CONVOLVULACEAE

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A predominantly tropical family of twining vines and lianas, with fewer that are erect herbs or shrubs (e.g., *Evolvulus, Ipomoea, Jacquemontia, Merremia*), and a few trees (*Humbertia, Ipomoea*); several species extend into temperate zones. About 750 of the ca. 918 species in the Americas are vines and lianas. In the Neotropics, climbers are predominant in lowland moist forests, savannas, gallery forests, and in open disturbed vegetation. There are more erect species in the dry lands of Mexico and Brazil than in other habitats, but each community has its specialties.

**Diagnostics**: 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. There are, however, some genera that are woody almost throughout (e.g., Bonamia, Calycobolus, Dicranostyles, Itzaea, Lysiostyles, Maripa, and some Ipomoea). Woody stems are largely 1-5 cm in diameter in many of these genera, but in Dicranostyles, Lysiostyles, and Maripa they may reach 10-35 cm and climb 30-35 m into the canopy of tropical forests. Stem shape varies from cylindrical to 1-2- or 3-lobed and is often asymmetrical or flat in species of Maripa.

Cross sections of stems in Convolvulaceae show different anatomical arrangements which are developed either by a single cambium or by numerous, successive cambia as follows. Single cambium: A) 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 (fig. 1a-b; fig. 2e), in species of Distimake, this differential growth is less pronounced and leads to a xylem that is sinuate, i.e., is intruded by shallow phloem wedges or arcs (fig. 1d); B) dispersed or fissured xylem, found in Jacquemontia and some Ipomoea, where non-lignified parenchyma proliferate, fissuring the xylem into irregular segments or islands (fig. 1a-b, e & 2e, Angyalossy et al., 2015; Carlquist, 1991; Obaton, 1960); C) regular anatomy, found in Porana nutans (Choisy) O’Donell where the xylem forms a continuous large cylinder traversed by narrow rays (fig. 1d).

Successive cambia are found in numerous genera and produce different anatomical arrangements such as A) Concentric or eccentric, alternate rings or bands of vascular tissue, e.g., Dicranostyles, some Ipomoea, and Maripa; (Austin, 1970; Mennega, 1969; Obaton, 1960; Schenck, 1892); for the most part, these bands are discontinuous or asymmetrical and rarely form a continuous ring, these are often dissected by narrow rays, joined by conjunctive tissue, and the peripheral edge of the xylem is often sinuate (fig. 1c & 2b-c); B) Lobed stems with successive cambia active in the area where the lobes are produced, these made of successive alternate bands of vascular tissue (fig. 2a); C) 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, fig. 1e-f) and Ipomoea (e.g., I. furcyensis Urb.,
fig. 1b), the xylem within these islands in *D. tuberosus* is furrowed with shallow phloem wedges (fig. 1f).

The phloem in many genera of Convolvulaceae often show bands of *stratified fibers* [(fig. 2d), M.R. Pace, pers. comm.]. All Convolvulaceae (except *Cuscuta*) have *intraxylary phloem* strands in the periphery of the medulla (Metcalf & Chalk, 1957; fig. 1e), although not always easy to observe.

2. EXUDATES. Many species, especially the herbaceous ones, produce milky latex when the leaves or stems are cut (fig. 2c & 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 studies done by 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 (fig. 3). 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 are branches.

5. LEAVES. Leaf blades are predominantly simple and *cordiform* (fig. 4d), 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 (fig. 4b), less often subcordate. Much of the family has alternate, simple, unlobed leaves; others are variable from entire to 3-9-lobed. Lobing varies considerably even on the same individual in some genera like *Ipomoea*. However, a few have pinnatifid e.g., *Ipomoea quamoclit* L. (fig. 4c) or *pedately* lobed (*I. ternifolia* Cav.) blades, and a group of *Ipomoea* mostly from the Caribbean are *palmately compound*, while others are deeply *palmately lobed*. *Distimake* has several species that are palmately compound and others that are palmately lobed (fig. 4a). Petioles are variable, with the tropical lianas mostly being rounded and canalicate above.
Figure 1. Cross sections of Convolvulaceae stems. A. *Jacquemontia* sp., cylindrical with furrowed xylem. B. *Ipomoea furcycensis*, early stage, cylindrical with xylem in irregular plates and few incipient vascular bundles in the cortex. C. *Maripa scandens*, asymmetrical with successive bands of vascular tissue. D. *Porana nutans*, cylindrical with regular anatomy, phloem with bands of stratified fibers. E. *Distimake tuberosus*, early stage with xylem divided into 3 plates and incipient vascular bundles on the periphery of the phloem. F. *Distimake tuberosus*, mature stem with successive islands of vascular tissue. Photos by P. Acevedo.
Figure 2 Cross sections of Convolvulaceae stems. A. *Ipomoea corymbosa*, 3-4-lobed with successive bands of vascular tissue in the lobes. B. *Dicranostyles holostyla*, asymmetrical 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 phloem with bands of stratified fibers. E. *Jacquemontia nodiflora*, asymmetrical with dispersed xylem. Photos by P. Acevedo.
Figure 3. Tuberous roots in Ipomoea. A. *I. eggersii.* B. *I. furcyensis* Urb. Photos by P. Acevedo.
6. INFLORESCENCES. Inflorescences are axillary or distal, and either simple or compound cymes. However, this basic pattern has been modified into racemose (monochasial cymes) in various genera (e.g., *Ipomoea lobata* (Cerv.) Thell., *Dicranostyles*, *Maripa*).

7. PEDICELLS. Length varies markedly, from essentially absent to several cm (e.g., *Ipomoea*, *Jacquemontia*, and other genera).

8. FLOWERS. Mostly actinomorphic but symmetry varies depending on the pollination syndrome of the species. Flowers that are slightly zygomorphic are pollinated by hummingbirds (e.g., *Ipomoea lobata* (Cerv.) Thell., *I. lutea* Hemsl.), or bats (*Merremia platyphylla* (Fernald) O'Donell, *Ipomoea neei* (Spreng.) O'Donell). Calyx of 5 free sepals with quincuncial aestivation, their shape and comparative lengths are important for determining taxa in several genera (e.g., *Ipomoea*, *Jacquemontia*); corolla tubular (sometimes only at the base), 5-lobed, white to yellow, or more commonly some variation of mixtures of red and blue resulting in corollas that range from lavender to purple to deep blue or even red or orange (fig. 5); 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 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 (fig. 5c, d, e, g, & i) or exserted (fig 5a, 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* to absent in Old World *Erycibe*, stigmas 1 or 2, variable from cylindrical to ligulate to globose.

9. FRUITS. Recognition of several genera depends, in part, on examination of the fruit type. Most are loculicidal capsules (fig. 6b-d) but some are either fleshy or dry baccate (fig. 6a) (some *Ipomoea*, *Dicranostyles*, *Lysiostyles*, *Maripa*); others are highly specialized in unique ways (e.g., *Stictocardia*) and some have either indehiscent or tardily dehiscent fruits (e.g., *Aniseia*, *Bonamia* (fig. 6c), *Ipomoea corymbosa* (L.) Roth).
Figure 6. Fruits 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* sp. D. 4-valved, 4-seeded dehiscent capsule in *Aniseia* sp. Photos by P. Acevedo.
Figure 7. Seeds and cotyledons in Convolvulaceae. A. Longitudinal section of fruit of *Ipomoea alba* showing plicate cotyledons. B. Cross section of *Dicranostyles mildbraediana* fruit showing foliaceous, plicate cotyledons. C. Seed with long trichomes in *Bonamia agrostopolis*. D. Seed in *Ipomoea* sp. with velvety pubescence. Photos by P. Acevedo.
10. SEEDS. Most genera have a hard, woody seed coat that requires scarification to induce germination; glabrous, pubescent with long (fig. 7c) or short trichomes (fig. 7d) or both in varying patterns and some ornamented with bumps and tubercules. A few tropical genera are adapted for quick germination and lack the hard seed coat (e.g., *Dicranostyle, Lysiostyles, Maripa*). Species with hard seed coats have long life spans of up to at least 30 years; those of the tropical taxa lacking the hard seed coat live for a short time, perhaps as little as a week or so. Many species have a hard cartilaginous endosperm; others lack that and have distinctive perisperms (e.g., *Dicranostyles, Itzaea, Lysiostyles, Maripa*). The red perisperm in *Itzaea* is unique; the jelly-like perisperm in the other 3 genera attracts dispersal agents like bats, birds, monkeys, etc. The cotyledons are foliaceous and profusely plicate in *Dicranostyles* (fig 7b), *Maripa* and some *Ipomoea* (fig.7a).

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. The second species, known as *water spinach* or *kang-kong*, is an Asian specialty cultivated as edible greens (leaves, stems). This Old World plant is now propagated in the Americas, often illegally, to supply the tables of immigrants who crave a familiar food. 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. The maladies treated vary with region and genus, but at least the following are or have been used: *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. There was a resurgence of use as a recreational drug in Western cultures during the 1960s and 1970s. Later a cultivated *Argyreia* (now in *Ipomoea*) was added to the list. Regardless of the source, humans have made use of these compactly packaged mind-altering chemicals in several parts of the New World, either believing they are communicating with their deities or simply for recreation. 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.) Tul. (Clavicipitaceae), are still used medicinally in obstetrics, and to treat migraine and Parkinson's disease; those derived from Convolvulaceae are not.

Some species such as the “Mary’s bean” (*Merremia discoidesperma* (Donn. Sm.) O'Donell) were long thought to have miraculous healing powers because of the “cross” on their seed surface. In Mexico these seeds are sold as “tomate marino” and touted as “cures” for hemorrhoids, circulation problems, varicose veins, and high blood pressure. The treatment is achieved by carrying two seeds in a small bag after drinking water in which they floated overnight. Others consider the seeds a treatment for snakebite. People hold other beliefs about several others species.

**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 mesocarp;
   perisperm glutinous ................................................................................................. Maripa
9. Vines (herbaceous); fruits not woody, 2-locular, with spongy mesocarp; perispperm 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. Woody lianas; styles 1 or bifid .............................................................................. 14
13. Herbaceous twiners; 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 .................................................. 26
19. Stems (and often petioles, peduncles) winged; capsules with a thickened circumscissile lid
 that separates from ± 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. Scrambling shrubs or slender, subwoody twining vines with fistulose stems; fruits
 indehiscent, with peduncle connate to lower ½ of a foliaceous accrescent bract, that
together with the fruit are wind dispersed as a unit ........................................ Keraunea
23. Herbaceous to woody twining vines, with solid stems; fruits capsular, not as above .......... 24
24. Leaves narrow (linear or oblong-linear) with sagittate, truncate or hastate base, subsessile;
anthers strait-dehisced............................................................................ Xenostegia
24. Leaves ovate, cordiform, palmately compound or palmately lobed, commonly long petioled; anthers longitudinally dehiscing with slightly curved apex or spirally dehiscing ...........25
25. Leaves entire, sinuate to shallowly 3-lobed; fruits with non-accrescent sepals; seeds hairy

Merremia

25. Leaves palmately compound or palmately lobed (rarely simple or vestigial); fruits with large, accrescent sepals; seeds glabrous (rarely velvety puberulent, glabrescent) ........Distimake

26. Stems (and often petioles, peduncles) winged; corollas salverform, salmon, orange to red; fruits operculate 

Distimake

26. 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. **Leaf bases.** Mostly cordate leaves but several have bases that are predominantly acute to obtuse (e.g., Aniseia, Bonamia, Dicranostyles, Lysiostyles, Maripa).

2. **Leaf texture.** Several of the lianas have coriaceous leaves (e.g., Bonamia, Dicranostyles, Lysiostyles, and Maripa). Other genera typically vary from membranaceous to chartaceous. Ipomoea imperati (Vahl) Griseb., I. pes-caprae (L.) R. Br., and I. violacea L. have succulent leaves.

3. **Leaves reniform.** Several species of Ipomoea in the West Indies have reniform leaves that are produced in brachyblasts.

4. **Flower size.** Cuscuta, Dicranostyles, Lysiostyles, and Poranopsis typically have the smallest flowers in the family sometimes reaching 1 cm in length. Cuscuta can be told apart by its parasitic habit, while the other genera by the presence of compound inflorescences and woody habit. Flowers in Tetralocularia are about 8 mm long, but they are in racemose clusters.

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. Technically, they are berries and that is more obvious when they are alive. Even alive, the exocarp is leathery or woody.

8. *Dry berries*. Fruits of the Old World species of *Ipomoea* (formerly *Argyreia* and *Stictocardia*) are unlike anything native in the New World. The former has fleshy or dry-baccate fruits while in the latter they are unique within the family in being lantern-like.

9. *Multiple segmented exocarp*. Most genera with capsular fruits divide into 4 segments. *Jacquemontia* fruit segments may further divide into 8; those if *Itzaea* into 10-20. *Bonamia* typically has 2-4, but sometimes divides into 8.
GENERIC DESCRIPTIONS


Herbaceous vines, typically prostrate, the apices of the branches twining, glabrous or pubescent, reaching up to 7 m in length; latex is 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 funnelform, 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.

**Unique features:** The outer 2 sepals are greatly enlarged and conceal the much small inner 3 sepals; cuneate leaf bases and entire, linear-ovate to elliptic leaves easily distinguish the genus.
**Distribution:** A neotropical genus of 2 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.).

Perennial, herbaceous or woody, twining vines, trailing, procumbent or erect herbs, the stems a few decimeters to several meters long, smooth or lenticellate, glabrous to densely pubescent; cross sections cylindrical to 5-angled, with furrowed xylem at least in *B. maripoides* Hallier f. Leaves petiolate, subsessile or sessile, herbaceous to subcoriaceous, occasionally leathery, simple, entire, ovate, elliptic, ovate, lanceolate, oblong, linear or linear-lanceolate, apically acute, obtuse, acuminate, acute-mucronate, obtuse-mucronate or emarginated, acute, 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 interplicae; stamens
inserted or rarely exserted, the filaments filiform or somewhat dilated below, unequal, subequal or 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 pantocarpate, not spiniferous; ovary 2-carpellate, 2-locular, glabrous, long-pilose, or hirsute with two-armed trichomes, the disc annular, ovules 2 per locule, the styles 2, almost free to partially united, included in the corolla to partially exserted, the stigmatic branches equal to unequal, filiform, mostly glabrous, occasionally with scattered trichomes, the stigmas globose, subglobose, capitate, reniform, bilobed conical or rarely peltate, smooth or rugose, occasionally lobulate. Fruits capsular, dehiscing by valves, occasionally by circumcision, rarely remaining indehiscent for a long time. Seeds 1-4, valves 4-8, rarely 2, with thin, chartaceous to thick, ligneous walls, ovoid, globose or conical-ovoid, glabrous or with scattered trichomes. Seeds 1-4, brown to black, smooth or punctuate, glabrous or lanate, oval, with hard or rarely soft seed coat, covered with thin transparent perisperm.
Unique features: Woody lianas, high-climbing or scrambling; stigmas globose, with styles either 1 or 2, the usually dehiscent capsules lacking the spongy mesophyll that is characteristic of *Itzaea*, the only tropical genus with which *Bonamia* is usually confused with in the New World.

Distribution: Some 56 species are widespread across the tropics of the Old and New Worlds; 19 are endemic to the Americas. The species grow in a variety of habitats, from tropical forest to dry thorn-scrub. Those in dry lands tend to be shrubs (Florida and Texas to Argentina).


Twining lianas, the stems glabrous or pubescent, with indumentum of simple or T-shaped hairs; latex clear. 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-thyriseiform, composed of cymose units; peduncle hidden among flowers or quite long; bracts present, deciduous or persistent. Flowers small to medium-sized, slightly fragrant to odorless; 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, ovate, elliptic, to rhombic, tightly enveloping corolla base; corollas tubular to narrowly funnelform, white, limb subentire to vaguely lobed, erect, interplicae pubescent outside or glabrous; stamens subequal,
anthers oblong to linear-oblong, white, dehiscing lengthwise without twisting; pollen 3-colpate and pantocolpate, non-spinulose; ovary 2-locular, the locules 2-ovulate, the 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.

**Unique features:** Some *Jacquemontia*, *Bonamia peruviana* Ooststr. and *Porana nutans* (Choisy) O'Donell 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
- 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

**Distribution:** There are 16-28 species known in the Americas and the Old World where they are largely African. In the New World there are 3 species, while there is disagreement on the number of species in the Old World. American plants grow in tropical forests in southern South America.

**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
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 valvicial 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.

**Unique features:** Herbaceous twining vines or prostrate creepers; 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 dehiscing and curved at the apex or spirally dehiscing; 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; scrubs, grasslands, savannahs, dry forests, and disturbed open areas, in the lowland.

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.

**Unique features:** The stigma lobes are subulate, filiform, and typically rounded. Corollas mostly white; fruits capsular. Pollen 3-colpate.

**Distribution:** There are ca. 220 *Convolvulus* 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, distributed from Mexico to Argentina including the West Indies; dry forests, scrubs, and grasslands.

Herbs, parasitic, yellow or reddish, glabrous, the stems twining, filiform, obtaining nourishment from hosts by means of haustoria. 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, ± 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.

**Unique 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:** Cuscuta includes 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 about 10 species reach 2 or more m in length.
Twining vines or less often prostate subshrubs; latex white; stems slender, 1-2 m long, 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, spinulate; 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.

Unique features: Similar to *Merremia* by the presence of globose stigmas, twisted dehisced 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; secondary growth with discontinuous bands of vascular tissue (fig. 1e), 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.

Inflorescences racemose or thyrsoid, axillary. Flowers ca. 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 nut-like, ellipsoid to ellipsoid-cylindrical (fig. 4e), the pericarp thickly coriaceous to woody (fig. 5a, c). Seeds glabrous, ovate to oblong-ellipsoid, triangular if there are more than 1 per fruit, with distinctive perisperm (fig. 5a, c) and a coriaceous covering; embryo foliaceous and profusely plicate (fig. 5a-c).
**Unique features**: These lianas often grow to considerable heights into the canopy of tropical forests where they produce flowers less than 1 cm long; fruits woody to baccate, indehiscent. Likely to be confused only with *Maripa*, which has larger flowers, and *Lysiostyles*, which has distinctive long attenuate corolla lobes.

**Distribution**: This tropical American genus has 15 species, all but one being confined to South America. A single species has been found in Costa Rica (Hammel, 2010). These lianas are most common in wetland forests (*igapó, várzea*) but also occur in upland forests (*terra firme*). (Costa Rica and Amazon region)

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

Twining herbaceous or subwoody vines, less often erect, decumbent or creeping herbs or 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* (Carlquist & Hamson, 1991) and *D. tuberosus*. the latter species also with fissured stems, with islands of vascular tissue that form from successive cambial patches (fig. 2e-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, the apex 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 (12-zonocolpate in D. tuberosus and D. quinatus); 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. aegypi us (L.) A.R.Simões & Staples), trigonous, with two flat sides, glabrous.

Unique 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 about 44 species, 27 of which are found in the New World, with about 20 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 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 4 or fewer, black.

Unique 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.

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

Argyreia Lour. (1790), Rivea Chosy (1823), Stictocardia Hall.f. (1893), Turbina Raf. (1838).

Twining vines or lianas, seldom shrubs or small trees; stems herbaceous to woody, terete 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 ± 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 funnelform (fig.5g), less often campanulate, tubular (fig. 5b) or salverform (fig. 5a), 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.

**Unique features:** *Ipomoea* is separable with ease from *Merremia* and *Operculina* only by examination of the pollen. A 10x hand-lens will reveal the spines on the pollen, but 20x shows it
more clearly. Fruits of *Operculina* are pericarp; those in *Ipomoea* capsular. *Merremia* and *Ipomoea* are not easily separated by fruits.

**Distribution:** No one knows how many species there are in *Ipomoea* as currently defined, but the best estimate is about 600; there are 425 species in the Americas, with ca. 380 distributed in the Neotropics, and ca. 267 are climbers (as defined in this project), most of which are native. New species are described regularly. There is a growing body of morphological and molecular data indicating that *Ipomoea, Argyreia, Stictocardia, and Turbina* belong to a single complex clade, and therefore these genera are treated as synonyms of *Ipomoea* by Wood et al. (2020). 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.


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 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.

**Unique 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. These vines are commonly found along waterways climbing into gallery vegetation or even sprawling on the banks.


Lianas, twining to 15 m or perhaps longer, to 2.5 cm in diameter, woody, glabrous. Leaves petiolate, entire, simple, 9-16 cm long, 4.5-6.5 cm wide, membranaceous, ovate-elliptic, the base obtuse to cuneate or rounded, the apex acute, obtuse to acuminate, glabrous above, sericeous below. Inflorescences cymose or rarely thyrsiform or solitary, on comparatively short (0.2–0.5 cm) peduncles in the axils of leaves, shorter than the leaves. Flowers 2-7 per cluster,
whitish green, yellowish green or greenish-yellowish, aromatic; sepals ± equal, 3-5 mm long, more or less orbicular, seraceous, the apex rounded; corolla 1-1.2 cm long, campanulate, the limb green, reflexed, more or less entire, seraceous, the stamens exserted, anthers erect; ovary 1-locular, 4-ovulate, the styles 2, with globose stigmas. Fruits capsular, 10-14 mm long, more or less globose, although sometimes flattened-globose, striate, dehiscent into 10-20 longitudinal segments, pericarp smooth, subligneous, reddish brown. Seeds (1)3-4, these 6-7 mm long, ellipsoid, glabrous surrounded by a red pulp (perisperm) which colors the seed red or black when dry.

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

**Distribution:** Monotypic with *I. sericea* (Standl.) Standl. & Steyerm. endemic from southern Mexico to Costa Rica. These lianas grow in secondary vegetation and semi-evergreen forests.


Twining vines, herbs or subshrubs; stems herbaceous toward tips, procumbent to 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 dispersed xylem at least in *J. nodiflora* (Desr.) G. Don (fig. 2e). Leaves chartaceous to herbaceous, mostly cordate, glabrous or pubescent, usually with stellate trichomes, entire or variously repand, dentate, or lobate, petiolate. Inflorescences in scorpionid 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), subrotate, campanulate, or funnelform, deeply lobed, dentate or almost entire, glabrous or pubescent; stamens and styles included or exserted; pollen 3-colpate, 12- or 15-rugate; 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.

**Unique features:** Trichomes usually stellate; styles one, stigma lobes usually oblong to ellipsoid; flowers mostly blue although some are white. Pollen mostly 12-15 aggrecolpate in polar-equatorial-polar pattern, less often 3-colpate (e.g., *J. nodiflora*).

**Distribution:** As currently understood, ca. 120 species, but research in Brazil and Australia is showing that the number may be an underestimate. There are about 100 species in the Americas, distributed from southern United States to Argentina and Uruguay. Plants grow in grasslands, thickets, savannas, near beaches, low to median forests and as weeds in cultivated fields.


Scandent shrubs or slender, subwoody scrambling vines, with terete, fistulose stems to 4–5 mm in diam., and short (2.5–4.0 cm) axillary shoots with congested leaves; pubescence of erect, translucent, simple hairs; mature stems terete; bark brownish white, irregularly longitudinally ridged, flaking. Leaves simple, hirsute, ovate or elliptic, obtuse at the apex, with entire, ciliate margins; short petioled. Inflorescence

*K. capixaba*, photo by G.S. Siqueira
terminal on short axillary shoots, corymbose, of 3–5 congested flowers; bracts oblong-elliptic, shorter than the sepals, strigose. Calyx campanulate, green, forming a short tube at base, sepals 5, nearly equal, lanceolate, acuminate, strigose; petals 3.5–4 mm long, oblong-elliptic, connate into a very short tube at the base, midpetaline weakly developed; stamens 5, inserted at base of corolla tube, glabrous, anthers elongated, large, nearly sessile, basifixed, with an apical connective; disc annular; ovary subglobose, glabrous, 2-locular, with 2 ovules per locule, style conduplicate, stigmas two, sessile, truncate. Fruit inserted on the middle (pedicel connate to lower ½) of a large, accrescent, foliaceous bract; fruit wide-ellipsoid, indehiscent, crustaceous with persistent calyx at base, fruit and bract wind dispersed as a unit.

**Unique features:** Scrambling shrubs or twining subwoody vines, with short lateral shots; fruits small, indehiscent, with a large foliaceous bract adnate to the peduncle and wind dispersed as a unit.

**Distribution:** A Brazilian endemic genus of two species, (*K. brasiliensis* Cheek & Sim.-Bianch. and *K. capixaba* Lombardi) distributed in NE & SE Brazil, in deciduous forest on limestone substrate or in lowland, dense forests; 9-200 m.

**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 brochidodromus, glabrescent above, densely reddish pubescent underneath; petioles canaliculated. Inflorescence axillary, slender cylindric-thrysiform, 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. ½ 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 nut-like, 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 perisperm, the seed coat coriaceous, the albumen absent or scanty, the embryo with a radical folded against the lower part of the latiplicate incumbent cotyledons, ca. 15 mm long.

Unique features: Lianas in tropical forests, often high-climbing. 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: Monospecific L. scandens is endemic to the Guiana Shield region of northern South America. These are tropical forest climbers, often near streams and rivers.
Twining lianas, climbing to 35 m or more, some species (e.g., *M. scandens* Aubl., *M. densiflora* Benth., and *M. elongate* 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 (fig. 2c), the larger stems more than 20 cm in diameter, grooved, or sometimes flattened, the young stems often angular; latex clear or yellowish (fig. 1c). Leaves simple, alternate or occasionally subopposite, generally elliptic, ovate to obovate to oblong (fig. 2b), 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 1/3 to ½ its length or less, the stigma capitate, 2-lobed, the lobes narrowly appressed if style entire, or lobes free. Fruits nut-like, indehiscent, rounded to ellipsoidal, the pericarp woody, firm to hard. Seeds 1-4, ovoid to oblong-ellipsoid, rounded, compressed or triangular if there are more than 1 per fruit, glabrous.
**Unique features:** Lianas in tropical forests, often high-climbing. Leaves are 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:** There are some 20 species in the genus. Most are South American, but a few reach into Central American and southern Mexico. These lianas are most common in wetland forests (*igapó, várzea*) but also occur in non-flooded forests.

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

Twining lianas or herbaceous annual or perennial vines, the stems twining or prostrate; latex watery or milky. Leaves simple, entire, shallowly trilobed or 3-angled, undulate or distantly serrulate, sessile or if present the petiole slender, cylindrical, occasionally sulcate, or rarely scale-like. 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, the pedicels usually shorter than the peduncle, smooth, striate, or notably five-angled, slender, stout to distinctly clavate, the bracts glabrous or pilose, usually two, prominent and foliaceous to reduced or scale-like or absent, usually caducous, rarely persisting in fruit, the bracteoles, when present, similar to the bracts; sepals 5, persistent, imbricate, ovate-
lanceolate, herbaceous, membranaceous-coriaceous, glabrous, pilose-appressed, or hirsute, the margins entire, the apex obtuse or rounded or emarginate; 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, erect, glabrous, the anthers helicoid-contorted; pollen 3-colpate (Simões & Staples, 2017); ovary 2-3-locular, 4-6-ovulate, glabrous, styles 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.

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

**Distribution:** The genus as previously circumscribed was a wastebasket of all species not fitting into *Ipomoea*, *Operculina*, or even other genera with a total of about 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 *Camomea*, *Decalobanthus*, *Distimake*, and *Xenostegia*. Only about 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. *Merremia hederacea* was introduced in the Lesser Antilles, Cuba and Colombia, while *M. discoidesperma* is found in Mexico, Guatemala, Nicaragua, Costa Rica, Hispaniola, Cuba, and *M. platyphylla* is found in Mexico.


Perennial vines, twining, the stems pubescent with unbranched trichomes but glabrescent, the trichomes green-olive or copper colored. 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, villose; corolla campanulate-funnelform, villose along the midpetaline plicae; stamens included, somewhat curved after anthesis; pollen 6(-8)-colpate; ovary 2-locular, 4-ovulate, styles 1, longer than the stamens, the stigma 2-globose. Fruits capsular, the valves lacking, dehiscence irregular, black when dry, enveloped by the sepals and bracts. Seeds 1-4, smooth, glabrous, surrounded by persistent perisperm.

**Unique 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, the stems prostrate or climbing to 10 m long, smooth or striate, glabrous. Leaves ovate, broadly ovate, pinnately or palmately lobed or compound, the segments 5 or 7 or entire, glabrous, the 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 (exserted in *O. pteripes* (G. Don) O'Donell), the anthers twisted when fully mature; pollen 3-colpate; ovary glabrous, bilocular, each locule 2-lobed, the styles included (exserted in *O. pteripes*), filiform, the 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.

**Unique 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, peduncles) are winged in *Operculina*; they are terete or striate, and unwinged in *Merremia*.

**Distribution:** Spread in the tropics of the Old and New Worlds, *Operculina* has some 12 or so species, with 7 in the Americas, distributed from Mexico to Paraguay including the West Indies. Several of those native to the Americas have become naturalized in the Old World and Pacific regions. Plants grow in thickets, grasslands, and deciduous tropical forests.
Twining lianas, 7-10 m long; stems subglabrous, lenticellate, with regular secondary growth and clear latex (fig. 1a). Leaves simple, entire, chartaceous, venation pinnate, prominent beneath; 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/pedicel 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 exserted, filaments connate below to corolla tube, free above, glabrous, anthers ellipsoid, longitudinally dehiscing prior to anthesis; pollen 3-colpate, nonspinose; pistil exserted, 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 ± prominulous. Seed 1, rarely 2, scurfy at first, smooth later, glabrous; hilum basal, C-shaped.

**Unique 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 while that trait is absent in other twining members of the family in the Americas.

**Distribution:** There are only 2 species in the genus, one in central Mexico (P. nutans (Choisy) O'Donell) and the other in SE Asia. Reported from a 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 lianas, dull yellow or 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, ± funnelform, less than 8 mm long, the limb 5-lobed, outside villous apically, inside glabrous; stamens included or exserted, the anthers ellipsoidal, longitudinally dehiscent; pollen 3-colpate, not spiny; pistil included, disc ring-like or absent, the ovary unilocular, ovules 4, the

*P. paniculata*, photo by P. Acevedo
styles simple (nearly absent in 1 species), the stigma 2-globose. Fruit papery, indehiscent. Seed 1, smooth.

**Unique features:** Distinguished from *Porana* by the pedate leaf venation, the calyx covering ¼ or less of the corolla tube, and entire style. The many funnelform, 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 and does not appear to produce fruits there.


Herbs, twining, with cylindrical to angular branches, the stems with dense ferruginous pubescence in the young parts, the trichomes simple and straight or antorose. Leaves simple, entire or undulate, ovate, slightly cordate basally, apex obtuse, both sides densely ferruginous-tomentose, the simple trichomes with two cells, one small and the other very long, the petiole 2-6 cm. Inflorescence terminal, racemose, bracts lanceolate or subcordate, peduncle small or none, pedicels elongate, the 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, interplicae 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, depressed, glabrous, 4-lobed, 4-locular, 2-valved. Seeds 4 (or fewer), light brown, subglobose, glabrous, the cotyledons reniform.

Unique features: This monotypic genus is rare, having been collected only a few times in the areas where it is known (Amazonas, Brazil; Bolivia; Colombia; French Guiana). While the species is distinctive and not likely to be confused with anything else, the genus is poorly known. *Tetralocularia* has a 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: This monotypic genus is endemic to the Americas. *Tetralocularia pennellii* O’Donell is known only from northern South America in Colombia, Venezuela, French Guiana, northern Brazil and lowlands of Bolivia. Recorded as a vine on floating islands in floodplain forests, riparian forests, swamps, and marshes.


Twining or repent herbaceous vines to ca. 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, the 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, the filaments inserted 1.5-4.5 mm above corolla base, glabrous or sparsely pubescent basally, anthers ellipsoid
to sagittate, longitudinally dehiscing; pollen 15-30 pantoporate, smooth; ovary 2-locular, 4-ovulate, almost globose, glabrous or covered with straight trichomes, the style 1, filiform, the 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.

**Unique features:** *Xenostegia* is distinguished by its subsessile leaves, pantoporate pollen, papillose stigmas, and straight-dehisced anthers. It was thought that the hypogeal germination of seeds was a distinguishing trait of the genus, but that has been questioned.

**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.

**RELEVANT LITERATURE**


association between *Ipomoea asarifolia* (Convolvulaceae) and a clavicipitalean fungus. Plant Physiology 147: 296-305.


PICTURE VOUCHERS

Figure 1.
A. Jacquemontia sp. from Bahia (no voucher)
B. Ipomoea furcyensis Urb. (Acevedo 17250)
C. Maripa scandens Aubl. (Acevedo 10455)
D. Porana nutans (Choisy) O’Donell (Acevedo 16258)
E-F. Distimake tuberosus (L.) A.R. Simões & Staples, from São Paulo (no voucher)

Figure 2.
A. Ipomoea corymbosa (L.) Roth (Acevedo 16146)
B. Dicranostyles holostyla Ducke (Acevedo 7622)
C. Ipomoea abutiloides (Kunth) G. Don (Acevedo 16608)
D. Ipomoea megapotamica Choisy, from São Paulo (no voucher)
E. Jacquemontia nodiflora (Desr.) G. Don (Acevedo 17169)

Figure 3.
A. Ipomoea eggersiana Peter, from St. Thomas, US Virgin Islands. (no voucher)
B. Ipomoea furcyensis Urb. (Acevedo 17250)

Figure 4.
A. *Distimake tuberosus* (Benth.) Britton & Rose (Acevedo 14307)
B. *Maripa paniculata* Barb.Rodr. (Acevedo 16080)
C. *Ipomoea quamoclit* L., cultivated (no voucher)
D. *Jacquemontia polyantha* (Schltdl. & Cham.) Hallier f. (Acevedo 16188)

Figure 5.
A. *Ipomoea heredifolia* L. (Acevedo 3031)
B. *Ipomoea ternata* Jacq. (Acevedo 9584)
C. *Ipomoea triloba* L. (Acevedo 12677)
D. *Maripa paniculata* Barb.Rodr. (Acevedo 16080)
E. *Jacquemontia heterantha* (Nees & Mart.) Hallier f. (Acevedo 16771)
F. *Jacquemontia havanensis* (Jacq.) Urb. (Acevedo 4077)
G. *Ipomoea nervosa* (Burm.f.) J.R.I.Wood & Scotland (Acevedo 16396)
H. *Ipomoea microdactyla* Griseb. (Acevedo 17415)
I. *Ipomoea furcyensis* Urb. (Acevedo 17250)

Figure 6.
A. *Dicranostyles ampla* Ducke (Acevedo 8327)
B. *Camonea umbellata* (L.) A.R.Simões & Staples (Acevedo 16725)
C. *Bonamia* sp. (Acevedo 16848)
D. *Aniseia* sp. (Acevedo 13631)

Figure 7.
A. *Ipomoea alba* L. (Acevedo 16685)
B. *Dicranostyles mildbraediana* Pilger (Acevedo 14433)
C. *Bonamia agrostopolis* (Vell.) Hallier f. (Acevedo 16627)
D. *Ipomoea* sp. (no voucher)