
A REVISION OF *BOURRERIA* (BORAGINALES, EHRETIACEAE) IN SOUTH AMERICA¹

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ABSTRACT

A review of South American herbarium specimens of *Bourreria* P. Browne (Boraginales, Ehretiaceae) indicates that five species are readily distinguished. *Bourreria boliviensis* Gottschling & J. S. Mill. is described as new; *B. baccata* Raf., *B. exsucca* Jacq., and *B. mollis* Standl. have their nomenclature clarified; *B. exsucca* is epitypified; and a neotype has been designated for *Rhamnus cumanensis* Loebl. (= *B. exsucca*). *Bourreria boliviensis* and *B. exsucca* are common species in the northern South American flora. *Bourreria costaricensis* (Standl.) A. H. Gentry and *B. mollis* are Central American species that have not been previously reported for South America. *Bourreria baccata* is a Caribbean species with the southern end of its distribution on Tobago, but it also occurs in a small, isolated population in the Netherlands Antilles and on the adjacent Venezuelan coast, perhaps resulting from a single long-distance dispersal event. *Bourreria exsucca* and the new species *B. boliviensis* have their distribution restricted to South America and exhibit schizocarpous fruits. The other three species have drupaceous fruits. All five species have extent of occurrence above the threshold (> 2000 km²) to be considered vulnerable based on the IUCN Red List categories, and none of the five species that occur in South America appear to be threatened when evaluated solely on their distributions.

Key words: Boraginaceae, *Bourreria*, Colombia, dispersal, distribution, IUCN Red List, schizocarp, taxonomy, Venezuela.

Bourreria P. Browne (Boraginales, Ehretiaceae) comprises approximately 30 species of tropical trees and shrubs that grow mostly in dry scrubby habitats and deciduous forests. A few species such as *B. costaricensis* (Standl.) A. H. Gentry have secondarily colonized predominantly wet habitats. *Bourreria* has its center of diversity in the Caribbean and Central America (Al-Shehbaz, 1991; Miller & Sirot, 1997; Miller, 1999) but also occurs in northwestern Mexico, Florida, and northern South America.

The precise systematic position of *Bourreria* remains unclear at present, since there is still a need for comprehensive phylogenetic analysis of Ehretiaceae. Monophyly of New World *Bourreria* s. str. has been supported by ITS-1 sequence data (Gottschling & Hilger, 2001; Gottschling et al., 2004). The closest relative is *Hilsenbergia* Tausch ex Meisn. from East Africa and Madagascar (Miller, 2003). This is inferred from molecular trees and synapomorphies such as the valvate calyx, the overlapping lamellae on the abaxial

surface of the pyrenes (also called endocarps), and the additional placental ("sterile") chamber found in each pyrene (Gottschling, 2001, 2004; Gottschling & Hilger, 2001).

Basic taxonomy is challenging in *Bourreria* due to the high morphological plasticity of the species, and a comprehensive classification is still lacking. Several species appear closely related, including those with large flowers and corollas to 4 cm in diameter (approximately seven species), while the remaining species have smaller flowers and corollas about 15 mm in diameter or less. However, this grouping may be artificial and has no support from any rigorous phylogenetic analysis (Miller, 1999). Two fruit types are found in *Bourreria*, indehiscent drupes (ca. 25 species) and dry schizocarps (five species). This fruit character is unique in the entire Boraginales and argues unequivocally for the monophyly of the schizocarpous species group. Miers (1869) recognized its distinctiveness and segregated those species as *Crematomia* Miers.

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Table 1. Risk of extinction based on the IUCN Red List categories.

	Total no. of specimens	Total area of occurrence (km ²)	Total extent of occupancy (km ²)
<i>Bourreria baccata</i>	499	2988	2,476,206
<i>B. bolivarensis</i>	20	162	36,089
<i>B. costaricensis</i>	88	540	476,655
<i>B. exsucca</i>	88	666	308,352
<i>B. mollis</i>	180	1188	716,523

A review of herbarium specimens for the preparation of a comprehensive revision of *Bourreria* led to the present re-evaluation of the South American species. *Bourreria exsucca* Jacq. is epitypified, and a neotype has been designated to *Rhamnus cumanensis* Loeffl. Furthermore, new records of three otherwise Central American or Caribbean species are reported for the first time from South America, and the new species *B. bolivarensis* Gottschling & J. S. Mill. is described. Hypotheses on intraspecific variability of different organs and the distributions of the plants are presented.

The number of species in South America is relatively low but spans much of the morphological diversity found in *Bourreria*. In this revision, we discuss that the five South American representatives of *Bourreria* are a heterogeneous group of only distantly related species. Thus, the continent appears to have colonized several times independently from Central America and the West Indies, either by exceptional long-distance dispersal events due to their endozoochorous (drupes) or presumptively anemochorous fruits (schizocarps), or simply by migration.

IUCN CONSERVATION STATUS

Specimen data for all five species of *Bourreria* that occur in South America were reviewed and used to

calculate area of occurrence (AOO) and extent of occupancy (EOO) following IUCN (2001), and these values were used to estimate risk of extinction based on the IUCN Red List categories (Table 1). Only two of the five species that occur in South America are endemic, and the other three have significant parts of their ranges in Central America or the West Indies. All five species have EOOs above the threshold (> 2000 km²) to be considered vulnerable.

Although *Bourreria bolivarensis* has an AOO of 162 (below the < 500 km² threshold for endangered), *B. costaricensis*, *B. exsucca*, and *B. mollis* Standl. have AOOs below the 2000 km² threshold for vulnerability. This is likely due to a paucity of collections, rather than the rarity in the areas in which they occur. *Bourreria mollis*, for example, has been collected only infrequently south of Honduras, but it is abundant and frequently encountered in Belize and the Yucatán Peninsula of Mexico.

While the dry forest habitats in which four of the five South American species grow face tremendous threat, none of these species seem to have reached a threshold where they can be considered immediately threatened. Surveys of populations in the field will be required to confirm the provisional IUCN Red List assignments presented here (IUCN, 2001).

KEY TO *BOURRERIA* SPECIES IN SOUTH AMERICA BASED ON FLORAL CHARACTERS

- 1a. Flowers large; corolla mostly > 20 mm; tube long, usually > 15 mm 2
- 1b. Flowers small; corolla mostly < 20 mm; tube short, < 10 mm 3
- 2a. Style exserted, > 20 mm; calyx < 10 mm 4. *Bourreria exsucca*
- 2b. Style included, < 15 mm; calyx > 10 mm 3. *Bourreria costaricensis*
- 3a. Filaments at least slightly sericeous at their corolla tube insertion 2. *Bourreria bolivarensis*
- 3b. Filaments glabrous at their corolla tube insertion 4
- 4a. Style undivided; leaf apex predominantly rounded or obtuse 1. *Bourreria baccata*
- 4b. Style divided; leaf apex predominantly acuminate 5. *Bourreria mollis*

KEY TO *BOURRERIA* SPECIES IN SOUTH AMERICA BASED ON FRUIT CHARACTERS

- 1a. Fruits dry, schizocarpous (breaking into 4 units at maturity, each mericarpid attached to the gynobase by an apical fiber) 2
- 1b. Fruits drupaceous 3
- 2a. Fruits rather compact, with indistinct beak; coastal plants of Colombia and Venezuela 4. *Bourreria exsucca*
- 2b. Fruits rather slender, with prominent beak; Venezuelan plants of forest habitats south of the Orinoco River ... 2. *Bourreria bolivarensis*

- 3a. Fruits large, > 20 mm 3. *Bourreria costaricensis*
- 3b. Fruits small, < 15 mm 4
- 4a. Style undivided; leaf apex predominantly rounded or obtuse 1. *Bourreria baccata*
- 4b. Style divided; leaf apex predominantly acuminate 5. *Bourreria mollis*

TAXONOMY

Bourreria P. Browne, Civ. Nat. Hist. Jamaica: 168. 1756, nom. conserv. TYPE: *Bourreria baccata* Raf.
Morelosia Lex. in La Llave & Lex., Nov. Veg. Descr. 1: 1. 1824. TYPE: *Morelosia huanita* Lex. [= *Bourreria huanita* (Lex.) Hemsl.].
Crematomia Miers, Ann. Mag. Nat. Hist., Ser. IV, 3: 302. 1869. TYPE: *Crematomia cumanensis* (Loefl.) Miers (= *Bourreria exsucca* Jacq.).

Trees or shrubs; bark smooth or slightly striate when young, light to dark gray or brown, longitudinally fissured; indument absent or puberulent to velutinous or strigose, trichomes simple, unicellular, eglandular, or rarely glandular. Leaves alternate or fasciculate, deciduous or evergreen, simple, sometimes microphyllous, blade mostly elliptic to obovate, margin entire, texture membranaceous to coriaceous, venation brochidodromous, upper blade surface frequently with multicellular incrustations; stipules rare; petioles smooth or canaliculate on adaxial surface. Inflorescences terminal, rarely axillary, thyrsoid, fertile branching sympodial, lax or compressed, bracts and bracteoles frequent, leafy or inconspicuous. Flowers actinomorphic, bisexual, often fragrant, sessile or pedicellate; perianth 5-merous, buds ellipsoid or obovoid; calyx synsepalous, persistent, campanulate or tubular, coriaceous or membranaceous, dehiscence regular or irregular, perianth lobes valvate; corolla sympetalous, mostly white, predominantly membranaceous, rotate to funnel-shaped, dehiscence imbricate (quincuncial), tube short or elongate, lobes spreading or reflexed, mostly rounded, alternating with the sepals; stamens 5, antesepalous, epipetalous, well exerted or included, filaments adnate to corolla tube, anthers tetrasporangiate, narrowly elliptic or oblanceolate, dorsifixed, introrse, opening via longitudinal slits; ovary superior, sessile, bicarpellate, syncarpous, conical, with 4 ovules, style terminal, divided or undivided, stigmas 2 or rarely 1, ovary disc round, usually extensive, ovules anatropous, unitegmic. Fruits 4-seeded, indehiscent and drupaceous or schizocarpous and dry, exocarp thin or rarely extensive, mesocarp succulent or dry, endocarp separating into 4 pyrenes (endocar-pids), each usually with conspicuous abaxial lamellae, enclosing one seed and an additional sterile chamber, attached by an apical fiber (carphophore, originating from ventral vascular traces) to gynobase (columella) in schizocarpous fruits; testa with transfer cells (Diane

et al., 2002); embryo curved, endosperm copious, cotyledons flat. Chromosome number $n = 19$ (Al-Shehbaz, 1991).

1. *Bourreria baccata* Raf., Sylva Tellur.: 42. 1838.
Cordia bourreria L., Syst. Nat. ed. 10. 2: 936. 1759. *Ehretia bourreria* (L.) L., Sp. Pl. ed. 2. 1: 1.
Morelosia beureria Kuntze, Revis. Gen. Pl. 2: 439. 1891. *Bourreria bourreria* (L.) Huth, Helios 11: 133. 1893. TYPE: Jamaica. s. loc., s.d. (fl), *P. Browne* s.n. (lectotype, designated by Stearn, 1971: LINN 254.2!).

[Synonymy includes only names that have been considered for South American populations.]

Bourreria succulenta Jacq., Enum. Syst. Pl.: 14. 1760, nom. inval., Select. Stirp. Amer. Hist.: 44. 1763, descr. Syn. nov. TYPE: tab. 26 in Pl. 2, Observ. Bot., 1767, *N. J. Jacquin* (type, tab. 26 in Jacquin, 1767).
Bourreria recurva Miers, Ann. Mag. Nat. Hist., Ser. IV, 3: 203. 1869. Syn. nov. TYPE: Dominica, Saint John, Prince Rupert's Bay [at Portsmouth], 1792 (fl), *Lane* s.n. (holotype, BM 85833!; isotype, BM 85830!).

Trees or rarely shrubs, to 6 m, glabrous or with few scattered trichomes, lenticels few or absent. Leaves alternate, blade (0.6–)1.2–10.0(–13.4) × (0.4–)0.9–5.0(–7.7) cm, elliptic to obovate, frequently asymmetric, rarely widely obovate or ovate, texture coriaceous to membranaceous, primary vein sometimes very distinctively prominent, but also rather smooth, secondary veins (3)4 to 7(9), the tertiary veins reticulate or sometimes percurrent, occasionally inconspicuous, adaxial surface glabrous or with few trichomes at veins, frequently with multicellular incrustations, abaxial surface glabrous or with few trichomes at veins, apex rounded, acute, or apiculate, occasionally obtuse, retuse, or emarginate, base acute or cuneate, frequently asymmetric, sometimes decurrent, rarely obtuse; stipules absent; petioles (0.1–)0.2–1.1(–1.5) cm, slender, rarely robust, canaliculate on adaxial surface, rarely rather smooth, glabrous or with few scattered trichomes. Inflorescences 4.5–12 (–17.5) cm, terminal or rarely axillary, comprising usually to 10 flowers, but occasionally more (to more than 50), fertile branching sympodial, branches slender to robust, glabrous or with few trichomes, bracts frequent, leafy, bracteoles rare, if present leafy or small, lanceolate, and velutinous. Flowers fragrant, pedicels to 11 mm, but mostly shorter, buds widely obovoid, slightly apiculate; calyx (5–)6–8 mm, campanulate or sometimes tubular, coriaceous, indurate and frequently striate in fruit, glabrous or with few

trichomes outside, tomentose at tips inside, sometimes only at margin, usually regularly divided, but irregularly (into 3 + 2 or occasionally 2 + 2 + 1) almost to base in fruit, lobes 3 to 5, 1–3 mm, acute; corolla 9–13(–14) mm, funnel-shaped, membranaceous, white, the tube 5–8(–9) mm, funnel-shaped or rarely tubular, sometimes broadened at base, glabrous on both surfaces, the lobes 3–6 mm, rounded or obtuse, glabrous, papillose, slightly strigose outside, glabrous inside; stamens well or rarely slightly exerted, the filaments 8–12(–13) mm, glabrous, adnate to corolla tube for 3–6(–8) mm, anthers 1–2 mm; ovary glabrous, style (6–)7–10 mm, well exerted, undivided or rarely branches to 1 mm long, stigma capitate, sometimes significantly broader than width of style, ovary disc present. Fruits 6–10 × (7–)9–11 × 5–8 mm, drupaceous, widely to depressed ovoid, red, orange, or yellow, exocarp thin, mesocarp succulent, voluminous, pyrenes 4–6 × 2–4 × 2–3 mm, shape 1/4 of a sphere, abaxial surface with 5 to 6 conspicuous lamellae and additionally with some vertical ridges.

Distribution and habitat. *Bourreria baccata* is a widely distributed Caribbean species ranging from Tobago through the Lesser Antilles to the Greater Antilles and Mexico. An isolated population can be found on the Netherlands Antilles, specifically in Curaçao, Bonaire, and Aruba, with a few records from the adjacent Venezuelan mainland as well. *Bourreria baccata* occurs from sea level to elevations of 300 m.

IUCN Red List category. This species is known on the South American mainland from only two Venezuelan collections, but it occurs on the Netherlands Antilles and Trinidad and Tobago, and it is widespread and commonly collected throughout the West Indies. It is provisionally assigned an IUCN status of LC (Least Concern) (IUCN, 2001).

Notes. The description given here refers to material from the Netherlands Antilles and Venezuela, where the plants have smaller leaves generally, fewer flowers in the inflorescence, and larger flowers than found in the Lesser Antilles. *Bourreria baccata* is highly variable (Stearn, 1971) in leaf shape and indument, but especially in the sizes of the different organs. It remains to be determined whether *B. baccata* is really distinct from other Caribbean species such as *B. virgata* (Swartz) G. Don. Schulz (1911) used the depth of the division of the style to differentiate between the Caribbean species. However, this character can be variable within species of *Bourreria* (Gottschling & Miller, 2007), with undivided styles seen in most individuals of *B. baccata*, but occasionally individuals with divided styles occur (e.g.,

Arnoldo 1193, GH), which are rarely on the same plant (*von Proosdij et al.* 519, GH).

Additional specimens examined. NETHERLANDS ANTILLES. **Aruba:** Spanish Lagoon, *Chamberlaine* 36 (GH). **Bonaire:** Ceru Largu, *Arnoldo-Broeders* 3730 (A); Montagne, *Stoffers* 373 (A). **Curaçao:** *Arnoldo* 1193 (A), *Curran & Haman* 49 (BM, CAL, F, GH, K, S), *Curran & Haman* 243 (GH), *Killip & Smith* 21057 (BM, F, GH), *Stoffers* 216 (A, GH); Soto, *Arnoldo-Broeders* 3799 (GH, NY); near Willemstad, *Britton & Shafer* 2965 (F, GH); Jan Thiel, *Morton s.n.* 1970 (BM); Christoffelpark, *van Proosdij et al.* 519 (A); St. Willibrord, *Stoffers* 373 (K). TRINIDAD AND TOBAGO. **Tobago:** near Stoer Bay, *Broadway* 9166 (BM, GH, MO); Bacolet, *Eggers* 5517 (GH, K, S), *Howard* 10455 (BM, GH), *Purseglove* P.6207 (K, US); Pigeon Point, *Philcox & Raynal* 7898 (K). VENEZUELA. **Falcón:** San Rafael, *Bellestros* MB358 (MA); Santa Ana, *Steyermark & Brown* 94596 (GH, P); Silva, *Steyermark & Manara* 110383 (MO, VEN); Paraguaná, *Tamayo* 799 (F).

2. *Bourreria bolivarensis* Gottschling & J. S. Mill., sp. nov. TYPE: Venezuela. Bolívar: San Pedro de las Dos Bocas, 7 km N of jct. of Río Paragua and Caroni, 7°00'N, 62°54'W, 200 m, 27 July 1978 (fl, fr), *R. Liesner & A. C. González* 5719 (holotype, MO 2742482!). Figure 1.

Arbor vel frutex usque ad 12 m alta. Lamina glabra, elliptica, 2–8 cm longa, 1–4 cm lata, apice basique acuta; folia petiolo ca. 0.2–0.9 cm longo, glabro. Inflorescentia terminalis, thyrsioidea. Flos fragrans; calyce 4–7 mm longo, intus tomentosus; corolla alba, campanulata, 12–18 mm longa, 5-loba, tubo 3–6 mm longo, lobulis ovatis, 6–10 mm longis; filamentis ad insertionem puberulis. Fructus exsuccus, elongato-pyriformis, 13–20 mm altus.

Trees or rarely shrubs, to 12(–20) m, glabrous or varying tomentose, lenticels rare. Leaves fasciculate or alternate, blade (0.4–)2.0–8.0(–11.5) × (0.3–)1.0–4.0(–6.0) cm, elliptic to obovate, sometimes asymmetric, rarely ovate or widely elliptic to widely obovate, apex obtuse, acute, or apiculate, occasionally acuminate or retuse, base acute or obtuse, occasionally decurrent or asymmetric, texture membranaceous to coriaceous, primary vein prominent or sometimes rather smooth, secondary veins 4 to 6(8), tertiary veins reticulate or sometimes percurrent, adaxial surface glabrous or with few trichomes, rarely with multicellular incrustations, abaxial surface glabrous or with few trichomes; stipules absent; petioles 0.2–0.9(–1.4) cm, slender, rarely robust, smooth or adaxially canaliculate, glabrous to varying tomentose. Inflorescences 3–9(–12) cm, terminal or sometimes axillary, comprising 5 to 20(30) flowers, fertile branching sympodial, branches slender or occasionally robust, glabrous to varying tomentose, bracts frequent, leafy, bracteoles rare, if present leafy or small, lanceolate, velutinous. Flowers fragrant, pedicel to 6 mm, but mostly shorter, buds widely obovoid, distinctively apiculate; calyx campanulate, 4–7 mm, coriaceous to

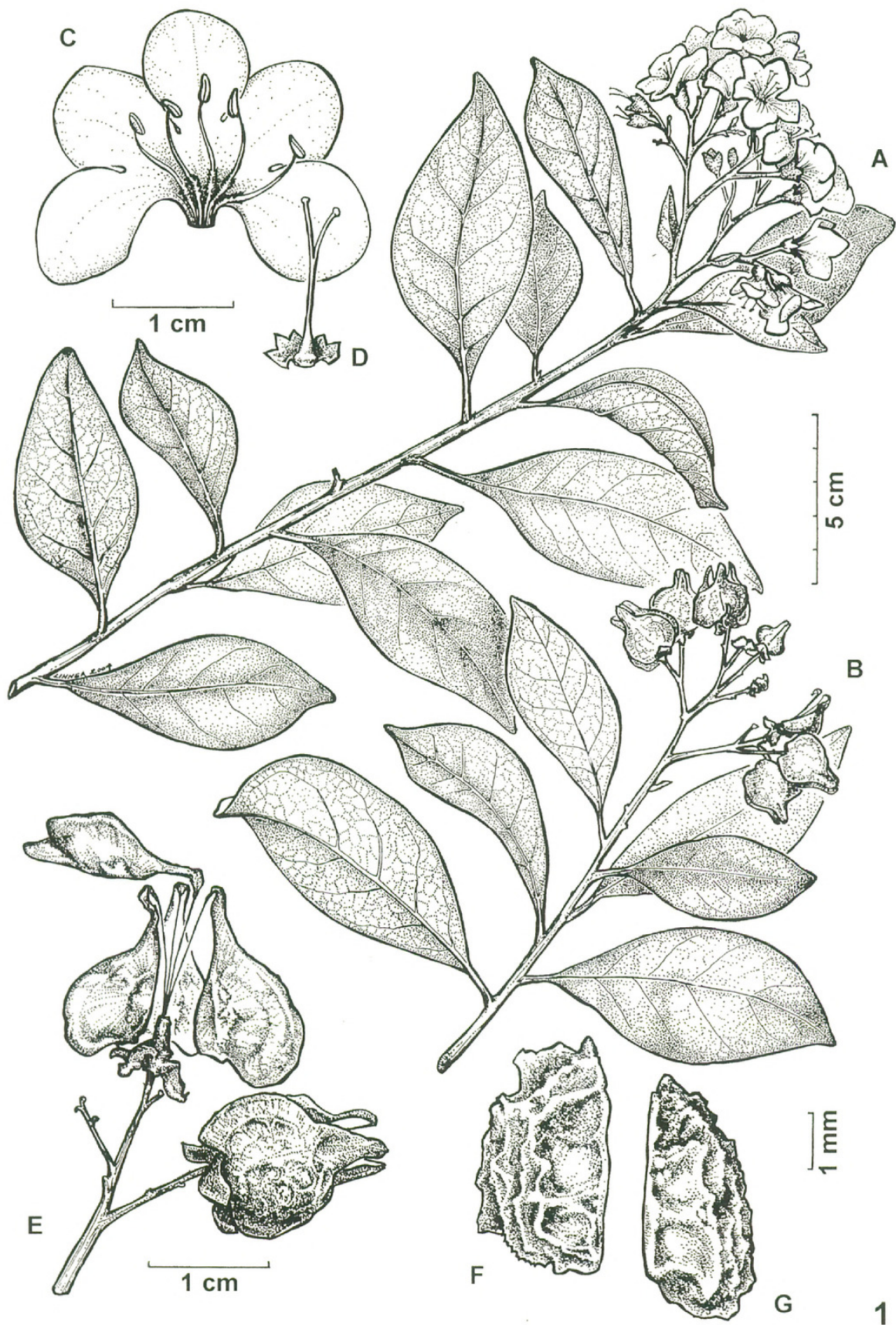


Figure 1. *Bourreria bolivarensis* Gottschling & J. S. Mill. —A. Flowering branch. —B. Fruiting branch. —C. Open corolla with stamens (note the hairy filaments at the point of insertion). —D. Open calyx with gynoecium. —E. Schizocarpous fruits (note the single mericarps with the apical fiber attached to the gynobase). —F, G. External surface of pyrene showing overlapping lamellae. A, *Davidse 4431* (MO); B and E, *Liesner & Gonz  les 5719* (MO); C and D, *Gentry et al. 10647* (MO); F and G, *Colella & Melina 1413* (MO).

membranaceous, sometimes indurate in fruit, glabrous or with few scattered trichomes outside, with few trichomes to tomentose at tips inside, rather regularly divided (almost to base in fruit), lobes (2)3 to 4, 1–3 mm, acute or acuminate, rarely obtuse, frequently brown and dry at tips, reflexed in fruit; corolla (10–)12–18(–20) mm, campanulate, membranaceous, glabrous on both surfaces, white or creamy, tube 3–6(–8) mm, funnel-shaped to campanulate, lobes (3–)6–10 (–12) mm, rounded; stamens well exerted, filaments 9–13(–17) mm, occasionally with some glandular trichomes, sericeous or at least with few trichomes at point of insertion for 1–3 mm, adnate to corolla tube for 2–4 mm, anthers 2–3 mm; ovary glabrous, style (8–)9–14(–17) mm, well exerted, divided, branches 1–4 mm, stigma capitate, ovary disc present. Fruits (11–)13–20 × (10–)12–19 × (8–)10–14 mm, schizocarpous, distinctively 4-angled, elongate pyriform, brown, gynobase 2–3 mm, carpophore (7–)9–12 mm, exocarp thin, mesocarp spongiose, dry, pyrenes 4–6 (–7) × 2–3 × 2 mm, shape 1/4 of a sphere, abaxial surface with 3 to 4 inconspicuous lamellae, reticulate.

Distribution and habitat. *Bourreria bolivarensis* grows in tropical wet forests, gallery forests, and adjacent savannahs in elevations 20–700 m and is geographically isolated from *B. exsucca* by the valley of the Orinoco River.

IUCN Red List category. This species is widely distributed in southeastern Venezuela, and its EOO is sufficient to provisionally assign this the IUCN status of LC. Although its AOO of 162 km² is below the threshold of 500 km², which would indicate EN (Endangered) status, this most likely reflects the paucity of collections made in the area and not the rarity of the plant; additional fieldwork will be necessary to confirm this provisional assignment (IUCN, 2001).

Notes. *Bourreria bolivarensis* may be the sister species of *B. exsucca*. Both are similar in appearance, but the most important difference between them is the distinctively shorter corolla tube of *B. bolivarensis* (3–6 mm vs. 15–19 mm in *B. exsucca*). Furthermore, fruits of *B. bolivarensis* appear more slender and have a more prominent beak than those of *B. exsucca*. The Guayana region south of the Orinoco River differs environmentally from coastal Venezuela and Colombia. The peculiar montane physiography of the Guayana region influences many of its floristic and ecological features (Berry et al., 1995). Such different habitat preferences also separate *B. bolivarensis* and *B. exsucca*.

Paratypes. VENEZUELA. **Bolívar:** betw. Botanamo & Comino, *Bernardi* 8055 (K); Sifontes, 3 km NE of Campto, *M. Colella* & *G. Molina* 1413 (MO); 10 km SW of Río Aro, betw.

Caicara & Ciudad Bolívar, *G. Davidse* 4481 (MO); Caroní, *W. A. Diaz* 3001 (MO); Piar, *C. Benítez* & *W. G. D'Arcy* 5303 (MO), *Fernandez* 2779 (MO); 10 km E of Ciudad Bolívar, *A. H. Gentry et al.* 10411 (MO); Tumeremo to Anacoco (N side of Cuyuni River), 72 km from Guyana frontier at Anacoco, *A. H. Gentry et al.* 10647 (MO); 18 km N of Upata, *A. H. Gentry* & *P. E. Berry* 14921 (AAU, MO); Rocio, *B. Stergios et al.* 3516 (MO); Carr. Casa Blanca (Tumeremo), *B. Stergios et al.* 3824 (MO); Reserva Forestal Imataca, *B. Stergios et al.* 3854 (MO), *B. Stergios et al.* 3866 (MO); betw. Upata & Altigracia, *J. A. Steyermark* 57726 (F); E of Miamo, *J. A. Steyermark* 88217 (F); La Paragua, *L. Williams* 12803 (F, S, U).

3. *Bourreria costaricensis* (Standl.) A. H. Gentry, *Phytologia* 26: 67. 1973. *Schlegelia costaricensis* Standl., *Publ. Field Mus. Nat. Hist., Bot. Ser.* 18: 1128. 1938. TYPE: Costa Rica. Alajuela: Cataratas de San Ramón, 6 Mar. 1931 (fl), *A. M. Brenes* 13570 (holotype, F 857116!; isotype, NY 22213!).

Bourreria panamensis I. M. Johnst., *J. Arnold Arbor.* 29: 229. 1948. *Bourreria superba* var. *glabra* Schery, *Ann. Missouri Bot. Gard.* 29: 366. 1942. TYPE: Panama. Bocas del Toro: Laguna de Chiriquí on Isla Colón, 3 June 1941 (fl), *H. v. Wedel* 2472 (holotype, GH 94387 not seen; isotypes, MO 1245306!, NY 126858!).

Trees, to 17 m, glabrous, lenticels absent. Leaves alternate, rarely subopposite, blade 7.0–17.5 × 5.1–9.7 cm, elliptic to widely obovate, frequently asymmetric, apex acuminate, but also apiculate, rounded, or retuse, base cuneate or acute, frequently asymmetric, texture coriaceous, rarely membranaceous, primary vein prominent, secondary veins 4 to 5(7), tertiary veins reticulate or rarely percurrent, both surfaces glabrous; stipules absent; petiole 1.0–2.5 cm, robust, canaliculate on adaxial surface, glabrous. Inflorescences 8 cm, terminal or rarely axillary, comprising up to 10 flowers, but frequently only 1 to 3 developed, fertile branching sympodial, branches robust, glabrous, bracts frequent, leafy, bracteoles absent. Flowers fragrant, pedicels to 15 mm; calyx 12–17 mm, campanulate, coriaceous, indurate and striate in fruit, glabrous outside, tomentose at tips inside, irregularly divided (into 3 + 2 lobes) almost to base in fruit or rarely rather regularly divided, lobes 4–6 mm, acute; corolla 38–47 mm, funnel-shaped, membranaceous, white or creamy, papillose outside, tube 20–25 mm, funnel-shaped, glabrous or with some curly trichomes (especially at level of anthers) inside, lobes 17 mm, rounded or obtuse, papillose inside; stamens included, filaments 15 mm, adnate to corolla tube for 4 mm, hirsute at point of insertion, anthers 2–3 mm; ovary glabrous, style 12–14 mm, included, branches 2–3 mm, stigma capitate, often significantly broader than width of style, ovary disc present. Fruits 28 × 33 × 10 mm, drupaceous, globose when young, later cylindrical, exocarp very extensive, mesocarp scanty, pyrenes 20 × 12 × 6 mm, shape of half of

a cylinder, abaxial surface with 5 to 7 conspicuous lamellae, additionally with some vertical ridges.

Distribution and habitat. *Bourreria costaricensis* occurs mainly at elevations between 800 and 1650 m in Nicaragua, Costa Rica, and Panama, with a few records also from Colombia. Its possible occurrence in Ecuador is inferred from one questionable record (Rubio & Quelal 1444, MO), which has only one very small flower and is tentatively assigned to this species.

IUCN Red List category. Although known from only a few widely scattered localities in Colombia and possibly Ecuador, this species is frequently collected in several protected areas in Costa Rica. Although its AOO is below the threshold for VU (Vulnerable), the combination of its large EOO with multiple populations that are known from protected areas support a provisional assignment of LC (IUCN, 2001).

Notes. *Bourreria costaricensis* is distinct in its unusually large flowers, and it has the largest drupes of any species of *Bourreria*. The variability of the species in size of vegetative and generative organs appears greater on the Central American mainland than in South America, as can be inferred from the small amount of South American collections. The closest relative is probably *B. grandicalyx* J. S. Mill. & Sirot, and their ancestor might have colonized secondarily wet forest habitats of southern Central America and South America. *Bourreria costaricensis* and *B. grandicalyx* appear to be derived from similar plants as *B. mollis* by enlargement of flowers and fruits. The relationship to other species with large flowers and/or drupes of *Bourreria* such as *B. moaensis* Britton from Cuba and *B. huanita* (Lex.) Hemsl. from Central America remains to be determined. However, the synonymous *B. panamensis* I. M. Johnst. is clearly not closely related to *B. superba* I. M. Johnst. from northern Mexico, even though Woodson and Schery (1942) initially described it as a variety of *B. superba*. The Mexican species has a densely velutinous interior calyx, which it shares with *B. huanita*, but which is not present in *B. costaricensis*.

Additional specimens examined. COLOMBIA. **Chocó:** Bahía Solano. *Espina et al.* 2860 (MO); Nuquí-Pangui. *Gómez et al.* 389 (HUA, MO). **Valle del Cauca:** Isla de Gorgona. *Cabrera* 3241 (CUVC).

4. *Bourreria exsucca* Jacq., Enum. Syst. Pl.: 14. 1760, nom. inval., Select. Stirp. Amer. Hist.: 45. 1763, descr. *Ehretia exsucca* (Jacq.) L., Sp. Pl. ed. 2. 1: 275. 1762. *Morelosia exsucca* (Jacq.) Kuntze, Revis. Gen. Pl. 2: 439. 1891. TYPE: tab. 173, fig. 17 in Select. Stirp. Amer. Hist., 1763,

N. J. Jacquin (type, tab. 173, fig. 17 in Jacquin, 1763). [EPITYPE: Colombia. Bolívar: Isla Barú, 10°09'N, 75°41'W, 5 m, 6 Aug. 1985 (fl, fr), *J. L. Zarucchi & H. Cuadros* 3951 (epitype, designated here, MO 3506236!; duplicate, JBG not seen).] Figure 2A.

Rhamnus cumanensis Loebl., Iter Hispan.: 182. 1758. Syn. nov. *Crematomia cumanensis* (Loebl.) Miers, Ann. Mag. Nat. Hist., Ser. IV, 3: 302. 1869. TYPE: Venezuela. Nueva Esparta: Isla de Margarita, El Valle, 15 July 1988 (fl, fr), *J. R. Johnston* 86 (neotype, designated here, GH!). Figure 2B.

Crematomia guildingiana Miers, Ann. Mag. Nat. Hist., Ser. IV, 3: 304. 1869. *Morelosia guildingiana* (Miers) Kuntze, Revis. Gen. Pl. 2: 439. 1891. TYPE: Grenadines, Saint Vincent: Botanical Garden (cult., from the South American mainland), *L. Guilding* s.n. (holotype, K!).

Crematomia jacquiniana Miers, Ann. Mag. Nat. Hist., Ser. IV, 3: 305. 1869. Syn. nov. TYPE: Colombia. Bolívar: Cartagena, s.d. (fl), *N. J. Jacquin* s.n. (holotype, BM 85819!).

Crematomia kunthiana Miers, Ann. Mag. Nat. Hist., Ser. IV, 3: 311. 1869. *Bourreria cumanensis* var. *kunthiana* (Miers) O. E. Schulz, in Urb., Symb. Antill. 7: 50. 1911. TYPE: Venezuela. Sucre: near Cumana, Llanos de Barcellona, 1799 (fl), *A. v. Humboldt & A. Bonpland* 101 (holotype, P-Bonpl., IDC 6209 63/19).

Trees or rarely shrubs, to 12 m, indument absent or rarely varying tomentose, lenticels frequent. Leaves alternate or fasciculate, blade (0.5–)0.8–7.3(–11.2) × (0.2–)0.5–4.0(–7.4) cm, elliptic to obovate, ovate, occasionally asymmetric, rarely widely elliptic to widely obovate, apex obtuse, acute, or apiculate, sometimes acuminate, rounded, retuse, or emarginate, base acute or obtuse, occasionally decurrent or asymmetric, texture membranaceous to slightly coriaceous, primary vein prominent or sometimes rather smooth, secondary veins 4 to 7(9), tertiary veins reticulate or sometimes percurrent, occasionally inconspicuous, adaxial surface glabrous or with few scattered trichomes, frequently with multicellular incrustations, rarely tomentose or somewhat scabrid, abaxial surface glabrous or with few trichomes at veins, rarely tomentose; stipules absent; petiole (0–)0.1–1.4(–1.8) cm, slender or robust, canaliculate on adaxial surface, glabrous or with few trichomes, rarely tomentose. Inflorescence (3–)6.5–10.0(–13) mm, terminal or sometimes axillary, comprising 15 to 20(30) flowers, fertile branching sympodial, sometimes compressed, branches slender or robust, glabrous or with few scattered trichomes, rarely tomentose, bracts frequent, leafy, bracteoles rare, if present leafy or small, lanceolate, and velutinous. Flowers fragrant, pedicels to 8 mm, but mostly shorter, buds ellipsoid or obovoid, distinctively apiculate; calyx (5–)7–9

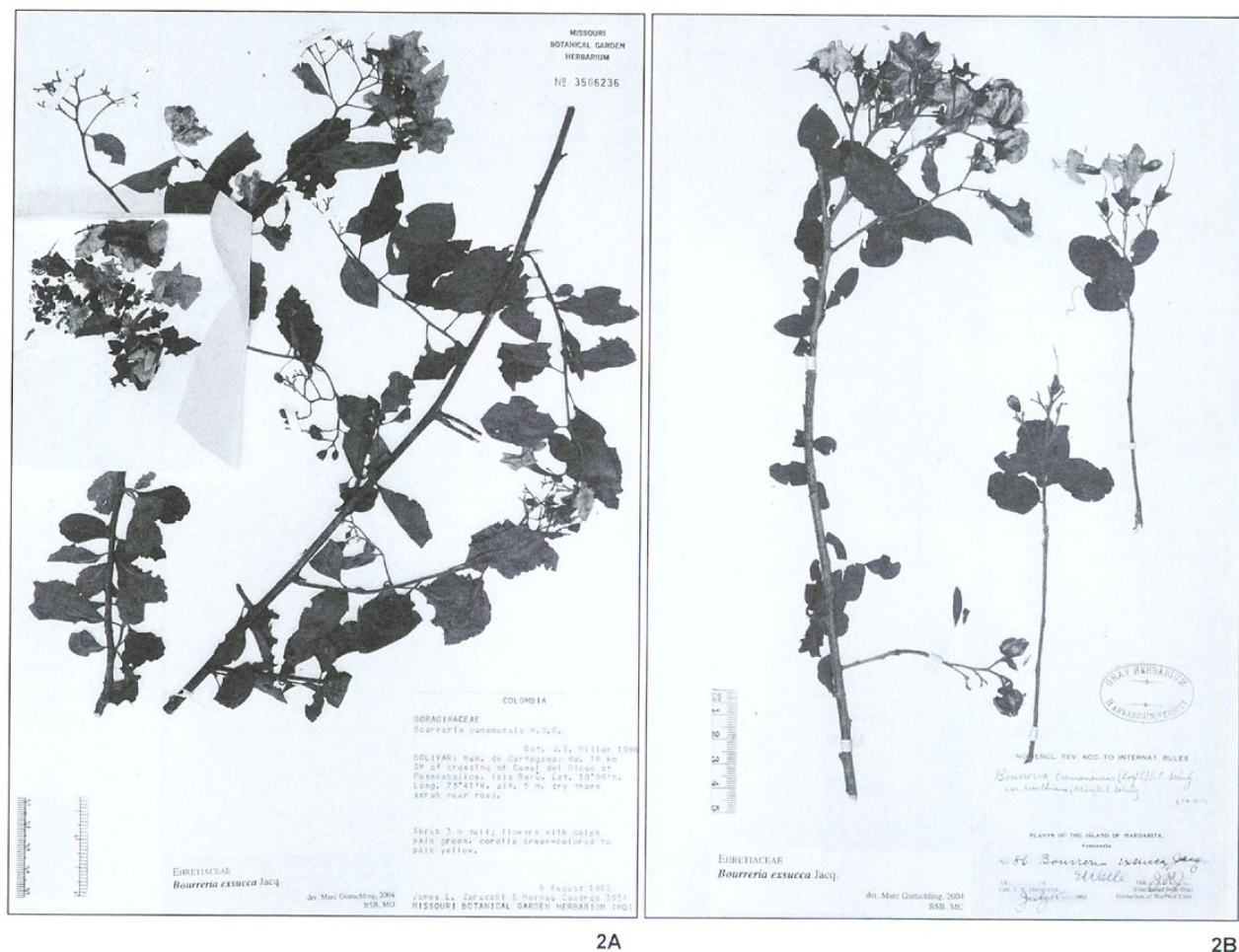


Figure 2. —A. Epitype of *Bourreria exsucca* Jacq. (*Zarucchi & Cuadros 3951*, MO 3506236). —B. Neotype of *Bourreria cumanensis* (Loefl.) O. E. Schulz (*Johnston 86*, GH).

(-11) mm, campanulate, coriaceous to membranaceous, indurate and sometimes striate in fruit, glabrous or with few scattered trichomes outside, tomentose at tips inside, rather irregularly divided (almost to the base in fruit), lobes 2 to 4(5), 1-4 mm, acute or acuminate, rarely obtuse, frequently brown and dry at tips, reflexed in fruit; corolla (20-)24-30(-40) mm, funnel-shaped or sometimes campanulate, membranaceous, glabrous on both surfaces, tube (12-)15-19(-22) mm, yellow, lobes (5-)9-12(-16) mm, rounded or obtuse, white, creamy, or pale yellow; stamens usually well exserted, filaments 23-29(-32) mm, occasionally with some glandular trichomes, sericeous at point of insertion for (3-)4-5(-7) mm, adnate to corolla tube for 3-4 mm, anthers 2-3 mm; ovary glabrous, style (17-)23-28(-34) mm, well exserted, divided, branches (2-)4-5(-7) mm, stigma capitate, ovary disc present. Fruit 14-23 × 14-25 × 9-20 mm, schizocarpous, evidently and strongly 4-angled pyriform, brown, gynobase (2-)3-4 mm, carpophore 9-12(-14) mm, exocarp thin, mesocarp spongy, dry, pyrenes 5-6(-7) × 3(-5)

× 2-3(-4) mm, shape 1/4 of a sphere or 1/2 of a cylinder, abaxial surface with 3 to 5 inconspicuous lamellae, reticulate.

Distribution and habitat. *Bourreria exsucca* is the most frequently encountered South American species, and it is found in dry coastal areas or occasionally in wet forests of Colombia to Venezuela from sea level to elevations up to 500(-2315) m. It is geographically isolated from the other schizocarpous species (*B. boliviarensis* in South America; *B. quirosii* Standl., *B. andrieuxii* (DC.) Hemsl., and *B. pulchra* (Mills) in Central America).

IUCN Red List category. Although this species has an AOO below the threshold for consideration as VU, it is widespread and has a large EOO. It also seems to occur in disturbed habitats and is hence best provisionally assigned to LC (IUCN, 2001).

Notes. The species is highly variable in size (leaves, corollas, fruits), shape (leaves), and indument (leaves, inflorescences), but it is distinct from the

other South American species by the combination of the large flowers, with a long tube, and the schizocarpous fruits.

Bourreria exsucca was first described as *Rhamnus cumanensis*, but Schulz's (1911) transfer to *Bourreria* was illegitimate, because Gürke (1893) had already used the combination *B. cumanensis* (DC.) Gürke, which is a heterotypic synonym of *Tournefortia hirsutissima* L. (Miller, 1989).

Pehr Löfving (1729–1756), an ambitious Linnaean student, collected plants with Benito Paltor in Venezuela in 1754. He described *Rhamnus cumanensis*, presumably based on material he collected in Cumaná and near the Franciscan mission in Píritu at Mt. Unare in Sucre. Löfving's surviving collections were deposited at LINN after his early death in 1756, but some of his collections, including those of this species, appear to be among those lost when a ship sank (Stafleu, 1971). In his catalogue of the Linnaean herbarium, Jackson (1912) includes the name *R. cumanensis* in italics, indicating that he was unable to locate a specimen. Johnston 86 (GH; Fig. 2B) is selected here as a neotype of *Bourreria cumanensis*, since it was collected close to the type locality specified in the protologue, where only one species of *Bourreria* occurs.

Bourreria exsucca was first described by Nicolaus Joseph von Jacquin (1729–1817) in 1763 but without clear designation of a type specimen. D'Arcy (1970) indicates that types of Jacquin names were most frequently found among collections at BM, LINN, MA, and W, but no Jacquin collections were located in these holdings. Jacquin illustrated many plants in the field, from which the Austrian artist Joseph Wagner (1706–1780) produced copper engravings (Stafleu in Jacquin, 1971). Jacquin may have never collected physical material for *B. exsucca*. However, the information available from the type is of limited utility, although the drawings of a flower and a fruit are consistent with Jacquin's protologue, so Zarucchi & Cuadros 3951 (MO) is selected as an epitype for *B. exsucca*. It was collected near the type locality (Cartagena), where only one species of *Bourreria* occurs, and it helps clarify the morphological circumscription of the species.

Additional specimens examined. COLOMBIA. **Atlántico:** near Baranquilla, Dugand 429 (F); betw. Ponadera & Santa Rita, Dugand 686 (F). **Bolívar:** Cartagena, Isla Barú, Gentry & Cuadros 47649 (MO); Manga Island, Cartagena, Killip & Smith 14005 (GH), Killip & Smith 14014 (GH); La Popa, near Cartagena, Killip & Smith 14053 (GH); Cartagena, Zarucchi & Cuadros 3928 (MO). **Guajira:** rd. betw. Riohacha & Cuestecitas, Cuadros 2380 (COL, MO). **Magdalena:** El Callao, Cuatrecasas & Castaneda 24943 (COL, F); N of La Paz, Haught 3874 (F, GH, S); near Riohacha, Haught 4415 (COL, GH, P).

Sucre: rd. betw. Colosó & Chalan, Ovejas, Cuadros & Gentry 4668 (JBGP, MO). **TRINIDAD AND TOBAGO.** **Chacachacare Island:** Comeau & Johnson 1992 (BM). **VENEZUELA.** **Anzoátegui:** Bahía de Mochima & Puerto La Cruz, Aristeguieta & Agostini 5571 (MO); Bruzual, Castillo & Franca 2969 (MO), Hwy. 9, Km 262, E of Barcelona, Croat 53926 (MO); Guanta, Curran & Haman 1233 (GH); Sotillo, Steyermark, Espinoza & Manara 107723 (MO). **Aragua:** E of Tejerías, Steyermark 56883 (F). **Distrito Federal:** Vargas, Castillo 2459 (MO), Castillo 2488 (MO); old rd. La Guaira–Caracas, Plowman 7653 (F); Caracas, Williams 12258 (F, GH, K, U); Silla de Caracas, Williams 12358 (F, GH). **Falcón:** La Ciénaga, Breteler 4379 (B, F, M, MA, MO, P); La Vela de Coro, Curran & Haman 426A (GH); Paraguana Peninsula, Curran & Haman 589 (GH); near Pueblo Zazárida, Liesner & Gonzáles 6024 (MO). **Guárico:** Altavracia, Aristeguieta 6079 (MO); 6 km S of Ortiz, Bunting 2206 (GH); 3 km W of Paso Real, Davidse 4195 (MO); 1 km from Est. C.A.N.T.V., Puebla 24 (MO, VEN); Roscio, Rodríguez 43 (F). **Lara:** Barquisimeto, Alston 6361 (F, GH), Pittier 13 (GH); 1 km N of Cabudare, Meijer & Burand 6 (MO); 20 km SW of Barquisimeto, Steyermark 56830 (F, GH). **Miranda:** near Tovar, Fendler 920 (GH); Santa Teresa, Johnson 3638–85 (MO). **Monagas:** Caicara de Maturín, Cardozo 512 (F, MY). **Nueva Esparta:** Isla de Margarita, Billiet & Jadin 7973 (MO), Miller & Johnston 10 (BM, F, GH, MO), Steyermark et al. 130918 (MO), Sugden 1299 (MO). **Sucre:** Golfo de Cariaco, Billiet & Jadin 7952 (MO); Cristobal Colon, Broadway 468 (GH); Río Caribe, Curran & Haman 1268 (GH); Las Piedras, Hahn & Grifo 3371 (MO); Peninsula de Araya, Liesner & Gonzáles 11977 (MO, WIS); Peninsula de Paria, Milliken et al. 123 (MO); Cabo Blanco, Pittier 10209 (GH); Ortiz, Roberston & Austin 189 (MO); betw. Saucedo & Cariaco, Rojas 884 (F); Isla Caracas del Este, Steyermark et al. 108342 (MO); Peninsula de Araya, Trujillo & Ponce 18639 (MO). **Testigos Islands:** s. loc., Ferry 1909 (F). **Trujillo:** La Vera, betw. Valera & S. Antonio vía Barquisimeto, Gaviria 487 (M). **Yaraeuy:** 3 km W of Yaritagna, Gentry & Puig-Ross 14227 (MO). **Zulia:** Mara, Carnevali & Lobo 679 (MO), Steyermark et al. 122987 (MO), Steyermark et al. 123038 (MO), Maracaibo Bot. Garden, Gentry 41256 (MO).

5. *Bourreria mollis* Standl., Trop. Woods 8: 5–6. 1926. TYPE: Belize, s. loc., s.d. (fl), H. W. Winzerling III–12 (holotype, US 1266030!; isotypes, F not seen, GH 94385!, NY!).

Bourreria oxyphylla Standl., Trop. Woods 16: 40–41. 1928. Syn. nov. TYPE: Belize, Cayo: San José, Nov. 1927 (fl), J. B. Aitken 4 (holotype, F 572622!; isotype, K!).

Bourreria wagneri Standl. in Yunck., Field Mus. Nat. Hist., Bot. Ser. 9: 328. 1940. TYPE: Honduras, Atlántida: La Ceiba, 23 July 1938 (fl. fr), T. G. Yuncker, J. M. Koepper & K. A. Wagner 8608 (holotype, F 941533!; isotypes, BM 85866!, GH 94393!, MO 1194412!, NY 334954!, NY 334955!, US 1747931!).

Trees, to 12 m tall, glabrous, lenticels absent. Leaves alternate, blade 3.5–10.0 × 1.5–5.0 cm, elliptic to obovate, occasionally asymmetric, apex acuminate, apiculate, rarely rounded or retuse, base acute, frequently asymmetric or decurrent, texture membranaceous to coriaceous, primary vein promi-

nent or rarely rather smooth, secondary veins 6 to 7, tertiary veins reticulate or sometimes percurrent, both surfaces glabrous; stipules absent; petioles 0.3–1.3 cm, slender, canaliculate on adaxial surface or rarely rather smooth, glabrous. Inflorescence 5–8.5 (–14) cm, terminal, comprising up to 50 flowers (or sometimes more), fertile branching sympodial, branches slender, glabrous, bracts frequent, leafy, bracteoles mostly absent. Flowers with pedicels to 3 mm, buds obovoid, slightly apiculate; calyx 5–6 mm, campanulate, coriaceous, glabrous or with few scattered trichomes outside, tomentose at tips inside, usually regularly divided, but irregularly (3 + 2) almost to base in fruit, lobes 5, 1–2 mm, acute, base narrowly cylindrical for 1–2 mm; corolla 10–12 mm, funnel-shaped, membranaceous, glabrous on both surfaces, white, tube 3–5 mm, tubular, sometimes broadened at base, lobes 5, 4–6 mm, rounded or obtuse; stamens well exerted, filaments (5–)8–9 mm, glabrous, adnate to corolla tube for (1–)3–4 mm, anthers 1–2 mm; ovary glabrous, style 8–9 mm, well exerted, divided, branches 3–4 mm, stigma capitate, ovary disc present. Fruits 7–9 × 8–9 × 7–9 mm, drupaceous, depressed ovoid, exocarp thin, mesocarp succulent, voluminous, pyrenes ca. 7 × 4 × 4 mm, shape 1/4 of a sphere, abaxial surface with 4 to 5 conspicuous lamellae and additionally with some vertical ridges.

Distribution and habitat. *Bourreria mollis* is highly variable and occurs mainly in Mexico, Belize, and Guatemala, but a few collections are found in Honduras, Panama, and Colombia.

IUCN Red List category. *Bourreria mollis* is a Central American species with a distribution that barely extends into South America. It occurs in scattered populations and is only rarely collected at the southern end of its distribution. However, it is very common and abundant in Belize and the Yucatán Peninsula of Mexico. The EOO of *B. mollis* is large, and it is provisionally assigned to LC, although its AOO is below the threshold for VU (IUCN, 2001).

Notes. *Bourreria mollis* is most closely related to a group of Caribbean species comprising *B. baccata* and its relatives (here referred to as *B. baccata* species group). Flowers and fruits of *B. mollis* are similar to those of other species of the *B. baccata* species group, but the species can be readily distinguished by leaf morphology. *Bourreria baccata* has broader leaves, with mostly rounded or retuse apices borne on robust petioles. *Bourreria mollis* has leaves that are narrower, with acuminate or apiculate apices borne on most frequently slender petioles. Further-

more, the base of the calyx is evidently constricted in *B. mollis*. This character is otherwise rarely found in *Bourreria*.

Additional specimens examined. COLOMBIA. **Antioquia:** Caucasia, *Brant & Escobar 1234* (HUA, MO), *Callejas et al. 4435* (F, MA, MO).

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