

GENERIC ADJUSTMENTS IN NEOTROPICAL MALPIGHIACEAE

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ABSTRACT. The genera *Bronwenia* W. R. Anderson & C. Davis and *Calcicola* W. R. Anderson & C. Davis are proposed to accommodate species segregated from *Banisteriopsis* and *Mascagnia*, respectively, and *Cottisia* Dubard & Dop is resurrected for the North American species formerly assigned to *Janusia*. All three genera are described, their morphology and relationships are discussed, and keys to the species are provided, with nomenclature for each species. For *Calcicola* and *Cottisia* distribution maps and descriptions of species are provided. The genus *Clonodia* is placed in synonymy under *Heteropterys*, with discussion of relationships, a key to clonodioid species, and nomenclature and a diagnostic description for each species. One new species is described [*Bronwenia peckoltii* W. R. Anderson & C. Davis] and 19 new combinations are proposed [*Bronwenia acapulcensis* (Rose) W. R. Anderson & C. Davis, *B. acapulcensis* var. *llanensis* (B. Gates) W. R. Anderson & C. Davis, *B. brevipedicellata* (B. Gates) W. R. Anderson & C. Davis, *B. cinerascens* (Benth.) W. R. Anderson & C. Davis, *B. cornifolia* (H. B. K.) W. R. Anderson & C. Davis, *B. cornifolia* var. *maracaybensis* (Adr. Juss.) W. R. Anderson & C. Davis, *B. cornifolia* var. *standleyi* (B. Gates) W. R. Anderson & C. Davis, *B. ferruginea* (Cav.) W. R. Anderson & C. Davis, *B. longipilifera* (B. Gates) W. R. Anderson & C. Davis, *B. mathiasiae* (W. R. Anderson) W. R. Anderson & C. Davis, *B. megaptera* (B. Gates) W. R. Anderson & C. Davis, *B. wurdackii* (B. Gates) W. R. Anderson & C. Davis, *Calcicola parvifolia* (Adr. Juss.) W. R. Anderson & C. Davis, *C. sericea* (Nied.) W. R. Anderson & C. Davis, *Cottisia californica* (Benth.) W. R. Anderson & C. Davis, *C. gracilis* (A. Gray) W. R. Anderson & C. Davis, *C. linearis* (Wiggins) W. R. Anderson & C. Davis, *Heteropterys complicata* (H. B. K.) W. R. Anderson & C. Davis, and *H. ovata* (Nied.) W. R. Anderson & C. Davis]. Ten species are illustrated.

INTRODUCTION

Phylogenetic studies of Malpighiaceae published in recent years (Cameron et al. 2001; Davis et al. 2001, 2002), and our recently acquired unpublished data, have revealed a number of genera that need to be divided or combined with other genera to produce a more nearly monophyletic classification. The purpose of this paper is to deal with four of those problems.

Although we give many synonyms below, we are omitting some of the less important infraspecific names; complete synonymy can be obtained by consulting the nomenclatural database on the Malpighiaceae website at <http://herbarium.lsa.umich.edu/malpigh>.

BANISTERIOPSIS AND BRONWENIA

In her monograph of *Banisteriopsis* C. B. Rob. and *Diplopterys* Adr. Juss., Gates (1982) recognized three subgenera in *Banisteriopsis* and considered *Diplopterys* a separate genus resembling *Banisteriopsis* subg. *Pleiopterys* (Nied.) B. Gates. Anderson

and Davis (2006) reported that *Banisteriopsis* sensu Gates is not monophyletic, and that *Diplopterys* is nested within *Banisteriopsis* subg. *Pleiopterys*. We resolved that problem by transferring all the species of *Banisteriopsis* subg. *Pleiopterys* to *Diplopterys*. The remaining two subgenera of Gates, however, require further taxonomic elucidation.

Some clarification of the subgeneric nomenclature is in order. Gates assumed that the earliest designation of a lectotype for *Banisteriopsis* was that of Cuatrecasas (1958, p. 486), who treated *B. cornifolia* (H. B. K.) C. B. Rob. as the "type" [lectotype]. On that basis Gates used the name subg. *Banisteriopsis* for the group of eight species containing *B. cornifolia*. The other two, much larger, subgenera she called subg. *Hemiramma* (Griseb.) B. Gates and subg. *Pleiopterys*. We now know, however, that there was an earlier designation of a lectotype for *Banisteriopsis* by Morton (1931), *B. argentea* (H. B. K.) C. B. Rob. [*B. muricata* (Cav.) Cuatrec.]. *Banisteriopsis muricata* belongs to the very large subgenus *Hemiramma*, so that has to become subg. *Banisteriopsis* and the generic name *Banisteriopsis* will remain (fortunately) with that largest group of species. The other, small subgenus that Gates called subg. *Banisteriopsis* is the subject of these notes. Our preliminary phylogenetic results (C. Davis & W. R. Anderson, unpubl.) indicate that the species assigned by Gates to her subg. *Banisteriopsis* do not form a clade with the greatly expanded subg. *Banisteriopsis*, and thus should not be retained in *Banisteriopsis* sens. str. (see Fig. 1, where the species in question are in boldface under the new name *Bronwenia*). We here segregate the eight species treated by Gates as *Banisteriopsis* subg. *Banisteriopsis* as a new genus, and include two additional ones not mentioned in her monograph.

Bronwenia W. R. Anderson & C. Davis, gen. nov.—TYPE: *Bronwenia ferruginea* (Cav.) W. R. Anderson & C. Davis.

Banisteria sect. *Monocentia* Nied., Ind. Lect. Lyc. Reg. Hos. Brunsberg, p. hiem. 1900–1901: 4. 1900.—LECTOTYPE, designated by Gates, 1982, p. 41: *Banisteria maracaybensis* Adr. Juss. [*Bronwenia cornifolia* var. *maracaybensis* (Adr. Juss.) W. R. Anderson & C. Davis].

Lianae lignosae vel frutices; petiolus eglandulosus vel prope apicem biglandulosus; lamina eglandulosa vel margine glandulis instructa; stipulae interpetiolares, distinctae; inflorescentia paniculata vel dichasialis, floribus in pseudoracemis 6–45-floris portatis; pedicelli sessiles vel brevipedunculati; glandulae calycinae pro parte maxima infra sepala affixae; petala lutea, plerumque glabra; antherarum connectivum loculos non superans; stigmata terminalia; samarae nux in lateribus laevis vel 1 crista vel alula instructa, ala dorsali elongata, adaxialiter incrassata; carpophorum nullum vel usque ad 1.5 mm longum, 1–2 mm latum.

Woody vines or shrubs, when shrubby the branches often twining. Leaves decussate; lamina with glands none or usually marginal (but see *B. peckoltii*), sessile, the distal glands (if present) minute, the 2 most proximal glands usually enlarged; petiole eglandular or biglandular at or somewhat below apex; stipules usually present, interpetiolar, distinct, triangular, minute (0.2 mm long) or small (up to 1.5 mm long). Inflorescence axillary or terminal, paniculate or dichasial, the flowers borne in short, usually dense pseudoracemes of 6–45; bracts and bracteoles eglandular, persistent; pedicels sessile or short-pedunculate. Flowers bilaterally symmetrical in calyx and corolla, and sometimes in androecium. Sepals leaving petals exposed during enlargement of bud, the lateral 4 bearing large paired abaxial glands and the anterior eglandular, the glands attached for most of their length below free part of sepal. Petals

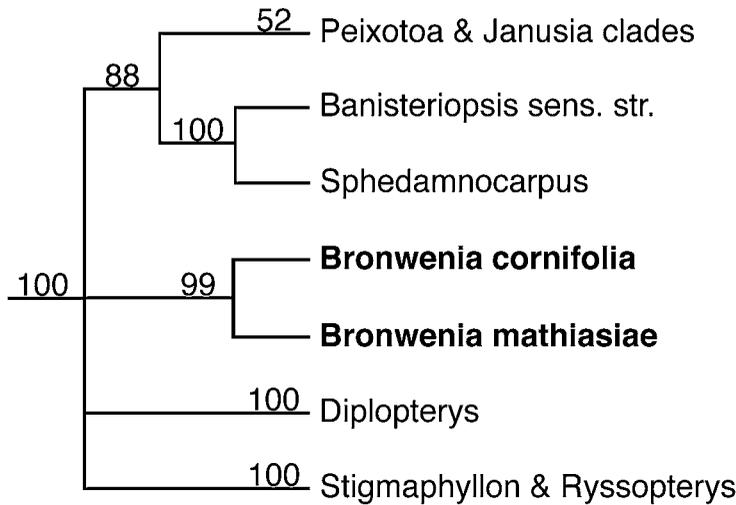


FIG. 1. Phylogenetic tree showing position of *Bronwenia* in the *Stigmaphyllon* clade of Malpighiaceae. Bootstrap values are given above branches. The reduced strict consensus tree shown here is extracted from a larger phylogenetic analysis of Malpighiaceae using combined DNA sequences from plastid *matK*, *ndhF*, and *rbcL*, nuclear *PHYC*, and morphology; all genes were sequenced for all taxa (C. Davis & W. R. Anderson, unpubl.). Vouchers for species of *Bronwenia* sequenced: *Bronwenia cornifolia*: Clark 1, MICH; *Bronwenia mathiasiae*: Nelson et al. 518, MICH.

yellow, glabrous (very rarely sericeous on abaxial midrib), the posterior petal different in size, shape, and stance from the lateral 4, and its margin often more deeply divided with the divisions (especially proximally) \pm glandular-thickened. Receptacle glabrous on both sides of filaments. Stamens 10, all fertile; anthers glabrous or pilose, the connective not or hardly exceeding locules at apex. Gynoecium 3-carpellate, the carpels 1 anterior and 2 posterior, all fertile; styles 3, distinct, mostly \pm alike; stigmas terminal, truncate or capitate. Fruit dry, breaking apart at maturity into 3 samaras (or fewer by abortion) separating from a low pyramidal torus; dorsal wing of samara well developed, elongated, thickened on the adaxial edge with the veins bending toward the thinner abaxial edge, a shallow triangular or rounded appendage usually present on adaxial edge at base; nut of samara smooth-sided or bearing a single ridge or winglet on each side parallel to areole; locule of nut glabrous within; carpophore absent or present but short (up to 1.5 mm long), broad (1–2 mm wide), and non-functional. Chromosome number: $n = 10$ (in *B. acapulcensis* var. *llanensis* [Gates 1982]).

Bronwenia is notable for its leaf glands usually marginal (if present), flowers borne in short dense pseudoracemes, calyx glands attached below the free part of the sepals, yellow, usually glabrous petals, and samaras with the sides of the nut smooth or bearing a single ridge or winglet parallel to the areole and the carpophore absent or short, broad, and apparently non-functional. Of the ten species recognized here, the eight that were treated in the same subgenus by Gates are morphologically coherent and readily recognized by their small petals. For descriptions of those species and their varieties, see Gates (1982). The two additional species of *Bronwenia* (*B. mathiasiae* and *B. peckoltii*) have much larger petals and other characteristics that set them apart from their congeners. For a description of *B. mathiasiae*, see its protologue (cited below), and for a discussion of its generic position see below. *Bronwenia peckoltii* is described below as new and its assignment to *Bronwenia* is discussed as part of its protologue.

The name *Bronwenia* honors Bronwen Elizabeth Gates (b. 1945), who was W. R. Anderson's first doctoral student and published an excellent monograph of *Banisteriopsis* and *Diplopterys*, a major contribution to the taxonomy of the Malpighiaceae.

The key that follows is modified from those in Gates (1982), with many of the data taken from her descriptions.

KEY TO THE SPECIES OF BRONWENIA

1. Lamina at least initially tomentose or appressed-tomentose below with the hairs loose or twisted, sometimes glabrescent at maturity.
 2. Styles 2–2.4 mm long, diverging from the base and \pm inflexed at apex; Bolivia, Amazonian Brazil (Roraima), and Guyana. *B. cinerascens*
 2. Styles 1.4–1.8 mm long, straight and parallel or diverging at apex; Mexico, Central America, Colombia, and Venezuela. *B. acapulcensis*
1. Lamina at least initially densely to thinly sericeous below with the hairs straight and strongly appressed, sometimes glabrescent at maturity.
 3. Lamina densely and persistently silver-sericeous below; Rio de Janeiro, Brazil. *B. peckoltii*
 3. Lamina sparsely sericeous to glabrate below at maturity; Mexico, Central America, and South America.
 4. Limb of lateral petals 7.5–11 mm long, 6–11 wide; glands on petiole 1.5–2.8 mm long; nut of samara without lateral winglets, smooth on the sides or at most with a low ridge up to 0.5 mm wide; Amazonian Peru, Bolivia, and Brazil, and Guyana. *B. mathiasiae*
 4. Limb of lateral petals 2.5–5.5 (–7) mm long, 2–4.5 (–5) mm wide; glands on petiole or base of lamina up to 2 mm long, mostly shorter; nut of samara with or without lateral winglets; Mexico, Central America, and South America.
 5. Styles 2–2.6 mm long, diverging from the base and \pm inflexed at apex; filaments of 3 anterior stamens free almost to base, those of stamens opposite anterior-lateral sepals flexuous and bent toward posterior petal; Panama and northern and western South America, as far east and south as French Guiana, central Brazil (Pará, Tocantins, Mato Grosso), and Bolivia. *B. wurdackii*
 5. Styles 1–2 mm long, straight and parallel or diverging throughout their length or at apex only; stamens subequal, erect, all their filaments somewhat connate at base; Mexico, Central America, and South America.
 6. Ultimate branches of inflorescence bearing 25–45 flowers.
 7. Lamina of larger leaves 13–15.4 cm long, 6–8.6 cm wide; pedicels 2–5 mm long; westernmost Amazonas, Brazil. *B. brevipedicellata*
 7. Lamina of larger leaves 4.5–11 cm long, 3–4.5 cm wide; pedicels 7–10 mm long; eastern Brazil, from Bahia to Paraná. *B. ferruginea*
 6. Ultimate branches of inflorescence bearing up to 24 flowers.
 8. Petiole biglandular at or somewhat below apex, the glands sometimes partly on margin of very base of lamina and partly on adjacent petiole.
 9. Pedicels 5–6 mm long; styles 1–1.2 mm long; samara with lateral winglets 2–6 mm wide, confluent at base below nut, the hairs on dorsal wing 1–1.5 mm long, stiff; Mato Grosso do Sul, Brazil. *B. longipilifera*
 9. Pedicels 7–12 mm long; styles 1.6–1.8 mm long; samara with lateral winglets absent or represented by a ridge up to 1 mm wide, not confluent below nut, the hairs on dorsal wing 0.2–0.7 mm long, soft; eastern Brazil (Piauí and Ceará to Rio de Janeiro). *B. megaptera*
 8. Petiole eglandular, the leaf glands wholly on margin of lamina near base.
 10. Petiole of larger leaves 8–20 mm long; nut of samara 9–11 \times 7–9 mm, the lateral winglets absent or represented by a ridge up to 1 mm wide; eastern Brazil (Piauí and Ceará to Rio de Janeiro). *B. megaptera*
 10. Petiole of larger leaves 6–10 (–15) mm long; nut of samara 5–8 \times 4–6 mm, usually bearing on each side a lateral winglet 1–5 mm wide; Mexico, Central America, northern South America (Colombia and Venezuela), and eastern Brazil (Bahia to Paraná).
 11. Lamina of larger leaves 5–10 (–13.5) cm long, 3.3–4.5 (–5.5) cm wide, mostly obtuse or truncate at base; styles 1.2–1.6 mm long; eastern Brazil (Bahia to Paraná). *B. ferruginea*

11. Lamina of larger leaves 10–14.5 (–17.9) cm long, 4–6.7 (–8.8) cm wide, mostly cuneate at base; styles 1.6–1.8 mm long; Mexico, Central America, and northern South America (Colombia and Venezuela). *B. cornifolia*

Bronwenia acapulcensis (Rose) W. R. Anderson & C. Davis, comb. nov. *Heteropterys acapulcensis* Rose, Contr. U.S. Natl. Herb. 5: 139. 1897. *Banisteria maracaybensis* var. *leiocarpa* Nied., Ind. Lect. Lyc. Reg. Hos. Brunsberg. p. hiem. 1900–1901: 6. 1900. *Banisteriopsis acapulcensis* (Rose) Small, N. Amer. Fl. 25: 132. 1910. *Banisteria cornifolia* var. *leiocarpa* (Nied.) Nied. in Engl., Pflanzenr. IV, 141: 405. 1928. *Banisteriopsis cornifolia* var. *leiocarpa* (Nied.) Cuatrec., Webbia 13: 496. 1958.—TYPE: MEXICO. Guerrero: near Acapulco, *Palmer 219* in 1894 (holotype: US!; isotypes: A! F! GH! MO! NY! UC! US!). [The lectotype of *Banisteria maracaybensis* var. *leiocarpa* is the NY specimen of *Palmer 219* in 1894 that came from Niedenzu's herbarium; it was designated by B. Gates, 1982, p. 44.]

Banisteria guatemalensis Nied., Ind. Lect. Lyc. Reg. Hos. Brunsberg. p. hiem. 1900–1901: 6. 1900. *Banisteriopsis guatemalensis* (Nied.) C. B. Rob. in Small, N. Amer. Fl. 25: 132. 1910.—TYPE: GUATEMALA. Llano Grande, Salamá, *Seler & Seler 2428* (holotype: B†, F neg. 12811, fragment NY!).

Banisteriopsis dugandii Cuatrec., Webbia 13: 496. 1958.—TYPE: COLOMBIA. Bolívar, *Dugand & Jaramillo 3335* (holotype: US!).

Fig. 2.

Gates (1982, pp. 45–48) recognized two varieties of this species, var. *acapulcensis* and var. *llanensis*, and we are doing the same. See her treatment for a key to the varieties.

Bronwenia acapulcensis var. *llanensis* (B. Gates) W. R. Anderson & C. Davis, comb. nov. *Banisteriopsis acapulcensis* var. *llanensis* B. Gates, Fl. Neotrop. Monogr. 30: 46. 1982.—TYPE: VENEZUELA. Guárico: E of Calabozo, *Gentry 10294* (holotype: MICH!; isotypes: MEXU! MO! NY!).

Bronwenia brevipedicellata (B. Gates) W. R. Anderson & C. Davis, comb. nov. *Banisteriopsis brevipedicellata* B. Gates, Fl. Neotrop. Monogr. 30: 50. 1982.—TYPE: BRAZIL. Amazonas: Mun. São Paulo de Olivença, *Krukoff 8758* (holotype: MO!; isotypes: A! G! K! MICH! NY! US!).

Bronwenia cinerascens (Benth.) W. R. Anderson & C. Davis, comb. nov. *Heteropterys cinerascens* Benth., London J. Bot. 7: 131. 1848. *Banisteria cinerascens* (Benth.) Griseb., Linnaea 22: 18. 1849. *Banisteriopsis cinerascens* (Benth.) B. Gates, Brittonia 31: 108. 1979.—TYPE: BRAZIL [“BRITISH GUIANA”]. Roraima: Cotinga/Suruma rivers, *Robert Schomburgk II 488/Richard Schomburgk 773* (holotype: K!; isotypes: BM [488]! F [488]! G [488]! GOET [773]! K [773]! NY [773]! P [488]! W [488]!).

Banisteriopsis sublucida Rusby, Bull. New York Bot. Gard. 8: 96. 1912. *Banisteria sublucida* (Rusby) Nied. in Engl., Pflanzenr. IV, 141: 452. 1928.—TYPE: BOLIVIA. La Paz: Apolo, *Williams 102* (holotype: NY!; isotype: US!).

Banisteria cinerascens var. *platyphylla* Nied. in Engl., Pflanzenr. IV, 141: 1928.—TYPE: BOLIVIA. Santa Cruz: *Steinbach 3260* (holotype: B†; lectotype, designated by Gates (1982, p. 54): NY!; isolectotypes: F! G! GH! MO! S!).

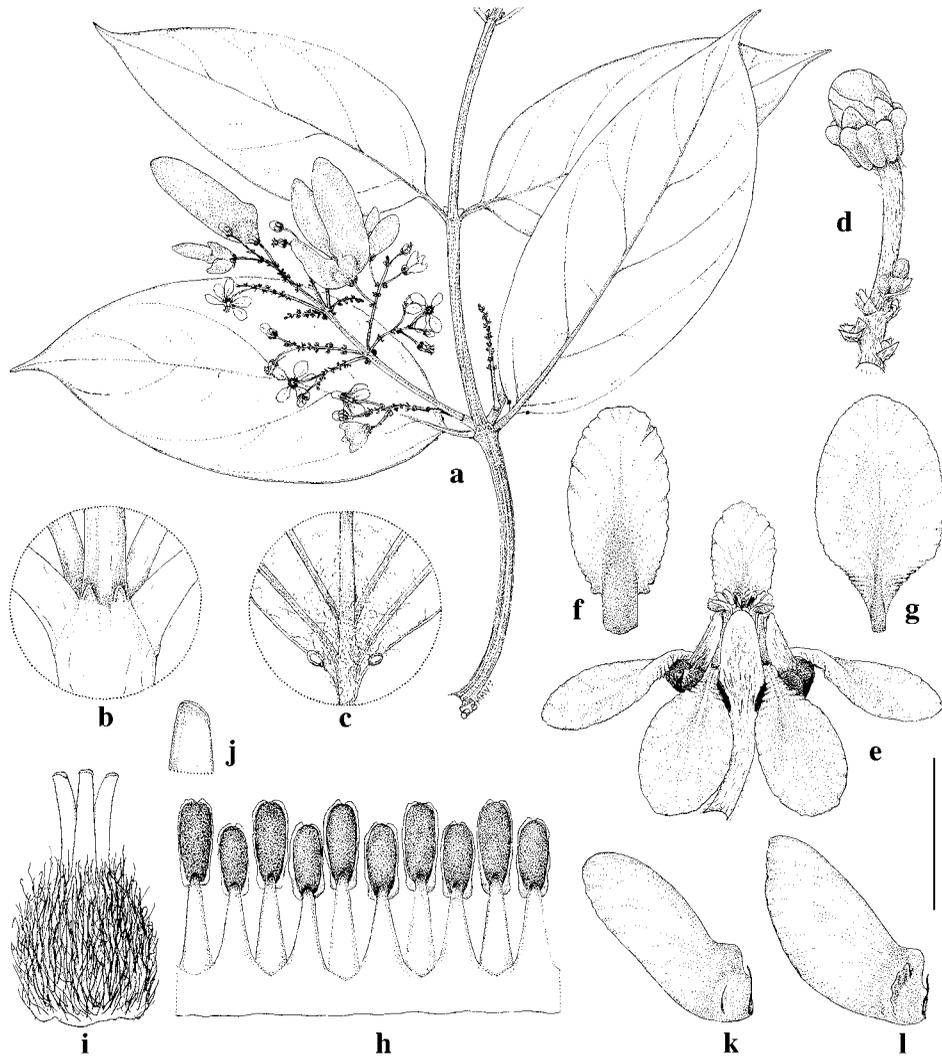


FIG. 2. *Bronwenia acapulcensis* var. *acapulcensis*. a. Branch with flowers and fruits. b. Node with interpetiolar stipules. c. Base of lamina, abaxial view. d. Flower bud and portion of inflorescence axis. e. Flower, posterior petal uppermost. f. Posterior petal, abaxial view. g. Lateral petal, abaxial view. h. Androecium laid out, abaxial view, stamen above letter "h" opposite posterior petal. i. Gynoecium. j. Apex of style. k. Samara with crest on side of nut. l. Samara with winglet on side of nut. Scale bar equivalents: a, 4 cm; b, 4 mm; c, d, 8 mm; e, 5.7 mm; f, g, 4 mm; h, i, 2 mm; j, 1 mm; k, l, 2 cm. (Based on: a, e-k, Burnham 977, MICH; b-d, Burnham 976, MICH; l, Almeda 3983, MICH.)

Bronwenia cornifolia (H. B. K.) W. R. Anderson & C. Davis, comb. nov. *Heteropterys cornifolia* H. B. K., Nov. Gen. Sp. 5 [quarto ed.] 165. 1822 ["1821"]. *Banisteria cornifolia* (H. B. K.) Spreng., Syst. Veg. 2: 388. 1825. *Banisteria maracaybensis* var. *cornifolia* (H. B. K.) Nied., Ind. Lect. Lyc. Reg. Hos. Brunsberg. p. hiem. 1900-1901: 5. 1900, nom. superfl. *Banisteriopsis cornifolia* (H. B. K.) C. B. Rob. in Small, N. Amer. Fl. 25: 132. 1910.—TYPE: COLOMBIA. Tolima: near Ibagué, *Humboldt & Bonpland* (holotype: P-HBK!).

Gates (1982, pp. 42–44) recognized three varieties of this species, var. *cornifolia*, var. *elliptica* [=var. *maracaybensis* here], and var. *standleyi*; we are doing the same. See her treatment for a key to the varieties.

We are following Gates in recognizing both *B. cornifolia* and *B. ferruginea*, but we are somewhat skeptical about the distinctions between those two species; eventually they may have to be combined under the older name, *B. ferruginea*.

Bronwenia cornifolia var. **maracaybensis** (Adr. Juss.) W. R. Anderson & C. Davis, comb. nov. *Banisteria maracaybensis* Adr. Juss., Ann. Sci. Nat. Bot., Sér. 2, 13: 285. 1840. *Banisteria maracaybensis* var. *elliptica* Nied., Ind. Lect. Lyc. Reg. Hos. Brunsberg. p. hiem. 1900–1901: 5. 1900, nom. superfl. *Banisteria cornifolia* var. *elliptica* Nied. in Engl., Pflanzenr. IV, 141: 405. 1928, nom. superfl. *Banisteriopsis cornifolia* var. *elliptica* B. Gates, Fl. Neotrop. Monogr. 30: 42. 1982, nom. superfl. *Banisteriopsis cornifolia* var. *maracaybensis* (Adr. Juss.) W. R. Anderson, Contr. Univ. Michigan Herb. 20: 15. 1995.—TYPE: VENEZUELA [“COLUMBIA”]. Zulia: Maracaibo, *Plée* (holotype: P!; isotypes: BR! F! P! P-JU!).

Bronwenia cornifolia var. **standleyi** (B. Gates) W. R. Anderson & C. Davis, comb. nov. *Banisteriopsis cornifolia* var. *standleyi* B. Gates, Fl. Neotrop. Monogr. 30: 44. 1982.—TYPE: GUATEMALA. Retalhuleu: vicinity of Retalhuleu, *Standley 88835* (holotype: F!; isotype: US!).

Bronwenia ferruginea (Cav.) W. R. Anderson & C. Davis, comb. nov. *Banisteria ferruginea* Cav., Diss. 9: 424, pl. 248. 1790. *Triopterys brasiliensis* Poir. in Lam., Encycl. 8: 105. 1808, nom. superfl. *Banisteriopsis ferruginea* (Cav.) B. Gates, Fl. Neotrop. Monogr. 30: 48. 1982.—TYPE: BRAZIL. Rio de Janeiro, *Commerston* (holotype: P-JU!; isotypes: C! MA! P! P-LAM! R!).

Banisteria unialata Vell., Fl. Flumin. 190; icones 4: pl. 157. 1829.—TYPE: Unknown.

Bronwenia longipilifera (B. Gates) W. R. Anderson & C. Davis, comb. nov. *Banisteriopsis longipilifera* B. Gates, Fl. Neotrop. Monogr. 30: 56. 1982.—TYPE: BRAZIL. Mato Grosso do Sul: E of Aquidauana, *Krapovickas & Schinini 32897* (holotype: MICH!; isotypes: CTES! MBM!).

Bronwenia mathiasiae (W. R. Anderson) W. R. Anderson & C. Davis, comb. nov. *Stigmaphyllon mathiasiae* W. R. Anderson, Bol. Mus. Bot. Munic. (Curitiba) 43: 3. 1981. *Banisteriopsis mathiasiae* (W. R. Anderson) W. R. Anderson, Contr. Univ. Michigan Herb. 20: 15. 1995.—TYPE: PERU. Ucayali: W of Tournavista, *Mathias & Taylor 6078* (holotype: MICH!; isotypes: COL! F! LA! MBM! MO! NY! RB! U! US! USM!).

Banisteria cornifolia var. *seibertii* J. F. Macbr., Field Mus. Publ. Bot. 13(3): 826. 1950.—TYPE: PERU. Madre de Dios: Iberia, *Seibert 2122* (holotype: US!; isotype: MO!).

Fig. 3.

Anderson originally described this species in *Stigmaphyllon* because of its dichasial inflorescence, which makes it look rather different from other species of *Bronwenia*, but in 1995 he transferred it to *Banisteriopsis* because by then he had become

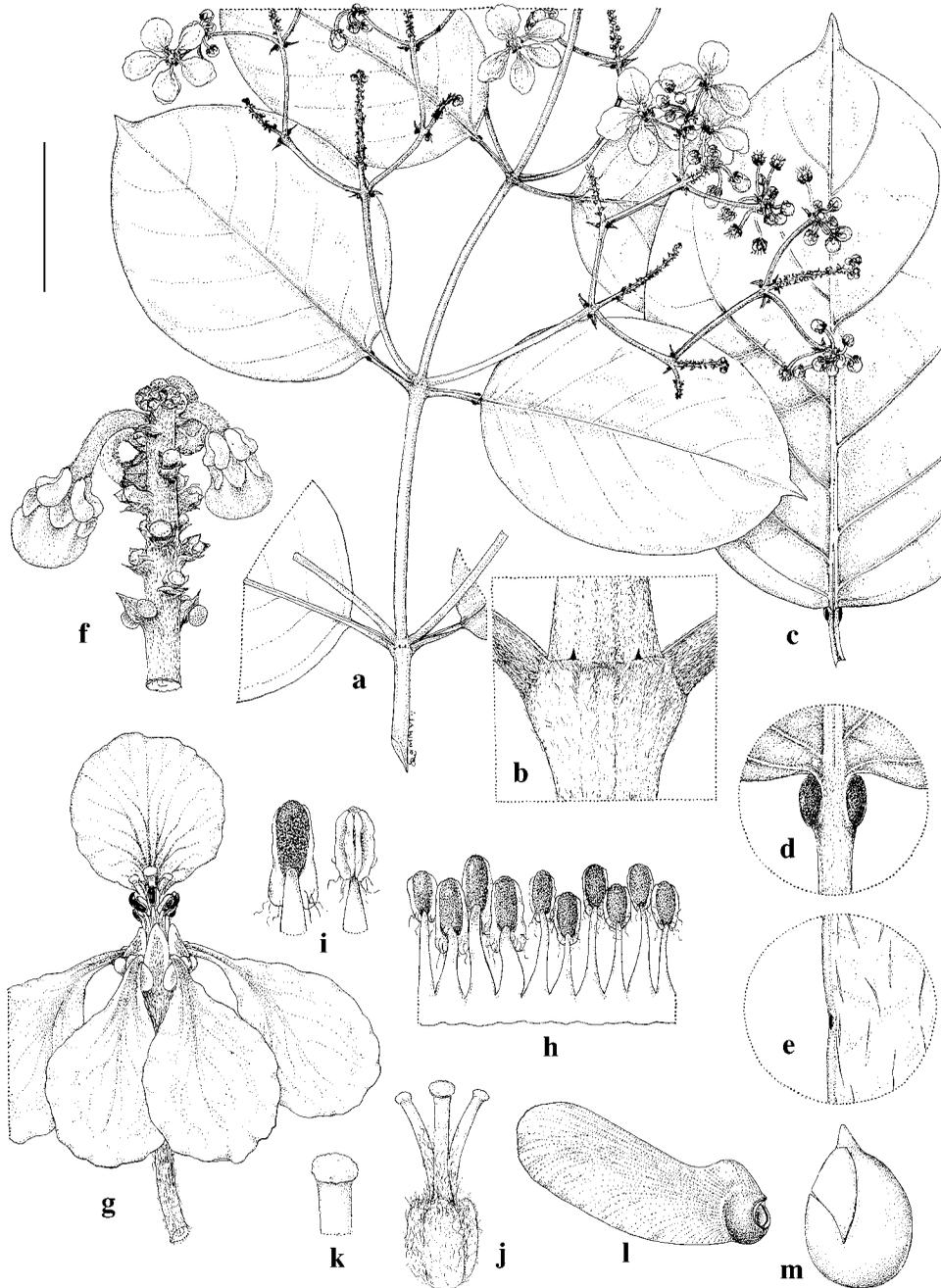


FIG. 3. *Bronwenia mathiasiae*. a. Flowering branch. b. Node with tiny interpetiolar stipules. c. Detached large leaf, adaxial view. d. Apex of petiole, abaxial view. e. Margin of lamina, abaxial view, to show tiny gland. f. Distal portion of inflorescence with flower buds. g. Flower, posterior petal uppermost. h. Androecium laid out, abaxial view, stamen third from right opposite posterior petal. i. Anthers: abaxial view of anther opposite anterior sepal (left) and adaxial view of anther opposite posterior petal (right). j. Gynoecium, the anterior style in center. k. Apex of anterior style. l. Samara. m. Embryo. Scale bar equivalents: a, 4 cm; b, 6.7 mm; c, 4 cm; d, 8 mm; e, 2 mm; f, g, 8 mm; h, 2.7 mm; i, 2 mm; j, 2.7 mm; k, 1.3 mm; l, 2.7 cm; m, 8 mm. (Based on: a, *Nelson et al. 518*, MICH, and *Stannard & Arrais 637*, MICH; b, *Gentry & Díaz 58617*, MICH; c, d, *Cid & Nelson 2680*, MICH; e, *Nelson et al. 518*, MICH; f–k, *Stannard & Arrais 637*, MICH; l, m, *Milliken 171*, MICH.)

convinced that its relationships lie with the species included here in *Bronwenia*. Our new data pair this species with *B. cornifolia* with 99% bootstrap support (Fig. 1), thus confirming its placement in *Bronwenia*, in spite of its dichasial inflorescence, large petals, and large petiole glands.

Bronwenia megaptera (B. Gates) W. R. Anderson & C. Davis, comb. nov. *Banisteriopsis megaptera* B. Gates, Fl. Neotrop. Monogr. 30: 49. 1982.—TYPE: BRAZIL. Minas Gerais: S of Itaobim, *Anderson 11734* (holotype: MBM!; isotypes: CAS! CTES! MICH! MO! NY!).

Banisteria ovata Nied., Ind. Lect. Lyc. Reg. Hos. Brunsberg. p. hiem. 1900–1901: 407. 1928, non *B. ovata* Cav., 1790.—TYPE: BRAZIL. Minas Gerais (fide Nienhüsen 1928): *Glaziou 12492* (holotype: B†, F neg. 12821, fragment NY!; isotypes: BR! C! G! NY! P! S!).

Bronwenia peckoltii W. R. Anderson & C. Davis, sp. nov.—TYPE: BRAZIL. Rio de Janeiro: Cantagalo, Jun fl/imm fr, *Peckolt 266* (holotype: W!; isotypes: F! W!).

Liana; lamina foliorum majorum 12–16.5 cm longa, 5–9 cm lata, abaxialiter dense et pertinaciter sericea; petiolus 22–30 mm longus, apice biglandulosus glandulis 1.5–3 mm longis; inflorescentia paniculata floribus in pseudoracemis 6–14-floris portatis; pedunculi 1–3.5 mm longi; pedicelli 10–27 mm longi; petala lutea, glabra; petala lateralia limbo 6–7 mm longo, 6–6.5 mm lato; petalum posticum limbo 4.5 mm longo, 3 mm lato; stamina glabra.

Woody vine; stems initially sericeous, glabrescent in age. Lamina of larger leaves 12–16.5 cm long, 5–9 cm wide, broadly elliptical, cuneate at base or somewhat decurrent onto petiole, rounded, obtuse, or abruptly short-acuminate at apex, initially thinly and loosely sericeous above but soon glabrate, densely and persistently silver-sericeous below with the hairs short, straight, and tightly appressed, eglandular (but see below under petiole), the principal lateral veins 5–6 on each side; petiole 22–30 mm long, thinly persistent or eventually glabrescent, bearing at apex (or on abaxial surface of decurrent base of lamina) 2 large bulging glands 1.5–3 mm long; stipules minute (0.2–0.4 mm long), often hidden under hairs, or apparently lacking. Inflorescence a terminal or axillary panicle, the axis thinly sericeous, the ultimate pseudoracemes 1.5–3 cm long, containing 6–14 flowers; bracts ovate or lanceolate, 1–2 (–3) mm long, 0.8–1 mm wide, abaxially sericeous, adaxially glabrous, eglandular but abaxially callose at base, appressed or somewhat spreading, persistent; peduncle 1–3.5 mm long, sericeous; bracteoles like bracts but smaller, borne at or slightly below apex of peduncle; pedicel 10–27 mm long, sericeous. Sepals 1–1.5 mm long and wide beyond glands, triangular, rounded at apex, abaxially sericeous proximally and glabrous distally, adaxially glabrous, the glands 2.5–3 mm long, obovate. Petals yellow, glabrous, entire or erose; lateral petals with limb 6–7 mm long, 6–6.5 mm wide, the claw 2 mm long; posterior petal with limb 4.5 mm long, 3 mm wide, the claw 2 mm long. Stamens glabrous; filaments 1.5–2 mm long, longer opposite sepals than opposite petals, connate at base; anthers 0.9–1.2 mm long, alike, the connective red, not exceeding locules. Ovary 1.5 mm high, densely sericeous; styles ca. 1.5 mm long, glabrous, stout, erect and straight or diverging distally, alike or the anterior slightly longer than the posterior 2 and more strongly divergent, the stigma terminal and capitate. Mature fruit unknown; very immature developing fruit with one elongating dorsal wing on each carpel and no lateral wings, but with a low ridge on each side parallel to areole.

Known only from the type collection; Peckolt's handwritten label has what is probably a more detailed locality, but we cannot decipher it.

This species is named in honor of the collector of the type, Theodor Peckolt (1822–1912), a botanist and pharmacist who was German by birth and training but spent most of his life (65 years) in his adopted country of Brazil. Peckolt collected extensively in the state of Rio de Janeiro and lived for 17 years in Cantagalo; it was probably during those years that he collected the plant described here (Ihering 1914).

The generic placement of this species is somewhat problematic. With its large flowers, long petioles, and huge petiole glands it bears little resemblance to other species in the genus except *B. mathiasiae*. Its metallic-sericeous leaves are unique in *Bronwenia*. In the enlarging fruits the carpels are clearly connate their whole length in the nut, whereas in most species (and indeed in most species of *Banisteriopsis* sensu Gates) the carpels are nearly distinct in the ovary. However, in specimens of *B. megaptera* with enlarging fruits the carpels show connation similar to that of *Peckolt 266*, which suggests that the usual condition of distinct carpels is not found consistently in *Bronwenia*. Even more worrisome is the fact that when the leaf glands are on the decurrent base of the lamina in this species, they are on the abaxial surface, not on the margin as in all other species. On the other hand, there are good reasons for placing this species in *Bronwenia*. The interpetiolar stipules, paniculate inflorescence with flowers ultimately disposed in short pseudoracemes, calyx glands attached mostly below the free part of the sepals, androecium of similar stamens with the connective not exceeding the locules, stout styles with a large terminal stigma, and glabrous yellow petals combine to say that if this plant belongs anywhere in *Banisteriopsis* sensu Gates, it must go among the species we are transferring here to *Bronwenia*. While the enlarging fruits are very young on this specimen, they suggest strongly that each samara at maturity will have one dominant dorsal wing with the lateral wings represented at most by a single ridge, which agrees with other samaras in *Bronwenia*. For these reasons we have decided to go ahead and describe this enigmatic species in *Bronwenia*, but its position should be re-evaluated when more and better specimens, especially ones with larger fruits, are available for study.

Bronwenia wurdackii (B. Gates) W. R. Anderson & C. Davis, comb. nov. *Banisteriopsis wurdackii* B. Gates, *Brittonia* 31: 109. 1979.—TYPE: VENEZUELA. Bolívar: Río Villacoa (Río Auyacoa), *Wurdack & Monachino 41145* (holotype: MICH!; isotypes: NY! VEN!).

Banisteria cinerascens var. *glabrescens* Nied. in Engl., *Pflanzenr.* IV, 141: 406. 1928.—TYPE: BRAZIL. Amazonas: Seringal São Francisco, Rio Acre, *Ule 9477* (holotype: B†; lectotype, designated here: G!; isotypes: L! MG!).

Fig. 4.

CALCICOLA AND MASCAGNIA

Mascagnia (Bertero ex DC.) Colla, as recognized by Niedenzu (1928), was an exceedingly polyphyletic genus (Anderson 1981, 1988, 2001a, 2001b; Cameron et al. 2001; Davis et al. 2001, 2002). Most of the segregates necessary to correct this problem have been described (Anderson 2006), but our recent work has uncovered a pair of species that will have to be removed from *Mascagnia* sens. str. (C. Davis & W. R. Anderson, unpubl.). They are *Mascagnia parvifolia* (Adr. Juss.) Nied. and *M. sericea*

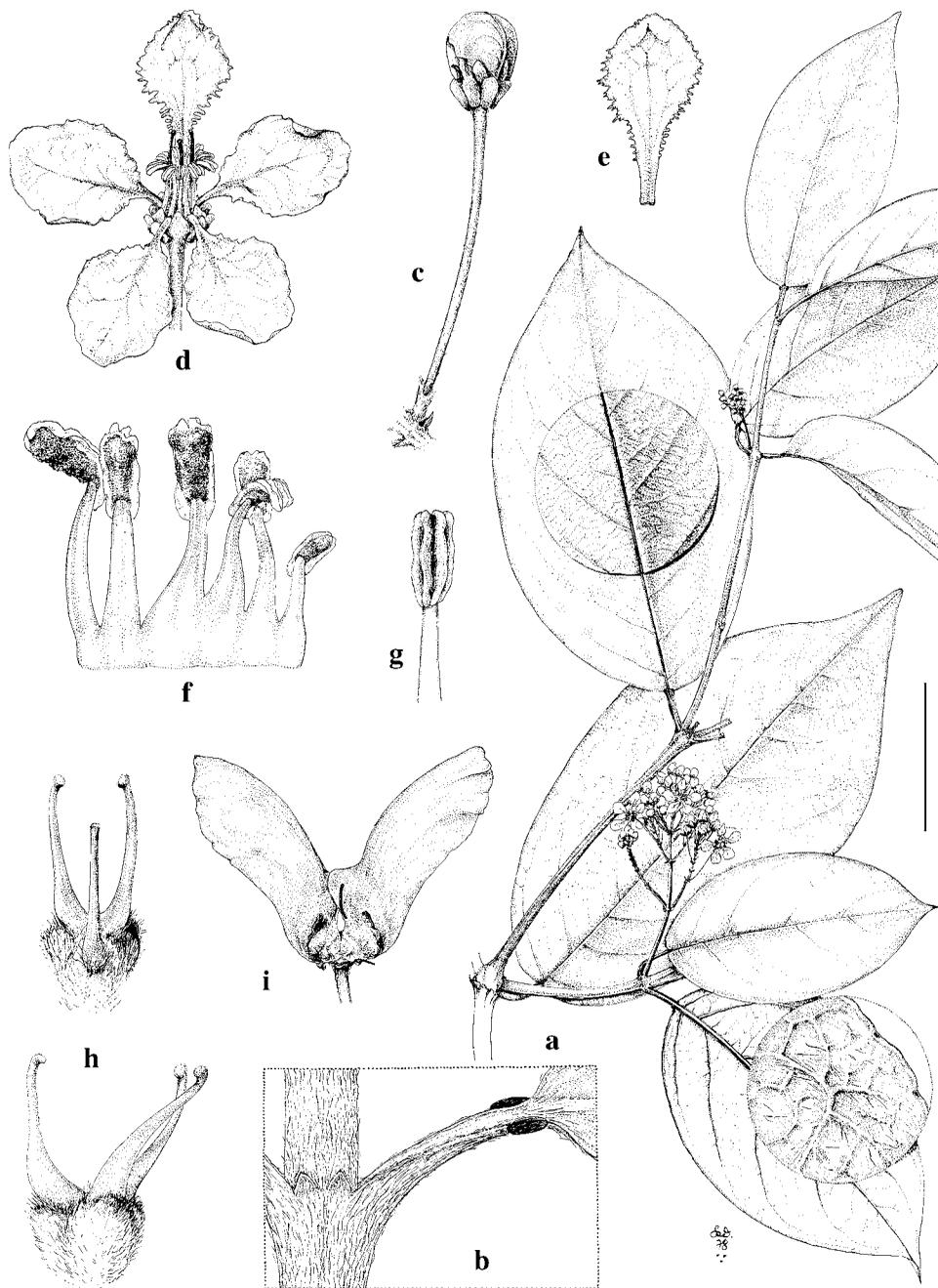


FIG. 4. *Bronwenia wurdackii*. a. Flowering branch, with enlargement of adaxial surface of lamina (above) and abaxial surface showing tiny marginal glands (below). b. Node and base of leaf to show interpetiolar stipules and petiole glands. c. Flower bud. d. Flower, posterior petal uppermost. e. Posterior petal, adaxial view. f. Portion of androecium laid out, abaxial view, stamen to right opposite posterior petal. g. Anther, adaxial view. h. Gynoecium, with anterior style in middle (above) and with anterior style to left (below). i. Fruit with two samaras developed. Scale bar equivalents: a, 4 cm (upper circle 2 cm, lower circle 4 mm); b, 4 mm; c–e, 5.7 mm; f–h, 2 mm; i, 2.7 cm. (Based on: a, *Wurdack & Monachino 40976*, MICH; b, *Murray & Johnson 1545*, MICH; c–h, *Pena 474*, IAN; i, *Wurdack & Monachino 41145*, MICH.) Modified from a drawing first published in *Mem. New York Bot. Gard.* 32: 156. 1981.

Nied., which form a well-supported clade and are more closely related to *Malpighia* and the Old World malpighioids than they are to *Mascagnia* (and *Triopterys*); see Fig. 5, where the species in question are in boldface under the name *Callicola*. Those two species are segregated here as a new genus.

Callicola W. R. Anderson & C. Davis, gen. nov.—TYPE: *Callicola parvifolia* (Adr. Juss.) W. R. Anderson & C. Davis.

Frutices; folia petiolis eglandulosis, laminis eglandulosis vel margine glandulis parvis cylindricis instructis; stipulae nullae vel interpetiolares; flores axillares, singulares vel in umbella 2–4-flora portatae; petala plerumque lilacina, caerulea, vel purpurea, interdum atroflorea; carpella stylique 2 vel 3; samara ala laterali orbiculari, membranacea, basi continua, apice continua vel usque ad nucem incisa.

Shrubs 0.3–2 (–3) m tall, occasionally described as small trees. Leaves decussate; lamina eglandular or bearing 1–5 small cylindrical glands on margin on each side of proximal half; petiole eglandular; stipules lacking or interpetiolar (borne on stem beside petioles), very small, distinct, triangular. Flowers borne singly or in umbels of 2–4 in axils of full-sized leaves; bracts and bracteoles eglandular, persistent, the bracteoles borne at or below apex of a well-developed peduncle. Flowers bilaterally symmetrical in calyx, corolla, and androecium. Sepals leaving petals exposed during enlargement of bud, the lateral 4 bearing large paired abaxial glands and the anterior eglandular. Petals mostly described as lilac, blue, or purple, sometimes as dark rose, sometimes with white or yellowish tints, glabrous, entire, erose, or dentate, abaxially smooth or carinate on claw, the posterior petal somewhat different in size, shape, and stance from the lateral 4. Receptacle glabrous on both sides of filaments. Stamens 10, all fertile, glabrous; filaments slightly connate at base, shortest opposite posterior petal; anthers subequal or larger opposite posterior-lateral petals, the connective not exceeding locules at apex. Gynoecium 2- or 3-carpellate, the carpels (when 3) 1 anterior and 2 posterior, all fertile, connate their whole length in ovary; styles 2 or 3, distinct, the anterior style shorter than the posterior 2; stigmas internal or nearly terminal. Fruit dry, breaking apart at maturity into 2 or 3 samaras separating from a high pyramidal torus; samara orbicular with the lateral wing well-developed, membranous with a prominent reticulum of arching anastomoses, continuous at base, the dorsal wing very small or absent or large and resembling one side of the lateral wing; fruit subtended by a fleshy 3-lobed disc or the disc rudimentary or lacking.

Callicola resembles *Mascagnia* in a number of characters, especially its mostly lilac, blue, or purple petals and its orbicular samaras with the wings membranous with reticulate venation. In several other respects, however, *Callicola* differs from all species of *Mascagnia*. Both species are shrubs that never climb, while most species of *Mascagnia* are twining woody vines. The leaf glands of *Callicola*, if any, are cylindrical and located on the margin of the lamina; in *Mascagnia* the glands are flat and borne in the abaxial surface between the midrib and the margin, sometimes lying very near the margin. The other significant difference is the inflorescence in the two genera. In *Mascagnia* the flowers are borne in pseudoracemes, sometimes crowded distally into corymbs or umbels. In *Callicola* the flowers are borne singly or in umbels of 2–4 in the axils of full-sized leaves. That is especially interesting given the fact that an identical inflorescence is found in many species of *Malpighia*; note that *Callicola* and *Malpighia* are in the same clade in our phylogenetic tree, with the Old World malpighioids (Fig. 5).

This genus is endemic to Mexico (Fig. 6), where both species grow on calcareous soils; the generic name *Callicola*, which means lime-dweller, refers to that habitat.

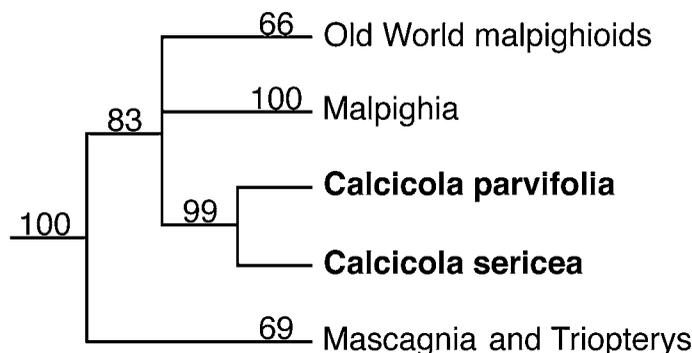


FIG. 5. Phylogenetic tree showing position of *Calcicola* in the *Malpighia* clade of Malpighiaceae. Bootstrap values are given above branches. The reduced strict consensus tree shown here is extracted from a larger phylogenetic analysis of Malpighiaceae using combined DNA sequences from plastid *matK*, *ndhF*, and *rbcL*, nuclear *PHYC*, and morphology; all genes were sequenced for all taxa (C. Davis & W. R. Anderson, unpublished data). Vouchers for species of *Calcicola* sequenced: *Calcicola parvifolia*: Salinas T. 5444, MICH; *Calcicola sericea*: Tenorio 6356, MICH.

KEY TO THE SPECIES OF CALCICOLA

1. Lamina of leaves elliptical, ovate, or orbicular, 1–1.7 times as long as wide, densely velutinous above and lanate below; petiole (1–) 2–4 (–6) mm long; samara with lateral wing continuous at both base and apex, the dorsal crest lacking or very small. *C. parvifolia*
1. Lamina of leaves narrowly elliptical or lanceolate, 2.4–5 times as long as wide, loosely sericeous on both sides or sometimes glabrescent above; petiole 0.5–1 mm long; samara with lateral wing continuous at base and cleft to nut at apex, the dorsal wing similar in size and shape to each side of the lateral wing or slightly smaller. *C. sericea*

Calcicola parvifolia (Adr. Juss.) W. R. Anderson & C. Davis, comb. nov. *Malpighia parvifolia* Adr. Juss., Arch. Mus. Hist. Nat. 3: 268. 1843. *Mascagnia parvifolia* (Adr. Juss.) Nied., Arbeiten Bot. Inst. Königl. Lyceum Hosianum Braunsberg 4: 5. 1912.—TYPE: MEXICO. Oaxaca: Galeotti 4327 (holotype: P!; isotypes: G! K! P-JU!).

Mascagnia seleriana Loes., Bull. Herb. Boissier 2: 543. 1894.—TYPE: MEXICO. Oaxaca: Tlacolula, near Mitla, Seler & Seler 120 (holotype: B†; lectotype, designated here: G!; isotypes: GH! US!).

Hiraea parviflora Rose, Contr. U.S. Natl. Herb. 5: 139. 1897. *Mascagnia pringlei* Nied., Arbeiten Bot. Inst. Königl. Lyceum Hosianum Braunsberg 3: 9. 1908, nom. superfl.—TYPE: MEXICO. Puebla: Near Tehuacán, Pringle 6274 (holotype: US!; isotypes: CAS! CM! F! G! GH! K! MEXU! MO! NY! UC!).

Fig. 7.

Shrub 0.3–2 (–3) m tall, occasionally described as a small tree. Lamina of larger leaves 10–55 mm long, 8–40 mm wide, elliptical, ovate, or orbicular, 1–1.7 times as long as wide, rounded or cordate at base, eglandular or bearing 1–5 small cylindrical glands on margin on each side of proximal half, densely and persistently velutinous above and lanate below; petiole (1–) 2–4 (–6) mm long. Flowers borne singly or (usually) in umbels of 2–4 on a common stalk. Petals mostly described as lilac, blue, or purple, with white or yellowish tints, occasionally as deep pink. Carpels 3; styles 3, dorsally truncate or slightly apiculate at apex, the stigma internal. Samara 15–22 (–28) mm in diameter, the lateral wing continuous at base and apex, entire or emarginate at

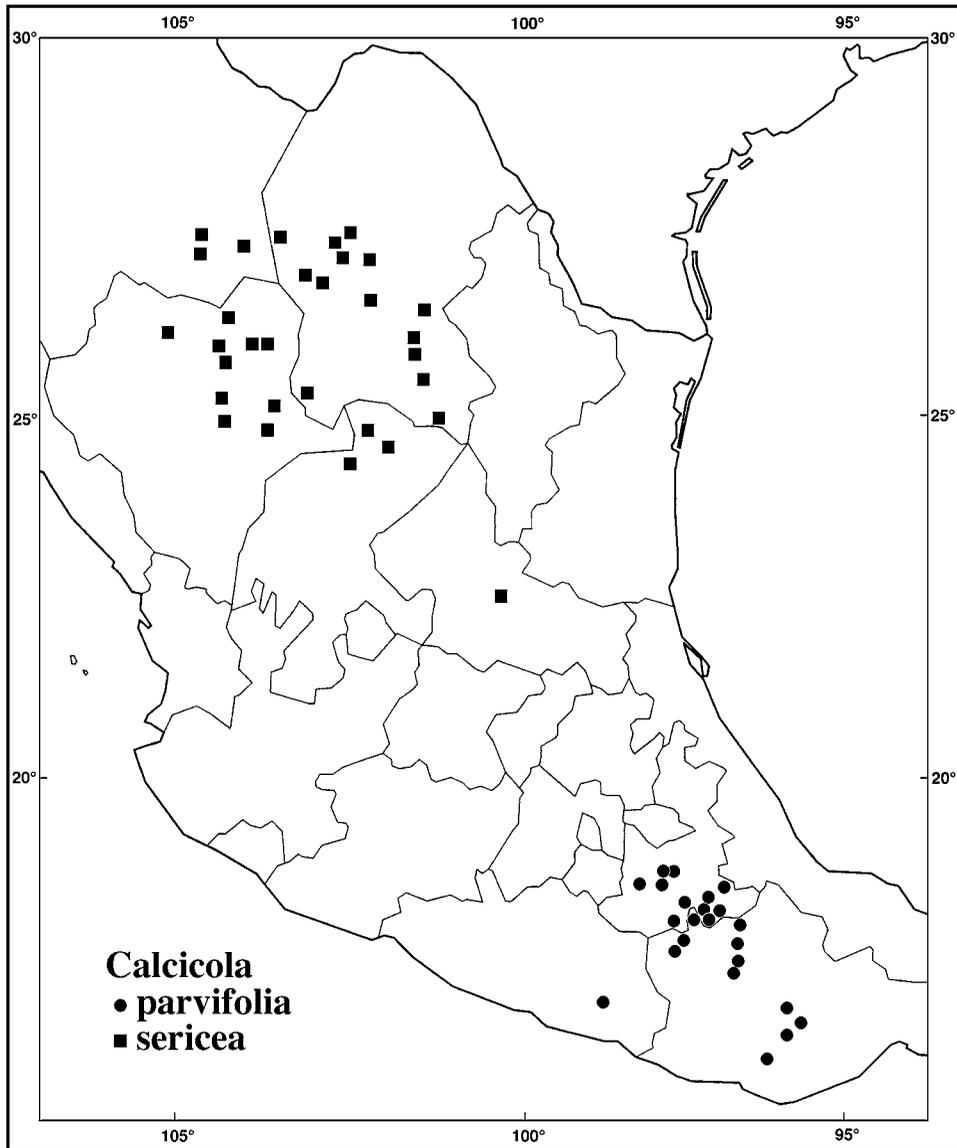


FIG. 6. Distribution of the species of *Callicola*.

apex; dorsal crest lacking or very small, with small irregular horizontal winglets often developing on sides of dorsal crest; disc below fruit well developed.

Southeastern Mexico (Puebla and Oaxaca, with one outlier population known from Guerrero) (Fig. 6). Low open deciduous woods or thorn-scrub on limestone slopes, 700–2000 m; collected with flowers and fruits in all months, but most often Jun–Nov.

Purpus 5913 (F, GH, MO, NY, US) and *Purpus 5919* (UC) were purportedly collected at Misantla, Veracruz, in June 1912, but that is probably not correct. Misantla (19°56'N, 96°52'W) is in tropical lowlands far from any known population of *Callicola* or suitable habitat for *Callicola*. Purpus is known to have collected in the vicinity of Tehuacán, Puebla, in 1912 before going to Misantla (Sousa S. 1969, pp. 6–7), and that was surely the source of these two collections.

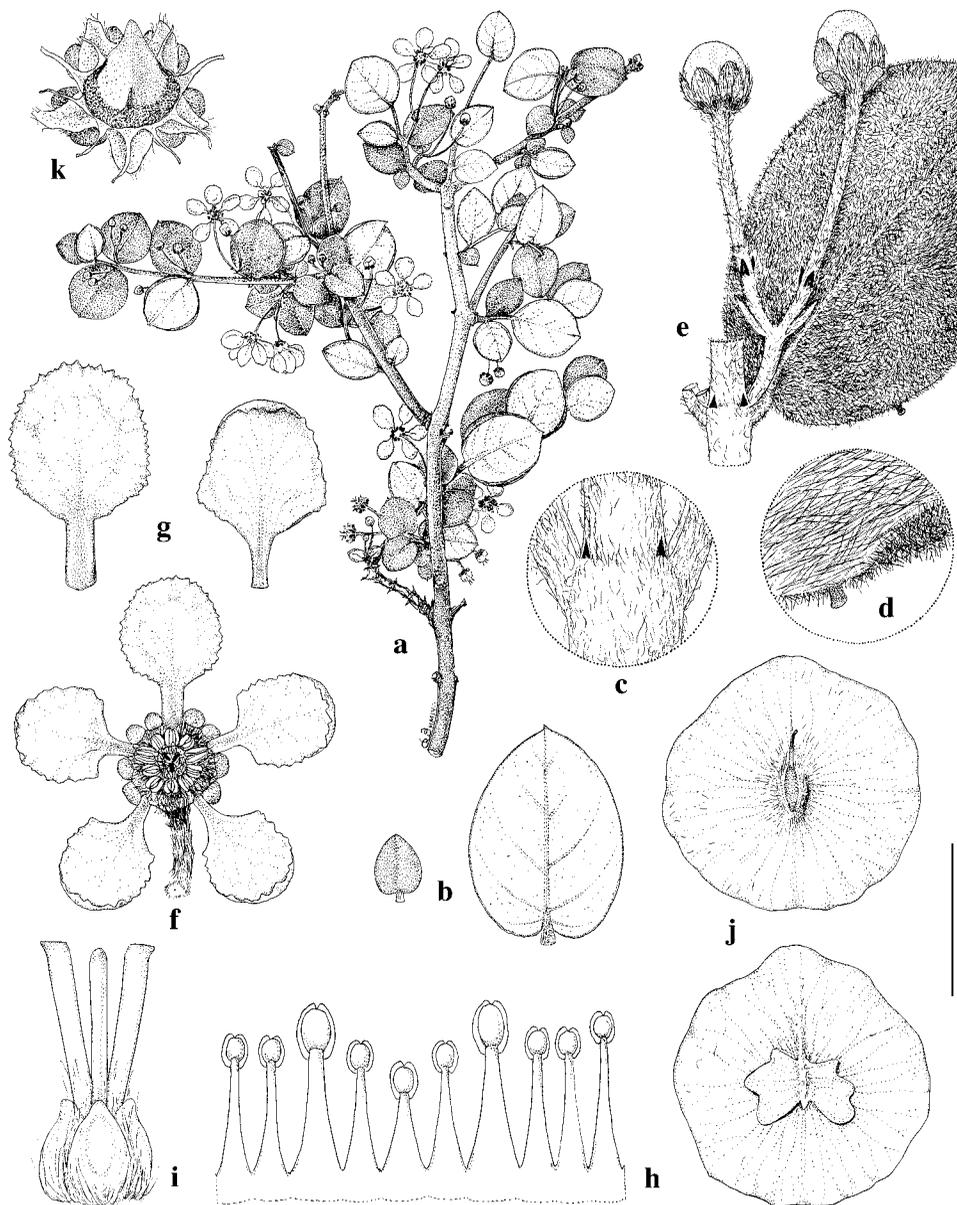


FIG. 7. *Calcicola parvifolia*. a. Flowering branch. b. Leaves to show range in size, adaxial view (left) and abaxial view (right). c. Node with interpetiolar stipules. d. Edge of lamina with marginal gland, abaxial view except where turned to show adaxial vestiture. e. Node and leaf (adaxial view) with axillary inflorescence. f. Flower, posterior petal uppermost. g. Posterior petal (left) and lateral petal (right), adaxial views. h. Androecium laid out, abaxial view, the shortest stamen opposite posterior petal. i. Gynoecium, anterior style in center. j. Samaras, adaxial view (above) and abaxial view (below). k. Old fruit after fall of samaras, with pyramidal torus in center, surrounded by lobed disc. Scale bar equivalents: a, b, 4 cm; c, d, 4 mm; e, f, 8 mm; g, 5.7 mm; h, 2.7 mm; i, 2 mm; j, 1 cm; k, 4 mm. (Based on: a, e–i, *Breckon et al.* 2343, MICH; b (left), *Rzedowski* 28187, MICH; b (right), *McVaugh* 24000, MICH; c, d, *Schoenwetter JSOX-91*, MICH; j, *García M.* 3297, MICH.)

The leaves in this species are exceedingly variable in size, probably reflecting availability of water in different populations, but the many collections seen clearly represent only one species (Anderson 1993b, p. 383).

Callicola sericea (Nied.) W. R. Anderson & C. Davis, comb. nov. *Mascagnia sericea* Nied., Arbeiten Bot. Inst. Königl. Lyceum Hosianum Braunsberg 3: 29. 1908. *Hiraea sericea* Engelm. in A. Gray, Pl. Wright. 1: 37. 1852, non. *H. sericea* Adr. Juss. *Mascagnia cana* Small, N. Amer. Fl. 25: 120. 1910, nom. superfl.—TYPE: MEXICO. Durango: Cadena, *Wizlizenus* 277 (lectotype, designated by Small in protologue of *M. cana*: MO!).

Fig. 8.

Shrub 0.4–1.5 (–3) m tall. Lamina of larger leaves 6–25 mm long, 2–9 mm wide, narrowly elliptical or lanceolate, 2.4–5 times as long as wide, narrowly to broadly cuneate or rounded at base, eglandular or bearing 1 (2) tiny cylindrical glands on margin on each side of proximal half, persistently loosely sericeous on both sides (or sometimes glabrescent above), the vestiture much denser below than above; petiole 0.5–1 mm long. Flowers borne singly or in umbels of 2 (3) on a common stalk. Petals mostly described as purple, sometimes as dark rose. Carpels 2 or 3; styles 2 or 3, dorsally rounded at apex, the stigma internal or nearly terminal. Samara 14–24 mm in diameter, the lateral wing continuous at base, cleft to nut at apex; dorsal wing similar in size and shape to each side of lateral wing or slightly smaller, usually confluent with lateral wing at base; small outgrowths sometimes present between dorsal and lateral wings; disc below fruit rudimentary or lacking.

North-central Mexico (Chihuahua, Coahuila, Durango, and Zacatecas, with one outlier population known from San Luis Potosí) (Fig. 6). Open desert scrub on dry rocky or sandy limestone slopes and flats, 1200–2200 m; collected with flowers and fruits May–Nov, most often Jul–Sep.

CLONODIA AND HETEROPTERYS

Clonodia Griseb. is a small group of riverine woody vines with lenticellate stems, an elongated pseudoraceme, alate pink or pink and white petals, and mericarps that have had all the wings of their samaras reduced to dissected winglets or crests, probably as an adaptation for dispersal by water. Niedenzu (1928) treated *Clonodia* in his subtribe Thryallidinae Nied., which was a mixture of disparate elements. He included three species, *C. ovata* Nied., *C. racemosa* (Adr. Juss.) Nied., and *C. sessilis* Nied.; the latter is now considered a synonym for *Niedenzuella stannea* (Griseb.) W. R. Anderson (Anderson 2006). Anderson (1981) added *C. complicata* (H. B. K.) W. R. Anderson, which Niedenzu (1928) had treated in *Mascagnia* under three different names [*M. complicata* (H. B. K.) Nied., *M. lehmanniana* Nied., and *M. nitida* (H. B. K.) Nied.]. As Anderson noted (1981), *Clonodia* is difficult to place with confidence, because its peculiar fruit is so reduced. If *Clonodia* is allied to *Mascagnia* sens. str., it could only be to the species with alate pink petals, like *M. cordifolia* (Adr. Juss.) Griseb., but this similarity is not convincing (see Anderson & Davis 2005). In particular, the three-lobed disc subtending the fruit that is always present in *Mascagnia* is lacking in *Clonodia*, and the carpels are only basally connate, whereas in most species of *Mascagnia* they are connate for their whole length. Anderson (1981) instead thought that the morphology was more supportive of a relationship to *Heteropterys* H. B. K. ser. *Rhodopetalis* Nied., in which one finds some species with the same punctiform lenticels, minute stipules on or beside the base of the petiole (or stipules lacking),

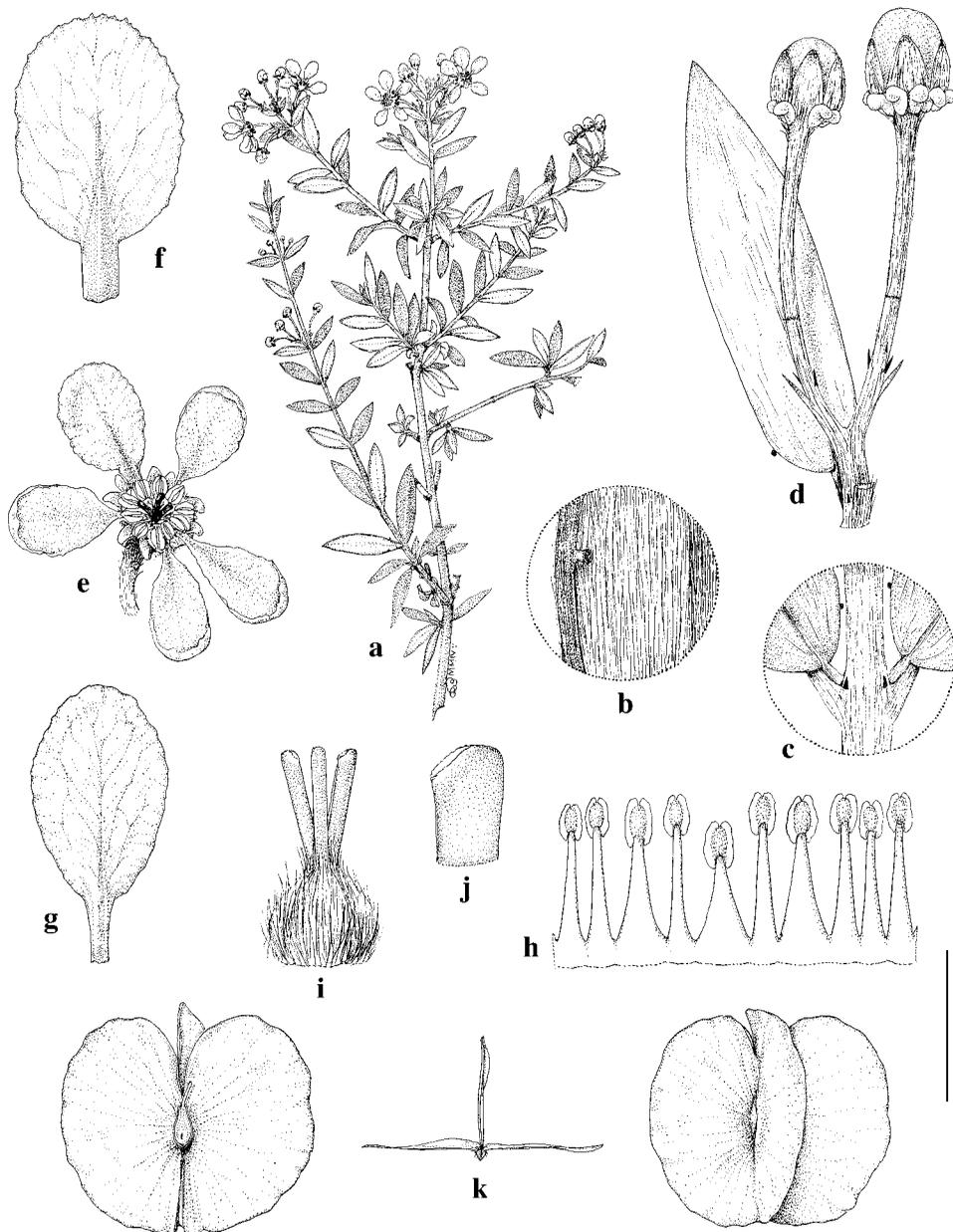


FIG. 8. *Calcicola sericea*. a. Flowering branch. b. Abaxial surface of lamina, showing cylindrical gland on revolute margin. c. Node showing interpetiolar stipules. d. Axillary pair of flower buds. e. Flower, posterior petal at upper left. f. Posterior petal, abaxial view. g. Lateral petal, abaxial view. h. Androecium laid out, abaxial view, the shortest stamen opposite posterior petal. i. Gynoecium. j. Enlarged stigma. k. Samaras, adaxial view (left), cross-section with dorsal wing uppermost (center), abaxial view (right). Scale bar equivalents: a, 4 cm; b, 2 mm; c, d, 4 mm; e, 8 mm; f, g, 4 mm; h, i, 2.7 mm; j, 0.8 mm; k, 1.6 cm. (Based on Johnston 7761, GH.)

a row of glands on the abaxial surface of the lamina between midrib and margin, winged pink or pink and white petals, carpels connate only at the base, and samaras with crests and winglets on the sides of the nut. That morphological argument still seems compelling to us, and we now have support for that placement from DNA

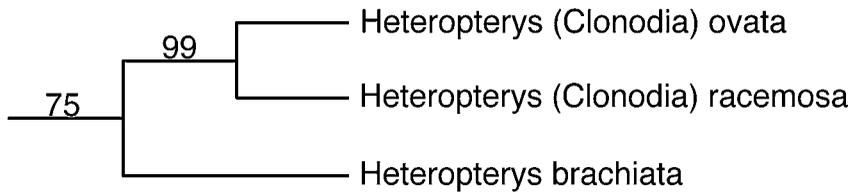


FIG. 9. Phylogenetic tree for three species of Malpighiaceae representing *Heteropterys* in the sense adopted in this paper (*Heteropterys* plus *Clonodia*). The parsimony tree shown here is extracted from a larger phylogenetic analysis of Malpighiaceae using combined DNA sequences from plastid *matK*, *ndhF*, and *rbcL*, nuclear *PHYC*, and morphology; all genes were sequenced for all taxa (C. Davis & W. R. Anderson, unpubl.). Bootstrap values given above branches. Vouchers for species sequenced: *H. brachiata*: FTG PRC-105, MICH; *H. ovata*: Beck 15105, MICH; *H. racemosa*: Rabelo et al. 3685, MICH.

sequences. Our data show that *Clonodia* is nested deep within *Heteropterys*, with its closest sister among the sampled species being *Heteropterys brachiata* (L.) DC., a pink-flowered species in Niedenzu's ser. *Rhodopetalis* (C. Davis & W. R. Anderson, unpubl.; Fig. 9). We are therefore including *Clonodia* in *Heteropterys*, proposing the necessary new combinations, and providing a key to the three species, synonymies, and brief synopses. Note that Jussieu originally described *Clonodia racemosa* in *Heteropterys*; we are not the first to recognize the similarity of these groups. The drawing we include here (Fig. 10) compares *Clonodia complicata* to another species of *Heteropterys* ser. *Rhodopetalis*, *H. alata* (W. R. Anderson) W. R. Anderson.

Cuatrecasas described these plants twice as new genera. One was *Atopocarpus* Cuatrec., *Webbia* 13: 454. 1958; type: *A. papillosus* Cuatrec. [*Heteropterys racemosa* Adr. Juss.]. The other was *Skoliopterys* Cuatrec., *Webbia* 13: 451. 1958; type: *S. lehmanniana* (Nied.) Cuatrec. [*Heteropterys complicata* (H. B. K.) W. R. Anderson & C. Davis]. Neither name ever gained any currency and both now become synonyms of *Heteropterys*.

Characteristics common to all three clonodioid species of *Heteropterys*: woody vines, sometime shrubby; stems with many punctiform lenticels; lamina bearing an abaxial row of impressed glands between midrib and margin; inflorescence simple or compound, with the flowers borne in an elongated pseudoraceme; sepals leaving petals exposed during enlargement of bud; petals pink or pink and white, the lateral 4 abaxially alate, the posterior carinate or alulate; mericarp without well-developed wings, only winglets or crests.

KEY TO THE CLONODIROID SPECIES OF HETEROPTERYS

1. Lamina abaxially densely tomentose to eventually glabrescent, the hairs stalked with the cross-piece sinuous to twisted. *H. ovata*
1. Lamina abaxially sericeous or soon glabrate, the hairs when present sessile, straight, ± appressed.
 2. Lamina of larger leaves (9–) 11–16.5 cm long, 4–9 cm wide, persistently sericeous below or eventually glabrate; petiole biglandular at or somewhat above base; mericarp with the nut 7 mm in diameter, bearing thick, often much-dissected winglets or crests with rounded edges and the veins obscure or invisible; most inflorescence hairs with a bulbous stalk and distally short-bifurcate; petals all papillose or verrucose adaxially. *H. racemosa*
 2. Lamina of larger leaves (5.5–) 7.5–11.5 (–13) cm long, (3–) 4–6 (–7) cm wide, soon nearly or quite glabrate; petiole eglandular or biglandular, often near middle; mericarp with the nut 4–5 mm in diameter, bearing thin winglets with clearly visible veins; inflorescence hairs with a slender stalk and long crosspiece at right angles; petals adaxially smooth or (especially the posterior) papillose. *H. complicata*

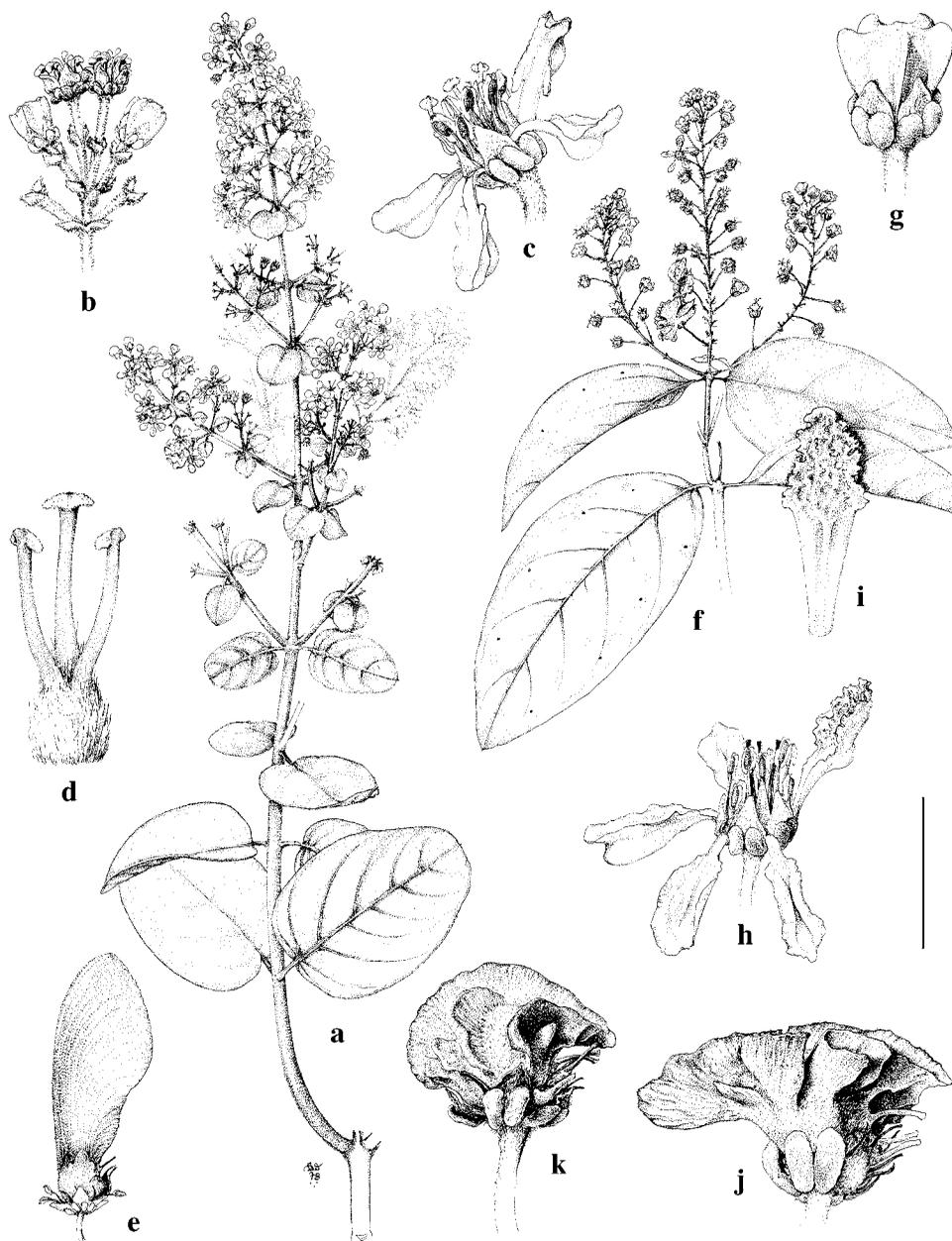


FIG. 10. *Heteropterys*. a–e, *H. alata*. a. Flowering branch. b. Cluster of flowers. c. Flower, posterior petal at upper right. d. Gynoecium, anterior style in center. e. Fruit, with only one samara developed. f–k, *H. complicata*. f. Branch with flowers and fruits. g. Flower bud. h. Flower, posterior petal at upper right. i. Posterior petal, showing papillose adaxial surface. j, k. Fruits, each with only one mericarp developed. Scale bar equivalents: a, 4 cm; b, 8 mm; c, 5.7 mm; d, 2 mm; e, 1.3 cm; f, 4 cm; g, 4 mm; h, 5.7 mm; i, 4 mm; j, k, 5 mm. (Based on: a–d, Wurdack & Monachino 39811, MICH; e, Wurdack & Monachino 39816, MICH; f–j, Breteleur 4829, US; k, Cardona 822, NY.) Drawing first published in Mem. New York Bot. Gard. 32: 207. 1981.

Heteropterys complicata (H. B. K.) W. R. Anderson & C. Davis, comb. nov. *Hiraea complicata* H. B. K., Nov. Gen. Sp. 5 [quarto ed.]: 171. 1822 ["1821"]. *Mascagnia complicata* (H. B. K.) Nied., Arbeiten Bot. Inst. Königl. Lyceum Hosianum Braunsberg 3: 4. 1908. *Clonodia complicata* (H. B. K.) W. R. Anderson, Mem. New York Bot. Gard. 32: 206. 1981.—TYPE: VENEZUELA. Bolívar: Río Orinoco near Carichana, *Humboldt & Bonpland* (holotype: P-HBK!).

Hiraea nitida H. B. K., Nov. Gen. Sp. 5 [quarto ed.]: 171. 1822 ["1821"]. *Mascagnia nitida* (H. B. K.) Nied., Arbeiten Bot. Inst. Königl. Lyceum Hosianum Braunsberg 3: 4. 1908.—TYPE: VENEZUELA. Amazonas: near Santa Bárbara, Alto Orinoco, *Humboldt & Bonpland* (holotype: P-HBK!).

Clonodia racemosa var. *orinocensis* Nied. in Engl., Pflanzenr. IV, 141: 580. 1928.—TYPE: VENEZUELA. Delta Amacuro: Manoa, *Rusby [& Squires] 166* (holotype: B†?; isotypes: G! NY!).

Mascagnia lehmanniana Nied., Arbeiten Bot. Inst. Königl. Lyceum Hosianum Braunsberg 8: 59. 1926. *Skoliopterys lehmanniana* (Nied.) Cuatrec., Webbia 13: 452. 1958.—TYPE: COLOMBIA. Río Meta, *Lehmann 8766* (holotype: B†, F neg. 12689, fragment NY!; isotype: K!).

Fig. 10f–k.

Lamina of larger leaves (5.5–) 7.5–11.5 (–13) cm long, (3–) 4–6 (–7) cm wide, originally sericeous below with sessile, straight, ± appressed hairs but soon nearly or quite glabrate; petiole eglandular or biglandular, the glands often near middle. Inflorescence hairs with a slender stalk and long crosspiece at right angles. Petals adaxially smooth or (especially the posterior) papillose. Mericarp with the nut 4–5 mm in diameter, bearing thin winglets with clearly visible veins. Southern Venezuela and eastern Colombia.

Heteropterys ovata (Nied.) W. R. Anderson & C. Davis, comb. nov. *Clonodia ovata* Nied., Arbeiten Bot. Inst. Königl. Lyceum Hosianum Braunsberg 8: 62. 1926.—TYPE: BRAZIL. Rondônia ["Matto Grosso"]: Rio Guaporé, *Comm. Rondon 2429* (holotype: B†?).

Lamina of larger leaves 4–11.7 cm long, 2.6–6.8 cm wide, densely tomentose to eventually glabrescent below, the hairs stalked with the crosspiece sinuous to twisted; petiole biglandular near middle. Inflorescence hairs various but the stalk not bulbous. Petals all papillose or verrucose adaxially. Mericarp with the nut 3–4 mm in diameter, the crests few, thick, low. Southwestern Brazil ("Mato Grosso," probably now Rondônia) and Beni, Bolivia.

Heteropterys racemosa Adr. Juss., Ann. Sci. Nat. Bot., Sér. 2, 13: 274. 1840. *Clonodia racemosa* (Adr. Juss.) Nied., Arbeiten Bot. Inst. Königl. Lyceum Hosianum Braunsberg 5: 13. 1914.—TYPE: BRAZIL. Amazonas: Coari, *Martius* (lectotype, designated by Cuatrecasas, Webbia 15(2): 397. 1960: M, F neg. 19403).

Clonodia verrucosa Griseb. in Mart., Fl. Bras. 12(1): 26. 1858.—LECTOTYPE collection, designated by W. R. Anderson, 1981, p. 205: BRAZIL. Amazonas: near Barra [Manaus], Dec–Mar 1850–51, *Spruce 1094* (BM! CGE! G! K! NY! P!).

Clonodia racemosa var. *mattogrossensis* Nied. in Engl., Pflanzenr. IV, 141: 581. 1928.—TYPE: BRAZIL. Mato Grosso: Rio Arinos, *Kuhlmann [Comm. Rondon 538]* (holotype: B†?).

Atopocarpus papillosus Cuatrec., Webbia 13: 454. 1958.—TYPE: COLOMBIA. Vaupés: Río Inírida, *Fernández 2202* (holotype: COL!).

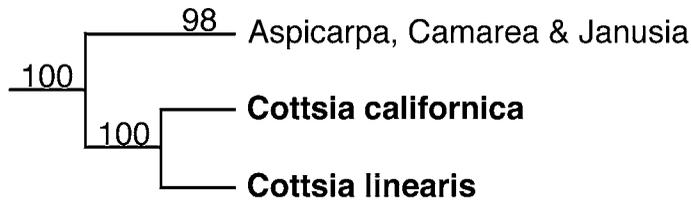


FIG. 11. Phylogenetic tree showing position of *Cottisia* (the North American species traditionally assigned to *Janusia*) as sister to the rest of the *Janusia* clade of Malpighiaceae. Bootstrap values are given above branches. The reduced strict consensus tree shown here is extracted from a larger phylogenetic analysis of Malpighiaceae using combined DNA sequences from plastid *matK*, *ndhF*, and *rbcL*, nuclear *PHYC*, and morphology; all genes were sequenced for all taxa (C. Davis & W. R. Anderson, unpubl.). Vouchers for species of *Cottisia* sequenced: *Cottisia californica*: Anderson 12539, MICH; *Cottisia linearis*: Anderson 12540, MICH.

Lamina of larger leaves (9–) 11–16.5 cm long, 4–9 cm wide, usually persistently sericeous below with sessile, straight, appressed hairs or eventually glabrate; petiole biglandular at or somewhat above base. Inflorescence hairs mostly with a bulbous stalk and distally short-bifurcate. Petals all papillose or verrucose adaxially. Mericarp with the nut 7 mm in diameter, bearing thick, often much-dissected winglets or crests with rounded edges and the veins obscure or invisible. Amazonian Colombia and Brazil.

COTTISIA AND JANUSIA

Janusia Adr. Juss. and its close relatives form a subclade within the larger stigmaphylloid clade (Davis et al. 2001); the *Janusia* clade continues to be strongly supported (C. Davis & W. R. Anderson, unpubl.; Fig. 11). The janusioids are distinguished by the loss of four or all five of the stamens opposite the petals, and most have only one style, borne on the anterior carpel. The type of *Janusia* is *J. guaranitica* (A. St.-Hil.) Adr. Juss., a widespread weedy herbaceous vine of southern South America. In the expanded sense of Anderson (1982, 1987) *Janusia* in South America comprises approximately 13 species. In northwestern Mexico and adjacent southwestern United States (Fig. 12) there is a small group of similar species that has traditionally been assigned to *Janusia*, although their differences have been recognized by the erection of sect. *Metajanusia* Nied. to accommodate them (Niedenzen 1928). Our data now show that the North American species of *Janusia* form a clade that is sister to the rest of the janusioids (Fig. 11, where the species in question are in boldface under the name *Cottisia*). The only way to maintain the North American species in the same genus as the South American species would be to treat the whole janusioid clade as one genus (in which case the name would have to be *Aspicarpa*), but we have rejected that course, so we are forced to take up the only generic name available for the North American species of *Janusia*, which is *Cottisia* Dubard & Dop.

Cottisia Dubard & Dop, Rev. Gén. Bot. 20: 359. 1908.—TYPE: *Cottisia scandens* Dubard & Dop [= *Cottisia californica* (Benth.) W. R. Anderson & C. Davis].

Janusia Adr. Juss. sect. *Metajanusia* Nied., Verz. Vorles. Königl. Lyceum Hosianum Braunsberg 1912–1913: 50. 1912. *Gaudichaudia* H. B. K. sect. *Erostratae* Chodat, Bull. Soc. Bot. Genève, Sér. 2, 9: 100. 1917, nom. superfl. *Aspicarpa* Rich. subsect. *Metajanusia* (Nied.) Hassl., Annuaire Conserv. Jard. Bot. Genève 20: 212. 1918.—LECTOTYPE, designated here: *Janusia gracilis* A. Gray [= *Cottisia gracilis* (A. Gray) W. R. Anderson & C. Davis].

Slender twining vines from a woody base, sometimes seeming shrubby when grazed; stems densely and persistently sericeous, eventually glabrescent. Leaves decussate; lamina eglandular on surface, sometimes eglandular on margin but usually bearing a pair of stalked glands or eglandular processes near base; petiole sericeous or glabrescent, eglandular; stipules borne on stem beside petiole, 0.1–0.8 mm long, triangular or subulate, glabrous or sericeous. Inflorescence sericeous or glabrescent, the flowers borne in umbels of 2–4 terminating lateral shoots; bracts 0.5–1.8 mm long, narrowly triangular or subulate, eglandular, persistent; peduncle (1–) 2–13 mm long; bracteoles like bract but usually smaller, borne at or somewhat below apex of peduncle, eglandular or one sometimes bearing a small stalked abaxial gland, persistent. Flowers all chasmogamous, bilaterally symmetrical in all whorls or the calyx radially symmetrical. Sepals leaving petals exposed during enlargement of bud, flat and appressed in anthesis, the glands 0.6–1.1 mm long, elliptical or obovate, detached and often reflexed distally, well separated on the sepal. Petals lemon-yellow, glabrous or bearing a few straight appressed hairs abaxially on claw or midrib, with the limb flat, the lateral 4 widely spreading, the posterior more erect, with a longer claw and a differently shaped limb. Receptacle glabrous on both sides of filaments. Fertile stamens 2, opposite posterior-lateral sepals, glabrous, nearly or quite distinct, erect and pressed against style, alike; staminodes (rudimentary filaments without anthers) 0–3, when present opposite anterior and anterior-lateral sepals; very rarely one of the filaments opposite an anterior-lateral sepal bearing an anther. Gynoecium 3-carpellate; carpels all fertile, 1 anterior and 2 posterior, connate their whole length in ovary; ovary 1–1.5 mm high, densely sericeous; style 1, borne on anterior carpel, straight and erect, the stigma terminal, truncate or capitate. Fruit dry, breaking apart at maturity into 3 samaras (or fewer by abortion) borne on a pyramidal torus 1.2–2 mm high, with each face of torus elliptical or obovate; samara 9–15 (–17) mm long, sericeous proximally; dorsal wing well developed, elongated, 7–12 (–15) mm long, 4–6 mm wide, thickened on the adaxial edge with the veins bending toward the thinner abaxial edge; nut 1.5–2.5 mm high, 3–4.5 mm long, without lateral wings but reticulate and often parallel-rugose on sides, flared and rounded at base and emarginate below to form a shallow groove to accommodate the short but functional carpophore 1–2 mm long, the nut usually forming a spur 0.2–0.5 mm long at end of carpophore; ventral areole 1–2 mm high, 0.8–1.3 mm wide, deeply concave. Embryo with the cotyledons subequal, flattened, folded back in the distal third.

The name *Cottisia* is based on an anagram of “Scott.” Dubard and Dop (1908) coined it to honor George Francis Scott Elliot (1862–1934), a Scottish botanist who collected plants in Madagascar in the late 1880s (Elliot 1891). They did that because their type, a single specimen in P, bore a label saying it was collected in Madagascar by Scott Elliot. Dubard and Dop recognized that the plant they were describing resembled the New World genera *Aspicarpa* and *Janusia*, and was unlike anything known from Madagascar, but apparently it did not occur to them that perhaps the specimen did not really come from Madagascar. Arènes (1943) argued that *Cottisia* should be considered a synonym of *Janusia* and transferred *Cottisia scandens* Dubard & Dop to *Janusia*, sect. *Metajanusia*, but did not question the unlikely disjunction from northwestern Mexico to Madagascar. In 1948 Arènes disclosed that the specimen in question is not from Madagascar after all; it is a mislabeled sheet of *Palmer 263* in 1887, from Sonora, Mexico. Arènes still insisted that it could not be a described species, but in fact *Palmer 263* in 1887 is a typical representative of *Janusia californica* Benth.

It is not surprising that the North American plants treated here as *Cottisia* have traditionally been placed in *Janusia*, because they are similar in a number of characteristics to the type species, *J. guaranitica*: herbaceous habit, flowers borne in umbels terminating short lateral shoots, five stamens opposite the sepals, one style on the anterior carpel, a terminal capitate stigma, and a small samara with a well-developed dorsal wing and a short but functional carpophore. The inflorescence, stigma, and samara characters are probably symplesiomorphies from a common ancestor of the stigmaphylloid clade, and the single style is probably a synapomorphy of the entire janusioid clade, which is found in all janusioids except for one small group of derived Mexican species that have reverted to three styles. In several important respects, however, *Cottisia* differs from *Janusia guaranitica*. Its petals are lemon-yellow, not carrot-yellow; the three anterior stamens lack anthers; its filaments are distinct even at the base; the carpels are connate their whole length in the ovary; the samara lacks a lateral winglet; and there are no cleistogamous flowers. The latter fact is especially interesting, because very specialized cleistogamous flowers are found in some species of all other genera in the janusioid clade (Anderson 1980). From a geographic perspective the simplest way to explain the North American distribution of *Cottisia* would be to suggest that it shares a more recent common ancestor with the North American janusioids than with those from South America, but this conclusion is not supported by our phylogenetic data. Moreover, if that were so one might expect to find cleistogamous flowers in *Cottisia*.

The very reduced androecium of *Cottisia* is intriguing, because some closely related species of *Camarea* and *Janusia* maintain six stamens, i.e., they have not lost the stamen opposite the posterior petal as in *Cottisia*. Moreover, in all cases studied the single stamen in cleistogamous flowers is the sixth stamen that has been lost in flowers with only five stamens (Anderson 1980), which argues for the evolution of cleistogamy in South American plants with six stamens. Another problematic feature of *Cottisia* is that its base chromosome number is $n = 10$, as is found in members representing more basal lineages of the stigmaphylloid clade, while the other janusioid genera have a base number of 20 pairs or a number aneuploid from 20 (17 or 19; Anderson 1993a). The low chromosome number and lack of cleistogamous flowers, taken in combination with the phylogenetic tree shown in Fig. 11, suggest that the ancestor of *Cottisia* diverged from the lineage leading to the remainder of the janusioids before doubling of the chromosomes and the origin of cleistogamy, and lost the sixth stamen (the one opposite the posterior petal) independently of the other janusioid species that lack it, such as *Janusia guaranitica*. If so, it must have reached northwestern Mexico independently of the migration of the ancestor of *Aspicarpa* north from South America. It seems clear that *Cottisia* occupies an enigmatic position in the family, and a better understanding of the sequence of events leading to its reduced morphology and isolated distribution will require further study.

Two other aspects of *Cottisia* merit comment. One is the fact that *C. linearis* usually has all five sepals biglandular, and that condition occurs sometimes in the other two species as well. Almost all other species in the more inclusive stigmaphylloid clade have the four lateral sepals biglandular and the anterior sepal eglandular (W. R. Anderson, unpublished data), so the condition in *C. linearis* must be a reversal to the ancestral condition of having five biglandular sepals (Anderson 1990). Even more interesting is the habitat of *Cottisia*. All three species grow in true desert. It is not rare for neotropical Malpighiaceae to grow in open more or less xeric places, but very few can survive in a place as hot and dry as the Sonoran desert; that is surely a derived adaptation of this genus.

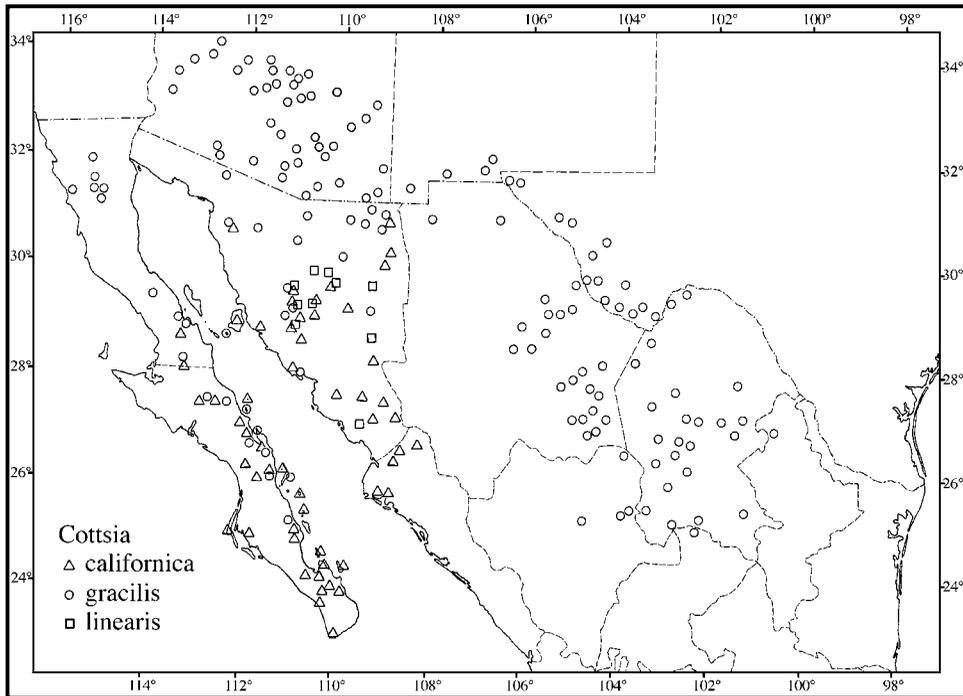


FIG. 12. Distribution of the species of *Cottisia*; *C. gracilis* may occur somewhat farther north in Arizona than shown here. Modified from a map first published in *Contr. Univ. Michigan Herb.* 19: 347. 1993.

The three species of *Cottisia* are sympatric in Sonora, Mexico (Fig. 12), where W. R. Anderson has collected them growing together, all flowering at the same time (*Anderson 12551, 12552, and 12553, MICH*). They represent two morphologically extreme species that have a chromosome number of $n = 10$ and an intermediate species with $n = 20$. Anderson (1993a) hypothesized that the intermediate species, *C. gracilis*, is an allotetraploid derived, possibly repeatedly, from hybridization between the diploids, *C. californica* and *C. linearis*, followed by doubling of the chromosome number. See the discussion below under *C. californica*.

KEY TO THE SPECIES OF COTTISIA

1. Lamina of larger leaves 1.2–10 times as long as wide, ovate to narrowly lanceolate or elliptical, flat at margin and very often bearing few to many marginal cilia or toothlike projections distal to basal pair; petiole 1–18 mm long; flowers 9–14 (–16) mm in diameter; lateral 4 sepals usually biglandular, the anterior sepal usually eglandular; style 1.5–2.3 mm long, the stigma usually borne at about the same height as anthers or slightly higher.
2. Lamina of larger leaves (6–) 9–36 (–47) mm wide, 1.2–2.2 (–2.5) times as long as wide, ovate, rounded or cordate at base; petiole 3–18 mm long; sepals adaxially glabrous; style 1.5–1.7 (–1.9) mm long. *C. californica*
2. Lamina of larger leaves (1.5–) 3–7 (–9) mm wide, 4–10 times as long as wide, narrowly lanceolate or elliptical, cuneate at base; petiole 1–3 (–5) mm long; sepals usually sericeous adaxially at base; style 1.9–2.3 mm long. *C. gracilis*
1. Lamina of larger leaves 12–40 times as long as wide, linear, moderately to strongly revolute at margin and without marginal cilia or teeth distal to basal pair of cilia or stalked glands; petiole 1–2 mm long; flowers 14–17 mm in diameter; all 5 sepals biglandular; style 2.1–3 mm long, the stigma usually borne well above anthers. *C. linearis*

Cottisia californica (Benth.) W. R. Anderson & C. Davis, comb. nov. *Janusia californica* Benth., Bot. Voy. Sulph. 8, pl. 4. 1844. *Gaudichaudia californica* (Benth.) Chodat, Bull. Soc. Bot. Genève, Sér. 2, 9: 100. 1917. *Aspicarpa californica* (Benth.) Hassl., Annuaire Conserv. Jard. Bot. Genève 20: 212. 1918.—LECTOTYPE, designated here: MEXICO. Baja California Sur: Magdalena Bay, *Hinds 1841* (lectotype: K!).

Cottisia scandens Dubard & Dop, Rev. Gén. Bot. 20: 359. 1908. *Janusia scandens* (Dubard & Dop) Arènes, Notul. Syst. (Paris) 11: 84. 1943. TYPE: MEXICO. Sonora: Guaymas, *Palmer 263* in 1887 (holotype: P!; isotypes: C! GH! NY! UC! US!).

Fig. 13a–f.

Leaves quite variable in size, the largest often on sterile shoots not represented in herbarium collections; lamina of larger leaves 15–55 mm long, (6–) 9–36 (–47) mm wide, 1.2–2.2 (–2.5) times as long as wide, ovate, rounded or cordate at base, flat at margin, obtuse, rounded, or slightly retuse and mucronate or apiculate at apex, initially densely sericeous on both sides but at maturity often thinly sericeous to glabrescent, very often bearing few to many distal cilia or toothlike projections along margin, the lateral veins and reticulum generally visible on both sides; petiole 3–18 mm long. Pedicel 3–7 (–9) mm long, 0.4–1.4 (–2) times as long as peduncle. Flowers 9–14 (–16) mm in diameter. Sepals 1.7–2.5 mm long, 1–1.4 mm wide, ovate or elliptical, acute, obtuse, or rounded at apex, abaxially sericeous to glabrate, adaxially glabrous, the anterior usually eglandular (occasionally bearing 1 or 2 glands), the lateral 4 usually biglandular (occasionally 1 or 2 of the most anterior glands lacking). Lateral petals with claw 1–2 mm long, the limb subtrotund, hardly decurrent, 3–5 (–6) mm long, 2.5–5 (–6) mm wide; posterior petal with claw 1.3–1.7 mm long, the limb 2.5–4.5 mm long, 2.2–5.5 mm wide. Fertile filaments 1.7–2.4 mm long; anthers 0.5–0.9 mm long; staminodes 1–3, 0.7–1.7 mm long. Style 1.5–1.7 (–1.9) mm long, glabrous or sericeous only at very base, the stigma usually borne at same height as anthers and with anthers pressed against it. Chromosome number: $n = 10$ (Anderson 1993a).

Endemic to northwestern Mexico (Sonora and adjacent Sinaloa, Baja California Sur and adjacent Baja California Norte) (Fig. 12). Thorn-scrub on gravelly plains and rocky hillsides, and in other xeric habitats, 10–1400 m; collected with flowers and fruits in most months, but most commonly Feb–Mar and Aug–Oct.

The leaves of this species are extremely variable in size and shape. When large leaves are present on the specimen it is usually easy to distinguish between *C. californica* and *C. gracilis*, because as the lamina gets larger it tends to become relatively broad in the former or relatively long in the latter. When all the leaves are very small, as they may be under some environmental conditions or in specimens where the collector failed to include leaves from stems below the inflorescence, the distinction between the two species can be difficult and the decision is sometimes arbitrary. Such apparently intermediate populations tend to be from western Sonora or Baja California Sur, where the two species are sympatric (Fig. 12), which suggests that the intermediate plants may represent backcrosses from *C. gracilis* to *C. californica*. If that is the case, and if the plants in question are fertile, they indicate that there may exist diploid populations of *C. gracilis*, in addition to the tetraploid populations sampled by Anderson (1993a). This problem merits further study by someone who has access to mixed populations in that area.

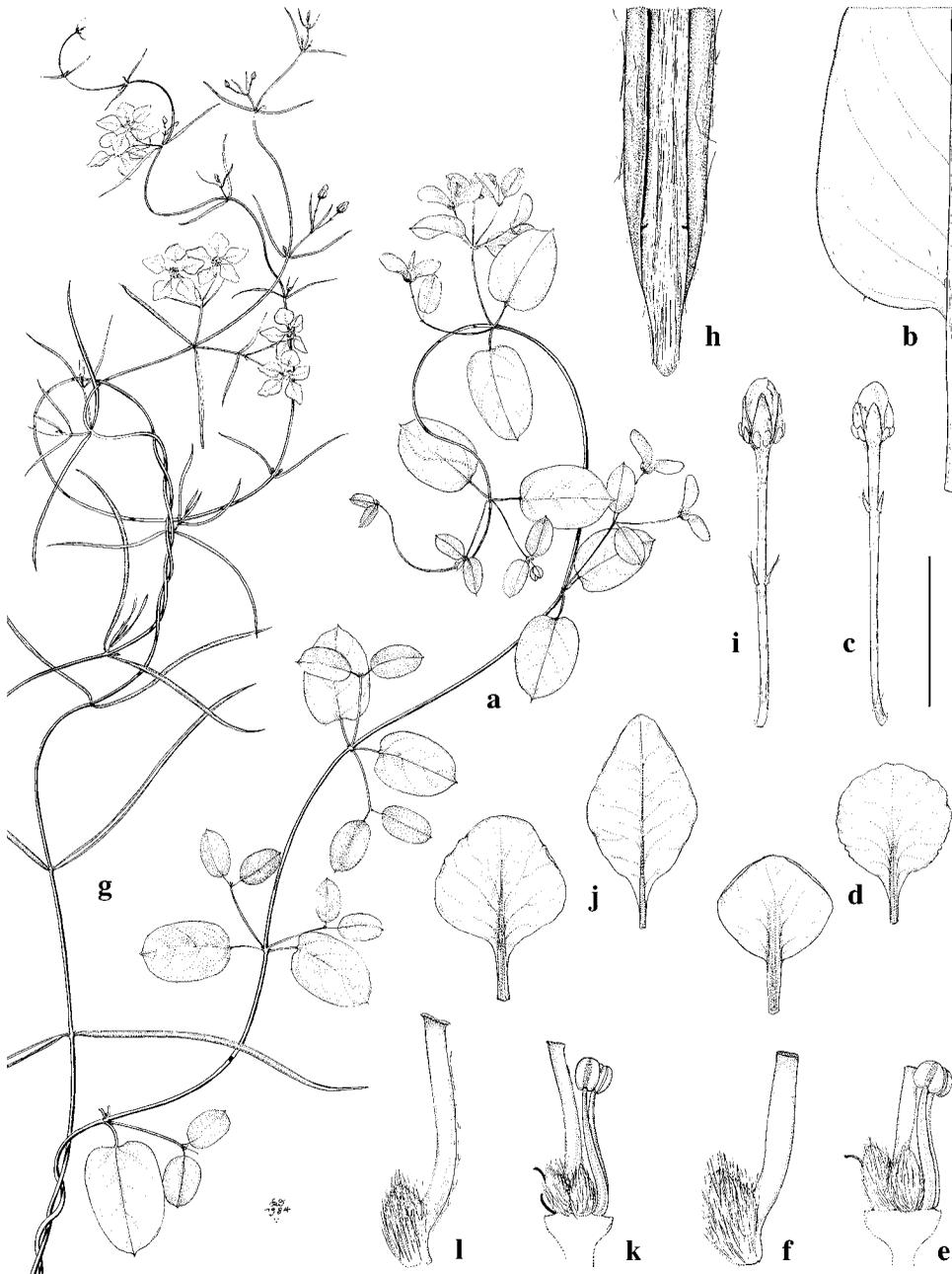


FIG. 13. *Cottsia*. a-f, *C. californica*. a. Fruiting branch. b. Base of leaf, abaxial view. c. Flower bud. d. Petals, adaxial view, posterior (left) and lateral (right). e. Androecium and gynoecium, lateral view, the two fertile stamens posterior. f. Anterior carpel. g-l, *C. linearis*. g. Flowering branch. h. Base of leaf, abaxial view. i. Flower bud. j. Petals, adaxial view, posterior (left) and lateral (right). k. Androecium and gynoecium, lateral view, the two fertile stamens posterior. l. Anterior carpel. Scale bar equivalents: a, g, 4 cm; b, 8 mm; c, i, 6.7 mm; d, j, 5.7 mm; e, k, 2.9 mm; f, h, l, 2 mm. (Based on: a-f, *Anderson 12536*, MICH; g-l, *Anderson 12551*, MICH.)

Cottisia gracilis (A. Gray) W. R. Anderson & C. Davis, comb. nov. *Janusia gracilis* A. Gray, Pl. Wright. 1: 37. 1852. *Gaudichaudia gracilis* (A. Gray) Chodat, Bull. Soc. Bot. Genève, Sér. 2, 9: 100. 1917. *Aspicarpa gracilis* (A. Gray) Hassl., Annuaire Conserv. Jard. Bot. Genève 20: 212. 1918. TYPE: U.S.A. Texas: mountains east of El Paso, Aug 1849, *Wright 96* (holotype: GH!; isotypes: G! GH! K! NY! US!). Fig. 14.

Lamina of larger leaves 12–40 (–50) mm long, (1.5–) 3–7 (–9) mm wide, 4–10 times as long as wide, very narrowly lanceolate or elliptical, cuneate or rounded at base, flat at margin, acute, obtuse, or occasionally rounded at apex, persistently sericeous on both sides or sometimes glabrescent, very often bearing few to many distal cilia or toothlike projections along margin, the lateral veins and reticulum visible on both sides in wider leaves; petiole 1–3 (–5) mm long. Pedicel 4–8 mm long, 0.7–1.8 times as long as peduncle. Flowers 10–14 mm in diameter. Sepals 2–2.5 mm long, 1–1.6 mm wide, ovate or triangular, acute, obtuse, or rounded at apex, abaxially sericeous, adaxially usually sericeous proximally and glabrous distally, the anterior usually eglandular (occasionally bearing 1 or 2 glands), the lateral 4 usually biglandular (occasionally 1 or 2 of the most anterior glands lacking). Lateral petals with claw (1.3–) 1.5–2 mm long, the limb trapezoidal to nearly round or somewhat oblate, decurrent or not at base, (2.5–) 3.5–5 mm long, 3–4.5 mm wide; posterior petal with claw 1.8–2.5 mm long, the limb usually oblate, (2.5–) 3–4.3 mm long, 3.6–5.2 mm wide. Fertile filaments 2.1–2.6 mm long; anthers 0.8–1 mm long; staminodes (2) 3, 1–2.5 mm long. Style 1.9–2.3 mm long, sparsely sericeous in proximal 1/3–2/3, the stigma borne at same height as anthers and with anthers pressed against it, or up to 0.3 (–0.5) mm above them. Chromosome number: $n = 20$ (Anderson 1993a).

Widespread in northern Mexico and extending into adjacent Texas, New Mexico, and Arizona (Fig. 12). Thorn-scrub and other xeric types of vegetation on diverse soils, 80–1900 m; collected with flowers and fruits in most months, but most commonly Apr–May and Jul–Oct.

See discussion above under *C. californica*. This species, one of only six Malpighiaceae native to the United States, occurs farther north than any other New World species.

Cottisia linearis (Wiggins) W. R. Anderson & C. Davis, comb. nov. *Janusia linearis* Wiggins, Contr. Dudley Herb. 3: 69. 1940. TYPE: MEXICO. Sonora: 18 mi S of Moctezuma, *Wiggins 7438* (holotype: DS!; isotypes: A! MICH! US!).

Fig. 13g–l.

Lamina of larger leaves 20–72 mm long, 1–5.5 mm wide, 12–40 times as long as wide, linear, cuneate at base, moderately to strongly revolute at margin, acute at apex, persistently sericeous on both sides or eventually glabrescent above, without distal cilia or teeth on margin, the lateral veins and reticulum not visible on either side; petiole 1–2 mm long. Pedicel (4–) 6–15 mm long, mostly 1.1–2.2 times as long as peduncle. Flowers 14–17 mm in diameter. Sepals 2.5–3 mm long, 0.9–1.5 mm wide, ovate or narrowly lanceolate, acute at apex, abaxially densely sericeous, adaxially sericeous proximally and glabrous distally, all biglandular. Lateral petals with claw 1–1.5 mm long, the limb trapezoidal, decurrent at base, 5–7.5 mm long, 4–6 mm wide; posterior petal with claw 1.5–2 mm long, the limb usually oblate, 4.5–5.5 mm long, 5.5–6.5 mm wide. Fertile filaments 2–2.7 mm long; anthers 0.6–0.8 mm long; staminodes 0–2, 1–1.8 mm long. Style 2.1–3 mm long, sericeous in proximal 1/2–3/4, the stigma usually borne well above anthers. Chromosome number: $n = 10$ (Anderson 1993a).

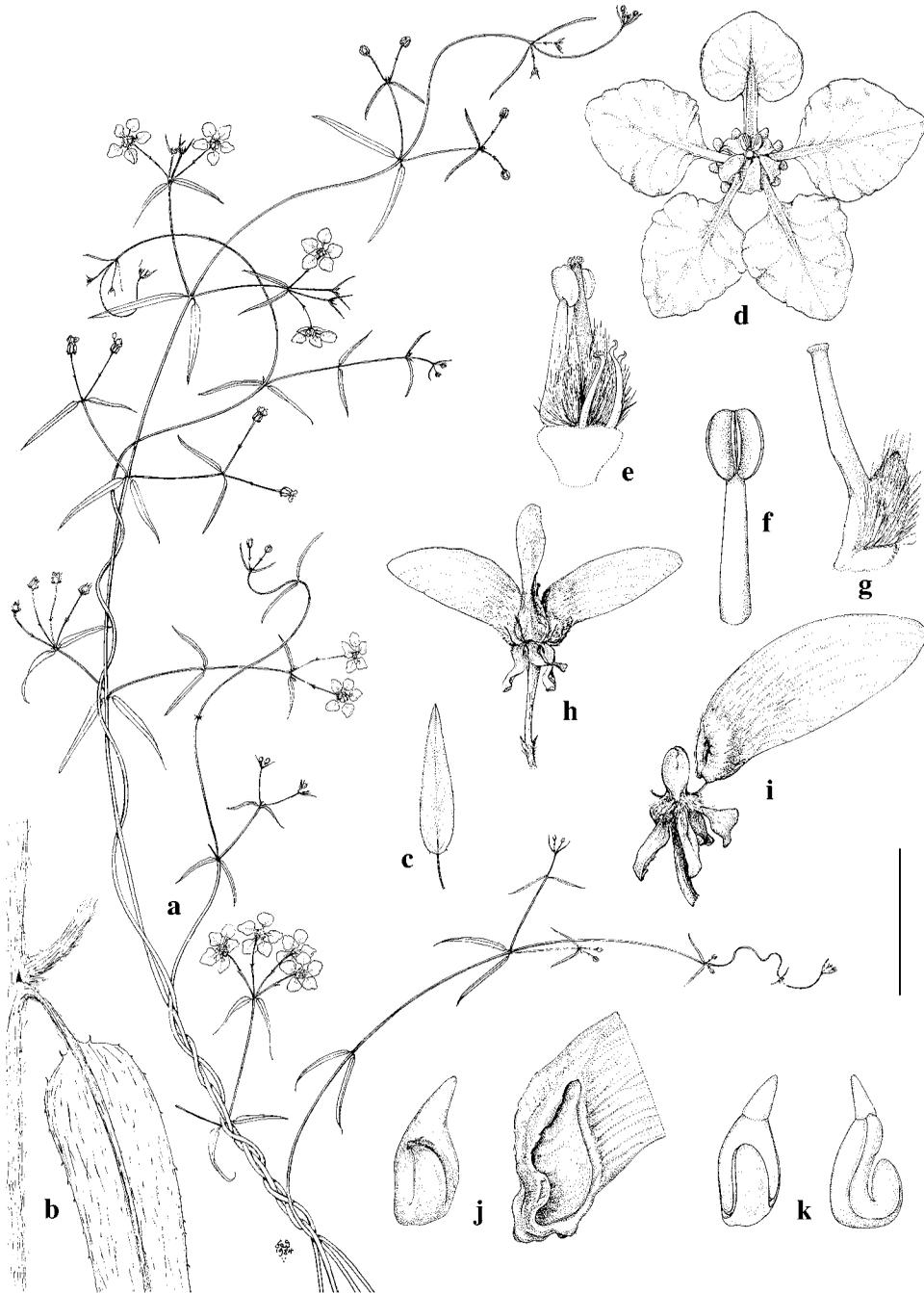


FIG. 14. *Cottisia gracilis*. a. Flowering branches. b. Base of leaf (abaxial view) and adjacent stem to show stipule and marginal processes. c. Detached, relatively broad leaf, adaxial view. d. Flower, posterior petal uppermost. e. Androecium and gynoecium, with two fertile posterior stamens and three anterior staminodes. f. Fertile stamen, adaxial view. g. Anterior carpel. h. Fruit. i. Fruit base and torus with one samara attached by carpophore. j. Seed (left) and nut of samara in longitudinal section with seed removed (right). k. Embryos. Scale bar equivalents: a, 4 cm; b, 4 mm; c, 4 cm; d, 5.7 mm; e, 2.9 mm; f, g, 2 mm; h, 1 cm; i, 5.7 mm; j, k, 4 mm. (Based on: a, b, *Monson 8*, CAS; c–g, *Anderson 12552*, MICH; h–k, *Anderson & Laskowski 3520*, MICH.)

Endemic to the Sonoran Desert of central Sonora, Mexico (Fig. 12). Thorn-scrub on gravelly plains and rocky hillsides, 200–700 m; collected with flowers and fruits Feb–Apr and Jul–Nov.

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