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## MALPIGHIACEAE

by William R. Anderson

Trees, shrubs, and vines, always perennial; hairs unicellular, usually medifixed or submedifixed. Leaves usually opposite, often bearing large multicellular glands on the petiole or blade (usually the abaxial side) or both; stipules usually present; blade simple, usually entire, rarely lobed or pseudodentate. Flowers usually bisexual, subtly to strongly bilaterally symmetrical. Sepals 5, eglandular or, most often, the lateral 4 or all 5 bearing (1)2 large multicellular abaxial glands; petals 5, distinct, clawed, alternating with the sepals, imbricate, the innermost (flag) petal posterior and often different from the lateral 4. Stamens mostly 10, fewer by reduction in some genera; anthers mostly dehiscent by longitudinal slits. Gynoecium superior, comprising (2)3 distinct to connate carpels, each fertile locule containing 1 pendent anatropous ovule; styles mostly 1 per carpel and distinct, sometimes connate or reduced in number. Fruits dry or fleshy, dehiscent or indehiscent, samaroid, nut-like, or drupaceous. Seeds without endosperm.

Tropics and subtropics (mostly between 30°N and 35°S, mostly New World but also found in the Old World, especially Africa and Madagascar); about 67 genera with over 1250 species, 23 genera and 153 species in the flora area.

Much of this treatment is modified from my paper on the Malpighiaceae of the Guayana Highland (Mem. New York Bot. Gard. 32: 21–305. 1981), which contains full descriptions of many of these species. Successful use of the keys to genera and species requires an understanding of what I mean by certain morphological terms. The ancestral inflorescence of the Malpighiaceae was a raceme of cincinni, but in many genera the cincinni have been reduced to one-flowered units. Each flower is borne on a *pedicel*, whose base is defined by a joint; below the joint the stalk is called the *peduncle*, and the peduncle bears two *bracteoles*, which can be borne anywhere on the peduncle but are most commonly at or near its summit; the peduncle is subtended by a single *bract*. The peduncle has been lost in several evolutionary lines, in which case the pedicel is described as sessile, subtended then by a cluster of the bract and two bracteoles.

The Malpighiaceae are notable for having highly stereotyped flowers (5 sepals mostly with paired abaxial glands on at least the lateral 4 in the New World, 5 clawed petals, mostly 10 stamens, mostly 3 carpels with distinct styles), and as a consequence identification to genus of flowering specimens can be difficult. Understanding the variation in styles and stigmas, and the terminology used to describe that variation, is essential. Most byrsonimoid genera (*Blepharandra*, *Burdachia*, *Byrsonima*, *Diacidia*, *Glandonia*, *Lophanthera*, and *Pterandra* in the flora area) have *subulate* styles, i.e., slender styles that taper gradually distally to minute stigmas (♦Fig. 71, A–C). In most cases the stigma is *terminal* on the style but in some species it is slightly *internal*, i.e., the stigmatic tissue is on the internal angle of the style apex. In all other genera in the flora area the styles are less tapered distally, such that the stigmas are larger, and their position is correspondingly easier to discern. Some of those genera have the stigmas *terminal* or nearly so, i.e., the stigmatic tissue is distributed ± evenly over the entire apex of the style. Our genera with consistently terminal stigmas on thick styles are *Banisteriopsis*, *Bunchosia*, *Diplopterys*, and *Spachea*, but similar styles also occur in some species of *Heteropterys*, *Malpighia*, *Mascagnia*, and *Tetrapteryx* (♦Fig. 71, D–F; see also figures of *Diplopteryx cabrerana* and *Spachea elegans* below). The rest of our Malpighiaceae, including all or most species of *Clonodia*, *Dicella*, *Excentradenia*, *Heteropterys*, *Hiraea*, *Jubelina*, *Lophopterys*, *Malpighia*, *Mascagnia*, *Mezia*, *Stigmaphyllon*, and *Tetrapteryx*, have the styles stigmatic on the internal angle of the apex; in the descriptions below these are called *internal stigmas* (♦Fig. 71, G–L; see also figures of *Dicella julianii*, *Excentradenia adenophora*, *Hiraea faginea*, and *Mezia huberi* below). Dorsally the apex of those styles is variable, and that variation has great systematic utility. Such a style tip may be dorsally rounded, truncate, acute, apiculate, or extended into a hook, and in *Stigmaphyllon* that extension often bears flap-like lateral outgrowths called folioles.

In contrast to their relatively uniform flowers, the fruits of Malpighiaceae are exceedingly diverse. Much of that diversity is represented in this flora. The principal dispersal agents for our Malpighiaceae are birds, wind, and water, but a few fruits have no obvious adaptation for dispersal. Three genera of shrubs and trees, representing different clades in the family, have independently evolved fleshy bird-dispersed fruits ranging in size from a pea to a small plum; they are *Bunchosia*, *Byrsonima*, and *Malpighia*. No one has ever actually studied their dispersal, so my statement that they are dispersed by birds represents an assumption, and it is possible that small mammals are also involved. Among the many genera of vines, most of which probably share a common ancestor, the usual fruit is a dry schizocarp, with

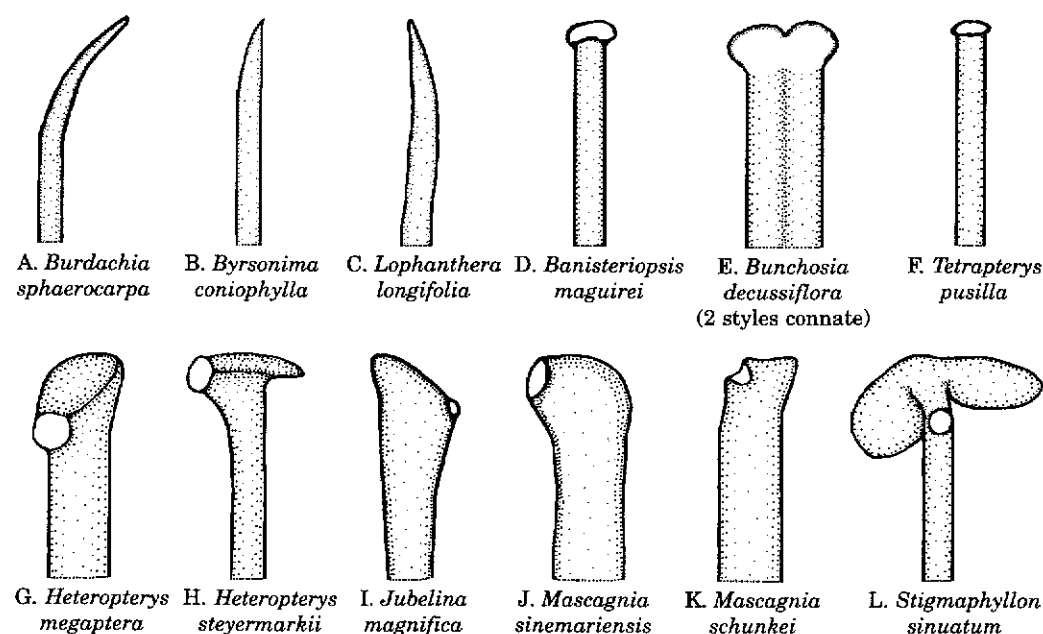


Fig. 71. Malpighiaceae styles and stigmas

each mericarp being a wind-dispersed samara. Two basic types of samaras have evolved, probably representing two aerodynamically optimal designs. Samaras with a single dorsal wing (the maple type) are found in *Banisteriopsis*, *Heteropteryx*, and *Stigmaphyllon*. Samaras with lateral wings, like that of elm, plus many variations, occur in *Excentradenia*, *Hiraea*, *Jubelina*, *Lophopteryx*, *Mascagnia*, *Mezia*, and *Tetrapteryx*. There are also two other types of wind-dispersed fruits in (or expected in) our flora. *Diacidia* is a genus of shrubs and trees in which the fruit proper is a tiny indehiscent nut without any adaptation for dispersal, but in all species except one (which is probably closest to the ancestor of the group) the sepals grow into dry veiny wings as the fruit matures and presumably aid in dispersal. Something similar happens in *Dicella*, a woody vine with a much larger nut-like fruit subtended at maturity by much-enlarged spreading wings derived from the sepals. The latter two genera are not closely related to each other or the samara-bearing genera; their adaptations for dispersal by wind clearly represent independent innovations. As might be expected in an area with extensive rivers, dispersal by water is common, both as the ancestral method and as a secondary adaptation in plants whose relatives are mostly dispersed by wind. *Lophanthera* is a genus of riparian trees in which the schizocarpic fruit breaks apart into small dry unwinged cocci half-filled with aerenchyma. *Spachea* is a related genus, probably sister to *Lophanthera*, and while the cocci are not as obviously adapted for floating, it seems probable that they are at least partially dispersed by water. *Burdachia* and *Glandonia* are sister genera of trees, in both of which the fruit is a relatively large, indehiscent, corky or fibrous nut, beautifully adapted for dispersal by water; all their species grow in lowland forests near water. Then there are the vines and shrubs that are obviously derived from groups with samaras. *Clonodia* and *Diplopteryx* are small genera in which the large wings of their ancestors have been replaced by crests and ruffles that probably help

the mericarps float by increasing the surface area and trapping air; *Diplopteryx* is clearly derived from *Banisteriopsis*, while *Clonodia* probably originated in either *Heteropteryx* or *Mascagnia*. Almost all the larger genera of samara-producing vines contain one or more species in which the samaras have had the principal wing(s) reduced or lost, often augmented by new supernumerary winglets or various kinds of aerenchyma or air-filled chambers. In our flora, that tendency is well developed in species of *Heteropteryx*, *Hiraea*, *Jubelina*, *Mezia*, *Stigmaphyllon*, and *Tetrapteryx*. Finally, there are a few groups in which the fruits seem to have no obvious adaptation for dispersal. *Pterandra* is a genus of trees and shrubs in which the distinct carpels grow into small dry indehiscent cocci without wings or flesh, although the areole may be surrounded by spongy tissue (see C. Anderson's revision, cited below under *Pterandra*). They are probably dispersed by water or by wind with other small bits of detritus. Given the nature of its fruits, the genus has achieved an impressive distribution, from Panama to southern Brazil, and an endemic species occurs at 1500 m on Cerro Sipapo in our area; one wonders how it got there! In *Blepharandra* and *Diacidia galphimiioides* the fruit is a tiny indehiscent nut without wings, flesh, or aerenchyma. These fruits also seem likely to be dispersed by wind with detritus. If the fruit were retained in the old flower the whole unit might aid dispersal by wind, but my observations on *B. hypoleuca* indicate that the fruits fall out and collect under the plant. The more derived species of *Diacidia* (*Sipapoa* sensu Maguire) have the sepals enlarged as an adaptation for dispersal by wind.

In addition to the 23 genera treated here, there are two additional genera at 1000 m or higher on the Serra Aracá of Amazonas, Brazil, either or both of which may eventually be found in the Venezuelan Guayana. These are *Acmanthera* (A. Juss.) Griseb. and *Verrucularia* A. Juss. Both are shrubs or trees with eglandular leaves and bracteoles, slender subulate styles, and unwinged fruits, so they will come out with *Blepharandra*, *Byrsonima*, *Diacidia*, and *Pterandra* in the keys to genera. In both *Acmanthera* and *Verrucularia* the inflorescence is an unbranched thyrse or pseudoraceme, corymbose or elongated, terminating a main axis or a lateral axis with one pair of leaves. *Acmanthera* has the outer anther locules winged for their whole length, white or pink petals, sessile pedicels, and deciduous stipules 15–110 mm long with the four at a node coherent or connate to form a sheath. In *Verrucularia* the outer anther locules bear a line or cluster of vesicular outgrowths toward the apex, the petals are yellow, the pedicels are pedunculate, and the persistent stipules are up to 2 mm long and distinct or basally connate. There is one species each of *Acmanthera* and *Verrucularia* on Serra Aracá. *Acmanthera parviflora* W.R. Anderson is described in my revision of the genus (Contr. Univ. Michigan Herb. 11: 41–50. 1975), and *Verrucularia piresii* W.R. Anderson is described in my 1981 paper on the Guayana Highland, cited above.

## Key to the Genera of Malpighiaceae based on flowering material

1. Styles slender and subulate, tapering to minute stigmas; shrubs or trees ..... 2
1. Styles slender to stout, of uniform thickness or widened at apex, the stigmas large; vines, shrubs, or trees ..... 8
- 2(1). Leaves bearing large glands on petiole or abaxial surface of blade; some bracteoles often bearing large apical or abaxial glands ..... 3

2. Leaves and bracteoles eglandular (except for tiny pellucid dots in blade and gland-tipped marginal teeth or cilia on bracts and bracteoles in some species) ..... 5
- 3(2). Anthers with 2 dark longitudinal wings on outer locules; carpels connate only along a narrow central axis, separating in fruit ..... 15. *Lophanthera*
3. Anthers unwinged; carpels broadly and persistently connate ..... 4
- 4(3). Stipules connate intrapetiolarly, persistent; flower buds spheroidal; connective of anthers enlarged, greatly exceeding the apically rounded locules; filaments glabrous ..... 4. *Burdachia*
4. Stipules connate interpetiolarly, caducous, leaving a large interpetiolar scar; flower buds pyramidal; connective of anthers exceeded by extensions of the apically tapered locules; filaments densely hirsute ..... 11. *Glandonia*
- 5(2). Inflorescence a tight umbellate fascicle, sessile or subsessile, axillary to leaves or bracts or leaf scars on older stems; carpels distinct; petals abaxially sericeous, at least on claw ..... 20. *Pterandra*
5. Inflorescence an elongated terminal thyrse or pseudoraceme; carpels connate, at least in flower; petals glabrous or rarely bearing a few hairs ..... 6
- 6(5). Anthers glabrous or bearing medifixed or submedifixed hairs, the apex without specially modified or directed hairs; hairs on leaves (if any) mostly medifixed or submedifixed or branched, rarely basifixed or sub-basifixed ..... 5. *Byrsonima*
6. Anthers bearing few to many basifixed awns or hairs, the apical ones  $\pm$  stiff and directed slightly forward; hairs on leaves (if any) mostly basifixed or sub-basifixed ..... 7
- 7(6). Petals all yellow; anthers with 2(-4) stout apical awn-like hairs, these strongly differentiated from other hairs on stamen, if any; stamens 6-10; ovary with only 2 locules developed and containing ovules ..... 7. *Diacidia*
7. Petals white and/or pink, or 4 white and the posterior pale yellow; anthers with apical hairs hardly or not at all different from other hairs on stamen; stamens 10; ovary with all 3 locules fertile, except in some populations of *B. fimbriata* (a few pink-flowered species of *Byrsonima* have anthers that mimic those of *Blepharandra*, from which they differ in having stipules connate to form an intrapetiolar pair, connective of anthers much exceeding fertile part of locules, and ovary sericeous at apex) ..... 2. *Blepharandra*
- 8(1). Petals pink or rose and/or white, or lilac ..... 9
8. Petals yellow, or yellow with a red central blotch or red flecks, or yellow turning red, or brownish ..... 15
- 9(8). Stipules large, 3-6 mm long, intrapetiolar and completely connate; leaf blades bearing 2-4 impressed glands in adaxial surface near apex ..... 21. *Spachea*
9. Stipules small, up to 2 mm long, interpetiolar or borne on base of petiole, distinct; leaf blades without adaxial glands ..... 10
- 10(9). Inflorescence an unbranched axillary umbel or corymb; shrubs or small trees ..... 17. *Malpighia*

10. Inflorescence an elongated pseudoraceme or compound panicle or cyme, or if an axillary corymb the plant a vine; woody vines or shrubs ..... 11
- 11(10). Petals (at least the lateral 4) with a prominent abaxial wing ..... 12
11. Petals abaxially smooth or at most carinate ..... 13
- 12(11). Ultimate units of inflorescence tight corymbs or umbels of 4-10 flowers ..... 12. *Heteropterys*
12. Ultimate units of inflorescence elongated pseudoracemes comprising (15-)20-50 flowers ..... 6. *Clonodia*
- 13(11). Styles with stigmas quite terminal and without any sort of dorsal extension at apex ..... 1. *Banisteriopsis*
13. Styles with apex stigmatic on internal angle and dorsally rounded, truncate, acute, or extended into a hook ..... 14
- 14(13). Calyx with 1 large central gland on each of the 4 lateral sepals, the anterior sepal eglandular; ultimate units of inflorescence umbels of 4 flowers or corymbs of 6; bracts and bracteoles 4-8 mm long ..... 14. *Jubelina*
14. Calyx with the 4 lateral sepals biglandular, the anterior eglandular; ultimate units of inflorescence pseudoracemes of (4-)7-50 flowers; bracts and bracteoles up to 3 mm long, mostly smaller ..... 18. *Mascagnia*
- 15(8). Styles with stigmas quite terminal and without any sort of dorsal extension at apex ..... 16
15. Styles with apex stigmatic on internal angle and dorsally rounded, truncate, acute, or extended into a hook or flap-bearing appendage ..... 23
- 16(15). Petals completely concealed by sepals during enlargement of bud, emerging only when flower opens ..... 18. *Mascagnia*
16. Petals (at least the outermost) exposed during enlargement of bud ..... 17
- 17(16). Stipules borne on base of petiole; carpels 2 or 3, completely connate in ovary, developing into an indehiscent fleshy fruit; styles as many as carpels, distinct or connate and then apparently only 1; trees or shrubs ..... 3. *Bunchosia*
17. Stipules interpetiolar or absent; carpels 3, centrally connate in ovary, the fruit dry and schizocarpic; styles 3, distinct; vines or shrubs ..... 18
- 18(17). Calyx bearing 10 glands; bracteoles wider than floriferous bracts and often longer, often bearing marginal or abaxial glands ..... 23. *Tetrapteryx*
18. Calyx bearing 8(9) glands or eglandular; bracteoles as large as bracts or smaller, eglandular ..... 19
- 19(18). Petals abaxially sparsely to densely sericeous ..... 20
19. Petals glabrous ..... 21
- 20(19). Petals abaxially sparsely sericeous, long-fimbriate ..... 9. *Diplopteryx*
20. Petals abaxially densely sericeous, denticulate to lacerate ..... 1. *Banisteriopsis*
- 21(19). Pedicels sessile ..... 1. *Banisteriopsis*
21. Pedicels raised on peduncles 1-6 mm long ..... 22
- 22(21). Flowers borne ultimately in umbels of 4-6; leaf blades abaxially glabrous or very thinly sericeous to glabrate ..... 23. *Tetrapteryx*
22. Flowers borne ultimately in pseudoracemes of 6-25, the terminal 4 sometimes crowded into an umbel; leaf blades abaxially sparsely to densely sericeous ..... 1. *Banisteriopsis*
- 23(15). Bracteoles larger than bracts, globose-cymbiform, borne just below flower, enclosing bud until flower opens; pedicels absent or up to 2(-5)

- mm long in fruit, the peduncles well developed ..... 19. *Mezia*
23. Bracteoles mostly similar to bracts or smaller than them, if larger not enclosing bud until flower opens; pedicels well developed relative to peduncles ..... 24
- 24(23). Calyx with 1 large central gland on each of the 4 lateral sepals, the anterior sepal eglandular ..... 16. *Lophopterys*
24. Calyx with 2 glands on each of the 4 lateral sepals or on all 5 sepals, or all sepals eglandular ..... 25
- 25(24). Pedicels sessile ..... 26
25. Pedicels pedunculate ..... 29
- 26(25). Flowers borne ultimately in pseudoracemes of 2–13 ..... 18. *Mascagnia*
26. Flowers borne ultimately in umbels of 3–15 or more ..... 27
- 27(26). Stipules well developed, epipetiole, often subulate, usually borne at or beyond middle of petiole, if borne near base of petiole the stipules  $\geq 2.5$  mm long; inflorescences axillary ..... 13. *Hiraea*
27. Stipules none or very small and triangular, borne on or beside base of petiole, if borne on base of petiole the stipules  $< 1$  mm long; inflorescences terminal or axillary and terminal ..... 28
- 28(27). Petioles biglandular at base ..... 12. *Heteropterys*
28. Petioles biglandular at apex, or eglandular with glands on abaxial base of blade ..... 22. *Stigmaphyllon*
- 29(25). Petals abaxially  $\pm$  densely sericeous or tomentose ..... 30
29. Petals glabrous or at most very sparsely sericeous ..... 32
- 30(29). Full-sized styles 2, posterior, the anterior style often present as a short, slender rudiment; ovary with only the 2 posterior locules developed and fertile; anthers with locules densely hairy ..... 8. *Dicella*
30. Styles 3, equal or the anterior slightly shorter; ovary with all 3 locules developed and fertile; anthers glabrous or at most sericeous on connective ..... 31
- 31(30). Bracteoles eglandular or bearing a row of stalked marginal glands ..... 18. *Mascagnia*
31. One of each pair of bracteoles bearing 1 large eccentric abaxial gland ..... 23. *Tetrapteryx*
- 32(29). Sepals erect or appressed in anthesis ..... 33
32. Sepals revolute at apex in anthesis ..... 37
- 33(32). Apex of styles (2 or all 3) dorsally extended into a long hook or flap-bearing appendage ..... 22. *Stigmaphyllon*
33. Apex of all styles dorsally rounded, truncate, acute, or short-hooked ... 34
- 34(33). Flowers borne ultimately in elongated to congested pseudoracemes .... 35
34. Flowers borne ultimately in umbels of 4–6 ..... 36
- 35(34). Bracteoles smaller than bracts, borne well below apex of peduncle; lateral 4 sepals biglandular, anterior eglandular; carpels with 1 crest on each side ..... 18. *Mascagnia*
35. Bracteoles mostly larger than bracts, borne at or slightly below apex of peduncle; all 5 sepals biglandular; carpels with 2 (or more) crests on each side ..... 23. *Tetrapteryx*
- 36(34). Stipules none or borne on base of petiole; carpels smooth-sided ..... 12. *Heteropterys*

36. Stipules interpetiolar, distinct or connate; carpels with lateral crests, developing into lateral wings in fruit ..... 23. *Tetrapteryx*
- 37(32). Sepals all abaxially biglandular ..... 38
37. Sepals all eglandular or the lateral 4 biglandular and the anterior eglandular ..... 39
- 38(37). Petals completely concealed by sepals during enlargement of bud, emerging only when flower opens ..... 18. *Mascagnia*
38. Petals (at least the outermost) exposed during enlargement of bud ..... 23. *Tetrapteryx*
- 39(37). Petioles eglandular ..... 12. *Heteropterys*
39. Petioles biglandular ..... 40
- 40(39). Flowers borne ultimately in umbels of 4, sometimes with an additional pair of flowers borne below the terminal umbel ..... 41
40. Flowers borne ultimately in elongated to congested pseudoracemes .... 42
- 41(40). Petioles 1–4 mm long ..... 12. *Heteropterys*
41. Petioles 10–20 mm long ..... 10. *Excentradenia*
- 42(40). Petiole glands borne between middle and apex ..... 12. *Heteropterys*
42. Petiole glands borne at or slightly above base ..... 43
- 43(42). Mature leaf blades abaxially metallic-sericeous, the hairs so dense and appressed as to completely conceal epidermis; inflorescence compound, paniculate, the ultimate pseudoracemes containing 2–16 flowers; bracts eglandular or biglandular; bracteoles eglandular ..... 18. *Mascagnia*
43. Mature leaf blades abaxially sericeous to glabrescent, the hairs never dense enough to completely conceal epidermis; inflorescence simple, containing 20–60 flowers; bracts eglandular; 1 of each pair of bracteoles bearing 1 large eccentric abaxial gland ..... 12. *Heteropterys*

## Key to the Genera of Malpighiaceae based on fruiting material

1. Fruits themselves unwinged, the sepals sometimes accrescent or wing-like in fruit; fruits schizocarpic or indehiscent ..... 2
1. Fruits winged, the wings reduced in some species to winglets or dissected crests; fruits schizocarpic ..... 12
- 2(1). Fruits schizocarpic, the mericarps dry, or the carpels distinct even in flower ..... 3
2. Fruits indehiscent, dry or fleshy ..... 5
- 3(2). Leaves and bracteoles eglandular (except for tiny pellucid dots in leaf blades of some species) ..... 20. *Pterandra*
3. Leaves bearing large glands on petiole or abaxial surface of blade; some bracteoles often bearing large apical or abaxial glands ..... 4
- 4(3). Styles slender and subulate, the stigmas minute; anthers longitudinally winged; leaf blades without adaxial glands ..... 15. *Lophanthera*
4. Styles stout, truncate or subpeltate at apex; anthers unwinged; leaf blades bearing 2–4 impressed glands in adaxial surface near apex ..... 21. *Spachea*
- 5(2). Woody vines; sepals greatly enlarged in fruit, forming narrowly elliptic or obovate wings 20–55 mm long, these strongly unequal, the posterior 2 longest, the anterior shortest ..... 8. *Dicella*

5. Shrubs or trees; sepals accrescent or not in fruit but not longer than 13 mm, equal or subequal ..... 6
- 6(5). Leaves and bracteoles eglandular (except for gland-tipped marginal teeth or cilia on bracts and bracteoles in some species) ..... 7
6. Leaves bearing large glands on petiole or abaxial surface of blade; bracteoles eglandular or some bracteoles bearing large abaxial glands ..... 9
- 7(6). Fruits 4–15 mm diameter or larger, the stone covered by a fleshy exocarp; hairs on leaves, if any, mostly medifixed or submedifixed or branched, rarely basifixed or sub-basifixed ..... 5. *Byrsonima*
7. Fruits up to 3.5 mm diameter, dry at maturity, the stone covered by a very thin, nonfleshy coat; hairs on leaves (if any) mostly basifixed ..... 8
- 8(7). Fruits with only 2 locules; anthers with 2(–4) stout apical awn-like hairs, these strongly differentiated from other hairs on stamen, if any; sepals slightly to greatly accrescent in fruit ..... 7. *Diacidia*
8. Fruits with up to 3 fertile locules (only 2 in some populations of *B. fimbriata*); anthers with apical hairs hardly or not at all different from other hairs on stamen; sepals not or hardly accrescent in fruit ..... 2. *Blepharandra*
- 9(6). Fruits without a soft fleshy exocarp, dry and corky or fibrous at maturity; inflorescence terminal, with each bract subtending a short cincinnus of 1–6 flowers; styles slender and subulate, distinct, the stigmas minute ..... 10
9. Fruits with an edible fleshy yellow, orange, or red exocarp at maturity; inflorescence lateral, with each bract subtending 1 flower; styles stout, distinct or connate, with large stigmas ..... 11
- 10(9). Stipules connate intrapetiolarly, persistent; filaments glabrous ..... 4. *Burdachia*
10. Stipules connate interpetiolarly, caducous, leaving a large interpetiolar scar; filaments densely hirsute ..... 11. *Glandonia*
- 11(9). Flowers borne in pseudoracemes; bracteoles (1 or both) often bearing 1 large abaxial gland, sometimes 2; styles 2 or 3, distinct or connate and then apparently only 1; stipules borne on base of petiole ..... 3. *Bunchosia*
11. Flowers borne in umbels or tight corymbs; bracteoles all eglandular; styles 3, distinct; stipules borne on stem between petioles ..... 17. *Malpighia*
- 12(1). Mericarps with wings very short relative to size of nut, often dissected and irregular or rudimentary ..... 13
12. Mericarps samaroid, with either dorsal or lateral wing(s) well developed ..... 18
- 13(12). Flowers borne ultimately in a pseudoraceme, sometimes reduced to a single pair ..... 14
13. Flowers borne ultimately in umbels or corymbs of (3)4(–8) ..... 16
- 14(13). Mericarps bearing a dorsal winglet but no lateral winglets, the sides smooth or at most somewhat rugose ..... 12. *Heteropterys*
14. Mericarps bearing a dorsal crest or winglet and several winglets or rounded or aculeate outgrowths on each side ..... 15
- 15(14). Pseudoracemes comprising (15–)20–50 flowers; woody vines, occasionally shrubby; blade of larger leaves (2.5–)4–6(–7) cm wide ..... 6. *Clonodia*

15. Pseudoracemes comprising 2–12(–22) flowers; shrubs 0.2–1 m tall; blade of larger leaves 0.9–2.8 cm wide ..... 23. *Tetrapteryx*
- 16(13). Stipules epipetiolar, usually borne at or beyond middle of petiole, often subulate ..... 13. *Hiraea*
16. Stipules interpetiolar, short, triangular ..... 17
- 17(16). Mericarps with a dorsal crest or winglet 1–5 mm wide and essentially 4 roughly parallel ridges or winglets 0.5–10 mm wide on each side, these irregular, dissected, and interconnected with transverse ridges ..... 9. *Diplopteryx*
17. Mericarps with a dominant triangular dorsal wing 4–9 mm long and several lateral ribs or crests radiating from the areole ..... 22. *Stigmaphyllon*
- 18(12). Samaras with dorsal wing dominant, the nut bearing on its sides only short winglets or crests or quite smooth ..... 19
18. Samaras with lateral wing(s) dominant, the dorsal wing smaller or reduced to a winglet or crest, occasionally absent ..... 21
- 19(18). Wing of samara with the abaxial edge thickened, the veins diverging and branching from it toward the thinner adaxial edge ..... 12. *Heteropteryx*
19. Wing of samara with the adaxial edge thickened, the veins diverging and branching from it toward the thinner abaxial edge ..... 20
- 20(19). Styles with stigmas quite terminal and without any sort of dorsal extension at apex ..... 1. *Banisteriopsis*
20. Styles with apex stigmatic on internal angle and a prominent dorsal extension of apex in the form of a hook or flap ..... 22. *Stigmaphyllon*
- 21(18). Bracteoles larger than bracts, globose-cymbiform, borne just below flower, enclosing bud until flower opens; pedicel absent or up to 2(–5) mm long in fruit, the peduncle well developed, 7–25 mm long in fruit ..... 19. *Mezias*
21. Bracteoles similar to bracts or smaller than them, or if larger not enclosing bud until flower opens; pedicel well developed relative to peduncle ..... 22
- 22(21). Calyx with 1 large central gland on each of the 4 lateral sepals, the anterior eglandular ..... 23
22. Calyx eglandular or with 2 glands on each of the 4 lateral sepals or on all 5 sepals ..... 24
- 23(22). Lateral wings of samara directed sideways, semicircular or up to twice as long as wide; bracteoles 4 mm long or longer; flowers borne ultimately in umbels of 4 or corymbs of 6; fertile locule of samara accompanied on each side by a parallel sterile cavity developed in base of lateral wing during maturation ..... 14. *Jubelina*
23. Lateral wings of samara directed forward, 3 or more times as long as wide; bracteoles 1.5–3 mm long; flowers borne ultimately in elongated pseudoracemes of 4–50; fertile locule of samara without parallel sterile cavities adjacent to it ..... 16. *Lophopteryx*
- 24(22). Pedicels sessile ..... 25
24. Pedicels pedunculate ..... 26
- 25(24). Flowers borne ultimately in pseudoracemes of 2–16; stipules short (≤ 0.5 mm long), triangular, borne on petiole at or somewhat above base ..... 18. *Mascagnia*

25. Flowers borne ultimately in umbels of 4; stipules mostly subulate, borne on petiole usually at or beyond middle, if borne near base of petiole the stipules  $\geq 2.5$  mm long ..... 13. *Hiraea*
- 26(24). Samaras with 4 discrete lateral wings, 2 on each side (in some species the 4 lateral wings may be accompanied by several long aculeate outgrowths between them) ..... 23. *Tetrapteryx*
26. Samaras with 1 continuous lateral wing or 2, 1 on each side ..... 27
- 27(26). Flowers mostly borne ultimately in pseudoracemes of (2-)4-50, these occasionally congested into corymbs or umbels; bracteoles eglandular or all bearing several small stalked marginal glands ..... 18. *Mascagnia*
27. Flowers borne ultimately in umbels of 4; one of each pair of bracteoles bearing 1 large, sessile, eccentric abaxial gland ..... 10. *Excentradenia*

1. **BANISTERIOPSIS** C.B. Rob. in Small, N. Amer. Fl. 25: 131. 1910.

*Banisteria sensu* A. Juss., Griseb., and Nied., non L. 1753.

Vines, shrubs, or rarely small trees. Leaves bearing glands on petiole or abaxial surface of blade or both; stipules small, distinct, interpetiolar. Floriferous bracts and bracteoles eglandular; pedicels usually sessile, raised on a peduncle in a few species. Petals yellow, pink, or white, usually the lateral 4 spreading or reflexed and the posterior erect. Stamens 10, all fertile; anthers alike or more commonly heteromorphic. Ovary with the 3 carpels adnate to a common torus, all fertile; styles 3, of uniform thickness or thicker distally, the stigmas terminal. Fruit breaking apart into 3 samaras separating from a short pyramidal torus, each samara having its largest wing dorsal, thickened on the adaxial (upper) edge, the veins terminating in the thinner abaxial edge; much shorter winglets, crests, or irregular outgrowths present on sides of nut in some species; nut usually with a functional carpophore.

Mexico, Central America, West Indies, and South America (all countries except Chile and Uruguay); 94 species, 19 in Venezuela, 10 of these in the flora area.

See *Banisteriopsis*, *Diplopteryx* (Malpighiaceae) by Bronwen Gates [Fl. Neotrop. Monogr. no. 30. 1982].

Key to the Species of *Banisteriopsis*

1. Leaf blades very densely and persistently metallic-sericeous abaxially ..... 2
1. Leaf blades glabrous or thinly sericeous to glabrate abaxially, the hairs at maturity never dense enough to completely hide the epidermis ..... 3
- 2(1). Petals pink, paler in age, the posterior yellow in proximal half; pedicels raised on a peduncle 0.5-3(-7) mm long; nut of samara rugose, tuberculate, muricate, or bearing irregular winglets on sides ..... *B. muricata*
2. Petals all yellow; pedicels mostly sessile, rarely raised on a peduncle up to 1 mm long; samara unknown, but its nut probably smooth-sided, or possibly bearing 1 winglet on each side ..... *B. lyrata*
- 3(1). Bracts and bracteoles deciduous before or during anthesis, or immediately afterwards; petals rose-pink turning white in age; nut of samara hairy on inner surface of locule ..... *B. caapi*
3. Bracts and bracteoles persistent; petals all yellow; nut of samara glabrous within locule ..... 4

- 4(3). Sepals all eglandular ..... 5
4. Lateral 4 sepals biglandular, anterior eglandular ..... 6
- 5(4). Flowers produced mostly on leafless stems, the inflorescences axillary to scars of leaves of previous seasons; styles densely bearded for  $1/4-1/2$  their length, the long spreading hairs especially extensive on anterior style; nut of samara bearing on each side 3-7 crest-like wings radiating from the areole ..... *B. cristata*
5. Flowers produced on currently leafy stems; styles glabrous; nut of samara unappendaged on sides, smooth or with reticulate veins prominent ..... *B. martiniana*
- 6(4). Specimens with flowers ..... 7
6. Specimens with fruits ..... 12
- 7(6). Petals, especially the lateral 4, densely sericeous abaxially ..... 8
7. Petals glabrous ..... 9
- 8(7). Petioles of larger leaves usually bearing 2 large glands at or slightly below apex; bracts and bracteoles 1-1.7 mm long, slightly concave to nearly flat, spatulate or subrotund, spreading to reflexed; anthers glabrous; nut of samara bearing several winglets on each side, nearly parallel to the areole ..... *B. krukoffii*
8. Petioles eglandular; bracts and bracteoles up to 1 mm long, cymbiform or triangular, erect to appressed; anthers with the locules pubescent; nut of samara with several to many ridges or crests on each side, radiating from the areole ..... *B. lucida*
- 9(7). Lateral petals subentire to denticulate, especially at base of limb; pedicels raised on a peduncle 0.5-2(-3) mm long ..... *B. wurdackii*
9. Lateral petals fimbriate or lacerate or at least distinctly dentate all around margin of limb; pedicels sessile ..... 10
- 10(9). Leaf blades deeply cordate at base, the lobes often equaling petiole; inflorescence usually glabrous, rarely sericeous to glabrate .... *B. pulcherrima*
10. Leaf blades truncate, rounded, or shallowly cordate at base; inflorescence hairy, the hairs usually persistent ..... 11
- 11(10). Inflorescence golden-sericeous; connective of anthers opposite 3 anterior sepals only slightly exceeding locules, by up to 0.5 mm; reduced leaves in inflorescence entire, the margin eglandular or bearing tiny glands ..... *B. maguirei*
11. Inflorescence minutely brown- or white-tomentose; connective of anthers opposite 3 anterior sepals greatly exceeding locules, by 0.6-1 mm; reduced leaves in inflorescence usually bearing well-developed glands or ciliate processes on margin ..... *B. martiniana*
- 12(6). Nut of samara unappendaged on sides, the veins sometimes prominent ..... go to couplet 10
12. Nut of samara bearing winglets, crests, or ridges on sides ..... 13
- 13(12). Flowers borne ultimately in short pseudoracemes of 10-25 ..... *B. wurdackii*
13. Flowers borne ultimately in umbels of 4(-6) ..... go to couplet 8

**Banisteriopsis caapi** (Griseb. in Mart.) C.V. Morton, J. Wash. Acad. Sci. 21: 486. 1931. —*Banisteria caapi* Griseb. in Mart., Fl. Bras. 12(1): 43. 1858. —Aya-huasca, Caapi, Yagé.

*Banisteriopsis inebrians* C.V. Morton, J. Wash. Acad. Sci. 21: 485. 1931. Woody vine; blade of larger leaves 10-22 x 4-10 cm, abaxially sparsely sericeous to glabrate; inflorescence with flowers borne ul-



timately in umbels of 4; bracts and bracteoles deciduous before or during anthesis, or rarely immediately afterward; sepals all eglandular or the lateral 4 biglandular; petals rose-pink turning white in age, fimbriate; anthers with locules sparsely pilose to glabrate, some with the connective much enlarged and glandular; samaras 21–47 × 8–22 mm, the nut ribbed or rarely short-aculeate on sides, hairy on inner surface of locule. Areas of evergreen lowland forests, 100–200 m; Amazonas (Caño Iguaña, Gavilán, Isla el Silencio in Río Orinoco basin, Río Marueta, San Carlos de Río Negro). Amazonian Colombia, Ecuador, Peru, Brazil, Bolivia, northernmost Argentina near Bolivia.

*Banisteriopsis caapi* is widely cultivated by native peoples of western Amazonia, and used by them as a principal ingredient in hallucinogenic concoctions. Unequivocally natural populations are not known, but the plants are often found naturalized near present or former villages.

**Banisteriopsis cristata** (Griseb.) Cuatrec., Ciencia (Mexico) 23: 141. 1964. —*Banisteria cristata* Griseb., Linnaea 22: 16. 1849.

*Banisteria orbicularis* Nied., Repert. Spec. Nov. Regni Veg. 33: 69. 1933.

Woody vine or shrub with twining branches; blade of larger leaves 3.5–9(–12) × 4–8 cm, soon glabrate on both sides except sericeous margin and midrib; inflorescences axillary to scars of leaves of previous seasons, the flowers borne ultimately in umbels of 4; bracts and bracteoles persistent; calyx eglandular; petals yellow, glabrous; anthers glabrous; styles bearded for up to 1/2 their length; samaras 29–39 × 9–11 mm, the nut bearing on each side 3–7 crest-like wings radiating from areole. Savannas, deciduous forests, 200–400 m; Bolívar (area of Ciudad Bolívar, Lago Guri, San Félix). Anzoátegui, common in northern coastal states of Venezuela; Guyana, Suriname.

**Banisteriopsis krukoffii** B. Gates, Fl. Neotrop. Monogr. 30: 200. 1982. —Bejuco de ratón.

Woody vine; petiole usually biglandular at or near apex; blade of larger leaves 10–21 × 5–9 cm, abaxially thinly sericeous with very

short hairs; inflorescence with flowers borne ultimately in umbels of 4; bracts and bracteoles 1–1.7 mm long, slightly concave to nearly flat, spatulate or subrotund, spreading to reflexed, persistent; 4 lateral sepals biglandular, anterior eglandular; petals yellow, abaxially densely sericeous, denticulate or short-fimbriate; anthers glabrous; nut of samara bearing several winglets on each side, nearly parallel to areole. Evergreen lowland and lower montane wet forests, 100–600 m; Bolívar (La Escalera), Amazonas (Río Mawarinuma, Solano). Brazil (Amazonas).

**Banisteriopsis lucida** (Rich.) Small, N. Amer. Fl. 25: 133. 1910. —*Banisteria lucida* Rich., Actes Soc. Hist. Nat. Paris 1: 109. 1792.

Woody vine; petioles eglandular; blade of larger leaves 8–16 × 3.5–7.5 cm, abaxially sparsely sericeous, sometimes glabrescent; inflorescence with flowers borne ultimately in umbels of 4(–6); bracts and bracteoles up to 1 mm long, cymbiform or triangular, erect to appressed, persistent; 4 lateral sepals biglandular, anterior eglandular; petals yellow, abaxially densely sericeous, dentate to lacerate; anther locules pubescent; samaras 41–73 × 14–25 mm, the nut with the sides prominently ridged or rarely cristate, the ridges radiating from areole. Evergreen lowland to montane forests, 100–1300 m; Delta Amacuro (Caño Güiniquina), Bolívar (Caño Majagua tributary of Río Parucito, Gran Sabana, upper Río Caroní, upper Río Caura, upper Río Paragua), southern Amazonas (Cariche, Río Baria/Mawarinuma, Río Casiquiare, Río Padamo, Río Siapa, Sierra de la Neblina, Tamatama). Apure, Aragua, Distrito Federal, Falcón, Lara, Sucre, Táchira, Zulia; Colombia, Trinidad, Guyana, Suriname, French Guiana, Ecuador, Peru, Brazil, Bolivia.

**Banisteriopsis lyrata** B. Gates, Brittonia 31: 108. 1979.

Woody vine; petioles biglandular at apex; blade of larger leaves 7–13 × 4.5–6.5 cm, abaxially densely and persistently golden-metallic-sericeous; inflorescence with flowers borne ultimately in short pseudoracemes of 3 or 4 pairs or umbels of 4, usually with 1

or 2 more proximal pairs below; pedicels sessile or rarely raised on a peduncle up to 1 mm long; bracts and bracteoles persistent; lateral 4 sepals biglandular, anterior eglandular; petals yellow, glabrous, long-fimbriate; anthers glabrous, some with the connective much enlarged and glandular; samaras unknown, the nut probably smooth-sided, possibly bearing 1 winglet on each side. Lowland forests, 100–200 m; Delta Amacuro (town of Sierra Imataca east-southeast of Los Castillos), Bolívar (Río Caura, Río Paragua). Brazil (Pará, Rondônia).

**Banisteriopsis maguirei** B. Gates, Brittonia 31: 108. 1979.

Woody vine; blade of larger leaves 6–12.5 × 3.5–10 cm, rounded or shallowly cordate at base, abaxially sparsely sericeous; inflorescence densely to sparsely golden-sericeous, the flowers usually borne ultimately in pseudoracemes of up to 7 pairs, rarely in umbels of 4 flowers; reduced leaves of inflorescence with margin eglandular or bearing tiny sessile glands; bracts and bracteoles persistent; lateral 4 sepals biglandular, anterior eglandular; petals yellow, glabrous, long-fimbriate; anthers glabrous; samaras 20–28 × 8–10 mm, the nut unappendaged on sides, sometimes with prominent veins. Tepui meadows, probably mostly in wooded ravines along streams, 1000–1900 m; western Bolívar (Cerro Guanay, Cerro Guaiquinima, Cerro Jaua, Sierra de Maigualida), Amazonas (Cerro Aracamuni, Cerro Coro Coro, Cerro Cuao, Cerro Duida, Cerro Guanay, Cerro Huachamacari, Cerro Marahuaka, Cerro Parima, Cerro Sipapo, Cerro Yutajé). Endemic.

**Banisteriopsis martiniana** (A. Juss.) Cuatrec., Webbia 13: 498. 1958. —*Banisteria martiniana* A. Juss., Ann. Sci. Nat. Bot. sér. 2, 13: 284. 1840.

*Banisteria leptocarpa* Benth., London J. Bot. 7: 130. 1848. —*Banisteriopsis leptocarpa* (Benth.) R.O. Williams, Fl. Trinidad 1: 131. 1929.

Woody vine, rarely shrubby; leaf blades obtuse to shallowly cordate at base, abaxially sparsely sericeous to soon glabrate; inflorescence minutely brown- or white-tomentose, the flowers borne ultimately in umbels of 4; reduced leaves in inflorescence with ±

well-developed glands or cilia on margin; bracts and bracteoles persistent; sepals all eglandular or lateral 4 biglandular and anterior eglandular; petals yellow, dentate to lacerate, glabrous; anthers glabrous, those opposite 3 anterior sepals with the connective much enlarged; samaras 18–35 × 5–12 mm, the nut unappendaged on sides, sometimes with prominent veins. Both recognized varieties occur in the Venezuelan Guayana.

#### Key to the Varieties of *B. martiniana*

1. Hairs of inflorescence rusty brown; leaf blades plane, 4.5–12.5 cm long, bearing cupulate marginal glands; Delta Amacuro and Bolívar ..... var. *martiniana*
1. Hairs of inflorescence white or gray; leaf blades falcate, 7–17 cm long, bearing minute marginal glands; Amazonas ..... var. *subnervia*

#### *B. martiniana* var. *martiniana*

Climbing in forests and sprawling in open places, near sea level to 2000 m; common in Delta Amacuro and eastern Bolívar, also northwestern Bolívar. Aragua, Sucre; Trinidad, Guyana, Suriname, French Guiana, Brazil. ♦Fig. 72.

#### *B. martiniana* var. *subnervia* Cuatrec., Webbia 13: 501. 1958.

*Banisteriopsis martiniana* var. *laevis* Cuatrec., Webbia 13: 502. 1958.

Evergreen lowland forests, 100–300 m; Amazonas (Río Yatua, San Carlos de Río Negro). Amazonian Colombia, Peru, Brazil.

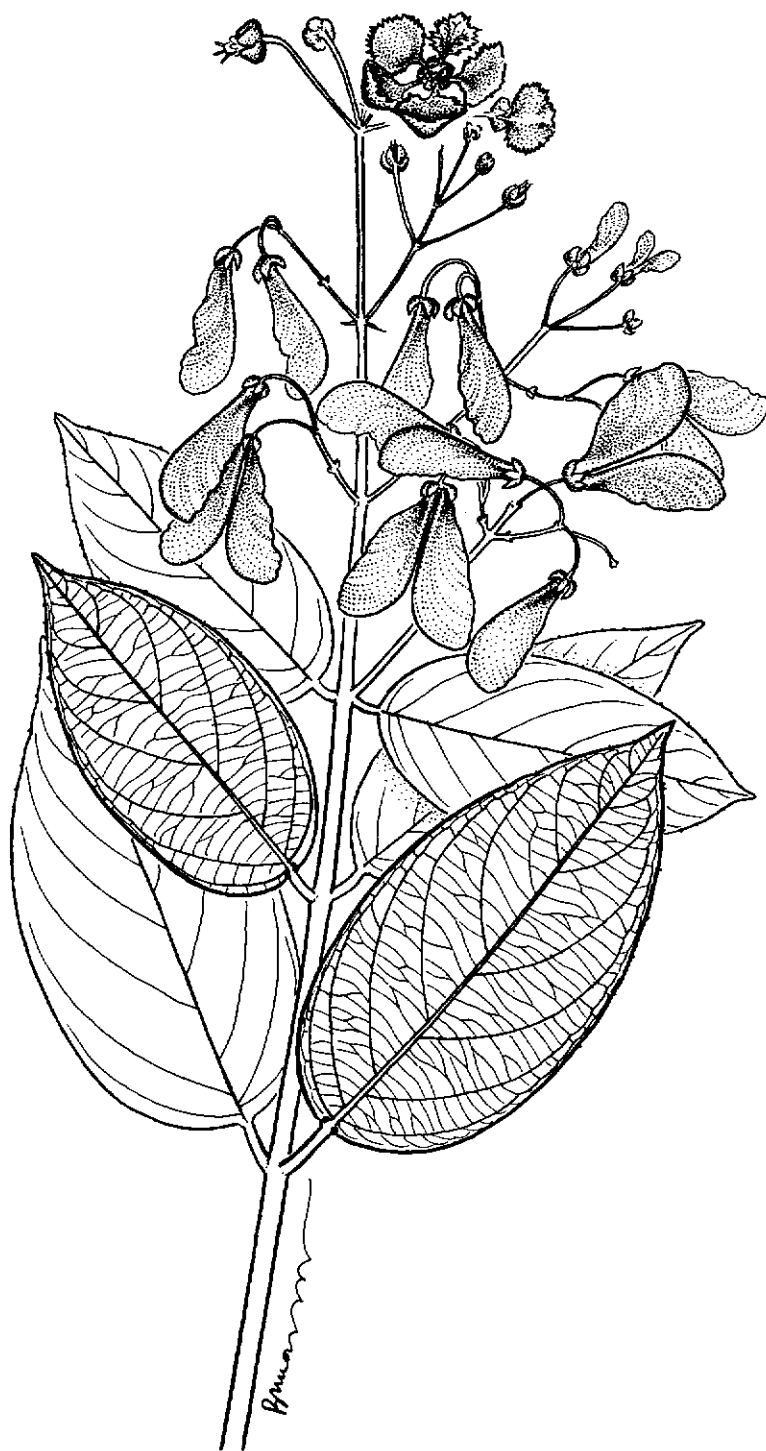
#### *Banisteriopsis muricata* (Cav.) Cuatrec., Webbia 13: 503. 1958. —*Banisteria muricata* Cav., Diss. 9: 423, pl. 246. 1790.

*Heteropterys argentea* H.B.K., Nov. Gen. Sp. 5: pl. 450. 1821. —*Banisteria argentea* (H.B.K.) Spreng., Syst. Veg. 2: 388. 1825. —*Banisteriopsis argentea* (H.B.K.) C.B. Rob. in Small, N. Amer. Fl. 25: 133. 1910.

*Banisteria metallicolor* A. Juss. in A. St.-Hil., Fl. Bras. Merid. 3: 46. 1832 [1833].

—*Banisteriopsis metallicolor* (A. Juss.) O'Donnell & Lourteig, Lilloa 9: 259. 1943.

*Banisteria schomburgkiana* Benth., London J. Bot. 7: 129. 1848. —*Banisteriopsis*

Fig. 72. *Banisteriopsis martiniana* var. *martiniana*

*schomburgkiana* (Benth.) C.B. Rob. in Small, N. Amer. Fl. 25: 133. 1910.

Woody vine, sometimes shrubby; blade of larger leaves 5.5–14 × 3–8 cm, abaxially (in the flora area) very densely and persistently metallic-sericeous (silver or golden); inflorescence with flowers borne ultimately in umbels of 4; pedicels raised on a peduncle 0.5–3(–7) mm long; bracts and bracteoles persistent; sepals all eglandular or the lateral 4 biglandular; petals glabrous, pink, paler in age, the posterior yellow proximally; anthers glabrous, some with the connective much enlarged and glandular; samaras (16–)24–40 (–50) × (9–)11–16(–20) mm, the nut rugose, tuberculate, muricate, or bearing irregular winglets on sides. Wet forests to drier, ± disturbed woods, often growing at edge of wooded areas along rivers and ravines, 100–400 m; common in northern Bolívar. Elsewhere in Venezuela known from most states; Mexico, Central America, Colombia, Guyana, French Guiana, Ecuador, Peru, Brazil, Bolivia, Paraguay, Argentina.

***Banisteriopsis pulcherrima*** (Sandwith) B. Gates, Brittonia 31: 109. 1979. —*Banisteriopsis elegans* var. *pulcherrima* Sandwith, J. Arnold Arbor. 24: 223. 1943.

Woody vine or shrub; blade of larger leaves 8–16 × 4–12 cm, deeply cordate at base, glabrous, usually with tooth-like marginal glands or ciliate processes; inflores-

cence usually glabrous, rarely sericeous to glabrate, the flowers borne ultimately in umbels of 4; reduced leaves in inflorescence with ciliate processes up to 6 mm long around margin; lateral 4 sepals biglandular, anterior eglandular; petals yellow, fimbriate, glabrous; anthers glabrous, those opposite the 3 anterior sepals with connective much enlarged; samaras 27–39 × 10–13 mm, the nut unappendaged on sides, sometimes with prominent veins. Wooded slopes, roadsides, savannas, 300–2200 m; southeastern Bolívar (Gran Sabana). Western Guyana.

***Banisteriopsis wurdackii*** B. Gates, Brittonia 31: 109. 1979.

Woody vine; blade of larger leaves 10–19 × 4.5–10.5 cm, abaxially sparsely sericeous; inflorescence with flowers borne ultimately in pseudoracemes of 10–25; pedicels raised on a peduncle 0.5–2(–3) mm long; bracts and bracteoles persistent; lateral 4 sepals biglandular, anterior eglandular; petals yellow, glabrous, subentire to denticulate, especially at base of limb; anthers glabrous; samaras 25–46 × 10–15 mm, the nut bearing on each side a single winglet parallel to areole. Semideciduous to evergreen lowland and lower montane forests, 50–400 m; northwestern Bolívar (El Manteco, Río Parguaza, Río Villacoa). Mérida; Costa Rica, Panama, Colombia, French Guiana, Ecuador, Peru, Brazil, Bolivia.

## 2. BLEPHARANDRA Griseb., Linnaea 22: 7. 1849.

Trees or shrubs, the hairs often basifixed or sub-basifixed. Leaves eglandular; stipules intra- and epipetiolar, distinct from each other but often basally connate with opposite stipules to form an interpetiolar sheath; blade with many (12–20 or more) fine parallel lateral veins interconnected by a fine elaborate reticulum. Inflorescence a thyrses or pseudoraceme composed of 1–several-flowered cincinni; bracts and bracteoles without abaxial glands. Sepals all abaxially biglandular; petals white, pink, or red (posterior petal pale yellow in 2 species), glabrous or bearing a few hairs on the claw. Stamens 10; filaments distinct, hirsute with straight basifixed hairs; anthers with locules bearing at least apical tufts of basifixed hairs and often hirsute on sides as well. Ovary of 3 completely connate carpels, all fertile or the anterior empty, glabrous; styles 3, slender and subulate with minute terminal stigmas. Fruit a tiny (2–3.5 × 2.5–3.5 mm), spheroidal or ovoidal, 3-angled, dry, indehiscent, nut-like capsule with a bony and often rugose endocarp.

Southern Venezuela, Guyana, Amazonian Brazil; 6 species, 4 in Venezuela, all in the flora area.



Key to the Species of *Blepharandra*

1. Stipules acute or acuminate at apex, deciduous before leaves; 500–2600 m ..... 2
1. Stipules rounded at apex, persistent on petiole; 50–400 m ..... 3
- 2(1). Sepals, most bracteoles, and some bracts bearing gland-tipped marginal processes 0.5–2 mm long; leaves light green abaxially, not or only thinly glaucous; leaves, vegetative internodes, and abaxial surface of stipules glabrous ..... *B. fimbriata*
2. Sepals, bracteoles, and bracts entire or denticulate; leaves white- or yellowish-glaucous abaxially; petioles, internodes, and abaxial surface of stipules at least initially densely hairy; leaf blades densely hairy to glabrate abaxially ..... *B. hypoleuca*
- 3(1). Petals all pink, turning white in age; sepals glabrous adaxially or sparsely sericeous near margin, sericeous abaxially; free lobes of stipules 2.5–4 mm long; pubescence of inflorescence light to dark brown; pedicels 5–6(–7) mm long; blade of larger leaves 1.5–3 cm wide, the margin thick and nonrevolute ..... *B. angustifolia*
3. Four lateral petals white, posterior petal pink; sepals densely sericeous on both sides; free lobes of stipules 4–7 mm long; pubescence of inflorescence white; pedicels 8–10(–13) mm long; blade of larger leaves (2.5–)3–7 cm wide, the margin thin and often revolute ..... *B. heteropetala*

***Blepharandra angustifolia*** (H.B.K.) W.R. Anderson, Mem. New York Bot. Gard. 32: 55. 1981. —*Byrsonima angustifolia* H.B.K., Nov. Gen. Sp. (quarto ed.) 5: 153, pl. 449. 1821 [1822].

Much-branched shrub or small tree 1–6 m tall; stipules persistent on petiole, the free lobes 2.5–4 mm long, rounded; petioles 7–11(–18) mm long; blade of larger leaves 4.5–7.5(–8.5) × 1.5–3 cm, elliptic or rectangular or narrowly obovate, thick and nonrevolute at margin; petals pink turning white in age. Savannas, usually on white sand, 100–400 m; Amazonas (base of Cerro Yapacana, Río Atabapo, Río Casiquiare, Río Guainía, Río Orinoco, Río Pasimoni). Brazil (Amazonas: upper Rio Negro). ♦Fig. 74.

***Blepharandra fimbriata*** MacBryde, Canad. J. Bot. 52: 2437. 1974.

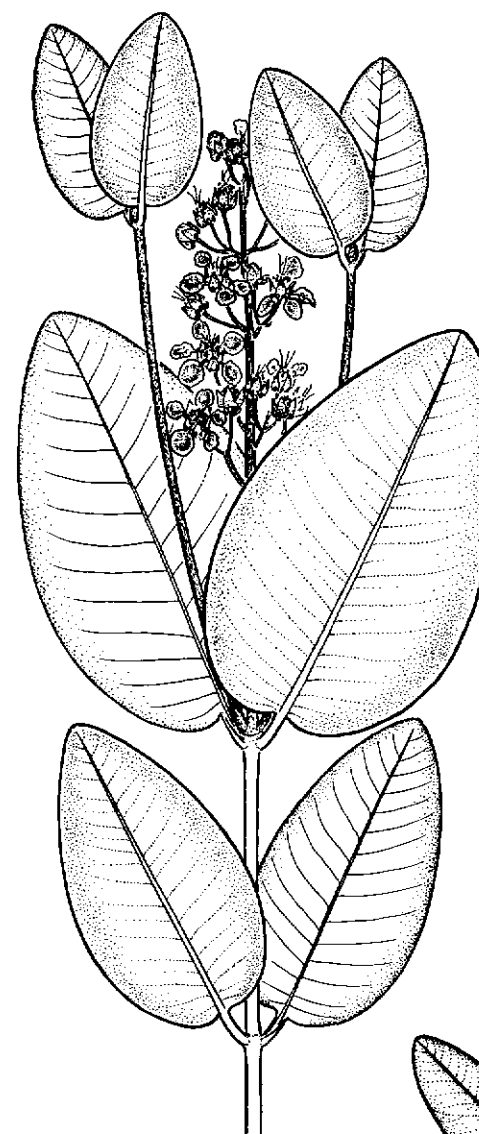
Weak shrub, prostrate to erect, to 2 m tall; vegetative internodes and leaves glabrous, except for tufts of hairs at nodes; stipules 11–30 × 4–7 mm, acute or acuminate at apex, deciduous before leaves; blade of larger leaves 3.5–8 × 1.7–3.8 cm, elliptic, not or only thinly glaucous abaxially, usually revolute at margin; some bracts, most bracteoles, and sepals

glandular-fimbriate; 4 lateral petals white, posterior petal pale yellow. Open scrub and rocky places along rivers, 600–1800 m; Bolívar (near Canaima, Cerro Guaiquinima, Uei-tepui). Guyana (Ayanganna Plateau). ♦Fig. 75.

***Blepharandra heteropetala*** W.R. Anderson, Mem. New York Bot. Gard. 32: 57. 1981.

Shrub or tree 2–7 m tall; stipules persistent on petiole, the free lobes 4–7 mm long, rounded; petioles (6–)8–12 mm long; blade of larger leaves 6–10 × (2.5–)3–7 cm, elliptic or ovate, often revolute at margin; 4 lateral petals white, posterior petal pink. Shrubby vegetation or scrub forests on white sand, 50–400 m; Amazonas (Cerro Cariche, Cerro Morocoto below San Fernando del Atabapo, Río Atabapo, between upper Río Orinoco and Cerro Autana, Río Sipapo). Brazil (Amazonas: campinas north and east of Manaus).

***Blepharandra hypoleuca*** (Benth.) Griseb., Linnaea 22: 7. 1849. —*Coleostachys hypoleuca* Benth., London J. Bot. 7: 125. 1848.

Fig. 73. *Blepharandra hypoleuca*Fig. 74. *Blepharandra angustifolia*Fig. 75. *Blepharandra fimbriata*

*Byrsonima cretacea* Gleason, Bull. Torrey Bot. Club 58: 378. 1931. —*Blepharandra cretacea* (Gleason) Steyerl., Fieldiana, Bot. 28: 280. 1952.

*Blepharandra ptariana* Steyerl., Fieldiana, Bot. 28: 282. 1952.

Shrub or small tree 1–8 m tall; vegetative internodes sericeous to glabrate; stipules 5–17(–22) × 3–9 mm, acuminate at apex, deciduous before leaves; blade of larger leaves 4.5–15.5 × 3–9.5 cm, elliptic or ovate, abaxially glaucous and densely hairy to glabrate; bracts, bracteoles, and sepals entire or denticulate; 4 lateral pet-

als white, posterior petal pale yellow. Sandy upland savannas and shrubby associations, often along rocky streams, 500–2600 m; Bolívar (Auyán-tepui, Cerro Guaiquinima, Cerro Jaua, Cerro Marutani, Ilú-tepui, Macizo del Chimantá, Ptari-tepui, upper Río Caroní, upper Río Paragua, Sierra Pakaraima), Amazonas (Cerro Aracamuni, Cerro Duida, Sierra Unturán). Western Guyana, Brazil (Amazonas: Serra Aracá). ♦Fig. 73.

*Blepharandra hypoleuca* is an extremely variable species; see discussion in Mem. New York Bot. Gard. 32: 53–55. 1981.

### 3. BUNCHOSIA H.B.K., Nov. Gen. Sp. (quarto ed.) 5: 153. 1821 [1822].

Shrubs or trees. Leaves usually bearing impressed glands abaxially on the blade; stipules distinct, borne on base of petiole. Inflorescence a pseudoraceme, simple or less commonly ternate, axillary without vegetative leaves or terminating a lateral shoot with 1 pair of vegetative leaves; 1 or both bracteoles often bearing 1(2) abaxial glands. Calyx bearing 8–10 often decurrent glands; petals yellow or whitish, glabrous. Stamens 10, usually glabrous; anthers ± alike. Gynoecium 2- or 3-carpellate; ovary with carpels connate and locules as many as carpels, every locule fertile; styles as many as carpels, distinct or partially to completely connate and then apparently only 1, stout, the large terminal stigmas subpeltate or apparently capitate. Fruit an indehiscent “drupe” (actually a berry), yellow, orange, or red at maturity, with 2 or 3 distinct 1-seeded pyrenes in a common fleshy exocarp, each pyrene with a smooth, brittle, cartilaginous wall.

Mexico, Central America, West Indies, South America (all countries except Chile and Uruguay); ca. 65 species, 11 in Venezuela, 6 of these in the flora area.

#### Key to the Species of *Bunchosia*

1. Inflorescence terminating a short lateral branch bearing a pair of sterile vegetative leaves (these sometimes deciduous, but leaving large leaf scars), or occasionally terminating a leaf-bearing main shoot; ovary glabrous or rarely sericeous, 2- or 3-carpellate ..... 2
1. Inflorescence axillary, with small bracts only, every bract subtending 1 uniflorous peduncle (or sometimes 2 in *B. glandulifera*); ovary sericeous, 2-carpellate ..... 3
- 2(1). Leaf blades abaxially densely velutinous or tomentose, the hairs less dense on fully expanded leaves than on young leaves but almost always persistent and nearly uniformly distributed; fully expanded leaf blades 6–18(–22) cm long; inflorescence 4–12 cm long, bearing 10–30 flowers ..... *B. mollis*
2. Leaf blades from the beginning densely velutinous on margin and abaxial midrib but bearing only a few hairs on surface between, glabrescent in age(?) or with hairs persistent on margin; leaf blades up to 4 cm long; inflorescence up to 3 cm long (in the only known collection, in which the

inflorescences are probably not fully elongated), bearing 8–12 flowers

- |   |                        |
|---|------------------------|
| .....   | <i>B. petraea</i>      |
| 3(1). Styles $\frac{2}{3}$ to completely distinct.....  | 4                      |
| 3. Styles connate, the stigmas distinct or connate.....   | 5                      |
| 4(3). Leaves persistently very densely silvery- or golden-sericeous abaxially, the epidermis completely concealed by hairs .....  | <i>B. argentea</i>     |
| 4. Leaves sparsely sericeous abaxially to apparently glabrate ....  | <i>B. armeniaca</i>    |
| 5(3). Leaves thinly but persistently sericeous abaxially, undulate and crispate at margin; pseudoracemes bearing 10–20 flowers, sometimes 2 in the axil of 1 bract; peduncles 2.5–5 mm long; style sericeous; dried fruits 20–28 × 15–20 mm, the wall smooth .....            | <i>B. glandulifera</i> |
| 5. Leaves nearly or quite glabrate, plane or slightly revolute at margin, entire or slightly indented near glands; pseudoracemes usually bearing 20–60 flowers, 1 per bract; peduncles 0.5–2 mm long; style glabrous; dried fruits up to 15 × 16 mm, the wall granulate ..... | <i>B. decussiflora</i> |

*Bunchosia argentea* (Jacq.) DC., Prodr. 1: 582. 1824. —*Malpighia argentea* Jacq., Fragm. Bot. 57, pl. 83. 1800–1809.

Shrub or tree (2–)3–20(–25) m tall; blade of larger leaves 10–23 × (5–)7–14 cm, abaxially densely and persistently silvery- or golden-sericeous; pseudoracemes 7–13 cm long, with 15–35(–50) flowers; anther connectives brown to red; ovary 2-carpellate, sericeous; styles distinct; fruits orange to red, 12–30 × 12–25 mm (dried), ± persistently sericeous. Evergreen lowland forests, 200–400 m; Bolívar (Río Nichare). Anzoátegui, Aragua, Barinas, Distrito Federal, Falcón, Lara, Mérida, Miranda, Monagas, Portuguesa, Táchira, Yaracuy; Costa Rica, Panama, Colombia, Guyana, French Guiana, Ecuador, Peru, Brazil. ♦Fig. 76.

There is great diversity in the plants to which this name has been applied; they may represent more than one species.

*Bunchosia armeniaca* (Cav.) DC., Prodr. 1: 582. 1824. —*Malpighia armeniaca* Cav., Diss. 8: 410, pl. 238. 1789. —Palo de colmena.

Tree 3–15 m tall; blade of larger leaves 10–27 × 5–10 cm, abaxially sparsely sericeous to nearly glabrate; pseudoracemes 6–17 cm long, with 8–60 flowers; anther connectives dark red to black; ovary 2-carpellate, densely sericeous; styles at least  $\frac{2}{3}$  distinct, glabrous or proximally sericeous; fruits reddish, 12–19 × 14–17 mm (dried), ± persistently sericeous. Wet forests, 50–300 m; Delta Amacuro (west of Caño Guayo and east

of Caño Sacupana, Río Cuyubini, town of Sierra Imataca east-southeast of Los Castillos), northern Bolívar (El Dorado, El Palmar, Pijiguaos, Río Caura). Colombia, Ecuador, Peru, Brazil, Bolivia.

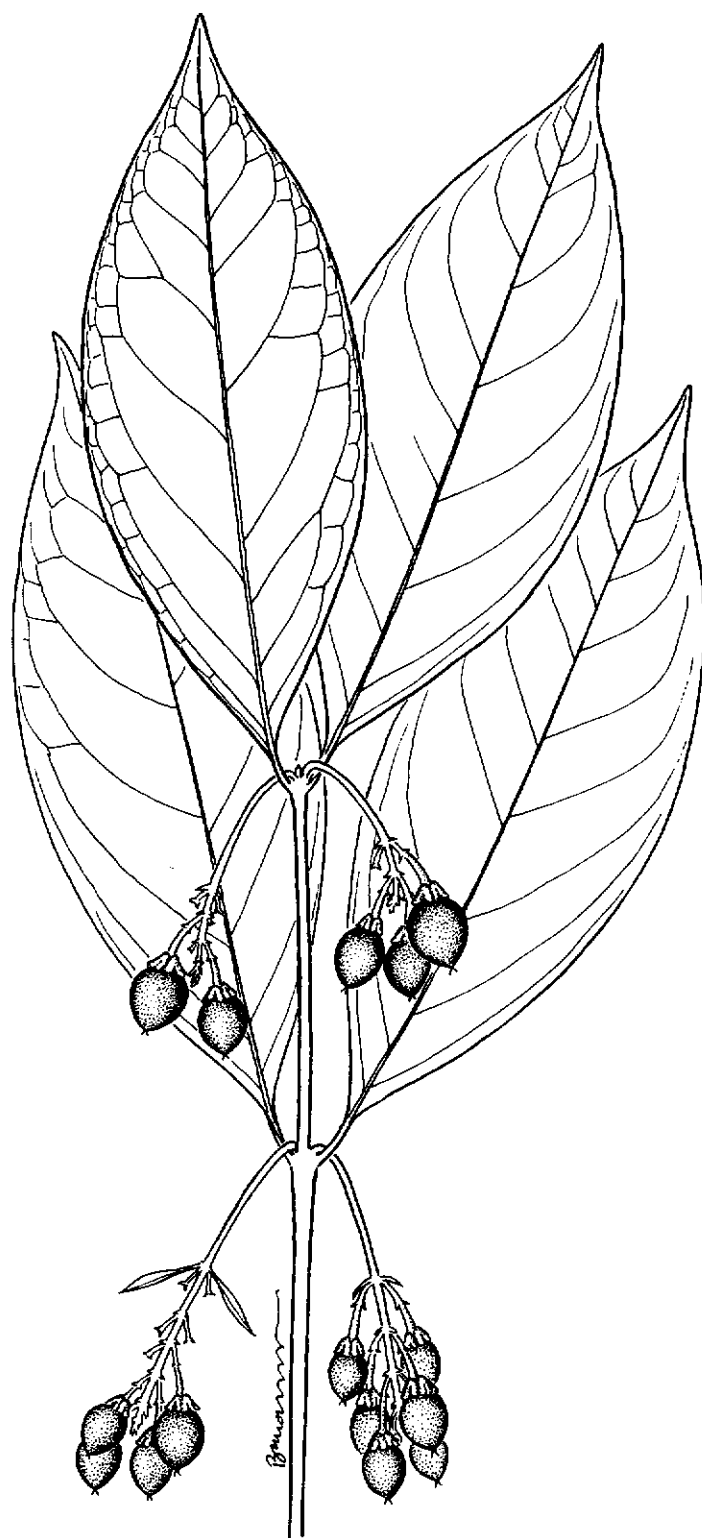
It is unlikely that everything passing under this name represents the same species. The styles are not always distinct in plants from Ecuador, but in Venezuela the character seems to be consistent.

*Bunchosia decussiflora* W.R. Anderson, Mem. New York Bot. Gard. 32: 279. 1981.

Shrub or tree 3–25 m tall; blade of larger leaves 12–19 × 4.5–10 cm, glabrate at maturity; pseudoracemes 8–15 cm long, with 20–60 flowers; peduncles 0.5–2 mm long; anther connectives brown or reddish; ovary 2-carpellate, sericeous; style (from 2 connate) glabrous; fruits yellow or reddish, 9–15 × 9–16 mm (dried), glabrate and granulate at maturity. Evergreen lowland to upper montane moist forests, 100–1300 m; southern Amazonas (Raudal de los Guaharibos on upper Río Orinoco, Río Ocamo, Río Ugueto, Sierra de la Neblina). Guyana, French Guiana, Brazil.

*Bunchosia glandulifera* (Jacq.) H.B.K., Nov. Gen. Sp. (quarto ed.) 5: 154. 1821 [1822]. —*Malpighia glandulifera* Jacq., Collectanea 4: 207. 1790 [1791]. —Ciruela, Ciruela de fraile.

Shrub or small tree 2–8 m tall; blade of larger leaves 8.5–18 × (4.5–)6–10(–12) cm, undulate and crispate at margin, abaxially

Fig. 76. *Bunchosia argentea*

thinly but persistently sericeous; pseudoracemes 5–11 cm long, with 10–20 flowers, the bracts sometimes subtending 2 flowers; peduncles 2.5–5 mm long; anther connectives yellow or light brown; ovary 2-carpellate, sericeous; style (from 2 connate) 3–3.5 mm long, sericeous; fruits orange to red, 20–28 × 15–20 mm (dried), beaked, the wall smooth, glabrate at maturity. Secondary woods, edges of forests, 50–100 m; Amazonas (La Esmeralda, Pimichín, Puerto Ayacucho, San Antonio del Sipapo, San Carlos de Río Negro). Anzoátegui, Aragua, Barinas, Carabobo, Distrito Federal, Guárico, Miranda, Portuguesa; West Indies, Colombia, Suriname, Ecuador, Peru, Brazil, Bolivia.

*Bunchosia glandulifera* has a very large fleshy red-orange fruit. It is widely cultivated for its handsome foliage and showy edible fruits. It is known only as an introduced tree in the West Indies, Peru, Brazil, and Bolivia, and seems likely to be native only in Colombia and Venezuela. Its wide distribution in northern Venezuela suggests that those may be natural populations. None of the collections I have seen from northern Venezuela were described as cultivated, but the possibility remains that in a long-settled area like the Distrito Federal (the type locality) the species was introduced early (perhaps before the arrival of Europeans) and then became naturalized through dispersal by birds. Most, but not all, of the collections from Amazonas were described by the collectors as cultivated. It seems unlikely to me that this showy species is indigenous to southern Venezuela; I would expect it to be better collected there if that were the case.

***Bunchosia mollis*** Benth., London J. Bot. 7: 127. 1848. —Ciruela de fraile, Ciruela montañera.

*Bunchosia rhombifolia* Turcz., Bull. Soc. Imp. Naturalistes Moscou 36: 582. 1863.

*Bunchosia schomburgkiana* Nied., Arbeiten Bot. Inst. Königl. Lyceum Hosianum Braunsberg 5: 45. 1914.

Shrub or small tree 1–5 m tall; blade of larger leaves 6–18(–22) × 3–12 cm, abaxially ± uniformly densely velutinous or tomentose, the T- or Y-shaped hairs stellate at base of stalk; inflorescence terminating a lateral shoot with 1 pair of full-sized leaves, 4–12 cm long beyond leaves, with 10–30 flowers; ovary glabrous or very rarely sericeous, 2- or 3-carpellate; styles distinct or up to ½ connate; fruits orange to red, 6–11 mm diameter (dried), glabrous. Savannas, scrub forests, gallery forests, near sea level to 300 m; common in northeastern Bolívar. Anzoátegui, Barinas, Guárico, Miranda, Monagas, Nueva Esparta, Sucre; Guyana, Brazil (Roraima).

***Bunchosia petraea*** W.R. Anderson, Contr. Univ. Michigan Herb. 21: 40. 1997.

Shrub 1.5 m tall; blade of larger leaves (not fully expanded?) 3–4 × 1.6–2 cm, velutinous on margin and abaxial midrib, some hairs with sharp spurs at base of very short stalk; inflorescence terminating a lateral shoot with 1 pair of full-sized leaves, up to 3 cm long (not fully elongated?), with 8–12 flowers; ovary glabrous, 2- or 3-carpellate; styles distinct; fruits unknown. Granitic outcrops, 50–100 m; Amazonas (Puerto Ayacucho–El Burro). Endemic.

#### 4. **BURDACHIA** A. Juss. in Endl., Gen. Pl. 1064. 1840.

*Tetrapodenia* Gleason, Bull. Torrey Bot. Club 53: 289. 1926.

Shrubs or trees. Leaves bearing abaxial glands; stipules intra- and epipetiolar, completely connate, the pair 3–11 mm long, coriaceous, persistent on petiole. Inflorescence terminal, single or 2 or 3 together, each usually divided near base into 3(–5) axes, each axis a raceme of short cincinni; lowest bracteole and alternate subsequent bracteoles bearing 1 large eccentric abaxial gland. Flower buds spheroidal. Sepals all biglandular; petals pink or white; posterior petal bearing 2–4 large glands on each side of base of limb and several smaller glands distally. Stamens 10, glabrous; anthers rounded at apex, often exceeded at apex by the thick, fleshy connective. Ovary of 3 completely connate carpels, 3-locular but 1 of the posterior locules empty and smaller; styles 3, slender and subulate; stigma slightly internal and decurrent. Fruit an indehiscent fibrous or aerenchymatous nut, dry at maturity and without a stony endocarp, usually containing only 1 locule completely filled by 1 large seed.

Amazonian Colombia, Venezuela, Guyana, Peru, Brazil; 2 or 3 species, 2 in Venezuela, both in the flora area.

The third species of *Burdachia*, if it is recognized, is *B. duckei* Steyerl., which occurs along the Rio Negro in Amazonian Brazil between Barcelos and the Rio Urubú. It is a segregate from *B. prismatocarpa*.

#### Key to the Species of *Burdachia*

1. Fruits pyramidal, bearing 8 or 9 longitudinal ribs, these extended at base into knobs or spurs; leaves minutely sericeous or tomentose abaxially to glabrate, with some hairs usually persisting on midrib; vegetative stems sericeous to glabrate; stipules abaxially sericeous to glabrate; peduncles sparsely to densely sericeous; ovary conoidal ... *B. prismatocarpa*
1. Fruits conoidal to spheroidal, round in cross section, the wall smooth; leaves and vegetative stems glabrous; stipules abaxially glabrous; peduncles glabrous or with a few hairs in a line; ovary depressed-globose ..... *B. sphaerocarpa*

***Burdachia prismatocarpa*** A. Juss., Ann. Sci. Nat. Bot. sér. 2, 13: 330. 1840.

*Burdachia williamsii* Steyerl., Fieldiana, Bot. 28: 285. 1952.

Shrub or tree 2–15 m tall; blade of larger leaves 10–21(–25) × (3–)4–12(–14) cm; fruits 9–20 × 7–17 mm. Along lowland rivers, 50–200 m; Bolívar (Cerro Marimarota, Río Horeda near Ciudad Bolívar, Río Parhueña), Amazonas (basins of upper Río Negro and upper Río Orinoco). Apure (Río Meta); Amazonian Colombia, Peru, Brazil. ♦Fig. 77.

Plants from Amazonas between San Fernando de Atabapo and Piedra Cocuy tend to have leaves < 6 cm wide, stipules only 3–5 mm long, a glabrous ovary, and fruits < 13 mm long, whereas elsewhere the leaves are mostly wider, the stipules are 6–10 mm long, the ovary is densely tomentose, and the fruits are mostly 14–20 mm long. The narrow-leaved form has been named as *Burdachia williamsii*, which I recognized in 1981. However, specimens that recombine the character states of these two taxa continue to accumulate. For example, *Davidse* 27754 (MICH, MO) and 27833 (MICH, MO, VEN) are *B. williamsii* with wide leaves; *Liesner* 8619 (MICH, MO, VEN), *Stergios & P. Stergios* 11293 (MICH, MO, NY, VEN), and *Stergios et al.* 11641 (MICH, VEN) are *B. williamsii* with a hairy ovary; *Maguire & C. Maguire* 35522 (MICH, NY, US, VEN) and *Davidse & González* 14086 from Apure (MICH) are *B. prismatocarpa* with short

stipules and fruits. Because of this variation I have decided to abandon *B. williamsii* as indefensible.

I have given the name *Burdachia prismatocarpa* var. *loretoënsis* W.R. Anderson to plants from Loreto, Peru, and adjacent Brazil. Given the variation discussed above, it may be that that variety will not continue to merit recognition. If it is recognized, the plants of Venezuela should be called *B. prismatocarpa* var. *prismatocarpa*.

***Burdachia sphaerocarpa*** A. Juss., Ann. Sci. Nat. Bot. sér. 2, 13: 330. 1840.

—*Burdachia prismatocarpa* var. *sphaerocarpa* (A. Juss.) Nied., Arbeiten Bot. Inst. Königl. Lyceum Hosianum Braunsberg 5: 60. 1914.

*Burdachia atractoides* Nied., Arbeiten Bot. Inst. Königl. Lyceum Hosianum Braunsberg 5: 59. 1914.

*Tetrapodenia glandifera* Gleason, Bull. Torrey Bot. Club 53: 289. 1926. —*Burdachia sphaerocarpa* var. *glandifera* (Gleason) W.R. Anderson, Mem. New York Bot. Gard. 32: 139. 1981.

Shrub or tree 3–15(–20) m tall; blade of larger leaves (8–)10–24 × 5–11(–13) cm; fruits 18–28 × 13–18 mm. Lowland primary and secondary forests, usually on the banks of rivers or streams or in periodically flooded areas, 50–100 m; Amazonas (Río Casiquiare, San Carlos de Río Negro). Guyana, Brazil (Amazonas, Pará). ♦Fig. 78.

Fig. 77. *Burdachia prismatocarpa*



Fig. 78. *Burdachia sphaerocarpa*

The type of *Tetrapodenia glandifera* came from the Amakura River, on the border between Guyana and Delta Amacuro, so the species must surely occur in Delta Amacuro too.

In 1981 I recognized the plants of western Amazonia as *Burdachia sphaerocarpa* var. *sphaerocarpa* and those of Guyana as *B.*

*sphaerocarpa* var. *glandifera*, on the basis of an apparent difference in petal color, pink in the west and white in the east. Subsequently collectors have described the petals of some western populations as white, so there seems to be no justification for recognizing two taxa within this species.

**5. BYRSONIMA** H.B.K., Nov. Gen. Sp. (quarto ed.) 5: 147. 1821 [1822].

*Alcoceratothrix* Nied., Arbeiten Bot. Inst. Königl. Lyceum Hosianum Braunschweig 1: 45. 1901.

Trees, shrubs, or subshrubs. Leaves eglandular; stipules intra- and epipetiolar, distinct or partially to completely connate, persistent on petiole in most species. Inflorescence terminal, a raceme of few-flowered cincinni or a pseudoraceme (i.e., a raceme of 1-flowered cincinni); floriferous bracts and bracteoles eglandular; pedicels sessile or sometimes raised on a short peduncle. Sepals all biglandular or all eglandular, connate as far as tips of glands, the glands green, yellow, white, or pink; petals yellow, white, pink, or red, glabrous in most species; lateral 4 petals with slender recurved claws, the anterior pair with deeply cup-shaped limbs, the posterior pair shallower; posterior petal with a stout, erect claw and the limb smaller, flat or crumpled and often reflexed. Stamens 10, the anthers  $\pm$  alike. Ovary with the 3 carpels completely connate, 3-locular, all locules fertile or the anterior sterile in some species; styles 3, slender and subulate, the stigmas minute and terminal or slightly internal. Fruit a drupe, the thin flesh green turning yellow, orange, red, purple, blue, or blue-black at maturity, the stone with a hard wall, 3-locular.

Mexico, Central America, West Indies, South America (all countries except Chile, Argentina, and Uruguay); at least 125 species, 44 known or expected in Venezuela, 40 of these in the flora area.

Key to the Species of *Byrsonima*

1. Pedicels long-pedunculate, the primary peduncle 5–15 mm long; petals yellow; anthers glabrous ..... *B. maguirei*
1. Pedicels sessile or short-pedunculate, the peduncle 0–3 mm long; petals yellow, white, pink, or red, if yellow the anthers mostly sericeous or tomentose between or on sides of locules ..... 2
- 2(1). Stipules distinct (Caution: This refers to the pair of stipules borne on the adaxial face of a single petiole, best viewed by removing the petiole, to which the stipules will remain attached. In a few species two stipules from opposite petioles are short-connate across the node, but that is *not* the connation to which this couplet refers); petals white, pink, or red, often changing from white to pink or red with age; anthers glabrous; ovary and fruit glabrous; bracts and/or bracteoles persistent to or past maturity of fruit ..... 3
2. Stipules  $\frac{1}{2}$  to completely connate beyond petiole; petals white, pink, red, or yellow; anthers glabrous or hairy; ovary and fruit glabrous or hairy; bracts and bracteoles persistent or deciduous ..... 15
- 3(2). Vegetative internodes, abaxial surface of stipules, petioles, and abaxial surface of leaf blades at least initially hairy, the hairs persistent or deciduous ..... 4

3. Vegetative internodes, abaxial surface of stipules, and leaves quite glabrous from the beginning except for short-hirsute axils of stipules (Caution: Do not confuse axis of inflorescence with vegetative internodes) ..... 9
- 4(3). Leaf blades with lateral veins very numerous and fine, not or hardly distinguishable from parallel veinlets and reticulum; flowers borne 1 per bract ..... 5
4. Leaf blades with principal lateral veins easily distinguished from finer veins and reticulum, usually 7–13 pairs, sometimes more in blades over 10 cm long; flowers borne 1–3 per bract ..... 7
- 5(4). Anther locules 1.8–3.1 mm long, cylindrical and unwinged or rarely bearing very narrow longitudinal wings  $< 0.1$  mm wide, the inner and outer thecae about the same length; pedicels straight or slightly nodding in fruit; leaf blades mostly obtuse or slightly acuminate at apex, sometimes nearly rounded ..... *B. coniophylla*
5. Anther locules 1–1.4 mm long, dorsiventrally flattened and bearing narrow membranous longitudinal wings, the outer thecae longer than the inner; pedicels usually decurved and sometimes twisted in fruit; leaf blades rounded or broadly obtuse at apex ..... 6
- 6(5). Leaf blades narrowly elliptic, 1.5–3(–3.6) cm wide, abaxially often persistently glaucous, the margin green; sepals revolute in anthesis; anther connective exceeding locules by 0.5–0.8 mm ..... *B. bronweniana*
6. Leaf blades elliptic or obovate, 3–5 cm wide, not glaucous abaxially, the margin yellow; sepals appressed in anthesis to eventually revolute; anther connective exceeding locules by 0.2–0.5 mm ..... *B. duidana*
- 7(4). Leaf blades abaxially persistently velutinous, the hairs on tissue between veins erect,  $\pm$  straight, basifixed, the hairs on veins denser, twisted, sub-basifixed ..... *B. cuprea*
7. Leaf blades abaxially glabrous or sparsely tomentose to glabrate between veins, tomentose to glabrate on principal veins, most densely so on midrib ..... 8
- 8(7). Blade of larger leaves 8.5–14.5  $\times$  4–8 cm, the petiole 10–19 mm long; stipules 3.5–7(–8) mm long, often acuminate; reticulum usually  $\pm$  concolorous with areolar tissue; inflorescence 9–18 cm long ..... *B. punctulata*
8. Blade of larger leaves 5–9(–10.5)  $\times$  3–4.5(–5) cm, the petiole 5–11 mm long; stipules 1.5–2.5(–3) mm long, acute or obtuse; fine reticulum visible (in dried leaves) abaxially or, usually, on both sides as a white mesh against darker areoles; inflorescence 5–10(–12.5) cm long ..... *B. leucophlebia*
- 9(3). Petioles slightly shorter than stipules to slightly longer, never twice as long ..... 10
9. Petioles at least twice as long as stipules, often longer ..... 11
- 10(9). Pedicels distally thickened, 2–3 mm diameter at apex, straight in bud; anther locules 1.6–2.2 mm long, the connective not or hardly exceeding them, by up to 0.1 mm; easternmost Bolívar ..... *B. pachypoda*
10. Pedicels up to 1 mm diameter in flower, 1.5 mm in fruit, circinate in bud; anther locules 1–1.3 mm long, the connective exceeding them by 0.1–0.5 mm; westernmost Bolívar and eastern Amazonas ..... *B. steyermarkii*

- 11(9). Pedicels decurved to eventually twisted in old flowers and fruits ..... 12
11. Pedicels ascending in old flowers and fruits ..... 13
- 12(11). Leaf blade with the abaxial epidermis deeply pitted, at maturity  $\pm$  densely and persistently glaucous ..... *B. luetzelburgii*
12. Leaf blade abaxially nearly or quite smooth and not or hardly glaucous ..... *B. laevis*
- 13(11). Pedicels becoming sigmoid in maturing fruits; petioles (18–)22–33 mm long; blade of larger leaves (11–)12.5–17.5  $\times$  (5–)6.5–8.5 cm ..... *B. sp. A*
13. Pedicels straight or curved but not sigmoid in fruits; petioles 5–17 mm long; blade of larger leaves 3–11(–13.5)  $\times$  1.5–6.5 cm ..... 14
- 14(13). Pedicels straight in bud, 2.5–3 mm long in flower, 5–7 mm long and 1.5–2 mm diameter in fruit; anther locules cylindrical and unwinged; sepals appressed in anthesis, not or only slightly revolute in fruit; stone of fruit apparently smooth; blade of larger leaves 3–5.5  $\times$  1.5–3.5 cm ..... *B. baccae*
14. Pedicels circinate in bud, 5–11 mm long in flower, 7–12 mm long and 0.7–1(–1.2) mm diameter in fruit; anther locules with the outer thecae dorsiventrally flattened and bearing narrow membranous longitudinal wings; sepals revolute at apex in anthesis, reflexed and revolute in fruit; stone of fruit rugose; blade of larger leaves (4.5–)6–11(–13.5)  $\times$  (2.5–)3–6.5 cm ..... *B. concinna*
- 15(2). Specimens with flowers ..... 16
15. Specimens with fruits ..... 42
- 16(15). Petals yellow, sometimes turning orange or red with age ..... 17
16. Petals white, pink, or red, often changing from white to pink or red with age ..... 25
- 17(16). Gnarled shrubs up to 60 cm tall; leaves mostly in dense clusters without measurable internodes ..... *B. verbascifolia*
17. Shrubs or trees (0.8–)1–35 m tall; internodes usually  $> 5$  mm long ..... 18
- 18(17). Leaf blades abaxially thinly to densely velutinous, the hairs with a straight, erect stalk, the branches mostly  $\leq$  stalk ..... 19
18. Leaf blades abaxially tomentose, sericeous, or glabrate, the hairs (if any) sessile, subsessile, or with a stalk much shorter than crosspiece or branches ..... 21
- 19(18). All or many hairs of abaxial surface of leaf blades stellate, i.e., with  $> 2$  branches; stipules (8–)10–25 mm long, deciduous ..... *B. stipulacea*
19. All hairs of leaf blades bifurcate, i.e., Y-shaped with only 2 branches; stipules 4–8 mm long, persistent on petiole ..... 20
- 20(19). Leaf blades  $\pm$  strongly revolute at margin and persistently velutinous adaxially over entire surface; sepals adaxially tomentose; ovary and fruit very densely and persistently hairy over entire surface, the hairs subappressed to suberect; bracts and bracteoles mostly persistent during maturation of fruit ..... *B. linguifera*
20. Leaf blades flat or only slightly revolute at margin, soon glabrescent adaxially or persistently velutinous or tomentose on midrib and sometimes on lateral veins; sepals adaxially glabrous; ovary and fruit glabrous or sparsely sericeous at apex; bracts and bracteoles mostly deciduous before maturity of fruit ..... *B. poeppigiana*

- 21(18). Posterior petal with 2 or more glands at apex of claw or occasionally on base of limb ..... 22
21. Posterior petal eglandular ..... 23
- 22(21). Ovary glabrous or very sparsely sericeous at apex; leaf blades abaxially  $\pm$  persistently subsericeous or appressed-tomentose, the hairs distinctly stalked, with slightly twisted, nonparallel crosspieces  $> 0.5$  mm long; leaf blades with 8–12 pairs of lateral veins strongly raised abaxially, parallel and anastomosing near margin, alternating with weaker, shorter, parallel veins; shrubs or small trees 2–5(–9) m tall ..... *B. chrysophylla*
22. Ovary sericeous; leaf blades abaxially appressed-sericeous to glabrate, the hairs sessile or subsessile, with short, straight, parallel crosspieces up to 0.5 mm long; leaf blades with 15–20 or more pairs of fine lateral veins parallel and anastomosing near margin, none very prominent abaxially; trees 3–25 m tall ..... *B. spicata*
- 23(21). Leaf blades abaxially tomentose to glabrate, the hairs  $\pm$  twisted, not parallel, not or only moderately appressed; petiole of larger leaves 5–13(–19) mm long ..... *B. crassifolia*
23. Leaf blades abaxially densely to sparsely sericeous or nearly glabrate, the hairs straight, appressed, and parallel; petiole of larger leaves (15–)20–40 mm long ..... 24
- 24(23). Leaf blades abaxially densely and persistently rusty brown-sericeous, occasionally belatedly glabrescent, the hairs 0.2–0.5 mm long; Delta Amacuro and eastern Bolívar ..... *B. aerugo*
24. Leaf blades abaxially sparsely sericeous to nearly glabrate, the hairs 0.1–0.2 mm long, never dense enough to hide epidermis; northwestern Bolívar and Amazonas ..... *B. crispa*
- 25(16). Anthers hairy ..... 26
25. Anthers glabrous ..... 31
- 26(25). Leaves sessile or subsessile, the petiole up to 2 mm long ..... *B. coccolobifolia*
26. Leaves petiolate, the petiole of larger leaves at least 5 mm long ..... 27
- 27(26). Anther locules rounded or acute at apex; bracts at least 3 mm long, mostly deciduous before maturity of fruit ..... 28
27. Anther locules extended at apex into slender, sterile projections; bracts up to 1.6(–2) mm long, persistent in fruit or some persistent and some deciduous in the same inflorescence ..... 29
- 28(27). Larger leaves with petiole 5–10 mm long, densely and  $\pm$  persistently tomentose, the blade (5–)7.5–15  $\times$  (3–)4–7 cm; anthers 1.8–2.8 mm long, the locules sparsely to moderately tomentose with  $\pm$  spreading and often twisted hairs that do not reach bulbous apex of connective; ovary glabrous; styles 2.7–3.7 mm long ..... *B. schomburgkiana*
28. Larger leaves with petiole (15–)23–48 mm long and glabrous, the blade (13–)15–23.5  $\times$  (6–)7–16 cm; anthers (2.5–)3–3.8 mm long, the locules very densely hirsute their whole length with straight, appressed, parallel hairs that often reach as high as tapered apex of connective or beyond; ovary densely sericeous on distal half; styles 4.5–6.5 mm long ..... *B. fernandezii*
- 29(27). Blade of larger leaves 5–8  $\times$  3–4 cm; lateral veins and reticulum barely or



- not visible in dried leaf blades; Gran Sabana, Bolívar ..... *B. dubia*
29. Blade of larger leaves 9–18.5 × 3.5–7.5(–8) cm; lateral veins and reticulum generally visible on one or both sides of dried leaf blades; basins of middle Río Orinoco west and south to upper Río Negro ..... 30
- 30(29). Leaves glabrous or thinly sericeous to glabrate on petiole and abaxial surface of blade, the hairs (if present) quite straight and very strongly appressed; peduncles 0–0.5 mm long; bracts 0.5–1(–1.5) mm long ..... *B. japurensis*
30. Leaves persistently appressed-tomentose or loosely subsericeous on petiole and abaxial surface of blade, or patchily glabrescent in age, the hairs sinuous to twisted, appressed to erect; peduncles 0–3 mm long in the same inflorescence, mostly 0.5–2 mm long; bracts 1.2–1.5(–2) mm long ..... *B. basiliana*
- 31(25). Ovary sericeous ..... 32
31. Ovary glabrous ..... 35
- 32(31). Bracts and bracteoles persistent past maturity of fruit; bracts 0.7–2(–2.5) mm long, ≤ bracteoles; flowers often borne 2(3) per bract; all 3 locules of ovary fertile ..... *B. christianeae*
32. Bracts and bracteoles all or most deciduous before or during anthesis; bracts 2.5–7 mm long, usually longer than bracteoles; flowers borne 1 per bract; only 2 locules of ovary fertile ..... 33
- 33(32). Leaf blades thinly to moderately sericeous abaxially with hairs not dense enough to completely conceal epidermis, sometimes eventually deciduous ..... *B. carraoana*
33. Leaf blades very densely and persistently sericeous or subsericeous abaxially, the hairs so dense as to completely conceal epidermis, even on older leaves ..... 34
- 34(33). Inflorescence 5–16 cm long; stipules 2.5–3.8 mm long; petioles 13–20 mm long; blade of larger leaves 6.5–12.5 × 3.3–7.5 cm; eastern Bolívar ..... *B. chalcophylla*
34. Inflorescence 18–26 cm long; stipules 4.5–9 mm long; petioles 20–28 mm long; blade of larger leaves 11–17 × 5.5–9 cm; Amazonas ..... *B. macrostachya*
- 35(31). Lateral petals adaxially pilose on claw, abaxially pilose on limb; stipules 6–11 mm long, completely and smoothly connate, the pair rounded at apex ..... *B. tillettii*
35. Petals glabrous; stipules 1.5–7.5 mm long, if ≥ 6 mm the pair triangular, acute at apex, sulcate in middle ..... 36
- 36(35). Leaf blades abaxially persistently dark brown-tomentose at maturity, the hairs very strongly twisted and so dense as to completely hide epidermis ..... *B. huberi*
36. Leaf blades abaxially glabrous or glabrate at maturity or, if persistently hairy, the hairs with nearly straight branches and never so dense as to completely hide epidermis ..... 37
- 37(36). Anthers with apex of connective about even with locules or exceeding them by no more than 0.3 mm ..... 38
37. Anthers with connective much enlarged at apex, exceeding locules by 0.7–1.6 mm ..... 39

- 38(37). Leaf blades with lateral veins very numerous and fine, not or hardly distinguishable from parallel veinlets and reticulum; petioles 8–16(–23) mm long; sepals abaxially glabrous or ciliate on margin and rarely bearing scattered hairs; hairs on filaments straight; fruit superior throughout development ..... *B. coniophylla*
38. Leaf blades with principal lateral veins easily distinguished from finer veins and reticulum, usually 5–8 pairs; petioles 2–6 mm long; sepals abaxially sericeous; hairs on filaments kinky; fruit developing half-immersed in enlarged, disk-like receptacle ..... *B. nitidissima*
- 39(37). Bracts and bracteoles persistent through anthesis and past maturity of fruit ..... *B. kariniana*
39. Bracts and bracteoles all or mostly deciduous before or during anthesis ..... 40
- 40(39). Bracts subtending only 1 flower, very rarely 2 ..... *B. frondosa*
40. Bracts (all or at least some in every inflorescence) subtending 2–4 flowers ..... 41
- 41(40). Pedicels decurved in old flowers and fruit; styles strongly bent in buds, ± straightening during anthesis; stipules 1.7–4(–5) mm long; calyx glands mostly absent or rudimentary, rarely well developed ..... *B. wurdackii*
41. Pedicels straight or bent upward in old flowers and fruit; styles nearly or quite straight in buds; stipules 4–7.5 mm long; calyx glands well developed ..... *B. cowanii*
- 42(15). Bracts and/or bracteoles persistent to or past maturity of fruit ..... 43
42. Bracts and bracteoles all or most deciduous before maturity of fruit .... 58
- 43(42). Leaves sessile or subsessile, the petiole up to 2 mm long ..... 44
43. Leaves petiolate, the petiole at least 4 mm long ..... 45
- 44(43). Leaf blades abaxially glabrous or very soon quite glabrate; stipules 1–2 mm long; fruits quite superior throughout development ..... *B. coccolobifolia*
44. Leaf blades abaxially sericeous or velutinous to glabrescent; stipules 2–5 mm long; fruits developing half-immersed in enlarged, disk-like receptacle ..... *B. nitidissima*
- 45(43). Bracts 3–5 times as long as bracteoles, strongly reflexed or revolute ..... 46
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- 46(45). Leaf blades densely velutinous on both sides, the hairs Y-shaped with a straight, erect stalk, the branches mostly shorter than stalk; leaf blades ± strongly revolute at margin; fruits persistently hairy over entire surface with hairs subappressed to suberect ..... *B. linguifera*
46. Leaf blades sericeous or glabrate, the hairs (if any) sessile or subsessile, straight, appressed; leaf blades flat at margin; fruits proximally glabrescent, distally sericeous to glabrate ..... 47
- 47(46). Leaf blades densely and persistently rusty brown-sericeous abaxially, occasionally belatedly glabrescent, the hairs 0.2–0.5 mm long; Delta Amacuro and eastern Bolívar ..... *B. aerugo*
47. Leaf blades sparsely sericeous to nearly glabrate abaxially, the hairs 0.1–0.2 mm long, never dense enough to hide epidermis; northwestern

- Bolívar and Amazonas ..... *B. crispa*
- 48(45). Leaf blades persistently dark brown-tomentose abaxially at maturity, the hairs very strongly twisted and so dense as to completely hide epidermis ..... *B. huberi*
48. Leaf blades glabrous or glabrate abaxially at maturity or, if persistently hairy, the hairs not dense enough to completely hide epidermis ..... 49
- 49(48). Fruits developing half-immersed in enlarged, disk-like receptacle ..... *B. nitidissima*
49. Fruits nearly to quite superior throughout development ..... 50
- 50(49). Sepals membranous in fruit, the portion beyond glands elongating to form a lingulate process at least twice as long as wide ..... *B. schomburgkiana*
50. Sepals  $\pm$  coriaceous in fruit, the portion beyond glands often somewhat accrescent but triangular, about as wide as long, often auriculate at base ..... 51
- 51(50). Pedicels straight or slightly nodding in fruit ..... 52
51. Pedicels strongly decurved and/or twisted in fruit ..... 55
- 52(51). Dried fruits 4–6 mm diameter; leaf blades with lateral veins very numerous and fine, not or hardly distinguishable from parallel veinlets and reticulum ..... *B. coniophylla*
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- 53(52). Blade of larger leaves 6.5–10.7 cm long; pedicels 2.5–6 mm long; bracts 2.5–7 mm long; fruits probably dark green or blue at maturity; 1450–2000 m ..... *B. kariniana*
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- 54(53). Blade of larger leaves 3.5–7.5(–8) cm wide; stipules 1.5–3(–4.5) mm long; fruits red at maturity, 10–16  $\times$  10–12 mm (dried); flowers 1 per bract; basins of middle Río Orinoco west and south to upper Río Negro ..... *B. japurensis*
54. Blade of larger leaves (6–)7–15 cm wide; stipules 3–5 mm long; fruits yellow or orange at maturity, 15–20 mm diameter (dried); flowers 1 per bract or more often a cluster of 2(3); expected in easternmost Bolívar ..... *B. christianeae*
- 55(51). Bracts (2.5–)3–5(–7) mm long, bracteoles 2–3 mm long; stipules 6–11 mm long, generally as long as petiole or longer, occasionally slightly shorter; flowers borne 1 or 2(3?) per bract ..... *B. tillettii*
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- 56(55). Blade of larger leaves 5–8  $\times$  3–4 cm; lateral veins and reticulum barely or not visible in dried leaf blades; Gran Sabana, Bolívar ..... *B. dubia*
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- 57(56). Leaves glabrous or thinly sericeous to glabrate on petiole and abaxial sur-

- face of blade, the hairs (if present) quite straight and very strongly appressed; peduncles 0–0.5 mm long; bracts 0.5–1(–1.5) mm long ..... *B. japurensis*
57. Leaves persistently appressed-tomentose or loosely subsericeous on petiole and abaxial surface of blade, or patchily glabrescent in age, the hairs sinuous to twisted, appressed to erect; peduncles 0–3 mm long in the same inflorescence, mostly 0.5–2 mm long; bracts 1.2–1.5(–2) mm long ..... *B. basiliiana*
- 58(42). Gnarled shrubs up to 60 cm tall; leaves mostly in dense clusters without measurable internodes ..... *B. verbascifolia*
58. Shrubs or trees 1–35 m tall; internodes mostly > 5 mm long, if shorter the plant at least 2 m tall ..... 59
- 59(58). Leaf blades thinly to densely velutinous abaxially, the hairs with a straight, erect stalk, the branches mostly  $\leq$  stalk ..... 60
59. Leaf blades tomentose, sericeous, glabrate, or glabrous abaxially, the hairs if present sessile, subsessile, or with a stalk much shorter than branches ..... 61
- 60(59). All or many hairs of abaxial surface of leaf blades stellate, i.e., with > 2 branches; stipules (8–)10–25 mm long, deciduous ..... *B. stipulacea*
60. All hairs of leaf blades bifurcate, i.e., Y-shaped with only 2 branches; stipules 4–8 mm long, persistent on petiole ..... *B. poeppigiana*
- 61(59). Leaves sessile or subsessile, the petiole up to 2 mm long; leaf blades usually rounded or cordate at base ..... *B. coccolobifolia*
61. Leaves petiolate, the petiole at least 5 mm long; leaf blades tapered, cuneate, or rounded at base ..... 62
- 62(61). Sepals membranous in fruit, the portion beyond glands elongating to form a lingulate process at least twice as long as wide ..... *B. schomburgkiana*
62. Sepals  $\pm$  coriaceous in fruit, the portion beyond glands often somewhat accrescent but triangular, about as wide as long, often auriculate at base ..... 63
- 63(62). Pedicels nearly or quite straight, or ascending, in fruit ..... 64
63. Pedicels strongly decurved or twisted in fruit ..... 69
- 64(63). Leaf blades abaxially nearly or quite glabrate as soon as expanded, with at most some appressed hairs persistent on midrib; fruit quite glabrous ..... 65
64. Leaf blades abaxially thinly to densely sericeous or subsericeous, the hairs persistent or eventually deciduous; fruit derived from a densely sericeous ovary and often bearing some hairs at maturity, especially at apex ..... 66
- 65(64). Bracts subtending only 1 flower, very rarely 2; inflorescence 6–15 cm long; stipules 1.5–2.5 mm long; blade of larger leaves 8–15  $\times$  3–7 cm ..... *B. frondosa*
65. Bracts (all or at least some in every inflorescence) subtending 2–4 flowers; inflorescence 15–35 cm long; stipules 4–7.5 mm long; blade of larger leaves 15–25  $\times$  7–13 cm ..... *B. cowanii*
- 66(64). Stipules completely and smoothly connate ..... *B. aerugo*
66. Stipules mostly incompletely connate, the pair sulcate and shallowly to

- deeply bidentate at apex ..... 67
- 67(66). Leaf blades thinly to moderately sericeous abaxially with hairs not dense enough to completely conceal epidermis, sometimes eventually deciduous ..... *B. carraoana*
67. Leaf blades very densely and persistently sericeous or subsericeous abaxially, the hairs so dense as to completely conceal epidermis, even on older leaves ..... 68
- 68(67). Inflorescence 5–16 cm long; stipules 2.5–3.8 mm long; petioles 13–20 mm long; blade of larger leaves 6.5–12.5 × 3.3–7.5 cm; eastern Bolívar ..... *B. chalcophylla*
68. Inflorescence 18–26 cm long; stipules 4.5–9 mm long; petioles 20–28 mm long; blade of larger leaves 11–17 × 5.5–9 cm; Amazonas ... *B. macrostachya*
- 69(63). Leaf blades with 15–20 or more pairs of fine lateral veins, none very prominent ..... *B. spicata*
69. Leaf blades with 5–12 pairs of principal lateral veins ..... 70
- 70(69). Leaf blades glabrous from the beginning or very soon nearly glabrate; petiole of larger leaves 15–48 mm long ..... 71
70. Leaf blades subsericeous to densely tomentose with hairs persistent or eventually mostly deciduous; petiole of larger leaves 5–15 mm long ..... 72
- 71(70). Fruits (dried) 12–17 × 10–16 mm, persistently sericeous at apex; calyx glands well developed ..... *B. fernandezii*
71. Fruits (dried) 6–7 mm diameter, quite glabrous; calyx glands mostly absent or rudimentary, rarely well developed ..... *B. wurdackii*
- 72(70). Blade of larger leaves 5–6.8 cm long, broadly obtuse to rounded at apex, adaxially rugose, abaxially persistently tomentose with hairs so dense as to completely hide epidermis, even on older leaves. .... *B. huberi*
72. Blade of larger leaves 6.5–17(–19) cm long, usually acute or acuminate at apex, sometimes narrowly obtuse, adaxially smooth or with veins slightly raised, abaxially tomentose or subsericeous to glabrescent, the hairs seldom so dense as to completely hide epidermis, especially on older leaves. .... 73
- 73(72). Fruits red at maturity, ovoid with a prominent apical beak ..... *B. basiliiana*
73. Fruits yellow at maturity, somewhat ovoid when young but nearly globose at maturity ..... 74
- 74(73). Sepals loosely sericeous adaxially; leaf blades elliptic, 2–3(–3.4) times as long as wide, persistently loosely subsericeous or appressed-tomentose abaxially, only rarely glabrescent in age ..... *B. chrysophylla*
74. Sepals usually glabrous adaxially; leaf blades mostly broadly elliptic to subrotund, 1.4–2 times as long as wide, mostly glabrescent abaxially in age, often patchily glabrescent, occasionally persistently tomentose ..... *B. crassifolia*

**Byrsonima aerugo** Sagot, Ann. Sci. Nat. Bot. sér. 6, 12: 178. 1881.

*Byrsonima ferruginea* var. *macrophylla* Benth., London J. Bot. 7: 119. 1848.

Tree (4–)15–45 m tall; stipules 2.5–4.5 mm long, completely connate; petioles (15–)20–40 mm long; blade of larger leaves

11–22(–25) × 4–9(–11) cm, densely and ± persistently rusty brown-sericeous abaxially, occasionally belatedly glabrescent; bracts and bracteoles persistent or deciduous in fruit; bracts 3.5–5 mm long, strongly reflexed or revolute; bracteoles 0.6–1.5 mm long; pedicels nearly or quite straight, or ascending,

in fruit; petals yellow, the posterior petal eglandular; anthers sericeous, especially between locules, the connective equaling locules or exceeding them by up to 0.6 mm; ovary densely sericeous; fruit yellow, 10–13 mm diameter (dried), sericeous to glabrate. Evergreen lowland to lower montane forests, 200–1300 m; Delta Amacuro (Caño Acoima, east-northeast of El Palmar, east-southeast of Imataca), widespread in eastern Bolívar to 63°W. Guyana, Suriname, French Guiana, Brazil (Roraima). ♦Fig. 85.

This species is close to *Byrsonima crispa* A. Juss., and when its leaf hairs are eventually deciduous instead of persistent (e.g., Cardona 2150 [MICH, MO, VEN] and 2164 [MICH, MO, US, VEN]) the distinction becomes difficult. Nevertheless, *B. aerugo* is a useful taxon and I am not yet ready to abandon it, especially because the two species seldom if ever occur together.

**Byrsonima baccae** W.R. Anderson, Contr. Univ. Michigan Herb. 20: 19. 1995.

Shrub or small tree 1–6 m tall; vegetative internodes glabrous except in axil of stipules; stipules 1.5–2.5 mm long, distinct; petioles 5–8 mm long; blade of larger leaves 3–5.5 × 1.5–3.5 cm, glabrous, rounded or broadly obtuse at apex; bracts and bracteoles persistent in fruit, 1.5–3.2 mm long, stiff; pedicels straight in bud, 2.5–3 mm long in flower, straight in fruit, becoming 5–7 mm long, 1.5–2 mm diameter; sepals appressed in anthesis, not or only slightly revolute in fruit; petals pink; anther locules glabrous, cylindrical, the connective exceeding locules by 0.3–0.6 mm; ovary and fruit glabrous; fruit 6–9 mm diameter (dried), the stone apparently smooth. On rocky slopes, in elfin forests, along streams, 1700–2200 m; Amazonas (Sierra Maigualida). Endemic.

**Byrsonima basiliiana** W.R. Anderson, Contr. Univ. Michigan Herb. 21: 45. 1997.

Shrub or small tree; stipules 1.5–2.5 mm long, connate, rounded; petioles 8–12 mm long; blade of larger leaves 9.5–13.5 × 3.5–5.7 cm, abaxially appressed-tomentose or loosely subsericeous to patchily glabrescent; bracts and bracteoles persistent or deciduous in fruit; bracts 1.2–1.5(–2) mm long; peduncles (0–)0.5–2(–3) mm long; bracteoles 0.7–1 mm long; pedicels decurved or twisted

in fruit; petals white and pink; anther locules sericeous, drawn out at apex into slender sterile extensions 0.5–1 mm long, the connective exceeding fertile part of locules by 0.5 mm; ovary glabrous or tomentose; fruit red, 8–9.5 × 6.5 mm (dried), beaked at apex, glabrous or tomentose to glabrate. Evergreen lowland forests, 100–200 m; Amazonas (Río Casiquiare, Río Emoni). Endemic.

**Byrsonima bronweniana** W.R. Anderson, Mem. New York Bot. Gard. 32: 107. 1981.

Shrub or tree 2–8 m tall; vegetative internodes sparsely sericeous to glabrate; stipules 1–2 mm long, distinct; petioles 6–13 mm long; blade of larger leaves 5–9.5 × 1.5–3(–3.6) cm, narrowly elliptic, rounded or obtuse at apex, sparsely sericeous to glabrate, abaxially often persistently glaucous, the lateral veins numerous and fine; bracts and bracteoles persistent in fruit; pedicels decurved or twisted in fruit; sepals revolute in anthesis; petals white turning pink; anthers glabrous, the locules 1–1.3 mm long, dorsiventrally flattened and narrowly winged, the connective exceeding locules by 0.5–0.8 mm, globose; ovary and fruit glabrous; fruits red or purplish, 5.5–7 mm diameter (dried). Along rivers, 50–200 m; Amazonas (basins of upper Río Orinoco and upper Río Negro). Colombia (Guainía), Brazil (Amazonas: upper Río Negro and Rio Uaupés). ♦Fig. 82.

**Byrsonima carraoana** Steyerl., Fieldiana, Bot. 28: 287. 1952. —*Byrsonima chalcophylla* var. *carraoana* (Steyerl.) W.R. Anderson, Mem. New York Bot. Gard. 32: 117. 1981.

*Byrsonima bolivarana* Steyerl., Fieldiana, Bot. 28: 287. 1952.

Shrub or tree (1.5–)3–12 m tall; stipules (2–)3–5 mm long, 2/3- to almost completely connate; petioles 7–18(–22) mm long; blade of larger leaves 5–12(–18.5) × 3–7(–10) cm, abaxially sericeous, sometimes eventually glabrescent, with hairs not dense enough to completely conceal epidermis; inflorescence 5–15 cm long; bracts and bracteoles deciduous before or during anthesis, 3–7 mm long or bracteoles shorter; pedicels nearly or quite straight in fruit; petals pink or pink in center and otherwise white; anther locules glabrous, cylindrical, the connective exceeding

locules by 0.8–1.7 mm; ovary densely sericeous; fruits 8–10 mm long (dried), sericeous to glabrate. Montane, often dwarf forests, 1200–2000 m; eastern Bolívar (Auyán-tepui and Sierra de Lema south and east to Roraima). Guyana (Pakaraima Mountains, upper Mazaruni River basin). ♦Fig. 81.

Since I treated this as a variety of *Byrsonima chalcophylla*, in 1981, accumulating collections have eroded the morphological differences between *B. carraoana* and *B. macrostachya*, and between *B. macrostachya* and *B. chalcophylla*. I now feel that *B. carraoana*, *B. chalcophylla*, and *B. macrostachya* should all have the same taxonomic status, and have elected to consider them a complex of three closely related species. One could also make the argument for treating them as three varieties of one species. *B. carraoana* is far better collected than the other two.

***Byrsonima chalcophylla*** Nied., Arbeiten Bot. Inst. Königl. Lyceum Hosianum Braunsberg 5: 57. 1914.

Tree 3–12 m tall; stipules 2.6–3.8 mm long, 1/2–3/4-connate; petioles 13–20 mm long; blade of larger leaves 6.5–12.5 × 3.3–7.5 cm, abaxially very densely and persistently sericeous; inflorescence 5–16 cm long; bracts and bracteoles deciduous before or during anthesis, 3–7 mm long or bracteoles shorter; pedicels nearly or quite straight in fruit; petals pink; anther locules glabrous, cylindrical, the connective exceeding locules by 0.6–1 mm; ovary densely sericeous; immature fruits 13 mm long (dried), sericeous to glabrescent. Tepui slope forests, ca. 1900 m; eastern Bolívar (Ilú-tepui, Roraima-tepui). Guyana.

*Byrsonima chalcophylla* is known from only three collections, the two in the flora area and one from ca. 1700 m on the slopes of Mount Roraima in Guyana.

See comments under *Byrsonima carraoana*.

***Byrsonima christianeae*** W.R. Anderson, Mem. New York Bot. Gard. 32: 112. 1981.

Tree (8–)12–25 m tall; stipules 3–5 mm long, completely connate or distinct at apex; petioles 20–35(–45) mm long; blade of larger leaves (16–)18–30 × (6–)7–15 cm, initially sparsely sericeous, soon glabrate; bracts and

bracteoles persistent in fruit, 0.7–2.5 mm long; pedicels straight in fruit; petals white turning red in age; anther locules glabrous, unwinged, the connective exceeding locules by 1.2–2.9 mm; ovary sericeous; fruits yellow or orange, 15–20 mm diameter (dried), sparsely sericeous or glabrate. Expected in eastern Bolívar.

*Byrsonima christianeae* is known presently only from mixed evergreen forests, 70–950 m, from Guyana (Mt. Ayanganna in the upper Mazaruni River basin) and Brazil (Amapá, Pará).

***Byrsonima chrysophylla*** H.B.K., Nov. Gen. Sp. (quarto ed.) 5: 150. 1821 [1822]. —Manteco.

Shrub or small tree 2–5(–9) m tall; stipules 2–3 mm long, completely and smoothly connate; petioles 5–15 mm long; blade of larger leaves 7–17 × 4–7(–9) cm, ± persistently subsericeous or appressed-tomentose abaxially, the hairs distinctly stalked, with slightly twisted, nonparallel crosspieces > 0.5 mm long, with 8–12 pairs of principal lateral veins strongly raised abaxially; bracts and bracteoles mostly deciduous before maturity of fruit; pedicels mostly decurved or twisted in fruit; sepals loosely sericeous adaxially; petals yellow, the posterior petal bearing 2 glands at apex of claw; anthers sericeous, especially between locules, the connective equaling or slightly exceeding locules; ovary glabrous or very sparsely sericeous at apex; fruits yellow, globose, 6–10 mm diameter (dried), glabrous. In or at the edges of savannas, or in woodlands along rivers, 100–200(–900) m; scattered in northwestern and southwestern Bolívar, common in Amazonas (basins of upper Río Orinoco and the Río Negro). Amazonian Colombia, Suriname, Peru, Brazil, Bolivia.

This species is close to *Byrsonima spicata*, and the placement of some collections in one species or the other can be rather arbitrary. Examples are Bunting et al. 3476 (MY) and Gentry & Berry 14694 (MICH, MO), both collected in the vicinity of Puerto Ayacucho.

***Byrsonima coccolobifolia*** H.B.K., Nov. Gen. Sp. (quarto ed.) 5: 148. 1821 [1822]. —Chaparro, Manteco merey.

*Byrsonima sessilifolia* Benth., London J. Bot. 7: 124. 1848.

Shrub or small tree 1–5 m tall; stipules 1–2 mm long, connate; petioles 0–2 mm long; blade of larger leaves 6–15.5 × 4–10 cm, usually rounded or cordate at base, glabrous or very soon quite glabrate; bracts and bracteoles mostly deciduous in fruit or rarely many persistent, 1.5–3.5(–5) mm long or bracteoles smaller; pedicels decurved or twisted in fruit; sepals lingulate-acrescent and membranous in fruit; petals white and/or pink; anther locules sericeous, the connective exceeding locules by (0–)0.2–1.3 mm; ovary and fruit glabrous; fruits green (yellow at maturity?), 6–8 mm diameter (dried). Savannas, 50–400 m; Delta Amacuro (Los Castillos), common in middle and northern Bolívar. Anzoátegui, Aragua, Barinas, Carabobo, Cojedes, Falcón, Guárico, Monagas, Sucre, Zulia; Cuba, Colombia, Guyana, Suriname, Peru, Brazil, Bolivia, Paraguay. ♦Fig. 80.

In the southwestern extreme of its range (Bolivia, Mato Grosso, Paraguay) this species may reach heights of 10 m, but in Venezuela and Guyana it seldom if ever exceeds 5 m.

***Byrsonima concinna*** Benth., London J. Bot. 7: 122. 1848.

*Byrsonima bracteolaris* Benth., London J. Bot. 7: 123. 1848.

Shrub or small tree 1.2–8(–15) m tall; vegetative internodes glabrous except in axil of stipules; stipules 1.5–2.5(–3.5) mm long, distinct; petioles 7–17 mm long; blade of larger leaves (4.5–)6–11(–13.5) × (2.5–)3–6.5 cm, glabrous, acute to rounded and often apiculate at apex; bracts and bracteoles persistent in fruit, (1–)2–5 mm long, usually spreading and often revolute; pedicels circinate in bud, 5–11 mm long in flower, straight or curved upward in fruit, becoming 7–12 mm long, 0.7–1(–1.2) mm diameter; sepals revolute at apex in anthesis, reflexed and revolute in fruit; petals pink(?) or white turning pink; anther locules glabrous, dorsiventrally flattened and bearing narrow membranous longitudinal wings, the connective exceeding locules by (0.2–)0.4–0.8 mm; ovary and fruit glabrous; fruits 4–8 mm diameter (dried), the stone rugose. Savannas, slope forests, (100–)400–2100 m; Bolívar (common in Gran Sabana and on tepuis as far west as Cerro Camarón), Amazonas (isolated populations on Cerro Marahuaka, Cerro Sipapo, Cerro

Yutajé, and Sierra de la Neblina). Western Guyana, Brazil (Roraima, on the border with Venezuela).

In Bolívar and adjacent Guyana this species is variable but reasonably homogeneous. However, in Amazonas most populations are somewhat different, with relatively large leaves, narrow anther wings, and short fruiting pedicels. One collection (Fernández et al. 6041, MICH, MO) has the pedicels apparently straight in bud. The complex containing *Byrsonima concinna* probably deserves re-evaluation in Amazonas.

A related species that may eventually be found in eastern Bolívar is *Byrsonima rubrobracteata* W.R. Anderson, Mem. New York Bot. Gard. 32: 105. 1981. It has been collected three times on the Ayanganna Plateau of western Guyana; other species from that area have been found in adjacent Venezuela. *Byrsonima rubrobracteata* is distinguished by its short dense inflorescence up to 6 cm long, with red bracts and bracteoles and only one flower per bract; its stipules are 3.5–5 mm long.

***Byrsonima coniphylla*** A. Juss., Ann. Sci. Nat. Bot. sér. 2, 13: 335. 1840.

Shrub or small tree 1–8 m tall, occasionally shorter; vegetative internodes hairy to glabrescent; stipules 2.5–4(–5) mm long, distinct to nearly connate; petioles 8–16(–23) mm long; blade of larger leaves 7–12(–15.5) × 2.5–4.7(–5.2) cm, mostly obtuse, broadly obtuse, or slightly acuminate at apex, sometimes rounded, thinly sericeous to glabrate, often persistently glaucous abaxially, the lateral veins numerous and fine; bracts and bracteoles persistent in fruit, 2.5–4 mm long or bracteoles smaller; pedicels straight or slightly nodding in fruit; petals white turning red in age; anther locules 1.8–3.1 mm long, glabrous, cylindrical and unwinged or rarely bearing very narrow longitudinal wings < 0.1 mm wide, the connective equaling locules or exceeding them by up to 0.3 mm; ovary and fruit glabrous; fruits red, purplish, or black, 4–6 mm diameter (dried). Sandy seasonally flooded savannas, 100–200 m; common in Amazonas (upper Río Orinoco and Río Atabapo south to Río Casiquiare, Río Guainía, and Río Pasimoni). Colombia (Guainía, Vaupés), Brazil (northern Amazonas, southwestern Roraima).

As I noted in my 1981 paper, plants from near the Río Atabapo sometimes have atypically small stature and leaves, which causes them to resemble their eastern relative *Byrsonima eugeniifolia* Sandwith. That species grows in sandy savannas of Guyana, Suriname, and Roraima and adjacent Amazonas, Brazil, including the tepui called Serra Aracá, but seems not to reach Venezuela.

***Byrsonima cowanii*** W.R. Anderson, Mem. New York Bot. Gard. 32: 123. 1981.

Tree (2-)4-12 m tall; stipules 4-7.5 mm long,  $\frac{1}{2}$ - $\frac{4}{5}$  connate, acute; petioles 11-21 (-25) mm long; blade of larger leaves 15-25 x 7-13 cm, sparsely sericeous to soon glabrate; inflorescence 15-35 cm long, the cincinni mostly 2-4-flowered; bracts and bracteoles deciduous during anthesis; bracts 3-8 mm long; bracteoles 1-3.5 mm long; pedicels straight or bent upward in fruit; calyx glands well developed; petals white and/or pink (white turning pink?); anther locules glabrous, unwinged, the connective exceeding locules by 0.8-1.5 mm; ovary and fruit glabrous; styles nearly or quite straight in bud; fruits dark blue, 7-10 mm diameter (dried). Forests, woodlands, often on granitic outcrops, 100-600 m; Amazonas (lowlands of the upper Río Orinoco and Río Atabapo from Río Cuao south to 3°12'N). Endemic? ♦Fig. 84.

In recent years, specimens resembling this species have been collected in Roraima, Brazil, and Loreto, Peru, but they are so incomplete that accurate identification is not possible.

***Byrsonima crassifolia*** (L.) H.B.K., Nov.

Gen. Sp. (quarto ed.) 5: 149. 1821 [1822].

—*Malpighia crassifolia* L., Sp. Pl. 426.

1753. —Chaparro, Chaparro manteco.

*Byrsonima ferruginea* H.B.K., Nov. Gen.

Sp. 5: pl. 446. 1821.

*Byrsonima laurifolia* H.B.K., Nov. Gen.

Sp. (quarto ed.) 5: 150. 1821 [1822].

Shrub or small tree (0.8-)1-8(-10) m tall; stipules 2-3(-4) mm long, completely and smoothly connate; petioles 5-13(-19) mm long; blade of larger leaves 6.5-11(-15.5) x 3-6.5(-8) cm, broadly elliptic to subrotund, densely tomentose to glabrate on both sides; bracts and bracteoles deciduous in fruit; pedicels decurved in fruit; sepals adaxially glabrous or rarely sparsely tomentose; petals

yellow, the posterior petal eglandular; anthers pilose with few to many spreading hairs, the connective equaling locules or exceeding them by up to 0.2(-0.4) mm; ovary glabrous or sparsely to densely tomentose-sericeous; fruits yellow, 8-10 mm diameter (dried), glabrous or sparsely tomentose to glabrate. Savannas, 50-1300 m; Delta Amacuro (near Los Castillos), throughout Bolívar and Amazonas. Common in savannas across northern Venezuela; Mexico, Central America, West Indies, Colombia, Guyana, Suriname, French Guiana, Brazil, Bolivia, Paraguay.

*Byrsonima crassifolia* is exceedingly variable through its range and may eventually yield defensible segregates, but within our area it is reasonably homogeneous. In my 1981 paper I recognized *B. laurifolia*, but subsequent study of the type has suggested that it is simply atypical material of this species. See discussion of probable hybrids under *B. verbascifolia*.

***Byrsonima crispa*** A. Juss., Ann. Sci. Nat.

Bot. sér. 2, 13: 335. 1840. —Manteco de agua.

*Byrsonima carmeniana* Cuatrec., Webbia 13: 615. 1958.

Tree (2.5-)6-30 m tall; stipules 3-4.5 mm long, completely connate; petioles 12-35(-40) mm long; blade of larger leaves (8-)11-20(-22) x (3-)4.5-8(-9) cm, sparsely sericeous to nearly glabrate abaxially; bracts (2.5-)3-4.5(-6) mm long, strongly reflexed or revolute, persistent or deciduous in fruit; bracteoles 0.5-1(-1.5) mm long, mostly persistent in fruit; pedicels mostly straight and ascending in fruit; petals yellow, the posterior petal eglandular; anthers sericeous, especially between locules, the connective equaling locules or exceeding them by up to 0.6 mm; ovary densely sericeous; fruits yellow, 10-13 mm diameter (dried), sericeous to glabrate. Nonflooded forests, 50-600 m; northwestern Bolívar (southeast of Pijiguaos, Túriba), Amazonas (Isla Ratón, Puerto Ayacucho, Río Cuao, Río Mawarín, San Antonio del Sipapo, Sierra Parima). Scattered in Costa Rica, Panama, Colombia, and Amazonian Peru, and common in Amazonian Brazil from Manaus east to Belém and south to Bolivia and Espírito Santo.

***Byrsonima cuprea*** Griseb. in Mart., Fl. Bras. 12(1): 19. 1858.

Shrub or tree (2-)3-8(-16) m tall; vegetative internodes velutinous; stipules 5-9 mm long, distinct, acuminate; petioles 9-20 mm long; blade of larger leaves 8-16 x 4-8 cm, abaxially persistently velutinous; bracts and bracteoles persistent in fruit, 1.5-2.5(-3.5) mm long or bracteoles smaller; pedicels decurved in fruit; petals white turning pink or red in age; anther locules glabrous, linear, the connective exceeding locules by 0.5-0.9 mm; ovary and fruit glabrous; fruits red, 5-6 mm diameter (dried). Riparian forests, 100-200 m; Amazonas (Río Atabapo, Río Atacavi, Río Casiquiare, Río Cuao, Río Negro, Río Orinoco, Río Pasimoni, Río Sipapo, Río Ventuari, Río Yatua). Brazil (Amazonas: upper Río Negro).

See discussion under *Byrsonima punctulata*.

***Byrsonima dubia*** W.R. Anderson, Contr. Univ. Michigan Herb. 17: 42. 1990.

Shrub or small tree 3-4 m tall; stipules 2-3 mm long,  $\frac{3}{4}$ - $\frac{5}{6}$  connate, the apical lobes obtuse to rounded; petioles 15-18 mm long; blade of larger leaves 5-8 x 3-4 cm, obovate to nearly elliptic, obtuse to rounded and apiculate at apex, thinly sericeous to glabrate, the lateral veins and reticulum obscure; bracts and bracteoles persistent in fruit, 1-1.6 mm long; pedicels decurved and/or twisted in fruit; petals probably pink or white; anther locules appressed-hirsute, with slender sterile extensions at apex, the connective exceeding fertile part of locules by 0.8-1 mm; ovary glabrous; fruits unknown. Thorn scrub in dry areas, 1400-1500 m; Bolívar (northwest of Cerro El Sol). Guyana (upper Potaro River).

*Byrsonima dubia* is known from only two collections, and although these lack petals, it is keyed with some confidence as having pink or white petals because it is apparently related to *B. gymnocalycina* A. Juss., of Guyana, and *B. laevigata* (Poir. in Lam.) DC., a tall tree of lowland forests in Suriname, French Guiana, and northeastern Brazil (Amapá, Bahia, Maranhão, and Pará).

***Byrsonima duidana*** W.R. Anderson, Contr. Univ. Michigan Herb. 19: 361. 1993.

Shrub or small tree 2-4 m tall; vegetative

internodes initially sericeous, soon or eventually glabrate; stipules 2-3 mm long, distinct; petioles 8-15 mm long; blade of larger leaves 5.5-10 x 3-5 cm, elliptic or obovate, rounded or obtuse and sometimes apiculate or retuse at apex, initially sparsely sericeous but soon glabrate, the lateral veins numerous and fine, the margin yellow; bracts and bracteoles persistent in fruit; pedicels decurved or twisted in fruit; sepals appressed in anthesis to eventually revolute, accrescent and reddish in fruit; petals white turning pink; anthers glabrous, the locules 1.1-1.3 mm long, dorsiventrally flattened and narrowly winged, the connective exceeding locules by 0.2-0.5 mm, globose; ovary and fruit glabrous; fruits 4.5-7 mm diameter (dried). Tepui scrub, edges of savannas, along valley forests, 50-2300 m; Amazonas (hills south and southeast of Cerro Camani, Cerro Duida, Cerro Marahuaka, Cerro Sipapo). Endemic. ♦Fig. 79.

This is the species that I treated as *Byrsonima bracteolaris* Benth. in my 1981 paper on the Malpighiaceae of the Guayana Highland. That name has fallen into synonymy under *B. concinna*. *Byrsonima duidana* belongs to a difficult complex that contains *B. laevis* and *B. luetzelburgii*, and the taxonomy of that group is not entirely satisfactory; see comments under *B. laevis*.

***Byrsonima fernandezii*** Cuatrec., Webbia 13: 612. 1958.

Tree (5-)10-25 m tall; stipules 1.5-3(-4) mm long, completely connate, obtuse or rounded at apex; petioles (15-)23-48 mm long; blade of larger leaves (13-)15-23.5 x (6-)7-16 cm, rounded and often apiculate at apex, glabrous; bracts and bracteoles deciduous before or during anthesis, or at the latest before maturation of fruit; bracts 3-5.5 mm long; bracteoles 1.5-2 mm long; pedicels decurved or twisted in fruit; petals white, perhaps turning pink in age(?); stamens densely hirsute; anthers (2.5-)3-3.8 mm long, the locules rounded at apex, the connective tapered, exceeding locules by 0.9-1.7 mm; ovary densely sericeous on distal half; styles 4.5-6.5 mm long; fruits 12-17 x 10-16 mm (dried), sericeous at apex. Lowland to lower montane forests, 100-800 m; Amazonas (Cerro Huachamacari, basin of upper Río Cuao, southeast of San Fernando de



Atabapo). Scattered in Colombia (Vaupés), Brazil (Amazonas: north of Manaus, vicinity of Humaitá, São Paulo de Olivença).

The type was said to have the flowers "moradas," i.e., purple, a color otherwise unknown in the genus and all but unknown in the family. More recent collections state that the petals are white, as I would have expected, given the other characteristics of the species.

**Byrsonima frondosa** A. Juss., Ann. Sci. Nat. Bot. sér. 2, 13: 334. 1840.

Tree 4–20 m tall; stipules 1.5–2.5 mm long, completely connate or the pair bidentate, triangular, acute or obtuse at apex; petioles 8–15(–18) mm long; blade of larger leaves 8–15 × 3–7 cm, initially sericeous but glabrate at maturity; inflorescence 6–15 cm long, the flowers borne 1(2) per bract; bracts and bracteoles deciduous before or during anthesis; bracts 3.5–5 mm long; bracteoles 1.5–2.5 mm long; pedicels straight in old flowers and fruit; calyx glands well developed; petals pink; anther locules glabrous, unwinged, the massive connective exceeding locules by 0.7–1.2 mm; ovary and fruit glabrous; styles nearly or quite straight in bud; mature fruits unknown. Wet forests along lowland rivers, ca. 100 m; Amazonas (Río Baría, Río Yatúa). Brazil (Amazonas: Rio Negro, Rio Uaupés).

**Byrsonima huberi** W.R. Anderson, Contr. Univ. Michigan Herb. 21: 48. 1997.

Tree 3 m tall; stems densely tomentose; stipules 3–4 mm long, completely and smoothly connate; petioles 8–12 mm long; blade of larger leaves 5–6.8 × 2.6–3.8 cm, broadly obtuse to rounded at apex, deeply rugose adaxially, abaxially very densely and persistently dark brown-tomentose; bracts and bracteoles persistent in fruit (? at least at nodes with maturing fruits); bracts 2.5–3.5 mm long, bracteoles similar but smaller; petals probably white or pink; anther locules glabrous, cylindrical, the connective not or hardly exceeding locules; ovary and fruit glabrous; fruits orange, 10 mm diameter (dried). Upper montane shrubby woodland/meadow ecotone, ca. 2000 m; Amazonas (Sierra Maimualida). Endemic.

*Byrsonima huberi* is known only from the type collection, which bears only extremely

immature flower buds and one detached fruit, so many of the character-states needed for placing this species in a key are not known with confidence, but the leaves are unlike those of any other species in the Guayana area.

**Byrsonima japurensis** A. Juss., Ann. Sci. Nat. Bot. sér. 2, 13: 335. 1840.

*Byrsonima inundata* Benth., London J. Bot. 7: 122. 1848.

*Byrsonima uvulifera* Spruce ex Nied., Arbeiten Bot. Inst. Königl. Lyceum Hosianum Braunsberg 1: 37. 1901.

*Byrsonima fluminensis* Nied., Arbeiten Bot. Inst. Königl. Lyceum Hosianum Braunsberg 1: 43. 1901. —*Byrsonima japurensis* subsp. *fluminensis* (Nied.) Cuatrec., Webbia 13: 627. 1958.

*Byrsonima japurensis* subsp. *silvatica* Cuatrec., Webbia 13: 626. 1958.

Shrub or tree (2–)3–21 m tall; stipules 1.5–3(–4.5) mm long, connate, the pair acute to rounded; petioles (8–)12–20(–25) mm long; blade of larger leaves 9–18.5 × 3.5–7.5(–8) cm, abaxially sparsely sericeous to usually glabrate; bracts and bracteoles persistent in fruit (at least the bracts), 0.5–1(–1.5) mm long; pedicels straight or decurved/twisted in fruit; petals white or pink; anther locules sparsely to densely sericeous, drawn out at apex into slender, sterile extensions 0.3–1.2 mm long, the connective exceeding fertile part of locules by 0.3–1.2 mm; ovary glabrous or sericeous; fruits red, 10–16 × 9–12 mm (dried), often beaked at apex, glabrous or glabrate. Riparian forests, 50–300 m; Bolívar (basins of Río Caura, Río Maniapure, Río Paragua, Río Parguaza, Río Orinoco, and Río Suapure), Amazonas (basins of Río Asisa, Río Casiquiare, Río Mavaca, Río Orinoco, Río Pamoni, Río Pasiba, Río Ventuari, and Río Siapa). Anzoátegui, Apure, Guárico; Amazonian Colombia, Ecuador, Peru, and Brazil.

**Byrsonima kariniana** W.R. Anderson, Mem. New York Bot. Gard. 32: 127. 1981.

Shrub to 4 m tall; stipules 3.4–5 mm long,  $\frac{1}{2}$ – $\frac{4}{5}$  connate, acute; petioles 12–19 mm long; blade of larger leaves 6.5–10.7 × 3–5.5 cm, glabrous (initially sericeous but very soon quite glabrate); inflorescence 6–13 cm

long; bracts and bracteoles persistent past maturity of fruit; bracts 2.5–7 mm long; bracteoles 2–3.5 mm long; pedicels 2.5–6 mm long, straight (or slightly decurved?) in fruit; petals pink (white turning pink?); anther locules glabrous, unwinged, the connective exceeding locules by 0.7–1(–1.5) mm; ovary and fruit glabrous; fruits blue(?) or dark green(?), ca. 10 mm diameter (dried). Tepui slope forests and savannas, 1400–2000 m; Amazonas (Cerro Sipapo). Apparently endemic.

Related species occur at high elevations in northern Venezuela and in Trinidad, but none of those populations seems to be conspecific with the plant of Cerro Sipapo.

**Byrsonima laevis** Nied., Arbeiten Bot. Inst. Königl. Lyceum Hosianum Braunsberg 1: 34. 1901.

Shrub or tree 1.5–12 m tall; vegetative internodes glabrous except in axil of stipules; stipules 1–2 mm long, distinct; petioles (3–)5–22 mm long; blade of larger leaves 6–10.5(–13) × 3–7 cm, glabrous; bracts and bracteoles persistent in fruit, 0.5–1.5 mm long; pedicels decurved or eventually twisted in old flowers and fruit; petals white turning pink; anther locules glabrous, dorsiventrally flattened and longitudinally winged, the connective exceeding locules by 0.1–0.3 mm; ovary and fruit glabrous; fruits 4–12 mm diameter (dried). Forests and savannas on white sand, 100–1500 m; southern Amazonas (Cerro Aracamuni, Maroa/Yavita, Río Atacavi, Río Guainía/Casiquiare, Río Manapiare, Río Mawarinuma, San Fernando de Atabapo, Sierra de la Neblina). Brazil (northwestern Amazonas).

The collections included here are a diverse lot, certainly closely related but perhaps not all one species. In my 1981 paper I recognized both *Byrsonima laevis* and *B. amoena* Cuatrec. as being in Amazonas, Venezuela. They were distinguished on the basis of size of leaves and fruits. Subsequent collections have eroded that distinction, and I can no longer justify recognizing both species in our area. I am using the older name, which happens to have been based on a type from near the mouth of Río Casiquiare. It remains to be seen whether *B. amoena* will stand as distinct elsewhere in western Amazonia.

**Byrsonima leucophlebia** Griseb. in Mart., Fl. Bras. 12(1): 15. 1858.

Shrub or small tree 2–5(–8) m tall; vegetative internodes hairy to glabrescent; stipules 1.5–2.5(–3) mm long, distinct, acute or obtuse; petioles 5–11 mm long; blade of larger leaves 5–9(–10.5) × 3–4.5(–5) cm, sparsely tomentose to glabrate except midrib, the reticulum white against dark areoles; inflorescence 5–10(–12.5) cm long; bracts and bracteoles persistent in fruit, 1–2 mm long or bracteoles smaller; pedicels usually decurved in fruit; petals white to pink or red in age; anther locules glabrous, linear, the connective exceeding locules by 0.3–0.7 mm; ovary and fruit glabrous; fruits red to black, 4–5 mm diameter (dried). Shrubby associations on sand, often near rivers, 300–500 m; Bolívar (Río Acanán, Canaima, Río Carrao, Salto Angel). Widespread in Amazonian Brazil (eastern Pará and Maranhão west and south into Amazonas and Rondônia) and Bolivia (Beni).

See discussion under *Byrsonima punctulata*.

**Byrsonima linguifera** Cuatrec., Webbia 13: 613. 1958.

Shrub or small tree 1.5–5(–6) m tall; stipules 4–7 mm long, smoothly and completely connate, the pair rounded at apex; petioles 4–10 mm long; blade of larger leaves 9.5–18 × 5–10 cm, obtuse or rounded at apex, ± revolute at margin, densely and persistently velutinous on both sides with Y-shaped hairs; many bracts and bracteoles persistent in fruit; bracts 5–7 mm long, linear, strongly reflexed, several times as long as short triangular bracteoles; pedicels strongly reflexed and twisted in fruit; sepals adaxially tomentose; petals yellow; anthers loosely sericeous, especially between locules, the connective equaling locules or exceeding them by up to 1 mm; ovary and fruit densely hairy; mature fruits not seen. Grassy savannas, 50–1100 m; Amazonas (Cerro Parí, Río Asisa). Colombia (Vichada), Brazil (southwestern Amazonas, Rondônia), Bolivia (Beni).

**Byrsonima luetzelburgii** Steyerl., Fieldiana, Bot. 28: 288. 1952.

*Byrsonima cretacea* Nied., Repert. Spec. Nov. Regni Veg. 33: 71. 1933, non Gleason 1931.



Shrub or tree 2–8 m tall; vegetative internodes glabrous except in axil of stipules; stipules 1.5–3 mm long, distinct; petioles (10–)15–25 mm long; blade of larger leaves 8–14 × (3.7–)4.5–8.3 cm, glabrous, the abaxial epidermis deeply pitted and ± densely and persistently glaucous at maturity; bracts and bracteoles persistent in fruit, 0.6–1.5 mm long; pedicels circinate in bud, decurved and eventually twisted in old flowers and fruit; petals pink or white and pink; anther locules glabrous, dorsiventrally flattened and longitudinally winged, the connective exceeding locules by 0.2–0.4 mm; ovary and fruit glabrous; fruits red at maturity, 4.5–6 mm diameter (dried). Riverbanks and lowland white-sand savannas, 100–200 m; Amazonas (Brazo Casiquiare, Caño Yagua, Cerro Yapacana, La Esmeralda, Río Autana, Río Manapiare, Río Ventuari). Brazil (northwestern Amazonas).

**Byrsonima macrostachya** W.R. Anderson, Mem. New York Bot. Gard. 32: 118. 1981.

Tree 14–20 m tall; stipules 4.5–9 mm long, 1/2-connate; petioles 20–28 mm long; blade of larger leaves 11–17 × 5.5–9 cm, abaxially very densely and persistently sericeous; inflorescence 18–26 cm long; bracts and bracteoles deciduous before or during anthesis, 2.5–4 mm long or bracteoles smaller; pedicels nearly or quite straight in fruit; petals pink; anther locules glabrous, cylindrical, the connective exceeding locules by 0.8–1.3 mm; ovary densely sericeous; immature fruits 12 mm long (dried), sericeous to glabrescent. Tepui slope forests, 1100–2000 m; Amazonas (Cerro Marahuaka, Cerro Parú). Endemic.

See comments under *Byrsonima carraoana*.

**Byrsonima maguirei** W.R. Anderson, Mem. New York Bot. Gard. 32: 81. 1981.

Shrub or tree 2–8 m tall; stipules 4–7 mm long, distinct or up to 1/2-connate, triangular; petioles 10–30 mm long; leaf blades 5–17 × 2.2–9.5 cm, obtuse at apex, abaxially tomentose to glabrate; bracts and bracteoles persistent in fruit; bracts 4–7 mm long; bracteoles 2.5–4 mm long; pedicels raised on peduncles 5–15 mm long, straight in fruit; petals yellow, turning pinkish in age?; anther locules

glabrous, linear, the connective not or hardly exceeding locules; ovary and fruit glabrous; fruits up to 20 mm diameter (dried). Scrub forests, tepui slopes, 1200–2200 m; Amazonas (Sierra de la Neblina). Endemic.

**Byrsonima nitidissima** H.B.K., Nov. Gen. Sp. (quarto ed.) 5: 152, pl. 448. 1821 [1822].

Shrub or tree 1.5–5(–10) m tall; stipules 2–5 mm long, usually completely and smoothly connate, rarely distinct at apex; petioles 2–6 mm long; blade of larger leaves 3.5–8.5 × 2–4.5 cm, rounded or broadly obtuse at apex, adaxially shining, abaxially sericeous or velutinous to glabrescent; bracts and bracteoles persistent in fruit; bracts 1.5–3 mm long, bracteoles slightly smaller; pedicels decurved in fruit; petals white or pinkish; filaments bearded with kinky rusty brown hairs; anther locules cylindrical, glabrous, the connective not or hardly exceeding locules; ovary and fruit glabrous; fruits dark purplish, developing half-immersed in enlarged, disk-like receptacle, 4–5 mm diameter (dried). Scrub forests on and beside granitic outcrops, 50–200 m; Bolívar (upper Río Orinoco south of Maniapure), Amazonas (upper Río Orinoco north of Río Sipapo). Apure; Colombia (Río Orinoco).

**Byrsonima pachypoda** W.R. Anderson, Mem. New York Bot. Gard. 32: 123. 1981.

Shrub 2–4 m or tree to 8(–10) m tall; vegetative internodes glabrous except in axil of stipules; stipules 3–6 mm long, distinct, acute or obtuse at apex; petioles 3–5(–7) mm long, glabrous; blade of larger leaves 6–14.5 × 3–8.3 cm, obovate, broadly obtuse or rounded at apex, glabrous; bracts and bracteoles persistent in fruit; bracts 2–3 mm long, bracteoles slightly shorter; pedicels distally thickened, straight in bud and fruit; petals white to pink in age; anthers glabrous, the locules linear and unwinged, the connective swollen but not or hardly exceeding locules; ovary and fruit glabrous; fruits red to black, 7–8 mm diameter (dried). Low scrub, low forests (8–10 m), low *Clusia-Magnolia* woodlands, 1400–1900 m; Bolívar (Ilú-tepui). Guyana (upper Mazaruni River basin, Mount Ayanganna, Mount Wokomung).

**Byrsonima poeppigiana** A. Juss., Ann. Sci. Nat. Bot. sér. 2, 13: 335. 1840.

Tree 6–25 m tall; stipules 4–8 mm long, completely connate, the pair rounded at apex; petioles 6–15(–18) mm long; blade of larger leaves 10–19(–24) × 4.5–10(–14.5) cm, abaxially thinly to densely velutinous with erect, bifurcate hairs; bracts and bracteoles mostly deciduous before maturation of fruit; bracts 1.5–4 mm long; bracteoles 0.5–1.5(–2) mm long; pedicels decurved or twisted in fruit; sepals glabrous on adaxial face; petals yellow; anthers loosely sericeous, at least between locules, the connective equaling or slightly exceeding locules; ovary glabrous or sparsely sericeous distally; fruits yellow, 8–10 × 6–8 mm (dried), glabrous or with a few hairs at apex. Nonflooded evergreen lowland forests, 100–200 m; Amazonas (Río Casiquiare, between San Carlos de Río Negro and Solano, Santa Rosa de Amanadona). Brazil (western Amazonas, Rondônia), Amazonian Peru (Loreto, Madre de Dios).

**Byrsonima punctulata** A. Juss., Ann. Sci. Nat. Bot. sér. 2, 13: 335. 1840.

*Byrsonima barkleyana* Cuatrec., Webb 13: 620. 1958.

Small tree 2.5–9 m tall, rarely a shrub only 1 m; vegetative internodes hairy to glabrescent; stipules 3.5–7(–8) mm long, distinct, often acuminate; petioles 10–19 mm long; blade of larger leaves 8.5–14.5 × 4–8 cm, tomentose to glabrate at maturity except abaxial veins and midrib, the reticulum and areoles ± concolorous; inflorescence 9–18 cm long; bracts and bracteoles persistent in fruit, 1.5–3 mm long or bracteoles smaller; pedicels usually decurved in fruit; petals white turning pink or red in age; anther locules glabrous, linear, the connective exceeding locules by 0.3–1 mm; ovary and fruit glabrous; fruits red to blue, 4–6 mm diameter (dried). On sandy soil beside rivers, sometimes in seasonally flooded savannas, 100–200 m; Amazonas (Río Atabapo, Río Sipapo). Colombia (Vaupés, Vichada), Brazil (Amazonas: basin of upper Río Negro, southern Roraima).

As noted in my 1981 paper, this species fills the morphological and geographical gap between *Byrsonima cuprea* and *B. leuco-*

*phlebia*, and may well have originated through hybridization between those two now-disjunct entities. Backcrossing to the putative parents probably continues, especially in the area of Manaus, where *B. punctulata* and *B. leucophlebia* co-occur, and the large-leaved plants of *B. punctulata* found in the region of San Fernando de Atabapo hardly differ from *B. cuprea* except in their hairs. Specimens of "*B. cuprea*" from the Atabapo area, in which the abaxial leaf hairs are sparser than usual, e.g., *Velazco* 244 (MO, PORT), are probably part of that hybrid complex, and call into question the feasibility of maintaining *B. cuprea* as a species. The name *B. punctulata* is the oldest in the complex.

**Byrsonima schomburgkiana** Benth., London J. Bot. 7: 123. 1848. —Chaparro manteco.

Tree 4–18 m tall, rarely a shrub only 1–2 m; stipules 2–4 mm long, smoothly connate; petioles 5–10 mm long, densely and ± persistently tomentose; blade of larger leaves (5–)7.5–17 × (3–)4–9 cm, elliptic to obovate, tomentose but soon ± glabrate; bracts and bracteoles mostly deciduous in fruit, occasionally persistent; bracts (2–)3–5(–9) mm long, narrowly lingulate, bracteoles similar but shorter; pedicels straight or decurved in fruit; sepals lingulate-acrescent and membranous in fruit; petals pink or pink and white; anthers tomentose, the bulbous connective exceeding locules by (0.3–)0.5–1.1 mm; ovary and fruit glabrous; fruits yellow, 6–10 mm diameter (dried). Dry forests and savannas, 100–800 m; Bolívar (Caicara south to Picachos de Sabana Nueva, Represa Guri, between Río Perro de Agua and Río Juasjualito west of San Antonio, San Félix to Puerto Ordaz, Sierra de Maigualida), Amazonas (Río Ocamo). Guyana (Rupununi area), Brazil (Roraima).

**Byrsonima spicata** (Cav.) DC., Prodr. 1: 580. 1824. —*Malpighia spicata* Cav., Diss. 8: 409, pl. 237. 1789. —*Byrsonima coriacea* var. *spicata* (Cav.) Nied. in Engl., Pflanzenr. IV. 141: 700. 1928, nom. superfl. —Manteco.

*Byrsonima propinqua* Benth., London J. Bot. 7: 120. 1848.

Tree 3–25 m tall; stipules 1–3 mm long, completely and smoothly connate; petioles 5–15(–20) mm long; blade of larger leaves 6.5–15(–16) × 1.7–5(–6) cm, tightly sericeous abaxially to usually eventually glabrate, the hairs sessile or subsessile with short, straight, parallel crosspieces up to 0.5 mm long, with 15–20 or more pairs of fine lateral veins, none very prominent; bracts and bracteoles deciduous in fruit; pedicels mostly decurved or twisted in fruit; petals yellow, the posterior petal bearing 2 or more glands at apex of claw or on base of limb; anthers sericeous, at least between locules, the connective equaling or slightly exceeding locules; ovary sericeous; fruits yellow-orange, 10–12 mm diameter (dried), sericeous to glabrate. Dry scrubland to wet forests, near sea level to 700(–1300) m; Delta Amacuro (near village of Morichito), common in Bolívar, Amazonas (Puerto Ayacucho to El Burro, Río Mawarinuma, Yutajé). Anzoátegui, Aragua, Barinas, Falcón, Lara, Mérida, Miranda, Monagas, Sucre, Táchira, Trujillo, Yaracuy, Zulia; Panama, West Indies, Colombia, Guyana, Suriname, French Guiana, Peru, Brazil, Bolivia.

The leaves of *Byrsonima spicata* are usually glabrescent at maturity. When the hairs persist (e.g., *Davidse & Miller 27179*, MICH, MO, VEN, *Huber et al. 12911*, MICH, MYF, VEN, *Steyermark et al. 113966*, MICH, VEN), the leaves have a different aspect, but I see no pattern suggesting that those plants deserve taxonomic recognition. In my 1981 paper (p. 96) I stated that *B. propinqua* is a name for such plants, but that was incorrect; the holotype of *B. propinqua* (K!) has rather large leaves for the species, but they are glabrescent.

***Byrsonima steyermarkii*** W.R. Anderson, Mem. New York Bot. Gard. 32: 124. 1981.

Tree 6–7 m tall; vegetative internodes glabrous except in axil of stipules; stipules 2–5 mm long, distinct; petioles 2.5–5 mm long; blade of larger leaves 6.5–12.2 × 4–7 cm, glabrous; bracts and bracteoles persistent in fruit, 1–2.5 mm long; pedicels straight in fruit; petals white; anther locules glabrous, unwinged, the connective exceeding locules by 0.1–0.5 mm; ovary and fruit glabrous; fruits 5–7.5 mm diameter (dried). Low forests on tepui slopes and summit, 1200–2100

m; Bolívar (Cerro Jaua), Amazonas (Cerro Parú). Endemic. •Fig. 83.

***Byrsonima stipulacea*** A. Juss., Ann. Sci. Nat. Bot. sér. 2, 13: 332. 1840. —*Alcoceratothrix stipulacea* (A. Juss.) Nied. in Engl., Pflanzenr. IV. 141: 762. 1928. —Chaparro manteco, Manteco, Manteco de agua.

*Byrsonima rugosa* Benth., London J. Bot. 7: 118. 1848. —*Alcoceratothrix rugosa* (Benth.) Nied., Arbeiten Bot. Inst. Königl. Lyceum Hosianum Braunsberg 1: 45. 1901.

Tree (5–)7–25(–35) m tall; stipules 8–25 mm long, amplexicaulous, completely connate, each pair deciduous independently of and often well before the leaf; petioles (6–)10–27 mm long; blade of larger leaves 12–27 × 6–13 cm, abaxially velutinous with a mixture of long, basifixed simple hairs, stalked stellate hairs, and sessile stellate hairs; bracts and bracteoles deciduous in fruit; bracts 5–10 mm long; bracteoles 2–5 mm long; pedicels straight or somewhat decurved in fruit; petals yellow; anthers loosely sericeous on both sides, the connective usually exceeding locules by 0.4–1.1 mm; ovary densely short-velutinous with an overlay of appressed hairs; fruits orange-yellow, 12–18 mm diameter (dried), tomentose to glabrate. Evergreen lowland to lower montane forests, 100–1300 m; Delta Amacuro (east-northeast of El Palmar), widespread in Bolívar to 63°W, rare farther west (Río Caura at 5°35'N). Guyana, Suriname, French Guiana, Brazil (Rondônia, Roraima, and Amapá south to Espírito Santo).

***Byrsonima tillettii*** W.R. Anderson, Mem. New York Bot. Gard. 32: 118. 1981.

Shrub or tree 2–5 m tall; stipules 6–11 mm long, completely connate, the pair rounded at apex; petioles 5–10 mm long; blade of larger leaves 9–11 × 4.5–6.5(–8) cm, abaxially sinuous-sericeous with hairs not dense enough to hide epidermis at maturity; bracts and bracteoles persistent in fruit; bracts (2.5–)3–5(–7) mm long; bracteoles 2–3 mm long; pedicels decurved in fruit; petals pink, the lateral 4 adaxially pilose on claw, abaxially pilose on limb; anthers glabrous, the connective exceeding locules by 0.7–1.2 mm; ovary and fruit glabrous; fruits 5–6 mm diameter (dried). Dense

scrub, low forests with trees to 8 m in savannas, ca. 1300 m; Bolívar (Wadaka-piapué-tepui west of Yuruaní-tepui). Guyana (Mount Ayanganna, upper Mazaruni River basin).

***Byrsonima verbascifolia*** (L.) DC., Prodr. 1: 579. 1824. —*Malpighia verbascifolia* L., Sp. Pl. 426. 1753.

*Byrsonima verbascifolia* var. *denudata* Cuatrec., Webbia 13: 605. 1958.

Gnarled shrub up to 60 cm tall, the leaves borne in dense sessile clusters on the thick corky stem, the internodes essentially lacking; stipules 6–12 mm long, connate, the pair triangular; petioles 10–35(–80) mm long; blade of larger leaves 14–25(–33) × 5–13(–15) cm, obovate or spatulate, attenuate at base, usually obtuse or rounded and apiculate at apex, densely and usually persistently villous adaxially and woolly abaxially, rarely eventually subglabrate adaxially or on both sides; bracts and bracteoles narrowly triangular or subulate, deciduous; bracts 5–11 mm long, bracteoles about half as long; pedicels decurved in fruit; petals yellow, the posterior petal eglandular; anthers loosely tomentose to glabrate, the connective not or hardly exceeding locules; ovary densely appressed-villous; fruits yellow, ca. 15 mm diameter (dried), thinly villous. Open savannas, often on white sand, 50–1200 m; common in Bolívar and Amazonas. Anzoátegui, Apure, Aragua, Barinas, Guárico, Mérida, Monagas; Honduras, Nicaragua, Colombia, Guyana, Suriname, French Guiana, Brazil, Bolivia.

Occasional plants in Venezuela have elongated internodes, short leaves with unwinged petioles, and small bracts. These have probably resulted from hybridization between *Byrsonima verbascifolia* and *B. crassifolia*, which is common and widespread and occurs in the same habitat.

This taxon is extremely variable through its range, and probably represents a complex of several related taxa rather than a single species. The descriptive notes above refer only to the form found in Venezuela and the Guianas.

***Byrsonima wurdackii*** W.R. Anderson, Mem. New York Bot. Gard. 32: 119. 1981.

Tree 3–19 m tall; stipules 1.7–4(–5) mm long, connate or distinct at apex, the pair tri-

angular, acute; petioles 15–35 mm long; blade of larger leaves 9.5–19 × 5–12 cm, sparsely sericeous to soon glabrate; inflorescence 10–25 cm long, the sessile cincinni 1–3(4)-flowered; bracts and bracteoles caducous; bracts 3–4 mm long; bracteoles 0.5–1.5 mm long; pedicels decurved in old flowers and fruits; calyx glands usually absent or rudimentary, rarely well developed; petals white turning pinkish; anther locules glabrous, unwinged, the connective exceeding locules by 0.8–1.6 mm; ovary and fruit glabrous; styles strongly bent at apex in bud; fruits 6–7 mm diameter (dried). Savannas and scrubby forests on white sand, 100–200 m; Amazonas (upper Río Atabapo and La Esmeralda south to Maroa and San Carlos). Brazil (Amazonas: upper Rio Negro, Rio Uaupés).

#### ***Byrsonima* sp. A**

Tree 3–15 m tall; vegetative internodes glabrous except in axil of stipules; stipules 2–2.5 mm long, distinct; petioles (18–)22–33 mm long; blade of larger leaves (11–)12.5–17.5 × (5–)6.5–8.5 cm, glabrous; bracts and bracteoles persistent in fruit, 1–3.5 mm long; pedicels ascending and becoming sigmoid in fruit, 8–12 mm long, 0.8–1 mm diameter; sepals abaxially sparsely velutinous or sericeous, elongating to 5–7 mm in fruit, the accrescent sepals often closely investing the enlarging fruit; petals and stamens unknown; fruits 6–8 mm diameter (dried), glabrous. Along black-water rivers, 100–200 m; Amazonas (Caño Caname, Río Atacavi, Río Autana, Río Cuchakén in Río Atabapo drainage). Otherwise known from one collection in Caquetá, Colombia.

I plan to describe this species in the near future, giving it the epithet "*flexipes*" in reference to the pedicels, which are peculiarly sigmoid-ascending in fruit. The species resembles *Byrsonima rodriguesii* W.R. Anderson, a plant from the vicinity of Manaus that differs in its longer stipules, glabrous sepals that are soon reflexed or revolute in the enlarging fruit, fruiting pedicels that are thicker and curved upward but not sigmoid, and larger fruits. The petals of the new species can be expected to be white turning red, as in *B. rodriguesii*, and for the same reason its anthers should have a large, glandular connective that extends well beyond flattened locules.

Fig. 79. *Byrsonima duidana*



Fig. 80. *Byrsonima coccolobifolia*



Fig. 81. *Byrsonima carraoana*

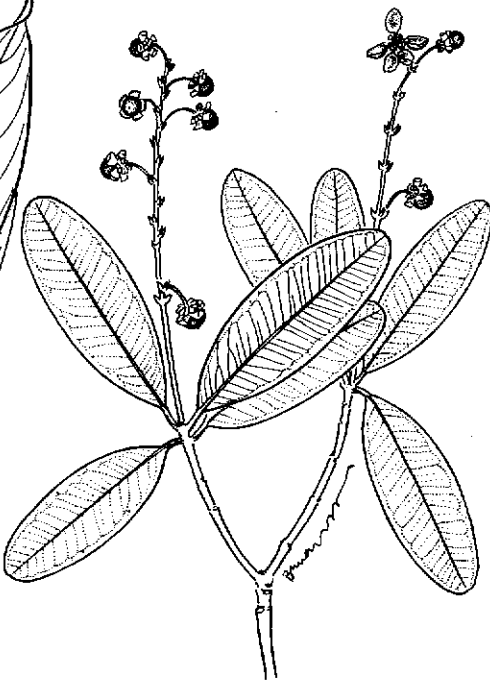


Fig. 82. *Byrsonima bronweniana*

Fig. 83. *Byrsonima steyermarkii*

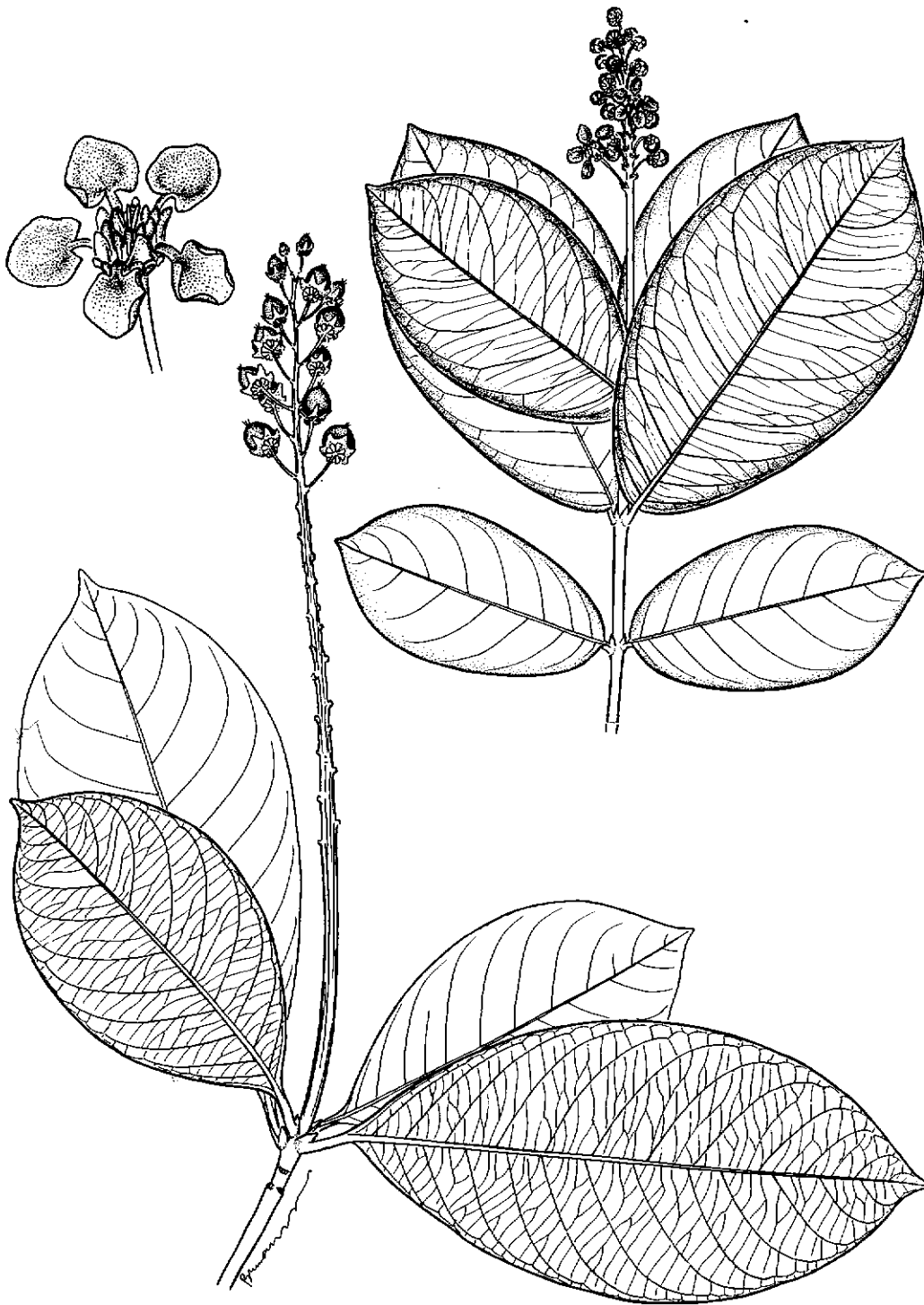
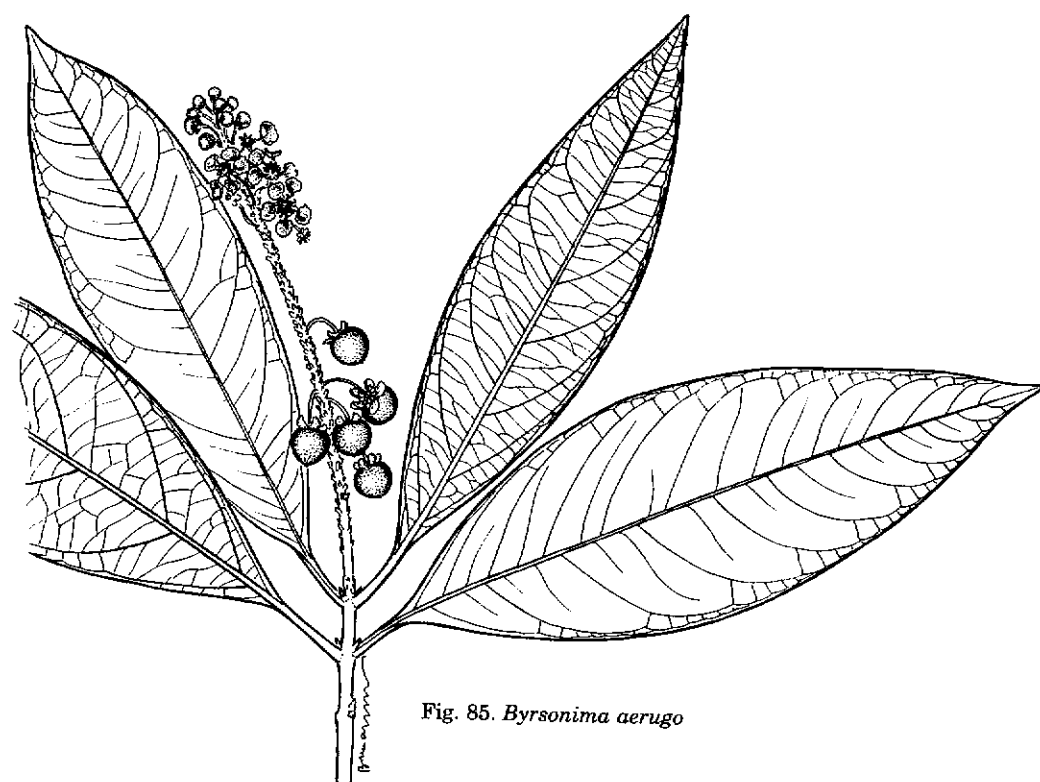


Fig. 84. *Byrsonima cowanii*

Fig. 85. *Byrsonima aerugo*

6. **CLONODIA** Griseb. in Mart., Fl. Bras. 12(1): 26. 1858.

*Atopocarpus* Cuatrec., Webbia 13: 454. 1958.

*Skoliopterys* Cuatrec., Webbia 13: 451. 1958.

Woody vines or shrubs; stems terete, with many tiny punctiform lenticels. Leaves decussate; stipules none(?) or minute (ca. 0.3 mm long), triangular, borne on stem at base of petiole. Inflorescence a pseudoraceme, simple or compound to form a panicle, terminal or terminal and lateral. Calyx bearing 8–10 glands; petals pink and/or white, abaxially winged. Stamens 10, glabrous; filaments basally to  $\frac{1}{2}$ -connate, straight or the posterior 3 (especially the 1 opposite posterior petal) sigmoid. Ovary of 3 carpels, connate at base, distinct distally; styles 3, stout, strongly unequal, the anterior thinner and usually shorter than the other 2, bent toward posterior petal, the 2 posterior styles turned toward anterior sepal; stigmas large, internal, the styles dorsally truncate to prominently hooked at apex. Fruit a schizocarp comprising 3 (or fewer by abortion) dry indehiscent mericarps separating from a short pyramidal torus; mericarp with the wings reduced to winglets or rounded outgrowths.

Amazonian Colombia, southern Venezuela, Brazil, Bolivia; 3 species, 1 in Venezuela.

*Clonodia complicata* (H.B.K.) W.R. Anderson, Mem. New York Bot. Gard. 32: 206. 1981. —*Hiraea complicata* H.B.K., Nov. Gen. Sp. (quarto ed.) 5: 171. 1821 [1822]. —*Mascagnia complicata* (H.B.K.) Nied., Arbeiten Bot. Inst. Königl. Lyceum

Hosianum Braunsberg 3: 4. 1908.

*Hiraea nitida* H.B.K., Nov. Gen. Sp. (quarto ed.) 5: 171. 1821 [1822]. —*Mascagnia nitida* (H.B.K.) Nied., Arbeiten Bot. Inst. Königl. Lyceum Hosianum Braunsberg 3: 4. 1908.

Fig. 86. *Clonodia complicata*

*Mascagnia lehmanniana* Nied., Arbeiten Bot. Inst. Königl. Lyceum Hosianum. Braunsberg 8: 59. 1926. —*Skoliopterys lehmanniana* (Nied.) Cuatrec., Webbia 13: 452. 1958.

*Clonodia racemosa* var. *orinocensis* Nied. in Engl., Pflanzenr. IV. 141: 580. 1928.

Woody vine, occasionally described as a shrub; petioles (3–)5–8 mm long; blade of larger leaves (4.5–)7.5–11.5(–13.5) × (2.5–)4–6(–7) cm, ovate, acute or obtuse at apex, loosely sericeous to ± glabrate at maturity; pseudoracemes comprising (15–)20–50 flow-

ers; petals, especially the posterior, sometimes papillose on adaxial face; styles dorsally truncate or with a very short hook at apex; mericarps bearing a dorsal winglet 0.5–2 mm wide and 3–5 winglets on each side, mostly at right angles to dorsal winglet, sometimes connate with it at apex. Usually near rivers or in marshy places, near sea level to 300 m; common along the Río Orinoco and its tributaries in Delta Amacuro, Bolívar, and Amazonas. Anzoátegui, Apure, Trujillo, Zulia; eastern Colombia. ♦Fig. 86.

7. **DIACIDIA** Griseb. in Mart., Fl. Bras. 12(1): 119. 1858.

*Sipapoa* Maguire, Mem. New York Bot. Gard. 8: 124. 1953.

Trees, shrubs, or subshrubs, with mostly basifixed or sub-basifixed hairs. Leaves eglandular, often glaucous, especially abaxially; proximal portions of stipules and petioles fused to form an interpetiolar sheath; distal portions of stipules (the

part extending beyond petiole) distinct or connate. Inflorescence a simple or compound thyrse (i.e., a raceme or panicle of cincinni) or a pseudoraceme (i.e., a raceme of 1-flowered cincinni); bracts and bracteoles eglandular, caducous or eventually deciduous. Sepals all biglandular, accrescent in fruit; petals yellow, often with red claws. Stamens 6–10; anthers with each half bearing at apex and angled forward 1 or occasionally 2 stout, basifixed, awn-like hairs. Ovary composed of 3 completely connate carpels but only 2-locular, the anterior carpel reduced to a ridge of tissue; styles 3, slender and subulate with minute slightly internal stigmas. Fruit a spheroidal or ovoidal, dry, indehiscent, nut-like capsule ca. 2.5 mm high and wide, with a thin exocarp and a bony, smooth or rugose endocarp and containing 2 seeds (or 1 due to abortion), subtended and enclosed by accrescent (in most species red, membranous, veiny, wing-like) sepals.

Endemic to the Guayana Shield in Colombia, southwestern Venezuela, and Brazil; 11 species, 10 in Venezuela, all in the flora area.

*Diacidia aracaënsis* W.R. Anderson was described from the Serra Aracá in Brazil, but may eventually be found in Venezuela. It is similar to *D. ferruginea*, but differs in having 8 fertile stamens, the anther connectives hardly enlarged, the sepals glabrous on the margin, and the leaves soon glabrescent adaxially.

#### Key to the Species of *Diacidia*

1. Stamens 10; sepals only slightly accrescent in fruit, up to  $3.5 \times 2.5$  mm; interpetiolar stipular sheath 2–3(–6) mm long, obscure, lacking median seams; 50–400 m ..... *D. galphimiioides*
1. Stamens 6–9; sepals greatly accrescent in fruit, forming membranous wings  $7-13 \times (2.5-4-12)$  mm; interpetiolar stipular sheath 4–26 mm long, marked by median seams; 300–2300 m ..... 2
- 2(1). Stipule lobes beyond petiole completely connate to form a single intrapetiolar structure ..... 3
2. Stipule lobes beyond petiole nearly or quite distinct ..... 6
- 3(2). Stipules 7–11 mm long beyond petiole, acute or obtuse at apex ..... *D. kunhardtii*
3. Stipules 28–90 mm long beyond petiole, broadly obtuse or rounded at apex ..... 4
- 4(3). Inflorescence a simple pseudoraceme, glabrous or very soon glabrate; bracts, bracteoles, and sepals glabrous; shrubs 0.5–3 m tall ..... *D. stipularis*
4. Inflorescence compound, with a terminal axis and few to many lateral axes, and with the cincinni several-flowered; inflorescence, bracts, bracteoles, and sepals densely and persistently hairy; shrubs or trees (1–)2–15 m tall ..... 5
- 5(4). Leaves glabrate abaxially or hairy only on veins; 600–1600 m ..... *D. glaucifolia*
5. Leaves densely and persistently rufous-sericeous abaxially over the whole surface; 1500–1900 m ..... *D. rufa*
- 6(2). Inflorescence a simple thyrse with several-flowered cincinni, glabrous; leaves glabrous or loosely sericeous to glabrate abaxially ..... *D. cordata*
6. Inflorescence a pseudoraceme, hairy; leaves hairy abaxially ..... 7

- 7(6). Vegetative internodes glabrous ..... *D. hypoleuca*
7. Vegetative internodes hairy ..... 8
- 8(7). Leaf blades glabrous or soon glabrescent adaxially except for very base; stipules 1–3 mm long beyond petiole ..... *D. ferruginea*
8. Leaf blades densely and persistently hairy adaxially; stipules 5–15 mm long beyond petiole ..... 9
- 9(8). Leaf blades woolly abaxially, the hairs much twisted and intertwined ..... *D. vestita*
9. Leaf blades sericeous abaxially, the hairs straight,  $\pm$  appressed, and parallel ..... *D. steyermarkii*

***Diacidia cordata*** (Maguire) W.R. Anderson, Mem. New York Bot. Gard. 32: 66. 1981.

—*Sipapoa cordata* Maguire, Mem. New York Bot. Gard. 18: 46. 1969.

Shrub 0.5–2(–3) m tall; vegetative internodes glabrous; stipules 7–10 mm long beyond petiole, distinct, acute at apex; petioles 5–10 mm long including petiole-stipule sheath; blade of larger leaves  $3-6.5 \times 1.5-4.5$  cm, deeply cordate at base, glabrous adaxially, glabrous or loosely sericeous to glabrate abaxially; inflorescence a simple thyrse, the cincinni 2–6(–8)-flowered, glabrous; fertile stamens 8 or 9; sepals in fruit up to  $7 \times 4$  mm. Brushy rocky tepui slopes, 300–1900 m; Amazonas (Sierra de la Neblina). Endemic. ♦Fig. 88.

***Diacidia ferruginea*** (Maguire & K.D. Phelps) W.R. Anderson, Mem. New York Bot. Gard. 32: 68. 1981. —*Sipapoa ferruginea* Maguire & K.D. Phelps, Mem. New York Bot. Gard. 8: 126. 1953.

Shrub or small tree 1–4 m tall; vegetative internodes persistently sericeous; stipules 1–3 mm long beyond petiole, distinct, acute at apex; petioles 5–9 mm long including petiole-stipule sheath; blade of larger leaves  $3-4.5 \times 1-2$  cm, adaxially glabrous or soon glabrescent except for sericeous base, abaxially densely and persistently rufous- or yellowish-sericeous; inflorescence a pseudoraceme, tomentose; stamens 6; sepals in fruit up to  $13 \times 12$  mm. Tepui savannas, 1100–2000 m; Amazonas (Cerro Parí). Endemic. ♦Fig. 89.

***Diacidia galphimiioides*** Griseb. in Mart., Fl. Bras. 12(1): 120. 1858.

*Diacidia duckeana* Maguire, Mem. New York Bot. Gard. 8: 124. 1953.

*Diacidia parvifolia* Cuatrec., Webbia 13: 632. 1958.

Shrub or small tree 0.5–2(–4) m tall; vegetative internodes sericeous; stipules 2–5 (–7) mm long beyond petiole, completely connate and rounded at apex; petioles 4–8 mm long including petiole-stipule sheath; blade of larger leaves  $(2-4-6(-9)) \times (0.7-1.2-2.7(-5))$  cm, loosely sericeous to subtomtose on both sides, occasionally glabrescent in age; inflorescence a simple thyrse with cincinni (1)2–10(–13)-flowered, glabrous or proximally sparsely sericeous; stamens 10; sepals in fruit up to  $3.5 \times 2.5$  mm. On or among granitic outcrops, 50–400 m; Bolívar (Río Caura at  $6^{\circ}14'N$ ), Amazonas (basins of upper Río Orinoco and upper Río Negro from Río Cuao south to Piedra de Cocuy). Adjacent Colombia and Brazil.

In my 1981 paper I recognized *Diacidia parvifolia* as distinct from *D. galphimiioides*. However, the accumulation of intermediates has convinced me that it is simply a small-leaved form that may not even have any genetic basis, reflecting nothing more than the extremely harsh conditions sometimes found on the granitic outcrops where it grows. Most of the characters I used in my earlier key overlap too much to be diagnostic, and the Venezuelan plants with the small leaves of *D. parvifolia* (Berry et al. 5114 [MICH], Morillo & Ishikawa 3470 [MICH, VEN], Morillo 6881 [MICH, VEN]) have the larger bracteoles of *D. galphimiioides*.

***Diacidia glaucifolia*** (Maguire) W.R. Anderson, Mem. New York Bot. Gard. 32: 63.

1981. —*Sipapoa glaucifolia* Maguire, Mem. New York Bot. Gard. 18: 48. 1969.

Shrub or tree (1–)2–15 m tall; vegetative internodes glabrous; stipules 70–90 mm long beyond petiole, completely connate and rounded at apex; petioles 34–53 mm long including petiole-stipule sheath; blade of



larger leaves 16–27 × 11–18 cm, glabrous adaxially, sericeous on midrib and veins to soon glabrate abaxially; inflorescence a compound thyrse, the cincinni mostly 4–10-flowered, laxly rufous-sericeous; stamens (8)9; sepals in fruit up to 9 × 4 mm. Tepui slope forests, 600–1600 m; Amazonas (Cerro Aracamuni, Sierra de la Neblina). Brazil (Amazonas: Serra Pirapucú).

***Diacidia hypoleuca*** (Maguire) W.R. Anderson, Mem. New York Bot. Gard. 32: 67. 1981. —*Sipapoa hypoleuca* Maguire, Mem. New York Bot. Gard. 8: 125. 1953.

Shrub or tree 3–10 m tall; vegetative internodes glabrous; stipules beyond petiole 10–18 mm long, connate for up to 3 mm and distally distinct, acute or acuminate at apex; petioles 16–25 mm long including petiole-stipule sheath; blade of larger leaves 5.5–10.5 × 3–6 cm, adaxially glabrous, abaxially densely and persistently white- or yellowish-sericeous; inflorescence a pseudoraceme, loosely sericeous; stamens 9; sepals in fruit up to 10 × 8 mm. Upper tepui slopes, 500–1200 m; Amazonas (Cerro Yapacana). Endemic.

***Diacidia kunhardtii*** (Maguire) W.R. Anderson, Mem. New York Bot. Gard. 32: 66. 1981. —*Sipapoa kunhardtii* Maguire, Mem. New York Bot. Gard. 8: 125. 1953.

Shrub or small tree to 4(–8) m tall; vegetative internodes glabrous; stipules 7–11 mm long beyond petiole, completely connate, acute or obtuse at apex; petioles 17–26 mm long including petiole-stipule sheath; blade of larger leaves 4–7 × 2.3–5 cm, adaxially sparsely sericeous to glabrate, abaxially spreading-sericeous on midrib and lateral veins; inflorescence a pseudoraceme (the cincinni rarely 2-flowered), villous; fertile stamens 8; sepals in fruit up to 13 × 4 mm. Tepui meadows and low woodlands on sandy soil, 1400–1600 m; Amazonas (Cuao-Sipapo massif). Endemic. ♦Fig. 90.

***Diacidia rufa*** (Maguire) W.R. Anderson, Mem. New York Bot. Gard. 32: 64. 1981. —*Sipapoa rufa* Maguire, Mem. New York Bot. Gard. 18: 48. 1969.

Shrub or tree 2–12 m tall; vegetative internodes glabrous; stipules 40–80 mm long

beyond petiole, completely connate and rounded at apex; petioles 20–40(–50) mm long including petiole-stipule sheath; blade of larger leaves 8.5–17(–22) × 5–10(–14) cm, glabrous adaxially or sericeous on midrib, laxly and persistently rufous-sericeous all over abaxial surface; inflorescence a compound thyrse, the cincinni mostly 2–6-flowered, densely rufous-sericeous; stamens (8)9; sepals in fruit up to 9 × 4 mm. Low tepui forests and bromeliad-scrub zone on escarpment slopes and ridges, 1500–1900 m; Amazonas (Sierra de la Neblina). Brazil (Amazonas: Serra Pirapucú).

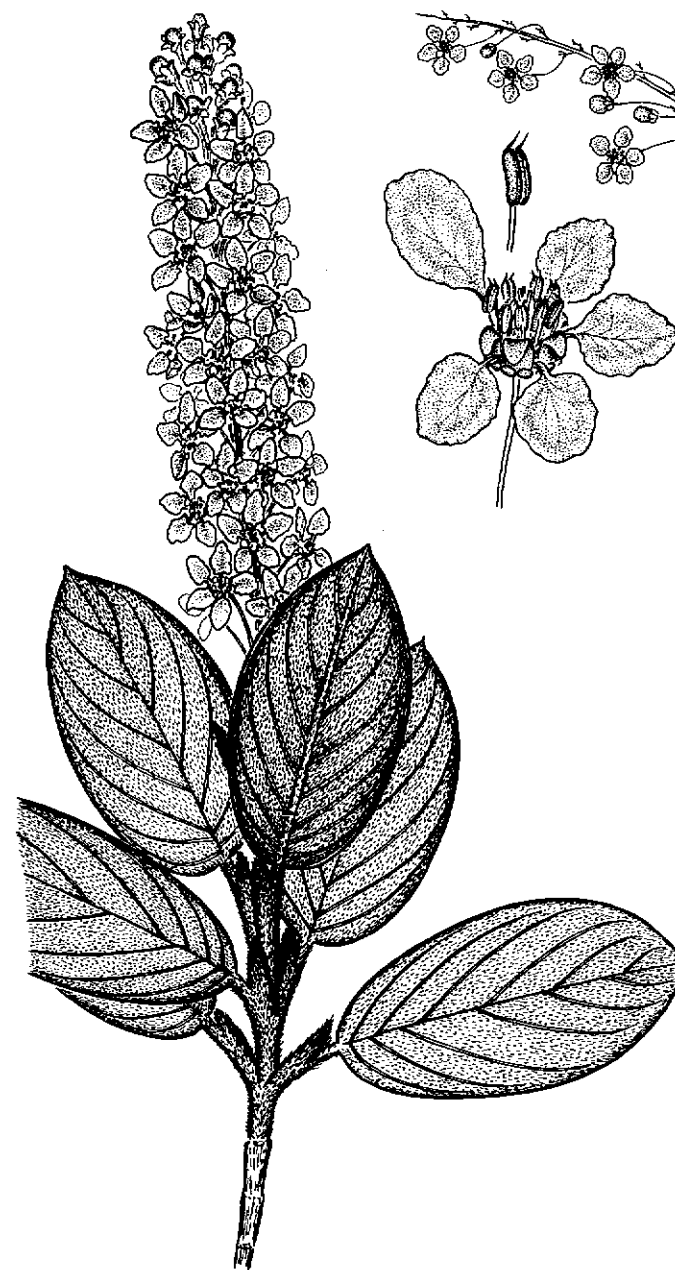
***Diacidia steyermarkii*** (Maguire) W.R. Anderson, Mem. New York Bot. Gard. 32: 71. 1981. —*Sipapoa steyermarkii* Maguire, Mem. New York Bot. Gard. 18: 54. 1969.

Shrub or tree (1–)3–8 m tall; vegetative internodes loosely sericeous to villous; stipules 9–15 mm long beyond petiole, distinct, acuminate at apex; petioles 23–30 mm long including petiole-stipule sheath; blade of larger leaves 6–10 × 3–4.5 cm, adaxially villous, abaxially densely sericeous; inflorescence a pseudoraceme, villous; stamens 8; sepals in fruit up to 9 × 4 mm. Tepui slope and summit vegetation, 1300–2300 m; Bolívar (Jaua-Sarisariñama massif). Endemic. ♦Fig. 87.

***Diacidia stipularis*** (Maguire & K.D. Phelps) W.R. Anderson, Mem. New York Bot. Gard. 32: 65. 1981. —*Sipapoa stipularis* Maguire & K.D. Phelps, Mem. New York Bot. Gard. 8: 127. 1953.

Shrub 0.5–3 m tall; vegetative internodes glabrous; stipules 28–62 mm long beyond petiole, completely connate, broadly obtuse or rounded at apex; petioles 12–24 mm long including petiole-stipule sheath; blade of larger leaves 4.5–13.5 × 2.5–9.5 cm, adaxially glabrous, abaxially densely and ± persistently white- or yellowish-sericeous; inflorescence a pseudoraceme, glabrous or very soon glabrate; stamens 6(7); sepals in fruit up to 12 × 5 mm. Tepui scrub, 1600–2000 m; Amazonas (Cerro Parú). Endemic.

***Diacidia vestita*** (Benth.) B.D. Jacks., Index Kew. 1: 741. 1895. —*Coleostachys*

Fig. 87. *Diacidia steyermarkii*Fig. 88. *Diacidia cordata*Fig. 89. *Diacidia ferruginea*



*vestita* Benth., London J. Bot. 7: 124. 1848. —*Sipapoa vestita* (Benth.) Maguire, Mem. New York Bot. Gard. 8: 127. 1953.

Shrub or small tree (1–)2–9 m tall; vegetative internodes loosely sericeous; stipules 5–11 mm long beyond petiole, distinct, acute or acuminate at apex; petioles 19–32 mm long including petiole-stipule sheath; blade of larger leaves 6–10(–13.5) × 2.8–5.5 cm, adaxially villous or subsericeous or subtomentose, abaxially woolly; inflorescence a pseudoraceme, villous; fertile stamens (7)8; sepals in fruit up to 13 × 7 mm. Open tepui slopes and woodlands, 1100–1900 m; Amazonas (Cerro Duida, Cerro Huachamacari, Cerro Marahuaka, Cerro Parú, Sierra Parima). Endemic.

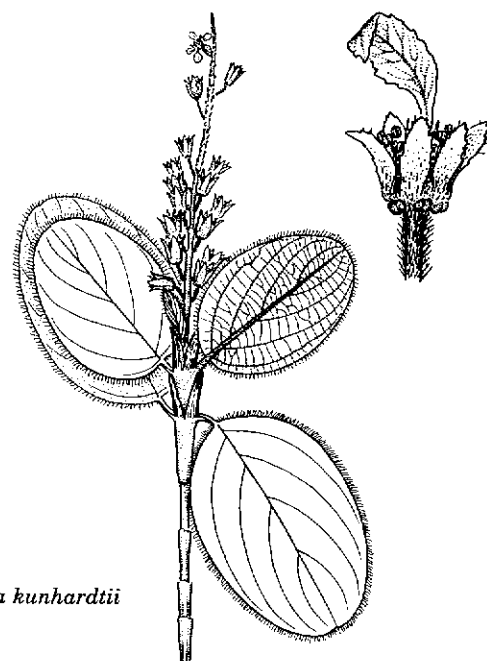


Fig. 90. *Diacidia kunhardtii*

#### 8. DICELLA Griseb., Linnaea 13: 249. 1839.

Woody vines. Stipules small, interpetiolar. Inflorescence a decompound panicle, the flowers borne ultimately in short pseudoracemes with decussate bracts, each bract subtending a 1-flowered peduncle with apical bracteoles. Sepals appressed in anthesis, the anterior eglandular, the lateral 4 biglandular, all accrescent in fruit; petals yellow, abaxially densely sericeous, adaxially glabrous or tomentose. Stamens 10; filaments and (in our species) the locules hairy. Ovary formed from 3 completely connate carpels, the 2 posterior locules full-sized and fertile, the anterior locule smaller and empty; styles distinct and straight, the posterior 2 stout, obliquely truncate or short-hooked at apex and with large internal stigmas, the anterior style absent or short, slender, rudimentary. Fruit composed of a dry, hard, indehiscent, nut-like structure with a thick, fibrous wall, containing 1 or 2 seeds, most often only 1, subtended by 5 dry wings formed by enlargement of the sepals.

Costa Rica, Colombia, Ecuador, Peru, Brazil, Bolivia, Paraguay, Argentina; 7 species, not yet known from Venezuela but 1 likely to occur there in the flora area.

See Mark W. Chase, 1981 [A revision of *Dicella* (Malpighiaceae), Syst. Bot. 6: 159–171].

***Dicella julianii*** (J.F. Macbr.) W.R. Anderson, Acta Amaz. 5: 279. 1975. —*Tetrapteryx julianii* J.F. Macbr., Publ. Field Mus. Nat. Hist., Bot. Ser., 13: 805. 1950. *Dicella amazonica* Pires, Bol. Técn. Inst. Agron. N. 38: 27. 1960.

Woody vine climbing to 30 m; petioles 13–24 mm long; blade of larger leaves 10–19(–22) × 5–11 cm, elliptic, acuminate at apex, abaxially persistently sericeous; bracts (4–)5–7 × 3–5 mm, bracteoles similar but smaller; fruit spherical, 13–18 mm diameter;

wings (enlarged sepals) subtending fruit 20–55 × 7–20 mm, unequal, the anterior eglandular one shortest, the anterior-lateral pair intermediate, the posterior-lateral pair longest. In forests near rivers, 200–400 m. Western Amazonia (Colombia, Ecuador, Peru, Brazil); known from Rio Maturacá, Rio Cauaburi, on the lower slopes of the Brazilian side of the Sierra de la Neblina, and therefore to be expected on the Venezuelan side. ♦Fig. 91.

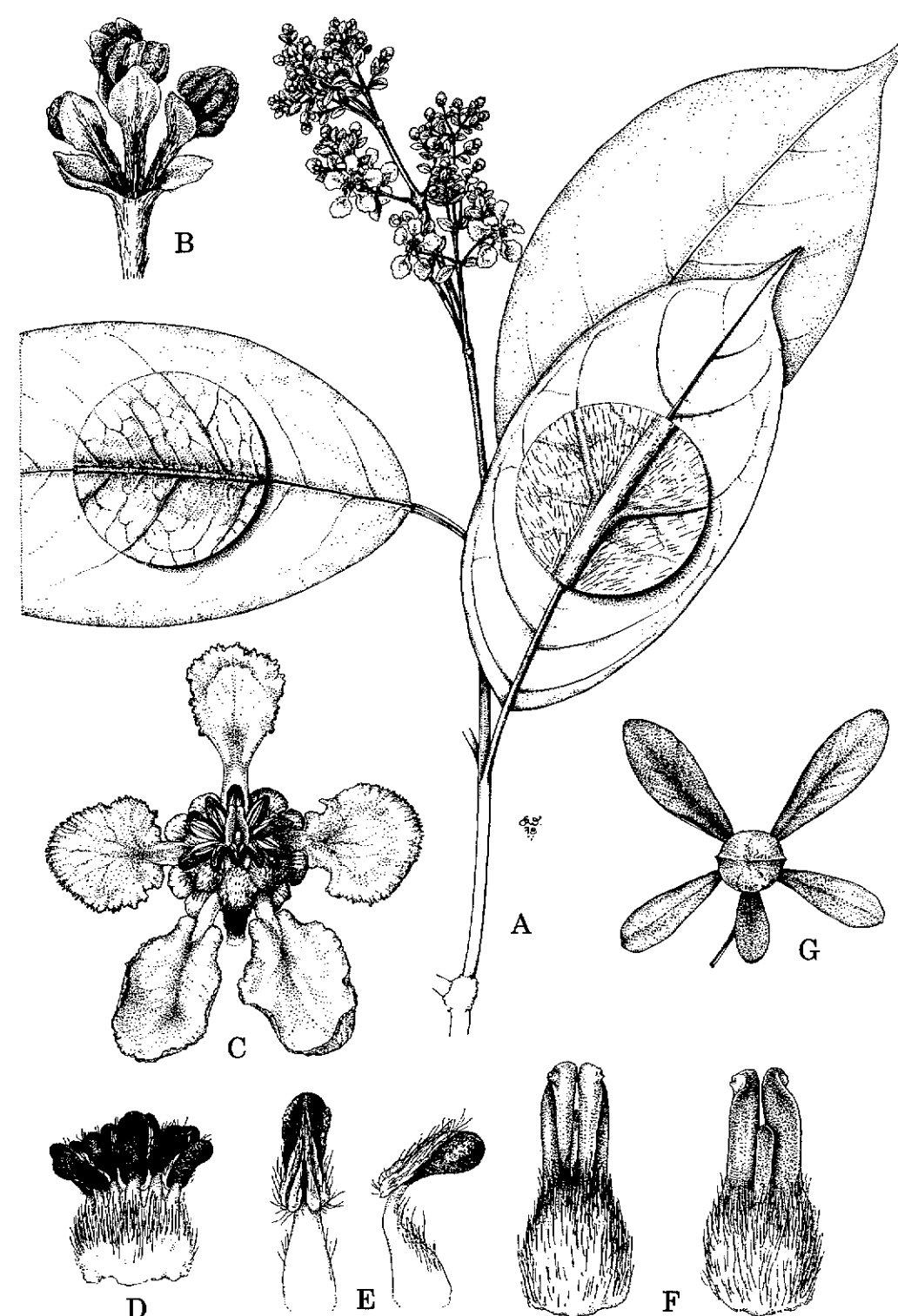


Fig. 91. *Dicella julianii*. —A. Flowering branch, ×0.5. —B. Decussate flower buds, ×2.1. —C. Flower, ×2.6. —D. Androecium, ×5.3. —E. Stamens, ×8.2. —F. Gynoecium, posterior view (left) and anterior view (right), ×8.2. —G. Fruit, ×5.3. ©New York Botanical Garden 1981.

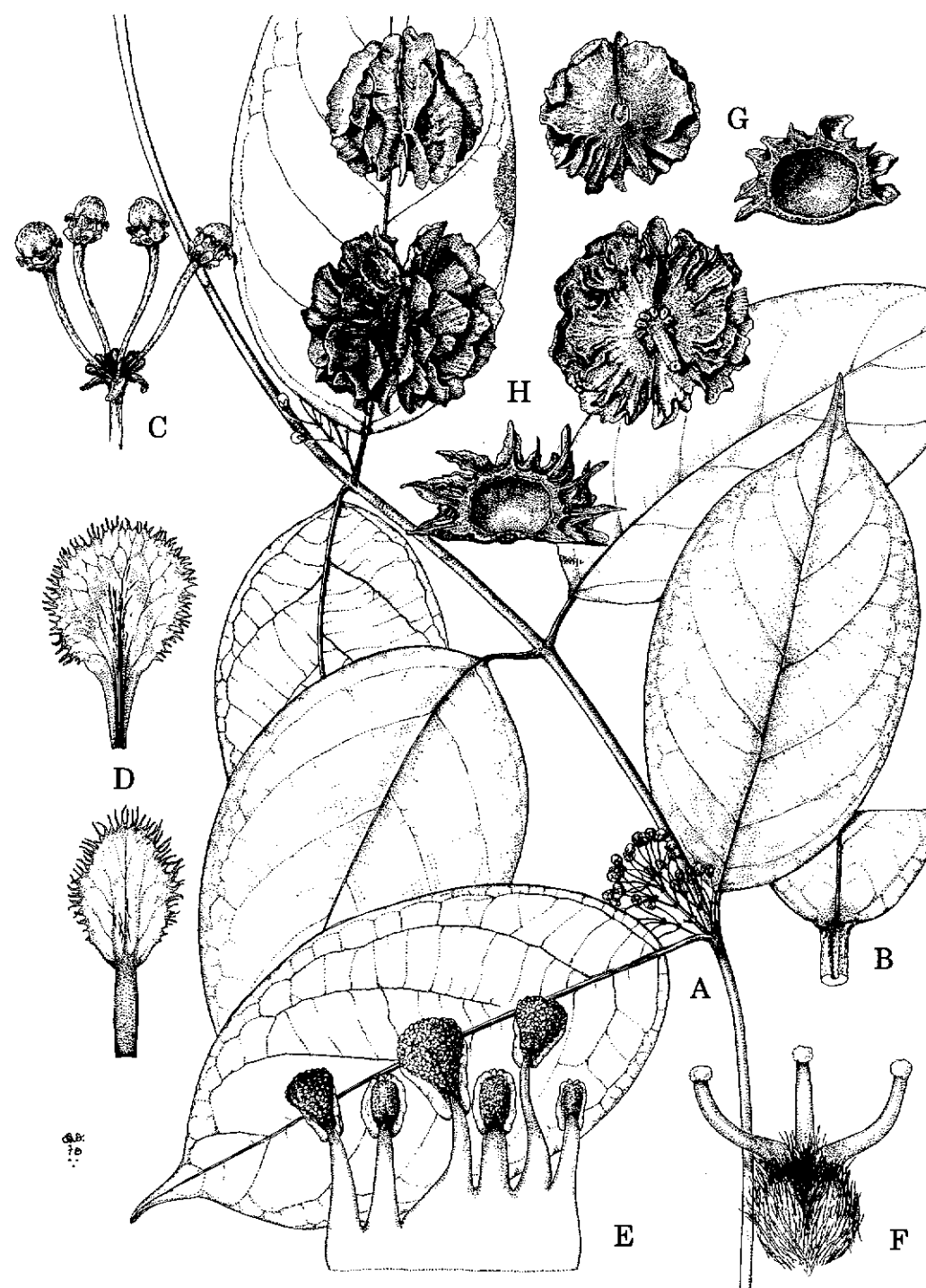


Fig. 92. *Diplopterys cabrerana*. —A. Flowering branch,  $\times 0.5$ . —B. Leaf base with glands,  $\times 1.6$ . —C. Umbel of 4 buds,  $\times 2.1$ . —D. Abaxial view of posterior-lateral petal (above) and posterior petal (below),  $\times 4.3$ . —E. Abaxial view of part of androecium, stamen to left opposite anterior sepal,  $\times 10.7$ . —F. Gynoecium, anterior style in center,  $\times 10.7$ . —G. Mericarp with short wings, abaxial view (left), adaxial view (middle), cross section (right),  $\times 1.1$ . —H. Mericarp with long wings, abaxial view (left), adaxial view (right), cross section (below),  $\times 1.1$ . ©New York Botanical Garden 1981.

### 9. *DIPLOPTERYS* A. Juss. in Deless., Icon. Sel. Pl. 3: 20. 1837 [1838].

Woody vines. Stipules small, distinct, interpetiolar. Inflorescence axillary, shorter than the subtending leaves, of 1–several simple 4-flowered umbels or 1–several racemes of up to 7 4-flowered umbels; pedicels sessile; bracts and bracteoles similar, lingulate, eglandular, spreading, persistent, borne in a cluster of 12 at base of umbel. Anterior sepal usually eglandular, rarely bearing 1 abaxial gland; 4 lateral sepals biglandular; petals yellow, long-fimbriate, abaxially sparsely sericeous. Stamens 10, all fertile; anthers unequal. Gynoecium of 3 free carpels adnate to a common torus; styles 3, distinct, with capitate terminal stigmas. Fruit dry, breaking apart into 3 mericarps; nut of mericarp with a hard woody pericarp, bearing a dorsal crest and 2–several lateral winglets or crests parallel to areole and interconnected by ridges.

Mexico, Colombia, Venezuela, Guyana, French Guiana, Ecuador, Peru, Brazil, Bolivia; 4 species, 1 in Venezuela.

See Bronwen Gates, 1982 [*Banisteriopsis*, *Diplopterys* (Malpighiaceae), Fl. Neotrop. Monogr. No. 30].

#### *Diplopterys cabrerana* (Cuatrec.) B.

Gates, Brittonia 31: 109. 1979. —*Banisteriopsis cabrerana* Cuatrec., Webbia 13: 493. 1958. —Yagé.

Woody vine; petioles (4–)8–15(–22) mm long, bearing 2 large convex glands on margin at apex; blade of larger leaves (8.5–)10–21(–26)  $\times$  (3–)4.1–9 cm, elliptic, long-acuminate at apex, abaxially sparsely sericeous; mericarp with nut up to 15 mm diameter, bearing a dorsal crest or winglet 1–5 mm wide and essentially 4 roughly parallel

ridges or winglets on each side 0.5–10 mm wide, these irregular, dissected, and interconnected with transverse ridges. Riparian forests, 100–200 m; Amazonas (Río Mawarimuma, Río Orinoco above San Fernando de Atabapo). Amazonian Colombia, Ecuador, Peru, Brazil. ♦Fig. 92.

*Diplopterys cabrerana* is widely used by indigenous peoples in western Amazonia as an admixture to *Banisteriopsis caapi* in the preparation of hallucinogenic concoctions.

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

Woody vines. Leaves with petiole biglandular; stipules small, triangular, borne on very base of petiole or on adjacent stem, or absent; blade eglandular or bearing small glands on margin, the tertiary veins strongly parallel (scalariform). Inflorescence a single axillary raceme of 3–7(–9) 4-flowered umbels, with 1 umbel terminal and the other 1–4 pairs axillary to bracts bearing stipules and often petiole glands; floriferous bracts small, persistent, eglandular; floriferous peduncle short or absent; bracteoles small, persistent, one of each pair bearing 1 bulging eccentric abaxial gland toward center of umbel; pedicels circinate in bud as far as known. Sepals all eglandular or the lateral 4 biglandular, revolute in anthesis; petals yellow, glabrous. Stamens 10, all fertile; anthers  $\pm$  alike. Ovary with the 3 carpels nearly distinct, all fertile; styles 3, inserted low on ventral face of carpels, the apex with a large internal stigma and dorsally truncate, apiculate, or bearing a hook up to 0.3 mm long. Fruits breaking apart into 3 samaras, each with a large, membranous, subcircular lateral wing borne on upper edge of nut, incised to nut at apex, usually continuous at base; dorsal wing small; intermediate winglets absent.

Venezuela, Guyana, Suriname, French Guiana, Brazil, Bolivia; 4 species, 1 in Venezuela.

Three of the species of *Excentradenia* are from north of the Amazon and the other is from Bolivia. It is close to *Hiraea* but differs in the small basal stipules, racemose branching of the inflorescence, eccentric bracteole glands, and samara wing

usually continuous at the base. Only the type species occurs in Venezuela and the flora area.

**Excentradenia adenophora** (Sandwith) W.R. Anderson, Contr. Univ. Michigan Herb. 21: 31. 1997. —*Hiraea adenophora* Sandwith, Kew Bull. 1951: 33. 1951.

Woody vine; leaves opposite, subopposite, or alternate; stipules 0.4–0.8 mm long, borne on petiole at very base; petioles 10–20 mm long; blade of larger leaves 8–15.5 × 4.5–10.3 cm, ovate or elliptic to orbicular, obtuse or rounded and abruptly short-acuminate at

apex; floriferous peduncles 1–2.5 mm long; pedicels 7–10 mm long; anterior sepal eglandular, the lateral 4 biglandular; styles bowed outward, dorsally apiculate at apex; samaras depressed-circular with the nut positioned below the center, 57–66 mm wide, ca. 50 mm high. Near streams, 100–200 m; Delta Amacuro (east side of Río Cuyubini), Bolívar (southwest of El Manteco on road to San Pedro de las Dos Bocas). Guyana. •Fig. 93.

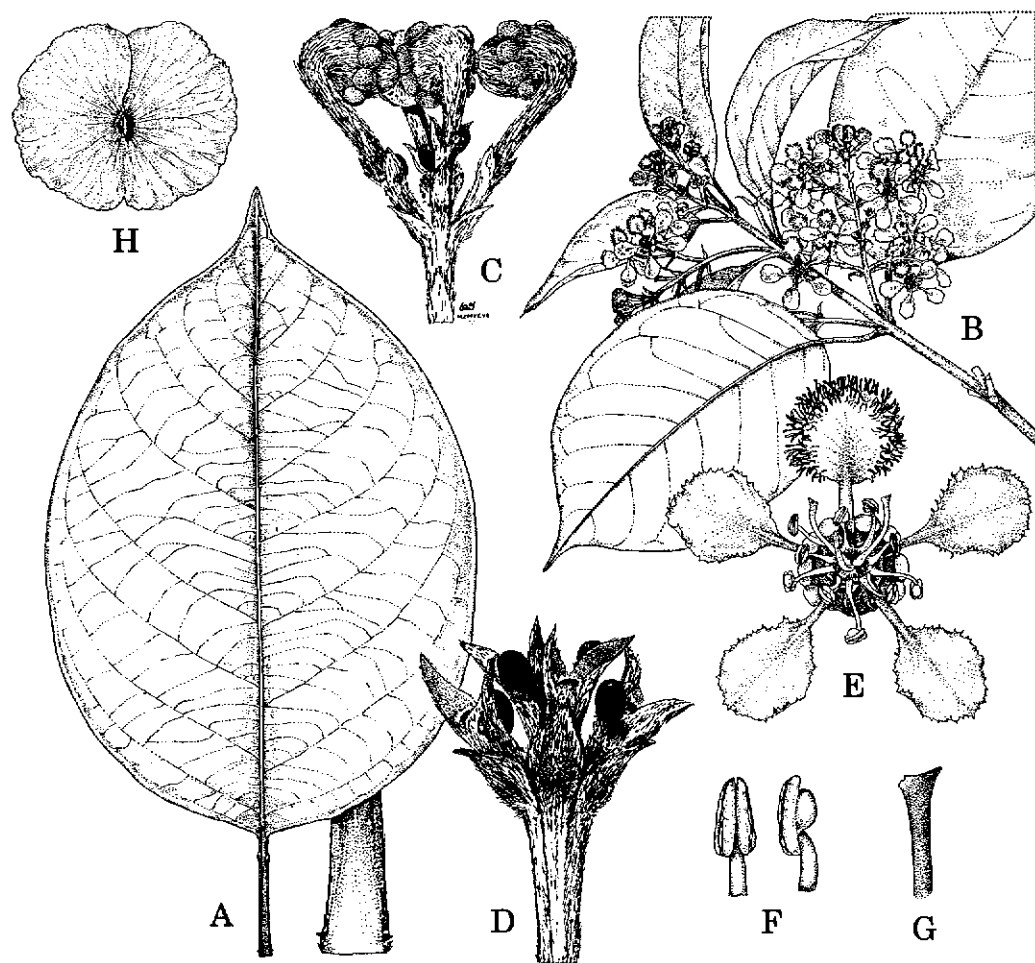


Fig. 93. *Excentradenia adenophora* A–G: —A. Large leaf, adaxial view,  $\times 0.54$ , and base of petiole with stipules,  $\times 2.7$ . —B. Flowering branch,  $\times 0.54$ . —C. Umbel of 4 circinate buds,  $\times 2.7$ . —D. Base of umbel enlarged to show eccentric glands on 4 bracteoles,  $\times 5.4$ . —E. Flower with posterior petal uppermost,  $\times 2.7$ . —F. Anthers, adaxial view (left), side view (right),  $\times 10.8$ . —G. Distal portion of style, side view,  $\times 10.8$ . —H. Abaxial view of samara of *E. propinqua* (similar to that of *E. adenophora*),  $\times 0.54$ . ©University of Michigan Herbarium 1997.

# **11. GLANDONIA** Griseb. in Mart., Fl. Bras. 12(1): 23. 1858.

Shrubs or trees. Leaves bearing abaxial glands; stipules interpetiolar, linear, 9–24 mm long, the adjacent stipules from opposite leaves connate in pairs, the 2 pairs at each node conduplicate and equitant over the apical bud, caducous, the members of a pair often splitting apart before falling off. Inflorescence terminal, usually unbranched, a raceme of short cincinni, the bracts and bracteoles persistent, the lowest bracteole and alternate subsequent bracteoles bearing 1 large eccentric abaxial gland. Flower buds pyramidal, with the conical-galeiform outermost petal completely covering the others. Sepals all biglandular; petals usually described as white, occasionally “yellow.” Stamens 10; filaments densely hirsute; anthers unwinged, tapering distally into 2 sterile awn-like extensions exceeding the slender connective. Ovary of 3 completely connate carpels, with all 3 locules fertile; styles 3, subulate; stigma minute and terminal. Fruit an indehiscent fibrous nut, cylindrical or truncate-conoidal, dry at maturity and without a stony endocarp, containing only 1 locule completely filled by 1 large seed.

Amazonian Colombia, Venezuela, and Brazil; 3 species, 1 in Venezuela.



***Glandonia williamsii*** Steyerl., Fieldiana, Bot. 28: 288. 1952.

Shrub or small tree 2–8(–15) m tall; blade of larger leaves 10–22 × 3.3–10.3 cm; posterior petal bearing ca. 10 glands on each side of base of limb and distally eglandular; fruits 14–22 × 12–14 mm, bearing 7–9 low, rounded, longitudinal ribs. Seasonally flooded riparian forests of black-water rivers, 100–200 m; Amazonas (Río Atacavi, Río Casiquiare, Río Cuao, Río Guainía, upper Río Orinoco, Río Pasimoni, Río Puruname, Río Sipapo, Río Temi, Río Yatua). Basin of upper Río Negro in Colombia and Brazil. •Fig. 94.

Fig. 94. *Glandonia williamsii*

**12. HETEROPTERYS** H.B.K., Nov. Gen. Sp. (quarto ed.) 5: 163. 1821 [1822], nom. cons.

Woody vines, shrubs, or small trees. Leaves usually bearing glands; stipules very small, distinct, triangular, borne on or beside base of petiole, or absent. Flowers borne in umbels, corymbs, or pseudoracemes, these single or grouped in racemes or panicles, axillary or terminal; petals mostly yellow or pink. Stamens 10; anthers  $\pm$  alike, the connective not or hardly exceeding locules (fertile stamens apparently only 6 or 7 in *H. maguirei*). Ovary with the 3 carpels partially connate, all fertile; styles 3, the apex with a large, usually internal stigma and dorsally rounded, truncate, acute, or hooked, the stigma very rarely terminal. Fruits breaking apart into 3 samaras, each samara having its largest wing dorsal, thickened on the abaxial (lower) edge and (in most species) bent upward, the veins terminating in the thinner adaxial edge; much shorter winglets or crests present on sides of nut in some species; dorsal wing rudimentary in a few species.

Mexico, Central America, West Indies, South America (all countries except Chile), western Africa (1 species); at least 125 species, 26 known or expected in Venezuela, 20 of these in the flora area.

Key to the Species of *Heteropterys*

1. Petioles biglandular at base ..... 2
1. Petioles eglandular or bearing glands near or above middle. .... 5
- 2(1). Pedicels sessile ..... 3
2. Pedicels pedunculate ..... 4
- 3(2). Woody vine; petioles 14–20 mm long; blade of larger leaves 10–15  $\times$  6–11 cm, tomentose abaxially with the hairs clearly stalked; inflorescence a raceme or panicle of umbels ..... *H. neblinensis*
3. Shrub or slender tree 1–3 m tall; petioles 5–10 mm long; blade of larger leaves 3–9  $\times$  2–5 cm, sericeous or appressed-tomentose or almost glabrous abaxially with the hairs nearly or quite sessile; inflorescence a single umbel terminating a leafy shoot ..... *H. steyermarkii*
- 4(2). Inflorescence compound, paniculate, with the flowers borne ultimately in umbels or tight corymbs of 4–10; bracteoles eglandular; petals pink or pink and white, with a prominent abaxial wing on the limb; sepals appressed ..... *H. cristata*
4. Inflorescence simple, an elongated pseudoraceme of 20–60 flowers; 1 of each pair of bracteoles bearing 1 large eccentric abaxial gland; petals yellow, abaxially smooth; sepals revolute at apex ..... *H. molesta*
- 5(1). Sepals erect or appressed; petals exposed early and through enlargement of bud, yellow, bronze, brown-maroon, pink, or white ..... 6
5. Sepals revolute at apex; petals concealed by sepals during enlargement of bud, yellow ..... 10
- 6(5). Mature leaf blades glabrous or glabrate abaxially or only sparsely sericeous, the hairs not apparent without a lens ..... 7
6. Mature leaf blades persistently and obviously sericeous or tomentose abaxially ..... 8
- 7(6). Petals yellow, abaxially smooth or with the midvein prominent; anthers loosely sericeous; petioles 12–22 mm long; blade of larger leaves 9–20  $\times$  4.5–12 cm; samaras 60–80 mm long, the nut smooth or rugose and

- without lateral crests or bearing a small crest 1.5 mm wide on each side. .... *H. megaptera*
7. Petals pink or pink and white, abaxially prominently winged; anthers glabrous; petioles 4–12(–15) mm long; blade of larger leaves 6–12.5  $\times$  3.3–6.5 cm; samaras 28–37 mm long, the nut bearing on both sides a lateral crest or wing 1–5 mm wide, subentire or dissected into several winglets ..... *H. cristata*
- 8(6). Leaf blades tightly and persistently sericeous abaxially; petals yellow, abaxially carinate; nut of samara with the sides quite smooth; blade of larger leaves 11–20  $\times$  6–11 cm ..... *H. macrostachya*
8. Leaf blades at least initially tomentose abaxially; petals pink or pink and white, 4 or all 5 abaxially prominently winged; nut of samara usually bearing short lateral crests or winglets; blade of larger leaves 4.5–12.5  $\times$  3–6.5 cm ..... 9
- 9(8). Leaf blades eventually glabrate abaxially, soon glabrate and shining adaxially; pedicels 5–9 mm long; bracteoles appressed; stigmas laterally compressed, higher than wide ..... *H. cristata*
9. Leaf blades persistently tomentose abaxially,  $\pm$  persistently tomentose adaxially and not shining; pedicels 2–3 mm long; bracteoles spreading; stigmas laterally expanded, at least twice as wide as high ..... *H. alata*
- 10(5). Bracts 4.5–8 mm long; bracteoles 3–5 mm long ..... 11
10. Bracts (0.5–)1–3(–4) mm long; bracteoles 0.5–2.5(–3) mm long ..... 12
- 11(10). Blade of larger leaves 23–33(–36)  $\times$  8–14(–19) cm, abruptly acuminate at apex; pseudoracemes 6–20 cm long; bracts 3–6 mm wide; bracteoles 3–4 mm wide; fertile stamens 10; styles 3.8–4.5 mm long, with a well-developed dorsal hook 0.3–0.6 mm long at apex; samara wing 22–37 mm wide ..... *H. leona*
11. Blade of larger leaves 8–10.5  $\times$  4.7–6.7 cm, very broadly obtuse or rounded and sometimes retuse and apiculate at apex; pseudoracemes 2–6(–9) cm long; bracts 1.3–3 mm wide; bracteoles 1–2.5 mm wide; fertile stamens 6 or 7 (as far as known); styles ca. 2.3 mm long, dorsally truncate or rounded at apex; samara wing 11–13 mm wide ..... *H. maguirei*
- 12(10). Inflorescence composed of umbels or corymbs of (3)4–6(–8) flowers or of short crowded pseudoracemes with 1–3 pairs of flowers and then a terminal umbel, the axis (excluding the floriferous peduncles and pedicels) up to 1.5 cm long (sometimes to 2.5 cm in *H. nervosa*) ..... 13
12. Inflorescence composed of elongated pseudoracemes not terminating in umbels, these mostly over 2.5 cm long, often much longer ..... 18
- 13(12). Leaf blades glabrous abaxially ..... 14
13. Leaf blades sparsely to densely sericeous or tomentose-sericeous abaxially (older leaves sometimes eventually glabrescent) ..... 15
- 14(13). Branches of inflorescence usually with 1–3 pairs of flowers below terminal umbel; samaras 19–40 mm long ..... *H. nervosa*
14. Branches of inflorescence usually without flowers developed below terminal umbel; samaras 40–50 mm long ..... *H. siderosa*
- 15(13). Bracts (and often bracteoles) reflexed or revolute; leaf blades sparsely sericeous abaxially, the hairs visible only with a lens ..... *H. siderosa*

15. Bracts and bracteoles ascending; leaf blades moderately to densely sericeous or tomentose-sericeous abaxially, the hairs visible without a lens ..... 16
- 16(15). Sepals proximally rusty brown, distally white; petals abaxially persistently sericeous; blade of larger leaves 5–7 cm wide ..... *H. dichromocalyx*
16. Sepals uniformly dark brown; petals sparsely pilose, especially on margins, to glabrate; blade of larger leaves 2–4.5 cm wide ..... 17
- 17(16). Woody vine; leaf blades acuminate at apex, the reticulum nearly or quite invisible on adaxial side; petiole of larger leaves 5–11 mm long; inflorescences short-stalked and crowded, mostly shorter than subtending leaves; anther connectives uniformly dark ..... *H. cuatrecasasii*
17. Shrub to 4 m tall; leaf blades obtuse or rounded and sometimes emarginate at apex, the reticulum readily visible on both sides; petioles 1–4 mm long; inflorescences long-stalked and open, often longer than subtending leaves; anther connectives with a dark red spot just above insertion of filament, otherwise yellow ..... *H. huberi*
- 18(12). Woody vines ..... 19
18. Shrublets, shrubs, or small trees ..... 20
- 19(18). Bracteoles (1 or both) usually bearing 1 or 2 prominent abaxial glands; petioles sometimes bearing 1 or 2 glands on distal half; samaras usually ca. 3 times as long as nut, the wing usually flabelliform, its abaxial edge often recurved ..... *H. orinocensis*
19. Bracteoles usually eglandular, rarely with minute marginal glands; petioles eglandular; samaras usually 4–5 times as long as nut or longer, the wing elongated, obovate or falcate, its abaxial edge usually curved or bent abruptly upward ..... *H. macradena*
- 20(18). Leaf blades densely and persistently tomentose to subsericeous abaxially, the hairs short-stalked, moderately sinuous to twisted, their cross-pieces 0.5–1 mm long ..... *H. quetepensis*
20. Leaf blades originally sparsely to moderately sericeous with sessile, straight, tightly appressed hairs 0.15–0.4 mm long but usually soon glabrescent to quite glabrate ..... 21
- 21(20). Leaves obtuse or rounded at apex, opposite, alternate, or whorled, the arrangement often variable on the same stem, seldom strictly decussate; petioles 0–5 mm long, eglandular ..... 22
21. Leaves mostly narrowly acute or acuminate at apex, strictly decussate (if somewhat obtuse at apex, the petioles mostly bearing 2 sunken glands near middle); petioles 4 mm long or longer, eglandular or bearing 1 or 2 pairs of glands between middle and apex ..... 23
- 22(21). Leaf blades moderately to strongly revolute, with the fine reticulum much more prominent adaxially than abaxially; vegetative internodes nearly or quite glabrous; abaxial leaf epidermis papillose (due to protruding starch grains in guard cells), often glaucous ..... *H. oblongifolia*
22. Leaf blades nearly or quite flat, with the reticulum about as prominent abaxially as adaxially or more prominent abaxially; vegetative internodes minutely sericeous to glabrate; abaxial leaf epidermis smooth or obscurely papillose, not glaucous ..... *H. atabapensis*
- 23(21). Leaf blades with the very fine reticulum equally visible on both sides in dried leaves, the finest subdivisions almost as prominent as the lateral

veins; most petioles bearing 2 sunken glands near middle, and occasionally 2 more near apex; bracts (and at least some bracteoles) deciduous before maturation of fruits; samaras 17–20 × 6–8 mm

- ..... *H. ayacuchensis*
23. Leaf blades with the reticulum more visible abaxially than adaxially, comprising 3 or 4 orders of prominence from lateral veins to finest and substantially less prominent veinlets; petioles eglandular; bracts and bracteoles mostly persistent; samaras usually 25 × 10 mm or larger ..... *H. macradena*

**Heteropterys alata** (W.R. Anderson) W.R. Anderson, Contr. Univ. Michigan Herb. 16: 75. 1987. —*Heteropterys beecheyana* var. *alata* W.R. Anderson, Mem. New York Bot. Gard. 32: 184. 1981.

Woody vine or shrub to 8 m tall; blade of larger leaves 4.5–7.5 × 3–5.2 cm, ovate, rounded or retuse and often mucronate at apex, densely and persistently tomentose on both sides, especially abaxially; flowers borne ultimately in umbels, corymbs, or short crowded pseudoracemes of 4–14; sepals erect or appressed in anthesis; petals pink or pink and white, the lateral 4 abaxially winged, the posterior carinate or with a narrow wing; samaras 18–30 × 7–12 mm, the nut usually bearing on both sides 1–several crests or winglets 0.5–2 mm wide. Open places in lowlands, especially in savannas and on granitic outcrops, 100–300 m; Bolívar (Cerro San Borja along lower Río Suapure), Amazonas (Cerro Parú, vicinity of Puerto Ayacucho). Cojedes, Miranda, Zulia; Colombia east of the Andes, especially common in the Llanos Orientales.

**Heteropterys atabapensis** W.R. Anderson, Mem. New York Bot. Gard. 32: 198. 1981.

Shrublet, shrub, or small tree 10 cm to 4 m tall; leaves alternate, opposite, or whorled, the arrangement often variable on the same stem; petioles 0–2 mm long, eglandular; blade of larger leaves 3.5–10(–12) × (0.5–)1–6.5(–7.2) cm, ovate or elliptic or rarely linear, obtuse or rounded at apex, soon glabrate; flowers borne in pseudoracemes; sepals revolute at apex; petals yellow; samaras 10–23 × 5–10 mm. White-sand savannas, 100–200 m; Amazonas (upper Río Guainía north to Río Atabapo, Río Orinoco, and Río Ventuari, found as far north as Cerro Cuao). Colombia (Vaupés).

For a discussion of the parallel variation found in this species and its morphological and geographical sister *Heteropterys oblongifolia*, see p. 196 in the 1981 paper where it was described.

**Heteropterys ayacuchensis** W.R. Anderson, Mem. New York Bot. Gard. 64: 227. 1990.

Shrub 1–2 m tall; petioles 4–7 mm long, mostly biglandular near middle and occasionally near apex; blade of larger leaves 5–8.8 × 2–4 cm, narrowly ovate, acute or acuminate or somewhat obtuse at apex, abaxially sericeous to soon ± glabrate, the very fine reticulum equally visible on both sides; flowers borne in pseudoracemes; sepals revolute at apex; petals yellow; samaras 17–20 × 6–8 mm. On and near granitic outcrops, 50–100 m; Amazonas (Puerto Ayacucho south to Morganito). Endemic.

**Heteropterys cristata** Benth., London J. Bot. 7: 131. 1848.

*Heteropterys carinata* Benth., London J. Bot. 7: 133. 1848.

Woody vine; petioles (4–)6–12(–15) mm long, usually biglandular near base; blade of larger leaves 6–12.5 × 3.3–6.5 cm, ovate, acute or acuminate at apex, initially sericeous or tomentose, soon glabrate and shining adaxially, soon to eventually glabrate abaxially; inflorescence with the flowers borne ultimately in umbels or tight corymbs of 4–10; sepals erect or appressed in anthesis; petals pink or pink and white, abaxially winged; samaras 28–39 × 13–15 mm, the nut bearing on both sides a crest or wing 1–5 mm wide, subtire or dissected into several winglets. Lowland to lower montane forests, often along rivers, 100–900 m; Bolívar (southwest of Roraima-tepui), Amazonas (Isla Ratón, Puerto Ayacucho, Río Ventuari,



San Juan de Manapiare, Sierra de la Neblina). Colombia, Guyana, Amazonian Peru, Brazil.

**Heteropterys cuatrecasii** W.R. Anderson, Mem. New York Bot. Gard. 32: 191. 1981.

Woody vine; petiole of larger leaves 5–11 mm long; blade of larger leaves 4–9 × 2–4 cm, ovate or elliptic, acuminate at apex, abaxially persistently tomentose-sericeous or eventually glabrescent; inflorescence short-stalked and crowded, the flowers borne ultimately in umbels or corymbs of 4–6(–8); sepals revolute at apex; petals yellow; samaras 21–33 × 9–16 mm. Sabanitas and tepui-slope forests, 1100–2000 m; Amazonas (Cerro Huachamacari, Cerro Marahuaka, Cerro Parú). Endemic.

**Heteropterys dichromocalyx** W.R. Anderson, Mem. New York Bot. Gard. 32: 193. 1981.

Woody vine; blade of larger leaves 11–12 × 5–7 cm, elliptic, acuminate at apex, abaxially thinly but ± persistently sericeous; flowers borne ultimately in umbels of 3–6; sepals revolute at apex, proximally rusty brown, distally white; petals yellow, abaxially persistently sericeous; samaras unknown. Montane forests, 1300–2000 m; Amazonas (expected on the slopes of Sierra de la Neblina). Brazil (Amazonas: Pico da Neblina).

**Heteropterys huberi** W.R. Anderson, Contr. Univ. Michigan Herb. 16: 78. 1987.

Shrub to 4 m tall; petioles 1–4 mm long; blade of larger leaves 5–8 × 2.5–4.5 cm, elliptic, obtuse or rounded and sometimes emarginate at apex, densely and ± persistently sericeous abaxially; inflorescence long-stalked and open, the flowers borne ultimately in umbels of 4, often with an additional proximal pair of flowers; sepals revolute at apex; petals yellow, sparsely pilose on margin or glabrate; immature samaras 12–14 × 5–5.5 mm. Open rocky shrubby places on tepui slopes, 600–800 m; Amazonas (Cerro Aracamuni). Endemic.

**Heteropterys leona** (Cav.) Exell, Cat. Vasc. Pl. S. Tomé 123. 1944. —*Banisteria leona* Cav., Diss. 9: 424, pl. 247. 1790.

*Malpighia reticulata* Poir. in Lam., Encycl. Suppl. 4: 8. 1816. —*Byrsonima reticulata* (Poir.) DC., Prodr. 1: 581. 1824. —*Heteropterys reticulata* (Poir.) Nied., Arbeiten Bot. Inst. Königl. Lyceum Hosianum Braunsberg 2: 54. 1903, non Griseb. in Mart. 1858. —*Banisteria reticulata* (Poir.) C.B. Rob. in Small, N. Amer. Fl. 25: 138. 1910.

*Banisteria multiflora* DC., Prodr. 1: 589. 1824. —*Heteropterys multiflora* (DC.) Hochr., Bull. New York Bot. Gard. 6: 277. 1910.

*Heteropterys africana* A. Juss., Ann. Sci. Nat. Bot. sér. 2, 13: 276. 1840, *nom. superfl.*

Woody vine; blade of larger leaves 23–33(–36) × 8–14(–19) cm, often smaller near inflorescence, ovate or elliptic to obovate, abruptly acuminate at apex, abaxially thinly sericeous to glabrate; pseudoracemes 6–20 cm long; bracts 5–8 × 3–6 mm; bracteoles 4–5 × 3–4 mm; sepals revolute at apex; petals yellow; styles with a dorsal hook at apex 0.3–0.6 mm long; samaras 35–50 × 22–37 mm, flabelliform to semicircular, the abaxial edge somewhat to strongly recurved, the nut flattened, trapezoidal, 17–25 mm diameter. Lowland riparian forests, near sea level to 100 m; Delta Amacuro (Caño Arature, Güini-quina, Río Cuyubini). Belize, Guatemala, Honduras, Nicaragua, Costa Rica, Panama, Colombia, Trinidad, Guyana, Suriname, French Guiana and adjacent Brazil (Amapá, Pará), west Africa.

*Heteropterys leona* has long been called *H. multiflora* in South America, but recent critical study by Christiane Anderson has shown that it is indistinguishable from the plant of west Africa, whose name is older and must be taken up for our species. I am grateful to C. Anderson for allowing me to cite her work here prior to its publication.

**Heteropterys macradena** (DC.) W.R. Anderson, Mem. New York Bot. Gard. 32: 202. 1981. —*Banisteria macradena* DC., Prodr. 1: 590. 1824.

Usually a woody vine, occasionally a shrub or small tree to 6 m tall; petioles eglandular; blade of larger leaves (5–)6.5–16(–18) × (2.5–)3.5–7(–8.5) cm, ovate or elliptic, occasionally obtuse or rounded at apex but mostly acuminate, originally sericeous on both sides, soon glabrate adaxially, the

hairs deciduous or sometimes ± persistent abaxially; bracteoles usually eglandular, rarely with minute marginal glands; flowers borne in a pseudoraceme; sepals revolute at apex; petals yellow; apex of styles usually extended dorsally into a hook up to 0.2 mm long; samaras (20–)25–42(–48) × (8–)10–15(–18) mm. Mostly in or near forests, often along streams, 50–500(–1300) m; throughout Bolívar and Amazonas. Elsewhere in Venezuela this species, interpreted in a broad sense, occurs in all or most states; Amazonian Colombia, Guyana, Suriname, French Guiana, Amazonian Peru and Brazil.

**Heteropterys macrostachya** A. Juss., Ann. Sci. Nat. Bot. sér. 2, 13: 275. 1840.

Woody vine, rarely a spreading shrub; petioles bearing 2–4 glands at or above middle; blade of larger leaves 11–22 × 6–11 cm, elliptic or slightly ovate or obovate, obtuse, short-acuminate, rounded, or retuse and mucronate at apex, soon glabrate adaxially, densely and persistently metallic-sericeous abaxially; inflorescence a raceme or panicle of 4–6-flowered umbels; sepals erect or appressed in anthesis; petals yellow, abaxially carinate; samaras 25–60 × 12–27 mm, the nut smooth-sided. Forests and thickets, especially along streams and rivers, 50–900 m; Bolívar (Río Caura, Río Orinoco, Río Paragua, Río Suapure), Amazonas (Río Cuao, Río Yawarui affluent of Río Matacuni). Apure, Aragua, Barinas, Carabobo, Distrito Federal, Falcón, Lara, Miranda, Nueva Esparta, Sucre, Táchira, Yaracuy; rare from Chiapas, Mexico, and Belize south to Nicaragua, ± common in Nicaragua, Costa Rica, Panama, Colombia, Guyana, Suriname, French Guiana, Ecuador, Peru, Brazil, Bolivia.

**Heteropterys maguirei** W.R. Anderson, Mem. New York Bot. Gard. 64: 225. 1990.

Woody vine or trailing shrub; blade of larger leaves 8–10.5 × 4.7–6.7 cm, elliptic, very broadly obtuse or rounded and sometimes retuse and apiculate at apex, abaxially ± persistently sericeous; pseudoracemes 2–6(–9) cm long; bracts 4.5–8 × 1.3–3 mm; bracteoles 3–5 × 1–2.5 mm; sepals revolute at apex; petals yellow; styles dorsally truncate or rounded at apex; samaras 26–32 × 11–13 mm. Upland white-sand savannas,

1000–1100 m; Bolívar (Gran Sabana, 194 km north of Santa Elena on road to El Dorado). Western Guyana.

The type collection has only 6 or 7 stamens fertile in each flower, whereas all other species of *Heteropterys* have all 10 stamens present and fertile. It remains to be seen whether that peculiarity will prove to be true of subsequent collections of this species; the type may have been abnormal and atypical. The second known collection is in fruit and sheds no light on this problem.

**Heteropterys megaptera** A. Juss., Ann. Sci. Nat. Bot. sér. 2, 13: 277. 1840.

*Heteropterys lasserii* W.R. Anderson, Mem. New York Bot. Gard. 32: 180. 1981.

Woody vine; petioles 12–22 mm long; blade of larger leaves 9–20 × 4.5–12 cm, broadly elliptic, rounded and abruptly short-acuminate at apex, abaxially sparsely sericeous or glabrate at maturity; inflorescence a panicle of 4–6-flowered umbels or 4-flowered umbels with another pair of flowers below; sepals erect or appressed in anthesis; petals yellow; anthers loosely sericeous; samaras 60–80 × 17–20 mm. Lower montane moist forests, 600–1200 m; Bolívar (La Escalera, Kavanayén, Río Venamo). Sucre (Península de Paria); Guyana, Atlantic Brazil (Bahia, Rio de Janeiro).

**Heteropterys molesta** W.R. Anderson, Contr. Univ. Michigan Herb. 21: 59. 1997.

Vine; petioles biglandular at base; blade of larger leaves 7.8–11.3 × 4–5.6 cm, elliptic or ovate, mostly obtuse and mucronulate at apex, adaxially loosely sericeous to glabrescent, abaxially tightly and persistently sericeous; inflorescence an unbranched axillary pseudoraceme of 20–60 flowers; 1 bracteole of each pair with 1 large eccentric abaxial gland; sepals revolute in anthesis; petals yellow; samaras unknown. Roadside thickets?, 50–100 m; Bolívar (between Upata and San Félix). Endemic.

This species is isolated in the genus, and until it is collected with fruits we will not even be certain it belongs in *Heteropterys*. See discussion in the protologue.

**Heteropterys neblinensis** W.R. Anderson, Mem. New York Bot. Gard. 32: 176. 1981.



Woody vine; petioles 14–20 mm long, biglandular at base; blade of larger leaves 10–15 × 6–11 cm, subcircular or broadly ovate or elliptic, rounded and apiculate at apex or abruptly short-acuminate, abaxially densely and persistently sulfur-tomentose; flowers borne ultimately in umbels of 5–15 (–20?); pedicels sessile; sepals appressed in anthesis; petals “bronze” or “pale yellow tinged with bronze”; samaras 32–35 × 11–12 mm. Amazonas (known only from escarpment overlooking Cañón Grande, Sierra de la Neblina, 1700–2000 m). Endemic.

**Heteropterys nervosa** A. Juss. in A. St.-Hil., Fl. Bras. Merid. 3: 26. 1832 [1833].

*Heteropterys suberosa* Griseb., Linnaea 13: 229. 1839.

*Banisteria mossii* C.V. Morton, Proc. Biol. Soc. Wash. 43: 157. 1930. —*Heteropterys mossii* (C.V. Morton) Cuatrec., Webbia 13: 478. 1958.

Woody vine; blade of larger leaves 7–13 (–17) × (2–)3–6.5 (–8) cm, elliptic, ovate, or somewhat obovate, acuminate at apex, glabrous; ultimate branches of inflorescence up to 1.5 (–2.5) cm long, terminating in umbels of 4–6 flowers usually subtended by 1–3 proximal pairs of flowers; sepals revolute at apex; petals yellow; samaras 19–40 × 8–13 (–16) mm. In lowlands, along rivers and in ± open savannas, often on white sand, 50–300 m; southern Amazonas (Caño Caname, La Esmeralda south to Río Negro and Río Baria, San Antonio). Eastern Colombia, Guyana, Suriname, French Guiana, Peru, Amazonian and central Brazil, Bolivia, Paraguay.

The plants to which I have applied this name are rather diverse through their range, and may represent more than one species.

**Heteropterys oblongifolia** Gleason, Bull. Torrey Bot. Club 58: 377. 1931.

Shrublet, shrub, or small tree 20 cm to 4 m tall; leaves alternate, opposite, or whorled, the arrangement often variable on the same stem; petioles 0–5 mm long, eglandular; blade of larger leaves 6–12 (–13.6) × 1–5 (–6.5) cm, narrowly to broadly elliptic or somewhat ovate or obovate, obtuse or rounded at apex, sparsely sericeous to soon glabrate; flowers borne in pseudoracemes; sepals revolute at apex; petals yellow; samaras 18–27 × 5–11 mm. Lowland savannas,

100–200 m; Amazonas (upper Río Orinoco and Río Guainía south to San Carlos de Río Negro and Río Pasimoni). Endemic. ♦Fig. 97.

See note under *Heteropterys atabapensis*.

**Heteropterys orinocensis** (H.B.K.) A. Juss., Ann. Sci. Nat. Bot. sér. 2, 13: 276. 1840. —*Banisteria orinocensis* H.B.K., Nov. Gen. Sp. (quarto ed.) 5: 162. 1821 [1822].

*Heteropterys acutifolia* A. Juss., Ann. Sci. Nat. Bot. sér. 2, 13: 276. 1840.

*Heteropterys helicina* Griseb. in Mart., Fl. Bras. 12(1): 67. 1858.

Woody vine; petioles often biglandular near apex; blade of larger leaves 9–18 (–20) × 3.5–7 (–8.5) cm, ovate or rarely elliptic, obtuse, acute, or acuminate at apex, thinly sericeous to glabrate; flowers borne in elongated pseudoracemes; one or both bracteoles usually bearing 1 or 2 prominent abaxial glands; sepals revolute at apex; petals yellow; samaras (16–)19–23 × (8–)11–13 mm, usually flabelliform, the abaxial edge often recurved. Common along rivers, 50–200 m; Bolívar (Río Orinoco and tributaries as far north as Caicara), Amazonas (Río Orinoco and Río Negro and their tributaries). Eastern Apure, southern Guárico; Amazonian Colombia, Peru, Brazil, Bolivia. ♦Fig. 96.

Some of the larger-leaved plants from Venezuela to which I have applied this name could pass for *Heteropterys riparia* Cuatrec., Webbia 13: 483. 1958, a species of Amazonian Colombia, Peru, and Brazil. I see no discontinuity that would allow me to recognize two species in Venezuela, which leads me to wonder whether *H. riparia* will survive careful study elsewhere.

**Heteropterys quetepensis** Steyer., Fieldiana, Bot. 28: 292. 1952.

Shrub or small tree 2–3 m tall; blade of larger leaves 6–11.2 × 3–6 cm, elliptic, mostly obtuse or rounded at apex, sometimes abruptly short-acuminate, abaxially persistently tomentose to subsericeous; flowers borne in pseudoracemes; sepals revolute at apex; petals yellow; samaras 20–28 × 8–11 mm. Dry rocky places with shrubby vegetation, near sea level to 200 m; Bolívar (between Caicara and Los Pijiguaos), Amazonas (northeast of Puerto Ayacucho). Anzoátegui, Apure, Cojedes, Guárico, Sucre.

**Heteropterys siderosa** Cuatrec., Webbia 13: 476. 1958.

Woody vine; blade of larger leaves 10–22 × 4–9 cm, elliptic or slightly obovate, acuminate to rounded at apex, abaxially sparsely sericeous to glabrate; ultimate branches of inflorescence terminating in umbels of 4–6 (–8) flowers; bracts (and often bracteoles) reflexed or revolute; sepals revolute at apex; petals yellow; samaras 40–50 × 12–21 mm. Evergreen lowland forests, 50–200 m; Amazonas (Caño Yagua, Río Casiquiare, Río Cataniapo, Río Cunucunuma, Río Yatua, Tamatama). Amazonian Colombia, Guyana, French Guiana, Amazonian Brazil.

**Heteropterys steyermarkii** W.R. Anderson, Mem. New York Bot. Gard. 32: 178. 1981.

Shrub or slender tree 1–3 m tall; petioles 5–10 mm long, biglandular at base; blade of larger leaves 3–9 × 2–5 cm, elliptic or slightly obovate, mostly obtuse or rounded and often apiculate at apex, rarely acute, sericeous or appressed-tomentose or almost glabrous abaxially with the hairs nearly or quite sessile; inflorescence an umbel of 3–11 flowers terminating a leafy shoot; pedicels sessile; sepals appressed in anthesis; 4 lateral petals brown-maroon, posterior petal white or pale yellow; samaras 18–30 × 8–14 mm. Rocky tepui slopes and marshy meadows, 1200–1900 m; Amazonas (Cerro Autana, Cerro Cuao, Cerro Sipapo). Endemic. ♦Fig. 95.

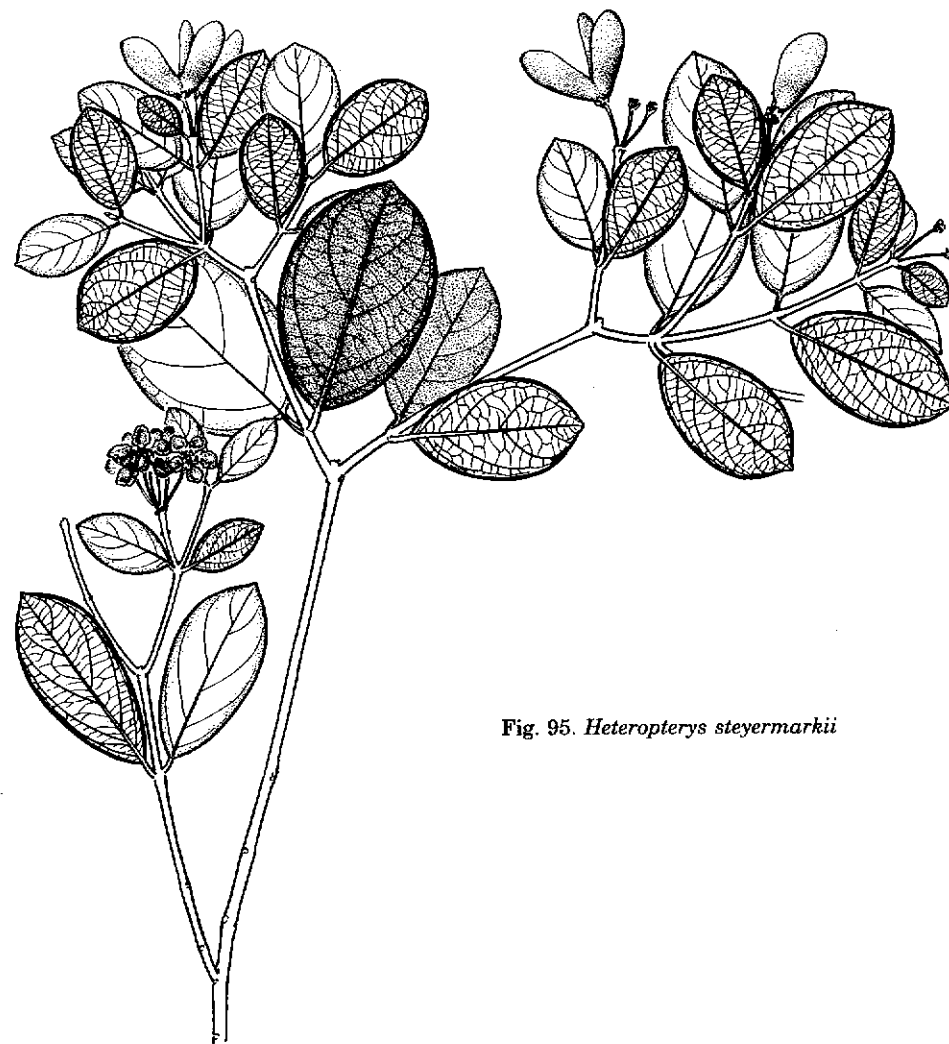


Fig. 95. *Heteropterys steyermarkii*

Fig. 96. *Heteropterys orinocensis*Fig. 97. *Heteropterys oblongifolia***13. HIRAEA** Jacq., Enum. Syst. Pl. 4. 1760.

Woody vines, sometimes shrubby. Leaves usually bearing glands distally on petiole or against abaxial base of midrib, and often on margin of blade, the tertiary veins often strongly parallel; stipules borne on petiole, from slightly above base to near apex, usually long and subulate. Inflorescences axillary, usually 1–several umbels of 4–many flowers, the umbels when 4-flowered often borne in a cyme; bracts and bracteoles eglandular; pedicels sessile. Anterior sepal eglandular, 4 lateral sepals biglandular or eglandular, with both forms present in some species; petals yellow, rarely red at maturity, glabrous. Stamens 10, all fertile; anthers  $\pm$  alike. Ovary with the 3 carpels nearly distinct, all fertile; styles 3, inserted low on ventral face of carpels, the apex with a large internal stigma and dorsally rounded to prominently hooked. Fruit breaking apart into 3 samaras, each butterfly-shaped with 2 discrete lateral wings, these coriaceous and reduced in a few species; dorsal wing small, sometimes reduced to a crest or lost; intermediate winglets or slender projections rarely present.

Mexico, Central America, West Indies, and South America (all countries except Chile and Uruguay); at least 47 species, ca. 20 in Venezuela, 10 of these in the flora area.

Key to the Species of *Hiraea*

1. Abaxial leaf hairs stalked, erect, Y- or T-shaped, occasionally with an admixture of V-shaped hairs (sessile with the 2 branches stiff and ascending) ..... *H. ternifolia*
1. Abaxial leaf hairs (if any) nearly or quite sessile and  $\pm$  appressed ..... 2
- 2(1). Leaf blades abaxially very densely and persistently sericeous, the hairs usually completely concealing the epidermis and producing a golden or silvery-metallic sheen ..... *H. faginea*
2. Leaf blades abaxially thinly sericeous or subtomentose to glabrate ..... 3
- 3(2). Umbel with a globose or depressed-globose, often dark glandular cushion, 0.7–2 mm diameter, in the center between bracteoles ..... 4
3. Umbel without a prominent central cushion, at most with a tiny obscure central body up to 0.3 mm diameter ..... 6
- 4(3). Leaf blades at least shallowly cordate at base; limb of lateral petals 6.5–8 mm long, 7.5–9 mm wide; petals long-fimbriate with the divisions 0.3–0.7 mm long ..... *H. fimbriata*
4. Leaf blades cuneate or rounded at base; limb of lateral petals 4–7 mm long and wide; petals subentire or short-fimbriate with the divisions up to 0.3 mm long ..... 5
- 5(4). Lateral veins prominent abaxially, hardly or not at all raised adaxially; limb of lateral petals 5–7 mm long and wide; nut of samara 3–4 mm diameter ..... *H. apaporiensis*
5. Lateral veins not or only slightly raised abaxially, almost as prominent adaxially as abaxially; limb of lateral petals 4–5 mm long and wide; nut of samara ca. 2 mm diameter ..... *H. tepuiensis*
- 6(3). Leaf blades bearing obscure or prominent glands on margin, at least distally ..... 7
6. Leaf blades with the margin eglandular ..... 8
- 7(6). Petiole of larger leaves 14–20 mm long; pedicels 14–28 mm long; stipules borne 5 mm or more below apex of petiole ..... *H. steyermarkii*

7. Petiole of larger leaves 7–11 mm long; pedicels 9–13 mm long (–15 mm in fruit); stipules borne at apex of petiole or up to 2 mm below ..... *H. fagifolia*
- 8(6). Lateral veins not or only slightly raised abaxially, almost as prominent adaxially as abaxially; stipules 0.5–1 mm long ..... *H. tepuiensis*
8. Lateral veins quite prominent abaxially, hardly or not at all raised adaxially; stipules 1–5 mm long ..... 9
- 9(8). Specimens with fruits (*H. celiana* is not known in fruit and is not keyed here) ..... 10
9. Specimens with flowers ..... 12
- 10(9). Samaras with the dorsal wing absent or represented by a rounded crest 0.2(–0.5) mm high; inflorescence an unbranched umbel, with 1–7 umbels in a vertical array in each axil ..... *H. affinis*
10. Samaras with a small but definite dorsal wing; inflorescence usually a cyme of 3 umbels, with 1–3 cymes in a vertical array in each axil, the cyme occasionally reduced to 1 umbel ..... 11
- 11(10). Blade of larger leaves up to 7.5 cm wide; stipules borne at apex of petiole or up to 2 mm below; pedicels up to 13 mm long (–15 mm in fruit) ..... *H. fagifolia*
11. Blade of larger leaves 8.5–17 cm wide; stipules borne slightly above middle of petiole; pedicels 11–20 mm long ..... *H. neblinensis*
- 12(9). Posterior petal glandular-fimbriate all around margin ..... *H. fagifolia*
12. Posterior petal with the margin dentate to fimbriate but the divisions not glandular-thickened ..... 13
- 13(12). Leaf blades cuneate at base; styles dorsally rounded or truncate at apex ..... *H. celiana*
13. Leaf blades rounded or cordate at base; styles with a short (ca. 0.2–0.3 mm), rounded dorsal hook at apex ..... 14
- 14(13). Petals dentate to short-fimbriate, with the divisions up to 0.2 mm long; inflorescence an unbranched umbel, with 1–7 umbels in a vertical array in each axil; petioles up to 11 mm long ..... *H. affinis*
14. Petals long-fimbriate, with the divisions 0.5–1 mm long; inflorescence usually a cyme of 3 umbels, with 1–3 cymes in a vertical array in each axil, the cyme occasionally reduced to 1 umbel; petioles 9–19 mm long ..... *H. neblinensis*

**Hiraea affinis** Miq., Linnaea 19: 133. 1847 [1846].

Large woody vine; stipules 1–2 mm long, borne somewhat below to somewhat above middle of petiole; petioles 4–11 mm long; blade of larger leaves 11–23 × (4–)5–12 cm, rounded or cordate at base, eglandular on margin, abaxially sparsely sericeous or glabrate at maturity; inflorescence a 4-flowered umbel, the umbels solitary in each axil or 2–7 in a vertical array; pedicels (9–)11–18 mm long; sepals adaxially glabrous; petals pale yellow, dentate or short-fimbriate with the divisions nonglandular; styles with a short

rounded dorsal hook at apex; samaras with lateral wings 22–30 mm wide, 35–56 mm high, membranous, the dorsal wing absent or represented by a rounded crest 0.2(–0.5) mm high. Lowland wet forests along rivers, 50–300 m; Delta Amacuro (Río Amacuro on the border with Guyana, east-northeast of El Palmar). Guyana, Suriname, French Guiana, Ecuador, Peru, Brazil, Bolivia.

**Hiraea apaporiensis** Cuatrec., Webbia 13: 404. 1958.

Woody vine; stipules 0.5–1(–1.5) mm long, borne between middle and apex of petiole;

petioles (4–)6–10(–12) mm long; blade of larger leaves 6–16(–21) × 3–6(–8) cm, cuneate or rounded at base, eglandular on margin, abaxially thinly sericeous at maturity, with the lateral veins prominent abaxially and hardly or not at all raised adaxially; inflorescence a 4-flowered umbel, the umbels solitary in each axil or 2 or 3 in a vertical array, each umbel with a dark glandular hemispherical or globose cushion in center between bracteoles; pedicels 8–13 mm long; petals subentire or short-fimbriate with the divisions nonglandular, the limb of lateral petals 5–7 mm long and wide; samaras with nut 3–4 mm diameter, lateral wings 7–11 mm wide, (6–)11–15 mm high. Evergreen lowland forests near rivers, 100–200 m; Amazonas (between San Fernando de Atabapo and the Río Orinoco). Amazonian Colombia, Brazil (western Amazonas).

**Hiraea celiana** W.R. Anderson, Mem. New York Bot. Gard. 32: 249. 1981.

Woody vine; stipules 1–1.5 mm long, borne between middle and apex of petiole; petioles 10–18 mm long; blade of larger leaves 12.5–28 × 5–12 cm, cuneate at base, eglandular on margin, abaxially thinly sericeous to glabrate at maturity; inflorescence a 4-flowered umbel, the umbels solitary in each axil or 2–4 in a vertical array; pedicels 16–22 mm long; sepals adaxially glabrous; petals all fimbriate with the divisions nonglandular; styles dorsally rounded or truncate at apex; samaras unknown. Mixed wet forests and scrub savannas, 100–1500 m; Amazonas (Cerro Cuao, Cerro Sipapo). Endemic.

**Hiraea fagifolia** (DC.) A. Juss., Ann. Sci. Nat. Bot. sér. 2, 13: 258. 1840. —*Banisteria fagifolia* DC., Prodr. 1: 590. 1824.

Woody vine, occasionally described as a shrub; stipules 2.5–5 mm long, borne within 2 mm of apex of petiole; petioles 7–11 mm long; blade of larger leaves 8.5–18.5 × 2.5–7.5 cm, rounded or subcordate at base, usually bearing several small glands on distal margin or occasionally eglandular, abaxially mostly glabrate at maturity except for sericeous midrib and sometimes the lateral veins; inflorescence a single axillary cyme of 3 4-flowered umbels; pedicels 9–13 mm long

(–15 mm in fruit); posterior petal glandular-fimbriate all around margin; samaras with lateral wings 13–20 mm wide, 20–30 mm high, membranous. Moist lower montane forests, 200–300 m; Bolívar (Altiplanicie de Nuria). Lara, Sucre; southeastern Mexico, Central America, Trinidad, all countries of South America except Chile and Uruguay.

See discussion below under *Hiraea faginea*. The specimens that I have called *H. fagifolia* sens. lat. came from Delta Amacuro (Río Amacuro) and Bolívar (upper Río Caura, Río Venamo).

**Hiraea faginea** (Sw.) Nied., Verz. Vorles. Königl. Lyceums Hosianum Braunsberg 1906/07: 16. 1906. —*Malpighia faginea* Sw., Prodr. 74. 1788. —*Hiraea swartziana* A. Juss., Ann. Sci. Nat. Bot. sér. 2, 13: 258. 1840, nom. superfl.

*Hiraea chrysophylla* A. Juss., Ann. Sci. Nat. Bot. sér. 2, 13: 258. 1840.

*Hiraea fulgens* A. Juss., Ann. Sci. Nat. Bot. sér. 2, 13: 258. 1840.

*Hiraea fulgens* var. *demerarensis* A. Juss., Arch. Mus. Hist. Nat. 3: 572. 1843. —*Hiraea demerarensis* (A. Juss.) Nied., Verz. Vorles. Königl. Lyceum Hosianum Braunsberg 1906/07: 15. 1906.

Woody vine, sometimes shrubby; stipules 2.5–5 mm long, borne between middle and apex of petiole; petioles 4–9(–11) mm long; blade of larger leaves (6–)8–15(–20) × 3–6(–8) cm, rounded or subcordate at base, usually bearing several small glands on distal margin, abaxially densely and usually persistently sericeous, the straight, appressed hairs giving lamina a golden or silvery-metallic sheen; inflorescence a single axillary cyme of 3 4-flowered umbels, sometimes reduced to a single umbel; pedicels (7–)8–11(–15) mm long; posterior petal glandular-fimbriate all around margin; samaras with lateral wings 5–15 mm wide and high, trapezoidal or rectangular, entire or lobed, usually coriaceous, often irregularly reduced. Riparian forests, near sea level to rarely as high as 200 m; Delta Amacuro (Caño Aragüao, Caño Güiniquina, Curipapo), Bolívar (Río Caura, Río Cuyuní, Río Paragüa), Amazonas (Isla Ratón, Río Casiquiare, Río Mavaca, Río Metacuni, Río Ocamo, upper Río Orinoco, Río Siapa). Ap-

parently not known from northern Venezuela; Nicaragua, Costa Rica, Panama, Lesser Antilles, Colombia, Guyana, Suriname, French Guiana, Brazil (north of the Amazon). ♦Fig. 98.

*Hiraea faginea* and *H. fagifolia* are very similar, and presumably closely related. Most specimens can immediately and unequivocally be assigned to one or the other, because in *H. faginea* the leaf blades are abaxially very densely and persistently metallic-sericeous, with the hairs completely hiding the epidermis, and in *H. fagifolia* the leaf blades are abaxially glabrous (or very early glabrate) except for the persistently sericeous midrib and sometimes the lateral veins. Moreover, the samara in *H. faginea* is usually  $\pm$  coriaceous and reduced, often very irregularly so, suggesting adaptation for dispersal by water; most fruiting collections of *H. fagifolia* have membranous, butterfly-shaped samaras obviously adapted for dispersal by wind. The two species have overlapping ecological requirements, but *H. faginea* seldom ventures much above sea level or away from rivers while *H. fagifolia* is much more likely to be found in upland forests, just as one would expect of a plant that has retained dispersal by wind. *H. fagifolia* has a much wider geographic range than *H. faginea*, and through much of their ranges the two species are allopatric, e.g., *H. fagifolia* is common in Peru, Bolivia, and Paraguay, while *H. faginea* is common in southern Venezuela and adjacent Brazil where *H. fagifolia* is hardly known. Their ranges do overlap, especially in the Venezuelan Guayana and the Guianas, and in those areas they seem to hybridize. I do not consider that sufficient reason to combine two taxa that are mostly distinct and distinctive, but the occasional intermediate plants do pose a problem for the users of this flora, because they will not key well. The putative hybrids have been found on the Río Caura and near the Río Cuyuní in Bolívar, in areas where "typical" *H. faginea* occurs. When the leaf blades are abaxially very thinly sericeous, so as to resemble most closely *H. fagifolia*, I am calling the intermediates *H. fagifolia sens. lat.* When the leaf blades are more densely sericeous, but with hairs not dense enough to hide the epidermis, I am using the name *H. faginea sens. lat.*

***Hiraea fimbriata*** W.R. Anderson, Mem. New York Bot. Gard. 32: 245. 1981.

Woody vine, occasionally described as a shrub 2–4 m tall; stipules 1–2.5 mm long, borne between middle and apex of petiole; petioles 4–10 mm long; blade of larger leaves 8–22  $\times$  4–10.5 cm, cordate at base, eglandular on margin, glabrate at maturity or with the midrib persistently sericeous; inflorescence a 4-flowered umbel, the umbels solitary in each axil or 2–4 in a vertical array, each umbel with a dark glandular hemispherical cushion in center between bracteoles; pedicels 7–14 mm long; petals long-fimbriate with the divisions nonglandular, the limb of lateral petals 6.5–8 mm long, 7.5–9 mm wide; mature samaras unknown. Riparian, seasonally flooded forests, 50–100 m; Bolívar (middle Río Orinoco and tributaries south of Río Caura), Amazonas (middle Río Orinoco and tributaries north of Río Sipapo). Anzoátegui, Apure; Colombia (Vichada: Río Meta).

***Hiraea neblinensis*** W.R. Anderson, Contr. Univ. Michigan Herb. 21: 66. 1997.

Large woody vine; stipules 2–3 mm long, borne slightly above middle of petiole; petioles 9–19 mm long; blade of larger leaves 13.5–31  $\times$  8.5–17 cm, shallowly cordate at base, eglandular on margin, abaxially mostly glabrate at maturity or with scattered hairs especially on midrib; inflorescence a cyme of 3 4-flowered umbels, sometimes reduced to a single umbel, the cymes solitary in each axil or 2 or 3 in a vertical array; pedicels 11–20 mm long; sepals adaxially sparsely sericeous; petals all long-fimbriate with the divisions 0.5–1 mm long and nonglandular; styles with a rounded dorsal hook ca. 0.2–0.3 mm long at apex; immature samaras with lateral wings 18 mm wide, 30 mm high. Evergreen lowland forests, 100–200 m; Amazonas (Río Mawarinuma). Endemic.

***Hiraea steyermarkii*** W.R. Anderson, Contr. Univ. Michigan Herb. 21: 69. 1997.

Woody vine; stipules 4.5–6 mm long, borne between base and middle of petiole or slightly higher; petioles 14–20 mm long; blade of larger leaves 14–23.5  $\times$  7–13.7 cm, cuneate to obtuse at base, bearing a series of large glands on distal  $\frac{1}{2}$ – $\frac{2}{3}$  of margin, abaxially nearly glabrate at maturity except

for sericeous midrib; inflorescence a cyme of 3–7 4-flowered umbels, the cymes solitary in each axil or 2, one above the other; pedicels 14–28 mm long; posterior petal fimbriate all around margin with the divisions  $\pm$  glandular-thickened, especially proximally; mature samaras unknown. Lowland forests, 100–300 m; Bolívar (east of Las Chicharras, Río Asa). Endemic.

The collection from near Las Chicharras is sterile and has much larger leaves than the type, and may represent a different species; more collections are needed to shed light on this problem.

***Hiraea tepuiensis*** Steyererm., Fieldiana, Bot. 28: 293. 1952.

Woody vine, rarely described as a small tree; stipules 0.5–1 mm long, borne at or above middle of petiole; petioles 6–15 mm long; blade of larger leaves 6–15  $\times$  3–6(–7) cm, cuneate or rounded at base, eglandular on margin, loosely sericeous or subtomentose to glabrescent except persistently sericeous on abaxial midrib, with lateral veins not or only slightly raised abaxially, almost as prominent adaxially as abaxially; inflorescence a 4-flowered umbel, the umbels solitary in each axil or 2–5 in a vertical array, each umbel without a prominent cushion in center between bracteoles, rarely with a small glandular knob; pedicels 8–15 mm long; petals erose or short-fimbriate with the divisions nonglandular, the limb of lateral petals 4–5 mm long and wide; samaras with nut ca. 2 mm diameter, the lateral wings 6–10 mm wide, 13–18 mm high. Moist montane to lower montane forests, often gallery forests in areas of savannas, (500–)700–1800 m; common in southeastern Bolívar (Gran Sabana and Macizo del Chimantá), Amazonas (Cerro Aratitoyope, Cerro Parí). Sucre. ♦Fig. 99.

***Hiraea ternifolia*** (H.B.K.) A. Juss., Ann. Sci. Nat. Bot. sér. 2, 13: 257. 1840. —*Malpighia ternifolia* H.B.K., Nov. Gen. Sp. (quarto ed.) 5: 146. 1821 [1822]. *Hiraea platytriphyllo* Hochr., Bull. New York Bot. Gard. 6: 276. 1910.

*Hiraea bifurcata* W.R. Anderson, Mem. New York Bot. Gard. 32: 242. 1981.

Woody vine forming thickets, shrub to 2.5 m tall, or small tree to 5 m tall; leaves ternate or decussate; stipules (1.5–)2–6 mm

long, borne from above base to near apex of petiole; petioles 5–11(–19) mm long; blade of larger leaves 7–16(–18.5)  $\times$  (3.5–)5–12 cm, broadly cuneate, rounded, or cordate at base, bearing several small glands on distal margin, adaxially densely velutinous with Y-shaped hairs to glabrescent in age, abaxially densely and persistently velutinous over whole surface with Y-shaped hairs; inflorescence usually an axillary cyme of 3 or 7 4-flowered umbels, sometimes a single umbel, sometimes 2 cymes, one above the other; pedicels 13–30(–35) mm long; posterior petal usually glandular-fimbriate all around margin; samara with the lateral wings 13–20 mm wide, 22–30 mm high, membranous. Open, dry forests on granitic outcrops, 50–400 m; Bolívar (Río Orinoco lowlands southward from Caicara), Amazonas (Río Orinoco lowlands northward from Samariapo). Mérida; Panama, Colombia.

*Hiraea ternifolia* is the oldest name in a difficult complex of species that extends from Mexico to eastern Brazil; species limits and the correct application of names in that complex are not at all clear. The description above applies to *H. ternifolia sens. str.* as I understand it. A second taxon in the complex, rather easily distinguished from *H. ternifolia sens. str.*, also occurs in the flora area. It differs from the above description in these ways: adaxial surface of leaf blade initially subsericeous, the hairs very short-stalked with a sinuous,  $\pm$  horizontal crosspiece often 1–1.5 mm long, glabrescent in age; abaxial surface of blade initially velutinous with Y- or T-shaped hairs but glabrescent in age with some hairs usually persistent on midrib and principal lateral veins. In addition, the leaf blade tends to be more deeply cordate at base and is often notably bullate. Such plants have been collected in forests, savannas, and thickets, 100–200 m, northwestern Bolívar (Caicara to El Burro) and northeastern Bolívar (El Palmar, El Miamo, north of Tumeremo, Reserva Forestal Imataca). I have seen similar plants from Zulía. For the present I am calling such plants *Hiraea aff. ternifolia* (H.B.K.) A. Juss. There are several published names that may eventually prove to be available for them, but I do not understand this group well enough to be willing either to apply one of those names to this taxon or to propose a new name in the complex at this time.

Fig. 98. *Hiraia faginea*Fig. 99. *Hiraia tepuiensis*

**14. JUBELINA** A. Juss. in Deless., Icon. Sel. Pl. 3: 19, pl. 32. 1837 [1838].

Woody vines. Leaves with the petiole eglandular; stipules small, borne on base of petiole; blade bearing impressed abaxial glands, the lateral veins interconnected by  $\pm$  parallel tertiary veins. Inflorescences axillary and terminal, decompound, thyriform, containing much-reduced bract-like leaves below the floriferous bracts, the flowers borne ultimately in umbels of 4 or corymbs of 6; bracts and bracteoles large, pubescent on both sides, persistent. Sepals narrowly ovate, oblong, or obovate, the anterior eglandular, the lateral 4 each biglandular or (in our species) bearing 1 large abaxial gland; petals yellow or (in our species) pink or pink and white. Stamens 10, glabrous. Ovary of 3 carpels adnate to a common axis; styles 3, the apex with a large internal stigma and dorsally truncate or short-hooked. Fruits breaking apart into 3 samaras, each bearing a semicircular dorsal wing and 2 large lateral wings confluent at base, each lateral wing with a sterile cavity in its base parallel to the fertile locule.

Central America, Colombia, Venezuela, Suriname, French Guiana, Ecuador, Peru, Brazil; 6 species, 2 in Venezuela, both in the flora area.

See W.R. Anderson, 1990 [The taxonomy of *Jubelina* (Malpighiaceae), Contr. Univ. Michigan Herb. 17: 21–37].

Key to the Species of *Jubelina*

1. Stems subsericeous or appressed-tomentose, the limb of hairs at right angles to the stalk; leaf blades bearing abaxially on each side 1 or 2 or occasionally 3 glands at base and 1–4 glands distally in a single row; calyx glands revolute at apex; samaras with lateral wings flat and lacking wings or winglets between them and dorsal wing, or at most a single flat crest or winglet 1–12 mm wide parallel to dorsal wing ..... *J. grisebachiana*
1. Stems velutinous, the hairs with a long fusiform stalk and very short erect branches; leaf blades bearing abaxially (4)5–15 scattered glands on each side; calyx glands attached for their whole length; samaras with strongly plicate or corrugated lateral wings consisting of an outer membranous wing, an inner dentate wing parallel to and hiding the central dorsal wing, and transverse winglets between them ..... *J. magnifica*

***Jubelina grisebachiana*** W.R. Anderson, Contr. Univ. Michigan Herb. 17: 30. 1990. —Bejuco de iguana, Bejuco de sapo.

*Jubelina bracteosa* auctt. non *Mascagnia bracteosa* Griseb. in Mart., Fl. Bras. 12(1): 97. 1858.

Woody vine; stems subsericeous or appressed-tomentose; petioles 14–23 mm long; blade of larger leaves 13–18 × 7–12 cm, broadly elliptic, rounded or abruptly short-acuminate at apex, persistently velutinous to tomentose on both sides or sometimes glabrescent adaxially; bracts and bracteoles

Fig. 100. *Jubelina grisebachiana*



pink, 4–6.5 × 1.5–2(–2.5) mm, narrowly obovate or spatulate; pedicels 5–7 mm long; sepals 4.5–6.5 × 1–1.5 mm, narrowly obovate, reflexed, distally inflated, the lateral 4 all bearing 1 large abaxial gland; petals pink, the lateral 4 sparsely to densely sericeous abaxially, the posterior glabrous; samaras elliptic, 60–90 × 25–40 mm, with the lateral wings flat. Open areas and secondary forests, 100–200 m; Amazonas (between Solano and San Carlos de Río Negro and San Simón de Cocuy). Basins of upper Río Negro and Río Vaupés in Colombia and Brazil. ♦Fig. 100.

**Jubelina magnifica** W.R. Anderson, Mem. New York Bot. Gard. 32: 228. 1981.  
Woody vine; stems velutinous; petioles 9–

20(–25) mm long; blade of larger leaves 18–28 × 10–18 cm, broadly ovate or elliptic, abruptly acuminate at apex, persistently velutinous on both sides; bracts and bracteoles pink, 6–8 × 3–4 mm, obovate or elliptic; pedicels 8–15 mm long; sepals 6.5–7 × 1.8–2.5 mm, narrowly obovate or oblong, reflexed, distally inflated, the lateral 4 all bearing 1 large abaxial gland; lateral petals pink, abaxially sericeous, posterior petal white with pink tints, glabrous; samaras subcircular, 40–50(–70) mm diameter, with the lateral wings strongly plicate or corrugated. Nonflooded riparian forests, 100–200 m; Amazonas (Río Baría, Río Mawarinuma, Río Siapa, Río Yaciba, Río Yatúa, San Carlos de Río Negro). Endemic.

**15. LOPHANTHERA** A. Juss., Ann. Sci. Nat. Bot. sér. 2, 13: 328. 1840.

Shrubs or trees, the stems often containing white latex. Leaves bearing glands on petiole or abaxial surface of blade or both; stipules intra- and slightly epipetiole,



Fig. 101. *Lophanthera longifolia*

$\frac{2}{3}$  to completely connate. Flowers borne in a usually terminal thyrse composed of few-flowered cincinni or dichasia or a pseudoraceme; 1 or both bracteoles usually bearing 1 large gland; petals pink or yellow, entire or minutely denticulate. Stamens 10, glabrous; anthers alike, their outer locules bearing dark longitudinal wings. Ovary of 3 fertile carpels connate along a central axis; styles 3, slender and subulate with minute terminal stigmas. Fruits breaking apart into 3 dry, unwinged, 1-seeded cocci, the mericarps indehiscent or slightly dehiscent along the keel but not enough so to release the spheroidal seed.

Costa Rica, Venezuela, Brazil, Bolivia; 5 species, 1 in Venezuela.

**Lophanthera longifolia** (H.B.K.) Griseb. in Mart., Fl. Bras. 12(1): 25. 1858.  
—*Galphimia longifolia* H.B.K., Nov. Gen. Sp. (quarto ed.) 5: 173. 1821 [1822].

Shrub or small tree 1–6(–10) m tall; stipules (6–)7–10 mm long; petioles (10–)14–30 mm long, usually bearing 2(–4) glands near middle; blade of larger leaves 12–30 × 4–10 cm, usually bearing few to many small abaxial glands; inflorescence 12–35 cm long, usually pendulous, the cincinni comprising

1–4(–10) flowers, 1 bracteole of each pair terminating in a sessile or stalked gland; sepals all biglandular; petals yellow; ovary glabrous; cocci 7–9 × 3–4 mm, glabrous, subcylindrical, the proximal half filled with aerenchyma, the distal half containing the seed. Along rivers, 100–200 m; Amazonas (from Isla Ratón and La Esmeralda on the upper Río Orinoco to San Simón de Cocuy on the Río Negro). Amazonian Brazil and Bolivia. ♦Fig. 101.

**16. LOPHOPTERYS** A. Juss. in Deless., Icon. Sel. Pl. 3: 18, pl. 29. 1837 [1838].

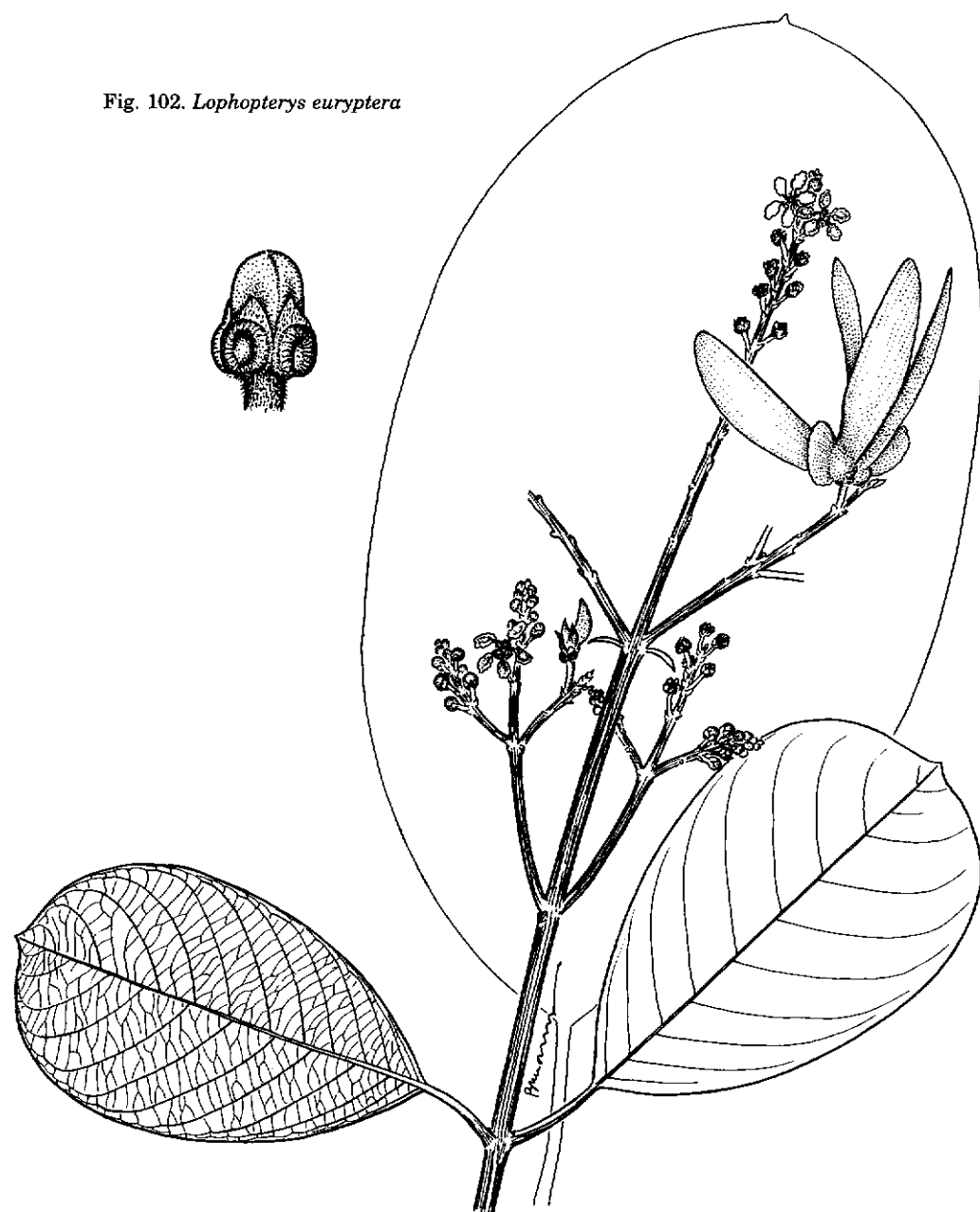
Woody vines or shrubs. Leaves densely and persistently sericeous abaxially; stipules minute or absent. Inflorescence paniculate (simple in 1 species not found in the flora area), the flowers borne ultimately in pseudoracemes. Anterior sepal eglandular, the 4 lateral sepals rarely eglandular, usually each bearing a single, very large, circular or elliptic, radially lineate gland; petals yellow, glabrous or very sparsely sericeous abaxially. Stamens 10. Ovary of 3 free carpels borne on a short pyramidal torus; styles 3, stout, with large internal stigmas. Fruits breaking apart into 3 samaras, each bearing a relatively short, flabellate or trapezoidal dorsal wing and 2 much longer, narrow, forward-pointing lateral wings 3 or more times as long as wide (lateral wings lacking in 1 species not found in the flora area).

Venezuela, Guyana, Suriname, French Guiana, Peru, Brazil, Bolivia; 8 species, 2 in Venezuela, both in the flora area.

Key to the Species of *Lophopterys*

1. Peduncles none or up to 1 mm long in fruit; blade of larger leaves 16–35 × 10–23 cm, obovate; petiole of larger leaves 20–60 mm long; pseudoracemes containing 10–50 flowers; samaras with nut 9–11 mm diameter, lateral wings 45–62 × 10–18 mm ..... *L. euryptera*
1. Peduncles well developed, 1.7–9 mm long; blade of larger leaves 8.9–19.8 × 3.4–10 cm, elliptic or ovate (i.e., widest at or below the middle); petiole of larger leaves 10–18(–22) mm long; pseudoracemes containing (2–)4–28 flowers; samaras with nut 3.4–4.5(–6) mm diameter, lateral wings 15–26 × 4–7 mm ..... *L. inpana*

**Lophopterys euryptera** Sandwith, Kew Bull. 1951: 34. 1951.  
Woody liana up to 35 m long. Evergreen lowland to lower montane forests, 50–400 m; Delta Amacuro (Río Acure, Río Grande east of El Palmar), Bolívar (upper Río Cuyuní). Northwestern Guyana. ♦Fig. 102.

Fig. 102. *Lophopterys euryptera*

**Lophopterys inpana** W.R. Anderson, Contr. Univ. Michigan Herb. 17: 46. 1990.

Woody vine or shrub up to 4 m tall. Evergreen lowland forests, roadside thickets, and

open savannas among sandstone outcrops, 100–200 m; Amazonas (southeast of San Fernando de Atabapo). Amazonian Peru, Brazil, and Bolivia.

# 17. MALPIGHIA L., Sp. Pl. 425. 1753.

Shrubs or small trees. Leaves usually bearing 2(–6) glands abaxially on blade, the petiole eglandular; stipules small, borne on stem between petioles. Inflorescence an axillary pseudoraceme congested into a dense corymb or umbel; bracts and bracteoles eglandular; pedicels pedunculate; petals pink, pale purple, or white. Sta-

mens 10, all fertile, glabrous; anthers alike or the 2 opposite the posterior-lateral petals larger. Ovary with the 3 carpels completely connate, the 3 locules all fertile; styles 3, the apex with a large internal or subterminal stigma and dorsally rounded, truncate, or hooked. Fruit a fleshy red or orange drupe (or berry), with 3 pyrenes united in the center or free at maturity but then usually retained in a common fleshy exocarp.

Mexico, West Indies, Central America, Colombia, Venezuela, Ecuador, Peru; 43 species, 2 in Venezuela, both in the flora area.

## Key to the Species of *Malpighia*

1. Leaves most often rounded or obtuse at apex and often emarginate and apiculate, but sometimes acute and rarely slightly acuminate, some pairs crowded in dense shoots with very short internodes, others separated by much longer internodes; umbels sessile or raised on a stalk 1–3(–5) mm long and containing 2–4 flowers; petals cuneate at base of limb, often sparsely sericeous abaxially on claw and in middle of limb, the lateral 4 with a narrow abaxial keel; styles divergent from the base, the posterior 2 bowed outward and then ascending; filaments opposite posterior-lateral petals notably thicker than the other 8; calyx glands 6–10 ..... *M. emarginata*
1. Leaves usually short- to long-acuminate at apex, occasionally acute, evenly spaced, successive pairs separated by well-developed internodes; umbels or corymbs raised on a stalk (2–)3–12(–22) mm long and containing (3)4–10(–12) flowers; petals rounded or truncate at base of limb, abaxially glabrous, smooth; styles ± straight, parallel or divergent distally; filaments ± alike in thickness; calyx glands 6 ..... *M. glabra*

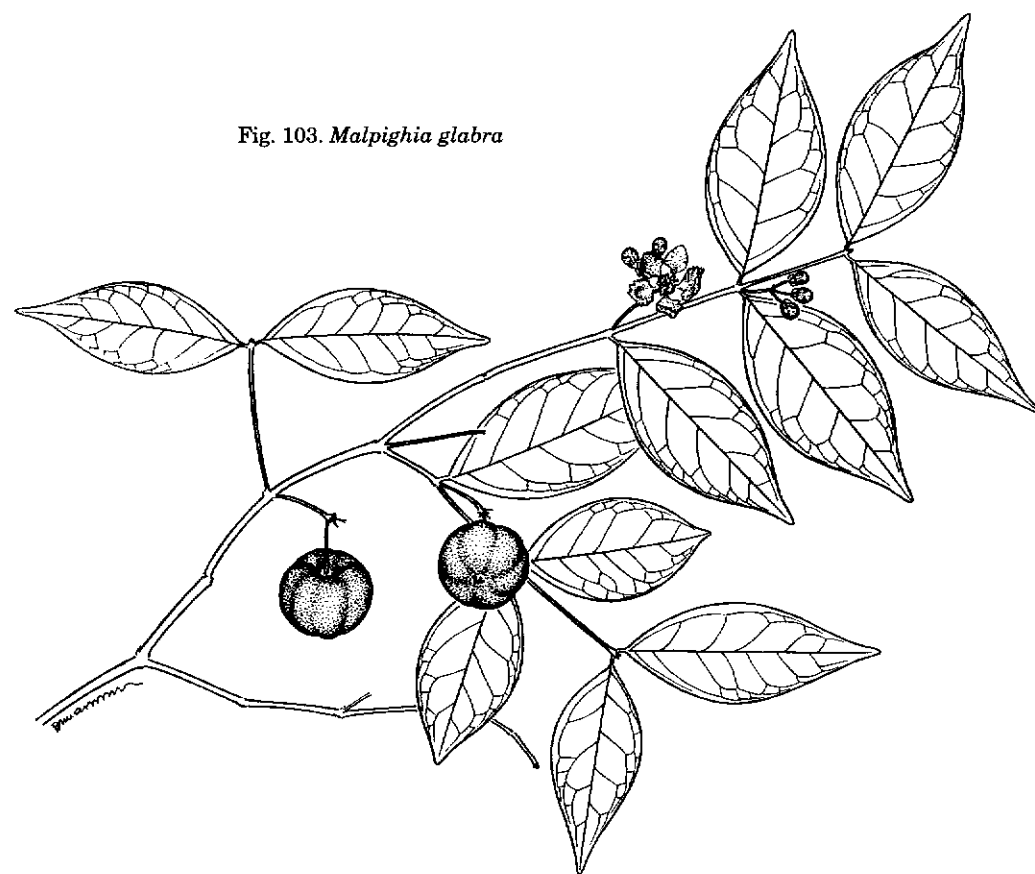
**Malpighia emarginata** DC., Prodr. 1: 578. 1824. —Acerola, Cereza, Semeruco.

*Malpighia puniceifolia* auctt. non L. 1762. Shrub or small tree 2–6 m tall; petioles (1–)2–4 mm long; blade of larger leaves 2.5–7 × 1.4–3.3 cm (up to 10 × 5 cm in cultivated plants), ovate, elliptic, or obovate, bearing 2(–4) abaxial glands in the proximal third, sparsely sericeous to glabrate; petals pink or purplish (in age?); styles with distinctly internal stigmas, dorsally truncate or apiculate at apex; fruits red, up to 17 × 22 mm. Dry areas with xerophytic vegetation, near sea level to 200 m; Delta Amacuro (Tucupita, cultivated), Bolívar (Ciudad Bolívar, Las Trincheras, Parque Cachamay near Río Caroní, Tumeremo, probably all cultivated or escaped from cultivation). Common in the coastal lowlands of northern Venezuela, where perhaps native, and elsewhere cultivated; apparently native from Mexico to Honduras, elsewhere in Central America and the West Indies probably escaped from cultivation, apparently native in Colombia(?) and coastal Ecuador.

Widely cultivated for the edible fruit, rich in vitamin C, and readily naturalized.

**Malpighia glabra** L., Sp. Pl. 425. 1753. —Cereza, Guayabito rojo, Semeruco. *Malpighia puniceifolia* L., Sp. Pl. ed. 2, 609. 1762.

Shrub or small tree 1–6 m tall; petioles 1–3 mm long; blade of larger leaves 3–10 × 1.5–5 cm, narrowly to broadly elliptic or ovate, bearing (0–)2–4 abaxial glands in proximal fourth, glabrous or very sparsely sericeous; petals pink or pale purple; styles truncate at apex with the stigma slightly internal or apparently terminal; fruits red, 7–10 × 10–13 mm. Relatively dry deciduous or semi-deciduous forests, occasionally in the understory of lowland evergreen forest, 200–300 m; Bolívar (vicinity of La Paragua). Northwestern Venezuela from Zulia to Miranda; U.S.A. (southern Texas), Mexico, Central America, Greater Antilles, Colombia, Ecuador, Peru (cultivated, native too?). ♦Fig. 103.

Fig. 103. *Malpighia glabra*

**18. MASCAGNIA** (Bertero ex DC.) Colla, Hortus Ripul. 85. 1824. —*Hiraea* sect. *Mascagnia* Bertero ex DC., Prodr. 1: 585. 1824.

Vines, mostly woody (a few species from outside the flora area are shrubs or small trees). Leaves usually bearing glands; stipules small, distinct, triangular, borne between petioles or on base of petiole. Inflorescence mostly axillary or terminal pseudoracemes, sometimes congested and reduced to form corymbs or umbels, single or grouped in panicles; floriferous peduncles usually well developed. Petals yellow or yellow and orange or yellow turning red, or pink, lilac, or white. Stamens 10; anthers  $\pm$  alike. Ovary with the 3 carpels connate along a central axis, all fertile; styles 3, the apex usually with a large internal stigma and dorsally rounded, truncate, acute, or short-hooked; stigma nearly or quite terminal in a few species. Fruits breaking apart into 3 samaras, each samara having its largest wings lateral, 2 discrete wings or a single wing continuous at the base or at both base and apex; dorsal wing small, sometimes reduced to a crest or lost; intermediate winglets present or absent; wings reduced or rudimentary in a few species.

Central America, West Indies, Mexico, South America (all countries except Chile and Uruguay); ca. 60 species, 16 in Venezuela, 15 of these in the flora area.

As I have noted in previous publications, *Mascagnia* as recognized here is a heterogeneous and probably unnatural genus, some of whose species will very likely have to be removed eventually to segregate genera. The species in our flora that will surely remain in *Mascagnia* even after that segregation are *M. cynanchifolia*, *M. dissimilis*, *M. divaricata*, *M. eggersiana*, *M. ovatifolia*, *M. schunkei*, and *M. sepium*.

Key to the Species of *Mascagnia* based on flowering material

1. Petals abaxially  $\pm$  densely and persistently tomentose or sericeous ..... 2
1. Petals glabrous or bearing a few abaxial hairs ..... 5
- 2(1). Margin of bracteoles and sepals with a row of stalked clavate or capitate glands ..... 3
2. Margin of bracteoles and sepals eglandular ..... 4
- 3(2). Leaf blades originally sericeous on both sides with sessile appressed hairs, glabrate at maturity or the hairs persistent abaxially and often on adaxial midrib ..... *M. glandulifera*
3. Leaf blades velutinous to glabrate adaxially, persistently velutinous abaxially with the prominently stalked hairs T- or Y-shaped ..... *M. surinamensis*
- 4(2). Petals lilac or pink; leaf blades abaxially persistently sericeous and bearing (1-)several small glands in a row parallel to but set in from the margin; sepals completely concealing petals in bud, revolute in anthesis; ultimate units of inflorescence  $\pm$  elongated pseudoracemes 2-9(-15) cm long ..... *M. macrodisca*
4. Petals yellow; leaf blades nearly or quite glabrate at maturity, bearing many tiny impressed glands on margin or on adaxial surface of revolute margin, abaxially eglandular between midrib and margin; sepals leaving outermost petal exposed during enlargement of bud, appressed in anthesis; ultimate units of inflorescence congested or corymbose pseudoracemes up to 1.5 cm long ..... *M. sinemariensis*
- 5(1). Petals pink, lilac, or white, or a combination of those colors ..... 6
5. Petals yellow or yellow turning red in age ..... 10
- 6(5). Inflorescence "simple," i.e., each pseudoraceme axillary to a well-developed vegetative leaf; bracteoles eglandular or 1 or both bearing 1 or 2 small abaxial glands ..... 7
6. Inflorescence usually "compound," i.e., pseudoracemes grouped in terminal or axillary panicles containing only tiny bracts or much-reduced leaves; bracteoles eglandular ..... 8
- 7(6). Leaf blades initially sericeous adaxially, usually soon glabrate; anthers glabrous; flowers  $\pm$  evenly distributed along axis of pseudoraceme; inflorescence sericeous ..... *M. schunkei*
7. Leaf blades persistently velutinous adaxially; anthers sericeous; flowers mostly congested in distal half of axis of pseudoraceme; inflorescence tomentose [petal color unknown; placed here on the basis of similarity in other characters to *M. schunkei*] ..... *M. cynanchifolia*
- 8(6). Anthers pilose; dried leaf blades smooth on adaxial surface, the reticulum not raised and hardly visible; petioles usually bearing 2-4 glands near middle, or eglandular ..... *M. divaricata*
8. Anthers glabrous (rarely very sparsely pilose); fine reticulum prominent on adaxial surface in dried leaf blades; petioles eglandular ..... 9
- 9(8). Leaf blades with a discolored band (0.5-)1-2 mm wide all around margin, the band reddish in dried leaves; pedicels quite glabrous or initially sericeous at very apex but usually soon glabrate; petioles 11-20 mm long; ovary and immature fruit sparsely to moderately sericeous with straight appressed hairs ..... *M. dissimilis*
9. Leaf blades uniformly green; pedicels initially loosely sericeous their whole length (sometimes only sparsely so), eventually  $\pm$  glabrescent;

- petioles 8–11(–18) mm long; ovary and immature fruit densely subto-mentose with loose sinuous ± spreading hairs ..... *M. ovatifolia*
- 10(5). Mature, full-sized leaves persistently golden-, silvery-, or brown-sericeous abaxially, the hairs so dense and appressed as to completely conceal epidermis and usually give leaf a metallic sheen; glands of leaf blade, if present, borne on very margin ..... 11
10. Mature, full-sized leaves abaxially glabrate or variously sericeous, velutinous, or tomentose, but the hairs never dense enough to completely conceal epidermis; glands of leaf blade, if present, borne on abaxial surface between midrib and margin ..... 13
- 11(10). Petioles biglandular near or above middle; anthers 0.5–0.7 mm long, glabrous; calyx glands (if present) 0.5–1.5 mm long; petals with limb up to 2.5 mm long; floriferous bracts eglandular ..... *M. poeppigiana*
11. Petioles biglandular at or just above base; anthers 1–1.5 mm long, usually sericeous between locules and bearing a few abaxial hairs; calyx glands 1.7–2.5 mm long; petals with limb 3.5–5 mm long; floriferous bracts often bearing 1 or 2 large glands, or eglandular ..... 12
- 12(11). Leaf blades abaxially golden- or silvery-sericeous, with the reticulum ± prominent ..... *M. stannea*
12. Leaf blades abaxially dark brown-sericeous, with the reticulum ± obscured by outer layer of hairs ..... *M. castanea*
- 13(10). Sepals completely concealing petals until flower opens, revolute afterwards; calyx glands 10 (all 5 sepals biglandular); petals yellow turning red in age; inflorescence densely and persistently sericeous or tomentose-sericeous with mostly white hairs, the overall aspect gray ..... *M. liesneri*
13. Sepals leaving outermost petal(s) exposed during enlargement of bud, appressed after flower opens; calyx glands 8 (lateral 4 sepals biglandular, anterior sepal eglandular); petals persistently yellow; inflorescence bearing yellowish, brownish, or reddish hairs, or glabrate, the overall aspect green or brown ..... 14
- 14(13). Leaf blades abaxially velutinous to subsericeous, occasionally glabrescent but the dark brown or reddish hairs persistent at least on midrib; stems velutinous to glabrescent in age; petiole of larger leaves 8–18(–22) mm long; pedicels sericeous or subvelutinous, with some hairs persistent in fruit at least on distal half; ovary densely tomentose-sericeous; samaras sparsely sericeous ..... *M. sepium*
14. Leaf blades abaxially glabrous or soon glabrate; stems soon glabrate; petioles 3–8 mm long; pedicels glabrous; ovary sparsely sericeous; samaras soon quite glabrate ..... *M. eggersiana*

Key to the Species of *Mascagnia* based on fruiting material

1. Lateral wings of samaras discrete, i.e., divided to nut at base and apex ..... 2
1. Lateral wing of samaras continuous at base, continuous at apex or incised part way or completely to nut ..... 6
- 2(1). Mature, full-sized leaves thinly sericeous to glabrate abaxially, the hairs never dense enough to completely conceal epidermis ..... 3

2. Mature, full-sized leaves persistently golden-, silvery-, or brown-sericeous abaxially, the hairs so dense and appressed as to completely conceal epidermis, usually giving leaf a metallic sheen ..... 4
- 3(2). Leaf blades abaxially persistently sericeous and bearing (1–)several small glands in a row parallel to but set in from margin; ultimate units of inflorescence ± elongated pseudoracemes 2–9(–15) cm long .... *M. macrodisca*
3. Leaf blades nearly or quite glabrate at maturity, bearing many tiny impressed glands on margin or on adaxial surface of revolute margin, abaxially eglandular between midrib and margin; ultimate units of inflorescence congested or corymbose pseudoracemes up to 1.5 cm long ..... *M. sinemariensis*
- 4(2). Petioles biglandular near or above middle; calyx glands (if present) 0.5–1.5 mm long; floriferous bracts eglandular ..... *M. poeppigiana*
4. Petioles biglandular at or just above base; calyx glands 1.7–2.5 mm long; floriferous bracts often bearing 1 or 2 large glands, or eglandular ..... 5
- 5(4). Leaf blades abaxially golden- or silvery-sericeous, with the reticulum ± prominent ..... *M. stannea*
5. Leaf blades abaxially dark brown-sericeous, with the reticulum ± obscured by outer layer of hairs ..... *M. castanea*
- 6(1). Margin of bracteoles and sepals with a row of stalked clavate or capitate glands ..... 7
6. Margin of bracteoles and sepals eglandular ..... 8
- 7(6). Leaf blades originally sericeous on both sides with sessile appressed hairs, glabrate at maturity or the hairs persistent abaxially and often on adaxial midrib ..... *M. glandulifera*
7. Leaf blades velutinous to glabrate adaxially, persistently velutinous abaxially with the prominently stalked hairs T- or Y-shaped ..... *M. surinamensis*
- 8(6). Calyx glands 10 (all 5 sepals biglandular) [species unknown in fruit, but placed here on the basis of fruits known in closest relatives] ... *M. liesneri*
8. Calyx glands 8 (lateral 4 sepals biglandular, anterior eglandular) ..... 9
- 9(8). Samaras with lateral wing entire at apex or emarginate or incised part-way or almost to nut and connate with dorsal wing; torus after fall of samaras surrounded by a 3-lobed disciform outgrowth of the receptacle; sepals appressed in anthesis ..... 10
9. Samaras with lateral wing incised to nut at apex and free from dorsal wing; torus not surrounded by disciform structure; sepals revolute in anthesis ..... *M. macrodisca*
- 10(9). Inflorescence "simple," i.e., each pseudoraceme axillary to a well-developed vegetative leaf; bracteoles eglandular or 1 or both bearing 1 or 2 small abaxial glands ..... 11
10. Inflorescence usually "compound," i.e., the pseudoracemes grouped in terminal or axillary panicles containing only tiny bracts or reduced leaves; bracteoles eglandular ..... 12
- 11(10). Leaf blades initially sericeous adaxially, usually soon glabrate; flowers ± evenly distributed along axis of pseudoraceme; inflorescence sericeous ..... *M. schunkei*
11. Leaf blades persistently velutinous adaxially; flowers mostly congested in distal half of axis of pseudoraceme; inflorescence tomentose ..... *M. cynanchifolia*

- 12(10). Disciform structure surrounding fruiting torus pilose; samaras usually distinctly wider than high ..... *M. ovatifolia*
12. Disciform structure surrounding fruiting torus glabrous; samaras higher than wide, about as high as wide, or a little wider than high ..... 13
- 13(12). Pedicels glabrous or initially sericeous at very apex but usually soon glabrate ..... 14
13. Pedicels at least initially sericeous, subvelutinous, or velutinous, eventually glabrescent in some species but with some hairs persisting, especially on distal half ..... 15
- 14(13). Leaf blades cordate at base, green and often crispate at margin; petioles 3–8 mm long ..... *M. eggersiana*
14. Leaf blades cuneate to rounded at base, smooth at margin and with a discolored band (0.5–)1–2 mm wide, the band reddish in dried leaves; petioles 11–20 mm long ..... *M. dissimilis*
- 15(13). Leaf blades  $\pm$  persistently velutinous or tomentose to subsericeous abaxially, the hairs dark brown or reddish (occasionally glabrescent but hairs persistent on midrib); hairs of inflorescence dark brown or reddish; petioles eglandular; leaf blades rounded or cordate at base ..... *M. sepium*
15. Leaf blades at maturity sparsely sericeous to glabrate, the hairs (if present) white or yellowish; hairs of inflorescence white or gray; petioles usually bearing 2–4 glands near middle, occasionally eglandular; leaf blades cuneate, truncate, or rounded at base, seldom cordate ..... *M. divaricata*

**Mascagnia castanea** (Cuatrec.) W.R. Anderson, Mem. New York Bot. Gard. 32: 218. 1981. —*Heteropterys castanea* Cuatrec., Webbia 13: 475. 1958.

Woody vine; leaf blades abaxially dark brown-sericeous, with the reticulum  $\pm$  obscured by outer layer of hairs; in other known characters this taxon (which has not been collected with fruits) is indistinguishable from *Mascagnia stannea*, which see. Evergreen lowland forests, 100–200 m; Amazonas (Caño Yagua). Brazil (Amazonas: Rio Dimiti).

This striking plant may not merit recognition, although its chestnut-brown leaves distinguish it immediately from *M. stannea*. I have decided to maintain it for now in order to draw attention to it as worthy of future study, which may reveal it to be nothing more than a trivial variant. It is worth noting that *Davidse et al.* 17463 (MICH, MO), which is *M. castanea*, and *Davidse et al.* 17374 (MO, VEN), which is *M. stannea*, were collected in the same area on the same day.

**Mascagnia cynanchifolia** Griseb. in Mart., Fl. Bras. 12(1): 95. 1858.

Woody vine; petioles 3–6 mm long, eglandular; blade of larger leaves 5–8.5  $\times$  2–4 cm, adaxially persistently velutinous, abaxially persistently sericeous; inflorescence a simple axillary pseudoraceme with flowers congested in distal half of axis; bracteoles eglandular or 1 or both bearing 1 or 2 abaxial glands; lateral 4 sepals biglandular; petals probably pink, glabrous; anthers sericeous; samaras suborbicular or broadly elliptic, 15–36 mm diameter, the lateral wing continuous at base, incised at apex ca. halfway to nut. Evergreen lowland forests, 100–200 m; Amazonas (area of San Fernando de Atabapo). Brazil (Amazonas: vicinity of Manaus).

No collection I have seen of this species records the color of the petals. I am assuming that they are probably pink, on the basis of the similarity of this species to *Mascagnia schunkei*, but that is a questionable assumption; see discussion under *M. schunkei*.

**Mascagnia dissimilis** C.V. Morton & Moldenke, Phytologia 1: 19. 1933.

Woody vine; petioles 11–20 mm long, eglandular; blade of larger leaves 11–25  $\times$  6–

11 cm, soon glabrate, broadly obtuse or rounded at base, with a discolored band (0.5–)1–2 mm wide at margin; inflorescence paniculate; pedicels glabrous or initially sericeous at very apex but usually soon glabrate; lateral 4 sepals biglandular; petals white or pink, glabrous; anthers glabrous; samaras ovate or orbicular, (20–)25–53 mm diameter, glabrate at maturity or with a few straight appressed hairs on nut, the lateral wing continuous at base, emarginate at apex. Evergreen lowland and lower montane forests, 100–300 m; Amazonas (Rio Cuao, Rio Cunucunuma, Tamatama). Western Amazonia (Colombia, Ecuador, Peru, Brazil, Bolivia).

**Mascagnia divaricata** (H.B.K.) Nied. in Engl. & Prantl, Nat. Pflanzenfam. III. 4: 55. 1890. —*Hiraea divaricata* H.B.K., Nov. Gen. Sp. (quarto ed.) 5: 169. 1821 [1822].

*Hiraea oblongifolia* DC., Prodr. 1: 585. 1824.

Woody vine; petioles 10–19(–24) mm long, eglandular or, usually, bearing 2–4 glands near middle; blade of larger leaves 6–13  $\times$  3.5–6.5(–8) cm, thinly sericeous to glabrate at maturity; inflorescence paniculate, the axes of ultimate pseudoracemes velutinous with very short gray hairs; 4 lateral sepals biglandular; petals lilac, pink, or pinkish lilac, glabrous; anthers pilose; samaras suborbicular, (18–)20–30 mm diameter, the lateral wing continuous at base, incised up to halfway to nut at apex. Evergreen lowland forests, 50–100 m; Delta Amacuro (Rio Acure between La Margarita and Puerto Miranda). Fairly common in northern Venezuela (Anzoátegui, Aragua, Carabobo, Distrito Federal, Falcón, Lara, Mérida, Portuguesa, Sucre); Nicaragua, Costa Rica, Panama, Colombia, Trinidad, Suriname, French Guiana, Ecuador, Peru, Brazil, Bolivia, Paraguay, Argentina.

*Mascagnia divaricata* is widely but erroneously known as *M. ovatifolia*; see discussions in Contr. Univ. Michigan Herb. 19: 380–383. 1993.

**Mascagnia eggersiana** (Nied.) W.R. Anderson, Mem. New York Bot. Gard. 32: 224. 1981. —*Mascagnia tenuifolia* var. *eggersiana* Nied., Arbeiten Bot. Inst. Königl.

Lyceum Hosianum Braunsberg 3: 10. 1908.

Woody vine; stems soon glabrate; petioles 3–8 mm long, eglandular; blade of larger leaves 8–19.5  $\times$  4–10.5 cm, cordate at base, often crispate at margin, soon glabrate; inflorescence paniculate, sparsely velutinous; pedicels glabrous; 4 lateral sepals biglandular; petals yellow, glabrous; samaras ovate, 20–35 mm diameter, soon glabrate, the lateral wing continuous at base, emarginate at apex or incised up to halfway to nut. Mostly in evergreen forests, also at edges of savannas and cultivated areas, 100–600 m; northwestern Bolívar (southeast of Pijiguaos, mouth of Rio Parguaza), Amazonas (Parhueña). Aragua, Distrito Federal, Falcón, Táchira, Trujillo, Yaracuy; Ecuador, Peru. ♦Fig. 105.

**Mascagnia glandulifera** Cuatrec., Webbia 13: 365. 1958.

Woody vine; stems sericeous to glabrate; petioles 8–13 mm long, bearing (2–)4–10 small glands in 2 rows; blade of larger leaves 11–14.5  $\times$  4.5–8 cm, sericeous to glabrate on both sides or the hairs persistent abaxially and on adaxial midrib; bracteoles and sepals bearing a row of small stalked glands on margin; sepals completely concealing petals until flower opens, the lateral 4 abaxially biglandular; petals yellow, abaxially densely tomentose; samaras 45–60 mm wide, the lateral wing continuous at base, divided to nut at apex. Evergreen lowland forests, ca. 100 m; Amazonas (northeast of San Carlos). Northwestern Amazonia (Colombia, Peru, Brazil).

**Mascagnia liesneri** W.R. Anderson, Contr. Univ. Michigan Herb. 17: 51. 1990.

Woody vine; petioles 10–20 mm long, eglandular or biglandular on distal half; blade of larger leaves 7–11.5  $\times$  3.8–5.8 cm, adaxially soon glabrate, abaxially thinly sericeous to glabrate, eglandular or with a row of tiny glands between midrib and margin; inflorescence paniculate, the flowers borne ultimately in pairs, 2 or 3 pairs usually congested to form corymbs or umbels; sepals all biglandular, completely concealing petals in bud, revolute in anthesis; petals yellow turning red in age, glabrous; stigmas terminal or nearly so; fruits unknown. Wet disturbed lowland forests, 100–200 m;



Amazonas (San Carlos de Río Negro north to the Brazo Casiquiare). Endemic.

The fruit of *Mascagnia liesneri* is not known, but it can be expected to resemble that of *Mascagnia leucanthele* Griseb. in Mart., in which the samaras are suborbicular with the membranous lateral wing continuous at the base and incised to the nut at the apex.

***Mascagnia macrodisca*** (Triana & Planch.) Nied., Arbeiten Bot. Inst. Königl. Lyceum Hosianum Braunsberg 3: 16. 1908.

—*Hiraea macrodisca* Triana & Planch., Ann. Sci. Nat. Bot. sér. 4, 18: 326. 1862.

Woody vine; petioles (8–)10–25 mm long, usually bearing 2–8 glands in 2 rows; blade of larger leaves 8–14.5(–18) × 4–9(–12) cm, abaxially persistently sericeous, bearing glands between midrib and margin; pseudoracemes 2–12(–16) cm long; sepals completely concealing petals in bud, revolute in anthesis, the lateral 4 biglandular; petals lilac or pink, abaxially densely sericeous or tomentose; samaras 20–62 × 25–70 mm, the lateral wing continuous at base or rarely divided nearly or quite to nut, divided to nut at apex. Evergreen lowland forests and secondary forests, 100–500 m; fairly common in Bolívar, rare in Amazonas (Mavaca). Apure, Barinas; Colombia, Guyana, Suriname, Amazonian Ecuador, Peru, Brazil (Acre, Amazonas, Pará), and Bolivia. •Fig. 106.

***Mascagnia ovatifolia*** (H.B.K.) Griseb., Fl. Brit. W.I. 121. 1860. —*Hiraea ovatifolia* H.B.K., Nov. Gen. Sp. (quarto ed.) 5: 170. 1821 [1822].

*Mascagnia nervosa* Nied., Arbeiten Bot. Inst. Königl. Lyceum Hosianum Braunsberg 3: 12. 1908.

Woody vine; petioles 8–11(–18) mm long, eglandular; blade of larger leaves 9.5–16.5 × 5–8.2 cm, soon glabrate, rounded at base; inflorescence paniculate; pedicels initially loosely sericeous, glabrescent in age; petals white or pink, glabrous; anthers glabrous or very sparsely pilose; samaras broadly elliptic, 17–30 × 25–37 mm, usually distinctly wider than high, the lateral wing continuous at base, emarginate or shallowly incised at apex; disciform structure surrounding fruiting torus pilose. Semideciduous forests, ca. 200 m; Bolívar (near El Manteco). Apure, Aragua, Barinas, Carabobo, Distrito Fe-

deral, Falcón, Mérida, Miranda, Monagas, Nueva Esparta, Portuguesa, Sucre, Táchira, Yaracuy, Zulia; Panama, Colombia, Trinidad.

This is not the species that has been called *Mascagnia ovatifolia* in all recent floras, which have continued the misapplication of that name by Niedenzu in Das Pflanzenreich. That species is treated here as *M. divaricata*. The type of *Hiraea ovatifolia* (P-HBK!), which Niedenzu never saw, is conspecific with his *M. nervosa*. See discussions in Contr. Univ. Michigan Herb. 19: 380–383. 1993.

***Mascagnia poeppigiana*** (A. Juss.) W.R. Anderson, Mem. New York Bot. Gard. 32: 219. 1981. —*Hiraea poeppigiana* A. Juss., Ann. Sci. Nat. Bot. sér. 2, 13: 260. 1840. —*Tetrapteryx poeppigiana* (A. Juss.) Griseb. in Mart., Fl. Bras. 12(1): 87. 1858.

*Mascagnia subsericea* Cuatrec., Webbia 13: 370. 1958.

*Mascagnia materdei* Cuatrec., Brittonia 11: 167. 1959.

Woody vine; petioles 7–9(–11) mm long, biglandular near or above middle; blade of larger leaves 8.5–15(–19) × 4.2–9 cm, abaxially very densely and persistently metallic-sericeous; floriferous bracts eglandular; all sepals eglandular or the lateral 4 biglandular, the glands 0.5–1.5 mm long; petals yellow, glabrous, the limb up to 2.5 mm long; anthers 0.5–0.7 mm long, glabrous; samaras 9–18 × 16–22 mm, butterfly-shaped, the lateral wing divided to nut at base and apex. Evergreen lowland forests, 100–200 m; Amazonas (Río Cunucunuma, Río Yureba). Colombia, Guyana, Peru, Brazil, Bolivia.

***Mascagnia schunkei*** W.R. Anderson, Mem. New York Bot. Gard. 32: 222. 1981.

*Mascagnia cordifolia* var. *peruviana* J.F. Macbr., Publ. Field Mus. Nat. Hist., Bot. Ser. 13: 787. 1950.

Woody vine; petioles 5–15 mm long, eglandular; blade of larger leaves 5.5–17 × 2.3–7 cm, adaxially sericeous to soon glabrate, abaxially persistently sericeous; inflorescence a simple axillary pseudoraceme with flowers ± evenly distributed along axis; bracteoles eglandular or 1 (rarely both) bearing 1 abaxial gland; lateral 4 sepals biglandular; petals pink or lilac(?), glabrous;

samaras suborbicular, 25–36 mm diameter, the lateral wing continuous at base, notched at apex or incised partway or almost all the way to nut. Evergreen lowland forests, 50–300 m; Amazonas (Mavaca, Puerto Ayacucho). Widespread in Amazonia [French Guiana, Peru, Brazil (Amapá, Amazonas, Mato Grosso, Pará), Bolivia].

When I described *Mascagnia schunkei* I admitted uncertainty as to whether the petals are yellow or pink. I now have available 2 collections from Peru for which the petals were described as yellow, and 7 from Peru, Brazil, Bolivia (Amapá and Pará), and French Guiana for which they were described as pink or lilac. In most other characters these collections are alike, so I still cannot say with confidence which form gets the name (the Peruvian type was in fruit). I am tentatively assuming the petals in the "true" *M. schunkei* to be pink, but that may prove to be wrong.

***Mascagnia sepium*** (A. Juss. in A. St.-Hil.) Griseb. in Mart. —*Hiraea sepium* A. Juss. in A. St.-Hil., Fl. Bras. Merid. 3: 19, pl. 165. 1832 [1833].

Woody vine; stems velutinous to glabrescent in age; petioles 8–18(–22) mm long, eglandular; blade of larger leaves 8–16 × 5–10.2 cm, rounded or cordate at base, abaxially velutinous or rarely tomentose to subsericeous with dark brown or reddish hairs, occasionally glabrescent; inflorescence paniculate, velutinous with dark brown or reddish hairs; pedicels at least sparsely sericeous or subvelutinous; 4 lateral sepals biglandular; petals yellow, glabrous; samaras ovate to orbicular, 16–34 mm diameter, sparsely and loosely sericeous, the lateral wing continuous at base and apex, often shallowly notched at apex. Evergreen lowland to lower montane forests, 50–1200 m; widespread in Bolívar and Amazonas. Apure, Distrito Federal, Falcón, Miranda, Sucre, Táchira, Yaracuy, Zulia; Colombia, Ecuador, Peru, Brazil. •Fig. 104.

Our plant is probably separable from true *Mascagnia sepium*, an exceedingly variable complex based on a type from Rio de Janeiro.

***Mascagnia sinemariensis*** (Aubl.) Griseb. in Mart., Fl. Bras. 12(1): 93. 1858. —*Banisteria sinemariensis* Aubl., Hist. Pl. Guiane 1: 462, pl. 185. 1775.

*Malpighia volubilis* Sims, Bot. Mag. 21: 809. 1805. —*Mascagnia volubilis* (Sims) Nied., Arbeiten Bot. Inst. Königl. Lyceum Hosianum Braunsberg 3: 22. 1908. *Hiraea schizoptera* Turcz., Bull. Soc. Imp. Naturalistes Moscou 36: 584. 1863. —*Mascagnia schizoptera* (Turcz.) Cuatrec., Webbia 13: 373. 1958.

*Mascagnia hondensis* C.V. Morton, Proc. Biol. Soc. Wash. 45: 52. 1932.

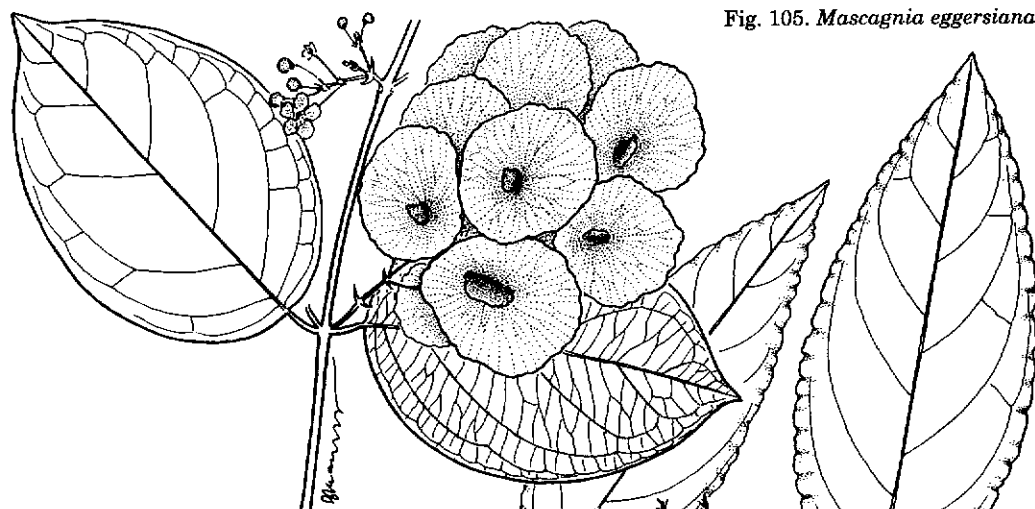
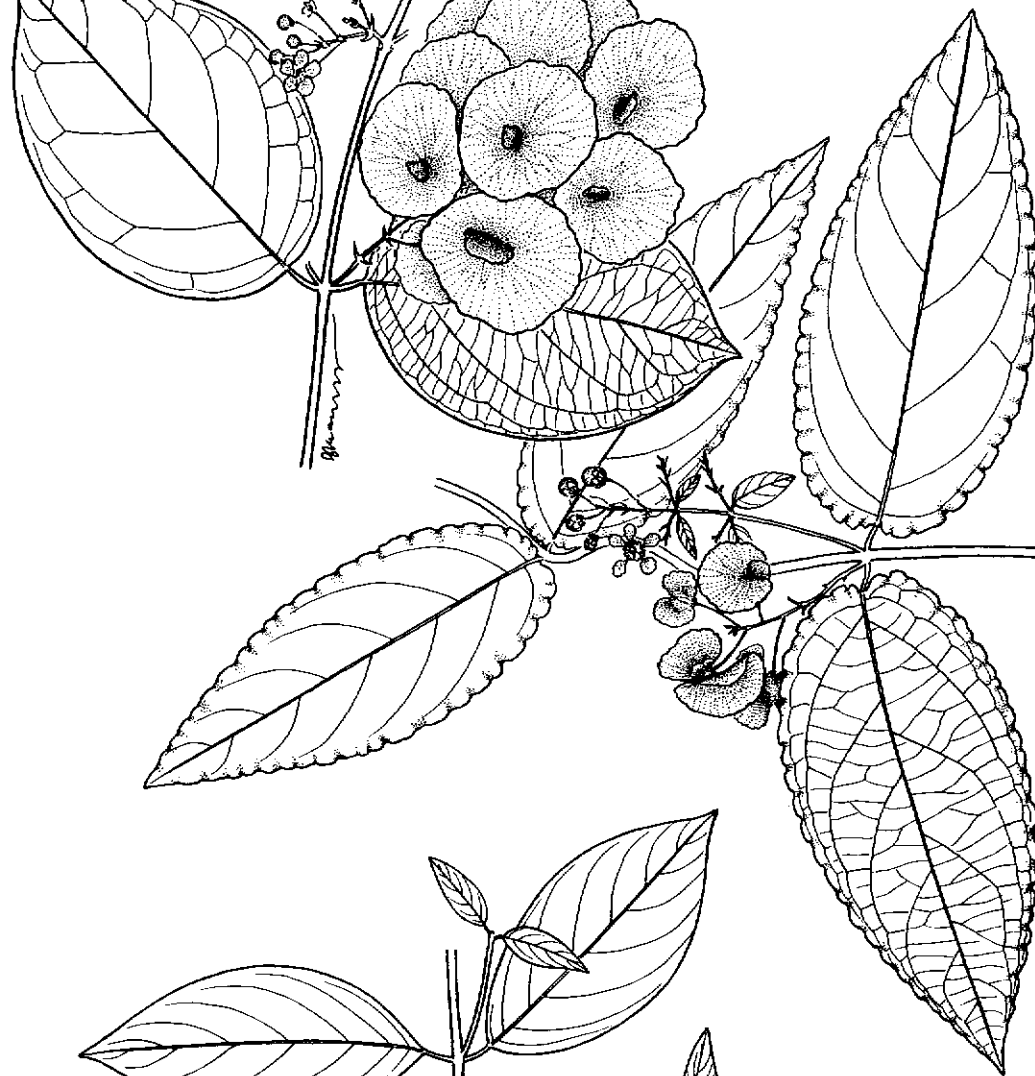
Woody vine; petioles (5–)8–15 mm long, usually bearing 2–6 glands in 2 rows; blade of larger leaves (6–)8–16.5 × (2.5–)4–9 cm, abaxially sparsely sericeous to glabrate, bearing impressed glands on margin; pseudoracemes up to 1.5 cm long, corymbose; sepals leaving petals exposed in enlarging bud, appressed in anthesis, the lateral 4 biglandular; petals yellow, abaxially densely sericeous; samaras 12–30 × 20–50 mm, butterfly-shaped with lateral wing divided to nut at base and apex, sometimes reduced and corky. Evergreen lowland forests, 100–300 m; Bolívar (50 km south of Caicara, El Dorado to Santa Elena de Uairén road, El Palmar, Isla Anacoco, Upata), Amazonas (Caño Yureba on lower Río Ventuari, Río Sipapo, Río Mavaca, Río Metacuni). Apure, Falcón, Mérida, Táchira, Zulia; Mexico, Central America, Lesser Antilles, Colombia, Guyana, French Guiana, Amazonian Ecuador, Peru, and Brazil.

***Mascagnia stannea*** (Griseb.) Nied., Verz. Vorles. Königl. Lyceum Hosianum Braunsberg 1912/13: 12. 1912. —*Heteropteryx stannea* Griseb., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1853: 46. 1854.

*Hiraea laurifolia* A. Juss., Ann. Sci. Nat. Bot. sér. 2, 13: 260. 1840, non *Mascagnia laurifolia* Nied. in Chodat & Hassl. 1907.

*Tetrapteryx benthamiana* Griseb. in Mart., Fl. Bras. 12(1): 88. 1858. —*Mascagnia benthamiana* (Griseb.) W.R. Anderson, Mem. New York Bot. Gard. 32: 217. 1981. *Mascagnia sericans* Nied. in Chodat & Hassl., Bull. Herb. Boissier sér. 2, 7: 284. 1907.

Woody vine, or a shrub with young branches twining when support is available; petioles 4–9 mm long, biglandular at or slightly above base; blade of larger leaves 10–19.5(–26) × 6.5–12(–14) cm, abaxially

Fig. 104. *Mascagnia sepium*Fig. 105. *Mascagnia eggersiana*Fig. 106. *Mascagnia macrodisca*

very densely and persistently golden- or silvery-metallic-sericeous; floriferous bracts mostly bearing 1 or 2 large abaxial glands, or eglandular; lateral 4 sepals biglandular, the glands 1.7–2.5 mm long; petals yellow, glabrous, the limb 3.5–5 mm long; anthers 1–1.5 mm long, usually sericeous between locules and bearing a few abaxial hairs; samaras 15–30 × 20–40 mm, butterfly-shaped, the lateral wing divided to nut at base and apex, sometimes much dissected. Evergreen lowland forests, often on riverbanks or in seasonally flooded places, 100–200 m; Amazonas (Caño Yagua, Cariche, Río Cuao). Costa Rica, Panama, Colombia, Peru, Brazil, Bolivia, Paraguay.

*Mascagnia stannea* is exceedingly variable in the size and shape of its leaves, but relatively consistent in its reproductive structures. The small-leaved populations in southern Brazil and Paraguay probably deserve segregation, but those in northern South America are not easily separable from the type of *Heteropterys stannea*, which came from Costa Rica. The descriptive notes given above apply only to the plants of southern Venezuela and nearby, and do not attempt to convey the variation throughout the taxon's range. I am recognizing here two segregates from this complex, *M. poeppigiana* and *M. castanea*. The former is fairly well supported by several characters and a distribution throughout western Amazonia. The latter has a much weaker claim to recognition; see the discussion under *M. castanea*.

Note that the oldest name for this species as it is defined here is *Hiraea laurifolia* A. Juss., but the combination cannot be made in *Mascagnia* because that would create a later homonym. However, if/when this species is transferred to a different genus, the epithet *laurifolia* should be taken up for it. On the other hand, if *M. poeppigiana* is combined with *M. stannea*, the epithet *poeppigiana*, which was published at the same time as *laurifolia*, can be used for it immediately, in *Mascagnia* or any other genus.

***Mascagnia surinamensis* (Kosterm.) W.R. Anderson**, Contr. Univ. Michigan Herb. 17: 53. 1990. —*Mascagnia multiglandulosa* var. *surinamensis* Kosterm., Meded. Bot. Mus. Herb. Rijksuniv. Utrecht 25: 5. 1936.

Woody vine; petioles 4–12 mm long, eglandular or biglandular in middle third; blade of larger leaves 6.5–12 × 3–7 cm, velutinous to glabrate adaxially, persistently velutinous abaxially with T- or Y-shaped hairs; bracteoles and sepals bearing a row of small stalked glands on margin; sepals leaving outermost petal(s) exposed in bud, the lateral 4 abaxially biglandular; petals yellow, abaxially densely tomentose; samaras 22–30(–40) mm wide, the lateral wing continuous at base, divided to nut at apex. Evergreen lowland forests, roadside thickets, 100–200 m; Amazonas (Puerto Ayacucho–Gavilán). Guyana, Suriname, Amazonian Brazil, Bolivia.

**19. MEZIA** Schwacke ex Nied. in Engl. & Prantl, Nat. Pflanzenfam. III. 4: 58. 1890.

—*Diplopterys* sect. *Mezia* (Schwacke ex Nied.) Nied., Arbeiten Bot. Inst. Königl. Lyceum Hosianum Braunsberg 4: 16. 1912.

Woody vines, shrubs, or small trees. Leaves with the petiole eglandular; stipules minute, interpetiolar, caducous; blade bearing impressed abaxial glands or eglandular. Inflorescence tightly reddish- or brown-sericeous throughout, axillary and terminal, often decompose, containing much-reduced bract-like leaves, the flowers borne ultimately in umbels of 4; bracts and bracteoles abaxially sericeous, adaxially glabrous or sparsely sericeous; bracts smaller than bracteoles, deciduous before maturation of fruits; peduncles well developed; bracteoles borne just below flower, large, globose-cymbiform, the inner enclosing bud until flower opens, the outer enclosing bud and inner bracteole, persistent or deciduous before maturation of fruits; pedicels absent or very short, up to 5 mm long in fruit; old flowers (not setting fruit) deciduous at base of peduncle, not at joint between peduncle and pedicel. Sepals narrowly oblong or spatulate, the anterior eglandular, the lateral 4 each bearing 2 large compressed glands, these distinct or partially to completely connate;

petals yellow. Stamens 10, dimorphic, the 5 opposite sepals differing from the 5 opposite petals in size and shape, and sometimes in pubescence. Ovary of 3 carpels adnate to a common axis; styles 3, the apex with a large internal stigma and dorsally truncate or short-hooked or pedaliform (i.e., with a short broad extension resembling from above the sole of a shoe), the anterior style shorter and often more slender than the 2 posterior styles. Fruits breaking apart into 3 samaras, each bearing 2 large lateral wings that are distinct or more often confluent at base, a smaller dorsal wing, and often additional wings, winglets, or crests between them or outside the lateral wings.

Panama, Colombia, Venezuela, Guyana, French Guiana, Ecuador, Peru, Brazil, Bolivia; ca. 12 species, 4 in Venezuela, all in the flora area.

#### Key to the Species of *Mezia*

1. Leaves very densely and persistently sericeous abaxially, the hairs producing a reddish or rusty brown metallic sheen ..... 2
1. Leaves glabrous or thinly sericeous to glabrate abaxially, the hairs on mature leaves not dense enough to completely conceal epidermis ..... 3
- 2(1). Shrub or small tree 2–8 m tall; blade of larger leaves 9–17 × 5–10 cm; petioles 10–15 mm long; samaras 30–42 mm diameter, the central dorsal wing and 2 parallel winglets flat, the latter not connected by transverse winglets to lateral wing; lateral wing of samara nearly flat, tomentose, the hairs sinuous and spreading ..... *M. huberi*
2. Woody vine; blade of larger leaves 19–29 × 10–18.5 cm; petioles 20–40 mm long; samaras 45–60 mm diameter, the central dorsal wing and 2 parallel winglets strongly corrugated and the latter connected to lateral wing by several transverse winglets; lateral wing of samara wrinkled or corrugated, sericeous, the hairs straight and appressed ..... *M. rufa*
- 3(1). Anthers opposite sepals densely tomentose, those opposite petals sparsely tomentose to glabrous ..... *M. curranii*
3. Anthers all glabrous ..... *M. includens*

***Mezia curranii*** W.R. Anderson, Mem. New York Bot. Gard. 32: 236. 1981.

*Diplopterys involuta* var. *ovata* Nied. in Engl., Pflanzenr. IV. 141: 227. 1928.

Woody vine; petioles 12–24 mm long; blade of larger leaves 12.5–23 × 4.5–9.5 cm, abaxially very sparsely sericeous to glabrate; anthers opposite sepals ± densely tomentose, those opposite petals sparsely tomentose to glabrous; samaras 55–65 mm diameter, the lateral wing continuous at base, flat to wrinkled, thinly and loosely sericeous, the central dorsal wing and 2 parallel winglets wavy or corrugated, the latter connected to lateral wing by several mostly transverse winglets. Evergreen lowland forests, Amazonas (Culebra). Amazonian Peru.

*Mezia curranii* is apparently little more than *M. includens* with hairy anthers, and it

remains to be seen whether that character is sufficient basis to justify its continued recognition, but it is true that the widespread and variable *M. includens* is generally consistent in its glabrous anthers.

***Mezia huberi*** W.R. Anderson, Contr. Univ. Michigan Herb. 19: 384. 1993.

Shrub or small tree 2–8 m tall; petioles 10–15 mm long; blade of larger leaves 9–17 × 5–10 cm, abaxially very densely and persistently reddish- or dark brown-sericeous; anthers glabrous; samaras suborbicular, 30–42 mm diameter, the lateral wing continuous at base, flat, tomentose with sinuous and spreading hairs, the dorsal wing and 2 intermediate winglets flat and parallel. Sandy savannas and adjacent gallery forests, 100–600 m; Amazonas (west of San Juan de Manapiare). Endemic. ♦Fig. 107.

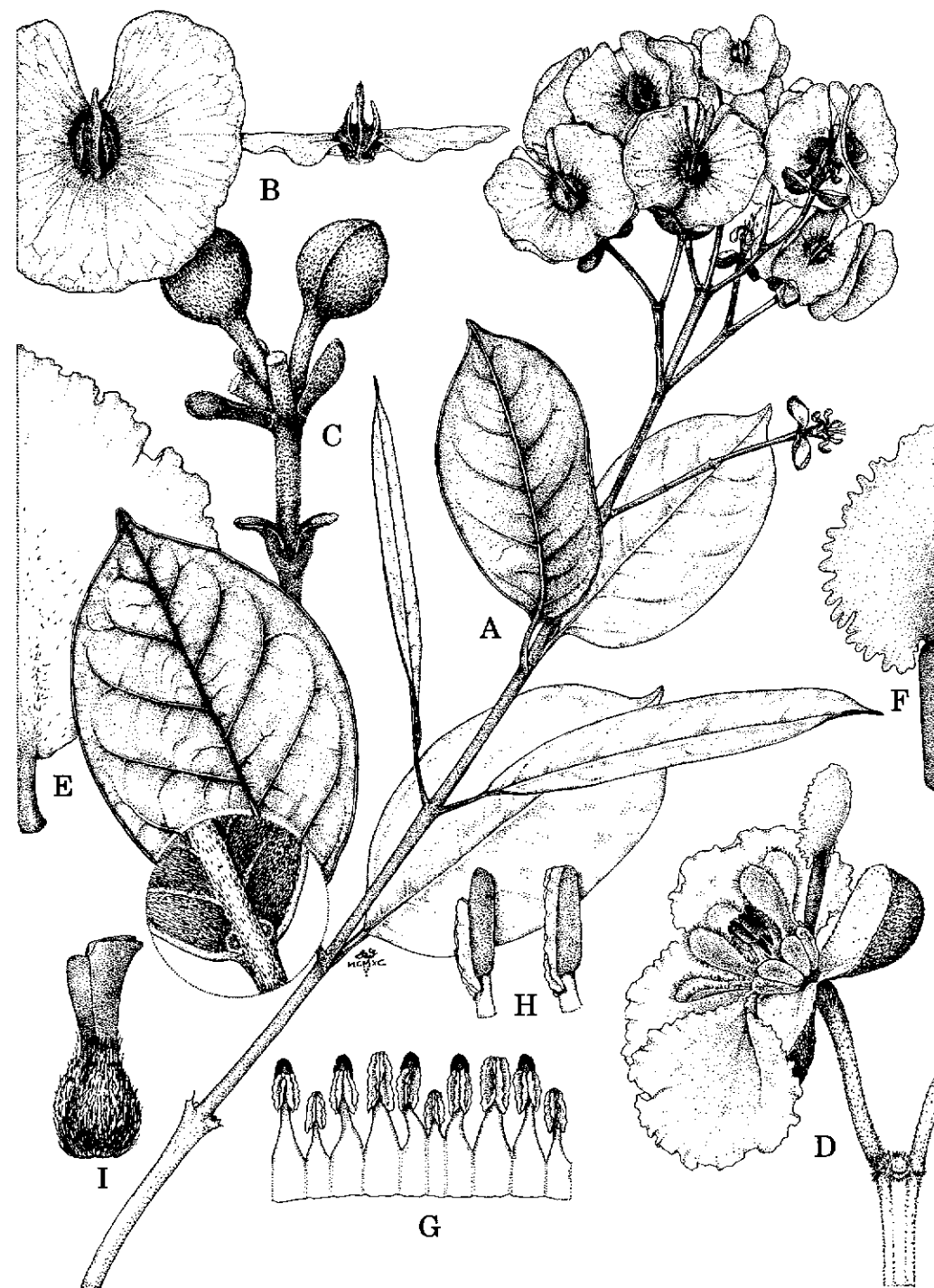


Fig. 107. *Mezia huberi*. —A. Fruiting branch, ×0.53. —B. Samara, abaxial view (left), side view looking into apical notch (right), ×1.1. —C. Umbel of 4 flower buds with 2 cut off, ×2.7. —D. Flower, side view with 1 posterior-lateral petal removed, ×2.7. —E. Lateral petal, abaxial view, ×5.3. —F. Posterior petal, abaxial view, ×5.3. —G. Androecium laid out, adaxial view, the stamen opposite anterior sepal to left, ×5.3. —H. Anthers, side view, from opposite a sepal (left) and opposite a posterior-lateral petal (right), ×10.6. —I. Gynoecium, side view, anterior style to left, ×8. ©University of Michigan Herbarium 1993.

**Mezia includens** (Benth.) Cuatrec., Webbia 13: 450. 1958. —*Tetrapterys includens* Benth., London J. Bot. 7: 133. 1848. —*Diplopterys includens* (Benth.) Nied. in Engl., Pflanzenr. IV. 141: 226. 1928. *Stenocalyx involutus* Turcz., Bull. Soc. Imp. Naturalistes Moscou 31: 394. 1858. —*Diplopterys involuta* (Turcz.) Nied. in Engl., Pflanzenr. IV. 141: 226. 1928.

Woody high-climbing vine; petioles 14–21(–25) mm long; blade of larger leaves 13–20(–21) × 6–9.5(–10.5) cm, abaxially initially ± densely sericeous, mostly glabrescent and thinly sericeous to glabrate at maturity; anthers glabrous; samaras suborbicular or wider than high, 70–110 mm across, the lateral wing continuous at base, wrinkled or corrugated, thinly sericeous, the central dorsal wing and 2 parallel winglets strongly corrugated, the latter connected to lateral wing by several transverse winglets. Evergreen lower montane forests, especially along rivers, 200–1300 m; Bolívar (east of 63°W, from Upata and Río Grande south to Río Icabarú, and upper Río Caura at 64°W), Amazonas (scattered localities from Puerto Ayacucho to Sierra Parima). Carabobo; Panama, Colombia, Guyana, French Guiana, Amazonian Ecuador, Peru, Brazil.

See discussion of *Bernardi 7170* under *Mezia rufa*.

**Mezia rufa** W.R. Anderson, Mem. New York Bot. Gard. 32: 234. 1981.

Woody vine; petioles 20–40 mm long; blade of larger leaves 19–29 × 10–18.5 cm, abaxially densely and persistently metallic-sericeous with the hairs usually giving blade

a rusty brown or reddish appearance; anthers glabrous; samaras 45–60 mm diameter, the lateral wing continuous at base or incised to nut, wrinkled or corrugated, sericeous with hairs straight and tightly appressed, the central dorsal wing and 2 parallel winglets strongly corrugated, the latter connected to lateral wing by several corrugated transverse winglets. Evergreen lowland forests, 100–300 m; Amazonas (Maroa to Yavita, base of Sierra de la Neblina). Brazil (Amazonas: Rio Maturacá, Rio Negro), Peru (Loreto).

*Mezia rufa* was described to accommodate plants with very large, persistently sericeous leaves. In characters of their flowers they resemble *M. includens*. The fruits of *M. rufa* are not well known; they seem to be mostly smaller than in *M. includens*, probably reflecting a shift toward dispersal by water, but they have complicated intermediate ruffles as in *M. includens*. The leaves of *M. includens* are often densely sericeous at first, but usually soon glabrescent and at most thinly sericeous abaxially at maturity, although occasionally the smaller leaves near the inflorescence are persistently sericeous. In one collection from Río Grande in north-eastern Bolívar (*Bernardi 7170* [G, MER, MICH]) the few leaves present, subtending branches of the inflorescence, are small but abaxially densely and persistently sericeous. Its samaras resemble those of *M. includens*. Given the small size of the leaves and the location, I suspect that *Bernardi 7170* represents *M. includens* rather than *M. rufa*; if larger leaves had been collected they probably would have been glabrate.

## 20. PTERANDRA A. Juss. in A. St.-Hil., Fl. Bras. Merid. 3: 72. 1832 [1833].

Shrubs or trees. Leaves often crowded at tips of branchlets, eglandular (except for tiny angular translucent dots often present in blade); stipules intra- and epipetiolar, basally to completely connate. Inflorescence reduced to fasciculate clusters in axils of leaves or bracts or above leaf scars; bracts and bracteoles eglandular; pedicels sessile; petals abaxially sparsely to densely sericeous on claw and in center of limb, often persistent in fruit. Stamens 10; anthers glabrous, the outer locules bearing introrse longitudinal wings. Ovary of 3 distinct carpels; styles 3, attached ventrally or subapically, slender and subulate with minute terminal stigmas. Fruits comprising up to 3 dry indehiscent cocci with a papery exocarp and a moderately thick, corneous but not bony endocarp.

Panama, Colombia, Venezuela, Guyana, Brazil, Bolivia; 14 species, 3 known or expected in Venezuela, all of these in the flora area.

See Christiane Anderson, 1997 [Revision of *Pterandra* (Malpighiaceae), Contr. Univ. Michigan Herb. 21: 1–27].

### Key to the Species of *Pterandra*

1. Stipules abaxially glabrous even in bud (but often with a sericeous patch at point of attachment to petiole); blade of larger leaves 9.5–14 cm long; bracts and bracteoles triangular, 1.2–1.5 × 1–1.5 mm; sepals strongly revolute ..... *P. guianensis*
1. Stipules initially densely sericeous abaxially, the hairs persistent or deciduous at maturity; blade of larger leaves up to 9.8 cm long; bracts and bracteoles linear or narrowly triangular, 1.7–3 × 0.4–1.3 mm; sepals appressed or slightly recurved. .... 2
- 2(1). Leaf blades white or yellow abaxially, bearing scattered, dark red or brown, short (up to 0.7 mm), straight, sessile hairs; lateral veins of leaf blade flush with abaxial surface or prominulous; petioles 15–27 mm long; anther wings 0.4 mm wide ..... *P. flavescens*
2. Leaf blades light green abaxially, densely brown- or white-sericeous, the hairs up to 1.2 mm long, straight to somewhat serpentine, sessile or short-stalked; lateral veins of leaf blade prominently raised abaxially; petioles 3–13 mm long; anther wings 0.2 mm wide ..... *P. sericea*

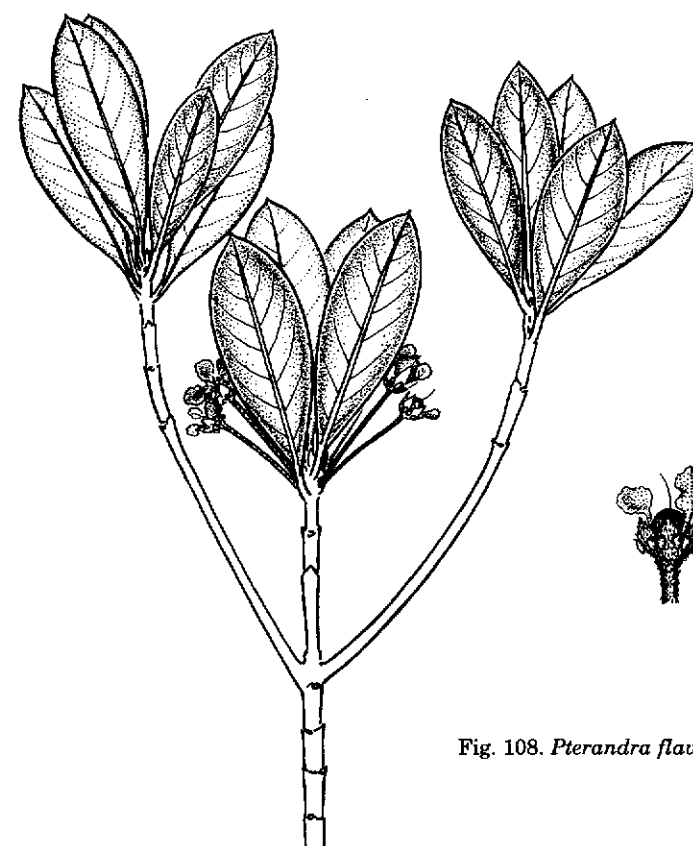


Fig. 108. *Pterandra flavescens*

**Pterandra flavescens** Maguire, Mem. New York Bot. Gard. 8: 128. 1953.

Shrub or small tree 2–10 m tall; stipules 3.5–4.5 mm long,  $\frac{2}{3}$ –completely connate, abaxially densely sericeous; petioles 15–27 mm long; leaf blades 5–9.8 × 2–5 cm, abaxially white or yellow and very sparsely sericeous; bracts and bracteoles linear or narrowly triangular, 1.7–3 × 0.6–1.3 mm; sepals all biglandular, appressed or slightly recurved; petals cream or pale yellow; anther wings 0.4 mm wide. Tepui meadows and boggy areas along river, ca. 1500 m; Amazonas (Cerro Sipapo). Endemic. •Fig. 108.

**Pterandra guianensis** W.R. Anderson, Mem. New York Bot. Gard. 32: 35. 1981.

Tree up to 20 m tall; stipules 3–3.7 mm long, nearly to completely connate, abaxially glabrous or with a sericeous patch at base; petioles 8–15 mm long; blade of larger leaves 9.5–14 × 3.5–6 cm; bracts and bracteoles triangular, 1.2–1.5 × 1–1.5 mm; sepals all

biglandular, strongly revolute; petals greenish yellow; anther wings 0.2 mm wide. Known only from the type, collected in mixed evergreen forest below 762 m on Mt. Ayanganna in western Guyana; to be expected in La Gran Sabana of southeastern Bolívar.

**Pterandra sericea** W.R. Anderson, Brittonia 28: 407. 1976 [1977].

Shrub or tree 2.5–10(–15) m tall; stipules 3–4 mm long, completely connate or notched at apex, abaxially densely sericeous to glabrescent; petioles 3–13 mm long; leaf blades 3–8.5 × 1.6–4.3 cm, abaxially light green and densely sericeous; bracts and bracteoles linear, 1.8–3 × 0.7–1 mm; sepals all biglandular or all eglandular, appressed; petals white to greenish white becoming pale yellow in age; anther wings 0.2 mm wide. By rivers in forests, 100–800 m; northwestern and eastern Bolívar (Apacará-tepui, Auyán-tepui, Cerro Bolívar, Río Ambutuir, Río Carrao, Río Caura). Western Guyana.

## 21. SPACHEA A. Juss. in Deless., Icon. Sel. Pl. 3: 19. 1837 [1838].

Shrubs or trees, the stems often containing white latex. Leaves bearing impressed glands in blade, abaxially at base and sometimes distally, adaxially near apex; stipules intra- and epipetiolar, connate. Inflorescence terminal, a raceme of short 1–several-flowered cincinni, 1 bracteole often bearing 1 large gland; petals pink or white. Stamens 10, the anthers unwinged, the connective shorter than the locules. Carpels 2 or 3, connate along a central axis, each bearing a stout, untapered style with the broad terminal stigma often becoming subpeltate or bilobed in anthesis. Plants morphologically gynodioecious but functionally dioecious, the pistillate flowers bearing flat unopened anthers with aborted pollen, the apparently bisexual flowers bearing large polleniferous anthers and a small ovary that does not mature into a fruit. Fruits breaking apart into 2 or 3 dry, unwinged, smooth, indehiscent, 1-seeded cocci bearing the persistent styles.

West Indies, Central America, and northern South America (Colombia, Venezuela, Guyana, Suriname, French Guiana, Peru, Brazil); ca. 6 species, 1 in Venezuela.

**Spachea elegans** (G. Mey.) A. Juss. in Deless., Icon. Sel. Pl. 3: 19, pl. 31. 1837 [1838]. —*Malpighia elegans* G. Mey., Prim. Fl. Esseq. 178. 1818.

Tree 4–15 m tall; stipules 3–6 mm long, completely connate; petioles 7–10 mm long; blade of larger leaves 6–12(–18) × 3–6(–7.5) cm, abaxially sparsely reddish-tomentose or subsericeous at least on midrib, bearing 2–4 impressed glands abaxially near base and often several distally, plus 2–4 glands on adaxial surface near apex; inflorescence a

pseudoraceme (i.e., all cincinni 1-flowered); bracts eglandular; some plants with 1 bracteole terminating in a ± stalked gland; calyx bearing 8 or 9 glands; petals pink; carpels 2(3); cocci of fruits 4.5–6 × 3–4 mm. Riparian forests, near sea level to 200 m; Delta Amacuro (Río Amacuro), Bolívar (Puerto Ordaz, Río Botanamo, lower Río Caroní, San Félix). West Indies (probably introduced), Trinidad, Guyana, Suriname, French Guiana, Brazil (Roraima). •Fig. 109.

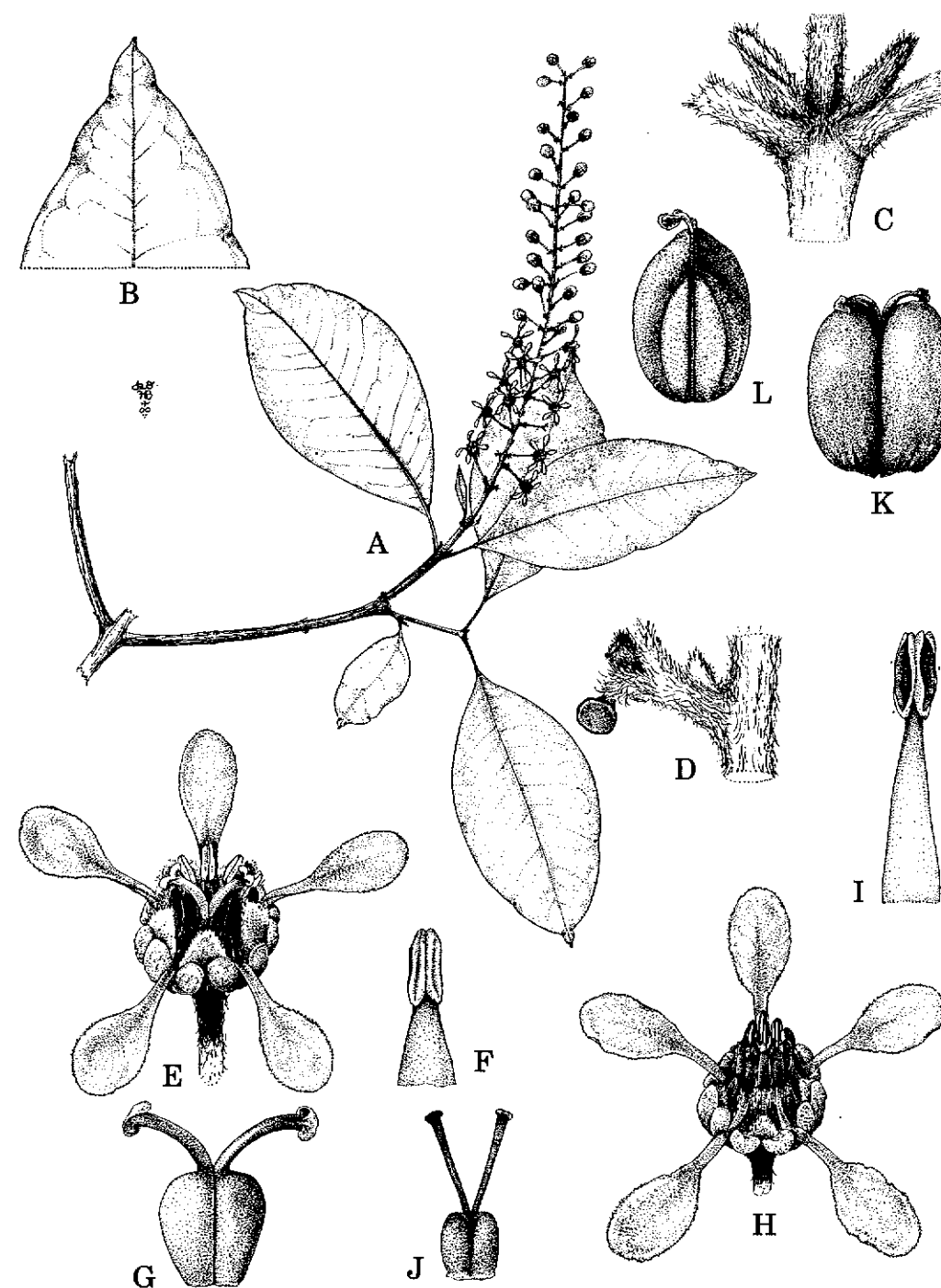


Fig. 109. *Spachea elegans*. —A. Flowering branch, ×0.6. —B. Adaxial view of leaf apex enlarged to show glands, ×1.1. —C. Node with stipules, ×5.5. —D. Bract, peduncle, and bracteoles (twisted peduncle makes bract appear above rather than below peduncle), ×5.5. —E–G. Flower, stamen, and gynoecium of functionally pistillate plant: E ×4.4, F ×11, G ×8.3. —H–J. Flower, stamen, and gynoecium of functionally staminate plant: H ×4.4, I ×11, J ×8.3. —K. Intact fruit, ×5.5. —L. Cocci, adaxial view, ×5.5. ©New York Botanical Garden 1981.



**22. STIGMAPHYLLON** A. Juss. in A. St.-Hil., Fl. Bras. Merid. 3: 48. 1832 [1833].*Brachypterys* A. Juss. in Deless., Icon. Sel. Pl. 3: 20. 1837 [1838].

Woody or herbaceous vines, a few species shrubby. Leaves with the blade entire or lobed; stipules small, distinct, interpetiolar; petioles often long, usually bearing 2 large glands at apex, these sometimes just above petiole on base of blade. Inflorescence unbranched or more commonly a dichasium (or occasionally a small thyrses) of congested pseudoracemes, these usually corymbose or umbellate. Lateral 4 sepals biglandular, the anterior usually eglandular; sepals erect or appressed in anthesis; petals yellow or yellow and red, glabrous or rarely pubescent abaxially, the limb largest in anterior-lateral pair, smaller in posterior-lateral pair, and smallest in posterior petal. Stamens 10, the filaments usually unequal in length and thickness; anthers very unequal in most species, the 4 opposite the lateral sepals often with reduced locules or sometimes sterile and the 1 opposite the posterior petal often small; anthers subequal in several species, including *S. bannisterioides* in our area. Ovary with the 3 carpels partially connate, all fertile; styles 3, the apex with an internal stigma and dorsally truncate, hooked, or bearing a foliaceous lateral appendage (foliole), the foliole symmetrical on the anterior style, 1-sided on the posterior styles. Fruits breaking apart into 3 samaras, each samara having its largest wing dorsal, thickened on the adaxial (upper) edge, the veins terminating in the thinner abaxial edge; much shorter winglets or crests present on sides of nut in some species; dorsal wing much reduced in a few species.

Mexico, Central America, West Indies, South America (all countries except Chile); 1 species, *S. bannisterioides*, also occurs in West Africa; 91 species, 11 known or expected in Venezuela, 5 of these in the flora area.

See Christiane Anderson, 1997 [Monograph of *Stigmaphyllon* (Malpighiaceae), Syst. Bot. Monogr. 51].

Key to the Species of *Stigmaphyllon*

1. Flowers (3)4(–6) per umbel; all 3 styles dorsally hooked but lacking folioles; "samaras" with dorsal wing reduced to a triangular apical crest 4–9 mm high ..... *S. bannisterioides*
1. Flowers 8–40 per umbel or pseudoraceme; all 3 styles or at least the posterior 2 bearing well-developed folioles; samaras with an elongated dorsal wing 25–55 mm long or with dorsal wing partially encircling nut and 30–44 mm long measured from base of nut ..... 2
- 2(1). Leaf blades abaxially pubescent with T-shaped hairs and bearing stipitate (nail-like) or peltate marginal glands 0.2–0.6 mm long and 0.2–0.4 mm diameter at the apex; samaras with nut 12–19 mm diameter, the locule surrounded by air chambers, and dorsal wing partially encircling nut ..... *S. adenodon*
2. Leaf blades abaxially glabrous or sparsely to densely sericeous with sessile or subsessile hairs and bearing sessile marginal glands 0.2–1.5 mm diameter and sometimes filiform glands up to 1.6 mm long; samaras with nut 2.8–7 mm diameter and dorsal wing not encircling nut ..... 3
- 3(2). Flowers 8–15 per umbel; petals fimbriate with fimbriae up to 0.6 mm long; anterior style and its opposing stamen longer than posterior styles and their opposing stamens; samaras with nut smooth-sided or with 1–5 prominent ribs, the wing widest at base ..... *S. puberum*

3. Flowers 15–40 per umbel or pseudoraceme; petals erose to denticulate-fimbriate with teeth or fimbriae up to 0.2 mm long; anterior style and its opposing stamen mostly shorter than posterior styles and their opposing stamens; samaras with nut usually bearing 1–3 coarsely toothed to lacerate lateral winglets and/or spurs and crests, rarely smooth, the wing narrowed beyond nut, widest distally ..... 4
- 4(3). Leaf blades abaxially sparsely to very densely sericeous, the hairs (0.2–)0.3–0.5(–0.7) mm long, usually touching to overlapping ..... *S. sinuatum*
4. Leaf blades abaxially appearing glabrous to the naked eye, but usually very sparsely sericeous, the hairs ca. 0.1(–0.2) mm long and widely spaced, never touching ..... *S. convolvulifolium*

**Stigmaphyllon adenodon** A. Juss., Ann. Sci. Nat. Bot. sér. 2, 13: 288. 1840.

*Stigmaphyllon grenadense* Nied., Ind. Lect. Lyc. Reg. Hos. Brunsberg. p. aest. 1900: 26. 1900.

Woody vine; petioles up to 115 mm long; blade of larger leaves 7–15 × 4–15 cm, cordate or ovate, cordate at base in larger leaves, abaxially pubescent with T-shaped hairs, the margin with stipitate nail-like or peltate glands; flowers 15–30(–40) in each umbel or congested pseudoraceme; peduncles 3.5–17.5 mm long; limb of petals erose or erose-denticulate; anthers pubescent; anterior style shorter than posterior styles, all 3 bearing folioles. Grenada, Trinidad, Amazonian Colombia, Venezuela, Ecuador, Amazonian Peru and Brazil; 2 varieties, 1 in Venezuela.

The second variety, var. *macropterum* C.E. Anderson, has a long samara wing similar to that of most other species of the genus. It is found in Ecuador and Peru.

**S. adenodon** var. **adenodon**

Samaras with nut 12–19 mm diameter including air chambers, the dorsal wing partially encircling nut, 30–44 mm long from base of nut. Wet areas along rivers, near sea level; Delta Amacuro (La Margarita–Puerto Miranda, Teima, Tucupita–La Horqueta). Sucre; Grenada, Trinidad, Amazonian Colombia, Peru, and Brazil.

**Stigmaphyllon bannisterioides** (L.) C.E. Anderson, Taxon 41: 328. 1992. —*Malpighia bannisterioides* L., Pl. Surin. 9. 1775.

*Banisteria ovata* Cav., Diss. 9: 429, pl. 257. 1790. —*Brachypterys borealis* A. Juss., Ann. Sci. Nat. Bot. sér. 2, 13: 291. 1840, nom. superfl. —*Stigmaphyllon*

*ovatum* (Cav.) Nied., Ind. Lect. Lyc. Reg. Hos. Brunsberg. p. aest. 1900: 31. 1900. —*Brachypterys ovata* (Cav.) Small, N. Amer. Fl. 25: 138. 1910.

Vine or twining shrub to 3 m tall; petioles up to 18 mm long; blade of larger leaves 5–11(–13) × 2–4.5(–5.5) cm, narrowly elliptic to ovate, attenuate or truncate at base, sparsely sericeous abaxially, the margin eglandular; flowers (3)4(–6) in each umbel; peduncles 0.2–2.5 mm long; limb of petals erose; anthers glabrous; styles subequal, all with a dorsal hook at apex and without folioles; mericarps with nut 8–11 mm diameter, bearing 4–6 ribs or crests on each side radiating from areole, without air chambers, and dorsal wing reduced to a triangular crest 4–9 × 5.5–7.5 mm. Seashores, mangrove swamps, salt marshes, sea level to 50 m; Delta Amacuro (Atoiba, Caño Güinipa, Caño Güiniquina, Curiapo, region of Pedernales). Miranda, Sucre, Yaracuy; Atlantic coast from southern Mexico through Central America, West Indies, Colombia, Guyana, Suriname, French Guiana, Brazil as far south as Ceará, Atlantic coast of western Africa.

**Stigmaphyllon convolvulifolium** A. Juss., Ann. Sci. Nat. Bot. sér. 2, 13: 289. 1840.

Vine to 15 m; petioles up to 100 mm long; blade of larger leaves 6–16 × 3–12 cm, ovate or cordate, cordate at base, abaxially very sparsely and minutely sericeous (apparently glabrous), the margin with sessile glands 0.2–0.5 mm diameter and filiform glands up to 1.6 mm long; flowers 15–40 in each congested pseudoraceme; peduncles 4–12.5 mm long; limb of petals erose to denticulate-fimbriate; anthers glabrous; anterior style shorter than posterior styles, all 3 bearing folioles; samaras with nut bearing short winglets, crests, or spurs on sides and dorsal

wing 34–42 × 12–20 mm, widest distally. Moist forests, along rivers, secondary growth, roadsides, near sea level to 300 m; expected in Delta Amacuro adjacent to Guyana. Guyana, Suriname, French Guiana, northeastern Brazil.

**Stigmaphyllon puberum** (Rich.) A. Juss., Ann. Sci. Nat. Bot. sér. 2, 13: 289. 1840.  
—*Banisteria pubera* Rich., Actes Soc. Hist. Nat. Paris 1: 109. 1792.

Woody vine; petioles up to 72 mm long; blade of larger leaves 9–18(–20) × 4.5–12.5 cm, elliptic to ovate, attenuate or truncate or sometimes cordate at base, ± densely sericeous abaxially, the margin with sessile glands 0.3–0.4 mm diameter; flowers 8–15 in each umbel; peduncles (0.8–)1.5–4.8 mm long; limb of petals digitate-fimbriate, the fimbriae up to 0.6(–0.8) mm long; anthers glabrous or pubescent; anterior style longer than posterior styles, all 3 bearing folioles; samaras with nut smooth-sided or with 1–5 prominent ribs and dorsal wing 25–41 × 9–

15 mm, widest at base. Evergreen lowland forests, gallery forests, river banks, mangrove swamps, near sea level to 100 m; Delta Amacuro (La Margarita–Puerto Miranda, Misión del Guayo, Río Amacuro, Río Cuyubini). Monagas; Central America, West Indies, Colombia, Guyana, Suriname, French Guiana, Amazonian Peru, Brazil.

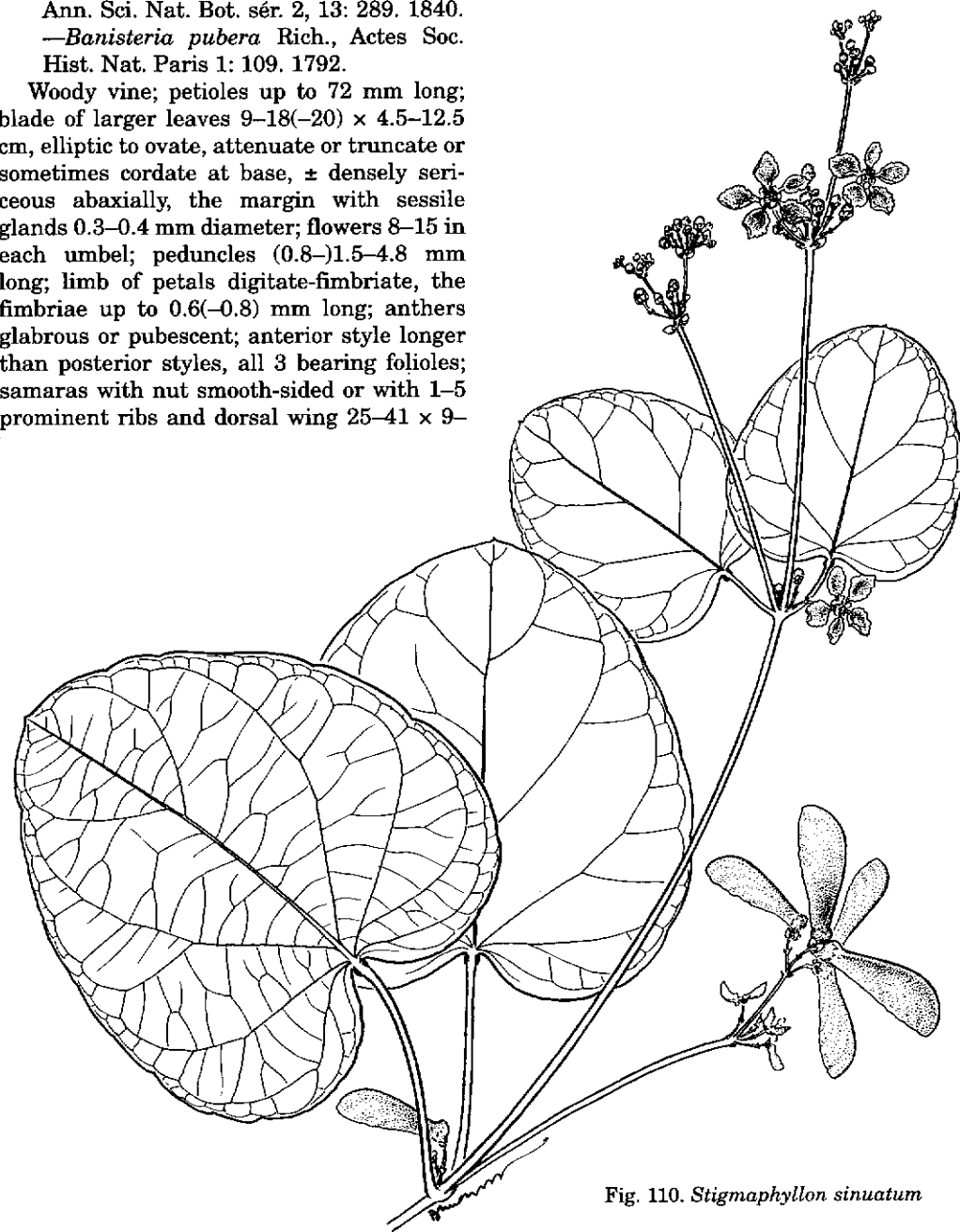


Fig. 110. *Stigmaphyllon sinuatum*

**Stigmaphyllon sinuatum** (DC.) A. Juss., Ann. Sci. Nat. Bot. sér. 2, 13: 288. 1840.  
—*Banisteria sinuata* DC., Prodr. 1: 588. 1824.

*Banisteria heterophylla* Willd., Sp. Pl. ed. 4, 2: 742. 1799, non *Stigmaphyllon heterophyllum* Hook. 1843. —*Banisteria splendens* DC., Prodr. 1: 588. 1824, nom. superfl. —*Stigmaphyllon fulgens* A. Juss., Ann. Sci. Nat. Bot. sér. 2, 13: 289. 1840, nom. superfl. —*Stigmaphyllon splendens* Cuatrec., Webbia 13: 531. 1958, nom. superfl.

*Stigmaphyllon martianum* A. Juss., Ann. Sci. Nat. Bot. sér. 2, 13: 289. 1840.

*Stigmaphyllon hypoleucum* Miq., Linnaea 18: 51. 1844.

*Stigmaphyllon brachiatum* Triana & Planch., Ann. Sci. Nat. Bot. sér. 4, 18: 316. 1862.

*Stigmaphyllon monancistrum* Nied., Ind. Lect. Lyc. Reg. Hos. Brunsberg. p. hiem. 1899–1900: 13. 1899.

Woody vine; petioles up to 130 mm long; leaf blades 6–21 × 4.5–20 cm, triangular or ovate to orbicular, acute to deeply auriculate at base, abaxially sparsely to very densely

silver-sericeous, the margin with sessile glands 0.4–1.5 mm diameter and sometimes with filiform glands up to 1.5 mm long; flowers 15–35(–40) in each congested pseudoraceme; peduncles 2.5–11 mm long; limb of petals erose to denticulate; anthers glabrous; anterior style ≤ posterior styles, all 3 bearing folioles; samaras with nut usually bearing short winglets, crests, or spurs on sides and dorsal wing 35–55 × 10–18 mm, widest distally. Primary and secondary forests, especially wet forests, but also in vegetation on white sand, along rivers, at roadsides, and in thickets, 50–900 m; Delta Amacuro (Río Grande, Sierra Imataca), widespread in lowlands of Bolívar and Amazonas. Present in most states of northern Venezuela; Colombia, Guyana, Suriname, French Guiana, Ecuador, northern Peru, northern Brazil, Amazonian Bolivia. ♦Fig. 110.

*Stigmaphyllon sinuatum* is common throughout much of Amazonia and excessively polymorphic. For a thorough discussion of its variability and comparison to similar species, see C. Anderson, Contr. Univ. Michigan Herb. 19: 393–413. 1993.

### 23. TETRAPTERYS Cav., Diss. 9: 433. 1790, nom. cons.

Woody vines or shrubs, occasionally described as small trees. Leaves usually bearing glands; stipules small, interpetiolar or epipetiolar, or absent. Flowers borne in umbels, corymbs, or pseudoracemes, these often grouped in panicles. Calyx usually bearing 8 or 10 glands, eglandular in a few species; petals yellow or pink. Stamens 10, all fertile; anthers ± alike. Ovary with the 3 carpels centrally connate, all fertile; styles 3, the apex with an internal to terminal stigma and dorsally smooth, truncate, or short-hooked. Fruits breaking apart into 3 samaras, each samara having its largest wings lateral, usually 4 discrete wings; dorsal wing smaller, sometimes reduced to a crest or lost; intermediate winglets or projections sometimes present; all wings reduced to rudimentary outgrowths in a few species.

Mexico, Central America, West Indies, South America (all countries except Chile and Uruguay); at least 70 species, ca. 18 in Venezuela, 11 of these in the flora area.

The taxonomy of this genus is far from satisfactory; as it is studied and better resolved in coming years the number of species recognized will probably increase substantially.

#### Key to the Species of *Tetrapteryx*

1. Inflorescence simple or compound, terminating in umbels of 4(–6) flowers; bracteoles smaller than floriferous bracts or the same size, eglandular or abaxially callose ..... 2

1. Inflorescence an axillary or terminal pseudoraceme, usually unbranched, rarely basally ternate, the flowers sometimes reduced to 1 pair or crowded distally to form a few-flowered corymb or umbel; bracteoles mostly larger than floriferous bracts (wider and often at least as long), often bearing marginal or abaxial glands ..... 4
- 2(1). Stipules distinct; styles slender, with small, discrete, nearly terminal stigmas; nonfloriferous bracts of the inflorescence inconspicuous, 5 mm long or less, lanceolate; bracteoles longer than wide; calyx glands (if present) becoming stalked in older flowers and fruits ..... *T. mucronata*
2. Stipules connate in interpetiolar pairs, often caducous but then leaving a prominent interpetiolar scar; styles stout, stigmatic on internal angle of apex with the stigmas decurrent; inflorescence containing conspicuous, often orbicular, foliaceous bracts 4–20 mm long, much smaller and thinner than vegetative leaves but much larger than floriferous bracts, the large bracts deciduous and usually absent from fruiting specimens; bracteoles about as wide as long or wider; calyx glands sessile ..... 3
- 3(2). Samaras with winglets or aculeate outgrowths between dorsal and lateral wings, the upper lateral wings 12–22(–25) mm long, the lower 4–10 mm long; stipule pair 1–2 mm wide, the scar stretched to 2.5 mm at older nodes; leaf blades (7.5–)9–14.5 × (3–)4–6.5 cm; petioles 7–12 mm long ..... *T. discolor*
3. Samaras usually devoid of outgrowths between dorsal and lateral wings, the upper lateral wings 22–35 mm long, the lower 11–15(–20) mm long; stipule pair 2.5–4 mm wide, the scar stretched to 5.5 mm at older nodes; leaf blades (11–)13–20 × (5–)6–10.5 cm; petioles (12–)14–20(–27) mm long ..... *T. crispa*
- 4(1). Calyx bearing 8 glands, i.e., lateral 4 sepals biglandular, anterior eglandular; petals abaxially ± abundantly appressed-tomentose or subsericeous ..... *T. maranhensis*
4. Calyx bearing 10 glands, i.e., all 5 sepals biglandular; petals glabrous or bearing a few appressed hairs abaxially ..... 5
- 5(4). Limb of lateral petals denticulate or entire; filaments densely to sparsely sericeous or rarely glabrous; glands on leaf blade marginal or none; nut of samara usually bearing aculeate outgrowths between dorsal and lateral wings ..... 6
5. Limb of lateral petals fimbriate; filaments glabrous; glands present on abaxial surface of leaf blade in most species, between midrib and margin; nut of samara usually devoid of outgrowths between dorsal and lateral wings (all wings reduced to thick, irregular outgrowths in *T. oleifolia*) ..... 8
- 6(5). Blade of larger leaves up to 6 cm long, persistently appressed-tomentose abaxially or eventually glabrescent, the hairs ± serpentine and loose ..... *T. aristeguietae*
6. Blade of larger leaves 3.5–15 cm long, thinly sericeous to glabrate abaxially, the hairs (if any) straight and appressed ..... 7
- 7(6). Woody vine or robust shrub 2–3 m tall, usually growing by rivers; leaf blades (2.5–)3.5–7 cm wide; calyx glands (2.5–)3–4 mm long; lateral wings of samara (7–)8–14 mm long, 4, subequal; anthers (1.3–)1.5–1.8 mm long; bracteoles 2–5 mm long ..... *T. styloptera*

7. Wiry-stemmed shrub 0.2–0.8(–1.5) m tall, in savannas; leaf blades 0.7–2.8 cm wide; calyx glands 1.2–2 mm long; lateral wings of samara 1–3(–5) mm long, variable in number, irregular and often unequal; anthers 0.9–1.1(–1.5) mm long; bracteoles up to 2 mm long ..... *T. gracilis*
- 8(5). Stems, inflorescence, and leaves very soon nearly or quite glabrate, except for golden-sericeous axillary buds; leaf blades with margin notably thickened and veins usually obscure or invisible; virgate shrubs 0.2–2(–3) m tall ..... *T. pusilla*
8. Stems and usually the inflorescence densely and persistently sericeous; leaves sericeous to glabrate; leaf blades with margin sometimes revolute but usually not or only slightly thickened, the veins visible on one or both sides; shrubs or vines. .... 9
- 9(8). Leaf blades abaxially thinly sericeous to glabrate, the epidermis and glands easily seen ..... *T. fimbripetala*
9. Leaf blades abaxially densely and persistently sericeous, the hairs nearly or completely concealing the epidermis and often hiding the glands, if any ..... 10
- 10(9). Leaf blades 2.5–5.1 cm wide, with a row of 9–20 abaxial glands between midrib and margin; lateral wings of samara normal, i.e., all 4 well developed, subequal, thin ..... *T. rhodopteron*
10. Leaf blades up to 2.4 cm wide, eglandular or with 2(–4) abaxial glands near base; lateral wings of samara reduced to rounded crests or thick or aculeate irregular outgrowths ..... *T. oleifolia*

**Tetrapteryx aristeguietae** W.R. Anderson, Mem. New York Bot. Gard. 32: 255. 1981.

Woody vine(?) or shrub or treelet 1–3.5 m tall; petioles 2–4 mm long; blade of larger leaves 2.3–6 × 1.3–3 cm, abaxially persistently appressed-tomentose to glabrescent, eglandular or with minute glands on margin; inflorescence a short axillary pseudoraceme; bracteoles larger than bracts, eglandular; sepals all biglandular; petals yellow, abaxially very sparsely sericeous, denticulate; filaments sericeous; samaras with lateral wings 2.5–10 mm long, irregular and unequal, with several long narrow projections between lateral wings and dorsal crest. Sandy savannas, semideciduous forests, rocky outcrops, 50–100 m; Bolívar near Río Orinoco (Cerro Carichana, Cerro El Jobito, Ciudad Bolívar, San Félix). Anzoátegui, Apure.

**Tetrapteryx crispa** A. Juss., Ann. Sci. Nat. Bot. sér. 2, 13: 265. 1840.

Woody vine; stipules connate in interpetiolar pairs, leaving a scar 2.5–5.5 mm wide; petioles (12–)14–20(–27) mm long; blade of larger leaves (11–)13–20 × (5–)6–10.5 cm, glabrate at maturity, with a row of

tiny abaxial glands between midrib and margin; flowers borne ultimately in umbels of 4; 4 lateral sepals biglandular, anterior eglandular; petals yellow, glabrous, entire or sinuate; stigmas internal, decurrent; upper lateral wings of samara 22–35 mm long, lower pair 11–15(–20) mm long, aculeate outgrowths usually not present between dorsal and lateral wings. Evergreen lowland to lower montane forests, usually near rivers, 100–700 m; Delta Amacuro (east-northeast of El Palmar, town of Sierra Imataca east-southeast of Los Castillos, Río Cuyubini), northeastern Bolívar (near San Felipe), southern Amazonas (Río Ocamo). Apure, Carabobo, Cojedes, Falcón, Lara, Miranda, Portuguesa, Yaracuy, Zulia; Panama, Colombia, Guyana, Suriname, French Guiana, Amazonian Ecuador, Peru, Brazil, and Bolivia.

**Tetrapteryx discolor** (G. Mey.) DC., Prodr. 1: 587. 1824. —*Triopteryx discolor* G. Mey., Prim. Fl. Esseq. 182. 1818.

Woody vine; stipules connate in interpetiolar pairs, leaving a scar 1–2.5 mm wide; petioles 7–12 mm long; blade of larger leaves (7.5–)9–14.5 × (3–)4–6.5 cm, soon glabrate,

with a row of tiny abaxial glands between midrib and margin; flowers borne ultimately in umbels of 4; 4 lateral sepals biglandular, anterior eglandular; petals yellow, glabrous, entire; stigma internal, decurrent; upper lateral wings of samara 12–22(–25) mm long, lower pair 4–10 mm long, several narrow winglets or rounded or aculeate outgrowths present between dorsal and lateral wings. Along rivers, in forests, at shrubby roadsides, 50–700 m; Delta Amacuro (east-northeast of El Palmar, southeast of Piacoa, Río Amacuro, upstream from San Victor), Bolívar (common north of 6°N, Río Karún). Anzoátegui, Apure, Falcón, Lara, Monagas, Sucre, Táchira; Mexico, Central America, West Indies, Colombia, Guyana, Suriname, French Guiana, Amazonian Ecuador, Peru, Brazil, and Bolivia.

**Tetrapteryx fimbripetala** A. Juss., Ann. Sci. Nat. Bot. sér. 2, 13: 263. 1840.

**Tetrapteryx huachamacariensis** W.R. Anderson, Mem. New York Bot. Gard. 32: 261. 1981.

Woody vine, sometimes a shrub 1–2.5 m tall; stems ± persistently sericeous; petioles (1–)2–11 mm long; blade of larger leaves 4–11(–15) × (1.5–)2.3–5(–6) cm, abaxially thinly sericeous to glabrate, with a row of 6–20 abaxial glands on each side between midrib and margin; inflorescence an axillary pseudoraceme of 4–16 flowers; bracteoles larger than bracts; sepals all biglandular; petals yellow, sometimes tinged with red, glabrous, fimbriate; filaments glabrous; samaras with lateral wings 12–20(–23) mm long, lacking outgrowths between dorsal and lateral wings. Along streams, edge of moist forests, occasionally in savannas, 50–2000 m; widespread in southern Bolívar and Amazonas. Guyana, Suriname, French Guiana, Brazil (Amazonas: Serra Aracá, Roraima), Peru (Huánuco). ♦Fig. 112.

**Tetrapteryx huachamacariensis** was based on shrubby plants from Cerro Duida and Cerro Huachamacari with leaves that are smaller than usual for the species. The additional collections of this complex that have accumulated over the last 20 years reveal that it is not rare for *T. fimbripetala* to be shrubby in various parts of its range, especially at higher elevations, and plants with small leaves also occur at scattered locali-

ties, in both shrubby and climbing plants. It therefore seems best to treat all of that variation as a single variable species.

**Tetrapteryx gracilis** W.R. Anderson, Mem. New York Bot. Gard. 32: 257. 1981.

Wiry-stemmed shrub 0.2–0.8(–1.5) m tall; petioles 3–6(–9) mm long; blade of larger leaves 3.5–6.5(–10) × 0.7–2.8 cm, soon glabrate, eglandular except for small impressed marginal glands; inflorescence an axillary pseudoraceme of 4–12(–26) flowers; bracteoles larger than bracts, often bearing abaxial glands; sepals all biglandular; petals yellow, glabrous or bearing a few abaxial hairs, entire or denticulate; filaments sericeous to subglabrous; samaras with lateral wings 1–3(–5) mm long, variable in number, irregular and often unequal. Sandy savannas, 100–200 m; Bolívar? (see discussion below), Amazonas (Río Cuao to Río Pasimoni). Colombia (Vaupés).

**Tetrapteryx gracilis** was described to accommodate plants that are obviously closely related to *T. styloptera* but differ from it in their habitat, habit, size of various parts, and reduced, irregular samaras. Most plants have very narrow leaves and low stature and look quite different from the riparian vines of *T. styloptera*, but occasional plants have higher stature and wider leaves and then resemble *T. styloptera* more strongly. One very anomalous plant is *Stergios et al.* 6266 (MICH, MO, PORT), which was found in rain forest on the Río Cuyuní in northeastern Bolívar, far from all populations of *T. gracilis* and in the wrong habitat. It was a shrub with leaves that are large for *T. gracilis* and toward the small end of the range for *T. styloptera*. Its fruits bear much-dissected, rudimentary, rounded outgrowths instead of wings, and therefore fit *T. gracilis* well. Assuming that *T. gracilis* deserves recognition, it may be that we should consider *Stergios et al.* 6266 to be that species, but it may also be that it represents a population of *T. styloptera* in which the fruits have become reduced independently of and in parallel to the same tendency in *T. gracilis*.

**Tetrapteryx maranhamensis** A. Juss., Arch. Mus. Hist. Nat. 3: 537. 1843.

**Hiraea gracilis** Benth., London J. Bot. 7: 135. 1848.

Woody vine or shrub 1–2 m tall; stems soon glabrate; blade of larger leaves 4–8.5 × 1.5–3.8 cm, abaxially loosely sericeous to glabrate, with 1–5 glands in a row between midrib and margin; inflorescence an axillary or terminal pseudoraceme of 8–30 flowers; bracteoles wider than bracts but often not as long, one of each pair bearing 1 large eccentric abaxial gland; 4 lateral sepals biglandular, anterior eglandular; petals yellow, abaxially ± abundantly appressed-tomentose or subsericeous, erose; filaments glabrous; samaras with lateral wings 9–14 mm long, bearing irregular outgrowths between dorsal and lateral wings. Evergreen lowland and lower montane forests and thickets, 50–300 m; Bolívar (south of Altiplanicie de Nuria and southeast of Campamento CVG-Las Flores, El Dorado). Guyana, Amazonian Brazil and Bolivia.

**Tetrapteryx mucronata** Cav., Diss. 9: 434, pl. 262. 1790.

**Tetrapteryx crebriflora** A. Juss. in A. St.-Hil., Fl. Bras. Merid. 3: 9. 1832 [1833].

—**Tetrapteryx mucronata** subsp. **crebriflora** (A. Juss.) Kosterm. in Pulle, Fl. Surinam. 2: 182. 1936. —**Tetrapteryx mucronata** var. **crebriflora** (A. Juss.) J.F. Macbr., Publ. Field Mus. Nat. Hist., Bot. Ser., 13: 807. 1950.

**Tetrapteryx glaberrima** Benth., London J. Bot. 7: 134. 1848.

**Tetrapteryx silvatica** Cuatrec., Webbia 13: 425. 1958.

Woody vine, rarely described as a shrub or small tree; stipules minute, distinct; petioles 5–15(–20) mm long; blade of larger leaves (4–)6–15(–17) × (2–)3–8(–10.5) cm, abaxially glabrous or very thinly sericeous to glabrate, with 2 glands at base and usually a distal row between midrib and margin; flowers borne ultimately in umbels of 4–6; bracteoles narrowly triangular, smaller than bracts; sepals all eglandular or the lateral 4 biglandular, the glands becoming stalked in age; petals yellow, often with reddish flecks, glabrous, entire or denticulate; stigmas internal or nearly terminal; lateral wings of samara 5–22 mm long, the upper pair ca. twice as long as the lower, aculeate outgrowths usually present between dorsal and lateral wings. Evergreen lowland forests, along streams, in roadside shrubs, 50–400

m; common in Bolívar and Amazonas. Apure; Costa Rica, Colombia, Guyana, Suriname, French Guiana, Ecuador, Peru, Brazil (from Minas Gerais north), Bolivia.

**Tetrapteryx mucronata** is an exceedingly variable species, especially in the size and shape of its leaves, but it hangs together as a monophyletic taxon. Whether that should be considered one variable species or a complex of closely related taxa I shall leave to a future monographer to decide.

**Tetrapteryx oleifolia** (Benth.) Griseb. in Mart., Fl. Bras. 12(1): 86. 1858. —**Hiraea oleifolia** Benth., London J. Bot. 7: 136. 1848. —**Heteropteryx oleifolia** (Benth.) Griseb., Linnaea 22: 19. 1849.

Shrub 0.5–1 m tall; stems densely and persistently golden-sericeous; petioles 4–13 mm long; blade of larger leaves 5.5–10 × 0.9–2.4 cm, abaxially densely and persistently sericeous to belatedly glabrescent, eglandular or with 1(2) pairs of impressed glands (often hidden under hairs) near base; inflorescence an axillary pseudoraceme of 2–6 flowers; bracteoles larger than bracts; sepals all biglandular; petals yellow, sometimes tinged with red, glabrous, fimbriate; filaments glabrous; mericarp bearing a dorsal crest up to 2 mm wide and several short, rounded or aculeate lateral outgrowths. Upland areas along streams or in sandy savannas, 1000–1400 m; Bolívar (Cerro La Danta northwest of Cerro Venamo, Gran Sabana, Río Aponguao, southwest of Roraima-tepui). Western Guyana. ♦Fig. 113.

As I noted in 1981, the fruit of **Tetrapteryx oleifolia**, which apparently has only rudimentary wings, is known only from *Steyermark et al.* 105495 (NY), in which the fruits are immature. No other fruiting collections have come to my attention in the last 19 years.

**Tetrapteryx pusilla** Steyermark., Fieldiana, Bot. 28: 294. 1952.

Virgate subshrubs or shrubs 0.2–2(–3) m tall; vegetative parts glabrous or soon glabrate except for golden-sericeous axillary buds; petioles 1.5–3(–5) mm long; blade of larger leaves 2.5–6(–7) × 1.3–3(–3.5) cm, with several abaxial glands between midrib and thickened margin; inflorescence an axillary pseudoraceme; bracteoles larger than

with a row of tiny abaxial glands between midrib and margin; flowers borne ultimately in umbels of 4; 4 lateral sepals biglandular, anterior eglandular; petals yellow, glabrous, entire; stigma internal, decurrent; upper lateral wings of samara 12–22(–25) mm long, lower pair 4–10 mm long, several narrow winglets or rounded or aculeate outgrowths present between dorsal and lateral wings. Along rivers, in forests, at shrubby roadsides, 50–700 m; Delta Amacuro (east-northeast of El Palmar, southeast of Piacoa, Río Amacuro, upstream from San Victor), Bolívar (common north of 6°N, Río Karún). Anzoátegui, Apure, Falcón, Lara, Monagas, Sucre, Táchira; Mexico, Central America, West Indies, Colombia, Guyana, Suriname, French Guiana, Amazonian Ecuador, Peru, Brazil, and Bolivia.

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*Tetrapteryx huachamacariensis* W.R. Anderson, Mem. New York Bot. Gard. 32: 261. 1981.

Woody vine, sometimes a shrub 1–2.5 m tall; stems ± persistently sericeous; petioles (1–)2–11 mm long; blade of larger leaves 4–11(–15) × (1.5–)2.3–5(–6) cm, abaxially thinly sericeous to glabrate, with a row of 6–20 abaxial glands on each side between midrib and margin; inflorescence an axillary pseudoraceme of 4–16 flowers; bracteoles larger than bracts; sepals all biglandular; petals yellow, sometimes tinged with red, glabrous, fimbriate; filaments glabrous; samaras with lateral wings 12–20(–23) mm long, lacking outgrowths between dorsal and lateral wings. Along streams, edge of moist forests, occasionally in savannas, 50–2000 m; widespread in southern Bolívar and Amazonas. Guyana, Suriname, French Guiana, Brazil (Amazonas: Serra Aracá, Roraima), Peru (Huánuco). ♦Fig. 112.

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Wiry-stemmed shrub 0.2–0.8(–1.5) m tall; petioles 3–6(–9) mm long; blade of larger leaves 3.5–6.5(–10) × 0.7–2.8 cm, soon glabrate, eglandular except for small impressed marginal glands; inflorescence an axillary pseudoraceme of 4–12(–26) flowers; bracteoles larger than bracts, often bearing abaxial glands; sepals all biglandular; petals yellow, glabrous or bearing a few abaxial hairs, entire or denticulate; filaments sericeous to subglabrous; samaras with lateral wings 1–3(–5) mm long, variable in number, irregular and often unequal. Sandy savannas, 100–200 m; Bolívar? (see discussion below), Amazonas (Río Cuao to Río Pasimoni). Colombia (Vaupés).

*Tetrapteryx gracilis* was described to accommodate plants that are obviously closely related to *T. styloptera* but differ from it in their habitat, habit, size of various parts, and reduced, irregular samaras. Most plants have very narrow leaves and low stature and look quite different from the riparian vines of *T. styloptera*, but occasional plants have higher stature and wider leaves and then resemble *T. styloptera* more strongly. One very anomalous plant is *Stergios et al.* 6266 (MICH, MO, PORT), which was found in rain forest on the Río Cuyuní in northeastern Bolívar, far from all populations of *T. gracilis* and in the wrong habitat. It was a shrub with leaves that are large for *T. gracilis* and toward the small end of the range for *T. styloptera*. Its fruits bear much-dissected, rudimentary, rounded outgrowths instead of wings, and therefore fit *T. gracilis* well. Assuming that *T. gracilis* deserves recognition, it may be that we should consider *Stergios et al.* 6266 to be that species, but it may also be that it represents a population of *T. styloptera* in which the fruits have become reduced independently of and in parallel to the same tendency in *T. gracilis*.

**Tetrapteryx maranhamensis** A. Juss., Arch. Mus. Hist. Nat. 3: 537. 1843.

*Hiraea gracilis* Benth., London J. Bot. 7: 135. 1848.

Woody vine or shrub 1–2 m tall; stems soon glabrate; blade of larger leaves 4–8.5 × 1.5–3.8 cm, abaxially loosely sericeous to glabrate, with 1–5 glands in a row between midrib and margin; inflorescence an axillary or terminal pseudoraceme of 8–30 flowers; bracteoles wider than bracts but often not as long, one of each pair bearing 1 large eccentric abaxial gland; 4 lateral sepals biglandular, anterior eglandular; petals yellow, abaxially ± abundantly appressed-tomentose or subsericeous, erose; filaments glabrous; samaras with lateral wings 9–14 mm long, bearing irregular outgrowths between dorsal and lateral wings. Evergreen lowland and lower montane forests and thickets, 50–300 m; Bolívar (south of Altiplanicie de Nuria and southeast of Campamento CVG-Las Flores, El Dorado). Guyana, Amazonian Brazil and Bolivia.

**Tetrapteryx mucronata** Cav., Diss. 9: 434, pl. 262. 1790.

*Tetrapteryx crebriflora* A. Juss. in A. St.-Hil., Fl. Bras. Merid. 3: 9. 1832 [1833].

—*Tetrapteryx mucronata* subsp. *crebriflora* (A. Juss.) Kosterm. in Pulle, Fl. Surinam. 2: 182. 1936. —*Tetrapteryx mucronata* var. *crebriflora* (A. Juss.) J.F. Macbr., Publ. Field Mus. Nat. Hist., Bot. Ser., 13: 807. 1950.

*Tetrapteryx glaberrima* Benth., London J. Bot. 7: 134. 1848.

*Tetrapteryx silvatica* Cuatrec., Webbia 13: 425. 1958.

Woody vine, rarely described as a shrub or small tree; stipules minute, distinct; petioles 5–15(–20) mm long; blade of larger leaves (4–)6–15(–17) × (2–)3–8(–10.5) cm, abaxially glabrous or very thinly sericeous to glabrate, with 2 glands at base and usually a distal row between midrib and margin; flowers borne ultimately in umbels of 4–6; bracteoles narrowly triangular, smaller than bracts; sepals all eglandular or the lateral 4 biglandular, the glands becoming stalked in age; petals yellow, often with reddish flecks, glabrous, entire or denticulate; stigmas internal or nearly terminal; lateral wings of samara 5–22 mm long, the upper pair ca. twice as long as the lower, aculeate outgrowths usually present between dorsal and lateral wings. Evergreen lowland forests, along streams, in roadside shrubs, 50–400

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*Tetrapteryx mucronata* is an exceedingly variable species, especially in the size and shape of its leaves, but it hangs together as a monophyletic taxon. Whether that should be considered one variable species or a complex of closely related taxa I shall leave to a future monographer to decide.

**Tetrapteryx oleifolia** (Benth.) Griseb. in Mart., Fl. Bras. 12(1): 86. 1858. —*Hiraea oleifolia* Benth., London J. Bot. 7: 136. 1848. —*Heteropteryx oleifolia* (Benth.) Griseb., Linnaea 22: 19. 1849.

Shrub 0.5–1 m tall; stems densely and persistently golden-sericeous; petioles 4–13 mm long; blade of larger leaves 5.5–10 × 0.9–2.4 cm, abaxially densely and persistently sericeous to belatedly glabrescent, eglandular or with 1(2) pairs of impressed glands (often hidden under hairs) near base; inflorescence an axillary pseudoraceme of 2–6 flowers; bracteoles larger than bracts; sepals all biglandular; petals yellow, sometimes tinged with red, glabrous, fimbriate; filaments glabrous; mericarp bearing a dorsal crest up to 2 mm wide and several short, rounded or aculeate lateral outgrowths. Upland areas along streams or in sandy savannas, 1000–1400 m; Bolívar (Cerro La Danta northwest of Cerro Venamo, Gran Sabana, Río Apongauo, southwest of Roraima-tepui). Western Guyana. ♦Fig. 113.

As I noted in 1981, the fruit of *Tetrapteryx oleifolia*, which apparently has only rudimentary wings, is known only from *Steyermark et al.* 105495 (NY), in which the fruits are immature. No other fruiting collections have come to my attention in the last 19 years.

**Tetrapteryx pusilla** Steyermark., Fieldiana, Bot. 28: 294. 1952.

Virgate subshrubs or shrubs 0.2–2(–3) m tall; vegetative parts glabrous or soon glabrate except for golden-sericeous axillary buds; petioles 1.5–3(–5) mm long; blade of larger leaves 2.5–6(–7) × 1.3–3(–3.5) cm, with several abaxial glands between midrib and thickened margin; inflorescence an axillary pseudoraceme; bracteoles larger than



bracts, bearing small abaxial glands; sepals all biglandular; petals yellow, glabrous, fimbriate; filaments glabrous; styles with stigma internal to apparently terminal; samaras with lateral wings 5–7 mm long, subequal, lacking outgrowths between lateral wings and dorsal crest. Sandy upland savannas and tepui meadows, rocky slopes, 500–1400(–2600) m; Bolívar (common in the Gran Sabana, Ilú-tepui). Western Guyana. ♦Fig. 111.

***Tetrapteryx rhodopteron*** Oliv., Timehri 5: 190. 1886.

*Tetrapteryx phylladenophora* Maguire & Steyerl., Mem. New York Bot. Gard. 9: 481. 1957.

Woody vine, sometimes a shrub 0.5–2.5 m tall; stems persistently sericeous; petioles 6–12 mm long; blade of larger leaves 6–10.5 × 2.5–5.1 cm, abaxially densely and persistently sericeous, with a row of 9–20 glands on each side between midrib and margin; inflorescence an axillary pseudoraceme of 4–16 flowers; bracteoles larger than bracts; sepals all biglandular; petals yellow, sometimes tinged with red, glabrous, fimbriate; filaments glabrous; samaras with lateral wings 8–17 mm long, lacking outgrowths between dorsal and lateral wings or rarely with 1 aculeate outgrowth. Near streams, apparently often in open rocky or sandy places but also reported from gallery forests, 400–1700 m; Bolívar (common in the Gran Sabana from Auyán-tepui east and south). Western Guyana.

*Tetrapteryx rhodopteron* is essentially identical to *T. fimbripetala* except for the fact that the leaf blades are densely and persistently sericeous abaxially in *T. rhodopteron*, thinly sericeous to glabrate in *T. fimbripetala*. Distinguishing between the two taxa is generally easy, but it may be that *T. rhodopteron* simply represents the extreme of a cline of variation and does not merit recognition. In two Bolívar collections that I am calling *T. rhodopteron*, Holst & Liesner 2419 (MICH, MO) from Río Samay and Liesner & Holst 18822 (MICH, MO) from near El Paují, the hairs are of intermediate density and the distinction is somewhat arbitrary.

***Tetrapteryx styloptera*** A. Juss., Ann. Sci. Nat. Bot. sér. 2, 13: 262. 1840.

*Bunchosia squarrosa* Griseb., Linnaea 22: 11. 1849. —*Tetrapteryx squarrosa* (Griseb.) Griseb. in Mart., Fl. Bras. 12(1): 87. 1858.

*Tetrapteryx boliviensis* Nied., Verz. Vorles. Königl. Lyceum Hosianum Braunsberg 1909/10: 17. 1909.

Woody vine, rarely described as shrub or tree 2–3 m tall; petioles (3–)4–9(–11) mm long; blade of larger leaves (4.5–)7–15 × (2.5–)3.5–7 cm, abaxially thinly sericeous to glabrate, eglandular except for small impressed marginal glands; inflorescence an axillary or terminal pseudoraceme of 8–24 or more flowers; bracteoles larger than bracts, often bearing 1 or 2 abaxial glands; sepals all biglandular; petals yellow, glabrous or abaxially very sparsely sericeous, denticulate; filaments usually sericeous; samaras with 4 subequal lateral wings (7–)8–15 mm long, bearing several slender outgrowths between dorsal and lateral wings. Along rivers, often at edge of gallery forests, occasionally in open savannas, near sea level to 1200 m; common throughout much of Bolívar and Amazonas. Carabobo, Distrito Federal, Falcón, Lara, Mérida, Miranda, Táchira, Trujillo, Yaracuy, Zulia; Nicaragua, Panama, Colombia, Guyana, Suriname, French Guiana, Amazonian Peru, Brazil, and Bolivia. ♦Fig. 114.

See discussion of Stergios *et al.* 6266 under *Tetrapteryx gracilis*.



Fig. 111. *Tetrapteryx pusilla*

Fig. 112. *Tetrapteryx fimbripetala*



Fig. 113. *Tetrapteryx oleifolia*



Fig. 114. *Tetrapteryx styloptera*