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NEW SERIES NO. 33

FLORA COSTARICENSIS

William Burger, Editor

Family #202 Rubiaceae

William Burger

Charlotte M. Taylor

December 30, 1993

Publication 1454

PUBLISHED BY FIELD MUSEUM OF NATURAL HISTORY

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William Burger

*Curator
Department of Botany
Field Museum of Natural History
Chicago, Illinois 60605-2496*

Charlotte M. Taylor

*Missouri Botanical Garden
St. Louis, Missouri 63166-0299*

Accepted April 16, 1993

Published December 30, 1993

Publication 1454

BIOLOGY LIBRARY
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JUN 23 1994

PUBLISHED BY FIELD MUSEUM OF NATURAL HISTORY

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Library of Congress Catalog Card Number: 93-73814

ISSN 0015-0746

PRINTED IN THE UNITED STATES OF AMERICA

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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.

Acknowledgments

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 (Spermacoaceae), 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 Spermacoaceae), nearly always pinnately veined (palmately veined in some weedy Spermacoaceae), 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 panicle 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 or 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. Spermaceae
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 *Schradera*
- 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 cincinnoid *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 *Duroioa*
- 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*
- 1b. Shrubs or trees, stems not slender and clambering 2
- 2a. Anthers dimorphic or trimorphic *Ferdinandusa*
- 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 sessile] *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 exerted; 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. NAUCLEAEAE

- 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 carnosy; 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 involucrate *Galium*
- 2b. Rare introduced procumbent herbs; flowers 4–10 and subsessile in distal involucrate 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

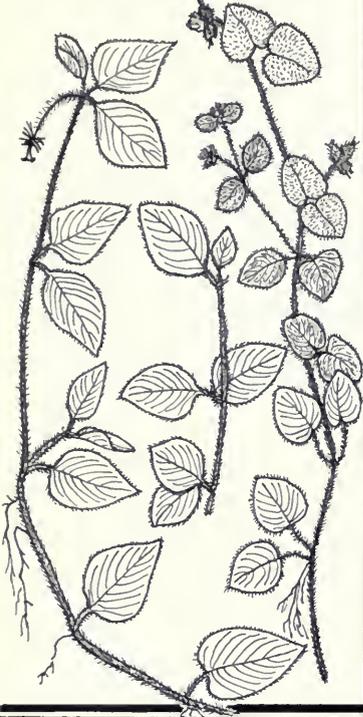
38a.	Expanded calyx lobes densely pubescent, dull red (white in some forms); cultivated (<i>Mussaenda</i>)	Fig. 16
38b.	Expanded sepals glabrous to glabrescent; calyx lobes white or red; native and also planted for ornament	39
39a.	Corolla tube 3 mm long, white (<i>Calycophyllum</i>)	Fig. 16
39b.	Corolla 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>Guettarda 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>Sommerera</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>Sommerera</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 arenchymatous 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 spatheaceous 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 <i>Psychotria</i>)	90
89a.	<i>Heteropsychotria</i> : large-leaved and pubescent	Fig. 54
89b.	<i>Heteropsychotria</i> : smaller-leaved species	Fig. 55
89c.	<i>Heteropsychotria</i> : smaller inflorescences	Fig. 56
89d.	<i>Heteropsychotria</i> : large open inflorescences	Fig. 57
89e.	<i>Heteropsychotria</i> : conspicuous inflorescences	Fig. 58
89f.	<i>Heteropsychotria</i> : deciduous and other species	Fig. 59
90a.	Subg. <i>Psychotria</i> : species with very small leaves	Fig. 60
90b.	Subg. <i>Psychotria</i> : species with small leaves	Fig. 61
90c.	Subg. <i>Psychotria</i> : species with <i>Ficus</i> -like stipules	Fig. 62
90d.	Subg. <i>Psychotria</i> : species with dense pubescence	Fig. 63
90e.	Subg. <i>Psychotria</i> : species with larger leaves	Fig. 64
90f.	Subg. <i>Psychotria</i> : deciduous and unusual species	Fig. 65
90g.	Subg. <i>Psychotria</i> : miscellaneous unusual species	Fig. 66

Coccocypselum hirsutum



C. cordifolium



Coccocypselum lanceolatum



Geophila repens



G. cordifolia



Geophila macropoda

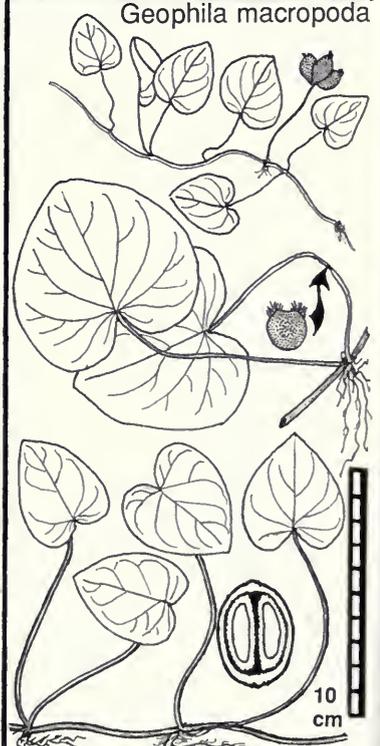


FIG. 2. Twining herbs: species of *Coccocypselum* and *Geophila*.

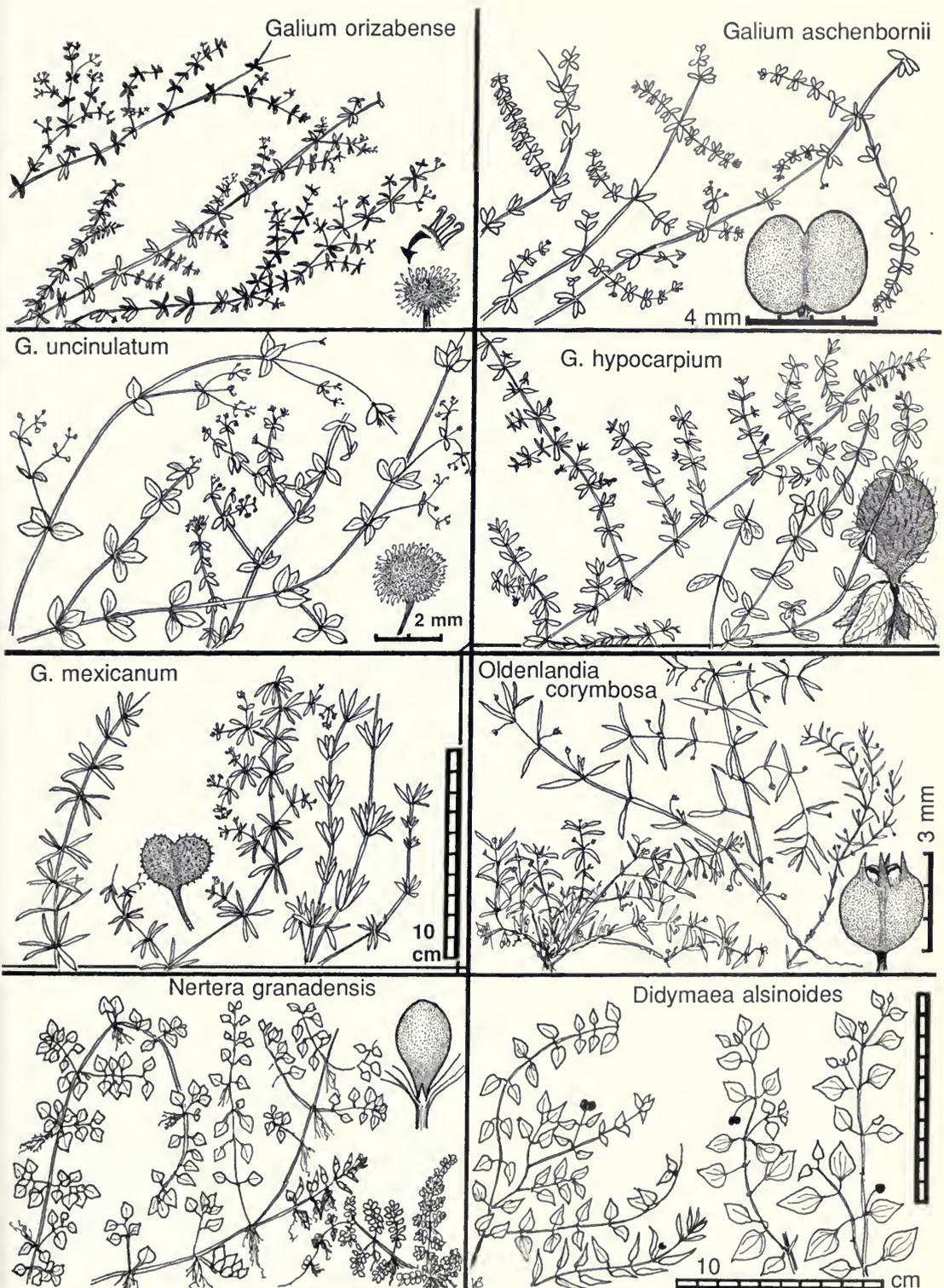


FIG. 3. Herbs with small leaves and slender stems: species of *Didymaea*, *Galium*, *Nertera*, and *Oldenlandia*.



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

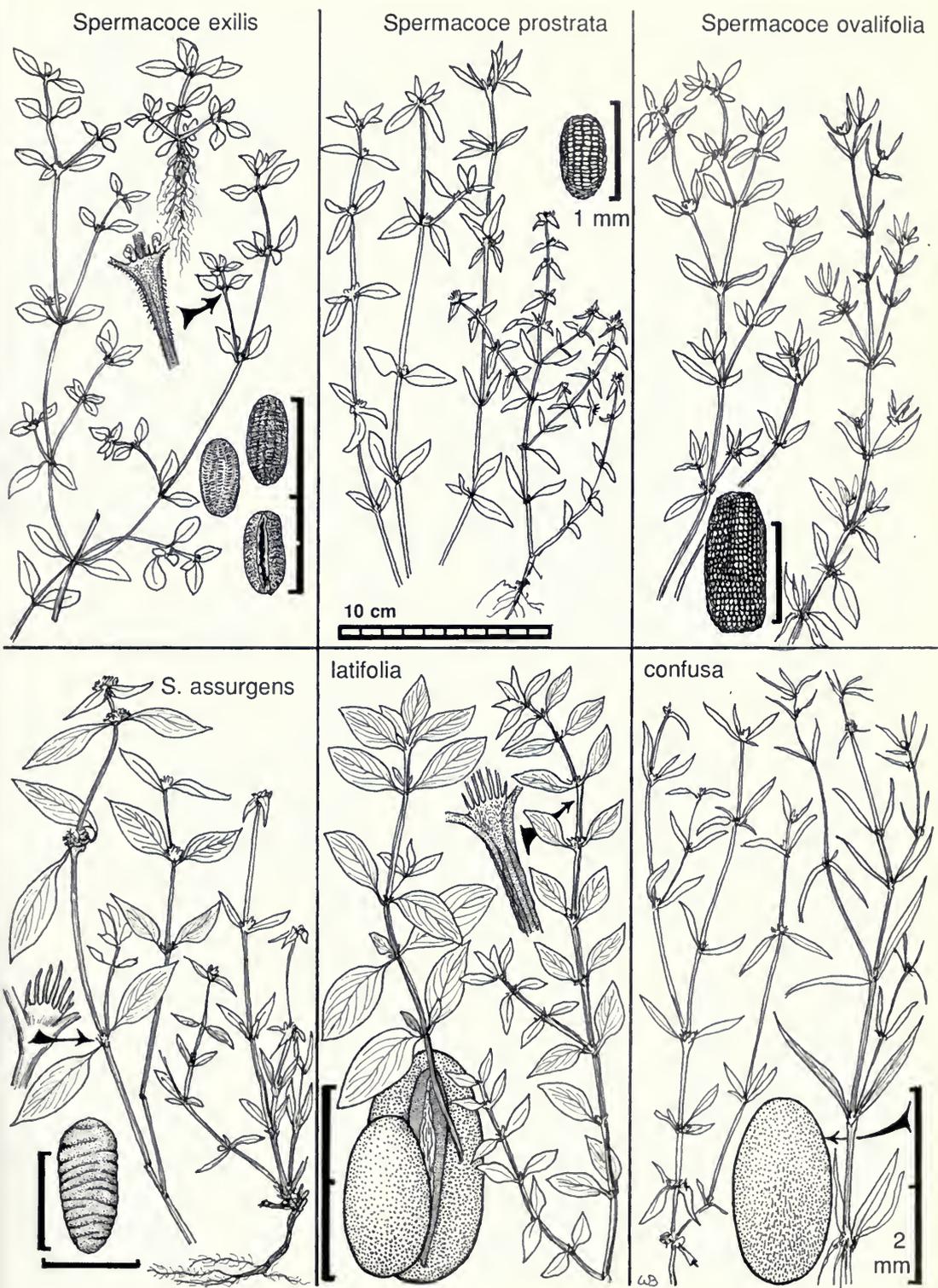


FIG. 5. Erect herbs with narrow lanceolate leaves: *Spermacoce* spp.

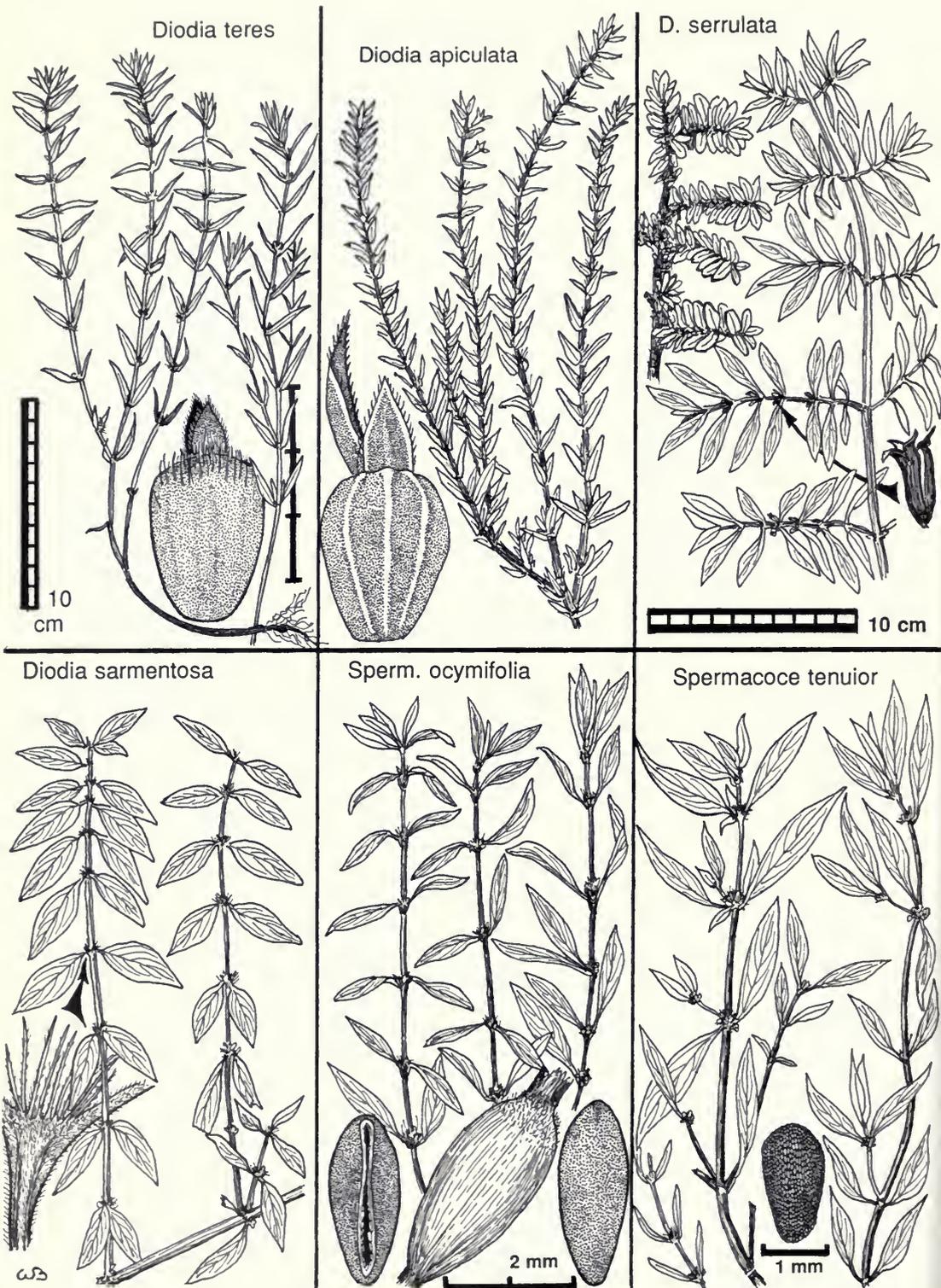
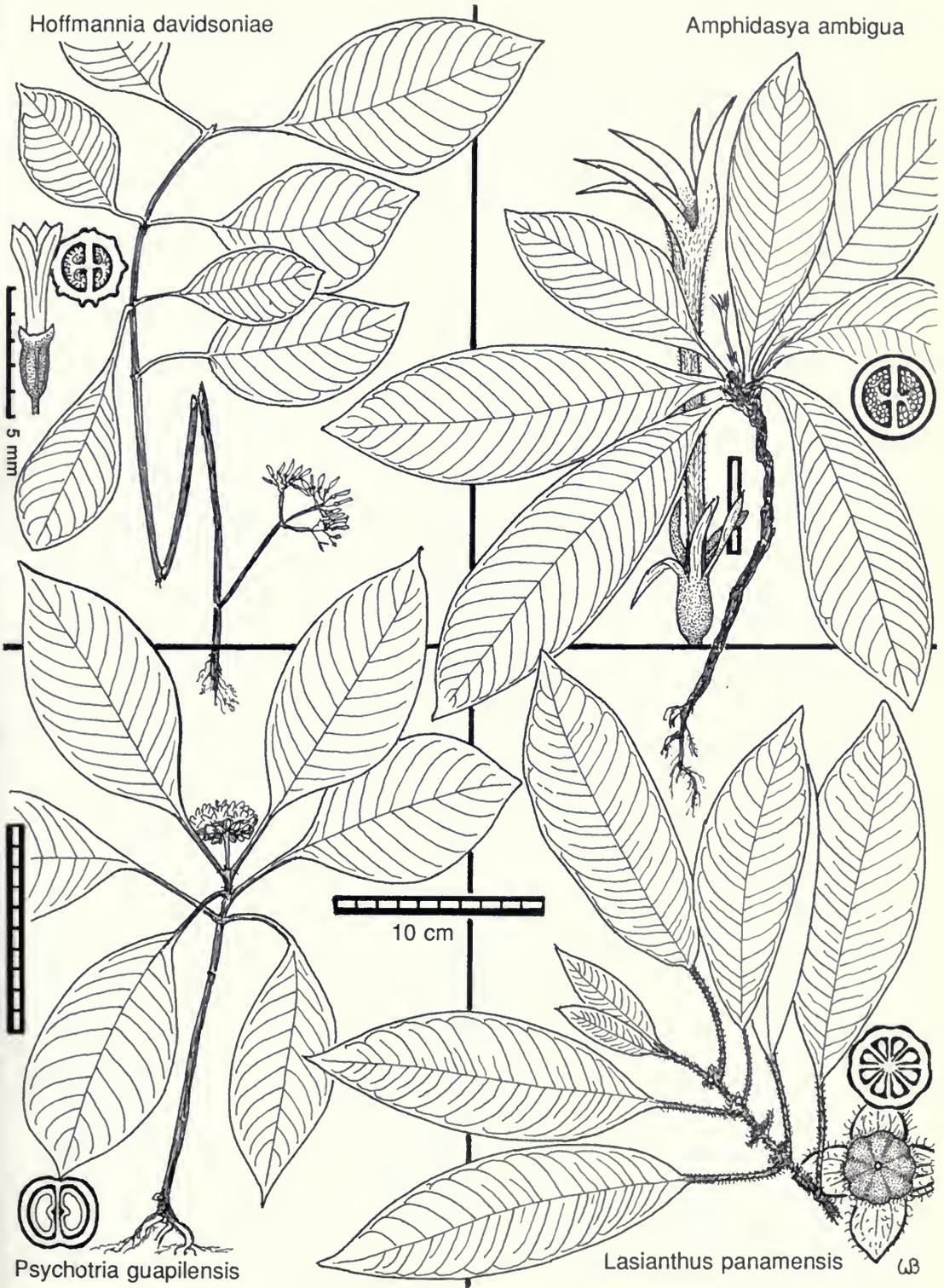


FIG. 6. Erect herbs with narrow lanceolate leaves: *Diodia* spp. and two species of *Spermacoe*.

Hoffmannia davidsoniae

Amphidasya ambigua



Psychotria guapilensis

Lasianthus panamensis ♂

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*.

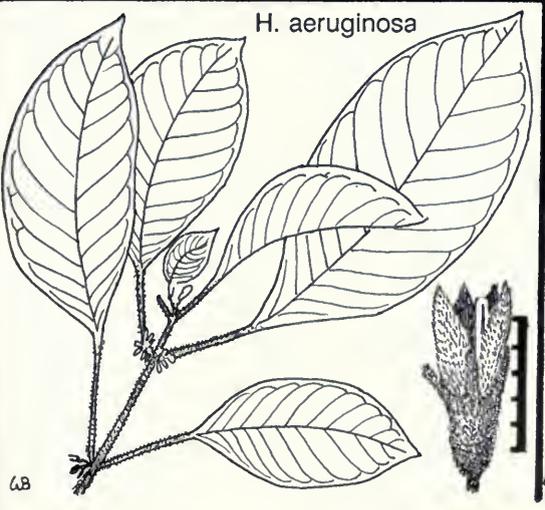
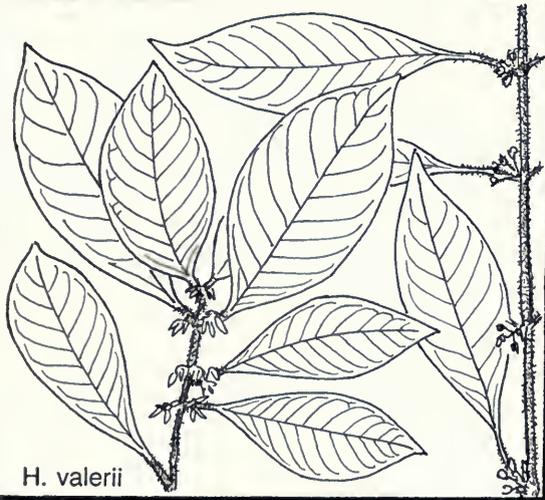
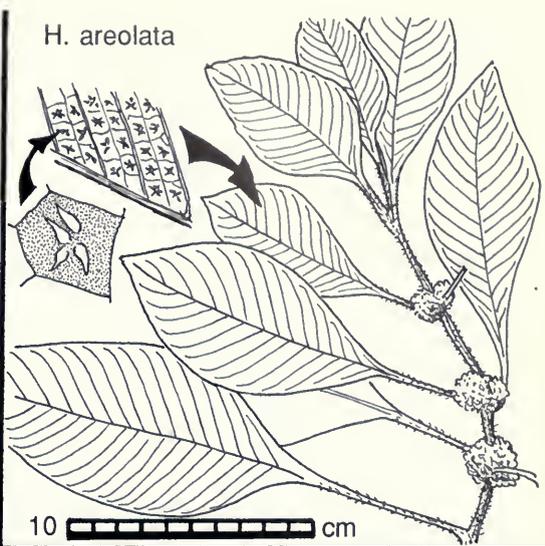
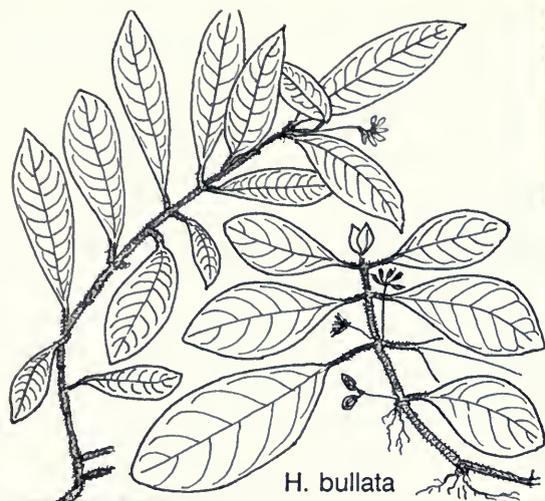


FIG. 9. Herbs or subshrubs with axillary flowers: pubescent species of *Hoffmannia* and *H. congesta*.



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

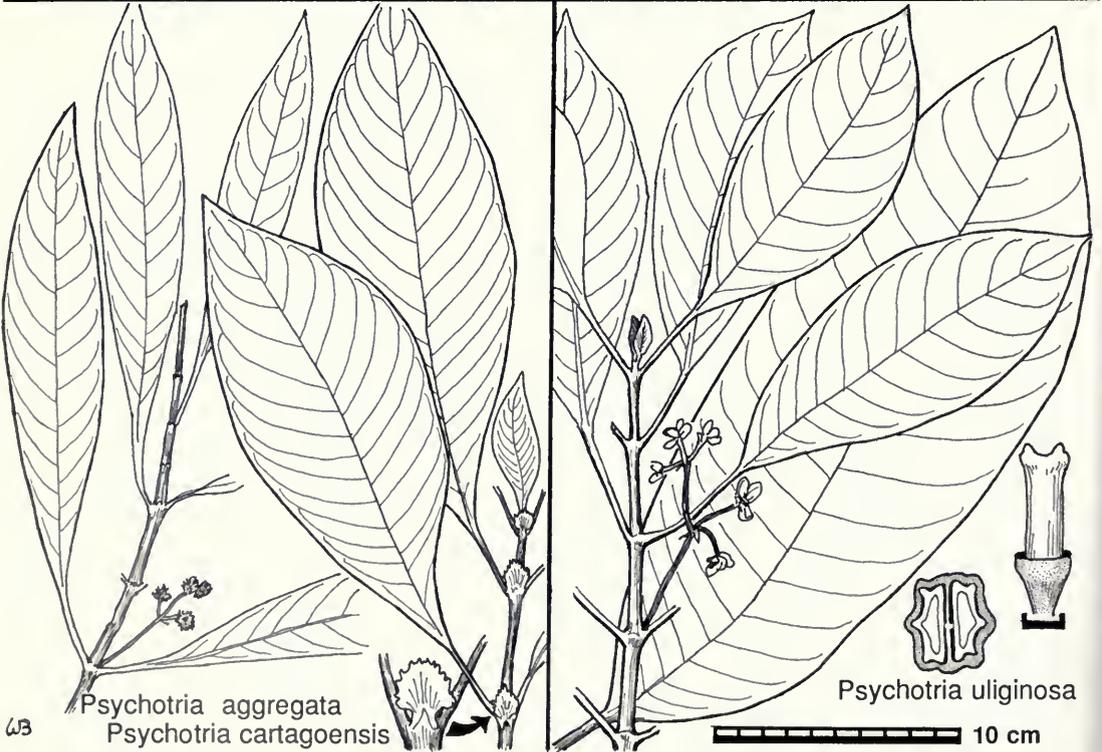


FIG. 12. Subshrubs with axillary flowers: species of *Psychotria*.



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

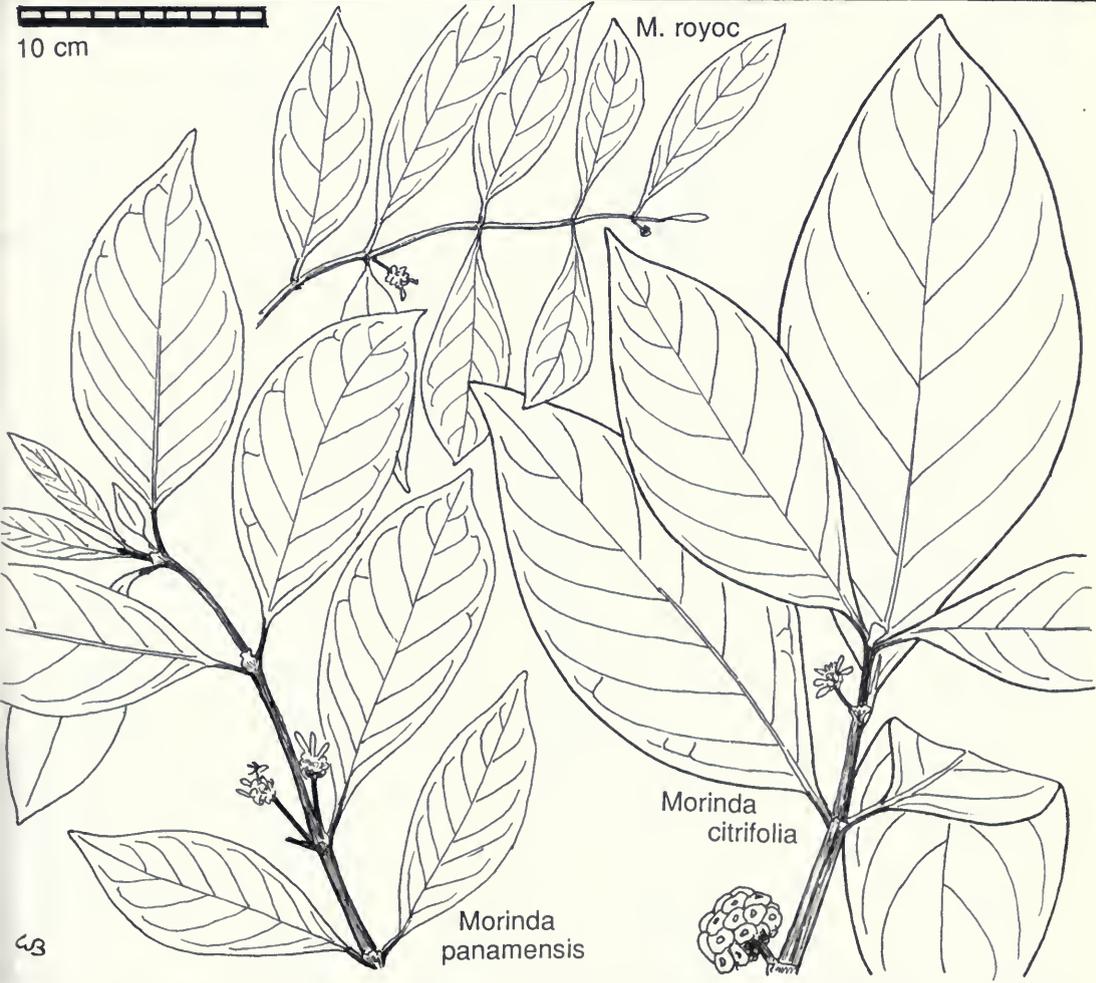


Schradera costaricensis



10 cm

M. royoc



Morinda panamensis

Morinda citrifolia

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*.

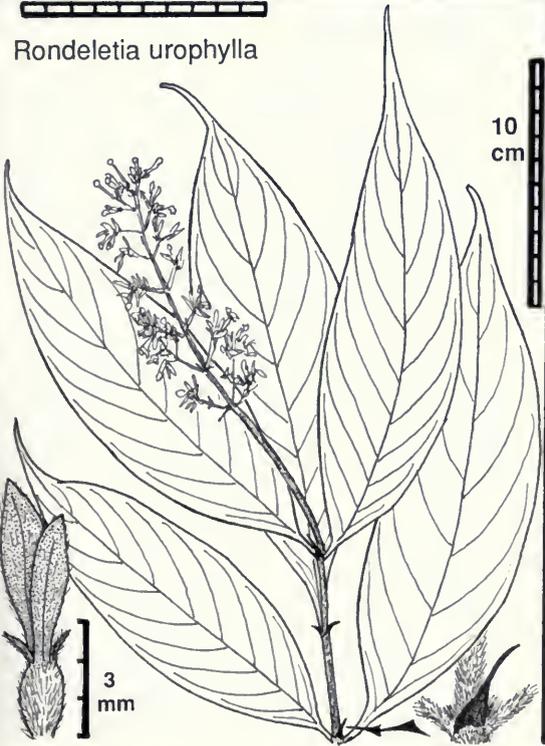
Rondeletia brenesii



Rondeletia buddleoides



Rondeletia urophylla



Gonzalagunia bracteosa



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

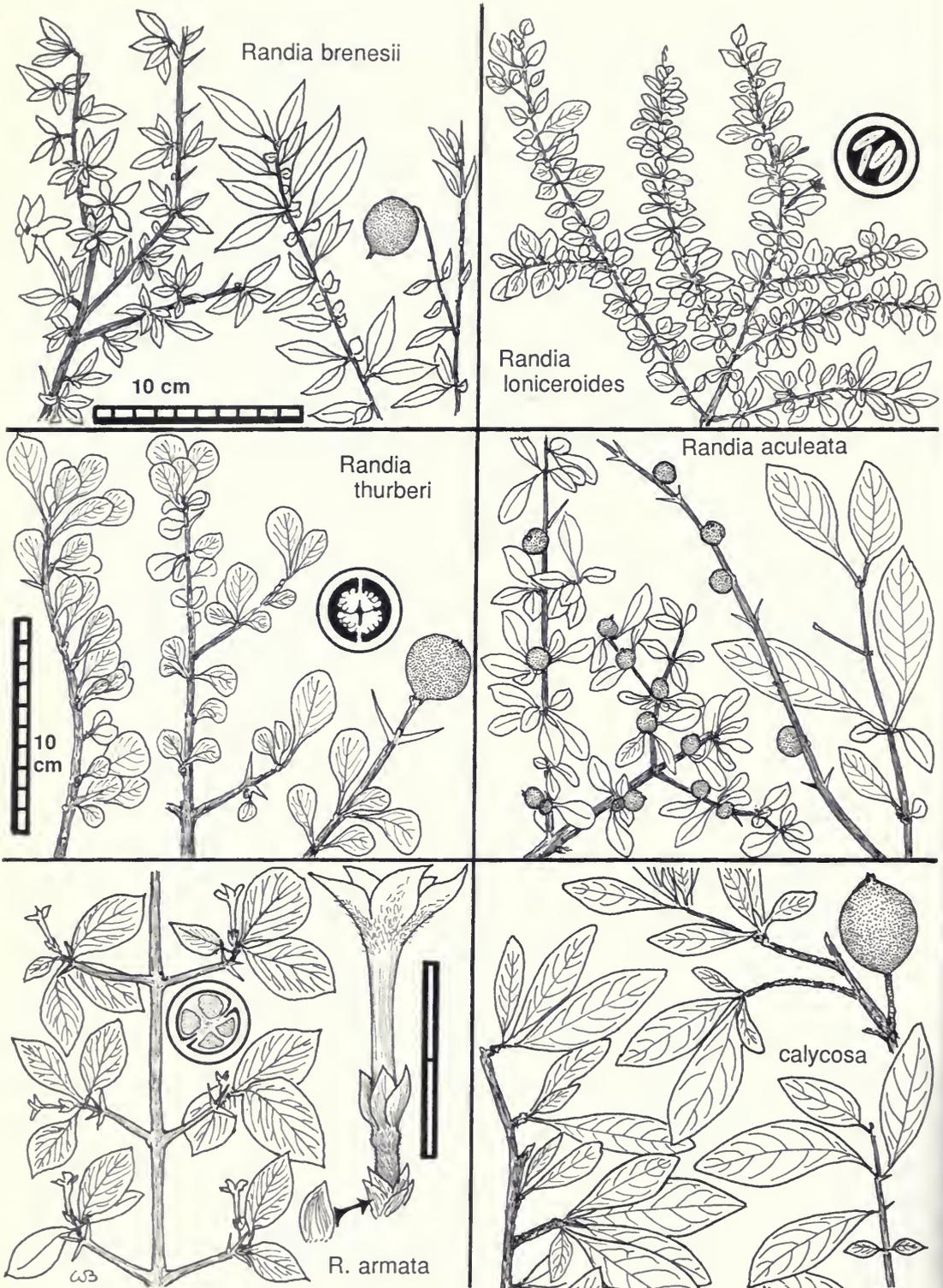


FIG. 22. Fruits usually terminal and solitary: species of *Randia* with small leaves.

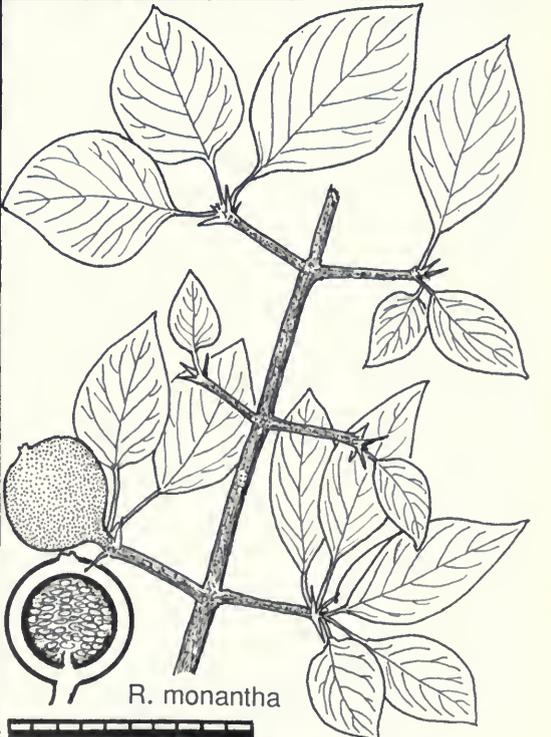
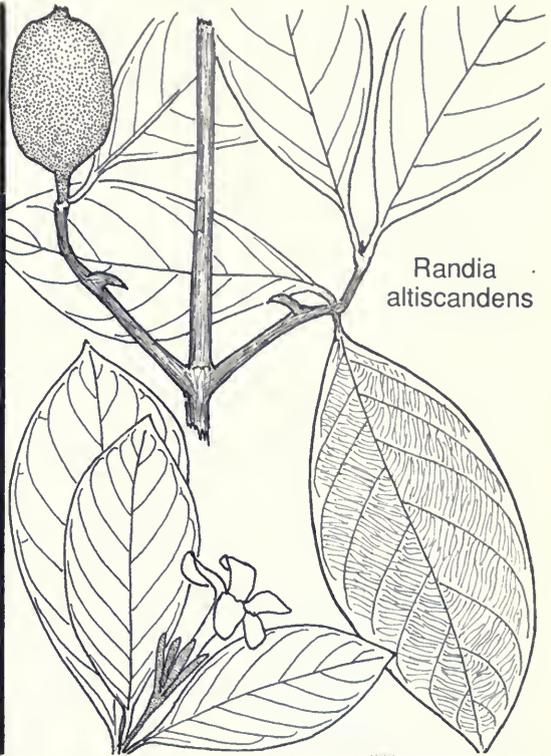


FIG. 23. Fruits usually terminal and solitary: species of *Randia* with medium-sized leaves.

R. genipoides



Randia grayumii



Randia mira

R. matudae

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*.

Genipa americana



G. williamsii



B. atlantica



Borojoa panamensis



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

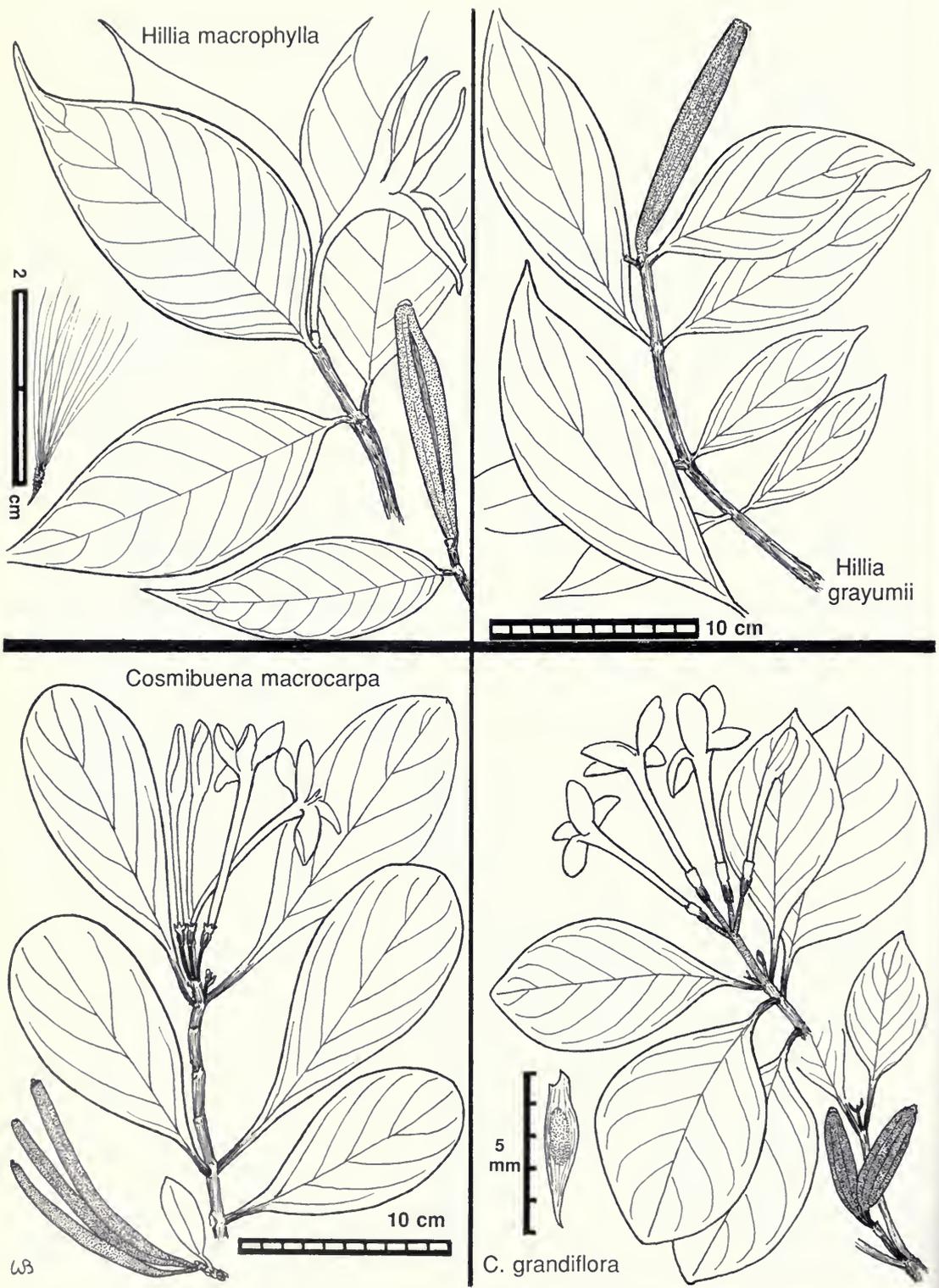


FIG. 28. Plants usually epiphytic: species of *Cosmibuena* and *Hillia* with larger leaves.



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*.

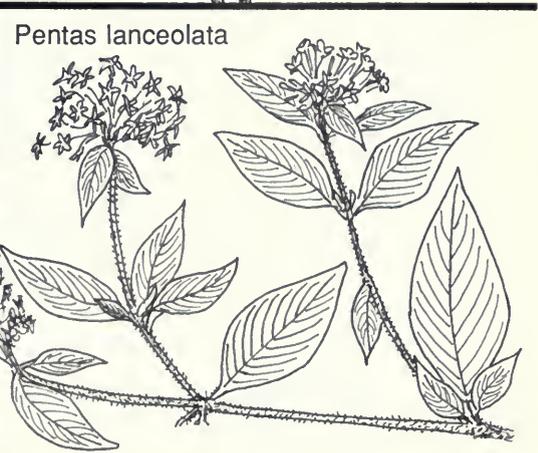
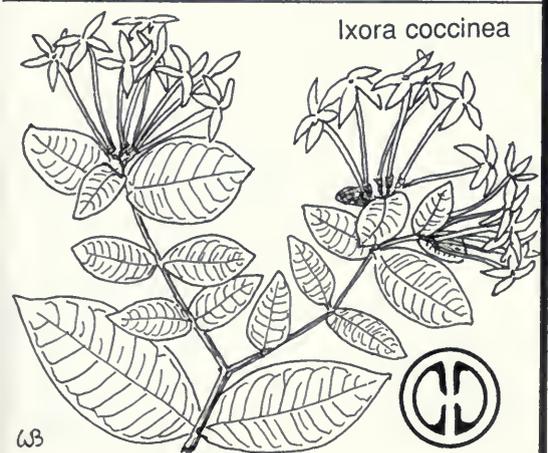
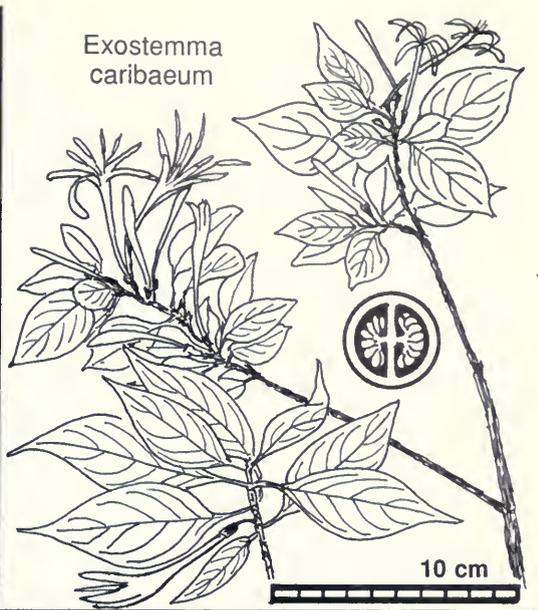


FIG. 31. Showy flowers: species of *Coutarea*, *Crusea*, *Exostemma*, *Ixora*, and *Pentas*.

Guettarda crispiflora



10 cm

G. tournefortiopsis



G. poasana



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

69

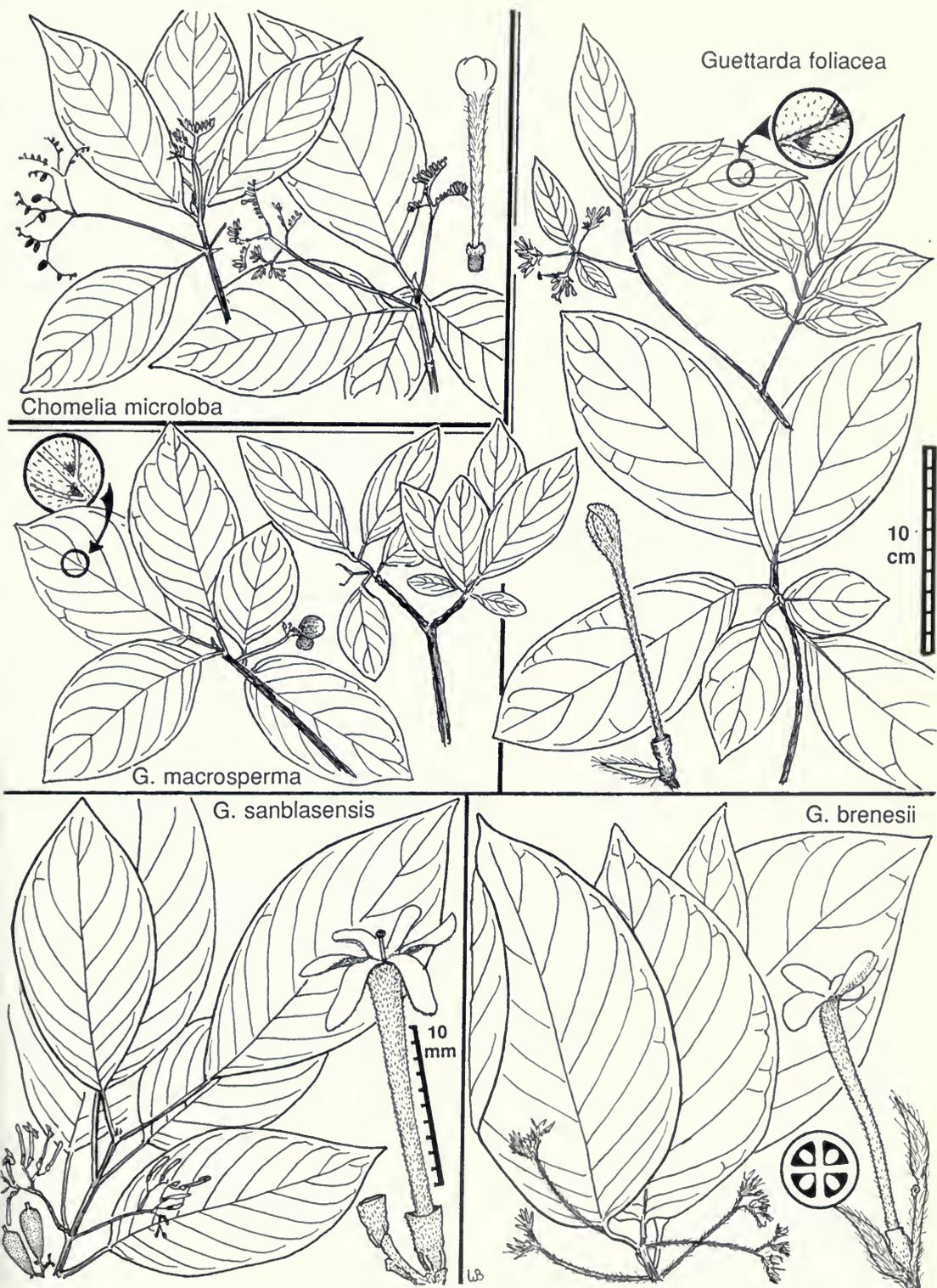


FIG. 33. Flowers with narrow corolla tubes: species of *Guettarda* and a species of *Chomelia*.

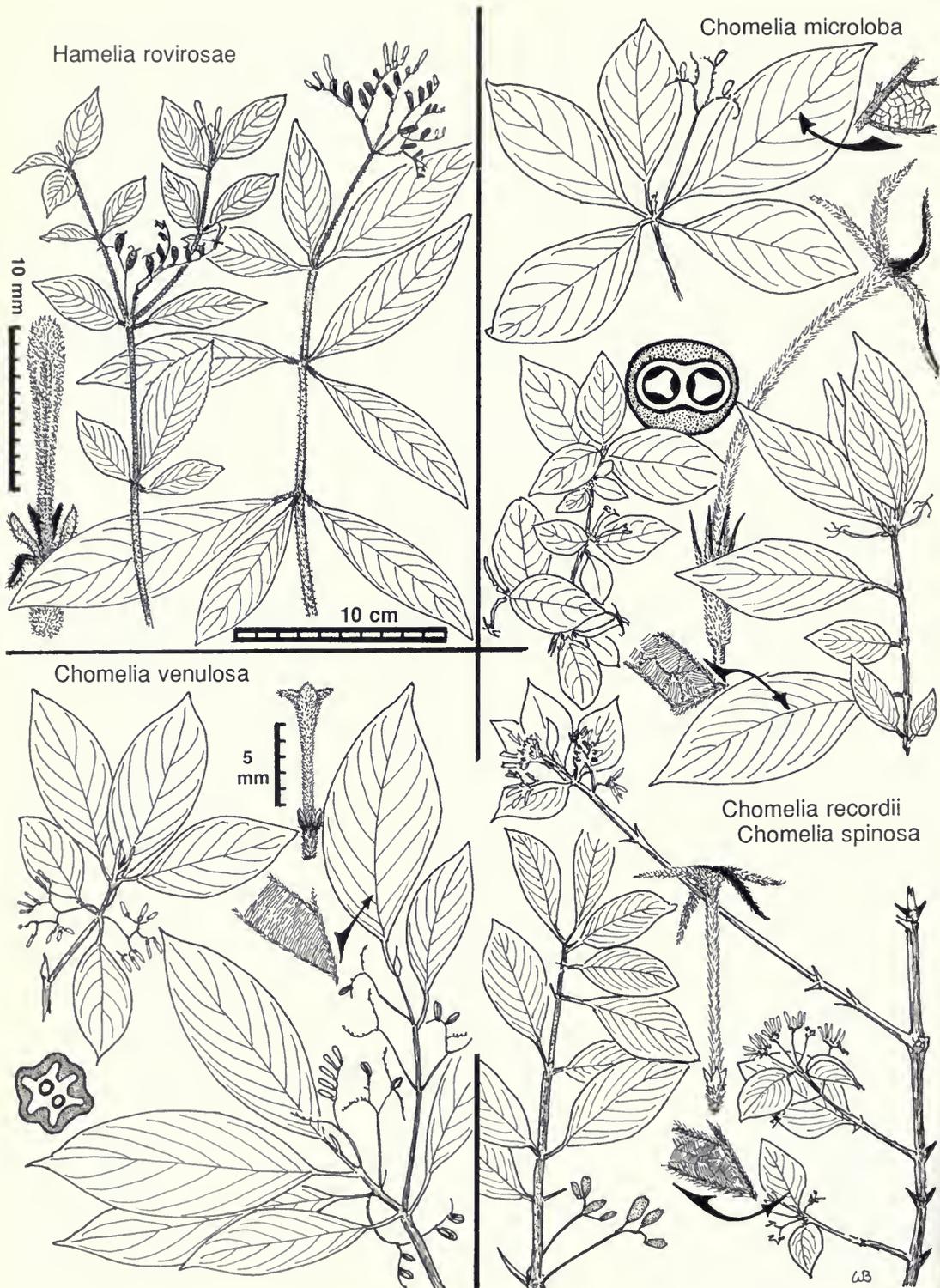


FIG. 34. Flowers with narrow corolla tubes: species of *Chomelia*, *Guettarda*, and *Hamelia*.

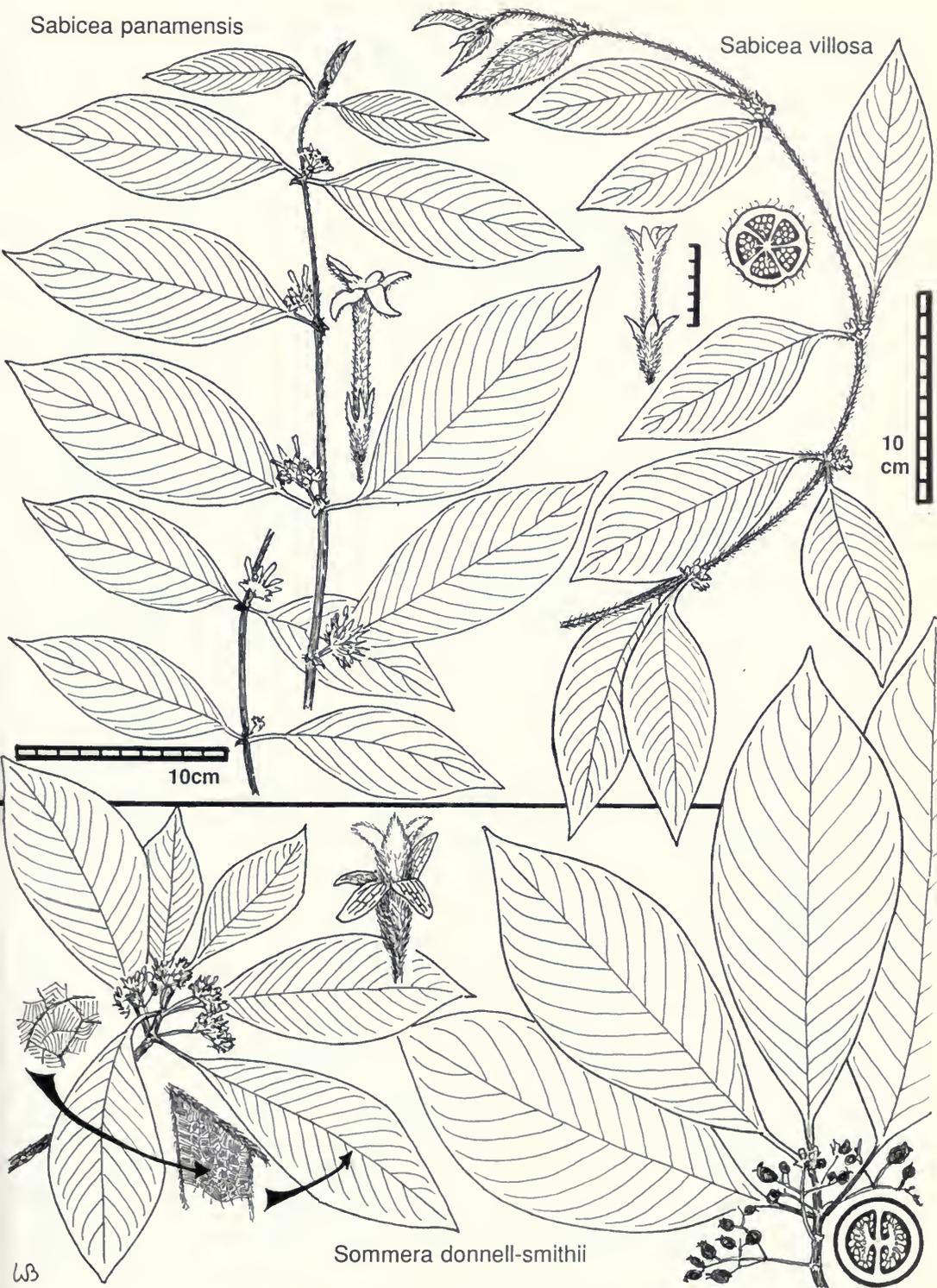


FIG. 35. Inflorescences mostly axillary: species of *Sabicea* (vines) and *Sommera* (trees).



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

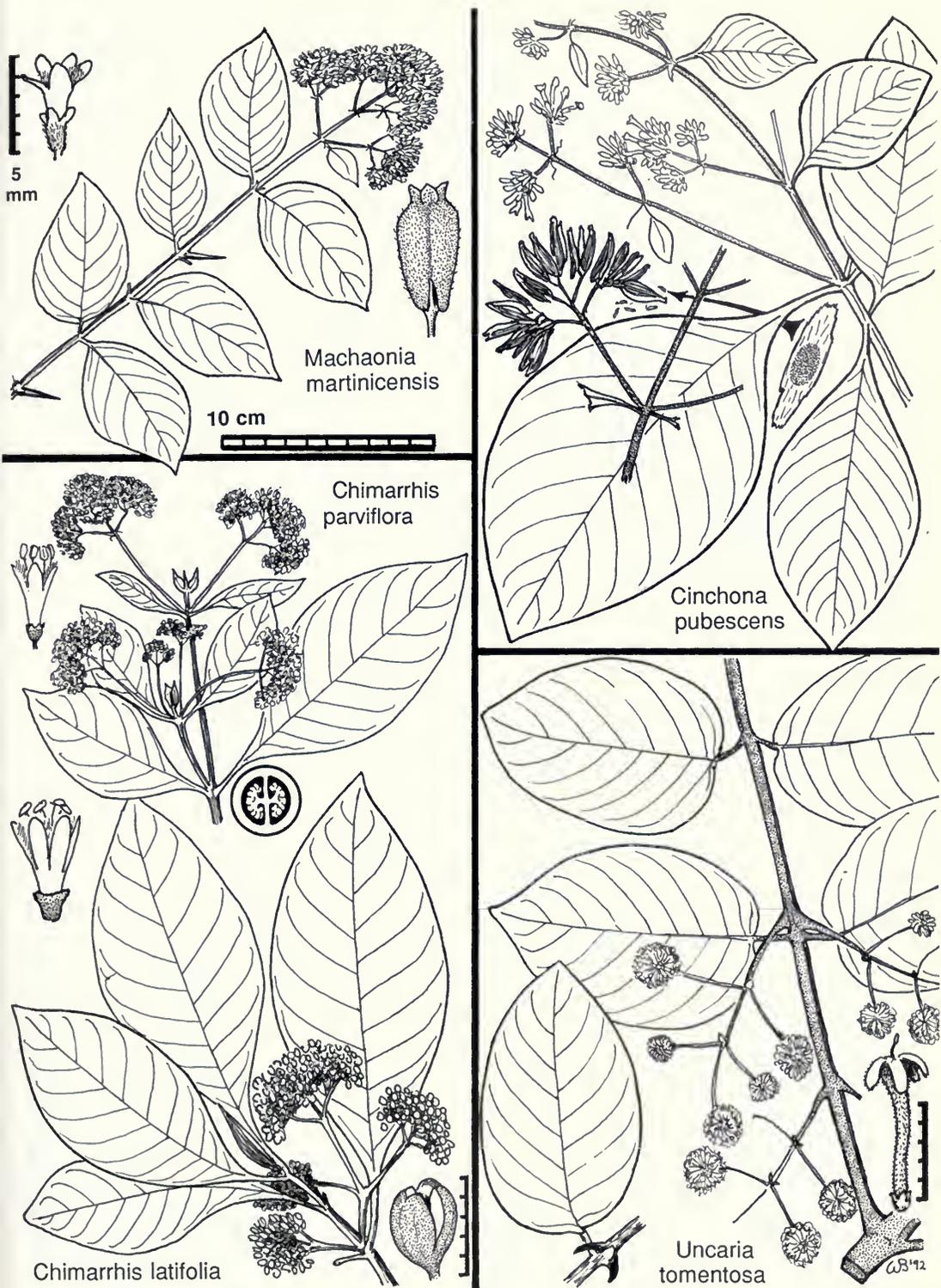


FIG. 37. Many small flowers in dense inflorescences: species of *Chimarrhis*, *Cinchona*, *Machaonia*, and *Uncaria*.



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*.

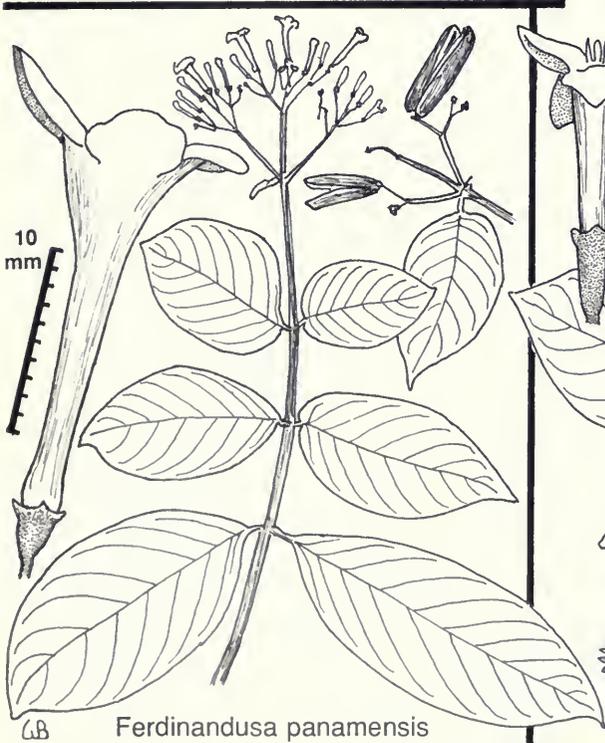
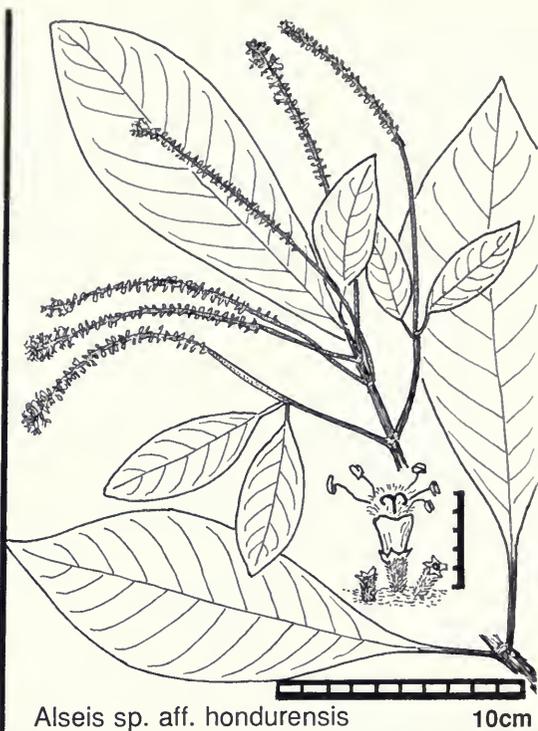
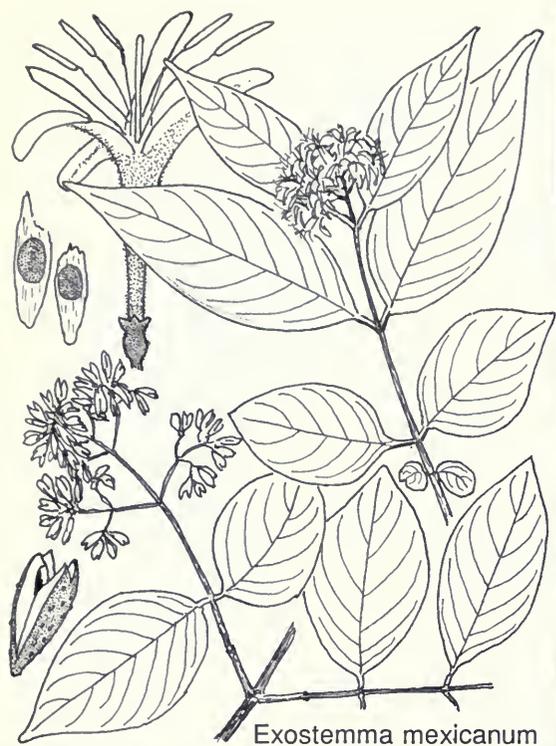


FIG. 40. Small flowers and capsular fruits: species of *Alseis*, *Exostema*, *Ferdinandusa*, and *Macrocnemum*.



FIG. 41. *Rondeletia* spp.



FIG. 41A. *Rondeletia* spp.



FIG. 42. *Hamelia* spp.

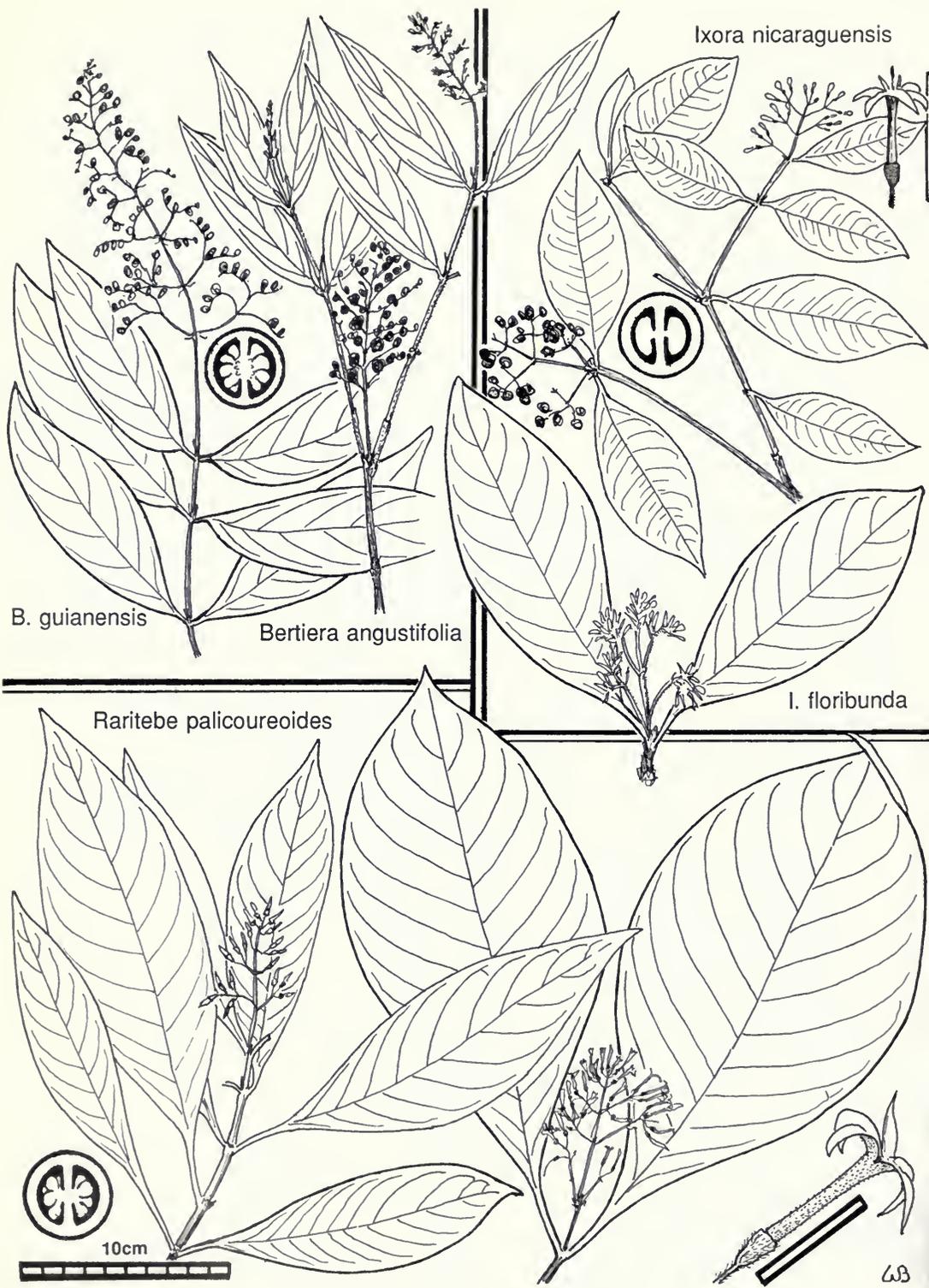


FIG. 43. *Bertiera*, *Ixora*, and *Raritebe* spp.

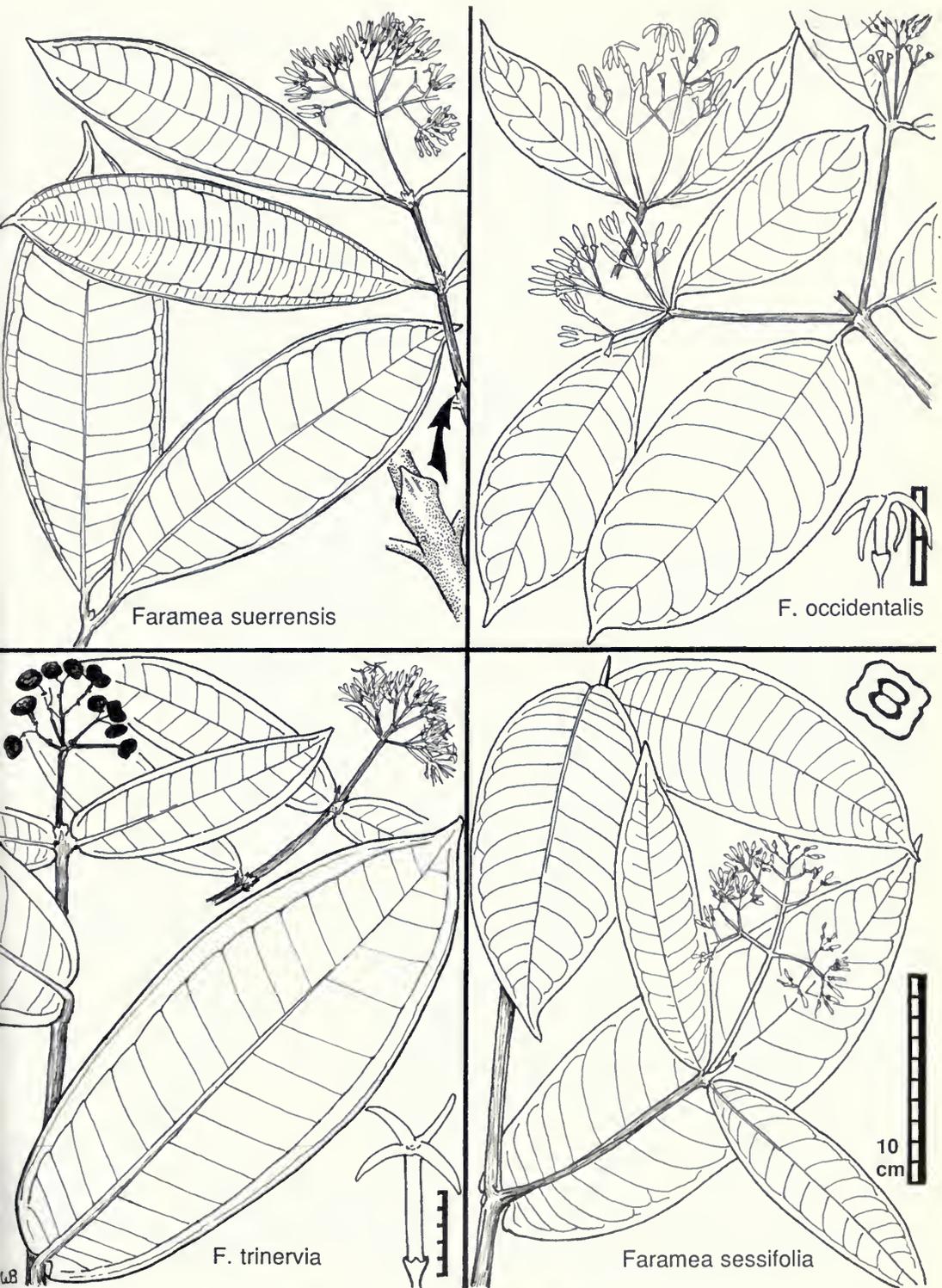


FIG. 44. *Faramaea*: species with larger leaves.

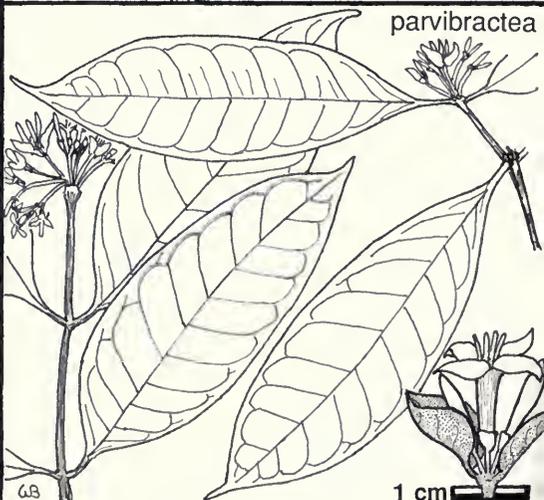
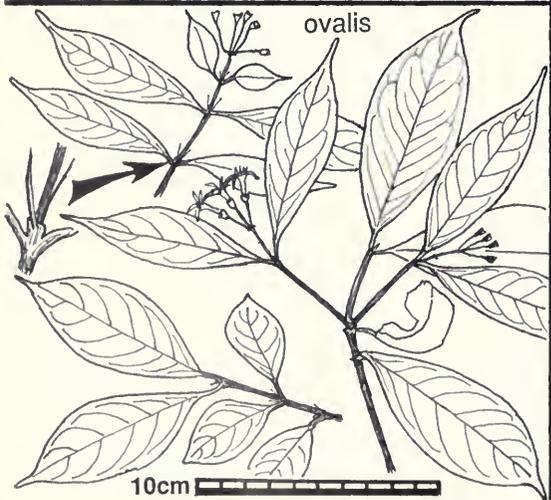
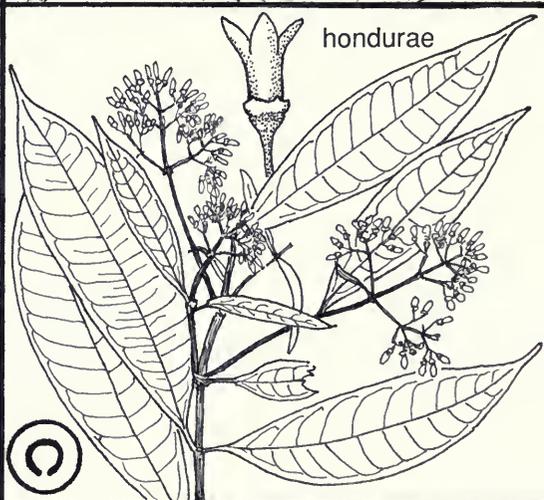
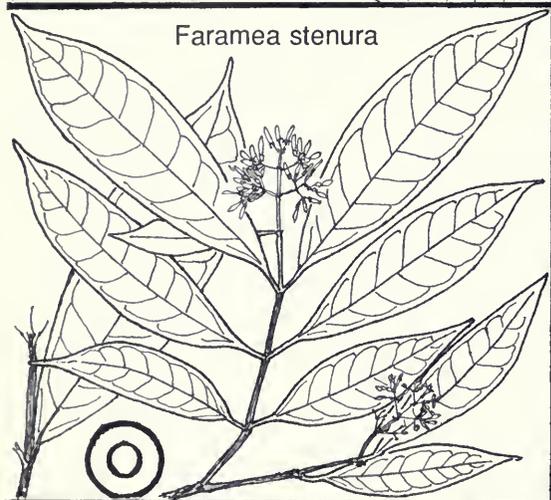
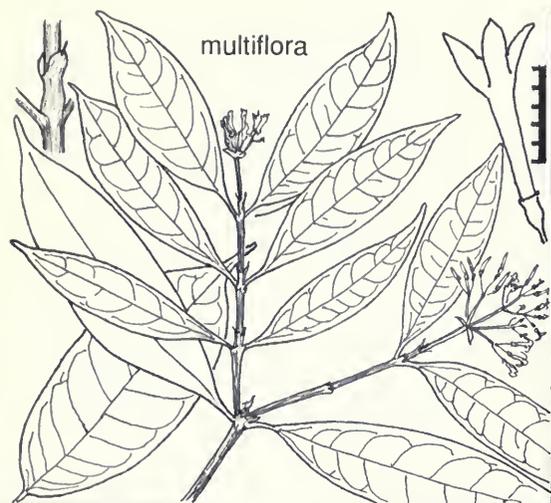


FIG. 45. *Faramaea*: species with smaller leaves.



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

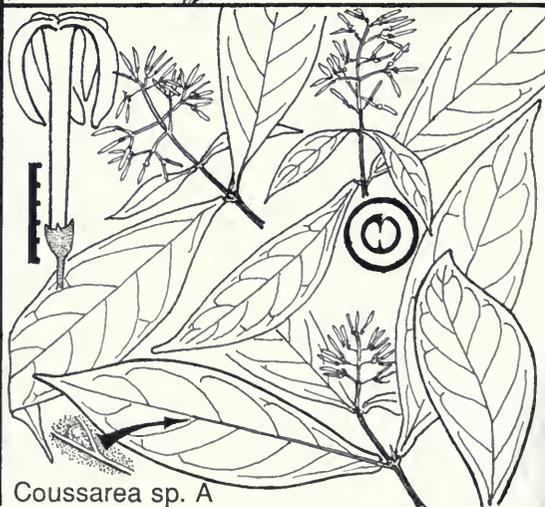
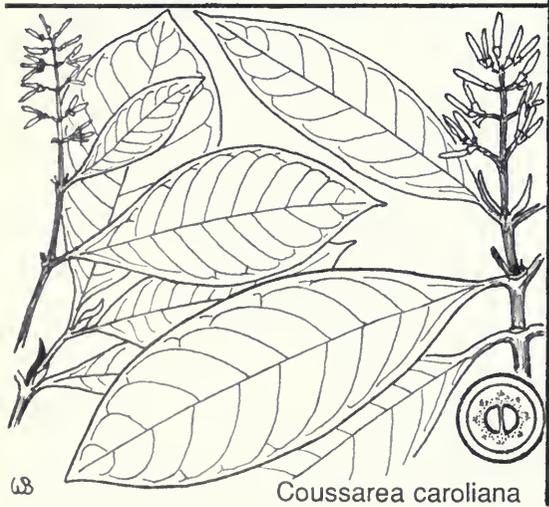
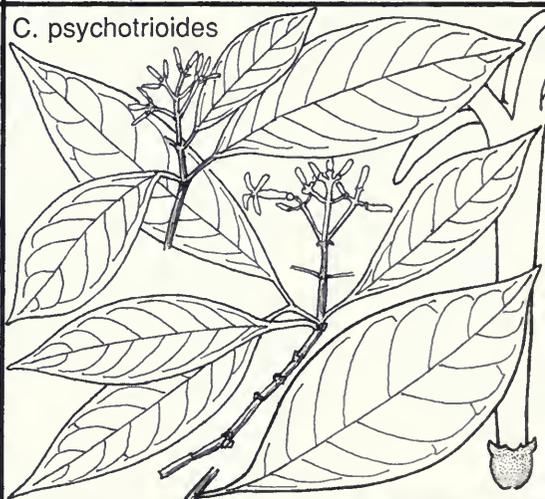
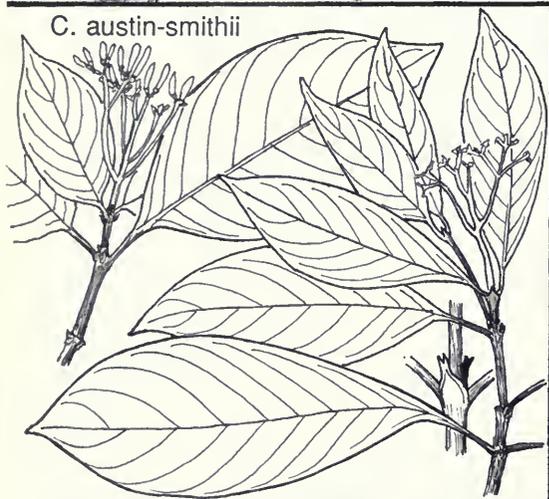
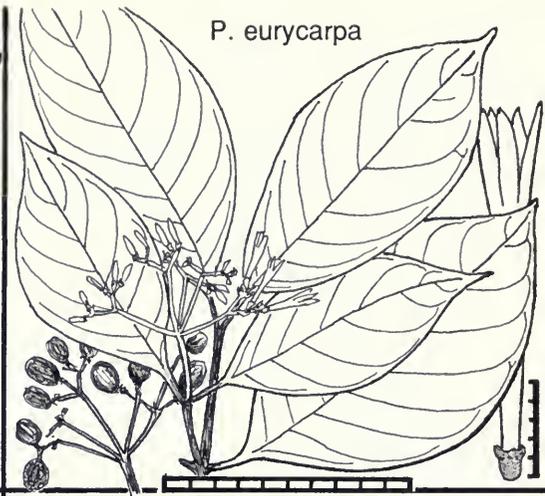
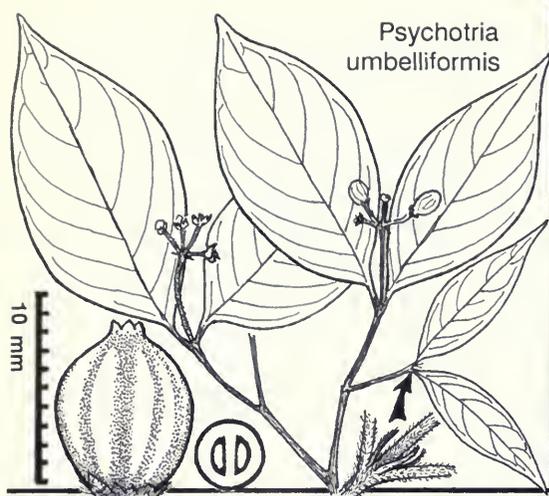


FIG. 47. *Coussarea* spp. and two similar *Psychotria* spp.

Coussarea talamancana

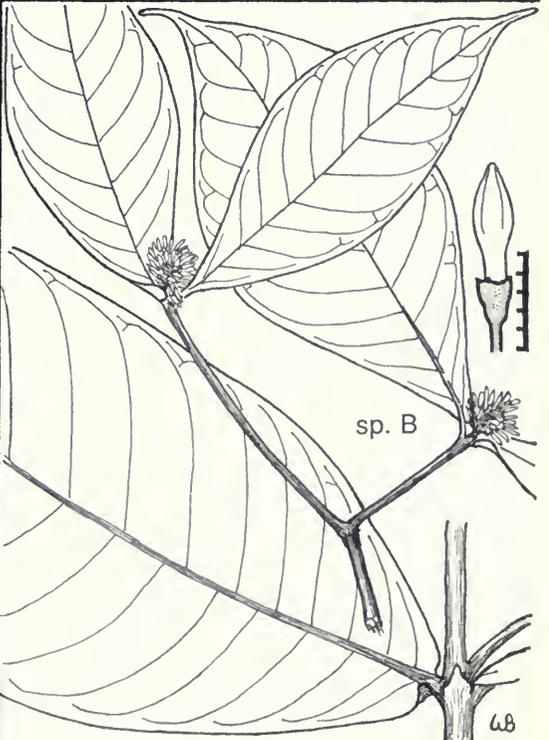
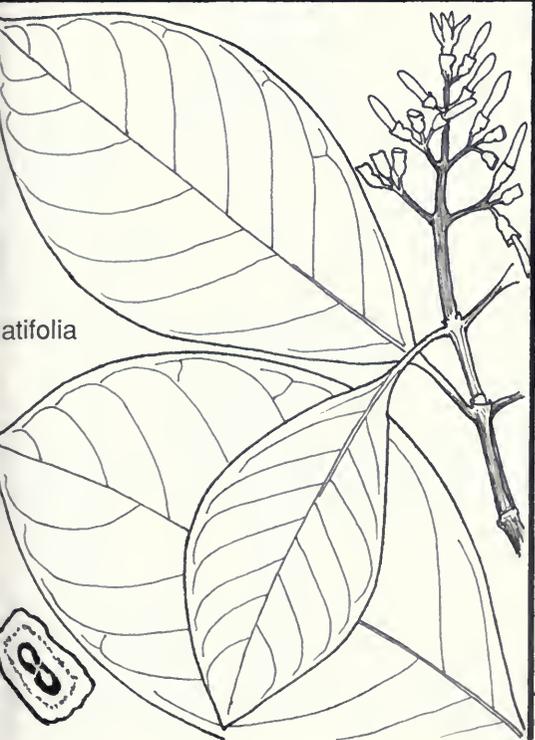
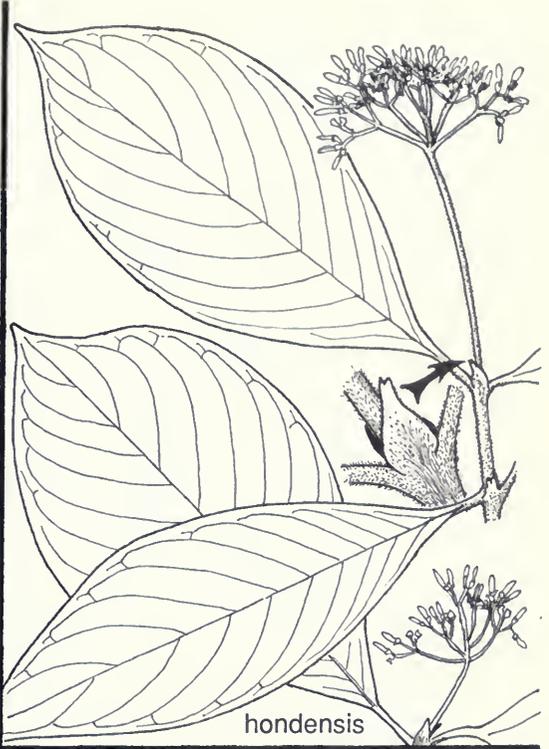
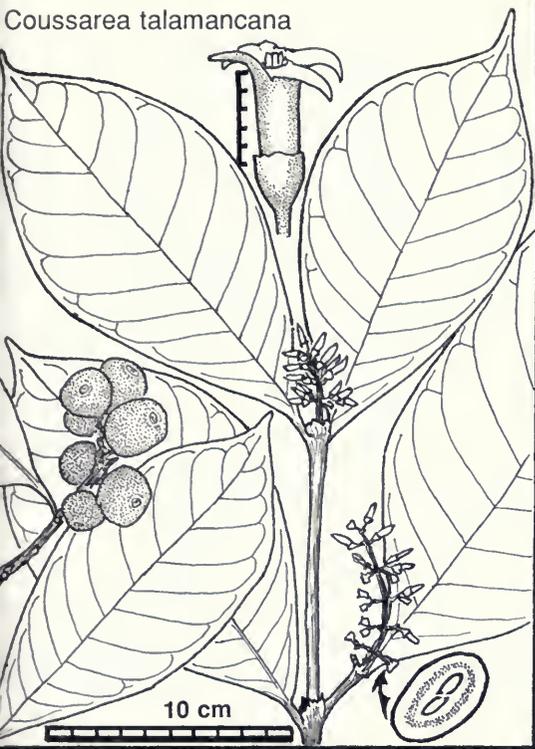


FIG. 48. *Coussarea*: species with larger leaves.

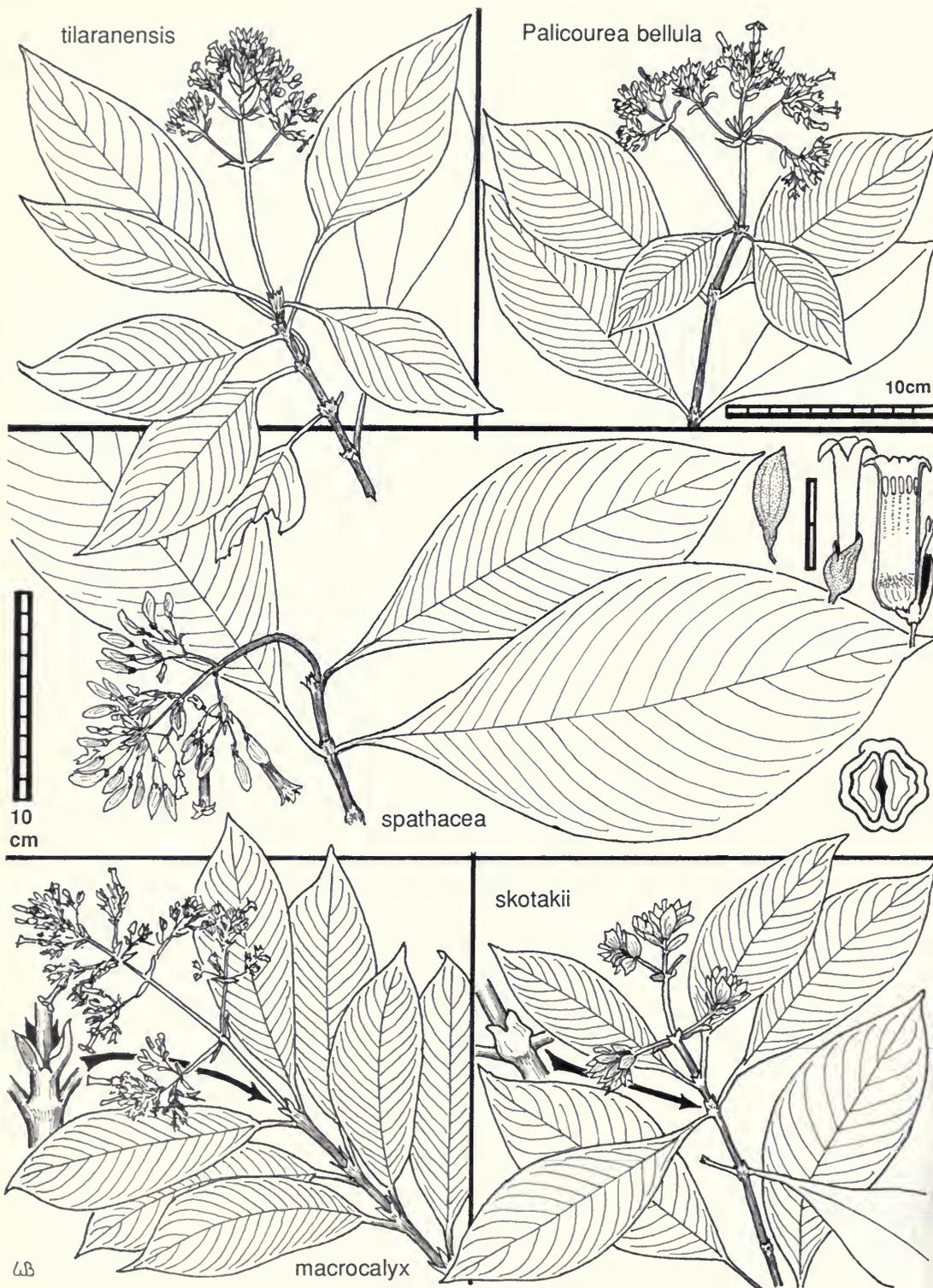


FIG. 49. *Palicourea*: species with conspicuous bracts.

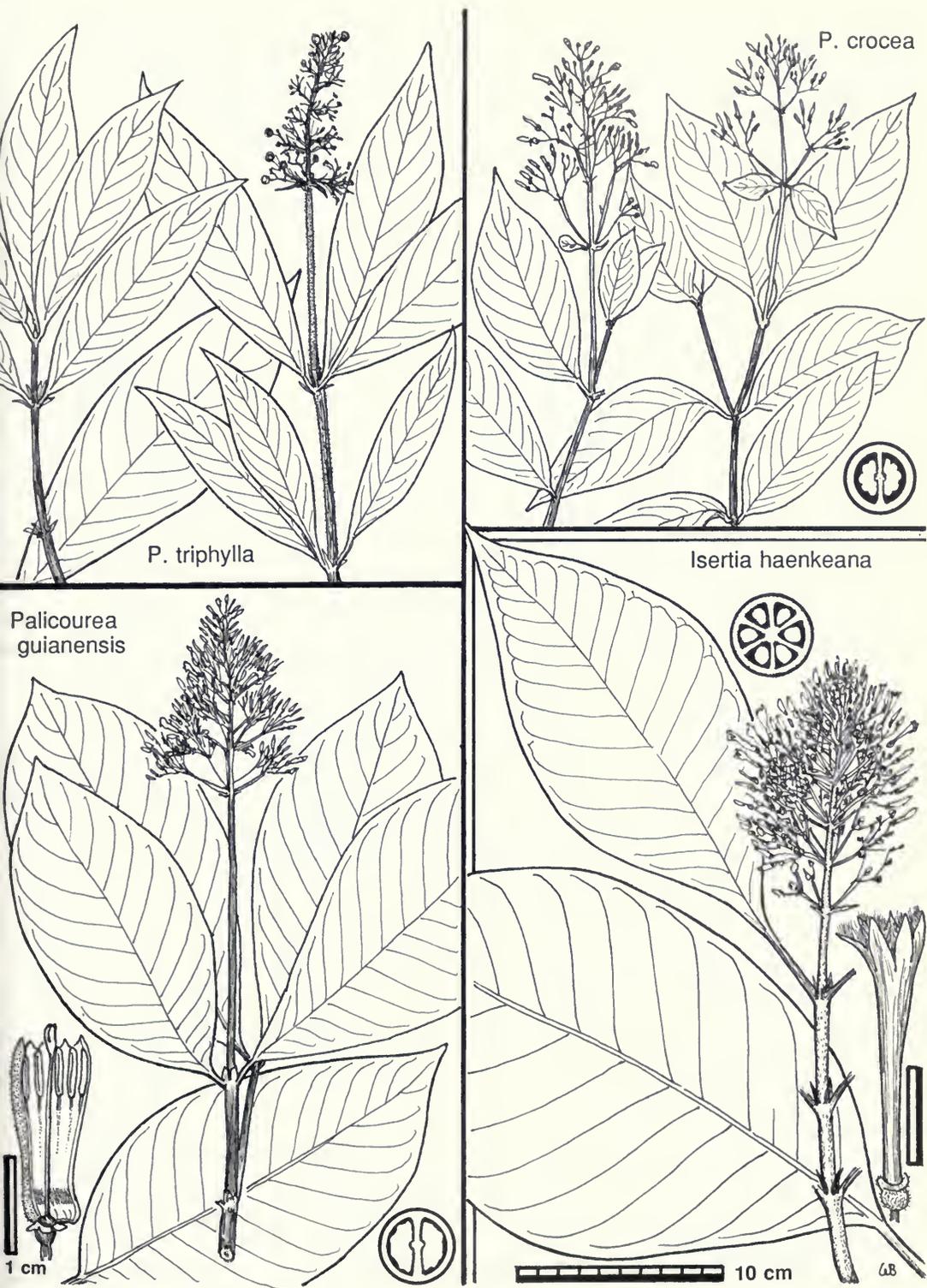
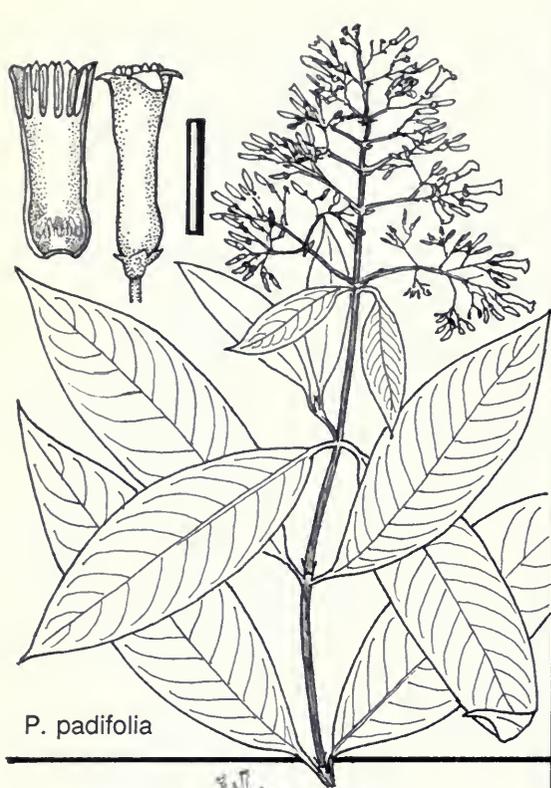


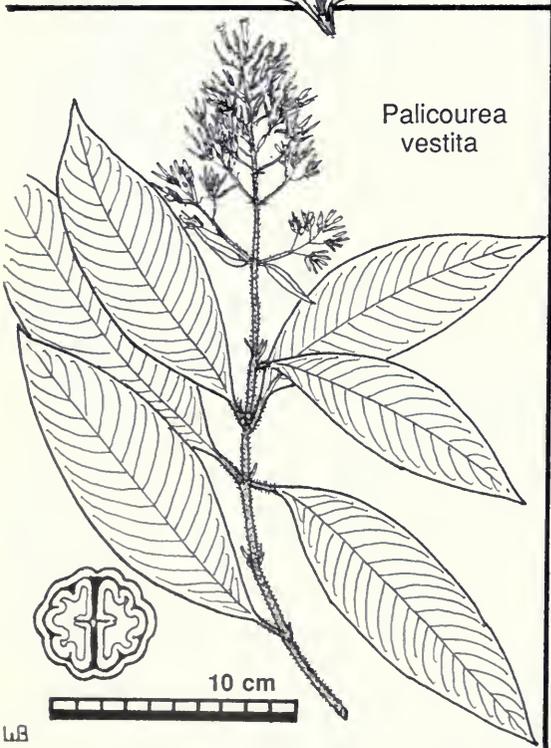
FIG. 50. *Palicourea*: species of lower elevations and a species of *Isertia*.



P. padifolia



P. orosiana



Palicourea vestita

10 cm

LB



P. lasiorrhachis

1 cm

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.

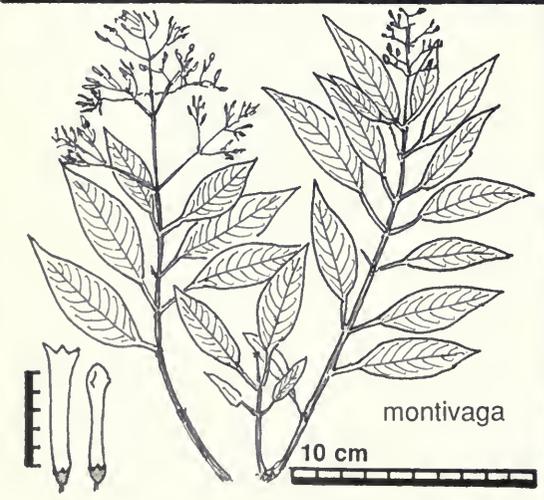
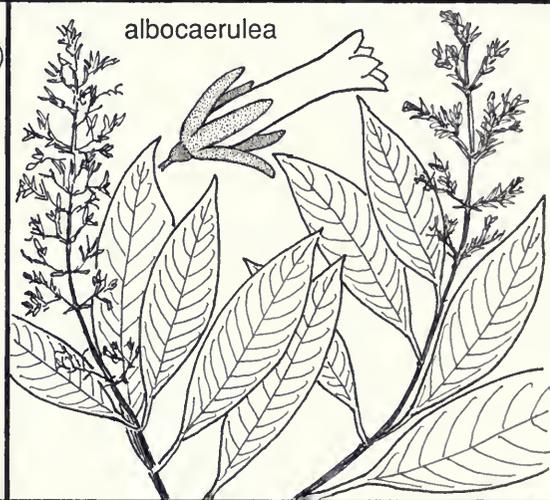
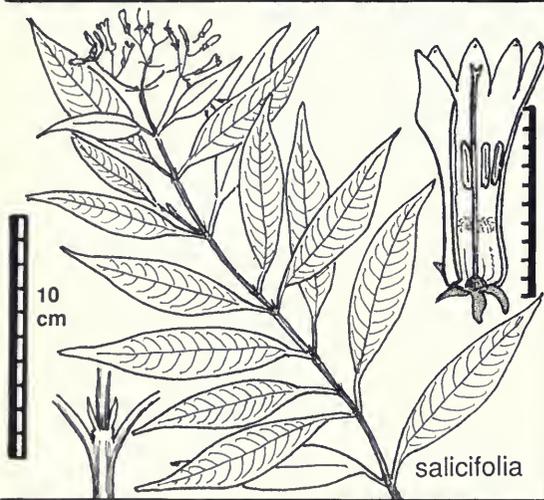
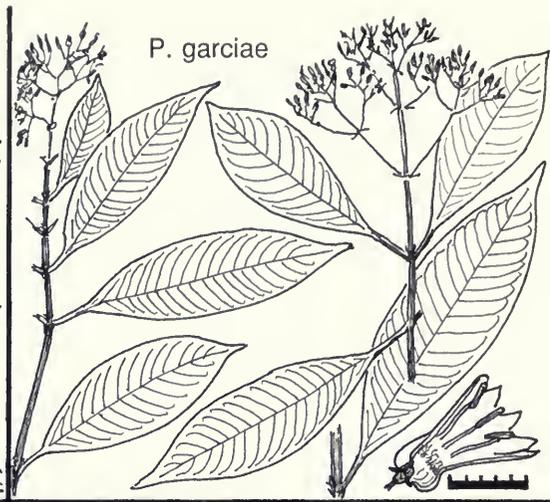
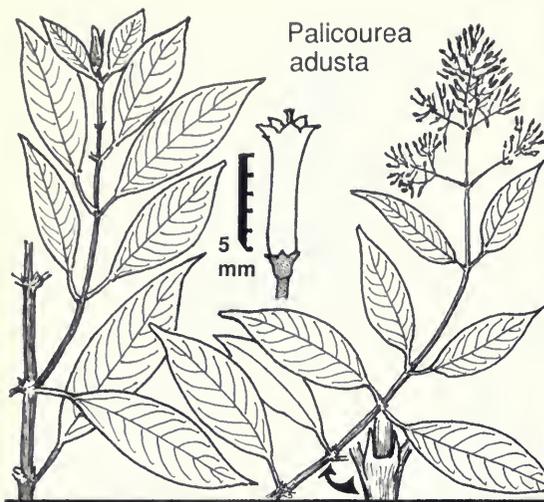
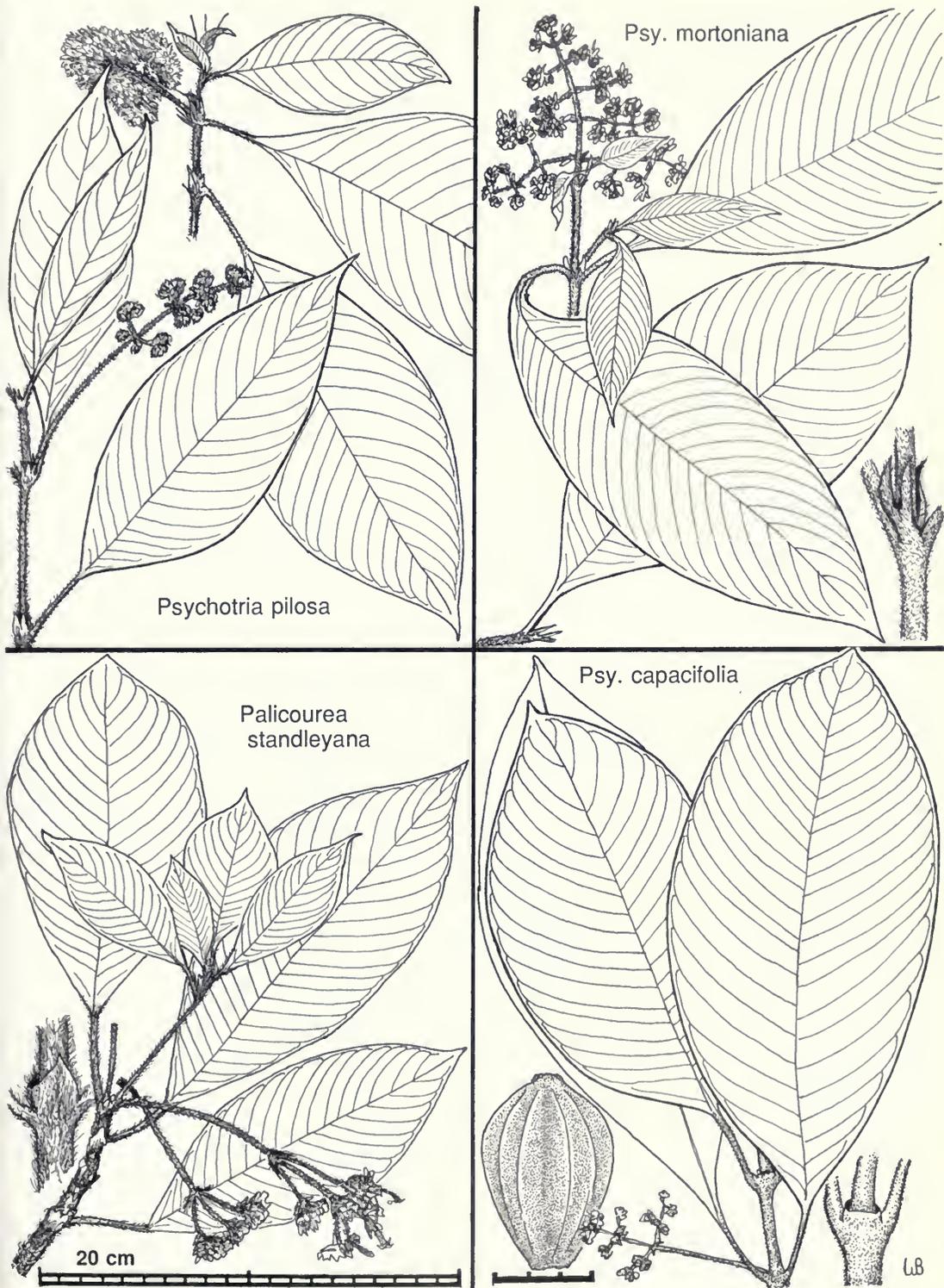


FIG. 53. *Palicourea*: species with smaller leaves.



Psychotria pilosa

Psy. mortoniana

Palicourea standleyana

Psy. capacifolia

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



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

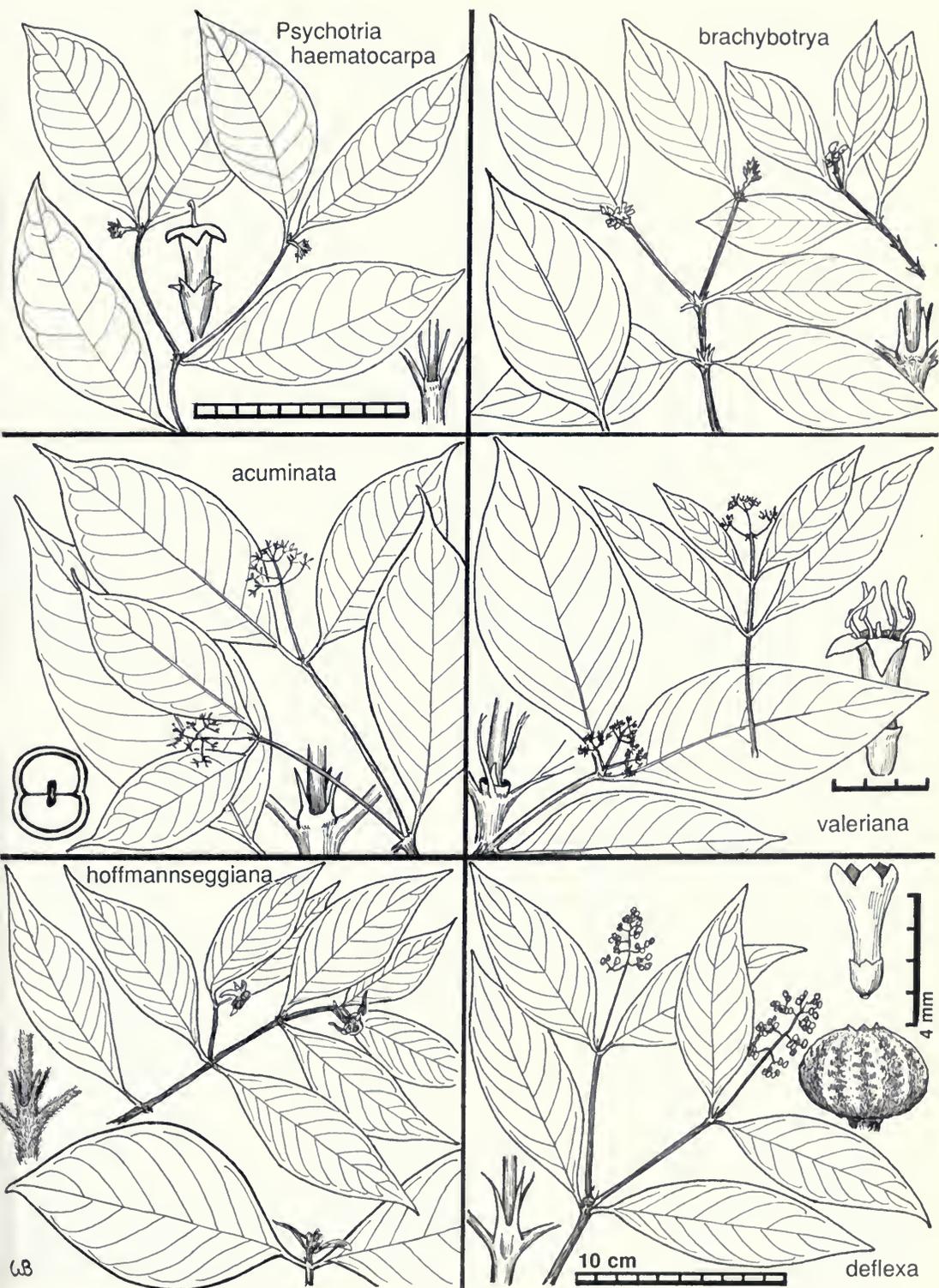


FIG. 56. *Psychotria* subg. *Heteropsychotria*: species with very small inflorescences.

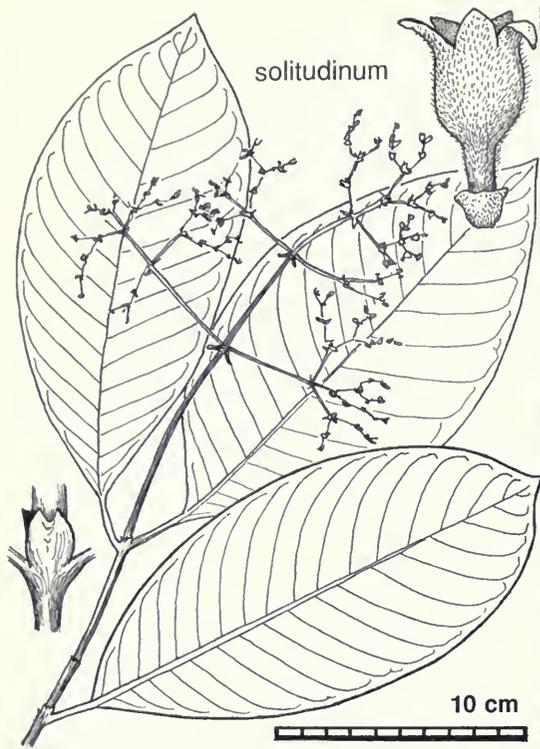


FIG. 57. *Psychotria* subg. *Heteropsychotria*: species with larger open inflorescences.



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



FIG. 59. *Psychotria* subg. *Heteropsychotria*: species of deciduous habitats and some with smaller 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.

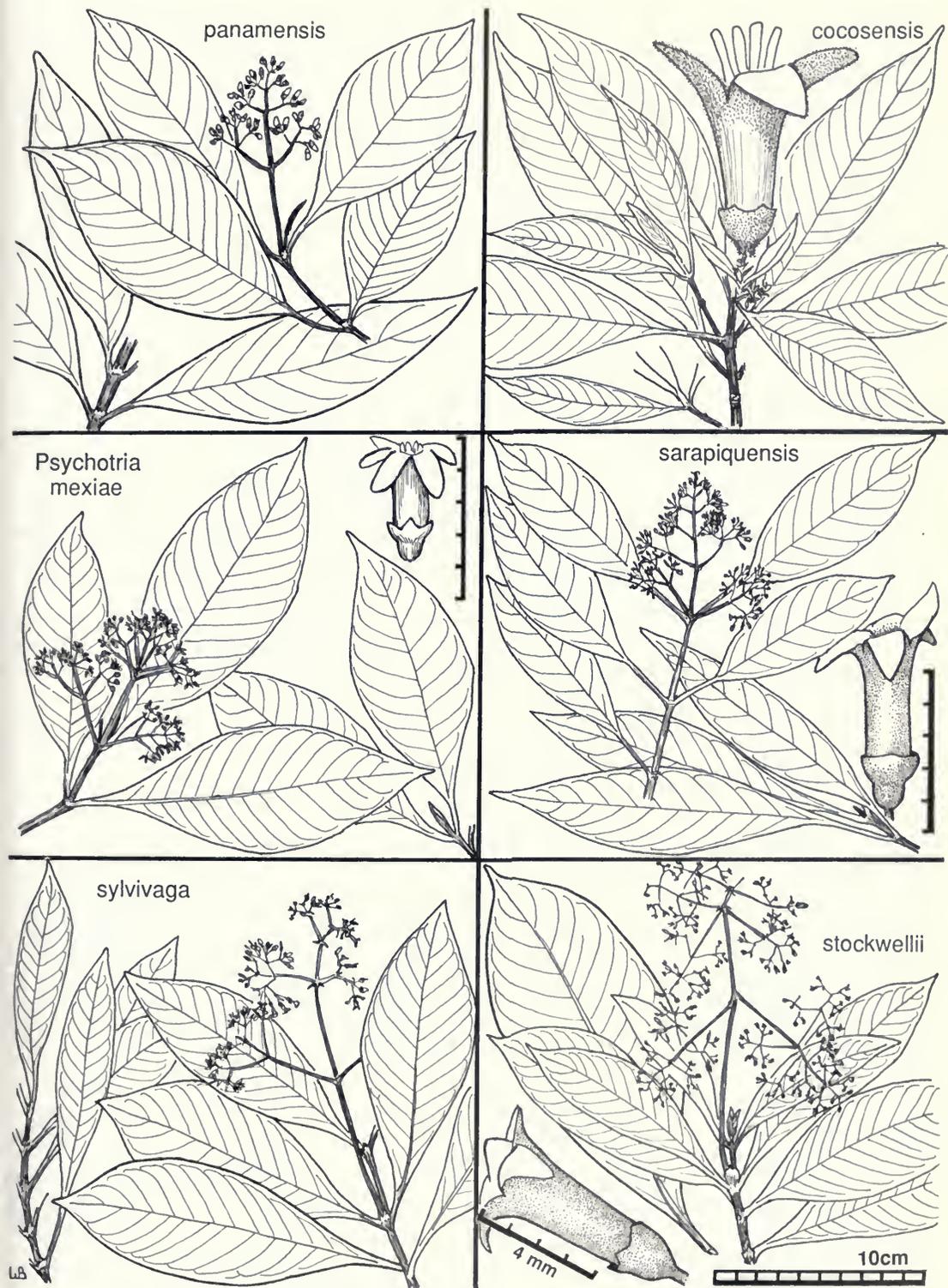


FIG. 62. *Psychotria* subg. *Psychotria*: high-elevation species and those with *Ficus*-like stipules.

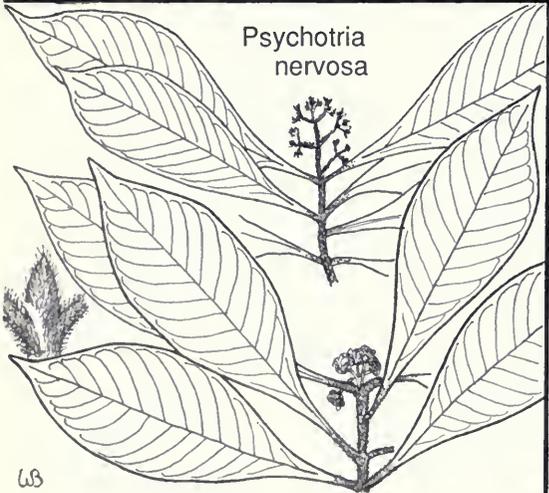
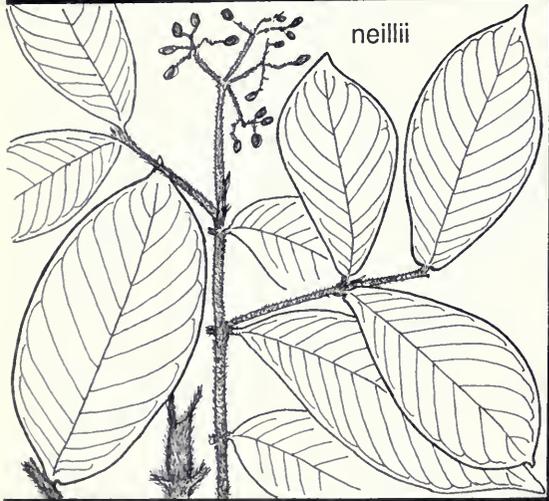
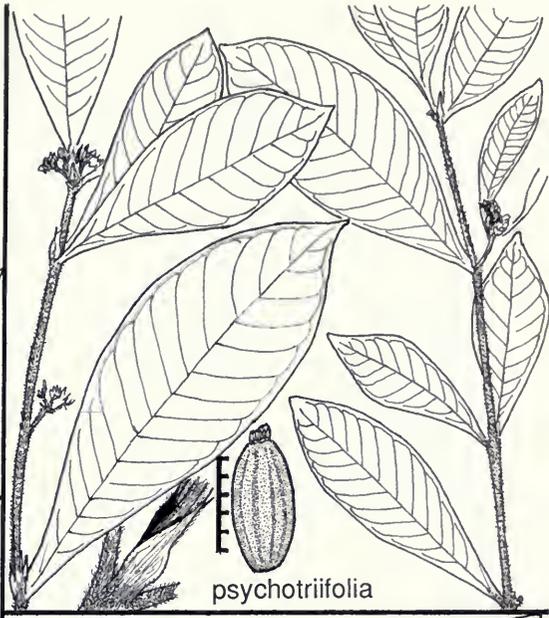
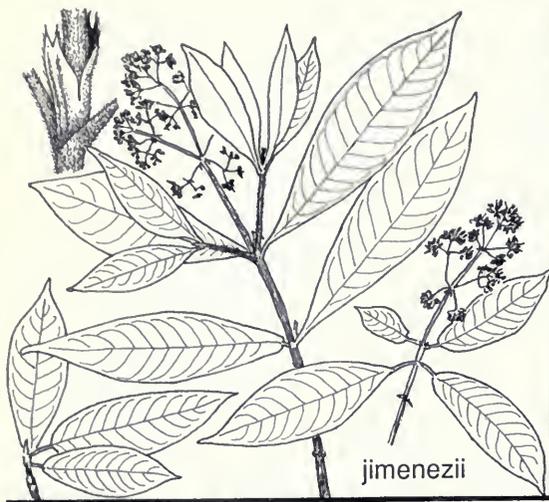


FIG. 63. *Psychotria* subg. *Psychotria*: densely pubescent species.

63

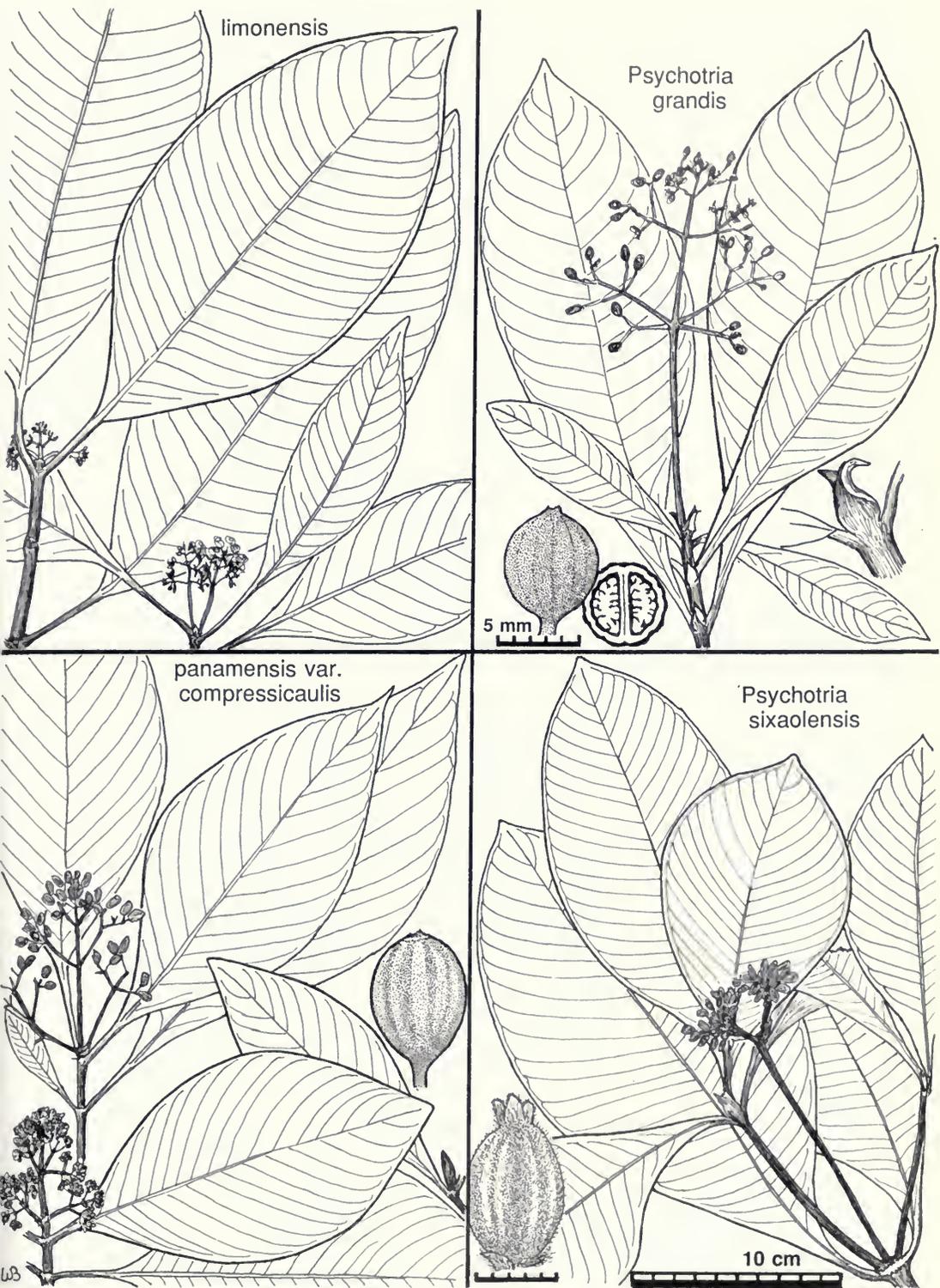


FIG. 64. *Psychotria* subg. *Psychotria*: large-leaved species.

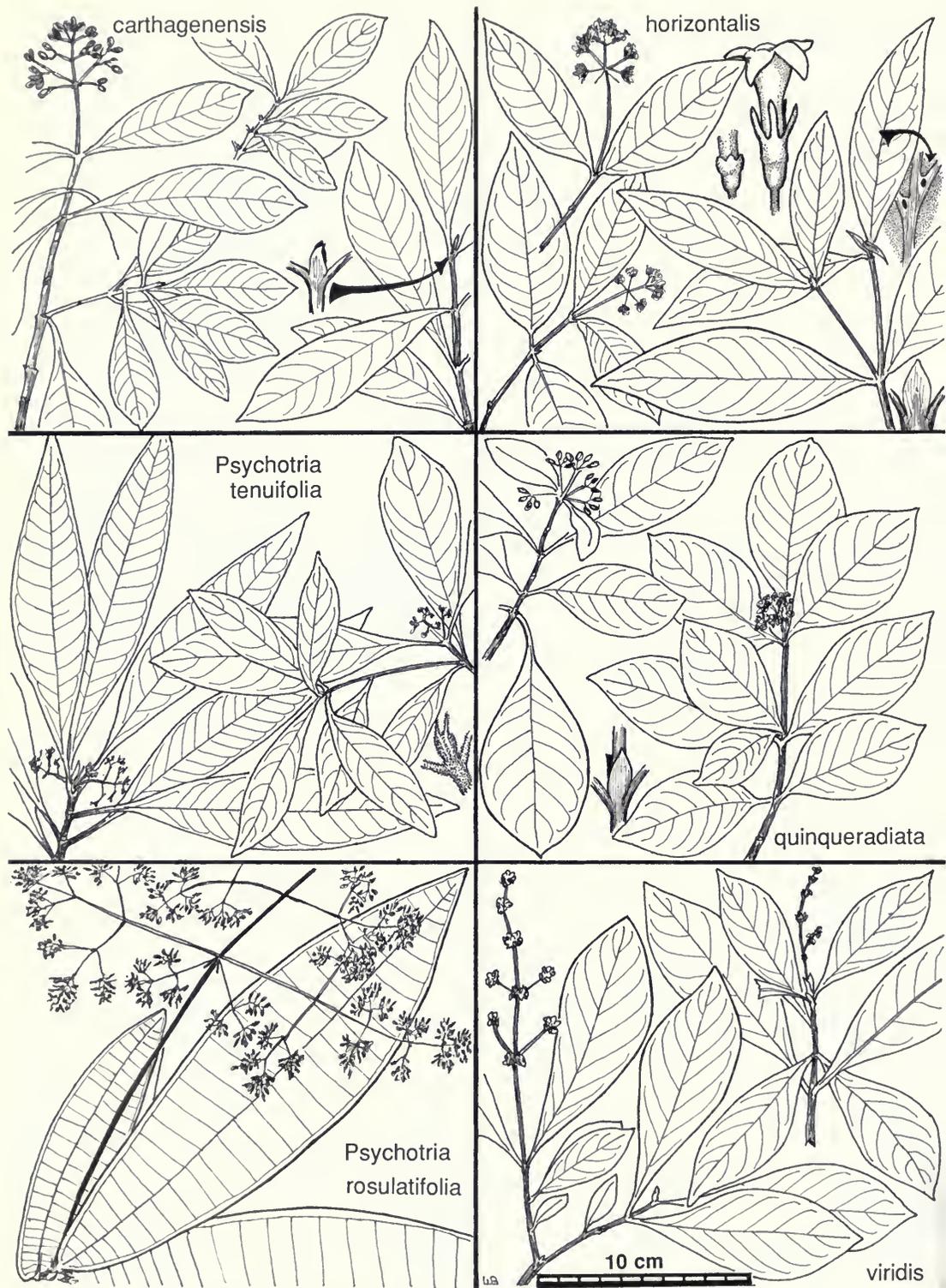


FIG. 65. *Psychotria* subg. *Psychotria*: deciduous and unusual species.

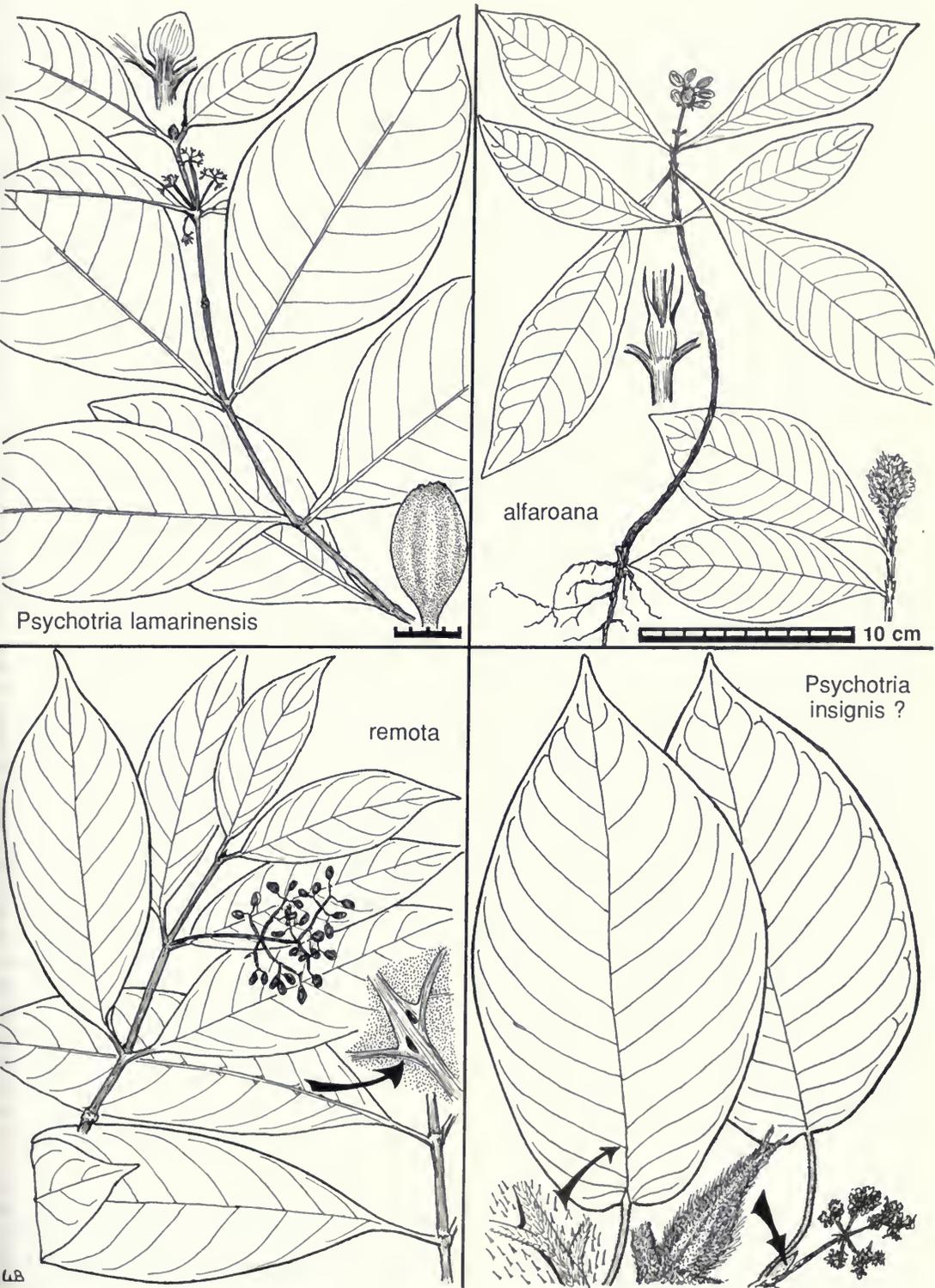


FIG. 66. *Psychotria* subg. *Psychotria*: several unusual species.

Alibertia A. Richard

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.

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*.

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

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 (thyrses) 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, exerted 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 exerted, 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, cylindrical 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 exerted, 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 Bahia 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-

time 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 lacinate 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.

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.

Arcytophyllum Willdenow ex Schultes

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

Key to the Species of *Arcytophyllum*

- 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*

Arcytophyllum lavarum K. Schum. ex Standl., Contr. U.S. Natl. Herb. 18: 127. 1916. *Mallostoma lavarum* (K. Schum.) J. D. Smith, Enum. Pl. Guatem. 5: 36. 1899, nom. nud. (based on *A. lavarum* K. Schum. in herb.). *A. chirropoënsis* 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;

Arcytophyllum (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 I: 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, muriccate.

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, thyrse-like 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.-Ex-act. 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 exerted in thrum flowers; **ovary** 2-locular, ovules many on a peltate placenta borne from the lower part of the septum, style 1, slender, exerted in pin flowers and included in thrum flowers. **Fruits** capsular, globose or obovate, didymous-globose, dehiscent 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 petiole and petal-like blade; **corolla** short funnelform 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, exerted; **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 (obtus), 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 petiole (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 shears 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 shears 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, exocarpe 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 bivalved 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 paniculate, 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.

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.

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; (?700–)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;

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 paniculate, 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** funnel-form, 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, funnel-form 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, sub-acuminate 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** funnel-form, 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, paniculate 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^o 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* Steyererm., 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, carnos, 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, exerted. **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 exerted 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 funnellform, 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 exerted, 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 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 cremaea, 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/size, 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, colleters 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 exocarpy; **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 exerted; **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 exerted, 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 paniculate 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, exerted; **ovary** 2-locular, ovules many in each locule from axile placentas, style narrow, stigmas oblong, exerted. **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 carnosae, 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 exerted, 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. impetolaris*
- 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. caroliana*
- 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
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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–Zarcelero), 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 caroliana 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** fragrant, 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 caroliana 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 colleters 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, ca. 2 mm broad, narrowly oblong; **corolla** salverform, white, tube 20–30 mm long and 3–4 mm diam., with ascending hairs ca. 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, paniculate or corymbiform 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 subsessile 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 curvigemmia* Dwyer of central Panama with smaller flowers is also closely related; see the discussions under *Coussarea* spp. A & B aff. *C. curvigemmia*. 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 jiminezii 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 cy-mose 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. talamancaum* 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. curvigemma* 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 curvigemma*, 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 *Faramea*.

Coussarea sp. B aff. *C. curvigemma*. 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 funnelliform 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, exerted 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, dehiscent 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, ca. 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** funnelform–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** funnelform 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 ⅓ 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, funnellform, 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., Linnæa 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 colleters, 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, funnelliform, 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** funnelliform 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 exerted; **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 paniculate 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, exerted 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, exserted, 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, capitulate 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 exerted, 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 ocyimifolia*
- 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** funnelliform 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 pseudoverticillate 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 pseudoverticillate 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 Cycles 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** tube 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, circumsissile 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.

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

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

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; venis lateralibus 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 on 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.) Steyerl., 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 sessile; **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 exerted; **ovary** 2-locular, placentas peltate on the septum with many ascending ovules, style filiform, usually exerted, 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 exerted 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 exerted 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, oblancoelate-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, exerted 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 subsessile); **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 exerted; **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. hondurae*

***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;* *Dryer 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, paniculate 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.

Suffrutices 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 Orosi). 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 Chiriqui 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** exerted, 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.

Faramea 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.

Faramea 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.

Faramea 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: *Herrera 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 *Cousarea enneantha* (fig. 46).

Faramea 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.

Faramea 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. suerrensis* of lowland formations.

Faramea 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.

Faramea 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.

Faramea 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.

Faramea 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.

Faramea suerrensis (J. D. Smith) J. D. Smith, Bot. Gaz. 44: 112. 1907. *Faramea trinervia* K. Schum. & J. D. Smith var. *suerrensis* 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-ob lanceolate, 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, exocarpy 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 suerrensis 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–

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 (*I. 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. suerrensis* (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. suerrensis*, 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, petiole, 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 *café cillo* 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 rootstock, 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, pinnately 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 exerted, 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, carnosose, 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, carnosose, 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 exerted; 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-petiole 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* Steyerem., 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, funneliform, 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 thyriform, 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** funnelliform, 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-quadangular 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 cymules 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-

floriscences 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-petiole 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. veraguensis* 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 glabrous, 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 deciduous. **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. **Inflorescences** 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), hypanthium ovoid to globose or tubular, calyx tube cupulate 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, globose 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 inflorescences 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 strongly ascending. Domatia are often present, and the 3° veins are usually subparallel. The inflorescences are always axillary, and the flowers are all salverform in Costa Rican species. This treatment benefited from the annotations made by Alfredo Grjalva 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 tomentulose, 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, glabrous, 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 funnelliform 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 funnelliform 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, calyx 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, panicleate 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 villosulous in variety *patens*) above, glabrous to densely villosulous 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-villosous, 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 treelets 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 funnelform, 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 funnelform 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 funnelform 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 longiflamentosa 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, carnose, 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, subtentire; **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 m 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 m 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