltoid to broadly deltoid, dark brown, densely strigillose externally. **Leaves** opposite, those of a node equal or subequal, petioles 1–3.5 cm long, 1–1.2 mm diam., narrowly winged distally, densely strigillose; **leaf blades** (5.5–)6.5–19.5 cm long, (2–)3–8.2 cm broad, elliptic to ovate, apex acuminate with an abrupt, straight or falcate acumen 1–2 cm long, base acute, usually attenuate and decurrent along the petiole, thinly to thickly chartaceous, drying brownish green, adaxially with scattered strigillose hairs on surfaces, denser on the veins and costa, glabrescent, abaxially densely strigillose, on veins and costa, hairs persistent, 2° veins 7–9/side, arcuate, brochidodromous. **Inflorescences** terminal, 5.5–16 cm long, 5–11.5 cm broad, corymbiform-cymose with 20–30(–60) flowers, sessile or the peduncles 4–8 cm long, axes trichotomous and densely fulvous strigillose-velutinous, branching to the 3°, with 2 pairs of 1° branches, these 1–7 cm long, branching again 1(–2) times dichasially, ending in cymes of 2–3 flowers, branches and cymes subtended by subulate bracteoles 1 mm long, pedicels 0–2 mm long, densely strigillose-velutinous. **Flowers** 4-merous, hypanthium 1.5–2 × 1.2–1.5 mm, obovoid, calyx cup 0.6–0.8 mm deep, calyx cup and hypanthium densely strigillose-velutinous, calyx lobes subequal, 1.5–2.5 × 0.8–1.5 mm, broadly elliptic, ovate or obovate, apex obtuse or rounded, both surfaces strigillose, green when fresh; **corolla** white, salverform,

tube 9–10 mm long, 1.2–1.4 mm diam. medially, externally densely strigillose-velutinous, internally hirtellous in basal 1/3, lobes 2–3 × 2–3 mm, subcircular or obovate, spreading, densely strigillose basally, internally minutely papillose-puberulent, basally with larger white bulbous trichomes; **stamens** in long-styled flowers sessile, attached 3 mm below throat, anthers 2–2.5 mm long, ellipsoid, included; style 10–11 mm long in long-styled flowers, tip exerted, glabrous except for a few hairs toward base, stigmas 0.8 mm long, ellipsoid. **Fruits** (immature) 6–7 × 4.5–5 mm, ovoid, bisulcate and crowned by the persistent calyx, strigillose; **seeds** not seen.

Plants of the premontane and montane tropical wet forest on the Caribbean slope of the Cordillera de Talamanca, 850–1350 m elevation. Flowers and immature fruits were collected in April. Only two collections have been seen, the type and *Robles & Chacón 2664* (CR, MO, PTGB), also from the Fila Matama (Cerro Muchilla) at 850 m elevation, Limón Province. Endemic.

Rondeletia tayloriae belongs to subgenus *Arachnothryx*, section *Calycosae*. This species is most closely related to *R. torresii*, which differs by its strongly unequal calyx lobes—the three small ones 1.5–3 mm long and linear to subulate with acute apices and the large one 4–5 mm long, obovate-elliptic to oblanceolate with an acute to obtuse apex—and larger corolla lobes 3–4 × 4–5 mm. This new species is also related to *R. calycosa*, a species that differs in having a pubescence of longer silky trichomes, linear-lanceolate calyx lobes 3–7 mm long with acute or acuminate apices, and dark pink or rose red corollas. I take pleasure in naming this species for Charlotte M. Taylor. [Description and discussion contributed by D. Lorence.]

***Rondeletia torresii* Standl., J. Wash. Acad. Sci. 18: 163. 1928. Figure 41.**

Shrubs or small trees, 1.5–5 m tall, leafy branchlets 1–3 mm thick, minutely puberulent with thin whitish ascending hairs 0.2–0.5 mm long, glabrescent; **stipules** 2–5 mm long, triangular, strigulose, deciduous. **Leaves** opposite, petioles 6–40 mm long, 0.5–1 mm thick, strigulose; **leaf blades** 5–12(–18) cm long, 2–5.5(–7) cm broad, elliptic to narrowly ovate-elliptic or elliptic-lanceolate, apex acuminate with tip 5–11 mm long, base acute to obtuse, drying thin-chartaceous, usually much darker above than below, glabrescent or minutely puberulent on the veins above, with short (0.2–0.4 mm) hairs along the veins beneath and occasionally with tufted hairs 0.5 mm long in some of the vein axils (domatia), 2° veins 5–7/side. **Inflorescences** terminal, 3.5–10 cm long, 2–8 cm broad, open pyramidal with spreading or compact opposite branches, peduncles 0.5–7 cm long, 0.5–1.5 mm thick, appressed-puberulent, bracts 3–12 mm long and

linear (or basal bracts larger and leaf-like), flowers usually borne in terminal cymes, pedicels 0–2 mm long. **Flowers** with hypanthium 2–3 mm long, 1.5–2 mm diam., turbinate, densely ascending sericeous, calyx tube ca. 1 mm long, calyx lobes 4 and strongly dimorphic, the 3 smaller lobes 1.5–3.5 mm long and linear, the single larger lobes 4–6 mm long and 1–3 mm broad; **corolla** white, densely sericeous with ascending whitish hairs externally, tube (6–)11–15 mm long, 1–2 mm diam., lobes 4, 3–4 mm long, 3–5 mm broad, rounded-truncate at the apex; anthers included. **Fruits** 6–8 mm long, 4–6 mm broad, narrowly ovoid to rounded-oblong, minutely puberulent and with prominent longitudinal ribs, the calyx persisting until dehiscence.

Plants of evergreen montane rain forest formations along the Caribbean escarpment and continental divide, from 900 to 2200 m elevation. Flowering in January–May and July; fruiting in May–September. As presently known, this species is endemic to the area ranging from the Cordillera de Tilarán, Guanacaste, to Tapantí, Cartago.

Rondeletia torresii is recognized by the thin often long-petiolate leaves, calyx with a single enlarged lobe, slender corolla tubes, and montane cloud forest habitat. There seems to be considerable variation in the form of the inflorescences and the development of the calyx lobes in different collections, but this variation does not appear to be correlated with other attributes.

***Rondeletia urophylla* Standl. & L. O. Williams,**
Phytologia 26: 129. 1973. Figure 21.

Shrubs or slender treelets, 4–9 m tall, leafy stems 2–4 mm thick, densely strigillose with appressed-ascending hairs 0.5–1 mm long, glabrescent in age; **stipules** 6–10 mm long, to 4 mm broad at the base, subulate with a long-linear tip from a short (2 mm) broadly triangular base. **Leaves** opposite and often unequal at each node, petioles 4–18 mm long, 1.2–1.8 mm thick, densely appressed-puberulent; **leaf blades** 10–22 cm long, 3–7 cm broad, elliptic to elliptic-oblong or elliptic-lanceolate, apex tapering gradually and long-acuminate with tip 15–30 mm long, base acute or obtuse and slightly decurrent on petiole, drying thin-chartaceous, dark brown above, glabrescent and often lustrous above, with short (0.3–0.5 mm) thin appressed hairs on the veins beneath, 2° veins 7–9/side. **Inflorescences** terminal, solitary, ca. 16 cm long, 2.5–5.5 cm broad, narrow thyrsoid panicles, peduncles 4–6 cm long, 1.1–2.2 mm thick, appressed-puberulent, secondary peduncles of the lateral branches 4–14 mm long, bracts 3–10 mm long, linear, flowers in short distal scorpioid dichasia, pedicels 0–1.5 mm long. **Flowers** with hypanthium 1.5–2 mm long, ca. 1 mm diam., appressed-puberulent, calyx lobes 4, clearly unequal with the 2 smaller 1–3 mm long and 0.5–1 mm broad, the larger calyx lobes usually 2 and opposite, ca. 5 mm long and 1.5–2 mm broad, with 3 palmate veins, lanceolate, white, sparsely puberulent; **corolla** white, gla-

brous externally, tube 7–10 mm long, 0.7–1.3 mm diam., lobes 4, 2–3.5 mm long, 2–3 mm broad, broadly oblong or ovate and rounded distally; style branches linear, stigmas ca. 2.5 mm long. **Fruits** ca. 3 mm long, 4–5 mm wide after opening.

Plants of the lowland Pacific rain forest formations around the Golfo Dulce area, 30–300 m elevation. Flowering in July–August (*Allen 6291* holotype F, EAP), with older fruits in February. Endemic to southern Costa Rica.

Rondeletia urophylla is recognized by the larger long-acuminate leaves, the long narrow inflorescences, the glabrous corolla tubes, the four unequal calyx lobes usually in two opposite pairs, and the restricted range. There seems to be considerable variation in the development of the calyx lobes. This species is similar in general appearance to *R. bertierioides*.

Rudgea Salisbury

Shrubs or small trees, stems usually terete, glabrous or sparsely puberulent; **stipules** interpetiolarly, coriaceous, sometimes also united intrapetiolar to form a cap over the shoot apex, with cartilaginous appendages along the distal edge or on abaxial surface, the appendages digitate (and thickened) to dentate or aristate, persisting or deciduous. **Leaves** opposite (rarely 3 or 4/node), short-petiolate or sessile; **leaf blades** entire and pinnately veined, chartaceous to coriaceous, often with thin vein-like tissue along the edge, domatia present or absent. **Inflorescences** terminal and solitary (in Central America), paniculate to umbellate or capitate (reduced to a single flower in *R. monofructus*), pedunculate, flowers often in cymose groups. **Flowers** bisexual, monomorphic or distylous, radially symmetrical, 5-parted (rarely 4- to 8-parted), hypanthium generally ovoid to obconic, calyx tube short or long, calyx lobes 4–6 or absent, usually small; **corolla** salverform to funnellform or tubular, white, the throat glabrous or puberulent, corolla lobes 5 (rarely 4 or 6–8), valvate in bud; **stamens** borne in the throat of the tube or on the lower half, anthers dorsifixed, included or exserted; **ovary** 2-locular with 1 erect ovule in each locule from the base of the septum. **Fruits** baccate or dry, rounded and made up of 2 pyrenes (rarely 1), the pyrenes plano-convex, 1-seeded; **seeds** ellipsoid, with an incurved ventral (adaxial) surface.

A genus of ca. 160 species, ranging from Mexico and the West Indies through tropical South America. A great majority of species are South American. This genus is characterized by the two-locular ovary with only two ovules, the baccate fruit without prominent longitudinal ribs, the seeds with incurved ventral surface, and the unusual stipular developments. While the stipules with their indurated teeth may be distinctive, they are often

caducous and may be lacking in some species. The inflorescence branches often have a succulent rather-jointed appearance and they usually lack bracts. Specimens of this genus may be difficult to differ-

entiate from species of *Psychotria* and *Coussarea*, and some may resemble species of *Faramea* and *Raritebe* as well.

Key to the Species of *Rudgea*

- 1a. Hypanthium and calyx 1.5–3 mm long; stipules with the teeth usually borne along the broadly rounded distal margin or hidden within the distal stipule margin; domatia often present on undersides of leaf blades 2
- 1b. Hypanthium and calyx 3.5–9 mm long; stipules rounded distally with the thickened teeth only in the center of the distal edge and with broad rounded distal margins; domatia absent on undersides of leaf blades 5
- 2a. Leaf blades 14–25 cm long, 4–12 cm broad, usually narrowly obovate [drying darker greenish]; domatia absent; inflorescences with 3–4 branches at the first node [Caribbean slopes, mostly at 600–900 m elevation] *R. reducticalyx*
- 2b. Leaf blades 4.5–15 cm long, 2–7 cm broad, elliptic to oblanceolate; pit domatia often present; inflorescences with 2 lateral branches at the first node 3
- 3a. Leaf blades sessile, oblanceolate to narrowly obovate-oblong; corolla tubes 12–14 mm long *R. amplexicaulis*
- 3b. Leaf blades rarely sessile oblanceolate or narrowly obovate-oblong; corolla tubes 3–8 mm long 4
- 4a. Leaf blades drying pale grayish green, petioles 0–5 mm long; 50–400(–700) m elevation *R. cornifolia*
- 4b. Leaf blades drying dark greenish or yellowish brown, petioles 5–16 mm long; ca. 1500 m elevation *Coussarea chiriquiensis*
- 5a. Flowers usually solitary [corolla lobes ca. 11 mm long and with recurved tips 3–4 mm long; leaf blades usually acute at the base]; Caribbean slope of northern Costa Rica *R. monofructus*
- 5b. Flowers in open panicles of (3–)5–15 flowers; plants of central and southern Costa Rica 6
- 6a. Leaf blades often slightly auriculate at the base [drying chartaceous and abruptly acuminate]; corolla lobes 3–7 mm long, with or without distal appendages to 2 mm high [calyx and hypanthium 4–6 mm long; southern Costa Rica to Panama] *R. skutchii*
- 6b. Leaf blades acute to obtuse at the base; corolla lobes ca. 6–8 mm long with erect tips 1.5–6 mm long 7
- 7a. Calyx and hypanthium 5–8 mm long; leaf blades to 16 cm long and stiffly chartaceous; Caribbean slopes and lowlands of the Talamanca range *R. trifurcata*
- 7b. Calyx and hypanthium 4–5 mm long; leaf blades to 27 cm long and subcoriaceous; evergreen Pacific lowlands *R. raveniana*

Rudgea amplexicaulis Dwyer, Ann. Missouri Bot. Gard. 67: 475. 1980.

Sprawling or clambering shrubs to 2 m long, stems glabrous; stipules to 1.5(–3) mm long, usually entire and cupulate or with a few stiff collectors within. Leaves sessile or the petioles to 3 mm long; leaf blades 5–16 cm long, 2–5 cm broad, oblanceolate to narrowly obovate-oblong, apex acuminate, base tapering gradually and auriculate or slightly rounded, drying chartaceous, green, 2° veins 7–11/side, weakly loop-connected distally. Inflorescences solitary, terminal, 2–4 cm long, cymose-paniculate with ca. 3 branches and 7–9 flowers, peduncles to 8–35 mm long, pedicels 0–6 mm long. Flowers with

hypanthium 1–2 mm long (continuous with the pedicels), calyx tube 0.5–1 mm long, lobes poorly developed; corolla white, funnelform, tube 11–14 mm long, lobes 5, 3–6 mm long. Fruits ca. 10 mm long and 6 mm diam., ovoid.

Rudgea amplexicaulis is distinguished by its clambering habit, small inflorescences, and relatively large corollas. The type (*Croat 33133* mo) from 1200 to 1500 m in Chiriquí, Panama, was flowering in March. Costa Rican material ascribed to this species is more likely to be *R. cornifolia*,

where occasional individuals can have similarly narrow subsessile leaves.

Rudgea cornifolia (Humb. & Bonpl. ex Roem. & Schult.) Standl., Publ. Field Columb. Mus., Bot. Ser. 7: 432. 1931. *Psychotria cornifolia* Humb. & Bonpl. ex Roem. & Schult., Syst. Veg. 191. 1819. *P. fimbriata* Benth., J. Bot. 3: 226. 1841. *R. fimbriata* (Benth.) Standl. in Standl. & Calderon, Lista Pl. Salv. 274. 1925. *R. ceratopetala* J. D. Smith, Bot. Gaz. 35: 3. 1903. Figure 46.

Shrubs or small treelets, 1.5–6(–10) m tall, leafy stems 1.2–3 mm thick, glabrous, terete, drying grayish to yellowish green, the nodes conspicuously thickened; **stipules** 2–7 mm long, 2.5–5 mm broad, oblong or broader than long, with a truncated apical margin with (1–)3–5 short (0.5–1 mm) stiff teeth. **Leaves** subsessile or petiolate, petioles 1.5–6 mm long, to 2 mm thick, glabrous; **leaf blades** 4.5–15(–18) cm long, 2–7(–9) cm broad, broadly elliptic to narrowly elliptic, elliptic-oblong, elliptic-obovate or ovate, apex acuminate with tip 7–15 mm long, base obtuse to narrowed and often slightly rounded (subcordate), drying chartaceous, pale grayish or yellowish green, glabrous above and beneath, 2° veins (3–)5–9/side, usually with a very slender veinlet along the margin, often with slit-like or rounded pit domatia along the midvein beneath. **Inflorescences** solitary or rarely 2, 3–7 cm long, 2–5 cm broad, few-branched open pyramidal, the first node with 2 lateral branches, peduncles 1–5 cm long, 0.5–1 mm thick, glabrous, bracts vestigial, distal branches cymose with 3–5 flowers and white in life, flowers sessile or with pedicels to 5 mm long. **Flowers** glabrous, distylous, hypanthium 0.6–1.3 mm long, oblong to obconic, calyx tube 0.6–1.2(–2) mm long, broadly cupulate to almost tubular, 1.5–2 mm in diameter distally, calyx lobes very short (0–0.5 mm) and broadly triangular or obsolete; **corolla**, salverform, white, tube (3–)4–5(–7) mm long and 1 mm diam., lobes 3–4.5 mm long, 0.8–1.5 mm broad, oblong. **Fruits** 6–9 mm long, 5–9 mm diam., oblong-ellipsoid or subglobose, glabrous, becoming white and fleshy, often with a prominent coriaceous calyx tube 0.5–3 mm long and ca. 2 mm diam. at the apex.

Plants of evergreen rain forest and wet forest formations of the Caribbean slope and southern Pacific slope in Costa Rica, from 50 to 800 m elevation. Flowering in February–September (mostly in June–July); fruiting in January–March and July–November. The species ranges from eastern Mexico through Central America to Brazil and Bolivia.

Rudgea cornifolia is recognized by the unusual stipules with little digitate projections on the distal edge, lack of puberulence on all parts, leaves often subsessile and tapering to a slightly auriculate base, small inflorescences with few opposite branches,

small flowers with poorly developed calyx lobes, and smooth rounded fruit (often with a persistent calyx tube). The leaves usually dry grayish green beneath and can differ greatly in form on different plants. Some specimens may resemble material of *Coussarea*. Breeding biology was studied by Bawa and Beach (1983).

Rudgea monofructus Gómez-Laurito & Dwyer, Novon 1: 50. 1991.

Shrubs or small treelets, 2–4.5 m tall, to 13 cm dbh, leafy branchlets 1.2–3.5 mm thick, glabrous and drying yellowish or grayish, soon becoming terete; **stipules** 3–10 mm long, 3–5 mm broad, oblong to broadly obovate, rounded distally with small (ca. 0.5 mm) fimbriate teeth clustered in the center of the distal margin, succulent and glabrous, caducous. **Leaves** clustered distally or distant, decussate, petioles 3–12 mm long, 0.8–2 mm thick, glabrous; **leaf blades** 7–15(–18) cm long, 2.5–7(–9) cm broad, elliptic-oblong to elliptic-obovate or obovate, apex abruptly narrowed and acuminate, tip 8–16 mm long, base acute, drying thin-chartaceous to chartaceous, dark grayish green above (distinctly paler or yellowish green beneath), glabrous above and below, 2° veins 4–8/side, edge of the leaf often with vein-like tissue, domatia absent. **Inflorescences** of solitary (rarely 2–3) terminal flowers, peduncles/pedicels 12–32(–40) mm long, 1–1.5 mm thick, glabrous, articulate but lacking bracts along their length and emerging from the terminal stipule pair, pedicels ca. 2 mm long on lateral flowers when more than 1 flower is present. **Flowers** glabrous, hypanthium and calyx not differentiated, 8–10 mm long, 4–5 mm diam., rounded at the base and tubular distally (slightly expanded distally), coriaceous, calyx lobes 3 or 4, 1.5–4 mm long and ca. 3 mm broad at the base, rounded-obtuse at the apex or irregular; **corolla** salverform-rotate, white, carnos, tube 5–9 mm long and equal to or slightly longer than the calyx tube, ca. 5 mm diam., lobes 6 (5, 7), apparently held horizontally (to 3 cm diam.), 8–12 mm long with an additional recurved or vertical tip 3–5 mm long; **stamens** included, filaments ca. 1 mm long, anthers ca. 3.5 mm long with a small (0.4 mm) appendage. **Fruits** 12–20 mm long (including calyx), 10–14 mm diam., ovoid-oblong and crowned with the persisting calyx tube 2–6 mm long and 4–6 mm diam., becoming greenish white.

Plants of evergreen rain forest formations on the Caribbean slope, from 600 to 1200 m elevation. Flowering in July–November; fruiting in February, June, August, and October–December. The species is only known from the Caribbean slopes of northern Costa Rica (Upala area to Ciudad Quezada) in Alajuela Province.

Rudgea monofructus is characterized by its usually solitary flowers (rarely with two to three flowers from a terminal node), large cylindrical hy-

panthium/calyx tube, and the long corolla lobes with distal recurved or erect tips. Many similarities (especially the flowers and stipules) suggest a close relationship with *R. skutchii* and *R. trifurcata*. The flowers are very unusual in being solitary and having the corolla tube largely hidden within the calyx tube. In addition, the usually six horizontal petals have conspicuous erect distal appendages.

***Rudgea raveniana* W. Burger, sp. nov.**

Frutices vel arbores ad 6 m altae, ramulis glabris; stipulis 0.5–3 mm longis, integris. Foliae lamina 10–21 cm longa, 3.5–8 cm lata, anguste vel late elliptica, glabra, venis lateralibus 6–11. Inflorescentiae terminales, solitariae, 5–7 cm longae, flores 5–15 gerentes. Flores extus glabri; corolla hypocrateriformi, tubo 10–14 mm longo, lobis 5, ca. 6 mm longis. Fructus maturus non visus.

TYPUS—*Burger & Liesner 7251* (holotypus CR, isotypus F), from Rincón de Osa, Costa Rica.

Shrubs or small trees, 1.5–6 m tall, leafy twigs 1.2–5 mm thick, glabrous, flattened in early stages, becoming terete and grayish; stipules united to form a very short (0.5–3 mm) entire collar or cup (rarely with ca. 8 apical closely crowded teeth 1–2 mm long and these caducous). Leaves with petioles 4–20 mm long, 1.5–3.5 mm thick, glabrous and drying dark; leaf blades (10–)14–21(–27) cm long, (3.5–)4.5–8(–15) cm broad, broadly to narrowly elliptic, elliptic-oblong or slightly obovate, apex short-acuminate or acute (acuminate in the smaller leaves), base acute to obtuse, laminae drying subcoriaceous, dark olive green above (paler grayish green or yellowish green beneath), glabrous above and below, 2° veins 6–11/side (largest leaves with 10–11). Inflorescences terminal and solitary, 5–7 cm long, panicleate-cymose, with 1 or 2 pairs of lateral branches and a distal branch (each usually terminating with 3 flowers for a total of 9–15), peduncles 14–25 mm long (to 35 mm in fruit), 1.2–1.8 mm thick and glabrous, bracts rudimentary (< 1 mm), pedicels 2–9 mm long. Flowers glabrous externally, white, hypanthium ca. 2 mm long and 1.3 mm thick, calyx limb 2–3 mm long, 3–4 mm broad, calyx lobes 5–7, minute; corolla salverform with recurved lobes, tube 10–14 mm long, ca. 1.7 mm diam. in the center and 3 mm near the mouth, lobes 5, ca. 6 mm long and 1.6 mm broad, with a distal reflexed appendage 1.5 mm long; stamens 5, anthers ca. 5 mm long and 0.4 mm broad, exerted. Fruits ca. 20 mm long and 8 mm diam. (not fully mature?), with a 2–4 mm high persisting calyx tube), ellipsoid, smooth and drying black.

Plants of evergreen forest formations in the Pacific lowlands of southern Costa Rica, 50–300 m elevation. Flowering in January (the type), late flowers with fallen corollas in March (*Croat & Grayum 59753* CR, MO), immature fruits in February (*Burger et al. 12242* CR, F, MO, *Hammel et al. 18081* CR, MO), and more mature fruits in May

(*Hammel 15211* CR, MO). The species is only known from the hills north of Quepos and near Rincón de Osa.

Rudgea raveniana is recognized by its larger stiff glabrous leaves, few-flowered panicleate inflorescences with distal triads of flowers, petal lobes with distal reflexed appendages, and ellipsoid fruit. The teeth on the stipules appear to be early caducous or undeveloped at many nodes, with the stipular tube entire. This species is related to *R. trifurcata* and *R. skutchii* but differs in leaf size and texture and in the flower and inflorescence. The ovary of the flower appears to have two well-developed locules (each with an ovule), but only one seed develops in the ellipsoid fruits, which are similar to other species of *Rudgea*. The fruiting collection from near Quepos (*12242*) has unusually large leaves whose measurements are given in parentheses (not included in the Latin description). The species is named in honor of Peter Raven, who made important collections in southern Costa Rica and whose leadership of the Missouri Botanical Garden has supported floristic research in many parts of the world.

***Rudgea reducticalyx* Dwyer, sp. nov. Figure 46.**

Frutices 1.5–3 m alti, ramulis glabris. Folia anguste obovata vel anguste elliptico-oblonga, 15–27 cm longa, 5–12 cm longa, 5–12 cm lata, chartacea, glabra; petiolis ad 20 mm longis; stipulis 3–6 mm longis. Inflorescentiae terminales paniculatae vel umbellatae, 5–12 cm longae, 4–7 cm latae, pedunculo ad 8 cm longo. Flores hypanthio glabro 0.5–1 mm longo, dentibus calycinis nullis vel minutis; corolla alba, tubo ad 6 mm longo, lobis 4 vel 5, 2–3 mm longis. Fructus 7–8 mm longus, glaber.

TYPUS—*Croat 36330* (holotypus CR, isotypus MO), from near Bijagua, Alajuela, Costa Rica.

Shrubs, 1.5–2.5(–3) m tall, with spreading branches, leafy stems 2–8 mm thick, glabrous and terete; stipules 3–6 mm long, 4–6 mm broad, united to form a short (1–2 mm) tube, often ovate and rounded distally, thick and drying dark, indurated teeth along the distal edge or hidden within, caducous and leaving a circular scar above the petiole. Leaves subsessile or with petioles 3–8(–20) mm long, 1.5–2.5 mm thick, glabrous; leaf blades (13–)15–20(–27) cm long, (4–)5–9(–12) cm broad, narrowly obovate to narrowly elliptic-oblong or oblanceolate (rarely broadly elliptic), apex gradually or abruptly short-acuminate with tip 5–9 mm long, base gradually narrowed and abruptly rounded or auriculate at the petiole, drying chartaceous, olive green above, glabrous on both surfaces, 2° veins 8–12/side, arcuate-ascending distally but not loop-connected, the leaf edge with thin vein-like tissue. Inflorescences 5–12 cm long, 4–7 cm broad, open panicleate or subumbellate with 3–4 branches at the first node, white, peduncles becoming 3–8 cm long in fruit, 1–2.5 mm thick, glabrous or minutely papillate-

puberulent, bracts and floral bracts minute (0.5 mm) or reduced to ridges, flowers mostly in distal 3-flowered cymes, pedicels 0–5 mm long. **Flowers** glabrous, with hypanthium 0.5–1 mm long, ca. 0.7 mm diam., cylindrical to obconic, calyx limb 0.5–1 mm long, ca. 1 mm diam. distally, calyx lobes absent or small and broadly triangular, essentially glabrous; **corolla** tubular-slaver-form, white, minutely papillate-puberulent, tube 4–6 mm long, 0.7 mm diam. at base and 1.3 mm distally, lobes 4–5, 2.3–3 mm long. **Fruits** 7–8 mm long, 6–7 mm diam., globose-oblong, with smooth surfaces and bisulcate at maturity, persisting calyx 0.5 mm long and usually entire.

Plants of the very wet forests of the Caribbean slopes of the Meseta Central and Cordillera de Tilarán, (100–)400–800(–1100) m elevation. Flowering in December–July; fruiting December–February. This species is endemic to northern and central Costa Rica.

Rudgea reducticalyx is recognized by its longer obovate subsessile (or short-petiolate) leaf blades with short-acuminate apices and leaf edges with thin vein-like tissue. The apparently ebracteate inflorescences with three to four branches at the first node and small flowers with subentire calyx tube and very minute puberulence (or the puberulence not apparent) are also distinctive. The stipules do not always display the indurated teeth that characterize the genus. These teeth may be hidden within (adaxially) and are caducous with the stipules. This species is very similar to *Coussarea impetiolaris*, but that species has more elliptic leaves, smaller inflorescences, and much larger lenticellate single-seeded fruit. Material of this species collected in the 1920s was misidentified as *R. fimbriata* (Benth.) Standl. by Standley (in herb. US); that name is a synonym of *R. cornifolia* according to Steyermark (1972). The following collections are placed here: *Burger & Antonio 11103*, *Grayum & Herrera 7819*, *Hammel et al. 12812*, *INBio 19*, *A. Jiménez 1339*, *Standley & Valerio 45382 & 44593*, and *Utley & Utley 3908*.

Rudgea reducticalyx may be represented by an atypical population or a closely related and undescribed species on the Osa Peninsula. The leaves are subsessile and up to 38 × 17 cm, and the rounded fruits are 2 cm long (*Burger & Liesner 7242 CR*, *F. Liesner 3225 MO*).

***Rudgea skutchii* Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 1374. 1938. Figure 46.**

Shrubs or small trees, 1–6 m tall, leafy stems 1–3.5 mm thick, glabrous, at first somewhat flattened but becoming terete, nodes thickened; **stipules** (3–)4–8 mm long,

2–4 mm broad, ovate-oblong or obovate, at first united and forming a 4-angled cap over the apex, coriaceous and glabrous, the thickened apical teeth becoming 1 mm long and borne in a small (0.5–1.5 mm) tight group at the center of the rounded apical margin, soon turning brown and deciduous. **Leaves** subsessile or petiolate (on different plants), petioles 0–5(–10) mm long, ca. 1.5 mm thick, glabrous; **leaf blades** 6–14(–17) cm long, 2–5.5(–7) cm broad, elliptic to elliptic-oblong or obovate, apex gradually or abruptly narrowed and acuminate, tip 6–17(–25) mm long, base quite variable (acute to obtuse or more often slightly auriculate at the petiole), drying chartaceous, grayish green to dark brownish, glabrous on both surfaces, 2° veins 5–11/side, with vein-like tissue at the leaf edge, pit domatia rarely present. **Inflorescences** 4–14 cm long, 3–10 cm broad, open-branched panicles with relatively few (5–15) flowers, with 2 lateral branches at the first node, peduncles 2–6 cm long, 0.7–1.6 mm thick, glabrous, bracts to 1 mm long or absent, flowers sessile or on pedicels to 7(–12) mm long. **Flowers** glabrous, hypanthium difficult to distinguish from the calyx tube, ca. 2 mm long, calyx tube 2–4 mm long, 2–3 mm diam. distally, entire or with 5 short lobes; **corolla** white, tube 3–7 mm long, 1.3–2 mm diam., lobes 5, 3–7 mm long, with a distal small (0.5–1 mm) thickened area or recurved appendage 1–3 mm long (as in the type, *Skutch 2836 us*); **stamens** 5, anthers 2.5–3 mm long. **Fruits** 6–8 mm long (not including calyx), 6–8 mm diam., subglobose with a persisting tubular calyx 1–2 mm long.

Plants of evergreen rain forest and wet forest formations on both the Caribbean and Pacific slopes, from 50 to 1300 m elevation (but not below 600 m on the Pacific slope). Flowering in February–November; fruiting in July–August and October–January. The species ranges from Monteverde and the Cordillera de Talamanca southward to the Chocó area of Colombia.

Rudgea skutchii is recognized by the unusual stipules, lack of pubescence, subsessile leaves, few-flowered inflorescences, prominent calyx tube, and the appendaged corolla lobes. This species is related to *R. trifurcata* and *R. monofructus*, but those species have larger flowers and inflorescences with little or no branching. It differs from *R. cornifolia* in the much more open inflorescences and larger flowers. Material from Bocas del Toro often has simpler inflorescences, resembling those of *R. trifurcata* (see below).

***Rudgea trifurcata* Gómez-Laurito, Brenesia 33: 139. (1990) 1991. Figure 46.**

Small trees, 3–6 m tall, leafy stems 0.7–3 mm thick, glabrous, becoming pale grayish; **stipules** 3–7 mm long, 4–6 mm broad, ovate to oblong, thick, rounded distally but with a group of thickened teeth at the apex 1–2 mm broad and 1 mm long (rarely absent), deciduous. **Leaves** with petioles 3–10 mm long, 0.7–1.8 mm thick, glabrous,

sulcate above, drying yellowish or brown; **leaf blades** 7–16 cm, 2.5–8(–10) cm broad, elliptic to elliptic-ovate or obovate, apex acuminate to caudate-acuminate, tip ca. 10 mm long, base obtuse to acute, drying stiffly chartaceous, dark green above, glabrous above and below, 2° veins 5–7/side. **Inflorescences** solitary and terminal, 4.5–10 cm long, 4–5 cm broad, paniculate with 3 major branches from the apex of the peduncle (each usually cymose with 3 flowers), usually with 9 flowers, peduncle 2.5–6 cm long, 0.7–1.7 mm thick, glabrous and drying yellowish green or yellowish brown, bracteoles minute and caducous, pedicels 3–10 mm long. **Flowers** glabrous externally, hypanthium and calyx difficult to distinguish, 5–8 mm long, 2.5–4 mm diam. distally, calyx lobes 0.5 mm high or poorly developed; **corolla** white, salverform with rotate lobes, 2 cm diam., tube 7–11 mm long and 2 mm diam. distally, lobes 5, 6–8 mm long (not including the 2–5 mm long distal appendages held vertically at 90°); **stamens** 4, subsessile, anthers 4–4.5 mm long. **Fruits** unknown.

Plants known only from the Caribbean slopes and lowlands below the Cordillera de Talamanca, 50–1300 m elevation. Flowering in January (*León 345* us) and November (*Baker & Burger 66* CR, F). *Gómez-Laurito & Vargas 11957* CR is the holotype. This species ranges from Moravia, Cartago, on the Caribbean slope of the Talamanca range southward to the mountains of Bocas del Toro Province, Panama.

Rudgea trifurcata is distinguished by the few-flowered inflorescences, relatively large flowers with long calyx and short corolla tube, and the long corolla lobes with distal vertical appendages. This species is closely related to both *R. skutchii* and *R. monofructus*. The higher-elevation collections from Moravia (*León 345* us) and San Ramón

(*Loiselle 149* MO) have smaller flowers and may be intermediate with *R. skutchii*.

Rustia Klotzsch

REFERENCE—D. Simpson, Studies in Neotropical Rubiaceae. 1. *Rustia*. Phytologia 33: 4–8. 1976.

Trees, branchlets glabrous; **stipules** interpetiolar and free (rarely intrapetiolar), entire or bifid, large and deciduous. **Leaves** opposite, petiolate; **leaf blades** medium to large in size, entire and pinnately veined, often with punctate oil glands, domatia absent. **Inflorescences** terminal and solitary, long-paniculate with decussate opposite branching, the lateral branches usually monochasial. **Flowers** with hypanthium turbinate or cupulate, calyx tube short and cupular, truncate or with small calyx teeth; **corolla** campanulate to funnelform, corolla tube glabrous or puberulent within, lobes 4–5, valvate in bud; **stamens** borne on the throat of the tube, filaments very short, anthers basifixed, opening by terminal slits or 2 pores beneath the apex, included or exerted; **ovary** 2-locular, placentation axile with many horizontal ovules in each locule. **Fruits** capsules, coriaceous, narrowly obovate to subglobose-obovate, dehiscent loculicidally into 2 valves; **seeds** small, pointed at the ends, angular or with minute marginal wings.

A genus of about 12 species, found in Mexico, the West Indies, southern Central America, and tropical South America. The genus is easy to recognize because of the anthers usually opening by terminal pores and the leaves with pellucid dots. Standley's genus *Stomandra* is a synonym of *Rustia* (D. Lorence, pers. comm.).

Key to the Species of *Rustia*

- 1a. Flowers pink, corolla tubes 6–9 mm long; larger leaf blades 4–11 cm broad; fruit 8–12 mm long; shrubs 2–5 m tall *R. occidentalis*
- 1b. Flowers white, corolla tubes 1–2 mm long; larger leaf blades 9–19 cm broad; fruit ca. 5 mm long; trees 5–10 m tall *R. costaricensis*

Rustia costaricensis (Standl.) Lorence, comb. nov.

Stomandra costaricensis Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 23: 247. 1947. *R. panamensis* Dwyer, Ann. Missouri Bot. Gard. 67: 483. 1980. Figure 38.

Trees to 12 m tall, leafy stems ca. 4 mm thick, terete, glabrous and grayish; **stipules** not seen, caducous. **Leaves** opposite, petioles (1–)2–6 cm long, ca. 2.5 mm thick, glabrous, with 2 slightly elevated adaxial ridges, thickened at the base; **leaf blades** 15–45 cm long, 7–19 cm broad, oblong to narrowly oblong-obovate, apex obtuse

to short-acuminate, base obtuse, drying stiffly chartaceous and brown, glabrous above and below, 2° veins 12–17/side, lower surfaces with small (0.2–0.3 mm) circular projections. **Inflorescences** 1–3 at the ends of stems, 20–26 cm long, to 20 cm broad, open paniculate with opposite branching from the central rachis, peduncles 2–4.5 cm long, 2–3.5 mm thick, glabrous, dark brown, distal bracts 1–2 mm long and ovate, bracteoles subtending the flowers 1–1.5 mm long, flowers alternate on the distal branches or in cymes, pedicels 0–2 mm long. **Flowers** glabrous externally, hypanthium 1–1.5 mm long, ca. 1 mm diam., turbinate, calyx limb 0.5 mm long, calyx lobes poorly developed (distal margin undulate); **corolla** white, tube 1–2 mm long, ca. 1.5 mm diam., lobes 4–6,

1.5–2 mm long, narrowly ovate to triangular, thick; **stamens** 5, filaments ca. 1 mm long, anthers 1.5–2 mm long, partly exerted; style to 4 mm long. **Fruits** to 5 mm long, broadly oblong to subglobose, subsessile; **seeds** ca. 0.8 mm long.

Plants of evergreen forest formations of the Pacific slope at 200–800 m elevation. Flowering in February–March and August. The species is only known from southeastern Costa Rica and western Panama.

Rustia costaricensis is recognized by its long-petiolate narrow or oblong leaves with pellucid dots, glabrous parts, large inflorescences, small flowers, anthers with distal pores, and small capsular fruit. This species has been collected from the General Valley (*Skutch 4777 F* the holotype) and in the hills northeast of Quepos (*Burger et al. 12314 CR, F*).

***Rustia occidentalis* (Benth.) Hemsl., Biol. centr. amer. Bot. 2: 14. 1881. *Exostemma occidentale* Benth., Bot. voy. Sulph. 104. 1844. Figure 38.**

Much-branched **shrubs** or small trees, 2–6(–12) m tall, leafy stems 3–6 mm thick, glabrous and smooth, terete, often pale grayish; **stipules** 16–24 mm long, 2–4 mm broad, tapering gradually to the acute apex, glabrous and drying brown, caducous. **Leaves** opposite or subopposite, petioles 13–35 mm long, 1.2–2.5 mm thick, glabrous, usually thickened at the base; **leaf blades** 13–33 cm long, 4–11 cm broad, oblanceolate to narrowly oblong-oblanceolate or narrowly obovate, apex tapering gradually and long-acuminate, tip to 35 mm long and often curved, base tapering gradually, drying stiffly chartaceous and brownish, glabrous above and below, with small (0.1–0.3 mm) rounded scale-like projections on upper and lower leaf surfaces, 2° veins 9–12/side. **Inflorescences** 4–15 cm long, to 8 cm broad in fruit, paniculate or racemiform, peduncles 5–30 mm long, 1.2–2.8 cm thick, glabrous, lateral branches to 3.5 cm long, with 1–5 flowers, bracts 1–2 mm long, triangular, pedicels 3–12 mm long. **Flowers** glabrous externally, hypanthium 3–5 mm long, narrowly turbinate, calyx tube ca. 1 mm long, calyx lobes not well developed (to 0.3 mm high); **corolla** pink or violet, tube 6–9 mm long, 2.5–3.5 mm diam., constricted above the base, lobes 4 or 5, 5–6 mm long and 3 mm broad near the base; **stamens** 5, ca. 6 mm long and 1.8 mm broad. **Fruits** 8–12 mm long, 6–8 mm diam., broadly obovoid to subglobose, drying very dark brown, truncated at the apex, the persisting calyx ca. 0.5 mm high, 3.5–5 mm diam., open valves with a conspicuous median septum.

Key to the Species of *Sabicea*

- 1a. Inflorescences to 4 cm broad, often on short peduncles, pedicels to 5 mm long; corolla tube 6–8 mm long; leaf blades obtuse to acute at the base but not usually decurrent on the petiole; hairs to 1 mm long and appressed *S. panamensis*

Plants of evergreen rain forest formations, from 5 to 300 m elevation. Flowers and fruits have been collected in February–April. This species seems to have a disjunct distribution of small populations. It is found near Bluefields, Nicaragua, near Moin (Limón), in Bocas del Toro, Panama (all along the Caribbean coast), and Cocos Island. This species is also reported from the lowlands of Chocó, Colombia (Dwyer, 1980).

Rustia occidentalis is recognized by its narrow and long-acuminate leaf blades with pellucid dots, glabrous parts, narrow inflorescences, short pink corollas, thick anthers opening by pores, and the capsule breaking into two valves. The species appears to be restricted to wet or swampy sites at very low elevations.

Sabicea Aublet

Vines, shrubs with clambering branches, or erect shrubs, stems usually pubescent, terete; **stipules** interpetiolar, erect or recurved, ovate to lingulate, persisting. **Leaves** opposite or verticillate, petiolate, entire, venation pinnate, domatia absent. **Inflorescences** axillary, sessile or pedunculate, corymbose to glomerulate or capitate, with bracts and bracteoles, the flowers often in distal cymes, pedicellate or sessile. **Flowers** bisexual, monomorphic or distylous, radially symmetrical, small or medium, hypanthium turbinate to urceolate, calyx lobes 3–6, persisting; **corolla** funnelliform or salverform, tube pubescent at the mouth, lobes 4–6, valvate in bud; **stamens** 4–6, anthers dorsifixed, included or partly exerted; **ovary** (2–)3–5-locular, ovules numerous and horizontal on axile placentas, style with 3–5 stigmatic branches. **Fruits** baccate, with persisting sepal lobes; **seeds** small, ovoid or angulate, reticulate to foveolate.

A genus of about 130 species in tropical America, Africa, and Madagascar. Our species of this genus are recognized by the climbing habit (or with clambering branches), prominent pubescence on most parts, small axillary inflorescences, small flowers, and baccate puberulent fruit with persisting calyx lobes and many small seeds. Our two species are very similar in appearance; some collections may be difficult to place with certainty and may represent hybrids. Alternatively, it is possible that Costa Rican material does not represent two distinct species.

- 1b. Inflorescences to 2 cm broad, sessile and the flowers sessile; corolla tube 4–5 mm long; leaf blades usually decurrent on the petioles; hairs to 2 mm long, spreading or appressed *S. villosa*

Sabicea panamensis Wernham, Monogr. Sabicea 30. 1914. *S. costaricensis* Wernham, Monogr. Sabicea 31. 1914. Figure 35.

Vines or shrubs with clambering branches, to 5 m high, leafy stems 1–4 mm thick, with appressed-ascending straight, yellowish hairs 0.7–1.4 mm long, terete; stipules 5–10 mm long, 4–5 mm broad, ovate with an acute apex, strigose externally, glabrous and dark brown within, persisting and often recurved. **Leaves** opposite, petioles 5–15(–20) mm long, 0.7–1.6 mm thick, strigose; **leaf blades** 5–16 cm long, 2–7 cm broad, elliptic to elliptic-oblong or lanceolate, apex acuminate (acute), base acute to obtuse, drying chartaceous, often dark brown, with thin appressed-ascending hairs to 1 mm long on the upper surface, more densely strigose on the veins beneath, and with shorter hairs between the hairs beneath, 2° veins 7–11/side. **Inflorescences** 1.5–3 cm long, to ca. 2 cm broad, corymbose, peduncles 0.7(–1.5) mm long, ca. 1 mm thick, with ascending strigose hairs, basal bracts broadly involucrate but tearing (stipule-like) and to 8 mm long, distal bracts ca. 3 mm long and narrow, pedicels 2–7 mm long. **Flowers** monomorphic, with slender appressed-ascending hairs ca. 1 mm long externally, hypanthium and calyx tube ca. 2 mm long and 1.3 mm diam., calyx lobes 5, 2.3–3(–4) mm long, ca. 1.2 mm broad, glabrous on the inner surface; **corolla** white, sericeous, tube 6–8 mm long, ca. 1 mm diam. near the base and 2 mm diam. at the apex, lobes 5, 2–4 mm long, narrowly triangular; **stamens** 5, anthers ca. 2 mm long. **Fruits** 5–9 mm diam., globose, appressed-strigulose, pink to red then purple-black at maturity; **seeds** ca. 0.5 mm long.

Plants of evergreen forest formations throughout Costa Rica, from 20 to 1200 m elevation. Flowering throughout the year; probably fruiting throughout the year. The species ranges from Belize to Colombia.

Sabicea panamensis is recognized by the vining habit, appressed pubescence, axillary inflorescences with evident peduncle or prominent pedicels, small white flowers, and fleshy red fruit. This species can become a high-canopy liana (*Stevens* 24620 MO). The differences between this species and its local congener are minor; it would be interesting to know if there are naturally occurring intermediates.

Sabicea villosa Willd. ex Roem. & Schult., Syst. Veg. 5: 265. 1819. *S. hirsuta* H.B.K., Nov. gen. sp. 3: 417 (quarto). 1820. *S. hirsuta* var. *adpressa* Wernham, Monogr. Sabicea 55. 1914. *S. villosa* var. *adpressa* (Wernham) Standl., Publ.

Field Columb. Mus., Bot. Ser. 7: 52. 1930. Figure 35.

Vines or shrubby vines to 4 m high, leafy stems 0.7–3 mm thick, with thin spreading hairs 1–2 mm long (in variety *villosa*) or with appressed hairs ca. 1.2 mm long (in variety *adpressa*), terete; stipules 3–8 mm long, 4–8 mm broad, broadly ovate, glabrous on the inner side, becoming reflexed, persisting. **Leaves** opposite, petioles 6–20 mm long, 0.5–1.2 mm thick, densely spreading-villose or appressed-strigose; **leaf blades** (4–)5–14 cm long, (2–)2.5–6 cm broad, elliptic to ovate-elliptic, elliptic-rhomboid, or elliptic-obovate, apex bluntly acute to short-acuminate, base obtuse to acute and slightly decurrent on the petiole, drying thin-chartaceous, dark brown or dark green above, smooth or slightly scabrous to the touch, with thin spreading hairs ca. 1.5 mm long (in variety *villosa*) or with appressed hairs 0.3–1.2 mm long (in variety *adpressa*) above, more densely puberulent below (especially on the secondary veins), 2° veins 7–11(–13)/side. **Inflorescences** 5–15 mm long, present at almost all distal internodes, capitate, peduncles not apparent among the closely crowded stipules, bracts and sessile flowers. **Flowers** monomorphic, hypanthium and calyx tube covered with thin straight ascending yellowish white hairs, calyx lobes 5, 2.5–4 mm long, 1.2 mm broad, usually glabrous within; **corolla** white, tube 4–6 mm long and 1 mm diam., with stiff ascending hairs, lobes 5, 1–3 mm long. **Fruits** sessile, 5–10 mm diam., globose to oblong, with thin yellowish hairs and becoming red or pink to lavender, calyx lobes persisting and usually reflexed; **seeds** ca. 0.3 mm long.

Plants of evergreen forest formations, from near sea level to 600 m elevation. Probably flowering and fruiting throughout the year. The species is found primarily along the Caribbean coast in Central America, but there are a few collections from Nicoya to the Golfo Dulce region along the Pacific coast. The species ranges from southern Mexico and the West Indies to Brazil and Peru.

Sabicea villosa is recognized by the climbing habit, very small compact axillary inflorescences, small white flowers, and fleshy reddish or pink fruit. This species is not as common in Costa Rica as *S. panamensis*. Variation within this species can make separation from *S. panamensis* difficult; compare material of that species.

Schradera Vahl

Epiphytic shrubs, or lianas with rooting branches, stems glabrous; stipules interpetiolar and intrapetiolar, united and forming a terminal cap over the nonflowering shoot apices, caducous. **Leaves** opposite, petiolate; **leaf blades**

entire and pinnately veined, usually coriaceous, domatia absent. **Inflorescences** terminal and solitary or 3, pedunculate (rarely sessile), capitate and subtended by a broad involucre or with each flower with a small involucre and in an umbellate arrangement, the flowers sessile. **Flowers** bisexual and radially symmetrical, hypanthium turbinate, calyx tube short-cupulate, truncated and without lobes or with small teeth; **corolla** salverform to tubular, white and thick, villous within the throat, lobes 5–8(–10), narrow, valvate in bud, spreading or reflexed at anthesis; **stamens** 5–8(–10), filaments very short and adnate to the tube, anthers dorsifixed, linear, included or exerted; **ovary** 2–4-locular, with many ovules in each locule on axile

placentas. **Fruits** closely clustered or united into a syncarp, fleshy and baccate; **seeds** numerous, small, horizontal, compressed, suborbicular.

A genus of about 40 species, mostly South American and with a few in the West Indies; two species are found in Costa Rica and adjacent Panama. The epiphytic habit, pedunculate capitula with a small involucre, and semisucculent flowers that dry black make this a very distinctive genus. Compare *Appunia*.

Key to the Species of *Schradera*

- 1a. Leaf blades rounded at the apex; capitula always solitary; corolla tubes to 8 mm long; Costa Rica *S. costaricensis*
- 1b. Leaf blades acuminate at the apex; capitula solitary or 3; corolla tubes to 30 mm long; western Panama *S. blumii*

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

Scandent or epiphytic **shrubs**, leafy stems 2–5 mm thick, glabrous, at first quadrangular; **stipules** not seen, united at the base and leaving a conspicuous scar between the leaf bases and a narrower scar above the petioles. **Leaves** opposite and in a single plane, petioles 5–14 mm long, 0.6–2 mm broad, glabrous, with lateral or adaxial margins continuous with the lamina margins; **leaf blades** 4–11(–15) cm long, 2–5 cm broad, oblong to elliptic-oblong or ovate-oblong, apex acuminate with tip 8–12 mm long, base acute to obtuse or rounded, drying stiffly chartaceous to subcoriaceous, very dark brown, glabrous above and below, 2° veins 10–12/side and weakly loop-connected near the margin (a thinner 2° vein usually present and parallel between two major 2° veins). **Inflorescences** solitary or 3 at the end of a stem, 4–7 cm long, 2–4 cm broad, peduncles 12–25 mm long, 1–3.3 mm thick, glabrous and drying black, involucre ca. 1 cm long and to 2.5 cm broad, glabrous and drying black, flowers sessile or subsessile. **Flowers** glabrous externally and drying black, hypanthium 4–6 mm long, calyx tube 4–6 mm long, entire distally (calyx teeth absent); **corolla** not seen at anthesis, white, tube to 30 mm long, slender, lobes 4, ca. 30 mm long, thick, villous within near the base; **stamens** 5, filaments ca. 1 mm long, anthers ca. 5 mm long. **Fruits** united near the base and borne tightly together (not truly connate?) on the involucre apex of the peduncle, body of the fruit subglobose and ca. 8 mm diam. (dried), the persisting calyx forming a distal tube 6–8 mm long and ca. 4 mm diam.

Schradera blumii occurs in cloud forest on the Pacific slope of Panama in Coclé and Chiriquí provinces at about 500–1500 m elevation. The epiphytic/climbing habit, glabrous parts, acuminate leaves, involucre heads, and prominent ca-

lyx tubes without calyx lobes are distinctive features of this species.

Schradera costaricensis Dwyer, sp. nov. Figure 19.

Frutices epiphytici. Folia oblonga vel anguste oblonga, coriacea, glabra, 4–8 cm longa, 1.4–3 cm lata, venis lateralibus ca. 10; petiolis ad 1.6 cm longis; stipulis terminalibus ad 1.8 cm longis. Inflorescentiae terminales solitariae capitatae involucreatae, pedunculo 2.5–4 cm longo. Flores tubis calycinis 3–4 mm longis; corolla alba, tubo ad 8 mm longo, 4 mm lato, lobis ad 8 mm longis. Fructus non visus.

TYPUS—*G. Herrera* 2004 (holotypus CR, isotypi F, MO), from Bijagua, Alajuela, Costa Rica.

Epiphytic **shrubs** ca. 1–2 m tall, leafy stems 2–5 mm thick, glabrous, with 4 prominent ridges (apparently semisucculent and becoming distorted on drying), pale grayish; **stipules** 7–10 mm long and 3–8 mm broad (to 18 mm long beneath the inflorescences), oblong, rounded at the apex, glabrous and drying black, caducous. **Leaves** loosely clustered at the ends of branches, petioles 6–16 mm long, ca. 1.3 mm thick, glabrous and drying black; **leaf blades** 4–8 cm long, 1.4–3 cm broad, oblong to narrowly oblong, apex rounded, base acute to obtuse and slightly decurrent on petiole, drying stiffly chartaceous or subcoriaceous, gray to blackish above, the margin often revolute when dry, glabrous above and below, 2° veins 8–12/side and loop-connected near the margin (but difficult to see). **Inflorescences** terminal and solitary, 4–7 cm long, drying black, the capitulum 15–25 mm diam. (not including the corollas), hemispherical or subglobose, peduncles 25–40 mm long, 2–3.5 mm thick, glabrous, drying black, involucre ca. 15 mm broad (4–6 mm from edge to peduncle), flowers sessile or subsessile and closely compressed, with hairs below the flower bases. **Flowers**

drying black, glabrous externally, hypanthium ca. 3 mm diam., calyx tube 3–4 mm long, 3–4 mm diam., entire or subentire; **corolla** white, tube 3–8 mm long, 2–3 mm diam., lobes 5, 4–10 mm long, 1–2 mm broad, recurved; anthers 3.5 mm long, yellow. **Fruits** apparently united basally in a syncarpous capitulum with the distal part of the individual fruits separate, calyx tube persisting and succulent.

Plants of evergreen cloud forest formations on the Caribbean slope, at 700–950(–1100?) m elevation. Flowering in January–March, May, July, and October. This species has been collected near Bijagua (Alajuela), at the Monteverde reserve, and the Reserva Forestal de San Ramón. A collection has also been made at Alto Urén near the border with Panama.

Schradera costaricensis is recognized by its epiphytic habit, small stiff oblong leaves rounded at the apex, solitary capitulum with flowers subtended by a small circular involucre, and the small flowers with long calyx tube. The restricted altitudinal range is also distinctive. The following collections are placed here: *Burger et al.* 12139 & 12465, *Gómez-Laurito* 11147, *Haber & Bello* 8077 & 8192, and *Herrera* 452, 2004 & 3325.

Serissa Commerson ex Jussieu

Shrubs, glabrous or puberulent, tissues giving off a fetid odor when crushed; **stipules** united to form a broad sheath between the petiole bases and with stiff distal awns, persisting. **Leaves** opposite, small, subsessile, without domatia. **Inflorescences** axillary or terminal, of solitary or few fascicled flowers. **Flowers** bisexual and radially symmetrical, small, hypanthium obconic, calyx lobes 4–6; **corolla** funnelform, white, tube and throat pilose within, lobes 4–6; **stamens** 4–6; **ovary** 2-locular, with 1 ovule in each locule, stigmas 2. **Fruits** subglobose drupes, usually 2-seeded.

A genus of one (or three) species of southeast and east Asia. A cultivar is widely planted.

Serissa japonica (Thunb.) Thunb., Nov. gen. pl. 9: 132. 1798. *Lycium japonicum* Thunb., Nov. Act. Roy. Soc. Sci. Upsal. 3: 207. 1780. *Lycium foetidum* L.f., Suppl. Pl. 150. 1781.

Shrubs to ca. 0.8 m tall, leafy stems 0.4–1.7 mm thick, with short (0.1–0.3 mm) hairs in 2 opposite longitudinal lines, grayish and glabrescent in age; **stipules** with a sheath 0.5–1 mm long and 3 awns (6/node) to 3 mm long. **Leaves** opposite or pseudovercillate by reduction of internodes, petioles 0–2 mm long, poorly differentiated; **leaf blades** 4–10(–20) mm long, 1.5–4(–12) mm broad,

elliptic to lanceolate or obovate, apex usually acute, base cuneate and decurrent on petiole, stiff, drying grayish green and with margins enrolled, 2° veins 2–3/side. **Inflorescences** of solitary or few flowers mostly terminal on short-shoots, subsessile and subtended by the distal leaves. **Flowers** glabrous externally, calyx lobes ca. 1 mm long, triangular; **corolla** pink in bud but becoming white, tube 4–5 mm long, lobes 2–4 mm long. **Fruits** 1–2 mm diam.

Ornamental small shrubs sometimes used as hedges. Some cultivars have double flowers and variegated leaves. They have been planted in the Meseta Central. Leafy stems resemble those of *Diodia polymorpha* or *Arcytophyllum lavarum* (see fig. 1).

Sherardia Linnaeus

Annual **herbs**, with straight stiff trichomes; **stipules** most apparent (transformed to become leaf-like). **Leaves** 4–6/node and subsessile or up to 10 and united at the base to form an involucre at the ends of flowering shoots, domatia absent. **Inflorescences** of subsessile flowers in terminal involucreate capitula. **Flowers** bisexual and radially symmetrical, calyx with 4–6 lobes; **corolla** funnelform, pink to blue, lobes 4–6, valvate in bud; **stamens** 4–6; **ovary** with 2 locules and 1 ovule in each locule, style with 2 unequal branches, stigmas subcapitate. **Fruits** splitting into 2 dry 1-seeded mericarps.

A genus with only a single Eurasian species, now found as a weed in many parts of the world.

Sherardia arvensis L., Sp. Pl. 102. 1753.

Procumbent **herbs**, leafy stems 0.3–0.9 mm thick (dried), with 4 longitudinal ridges, hairs erect and whitish, 0.4–0.7 mm long; **stipules** leaf-like. **Leaves** 4–6(–10)/node, subsessile or the terminal involucre leaves united for 1–2 mm; **leaf blades** 4–9(–17) mm long, 0.8–3(–5) mm broad, lanceolate to elliptic or ovate, apex acute, pale grayish green when dried and with revolute margins, with scabrid hairs along the margins and scattered thin straight hairs ca. 0.5 mm long. **Inflorescences** 1–2 cm broad, usually on the ends of short-shoots, with 4–10 flowers. **Flowers** with corolla 4–5 mm long, lilac to pink or blue. **Fruits** 2–5 mm long (including the sepal lobes), splitting into 2 mericarps 1.2–1.5 mm diam., with minute stiff hairs.

Sherardia arvensis is a small weed resembling *Galium* and some *Spermacoce*. The stiff whorled leaves, lack of apparent stipules, and involucreate inflorescences are distinctive. It has only been collected near the cities of Turrialba and San José in Costa Rica.

Simira Aublet

Trees or shrubs, the wood often turning red or rose-purple after being cut (the color then fading with exposure to light); **stipules** interpetiolar, often large, glandular at the base within, caducous or persisting. **Leaves** opposite, petiolate; **leaf blades** entire or slightly pinnately lobed distally, pinnately veined, usually large, a few species with domatia. **Inflorescences** terminal or axillary to distal leaves, paniculate with decussate branching or congested and capitate, pedunculate, usually with many flowers, the flowers sessile or pedicellate, bibracteolate. **Flowers** bisexual and monomorphic, radially symmetrical, small to medium in size, fragrant, calyx tube cupular or campanulate, 4–6-dentate or entire; **corolla** campanulate to funnellform, white to yellowish or greenish white, tube with hairs at the stamen bases, lobes 4–5(–6), imbricate or open in bud; **stamens** 4–6, filaments borne on the lower half of the tube, anthers dorsifixed in the middle, sagittate at the base, conspicuously exerted; **ovary** 2-locular, ovules many in each locule, horizontally biserial on axile placentas. **Fruits** capsules, usually globose and woody, 2-locular and 2-valvate with loculicidal dehiscence; **seeds** large, numerous, lunate to semioblong, with a membranous marginal wing.

A genus of about 35 species, ranging from Mexico and Central America into tropical South America. This genus is now circumscribed to include the genus *Sickingia*. The small flowers, stamens with hairs along the base of the filaments, locules with many seeds, capsular or rounded fruits with flat horizontal seeds, and reddish wood (in some species) characterize this genus.

Simira maxonii (Standl.) Steyerf., Mem. New York Bot. Gard. 23: 306. 1972. *Genipa maxonii* Standl., J. Wash. Acad. Sci. 8: 642. 1918. *Sickingia maxonii* (Standl.) Standl., Trop. Woods 14: 30. 1928. Figure 38.

Trees, to 20 m tall, trunks to 30 cm dbh, cut wood often remaining pinkish, stems glabrous or puberulent at first but soon glabrescent, quadrangular but soon terete; **stipules** 2.5–4 cm long flattened and 6 mm broad, glabrous or minutely appressed-puberulent at the base. **Leaves** large, subsessile with petioles 3–9(–18) mm long, 3–6 mm thick, glabrous; **leaf blades** 22–48(–60) cm long, 10–26(–40) cm broad, broadly elliptic to elliptic-obovate or rhombic, sometimes lobed distally along the edge (with lobes 3–10 mm long), apex acuminate with a narrowed tip 8–20 mm long, base gradually narrowed and slightly rounded (subauriculate) at petiole, drying stiffly chartaceous, dark green or brown above, slightly paler or reddish beneath, glabrous above, glabrous or with short (0.1–0.2 mm) stiff hairs on the veins beneath, 2° veins 12–18/side, 3° veins subparallel and perpendicular to 2° veins. **Inflorescences** 6–15(–22) cm long, to 14(–18) cm broad, a compact panicle with many closely spaced

branches, peduncles 0–3(–5) cm long, 5–6 mm thick, minutely puberulent or glabrous, flowers sessile or on short (1–3 mm) pedicels. **Flowers** with hypanthium 3–5 mm long, obconic, sparsely and minutely puberulent or glabrous, calyx tube 1–2 mm long, broadly cupulate, calyx lobes 5, 0.5–1 mm long and 2 mm broad, minutely ciliate along the edge; **corolla** broadly funnellform or campanulate, greenish yellow to cream or orange, tube 4–5 mm long, ca. 4 mm diam. distally, lobes 5, 2–3 mm long; **stamens** 5, anthers 3–4 mm long, purplish, exerted. **Fruits** hard, 5–9 cm long, 3–7 cm diam., globose to rounded-oblong, smooth and grayish externally, pericarp 4–5 mm thick; **seeds** 12–25 mm long and 2–3 mm thick.

Trees of evergreen rain forest formations along the Caribbean lowlands and on the Osa Peninsula, from near sea level to 300 m elevation. Flowering in January–February, June–July, and September; fruiting in February–March, June–August, and November. The species ranges from southernmost Nicaragua to central Panama.

Simira maxonii is recognized by the large opposite leaves on very short petioles, the compact densely flowered inflorescences, the hard round fruit with large flat horizontal seeds, and the reddish coloring of wood, anthers, and undersides of young leaves (when present). This very distinctive species is often found in poorly drained sites and along stream edges. The large leaves of some collections have small distal lobes, a rarity in Rubiaceae. The fruits are reported to require 2 years to mature. The distal stems sometimes harbor ants (*Frankie 191c* from La Selva). Common names are “inkwood,” *guaiatil*, *guayatil colorado*, *jagua colorado*, and *jagua de montaña*.

Sipanea Aublet

Herbs, erect to clambering or decumbent, usually puberulent; **stipules** interpetiolar, small and inconspicuous to well developed, broadly triangular, acute or with a long narrow awn. **Leaves** opposite, sessile, subsessile or petiolate; **leaf blades** entire and pinnately veined, domatia absent. **Inflorescences** terminal or axillary, of 1–3 flowers or branched and paniculate to corymbose or cymose, branches often monochasial, bracts narrow, bracteoles absent, flowers sessile to short-pedicellate. **Flowers** bisexual and radially symmetrical, calyx lobes 4–5, linear to lanceolate; **corolla** salverform to funnellform, pink to rose or white, tube glabrous to villous at the mouth, lobes 5, convolute in bud; **stamens** 5, inserted in the middle or lower part (rarely near the apex) of the tube, anthers dorsifixed and linear; **ovary** 2-locular, with many ovules on axile placentas. **Fruits** thin-walled capsules, 2-locular and dehiscing loculicidally; **seeds** numerous, small, reticulate.

A South American genus of about 17 species; a

single species reaches Costa Rica and Panama. The delicate herbaceous habit, narrow-tubular flowers with corolla lobes contorted in bud, many-seeded capsules, and nonsagittate stamens characterize this genus. The following species has recently been collected in Costa Rica. Compare *Oldenlandia*.

Sipanea biflora (L.f.) Cham. & Schlechtend., *Linnaea* 4: 168. 1829. *Virecta biflora* L.f., Suppl. 134. 1781. *Rondeletia biflora* (L.f.) Rottb., *Descr. rar. pl. surin.* 8, pl. 2. 1798. *Manettia hydrophila* Dwyer, *Ann. Missouri Bot. Gard.* 67: 280. 1980.

Low creeping or erect **herbs** to 20(–50) cm tall, leafy stems 0.3–1.7 mm thick, somewhat succulent in life, minutely puberulent with thin curved hairs 0.1–0.3 mm long; **stipules** 0.3–1 mm long, bifid or entire distally, minutely ciliate. **Leaves** evenly spaced and distant along the stems, petioles 4–18 mm long, ca. 0.5 mm broad, minutely appressed-puberulent; **leaf blades** 12–42(–55) mm long, 6–22(–25) mm broad, ovate, apex obtuse to subacute, base obtuse to subtruncate and acute-decurrent on petiole, drying membranaceous, dark above, glabrous or with sparse short (ca. 0.3 mm) appressed-ascending hairs on the upper surface, usually appressed-puberulent on the veins beneath, 2° veins 3–5/side, ascending. **Inflorescences** usually terminal and spicate, to 6 cm long with 2–5 alternate subsessile flowers (or paniculate with lateral branches bearing 1–2 flowers), peduncles to 15 mm long, ca. 0.4 mm thick, glabrous, pedicels of the distal flowers 5–15 mm long, bracts 0.5–1.5 mm long, linear. **Flowers** with hypanthium and calyx tube 1–2 mm long, covered with straight stiff ascending hairs, calyx lobes 5, 1–3(–4.5) mm long, linear to narrowly triangular, sparsely minutely puberulent; **corolla** pink or pale purple (white around the throat), glabrous or with a few small hairs externally, tube 5–14 mm long, ca. 1 mm diam., lobes 5, 4–8 mm long, 2–5 mm broad, obovate-oblong; anthers 2.5 mm long, included. **Fruits** globose capsules, 3–4 mm long (not including the persisting calyx lobes) and 4 mm diam., bisulcate and splitting from the top, with stiff appressed ascending hairs 0.2–0.4 mm long; **seeds** ca. 0.5 mm thick.

Plants of poorly drained moist sites in the evergreen Caribbean coastal plain, 2–20 m elevation. Flowering and fruiting in March–April and September–November. This species ranges from central Costa Rica southward to Venezuela and northern Brazil.

Sipanea biflora is recognized by the semiaquatic or poorly drained lowland habitat, the small herbaceous habit, slender stems with minute curved hairs, thin ovate leaves, few-flowered inflorescences, hispidulous ovaries, and subglobose capsules with persisting linear calyx lobes. The above

description is based, in part, on Steyermark (1974) and Venezuelan material. Compare *Pentodon pentandrus*.

Sommeria Schlechtendal

REFERENCE—L. O. Williams, *Sommeria* (Rubiaceae) in North America. *Phytologia* 26: 121–126. 1973.

Shrubs or small trees, branchlets usually terete and pubescent; **stipules** interpetiolar, large, triangular, caducous. **Leaves** opposite, petiolate; **leaf blades** usually large, entire and pinnately veined, the minor venation (between the 3° and 4° veins) conspicuously parallel (lineolate), domatia present or absent. **Inflorescences** solitary in the distal leaf axils (2/node), corymbose to racemose, pedunculate, the flowers usually small and often in distal cymes, bracts and bracteoles present. **Flowers** usually small, hypanthium turbinate, calyx lobes 5, equal or unequal, usually broad and conspicuous, persisting; **corolla** funnelform to subcampanulate, sericeous externally, somewhat fleshy, corolla tube villous on the throat within, lobes 5, valvate in bud; **stamens** 5, filaments short and barbate, borne at the throat of the tube, anthers dorsifixed, oblong, obtuse at each end; **ovary** 2-locular, ovules many on placentas borne on the septum, style short with 2 long style branches, glabrous or hirsute. **Fruits** baccate, globose to ovoid, 2-locular; **seeds** numerous and minute, subglobose, testa thin and foveolate.

A genus of about 15 species, ranging from Mexico and Central America into Andean South America. The genus is recognized by the pubescence on all parts, larger leaves with unusual parallel (lineolate) minor venation, small flowers with large calyx lobes, and fleshy two-locular fruit with many small seeds.

Sommeria donnell-smithii Standl., *Contr. U.S. Natl. Herb.* 17: 436. 1914. *S. mesochroa* Standl., loc. cit. 439. 1914. *S. dunlapii* L. O. Williams, *Phytologia* 26: 122. 1973. *S. rivularis* L. O. Williams, loc. cit. 125. 1973. Figure 35.

Shrubs or small trees, 1.5–8(–15) m tall, leafy stems 2–7 mm thick, young stems densely strigulose with yellowish ascending hairs 0.3–0.9 mm long, becoming terete and dark brown; **stipules** 14–35 mm long and 3.5–8 mm broad, lanceolate, glabrous or puberulent on the midrib and base abaxially, glabrous on the inside, drying reddish brown, deciduous. **Leaves** with petioles 12–44 mm long, 1–2.4 mm thick, with thin ascending hairs 0.3–0.9 mm long; **leaf blades** 10–28(–32) cm long, 5–12(–14) cm broad,

obovate to elliptic-obovate, oblong or oblong-obovate, apex acuminate with tip 5–15 mm long, base tapering gradually and acute or obtuse, slightly decurrent on petiole, drying stiffly chartaceous, brown or yellowish brown, with small (0.5 mm) scattered hairs on the upper surface, appressed-puberulent on the veins beneath with yellowish hairs 0.3–1.2 mm long, 2° veins 11–15/side, tufts of hairs or depressions (domatia) often present in the vein axils beneath, smallest veins parallel. **Inflorescences** 3–7 cm long, to 5 cm broad, paniculate with opposite branching or with 3 major branches, peduncles 1–3 cm long, ca. 1 mm thick and densely puberulent, flowers in corymbs, cymes or racemes, bracts to 10 mm long, linear-lanceolate, pedicels 0–4 mm long. **Flowers** 5-parted, hypanthium ca. 2 mm long, with dense appressed ascending yellowish hairs, calyx lobes unequal, (1–)2–4(–5) mm long, 1–3 mm broad, usually glabrous on the surfaces and drying pale brown, with parallel or reticulate venation; **corolla** white, funnelform, tube 3–4 mm long, ca. 2 mm diam., densely appressed-puberulent, lobes 2–3 mm long; anthers 0.8 mm long. **Fruits** becoming 6–10 mm diam., globose to oblong, becoming dark red or maroon, with ascending hairs and persisting sepal lobes, the infructescence often with elongated branches; **seeds** angular, 0.9–1.5 mm long, smooth.

Plants often found along rivers and in stream valleys in evergreen rain forest formations, from (100–)400 to 1400 m on the Caribbean slope and from (100–)500 to 1600 m on the Pacific slope. Flowering and fruiting throughout the year. The species occurs in Costa Rica and Panama.

Sommeria donnell-smithii is recognized by its large obovate leaves with parallel (lineolate) minor venation, the dense yellowish puberulence, axillary inflorescences, small flowers with large calyx lobes and short corolla tube, and fleshy many-seeded fruit. The flowers and inflorescences are quite variable and give little support for delimiting additional species in our area. Williams based two new species on unusual lowland collections: *S. dunlapii* from Bocas del Toro, Panama (Dunlap 351 F) and *S. rivularis* from southern Puntarenas (Allen 5431 EAP, F, US). It is noteworthy that collections from below 200 m are quite rare (3 of 31 collections at F). *Sommeria grandis* (Bartl.) Standl., listed by Standley (1938), is a species of Mexico.

Spermacoe Linnaeus

REFERENCES—C. D. Adams (manuscript submitted to Novon, 1992). W. T. Gillis, The confused *Spermacoe*. *Phytologia* 29: 185–187. 1974.

Annual or perennial **herbs** or small subshrubs, erect

to prostrate, stems quadrangular, glabrous or pubescent; **stipules** united with the petiole bases to form a sheath, with 3–15 stiff erect awns arising from the truncated (transverse) distal margin, persisting. **Leaves** opposite or pseudoverticillate (with pairs of smaller axillary leaves), petiolate or sessile; **leaf blades** usually narrow with strongly ascending secondary veins, entire, often scabrous, without domatia. **Inflorescences** axillary or terminal, peduncles absent (in ours), the flowers fasciculate and verticillate or congested into heads, terminal heads subtended by 2 or more leaves (these sometimes involucrate), bracteoles filiform when present, flowers sessile or subsessile. **Flowers** bisexual and monomorphic or distylous, small, hypanthium obovoid to turbinate, calyx tube short or absent, calyx lobes usually 4 (2–8), lobes acute to dentate and green; **corolla** funnelform or salverform, white to lavender, lobes 4 (3), valvate in bud; **stamens** 4 (3), filaments short, anthers linear to oblong, included or slightly exserted, often bluish; **ovary** 2-locular with 1 ovule borne on the middle of the septum in each cell, style slender, stigma capitate or bilobed. **Fruits** capsular, 2-lobed and resulting in 2 cocci (both dehiscent adaxially or 1 dehiscent adaxially and the other indehiscent) or splitting down the center to expose both seeds, the calyx often persisting; **seeds** oblong to ellipsoid, with a narrow longitudinal ventral sulcus and lustrous minutely pitted dorsal (abaxial) surface.

A pantropical genus of over 150 species, with many species in the American tropics. This genus is now interpreted to include *Borreria*. *Spermacoe* is difficult to separate from *Crusea* and *Diodia*, in which the cocci do not open. The often narrow subsessile leaves, small capitulate or axillary sessile inflorescences, four-lobed corolla, single-seeded cocci, and herbaceous weedy growth form distinguish these plants and their close relatives: *Crusea*, *Diodia*, *Mitracarpus*, and *Richardia*. All these plants are characterized by a stipular sheath united to the leaf bases and truncated distally (straight or convex) with slender stiff awns or setae; all have strongly ascending secondary veins, and many have scabrous leaves. A number of our species appear to be recently introduced weeds, having been collected only a few times near the larger cities. As in the case of many other weedy plants, different individuals of the same *Spermacoe* species can differ greatly in overall size, form of the leaves, and development of inflorescences. This can make their identification difficult. Consequently, seeds are often necessary to confirm an identification.

We gratefully acknowledge the suggestions, determinations, and measurements provided by C. D. Adams, who has clarified the nomenclature and many of the species problems in this group; he is treating the *Spermacoeae* for the Flora Mesoamericana.

Key to the Species of *Spermacoce*

- 1a. Mature fruits splitting into 2 cocci, one of which does not open and the other of which splits longitudinally along the inner face, *or* with the mature fruits opening at the base and occasionally opening slightly at the apex 2
- 1b. Mature fruit splitting into 2 cocci, both of which open along the inner face, or open broadly at the top to release both seeds; seeds 0.6–3 mm long and usually easily removed from the cocci at maturity by crushing between the fingers (species formerly placed in *Borreria*) 4
 - 2a. Fruits splitting into 2 and often opening slightly at the bottom; seeds 2–3 mm long [commonly collected and wide-ranging] *S. ocymifolia*
 - 2b. Mature fruits splitting into 2 cocci, one of which does not open and the other of which splits longitudinally along the inner face; seeds 1.4–2.2 mm long (species of *Spermacoce sensu stricto*) 3
 - 3a. Leaves scabrous above; calyx lobes ciliate along the margins; fruits puberulent; rarely collected (in Costa Rica) in open weedy sites *S. confusa*
 - 3b. Leaves smooth above; calyx lobes glabrous along the margins; fruits glabrous; usually growing along river edges and wet depressions *S. tenuior*
- 4a. Leaves often linear to lanceolate and pseudoverticillate; stems with larger rounded terminal inflorescences and only 1 (2, 3) additional nodes with axillary inflorescences (except *S. densiflora*) 5
- 4b. Leaves lanceolate to ovate, opposite or less often pseudoverticillate; stems usually with inflorescences in the axils of many nodes along the stem, but with larger (> 1 cm) rounded terminal inflorescences only in *S. assurgens* and *S. vegeta* 8
 - 5a. Plants growing in water or wet mud; calyx lobes 4; fruits 6–7 mm long (including calyx lobes); rarely collected in Costa Rica *S. scabiosoides*
 - 5b. Plants not semiaquatic, not restricted to shallow water and wet mud; calyx lobes 2–4; fruits 1.5–5 mm long; commonly collected species 6
 - 6a. Terminal capitulae usually exceeding 16 mm diam., often with well-developed capitulae at the distal 3 nodes; calyx lobes 2; body of the fruits 2.5–5 mm long (seeds 1.4–2.2 mm long); widespread *S. densiflora*
 - 6b. Terminal capitulae not usually exceeding 16 mm diam., capitulae usually only well developed at the distal node; calyx lobes 2–4; body of the fruits 1.5–3 mm long; plants mostly confined to the seasonally dry Pacific slope in Costa Rica 7
 - 7a. Calyx lobes 2(–3) or with 2 larger and 2 very small lobes, narrowly clavate to acute, often lacking a slender central pigmented midvein; seeds 1.3–1.6 mm long *S. verticillata*
 - 7b. Calyx lobes 4 (rarely 3), usually pigmented along the slender midvein, narrowly acute; seeds 1.6–2.2 mm long *S. suaveolens*
- 8a. Seeds with transverse sulci or depressions on the abaxial surface and easily seen with a hand lens ($\times 10$); plants often with hemispheric terminal heads 1–2 cm diam.; calyx lobes 4, but often unequal 9
- 8a. Seeds without transverse sulci easily seen with a hand lens (minute transverse pits present in some species but seen clearly only at $\times 40$); plants rarely with hemispheric terminal heads; calyx lobes 2–4 10
 - 9a. Calyx lobes ovate to broadly triangular, often rounded distally; seeds 2–2.2 mm long; upper leaf surface usually glabrous or scabrous; rarely collected in southern Central America *S. vegeta*
 - 9b. Calyx lobes narrowly triangular, never rounded distally; seeds 1.1–2.1 mm long; upper leaf surfaces glabrous or with thin hairs; plants of wide distribution *S. assurgens*
- 10a. Corolla tubes 2–5 mm long, calyx lobes 4, 0.4–1.2 mm long; leaves often becoming more than 15 mm broad 12
- 10b. Corolla tubes 0.5–2 mm long, calyx lobes 2–4, 0.4–2 mm long; leaves rarely becoming more than 13 mm broad 12
 - 11a. Seeds 1.7–2.9 mm long, smooth or minutely reticulate; stems often with thin green longitudinal wings to 0.4 mm high; stipule sheath not beginning below the leaf bases; flowers white, lavender, or blue *S. latifolia*
 - 11b. Seeds 1.2–2.1 mm long, reticulate or transversely sulcate; stems with longitudinal ridges only

- 0.1–0.2 mm high; stipule sheath beginning well below the leaf bases; flowers white or tinged with pink *S. assurgens*
- 12a. Calyx lobes 2 (often on only 1 side of the capsule); stems often with ciliate hairs along the longitudinal ribs beneath the nodes, leaves not more than 25 mm long; capsule wall thin and fragmenting, seeds 0.7–0.9 mm long, often yellowish, surface reticulate ($\times 40$) *S. exilis*
- 12b. Calyx lobes 4 (rarely 3 or 2); stems rarely with ciliate hairs along the ribs beneath the nodes, leaves often exceeding 25 mm length; capsule wall firmly cartilaginous, seeds 0.7–2.2 mm long, usually dark reddish brown, smooth or clearly reticulate 13
- 13a. Calyx lobes 4 or fewer, often unequal with the 2 smaller deciduous; seeds 0.7–1.2 mm long, with clearly reticulate surface and larger (0.05–0.1 mm) pits; plants erect to prostrate or decumbent, usually glabrous *S. prostrata*
- 13b. Calyx lobes 4 and equal, persisting; seeds 1.4–1.8 mm long, with finely reticulate (minutely pitted) surface; plants usually erect with slender stiff stems *S. ovalifolia*

Spermacoce assurgens Ruiz & Pav., Fl. Peruv. 1: 60, t. 92. 1798. *Spermacoce laevis sensu auctores* non Lam., Tabl. Encycl. 1: 231. Figure 5.

Herbs, 20–80 cm tall, erect or spreading, leafy stems 0.8–3 mm diam., with thin whitish hairs 0.1–0.4 mm long, glabrescent, the hairs often in narrow longitudinal ridges; **stipule** sheaths 1.5–5 mm high, 2–4 mm broad (to 8 mm beneath inflorescences), often obconic and arising from beneath the leaf bases at sterile nodes, with 3–9 awns 1–6 mm long, glabrous or sparsely pubescent. **Leaves** opposite or rarely pseudoverticillate, petioles 0–6 mm long, slender; **leaf blades** 1–5(–7) cm long, 0.5–2.5(–3) cm broad, lanceolate to ovate-lanceolate or ovate-elliptic, apex acute to obtuse, base obtuse to cuneate or rounded, drying stiffly chartaceous, darker grayish green above, usually glabrous and scabrous above, glabrous or with stiff scabrous or thin hairs to 0.5 mm long beneath, 2° veins 4–6/side. **Inflorescences** terminal or axillary, globose to verticillate, 3–13 mm long, 5–15 mm diam., subtended by 2–4 leaf-like bracts 1–5 cm long, flowers sessile or subsessile and crowded. **Flowers** monomorphic, hypanthium ca. 1.5 mm long, calyx lobes 4, 0.3–0.7(–1) mm long, acute or blunt; **corolla** white, tube ca. 2 mm long, lobes ca. 1 mm long, triangular. **Fruits** 2–2.5 mm long (not including the calyx lobes), ca. 2 mm broad; **seeds** 1.2–2.2 mm long, 0.6–1.1 mm broad, dark reddish brown, minutely reticulate and usually with narrow transverse sulci abaxially.

Weedy plants of open sites in evergreen and partly deciduous forest areas, 0–1700(–2000) m elevation in Costa Rica. Flowering and fruiting throughout the year. This species ranges widely over the tropics and subtropics of the world.

Spermacoce assurgens is recognized by the stipular sheath arising from well beneath the leaf bases (especially noticeable at sterile nodes), having both terminal and axillary capitula, four small sepal lobes, small corollas, and seeds with transverse sulci (not always easily seen). Rare individual plants may occur with thin hairs over many surfaces and long-hirsute on ridges of the stems, but intermediates can be found in Central America (see Ad-

ams cited above). This is one of the most common species of *Spermacoce* in Central America. Compare *S. vegeta*, a closely related species.

Spermacoce confusa Rendle ex Gillis, Phytologia 29: 185. 1974 (Rendle's description in J. Bot. 74: 12. 1936, lacked a Latin diagnosis). *S. tenuoir sensu auctores* non L. Figure 5.

Annual **herbs** or subshrubs to 80 cm tall, with few or many branches, leafy stems 0.5–2.5 mm thick, with 4 prominent longitudinal ridges and with scabrid hairs along the ridges; **stipule** sheath ca. 1 mm long, 1–3 mm broad, with 3–7 filiform awns 1–4 mm long, glabrous. **Leaves** usually opposite and subsessile, petioles 0–3(–6) mm long; **leaf blades** 2–6 cm long, 2–10(–13) mm broad, lanceolate to oblanceolate or linear-lanceolate, apex acute to acuminate, base narrowed, with minute (0.1–0.2 mm) scabridulous hairs above, glabrous beneath, 2° veins 2–3/side, usually impressed above. **Inflorescences** small and axillary, few-flowered, ca. 4–6 mm long, of 6–15 flowers, the flowers sessile or subsessile. **Flowers** with hypanthium and calyx tube 1–1.5 mm long, calyx lobes 4, 0.4–1 mm long, triangular-lanceolate to linear-lanceolate, conspicuously ciliolate along the edges; **corolla** white, rose, lavender, or blue, tube ca. 1.5 mm long and 1 mm diam., lobes 0.5–1 mm long, 0.4–0.5 mm broad, ovate-oblong, obtuse at the apex, minutely puberulent distally; filaments ca. 0.2 mm long, borne at the base of the tube, anthers ca. 0.3 mm long. **Fruits** 1.5–3 mm long, obovoid to ellipsoid or subglobose, with short ascending hispidulous hairs to 0.5 mm long, with persisting calyx lobes 0.5–1 mm long; **seeds** 1.1–2 mm long, 0.5–1 mm broad, ellipsoid-oblong to obovoid-ellipsoid, bluntly rounded at both ends, yellowish to dark brown, lustrous, with minute shallow pits ($\times 40$), sinus less than $\frac{1}{3}$ the width of the seed and constricted in the middle.

Plants of open weedy sites, from near sea level to 1000 m elevation (to 1600 m in Guatemala). Flowering probably primarily in the wet season: July–December. The species ranges from Mexico through Central America and the West Indies into South America.

Spermacoce confusa is recognized by the very narrow scabrous leaves, small compact inflorescences, and the asymmetric unevenly setose capsule that breaks into two parts, with one failing to open. Rarely collected in Costa Rica (all from the Pacific slope and lowlands: Guanacaste, Puntarenas, and San José provinces).

Spermacoce densiflora (DC.) Liogier, *Phytologia* 54: 113. 1983. *Borreria densiflora* DC., *Prodr.* 4: 542. 1830. *S. spinosa* L., *Sp. Pl.* ed. 2, 148. 1762, nom. illeg. (cf. Steyermark, 1972, p. 814). *B. spinosa* (L.) Cham. & Schlechtend., *Linnaea* 3: 340. 1828. Figure 4.

Herbs from a woody rootstock, 0.3–1 m tall, with few distal branches, leafy stems 1–4 mm thick, with 4 longitudinal ridges, usually glabrous but scabrous; **stipule** sheaths 2–5 mm long, to 5(–11) mm broad, awns 3–9, 2.5–7 mm long, usually glabrous and pale yellowish gray. **Leaves** opposite or more often pseudoverticillate with 2 larger and 2–6 smaller leaves at the same node, petioles absent or poorly differentiated; **leaf blades** 1–6(–7) cm long, 1–8(–15) mm broad, linear to linear-lanceolate or linear-oblong, apex acute, base narrowly cuneate, drying grayish with incurved scabrid margins, stiffly chartaceous to subcoriaceous, glabrous but with scabrous surfaces, 2° veins 3–6/side. **Inflorescences** terminal and axillary to the distal 2(–3) nodes, 8–18 mm long and 14–28 mm broad, capitate and hemispheric or verticillate, subtended by leaf-like bracts 1–5 cm long, flowers sessile and tightly congested. **Flowers** with hypanthium 2.5 mm long, pilose distally, calyx lobes 2, 0.9–2.5 mm long, narrow, ciliolate or glabrous; **corolla** white, campanulate, tube ca. 1 mm long, lobes ca. 1 mm long; anthers ca. 0.4 mm long. **Fruits** 3–5 mm long not including the calyx lobes; **seeds** 1.5–2.1 mm long and 0.4–0.6 mm broad, narrowly oblong, dark brown, surface weakly reticulate ($\times 10$) with minute pits ($\times 40$).

Weedy plants of open sites in both evergreen and deciduous forest areas, from near sea level to 800 m (to 1200 m in Guatemala). Flowering in October–February. This species ranges from Mexico and the West Indies to northern South America.

Spermacoce densiflora is recognized by the larger terminal hemispheric or subglobose heads, very narrow leaves, stipular sheaths often drying pale grayish, and narrow seeds.

Spermacoce exilis (L. O. Williams) C. D. Adams, *Novon* (in press). *Borreria exilis* L. O. Williams, *Phytologia* 28: 227. 1974, nom. nov. for *Borreria gracilis* L. O. Williams, *Phytologia* 26: 487. 1973, not *B. gracilis* Miq. in Hook. f., nor

Scheele. *S. mauritiana* Gideon, *Kew Bull.* 37: 547. 1983, nom. nov. for *Borreria repens* DC. non *Spermacoce repens* Cham. & Schlechtend. Figure 5.

Annual herbs, prostrate or clambering, to 30 cm long with few branches, leafy stems 0.6–1.8 mm thick, glabrous or with ciliate hairs 0.2–0.5 mm long (especially along the raised longitudinal ribs below the node); **stipule** sheath 0.5–2 mm long, 1.5–6 mm broad, with 5–9 awns 1–2 mm long. **Leaves** usually opposite, less often verticillate with short axillary leaves, petioles 0–3 mm long, lateral margins continuous with the lamina margins; **leaf blades** 7–24 mm long, 3–11 mm broad, ovate-elliptic to ovate-oblong, ovate or elliptic, apex acute to obtuse, base cuneate and decurrent, drying grayish or yellowish green above, membranaceous to thin-chartaceous, glabrous or with thin hairs 0.1–0.4 mm long, scabrous above and along the margins, 2° veins 2–4/side. **Inflorescences** mostly axillary and verticillate with few sessile flowers, ca. 2 mm high and 6 mm broad, subtended by the stipules and leaves. **Flowers** with hypanthium 0.5–1 mm long, calyx lobes 2, ca. 0.5 mm long, linear and blunt or acute at the apex; **corolla** white or purplish white, tube ca. 0.5 mm long. **Fruits** 0.8–1 mm long, 1–2 mm broad when open, persisting calyx often recurved; **seeds** 0.7–0.9 mm long, 0.3–0.5 mm thick, oblong, sometimes appearing to have longitudinal ridges ($\times 10$) but with minute transverse pits ($\times 40$), yellowish to dark brown.

Weedy plants of open sites mostly in evergreen areas, 50–600 m elevation (higher elsewhere). Probably flowering throughout the year but primarily in the wet season: May–December. The species ranges from southern Mexico to South America and the West Indies. It occurs on Cocos Island and may be widely distributed in the Old World.

Spermacoce exilis is recognized by its small stature, little leaves, axillary inflorescences, stems often with ciliolate ridges below the node, minute flowers with two small calyx lobes, and small seeds. The seeds appear to be smooth but are characterized by transversely elongated pits in vertical rows on the abaxial surface ($\times 40$) with neither row orientation dominant (C. D. Adams, pers. comm., June 1991); see illustration, upper right. The type of *S. exilis*, from Cocos Island, lacks the ciliolate ridges seen in most other collections but has the characteristic seed. This may be *S. gracilis* Ruiz & Pav. as used in the Flora of La Selva (Taylor 1991).

Spermacoce latifolia Aubl., *Hist. pl. Guiane* 1: 55, pl. 19, f. 1. 1775. *Borreria latifolia* (Aubl.) K. Schum. in Mart. *Fl. Bras.* 6(6): 61, pl. 80. 1888. Figure 5.

Herbs, prostrate, clambering or erect to 1 m high, branched mostly near the base, leafy stems 1–4.5 mm thick, quadrangular and usually with thin greenish longitudinal ridges ca. 0.3 mm high, glabrous or with thin hairs to 0.7 mm long; **stipule** sheath 1–3 mm long, 2–7 mm broad, with 5–7 slender awns 1–6 mm long, glabrous or with thin hairs to 2 mm long. **Leaves** opposite and well separated along the stem, petioles 0–8 mm long, poorly differentiated from the lamina; **leaf blades** 10–45(–80) mm long, 4–25(–40) mm broad, ovate-elliptic to obovate, elliptic or broadly elliptic, apex acute, base obtuse to cuneate and decurrent on petiole, drying membranaceous to stiffly chartaceous, usually greenish above, subglabrous with minute (0.1 mm) hairs or with hairs to 0.9 mm long, 2° veins 3–6/side. **Inflorescences** axillary, 3–8 mm long, 7–15 mm broad, few-flowered, sessile and glomerulate, separate or verticillate, subtended by the inconspicuous stipule sheath and leaves, flowers sessile. **Flowers** with hypanthium 1–1.5 mm long, turbinate, sparsely puberulent with ascending hairs, sepal lobes 4, ca. 1 mm long, triangular; **corolla** salverform, white to lavender or blue, 2.5–5 mm long, tube ca. 3 mm long, 0.5–1 mm diam., anthers 0.5–1 mm long. **Fruits** 2.5–4 mm long, 3–4 mm broad when open, minutely pilose; **seeds** 1.7–2.9 mm long, 1–1.7 mm broad, oblong, minutely reticulate or smooth, pale yellowish brown to dark brown.

Weedy plants of evergreen forest formations, from near sea level to ca. 1100 m elevation. Probably flowering and fruiting throughout the year. The species ranges from Mexico and the West Indies to South America and is found in the Old World as well.

Spermacoce latifolia is distinguished by the broader (usually thin) opposite leaves, stems with conspicuous (often winged) longitudinal ridges, small axillary inflorescences, and larger seeds with very minutely reticulate surface. The leaves and stems are glabrous or only sparsely puberulent. The axillary inflorescences often have only a few (3–7) flowers and the leaves usually dry yellowish green. *Mielcillo* and *chiritillo* have been reported as common names.

Spermacoce ocymifolia Willd. ex Roem. & Schult., Syst. Veg. 3: 530. 1818. *Hemidiodia ocymifolia* (Willd. ex Roem. & Schult.) K. Schum. in Mart., Fl. Brasil. 6(6): 30, pl. 72. 1889. *Diodia ocymifolia* (Willd. ex Roem. & Schult.) Bremek., Rec. Trav. Bot. Neerl. 31: 305. 1934. Figure 6.

Herbs or subshrubs, 30–90(–150) cm tall, branches erect or spreading and decumbent, distal branchlets simple or less often branched, leafy stems 0.5–3 mm thick, with 4 obscure longitudinal ribs and becoming terete, usually sparsely pubescent with thin whitish hairs 0.1–0.3 mm long; **stipule** sheath 2–6 mm long, 2–6 mm broad, conical (often difficult to see beneath the inflorescences),

pubescent, with (3–)5–11 unequal erect or spreading awns on each side, 2–8 mm long. **Leaves** opposite, petioles 0–12 mm long, 0.4–2 mm wide, sometimes with winged margins continuous with the leaf margins; **leaf blades** 2–8(–11) cm long, 0.6–2(–3) cm broad, narrowly elliptic, narrowly elliptic-oblong or elliptic-lanceolate, apex tapering gradually and acute or acuminate, base attenuate and decurrent on petiole, the margins becoming revolute, leaves drying stiffly chartaceous, slightly scabrous above and glabrous or sparsely puberulent, glabrous or scabrous beneath with short (0.1–0.2 mm) stiff hairs. 2° veins 3–6/side, strongly ascending. **Inflorescences** axillary and verticillate, 6–14 mm broad and 4–8 mm high, subtended by the petiolar sheath and its linear awns, the flowers densely crowded and sessile or subsessile. **Flowers** with hypanthium 1–2 mm long, narrowly oblongoid, with short stiff hairs, calyx lobes 0.3–0.5 mm long and ca. 0.4 mm broad, acute; **corolla** white, funnellform, tube 1.3–2.5 mm long, ca. 0.6 mm diam. at the base and 1 mm at the mouth, glabrous externally, with short hairs at the mouth within, lobes 3–4, 1–2 mm long and ca. 0.5 mm broad, oblong-lanceolate; **stamens** 3–4, filaments 0.6–2 mm long, anthers 0.6–0.9 mm long, oblong; style ca. 2.5 mm long. **Fruits** 2.5–4 mm long, 1.5–2 mm broad, oblong-turbinate to obovoid-oblong, glabrous near the base and with thin erect hairs 0.2–0.3 mm long distally, persisting calyx 0.3 mm long, splitting into 2 mericarps; **seeds** 2–3 mm long, 0.6–1.3 mm thick, narrowly oblong, smooth or with obscure transverse depressions abaxially ($\times 10$) and minutely pitted surface ($\times 40$), dark reddish brown.

Weedy plants of open sites in evergreen or partly deciduous areas, from near sea level to 1200 m elevation in Costa Rica. Collected on the Caribbean slope and through the length of the cordilleras. This species has not been collected in the drier deciduous or semideciduous Pacific slope (0–500 m) of Central America. Probably flowering and fruiting throughout the year. The species ranges from Mexico, Central America, and the West Indies to Paraguay. It is found on Cocos Island and in the Old World.

Spermacoce ocymifolia is recognized by the short weedy habit, erect stems, the narrow opposite leaves with strongly ascending veins, sheathing stipules with long narrow awns, the densely crowded small verticillate flowers, and the obovoid capsular fruit with short thin erect hairs and short (0.5 mm) calyx lobes. The capsule splits into two mericarps, which tend to open near the base adaxially but occasionally the capsules open slightly at the top before separating from the base. These plants closely resemble species of *Crusea* and *Diodia*.

Spermacoce ovalifolia (M. Martens & Galeotti) Hemsl., Biol. centr. amer. Bot. 2: 59. 1881. *Borreria ovalifolia* M. Martens & Galeotti, Bull. Acad. Roy. Sci. Bruxelles 11: 129. 1844. *S. prin-*

glei S. Watson, Proc. Amer. Acad. Sci. 25: 152. 1890. *S. ernstii* R. Fosberg & D. Powell, Smiths. Contr. Bot. 45: 29. 1980. Figure 5.

Annual **herbs** to 40 cm tall, often branched near the base and with few distal branches, leafy stems 0.5–2 mm thick, with 4 longitudinal ribs ca. 0.2 mm high, glabrous or minutely puberulent at the nodes; **stipule** sheath 0.5–3 mm high, often obscured by the inflorescences, with 3–11 awns 1–5 mm long. **Leaves** opposite (occasionally pseudoverticillate) with 2–4 smaller axillary leaves, petioles 0–5 mm long, with lateral margins continuous with the leaf margins; **leaf blades** 6–48 mm long, 2–16 mm broad, elliptic to narrowly elliptic, elliptic-lanceolate or ovate-elliptic, apex acute, base acute to cuneate, drying membranaceous, brownish or dark green above, glabrous or with a few scabrous hairs above, subglabrous or with minute (0.1–0.2 mm) stiff hairs beneath, scabrous on the edges, 2° veins 2–5/side. **Inflorescences** axillary and verticillate or terminal and subtended by 2–6 leaves, 2–4 mm high, 3–6 mm broad, with few (5–12) flowers. **Flowers** with 4 calyx lobes 0.6–1.1 mm long, 0.1–0.2 mm broad, linear-aculeate, persisting; **corolla** minute. **Fruits** ca. 2 mm long and 2 mm broad when opened, body of the capsule ca. 1.5 mm long, glabrous externally or minutely (0.05–0.1 mm) hispid distally; **seeds** (1.3–)1.5–1.8 mm long, 0.8–0.9 mm broad, very finely reticulate ($\times 10$) and minutely pitted ($\times 40$), dark reddish brown.

Weedy plants of open sites in evergreen and partly deciduous areas of the Meseta Central, 900–1400 m elevation. Flowering in the wet season: July–December. The species ranges widely, from the southern United States to South America, the West Indies, and the Old World.

Spermacoe ovalifolia is recognized by its short stature, mostly opposite (not verticillate) leaves, small axillary inflorescences, and slightly larger seeds with minutely pitted surface. Many of our specimens were earlier placed under the name *Borreria ocyroides* (Burm.) DC., an Asian species. These plants are very similar to *S. exilis* and *S. prostrata*, with smaller seeds. This species is rare in Costa Rica and perhaps a recent introduction.

Spermacoe prostrata Aubl., Hist. pl. Guiane 1: 58, pl. 20. f. 3. 1775. *Borreria repens* DC., Prodr., 4: 533. 1830. *B. parviflora* G. F. W. Meyer, Prim. fl. Esseq. 83. 1818. Figure 5.

Prostrate or decumbent annual **herbs** to 40 cm tall, branching mostly near the bases, leafy stems 0.4–2 mm thick, glabrous or rarely with thin hairs to 0.8 mm long, with 4 longitudinal ribs 0.1–0.3 mm high; **stipule** sheaths 1–3 mm high, 1.5–6 mm broad, with 3–9 awns 1–2 mm long. **Leaves** opposite or pseudoverticillate with 2–4 smaller axillary leaves at each node, sessile or subsessile; **leaf blades** 10–35 mm long, 2–18 mm broad, elliptic to

narrowly elliptic or elliptic-lanceolate, apex acute (obtuse), base cuneate and decurrent on petiole, drying membranaceous to chartaceous, greenish or yellowish brown, glabrous or with minute (0.2 mm) stiff hairs above and below, scabrous on the margin, 2° veins 2–4/side. **Inflorescences** mostly axillary (sometimes terminal), 2–4 mm high and 3–8 mm broad, flowers few (3–8) to many (ca. 20) and sessile. **Flowers** with hypanthium 0.5–1 mm long, calyx lobes usually 2 larger and 2 smaller, 0.6–1 mm long; **corolla** white, less than 3 mm long. **Fruits** ca. 2 mm long, body of the fruit 0.8–1.2 mm long; **seeds** 0.7–1.2 mm long, 0.3–0.5 mm broad, reticulate, often with longitudinal ridges ($\times 10$) and distinctive transversely elongated pits ($\times 40$), dark reddish brown.

Common weedy plants of open sites in evergreen and partly deciduous forest regions (only rarely collected in deciduous forest areas), from near sea level to 1900 m elevation. Probably flowering and fruiting throughout the year. The species ranges from the southern United States to South America and the West Indies.

Spermacoe prostrata is recognized by the small weedy habit, usual lack of puberulence, often sessile leaves, minute flowers, and small seeds with reticulated surface of distinctive pits. These pits are larger (0.05–0.1 mm) than in *S. exilis* or *S. ovalifolia* and they are transversely oblong ($\times 40$); see Figure 5, upper center. The fruits usually appear to have only two calyx lobes because the two smaller lobes fall off. Many of these specimens were earlier placed under the name *Borreria ocyroides* (Burm.) DC., an Asian species. Compare with *S. exilis*.

Spermacoe scabiosoides (Cham. & Schlechtend.) O. Kuntze, Rev. gen. pl. 3: 123. 1898. *Borreria scabiosoides* Cham. & Schlechtend., Linnaea 3: 318. 1828.

Semiaquatic **herbs**, floating, procumbent or erect, to 1 m tall, distal stems with long (3–10 cm) internodes and few or no lateral branches, leafy stems 1–5 mm thick, glabrous or rarely with slender hairs to 1.5 mm long at the nodes, terete; **stipule** sheaths 3–9 mm long, beginning well below the petiole base, 3–12 mm broad, with 3–7 awns 2–7 mm long. **Leaves** opposite or occasionally pseudoverticillate, petioles 3–10 mm long, with winged lateral margins continuous with the lamina margins; **leaf blades** 2–10 cm long, 3–16 mm broad, linear-lanceolate to narrowly lanceolate or linear-oblong, apex tapering gradually and narrowly acuminate, base tapering gradually and cuneate-decurrent, drying chartaceous, dark above, glabrous or with scabrid hairs, 2° veins 3–4/side. **Inflorescences** terminal or axillary, 3–12 mm long, 8–16 mm broad, capitate or verticillate, subtended by 1–2 pairs of narrow leaves (rarely without leaves and appearing pedunculate), flowers tightly congested and sessile, often few-flowered. **Flowers** ca. 8 mm long, calyx

puberulent distally, lobes 4, 1–2 mm long, 0.2–0.3 mm wide, narrow and acute; **corolla** white, funnellform, puberulent distally on the interior and exterior, tube 3–4 mm long, 1.5–3 mm diam. distally, lobes 1.3–2 mm long, triangular; anthers 1–1.5 mm long. **Fruits** ca. 5 mm long (not including the calyx lobes), ca. 2.5 mm broad distally, obovoid, glabrous in the lower half, splitting from above; **seeds** 2.6–3 mm long, narrow.

Aquatic plants of evergreen or deciduous lowland vegetation. Collected in Santa Rosa National Park (*Liesner* 5261 CR, MO), flowering in February, and growing in persisting water of a lagoon. The species ranges from Costa Rica and Panama to Brazil and Argentina.

Spermacoce scabiosoides is distinguished by its growth in shallow water or wet mud, stipular sheath beginning well below the petiole bases, glabrous vegetative parts (but with slender longer hairs occasionally at the nodes), narrow leaves to 10 cm long, congested flower, and larger corolla and fruits.

Spermacoce suaveolens (G. F. W. Meyer) O. Kuntze, *Rev. gen. pl.* 3: 124. 1898. *Borreria suaveolens* G. F. W. Meyer, *Prim. Fl. Esseq.* 81, pl. 1. 1818. Figure 4.

Herbs from a woody base, usually erect 15–40 (–60) cm tall, branched from the base and often forming dense tufts, distal branches few, leafy stems 0.7–4 mm thick, with 2 or 4 well- or poorly defined longitudinal ridges, puberulent with minute (0.1–0.3 mm) hairs or subglabrous with a few hairs at the nodes; **stipule** sheaths 1–3 mm high, 1–4 mm broad, with 3–7 stiff yellowish awns to 6 mm long. **Leaves** opposite or more often pseudover-ticillate, 1 pair of larger leaves and 2–4 additional pairs of smaller leaves at a node, petioles usually absent; **leaf blades** 6–45 (–60) mm long, 1–3 (–4) mm wide, linear-lanceolate to linear or linear-oblong, apex tapering gradually and acute, base tapering gradually and narrowly cuneate, usually drying stiffly chartaceous, grayish, glabrous above, minutely puberulent beneath, 2° veins 2–3/5. **Inflorescences** terminal (or sometimes axillary and verticillate at the next-to-last node), 4–10 mm high, 8–16 mm broad, dense hemispheric (subglobose) capitula, usually subtended by 4 leaves 1–4 cm long and 1–3 mm broad, often with slender awns among the sessile flowers. **Flowers** with a hypanthium 0.8–1.7 mm long, with thin whitish hairs near the apex, calyx lobes 4 (rarely 3 or 2), 1.4–2 (–2.5) mm long, narrowly triangular and acute at the apex; **corolla** white to pale pink, tube 1.1–2.3 mm long, 0.4–1.1 mm diam., lobes 4, 1–1.5 mm long; anthers 0.8–1.2 mm long. **Fruits** ca. 3 mm long and 1.5 mm diam; **seeds** 1.7–2.2 mm long, 0.6–0.7 mm thick, dark reddish brown with minutely reticulate surfaces.

Plants of savannas and open sites in deciduous and partly deciduous areas of the Pacific slope

(rarely in evergreen formations of the central highlands), 20–1300 m elevation in Costa Rica. It is found around 2000 m elevation on Volcán Baru, Chiriquí, Panama. Flowering is largely in the wet season: May–December. The species ranges from Mexico and the West Indies to southern South America.

Spermacoce suaveolens is recognized by its stiff erect stems usually with four to eight unequal leaves at a node, the rounded terminal inflorescences, the four narrow sepal lobes, and the seeds with reticulate surfaces. Dried specimens may be virtually identical to those of *S. verticillata*; flowers need to be carefully examined to distinguish the two species. Compare this material with *S. capitata* Ruiz & Pav. and *Borreria capitata* (Ruiz & Pav.) DC. of South America.

Spermacoce tenuior L., *Sp. Pl.* 102. 1753. *S. glabra* auct. non Michx., *S. riparia* Cham. & Schlechtend., *Linnaea* 3: 355. 1828. Figure 6.

Perennial **herbs** to 80 cm tall, woody at the base, twigs ascending and with few branches, leafy stems 0.2–2.8 mm thick, with 4 longitudinal smooth or scabrous ridges, glabrous or with a few hairs; **stipule** sheath 0.5–2.5 mm long, with 3–7 awns 1.5–4 mm long. **Leaves** with petioles 3–7 mm long, glabrous; **leaf blades** 3–6 cm long, 3–17 (–21) mm broad, lanceolate to linear-lanceolate or oblong-lanceolate, apex acute to acuminate, base acute, glabrous on both sides but scabrous, 2° veins 3–5/5ide. **Inflorescences** small and axillary, usually verticillate, 5–10 mm broad, with 10–20 flowers, bracts 1.5–3 mm long, filiform. **Flowers** with hypanthium ca. 2.2 mm long and 1 mm diam., calyx lobes 4, 0.5–0.9 (–1.2) mm long, lanceolate to linear-lanceolate, ciliolate only at the base; **corolla** white, rotate, lobes 0.8–1.2 mm long, 0.4 mm broad, longer than the tube; filaments ca. 0.2–0.3 mm long, borne in the middle of the tube, anthers ca. 0.5 mm long, included. **Fruits** 2.5–3 mm long, obovoid or oblong-pyriform, usually glabrous; **seeds** 1.4–2 mm long, 0.7–1 mm broad, dark reddish brown to purplish brown, rounded at both ends, surface, minutely foveolate ($\times 40$) with circular pits at the broader apical end and slightly vertically elongated pits at the basal end, in 10–16 vertical rows and 25–28 transverse rows, sinus more than $\frac{1}{3}$ the width of the seed.

Herbs of open sites, especially along streams and wet depressions, 0–1200 m elevation. Flowering in January–August in Central America. The species ranges from the southeastern United States, the West Indies, Mexico, and Central America through most of South America.

Spermacoce tenuior is recognized by its preference for wet habitats, narrow glabrous leaves (scabrous on the edges), small sessile inflorescences,

little white flowers, and minutely pitted seeds. The fruit splits from the top into an open half releasing the seed and an indehiscent half tightly enclosing the other seed.

Spermacoce vegeta (Standl. & Steyererm.) C. D. Adams, Novon (in press). *Borreria vegeta* Standl. & Steyererm., Publ. Field Mus. Nat. Hist., Bot. Ser. 23: 21. 1943.

Annual **herbs**, erect, 10–30 cm tall, leafy stems 1–5 mm diam., longitudinal ribs obscure in early growth, sparsely to densely puberulent with thin crooked whitish hairs 0.2–0.6 mm long; **stipule** sheath 3–8 mm long, 6–23 mm broad, often marked with reddish spots, with 7–13 subequal awns to 9 mm long. Leaves opposite or more often pseudoverticillate with smaller axillary leaves, petioles 3–10 mm long, with broad lateral margins; **leaf blades** 25–90 mm long, 6–40 mm broad, elliptic-lanceolate to ovate-elliptic or lanceolate, apex tapering gradually and attenuate-acuminate, base abruptly narrowed and obtuse or cuneate, decurrent on the winged petiole, drying chartaceous, grayish green or yellowish green above (paler grayish beneath), glabrous or with short scabrous hairs above, sparsely to densely puberulent with thin whitish hairs 0.2–0.5 mm long beneath, 2° veins 4–7/ side. **Inflorescences** terminal or axillary, hemispheric or verticillate, to 15 mm high and 25 mm broad, subtended by the leaves and enlarged stipular sheath, flowers densely congested. **Flowers** with 4 calyx lobes, 0.5–1.3 mm long, ca. 1 mm broad at the base, ovate or suborbicular to broadly triangular, rounded to obtuse at the apex, ciliolate; **corolla** white, ca. 2.5 mm long, anthers ca. 0.4 mm long. **Fruits** ca. 3 mm long, villose to glabrous; **seeds** 2–2.2 mm long, 0.8–0.9 mm broad, narrowly oblong, with prominent transverse sulci, dark reddish brown.

Plants of open sites in partially deciduous or evergreen areas, from 600 to 900 m elevation in Guatemala and Honduras (1600 m in Chiriquí). Flowering and fruiting occur in the latter part of the wet season: September–January. This species is native to northern Central America and appears to have been introduced in Costa Rica and Panama.

Spermacoce vegeta is distinguished by its erect stature, larger elliptic-lanceolate leaves, larger terminal and axillary inflorescences that are subtended by leaves and expanded stipular sheaths, broad calyx lobes, and seeds with clearly demarcated transverse depressions. It is closely related to *S. assurgens*, but that species is smaller and prostrate to decumbent.

Spermacoce verticillata L., Sp. Pl. 102. 1753. *Borreria verticillata* (L.) G. F. W. Meyer, Prim. Fl. Esseg. 83. 1818. Figure 4.

Erect **herbs**, 15–60(–100) cm tall, perennial from a woody base, branching from the base and with opposite branches along the stems, leafy stems 0.6–4 mm thick, usually with 4 slightly elevated longitudinal ridges, glabrous or minutely (0.1–0.2 mm) puberulent near the nodes; **stipule** sheaths ca. 1 mm long, to 3 mm broad, with 3–5 yellowish awns 1–5 mm long. **Leaves** opposite or pseudoverticillate (4, 6, 8 per node), separated by 2–5 cm along the stem, a well-defined petiole absent; **leaf blades** 1–4 cm long, 0.7–(–8) mm wide, linear to linear-lanceolate, lanceolate or narrowly oblong, apex tapering gradually and acute, base narrowly cuneate, drying stiffly chartaceous to subcoriaceous, grayish with the outer margins becoming involute, glabrous above and below, 2° veins 2–3/ side. **Inflorescences** mostly terminal, a few axillary to distal nodes (rarely more than 2 on a distal stem), 8–14 mm diam., globose to hemispheric capitula, subtended by 2–4 slender leaf-like bracts 1–2 cm long, flowers sessile and densely congested. **Flowers** 2.5–4.5 mm long, hypanthium 0.5–1 mm long, glabrous or sparsely puberulent, calyx lobes 2(–3–4), ca. 1 mm long and 0.2–0.3 mm broad, narrowly clavate and blunt at the apex or acute, often more darkly pigmented distally, lobes often connected at the base by hyaline tissue 0.4 mm high; **corolla** white, salverform, tube 1–3 mm long, ca. 1 mm diam., lobes 0.8–1.4 mm long; anthers 0.5–0.8 mm long. **Fruits** ca. 1.8 mm long (not including the sepal lobes); **seeds** 1.3–1.6 mm long, 0.4–0.6 mm thick, narrowly oblong, dark brown and minutely reticulate.

Weedy plants of the seasonally very dry and deciduous Pacific lowlands, 0–300 m elevation (to 900 m in Honduras). Flowering in the wet season: May–November. The species ranges from the southern United States to southern South America, the West Indies, and the Old World.

Spermacoce verticillata is distinguished by its erect stems with opposite branches and short narrow subsessile verticillate leaves, dense terminal heads, two-lobed calyx, minute corolla, and small reticulate seeds. There may be two minute calyx lobes between the two well-developed lobes. Dried material of this species can be virtually identical to that of the more commonly collected *Spermacoce suaveolens*.

Tocoyena Aublet

REFERENCES—J. D. Dwyer, *Borojoa* and *Tocoyena* (Rubiaceae) in Panama. Phytologia 17: 445–449. 1969. I. Silberbauer-Gottsberger, G. Gottsberger and F. Ehrendorfer, Hybrid speciation and radiation in the Neotropical woody genus *Tocoyena* (Rubiaceae). Pl. Syst. Evol. 181: 143–169. 1992.

Trees or shrubs, stems terete, mostly glabrous; **stipules** interpetiolar, free or connate (intrapetiolar) at the base, narrowly triangular to ovate, usually persisting. **Leaves** opposite or 3/node, petiolate; **leaf blades** entire and pin-

nately veined, drying black or dark brown, stiffly chartaceous to coriaceous. **Inflorescences** terminal or subterminal, corymbose, capitate or cymose, without bracts, flowers sessile to pedicellate. **Flowers** bisexual, radially symmetrical (or curved), large, very fragrant, hypanthium/ovary cylindrical-turbinate to obovoid, calyx lobes 4–6, persisting; **corolla** long, white or cream, salverform to tubular, corolla tube usually with a puberulent mouth, lobes 4–6, convolute in bud; **stamens** 4–6, inserted at the corolla mouth, anthers dorsifixed, 2-lobed at the base, exserted; **ovary** 2-locular, with many horizontal ovules on axile placentation. **Fruits** baccate or hard, globose to ovoid or oblong, pericarp thick and usually coriaceous, 2-locular; **seeds** many, horizontal and somewhat flattened, imbedded in a pulp.

A genus of ca. 18 species, nearly all South American. The very long narrow corolla tubes, flowers closely clustered on a terminal inflorescence, and large solitary fruit with horizontally oriented seeds in a fleshy pulp characterize our species. Despite the numerous flowers within each inflorescence, apparently only one large fruit develops at the tips of fruiting branches.

Tocoyena pittieri (Standl.) Standl., Contr. Arnold Arbor. 5: 151. 1933. *Posoqueria pittieri* Standl., J. Wash. Acad. Sci. 18: 167. 1928. *Tocoyena obliquinervia* (Standl.) Standl., Contr. Arnold Arbor. 5: 152. 1933. *Posoqueria obliquinervia* Standl., J. Wash. Acad. Sci. 18: 167. 1928. *T. cuatrecasii* Steyerf., Acta Biol. Venez. 4: 113. 1964. Figure 30.

Trees, 10–18 m tall, trunk 30–60 cm diam., leafy branchlets 4–12 mm thick, glabrous and drying grayish; **stipules** 7–10 mm long, triangular, acute to acuminate, glabrous, persisting. **Leaves** with petioles (1–)2–4.5 cm long, 1.5–3.5 mm broad, glabrous; **leaf blades** 20–35 cm long, 8–20 cm broad, obovate to obovate-elliptic or broadly elliptic, apex abruptly narrowed or rounded and short-acuminate, tip 5–10 mm long, base gradually narrowed and obtuse or cuneate, drying chartaceous, usually blackish, glabrous above and below or with few minute hairs on the major veins beneath, sometimes with tufted hairs (domatia) in the vein axils beneath, 2° veins 9–13/ side. **Inflorescence** terminal and solitary or 3, 5–17 cm long (including corollas), to 15 cm broad, a dense corymb or panicle with crowded cymose branches, peduncles very short (1–5 mm) beneath the primary branches, glabrous, bracts and bracteoles minute (1–2 mm long) and triangular-acuminate, pedicels 0–5 m long, merging with the hypanthium. **Flowers** glabrous externally and drying blackish, hypanthium 4–5 mm long, oblong-turbinate, calyx tube 2–3 mm long, calyx lobes minute, broadly triangular or rounded and apiculate; **corolla** long-tubular, carnose, yellow, tube 5–8 cm long, 1.5–3 mm diam., lobes 6–12 mm long, 5–7 mm broad, rounded distally and spatulate, imbricate, minutely papillate within. **Fruits** apparently solitary and sessile, ca. 10 cm long and 9 cm

diam., subglobose, the wall thick (8–10 mm dried) and warty lenticellate; **seeds** to 20 mm long, 13–16 mm wide, and 3–4 mm thick, imbedded in a fleshy matrix.

Trees of lowland rain forest or partly deciduous forest formations, from near sea level to 300 m elevation. Immature flowers were collected in March (*Jiménez & Zuniga 814 CR, Tonduz 9528*); mature flowers were collected in April (*Hammel & Bozzoli 16628 CR, F, MO*, and *Q. Jiménez et al. 579 CR, F*). Fruiting in April. The type of *T. obliquinervia* (*Tonduz 9528 US*) was collected from 200 to 250 m elevation along Río Naranjo, San José; the other collections are from the Reserva Biológica Carara and the Golfo Dulce region. The species ranges southward to Colombia.

Tocoyena pittieri is distinguished by the large leaves, long-tubed flowers in crowded inflorescences, and large round fruit with many horizontal seeds in a fleshy pulp. Nearly all parts of the plant (excepting the stems) turn black on drying. At first, it appeared that Standley was correct in separating *T. obliquinervia* as a separate species. However, recently collected material suggests that all our collections are part of the variation to be expected within *T. pittieri*. The fruit requires a year to mature, according to Croat (1978).

Uncaria Schreber

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

Woody **lianas** or clambering shrubs, climbing with the aid of recurved spines (developed from partly formed peduncles), young stems quadrangular or terete, glabrous or puberulent; **stipules** interpetiolar, entire to bifid, usually with colleters at the base within. **Leaves** opposite, decussate, petiolate; **leaf blades** entire and pinnately veined, domatia often present in the vein axils beneath. **Inflorescences** axillary or terminal, flowers in globose capitula, solitary and pedunculate or on open opposite-branched panicles of 3–5 heads, flowers closely congested, sessile or pedicellate and bracteolate. **Flowers** bisexual and monomorphic, radially symmetrical, greenish white to yellowish or orange, hypanthium turbinate, glabrous to densely puberulent, calyx lobes 5; **corolla** salverform or slightly funnelform, puberulent to glabrous externally, lobes 5, valvate in bud; **stamens** 5, filaments short, inserted in the throat of the tube, anthers oblong and sagittate at the base (or sterile and not sagittate), exserted; **ovary** 2-locular, ovules numerous ascending, placentation from the upper part of the septum, stigma capitate. **Fruits** thin-walled capsules, 2-locular, septicidally dehiscent into 2 valves that usually remain united at the base, each valve slightly 2-parted from the top;

seeds many, imbricate, winged at both ends with the lower end deeply bifid.

A genus of 34 species: 2 species are American, 3 species occur in Africa and Madagascar, and 29 species are found in Asia, Australia, and nearby areas. The woody vining habit, paired recurved spines at many nodes, flowers in globose heads and capsular fruits with many imbricate winged seeds distinguish this genus. Only one species is found in Central America. The flowers and capitula are similar to those of *Cephalanthus occidentalis* L., which ranges from southeastern Canada to Guatemala.

***Uncaria tomentosa* (Willd. ex Roem. & Schult.)**

DC., Prodr. 4: 349. 1830. *Nauclea tomentosa* Willd. ex Roem. & Schult., Syst. Veg. 5: 221. 1819. *N. aculeata* H.B.K., Nov. gen. sp. 3: 382 (quarto). 1819, non Willd. 1790. Figure 37.

Vines or woody lianas to 30 m high, 8–25 cm diam. near the ground, leafy stems 2–6 mm thick, minutely appressed-puberulent with pale brownish hairs 0.1–0.4 mm long, quadrangular and becoming terete, hooked thorns to 15(–20) mm long and 6–10 mm broad at the base, recurved; stipules 6–14 mm long, to 9 mm broad at the base, ovate-triangular, minutely puberulent, persisting or deciduous. Leaves usually distichous in a single plane, petioles 8–18 mm long, 1.2–2 mm thick, minutely puberulent; leaf blades 7–15 cm long, 4–9 cm broad, ovate to broadly oblong, apex obtuse to subacuminate, base obtuse to subtruncate or rounded and subcordate, drying stiffly chartaceous, much darker above than below, glabrous and often lustrous above, pale grayish beneath and glabrous or with longer (0.3–0.7 mm) thin ascending hairs, 2° veins 5–8/side, pit domatia sometimes present in the vein axils beneath. Inflorescences axillary, 6–15 cm long, of 3 or 5 spherical heads on an open opposite-branched panicle, heads 15–25 mm diam. at anthesis, peduncles 1.2–4(–7) cm long, to 5 mm thick at the base (and resembling the recurved spines), minutely appressed-puberulent, lateral branches subtended by broadly ovate stipule-like bracts, flowers sessile and tightly clustered, bracteoles obscure. Flowers yellowish white to golden yellow, hypanthium 1–1.5 mm long, obconic, calyx tube ca. 0.5 mm long, calyx lobes 0.2–0.3 mm long and 0.4 mm broad at the base, rounded distally; corolla tubular-salverform, tube 4.5–6 mm long and 0.5–0.9 mm diam., with minute whitish hairs, lobes 1–1.8 mm long, ca. 0.8 mm broad, oblong, glabrous within; anthers sessile on the mouth of the tube, partly exerted, ca. 1.3 mm long; the ellipsoid stigma extended to 4 mm beyond the mouth of the tube. Fruits 7–9 mm long and 4 mm broad, ellipsoid with a short crown of persisting calyx, longitudinally ribbed and puberulent; seeds 3–4 mm long and 0.4 mm broad (including the unequal wings), body of the seed ca. 0.5 mm long.

Plants of evergreen rain forest formations of the

Caribbean lowlands, from 10 to 300 m elevation. Probably flowering primarily in January–April; fruiting in April–September. The species ranges from Guatemala and Belize through Central America to Colombia, Ecuador, and Venezuela.

Uncaria tomentosa is recognized by the climbing habit and thick recurved thorns, the opposite-branched inflorescences of closely compacted sessile flowers in globose heads, the slender corolla tubes, and the small capsules with narrowly winged seeds. These lianas can grow into the canopy to 30 m high (Croat, 1978). The leaves are often whitish below in life. The sharp thorns can easily cause injury and make these plants troublesome weeds (called *rangayo* in Costa Rica).

***Vangueria* Jussieu**

Shrubs or small trees, glabrous or pubescent, usually without spines; stipules interpetiolar, often broad at the base, villous within. Leaves opposite, short-petiolate, blades entire, glabrous or pubescent, domatia absent. Inflorescences axillary, usually arising from older leafless nodes, paniculate or racemose, flowers in distal cymose groups, bracteate. Flowers bisexual, calyx conic to rounded, 5-lobed, usually persisting, glabrous or pubescent; corolla campanulate or salverform, villous in the throat, lobes 5, valvate in bud, often as long as the tube; stamens 5, borne near the apex of the tube, filaments short, anthers oblong to ovate; ovary 5-locular, 1 ovule per locule pendulous from the apex, stigma thick, usually 5-lobed. Fruits drupaceous, usually crowned by the persisting sepal lobes, usually 5-seeded; seeds oblong to subglobose, with bony testa.

A genus of 27 species of tropical Africa and Madagascar. One species is occasionally planted or escaped in the New World tropics.

***Vangueria madagascariensis* J. F. Gmelin, Syst.**

Nat. ed. 13, 2: 367. 1791. *V. edulis* Vahl, Skr.

Naturh.-Selskr. Kjobenhavn 2: 208, t. 7. 1792.

Shrubs or small trees, 5–15 m tall, leafy stems 1.5–5 mm thick, glabrous; stipules 4–7 mm long, ca. 3 mm broad at the base, triangular with narrow acute apex, united for 0.5–1 mm above the petiole. Leaves with petioles 5–16 mm long, ca. 1 mm thick, glabrous; leaf blades 7–20(–28) cm long, 4–10(–15) cm broad, ovate to ovate-elliptic or elliptic, minutely puberulent on the veins above, 2° veins 7–9/side. Inflorescences 3–6 cm long, equally broad, branched near the base, peduncles 2–5 cm long, ca. 1 mm thick, with ascending or curled hairs 0.2–0.5 mm long, pedicels to 4 mm long, minutely pubescent. Flowers with hypanthium 0.5–0.7 mm long, conic, calyx lobes 0.5–1.5 mm long, triangular; corolla pale yellow, usually glabrous, tube 3.5–4 mm long, ca. 2.2 mm diam.,

lobes ca. 2 mm long, becoming reflexed; **stamens** bluish lilac. **Fruits** 2.5–5 cm diam., green to brownish, with 4–5 thick woody pyrenes.

Known from only a single collection in Costa Rica: *Chacón & Chacón 2258* CR, flowering in September near Volcón Cacao at 1000 m elevation in Guanacaste Province. The species, native of Africa, is grown in gardens and called “tamarind of the Indies.”

Warszewiczia Klotzsch

Trees or shrubs; **stipules** interpetiolar, with glandular collectors at the base within, persisting. **Leaves** opposite and decussate or verticillate, petiolate; **leaf blades** large, entire and pinnately veined, domatia rarely present. **Inflorescences** terminal or in the axils of distal leaves, made up of small trichotomous cymes along an elongate racemiform axis, with or without expanded colorful calyx lobes. **Flowers** bisexual and monomorphic, small, hypanthium and calyx tube campanulate to cupulate, calyx lobes 5, 1 of the lobes often expanded into a large colorful leaf-like blade; **corolla** funnelform to salverform, corolla tube villous within, lobes 5, imbricate in bud; **stamens** 5, filaments borne in the throat of the tube, anthers dorsifixed and versatile, sagittate at the base; **ovary** 2-locular, ovules many and horizontal, placenta borne on the septum. **Fruits** woody capsules with septicidal basipetal dehiscence, the 2 valves entire or slightly bifid at the top; **seeds** many, horizontal, with a narrow margin around the edge.

A genus of about six species, ranging from Central America into South America. The genus is represented by a single very distinctive species in Costa Rica. *Warszewiczia coccinea* is perhaps our most colorful native species of Rubiaceae, having long inflorescences with small opposite flower clusters, each with a single brilliant calyx lobe.

Warszewiczia coccinea (Vahl) Klotzsch, Monatsber. Königl. Preuss. Akad. Wiss. Berlin 1853: 497. 1853. *Macrocnemum coccineum* Vahl, Symb. Bot. 2: 38. 1791. *Mussaenda coccinea* (Vahl) Poir. in Lam., Encycl. 4: 394. 1797. *Calycophyllum coccineum* (Vahl) DC., Prodr. 4: 367. 1838. Figure 16.

Shrubs or small trees, 2–10(–15) m tall, leafy branches

3.5–12 mm thick, minutely (0.2 mm) appressed-puberulent and glabrescent, flattened at first but becoming terete; **stipules** 1–4 cm long, 6–12 mm broad at the base, narrowly triangular and acute to acuminate, minutely appressed-puberulent or glabrous distally, slightly (1 mm) united (intrapetiolar) above the petioles. **Leaves** 2 or 3/node, petioles (5–)12–25(–50) mm long, 2–4.5 mm thick, minutely appressed-puberulent; **leaf blades** (15–)20–36(–60) cm long, 7–15(–23) cm broad, elliptic to elliptic-oblong or elliptic-obovate, apex obtuse to acuminate, base gradually narrowed and obtuse or acute, slightly decurrent on the petiole, drying chartaceous, dark brown, glabrous and slightly lustrous above, with short (0.3 mm) thin appressed hairs beneath, 2° veins 13–20/side. **Inflorescences** terminal or axillary, 20–80 cm long, racemiform, primary peduncles to 10 cm long and ca. 4 mm thick, appressed-puberulent, the broad cymose flower clusters 1–5 cm distant and opposite or subopposite along the central rachis, to 2 cm long on short (4–15 mm) lateral peduncles, subtended by broad-based bracts to 10 mm long, mostly glabrous and drying black, each flower cluster with 5–30 flowers and 1 greatly enlarged red sepal lobe, the enlarged sepal lobes with slender petiole-like stipes 12–38 mm long and blades 3–10 cm long and 1–4 cm broad, ellipsoid to rhombic, flowers mostly sessile. **Flowers** with hypanthium 1–2 mm long, obconic and densely sericeous with ascending yellowish hairs, calyx tube ca. 1 mm long, calyx lobes 0.3–1 mm long and 1–1.3 mm broad, rounded distally, glabrous (1 lobe per lateral inflorescence branch greatly expanded; see above); **corolla** yellow-orange or orange and red, tube 3–5 mm long, 1.5–2 mm diam., glabrous externally except for 4 longitudinal lines of appressed hairs, lobes 2–4 mm long and 1.5 mm broad, acute, anthers 1.5–2 mm long. **Fruits** 3–5 mm long, 3–4 mm diam., obconic to subglobose, appressed-puberulent; **seeds** 0.2–0.5 mm long.

Plants of evergreen lowland rain forest formations, from 10 to 300 m elevation. Growing in forest light-gaps, forest edges, and secondary growth. Flowering throughout the year, but the principal flowering period appears to be in April–September. The species ranges from southern Nicaragua to Peru and Bolivia.

Warszewiczia coccinea is readily identified by its brilliant and elongate racemiform inflorescences with each opposing flower cluster bearing a single brilliant crimson leaf-like calyx lobe. Distal branches often bear three inflorescences: a terminal one and two laterals. This is one of Costa Rica's most showy trees, but it is not common. Breeding biology was studied by Bawa and Beach (1983). Also referred to as *bandera*, *curcero*, *guna*, and *sangrenaria*.

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List of Accepted Species

Key: ! = new species (15); # = new combinations or new names (12); CR = endemic to continental Costa Rica (68); (*) = endemic to Cocos Island; ** = endemic to Costa Rica and western Panama (21); CULT = introduced ornamental and useful species (11); (N) = in adjacent Nicaragua, not recorded for Costa Rica; (P) = in adjacent Panama, not recorded for Costa Rica. Total = 406 species in 84 genera.

<i>Alibertia edulis</i>	<i>Crusea hispida</i>	<i>Guettarda combsii</i> (N)
<i>Alibertia garapatica</i>	<i>Crusea longiflora</i>	<i>Guettarda conferta</i>
<i>Allenanthus erythrocarpa</i>	<i>Crusea parviflora</i>	<i>Guettarda crispiflora</i>
<i>Alseis</i> sp. aff. <i>A. hondurensis</i> CR		<i>Guettarda foliacea</i>
<i>Amaioua corymbosa</i>	<i>Declieuxia fruticosa</i>	<i>Guettarda macrosperma</i>
<i>Amaioua pedicellata</i>	<i>Deppea grandiflora</i>	<i>Guettarda poasana</i> CR
<i>Amphidasya ambigua</i>	<i>Didymaea alsinoides</i>	<i>Guettarda sanblasensis</i>
<i>Appunia guatemalensis</i>	<i>Diodia apiculata</i>	<i>Guettarda tournefortiopsis</i>
<i>Arcytophyllum lavarum</i> **	<i>Diodia brasiliensis</i>	<i>Guettarda turrialbana</i> CR
<i>Arcytophyllum muticum</i>	<i>Diodia sarmentosa</i>	
	<i>Diodia serrulata</i>	<i>Hamelia axillaris</i>
<i>Bathysa veraguensis</i>	<i>Diodia teres</i>	<i>Hamelia calycosa</i> (P)
<i>Bertiera angustifolia</i>	<i>Duroia costaricensis</i>	<i>Hamelia macrantha</i>
<i>Bertiera guianensis</i>	<i>Duroia utleyorum</i> CR!	<i>Hamelia magnifolia</i> **
<i>Borojoa atlantica</i>		<i>Hamelia patens</i>
<i>Borojoa panamensis</i> (sensu lato)	<i>Elaeagia auriculata</i>	<i>Hamelia rovirosae</i>
<i>Bouvardia glabra</i> CULT	<i>Elaeagia myriantha</i>	<i>Hamelia xerocarpa</i>
	<i>Elaeagia nitidifolia</i>	<i>Hillia allenii</i>
<i>Calycophyllum candidissimum</i>	<i>Elaeagia uxpanapensis</i>	<i>Hillia grayumii</i> CR
<i>Chimarrhis latifolia</i> **	<i>Exostema caribaeum</i>	<i>Hillia longifilamentosa</i> **
<i>Chimarrhis parviflora</i>	<i>Exostema mexicanum</i>	<i>Hillia loranthoides</i>
<i>Chiococca alba</i>		<i>Hillia macrophylla</i>
<i>Chiococca pachyphylla</i>	<i>Faramaea capulifolia</i> **!	<i>Hillia maxonii</i>
<i>Chiococca phaenostemon</i>	<i>Faramaea eurycarpa</i>	<i>Hillia panamensis</i>
<i>Chiococca semipilosa</i>	<i>Faramaea hondurae</i>	<i>Hillia triflora</i>
<i>Chione sylvicola</i>	<i>Faramaea multiflora</i>	<i>Hippotis albiflora</i>
<i>Chomelia microloba</i>	<i>Faramaea myrticifolia</i> CR!	<i>Hoffmannia aeruginosa</i>
<i>Chomelia recordii</i>	<i>Faramaea occidentalis</i>	<i>Hoffmannia amplexifolia</i>
<i>Chomelia spinosa</i>	<i>Faramaea ovalis</i>	<i>Hoffmannia arborescens</i> CR
<i>Chomelia venulosa</i> CR!	<i>Faramaea parvibractea</i>	<i>Hoffmannia areolata</i> **
<i>Chomelia</i> sp. A, aff. <i>C. spinosa</i>	<i>Faramaea pauciflora</i>	<i>Hoffmannia asclepiadea</i>
<i>Cinchona pubescens</i>	<i>Faramaea scalaris</i> (P)	<i>Hoffmannia bullata</i>
<i>Coccocypselum cordifolium</i>	<i>Faramaea stenura</i> CR	<i>Hoffmannia congesta</i> #
<i>Coccocypselum guianense</i>	<i>Faramaea suerensis</i>	<i>Hoffmannia davidsoniae</i> **
<i>Coccocypselum herbaceum</i>	<i>Faramaea trinervia</i> **	<i>Hoffmannia decurrens</i> CR
<i>Coccocypselum hirsutum</i>	<i>Ferdinandusa panamensis</i> **	<i>Hoffmannia dotae</i> **
<i>Coccocypselum lanceolatum</i>		<i>Hoffmannia hamelioides</i> CR
<i>Coffea arabica</i> CULT	<i>Galium aschenbornii</i>	<i>Hoffmannia hammelii</i> CR!
<i>Coffea liberica</i> CULT	<i>Galium hypocarpium</i>	<i>Hoffmannia inamoena</i> CR
<i>Condaminea corymbosa</i>	<i>Galium mexicanum</i>	<i>Hoffmannia laxa</i>
<i>Cosmibuena grandiflora</i>	<i>Galium orizabense</i>	<i>Hoffmannia leucocarpa</i> CR
<i>Cosmibuena macrocarpa</i>	<i>Galium uncinulatum</i>	<i>Hoffmannia liesneriana</i> CR
<i>Cosmibuena valerii</i>	<i>Gardenia augusta</i> CULT	<i>Hoffmannia longipetiolata</i>
<i>Coussarea austin-smithii</i> CR	<i>Genipa americana</i>	<i>Hoffmannia nesioti</i> (*)
<i>Coussarea caroliniana</i> CR	<i>Genipa williamsii</i>	<i>Hoffmannia pallidiflora</i>
<i>Coussarea chiriquiensis</i> **#	<i>Geophila cordifolia</i>	<i>Hoffmannia piratarum</i> (*)
<i>Coussarea enneantha</i>	<i>Geophila gracilis</i> (P)	<i>Hoffmannia pittieri</i> **
<i>Coussarea hondensis</i>	<i>Geophila macropoda</i>	<i>Hoffmannia psychotriifolia</i>
<i>Coussarea impetiolaris</i> CR	<i>Geophila repens</i>	<i>Hoffmannia subauriculata</i>
<i>Coussarea latifolia</i>	<i>Gonzalagunia bracteosa</i> CR	<i>Hoffmannia valerii</i>
<i>Coussarea nebulosa</i>	<i>Gonzalagunia brenesii</i>	<i>Hoffmannia vesiculifera</i>
<i>Coussarea nigrescens</i> (P)	<i>Gonzalagunia ovatifolia</i>	
<i>Coussarea psychotrioides</i> CR	<i>Gonzalagunia panamensis</i>	<i>Isertia haenkeana</i>
<i>Coussarea talamancana</i> **	<i>Gonzalagunia rosea</i>	<i>Isertia laevis</i>
<i>Coussarea</i> sp. A, aff. <i>C. curvigemma</i>	<i>Gonzalagunia rudis</i>	<i>Ixora coccinea</i> CULT
<i>Coussarea</i> sp. B, aff. <i>C. curvigemma</i>	<i>Gonzalagunia stenostachya</i> CR#	<i>Ixora finlaysonianae</i> CULT
<i>Coutarea hexandra</i>	<i>Guettarda brenesii</i> CR	<i>Ixora floribunda</i>
<i>Crusea coccinea</i>		<i>Ixora nicaraguensis</i>

Ladenbergia brenesii CR
Ladenbergia sericophylla CR
Ladenbergia valerii CR
Lasianthus panamensis
Lindenia rivalis

Machaonia acuminata (P)
Machaonia martinicensis
Macrocnemum glabrescens
Malanea colombiana
Manettia barbata
Manettia flexilis
Manettia reclinata
Mitracarpus hirtus
Morinda citrifolia
Morinda panamensis
Morinda royoc (N)
Mussaenda erythrophylla CULT

Neolamarckia cadamba CULT
Nertera granadensis

Oldenlandia callitrichoides
Oldenlandia corymbosa
Oldenlandia herbacea
Oldenlandia lancifolia
Osa pulchra CR

Palicourea adusta CR
Palicourea albocaerulea CR
Palicourea angustifolia
Palicourea bella
Palicourea bellula CR
Palicourea brenesii CR
Palicourea copensis
Palicourea crocea
Palicourea discolor **
Palicourea garciae
Palicourea guianensis
Palicourea hammelii
Palicourea lancifera CR
Palicourea lasiorrhachis
Palicourea macrocalyx CR
Palicourea montivaga CR
Palicourea orosiana CR
Palicourea padifolia
Palicourea purpurea **
Palicourea salicifolia CR
Palicourea skotakii CR
Palicourea spathacea CR
Palicourea standleyana
Palicourea tilaranensis CR
Palicourea triphylla
Palicourea vestita
Pentagonia costaricensis ***
Pentagonia donnell-smithii
Pentagonia gymnopoda
Pentagonia hirsuta CR
Pentagonia macrophylla
Pentagonia tinajita
Pentagonia wendlandii
Pentas lanceolata CULT
Pentodon pentandrus
Pogonopus speciosus
Posoqueria coriacea
Posoqueria grandiflora CR

Posoqueria latifolia
Psychotria acicularis CR!
Psychotria acuminata
Psychotria aggregata
Psychotria alfaroana **
Psychotria allenii **
Psychotria angustiflora
Psychotria aubletiana
Psychotria aurantibractea CR#
Psychotria berteriana
Psychotria boquetensis
Psychotria borucana #
Psychotria brachiata
Psychotria brachybotrya
Psychotria calochlamys
Psychotria camponutans
Psychotria capacifolia
Psychotria capitata (N)
Psychotria cartagoensis CR
Psychotria carthagenensis
Psychotria chagensis
Psychotria chiapensis
Psychotria chiriquiensis ***
Psychotria chiriquina **
Psychotria chitariana CR
Psychotria cincta
Psychotria clivorum
Psychotria cocosensis (*)
Psychotria cooperi
Psychotria correae #
Psychotria deflexa
Psychotria dichroa #
Psychotria domingensis
Psychotria dukei
Psychotria elata
Psychotria emetica
Psychotria erecta
Psychotria eurycarpa CR
Psychotria fruticetorum
Psychotria glomerulata
Psychotria goldmanii
Psychotria graciliflora
Psychotria grandis
Psychotria guadalupensis
Psychotria guapilensis
Psychotria haematocarpa
Psychotria hazenii
Psychotria hebeclada
Psychotria hoffmannseggiana
Psychotria horizontalis
Psychotria insignis (?)
Psychotria ipecacuanha
Psychotria jimenezii CR
Psychotria lamarinensis CR
Psychotria laselvensis CR
Psychotria limonensis
Psychotria longipedunculoides #
Psychotria luxurians
Psychotria macrophylla
Psychotria marginata
Psychotria maxonii
Psychotria mexiae
Psychotria micrantha
Psychotria microbotrys
Psychotria microdon
Psychotria monteверdensis CR

Psychotria mortoniana **
Psychotria neillii
Psychotria nervosa
Psychotria officinalis
Psychotria orosiana
Psychotria panamensis
Psychotria parvifolia
Psychotria phanaerandra
Psychotria pilosa
Psychotria pithecobia
Psychotria pittieri
Psychotria platypoda
Psychotria poeppigiana
Psychotria polyphlebia
Psychotria psychotriifolia
Psychotria pubescens
Psychotria quinqueradiata
Psychotria racemosa
Psychotria remota
Psychotria rosulatifolia
Psychotria sarapiquensis
Psychotria siggersiana
Psychotria sixaolensis **
Psychotria solitudinum
Psychotria steyermarkii
Psychotria stockwellii **
Psychotria suerensis
Psychotria sylvivaga **
Psychotria tapantiensis CR!
Psychotria tenuifolia
Psychotria turubarensis CR
Psychotria uliginosa
Psychotria umbelliformis
Psychotria valeriana CR
Psychotria viridis
Psychotria sp. A (Cocos Island, in-det.)
Psychotria sp. B, aff. *P. papantlense*

Randia aculeata
Randia altiscandens #
Randia armata
Randia brenesii
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Families of seed plants known or expected to occur in Costa Rica and adjacent areas numbered according to the sequence of Engler's *Syllabus der Pflanzenfamilien*, edition 11, reworked by L. Diels (1936).

1	Cycadaceae	71	Nymphaeaceae	140	Quinaceae
2	Taxaceae	72	Ceratophyllaceae	141	Theaceae
3	Podocarpaceae	73	Ranunculaceae	142	Guttiferae
4	Araucariaceae	74	Berberidaceae		incl. Hypericaceae
5	Pinaceae	75	Menispermaceae	143	Elatinaceae
6	Cupressaceae	76	Magnoliaceae	144	Cistaceae
7	Gnetaceae	77	Annonaceae	145	Bixaceae
8	Typhaceae	78	Myristicaceae	146	Cochlospermaceae
9	Potamogetonaceae	79	Monimiaceae	147	Violaceae
10	Najadaceae	80	Lauraceae	148	Flacourtiaceae
11	Alismataceae	81	Hernandiaceae	149	Turneraceae
12	Butomaceae	82	Papaveraceae	150	Passifloraceae
13	Hydrocharitaceae		incl. Fumariaceae	151	Caricaceae
14	Triuridaceae	83	Capparidaceae	152	Loasaceae
15	Gramineae	84	Cruciferae	153	Begoniaceae
16	Cyperaceae	85	Tovariaceae	154	Cactaceae
17	Palmae	86	Resedaceae	155	Thymelaeaceae
18	Cyclanthaceae	87	Moringaceae	156	Elaeagnaceae
19	Araceae	88	Droseraceae	157	Lythraceae
20	Lemnaceae	89	Crassulaceae	158	Punicaceae
21	Mayacaceae	90	Saxifragaceae	159	Lecythidaceae
22	Xyridaceae	91	Brunelliaceae	160	Rhizophoraceae
23	Eriocaulaceae	92	Cunoniaceae	161	Combretaceae
24	Bromeliaceae	93	Hamamelidaceae	162	Myrtaceae
25	Commelinaceae	94	Rosaceae	163	Melastomataceae
26	Pontederiaceae	95	Connaraceae	164	Onagraceae
27	Juncaceae	96	Leguminosae	165	Haloragaceae
28	Liliaceae	97	Krameriaceae	166	Araliaceae
29	Haemodoraceae	98	Oxalidaceae	167	Umbelliferae
30	Amaryllidaceae	99	Geraniaceae	168	Cornaceae
31	Velloziaceae	100	Tropaeolaceae	169	Clethraceae
32	Dioscoreaceae	101	Linaceae	170	Monotropaceae
33	Iridaceae		incl. Huminiaceae	171	Pyrolaceae
34	Musaceae	102	Erythroxylaceae	172	Ericaceae
35	Zingiberaceae	103	Zygophyllaceae	173	Theophrastaceae
36	Cannaceae	104	Rutaceae	174	Myrsinaceae
37	Marantaceae	105	Simarubaceae	175	Primulaceae
38	Burmanniaceae	106	Burseraceae	176	Plumbaginaceae
39	Orchidaceae	107	Meliaceae	177	Sapotaceae
40	Casuarinaceae	108	Malpighiaceae	178	Ebenaceae
41	Piperaceae	109	Trigoniaceae	179	Symplocaceae
42	Chloranthaceae	110	Vochysiaceae	180	Styracaceae
43	Laciniaceae	111	Polygalaceae	181	Oleaceae
44	Salicaceae	112	Dichapetalaceae	182	Loganiaceae
45	Garryaceae	113	Euphorbiaceae	183	Gentianaceae
46	Myricaceae	114	Callitrichaceae	184	Apocynaceae
47	Juglandaceae	115	Buxaceae	185	Asclepiadaceae
48	Batidaceae	116	Coriariaceae	186	Convolvulaceae
49	Betulaceae	117	Anacardiaceae	187	Polemoniaceae
50	Fagaceae	118	Cyrillaceae	188	Hydrophyllaceae
51	Ulmaceae	119	Aquifoliaceae	189	Boraginaceae
52	Moraceae	120	Celastraceae	190	Verbenaceae
53	Urticaceae	121	Hippocrateaceae	191	Labiatae
54	Podostemonaceae	122	Staphyleaceae	192	Solanaceae
55	Proteaceae	123	Icacinaceae	193	Scrophulariaceae
56	Olaceae	124	Hippocastanaceae	194	Bignoniaceae
57	Opiliaceae	125	Sapindaceae	195	Pedaliaceae
58	Loranthaceae	126	Sabiaceae	196	Martyniaceae
59	Aristolochiaceae	127	Balsaminaceae	197	Orobanchaceae
60a	Hydnoraceae	128	Rhamnaceae	198	Gesneriaceae
60b	Rafflesiaceae	129	Vitaceae	199	Lentibulariaceae
61	Balanophoraceae	130	Elaeocarpaceae	200	Acanthaceae
62	Polygonaceae	131	Tiliaceae	201	Plantaginaceae
63	Chenopodiaceae	132	Malvaceae	202	Rubiaceae
64	Amaranthaceae	133	Bombacaceae	203	Caprifoliaceae
65	Nyctaginaceae	134	Sterculiaceae	204	Valerianaceae
66	Phytolaccaceae	135	Dilleniaceae	205	Dipsacaceae
67	Aizoaceae	136	Actinidiaceae	206	Cucurbitaceae
68	Portulacaceae	137	Ochnaceae	207	Campanulaceae
69	Basellaceae	138	Caryocaraceae	208	Compositae
70	Caryophyllaceae	139	Marograviaceae		



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