GUIDE TO THE GENERA OF LIANAS AND CLIMBING PLANTS IN THE NEOTROPICS

MALPIGHIACEAE

By Christiane Anderson



Stigmaphyllon ciliatum (photo: S. G. Weller)

A warm-temperate and tropical family of ca. 70 genera and ca. 1300 species of trees, shrubs, erect or trailing subshrubs or herbs with perennial underground structures, or woody to herbaceous, vines, predominantly neotropical but with some genera in Africa, Madagascar, southeast Asia, eastern Australia, New Guinea, and parts of Oceania. Vines are represented in the Neotropics by 33 genera and ca. 600 species that occur in diverse habitats, except at highest elevations.

Diagnostics: The hairs are unicellular and medifixed (stellate in *Thryallis*). Leaves are simple and opposite, commonly stipulate. Sepals commonly bearing a pair of large oil glands; petals clawed; androecium, with some

exceptions, comprises 10 stamens; gynoecium as a rule is 3-carpellate with usually three styles. In the majority of genera, fruits break into three samaras or mericarps.

General Characters

- 1. STEMS¹. Stems are terete (fig. 1a-e), lobed (fig. 1i, k; 2f, k), asymmetrically lobed (fig. 1g, h, j; 2b, e, i) or less often **flattened** or **4-angled** (fig. 11); straight (fig. 3a) or twisted (fig. 3b, e, f), from < 1 cm to 30 cm in diam. (fig. 3f) and up to 30–40 m long. Bark is usually smooth, gravish and lenticellate (fig. 3a), or dark grav and shaggy or corky in species of *Diploptervs* (fig. 3d), Peixotoa (fig. 1i), and Stigmaphyllon (fig. 3c). Stems with regular secondary growth are found in several genera; of these species of Adelphia, Aenigmatanthera, Amorimia, Heteropterys, Stigmaphyllon (fig. 1f), and Tetrapterys (fig. 1c) have inconspicuous rays, whereas species of Banisteriopsis, Echinopterys (fig. 1b), Hiraea, Gaudichaudia, Mascagnia and Tetrapterys (fig.1a) may have conspicuous rays. Stems may also present cambial variations classified as: **dispersed xylem** (also known as fissured stems) found in Alicia (fig. 2j), Banisteriopsis, Callaeum (fig. 2g; Cabanillas et al. 2017), Carolus (fig. 11), Christianella (fig. 2k), Diplopterys (fig. 2c, i), Jubelina, Mascagnia (fig. 2b), Malpighiodes, Mezia, and Peixotoa (fig. 1i, k), this type of cambial variation is only visible in mature stems (> 2 cm diam.) as their young stems only present deep phloem wedges; *interxylary phloem* found in *Dicella* (fig. 1e); *interxylary cambia* have been documented in several species of *Stigmaphyllon* (fig. 2a) and *Banisteriopsis nummifera* group (fig. 2d, Pace et al. 2018); and deep **phloem wedges** in species of *Banisteriopsis*, *Diplopterys* (fig. 2f), Heteropterys, Mascagnia (fig. 2h), Niedenzuella, Peixotoa (fig. 1i), and Stigmaphyllon, while some species retain this feature throughout their life cycle, others may transform into dispersed xylem (Pace, 2015).
- EXUDATES¹. For the most part, exudates are inconspicuous or clear; in species of *Tetrapterys* (fig. 1c) and possibly *Heteropterys* exudates can be reddish. The exudate generally is tasteless, but in species of *Tetrapterys* (e.g., *T. inaequalis*) it has a strong bitter taste.

¹ By P. Acevedo-Rodríguez and M.R. Pace.



Figure 1. Cross sections of stems of climbing Malpighiaceae. A. *Tetrapterys calophylla* A. Juss. B. *Echinopterys eglandulosa* (A. Juss.) Small. C. *Tetrapterys crispa* A. Juss. D. Unidentified Malpighiaceae. E. *Dicella macroptera* A. Juss. F. *Stigmaphyllon sinuatum* (DC.) A. Juss. G. *Heteropterys imperata* Amorim. H. *Heteropterys nordestina* Amorim. I. *Peixotoa adenopoda* C.E. Anderson. J. *Stigmaphyllon macropodum* A.
Juss. K. *Peixotoa sericea* C.E. Anderson. L. *Carolus chasei* (W.R. Anderson) W.R. Anderson. Photos by P.
Acevedo.



Figure 2. Cross sections of stems of climbing Malpighiaceae. A Stigmaphyllon acuminatum A. Juss. B.
Mascagnia cordifolia (A. Juss.) Griseb. C. Diplopterys patula (B. Gates) W.R. Anderson & C. Davis. D.
Banisteriopsis nummifera (A. Juss.) B. Gates. E. Tetrapterys crispa A. Juss. F. Diplopterys longialata (Nied.)
W.R. Anderson & C. Davis. G. Callaeum psilophyllum (A. Juss.) D.M. Johnson. H. Mascagnia sepium (A.
Juss.) Griseb. I. Diplopterys lutea (Rich.) W.R. Anderson & C. Davis. J. Alicia macrodisca (Triana & Planch.)
W.R. Anderson. K. Christianella mesoamericana (W.R. Anderson) W.R. Anderson. Photos: A by C.L. Bastos;
B-K by P. Acevedo.



Figure 3. Stems of climbing Malpighiaceae. A. Stigmaphyllon sp. B. Christianella mesoamericana (W.R. Anderson) W.R. Anderson. C. Stigmaphyllon floribundum (DC.) C.E. Anderson. D. Diplopterys patula (B. Gates) W.R. Anderson & C. Davis. E. Heteropterys cordifolia A. Juss. F. Alicia sp. Photos: A-D & F by P. Acevedo; E. by M. Pace.

- CLIMBING MECHANISMS. All genera climb by twining stems (fig. 3), with the exception of *Mascagnia almedae* and *M. vacciniifolia*, which climb by adventitious rootlets. In some genera, e.g., *Peixotoa*, plants may be shrubs but distally twining if adjacent vegetation offers support.
- 4. HAIRS. Hairs are unicellular, medifixed, and usually **2-armed**. The hairs may be straight to wavy and tightly appressed, or the arms may form a V. The trabecula, i.e., the crosspiece,

may be borne on a small stalk, and the hairs T- or Y-shaped and spreading; the arms may be curled, as in tomentose vesture. Occasionally, one arm of a Y-shaped hair may be greatly reduced and the hair appearing basifixed, but usually careful observation will show a rudiment of the reduced arm. Very rarely basifixed hairs are present, e.g., the samara vesture in species of *Christianella*. *Thryallis* is exceptional in the family in having stellate hairs.

- 5. STIPULES. Stipules are usually present beside (fig. 4a) or on the petiole (fig. 4 b) or axillary to it (fig. 4c), but absent in some genera or species. They are usually small, triangular, and distinct. In some species of *Tetrapterys*, the stipules are partly or entirely connate, and in *Peixotoa*, they are fused across the node, forming large interpetiolar heart-shaped structures that act as bud scales (fig. 4d).
- 6. LEAVES. Leaves are mostly opposite and decussate (fig. 4e), sometimes ternate or whorled, subopposite, or rarely alternate (e.g., *Barnebya*). Commonly they bear a pair of large multicellular glands on the petiole (usually at or near the apex (fig. 4f) but also near the middle or at the base) or near the base of the lamina. In addition, the lamina may bear glands along the margin (fig. 4g) and also on the surface (usually abaxially). The lamina is simple, mostly entire, rarely lobed or crenate (e.g., *Stigmaphyllon crenatum*), the margin never truly toothed but sometimes pseudodentate or ciliate at the location of marginal glands or stout bristle-like hairs. In general, the lamina varies from elliptical to ovate or sometimes orbicular. Petioles are commonly 0.5–2 cm long. In most species of *Stigmaphyllon* the lamina is heart-shaped and borne on much longer petioles.
- 7. INFLORESCENCES. Inflorescences are terminal or axillary, very diverse, most often racemose or paniculate but also dichasial (fig. 5). The flowers are often borne ultimately in umbels or corymbs of 4 or more; in the monotypic genera *Cordobia*, *Gallardoa*, and *Mionandra* the flowers are solitary and axillary. Each "flower" represents a reduced cincinnus, where the flower is borne on a pedicel, subtended by a pair of bracteoles, which itself is borne on a peduncle, subtended by a bract (fig. 6). In some genera the peduncle may be greatly reduced or absent (e.g., *Banisteriopsis*); if absent, the pedicel is subtended by the bract and the



Figure 4. Leaf features in climbing Malpighiaceae. A. Stipules lateral to petioles, laminar glands in *Banisteriopsis adenopoda* (A. Juss.) B. Gates. B. Stipules on petiole in *Hiraea faginea* (Sw.) Nied. C. Intrapetiolar stipules and petiolar glands in *Callaeum malpighioides* (Turcz.) D.M. Johnson. D. Stipules connate across the node (interpetiolar) in *Peixotoa sp.* E. Opposite, decussate leaves in *Banisteriopsis adenopoda*. F. Petiole glands in *Diplopterys patula*. G. Marginal glands and trichomes on leaf of unidentified Malpighiaceae. Photos by P. Acevedo.



Figure 5. Inflorescences in climbing Malpighiaceae. **A.** Racemose inflorescence in *Amorimia amazonica* (Nied.) W.R. Anderson. **B**. Paniculate inflorescence in *Heteropterys laurifolia* (L.) A. Juss. **C**. Dichasial cymes in *Heteropterys wydleriana* A. Juss. Photos by P. Acevedo.



Figure 6. Flowers in climbing Malpighiaceae. **A**. Pedicels subtended by 2 bracteoles in *Tetrapterys sp.* **B**. Pedicels of darker color than the peduncle (bracteoles deciduous) in *Mascagnia polybotrya* (A. Juss.) Nied. Photos by P. Acevedo.

bracteoles (e.g., *Peixotoa*). Old flowers (i.e., not pollinated) abscise at the joint between the pedicel and peduncle in all but one genus. The exception is *Mezia* in which the pedicel is greatly reduced or rudimentary, and the peduncle is well developed; abscission is at the base of the peduncle.

- 8. FLOWERS. The flowers are epigynous, except perigynous in *Barnebya*. They vary from small (about 6 mm in diameter) to large (about 4 cm in diameter). In the New World they are mostly bisexual, chasmogamous, and subtly to mostly strongly bilaterally symmetrical (radially symmetrical in *Psychopterys*); *Lasiocarpus* and *Spachea*, neither vining, are dioecious or functionally dioecious. A few genera have showy chasmogamous flowers and tiny reduced cleistogamous flowers borne ± simultaneously (*Gaudichaudia*, *Janusia*). Most Old World genera differ from the pattern described here in that the flowers are radially symmetrical and lack oil glands on the sepals, and in some genera all or some species are dioecious.
- 9. CALYX. The calyx consists of five sepals, distinct or partially connate at base or adnate to the receptacle. In the majority of New World genera the lateral (sometimes all) sepals each bear a pair of large oil glands (fig. 6a,b), and the flowers are visited by oil-collecting bees (e.g., *Centris*; Buchman, 1987). Occasionally, the sepals of some individuals are eglandular even though biglandular sepals are the norm for a particular species. Sepal glands are sessile in all but two genera; they are stalked in *Heladena* and *Henleophytum*. In genera lacking oil-glands the pollinator reward is pollen, and the anthers are large (e.g., *Thryallis*). In a few genera, e.g., *Dicella* and *Thryallis*, the calyx becomes papery and wing-like, and subtends the mature fruit.
- 10. COROLLA. The corolla is composed of five petals that are distinct, mostly clawed, alternating with the sepals, and imbricated with the posterior innermost and one of the anterior-lateral pair outermost. The petals are most often yellow, but also pink or white, sometimes other colors but rarely blue. The posterior petal, the "flag", usually differs from the lateral four, and the posterior-lateral pair may also differ from the anterior-lateral two.

- 11. ANDROECIUM. In most genera the androecium consists of 10 stamens, all fertile or some reduced to staminodes. A few genera have a reduced androecium; among vining genera are *Cottsia* (a warm temperate genus) with two fertile stamens and 0–3 staminodes, *Gaudichaudia* with five stamens, all fertile or two or three staminodes, and *Janusia* with five or six fertile stamens. The stamens may be homo- or heteromorphic, and the filaments and/or anthers variously pubescent or glabrous.
- 12. GYNOECIUM. The gynoecium is superior and 3-carpellate, mostly one anterior on the plane of symmetry and two posterior on each side of the plane of symmetry. The carpels are mostly all fertile, each fertile locule containing one pendent anatropous ovule. The styles number three and are mostly distinct, but connate or reduced in number in a few genera. Exceptions among vining genera are *Cottsia* (a warm temperate genus) and *Janusia* with one style, *Dicella*, with two styles and the anterior locule rudimentary, and *Gaudichaudia* with 1 (-3) styles. The style apex may be capitate or dorsally blunt or extended into a spur or hook; in *Ectopopterys* and most species of *Stigmaphyllon* the style apex is foliolate. The stigma is terminal or placed at the internal angle.
- 13. FRUIT. In most of the vining genera the fruit is a dry schizocarp that breaks into three samaroid mericarps ["samaras"] or cocci, each containing a seed lacking endosperm. Samaras may have the dorsal wing dominant and usually elongate, and the nut laterally with small winglets and/or crests or smooth. The dorsal wing is thickened along the adaxial margin (fig. 7a & c) in all genera, except *Heteropterys* (fig. 7b). If the lateral wings are dominant, they may be free and the samara butterfly-shaped (fig. 7d), or basally confluent and the samara circular (fig. 7e); the dorsal wing is small or sometimes absent. In some species, especially those water-dispersed, the wings are somewhat to greatly reduced (fig. 7f). Cocci may have a dorsal crest or be smooth; in *Echinopterys* and *Henleophytum* they are covered with setae and bristly (fig. 7g). In the aberrant *Dicella* the fruit is an indehiscent nutlike structure containing 1 (-2) seeds (fig. 7h). Fleshy fruits occur in *Bunchosia, Byrsonima*, and *Malpighia*, which include only trees and shrubs.



Figure 7. Fruits in climbing Malpighiaceae. **A.** *Niedenzuella stannea* (Griseb.) W.R. Anderson, dorsal wing of samara thickened adaxially. **B.** *Heteropterys brachiata* (L.) DC., dorsal wing of samara thickened abaxially. **C.** *Stigmaphyllon emarginatum* (Cav.) A. Juss., dorsal wing of samara thickened adaxially. **D.** *Hiraea sp.* with butterfly-shaped mericarps, the lateral wings dominant. **E.** *Mascagnia polybotrya*, lateral wings of samara confluent. **F.** *Diplopterys sp.*, immature fruit, mericarps with reduced winglets. **G.** *Echinopterys eglandulosa* (A. Juss.) Small, fruit composed of three bristly mericarps. **H.** *Dicella macroptera* A. Juss., with indehiscent nut-like fruit. Photos by P. Acevedo.

Key to the genera of climbing Malpighiaceae

1. Hairs of vesture stellate; Brazil and adjacent Paraguay and Bolivia
1. Hairs of vesture straight, crisped, or curly, or V-, Y-, or T-shaped, or plants glabrous 2
2. Sepal glands raised on stout stalks to 2 mm long at anthesis
2. Sepal glands sessile, flush or prominent, or sepals eglandular
3. Pedicels pedunculate, petals abaxially thinly sericeous on claw and proximally on midrib
of limb; mericarps smooth except for a rudimentary dorsal crest; southern Brazil,
Paraguay, and northeastern Argentina
3. Pedicels sessile or very short-pedunculate; petals abaxially densely appressed-tomentose
on claw and limb; mericarps with plumose setae; Cuba
4. Styles 1 or 2 (in <i>Dicella</i> sometimes with a third rudimentary style on anterior carpel) 5
4. Styles 3 7
5. Fertile stamens 10; styles 2 (sometimes with a rudimentary style on anterior carpel); fruit
a hard, indehiscent, obconic or spherical, nutlike structure, subtended by dry wings
formed by enlargement of the sepals; Costa Rica, South America Dicella
5. Fertile stamens 5–6; style 1; fruit breaking into three samaras
6. Laminas with glands on margin or on abaxial surface or a pair of glands at base; petals
yellow or pink and white; dominant wing of samara dorsal, the nut often with a pair of
lateral wings at the base and forming a rostrum Janusia
6. Laminas eglandular but often bearing on each side near base a small marginal process,
this eglandular or glandular at tip; petals yellow; dominant wing of samara lateral
(resembling a large dorsal wing), or the lateral wings continuous at base and forming a
circular or 3-lobed wing; Mexico and Central America (not reported from Panama), one
species-complex extending as far south as Colombia and Venezuela Gaudichaudia
7. Corolla radially symmetrical, petals subequal, white; Mexico, Guatemala, and Belize
Psychopterys
7. Corolla bilaterally symmetrical, the posterior petal differing somewhat to greatly from
the lateral 4, petals yellow, white, pink, pink and white, lilac, violet, blue, red, or
bronze
8. Sepals valvate or imbricate, concealing petals during enlargement of bud (sepals slightly

separating in a few species of <i>Niedenzuella</i> and strongly revolute at anthesis)
8. Sepals leaving petals exposed during enlargement of bud
9. Flowers borne singly; Paraguay and Argentina Cordobia
9. Flowers grouped into various inflorescences, rarely two in leaf axils
10. Fertile stamens 5, alternating with 5 staminodes; stipules connate, cordate and large,
acting as valvate bud scales enclosing the developing shoot or inflorescence;
southeastern Brazil and adjacent Bolivia and Paraguay Peixotoa
10. Fertile stamens 10; stipules distinct, triangular, small, or stipules absent 11
11. Petals white, white and pink, pink, or lilac, abaxially densely tomentose or
subsericeous; South America, except Chile and Uruguay
11. Petals yellow, abaxially glabrous or thinly sericeous
12. Sepals all biglandular; samara suborbicular or transversely elliptical (in M. bracteosa
mericarps with wings reduced to coriaceous or corky outgrowths); Amazonian
Venezuela and Brazil, the Guianas
12. Sepals with the anterior eglandular and the lateral 4 biglandular, or all eglandular;
samara butterfly- or X-shaped, sometimes lateral wings irregularly divided; Central and
South America
South AmericaNiedenzuella13. Stipules borne on petiole, at base or distally, distinct, or stipules absent (Mezia has
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samara with medifixed hairs and lacking dark spots
16. Lateral sepals each with one large gland (except in Jubelina uleana lateral sepals with
6-8 distinct glands and adaxially tomentose) 17
16. Lateral sepals each with a pair of glands or eglandular
17. Stipules absent; flowers borne in pseudoracemes; petals yellow; samara with 2 long,
narrow, forward-pointing, parallel-sided lateral wings and a short, inequilaterally
trapezoidal or flabellate dorsal wing (in L. splendens with very short dorsal crest and
the lateral wings reduced to ridges or lost), intermediate winglets absent; South
America, south to about 23°S Lophopterys
17. Stipules present; flowers borne in umbels of 4 or corymbs of 6; petals pink, violet, or
yellow; samara orbicular or transversely elliptical, the lateral wings cleft to nut at apex,
usually confluent at base, frequently bearing additional wings, winglets, crests, or
irregular outgrowths between outer wing and central dorsal wing; Central America and
northern South America
18. Anthers abundantly pubescent
18. Anthers glabrous (rarely with a few hairs in <i>Heteropterys</i> and <i>Tetrapterys</i>) 20
19. Sepals eglandular; styles distally coherent at or below stigmas; mericarps covered with
setae; Mexico Echinopterys
19. Sepals all biglandular or only on the lateral 4 or eglandular; styles distinct; samaras
butterfly-shaped
20. Leaves alternate; all sepals biglandular; outermost petal (one of anterior-lateral pair)
deeply concave; styles subulate
20. Leaves opposite or whorled (rarely alternate); anterior sepal or all sepals eglandular;
anterior-lateral petals equal; styles not tapered
21. Peduncles absent (or very short in Excentradenia); laminas with the tertiary venation
scalariform; inflorescences axillary, the flowers ultimately borne in umbels
21. Peduncles well developed; laminas with the tertiary venation reticulate; inflorescences
axillary or terminal, the flowers ultimately borne in umbels, pseudoracemes, or
corymbs
22. Bracteoles eglandular; inflorescence a cyme of 3–7, 4-flowered umbels or a single
umbel of 4-many flowers; samara butterfly-shaped (wings greatly reduced in H.

brachyptera and H. quapara); western Mexico to South America (H. faginea rare in 22. Bracteoles with one of each pair with a large bulging gland; inflorescence a single short raceme of 3–7 (–9), 4-flowered umbels, with 1 umbel terminal and the other 1–4 pairs axillary to bracts; samara circular in outline; northern South America Excentradenia 23. Samara with the dorsal wing dominant and thickened along the abaxial margin; petals yellow, pink, or pink and white (rarely white, bronze, or dark red); northern Mexico and the West Indies to northern Argentina and southeastern Brazil Heteropterys 23. Samara with the lateral wings dominant, butterfly- or X-shaped; petals yellow 24 24. Anthers of the posterior 3 stamens fertile or sterile, smaller than the other 7 and borne on smaller filaments; samara butterfly-shaped, dorsal wing small to nearly equal to lateral wings; Mexico, Central America, and South AmericaCallaeum 24. Anthers \pm alike, all fertile; samara X-shaped, with 4 discrete lateral wings, 2 on each side (in some species with several long aculeate outgrowths between them), all wings reduced to rudimentary outgrowths in a few species; Mexico and the West Indies to 25. Bracteoles very large, borne just below flower, the inner enclosing bud until anthesis, the outer enclosing bud and inner bracteole; peduncles well developed, pedicels absent or rudimentary; South America (M. includens extending into Panama)Mezia 25. Bracteoles small and bract-like, not enclosing flower bud; peduncles present or absent, 26. Stamens 5, opposite sepals, all fertile or 2 or 3 represented by staminodes; petiole eglandular; Mexico and Central America (not reported from Panama), one speciescomplex extending as far south as Colombia and Venezuela Gaudichaudia 26. Stamens 10, all fertile or a few with locules reduced or sterile; petiole with glands or 28. Samaras X-shaped, with 4 discrete lateral wings, 2 on each side (some species with several long aculeate outgrowths between them); Mexico and the West Indies to

Argentina
28. Samaras with the dorsal wing dominant or sometimes reduced to a crest
29. Petals pink or white, glabrous; Mexico to South America and the West Indies
Banisteriopsis
29. Petals yellow, glabrous or pubescent
30. Flowers borne in short, usually dense, 6-45-flowered pseudoracemes, these in
paniculate or dichasial arrangements; pedicels short-pedunculate (rarely sessile); petals
glabrous abaxially (rarely with a few hairs); Mexico to South America Bronwenia
30. Flowers borne in open 4- (6-)flowered umbels, corymbs, or pseudoracemes, these
grouped in panicles or cymes or borne singly, or in Diplopterys also with up to 8 pairs
of flowers in condensed axillary pseudoracemes; pedicels sessile (rarely short-
pedunculate); petals glabrous or abaxially sericeous
31. Petals abaxially sericeous (if glabrous, flowering plants leafless); styles with spreading
hairs at base and up to 2/3 of length (rarely glabrous); samara with a well-developed
dorsal wing thickened on the adaxial margin and usually with a triangular or rounded
appendage at base, nut smooth-sided, rugose, ribbed, or alulate; in a few species the
dorsal wing reduced to a crest and the nut bearing 2 to several lateral winglets or crests
parallel to the areole and interconnected by ridges; southeastern Mexico to South
America, Trinidad Diplopterys
31. Petals glabrous abaxially (flowering plants leafy); styles glabrous or sometimes
appressed-sericeous at base; samara with a well-developed dorsal wing thickened on
the adaxial margin and without appendage at base, the dorsal wing reduced to a crest
and the nut unornamented or with a single winglet on each side in a few species;
Mexico to South America and the West Indies Banisteriopsis
32. Anthers strongly heteromorphic in shape and/or size
32. Anthers ± alike
33. Sepals eglandular; lamina with glands on the abaxial surface; anterior style foliolate;
samara with the dominant wing elongated and apparently dorsal, thickened on abaxial
margin (resembling a samara of <i>Heteropterys</i>); Colombia, Ecuador, and Peru
Ectopopterys
33. Sepals biglandular; lamina eglandular or with glands on or just inside margin; anterior

- 35. Samara with the dorsal wing dominant and usually elongate, sometimes reduced...... 36
- 36. Dorsal wing thickened along abaxial margin; apex of styles efoliolate; petals yellow, pink, or pink and white (rarely white, bronze, or dark red); flowers in umbels, corymbs, or pseudoracemes, these solitary or grouped in racemes or panicles; northern Mexico to northern Argentina and southeastern Brazil, including the West Indies

- 37. Samaras X-shaped, with 4 discrete lateral wings, 2 on each side (in some species with several long aculeate outgrowths between them), all wings reduced to rudimentary outgrowths in a few species; Mexico to Argentina and the West Indies *Tetrapterys*

- 40. Lamina eglandular or with small glands on margin, the tertiary veins scalariform; peduncles absent or very short; flowers ultimately borne in umbels; petals yellow; samaras circular; northern South America Excentradenia

GENERIC DESCRIPTIONS

ADELPHIA W. R. Anderson, Novon 16: 170. 2006.

Woody vines. Leaves opposite; stipules minute, distinct, triangular, borne on stem



A. hiraea

beside base of petiole; petiole usually biglandular above middle, the glands when present protuberant, usually large and knoblike; lamina eglandular or bearing very small marginal glands, on distal half and especially near apex, often drawn out into vascularized cilia; tertiary veins reticulate. Inflorescence an open, elongated, axillary or terminal panicle or pseudoraceme with the flowers borne singly or (most often) in 2s, 3s, or 4s; floriferous bract eglandular; pedicels pedunculate; bracteoles borne at apex of peduncle, one of each pair bearing 1 bulging eccentric abaxial gland.

Sepals leaving petals exposed during enlargement of bud, all 5 or only the lateral 4 abaxially biglandular; glands sessile. Corolla bilaterally symmetrical, the posterior petal strongly

differentiated from the lateral 4 and longfimbriate; petals bright yellow or the posterior yellow and red, glabrous. Stamens 10, all fertile, glabrous; filaments connate at base, longer opposite sepals, shorter opposite petals; anthers mostly larger on the longer filaments. Styles 3, free, subequal, ± bowed or



A. hiraea (left), A. mirabilis (right)

lyrate, the anterior mostly shorter and less strongly bent than the posterior 2, apex dorsally truncate, apiculate, or bearing a hook up to 0.5 mm long, the stigma at internal angle. Fruit dry, breaking apart into 3 samaras separating from a short pyramidal torus; samara orbicular to butterfly-shaped, the lateral wings cleft to nut at apex and base (lateral wings rudimentary and the small dorsal wing dominant in *A. mirabilis*); dorsal wing smaller and distinct from

lateral wings at both apex and base; intermediate winglets absent; ventral areole orbicular to ovate.

Distinctive features: Petioles with two large knob-like glands at or above the middle; one bracteole of each pair with a large gland; posterior petal with the limb long-fimbriate.

Distribution: Four species in western South America; one (*A. hiraea*) extending to northern Venezuela and through Central America to southeastern Mexico, and on Jamaica.

AENIGMATANTHERA W. R. Anderson, Novon 16: 173. 2006.

Woody vines, occasionally described as shrubs. Leaves opposite; stipules minute,



A. lasiandra

distinct, triangular, borne on petiole at or slightly above base, or sometimes apparently absent; petiole eglandular or biglandular at or above middle; lamina eglandular or bearing several tiny glands embedded in the margin; tertiary veins reticulate. Inflorescence axillary or terminal pseudoracemes or a panicle of pseudoracemes, flowers decussate and sometimes crowded distally to form a corymb or umbel; floriferous bract eglandular; pedicels pedunculate;

bracteoles borne at or slightly below apex of peduncle, eglandular. Sepals leaving petals

exposed during enlargement of bud, the anterior eglandular and the lateral 4 biglandular, or all 5 biglandular; glands sessile. Corolla bilaterally symmetrical, the posterior petal differentiated from the lateral 4, bright yellow, glabrous or with a few hairs abaxially in center. Stamens 10, all fertile; filaments connate at base, longer opposite sepals than opposite petals, glabrous or distally sericeous; anthers



A. lasiandra

alike, abaxially densely white-sericeous on connective, at least proximally. Styles 3, free,

subequal, erect or slightly spreading, apex dorsally rounded, the stigma terminal or at internal angle, circular or laterally compressed. Fruit dry, breaking apart into 3 samaras separating from a short pyramidal torus; samara butterfly-shaped, the lateral wings cleft to nut at apex and base; dorsal wing smaller and distinct from lateral wings at both apex and base; intermediate winglets absent; ventral areole orbicular to ovate.

Distinctive features: Stipules borne on petiole; anthers alike and abaxially pubescent.

Distribution: Two species in Brazil and Bolivia.

ALICIA W. R. Anderson, Novon 16: 174. 2006.

Woody vines. Stems cylindrical, with dispersed xylem. Leaves opposite; stipules



A. anisopetala

minute, distinct, triangular, borne on petiole at or slightly above base; petiole bearing 2-4 (-8) small glands in 2 rows; lamina bearing few to many small glands impressed in abaxial surface in a row parallel to but set in from the margin; tertiary veins reticulate. Inflorescence a terminal and lateral panicle with the flowers borne decussate or distally irregularly in short to elongated pseudoracemes; floriferous bracts eglandular; pedicels pedunculate; bracteoles borne between middle and apex of peduncle or near apex, eglandular. Sepals valvate, completely concealing petals during enlargement of bud, the anterior usually eglandular,

the lateral 4 biglandular; glands sessile. Corolla bilaterally symmetrical to almost radial, the posterior petal strongly differentiated from the lateral 4 in size and shape; petals white, white and pink, pink, or lilac, abaxially densely tomentose or subsericeous, adaxially glabrous or sparsely tomentose, especially the lateral 4. Stamens 10, all fertile, glabrous; filaments \pm alike, 1/3-2/3-connate; anthers alike. Styles 3, free, subequal, straight or



nearly so, apex dorsally rounded, truncate, or apiculate, the stigma at internal angle. Fruit

dry, breaking apart into 3 samaras separating from a short pyramidal torus; samara suborbicular or transversely elliptical, the lateral wings cleft to nut at apex, usually continuous at base (rarely cleft to nut at base); dorsal wing smaller than lateral wings, distinct at apex, distinct at base or very abruptly confluent with lateral wing; intermediate winglets none; ventral areole orbicular or ovate.

Distinctive features: Stipules borne on petiole; petioles glands up to 8 in two rows; petals abaxially tomentose, the posterior much larger than the lateral four.

Distribution: Two species in South America (except Chile and Uruguay).

AMORIMIA W. R. Anderson, Novon 16: 176. 2006.

Woody vines or scandent shrubs. Leaves usually opposite, sometimes subopposite

or alternate near inflorescence; stipules minute,

distinct, triangular, borne on stem between petioles or

on petiole in leaves associated with inflorescences;

petiole eglandular or rarely biglandular near apex;

lamina eglandular or bearing 2-many small glands

impressed in abaxial surface between midrib and

margin, on margin at base in A. concinna, but usually

somewhat set in from margin in other species.

Inflorescence with the flowers borne in elongated

terminal or axillary pseudoracemes or panicles;



A. kariniana

often bearing 1 (-3) pairs of

bract

floriferous

submarginal or marginal glands or sometimes eglandular; pedicels pedunculate; bracteoles borne at apex of peduncle, eglandular or with 1 (-2) pairs of glands. Sepals leaving petals exposed during



A. rigida

enlargement of bud, the anterior eglandular (rarely bearing 1 or 2 small glands), the lateral 4 biglandular (occasionally the 2 glands adjacent to anterior sepal absent), glands sessile. Corolla bilaterally symmetrical, the posterior petal differentiated from the lateral 4 and usually smaller; petals yellow or yellow turning red-orange in age (especially the claws), abaxially densely velutinous, tomentose, or sericeous, at least on proximal half (only thinly sericeous in *A. concinna*), adaxially glabrous or densely to sparsely hairy on distal half. Stamens 10, all fertile; filaments connate at base, straight, subequal or longer opposite sepals than opposite petals, glabrous; anthers alike, glabrous or pubescent at apex and/or base. Styles 3, subequal, erect and straight to recurved, glabrous, the apex dorsally rounded or truncate or acute to short-hooked, the stigma at internal angle. Fruit dry, breaking apart into 3 samaras separating from a short or moderately high pyramidal torus; samara butterfly-shaped to depressed-elliptical with lateral wings chartaceous, continuous at base or cleft part-way or completely to nut; dorsal wing small, distinct at apex and base or confluent with lateral wings at base; intermediate winglets absent; nut almost always smooth between lateral and dorsal wings; ventral areole ovate or circular to very narrowly elliptical.

Distinctive features: Floriferous bract bearing glands; petals abaxially tomentose or sericeous; samaras without intermediate winglets.

Distribution: Fifteen species, Colombia, Ecuador, Peru, Brazil, Bolivia.

BANISTERIOPSIS C. B. Robinson in Small, N. Amer. Flora 25: 131. 1910.

Vines, shrubs, or rarely small trees. Stems cylindrical or nearly so, with regular



B. angustifolia (photo W. R. Anderson)

growth, phloem wedges, dispersed xylem, or interxylary cambia. Leaves opposite or ternate, rarely alternate; stipules small, triangular, interpetiolar; petiole eglandular or bearing 2-4 small raised glands on distal half, lamina usually bearing glands along margin or abaxially on surface or on the costa at base; tertiary veins reticulate. Inflorescence axillary or terminal, flowers borne in 4(-6)-flowered umbels. corymbs. or

pseudoracemes, these grouped in panicles or cymes or borne singly; floriferous bract eglandular; pedicels sessile or rarely borne on a short peduncle; bracteoles eglandular. Sepals mostly leaving petals exposed during enlargement of bud, the anterior usually eglandular or sometimes biglandular, the lateral 4 biglandular, or sometimes all eglandular; glands sessile. Corolla bilaterally symmetrical, the posterior petal differentiated from the lateral 4 and usually smaller; petals yellow, pink, or white, glabrous. Stamens 10, all fertile; filaments subequal or unequal, glabrous, proximally connate; anthers equal or unequal with the connective enlarged, glabrous or pubescent. Styles 3, free, equal or sometimes the anterior differing from the posterior two, glabrous or pubescent, rarely only the anterior style developing, the stigma terminal. Fruit dry, breaking apart into 3 samaras separating from a short pyramidal torus; in most species samara with a well-developed dorsal wing thickened on the adaxial margin; nut spherical or ovoid, smooth, ribbed, or bearing diverse winglets; dorsal wing reduced in a few species; ventral areole orbicular to elliptical.



B. muricata (left; photo P. Acevedo); *B. megaphylla* (center), *B. paraguariensis* (right), photos W. R. Anderson

Distinctive features: Inflorescences cymose or paniculate; pedicels mostly sessile; all stamens fertile; stigma terminal.

Distribution: 66 species, Mexico to South America and Cuba.

BARNEBYA W. R. Anderson & B. Gates, Brittonia 33: 275. 1981.



B. harleyi (photo A. A. Conceição)

Trees or woody vines. Leaves alternate, appearing opposite when crowded; stipules absent; petiole eglandular; lamina with 0–4 glands abaxially; tertiary veins reticulate. Inflorescence terminal, unbranched or with a dominant axis and many weaker axes from near base, each axis with 1–3 flowers; flowers perigynous; floriferous bract eglandular; peduncle pedunculate; bracteoles borne at or below apex of peduncle, eglandular. Sepals leaving outermost petal exposed during enlargement of bud, all biglandular; glands sessile.

Corolla bilaterally symmetrical, the posterior petal differentiated from the lateral 4, one of anterior-lateral petals (the outermost) deeply concave and larger than other petals; petals

yellow, glabrous or thinly sericeous abaxially on claw. Stamens 10, all fertile, glabrous; filaments alike, distinct; anthers \pm alike, those opposite sepals longer than those opposite petals. Styles 3, alike, subulate, glabrous, stigma at internal angle or subapical. Fruit dry, breaking apart into 3 samaras separating from a pyramidal torus; samara with an elongated



a, b, c, B. dispar, d. B. harleyi

dorsal wing thickened on adaxial margin; nut spherical or ovoid, reticulate, without lateral winglets; ventral areole narrowly elliptical.

Distinctive features: Leaves alternate; stipules absent;

flowers perigynous; sepals all biglandular; outermost petal (one of anterior-lateral pair) deeply concave; styles subulate; nut without lateral winglets.

Distribution: Two species in eastern Brazil, from Piauí and Pernambuco to São Paulo.

BRONWENIA W. R. Anderson & C. Davis, Contr. Univ. Michigan Herb. 25: 138. 2007. Woody vines or shrubs, when shrubby the branches often twining. Leaves opposite;



B. acapulcensis

stipules minute (0.2 mm long) or small (up to 1.5 mm long), distinct, triangular, borne on stem between petioles or sometimes absent; petiole eglandular or biglandular at or somewhat below apex; lamina usually bearing marginal glands, the distal glands (if present) minute, the 2 most proximal glands usually enlarged, or eglandular. Inflorescence axillary or terminal, paniculate or dichasial, the flowers borne

in short, usually dense pseudoracemes of 6–45 flowers; floriferous bract eglandular; pedicels mostly short-pedunculate, sometimes sessile; bracteoles borne at apex of peduncle, eglandular. Sepals leaving petals exposed during enlargement of bud, the anterior eglandular, the lateral 4 biglandular; glands sessile. Corolla bilaterally symmetrical, the posterior petal differentiated from the lateral 4; petals yellow, glabrous (very rarely sericeous on abaxial midrib). Stamens 10, all fertile; filaments unequally long, connate at base; anthers unequal in size, glabrous or pilose. Styles 3, free, subequal, erect or divergent, apex with a terminal, truncate or capitate stigma. Fruit dry, breaking apart into 3 samaras (or fewer by abortion) separating from a short pyramidal torus; dorsal wing of samara well developed, elongated, thickened on the adaxial margin, a shallow triangular or rounded appendage usually present on adaxial edge at base; nut smooth-



B. acapulcensis

sided or bearing a single ridge or winglet on each side parallel to areole; ventral areole triangular to circular.

Distinctive features: Leaf glands (if present) usually marginal; flowers are borne in dense, 6–45-flowered pseudoracemes.

Distribution: Ten species, South America to Mexico.

CALLAEUM Small, N. Amer. Fl. 25: 128. 1910.



C. macropterum (photo S. G. Weller)

Woody vines, or shrubs with scandent or trailing branches. Stems with dispersed xylem. Leaves opposite; stipules minute, distinct, triangular or linear, borne on petiole at or just above base (somewhat below to beyond middle of petiole in *C. johnsonii*), occasionally absent; petiole biglandular near or beyond middle or eglandular; lamina bearing small glands at or on margin in proximal half, occasionally eglandular; tertiary veins reticulate. Inflorescences axillary or terminal, simple or



compound, the flowers in few-flowered umbels or corymbs or in short, mostly decussate pseudoracemes; floriferous bract

eglandular;

pedicels

C. macropterum (left), C. psilophyllum (center), C. antifebrile (right)

pedunculate; bracteoles borne at or (often) below apex of peduncle, eglandular. Sepals leaving petals exposed during enlargement of bud, the anterior eglandular, the lateral 4 biglandular; glands sessile. Corolla bilaterally symmetrical, the posterior petal differentiated from the lateral 4 in shape and size; petals lemon-yellow, glabrous or abaxially sericeous or tomentose. Stamens 10, all fertile or the posterior 3 occasionally sterile, glabrous; filaments 1/3-2/3 or more connate; anterior 7 anthers \pm alike, usually larger than the posterior 3. Styles 3, free, subequal, erect or divergent from base, nearly straight or slightly sigmoid, apex dorsally rounded, the stigma at internal angle but transversely expanded. Fruit dry, breaking apart into 3 samaras separating from a pyramidal torus (in *C. antifebrile* 3 nutlike mericarps with vestigial wings); samara butterfly-shaped to depressed-elliptical, the lateral wings cleft to nut at apex, continuous at base or cleft part-way or completely to nut; dorsal wing varying from small to nearly as large as lateral wings, distinct at apex and base or connate with lateral wings at base, a few species with ruffles or winglets between dorsal and lateral wings; ventral areole ovate to linear.

Distinctive features: Minute stipules borne on petiole at or above base; petiole glands (if present) at or above middle; posterior three stamens smaller than the anterior seven; stigma transversely expanded.

Distribution: Eleven species of Mexico, Central America, and South America.

CAROLUS W. R. Anderson, Novon 16: 186. 2006.

Woody vines. Stems cylindrical or obtusely quadrangular, with dispersed xylem.



C. sinemariensis

Leaves opposite; stipules minute, triangular, borne on stem between petioles or beside base of petiole; petiole eglandular or bearing 2–4 (–6) small glands; lamina eglandular or bearing 2–many tiny glands on or embedded in margin; tertiary veins reticulate. Inflorescences axillary or terminal, pseudoracemes or umbels or panicles of pseudoracemes or umbels, the flowers mostly decussate; floriferous bracts eglandular; pedicels pedunculate (to sessile in some populations); bracteoles borne at apex of peduncle, eglandular. Sepals leaving petals exposed during

enlargement of bud, all 5 eglandular or the lateral 4 biglandular; glands sessile. Corolla bilaterally symmetrical, the posterior petal differentiated from the lateral 4; petals yellow,

adaxially glabrous, abaxially densely sericeous on claw and limb except near margin. Stamens 10, all fertile; filaments glabrous, connate in proximal 1/4–1/2, sometimes subequal but mostly of differing lengths, often longest opposite anterior sepal and shortest opposite posterior petal, the 2 opposite posterior-lateral petals often stouter than others; anthers alike or



C. sinemariensis

subequal, glabrous or sparsely hairy. Styles 3, free, subequal, erect and straight or somewhat bowed or spreading, apex dorsally rounded to short-apiculate or short-hooked and laterally compressed or terete, the stigma at internal angle. Fruit dry, breaking apart into 3 samaras separating from a high pyramidal torus; samara butterfly-shaped, the lateral wings cleft to nut at apex and base, the margin sinuate to coarsely dentate; dorsal wing absent or small, distinct at base and apex; ventral areole ovate to linear; samara of *C. sinemariensis* reduced or highly modified in some populations: in the Yucatan peninsula mericarps with very short lateral wings and sometimes outgrowths between lateral and dorsal wings, in the Guianas and adjacent Brazil lateral wings modified into narrow projections or reduced to corky outgrowths on enlarged nut.

Distinctive features: Petals yellow and abaxially densely sericeous; samaras butterflyshaped; pyramidal torus high.

Distribution: Six species of Mexico, Central America, the Lesser Antilles, and South America.

CHRISTIANELLA W. R. Anderson, Novon 16: 190. 2006.

Woody vines, or shrubby in open habitats. Stems lobed, sometimes asymmetrical, with dispersed xylem. Leaves opposite; stipules minute, distinct, triangular, borne on petiole near base; petiole eglandular or bearing 2–10 large to small glands in 2 rows; lamina



C. multiglandulosa (photo: M. Pace)

eglandular or bearing several small sessile glands on margin on proximal half; tertiary veins reticulate. Inflorescences terminal or axillary, single or (usually) grouped in panicles; flowers decussate to irregularly inserted in short to elongated pseudoracemes; floriferous bract eglandular or bearing several subsessile to long-stalked, clavate or capitate marginal glands; pedicels pedunculate; bracteoles borne at apex of peduncle, eglandular or with several subsessile to long-stalked, clavate or capitate marginal glands. Sepals elongated but

separating to expose petals during enlargement of bud, the anterior eglandular, the lateral 4 biglandular, all 5 bearing a row of small sessile or subsessile to long-stalked, clavate or capitate marginal glands. Corolla bilaterally symmetrical, the posterior petal differentiated from the lateral 4; petals yellow, adaxially glabrous, abaxially densely tomentose. Stamens 10, glabrous; filaments connate at base, straight, strongly heteromorphic, longest and much thickened opposite the 2 posterior-lateral petals, usually long but slender opposite the

anterior sepal, shortest opposite the posterior petal; anthers alike or larger on stouter filaments. Styles 3, free, the anterior straight and shorter than the other two, the posterior two straight or bowed from the base, apex dorsally truncate to short-hooked, the stigma at internal angle. Fruit dry, breaking apart into 3 samaras separating from a short pyramidal torus; samara orbicular to butterfly-shaped, the lateral wings membranous, cleft to nut at apex, continuous at base or cleft to nut, bearing stiff, usually basifixed or sub-basifixed hairs mostly



C. multiglandulosa (photo: M. Pace)

inserted at dark spots; dorsal wing extended forward at apex through gap in lateral wing, distinct at base or confluent with lateral wing; intermediate winglets mostly absent, rarely 1, narrow; ventral areole circular or broadly ovate.

Distinctive features: Stipules epipetiolar; bracts, bracteoles, and sepals with glandular margins; petals abaxially tomentose; samara wings with stiff hairs inserted at dark spots.

Distribution: Five species in southeastern Mexico, Central America, and South America.

CORDOBIA Niedenzu, Verz. Vorles. Königl. Akad. Braunsberg 1912/13: 41. 1912.

Vining shrubs to ca. 2 m, all vegetative parts densely sericeous, except older stems. Leaves opposite; stipules small, triangular, connate across the node and bifid or sometimes



C. argentea

distinct, borne on stem beside petioles; petiole eglandular; lamina with a pair of tiny glands near the base (sometimes hidden by the dense vesture); tertiary veins reticulate. Inflorescence a single, terminal or axillary flower; floriferous bract eglandular; pedicels pedunculate; bracteoles borne at apex of peduncle, eglandular. Sepals valvate, completely concealing petals during enlargement of bud, the anterior eglandular, the lateral 4 biglandular, adaxially red; glands sessile. Corolla bilaterally symmetrical, the posterior petal somewhat differentiated

from the lateral 4; petals yellow, glabrous. Stamens 5, all fertile, glabrous, alternating with 5 or fewer filiform staminodes; filaments basally connate, the longest opposite posterior petal; anthers \pm alike. Styles 3, free, subequal, straight, apex dorsally truncate, the stigma a line along the flattened slightly recurved apex. Fruit dry, breaking apart into 3 samaras separating from a pyramidal torus; samara bearing



C. argentea

a sub-trapezoidal dorsal wing with the adaxial margin thickened; nut bearing a pair of tiny lateral wings or crests; ventral areole ovate.

Distinctive features: Petioles with two large knob-like glands at or above the middle; flowers borne singly; one bracteole of each pair with a large gland; posterior petal with the limb long-fimbriate.

Distribution: One species, Cordobia argentea in Paraguay and Argentina.

DICELLA Grisebach, Linnaea 13: 249. 1839.

Woody vines. Stems cylindrical, xylem with interxylary phloem. Leaves opposite;



stipules minute, distinct, triangular, borne on stem at base of petioles; petiole eglandular or bearing 2 small glands near middle; lamina eglandular or bearing 2–6 glands on the abaxial surface (sect. *Dicella*) or 2–8 glands on the margin (sect. *Macropterys*); tertiary veins reticulate. Inflorescence terminal or axillary, a decompound panicle, the flowers ultimately borne in short pseudoracemes; floriferous bract eglandular; pedicels pedunculate; bracteoles borne at apex of peduncle, eglandular. Sepals leaving petals

exposed during enlargement of bud, the anterior eglandular, the lateral 4 biglandular; glands sessile; in fruit all sepals much enlarged and becoming papery and wing-like, shorter than or subequal to mature fruit in sect. Dicella, much longer than mature fruit in sect. Macropterys. Corolla bilaterally symmetrical, the posterior petal strongly differentiated from the lateral 4; petals yellow, turning red in age in some species, adaxially glabrous or tomentose, abaxially densely sericeous or lanate. Stamens 10, all fertile; filaments alike, abaxially sparsely to densely sericeous and adaxially glabrous, 1/4-1/2 connate; anthers \pm alike (the pair opposite the anterior-lateral petals smaller than the others), all strongly reflexed in anthesis, the connectives large and reddish, not exceeding locules (sect. *Dicella*) or exceeding locules, especially those of anthers opposite sepals (sect. *Macroptervs*). Ovary with the anterior locule rudimentary and empty, the 2 posterior locules full-sized and fertile; anterior style much reduced or absent, the 2 posterior styles distinct, stout, glabrous, apex obliquely truncate or short-hooked, the stigma at internal angle. Fruit a dry, hard, indehiscent, obconic or spherical, nutlike structure with a thick fibrous wall, containing 1-2 seeds (most often only 1), and subtended by dry wings formed by enlargement of the sepals.



D. nucifera, sect. Dicella, left; D. conwayi, sect. Macropterys, right (photos: W. R. Anderson)

Distinctive features: Petals abaxially sericeous or lanate; ovary with two stout posterior styles, the anterior style rudimentary or absent; fruit round and nutlike, with the sepals enlarged and wing-like.

Distribution: Seven species in two sections; sect. *Dicella*: two species in southeastern Brazil and adjacent Paraguay and Argentina; sect. *Macropterys*: five species, one (*D. aciculifera*) in Costa Rica, four in South America.

DIPLOPTERYS A. Jussieu in Delessert, Icon. Sel. Pl. 3: 20, pl. 33. 1838 ["1837"].

Woody vines or shrubs, when shrubby the branches often twining. Stems cylindrical



D. hypericifolia (photo: W. R. Anderson)

or asymmetrical (slightly flattened), with dispersed xylem or deep phloem wedges. Leaves opposite; stipules minute to small, triangular, borne on stem beside base of petiole; petiole eglandular or bearing 2 (rarely 4) glands on distal half; lamina with glands (often minute) on or just within margin (on the abaxial surface in one species); tertiary veins reticulate. Inflorescence axillary or occasionally terminal, flowers grouped in 4- to 6-flowered umbels borne singly or in short racemes or cymes, or in condensed axillary

pseudoracemes of up to 8 pairs of flowers; floriferous bract eglandular; pedicels sessile; bracteoles eglandular. Sepals mostly leaving petals exposed during enlargement of bud (valvate in *D. valvata*), all 5 eglandular or the lateral 4 biglandular; glands sessile. Corolla bilaterally symmetrical, the posterior petal strongly differentiated from the lateral 4; petals yellow, glabrous or abaxially sparsely to densely sericeous or tomentose. Stamens 10, all fertile; filaments unequal, glabrous, variously connate;



D. pubipetala (photo: T. F. Daniel)

anthers unequal, glabrous to tomentose. Styles 3, free, subequal or the anterior longer than the posterior two, mostly bearing long spreading hairs at least at base or up to 2/3 of their length, rarely glabrous, the stigma terminal, capitate or occasionally truncate. Fruit dry, breaking apart into 3 samaras separating from a short pyramidal torus; in most species samara with a well-developed dorsal wing thickened on the adaxial margin and usually with a triangular or rounded appendage on adaxial margin at base; nut spherical and smoothsided, rugose, ribbed, or bearing diverse winglets; in a few species the dorsal wing reduced
to a crest and nut bearing 2 to several lateral winglets or crests parallel to the areole and interconnected by ridges; ventral areole orbicular to elliptical.

Distinctive features: Pedicels sessile; styles pubescent in proximal half; nut of samara spherical, smooth-sided, rugose, ribbed, or bearing diverse winglets.

Distribution: 31 species, 30 in South America (including Trinidad) with two of those extending west into southern Central America; one species (D. mexicana) in southeastern Mexico.

ECHINOPTERYS A. Jussieu, Arch. Mus. Hist. Nat. 3: 342. 1843.



E. eglandulosa

Shrubs or woody vines, occasionally described as small trees. Stems cylindrical, with regular growth and conspicuous rays. Leaves alternate, or alternate and

opposite, rarely all or most opposite; stipules small, triangular, borne on petiole at base: petiole eglandular; lamina

eglandular; tertiary veins reticulate. Inflorescence a pseudoraceme terminating a leafy stem; floriferous bract eglandular; pedicels pedunculate; bracteoles borne at



E. eglandulosa

apex of peduncle, eglandular. Sepals leaving petals exposed during enlargement of bud, eglandular. Corolla bilaterally symmetrical, the posterior petal differentiated from the lateral 4; petals yellow, abaxially moderately to densely sericeous or appressed-tomentose on claw and in center of limb. Stamens 10, all fertile and alike; filaments connate at base; filaments and anthers densely appressed-tomentose or tomentose. Styles 3, distinct for proximal 2/3 or more of their length but coherent distally in stigmas or below distinct stigmas, the cluster of styles curved toward posterior petal, the stigma terminal and capitate, coherent or distinct. Fruit dry, apparently indehiscent or only very tardily schizocarpic (*E. eglandulosa*), or soon breaking apart into 3 mericarps separating from a short pyramidal torus (*E. setosa*); mericarp covered on back and sides with many long, slender, vascularized setae arrayed in several roughly vertical rows but giving the impression of completely covering abaxial surface of nut; ventral areole narrowly ovate.

Distinctive features: Eglandular and often alternate leaves; hairy petals and stamens; coherent styles; bristly fruits.

Distribution: Two disjunct species (*E. eglandulosa*, *E. setosa*) in Mexico.

ECTOPOPTERYS W. R. Anderson, Contr. Univ. Michigan Herb. 14: 11. 1980.

Woody vine. Leaves opposite; stipules small, triangular, borne on stem between petioles, distinct or adjacent stipules connate; petiole eglandular or distally biglandular; lamina bearing



glands on abaxial surface; tertiary veins reticulate. Inflorescence a terminal and lateral panicle, the flowers borne in decussate 4-flowered umbels, 6-flowered corymbs, or pseudoracemes; floriferous bract eglandular; pedicels pedunculate; bracteoles borne at apex of peduncle, eglandular. Sepals leaving petals exposed during enlargement of bud, eglandular, strongly reflexed in anthesis; glands sessile. Corolla bilaterally symmetrical, the posterior petal differentiated from the lateral 4; petals light yellow, glabrous. Stamens 10, all fertile; filaments longer opposite sepals than opposite petals, glabrous, connate at base; anthers all bearing tufts of hairs at base and apex of locules, strongly heteromorphic, of 3 types: 5 anthers opposite sepals introrse, the locules much exceeded by the globose glandular connective; 3 anthers opposite anterior-lateral petals and posterior petal like those opposite sepals but with the glandular connective not or barely exceeding the locules; 2 anthers opposite posterior-lateral petals latrorse, much reduced, the connective hardly developed and eglandular. Styles 3, free, anterior style dorsally extended at apex in a hook bearing pendent triangular folioles; 2 posterior styles laterally flattened, truncate at apex and coherent or connate along their upper edges, the stigma at internal angle. Fruit dry, breaking apart into 3 samaras separating from a short pyramidal torus; samara with the dominant wing elongated and apparently dorsal, thickened on abaxial edge and bent upward (resembling a samara of *Heteropterys*); nut bearing 1 or 2 winglets or crests on one side; ventral areole circular.

Distinctive features: Eglandular reflexed sepals; androecium with two anthers reduced and five with an elongated glandular connective; anterior style foliolate; samaras superficially resembling those of *Heteropterys*.

Distribution: One species, E. soejartoi W.R. Anderson, in Colombia, Ecuador, and Peru.

EXCENTRADENIA W. R. Anderson, Contr. Univ. Michigan Herb. 21: 29. 1997.

Woody vines. Leaves opposite, subopposite, or alternate; stipules small, triangular, borne on petiole at base or on adjacent stem, or absent; petiole biglandular at or above middle; lamina



eglandular or bearing small glands on margin; tertiary veins scalariform. Inflorescence a single short axillary raceme of 3–7 (–9) 4flowered umbels; with 1 umbel terminal and the other 1–4 pairs axillary to bracts bearing stipules and often petiole glands; floriferous bract eglandular; peduncles short or absent; bracteoles small, one of each pair bearing 1 bulging eccentric abaxial gland toward center of umbel. Sepals leaving petals at least somewhat exposed during enlargement of bud, all 5 eglandular or the lateral 4 biglandular; glands sessile. Corolla bilaterally symmetrical, the posterior petal strongly differentiated from the lateral 4; petals bright yellow, glabrous. Stamens 10, all fertile, glabrous; filaments alike or those opposite sepals slightly longer than those opposite petals, briefly connate at base; anthers \pm alike. Styles 3, free, the anterior style shorter than the posterior styles, apex dorsally truncate, apiculate, or bearing a hook up to 0.3 mm long, the stigma at internal angle. Fruit dry, breaking apart into 3 samaras separating from a short pyramidal torus; samara usually subcircular, the lateral wings cleft to nut at apex and continuous at base or occasionally cleft to nut at both apex and base; dorsal wing small; intermediate winglets absent; ventral areole circular.

Distinctive features: Laminas with scalariform tertiary venation; one bracteole of each pair with a large gland.

Distribution: Four species in northern South America.

GAUDICHAUDIA Kunth in Humboldt, Bonpland & Kunth, Nov. Gen. Sp. 5: pl. 445. 1821. Slender vines or small erect shrubs. Leaves opposite; stipules small, distinct, triangular,



borne on stem beside base of petiole; petioles eglandular; laminas eglandular, but often bearing on each side near base a small marginal process, this eglandular or glandular at tip and terminating lobe-like enlargements of the lamina in some species; tertiary veins reticulate. Inflorescences composed of flowers of 2 kinds: chasmogamous (showy, present in all species) and cleistogamous (inconspicuous, present in some species). Chasmogamous flowers borne typically in (2–) 4 (–6)-flowered umbels; floriferous bract eglandular; pedicels pedunculate; bracteoles borne at apex of peduncle, eglandular. Sepals leaving petals exposed during enlargement of bud, the anterior eglandular, the lateral 4 biglandular; glands sessile. Corolla bilaterally symmetrical, the posterior petal differentiated from the lateral 4 or only slightly so; petals orange-yellow, glabrous. Stamens 5, opposite sepals, all fertile or 2 or 3 represented by staminodes, these sometimes much reduced in size, glabrous; filaments basally connate, those of staminodes more slender than of fertile stamens; anthers of fertile stamens alike. Styles 1(-3), regularly 3 in some species and free, straight and erect, when single borne on the anterior carpel, the stigma terminal and capitate. Cleistogamous flowers borne in axillary clusters, usually nearly or quite sessile, tiny, ca. 1–2 mm long, elongating to 4 mm as fruit develops, composed of 5 eglandular sepals, 1 (-2) rudimentary petals, 1 (-2) minute stamens, and 2 fertile carpels without styles. Fruit dry, breaking apart at maturity into 3 samaras (chasmogamous flowers) or 2 samaras (cleistogamous flowers), each samara having its largest wings lateral, a single wing continuous at the base or at both base and apex, or a 3-lobed wing with the lobes alike or, more commonly, with 1 upper lobe larger; dorsal wing small, sometimes reduced to a crest or absent; ventral areole orbicular to ovate.

Distinctive features: Presence of cleistogamous flowers in some species; five stamens; single style in some species; samaras circular or with one lateral wing dominant.

Distribution: About 25 species of Mexico and Central America (not reported from Panama), with one species-complex extending as far south as Colombia and Venezuela.

HELADENA A. Jussieu, Ann. Sci. Nat. Bot., Sér. 2, 13: 321. 1840.

Woody vine, occasionally described as a shrub or small tree. Leaves opposite; stipules linear-subulate, distinct, borne on petiole at base; petiole sometimes biglandular at apex; laminas



H. multiflora

usually bearing 1–3 pairs of small protuberant glands on margin near base, often on shallow tooth-like extensions of margin; tertiary veins reticulate. Inflorescences unbranched, terminating a leafy branch with full-sized leaves or lateral, axillary to a full-sized leaf and then usually bearing 1 pair of much-reduced

leaves, these often deciduous; floriferous bracts eglandular; pedicels pedunculate; bracteoles borne at apex of peduncle, eglandular. Sepals leaving petals exposed during enlargement of bud, the anterior eglandular, the lateral 4 biglandular; glands peltate, raised on stout stalks that elongate to 0.7–1.5 mm during anthesis, borne below free part of sepals. Corolla bilaterally symmetrical, the posterior petal differentiated from the lateral 4; petals abaxially thinly sericeous on claw and proximally on midrib of limb, adaxially glabrous; lateral petals lacerate on proximal half, distally subentire; posterior petal lacerate all around margin. Stamens 10, all fertile; filaments alike or longer opposite sepals than opposite petals, glabrous or abaxially sericeous distally, connate only at very base; anthers alike, glabrous or rarely sparsely sericeous. Styles 3, weakly coherent in bud but soon separating during anthesis, subequal, straight, the anterior longer than the posterior 2, the large stigma apical, elliptical-capitate and eccentric, dorsally elongated away from axis of flower. Fruit dry, breaking apart into 3 ellipsoidal mericarps (cocci) separating from an elongated pyramidal torus; mericarp without wings or setae, bearing a rudimentary dorsal crest and otherwise completely smooth; ventral areole elongate-elliptical.

Distinctive features: Stalked peltate calyx glands; elliptical-capitate stigmas; smooth cocci.

Distribution: One species, *H. multiflora* (Hook. & Arn.) Nied., in southern Brazil, Paraguay, and northeastern Argentina.

HENLEOPHYTUM H. Karst., Fl. Columbiae 1: 158. 1861.

Slender twining woody vine. Leaves opposite; stipules minute, triangular, borne on



H. echinatum

petiole at base; petiole eglandular; lamina usually bearing 2 small glands embedded in margin near its base (these occasionally apparently on petiole when lamina is decurrent), rarely eglandular; tertiary veins reticulate. Inflorescences unbranched, mostly axillary to scars of leaves from previous seasons, leafless or bearing a pair of much-reduced, soon-deciduous leaves subtending lowest flowers; floriferous bracts eglandular or bearing 2 tiny marginal glands near base; pedicels sessile or short-pedunculate; one or both bracteoles usually bearing (1–) 2 small marginal glands near base. Sepals leaving petals exposed during enlargement of bud, all 5

biglandular but those of the anterior sepal connate with adjacent glands to form 2 larger compound glands; glands peltate, raised on stout stalks that elongate to 1–2 mm during anthesis,

borne below free part of sepals. Corolla bilaterally symmetrical, the posterior petal strongly differentiated from the lateral 4; petals yellow, abaxially densely appressed-tomentose on claw and limb and somewhat hairy adaxially on claw. Stamens 10, all fertile; filaments diminishing in length from front to back, the anterior 3 longest and the posterior 3 shortest, abaxially thinly sericeous, connate at base; anthers alike, glabrous. Styles 3, initially coherent but usually separating during anthesis, subequal (the



H. echinatum

anterior sometimes slightly shorter than the posterior 2), straight or slightly bent outward, the large distinct stigma apical, elliptical-capitate and eccentric, dorsally elongated away from axis of flower. Fruit dry, breaking apart into 3 mericarps (cocci) separating from a short pyramidal

torus; mericarp covered on back and sides with many long, slender, vascularized setae arrayed in several roughly vertical rows but giving the impression of completely covering abaxial surface of nut, each seta plumose its whole length with short soft spreading white hairs; ventral areole ovate.

Distinctive features: Stalked peltate calyx glands; petals abaxially hairy; elliptical-capitate stigmas; bristly fruits.

Distribution: One species, Henleophytum echinatum (Griseb.) Small, in Cuba.

HETEROPTERYS Kunth in Humboldt, Bonpland & Kunth, Nov. Gen. Sp. 5 [quarto ed.]: 163. 1822 ["1821"].

Woody vines, shrubs, or small trees. Stems cylindrical or deeply lobed, with regular growth and conspicuous rays. Leaves opposite or very rarely alternate or whorled; stipules very small, distinct, triangular, borne on edge of petiole at its base or on stem beside petiole, or



H. purpurea (photo: P. Acevedo)

absent; petiole usually with 2 glands borne at base to apex; lamina usually bearing glands on lamina, at base and/or on surface and/or along margin; tertiary veins reticulate. Inflorescence with the flowers borne in umbels, corymbs, or pseudoracemes, these single or grouped into racemes or panicles, axillary or terminal or both; floriferous bract eglandular or with 1–2 glands; pedicels pedunculate or sometimes sessile; bracteoles borne at or below apex of peduncle, eglandular or sometimes one bracteole of a pair with a gland. Sepals leaving outermost petal

exposed in enlarging bud or concealing petals until anthesis, eglandular or the lateral 4 biglandular, or perhaps occasionally all 5 biglandular with the glands on anterior sepal connate with adjacent glands. Corolla bilaterally symmetrical, the posterior petal \pm strongly differentiated from the lateral 4 petals; petals light yellow or pink or pink and white in most species, white,

bronze, or dark red in a few species, glabrous in all but a few species. Stamens 10, all fertile; filaments mostly connate proximally, generally longer opposite sepals and posterior-lateral petals, the latter 2 often thicker than others, glabrous; anthers \pm alike, the posterior 3 sometimes smaller than others, glabrous in all but a few species. Styles 3, free, anterior style mostly differing at least somewhat from the posterior in length and shape; apex dorsally rounded, truncate, acute, or hooked, the stigma at internal angle or rarely terminal. Fruit dry, breaking apart into 3 samaras or mericarps separating from a short pyramidal torus; samara with a welldeveloped dorsal wing thickened on the abaxial margin; nut smooth or with much shorter lateral winglets or crests in some species; ventral areole elliptical to ovate to orbicular.



a. H. brachiata, b. H. laurifolia, c. H. leona, d. H. lindeniana, e. H. subhelicina

Distinctive features: Stamens alike in shape but varying in size; anthers glabrous (except in a few species); samara with dorsal wing thickened along abaxial margin.

Distribution: More than 140 species; northern Mexico and the West Indies to northern Argentina and southeastern Brazil. One species, *H. leona* (Cav.) Exell, also established in coastal West Africa from Senegal to Angola. HIRAEA Jacquin, Enum. Syst. Pl. 4. 1760.

Woody vines, sometimes shrubby or a small tree. Stems cylindrical with regular growth



H. faginea

and inconspicuous rays. Leaves mostly opposite, sometimes ternate; stipules usually long, triangular to subulate, borne adaxially on petiole, from slightly above base to near apex; petiole usually biglandular distally or the pair of glands borne at base of lamina; lamina often glandular on margin in addition to basal glands; tertiary veins scalariform. Inflorescence axillary, either 1–several umbels of 4–6 flowers, often borne in a cyme or compound arrangement, or umbels multi-flowered and mostly solitary in each axil; floriferous bract eglandular; pedicels sessile; bracteoles eglandular. Sepals leaving

petals exposed during enlargement of bud, the anterior eglandular, the lateral 4 biglandular or all eglandular; glands sessile. Corolla bilaterally symmetrical, the posterior petal commonly strongly differentiated from the lateral 4; petals mostly yellow or yellow turning orange or red in age, glabrous. Stamens 10, all fertile, glabrous, varying only in size; filaments connate only at base; anthers \pm alike. Styles 3, free, subequal or the anterior longer than the posterior 2, erect or divergent, apex dorsally rounded to prominently hooked, the stigma at internal angle. Fruit dry, breaking apart into 3 samaras separating from a very short pyramidal torus; samara mostly butterfly-shaped, the lateral wings cleft to nut at apex and base (lateral wings \pm reduced in a few species, turned into many short winglets in *H. quapara*); dorsal wing small, sometimes reduced



a. H. barclayana, b. H. smilacina, c. H. brachyptera, d. H. quapara

to a crest or lost; intermediate winglets or slender projections rarely present; ventral areole orbicular to ovate.

Distinctive features: Scalariform leaf venation; stipules borne on petiole; inflorescences axillary, umbels either multi-flowered and solitary, or 4 (–6)-flowered and borne singly, in cymes, or small compound inflorescences; samaras butterfly-shaped.

Distribution: 70–80 species, from western Mexico to Paraguay, adjacent Argentina, and southeastern Brazil; absent from the West Indies, except for the Lesser Antilles (Grenada, St. Lucia).

JANUSIA A. Jussieu, Ann. Sci. Nat. Bot., Sér. 2, 13: 250. 1840.

Vines, small shrubs or perennial herbs. Leaves opposite; stipules small, distinct, triangular to subulate, borne on stem beside base of petiole, or absent; petioles eglandular or with



J. anisandra

a pair of glands at or near apex or at middle; laminas with glands on margin or on abaxial surface or a pair of glands at base; tertiary veins reticulate. Inflorescences composed of flowers of 2 kinds: chasmogamous (showy, present in all species) and cleistogamous (inconspicuous, present in some species). Chasmogamous flowers borne in umbels of 4 (occasionally reduced to 2 or 3), or in 1-flowered units derived from the reduction of 4 flowers to 1 (the missing flowers denoted by various numbers of sterile bracts), grouped into irregular cymose or paniculate arrangements; floriferous bract eglandular; pedicels pedunculate or sessile; bracteoles usually borne at apex of peduncle or sometimes slightly below, eglandular. Sepals leaving petals exposed during enlargement of bud, the anterior eglandular, the lateral 4 biglandular or rarely all biglandular;

glands sessile. Corolla bilaterally symmetrical, the posterior petal differentiated from the lateral 4; petals vellow, pink, or pink and white, glabrous. Stamens all fertile, 5 opposite sepals, anthers glabrous, or stamens 5 opposite sepals and 1 opposite posterior petal, anthers densely to sparsely hairy; stamens greatly heteromorphic in size of filaments and/or anthers, filaments slightly connate at base or the posterior 3 connate in proximal 1/2, variously curved; or stamens alike, filaments \pm straight. Style 1, borne on the anterior carpel, erect or variously bowed or curved, the stigma terminal and capitate or somewhat oblique, or the style tapering to a pointed apex with the small, flat, elliptical stigma displaced to one side so that it points upward. Cleistogamous flowers often borne singly or in umbels, or in clusters of several raised on a slender axillary stalk, but also (usually lower on the same plant) sessile or subsessile in axils of full-sized leaves; flowers minute, ca. 1.5 mm in diameter, resembling undeveloped flower buds, composed of 5 eglandular sepals, 0–1–5 rudimentary petals, 1–2 stamens or sessile anthers, and 2–3 fertile carpels with 0–1 rudimentary style. Fruit dry, breaking apart at maturity into 3 samaras from a low pyramidal torus; dorsal wing of samara well developed, elongated, thickened on the adaxial margin, with or without a rounded or triangular projection at adaxial base; nut spherical or ovoid, smooth, ribbed, or with low crests or dissected outgrowths, with or without a pair of lateral winglets at or near base, these connate and forming a straight or decurved apparent extension of nut ("rostrum"); ventral areole elliptical or ovate.

Distinctive features: Cleistogamous flowers present in some species; stamens 5 or 6; style single; samara in most species with a basal rostrum formed by lateral winglets.

Distribution: Fifteen species, in Argentina, Bolivia, Brazil, Paraguay, and Uruguay; *J. caudata* Griseb. also recorded from the Guayana region.

JUBELINA A. Jussieu in Delessert, Icon. Sel. Pl. 3: 19, pl. 32. 1838 ["1837"].

Woody vines. Stems with dispersed xylem. Leaves opposite; stipules small or minute,



distinct, triangular, borne on base of petiole; petiole eglandular; lamina bearing glands impressed abaxially or rarely eglandular; tertiary veins \pm scalariform. Inflorescences axillary and terminal, decompound, containing much-reduced bract-like leaves below the floriferous bracts, the flowers ultimately borne in umbels of 4 or corymbs of 6; floriferous bract eglandular; pedicels pedunculate; bracteoles borne at apex of peduncle, eglandular. Sepals leaving petals exposed during enlargement of bud, revolute or reflexed in anthesis, the anterior eglandular, the lateral 4 each

usually bearing 1 large gland formed by \pm complete fusion of 2 (except in *J. uleana*, with 6–8 distinct glands), occasionally all sepals eglandular. Corolla bilaterally symmetrical, the posterior petal differentiated from the lateral 4; petals pink, violet, or yellow, at least the anterior-lateral 2 abaxially sericeous. Stamens 10, all fertile, glabrous; filaments very stout opposite posterior-lateral petals, proximally connate; anthers \pm alike. Styles 3, free, subequal, erect or divergent, apex dorsally truncate or short-hooked, the stigma at internal angle. Fruit dry, breaking apart into 3 samaras separating from a high pyramidal torus; samara orbicular or transversely elliptical, the lateral wings cleft to nut at apex, usually confluent at base, each lateral wing with a complex structure comprising at least an outer membranous wing and a sterile cavity developed in its base, parallel to the fertile locule, during maturation of the fruit, and frequently bearing additional wings, winglets, crests, or irregular outgrowths between outer wing and central dorsal wing; dorsal wing often extended forward at apex between lateral wings; ventral areole narrowly elliptical or linear.



J. rosea (left), J. magnifica (right)

Distinctive features: Leaves with scalariform tertiary venation; at least the anterior-lateral petals abaxially sericeous; samara with complex lateral wings.

Distribution: Six species of Central America and northern South America.

LOPHOPTERYS A. Jussieu in Delessert, Icon. Sel. Pl. 3: 18. 1838 ["1837"].

Woody vines or shrubs (or small trees?). Leaves opposite or subopposite; stipules absent or vestigial, borne on adaxial edges of petiole 1–2 mm above base; petiole eglandular or bearing 1–7 pairs of small glands at various distances from base along adaxial edges; lamina mostly



eglandular, occasionally biglandular on margin at base; tertiary veins reticulate or scalariform. Inflorescence paniculate, rarely simple, the flowers ultimately borne in pseudoracemes; floriferous bract eglandular; pedicels sessile to pedunculate; bracteoles borne at apex of

peduncle (when present), eglandular. Sepals leaving petals exposed during enlargement of bud, the anterior eglandular, the lateral 4 each mostly bearing a single, very large, circular or

transversely elliptical gland (all sepals eglandular in some populations of *L. inpana*); glands sessile. Corolla bilaterally symmetrical, the posterior petal strongly differentiated from the lateral 4; petals bright yellow, glabrous or only very sparsely sericeous abaxially. Stamens 10, all fertile, glabrous; filaments longer opposite sepals, shorter opposite petals, 1/3-2/3 connate or only at base; anthers \pm alike. Styles 3, free, straight or nearly so, the anterior shorter than the posterior 2, the stigma at internal angle to nearly terminal. Fruit dry, breaking apart into 3 samaras separating from a short pyramidal torus; samara with 2 long, narrow, forward-pointing, parallel-sided lateral wings 3 or more times as long as wide; dorsal wing relatively short, inequilaterally trapezoidal or flabellate, with its greatest width toward base of nut (in *L. splendens* A. Juss. the lateral wings reduced to ridges or lost, and with a very short dorsal crest); ventral areole ovate to round.

Distinctive features: Lateral sepals with one large gland; samaras with two long forwardpointing, parallel-sided lateral wings and a short, inequilaterally trapezoidal or flabellate dorsal wing.

Distribution: Seven species in South America, south to about 23°S.

MALPIGHIODES Niedenzu, Verz. Vorles. Königl. Lyceum Hosianum Braunsberg 1909 (10): 31. 1909.



Woody vines. Stems cylindrical or nearly so, with dispersed xylem. Leaves opposite; stipules minute, triangular, borne on proximal half of petiole or at junction of petiole and stem, or apparently absent; petiole eglandular or bearing 2–8 small glands in 2 rows; lamina usually bearing few to many small glands impressed abaxially in 1-3 rows between midrib and margin; tertiary veins reticulate. Inflorescence a terminal or lateral compound dichasium or paniculate dichasium, strictly decussate, with the flowers borne in pairs or umbels or corymbs of 4 (–8);

floriferous bract eglandular; pedicels pedunculate; bracteoles broad and rounded (elliptical or

obovate), borne between middle and apex of peduncle, eglandular. Sepals valvate, completely concealing petals during enlargement of bud, revolute in anthesis, all 5 biglandular; glands sessile. Corolla bilaterally symmetrical, the posterior petal differentiated from the lateral 4; petals yellow turning red in age, glabrous. Stamens 10, all fertile; filaments opposite sepals slightly longer than those opposite petals, ca. 1/2-connate, glabrous or sparsely sericeous; anthers alike, glabrous. Styles 3, free, subequal, \pm straight, stout, apex truncate, the stigma terminal or nearly so. Fruit dry, breaking apart into 3 samaras separating from a prominent pyramidal torus; samara suborbicular or transversely elliptical (in *M. bracteosa* the mericarps with the wings reduced to coriaceous or corky outgrowths), the lateral wings membranous, cleft to nut at apex, continuous at base; dorsal wing free from lateral wing at base, extended forward at apex through gap in lateral wing; intermediate winglets none or 1–several seta-like structures as high as width of dorsal wing or smaller; ventral areole broadly ovate.



M. guianensis (left), M. bracteosa (right)

Distinctive features: Dichasial inflorescence; bracteoles broad and rounded; all five sepals biglandular; petals yellow becoming red in age.

Distribution: Four species of northern South America, in Amazonian Venezuela and Brazil, and the Guianas).

MASCAGNIA (Bertero ex DC.) Bertero in Colla, Hortus Ripul. 85. 1824, nom. cons. *Triopterys* Linnaeus, Sp. Pl. 428. 1853, nom. rej.

Woody vines, occasionally described as shrubby, two species climbing by rootlets (M.



M. lilacina (photo: T. F. Daniel)

almedae, M. vacciniifolia). Stems in some species with dispersed xylem, while regular or with phloem wedges in others. Leaves opposite; stipules small, distinct, triangular, or rarely connate in interpetiolar pairs, borne on stem beside petioles; petiole eglandular or biglandular at base or between base and apex; lamina in most species bearing glands abaxially; tertiary veins reticulate. Inflorescences elongated or occasionally congested pseudoracemes, single or grouped in panicles; floriferous bract eglandular;

pedicels pedunculate; bracteoles borne at various heights on peduncle, eglandular or one of each pair bearing one abaxial gland. Sepals leaving petals exposed during enlargement of bud, the anterior eglandular, the lateral 4 biglandular; glands sessile. Corolla bilaterally symmetrical, the posterior petal differentiated from the lateral 4; petals yellow, pink, white, or various shades of lilac, blue, or purple, glabrous. Stamens 10, all fertile; filaments connate at base, differing in size and shape, glabrous; anthers ± alike, glabrous or hairy. Styles 3, free, subequal or the anterior style shorter than the posterior 2, apex dorsally rounded, truncate, or short-hooked, the stigma at internal angle. Fruit dry, subtended by a fleshy 3-lobed disc, the disc sometimes much reduced, breaking apart into 3 samaras separating from a long pyramidal torus; samara mostly elliptical or orbicular (occasionally triangular), the lateral wings in most species continuous at base (divided to the nut in a few species) and entire to deeply cleft at the apex, sometimes strongly reduced or dissected, in a few species indented at the sides and Y-shaped (*"Triopterys"*); dorsal crest or winglet small or absent; ventral areole narrowly to broadly elliptical to ovate.



M. divaricata (left), M. lucida (center), M. violacea (right)

Distinctive features: Petiole gland, if present, at base or between base and apex; in most species with glands on the surface of the lamina (never marginal); flowers in pseudoracemes (never in umbels); bracteoles borne on peduncle at varying heights, often one bracteole of a pair with a large gland.

Distribution: Ca. 45 species, northern Mexico to northern Argentina and southeastern Brazil, Greater Antilles, and Bahamas.

MEZIA Niedenzu in Engler & Prantl, Nat. Pflanzenfam. III, 4: 58. 1890.

Woody vines, shrubs, or small trees. Stems with dispersed xylem. Leaves opposite;



M. angelica (photo: M. Pace)

stipules minute, borne on stem beside base of petiole, caducous; petiole eglandular; lamina bearing impressed glands on abaxial surface at base or eglandular; tertiary veins reticulate. Inflorescences tightly reddish or brown-sericeous throughout, axillary and terminal, containing much-reduced bract-like leaves, the flowers ultimately borne in an umbel of 4 terminating a stalk bearing 1 (–3) pairs of sterile bracts and, at its apex, 4 floriferous bracts subtending the 4 peduncles; floriferous bract eglandular; peduncles well developed, pedicels absent or rudimentary; bracteoles borne just below rudimentary pedicel and flower, the inner enclosing bud until anthesis, the outer enclosing bud and inner bracteole; old flowers (not setting fruit) deciduous at base of peduncle (not at joint between peduncle and pedicel). Sepals leaving petals exposed during enlargement of bud, narrowly oblong or spatulate, the anterior eglandular, the lateral 4 each with 2 distinct or partially to completely connate glands; glands sessile. Corolla bilaterally symmetrical, the posterior petal differentiated from the lateral 4; petals yellow, the posterior petal often red in center, glabrous or abaxially hairy. Stamens 10, all fertile, the 5 opposite sepals differing from the 5 opposite petals in size and shape of filaments and/or anthers; filaments 1/4–2/3 connate or only at base, glabrous to tomentose; anthers alike or not, glabrous to sparsely hairy to tomentose. Styles 3, free, the anterior style shorter and often slenderer than the posterior two, stout and mostly erect or slender and lyrate to sigmoid, the apex dorsally truncate, short-hooked, rounded, or pedaliform, the stigma at internal angle. Fruit dry, breaking apart into 3 samaras separating from a short pyramidal torus; samara orbicular (butterfly-shaped



M. curranii (left), *M. mariposa* (right)

in *M. mariposa*), the membranous lateral wings cleft to nut at apex and confluent at base (except in *M. mariposa*); dorsal wing present, and

often additional wings, winglets, or crests developed between dorsal and lateral wings or outside lateral wings; ventral areole ovate or broadly to narrowly elliptical.

Distinctive features: Large bracteoles enclosing flower bud; rudimentary pedicel; abscission of old flowers at base of peduncle; orbicular samaras (3-) 5–11 cm in diameter (except *M. mariposa*).

Distribution: Fifteens species of South America, with one (*M. includens*) extending into Panama.

NIEDENZUELLA W. R. Anderson, Novon 16: 190. 2006.

Woody vines, sometimes shrubby. Stems cylindrical, with regular growth or phloem wedges. Stipules very small, triangular or subulate, borne on petiole at base or distally, as high as



N. stannea

middle of petiole, persistent, sometimes absent. Petiole eglandular or with 2–4 or more glands; lamina eglandular or bearing few to many small glands on margin; tertiary veins reticulate. Inflorescence a terminal or axillary panicle, the ultimate branches short pseudoracemes with 2–30 flowers, the flowers mostly strictly decussate, occasionally subopposite distally; floriferous bracts eglandular or biglandular; pedicels pedunculate to sessile; bracteoles borne at apex of peduncle or slightly below, usually eglandular, rarely with 1 or 2 small glands. Sepals long and imbricated, mostly concealing petals throughout enlargement of bud (separating to expose petals in bud in a few species), strongly revolute at anthesis, the anterior eglandular, the lateral 4 biglandular, or all 5

eglandular. Corolla bilaterally symmetrical to nearly radial, the posterior petal with its claw usually somewhat longer or thicker than the 4 lateral petals; petals bright yellow, glabrous or abaxially thinly sericeous. Stamens 10, all fertile; filaments connate at base, alike or the 2 opposite the posterior-lateral petals thicker than others, glabrous or abaxially sericeous; anthers \pm alike, glabrous or sericeous. Styles 3, free, alike, straight and erect to distally spreading or recurved, apex dorsally rounded or truncate, the stigma at internal angle to nearly terminal. Fruit dry, breaking apart into 3 samaras or 3 mericarps with all wings more or less reduced or rudimentary and replaced by crests or irregular outgrowths, the samaras/mericarps separating



from a flat or shortpyramidal torus; samara (when not reduced) butterfly-

N. stannea (left), N. multiglandulosa (center), N. acutifolia (right)

shaped or X-shaped, the lateral wings chartaceous, cleft to nut at apex and base, each side trapezoidal with the margin coarsely toothed or sometimes deeply and irregularly lobed, or

divided to the nut into 2 elongated, 6 parallel-sided wings; dorsal wing or crest small, distinct from lateral wings, often extended forward at apex between lateral wings; irregular outgrowths present between dorsal and lateral wings in some species; ventral areole ovate.

Distinctive features: Stipules borne on petiole; sepals longer than petals and imbricated in bud, strongly revolute in anthesis; samaras butterfly-shaped or X-shaped.

Distribution: 16 species, Central and South America.

PEIXOTOA A. Jussieu in A. St.-Hilaire, Fl. Bras. Merid. 3: 59. 1833 ["1832"].

Shrubs, subshrubs, or vines. Stems cylindrical or nearly so, xylem with conspicuous wide rays or deep phloem wedges. Leaves opposite; stipules borne on stem beside petioles, much



P. reticulata (photo: W. R. Anderson)

enlarged, each pair of stipules from opposite leaves connate to form a large cordate "stipule," with the 2 stipule-pairs at each node acting as valvate bud scales enclosing the vegetative tip or the 4 flower buds of an umbel until they emerge, eventually deciduous and leaving wide scars across the node; petiole eglandular; lamina bearing glands on abaxial surface between midrib and margin; tertiary veins reticulate. Inflorescences terminal and/or axillary, flowers borne in umbels of 4 (8 in *P. octoflora*) and variously grouped in compound inflorescences; floriferous bract and bracteoles

eglandular, usually present and persistent but very small, or absent; pedicels usually sessile (short-pedunculate in *P. octoflora*). Sepals valvate, concealing petals during enlargement of bud, recurved or revolute in anthesis, the anterior eglandular, the 4 lateral biglandular; glands sessile. Corolla bilaterally symmetrical, the posterior petal strongly differentiated from the lateral 4 and much smaller; petals yellow, glabrous. Stamens 10, glabrous, the five opposing the petals fertile, stamens opposite sepals sterile; filaments unequal, connate at base; anthers of fertile stamens alike; staminodes with a large apical gland (a modified sterile connective), these differing in size and shape and in length of adaxial groove. Styles 3, free, divergent, glabrous, the anterior \pm different from posterior 2 in length, thickness, and stance, the stigma usually terminal and capitate, in *P. jussieuana* and *P. magnifica* the stigma of the anterior style oblong and borne on

the abaxial surface at the apex of a long, strongly curved style. Fruit dry, breaking apart into 3 samaras borne on a pyramidal torus; dorsal wing of samara well developed, elongated, thickened on the adaxial margin; nut ovoid, usually bearing 2 much smaller lateral winglets, one on each side (winglets absent or much reduced in *P. hatschbachii*); ventral areole ovate.



P. cordistipula (photo: W. R. Anderson)

Distinctive features: Large cordate stipules; ultimate inflorescence unit a 4-flowered umbel; pedicels sessile; androecium of fertile stamens alternating with staminodes; samara with one lateral winglet on each side of nut (except *P. hatschbachii*).

Distribution: 29 species of southeastern Brazil and adjacent Bolivia and Paraguay.

PSYCHOPTERYS W. R. Anderson & S. Corso, Contr. Univ. Michigan Herb. 25: 116. 2007. Woody vines, occasionally described as shrubs or small trees. Leaves opposite; petiole



P. dipholiphylla

usually with 2 glands between middle and apex, occasionally eglandular; stipules minute, triangular, borne on petiole at or slightly

above base or on stem beside base of petiole, occasionally absent; lamina eglandular or rarely biglandular on margin at very base; tertiary veins reticulate. Inflorescences axillary and terminal,



P. dipholiphylla

paniculate, open and many-flowered, the flowers ultimately borne in pseudoracemes; floriferous bract eglandular; pedicels sessile; bracteoles borne at apex of peduncle, eglandular. Sepals leaving petals exposed during enlargement of bud, all eglandular. Corolla radially symmetrical or nearly so; petals subequal, white, spreading to (usually) strongly reflexed during anthesis. Stamens 10, all fertile; filaments longer opposite sepals than opposite petals or subequal, glabrous, very briefly connate at base; anthers \pm alike, mostly glabrous but rarely abaxially sparsely sericeous. Styles 3, alike or 1 shorter than the other 2, of uniform diameter, truncate or slightly capitate, the stigma terminal or slightly at internal angle. Fruit dry, breaking apart into 3 samaras separating from a short pyramidal torus; samara butterfly-shaped, the lateral wings cleft to nut at apex and base; dorsal wing small to absent; intermediate outgrowths absent or present; ventral areole orbicular to ovate.

Distinctive features: Flowers radially symmetrical; sepals eglandular; petals white, reflexed.

Distribution: Eight species; southern Mexico, Guatemala, and Belize.

STIGMAPHYLLON A. Jussieu in A. St.-Hilaire, Fl. Bras. Merid. 3: 48. 1833 ["1832"] Woody or herbaceous vines, a few species shrubs. Stems cylindrical or lobed and flattened, with regular growth or interxylary cambia. Leaves opposite or rarely alternate; stipules



S. jatrophifolium (photo: W. R. Anderson)

triangular, borne on stem beside base of petiole, distinct or sometimes connate across the node into a bifid structure; in *S. calcaratum* each stipule a gland with a minute triangular tip; petiole mostly long, usually bearing 2 large glands at apex, these sometimes just above petiole on base of lamina, or sometimes glands absent; lamina eglandular, or with glands on margin or just within margin on the abaxial surface; tertiary veins reticulate. Inflorescence axillary and terminal, flowers grouped in an umbel or pseudoraceme, these sometimes solitary but more commonly borne in dichasia or compound dichasia or small thyrses; floriferous



S. florosum (photo: M. Pace); S. sinuatum (photo: P. Acevedo); S. paralias (photo: W. R. Anderson)

bract eglandular; pedicels usually pedunculate, peduncles sometimes reduced or rudimentary; bracteoles borne at apex of peduncle, eglandular or with (1–) 2 glands. Sepals mostly leaving petals exposed during enlargement of bud, the anterior eglandular or rarely biglandular, the lateral 4 biglandular; glands sessile. Corolla bilaterally symmetrical, the posterior petal strongly differentiated from the lateral 4; petals yellow or yellow marked with red, glabrous or rarely abaxially sparsely sericeous. Stamens 10; filaments unequal, proximally connate; anthers glabrous or pubescent, subequal in several species, in most species very unequal, the 4 opposite the lateral sepals often with reduced locules or sometimes sterile and the 1 opposite the posterior petal often small. Styles 3, free, glabrous or pubescent, the anterior shorter (longer in a few species) than the posterior two, erect or slightly recurved, apex with two equal lateral folioles or only laterally expanded or linear and distally blunt or distally extended into a spur or hook; posterior styles mirror images of each other, lyrate or sometimes erect, apex with a lateral foliole or lip or linear and distally blunt or distally extended into a spur or hook, the stigma at internal angle. Fruit dry, breaking apart into 3 samaras separating from a pyramidal torus; in most species samara with a well-developed dorsal wing thickened on the adaxial margin; nut spherical or ovoid (lenticular in S. ciliatum), with small lateral winglets and/or spurs and/or crests or only prominently ribbed or smooth (in S. calcaratum the nut covered with numerous bulbous and warty excrescences composed of spongy tissue), rarely the dorsal wing reduced or a crest (e.g., S. *bannisterioides, S. calcaratum*); ventral areole orbicular to elliptical or ovate or triangular.

Distinctive features: Long petioles with a pair of large glands at apex; inflorescences dichasial; style apex foliolate or with a hook or spur; stigma at internal angle.

Distribution: 117 species; 95 species in subg. *Stigmaphyllon* in the New World: southern Mexico and the Caribbean to northern Argentina, one species (*S. bannisterioides*) also established in coastal West Africa; 22 species in subg. *Ryssopterys* in the Old World.

TETRAPTERYS Cavanilles, Diss. 9: 433. 1790.

Vines or shrubs, occasionally described as small trees. Stems cylindrical, with regular



T. goudotiana (photo: T. F. Daniel)

xylem, sometimes with red latex. Leaves opposite; stipules small, triangular, distinct or connate across the node or epipetiolar, apparently sometimes absent; petiole eglandular or with 2 glands; lamina bearing glands on the abaxial surface, or with a few to many small glands on margin, or eglandular; tertiary veins reticulate. Inflorescence terminal or axillary, flowers borne in umbels, corymbs or pseudoracemes, these often grouped in panicles; floriferous bract eglandular; pedicels pedunculate; bracteoles borne at apex of peduncle or slightly below, eglandular or glandular, sometimes larger than floriferous bract. Sepals leaving petals exposed during enlargement of bud, the anterior eglandular and the lateral 4

biglandular, or all 5 biglandular, or sometimes all 5 eglandular. Corolla bilaterally symmetrical, the posterior petal strongly differentiated from the lateral 4; petals yellow or yellow turning orange or red in age or marked with red, mostly glabrous or abaxially sericeous. Stamens 10, all fertile; filaments connate at base, differing in length, glabrous or abaxially sericeous; anthers \pm alike, usually glabrous. Styles 3, free, alike, straight and erect to spreading, apex dorsally rounded or truncate or short-hooked; stigma terminal or at internal angle. Fruit dry, breaking

apart into 3 samaras, these commonly X-shaped or sometimes butterfly-shaped, each samara having its largest wings lateral, usually 4 discrete wings; dorsal wing smaller, sometimes reduced to a crest or lost; intermediate winglets or outgrowths sometimes present; all wings reduced to rudimentary outgrowths in a few species; ventral areole ovate.



a. T. styloptera, b. T. tinifolia, c. T. ramiflora, d. T. gracilis

Distinctive features: Stipules connate across the node in some species; samaras X-shaped or butterfly-shaped.

Distribution: Ca. 80 species, from Mexico and the West Indies to Argentina.

THRYALLIS Martius, Nov. Gen. Sp. Pl. 3: 77. 1829.

Scandent shrubs and woody vines; vegetative hairs stellate. Leaves opposite; stipules



T. longifolia (photo: W. R. Anderson)

minute, narrowly triangular, borne on petiole at base; leaves bearing 1 or 2 pairs of glands at apex of petiole and/or on base of lamina. Inflorescences terminal and lateral, flowers borne (sub) opposite on axis, grouped in in dichasia, compound dichasia, or thyrses; floriferous bract eglandular; pedicels short-pedunculate or subsessile; bracteoles borne at apex of peduncle, eglandular. Sepals imbricated and completely concealing petals in enlarging bud, eglandular, reflexed to revolute

in anthesis, elongating and becoming stiff and spreading

in fruit. Corolla bilaterally symmetrical, the posterior petal slightly smaller than the lateral 4;

petals lemon-yellow, glabrous, the limb wider than long. Stamens 10, all fertile, glabrous; filaments alike, proximally connate; anthers slightly longer opposite sepals than opposite petals. Styles (2–) 3, free, slender, erect, the anterior slightly longer than the posterior 2, the stigma terminal, capitate but somewhat reflexed abaxially and briefly decurrent adaxially. Fruit dry, probably dispersed intact with the enlarged wing-like sepals, tardily schizocarpic into (2–) 3 small nutlets; nutlet rugose, with a prominent dorsal ridge or rudimentary winglet.



T. longifolia

Distinctive features: Vesture stellate; stipules epipetiolar; sepals persistent, stiff and spreading, subtending the fruit; mericarp a rugose nutlet.

Distribution: Five species; Brazil and adjacent Paraguay and Bolivia.

RELEVANT LITERATURE

- Almeida, R. F. de. 2018. Taxonomic revision of *Amorimia* W. R. Anderson (Malpighiaceae). Hoehnea 45: 238–306.
- Amorim, A. M. 2003. The anomalous-stemmed species of *Heteropterys* subsect. *Aptychia* (Malpighiaceae). Brittonia 55: 127–145.
- Anderson, C. 1982. A monograph of the genus *Peixotoa* (Malpighiaceae). Contr. Univ. Michigan Herb. 15: 1–92.
- Anderson, C. 1995. Revision of *Thryallis* (Malpighiaceae). Contr. Univ. Michigan Herb. 20: 3–14.
- Anderson, C. 1997. Monograph of *Stigmaphyllon* (Malpighiaceae). Syst. Bot. Monogr. 51: 1–313.

- Anderson, C., and W. R. Anderson. 2018 [in press]. Revision of *Mezia* (Malpighiaceae). Edinburgh Journal of Botany.
- Anderson, W. R. 1980. *Ectopopterys*, a new genus of Malpighiaceae from Colombia and Peru. Contr. Univ. Michigan Herb. 14: 11–15.
- Anderson, W. R. 1981. Malpighiaceae. In: The botany of the Guayana Highland—Part XI, ed. B. Maguire. Mem. New York Bot. Gard. 32: 21–305.
- Anderson, W. R. 1988. Malpighiaceae. In: Flora of the Lesser Antilles, ed. R. A. Howard, 4: 596–633.
- Anderson, W. R. 1990a. The taxonomy of *Jubelina* (Malpighiaceae). Contr. Univ. Michigan Herb. 17: 21–37.
- Anderson, W. R. 1997. *Excentradenia*, a new genus of Malpighiaceae from South America. Contr. Univ. Michigan Herb. 21: 29–36.
- Anderson, W. R. 2006. Eight segregates from the neotropical genus Mascagnia (Malpighiaceae). Novon 16: 168–204. [Adelphia, Aenigmatanthera, Alicia, Amorimia, Carolus, Christianella, Malpighiodes, Mascagnia, Niedenzuella]
- Anderson, W. R., and S. Corso. 2007. *Psychopterys*, a new genus of Malpighiaceae from Mexico and Central America. Contr. Univ. Michigan Herb. 25: 113–135.
- Anderson, W. R., and C. C. Davis. 2001. Monograph of *Lophopterys* (Malpighiaceae). Contr. Univ. Michigan Herb. 23: 83–105.
- Anderson, W. R., and C. C. Davis. 2006. Expansion of *Diplopterys* at the expense of *Banisteriopsis* (Malpighiaceae). Harvard Pap. Bot. 11: 1–16.
- Anderson, W. R., and C. C. Davis. 2007. Generic adjustments in neotropical Malpighiaceae. Contr. Univ. Michigan Herb. 25: 137–166. [*Bronwenia, Calcicola, Cottsia*]
- Anderson, W. R., and C. C. Davis. 2013. Combination of *Mascagnia* and *Triopterys*. Mem. New York Bot. Gard. 108: 191–203.
- Anderson, W. R., and B. Gates. 1981. *Barnebya*, a new genus of Malpighiaceae from Brazil. Brittonia 33: 275–284.
- Buchmann, S. L. 1987. The ecology of oil flowers and their bees. Ann. Rev. Eco. Syst. 18: 343–369.
- Cabanillas, P. A., M. R. Pace, and V. Angyalossy. Structure and ontogeny of the fissured stems of *Callaeum* (Malpighiaceae). IAWA J. 38: 49-66.

- Chase, M. W. 1981. A revision of *Dicella* (Malpighiaceae). Syst. Bot. 6: 159–171.
- Cuatrecasas, J. 1958. Prima Flora Colombiana. Malpighiaceae. Webbia 13: 343-664.
- Davis, C. C., and W. R. Anderson. 2010. A complete generic phylogeny of Malpighiaceae inferred from nucleotide sequence data and morphology. Amer. J. Bot. 97: 2031–2048.
- Gates, B. 1982. Banisteriopsis, Diplopterys (Malpighiaceae). Fl. Neotropica 30: 1-238.
- Johnson, D. M. 1986. Revision of the neotropical genus *Callaeum* (Malpighiaceae). Syst. Bot. 11: 335–353.
- Jussieu, Adr. de. 1843. Monographie de la famille des Malpighiacées. Arch. Mus. Hist. Nat. 3: 5–151, 255–616, pl. 1–23.
- Niedenzu, F. 1888–94. Malpighiaceae. In: Die Natürlichen Pflanzenfamilien, ed. A. Engler and K. Prantl; 3(4): 41–48 (1888), 3(4): 49–74 (1891), 3(4): 352–353 (1894); supplements in Nachträge zum II.–IV. Teil, pp. 205–207 (1897) and Nachträge III, Ergänzungshefte II, pp. 182–186 (1906).
- Niedenzu, F. 1928. Malpighiaceae. In: A. Engler (ed.), Das Pflanzenreich IV, 141 (Heft 91, 93, 94): 1–870.
- Pace, M. R. 2015. Evolution of the vascular system in lineages that contain lianas. Doctoral Dissertation. University of São Paulo, Brazil.
- Pace, M. R., P. Acevedo-Rodríguez, A. M. Amorim, and V. Angyalossy. 2018. Ontogeny, structure and occurrence of interxylary cambia in Malpighiaceae. Flora 241: 46-60.
- Sebastiani, R., and M. C. H. Mamede. 2010. Estudos taxonômicos em *Heteropterys* subsect. *Stenophyllarion* (Malpighiaceae) no Brasil. Hoehnea 37: 337–366.