

RUBIACEAE

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The fourth largest family of flowering plants, with 600–650 genera and more than 13,000 species. A predominantly tropical family with a few genera in temperate regions; 217–220 genera and more than 5,000 species in the Neotropics. These are most commonly terrestrial, rarely epiphytic, rheophytic, semi-aquatic (amphibious) or aquatic, presenting a wide range of habits, such as herbs, shrubs, small to large trees, and herbaceous to woody climbers. Climbers are represented by 31 genera and a total of 259 species occurring in a wide range of habitats, including moist, wet or dry forests, scrublands, savannas, and sometimes open disturbed biomes; 0–2,400 m elevation.

Diagnosics: In the absence of fertile material, climbing Rubiaceae are distinguished from climbers in other families that have simple, commonly opposite (rarely whorled) leaves, with entire margins by the interpetiolar stipules, and the watery, clear exudates of stems. Climbing mechanisms are diverse but never include tendrils. Twining woody Rubiaceae may be confused with species of *Trigonía* (Trigoniaceae) but in the absence of fertile material, *Trigonía* can be distinguished by the stem cross section with a square medulla and the presence of four, shallow phloem wedges or arcs, a combination of characters never present in climbing Rubiaceae.

General Characters

1. **STEMS.** Herbaceous or woody with moderate secondary growth, some species attaining 25–30 m in length and up to 20 cm in diam. in some genera (e.g., *Schradera*, *Uncaria*, *Chiococca*, and *Manettia*). Most climbing neotropical Rubiaceae are herbaceous, although sometimes they are woody at the base, and only a few genera are lianas with thick, woody

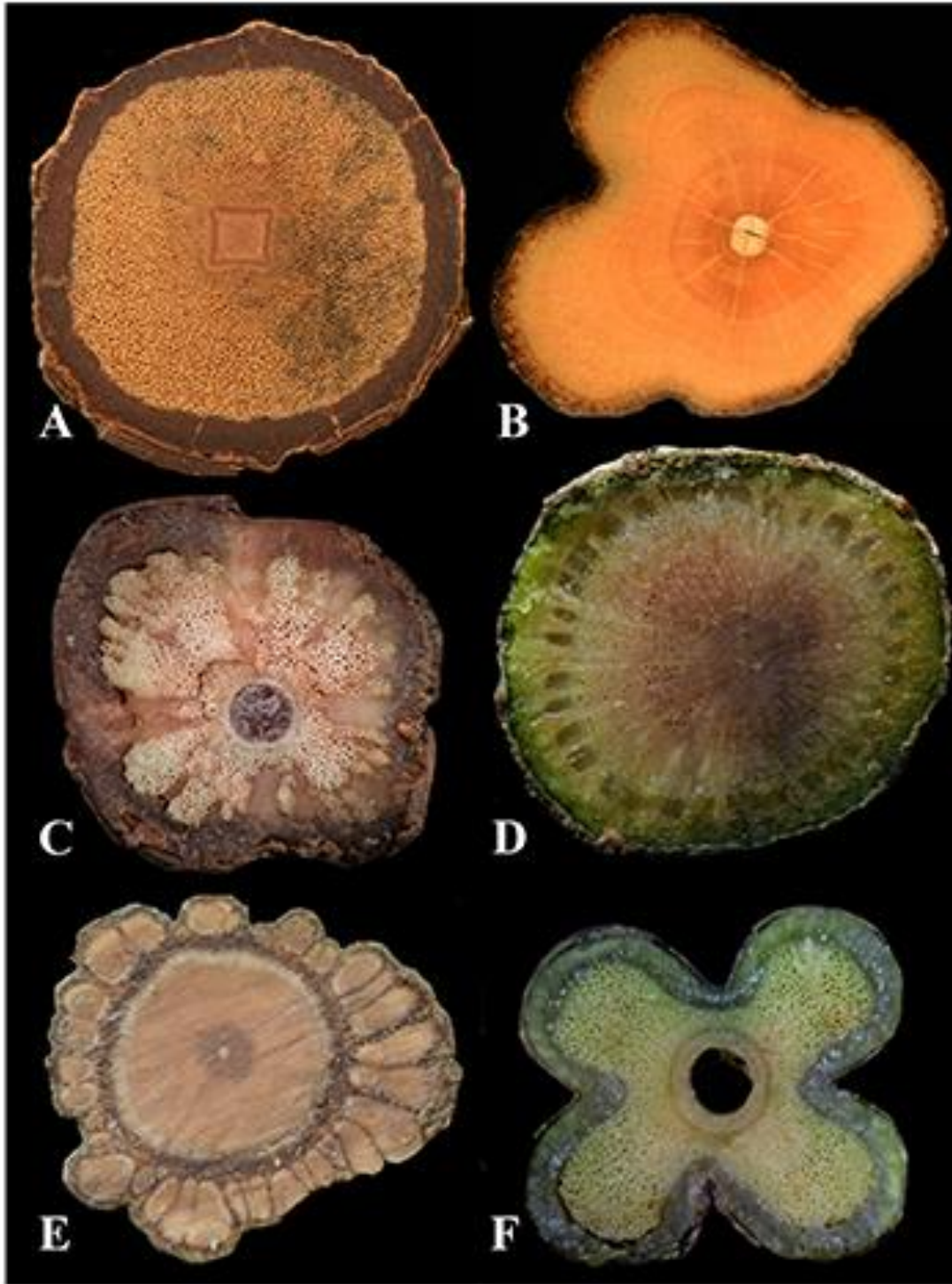


Figure 217. Cross sections of stems in Rubiaceae. **A.** Simple stem in *Uncaria guianensis*, young stems quadrangular (see square medulla) becoming cylindrical with age. **B.** Asymmetrical, lobed stem in *Randia* sp. **C.** Sub-quadrangular stem with deep phloem wedges in *Hexasepalum sarmentosum*. **D.** Cylindrical stems in *Schradera exotica*, axial elements divided in radial segments. **E.** Neoformations in *Chiococca alba* during late stages of secondary growth. **F.** 4-lobed, fistulose in *Emmeorhiza umbellata*. Photos by P. Acevedo.

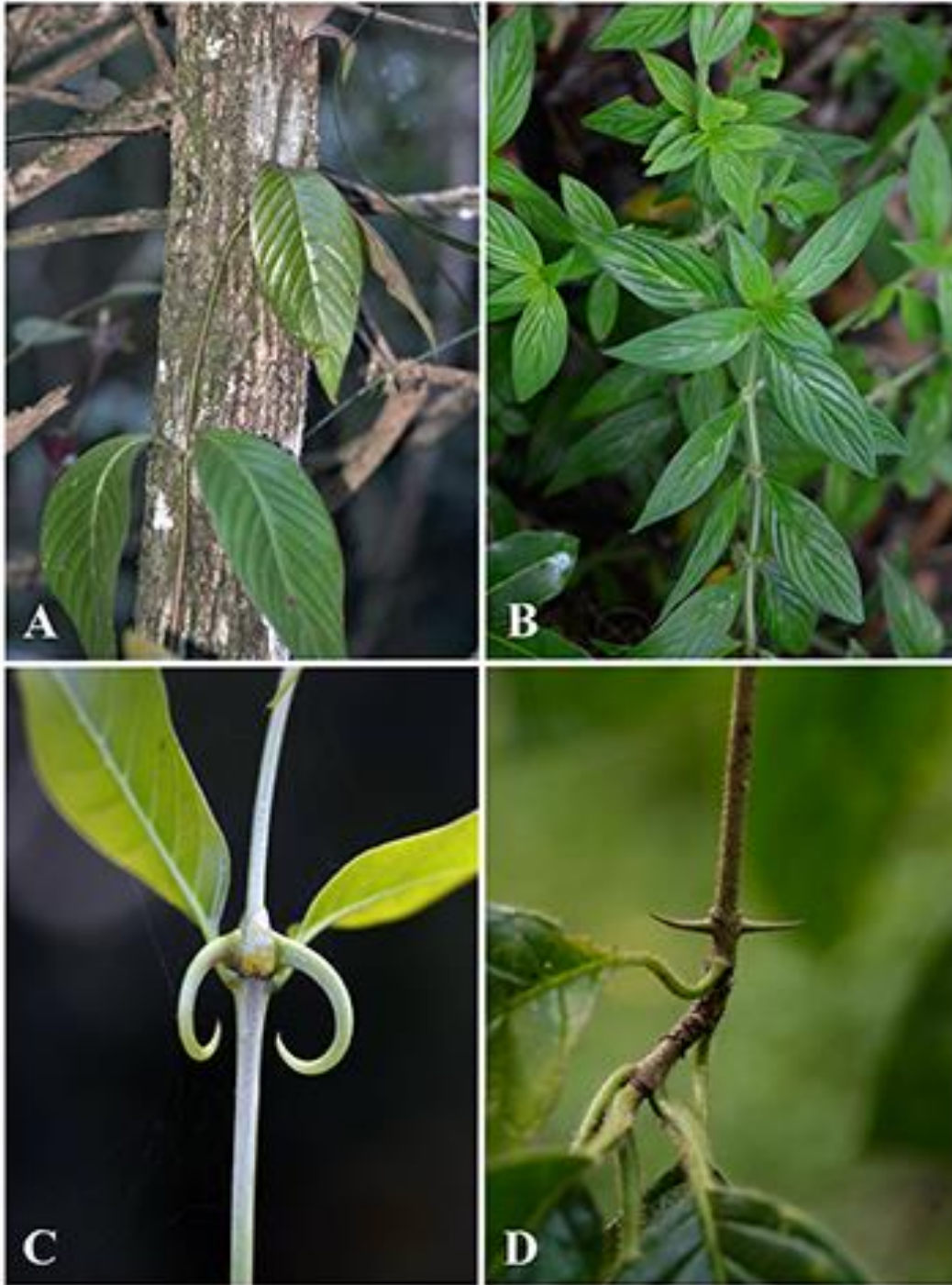


Figure 218. Climbing mechanisms in Rubiaceae. **A.** Root-climber, *Malanea macrophylla*. **B.** Scrambler, *Hexasepalum sarmentosum*. **C.** Scrambler aided by recurved, hook-like thorns, *Uncaria guianensis*. **D.** Scrambler aided by straight thorns in *Randia retroflexa*. Photos by P. Acevedo.

stems throughout (e.g., *Chiococca*, *Guettarda*, *Manettia*, *Schradera*, and *Uncaria*). Stems are cylindrical, quadrangular, lobed, or asymmetrical in cross section (Figure 217). Most genera have regular anatomy with xylem forming a continuous cylinder, however, the following anatomical variations have been documented in the family: neoformations in *Chiococca alba* (L.) Hitchc. (Figure 217E); phloem wedges in *Hexasepalum sarmentosum* (Sw.) J.H. Kirkbr. & Delprete (Figure 217C); deeply lobed stems in *Randia* and *Emmeorhiza* (Figure 217B, F); and axial elements divided in radial segments in *Schradera* (Figure 217D). Metcalfe & Chalk (1957) report that stems in *Randia asperifolia* (Sandw.) Sandw. (Guyana and Suriname) has successive, concentric cambia, however, we only have seen young stems with regular anatomy in this species. Stems of *Uncaria* exhibit overlapping layers of sclerenchyma in the cortex (Figure 217A).

2. EXUDATES. Generally watery, odorless, and colorless. The genus *Salzmannia* has stipular colleters that produce resin droplets, which later covers the stems.
3. CLIMBING MECHANISMS. Most climbing Rubiaceae are scramblers that lean on and grow over the phorophytes, these are sometimes aided by the presence of thorns (modified axillary branches) that are straight, stout or acicular (2–4 per node in *Randia*, Figure 218D; or 2 per node in *Chomelia*, *Guettarda* and *Machaonia*), or recurved and hook-like in *Uncaria* (Figure 218C). Some Rubiaceae (e.g., *Chiococca*, *Malanea*, and *Morinda*) are shrubby in early stages, later becoming scramblers. Twiners are present in *Emmeorhiza*, *Manettia*, *Paederia*, *Sabicea*, and in some species of *Chiococca*, *Cosmibuena*, *Malanea*, *Morinda*, and *Randia*. Root climbers are known in *Malanea*, *Hillia* and *Schradera* (the latter two genera have dimorphic juvenile and adult stages).

4. STIPULES. An important diagnostic character at the generic level. They are interpetiolar in all climbing genera, minute to large (sometimes foliaceous, e.g., *Galium*), entire, divided or bifid, lacinate, or fimbriate, early or late caducous, persistent and withering on the stem, or falling off by irregular fragmentation.
5. LEAVES. Simple, commonly opposite and decussate, less frequently ternate or 4 (6– 8) per node (e.g., *Galium*). Leaf margins entire or exceptionally undulate. Leaf domatia, when present, always on the abaxial side and located on secondary (less often tertiary) vein axils, these with sparse or dense tufts of hairs, hairy pockets, ciliated pits, and crypts, ciliated or not.
6. INFLORESCENCES. Most genera either have terminal or axillary inflorescences, but some genera may have both, terminal and axillary inflorescences; inflorescence position represents a good diagnostic character at the generic level. Sometimes, the inflorescences are frondose, i.e., bearing leaf-like bracts (pherophylls) that subtend lateral branches. Flowers are produced in cymes, panicles, umbels, racemes, spikes, heads, or sometimes solitary. In several dioecious genera of the tribe Gardenieae, female flowers are solitary, while male flowers are produced in inflorescences, e.g., *Randia* where male inflorescence are fasciculate (or rarely uniflorous).
7. FLOWERS. Commonly heterostylous, actinomorphic or rarely zygomorphic (e.g., *Coutarea*), bisexual, rarely unisexual or functionally unisexual where plants are dioecious or polygamous-dioecious, mostly 4–6(–10)-merous in climbing genera. Calyx commonly tubular and distally truncate, undulate, toothed or lobed, or sometimes the tube reduced or absent with free lobes; sepals of similar shape and size, slightly unequal or conspicuously unequal; sometimes one or several calyx lobes are enlarged into colored calycophylls that

may serve to attract pollinators and/or to aid seed dispersal; corolla sympetalous, tubular, hypocrateriform, infundibuliform, campanulate or rotate, with valvate, contorted or imbricate aestivation (a generic diagnostic character); stamens as many as the corolla lobes and alternate to them, with dorsifixed or basifixed anthers with longitudinal dehiscence; ovary inferior, 2(-7)-locular, surrounded by a hypanthium, placentation axile, rarely incompletely axile or parietal (e.g., *Randia*), with ovules solitary or numerous.

8. FRUITS. Simple or rarely multiple (e.g., *Morinda*), including berries, either fleshy (e.g., *Sabicea*), leathery or thinly woody with a gelatinous pulp (e.g., *Randia*); drupes with woody pyrenes (e.g., *Chiococca*, *Palicourea*); or dry capsules, either loculicidal (e.g., *Rondeletia*) or septicidal (e.g., *Emmeorrhiza*); schizocarps, either separating into free mericarps (e.g., *Machaonia*) or with mericarps suspended by thin carpophores (e.g., *Paederia*).
9. SEEDS. One to many per locule; one (rarely two) per pyrene in drupes, or mericarp in schizocarps, and sometimes in capsules; numerous in berries and capsules. They are smooth or sculptured (e.g., reticulate, foveolate, etc.), wingless, rarely winged (e.g., *Coutarea* and *Hintonia*) or comose (e.g., *Hillia*).

USES

Rubiaceae is a family with great economic importance, being the source of coffee, one of the most important crops in the world. Many genera are the source of commercial and traditional medicines. In addition, many species are cultivated as ornamentals for their beautiful flowers, foliage and forms, and several genera are a significant source of timber in the tropics. Climbing Rubiaceae are not the exception, with several species cultivated as ornamentals in private and public gardens (e.g., *Chiococca*, *Guettarda*, *Manettia* and *Nertera*). Other species are used in

traditional medicine, e.g., the bark of *Coutarea hexandra* (Jacq.) K. Schum. as a secondary source of quinine for the treatment of malaria; the roots, stems and fruits of species of *Morinda* as a tonic, appetite stimulant, purgative or aphrodisiac; the bark, leaves and fruits of the neotropical species of *Uncaria*, the most celebrated medicinal climbing Rubiaceae throughout tropical America (commonly known as *uña de gato*, *cat claw*, or *gambier*) are used as a sustainable source of tannins, iridoid glycosides and alkaloids for the treatment of diarrhea, inflammation, diabetes, rheumatic pains, acne, and respiratory problems (Azevedo et al. 2018; El-Saber et al. 2020; Honório et al. 2018; Zanetti et al. 2020; Zhang et al. 2015).

Key to genera of climbing Rubiaceae

1. Plant with a strong fetid odor; fruit a laterally compressed, dry, schizocarp, with mericarps suspended by thin carpophores upon splitting.....***Paederia***
1. Plant without fetid odor; fruit various, if schizocarpic, then not suspended by a carpophore2
2. Stipules fimbriate, with (1)3–9 setae3
2. Stipules entire or bifid (not fimbriate)6
3. Fruit schizocarpic, breaking up into 2 indehiscent mericarps.....***Hexasepalum***
3. Fruit capsular, septicidal4
4. Inflorescences terminal, paniculate, with secondary branches terminating in many-flowered umbels..... ***Emmeorhiza***
4. Inflorescences terminal and/or axillary, thyrsoid with flowers in fascicles or glomerules, or capitate5

5. Inflorescence thyrsoid, with flowers in fascicles, or flowering branches with terminal and axillary glomerules subtended by minute or small bracts; fruit capsular, dehiscent septically from the apex down to the seed insertion, with both cocci dehiscent; seed margin with a very narrow wing..... ***Denscantia***
5. Flowering branches with few- to many-flowered glomerules, these usually subtended by leaf-like bracts; fruit schizocarpic, separating into two indehiscent mericarps, or a septicidal capsule with two dehiscent cocci; seed margin without a narrow wing.....***Spermacoce***
6. Stipules truncate or bifid (connate or sheathing at base, with two triangular to linear lobes on each side of the stem)7
6. Stipules entire8
7. Stipules connate at base to sheathing, often connate to the petioles, truncate or bifid, with interpetiolar appendages, these conical, linear, shortly bifid, bilobed, fimbriate at the apex, with glandular apical projections or laminar and erose or lacinate***Notopleura***
7. Stipules sheathing at base, bifid, with two short to long triangular lobes on each side of the stem, without interpetiolar appendages***Palicourea***
8. Stems with hook-like thorns, slightly or strongly recurved, or coiled.....***Uncaria***
8. Stems unarmed or with straight thorns9
9. At least some portions of the stems armed with straight thorns10
9. Stems unarmed.....13
10. Thorns 2–4 per node, simple, without vestigial nodes or reduced leaves; plant dioecious; flowers functionally unisexual; male flowers in few- to many-flowered fasciculate or corymbose inflorescence (rarely uniflorous); female flowers solitary; ovules many per locule***Randia***

10. Thorns 2 per node, simple or compound (sometimes dendroid in *Machaonia*), often with vestigial nodes, sometimes with reduced leaves; plant monoecious or polygamous-dioecious; inflorescences with flowers of both sexes or with hermaphroditic flowers; ovules 1 per locule11
11. Fruit schizocarpic, chartaceous or thinly woody, splitting into 2 indehiscent mericarps with corky ornamentation *Machaonia martineziorum*
11. Fruit drupaceous, fleshy or succulent, with 2–7 woody pyrenes12
12. Flowers 4-merous, bisexual; corolla lobes valvate; style 2-lobed; ovary 2-locular; ovules pendulous; drupes with 2 pyrenes *Chomelia obtusa*
12. Flowers (4–)5–7(–9)-merous, bisexual, or unisexual and bisexual on the same individual; corolla lobes imbricate-quincuncial; style commonly subcapitate or shortly (2)4–7(–9)-lobed; ovary (2–)4–7(–9)-locular; ovules inserted at the middle of the placenta, vertical; drupes with (2–)4–7(–9) pyrenes *Guettarda*
13. Leaves whorled, commonly 4 (6–8) per node, including 2 leaf-like stipules; stipules commonly of same shape and size of leaves *Galium*
13. Leaves opposite or rarely ternate; stipules much smaller than leaves14
14. Inflorescence a globose head of many flowers with connate ovaries; infructescence forming a fleshy, oblong-globose, ellipsoid to ovoid, multiple fruit *Morinda*
14. Inflorescence not capitate, flowers free from each other; infructescence of free fruits15
15. Fruits dry, capsular or schizocarpic16
15. Fruits fleshy or spongy, baccate or drupaceous, or a leathery or thinly woody berry with a gelatinous pulp in *Randia*24

16. Fruit schizocarpic, chartaceous, splitting into 2 indehiscent mericarps, and leaving a persistent septum *Machaonia martinicensis*
16. Fruits capsular, septicidal or loculicidal17
17. Plant epiphytic or hemi-epiphytic, rarely terrestrial in juvenile stages; young branchlets fleshy; leaf secondary veins inconspicuous; corolla large, tube 24–150 mm long; capsules (2–)3–15 cm long.....18
17. Plant terrestrial (rarely hemiepiphytic lianas in a few species of *Manettia*); young branchlets woody or herbaceous; leaf secondary veins abaxially conspicuous or prominent; corolla small to medium-sized, tube less than 24 mm long or 1.8–45 mm long in *Manettia*; capsules less than 2.5 cm long19
18. Stipules shallowly fused at base; calyx tubular, truncate or shallowly to deeply lobed; corolla lobes imbricate (quincuncial) or rarely convoluted; capsules cylindrical, sometimes lenticellate; seeds elliptic, dorsoventrally compressed, with a narrow rhombic, membranaceous, entire or irregularly erose wing.....*Cosmibuena*
18. Stipules free at base; calyx with free lobes, not tubular; corolla lobes convoluted (i.e., right-contorted); capsules oblong to narrowly oblong, slightly compressed, septicidal, mericarps secondarily splitting at apex; seeds fusiform, comose at distal end*Hillia*
19. Terrestrial, herbaceous or woody twiners, rarely hemiepiphytic lianas with adventitious roots at nodes; inflorescence axillary, thyrsoïd, dichasial or fasciculate, pauci- or multi-florous, rarely uniflorous; capsule septicidal*Manettia*
19. Terrestrial shrubs or small to medium-sized trees, rarely climbing shrubs or woody vines; inflorescence terminal or axillary, cymose, paniculate or corymbose, pauci- or multi-florous; capsules loculicidal (secondarily septicidal) or septicidal.....20

20. Corollas campanulate or broadly infundibuliform, tube 2–7.5 cm long; filaments basally connate, inserted at base of the corolla tube; capsules more than 1.8 cm long21
20. Corollas hypocrateriform, tube up to 2 cm long; filaments free, inserted at median or distal portion of the corolla tube; capsules less than 1.8 cm long22
21. Flowers actinomorphic, 8-merous; corolla straight, with equal stamens; corolla tube 2.5–6 cm long; capsule septicidal, ellipsoid or globose, 2–3.5 cm long, terete in cross section *Hintonia octomera*
21. Flowers zygomorphic, 6-merous; corollas curved, with unequal stamens; corolla tube 1.9–7.5 cm long; capsule loculicidal, obovate to oblong-ovate in outline, 1.8–7 cm long, laterally compressed *Coutarea hexandra*
22. Corolla mouth glabrous, lacking a thick fleshy ring; capsules septicidal or loculicidal *Arachnothryx*
22. Corolla mouth with a thick fleshy ring, or a ring of yellow or white hairs; capsules loculicidal23
23. Corolla with a ring of yellow or white hairs within the mouth; seeds horizontal (perpendicular to the septum), small, angular, globose, fusiform or falciform, narrowly or partially winged; wing bipolar or unipolar, rarely absent *Rogiera*
23. Corolla with a thick fleshy glabrous ring at mouth; seeds vertical, with a central hilum, dorsoventrally compressed, fusiform or irregularly elliptic, winged; wing bipolar *Rondeletia*
24. Fruit drupaceous, fleshy or spongy, with 2–several woody pyrenes25
24. Fruit a fleshy, many-seeded berry.....35
25. Herbaceous vines; stipules withering on the stem *Didymaea*
25. Woody vines (lianas), or scrambling shrubs; stipules not withering on stems.....26

26. Stipules persistent, becoming indurate, distal portion falling off by fragmentation, entire, dentate, or with 1–2 short acumens or with 1–2 aristae, these sometimes with 1–2 caducous glandular appendages; pyrenes with 2 marginal germination slits extending to the middle and sometimes also with several shorter dorsal slits *Eumachia*
26. Stipules not becoming indurate; pyrenes with germination apertures not marginal.....27
27. Distal portion of branches covered with resinous exudates; apical stipules producing a small globe of resinous exudate; scrambling shrubs *Salzmannia*
27. Distal portion of branches not covered with resinous exudates; apical stipules not producing a globe of resinous exudate; terrestrial or epiphytic shrubs, woody vines, lianas, twining or scrambling, sometimes shrubs, treelets or trees with scandent or clambering branches28
28. Stipules with interpetiolar appendages, these conical, linear, shortly bifid, bilobed or fimbriate at apex, with glandular apical projections or laminar and erose or lacinate; fruits with 2 pyrenes *Notopleura*
28. Stipules without interpetiolar appendages; fruits with 2–7 pyrenes29
29. Stipules bifid, with two short to long triangular lobes on each side of the stem
..... *Palicourea*
29. Stipules entire, broadly to narrowly triangular, acuminate (rarely bifid at tip), narrowly ovate, obovate, elliptic, oblong or oblanceolate30
30. Ovary 2-locular, with 2 ovules per locule, sometimes appearing as 4-locular due to thick placenta within each locule; pyrenes (2–3) 4 per fruit *Appunia megalantha*
30. Ovary 2–7-locular, with 1 ovule per locule; pyrenes 2–7 per fruit.....31
31. Corolla tubular-subcylindrical; filaments inserted at base of corolla tube (forming a minute tube at base of corolla); fruits with 2 pyrenes, or rarely with 1 pyrene (by abortion).....32

31. Corolla hypocrateriform or infundibuliform; filaments inserted just below or at the corolla mouth; fruit with (1)2–7 pyrenes33
32. Stems not resinous; inflorescence paniculate or racemose; calyx extremely reduced, lobes broadly to narrowly triangular; corolla campanulate or broadly infundibuliform, white, cream-white to pale yellow throughout, the tube narrowly reduplicate; fruits globose to oblong-cylindrical, sometimes laterally compressed..... *Chiococca*
32. Stems often slightly resinous; inflorescence cymose; calyx tube narrowly obovoid, shallowly lobed; corolla purple-brown outside and deep yellow inside, the tube not reduplicate; fruit subglobose to obovoid (endemic to eastern Cuba) *Ramonadoxa*
33. Flowers (4–)5–7(–9)-merous, bisexual or unisexual and bisexual on same individual (polygamous-dioecious); corolla lobes imbricate (quincuncial), with entire, undulate or fringed margin; ovary (2–)4–7(–9)-locular; fruit globose, ovoid or oblong-ovoid, with (2–)4–7(–9) pyrenes *Guettarda*
33. Flowers 4(5)-merous, bisexual; corolla lobes valvate or valvate-induplicate, with entire margin; ovary (1)2–3-locular; fruit fusiform, ellipsoid, oblong-ellipsoid or cylindrical, with (1) 2–3 pyrenes34
34. Flowers 4(5)-merous, heterostylous or possibly homostylous; corolla lobes valvate or valvate-induplicate, ovate, lanceolate, oblong, oblong-ovate, linear-lanceolate or linear, round, ovate or acute at apex, sometimes short- or long-acuminate at apex, sometimes with a rhomboidal or triangular internal appendix at apex *Chomelia*
34. Flowers 4-merous, heterostylous; corolla lobes valvate, narrowly ovate, lanceolate, oblong or ligulate, round or acute at apex, without an internal apical appendix *Malanea*

35. Twining or scrambling vines, rarely a shrub with scrambling branches; plants monomorphic, without adventitious roots; stipules persistent, free at base; inflorescences axillary, 1 or 2 per node, compact-verticillate, fascicled, glomerulate, capitate or laxly paniculate; flowers free from each other; ovary 4–5(–7)-locular; fruits free from each other*Sabicea*
35. Terrestrial or epiphytic vines; plants with distinct juvenile and adult stages (juvenile with adventitious roots); stipules caducous, sheathing at base; inflorescences axillary or terminal, 2 or 3 per node, a pedunculate capitulum subtended by a discoid involucre; flowers congested, free or basally connate; ovary 2(4)-locular, basally connate with those of the same head; fruits usually basally connate forming a head *Schradera*

Identification of genera based on vegetative characters

Stipules (interpetiolar).

- A) Entire. Triangular, ovate, elliptic, obovate, oblong, ligulate, linear: *Appunia*,
Arachnothryx, *Chiococca*, *Cosmibuena*, *Coutarea*, *Didymaea*, *Eumachia*, *Guettarda*,
Hillia, *Hintonia*, *Machaonia*, *Malanea*, *Manettia*, *Morinda*, *Paederia*, *Randia*,
Rogiera, *Rondeletia*, *Sabicea*, *Salzmannia*, *Schradera*, and *Uncaria*;
- B) Fimbriate. With (1)3–7(–9) setae: *Denscantia*, *Emmeorhiza*, and *Hexasepalum*.
- C) Withering. Withering on the stem (no abscission layer). Stipules persistent, deltoid to narrowly triangular, and remaining on stem as a series of triangular units on either side of the nodes: *Didymaea*.
- D) Indurate. Stipules become hardened when old, with the distal portion falling off by fragmentation; they are dentate or with 1–2 short acumens or aristae, these sometimes with 1–2 caducous glandular appendages: *Eumachia*.

E) Resinous. Stipules with abundant resinous exudate, forming a globose structure at the distal nodes, and covering stems: *Salzmannia*.

F) Foliaceous. Stipules are leaf-like, giving the impression of whorled leaves, 4–6(–8) per node: *Galium*.

Thorns. Present in a few genera. Some species may develop thorns or not, which may be variable on different portions of the stem. In *Randia*, thorns are straight stout or acicular and 2–4 per node. In *Chomelia* and *Guettarda*, they are straight or slightly curved, stout or acicular, simple (without vestigial nodes) and two per node. In *Uncaria*, thorns are hook-shaped, slightly or strongly recurved and one or two per node.

Involucral bract. The pedunculate flowering heads subtended by an involucral, discoid or cup-shaped bract that sometimes splits irregularly with age: *Schradera*.

Heterophylly. Juvenile shoots with small leaves, thin flattened stems, climbing by means of adventitious roots and adult shoots with large leaves, with thick, woody stems, that hang down from the phorophyte: *Hillia* and *Schradera*.

APPUNIA J. D. Hooker in Bentham & J. D. Hooker, Gen. Pl. 2: 120. 1873.

Weakly branching shrubs or small trees, sometimes scrambling lianas, unarmed. Stipules



Appunia guatemalensis, photo by Jan Meerman.

persistent or
caducous, free or
briefly connate at
base, broadly to
narrowly triangular,
acuminate or bifid at
tip. Leaves opposite
(ternate in non-
climbing species),
petiolate; blades

elliptic, ovate, lanceolate to oblanceolate, membranaceous, chartaceous to subcoriaceous; domatia absent. Inflorescences leaf-opposed, with 1 or 3 leaves opposed to the peduncles (due to extreme reduction of internode), or occasionally terminal, pedunculate, sometimes with secondary peduncles, capitate, with 2–10(–15) flowers per head; ovaries of individual flowers congested but not fused. Flowers 4–5(6)-merous, heterostylous. Calyx persistent, extremely reduced, tubular or funnelform, truncate, undulate or with small, broadly triangular lobes; corolla hypocrateriform or narrowly infundibuliform, pale green to white, tube adaxially glabrous or pilose near the base; lobes 4–5(6), valvate, reflexed, linear-lanceolate, margins entire or ciliate, dorsally corniculate; stamens included, inserted near middle of tube or near mouth of corolla, glabrous, anthers oblong; ovary 2-locular, with 2 ovules per locule, sometimes appearing as 4-locular due to thick placenta within each locule; style included or exerted just beyond corolla mouth, obtuse to capitate, or shortly bifid. Infructescence a head of a few to many fruits

congested but not fused. Fruit drupaceous, globose to oblong-ovoid, passing from red to maroon or purple-black at maturity; pyrenes 4 or fewer per fruit (due to the abortion of 1–2 ovules), vertical, woody, ovoid to reniform, angled at the ventral edge.

Distinctive features: Recognized by the leaf-opposed inflorescences. Inflorescences often with 2 or 3 peduncles per node, capitate, with individual flowers congested but not fused; ovary 2-locular, commonly with 2 ovules per locule. Fruits fleshy drupes, congested but not fused, with (2–3) 4 pyrenes.

Distribution: About 12 species distributed from Central America to northern South America, with a few species in the Amazon basin; highest diversity in Venezuela and the Guianas. Only *A. megalantha* C. M. Taylor & Lorence, from Colombia, Ecuador and northern Peru, is reported as a liana; wet forests; 320–850 m.

ARACHNOTHRYX Planchon, Fl. Serres Jard. Eur. 5: 442. 1849.

Shrubs or small trees, rarely scrambling shrubs or woody vines, unarmed. Stipules caducous, free or sheathing at base, oblong-ovate, acute to acuminate. Leaves opposite, isophyllous or anisophyllous, short- to long-petiolate; blades elliptic to oblanceolate, chartaceous, domatia absent; tertiary venation clathrate. Inflorescence terminal, frondose or not, thyrsoid, pauci- or multi-florous. Flowers 4(5)-merous, heterostylous, fragrant. Calyx lobes lanceolate, acute; corolla actinomorphic, hypocrateriform, pink, glabrous and lacking a fleshy ring at mouth, tube arachnoid-tomentose or glabrous outside, lobes imbricate, round, margin eroded or crisped; stamens included (in long-styled flowers) or partially exerted (in short-styled flowers), filaments inserted at median or distal portion of the tube, anthers short, narrowly oblong, basifixed; style exerted just beyond the corolla mouth (in long-styled flowers) or

included (in short-styled flowers), terete, glabrous, with 2 oblong lobes; ovary 2-locular; placentation axile, ovules many per locule. Fruit a globose, crustaceous capsule dehiscing basipetally. Seeds horizontal, rhomboid or multi-angular, margins undulate, fringed, or narrowly winged; testa foveolate, rugulose.

Distinctive features: Similar to *Rondeletia* and *Rogiera* in being woody and by having capsular fruits but distinguished by the glabrous corolla mouth lacking a fleshy ring or a ring of hairs (vs. thick fleshy ring in *Rondeletia* or with a ring of yellow or white hairs in *Rogiera*).

Distribution: About 80 species, of which only *A. darienensis* (Standl.) Borhidi, from Panama (Darien) and Colombia (Chocó), has a variable habit that includes scrambling shrubs or lianas; moist forests; 20–274 m.

CHIOCOCCA P. Browne, Civ. Nat. Hist. Jamaica 164. 1756.

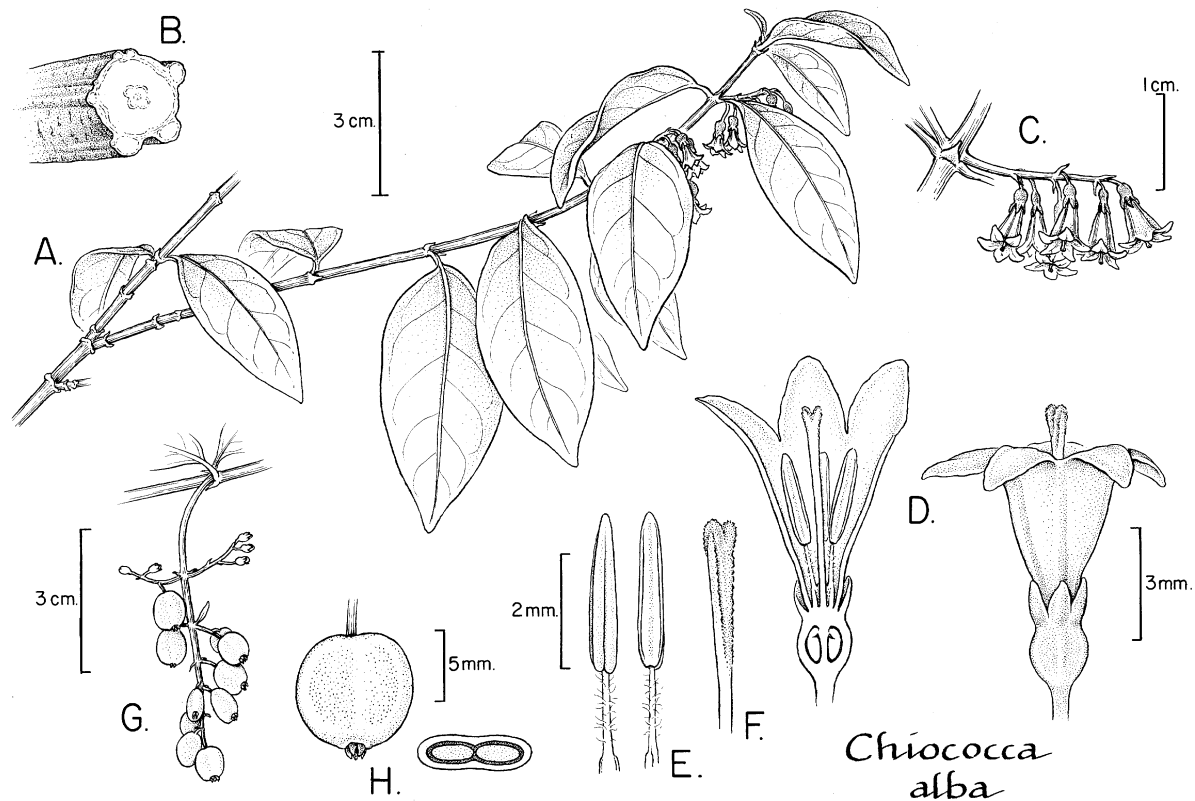
Scrambling or twining lianas, shrubs or treelets with scrambling branches; unarmed. Lianas



Chiococca alba, photo by P. Acevedo.

with twisted, deeply furrowed stems, reaching 10–15 m in length and up to 6 cm in diam.; commonly with short, opposite, plagiotropic branches; cross sections (known only for *C. alba* (L.) Hitchc.) with neofomed vascular cylinders in the cortex

(Figures 4F; 217E). Stipules persistent, connate at base, deltoid or narrowly triangular. Leaves



Chiococca alba. **A.** Flowering branch. **B.** Cross section of mature stem showing neoformations. **C.** Inflorescence. **D.** Flower, longitudinal section & lateral view. **E.** Stamens. **F.** Distal portion of style showing stigmatic area. **G.** Infructescence. **H.** Fruit, lateral view and cross section. Drawing courtesy of Bobbi Angell.

opposite, subsessile or short-petiolate; domatia absent. Inflorescences axillary, paniculate or racemose, sparsely branched. Flowers 4–5(–6)-merous, homostylous. Calyx persistent, extremely reduced, lobes broadly to narrowly triangular; corolla < 1 cm long, campanulate or broadly infundibuliform, white, cream-white, greenish white or yellow; tube narrowly reduplicate, glabrous or puberulous outside, glabrous or pubescent inside, lobes valvate or narrowly imbricate, broadly to narrowly triangular; stamens included or partially exerted, filaments inserted at base of corolla, basally connate forming a short tube, anthers elliptic to linear; ovary 2-locular, with 1 pendulous ovule per locule, style exerted just beyond corolla mouth, glabrous,

capitate. Fruit drupaceous, fleshy or spongy, white, globose to oblong-cylindrical, terete or laterally compressed, with (1)2 woody, 1-seeded pyrenes. Seeds pendulous, laterally compressed.

Distinctive features: Corolla small, campanulate or broadly infundibuliform, white, cream-white, greenish white or yellow, with tube narrowly reduplicate, and lobes valvate or narrowly imbricate. Fruits are fleshy or spongy drupes, white, circular to ovate more or less laterally compressed. The widespread *C. alba* is easily recognized by the twining branches, deeply furrowed stems with numerous neoformations of vascular cylinders, and white laterally compressed drupes.

Distribution: A neotropical genus with ~20 species, seven of which are reported as climbers; distributed in United States (Florida), Mexico through Central America, the West Indies, and South America in Colombia, Venezuela, the Guianas, Ecuador, Peru, Bolivia, Brazil, Paraguay and northern Argentina; dry to moist forests; 0–2,400 m.

CHOMELIA Jacquin, Enum. Syst. Pl. 1, 12. 1760 (nom. cons.).

Shrubs or trees, sometimes with leaning branches, a few species growing as scrambling vines or lianas up to 6 m long; branches short and opposite; unarmed or with axillary pairs of



Chomelia psilocarpa, photo by A. Hernández.

straight, acicular thorns, simple, or compound (brachyblasts, sometimes with vestigial nodes and vestigial leaves). Stipules persistent or caducous, free or connate at base, broadly to narrowly triangular. Leaves opposite, short- to long-

petiolate; blades chartaceous to subcoriaceous, sometimes with sunken secondary veins; domatia tufts of dense hairs or absent. Inflorescence axillary or terminal on axillary short shoots of 3–5 nodes, cymose, pauci- or multi-florous, sometimes with scorpioid branches, or dichasial cymes, fasciculate or uniflorous. Flowers 4(5)-merous, heterostylous or possibly homostylous; hypanthium ovoid, narrowly obovoid, obovoid, oblate or turbinate. Calyx persistent, short- to long-tubular, lobes ovate, oblong, narrowly triangular or linear; corolla narrowly infundibuliform, white to cream-white or yellowish white, glabrous, the tube sometimes strigose or sericeous outside, lobes valvate or valvate-induplicate, acute (acuminate) at apex, with a rhomboidal or triangular internal appendix at apex; stamens included or partially exserted, inserted near the corolla mouth, filaments short, equal, glabrous, anthers subsessile, elliptic narrowly elliptic, oblong to narrowly oblong, sometimes with pointed extension or tailed at base, dorsifixed near the base; ovary 2(3)-locular; placentation axile, ovules 1 per locule, apically

inserted, pendulous, style 2(3)-lobed. Fruit drupaceous, fleshy, fusiform or ellipsoid, turning red to purple to bluish black when mature; pyrenes 2(3), pendulous, woody, dorsoventrally convex. Seeds cylindrical.

Distinctive features: Similar to *Guettarda* but differs by the 4(5)-merous flowers, valvate corolla lobes in bud, style 2(3)-lobed, ovary 2(3)-locular and fruits with (1)2(3) pyrenes [vs. flowers (4–)5–7(–9)-merous, corolla lobes imbricate-quincuncial, style subcapitate or (2–)4–7(–9)-lobed, ovary (2–)4–7(–9)-locular and fruits with (2–)4–7(–9) pyrenes in *Guettarda*].

Distribution: A neotropical genus of ~70 species, five of which sometimes grow as scrambling vines; from Panama to Bolivia, including the Guianas and the Amazon basin; lowland, moist forests; 0–1,200 m.

COSMIBUENA Ruiz & Pavón, Fl. Peruv. 3: 2. 1802 (nom. cons.).

Shrub or trees, epiphytic, rarely terrestrial, rarely climbing with twining or scrambling,



Cosmibuena grandiflora, photo by C. Galdames.

unarmed branches; terminal branchlets commonly succulent. Stipules caducous (those subtending flowers somewhat persistent), connate to sheathing at base, free portion obovate to oblanceolate.

Leaves opposite, petiolate; blades ovate, elliptic, obovate, or oblong,

subcoriaceous, coriaceous to succulent;

domatia absent. Inflorescences terminal,

cymose, multiflorous or rarely uniflorous. Flowers (4–)5–6(–7)-merous, homostylous, nocturnal.

Calyx persistent or deciduous, membranaceous to coriaceous, truncate or shallowly to deeply divided; corolla hypocrateriform, white, cream-white, greenish white, turning cream to yellow after anthesis, tube long and narrow, glabrous (rarely papillose) inside and outside, lobes imbricate or rarely convolute, elliptic, elliptic-oblong to oblong, or rarely ovate; stamens included or partially exerted, filaments inserted at distal portion of tube, anthers oblong; ovary 2-locular; ovules many per locule, vertical, imbricate, style exerted just beyond corolla mouth, glabrous, branches 2, elliptic to ovate. Fruit capsular, septicidal, cylindrical, woody, dark brown when dry, smooth or with several lenticels. Seeds elliptic, dorsoventrally compressed, with a narrow rhombic, membranaceous wing, margin entire or irregularly erose.

Distinctive features: *Cosmibuena* and *Hillia* are similar in being epiphytic or hemi-epiphytic, shrubs or trees, with succulent terminal branches, coriaceous or succulent leaves, large flowers, and large capsules. *Cosmibuena* differs from *Hillia* by the stipules shallowly fused at base, calyx truncate or divided, and seeds with a membranaceous wing; while in *Hillia* stipules are free, calyx lobes free at base (tube absent), and seeds with a tuft of long hairs at distal end.

Distribution: A genus of four species, commonly of erect shrubs or trees, sometimes with scrambling lateral branches; Mexico to Peru, Bolivia and southern Brazil; *Cosmibuena grandiflora* (Ruiz & Pav.) Rusby, although commonly a tree, is known to grow in Venezuela (*Tillett 45481*) as a liana 30 m long; moist forest, savanna; 0–1,300 m.

COUTAREA Aublet, Hist. Pl. Guiane 1: 314. 1775.

Shrubs or small to medium-sized (rarely tall) trees, or rarely scrambling (?) lianas;



Coutarea hexandra, photo by A. Popovkin.

unarmed; bark fissured; young branches often lenticellate.

Stipules free at base, broadly triangular to deltoid, persistent.

Leaves opposite, short-petiolate; blades ovate to

elliptic, chartaceous to thinly coriaceous; domatia tufts of

sparse or dense hairs, or absent.

Inflorescences terminal, paniculate, frondose or not, sparsely branched. Flowers (5–)6–7-merous; flower buds curved. Calyx cup-shaped, persistent, lobes linear; corolla campanulate, zygomorphic, white, cream-white, pale green, pink, red, violet to purple, tube reduplicate at edges, glabrous throughout, lobes imbricate, ovate to deltoid, margin entire, rounded at apex; stamens partially exerted, filaments long, unequal, glabrous throughout or puberulent at basal portion inserted at base of corolla, anthers linear, dorsifixed near base; ovary 2-locular, placentation axile, peltate to entire length of septum, ovules many per locule, style exerted just beyond corolla, glabrous, style 2-branched. Fruit capsular, dehiscent loculicidally from apex, obovate to oblong-ovate in outline, laterally compressed, woody, often lenticellate. Seeds many, ascendingly imbricate, oblong-ovate in outline; wing concentric, membranous, with entire margin.

Distinctive features: Characterized by the large, campanulate, zygomorphic corollas, with a curved tube, reduplicate at edges, lobes imbricate in bud; hypanthium laterally compressed; and

filaments connate at base, inserted at base of corolla tube, and of different lengths. Capsules laterally compressed, obovate to oblong-ovate in outline and often lenticellate.

Distribution: A genus of two species; Mexico throughout Central America to Peru, Bolivia, Brazil to northern Argentina. *Coutarea hexandra* (Jacq.) K. Schum., although commonly a shrub or a small to large tree, sometimes grows as a shrub with scrambling branches or as a liana; scrublands to dense forests; 0–1,730 m.

DENSCANTIA E.L. Cabral & Bacigalupo, *Darwiniana* 39: 353. 2002.

Scrambling herbaceous or subwoody vines; unarmed; stems basally woody. Stipules



Denscantia cymosa, photo by W. Oliveira Fonseca.

persistent, often withering on the stem, sheathing and connate to the petioles, fimbriate, with 1 or 3–8 setae, each seta with an apical colleter. Leaves opposite, sometimes seeming whorled by the presence of axillary short shoots (brachyblasts), subsessile or short-petiolate; blades elliptic, obovate, narrowly elliptic to elliptic-lanceolate, membranaceous, chartaceous or papyraceous.

Inflorescence terminal, thyrseoid, frondose or not, lateral branches with flower glomerules, or flowering branches with terminal and axillary

flower fascicles or glomerules. Flowers 4-merous,

homostylous. Calyx persistent, lobes small, narrowly triangular; corolla infundibuliform to tubular, white, cream-white to pink, tube externally glabrous or puberulent, internally glabrous,

puberulent or pubescent with moniliform hairs, lobes valvate, narrowly ovate, narrowly triangular or oblong; stamens exerted well beyond the corolla, filaments inserted near the mouth of the corolla tube or at lobe sinuses, anthers elliptic or oblong; ovary 2-locular, ovules 1 per locule, centrally inserted, vertical, style exerted well beyond the corolla, capitate-bilobed. Fruit capsular, ovoid, obovoid, oblong-ovoid, dehiscent septicidally from the apex down to the seed insertion, both cocci dehiscent, thinly woody or crustaceous. Seeds vertical, plano-convex, oblong-ovate in outline, ventrally sulcate, margin with a very narrow wing.

Distinctive features: Climbing herbs or subshrubs, with sheathing fimbriate stipules bearing (1)3–8 setae, often withering on the stem, and a thyrsoid inflorescence with flowers in fascicles or glomerules. Capsules with both cocci dehiscent septicidally from the apex down to the seed insertion. Similar to *Spermacoce* (see discussion under that genus).

Distribution: A genus of five species endemic to the Atlantic coastal forests of Brazil, from Alagoas to Rio de Janeiro; 50–800 m.

DIDYMAEA J. D. Hooker in Bentham & J. D. Hooker, Gen. Pl. 2: 150. 1873.

Procumbent herbs or scrambling vines to 4.5 m long; stems terete, unarmed. Stipules



Didymaea mexicana, photo by M. Jiménez Chimil.

persistent, free at base, deltoid to narrowly triangular, withering on the stem as a series of triangular units on either side of the nodes. Leaves opposite; sessile, or short- to long-petiolate; blades ovate, broadly ovate, narrowly ovate,

elliptic, broadly elliptic, narrowly lanceolate, lanceolate, cordate, or orbicular; membranaceous or chartaceous; domatia absent. Inflorescence axillary, cymose, pauciflorous, or uniflorous; bracts small. Flowers 4-merous, homostylous. Calyx tube extremely reduced, persistent, truncate or undulate; corolla campanulate or rotate, actinomorphic, greenish brown, yellowish white, purplish, violet to purple, tube glabrous, lobes valvate, narrowly triangular; stamens partially exserted or exserted just beyond the corolla, filaments inserted on upper portion of tube or near the mouth of the corolla, short or long, shorter than the corolla tube, equal, glabrous, anthers elliptic, round at base and at apex; ovary 2-locular, ovules 1 per locule, basally inserted, style exserted or partially exserted, glabrous, stigmatic lobes 2, ovate. Fruit drupaceous, fleshy, didymous or globose, bluish black to purplish black. Pyrenes (1)2, ascending, hemispherical, woody, 1-seeded. Seeds minute, reniform.

Distinctive features: Scrambling herbs or herbaceous vines to 4.5 m long, with deltoid to narrowly triangular stipules withering on the stem as a series of triangular units on both sides of the nodes. Drupes fleshy, bluish black to purplish black.

Distribution: A neotropical genus of eight species of which only *D. mexicana* Hook. f. grows as a vine that reaches more than 2 m in length; northeastern Mexico to Panama; moist tickets, cloud forests and rocky slopes; 1,500–2,300 m.

EMMEORHIZA Pohl ex Endlicher, Gen. Pl. 565. 1838.

Twining vines, often with short plagiotropic branches; stems woody at the base, unarmed



Emmeorhiza umbellata, photo by P. Acevedo.

5–10 m long and ~1 cm in diam.; cross section deeply 4-lobed and often fistulose (Figure 217F). Stipules persistent, often withering on stem, sheathing, connate to petioles, fimbriate, with 3–9 setae, each seta with an apical colleter.

Leaves opposite or ternate, often seemingly whorled by the presence of axillary short shoots (brachyblasts) with fasciculate leaves, sessile to short-petiolate; blades ovate, narrowly ovate, broadly to narrowly elliptic, rhombic to oblong, chartaceous to papyraceous; domatia absent.

Inflorescences terminal, paniculate, with secondary branches terminating on many-flowered

umbels. Flowers 4-merous, homostylous. Calyx persistent, tube extremely reduced, lobes minute or small, narrowly triangular, lanceolate, narrowly lanceolate to linear; corolla broadly infundibuliform, white or cream-white, tube externally glabrous, internally pubescent or villous at medial-basal portion, lobes valvate, narrowly ovate; stamens exserted well beyond the corolla, filaments inserted near the mouth of corolla tube or at lobes sinuses, anthers elliptic to narrowly elliptic; ovary 2-locular, ovules 1 per locule, centrally inserted, style exserted well beyond the corolla mouth, branches 2, oblong. Fruit capsular, narrowly obconical to turbinate, dehiscent septicidally from the apex down to the seed insertion, valves indehiscent. Seeds 2 per capsule, vertical, laterally compressed, narrowly oblong in outline; wings bipolar, somewhat acute at both ends, margin entire.

Distinctive features: Twining, subwoody vine; stems deeply lobed, fistulose; inflorescences paniculate with flowers clustered in umbels. Fruit capsular, dehiscent septicidally from the apex down to the seed insertion, with indehiscent valves.

Distribution: A genus of a single species, *E. umbellata* (Spreng.) K. Schum.; Colombia, Venezuela, Trinidad, the Guianas south to Brazil, Bolivia and northern Argentina; moist forests; 30–2,500 m.

EUMACHIA A.P. de Candolle, Prodr. 4: 478. 1830.

Subshrubs, shrubs or trees, rarely creeping or climbing herbs, or scrambling vines;



Eumachia microdon, photo by M. Caraballo-Ortiz.

unarmed; stem in *E. microdon* (DC.) Delprete & J.H. Kirkbr. quadrangular to slightly flattened, 2–2.5 m long. Stipules persistent, becoming indurate, distal portion falling off by fragmentation, free at base, entire. Leaves opposite, long-petiolate; blades ovate, elliptic, obovate, oblong or narrowly

elliptic, chartaceous or papyraceous; domatia absent. Inflorescences terminal, pedunculate, subcapitate or paniculate with 2–several pairs of secondary branches, few- to many-flowered, with 2–8 bracts, either subtending inflorescence or inserted on inflorescence branches. Flowers 5-merous, heterostylous. Calyx persistent, minute, cyathiform or cup-shaped, lobed or undulate, lobes (when present) small, broadly to narrowly triangular; corolla actinomorphic, hypocrateriform, infundibuliform or campanulate, white or cream-white, tube glabrous outside, lobes valvate, ovate-triangular, oblong-ovate, ovate to oblong-lanceolate to elliptic-ovate, appendiculate on the adaxial side; stamens included in long-styled flowers, as long as the corolla tube or exerted in short-styled flowers, anthers ovoid to ellipsoid; ovary 2-locular, ovules 1 per locule, basally inserted, erect, style glabrous, 2-branched. Fruit drupaceous, subglobose to ellipsoid, fleshy, with 2 pyrenes, turning from orange-red to red to purplish red to bluish or purplish black at maturity; pyrenes woody, plano-convex, ovate to elliptic in outline, with 2

marginal germination slits extending to the middle and sometimes also with several shorter dorsal slits, dorsally multicostate, ventrally flat.

Distinctive features: Scrambling shrubs with persistent, indurate stipules with distal portion falling off by fragmentation; drupes subglobose to ellipsoid, turning from orange-red to red to purplish red to bluish or purplish black at maturity; pyrenes dorsally multicostate, ventrally flat, with 2 marginal germination slits extending to the middle, and sometimes also with several shorter dorsal slits.

Distribution: A pantropical genus of ~90 species, with 27–30 in the Neotropics, of which *E. microdon* is the only species that grows as a scrambling shrub in addition to being an erect shrub; Mexico to Panama, Greater and Lesser Antilles, Guyana, Venezuela, Colombia, Ecuador, and Peru; understory of evergreen or seasonal forests; 50–1,050 m.

GALIUM Linnaeus, Sp. Pl. 105. 1753.

Erect, sprawling or scrambling herbs (to 4 m long), annual or perennial herbs, or



Galium hypocarpium, photo by B. Hammel.

subshrubs; unarmed.

Stipules persistent,
commonly of same
shape and size of leaves.

Leaves whorled,
commonly 4 (rarely 6–8)
per node (including the 2
leaf-like stipules),

subsessile or sessile;

blades ovate, narrowly ovate, elliptic, narrowly elliptic, oblong, lanceolate or linear, membranaceous or chartaceous; domatia absent. Inflorescences axillary or terminal, paniculate or cymose, frondose or not, 1-, few- or many-flowered. Flowers (3–)4–5-merous, bisexual, unisexual or functionally unisexual (male and female flowers on separate individuals), or unisexual and bisexual on same individual (polygamous-monoecious). Calyx lobes free, caducous, ovate, lanceolate to narrowly ovate; corolla campanulate, urceolate or rotate, white, cream-white, greenish white, yellow, yellowish white, pink, red or maroon, tube (when present) glabrous, internally glabrous, pubescent or hispid, lobes valvate, ovate, margin entire; stamens inserted at sinuses of corolla lobes, filaments short, glabrous, anthers elliptic or oblong; ovary 2-locular, placenta axile, reduced, ovules 1 per locule, centrally inserted, vertical; styles 2, sometimes united at base, capitate, glabrous. Fruits didymous, baccate, fleshy, white, orange, red or blackish red, or dry, schizocarpic, splitting into 2 dehiscent cocci. Seeds 2, vertical, dorsally convex.

Distinctive features: Scrambling herbs to 4 m long; leaves 4 (6–8) per node, including the 2 leaf-like stipules. Fruits baccate, fleshy, didymous, orange.

Distribution: A cosmopolitan genus of ~400 species occurring in tropical and temperate environments; in the New World there are ~160 species ranging from Alaska to southern Argentina and Chile, 92 of which are found in the Neotropics, with only five species consistently reported as vines that attain 2 or more m in length; forest understory, forest margins, high altitude mountain vegetation, secondary vegetation; 50–3,400 m.

GUETTARDA Linnaeus, Sp. Pl. 991. 1753.

Shrubs, small to tall canopy trees, or scrambling lianas. Axillary thorns when present,



Guettarda comata, from Schunke-Vigo 6636 (US).

straight or slightly curved, stout, with vestigial nodes and sometimes with reduced leaves. Stipules persistent or readily caducous, free at base, deltoid or narrowly triangular. Leaves

opposite or whorled, 3–4 per node, short- to long-petiolate; blades ovate, elliptic or oblong, chartaceous, papyraceous or subcoriaceous; domatia of hairy-pockets, or absent. Inflorescences axillary, sessile or pedunculate, cymose or dichasial, with 2–7 scorpioid branches, or rarely subcapitate, frondose or not, few- to many-flowered. Flowers (4–)5–7(–9)-merous, bisexual, sometimes unisexual flowers also present (polygamous-dioecious), sessile or pedicellate. Calyx persistent, cup-shaped, lobes small, broadly triangular, deltoid or ovate; corolla hypocrateriform or broadly infundibuliform, white, cream-white, yellow, bluish white, pale blue, violet to purple, tube externally pubescent, internally glabrous or pubescent, with or without a pubescent ring at base, lobes (4–)5–7(–9), imbricate (quincuncial), ovate, round or oblong, margin entire, undulate or fringed; stamens included or partially exerted, filaments inserted near mouth of corolla tube, anthers subsessile, oblong or linear; ovary (2–)4–7(–9)-locular, ovules 1 per locule, pendulous, inserted near the roof of the locule, style included, terete, glabrous or antrorsely puberulent, capitate or with (2–)4–7(–9) short lobes, these ovate, oblong to linear. Fruit drupaceous, fleshy,

globose, ovoid or oblong-ovoid, white, red, purple to black. Pyrenes (2–)4–7(–9), woody, plano-convex. Seeds pendulous, compressed, oblong.

Distinctive features: Scrambling lianas, sometimes armed with axillary thorns; flowers (4–) 5–7(–9)-merous, bisexual or unisexual; calyx persistent, cup-shaped with broadly triangular, deltoid or ovate lobes; drupes fleshy, white, red, purple to black, and with (2–)4–7(–9) woody pyrenes inserted near the apex of the locule.

Distribution: A pantropical genus of ~120 species, 80–90 of which occur in the Neotropics, of these, only *G. comata* Standl. (Colombia), and *G. tikalana* Lundell (Mexico and Belize) are reported as lianas; primary and secondary forests; 100–800 m.

HEXASEPALUM Bartling ex A.P. de Candolle, Prodr. 4: 561. 1830.

Annual or perennial, erect or decumbent herbs, sometimes scrambling subwoody vines;



Hexasepalum sarmentosum, photo by P. Acevedo.

unarmed. Stems sub-quadrangular, reaching 8–10 m in length and ~2 cm diam. in *H. sarmentosum* (Sw.) J.H. Kirkbr. & Delprete; cross section with deep phloem wedges in *Hexasepalum sarmentosum* (Figure 217C). Stipules persistent, often withering on stem, sheathing and connate to petioles, fimbriate, with 3–13 setae, each seta commonly with an apical colleter. Leaves opposite, sessile, subsessile to short-petiolate; blades ovate, elliptic, oblong, narrowly oblong to lanceolate, chartaceous, papyraceous or subcoriaceous; domatia absent. Inflorescences

axillary, glomerules, 1- to few-flowered. Flowers 4-merous, homostylous. Calyx persistent, tube extremely reduced, lobes ovate, oblong, lanceolate, narrowly lanceolate to linear; corolla hypocrateriform or narrowly infundibuliform, white, cream-white, pinkish white, pink, bluish white, pale blue to lilac, tube externally glabrous, internally pubescent, usually with moniliform hairs, lobes valvate, ovate, oblong-ovate to narrowly ovate; stamens partially exerted or shortly exerted, filaments inserted near mouth of corolla tube or at lobes sinuses, glabrous, anthers elliptic, narrowly elliptic or short-oblong; ovary 2-locular, ovules basally or medially inserted, 1 per locule, style exerted just beyond or well beyond corolla, glabrous, capitate or with 2 short, elliptic, oblong or narrowly oblong branches. Fruit schizocarpic, obovoid, thinly woody to coriaceous, breaking up into 2 mericarps; mericarps indehiscent, plano-convex, 1-seeded. Seeds vertical, obovate or subellipsoid, plano-convex, dorsal side smooth or reticulate-foveolate, ventral side with a narrowly ellipsoid depression and two apical extensions, Y-shaped.

Distinctive features: Scrambling vines with fimbriate stipules bearing 3–13 setae, and schizocarpic fruits that split into 2, indehiscent, 1-seeded mericarps.

Distribution: A genus of ~12 species naturally found in the Americas and Africa, of which *H. gardneri* (K. Schum.) J.H. Kirkbr. & Delprete (from Brazil), *H. sarmentosum* (from Tropical America and Tropical Africa), and *H. scandens* (Sw.) J.H. Kirkbr. & Delprete (from Hispaniola) are scrambling vines; thickets, pastures, forest edges, and secondary growths, in moist areas; 0–1,600 m.

HILLIA Jacquin, Enum. Syst. Pl. 3, 18. 1760.

Erect or scrambling epiphytic shrubs or small trees, sometimes with pendulous branches, glabrous throughout; unarmed. Stipules readily caducous, free at base, ovate, oblong,



Hillia parasitica, photo by P. Acevedo.

oblanceolate or ligulate. Leaves opposite, isophyllous or anisophyllous, sessile to short-petiolate; blades ovate, elliptic, oblanceolate to lanceolate, subcoriaceous to coriaceous, sub-succulent to succulent. Inflorescences terminal, cymose, 3-flowered, or uniflorous. Flowers 4–10-merous. Calyx lobes free, round, narrowly triangular or lanceolate. Corolla tubular, hypocrateriform or broadly infundibuliform, often inflated at the middle, white, cream-white, yellow, or pale to bright green, orange, pink, red or violet to purple; tube glabrous throughout, lobes right-contorted, round, elliptic, broadly to narrowly triangular or linear, reflexed at anthesis; stamens included, partially exerted or exerted just beyond the corolla mouth, filaments inserted at middle or near the corolla mouth, anthers sessile, narrowly elliptic or oblong; ovary 2-locular, ovules many per locule, style included or as long as corolla tube, branches 2, ovate or long-linear. Fruit capsular, septicidal, oblong to narrowly oblong, crowned by the permanent calyx and the disk, woody, valves secondarily splitting at apex. Seeds many, imbricate, fusiform, with a tuft of long hairs (exotestal extensions) at distal end.

Distinctive features: *Hillia* and *Cosmibuena* are similar in being epiphytic or hemi-epiphytic (rarely terrestrial), vines with succulent distal branches, coriaceous or succulent leaves, large flowers, and large, septicidal capsules. See discussion under *Cosmibuena*.

Distribution: A neotropical genus of ~24 species, seven of which are often described as climbing shrubs or lianas; Mexico throughout Central America to Colombia, Bolivia, and Brazil, including the Greater and Lesser Antilles; wet or cloud forests; 600–2,750 m.

HINTONIA Bullock, Hooker's Icon. Pl. 33(4): tab. 3295. 1935.

Shrubs, or small to medium-sized trees, rarely scrambling woody vines > 5 m long, with



Hintonia octomera, photo by W.J. Hayden.

short, opposite branches; unarmed.

Stipules persistent, or sub-caducous, free or connate at base, broadly triangular. Leaves opposite, short- to long-petiolate; blades ovate, elliptic, oblong, or lanceolate, chartaceous or papyraceous; domatia tufts of sparse or dense hairs, or absent.

Inflorescence axillary, cymose,

pauciflorous or uniflorous. Flowers 6- or 8-merous. Calyx lobes free or shallowly connate at base, caducous, narrowly lanceolate or linear; corolla actinomorphic, campanulate, narrowly campanulate, or broadly infundibuliform, white, cream-white, yellowish white, pink, purplish, violet to purple; tube reduplicate, glabrous or basally pubescent outside, lobes imbricate or left-contorted, broadly triangular, margin entire, round or obtuse at apex; stamens partially exerted, filaments inserted at base of the corolla tube, basally connate into a minute tube, slender, long, equal, glabrous, anthers linear, basifixed; ovary 2-locular, placentation axile, with many ovules per locule, perpendicular to the central septum, style exerted just beyond the corolla, terete,

glabrous, unlobed, with stigmatic lines along style. Fruit capsular, septicidal, dehiscing basipetally, ellipsoid or subglobose, woody, sometimes lenticellate, the valves sometimes secondarily splitting at apex. Seeds imbricate, horizontal or basipetal, large, dorsoventrally compressed, elliptic to narrowly elliptic in outline, with concentric wing along the entire margin.

Distinctive features: Scrambling woody vines > 5 m long, flowers 5–7 cm long, 6- or 8-merous, with campanulate or broadly infundibuliform corolla, filaments basally connate, inserted at base of the corolla, anthers linear, basifixed. Similar to *Coutarea* but distinguished by the actinomorphic flowers with straight corolla, the stamens of equal length, and by the terete, septicidal capsules (vs. zygomorphic, curved corollas with unequal stamens and laterally compressed, loculicidal capsules).

Distribution: A genus of four species; Mexico, Guatemala, El Salvador and Costa Rica of which *Hintonia octomera* (Hemsl.) Bullock (from SE Mexico and Guatemala) is often reported as a liana or a climbing shrub; primary and secondary forests, seasonal forests, and rarely on coastal dunes; 5–100 m.

MACHAONIA Bonpland in Humboldt & Bonpland, Pl. Aequin. 1: 101, pl. 29. 1806.

Shrubs or small trees, sometimes with scandent lateral branches, and rarely subwoody scrambling shrubs or vines, reaching 5 m in length; young stems often lenticellate. Thorns when



Machaonia martinicensis, photo by Reinaldo Aguilar.

present, 2 per node, stout, straight, simple or dendroid, often with vestigial nodes, and sometimes with reduced leaves. Stipules persistent, free at base, broadly triangular. Leaves opposite, but often seemingly fasciculate due to the extreme reduction of nodes in lateral shoots (brachyblasts),

subsessile or short-petiolate; blades ovate, elliptic to very narrowly elliptic or obovate, chartaceous or papyraceous; domatia tufts of sparse hairs, or absent. Inflorescence terminal, frondose or not, paniculate or cymose, densely or sparsely branched, few- to many-flowered. Flowers 4–5-merous, heterostylous. Calyx persistent, tube extremely reduced, rotate or cup-shaped, lobes small, elliptic, ligulate, oblong, ovate; corolla < 1 cm long, broadly infundibuliform, white, cream-white or yellowish white, tube pubescent at mouth but not forming a ring, lobes imbricate, ovate or round; stamens well exerted in short-styled flowers or exerted among the corolla lobes in the long-styled flowers; ovary 2–3-locular, ovules 1 per locule, inserted at top of the locule, pendulous, style branches 2, ovate or elliptic. Fruit schizocarpic, narrowly turbinate, laterally compressed, chartaceous or thinly woody, splitting

into 2 pendulous, indehiscent, 1-seeded cocci that remain attached to a persistent septum. Seeds narrowly oblong-cylindrical.

Distinctive features: Scrambling shrubs, sometimes with axillary, straight, simple thorns; fruits small, schizocarpic, splitting into 2, indehiscent, pendulous, 1-seeded cocci that remain attached to a persistent septum.

Distribution: A neotropical genus of ~20 species ranging from Mexico throughout Central America to South America and the West Indies. *Machaonia martineziorum* Lorence (armed species ranging from southern Mexico and Guatemala) and *M. martinicensis* (DC.) Standl. (unarmed species ranging from Nicaragua to Colombia, Jamaica and Martinique) are sometimes reported as scrambling shrubs or lianas; flooded forests and thickets and coastal vegetation; 0–160 m.

MALANEA Aublet, Hist. Pl. Guiane 1: 106, t. 49. 1775.

Twining, root-climbing or scrambling, subwoody vines or lianas, shrubs, or small trees;



Malanea glabra, photo by Alex Popovkin.

unarmed. Stipules partly or readily caducous, free or connate at base, narrowly triangular, narrowly ovate, obovate, elliptic, oblong or oblanceolate. Leaves opposite,

subsessile or short-petiolate; blades broadly ovate to ovate, broadly elliptic to elliptic, papery or subcoriaceous; domatia absent. Inflorescence axillary, paniculate or spiciform, with short-fasciculate lateral branches, or cymose with the flowers borne in sessile glomerules or cymules along the primary, secondary and tertiary axes. Flowers 4-merous, heterostylous. Calyx persistent, campanulate, lobes ovate or broadly to narrowly triangular; corolla broadly infundibuliform, white, cream-white, yellowish white to orange; tube internally pubescent, not forming a ring, lobes 4, valvate, narrowly ovate, lanceolate, oblong or ligulate, round or acute at apex; stamens well exerted above the corolla lobes in short-styled flowers or included or partially exerted among the corolla lobes in long-styled flowers; ovary (1) 2–3-locular, ovules 1 per locule, inserted at top of septum, pendulous, style 2–3-branched. Fruit drupaceous, fleshy, oblong-ellipsoid, fusiform or cylindrical, red, purple or black at full maturity; pyrenes (1) 2–3, plano-convex, dorsal side 3–4-costate, ventral side flat. Seed 1 per pyrene, pendulous, cylindrical.

Distinctive features: Twining, root-climbing or scrambling vines or lianas with 1–3-locular ovaries with a pendulous ovule per locule; pyrenes dorsally 3–4 costate and ventrally flat. Similar to *Guettarda* in having drupaceous fruits with pendulous pyrenes but differs by the 4-lobed corollas, valvate in bud, with entire margin, and the (1) 2–3-locular ovaries and fruits [vs. (4–)5–7(–9)-lobed corollas, which are valvate, imbricate or left-contorted in bud, with entire, undulate or fringed margins, and the 2–7-locular ovaries and fruits]. In addition, climbing *Guettarda* are scramblers, never twiners or root-climbers.

Distribution: A neotropical genus of ~33 species, 29 of which are reported as climbers, however, several species are erect shrubs during early stages and only become climbers as they grow old; known from Guatemala, Belize, and from Costa Rica to SE Brazil and the Lesser

Antilles; seasonally dry forests, gallery forests, wet forests, and secondary vegetation; 0–1,400 m.

MANETTIA Mutis ex Linnaeus, Mant. 2: 553, 558. 1771 (nom. cons.).

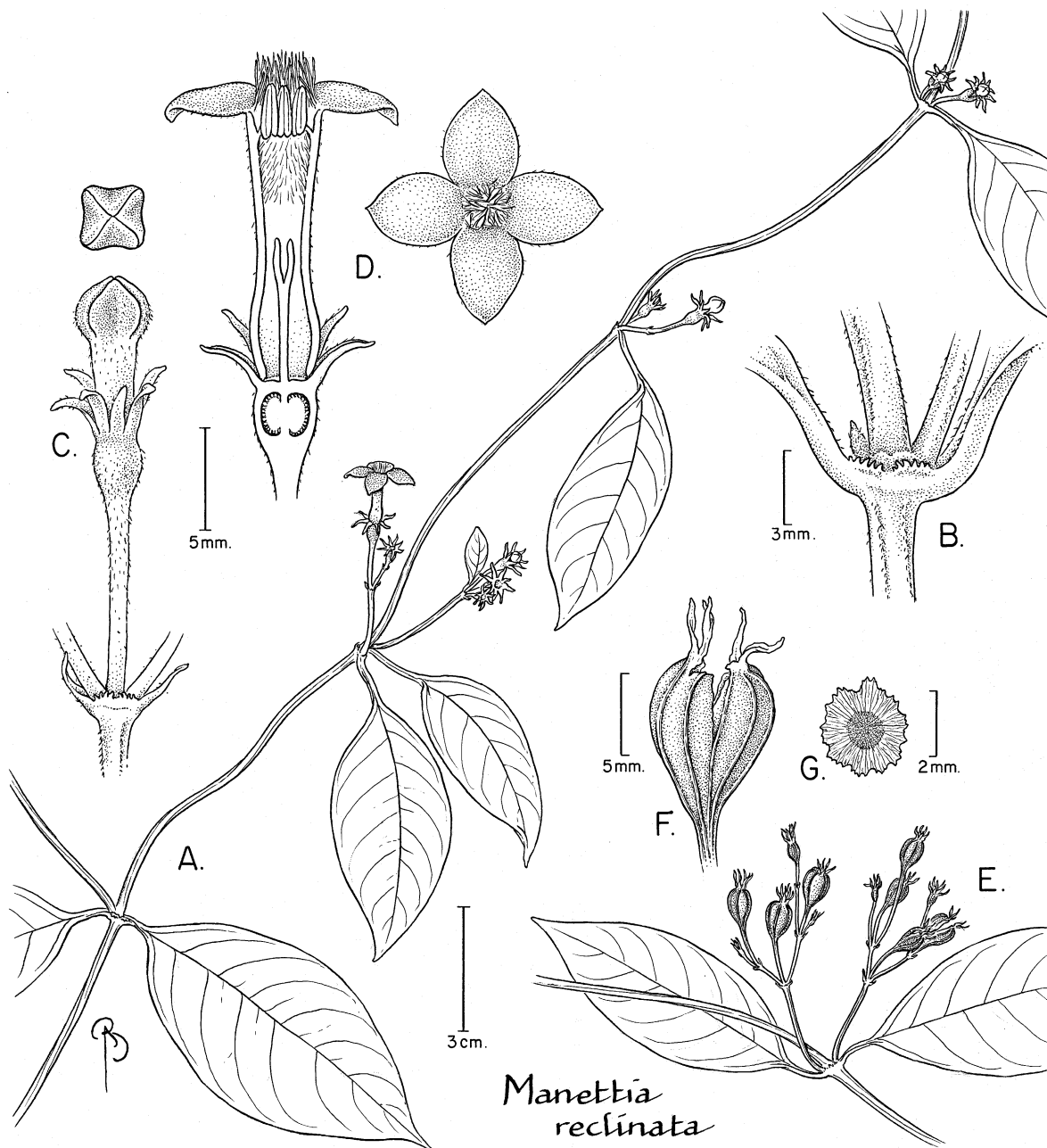
Twining herbaceous or woody vines to 10 m long, rarely hemiepiphytic, root-climbing



Manettia cordifolia, photo by P. Acevedo.

lianas or very rarely erect subshrubs. Stipules persistent, free at base, broadly triangular to deltoid. Leaves opposite, short- to long-petiolate; blades ovate, elliptic, oblong, lanceolate or almost linear, chartaceous or papyraceous; domatia tufts

of sparse hairs, or absent. Inflorescence axillary, frondose or not, thyrsoïd, dichasial or fasciculate, rarely uniflorous. Flowers commonly heterostylous. Calyx persistent, tube extremely reduced or cup-shaped, truncate or with small to foliose, lobes 4(5, or 8) narrowly triangular, lanceolate, ovate or linear; corolla tubular, urceolate, hypocrateriform or narrowly infundibuliform, white, cream-white, yellow, pink, red, bluish white to pale blue, or bicolorous (tube red and lobes yellowish or greenish), tube glabrous, puberulent or pubescent, lobes 4(5), valvate, deltoid, narrowly triangular or elliptic; stamens included or partially exerted in long-styled flowers or exerted just beyond the corolla mouth in short-styled flowers, filaments inserted on distal half of the corolla tube, anthers narrowly elliptic or oblong; ovary 2-locular,



Manettia reclinata. **A.** Flowering branch. **B.** Node showing interpetiolar stipules. Flower bud with nectary, frontal, lateral, & dorsal views & longitudinal section of nectary. **C.** Flower bud. **D.** Flower, longitudinal section & top view. **E.** Fruiting branch. **F.** Partly dehiscent fruit. **G.** Seed. Drawing courtesy of Bobbi Angell.

placenta peltate to the entire length of the septum, ovules many per locule, style included in short-styled flowers or exserted just beyond the corolla in long-styled flowers, glabrous,

branches 2, oblong or ligulate. Fruit capsular, dehiscent septically from apex, oblong, ovoid to subglobose, often laterally compressed, crustaceous or thinly woody, the valves sometimes secondarily splitting at apex. Seeds many, membranaceous, round, broadly to narrowly elliptic in outline, with a concentric, narrow, membranaceous wing, with entire or irregular margin.

Distinctive features: Twining or less often root-climbing vines or lianas, with slender stems and small to large corollas that are tubular, urceolate, hypocrateriform or narrowly infundibuliform, white, cream-white, yellow, pink, red, bluish white to pale blue, or bicolorous; capsules septical, oblong, ovoid to subglobose, often laterally compressed.

Distribution: A genus of 90–100 species most of which are reported as climbers; Mexico, throughout Central America, Greater and Lesser Antilles to Colombia, Bolivia, Brazil, and northern Argentina; primary and secondary forests, seasonal forests, Andean cloud forests; 200–3,000 m.

MORINDA Linnaeus, Sp. Pl. 176. 1753.

Shrubs, trees or less often twining or scrambling, subwoody vines, 3–4 m in length; unarmed. Stipules caducous or persistent, free or connate at base or sheathing, oblong, triangular, ligulate, spatulate or bifid. Leaves opposite or ternate, isophyllous or anisophyllous, short- to long-petiolate; blades ovate, broadly elliptic, oblong, oblanceolate, chartaceous or stiffly chartaceous; domatia tufts of sparse or dense hairs, or absent. Inflorescence axillary or distal, solitary or fasciculate, pedunculate, capitulum of many fused flowers. Flowers homostylous or distylous. Calyx caducous, tube extremely reduced or short tubular, truncate, undulate or lobed,



Morinda royoc, photo by P. Acevedo.

lobes when present,
4–7, broadly
triangular; corolla
hypocrateriform or
narrowly
infundibuliform,
white, cream-white,
or rarely pale blue;
tube externally
glabrous or

puberulous, glabrous throughout or puberulent inside, lobes 4–7, valvate, lanceolate or oblong, with narrow dorsal extension at apex (usually caducous); stamens 4–7, included, partially exerted, or exerted just beyond the corolla mouth, filaments attached at the middle of the corolla tube, long, anthers narrowly oblong or elongate, with acute extensions at apex; ovary 2-locular, with 2 ovules per locule, or partly 4-locular, with 1 ovule per locule, ovules basally inserted, ascending, style included or exerted just beyond the corolla, capitate, bilobed or 4-lobed, lobes ovate, oblong or linear. Fruits multiple, fleshy, oblong-globose, ellipsoid to ovoid, grayish white to yellowish white at maturity; single fruits drupaceous, fleshy; pyrenes commonly 4 per fruit, or 2–3 per fruit by the abortion of 1–2 ovules, oblong or narrowly ovoid. Seeds vertical, ovoid to obovoid or reniform.

Distinctive features: Twining vines with multiple, fleshy fruits, formed by the fusion of many ovaries.

Distribution: A genus of 60–80 species worldwide, 20 of which are present in the Neotropics, with *M. royoc* L. as the only species of vine; distributed in SE United States (Florida), southern Mexico to NW South America (Venezuela, Colombia, Ecuador), Cuba, Jamaica, Hispaniola and the Bahamas; wet forests, coastal scrubs, dry and semi deciduous forests and disturbed vegetation; 0–400 m.

NOTOPLEURA (Bentham) Bremekamp, Recueil Trav. Bot. Néerl. 31: 289. 1934.



Notopleura pithecobia, photo by Monica Álvarez.

Mostly terrestrial, erect shrubs or trees, rarely subshrubs, epiphytic herbs, scrambling vines or root-climbing vines, unarmed; stems commonly succulent. Stipules persistent to caducous, connate at base or sheathing, often connate to the petioles,

truncate or bifid, with interpetiolar appendages, these conical, linear, shortly bifid, bilobed, fimbriate at the apex, with glandular apical projections or laminar and erose or lacinate. Leaves opposite, short- to long-petiolate; blades ovate, elliptic, obovate, oblong, oblanceolate or lanceolate, chartaceous, papyraceous, subcoriaceous to succulent in epiphytic species; domatia absent. Inflorescence pseudo axillary or terminal, paniculate, sparsely or densely branched, or capitate, sometimes subtended by bracts. Flowers 4–5(6)-merous, heterostylous, rarely homostylous. Calyx persistent, tube extremely reduced or cup-shaped, lobes small, broadly to

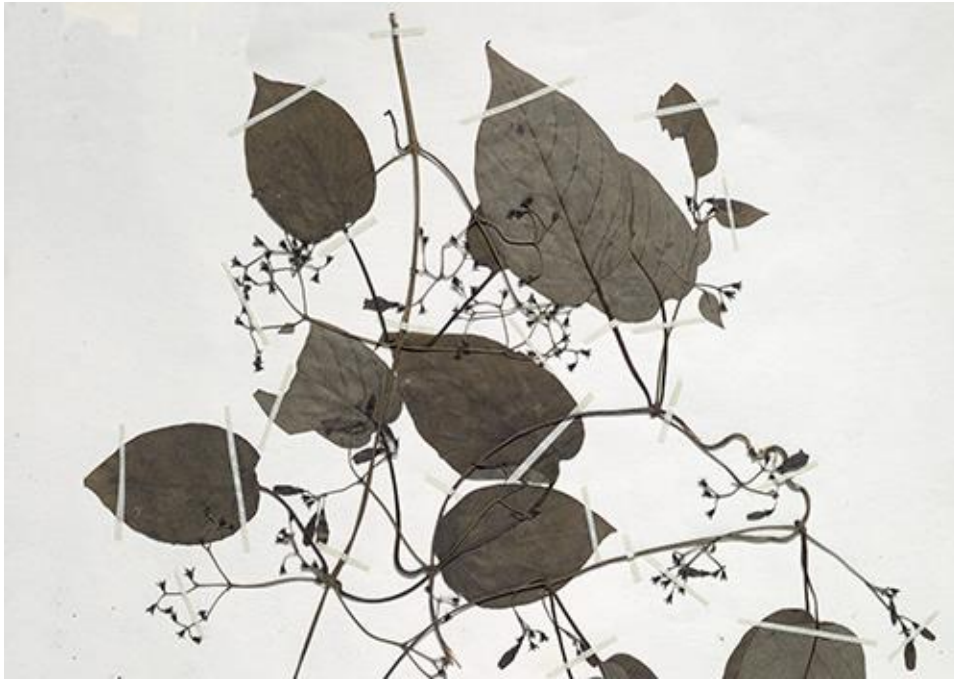
narrowly triangular; corolla tubular or narrowly infundibuliform, white, cream-white, pinkish white, yellow, yellowish orange or orange, tube externally and internally glabrous or pubescent; lobes 4–5(6), valvate, deltoid to narrowly triangular, short-acuminate at apex, sometimes with pronounced dorsal appendages; stamens 4–5, filaments short or long, included, inserted at basal or median portion of corolla tube in long-styled flowers, or included or partially exerted and inserted at medial or distal portion of corolla tube in short-styled flowers, anthers narrowly elliptic, oblong or narrowly oblong; ovary 2–4(6)-locular, with 1 ovule per locule, basally inserted, style branches 2–4(6), oblong to linear. Fruit drupaceous, fleshy or spongy, subglobose, ellipsoid, narrowly ovoid, white, orange, red or black, with 2–4(6) pyrenes. Pyrenes ascending, dorsoventrally convex, dorsal side smooth or with 1–5 ridges, ventral side sulcate.

Distinctive features: Stems commonly succulent; stipules connate at base or sheathing, truncate or bifid, and with interpetiolar appendages; inflorescence pseudoaxillary or terminal, paniculate or capitate, sometimes subtended by bracts; ovary 2–4(6)-locular, with 1 ovule per locule, basally inserted; fruit drupaceous, fleshy or spongy, white, orange, red or black, with 2–4(6) pyrenes.

Distribution: A genus of ~73 species, distributed from Mexico to South America, and the West Indies (Taylor, 2001). Only two species, i.e., *N. episcandens* C.M. Taylor & Lorence from Panama and *N. pithecobia* (Standl.) C.M. Taylor from Costa Rica to Ecuador, in addition to growing as epiphytic shrubs are reported as scrambling or root-climbing vines that can reach 2–3 m in length; wet forests; 400–1,800 m.

PAEDERIA Linnaeus, Syst. Nat., ed. 12: 135, 189. 1767.

Twining herbaceous or woody vines, with strong fetid odor; unarmed. Stipules caducous,



Paederia brasiliensis, from Venturi 9052 (US).

free at base,
triangular, rarely
bilobed at apex.
Leaves opposite or
whorled, 3–4 per
node, long-
petiolate; blades
ovate, elliptic or
cordate, chartaceous
or papyraceous;
domatia tufts of

hairs or hairy-pockets, or absent. Inflorescence terminal or terminal on lateral branches, paniculate or thyrsoid, sparsely branched. Flowers 4–6-merous, bisexual or unisexual and bisexual on the same individual (polygamous-dioecious), homostylous. Calyx persistent, tube extremely reduced, with small, broadly to narrowly triangular or linear lobes; corolla tubular, reddish to purple inside, greenish white outside, tube narrowly infundibuliform, internally densely pubescent at distal portion, lobes 4–6, valvate, narrowly triangular or narrowly ovate, margin undulate or fringed; stamens included, inserted at about the middle of the corolla tube, anthers subsessile, narrowly oblong; ovary 2-locular, with 1 ovule per locule, basally inserted, style bifid, divided almost to the base. Fruit schizocarpic, dry, ovate or elliptic in outline, laterally compressed, crustaceous to chartaceous, with 2 flat mericarps that remain suspended by thin carpophores; mericarps indehiscent, with seed enclosed in endocarp tissue, dorsoventrally

flat, narrowly to broadly elliptic in outline, with narrow or large, concentric, membranaceous wings, and entire margin.

Distinctive features: Twining vines with strong fetid odor, due to Sulphur containing compounds (Takeda et al., 1991); fruits are unique in being laterally compressed, crustaceous to chartaceous, brittle, splitting into two flat mericarps that remain suspended by thin carpophores and later dispersed by the wind.

Distribution: A pantropical genus of ~30 species distributed in Asia, Africa and Madagascar, with only two species native to the Neotropics, i.e., *P. ciliata* (Bartl. ex DC.) Standl., endemic to Mexico, and *P. brasiliensis* (Britton) Standl., distributed in Brazil, Peru, Bolivia, Paraguay and Argentina; common in calcareous substrates; 0–1,200 m.

PALICOUREA Aublet, Hist. Pl. Guiane 1: 172. 1775, *sensu lato* (incl. *Psychotria* subgen. *Heteropsychotria*, *Cephaelis*)

Erect shrubs, small trees, or scrambling or clambering shrubs; unarmed. Stipules persistent, sheathing at base, bifid, with two short–long, triangular lobes on each side of the stem (without interpetiolar appendages). Leaves opposite, petiolate; blades chartaceous, papyraceous, or subcoriaceous. Inflorescence (in climbing species) terminal or subaxillary, paniculate or corymbiform, terminating in flowering heads or cymules. Flowers 4–5-merous, heterostylous. Calyx persistent, tube reduced, lobed; lobes narrowly triangular or lanceolate; corolla narrowly funnelform, white or cream-white, tube glabrous outside, glabrous or puberulent, without a pubescent ring at base inside (in climbing species); lobes valvate, ovate to narrowly ovate, margin entire; stamens included (in long-styled flowers), partially exerted or exerted just beyond or well beyond the corolla (in short-styled flowers), filaments inserted at the lower,

middle or upper part of the corolla tube or near the mouth of corolla tube, short to long, anthers elliptic; ovary 2-locular (in climbing species); ovules 1 per locule, basally inserted, style included (in short-styled flowers) or exerted just beyond or well beyond the corolla (in long-styled flowers), branches as many as the locules, ovate, elliptic, oblong or linear. Fruit drupaceous, fleshy, subglobose, with 2 pyrenes (in climbing species). Pyrenes woody, dorsoventrally convex, dorsally costate, ventrally sulcate.

Distinctive features: *Palicourea*, as currently delimited, has a very variable habit, ranging from erect, trailing, decumbent, scrambling or rarely epiphytic, herbs, shrubs or trees. It is characterized by the stipules basally sheathing with two triangular lobes on each side of the stem, and without interpetiolar appendages (present in *Notopleura*).

Distribution: *Palicourea* (*sensu lato*) is a neotropical genus of ~650 species occurring in Mexico, Central America, Greater and Lesser Antilles, and South America south to Bolivia and southern Brazil. At least *P. scandens* C.M. Taylor from the Pacific slopes of the Colombian Andes is sometimes reported as a climber (Taylor, 2019); primary and secondary forests, Andean cloud forests; 100–1,900 m.

RAMONADOXA Paudyal & Delprete, Bot. J. Linn. Soc. 187: 389. 2018.

Erect shrubs, treelets or scrambling woody vines; unarmed. Branches glabrous, terete; young branches sometimes slightly resinous; basal internodes often laterally compressed below nodes. Stipules persistent, connate at base, deltoid to narrowly triangular. Leaves opposite, petiolate; blades chartaceous to coriaceous, ovate to oblong, domatia absent. Inflorescence axillary, paniculate, pedunculate, many-flowered; bracts small, lanceolate or triangular. Flowers 4-merous, homostylous. Calyx persistent, tube narrowly obovoid, shallowly lobed; corolla

tubular-subcylindrical, slightly inflated at the middle, purple-brown outside, deep yellow inside; tube not reduplicate, glabrous throughout, lobes 4, narrowly imbricate in bud, short, ovate, obtuse at tip; stamens included, filaments connate into a short tube at base, inserted at base of corolla tube, lower half puberulent, anthers linear; ovary 2-locular, with 1 ovule per locule, apically inserted, pendulous, style exerted, filiform, basally puberulent, capitate, with 2 minute, connivent style branches. Fruit drupaceous, spongy, white, subglobose to obovoid; pyrenes 2, woody, hemi-ellipsoidal, 1-seeded. Seeds cylindrical, terete.

Distinctive features: A recent segregate of *Chiococca*, distinguished by the narrowly obovoid, shallowly lobed calyx tube, the tubular-subcylindrical corollas, with tube not reduplicate and slightly inflated at the middle, purple-brown outside and deep yellow inside; while in *Chiococca* the calyx tube is extremely reduced, with lobes broadly to narrowly triangular, the corollas are campanulate to funnelform, with tube narrowly reduplicate, white, cream-white to pale yellow throughout.

Distribution: A monotypic Cuban genus; thickets and pinelands of eastern Cuba; 300–450 m.

RANDIA Linnaeus, Sp. Pl. 1192. 1753.

Basanacantha J. D. Hooker (1873).



Randia retroflexa, photo by P. Acevedo.

Dioecious shrubs or small to medium-sized trees, sometimes scrambling shrubs or rarely twining lianas; unarmed or armed with 2–4 axillary, straight, stout, or acicular thorns per node (Figure 218D). Stipules persistent, connate at base, broadly to narrowly triangular, broadly ovate or lanceolate. Leaves opposite, sessile or short- to long-petiolate; blades broadly ovate, ovate, elliptic, obovate, oblong to lanceolate, chartaceous, papyraceous or subcoriaceous; domatia tufts of sparse or dense hairs, or absent. Inflorescence axillary or terminal on axillary, short shoots, rarely cauliflorous; male inflorescence fasciculate or corymbose, few- to many-flowered, or rarely uniflorous; female inflorescences 1-flowered. Staminate and pistillate flowers dimorphic with respect to the perianth. Calyx persistent, tube cupular or tubular, truncate, with small teeth or lobed, or tube absent, with free small to foliose lobes; corolla hypocrateriform or narrowly infundibuliform, white to cream-white, or yellowish white, turning pale yellow to yellow at later stages of anthesis, tube internally glabrous, pubescent or villous without a pubescent ring inside, lobes left-contorted, ovate, suborbicular, oblong, oblong-

ovate to lanceolate. Staminate flowers: 4–6-merous; hypanthium and ovary absent; stamens included, partially exerted or exerted just beyond the corolla, filaments inserted at distal portion of corolla tube or near the corolla mouth, short or long, anthers elliptic, narrowly elliptic to oblong; style nonfunctional, included. Pistillate flowers: 5–7-merous; stamens non-functional, included or partially exerted; ovary 1-locular, with incomplete placenta, or 2-locular, with parietal placentation, ovules many per locule, style partially exerted or exerted just beyond the corolla, with 2 ovate branches. Fruit baccate, leathery or somewhat woody, ovoid to oblate, with seeds surrounded by a gelatinous pulp that turns black when exposed to air. Seeds horizontal, perlaceous, dorsoventrally compressed, irregularly elliptic in outline.

Distinctive features: Dioecious scrambling shrubs or rarely twining lianas with straight, stout or acicular thorns that are opposite or whorled, 3–4 per node, and lack vestigial nodes (present in *Chomelia*, *Guettarda* and *Machaonia*). Inflorescence in *Randia* is axillary or terminal on lateral short shoots, or rarely cauliflorous. In staminate individuals, the inflorescence is fasciculate or corymbose, few- to many-flowered, or very rarely uniflorous. In pistillate individuals, the inflorescences are always single-flowered. Fruits are characteristic in being externally leathery or thinly woody with seeds surrounded by a gelatinous pulp that usually turns black when exposed to air.

Distribution: A neotropical genus of ~90 species, nine of which are reported as lianas which are mostly found in Mexico with a few species in Central America, and lowlands of South America; moist forests; 0–900 m.

ROGIERA Planchon, Fl. Serres Jard. Eur. 5: 442. 1849.

Shrubs, or small to medium-sized trees, rarely scrambling shrubs or woody vines;



Rogiera edwardsii, photo by N. Ramírez Marcial.

unarmed. Stipules persistent or caducous, free or connate at base, triangular to linear, erect or reflexed. Leaves opposite (rarely ternate), isophyllous or anisophyllous, short- to long-petiolate; blades ovate, elliptic, or ovate-oblong, chartaceous, subcoriaceous or coriaceous;

domatia tufts of sparse or dense

hairs, or hairy pockets, or absent. Inflorescence terminal or axillary, cymose, paniculate or corymbose, pauci- or multi-florous. Flowers heterostylous, fragrant. Calyx lobes free or shallowly connate at base, 4–6(–7), usually unequal, oblong to ovate-triangular to narrowly triangular, persistent; corolla actinomorphic, hypocrateriform, white, yellowish white, yellow, red, or purple, tube glabrous or pubescent and with a ring of yellow or white hairs at the mouth, lobes 4–6(–7), imbricate, oblong, triangular-ovate to round, margin entire, undulate or crisped, rounded at apex; stamens included in long-styled flowers or partially exerted in short-styled flowers, filaments inserted at median or distal portion of tube, shorter than the tube or absent, equal, glabrous, anthers narrowly oblong to linear, basifixed; ovary 2-locular with axile placentation, ovules many per locule, style exerted just beyond the corolla mouth in long-styled flowers or included in short-styled flowers, terete, glabrous, 2 lobed. Fruit capsular, loculicidal,

woody, globose, ellipsoid or obovoid. Seeds horizontal, small, angular, globose, fusiform or falciform, narrowly or partially winged; wing bipolar or unipolar, rarely absent.

Distinctive features: *Rogiera*, *Arachnothryx* and *Rondeletia* are similar in being woody plants with capsular fruits. *Rogiera* is similar to *Rondeletia* by the loculicidal capsules, from which it differs by the corolla with a ring of yellow or white hairs at mouth (vs. corolla with a thick fleshy glabrous ring at mouth in *Rondeletia*), and the horizontal, angular, globose, fusiform or falciform seeds (vs. vertical, dorsoventrally compressed, fusiform, irregularly elliptic or bipolar seeds in *Rondeletia*). *Arachnothryx* differs from *Rogiera* by the corolla mouth glabrous, without a thick fleshy ring or a ring of yellow or white hairs.

Distribution: A neotropical genus of 10 species, of which *R. breedlovei* (Lorence) Borhidi always grows as a climbing shrub, while *R. edwardsii* (Standl.) Borhidi, *R. gratissima* Planch. & Lind, and *R. ligustroides* (Hemsl.) Borhidi are trees or shrubs that sometimes grow as scrambling shrubs, these are distributed from southern Mexico to Guatemala and Honduras; evergreen primary and secondary forests, cloud forests, and disturbed vegetation; 600–2,800 m.

RONDELETIA Linnaeus, Sp. Pl. 72. 1753.

Shrubs, or small to medium-sized trees or rarely scrambling shrubs or woody vines; unarmed. Stipules persistent or caducous, free at base, ovate, triangular, narrowly triangular to subulate, erect. Leaves opposite, short-petiolate; blades ovate or elliptic, chartaceous; domatia tufts of hairs. Inflorescence terminal, cymose, paniculate-thyrsoid, multi-florous. Flowers 5-merous, heterostylous, fragrant. Calyx lobes equal, ovate, narrowly triangular, persistent. Corolla actinomorphic, hypocrateriform, white, with a thick fleshy glabrous ring at mouth; tube glabrous outside; glabrous inside; lobes imbricate, equal to subequal, obovate, margin entire or slightly

undulate, round at apex. Stamens included or partially exerted (only tips exerted); filaments inserted at distal portion of the corolla tube, short, equal, glabrous; anthers narrowly oblong; round at base and at apex, dorsifixed. Style exerted just beyond the corolla mouth (long-styled flowers) or included (short-styled flowers), terete, glabrous; lobes 2, oblong to linear. Ovary 2-locular; placentation axile; placenta peltate to the entire length of the septum; ovules many per locule. Fruit capsular, loculicidal, dehiscent basipetally, globose, woody. Seeds vertical, with a central hilum, dorsoventrally compressed, fusiform or irregularly elliptic, winged, wing bipolar.

Distinctive features: *Rondeletia* is similar to *Rogiera* and *Arachnothryx* by being woody plants with small, globose, subglobose, ellipsoid or obovoid capsular fruits. The diagnostic characters to differentiate these three genera are compared under *Rogiera* (see above).

Distribution: A genus of ~140 species, with *R. purdiei* Hook. f., native to Colombia and northern Venezuela, as the only species that grows as a climber in addition to being a tree or a shrub (Bernal et al. 2015, onwards); primary and secondary dry forests, Caribbean coastal forests, 5–900 m.

SABICEA Aublet, Hist. Pl. Guiane 1: 192, t. 75. 1775.

Herbaceous to woody, twining or scrambling vines, rarely subshrubs; unarmed; stems



Sabicea panamensis, photo by P. Acevedo.

slender (up to 1.7 cm in diam.) and in some species reaching > 10 m in length; cross section with regular anatomy, the xylem with shallow phloem arcs and inconspicuous rays. Stipules

persistent, free at base,

ovate to broadly triangular, sometimes ligulate or lanceolate. Leaves opposite, petiolate; blades narrowly elliptic to obovate, ovate to lanceolate, papyraceous to subcoriaceous. Inflorescence axillary, one or two per node, compact-verticillate, fascicled, glomerulate, capitate or laxly paniculate cymes, sometimes subtended by broadly lanceolate or ovate involucre bracts.

Flowers 4–5-merous, homostylous, or rarely heterostylous, sessile to shortly pedicellate. Calyx persistent, campanulate to infundibuliform, lobes antrorse to reflexed, lanceolate to elliptic, ligulate, triangular or linear; corolla salverform or hypocrateriform, white, cream-white or pink (rarely purple), lobes valvate, ovate to lanceolate; stamens 4–5(–10), included, filaments short, anthers oblong; ovary 4–5(–7)-locular, with many ovules per locule, style included in short-styled flowers or exerted beyond corolla mouth in long-styled flowers, style branches 4–5(–10), oblanceolate, elliptic, oblong or linear. Fruit baccate, fleshy, globose, subglobose, ellipsoid to

turbinate, red to red-purple, dark violet or maroon, crowned by the persistent calyx. Seeds many, minute, variously angular, brownish orange.

Distinctive features: Twining herbaceous or subwoody vines with ovate or widely triangular stipules, or less often scrambling vines; corolla salverform or hypocrateriform, white, cream-white or pink with valvate lobes; fruit a fleshy, multi-seeded berry, crowned by the persistent calyx.

Distribution: A pantropical genus of ~170 species, represented in the Neotropics by ~54 species of which 42 are climbers that reach two or more m in length; Mexico, Central America, Greater Antilles, most of South America, to southern Brazil and Bolivia (Khan 2007); seasonal forests, savanna formations, low altitude rainforests, primary and secondary cloud forests; 0–1,800 m.

SALZMANNIA A.P. de Candolle, Prodr. 4: 617. 1830.

Shrubs or trees with erect or scandent branches, sometimes leaning shrubs; unarmed; branches covered with copious resinous exudates. Stipules persistent, sheathing at base, triangular, shallowly orbicular or truncate, glabrous, with internal colleters exuding abundant resinous exudate. Leaves opposite, short- to long-petiolate; blades lanceolate, elliptic, broadly elliptic, oblong to obovate, chartaceous, subcoriaceous to coriaceous; domatia absent.

Inflorescence axillary or subterminal, sessile, subsessile or pedunculate, uniflorous or 3–18-flowered heads; bracts when present often foliaceous, lucid, glabrous. Flowers 4–5-merous, homostylous, sessile or pedicellate. Calyx persistent, cupular, shortly lobed, lobes broadly triangular, ovate, orbicular-ovate, triangular or deltoid, imbricate, persistent, glabrous or pubescent; corolla actinomorphic, tubular, pale green to greenish yellow, rarely with reddish or

purplish tinge on lobes, tube cylindrical or tetragonal, not reduplicate, glabrous, lobes narrowly imbricate in bud, much shorter than tube, ovate, deltoid or narrowly triangular, glabrous; stamens included, filaments inserted at base of the corolla tube, connate at base into a minute, slender, glabrous or pubescent, anthers narrowly oblong to linear, basifixed; ovary 2-locular with axile placentation, ovules 1 per locule, inserted near the roof of the locule, style as long as the corolla tube, terete, glabrous, with 2 linear lobes. Fruit drupaceous, fleshy, globose, ovoid to ellipsoid, pinkish red, lavender, red to purple-blue; pyrenes 2, woody, plano-convex. Seeds pendulous, narrowly ovoid to narrowly obovoid.

Distinctive features: Scrambling shrubs, similar to *Chiococca* but distinguished by the stems covered by abundant resinous exudate, the tubular corollas with a non-reduplicate tube, and the fruits that are pink to red or purplish blue; whereas in *Chiococca* the stems aren't resinous, the corollas are campanulate or broadly infundibuliform with a narrowly reduplicate tube, and the fruits are white or yellowish white.

Distribution A neotropical genus of 4–5 species with disjunct distribution, one species in Venezuela, and 3–4 species in the coastal dunes “*restingas*” and forested vegetation of north-eastern Brazil; only *S. nitida* DC. from NE Brazil is reported as a scrambling shrub; 0–140 m.

SCHRADERA Vahl, *Eclog. Amer.* 1: 35. 1797 [“1796”].

Herbaceous or woody vines, rarely terrestrial, hemiepiphytic or epiphytic shrubs, or



Schradera exotica, photo by P. Acevedo.

woody lianas; unarmed.

Plants with a juvenile phase morphologically different from the adult phase. Juvenile plants < 1 m long, slender, sparsely branched, with adventitious roots at the nodes, and small,

membranaceous, crenate leaves. Adult plants developing into woody vines with scandent or hanging branches and larger, coriaceous, entire leaves; stem up to 20 cm diam. and 25–30 m long; cross section with axial elements divided in radial segments by wide rays in *Schradera exotica* (J. F. Gmel.) Standl. (Figure 217D). Stipules large, caducous, sheathing at base, forming a basal tube, lobes round, ovate to triangular, appressed to each other or imbricate. Leaves opposite, petiolate; blades elliptic, elliptic-oblong to oblanceolate, chartaceous to coriaceous; domatia absent. Inflorescences axillary or terminal, 2 or 3 per node, pedunculate, hemispherical or globose capitula, commonly pauci- or multi-florous (rarely uniflorous), subtended by a discoid, small to large involucre, that is truncate, undulate or irregularly divided at later stages. Flowers free or basally connate, 5–6(–10)-merous, bisexual, sessile, heterostylous, fragrant, and nocturnal. Calyx persistent, tubular, margin truncate or undulate; corolla hypocrateriform, white, tube pilose at distal portion inside, lobes valvate, reflexed, narrowly lanceolate to linear, fleshy, and entire; stamens 5–6(–10), included, inserted near middle of the corolla tube in long-styled

flowers or partially exerted, inserted near the mouth of corolla tube in short-styled flowers, filaments glabrous, anthers oblong; ovary 2(4)-locular, with many horizontal ovules per locule, style included in short-styled flowers or exerted in long-styled flowers, stigmatic branches 2(4), linear. Fruits commonly basally connate, individual fruits few to many (per head), baccate, globose to subglobose, fleshy, smooth, greenish white, white or yellowish white. Seeds many, horizontal, dorsoventrally compressed, quadrangular.

Distinctive features: Root-climbing or epiphytic lianas with juvenile and adult phases, bearing pedunculate heads subtended by a discoid involucre, with congested, free or basally connate flowers.

Distribution: A pantropical genus of ~65 species distributed in tropical America, Southeast Asia and New Guinea, of which 40 are distributed in the Neotropics, 22 of which are reported as climbers; Costa Rica south to the Amazon basin and the Atlantic Forest in Brazil, including the West Indies; premontane forests, low and high altitude rainforests, cloud forests; 150–1,700 m.

SPERMACOCE Linnaeus, Sp. Pl. 102. 1753.

Borreria G. Mey. (1818).

Annual or perennial herbs, subshrubs, sometimes scrambling or leaning, up to 4 m long; unarmed. Stipules persistent, often withering on the stem, sheathing and connate to the petioles, fimbriate, with 5–9 setae, each seta with an apical colleter. Leaves opposite, sometimes seemingly whorled, subsessile or short-petiolate; blades narrowly ovate, elliptic to narrowly elliptic, membranaceous, chartaceous or papyraceous; domatia tufts of sparse hairs, or absent. Flowering branches with 3–13 terminal and axillary flowering glomerules; glomerules 13–32-flowered, usually subtended by leaf-like bracts. Flowers 4-merous, heterostylous. Calyx

persistent, lobes narrowly triangular or linear; corolla infundibuliform, white to bluish white, tube glabrous or puberulent outside, glabrous, puberulent or pubescent at medial or distal portion inside, with moniliform hairs, lobes valvate, ovate-triangular; stamens partially exerted or exerted just beyond the corolla, inserted at distal portion, near the mouth of the corolla tube or at lobes sinuses in short-styled flowers or included, inserted at median portion of corolla tube in long styled flowers, filaments short or long, anthers oblong; ovary 2-locular, ovules 1 per locule, centrally inserted, vertical, style glabrous, branches 2, oblong. Fruit (in climbing species) dry, schizocarpic, separating into two indehiscent mericarps, or a septicidal capsule with two dehiscent cocci. Seeds vertical, centrally inserted, plano-convex, obovate or elliptic in outline, dorsoventrally compressed, finely foveolate or transversally sulcate on the dorsal side, with a well-developed strophiole on the ventral side.

Distinctive features: Scrambling herbs (sometimes woody at base); stipules basally sheathing and fimbriate, with 5–9 setae, each of which has an apical colleter; flowers heterostylous; fruits schizocarpic, separating into two indehiscent mericarps (e.g., *S. schumannii* (Standl. ex Bacigalupo) Delprete) or a septicidal capsule (e.g., *S. valens* (Standl.) Govaerts). *Spermacoce* resembles *Denscantia* in the fimbriate stipules and the capsular fruits. However, *Denscantia* is distinguished by the thyrsoid inflorescences with branchlets terminating in fascicles or glomerules, homostylous flowers, capsules apically dehiscent down to the seed insertion and seeds with very narrow wings (vs. inflorescence capitate, usually subtended by leaf-like bracts, and sometimes on flowering branches as a series of few- to many-flowered glomerules, flowers heterostylous, capsules usually dehiscent down to the base, and seed wingless in *Spermacoce*).

Distribution: A pantropical genus of ~300 species, with ~80 species in the Neotropics, of which *S. valens* from Minas Gerais, Brazil, and *S. schumannii* from Colombia, Brazil, Paraguay and

Argentina, sometimes grow as scrambling herbs up to 4 m in length; humid and seasonal forests, savanna formations, rocky outcrops, secondary vegetation and ruderal areas; 170–1,200 m.

UNCARIA Schreber, Gen. 125. 1789 (nom. cons.).

Monoecious or rarely dioecious, scrambling lianas or shrubs with scrambling lateral



Uncaria guianensis, photo by P. Acevedo.

branches. Stems initially quadrangular, turning cylindrical with age, up to 15 cm in diam. and > 20 m in length; cross section regular, often with a quadrangular medulla, inconspicuous rays, and the cortex exhibiting overlapping layers of sclerenchyma (Figure 217A). Axillary, hook-shaped thorns (Figure 218C) helping the plant to hold on to the phorophyte. Stipules persistent or caducous, free at base, deltoid, obovate or cordate. Leaves opposite, short- to long-petiolate; blades ovate, elliptic, obovate or oblong, subcoriaceous to coriaceous; domatia tufts of

sparse hairs, hairy-pockets or tuft-pits, or absent. Inflorescence terminal, paniculate, with branches terminating in globose few- to many-flowered heads, sometimes at the top of lateral thorns. Flowers 4–5(-6), bisexual or functionally unisexual (staminate and pistillate flowers on separate individuals). Calyx persistent, funnel-shaped or short tubular, lobes broadly to narrowly ovate; corolla hypocrateriform, white to cream-white, or yellow when young and turning red at later stages, tube externally retrorsely puberulous, villous or sericeous, internally glabrous or

sericeous, lobes narrowly imbricate, round, ovate, narrowly ovate or oblong; stamens partially exerted, filaments inserted near the mouth of the tube, anthers elongate, with a pointed extension at base and an acute extension at apex; ovary 2-locular with many ovules per locule, peltate or along the entire length of the septum, style exerted well beyond the corolla, glabrous, capitate. Fruit capsular, dehiscent septically from the apex, thinly woody, ovoid, narrowly ovoid to turbinate, sessile or long-pedicellate. Seeds many, ascendingly imbricate, laterally compressed, membranaceous, irregularly narrowly oblong to fusiform in outline, wings bipolar, margin entire.

Distinctive features: Scrambling lianas or shrubs with hook-shaped axillary thorns; inflorescences terminal, paniculate, with branches terminating in globose heads.

Distribution: A genus occurring in tropical Africa and tropical America, with ~34 species, two of which are found in the Neotropics. *Uncaria guianensis* (Aubl.) J.F. Gmel. from South America is recognized by the strongly recurved thorns, glabrous branches and leaves and the long-pedicellate capsules, while *U. tomentosa* (Schult.) DC., from southern Mexico south to the Amazon Basin, is recognized by the slightly curved thorns, sparsely pubescent branches and leaves, and the sessile capsules; along rivers, moist forests, secondary forests; 0–300 m.