

CONVOLVULACEAE

By Dan Austin † and P. Acevedo-Rodríguez

A predominantly tropical family of twining vines and lianas, sometimes erect herbs or shrubs (e.g., *Evolvulus*, *Ipomoea*, *Jacquemontia*, *Merremia*), or even trees (*Humbertia*, some *Ipomoea*); several species extend into temperate zones. There are 22 genera (including 3 introduced genera) of climbing Convolvulaceae in the Neotropics and ~415 species predominantly found in lowland moist forests, savannas, gallery forests, and in open disturbed vegetation.

Diagnosics: Sterile material is problematic to identify but the twining stems, alternate, mostly cordate leaves with largely pinnate venation, absence of stipules and tendrils, and milky latex (when present) are the best indicators of the family. Lianas are recognized by more or less oblong, coriaceous leaf blades that are uniform in that they lack glands, swellings, or pulvini, and are glabrous or sericeous. Stellate trichomes are mostly confined to *Jacquemontia* and *Distimake*, but also appear in some *Ipomoea* and *Maripa*. Woody lianas usually have stems with bands of successive vascular tissue resulting from successive cambial tissue.

General Characters

1. **STEMS.** Commonly herbaceous although many become woody with age, at least toward the base. However, some genera are woody almost throughout (e.g., *Bonamia*, *Calycobolus*, *Dicranostyles*, *Itzaea*, *Lysiostyles*, *Maripa*, and some *Ipomoea*). Woody stems are largely 1–5 cm in diam. in many of these genera, but in *Dicranostyles*, *Lysiostyles*, and *Maripa* they may reach 10–35 cm in diam. and 30–35 m in length. Stem shape varies from cylindrical to 1–2- or 3-lobed and is often non-cylindrical or flat in species of *Maripa*. Cross sections of stems show different anatomical

arrangements that are developed either by a single a single cambium or by numerous, successive cambia as follows.

A. Single cambium:

- i. Xylem furrowed by phloem wedges found in *Bonamia*, *Jacquemontia*, and some *Ipomoea*, where the xylem is intruded by deep phloem wedges that are the result of differential production of xylem and phloem in regions of the cambium (Figures 86A, B; 87E), in species of *Distimake*, this differential growth is less pronounced and leads to a xylem that is sinuate (Figure 86E).
- ii. Fissured stems, found in *Jacquemontia* and some *Ipomoea*, where non-lignified parenchyma proliferate, fissuring the xylem into irregular segments or islands (Figures 86A, B, E; 87E; Angyalossy et al. 2015; Carlquist 1991; Obaton 1960).
- iii. Regular anatomy, found in *Porana nutans* (Choisy) O'Donnell where the xylem forms a continuous large cylinder traversed by narrow rays (Figure 86D).

B. Multiple cambia (successive) are found in numerous genera and produce different anatomical arrangements such as:

- i. Concentric or eccentric, alternate rings or bands of vascular tissue, found in *Dicranostyles*, *Maripa*, and many *Ipomoea* (Schenck 1892; Obaton 1960; Mennega 1969); for the most part, these bands are discontinuous or asymmetrical and rarely form a continuous ring, these are often dissected by narrow to wide rays joined by conjunctive tissue; the peripheral edge of the xylem is often sinuate (Figures 86C; 87B, C).

- ii. Lobed stems with successive cambia active in the area where the lobes are produced, these made of successive alternate bands of vascular tissue (Figure 87A).
- iii. Successive cambial patches responsible for the development of islands of vascular tissue separated from each other by a matrix of parenchyma are produced in *Distimake* (e.g., *D. tuberosus* (L.) A.R. Simões & Staples, Figure 86E, F) and *Ipomoea* (e.g., *I. furcyensis* Urb., Figure 86B), the xylem within these islands in *D. tuberosus* is furrowed with shallow phloem wedges (Figure 86F).

The phloem in many genera of Convolvulaceae is stratified, with alternating bands of fibers (Figure 87D). All Convolvulaceae (except *Cuscuta* and *Humbertia*) have intraxylary phloem strands in the periphery of the medulla (Metcalf & Chalk 1957; Figure 86C), although not always easy to observe.

2. EXUDATES. Many species, especially the herbaceous ones, produce milky latex when the leaves or stems are injured (Figure 87C, D). In many lianas, the latex is clear or sometimes yellowish. Coloration of exudates is variable within genera or even within species, where the exudate is sometimes milky or clear. According to Hallier (1893), most, if not all genera, have latex cells whether or not they show milky sap.
3. ROOTS. Some *Ipomoea* are known to have large, fleshy roots that store nutrients (Figure 88). A well known example is *I. batatas*, the common sweet potato, which is widely cultivated for its edible starchy roots.
4. CLIMBING MECHANISM. All climbers in Convolvulaceae are twiners. Various species of *Maripa* produce short, sympodial, twining tendril-like branches that may be distally

devoid of leaves; these were considered in the past by some as tendrils, but in reality, they are branches.

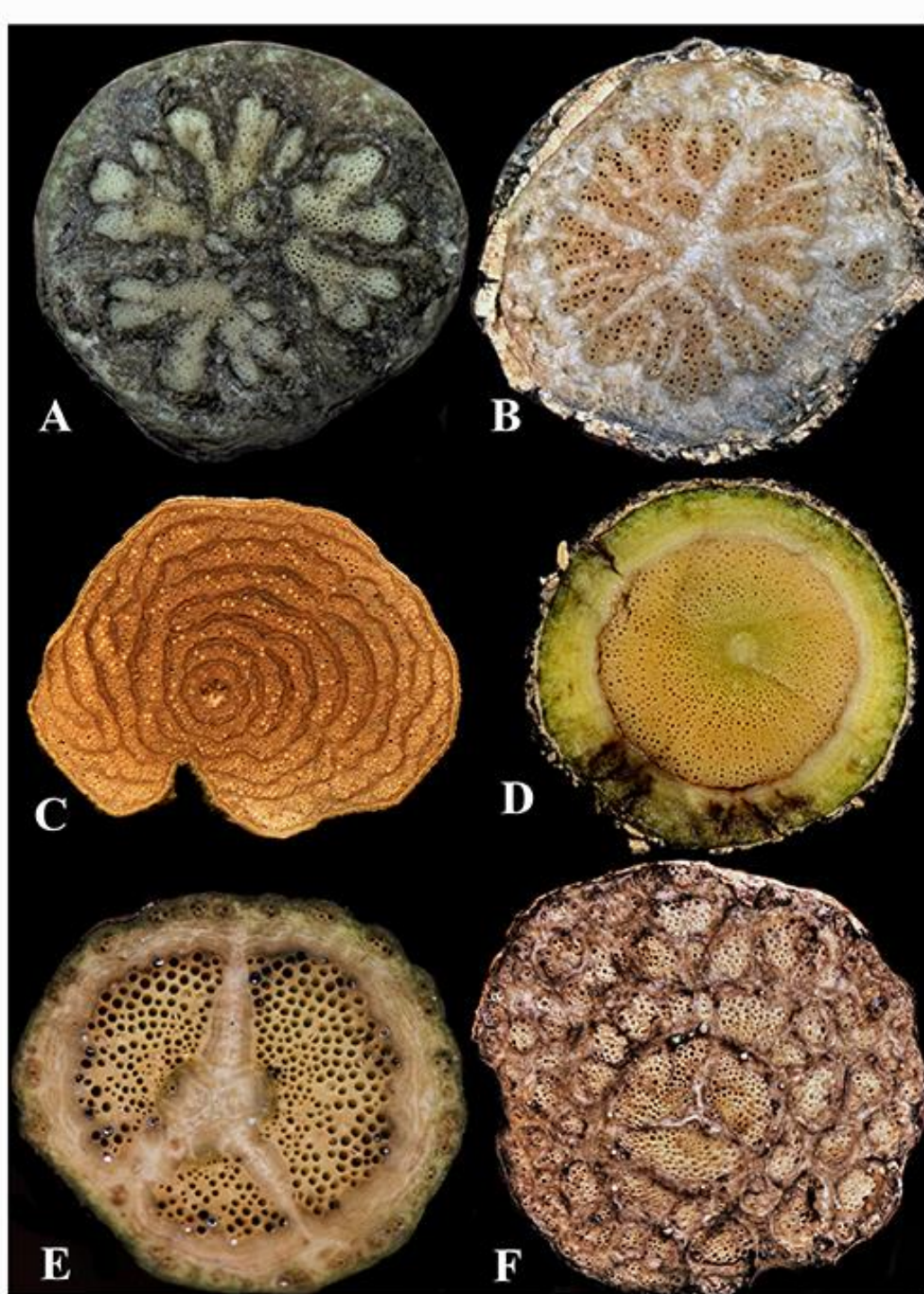


Figure 86. Cross sections of Convolvulaceae stems. **A.** *Jacquemontia* sp., cylindrical with furrowed xylem. **B.** *Ipomoea furcyensis*, early stage, cylindrical with xylem in irregular plates and few incipient

neoformed vascular cylinders in the inner bark. **C.** *Maripa scandens*, asymmetrical with successive bands of xylem and phloem. **D.** *Porana nutans*, cylindrical with regular anatomy, stratified phloem with bands alternating fibers. **E.** *Distimake tuberosus*, early stage with xylem divided into 3 plates and incipient neoformed vascular cylinders on the periphery of the phloem. **F.** *Distimake tuberosus*, mature stem with successive islands of xylem and phloem. Photos by P. Acevedo.

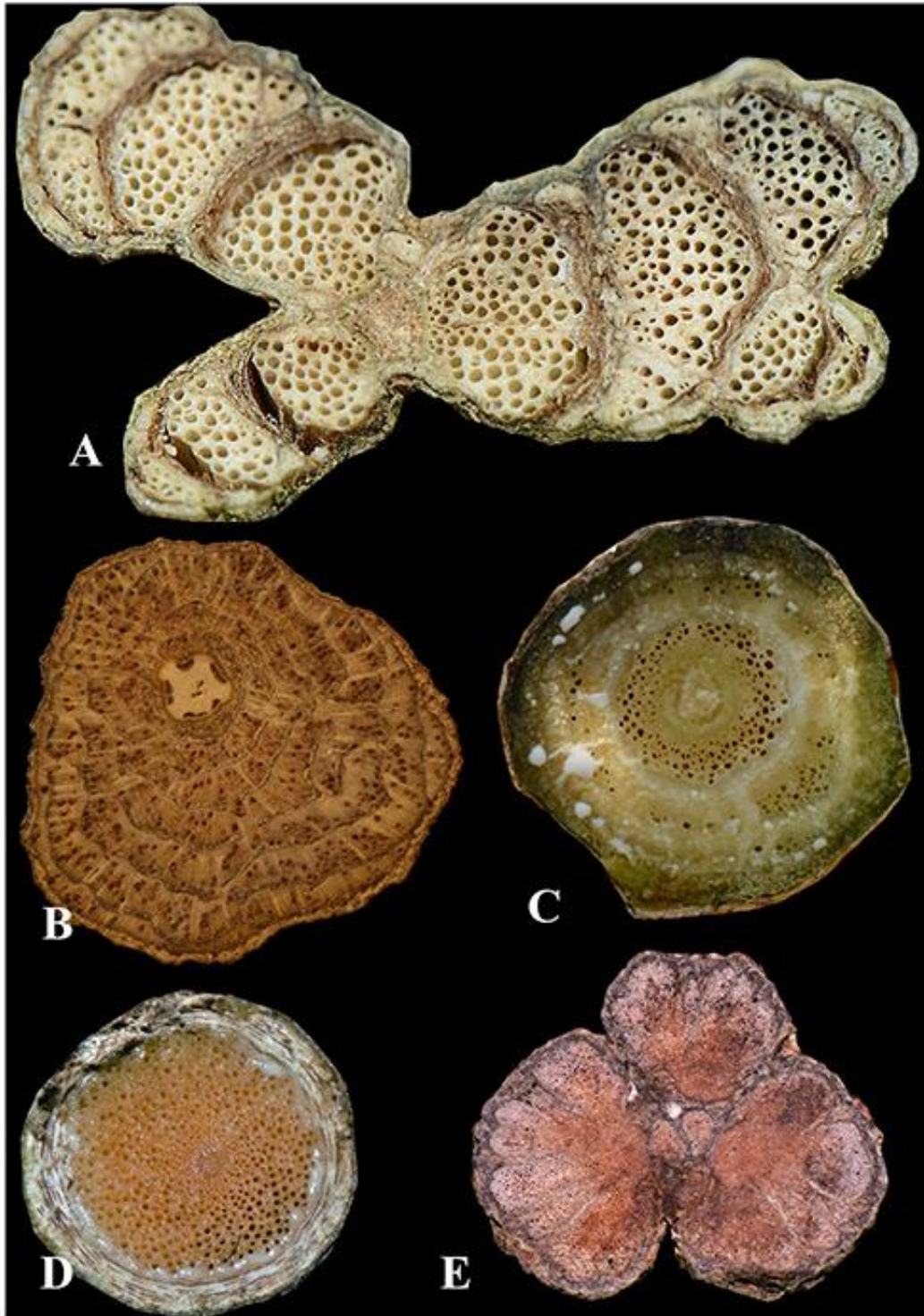


Figure 87 Cross sections of Convolvulaceae stems. **A.** *Ipomoea corymbosa*, 3- 4-lobed with successive bands of vascular tissue in the lobes. **B.** *Dicranostyles holostyla*, trigonous with successive discontinuous bands of vascular tissue. **C.** *Ipomoea abutiloides*, cylindrical with discontinuous, successive, concentric rings of vascular tissue. **D.** *Ipomoea megapotamica*, cylindrical with regular anatomy, xylem cylindrical with inconspicuous rays and stratified phloem, with alternating bands of fibers. **E.** *Jacquemontia nodiflora*, asymmetrical with Fissured stem. Photos by P. Acevedo.

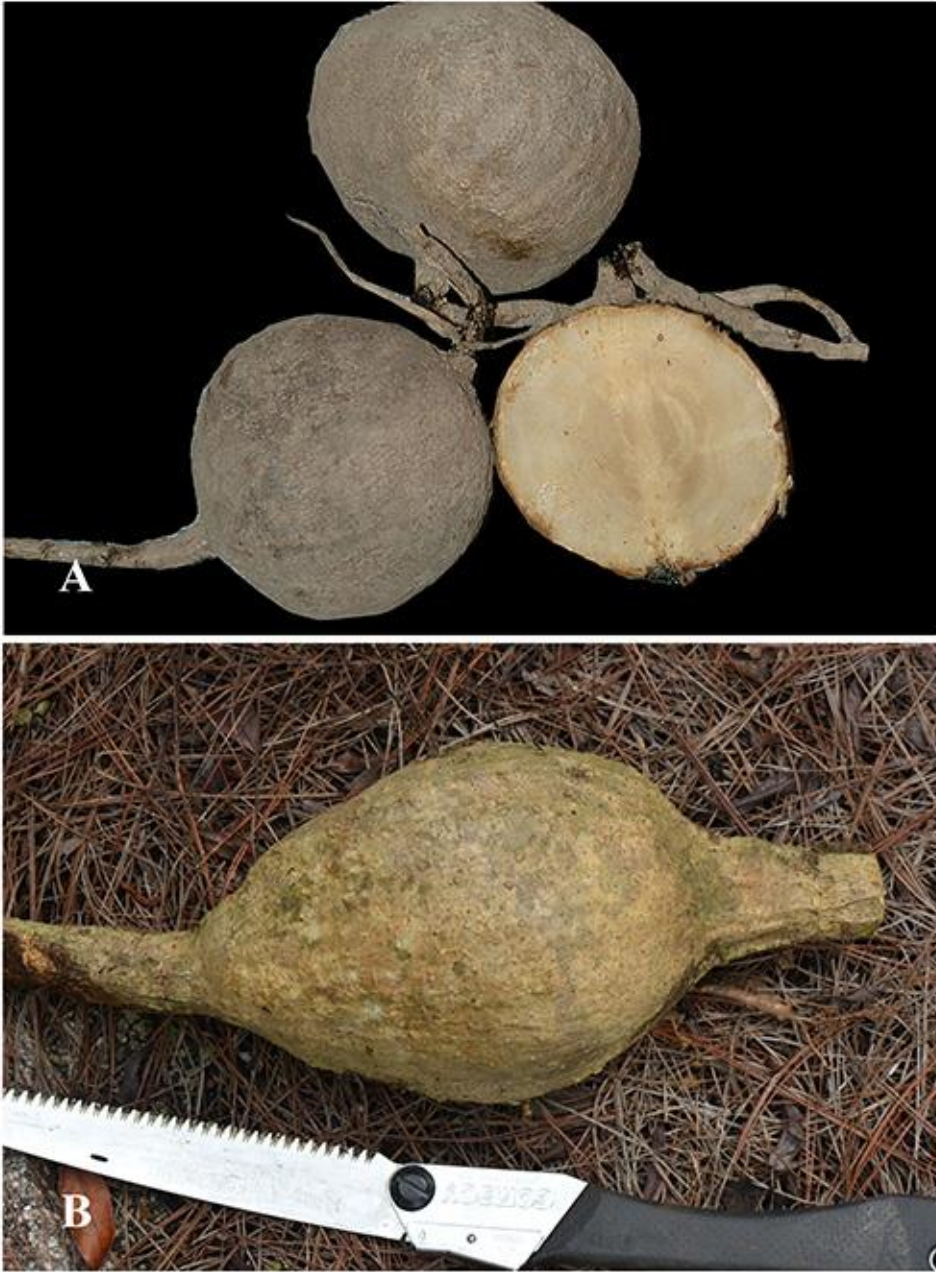


Figure 88. Tuberous, napiform roots in *Ipomoea*. **A.** *I. eggersii*. **B.** *I. furcyensis*. Photos by P. Acevedo.

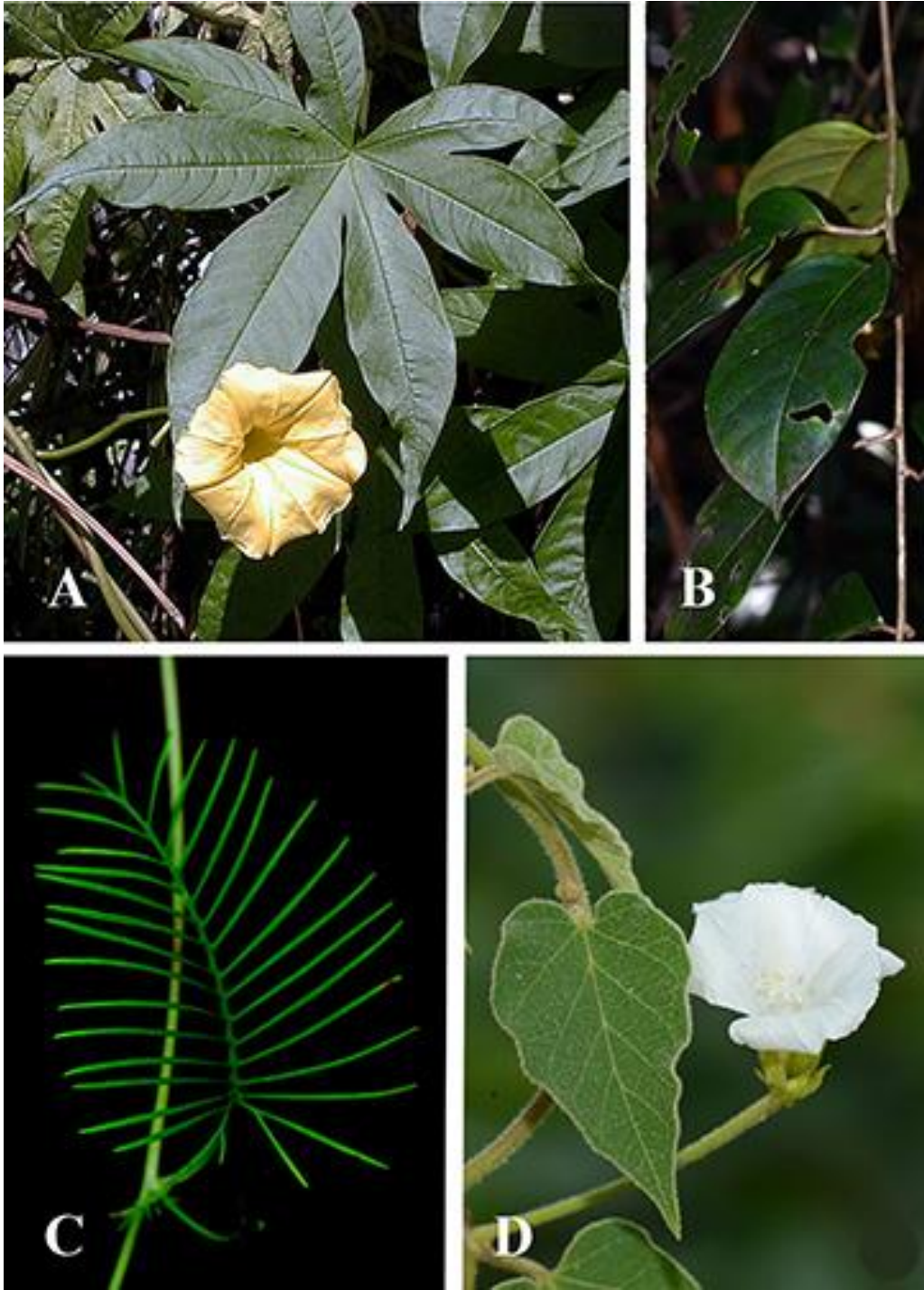


Figure 89. Leaves in Convolvulaceae. **A.** Palmately lobed in *Distimake tuberosus*. **B.** Oblong in *Maripa glabra*. **C.** Pinnatifid in *Ipomoea quamoclit*. **D.** Cordiform in *Jacquemontia polyantha*. Photos by P. Acevedo.

5. LEAVES. Leaf blades are predominantly simple and cordiform (Figure 89D), a shape that is often associated with the twining growth form. Most of the woody lianas have leaf blades that vary between ovate to oblong to lanceolate and are largely coriaceous while their bases are mostly obtuse to acute (Figure 89B), less often subcordate. Much of the family has alternate, simple, unlobed leaves; others are variable from entire to 3–9-lobed; deeply palmately lobed as in *Distimake tuberosus* (Figure 89A); pinnatifid as in *Ipomoea quamoclit* L. (Figure 89C); and palmately compound as in some *Ipomoea* from the Antilles. Petioles are variable, with the tropical lianas mostly being rounded and canaliculate above.
6. INFLORESCENCES. Axillary or distal, and either simple or compound cymes. In various genera, this basic pattern is modified into racemose, monochasial cymes, e.g., *Ipomoea lobata* (Cerv.) Thell., *Dicranostyles*, *Maripa*.
7. PEDICELS. Length varies markedly, from essentially absent to several cm (e.g., *Ipomoea*, *Jacquemontia*, and other genera).
8. FLOWERS. Mostly actinomorphic, or slightly zygomorphic as in species pollinated by hummingbirds (e.g., *Ipomoea lobata*, *I. lutea* Hemsl.) or bats (*Merremia platyphylla* (Fernald) O'Donell, *Ipomoea neei* (Spreng.) O'Donell). Sepals 5, free, quincuncial; corolla tubular (sometimes only at the base), 5-lobed, white to yellow, or more commonly lavender to purple to deep blue or even red or orange (Figure 90); buds are plaited or twisted, resulting in 5 areas of the corolla called plicae (portions folded in bud) and 5 interplicae (areas exposed in bud); absence or presence of indumenta and its type on the interplicae may aid in generic or specific identification; corolla appendages present in *Cuscuta* that are probably homologous to the glandular staminal trichomes on the bases of filaments in

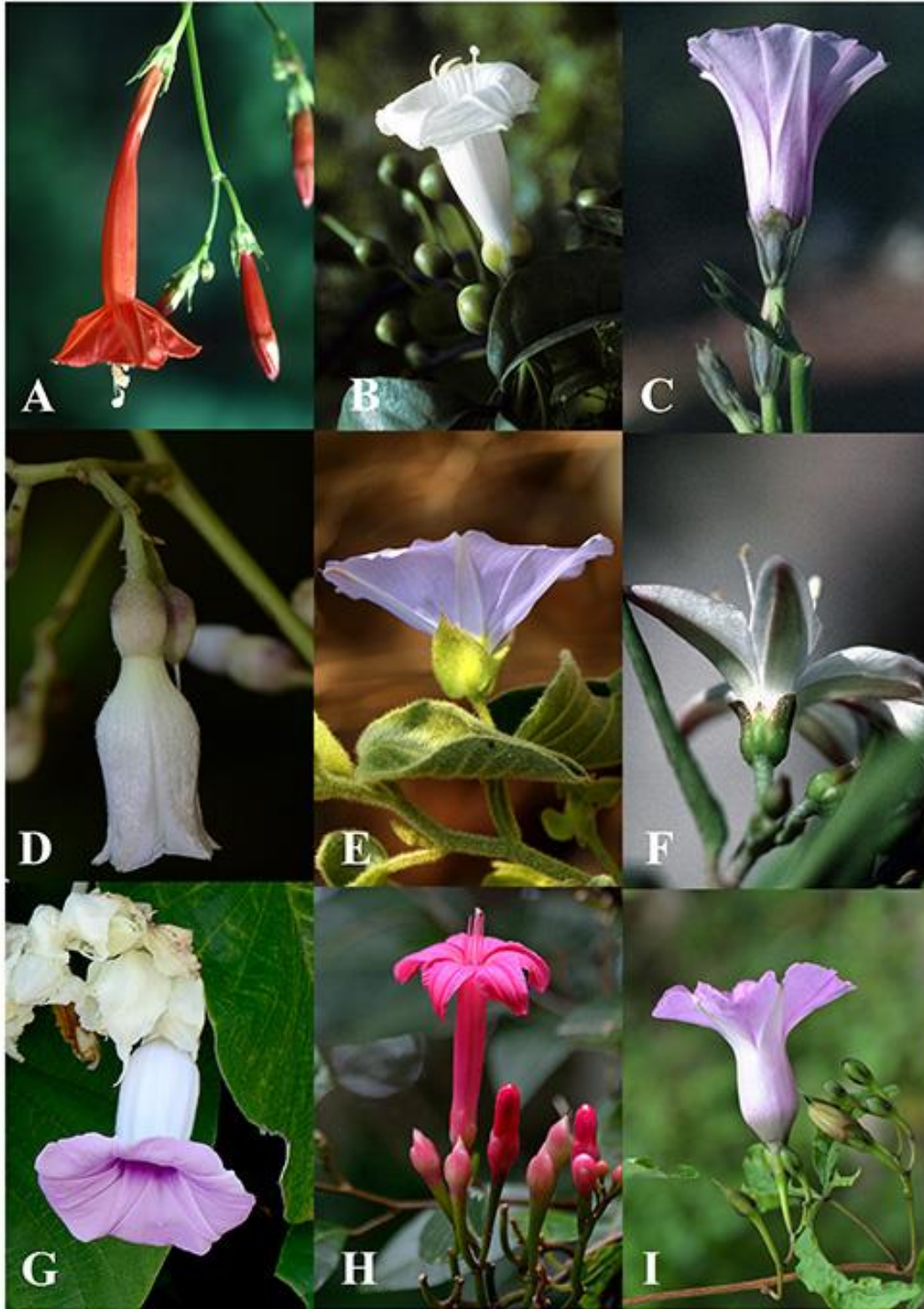


Figure 90. Flowers in Convolvulaceae. **A.** Salverform corolla in *Ipomoea hederifolia*. **B.** Funnel-campanulate corolla in *Ipomoea ternata*. **C.** Funnelform corolla in *Ipomoea triloba*. **D.** Campanulate corolla with short lobes in *Maripa paniculata*. **E.** Rotate corolla in *Jacquemontia heterantha*. **F.** Funnelform corolla with deep lobes in *Jacquemontia havanensis*. **G.** Funnelform corolla in *Ipomoea nervosa*. **H.** Salverform corolla in *Ipomoea microdactyla*. **I.** Funnelform corolla in *Ipomoea furcyensis*. Photos by P. Acevedo.



Figure 91. Frutis in Convolvulaceae. **A.** Indehiscent, woody fruit in *Dicranostyles ampla*. **B.** 4-valved, 4-seeded capsule in *Camonea umbellata*. **C.** 4-valved, late dehiscent capsule in *Bonamia agrostopolis*. **D.** 4-valved, 4-seeded dehiscent capsule in *Aniseia* sp. Photos by P. Acevedo.

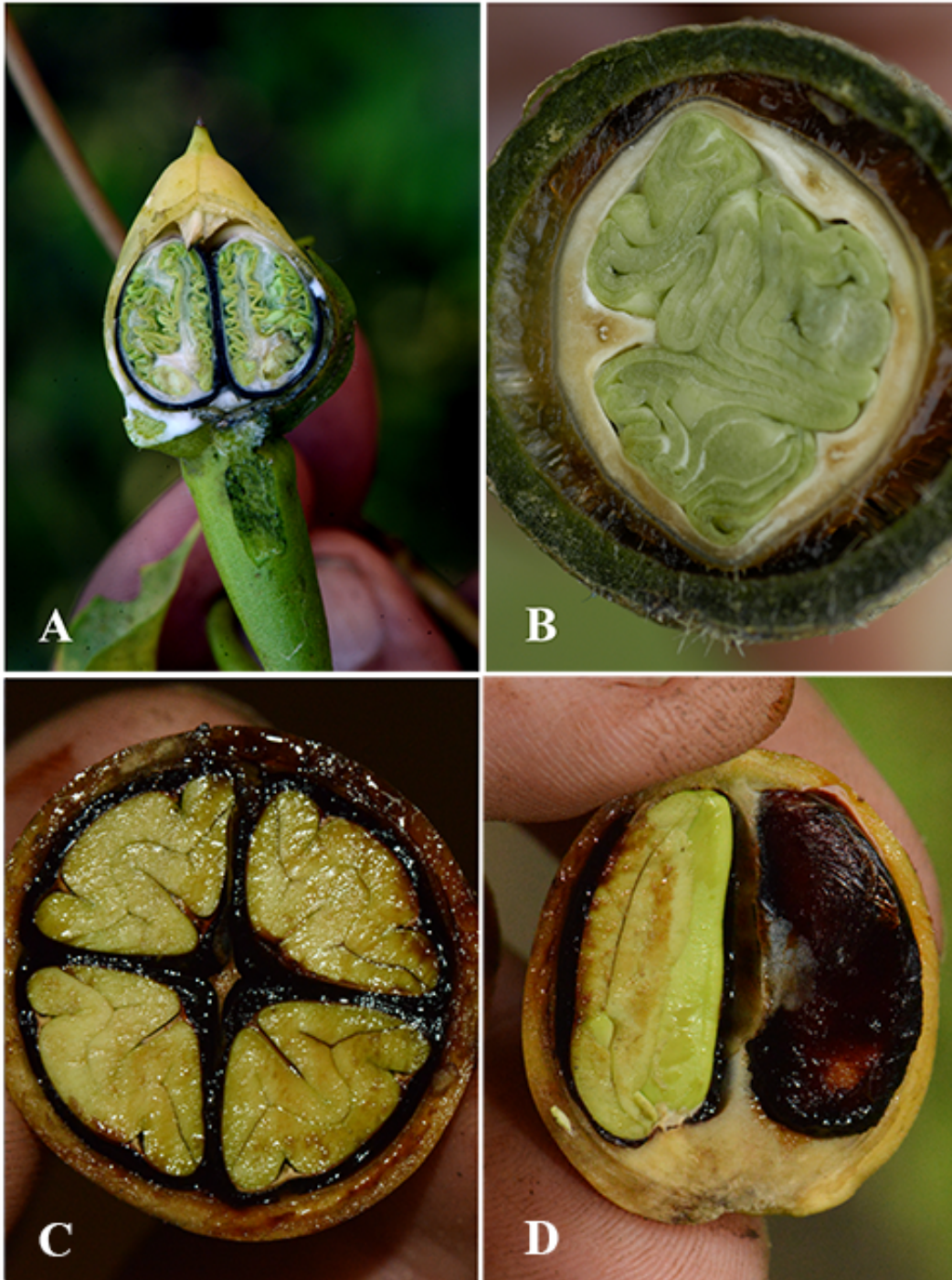


Figure 92. Seeds and cotyledons in *Convolvulaceae*. **A.** Longitudinal section of fruit of *Ipomoea alba* showing plicate cotyledons. **B.** Cross section of *Dicranostyles mildbraediana* 1-seeded fruit showing foliaceous, plicate cotyledons and gelatinous pulp around the seed. **C.** Cross section of *Maripa nicaraguensis* 4-seeded fruit, showing foliaceous plicate cotyledons and juicy gelatinous, brown pulp around the seeds. **D.** Longitudinal section of *M. nicaraguensis* fruit showing cotyledons (left) and seed (right) enveloped in a brown gelatinous pulp. Photos by P. Acevedo.

several other genera such as *Ipomoea*; nectaries intrastaminal, ring- or cup-shaped, often 5-lobed, absent in some lineages that are autogamous (e.g., *Ipomoea minutiflora* (M. Martens & Galeotti) House); stamens equal or unequal in length, inserted within the corolla (Figure 90C, D, E, G, I) or exserted (Figure 90A, B, F, H); ovary superior, bicarpellate, less often 3–5-carpellate, mostly 2-locular, but may be 4, 5, or 6 locular due to false septa, with axile placentation bearing 2 ovules per locule, styles 1 or 2, elongate in most species, almost absent in some *Dicranostyles*, stigmas 1 or 2, variable from cylindrical to ligulate to globose.

9. FRUITS. Mostly loculicidal capsules (Figure 91B–D), sometimes indehiscent or tardily dehiscent as in *Aniseia*, *Bonamia*, and *Ipomoea corymbosa* (L.) Roth (Figure 91C); fleshy or dry berries are found in *Dicranostyles*, *Lysiostyles*, *Maripa*, and some *Ipomoea* (Figure 91A).
10. SEEDS. (1)2–4 per fruit, glabrous or variously pubescent, sometimes ornamented with bumps and tubercles; seed coat hard and woody in most genera but soft in *Dicranostyle*, *Lysiostyles*, and *Maripa*. Hard-coated seeds may have life spans of up to at least 30 years, while soft-coated seeds live and germinate within a short time, perhaps as little as a week. Seeds of *Dicranostyles*, *Itzaea*, *Lysiostyles*, and *Maripa* are covered by a fleshy arillode or pulp, which is red in *Itzaea* and brownish gelatinous in the other three genera, a feature related to animal dispersal. Cotyledons are foliaceous and profusely plicate in *Dicranostyles*, *Maripa* and some *Ipomoea* (Figure 92).

USES

Only two edible species are of worldwide usage, *Ipomoea batatas* (L.) Lam. and *I. aquatica* Forssk. The former, *sweet potato*, *batata* or *camote*, is widely grown for its edible roots, and this American species is now a starch staple for several Old World countries. Additionally, sweet potato leaves are eaten as greens. There are other *Ipomoea* that have local uses as food because of their edible roots (e.g., *I. jicama* Brandegee and *I. plummerae* A. Gray). Fruits of *Maripa* are eaten by humans and other vertebrates (e.g., bats, birds, and monkeys) because of the sweet glutinous material surrounding their seeds; in the Guianas they are called “Monkey Syrup” (*hoa-soropan* in Arawak).

Because most genera are somewhat poisonous, many are used medicinally, e.g., *Calystegia*, *Convolvulus*, *Cuscuta*, *Dichondra*, *Evolvulus*, *Ipomoea*, *Jacquemontia*, *Merremia*, *Operculina*, and *Xenostegia*. There are numerous bioactive chemicals in the genera, including alkaloids, alkanes, calystegines, flavonols, flavonoids, phenols, resin glycosides (glycoresins), saponins, β -sitosterol, tannins, and terpenoids. Historically, the most well-known medicinal applications were as laxatives, due to the resin glycosides in several species (e.g., *Ipomoea jalapa* (L.) Pursh, *I. purga* (Wender.) Hayne, *Operculina* spp.), although many species have these compounds in lower concentrations.

Several American *Ipomoea* became famous in the 1930s and 1940s because of their hallucinogenic alkaloids used in religious context by indigenous peoples. It is now known that the plants themselves do not make ergoline alkaloids, but these chemicals are present in the epibiotic clavicipitaceous fungus *Periglandula* Steiner, Leistner & Leuchtm. The original ergoline alkaloids and their derivatives, originally from *Claviceps purpurea* (Fr.)

Key to the genera of climbing Convolvulaceae

- 1. Plants parasitic; stems yellow to orangish, without visible chlorophyll; leaves reduced to scales *Cuscuta*

- 1. Plants autotrophic (not parasitic); stems green to brown, with chlorophyll; leaves normally developed, green 2
- 2. Fruits indehiscent, nearly berries, dry or woody, mostly woody twiners 3
- 2. Fruits dehiscent, dry or woody, mostly herbaceous twiners, less often woody 10
- 3. Leaves cordate or subcordate basally 4
- 3. Leaves obtuse to acute basally 5
- 4. Flowers 5–6 mm long, in paniculate clusters with many flowers; cultivated *Poranopsis*
- 4. Flowers 2 cm long or longer, generally in simple or compound cymose clusters *Ipomoea*
- 5. Flowers smaller than 10 mm long 6
- 5. Flowers larger than 10 mm long 7
- 6. Anthers versatile, connective inconspicuous; corolla lobes apically acute to obtuse *Dicranostyles*
- 6. Anthers not versatile, with an enlarged connective, flattened and elongate, 1.5–2 times longer than the basifixed thecae; lobes of the corolla terminating in a mostly attenuate apex that is almost filiform *Lysiostyles*
- 7. Sepals markedly unequal in flower and fruit 8
- 7. Sepals more or less equal in flower and fruit 9
- 8. Outer 2 sepals much larger than inner 3; outer 2 sepals cordate at base, with distinct sinus between two lobes; third sepal similar to inner sepals, not markedly asymmetrical *Calycobolus*

8. Outer 3 sepals much longer than inner 2, outer 3 sepals narrowed into a claw-like base; third sepal narrower than outermost 2, distinctly asymmetrical on one side *Porana*
9. Lianas (woody); fruits woody to firm-baccate, incompletely 2-locular, lacking a spongy mesocarp; seeds covered by a gelatinous pulp *Maripa*
9. Vines (herbaceous); fruits not woody, 2-locular, with spongy mesocarp; pulp absent *Iseia*
10. Outer 2 sepals markedly larger than inner 11
10. Outer and inner sepals more or less equal or the outer shorter 13
11. Stigmas ellipsoid, flattened; trichomes stellate *Jacquemontia*
11. Stigmas globose; trichomes simple 12
12. Corollas white; leaf bases cuneate *Aniseia*
12. Corollas yellow with purple throat; leaf bases cordate *Hewittia*
13. Twining woody vines (lianas); styles 1 or bifid 14
13. Twining herbaceous vines; styles 1, entire or with 2 stigma lobes 15
14. Fruits 2–4 valvate but rarely break into 8 sections; endocarp absent; seeds brown to black
..... *Bonamia*
14. Fruits 3–4 valvate but break into 10–20 linear sections; spongy white endocarp supports and surrounds seeds; seeds red *Itzaea*
15. Stigmas subulate to ellipsoid 16
15. Stigmas globose to 2-globose 17
16. Stigmas subulate; trichomes simple, 2-branched..... *Convolvulus*
16. Stigmas ellipsoid, dorsoventrally flattened; trichomes stellate *Jacquemontia*
17. Corollas with midpetaline bands densely pubescent with long trichomes; fruit a 4-seeded capsule, enclosed by the persistent sepals and sepaloid bracts *Odonellia*

17. Corollas with glabrous or pubescent midpetaline bands sparsely to densely pubescent but
with small trichomes; fruit a 1–4 seeded capsule not enclosed by sepals and bracts 18
18. Flowers white to yellow, with or without a darker throat of red to purple 19
18. Flowers purple, blue, lavender, orange to scarlet, less often white to yellow, throat variable
but mostly darker or lighter shades of the limb 25
19. Stems (and often petioles, peduncles) winged; capsules with a thickened circumscissile lid
that separates from \pm papery and tardily shattering endocarp *Operculina*
19. Stems terete or striate, not winged; capsules dehiscing longitudinally or irregularly 20
20. Capsules 2-valved, 4-locular; inflorescences racemose; pubescence simple; stigmas
somewhat flattened-globose *Tetralocularia*
20. Capsules 4-valved or irregularly dehiscent, mostly 2–3 locular, less often 4 locular;
inflorescences cymose; pubescence simple or stellate; stigmas globose.....21
21. Inflorescence capitate, subtended by an involucre of acuminate, velutinous bracts .. *Daustinia*
21. Inflorescences umbellate, cymose, or corymbose.....22
22. Stems with a pair of spiniform projections at the nodes *Camonea*
22. Stems lacking spiniform projections at the nodes.....23
23. Leaves narrow (linear or oblong-linear) with sagittate, truncate or hastate base, subsessile;
anthers strait-dehisced..... *Xenostegia*
23. Leaves ovate, cordiform, palmately compound or palmately lobed, commonly long petioled;
anthers longitudinally dehiscing with slightly curved apex or spirally dehiscing24
24. Leaves entire, sinuate to shallowly 3-lobed; fruits with non-acrescent sepals; seeds hairy
..... *Merremia*

24. Leaves palmately compound or palmately lobed (rarely simple or vestigial); fruits with large, accrescent sepals; seeds glabrous (rarely velvety puberulent, glabrescent)*Distimake*
25. Stems (and often petioles, peduncles) winged; corollas salverform, salmon, orange to red; fruits operculate*Operculina*
25. Stems terete or striate, not winged; corollas mostly funnelform, some salverform, lavender to red; fruits valvately dehiscent*Ipomoea*

Identification of genera based on vegetative characters

The genera of climbing Convolvulaceae are defined by multiple traits; vegetatively the genera are mostly similar and difficult to tell apart. However, the following generalities can be useful in distinguishing the genera with a certain degree of confidence.

1. Acute to obtuse leaf bases: *Aniseia*, *Bonamia*, *Dicranostyles*, *Lysiostyles*, and *Maripa*.
2. Leaf texture.
 - a. coriaceous leaves: *Bonamia*, *Dicranostyles*, *Lysiostyles*, and *Maripa*.
 - b. succulent leaves: *Ipomoea imperati* (Vahl) Griseb., *I. pes-caprae* (L.) R. Br., and *I. violacea* L.
3. Leaves reniform. Several species of *Ipomoea* in the West Indies have reniform leaves that are produced in brachyblasts.
4. Small flowers (< 1 cm long): *Cuscuta*, *Dicranostyles*, *Lysiostyles*, *Poranopsis* and *Tetralocularia*.
5. Flower color. Yellow and white corollas dominate *Distimake*, *Hewittia*, *Merremia*, *Operculina*, and *Tetralocularia*. There are a few species of *Ipomoea* with yellow corollas, some of which are autogamous species such as *I. minutiflora* (M. Martens & Galeotti)

House. White corollas occur mostly in species adapted for moth pollination (e.g., *I. alba* L.) but also are found in genera with tiny or small flowers (e.g., *Dicranostyles*, *Jacquemontia*, *Poranopsis*), and as occasional mutations in species with typical colored flowers.

6. Enlarged outer sepals: *Aniseia*, *Calycobolus*, and *Porana* have 2 or more of the outer sepals markedly larger than the inner sepals.
7. Nut-like fruits. When dry, the fruits of *Dicranostyles*, *Lysiostyles*, and *Maripa* resemble nuts, being somewhat woody.
8. Multiple segmented exocarp. Most genera with capsular fruits divide into 4 segments. *Jacquemontia* fruit segments may further divide into 8; those of *Itzaea* into 10–20. *Bonamia* typically has 2–4, but sometimes divides into 8.

ANISEIA Choisy, Mém. Soc. Phys. Genève 6: 481. 1834.

Herbaceous vines typically prostrate, the apices of the branches twining, glabrous or pubescent, reaching up to 7 m in length; latex clear. Leaves short-petiolate, entire, linear-ovate to



elliptic, bases mostly cuneate, apices sometimes mucronate. Inflorescences axillary, solitary or in dichasia. Flowers 1–3; sepals 5, herbaceous, unequal, the outer 2 larger, sometimes decurrent on the peduncle; corollas funnellform, white, the limb 5-dentate or more or less entire, with 5 pubescent longitudinal

bands on the outside; stamens included, equal or unequal, with glandular trichomes on the

filament bases, the anthers ovate, extrorse; pollen pantocolpate; ovary 2-locular, the locules 2-ovulate, the style 1, slender, included, the stigma 2-globose. Fruits capsular, globose to ovoid, 2-locular, 4-valved, glabrous without, typically white and appressed pubescent within the valves. Seeds often 4, glabrous or with short erect trichomes around margins forming wing-like appendages, densely pubescent on all surfaces in one species, the hilum often somewhat triangular.

Distinctive features: The outer 2 sepals are greatly enlarged and conceal the much smaller inner 3 sepals; cuneate leaf bases and entire, linear-ovate to elliptic leaves easily distinguish the genus.

Distribution: A neotropical genus of two species, distributed from southern Mexico to NE Argentina, typically along the margins of wetlands, in some cases trailing from shore over the surface of the water; 0–100 m.

BONAMIA Thouars, Hist. Vég. Îles France 33. 1804 (nom. cons.).

Twining herbaceous or woody vines, or trailing, procumbent or erect herbs; stems up to



Bonamia menziesii, photo by G. Staples.

several meters long, smooth or lenticellate, glabrous to densely pubescent; cross sections cylindrical to 5-angled, fissured stems known from *B. maripoides* Hallier f. Leaves petiolate, subsessile or sessile, herbaceous to subcoriaceous, occasionally leathery, simple, entire, ovate,

elliptic, lanceolate, oblong or linear, basally attenuate, cordate, rounded or truncate, trichomes appressed, 2-armed, straight or crisped, scattered or dense, silvery grey or grayish white to pale brown, often rusty brown when dry. Inflorescence axillary or terminal, pedunculate or subsessile, of simple or compound dichasial cymes; bracts small and linear to distinctly foliaceous. Flowers 1–∞, medium to large; sepals ovate to oblong-orbicular, equal or unequal, apically acute, acuminate, obtuse, rounded or emarginated, ferruginous, sericeous or glabrous; corolla white, blue, red, yellow, yellowish white or greenish white, funnelform, the limb entire to lobulate, sparsely or densely pilose on interplacae; stamens inserted or rarely exerted, filaments unequal to equal, glabrous to densely villous or glandular-villous, frequently villous only on the basal dilated portions; anthers oblong or oblong-lanceolate, dorsifixed or apparently basifixed, frequently sagittate or cordate at the base, introrse or partially extrorse; pollen 3-colpate to pantocolpate, not spiny; ovary 2-carpellate, 2-locular, glabrous, long-pilose, or hirsute with two-armed trichomes, disc annular, ovules 2 per locule, styles 2, almost free to partially united, included in the corolla to partially exerted, the stylar branches equal to unequal, filiform, mostly glabrous, stigmas globose, subglobose, capitate, reniform, bilobed conical or rarely peltate. Fruits valvicular capsules, occasionally dehiscent by circumscission, or late dehiscent; valves 4–8, rarely 2, ovoid, globose or conical-ovoid, glabrous or with scattered trichomes, pericarp thin and chartaceous to thick and ligneous. Seeds 1–4, brown to black, smooth or punctate, glabrous or lanate, oval, with hard or rarely soft seed coat, surrounded by a thin, transparent pulp.

Distinctive features: High-climbing lianas; stigmas globose; styles 1 or 2; capsules lacking the spongy mesophyll that is characteristic of *Itzaea*, the only genus with which *Bonamia* is usually confused with in the Neotropics.

Distribution: Some 56 species widespread across the tropics, with 18 species endemic to the Neotropics, all of which are twining climbers; Mexico to Argentina; lowland tropical forests to dry thorn-scrubs.

CALYCOBOLUS Willdenow ex J. A. Schultes in J. J. Roemer & J. A. Schultes, Syst. Veg. 5: ii. 1819.

Twining lianas, stems glabrous or pubescent (simple or T-shaped hairs); latex clear.



Calycobolus sericeous, photo by P. Acevedo.

Leaves petiolate, simple, entire, chartaceous to coriaceous, base attenuate, acute, or obtuse, apex attenuate to obtuse, pinnately veined, densely appressed pubescent to glabrous. Inflorescences axillary or terminal on lateral branches, umbelliform to paniculate-thyriform, composed of cymose units; peduncle short or quite long; bracts present, deciduous or persistent. Flowers small to medium-sized;

sepals very unequal, outer 2 larger, cordiform, subtriangular, ovate or broadly reniform, tightly appressed to one another, base cordate, apex rounded to acute, inner 3 much smaller, decreasing in size toward innermost, tightly enveloping corolla base; corollas tubular to narrowly funnelliform, white, limb subentire to vaguely lobed, erect, interplacae pubescent outside or glabrous; stamens subequal, anthers oblong to linear-oblong, white, dehiscing lengthwise without twisting; pollen 3-colpate and pantocolpate, non-spinose; ovary 2-locular, locules 2-

ovulate, styles 2, free or partially fused below middle, stigmas 2, capitate or depressed-globose. Fruits enclosed in accrescent, chartaceous calyx; indehiscent, an utricle or utricle-like, 1- or 2-locular, ovoid to ellipsoid, mostly chartaceous. Seeds 1–4, ovoid to ellipsoid, black to brown, glabrous; hilum basal, often D-shaped.

Distinctive features: Some *Jacquemontia*, *Bonamia peruviana* Ooststr. and *Porana nutans* have been confused with *Calycobolus* in the Americas. The stellate trichomes and single style distinguish *Jacquemontia*. Simple or 2-armed trichomes and 2 styles are shared among the others. Subligneous to coriaceous capsules and twisted anthers separate *B. peruviana*. The other two genera may be distinguished as follows:

Outer 3 sepals much longer than inner 2, the outer 3 sepals narrowed into a claw-like base, and the third sepal narrower than outermost 2, distinctly asymmetrical on one side
.....*Porana nutans*

Outer 2 sepals much larger than inner 3, outer 2 sepals cordate at base, with distinct sinus between the two lobes, and the third sepal similar to the inner sepals and not markedly asymmetrical*Calycobolus*

Distribution: There are 16–28 species known in South America and Western Africa, with only three species in the Neotropics; northern half of South America; moist and gallery forests; 100–600 m.

CAMONEA Rafinesque, Fl. Tell. 4: 81. 1838 ['1836'].

Twining herbaceous vines; stems climbing or creeping, reaching 5 m long, with a pair of spiniform projections at the nodes; latex milky. Leaves simple, ovate or lanceolate, the margins



Camonea umbellata, photo by P. Acevedo.

undulate; petioles cylindrical, often longer than the blade. Inflorescences axillary, umbelliform cymes, 10–15-flowered, mostly diurnal; peduncles usually similar to the stems and petioles, longer than the sustaining petiole; pedicels much shorter than the peduncle, puberulous; bracts scale-like. Sepals 5, slightly unequal, glabrous, imbricate, oblong, the margins entire, the apex rounded, slightly emarginate; corollas bright yellow, infundibuliform, glabrous, tube widening

gradually with 10 obtuse lobes; stamens 5, white, included, inserted at the base of the corolla tube, anthers helicoid-contorted, pollen hexazonocolpate; ovary 2-locular, with 2 ovules per locule, styles 1, white, slightly exserted, stigmas 2, greenish. Fruit a valvicular dehiscent capsule, globose, brown, 4-valvate, glabrous, with persistent indurate sepals. Seeds 4, dark brown, obtusely trigonal, papillate, with a line of hairs on two of the edges.

Distinctive features: Twining vines; leaves entire or angulate-lobed, with a pair of spiniform projections at base of petioles; corolla glabrous, except for a tuft of hairs at apex of the midpetaline bands; anthers longitudinally dehiscent and curved at the apex or spirally dehiscent; capsule chartaceous, 4-valved; seeds velvety pubescent, with a line of longer hairs on two of the margins.

Distribution: A genus of 5 species centered in tropical Asia, with only *C. umbellata* (L.) A.R. Simões & Staples native and widespread in the Neotropics; in lowland scrubs, grasslands, savannahs, dry forests, and disturbed open areas.

CONVOLVULUS Linnaeus, Sp. Pl. 153. 1753.



Convolvulus arvensis L., photo by D.G. Carr.

Woody or herbaceous twining vines or shrubs, with clear latex. Leaves petiolate, rarely sessile; blades herbaceous to coriaceous, linear to ovate or elliptic with subtruncate cordate, sagittate or hastate bases, glabrous or pubescent, the margins usually undulate to crenate or irregularly lobed or laciniate. Inflorescences of solitary flowers or in cymose groups, on pedicels mostly 1–3 cm long, bracts and bracteoles linear, elliptic or ovate. Flowers 0.4–4 cm long in the Americas; sepals subequal, the inner three often somewhat longer, suborbicular, elliptic to ovate, pubescent or glabrous, obtuse to acute, usually mucronate; corollas white or rose to purple or blue on the limb and white or purplish within the tube, funnelform, the limb 5-angulate to 5-lobed, the midpetaline bands (interplicae) glabrous or pubescent; stamens included, unequal, with glandular trichomes on the filament base, the anthers oblong, basally auriculate, introrse; pollen 3-colpate; ovary 2-locular, 4-ovulate, ovoid to subglobose, glabrous or pubescent, the disc usually lobed; style one; with 2 filiform, papillose stigmas. Fruits capsular, 4-valved, mostly

brown, subglobose to ovoid, chartaceous, glabrous or pubescent. Seeds (1)2–4, each 2–6 mm long, smooth or warty, glabrous to densely puberulent or hirsute.

Distinctive features: The stigma lobes are subulate, filiform, and typically rounded. Corollas mostly white; fruits capsular.

Distribution: A genus of ~220 species, with the majority in the Mediterranean and Near East. In the New World, there are 16–19 species, but only 5 species are found within the Neotropics, 3 of which are climbers; distributed from Mexico to Argentina including the West Indies; dry forests, scrubs, and grasslands.

CUSCUTA Linnaeus, Sp. Pl. 124. 1753.

Twining parasitic vines, holding on to the host by means of haustoria; stems twining,



Cuscuta americana, photo by P. Acevedo.

filiform, yellow or reddish, glabrous. Leaves reduced to minute scales. Inflorescences sessile or short pedicellate, mostly in globular, spicate, racemose, or cymose clusters. Flowers few to many, 4- or 5-merous; bracts minute or absent; sepals gamosepalous, \pm deeply lobed, or free; corolla white, pinkish, or cream-colored, urceolate, tubular, globose or campanulate, inside with fimbriate or crenulate, membranous, infrastaminal scales at base of tube; stamens as many as corolla lobes, inserted on corolla above scales, alternating with corolla lobes; pollen smooth, 3-zonocolpate, although some 5–6-colpate or 8-colpate; ovary 2-locular, each locule with

2 ovules, the styles 1 or 2, stigmas 2, nearly globose or elongated, sometimes united. Fruits capsular, ovoid or globose, dry or sometimes fleshy, circumscissile or opening irregularly. Seeds 1–4, glabrous; embryo acotyledonous, filiform, spiral-curved.

Distinctive features: Parasitic and lacking obvious chlorophyll and leaves. While they may be rooted in the ground for a short while after germination, they soon break away to scramble through the branches of their host.

Distribution: At least 200 species widely spread across the world, except in Polar Regions.

Mihai Costea estimates that there are ca. 155 species in the Americas, but only ~10 species reach 2 or more m in length.

DAUSTINIA Buril & A.R. Simões, *Phytotaxa* 197(1): 60. 2015.

Austinia Buril & A.R. Simões (2014), nom. illeg.

Twining vines or less often prostrate subshrubs; latex white; stems slender, 1–2 m long,



Daustinia montana, photo by Bromelario Imperialis.

pubescent to velutinous, with simple trichomes. Leaves simple, unlobed or 3–5-lobed, with serrate or dentate margins, rarely serrulate or entire, abaxially white to yellowish cinereous; petiolate. Inflorescences axillary, capitate cymes, flowers nearly sessile, subtended by an

involucre of acuminate, velutinous bracts; peduncle 2.5–17 cm long. Sepals 5, persistent, shorter than the bracts, velutinous or pubescent; corolla bright yellow, rotate-funnelform, glabrous, limb

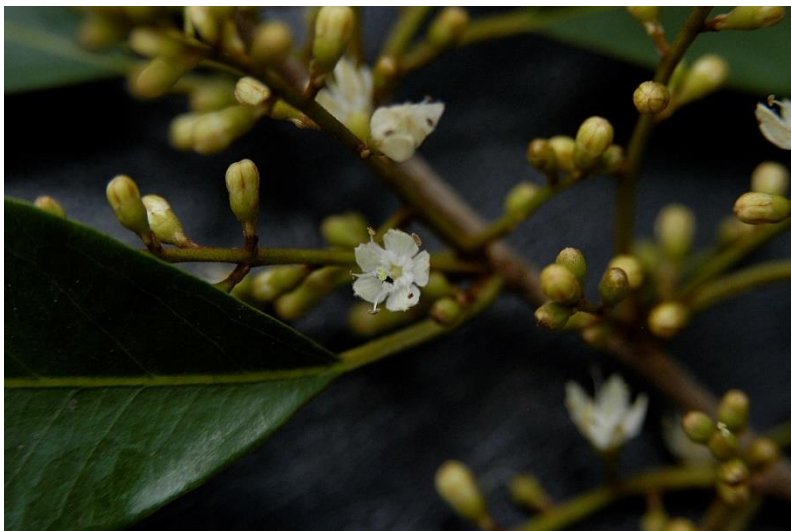
10-lobed; stamens subequal, included, pubescent at the base, anthers twisted at dehiscence; pollen grains 3-zonocolpate, spherical to prolate, perforate, spinulose; style as long as the stamens, stigmas 2, globose; disc 5-lobed; ovary 2-locular, 4-lobate, with 2 ovules per carpel. Fruit capsular, spherical, brown, glabrous, 4-seeded, dehiscing by 4 valves, enclosed by the persistent sepals and bracts. Seeds brown, glabrous, smooth.

Distinctive features: Similar to *Merremia* by the presence of globose stigmas, twisted dehiscent anthers, and 4-valvular capsules, but distinguished by the capitate inflorescence, large bracts, and unequal sepals.

Distribution: Monospecific, *D. montana* (Moric.) Buril & A.R. Simões is endemic to eastern Brazil (Piauí to Rio de Janeiro), occurring in caatinga, campos rupestres, cerrado and coastal sandy areas along the Atlantic Forest.

DICRANOSTYLES Bentham, London J. Bot. 5: 355. 1846.

Twining lianas with smooth or lightly striate stems (Figure 93); secondary growth with



Dicranostyles scandens, photo by P. Acevedo.

discontinuous bands of vascular tissue (Figure 87B), producing clear or yellowish latex. Leaves chartaceous to coriaceous, the base attenuate, acute to obtuse or rounded, cordate to truncate, the apex acuminate, rarely truncate, densely appressed-puberulent or erect-pubescent to glabrescent.

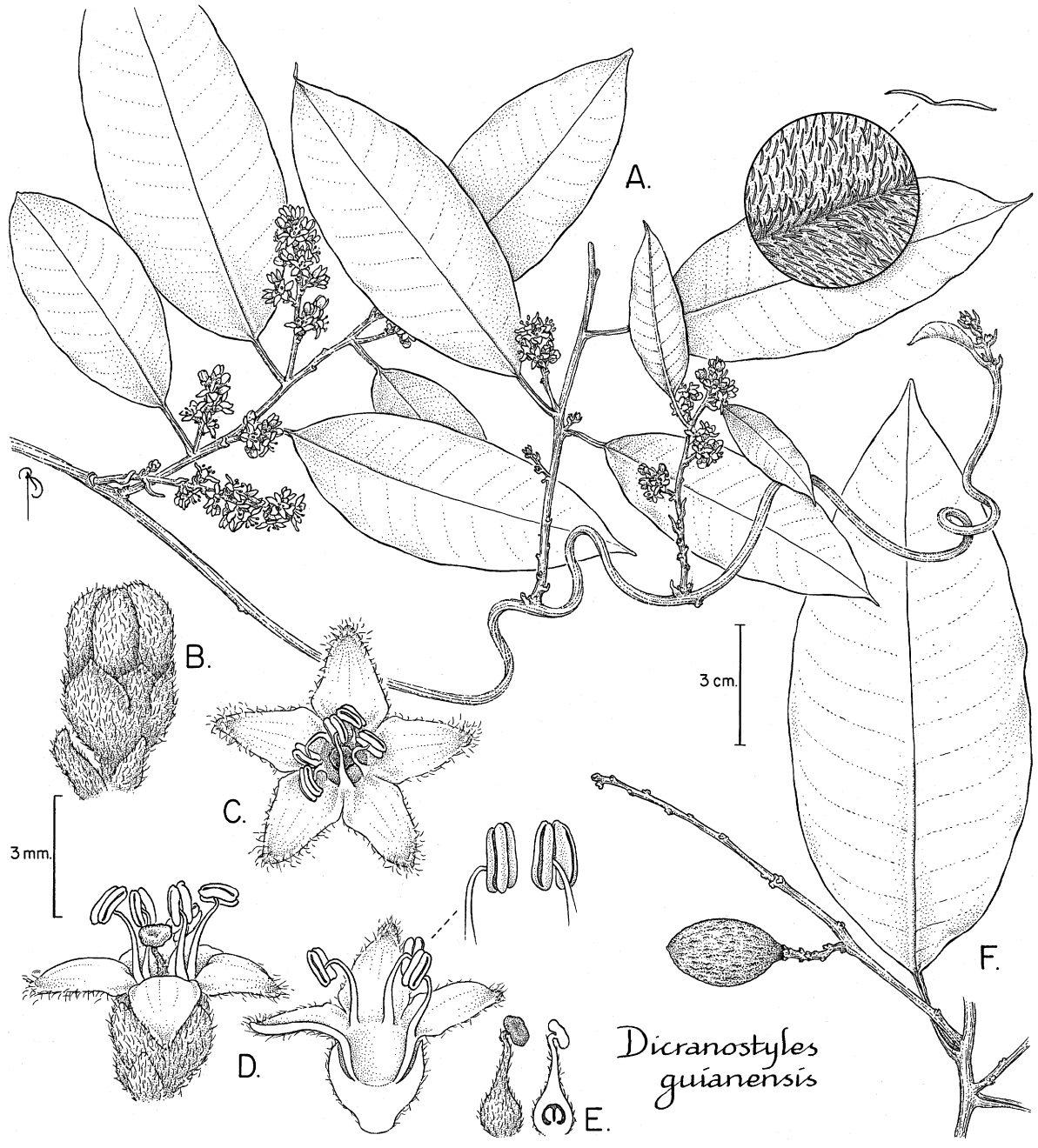


Figure 93. *Dicranostyles guianensis*. **A.** Flowering branch. **B.** Flower bud. **C.** Flower top view. **D.** Flower, lateral view & longitudinal section. **E.** Gynoecium, lateral view & longitudinal section. **F.** Fruiting branch. Drawing courtesy of Bobbi Angell.

Inflorescences racemose or thyrsoid, axillary. Flowers ~10 to many; sepals more or less equal, the outer ovate, the apex acute, the inner ovate to rounded, generally pubescent; corolla 5–8 mm long, rotate to funnelform, white to pinkish, lobed nearly to the base when rotate and near the midway when funnelform; pollen 3-colpate; ovary incompletely 2-locular, with a partial septum in the base, ovoid to obovoid, the locules 2-ovulate, mostly pubescent, styles 2, entire, divided into 2 short branches or completely divided, the stigmas capitate. Fruits indehiscent, ellipsoid to ellipsoid-cylindrical (Figure 91A), pericarp thickly coriaceous to woody (Figure 92B). Seeds 1–4, glabrous, ovate to oblong-ellipsoid, or triangular if there are more than 1 per fruit, covered in a distinctive jelly-like pulp (Figure 92B); embryo foliaceous and profusely plicate (Figure 92B).

Distinctive features: Lianas that grow to considerable heights into the canopy; flowers less than 1 cm long; fruits woody to baccate, indehiscent. Likely to be confused only with *Maripa*, which has much larger flowers, and *Lysiostyles*, which has distinctive long attenuate corolla lobes.

Distribution: Essentially a South American genus of 15 species, with *D. ampla* Ducke also found in Costa Rica (Hammel 2010); most common in periodically flooded forests (*igapó*, *várzea*) but also in non-flooded forests (*terra firme*); 80–460 m.

DISTIMAKE Rafinesque, Fl. Tell. 4: 82. 1838 ['1836'].

Twining herbaceous or subwoody vines, less often erect, decumbent or creeping herbs or



Distimake dissectus, photo by P. Acevedo.

subshrubs; stems cylindrical, twining or prostrate; pubescence when present of simple, glandular or stellate hairs; cross sections with successive cambia at least in *D. cissoides* (Lam.) A.R. Simões & Staples (Carlquist & Hamson 1991) and *D. tuberosus* (L.) A.R. Simões & Staples. The latter species also with fissured stems, with islands of vascular tissue that form from successive cambial patches (Figure 86E, F); latex watery or milky. Leaves simple, entire, palmately lobed or palmately

compound, leaflets or segments (3)5–9, ovate, elliptic or rarely linear, sessile, the margins entire or sinuate-serrulate; petioles short to long, sometimes absent. Inflorescences axillary, in dichasia or monochasia; peduncle commonly stout; pedicels commonly shorter than the peduncle; bracts lanceolate or linear, persistent or caducous. Flowers 1 to several, mostly diurnal; sepals 5, free, unequal or subequal, flat, imbricate, appressed to the corolla tube, ovate or lanceolate, longer than wide, accrescent in fruit, acute to rounded; corolla campanulate to infundibuliform, the tube widening gradually or abruptly with glabrous petaline bands, the limb more or less entire, the lobes 5–10, white, yellow, or rarely orange with tube sometimes of different coloration, glabrous; stamens 5, included, inserted at the base of the corolla tube, erect, unequal in length,

glabrous or pubescent, the anthers helicoid-contorted, white, yellow, cream or purplish; pollen trizonocolpate; ovary ovoid, 2–3-locular with 2 ovules per locule, style 1, white, glabrous, stigma 2-globose. Fruits capsular, globose, subglobose to quadrangular, 4-valved, glabrous. Seeds 1–4, brown or black (straw-colored in *D. aegyptius* (L.) A.R. Simões & Staples), trigonous, with two flat sides, glabrous.

Distinctive features: Robust herbaceous twining vines (rarely lianas) with white or watery sap; leaves alternate, commonly 5- to 7-palmately compound or lobed; sepals mostly flat and appressed to the corolla tube; corolla commonly white or light yellow, with or without a dark red center, entirely glabrous; anthers helicoid-contorted; capsules usually 4-valved, with greatly accrescent, reflexed sepals in fruit; seeds glabrous (less commonly sericeous). Distinguished from *Merremia* by the palmately compound or dissected leaves.

Distribution: A pantropical genus of ~44 species, 27 of which are found in the New World, with ~16 species of twining vines in the Neotropics; Mexico to southern South America, including the West Indies.

HEWITTIA Wight & Arnott, Madras J. Lit. Sci. 5: 22. 1837 (nom. cons.).

Vines, the stems twining or prostrate, herbaceous, pubescent. Leaves petiolate, base



Hewittia malabarica, photo from EfloraofIndia.

usually cordate, margin entire, angular, or lobed, ovate to broadly-ovate.

Inflorescences axillary cymes. Flowers 1- to few, the bracts 2, leaf-like, oblong to linear-lanceolate, borne well below calyx, persistent; sepals 5, apex mostly acute, herbaceous, the outer 3 larger, ovate, slightly enlarged in fruit, the

inner 2 much smaller, not accrescent; corollas campanulate or funnelform, the limb shallowly 5-lobed; stamens included, the filaments dilated basally, adnate to corolla tube, free distally, filiform; pollen 12-colpate, not spiny; the pistil included, the ovary 1-locular or imperfectly 2-locular apically, 4-ovuled, the disc ring-like, the style 1, filiform, the stigmas 2, ovate-oblong, complanate. Fruits capsular, unilocular, globose, 4-valved, pilose. Seeds four or fewer, black.

Distinctive features: In the New World tropics, *Hewittia* can be mistaken for *Aniseia*. It differs from *Aniseia* by the yellow to whitish corolla with a purple center and the large bracts below the calyx that are somewhat enlarged and persistent in fruit.

Distribution: Old World *Hewittia* was long thought to contain a single species but now includes two. Of these, only *H. malabarica* (L.) Suresh has been introduced into the New World; known only from Jamaica where it grows in disturbed coastal sites.

IPOMOEAE Linnaeus, Sp. Pl. 1: 159. 1753.

Argyreia Lour. (1790), *Rivea* Choisy (1823), *Stictocardia* Hallier f. (1893), *Turbina* Raf. (1838).

Twining vines or lianas, seldom shrubs or small trees; stems herbaceous to woody, terete



Ipomoea furcyensis, photo by P. Acevedo.

or slightly flattened, usually climbing, sometimes prostrate or floating, glabrous or pubescent; producing milky or less often watery latex; stems in herbaceous species with regular anatomy, subwoody vines and lianas with successive rings or bands of vascular tissue. Leaves variable

in shape and size; blades simple, lobed, divided or less often palmately-compound, petiolate. Inflorescences mostly axillary, in cymes, rarely paniculate. Flowers 1 to many, on long or short pedicels, the bracts scale-like to foliose; sepals herbaceous to \pm coriaceous, ovate to oblong or lanceolate, often somewhat enlarged in fruit but usually not markedly accrescent; corollas purple, red, pink, white, or less often yellow (flowers with white corollas sometimes occur among normally non-white flowers), regular or rarely slightly zygomorphic, mostly funnellform (Figure 90A), less often campanulate (Figure 90G), tubular or salverform (Figure 90A, H), the limb shallowly or rarely deeply lobed, the midpetaline bands well defined by 2 distinct veins; stamens included or less often exserted, the filaments filiform, often triangular-dilate at the base, mostly unequal in length; pollen pantoporate, globose, spinulose; ovary usually 2–4 locular, 4-ovulate, less often 3-locular, 6-ovulate or rarely more, the styles simple, filiform, included or less often exserted, the stigmas capitate, entire or 2 (3)-lobed, globose. Fruits globose to ovoid capsules, mostly 4 (–6)-valved or splitting irregularly, or indehiscent and 1-seeded, with a coriaceous or

subligneous pericarp. Seeds 1–4 (6 to 10 in *I. decasperma* Hallier f.), glabrous to pubescent along margins or over much of the surface.

Distinctive features: *Ipomoea* is separable with ease from *Merremia* and *Operculina* by the spikes on the pollen. Fruits of *Operculina* are operculate, those in *Ipomoea* capsular. *Merremia* and *Ipomoea* are not easily separated by fruits.

Distribution: A genus of nearly cosmopolitan distribution with most species centered in the tropics. No one knows how many species there are in *Ipomoea* as currently defined, but the best estimate is ~600; there are 425 species in the Americas, with ca. 380 distributed in the Neotropics, and ca. 234 are climbers (as defined in this project), most of which are native. New species are described regularly. Various species grow in most habitats, ranging from coastal beaches and mangroves into mixed coniferous forests at comparatively high elevations. The greatest diversity in both North America, southern South America, and the West Indies, is in drylands.

ISEIA O'Donell, Bol. Soc. Argent. Bot. 5: 77. 1953.

Herbaceous vines, the stems prostrate or climbing, the stems branched, to 3 m or more



long, with fibrous, adventitious roots.

Leaves entire, 1.5–12 cm long, 1.5–4

cm wide, entire, elliptic, oblong to

lanceolate, the base cuneate to

rounded, the apex obtuse to

mucronate, with silky appressed

pubescence at least along the

Iseia luxurians, photo by P. Acevedo.

principal nerves, glabrescent. Inflorescences in cymes, axillary. Flowers 1–10 in dichasia, rarely solitary; sepals 5, herbaceous, more or less equal, the outer elliptic to more or less orbicular, pubescent to less often glabrous; corolla funnelform, the limb 5-dentate to more or less entire, with 5 bands of dense longitudinal ferruginous trichomes along the exterior; stamens and styles included; pollen 3-colpate; ovary 2-locular, the locules 2-ovulate, with a pubescent apex, the style 1, slender, the stigma 2-globose. Fruits indehiscent, more or less globose, blackish, glabrous or with the upper part pubescent, the mesocarp spongy, the endocarp crustaceous, woody. Seeds 1–4, dark brown to almost black, glabrous to winged along the borders with small trichomes.

Distinctive features: The long leaves with cuneate to obtuse bases and apices in conjunction with the indehiscent fruits that have a spongy mesocarp are distinctive of *Iseia*. The obviously ferruginous bands on the outside of the white corollas, when added to the above traits, are also distinctive. Molecular genetic studies by Stefanović et al. (2002, 2003) suggest that *Iseia* and *Aniseia* should be combined into a single genus. The two are so morphologically distinctive that they are kept apart here.

Distribution: A genus of a single species, i.e., *I. luxurians* (Moric.) O'Donell, confined to Central America and northern South America; commonly along waterways, climbing into gallery vegetation or even sprawling on the banks; 10–920 m.

ITZAEA Standley & Steyermark, Publ. Field Mus. Nat. Hist., Bot. Ser. 23: 83. 1944.

Twining lianas, stems woody, glabrous, ≥ 15 m long and to 2.5 cm in diam. Leaves petiolate, entire, simple, membranaceous, ovate-elliptic, glabrous above, sericeous below. Inflorescences axillary, cymose or rarely thyriform or solitary, peduncles short (0.2–0.5 cm).

Flowers 2–7 per cluster, aromatic; sepals \pm equal, 3–5 mm long, ~orbicular, sericeous; corolla whitish green, yellowish green or greenish-yellowish, 1–1.2 cm long, campanulate, the limb green, reflexed, more or less entire, sericeous; stamens exserted, anthers erect; ovary 1-locular, 4-ovulate, styles 2, with globose stigmas. Fruits capsular, 10–14 mm long, ~globose, although sometimes flattened-globose, striate, dehiscent into 10–20 longitudinal segments, pericarp smooth, subligneous, reddish brown. Seeds (1)3–4, ellipsoid, 6–7 mm long, glabrous, covered by red arilode that sometimes turns black upon drying.

Distinctive features: While the corollas and general aspect of the plants are similar to *Bonamia*, the capsules with 10–20 longitudinal segments and the seed with a reddish brown pulp are unique. Specimens without fruits are much harder to distinguish from *Bonamia*.

Distribution: Monotypic with *I. sericea* (Standl.) Standl. & Steyerl. endemic from southern Mexico to Costa Rica; secondary vegetation and semi-evergreen forests; 200–470 m.

JACQUEMONTIA Choisy, Mém. Soc. Phys. Genève 6: 476. 1834.

Twining vines, herbs or subshrubs; stems herbaceous toward the tips, procumbent to



Jacquemontia tamnifolia, photo by P. Acevedo.

twining, perennials or occasionally annuals, glabrous or pubescent; latex clear; stems in some species reaching 15 m in length and 3.5 cm in diam.; cross section with fissured xylem at least in *J. nodiflora* (Desr.) G. Don (Figure 87E). Leaves

chartaceous to herbaceous, mostly cordate, glabrous or pubescent, usually with stellate trichomes, entire or variously repand, dentate, or lobate, petiolate. Inflorescences in scorpioid cymes, head-like cymes, umbelliform, or flowers solitary. Flowers on pedicels 5–30 mm long, the bracts small and linear or lanceolate or large and foliose; sepals equal or unequal, variable in shape, pubescent or glabrous; corollas blue, lilac, or white (red in one West Indian species), subtrotate, campanulate, or funnellform, deeply lobed, dentate or almost entire, glabrous or pubescent; stamens and styles included or exserted; mostly 12–15 aggregolate in polar-equatorial-polar pattern, less often 3-colpate (e.g., *J. nodiflora*); ovary 2-locular, 4-ovulate, glabrous or pubescent, the styles 1, filiform, the 2 stigmas ellipsoid or oblong and flattened. Fruits capsular, 2-celled, with 4 or 8 valves, globose to subglobose. Seeds 1–4, glabrous or pilose, or tuberculate, or winged.

Distinctive features: Trichomes usually stellate; styles one, stigma lobes usually oblong to ellipsoid; flowers mostly blue although some are white.

Distribution: A pantropical genus as currently understood with ca. 120 species, but research in Brazil and Australia is showing that the number may be an underestimate. There are ~100 species in the Americas, but only 67 with neotropical distribution. Plants grow in grasslands, thickets, savannas, near beaches, low to median forests and as weeds in cultivated fields.

LYSIOSTYLES Bentham, London J. Bot. 5: 356. 1846.

Lianas reaching 30 m, the stems 3.8 cm in diameter or larger; younger branches red-pubescent, the older branches greyish to brownish, irregularly angled, glabrous, the bark somewhat scaly, the pith ± round in cross section, light brown. Leaves simple, oblong to elliptic or obovate, 7.5–14 cm long and 5–10 cm wide, the base obtuse, the margins entire, the apex

shortly acuminate, coriaceous, venation brochidodromous, glabrescent above, densely reddish



Lysiostyles scandens, from Mori & Boom 8500 (US).

pubescent underneath; petioles canaliculated.

Inflorescence axillary, slender cylindrical-

thyrsiform, 2.5–8 cm long, often racemose

below and cymose above, dichasial, the rachis

and branches densely red-pubescent; bracts

triangular, densely red-pubescent. Flowers 2–5,

actinomorphic, sweet-scented; sepals broadly

ovate to orbicular, the outer lobes acute, the

inner lobes obtuse, about equal in length, red-

pubescent; corolla subrotate, white, the tube ca.

2 mm long, glabrous, the lobes 4–6 mm long,

triangular, acute, terminating in a long-

acuminate, almost filiform apex, the outside

villous, the inside glabrous; stamens shortly

exserted between corolla lobes, epipetalous, shorter than lobes of corolla, glabrous, filament ca. 1

mm long, the bases triangular, connected into a ring, the anthers oblong, obtuse, flattened

connective 1–1.5 mm long, the thecae on basal lobes of connective, ca. $\frac{1}{2}$ as long as connective,

functionally extrorsely dehiscent; ovary depressed-globose, ca. 1 mm long, ca. 1 mm in diameter,

incompletely bilocular with a partial septum in lower portion, villose, the ovules 4, the styles

fused to completely free, ca. 1 mm long, glabrous, the stigmas 2, capitate, spherical to short-

cylindrical, white when living; pollen 3-colpate, prolate. Fruits woody, indehiscent, 1-locular,

globose to oblong-globose, 2.5 cm long, 2.3 cm in diameter, the pericarp hard, the surface

ruminate, buff-gray. Seeds 1 through abortion, ellipsoid to oblong-ellipsoid, 16–18 mm long, 14–15 mm in diameter, glabrous, surrounded by dark pulp, seed coat coriaceous; embryo with a radical folded against the lower part of the latiplicate incumbent cotyledons, ca. 15 mm long.

Distinctive features: Often high-climbing lianas. Leaves coriaceous, densely golden-pubescent below; trichomes are unique in the family in being T-shaped with the stalk longer than the branches. The small flowers are unlike any others in having long attenuate apices on the ends of lobes.

Distribution: A single species, (*L. scandens* Benth.), endemic to the Guiana Shield region of northern South America; rainforests, often near streams and rivers; 0–500 (700) m.

MARIPA Aublet, Hist. Pl. Guiane 1: 230, t. 91. 1775.

Twining lianas, climbing to 35 m or more, some species (e.g., *M. scandens* Aubl., *M.*



Maripa panamensis, photo by P. Acevedo.

densiflora Benth., and *M. elongata* Ducke) bearing tendril-like branches with determinate growth; young stems with regular anatomy, but as they grow older the successive cambia starts producing

successive concentric, discontinuous rings of vascular tissue (Figure 86C), the larger stems more

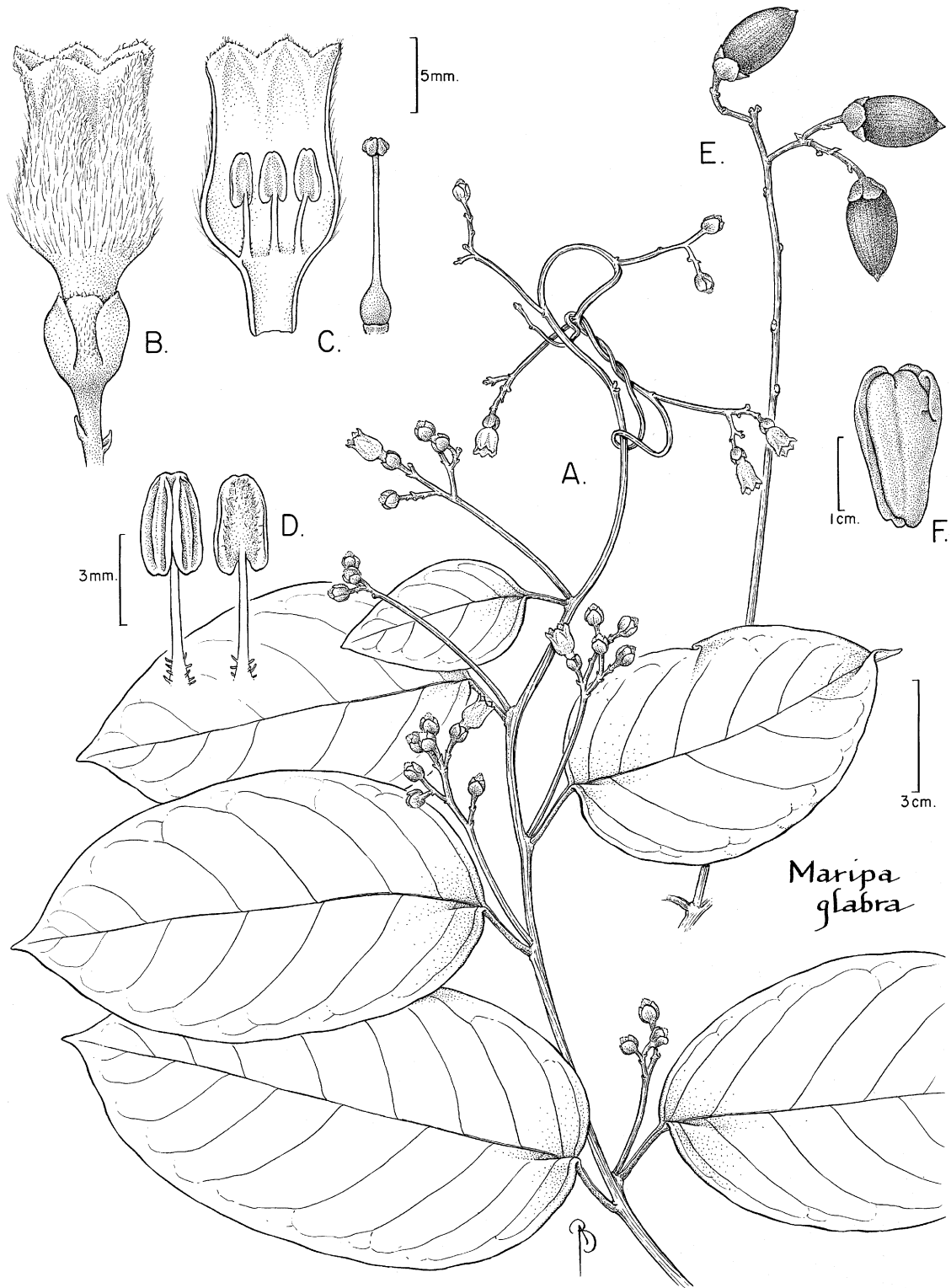


Figure 94. *Maripa glabra*. **A.** Flowering, twining branch. **B.** Flower, lateral view. **C.** Longitudinal section of corolla & gynoecium. **D.** Stamens, dorsal and ventral views. **E.** Infructescence. **F.** Cotyledons. Drawing courtesy of Bobbi Angell.

than 20 cm in diameter, grooved, or sometimes flattened, the young stems often angular; latex clear or yellowish (Figure 86C). Leaves simple, alternate or occasionally subopposite, generally elliptic, ovate to obovate to oblong (Figure 89B), glabrous or glabrescent, less often with stellate trichomes. Inflorescences in racemes or panicles that may be terminal or along lateral branches. Flowers few to many; sepals more or less equal, ovate to rounded, the outer often emarginate, the inner acute to rounded, generally coriaceous with membranaceous margins, glabrous to pubescent; corolla funnelform to campanulate, white to violet or dark pink, the lobes generally shallow, rounded to acute, pubescent along the internal folds from the bud; stamens usually included, the filaments basally triangular, glandular-pubescent, filiform above, the anthers more or less sagittate, narrowly ovate; pollen 3-colpate to 12–15-pantocolpate; ovary incompletely 2-locular with a partial septum in the base, usually glabrous, the apex occasionally pubescent, the style 1, entire, rarely divided $\frac{1}{3}$ to $\frac{1}{2}$ its length or less, the stigma capitate, 2-lobed, the lobes narrowly appressed if style entire, or lobes free. Fruits woody, indehiscent, rounded to ellipsoidal. Seeds 1–4, ovoid to oblong-ellipsoid, rounded, compressed or triangular if there are more than 1 per fruit, glabrous, covered by a juicy, gelatinous, sweet, brownish pulp (Figure 92D); cotyledons plicate (Figure 92C).

Distinctive features: High-climbing lianas; leaves coriaceous, fruits indehiscent, woody to almost berry-like. Typically confused only with *Dicranostyles* and *Lysiostyles*. *Maripa* can be distinguished from *Dicranostyles* and *Lysiostyles* by the densely pubescent corolla interplicae, which are glabrous in the latter two genera. In addition, fruits are smaller in *Dicranostyles* than in most *Maripa*; and in *Lysiostyles* they are distinctively wrinkled.

Distribution: A genus of ~21 species, most of which occur in the northern half of South America with one species extending north to southern Mexico; seasonally flooded forests (*igapó*, *várzea*) and wet, non-flooded forests; 50–700 m.

MERREMIA Dennstedt ex Endlicher, Gen. Pl. 1403. 1841 (nom. cons.).

Twining lianas or herbaceous vines, sometimes prostrate; latex watery or milky. Leaves



Merremia discoidesperma, photo by Federico Oviedo-Brenes (OTS).

simple, entire, shallowly trilobed or 3-angled, undulate or distantly serrulate, sessile or if present the petiole slender.

Inflorescences axillary, in dichasia or monochasia, sometimes umbellate.

Flowers 1–40, mostly diurnal; peduncles usually similar to the stems and petioles or reduced or absent, pedicels usually

shorter than the peduncle, smooth, striate, or notably five-angled, bracts glabrous or pilose, usually two, foliaceous to scale-like or absent, bracteoles, when present, similar to the bracts; sepals 5, persistent, imbricate, ovate-lanceolate, herbaceous, membranaceous-coriaceous, glabrous, pilose-appressed, or hirsute, entire, obtuse or rounded; corollas campanulate, often gibbous on one side, limb 10-lobed, yellow, glabrous, mid-petaline bands darkly veined; stamens 5, included, inserted at the base of the corolla tube, glabrous, the anthers helicoid-contorted; pollen 3-colpate (Simões & Staples 2017); ovary 2–3-locular, 4–6-ovulate, glabrous, style 1, white, glabrous, stigma biglobose. Fruits capsular, globose, conical or depressed-globose, brown,

glabrous, entire or shallowly 4-lobed, the locules 2–4, 4-valvular. Seeds 1–4, brown or black, rounded or 1–3-angled, hairy.

Distinctive features: As now defined, *Merremia* includes those species that have the dehiscent fruits of *Ipomoea* but the non-spiny pollen of *Operculina*.

Distribution: As currently circumscribed, an Asiatic genus of ~10 species. However, four species in the Neotropics are still retained in *Merremia* because there is no sufficient data to elucidate their phylogenetic placement. These include *M. discoidesperma* (Donn. Sm.) O'Donell and *M. platyphylla* (Fernald) O'Donell from Mexico, *M. calycina* (Meisn.) Hallier f. from Brazil and *M. wurdackii* D. F. Austin & Staples from Venezuela and Brazil. The Asiatic *M. hederacea* (Burm. f.) Hallier f., was introduced in the Neotropics more than a century ago (Colombia, Cuba, Guadeloupe and Martinique) where it may have become naturalized.

Note: *Merremia*, as previously circumscribed was a wastebasket of all species not fitting into *Ipomoea*, *Operculina*, or even other genera, with a total of ~100 species. Molecular studies by Simões and Staples (2017) confirmed the polyphyly of the genus and proposed a new classification where most species of *Merremia* were transferred to *Camonea*, *Decalobanthus*, *Distimake*, and *Xenostegia*. Only ~10 species (all of Asiatic origin) were recovered as closely allied to *M. hederacea* (Burm. f.) Hallier f., the type of the genus, and therefore are currently retained in *Merremia*. The neotropical species *M. discoidesperma* (Donn. Sm.) O'Donell and *M. platyphylla* (Fernald) O'Donell, both from Mexico, are retained in *Merremia* because they have not been analyzed and their alliances are not known. On the other hand, *M. calycina* (Meisn.) Hallier f. and *M. wurdackii* D. F. Austin & Staples are currently unassigned to any genera as they did not group with any other species in Simões and Staples analyses.

ODONELLIA K.R. Robertson, Brittonia 34: 417. 1982.

Twining herbaceous vines, 6-7 m long; pubescence of unbranched, green-olive or copper



Odonellia hirtiflora, photo by F. Logan.

trichomes. Leaves ovate to narrowly ovate, the base truncate or cordate, the apex acute to acuminate, mucronulate, pubescent. Inflorescence axillary with numerous flowers, in capitate-cymose clusters, with bracts resembling sepals, densely pubescent. Flowers numerous, but

rarely more than one or two open at any time; sepals unequal, ovate or oblong, apex rounded to acute or acuminate, the indumenta like the bracts and bracteoles; corolla campanulate-funnelform, villose along the midpetaline plicae; stamens included, somewhat curved after anthesis; pollen 6(–8)-colpate; ovary 2-locular, 4-ovulate, style 1, longer than the stamens, stigma 2-globose. Fruits capsular, with irregular dehiscence, lacking valves, black when dry, enveloped by the sepals and bracts. Seeds 1–4, smooth, glabrous; embryo plicate.

Distinctive features: Inflorescences of bracteate head-like, dense cymose clusters; trichomes simple; pollen 6(–8)-colpate.

Distribution: A genus of two species, distributed from tropical Mexico south to Bolivia and SE Brazil.; marshes to upland forests.

OPERCULINA Silva Manso, Enum. Subst. Braz. 16, 49. 1836.

Twining lianas or small herbs; stems prostrate or climbing to 10 m long, smooth or



Operculina macrocarpa, photo by P. Acevedo.

striate, glabrous.

Leaves ovate, broadly ovate, pinnately or 5- or 7-palmately lobed or compound, or entire, glabrous, petioles and pedicels sometimes winged, mostly glabrous.

Inflorescences in

axillary monochasia. Flowers few or solitary, often with foliose bracts; sepals equal or unequal, enlarging in fruit and becoming coriaceous, sometimes irregularly dentate on the margins, glabrous; corollas broadly campanulate, funnelform or salverform, white, yellow, or reddish to salmon, the interplicae pilose, the plicae glabrous; stamens included (rarely exerted), anthers twisted when fully mature; pollen 3-colpate; ovary glabrous, bilocular, each locule 2-lobed, the styles included (rarely exerted), filiform, stigma of 2 globose lobes. Fruits dehiscent, the upper part separating by a circumscissile epicarp, more or less fleshy and separating from the lower segment and from the endocarp, 2-locular. Seeds 1–4, ovoid to ovate, glabrous or pubescent.

Distinctive features: The circumscissile fruits are unique to *Operculina*. Pollen is smooth and not spiny as in *Ipomoea*. *Operculina* is more similar to *Merremia* than any other genus in the family and most likely to be confused with it. Without fruits it is often difficult to separate

Operculina from *Merremia*. Stems (and often petioles and peduncles) are winged in *Operculina* while they are terete or striate and unwinged in *Merremia*.

Distribution: Spread in the tropics of the Old and New Worlds, *Operculina* has ~14, with 10 distributed in the Neotropics from Mexico to Paraguay including the West Indies; thickets, grasslands, and deciduous tropical forests.

PORANA N. L. Burman, Fl. Indica 51. 1768.

Twining lianas, 7–10 m long; stems subglabrous, lenticellate, with regular secondary growth and clear latex (Figure 86D). Leaves simple, entire, chartaceous, venation pinnate; petiole sulcate. Inflorescence a thyrsiform, axillary or terminal, compound panicle; bracts foliaceous and petiolate, diminishing distally and becoming sessile; bracteoles 2, scale-like, borne at peduncle/pedicele junction. Flowers small, fragrant; sepals 5, free, quincuncial, outer ones half as long as corolla, equally or unequally accrescent in fruit; corolla campanulate or



broadly funnelform-campanulate, 5-lobed, lobes plicate and valvate (not twisted), interplicae pubescent outside, plicae diaphanous, glabrous; stamens 5, unequal, longest 2 or 3 exerted, filaments connate below to corolla tube, free above, glabrous, anthers ellipsoid, longitudinally dehiscent prior to anthesis; pollen 3-colpate, non-spinose; pistil exerted, disc annular, ovary unilocular or incompletely bilocular, ovules 4, style terminal, unequally 2-branched, stigmas reniform. Fruit a brittle chartaceous utricle, wall breaking irregularly or tardily splitting along suture in

acropetal direction, protruding from chartaceous, papery calyx, outer 3 or all 5 sepals greatly enlarged, 7–9-veined, the veins longitudinal, forming a subapical reticulum, veins \pm prominulous. Seed 1, rarely 2, scurfy at first, smooth later, glabrous; hilum basal, C-shaped.

Distinctive features: Similar to *Calycobolus* in having large sepals, but the outer 3 sepals are much longer than the inner 2 in *Porana*. In *Calycobolus*, the outer 2 are larger than the inner 3. In *Porana*, the outer 3 sepals are narrowed into a claw-like base while the outer ones in *Calycobolus* are cordate at the base with a distinct sinus between the two lobes. Fruits in both genera are utriculate and chartaceous, a trait that is absent in other twining members of the family in the Americas.

Distribution: A genus of two species, one in central Mexico (*P. nutans* (Choisy) O'Donnell) and the other in SE Asia; variety of habitats such as deciduous forest, disturbed tropical deciduous forest, desert thorn scrub, rocky hillsides, dry riverbeds, and steep hills.

PORANOPSIS Roberty, Candollea 14: 26. 1953 ["1952"].

Twining subwoody vines, reaching 5-7 m in length; stems slender, cylindrical, grayish villous or sericeous, glabrescent, with clear latex. Leaves simple, petiolate, cordate-ovate, papery, rugulose, abaxial surface densely pubescent; venation pedate or nearly palmate. Inflorescence an axillary or terminal bracteose panicle, the bracteoles 2, scale-like, basal to calyx, the pedicel filiform. Flowers tiny, often fragrant, fascicled; sepals free, quincuncial, unequally enlarged, outer 3 sepals greatly enlarged (inner 2 sepals slightly so), midvein 1, secondary veins reticulate; corolla white, \pm funnellform, less than 8 mm long, the limb 5-lobed, outside villous apically, inside glabrous; stamens included or exerted, the anthers ellipsoidal, longitudinally dehiscent; pollen 3-colpate, not spiny; pistil included, disc annular or absent;



Poranopsis paniculata, photo by P. Acevedo.

ovary unilocular, ovules 4, style simple (nearly absent in 1 species), stigma 2-globose. Fruit papery, indehiscent. Seed 1, smooth.

Distinctive features: Distinguished from *Porana* by the pedate leaf venation, the calyx covering $\frac{1}{4}$ or less of the corolla tube, and entire style. The many funnellform, white flowers are similar to those of *Dicranostyles* and *Lysiostyles* in size, but not so much in shape except for some species of *Dicranostyles*.

Distribution: There are 3 species native to the Old World. *Poranopsis paniculata* (Roxb.) Roberty is cultivated in the New World although does not

appear to produce fruits there.

TETRALOCULARIA O'Donell, Lilloa 30: 66. 1960.

Twining herbaceous vines; stems cylindrical to angular, with dense ferruginous pubescence in the young parts, the trichomes simple and straight or antrorse. Leaves simple, entire or undulate, ovate, slightly cordate basally, apex obtuse, both sides densely ferruginous-tomentose, petiole 2–6 cm long. Inflorescence terminal, racemose, bracts lanceolate or subcordate; peduncle small or none; pedicels elongate; bracteoles 2, linear to lanceolate. Flowers 1–30; sepals 5, unequal, the 2 outer oblong, semi-transparent with a long series of laticifers inside, apex obtuse to subacute, margins ciliate, tomentose outside; 3 inner ovate to oblong, smaller, ciliate only at the apex; corolla campanulate, white, ca. 8 mm long, 5-lobed, interplacae

pubescent only on the upper half; stamens 5, subequal, included, the filaments inserted near the base of corolla, with glandular trichomes at the base; pollen smooth; ovary subglobose, 4-locular, 4-ovulate, style 1, stigmas 2, globose, slightly compressed and concave. Fruits capsular, subglobose, glabrous, 4-lobed, 4-locular, 2-valved. Seeds 4 (or fewer), light brown, subglobose, glabrous; cotyledons reniform.

Distinctive features: Racemose inflorescence; almost globose or somewhat flattened stigmas; pubescent corollas, simple trichomes; and 2-valvular capsules with 4 locules. *Tetralocularia* is most likely to be confused with *Merremia* which has 4-valved or irregularly splitting capsules and either simple or stellate trichomes. *Tetralocularia* is also similar to *Jacquemontia*, but that genus differs in having mostly trichomes with 3 branches or more, cymose inflorescences, and 8-valved capsules.

Distribution: A poorly known genus of a single species (*Tetralocularia pennellii* O'Donell) known only from Colombia, Venezuela, French Guiana, northern Brazil and lowlands of Bolivia; floodplain forests, riparian forests, swamps, and marshes.

XENOSTEGIA D.F. Austin & Staples, *Brittonia* 32: 533. 1980.

Twining or creeping herbaceous vines to ~ 2 m long; with scanty milky latex. Leaves glabrous to less often pubescent, linear, oblong-linear, lanceolate-elliptic to oblanceolate or



spatulate, the base sagittate to truncate or hastate, basal lobes toothed or entire, the apex acute, obtuse, truncate to emarginate, mucronate to tridentate; petioles 0.5–3 mm long. Inflorescences cymose. Flowers 1–2(–3); sepals subequal or the 2 outer larger, oblong to oblong-ovate, acute to obtuse to rarely sagittate basally, the inner often narrower, lanceolate to lanceolate-acuminate; corolla broadly funnelform to campanulate, 10–23 mm long, pale yellow to almost white, the center often purplish, stamens included, equal or subequal, filaments inserted 1.5–4.5 mm above corolla base, glabrous or sparsely pubescent basally, anthers ellipsoid to sagittate, longitudinally dehiscent; pollen 15–30

pantoporate, smooth; ovary 2-locular, 4-ovulate, almost globose, glabrous or covered with straight trichomes, style 1, filiform, stigma biglobose, unlobed, papillose. Fruits globose to ovoid, 4-valved, apiculate, pericarp papery, glabrous or the upper part pubescent. Seeds 1–4, 2–3 mm long, ovoid, trigonous, brown to black, apices obtuse, glabrous.

Distinctive features: *Xenostegia* is distinguished by its sessile leaves; pantoporate pollen; papillose stigmas; and straight-dehiscent anthers.

Distribution: A pantropical genus of 5 species, widespread in E Africa, Madagascar, tropical Asia and Australia (Simões & Staples, 2017); only *X. tridentata* (L.) D.F. Austin & Staples has been introduced and naturalized to the New World in Puerto Rico where it grows in disturbed areas that are often sandy.