



Two New Species of *Burmeistera* (Campanulaceae: Lobelioideae) from the Cordillera de Talamanca of Costa Rica and Panama, with a Key to the Central American Species

Authors: Lagomarsino, Laura P., Aguilar, Daniel Santamaría, and Muchhala, Nathan

Source: Systematic Botany, 40(3) : 914-921

Published By: The American Society of Plant Taxonomists

URL: <https://doi.org/10.1600/036364415X689339>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Two New Species of *Burmeistera* (Campanulaceae: Lobelioideae) from the Cordillera de Talamanca of Costa Rica and Panama, with a Key to the Central American Species

Laura P. Lagomarsino,^{1,4} Daniel Santamaría Aguilar,² and Nathan Muchhala³

¹Department of Organismic and Evolutionary Biology, 22 Divinity Avenue, Harvard University Herbaria, Cambridge, Massachusetts, 02138, U. S. A.

²Current address: Harvard University Herbaria, 22 Divinity Avenue, Cambridge, Massachusetts 02138, U. S. A.

³Department of Biology, University of Missouri– St. Louis, R428 Research Building, St. Louis, Missouri, 63121, U. S. A.

⁴Author for correspondence (lagomarsino.l@gmail.com)

Communicating Editor: Ricarda Riina

Abstract—Two new species of *Burmeistera* (Campanulaceae: Lobelioideae) from the Cordillera de Talamanca are described, illustrated, and discussed with reference to similar species. One species, *B. serratifolia*, is endemic to Panama, while the second, *B. monroi*, is known from both Panama and Costa Rica. Additionally, these species are included in a dichotomous key to all Central American species of *Burmeistera*.

Keywords—Asterales, Central America, Mesoamerica, Talamanca Mountains, taxonomy.

Burmeistera Triana, with ~120 species, is the fourth largest genus of Lobelioideae in the family Campanulaceae (Lammers 2007). Species are found in the understory of cloud forests from Guatemala through northernmost Peru, but are absent in Belize, El Salvador, and Nicaragua. The highest species diversity of *Burmeistera* occurs in the northern Andes of Colombia and Ecuador (Garzón Venegas et al. 2014; Jeppesen 1981; McVaugh 1949). The genus comprises herbaceous to suffrutescent plants that are terrestrial or hemi-epiphytic. As in all Lobelioideae, *Burmeistera* is characterized by protandrous flowers: anthers are fused into an anther tube which releases pollen through the initial male phase as the style elongates within; the stigma then emerges from this tube, unfolds, and becomes receptive (Erbar and Leins 1995; Leins and Erbar 2006). Flowers are typically green or dark maroon and adapted to bat pollination, although some are yellow or pink, and at least one species is known to be hummingbird pollinated (Muchhala 2006b). Fruits are berries, which are often inflated or brightly colored and spongy.

Burmeistera is a subclade of the centropogonids, a clade that also includes the large Neotropical genera *Centropogon* C. Presl and *Siphocampylus* Pohl (Lagomarsino et al. 2014). This clade is unique within Lobelioideae for the combination of its Neotropical distribution, woody habit and corolla tube that is entire, neither fenestrate nor dorsally cleft (Lammers 2002; Muchhala and Lammers 2005). Unlike in *Centropogon* and *Siphocampylus*, the monophyly of *Burmeistera* is strongly supported (Antonelli 2008; Knox et al. 2008; Lagomarsino et al. 2014). Morphological synapomorphies of *Burmeistera* include a dilated anther orifice and seeds that are much longer than broad (Lammers 1998). Additionally, most species of *Burmeistera* have ebracteolate pedicels (Lammers 1998). At least two lineages of green-flowered, bat-pollinated *Centropogon* species are successively sister to *Burmeistera*; together, this clade is known as the burmeisterids and is defined morphologically by a ventricose, inflated corolla throat (Lagomarsino et al. 2014).

Burmeistera is a taxonomically difficult genus (Wilbur 1975, 1976). This is in part due to the wide overlap of characters between species and morphological variation within species, such as in the widespread *B. cyclostigmata* Donn. Sm. and *B. vulgaris* E. Wimm. The last comprehensive taxonomic treatment of the genus was Wimmer's monograph of Lobelioideae for Engler's Das Pflanzenreich (Wimmer 1943),

though the infrageneric taxonomy established in Wimmer (1943) does not reflect evolutionary relationships (Muchhala and Lammers 2005; Knox et al. 2008; Lagomarsino et al. 2014). Although a new infrageneric taxonomy is still outstanding, taxonomic knowledge of *Burmeistera* has substantially improved since Wimmer's treatment. There are now floristic treatments for the genus for most countries in which it occurs, including Guatemala (Nash 1976), Costa Rica (Wilbur 1975), Panama (Wilbur 1976, 1981), Colombia (ongoing), Ecuador (Jeppesen 1981), and Peru (Stein 1987). The ongoing floristic treatment of Colombia alone has resulted in the description of at least 10 new species and several range extensions (Garzón Venegas and González 2012; Garzón Venegas et al. 2012; Garzón Venegas et al. 2014; Garzón Venegas et al. 2013). Additionally, recent research on the pollination biology of *Burmeistera* has resulted in the description of new species (Muchhala and Lammers 2005; Muchhala and Pérez 2015) and a better understanding of the ecology and evolution of the group (Muchhala and Potts 2007; Muchhala 2003, 2006a, 2006b, 2007).

The Cordillera de Talamanca, shared between Costa Rica and Panama, is home to 21 species of *Burmeistera*, the highest species diversity outside of the Andean mountains. This mountain range stretches 320 km from the vicinity of San José and Cartago, Costa Rica to just beyond the Costa Rica–Panama border (Janzen 1983). The flora of the Cordillera de Talamanca, which has strong phytogeographical affinities with the northern Andes (Gentry 1982; Kappelle et al. 1992), is extremely diverse, particularly at mid-elevation. Important habitats in the Talamanca mountain range include cloud forests, oak forests, bogs, and the westernmost páramos (Lutelyn 1999). A large portion of this cordillera is protected by the Parque Internacional La Amistad (PILA), a UNESCO World Heritage Site shared between Costa Rica and Panama.

Here, we describe two new species of *Burmeistera* native to the Cordillera de Talamanca: *B. monroi* and *B. serratifolia*. We also provide a key to all known species of *Burmeistera* native to Central America.

MATERIALS AND METHODS

Herbarium specimens, including types, of Central American *Burmeistera* were examined at A, CR, GH, INB, MO, NY, PMA, and SCZ (herbarium abbreviations and throughout follow Thiers [2013]). Additional type

specimens were accessed from the Global Plants Initiative website (<http://plants.jstor.org/>). Material was examined under a Leica Stereo-Zoom 5 binocular microscope. Terminology in the taxonomic treatment and dichotomous key largely follows Wilbur (1975, 1976, 1981). The dichotomous key is adapted from Wilbur (1975, 1976, 1981) and includes the countries of occurrence for each species in parentheses (COL: Colombia; CR: Costa Rica; ECU: Ecuador; G: Guatemala; H: Honduras; P: Panama); these data were obtained from herbarium specimens, as well as from the Tropicos database (<http://www.tropicos.org/>).

TAXONOMIC TREATMENT

Burmeistera monroi D. Santam. & Lagom., sp. nov.—TYPE: PANAMA. Bocas del Toro: Ridges leading to Río Teribe, NE most ridge of Cerro Fábrega ridge, 09°09'07"N 082°51'52"W, 2,900 m, 07 Mar 2006 (fl), A. K. Monro & S. Knapp 5225 (holotype: PMA!; isotype: BM!).

Terrestrial herb 0.6–1 m in height, with ascending branches, producing white latex; branches 1.5–3 mm in diameter, fistulose, reddish to purple in living material, drying yellowish, indumentum villose with septate trichomes, internodes 1.8–5.5 cm long. Leaves distichous or spirally arranged; petiole 0.4–1.6 cm long, villose; blade 4.9–12.1 × 2.5–3.4 cm, elliptic or narrowly elliptic, apex acuminate, base cuneate, margin dentate, 2 short teeth per cm, round or minutely triangular; venation semicraspedodromous, with 6–12 pairs of lateral nerves, flat and barely visible on the adaxial surface, elevated on the abaxial surface; adaxial surface glabrous; abaxial surface pubescent, especially over the veins. Flowers solitary in the axils of distal leaves, pedicels 1.9–5.7 cm long, ebracteolate, straight, villose, bearing septate trichomes; hypanthium 3–4.7 × 3–5 mm, globose or hemispheric at anthesis, sparsely pubescent, green or green with dark purple; calyx lobes 2.3–5 × 1.2–1.5 mm, oblong to lanceolate with acute or obtuse apex, one central vein, the margins entire or dentate with 2–5 teeth per side, sometimes with marginal ciliate trichomes, glabrous on the adaxial surface, sparsely pubescent on the abaxial surface, erect or slightly recurved; corolla 22–25 mm long, green grading into dark purple or brownish externally, purple and green internally, sparingly to moderately short pubescent externally, glabrous internally, throat not ventricose at anthesis; corolla tube 14–16 × 2–3 mm, straight in anthesis; corolla lobes deflexed-falcate, narrowly linear, with an acute apex, dorsal lobes 8–12 × 1.5–2 mm, lateral lobes 5–7 × 1–1.2 mm, ventral lobe 4–6 × 1–1.2 mm; filament tube 18–21 × 1–1.8 mm, straight, completely glabrous, reddish-purple in living material, exerted between the dorsal corolla lobes 2–3 mm beyond the corolla; anther tube ca. 5–8 × 2–3 mm, purple, largely glabrous, but with appressed sparse pubescence in the suture between individual anthers, the two ventral anthers ca. 5 mm long, with penicillate white hairs at the apex but otherwise glabrous, the three dorsal anthers ca. 6 mm long, glabrous throughout. Berries 0.5 × 0.7 cm when immature (dried), 0.8 × 0.9 cm when mature (dried), globose, inflated, color unknown; seeds 0.5–0.8 mm long, light brown, elliptic. Figures 1–2.

Additional Specimens Examined—COSTA RICA. Puntarenas: Parque Internacional La Amistad, sendero al Valle del Silencio, sector entre el albergue y la línea divisora de aguas, 09°04'00"N, 82°59'00"W, 2,100–2,200, 20 Feb 2006 (fl & fr), D. Santamaría 3909 (GH, INB); Parque Internacional La Amistad. Casa Coca, punto 11, 09°05'61"N, 82°58'66"W, 2,550 m, 04 Apr 2011 (fl & fr), A. K. Monro & D. Santamaría 6986 (BM, GH, INB, MO); Parque Internacional La Amistad. Tararia. Valle del

Silencio, 09°06'61"N, 82°58'03"W, 2,500 m, 01 Sep 2001 (fl), E. Alfaro & O. Esquivel 3716 (MO).

PANAMA. Bocas del Toro: Cordillera de Talamanca, headwaters of the Río Culubre, 6 airline km NW of the peak of Cerro Echandi on the Costa Rican-Panamanian international border, 2,450–2,600 m, 02–03 March 1984 (fl & fr), G. Davidse et al. 25196 (CR, DUKE[image]).

Distribution and Habitat—*Burmeistera monroi* is restricted to the Parque Internacional La Amistad, where it is found on both the Costa Rican and Panamanian sides of this protected area. It grows in cloud forests on the Caribbean slope of the Cordillera de Talamanca between 2,100–2,900 m. The elevational range occupied by *Burmeistera monroi* is high for its genus, though not exceptional.

Phenology—Specimens of *Burmeistera monroi* were collected in flower in February–April and September. All except the September collections were also in fruit. This suggests a long flowering season, but phenology in the rest of the year is unknown.

Etymology—It is an honor to dedicate this new species to the British botanist Alexandre K. Monro (1968–), investigator at the Kew Royal Botanic Gardens in London and world authority of Urticaceae. Monro has led many botanical expeditions into the Cordillera de Talamanca and Parque Internacional La Amistad in Costa Rica and Panama that have substantially increased our understanding of the biodiversity in this species-rich region. During one of these trips, Monro collected the type specimen of the species that we describe here in his honor.

Notes—*Burmeistera monroi* is distinguished by its straight, narrow, sparsely pubescent corolla with narrowly linear corolla lobes and a non-ventricose throat. It is most similar to *B. nigropilosa* Luteyn ex Garzón & F. González from Antioquia, Colombia (Garzón Venegas and González 2012), but can be distinguished by its glabrous to sparsely-pubescent, smooth leaves (versus densely pubescent, bullate leaves), ebracteolate pedicels (versus bracteolate), dark purple or brown corolla tube that grades distally to green (versus green), and whitish and sparse corolla pubescence (versus dark or hyaline and dense).

Among Central American species, *Burmeistera monroi* is most similar to *B. chirripoensis* Wilbur, from which it can be distinguished by its dark purple to brown corolla tube grading into green (versus green), the corolla throat that is not ventricose (versus ventricose), and largely glabrous anthers (versus densely pubescent throughout). It is also similar to *B. virescens* (Benth.) Benth. & Hook. f. ex Hemsl. from relatively low elevations, ca. 500–2,000 m, in Guatemala and Honduras due to its narrow corolla tube, but can be readily distinguished by its villose stems (versus glabrous or puberulent), elliptic or narrowly elliptic leaves (versus oblong-elliptic to ovate), globose to hemispheric hypanthium at anthesis (versus obconic), corolla throat that is not ventricose (versus ventricose), and corolla tube that is dark purple to brown grading into green (versus green). *Burmeistera monroi* is vegetatively similar to *B. estrellana*, but differs in its corolla that is not ventricose (versus ventricose) with linear lobes (versus deltoid).

Burmeistera monroi is among three known species of *Burmeistera* in Central America with inflated fruits. The other species are *B. vulgaris* and *B. glauca* (E. Wimm.) Gleason. The former, *B. vulgaris*, is a widespread species that is readily distinguished from *B. monroi* by its ventricose corolla throat (versus not ventricose) and cylindric hypanthium (versus globose or hemispheric). The latter, *B. glauca*, can be distinguished



FIG. 1. *Burmeistera monroi*. A. Habit with flower buds, flower, and fruit. B. Flower in female phase. All drawings by L. Lagomarsino based on A. K. Monro 7142.



FIG. 2. *Burmeistera monroi*, photographs from field collections. A. Habit. B. Flower in female phase, lateral view. C. Flower in female phase, frontal view with detail of stigma and anthers. D. Flower in male phase, lateral view. E. Flowering branch with developing fruits. F. Abaxial leaf surface. All photos are of A. K. Monro 7142 except D, which is of A. K. Monro 6986. Photos by A. K. Monro.

from *B. monroi* by its hemi-epiphytic to epiphytic habit (versus terrestrial), glabrous corolla (versus sparsely to moderately pubescent), and oblong-ovoid berry (versus globose).

Burmeistera monroi is also among few species of its genus that does not have a ventricose corolla throat (as in e.g. *B. serratifolia*, Fig. 3D), thought to be an adaptation to bat pollination in some species (Muchhala 2006b). This species' corolla morphology (a long, straight corolla tube with falcate corolla lobes and a non-ventricose throat) is quite similar to the brevilibatid subclade of *Centropogon* (Lagomarsino et al. 2014), which includes the hummingbird-pollinated *C. valerioi* Standl. (Colwell et al. 1974) and *C. ferrugineus* (L. f.) Gleason from Costa Rica; these species are easily distinguished from *B. monroi* by their more robust, scandent subshrub habit (versus terrestrial herb less than 1 m in height), generally bright orange corolla tubes with yellow limb (versus brown grading into green), and a constricted anther orifice (versus dilated). The pollinator of *B. monroi* is unknown.

***Burmeistera serratifolia* Lagom. & D. Santam., sp. nov.—**

TYPE: PANAMA. Chiriquí: Ridges above and to W of Quebrada Alemán, trail to town of Fortuna, 08°45'N, 82°13'W, 1,200–1,500 m, 13 Aug 2000 (fl), S. Knapp & J. Mallet 9226 (holotype: PMA!; isotype: SCZ!).

Epiphytic herb producing white latex; branches 2.5–3 mm in diameter, fistulose, sparsely puberulent with simple trichomes, internodes 1.5–3 cm long. Leaves spirally arranged; petiole 0.6–1.5 cm long, sparsely pubescent; blade 10.2–15 × 1–1.7 cm, narrowly oblong-lanceolate, apex acuminate, base cuneate, sometimes slightly decurrent and asymmetric, margin strongly irregularly serrate, 15–17 conspicuous triangular teeth per cm; venation semicraspedodromous, lateral nerves 13–20 per side, flat and little visible on the adaxial surface, elevated on the abaxial surface; adaxial surface glabrous; abaxial surface glabrous except on the veins, which are pubescent. Flowers solitary in the axils of upper leaves, which are

sometimes reduced in size compared to mature leaves not associated with flowers; pedicels 7–11.2 cm long, straight or slightly curved towards the apex, ebracteolate, glabrous or sparsely pubescent, the trichomes not septate; hypanthium 9–11 × 2–4 mm, campanulate at anthesis, glabrous or sparsely pubescent with simple trichomes; calyx lobes 3–4.5 × 1–4.5 mm, oblong-lanceolate to triangular with acute apex, with one almost indistinct central vein, margins serrate, with 3–5 teeth per side, glabrous on both surfaces, straight or slightly curved; corolla ca. 21–40 mm long, green, glabrous on all surfaces, throat ventricose; tube 5–11 × 2–4.5 mm, straight; lobes oblong, falcate, with an acuminate or acute apex, dorsal lobes 13–15 × 3.5–5 mm, lateral lobes ca. 14 × 4 mm, ventral lobe ca. 14 × 2 mm; filament tube ca. 31 × 1.1 mm, straight in the proximal half and curved towards the distal end, glabrous except towards the apex where it is strigose, exserted between the pair of dorsal lobes ca. 15 mm; anther tube ca. 5 × 3 mm, glabrous or minutely pubescent, the two ventral anthers ca. 3–4 mm long, glabrous throughout, the three dorsal anthers ca. 5 mm long, glabrous throughout. Berries 1.8 × 0.6 cm (possibly not mature), more or less cylindrical, calyx lobes persistent, glabrous; seeds not seen. Seedlings produce finely divided leaves (information from label). Figure 3.

Distribution and Habitat—*Burmeistera serratifolia* is endemic to Panama, where it grows in premontane and montane forests on the Caribbean slope of the Cordillera de Talamanca between 1,200–1,500 m in elevation. It is only known from the type, collected in the Reserva Forestal Fortuna, Chiriquí, Panama.

Phenology—Flowers and fruits were collected from *Burmeistera serratifolia* in August, but phenology is otherwise unknown.

Etymology—This species' epithet refers to the characteristic serrate leaf margins of this species.

Notes—This species is exceptional for its oblong-lanceolate leaves with strongly serrate margins. *Burmeistera serratifolia* is most similar to *B. chiriquiensis* Wilbur from western Panama

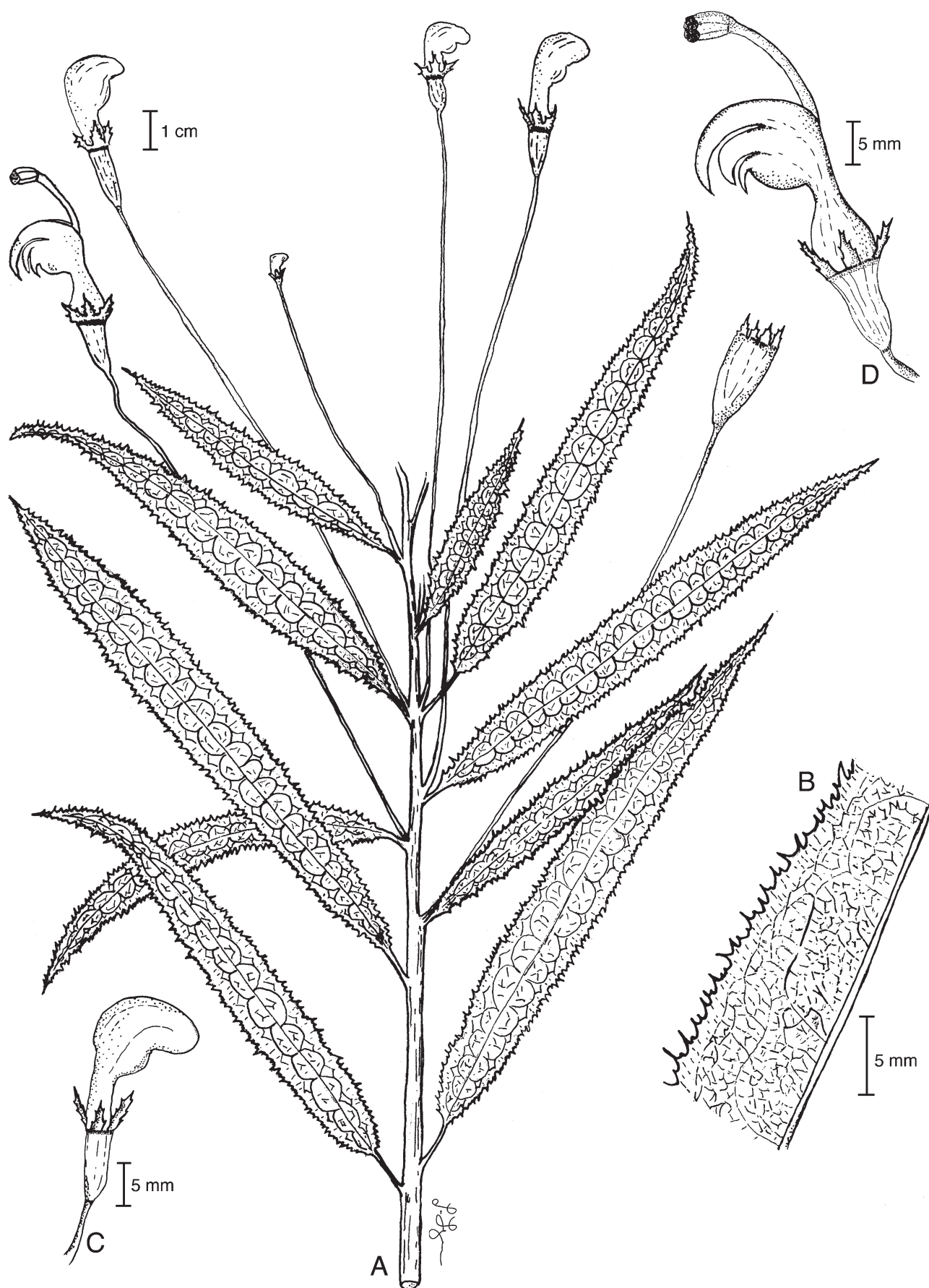


FIG. 3. *Burmeistera serratifolia*. A. Habit with flower buds, flower, and fruit. B. Detail of leaf margin and venation. C. Flower bud. D. Flower in male phase. All drawings by L. Lagomarsino based on the holotype.

and eastern Costa Rica, with which it shares its oblong-lanceolate leaves; it can be distinguished by its prominently and irregularly serrate leaf margins with more than 15 conspicuous teeth/cm (versus shallowly dentate leaf margins with one to two inconspicuous teeth/cm), secondary and tertiary venation that is easily distinguished and reticulate (versus secondary and tertiary venation that is not prominent), acuminate leaf apex (versus caudate), pedicel 7.0–11.2 cm long (versus ca. 3 cm long), campanulate hypanthium (versus obconic), filament tube 30 mm long (versus 23 mm long), and the glabrous tips of the ventral anthers (versus densely pilose). *Burmeistera intii* Gómez-Laur. & L.D. Gómez also has oblong-lanceolate leaves; however, they are less than 8 cm long (versus 10–15 cm in *B. serratifolia*). *Burmeistera silencioensis* Wilbur (ined.), which is soon to be validly published in conjunction with the Manual de las Plantas de Costa Rica, also produces elongate leaves. However, *B. serratifolia* can be distinguished from this entity, which would also belong near the third couplet of the key below, by its irregularly serrate leaf margins

(versus serrulate), acute leaf apices (versus acuminate to caudate), sepals with serrate margins (versus inconspicuously serrulate), and filament tube exerted 1.5 cm beyond the corolla (versus included or exerted less than 5 mm). The following specimens of *B. silencioensis* from Costa Rica and Panama were examined to compare to *B. monroi*: A. K. Monro 7117 (INB), D. Santamaría-Aguilar 9093 (INB), and T. Antonio 1608A (DUKE [image]). It is not our intention to validly publish this species name here.

Among Central American species, *Burmeistera serratifolia* shares its finely divided juvenile leaves only with *B. mcvaughii* Wilbur, from which it is readily distinguished by its long-lanceolate leaves with serrate margins bearing more than 15 teeth/cm (versus elliptic with serrulate to denticulate margins bearing 6–8 teeth/cm) and campanulate hypanthium (versus obconic). Additionally, two specimens currently identified as *B. dendrophila* (L. E. Skog 4056 [MO] and *B. Hammel* 6199 [MO]) also produce finely divided young leaves, though this does not appear to be common in this species.

KEY TO THE CENTRAL AMERICAN SPECIES OF *BURMEISTERA* (ADAPTED FROM WILBUR 1975, 1981)

1. Leaves > 5 times longer than wide.
 2. Leaves distichously arranged, ≤ 8 cm long; dorsal corolla lobes long-acuminate, > 4 times as long as the lateral and ventral lobes *B. intii* (CR)
 2. Leaves spirally arranged, ≥ 10 cm long; dorsal corolla lobes acute, < 1.5 times as long as the lateral and ventral lobes
 3. Leaf margins weakly dentate, 1–2 teeth per cm; venation pattern not readily apparent; pedicels ca. 3 cm long; filament tube not exerted from corolla tube *B. chiriquiensis* (CR,P)
 3. Leaf margins strongly serrate, 15 + teeth/cm; venation semicraspedodromous; pedicels > 6 cm long; filament tube exerted from corolla tube > 1 cm *B. serratifolia* (P)
1. Leaves < 5 times longer than wide
 4. Corolla < 1.5 cm long 5
 5. Corolla pink or green; filament tube ≤ 9 mm long *B. kirkbridei* Wilbur (P)
 5. Corolla bright yellow; filament tube ≥ 10 mm long *B. parviflora* E. Wimm. ex Standl. (CR, P)
 4. Corolla > 2 cm long 6
 6. Corolla throat not ventricose *B. monroi* (CR, P)
 6. Corolla throat ventricose
 7. Plants climbing, sometimes hemiepiphytic; branches arching to pendent; leaves distichously arranged 8
 8. Leaf margins lobed, undulate *B. quercifolia* Gómez-Laur. & L.D. Gómez (CR)
 8. Leaf margins crenate-serrate, flat 9
 9. Stems densely spreading-hirsute
 10. Cauline trichomes terete, tawny or reddish purple; pedicels and hypanthia glabrous *B. almedae* Wilbur (CR, P)
 10. Cauline trichomes flattened, tawny; pedicels and hypanthia pubescent *B. obtusifolia* E. Wimm. (CR, P)
 9. Stems glabrous, or with only a few scattered trichomes 11
 11. Anthers externally pilose with golden trichomes *B. microphylla* Donn. Sm. (CR, P, COL)
 11. Anthers externally glabrous 12
 12. Leaves 2.7–5 (–8) × 1.2–2.5 cm; petioles 0.4–0.7 cm long; flowers 30–35 mm long; hypanthium cylindric; berries oblong-ovoid, 3–6 cm long *B. glauca* (P)
 12. Leaves 5–9.5 × 2.5–3.9 cm; petioles 0.7–1 cm long; flowers 45–55 mm long; hypanthium obconic; berries globose, 0.9–1.1 cm long *B. zurquiensis* Wilbur (CR)
 7. Plants climbing or terrestrial; branches erect; leaves spirally arranged 13
 13. Hypanthium at anthesis obconic, acute-tapering at the base with the sides strongly divergent 14
 14. Leaves with conspicuously denticulate, serrulate, or crenate margins, with ≥ 6 teeth/cm 15
 15. Leaf margin subtire to coarsely and irregularly dentate or crenate; corolla lobes sublinear to linear, 6 × 1.5 mm *B. virescens* (G, H)
 15. Leaf margin denticulate or serrulate; corolla lobes falcately oblong to deltoid, 5–13 × 3–4 mm *B. mcvaughii* (P)
 14. Leaf margins entire to inconspicuously serrulate, with ≤ 4 teeth per cm 16
 16. Calyx lobes > 6 mm long (up to 20 mm), equaling or longer than the hypanthium *B. tenuiflora* Donn. Sm. (CR, P)
 16. Calyx lobes < 4 mm long, shorter than the hypanthium 17
 17. Corolla lobes greatly recurved; calyx lobes 1–1.5 mm long *B. toroensis* Wilbur (P)
 17. Corolla lobes erect or deflexed; calyx lobes > 2 mm long 18
 18. Distal leaves not markedly reduced, not giving the impression of a bracteate raceme, the flowers obviously borne singly 19
 19. Corolla lobes sublinear to linear *B. virescens* (G, H)
 19. Corolla lobes falcate and deltoid 20
 20. Leaf apex acute to short-acuminate, tertiary venation indistinct; filament tube exerted more than 1 cm beyond the corolla, largely glabrous, but distally puberulent *B. dendrophila* E. Wimm. (P)

20. Leaf apex long-acuminate, tertiary venation distinct; filament tube exerted less than 1 cm beyond the corolla or included, pubescent throughout *B. estrellana* E. Wimm. (CR)
18. Distal leaves that bear flowers greatly reduced, giving the impression of a bracteate raceme 21
 21. Pedicels > 7 cm long *B. utleyi* (P)
 21. Pedicels < 6 cm long 22
 22. Leaves and corolla puberulent; flowers ca. 40 mm long *B. chirripoensis* (CR)
 22. Leaves glabrous, the corolla glabrous to inconspicuously puberulent; flowers ca. 30 mm long *B. morii* Wilbur (P)
13. Hypanthium at anthesis cylindric to campanulate or urceolate, somewhat rounded at the base with the sides more or less parallel 23
23. Leaves with conspicuously denticulate or serrulate margins 24
 24. Stems puberulent with several-celled, yellowish-white hairs; pedicels 7–8 cm long; hypanthium 7.5 × 2 mm; anthers externally sparsely pubescent, naked at tips. *B. crebra* McVaugh (CR)
 24. Stems inconspicuously puberulous to glabrate; pedicels 3–4 cm long; hypanthium 4–5 × 3–4 mm; anthers externally appressed-pilosulose, pilose-fringed at tips *B. hammeli* Wilbur (P)
23. Leaves with shallowly crenate-serrate or inconspicuously serrulate margins 25
 25. Calyx lobes ≤ 5 mm long. 26
 26. Corolla moderately to densely puberulous; berry red *B. dukei* Wilbur (P)
 26. Corolla glabrous or occasionally sparsely puberulous; berry white or greenish turning black 27
 27. Upper corolla lobes ≥ 18 mm long and the 2 lateral lobes 12–14 mm long; corolla dark red; anthers externally glabrous *B. darienensis* Wilbur (P)
 27. Upper corolla lobes < 12 mm long and the 2 lateral lobes ca. 7 mm long; corolla greenish; anthers externally puberulous *B. pirrensis* Wilbur (P)
 25. Calyx lobes > 5 mm long 28
 28. Two ventral anthers densely bearded; leaves (except the most distal) ≥ 5 cm wide *B. panamensis* Wilbur (P)
 28. Two ventral anthers sparingly fringed apically or glabrous; leaves mostly < 5 cm wide 29
 29. Corolla predominantly purplish or green with a deep suffusion of maroon or dark purple; hypanthium and calyx lobes purplish, drying dark purple or black; berry fleshy and with a thick wall, 1–2(–3) × 1–2(–2.5) cm *B. cyclostigmata* (CR, P, COL, ECU)
 29. Corolla green or bronze; hypanthium and calyx lobes green, drying green or stramineous (rarely suffused with purple or maroon); berry greatly inflated with a thin, bladdery wall, 2.5–5 × 2–4 cm *B. vulgaris* (CR, P)

ACKNOWLEDGMENTS. The authors would like to thank the following herbaria for use of their collections and facilities: A, CR, GH, INB, MO, NY, PMA, and SCZ. We additionally would like to acknowledge the help of the following individuals: Carmen Galdames and Eric K. O. Hattori scanned herbarium specimens for study, Carlos Maldonado drew preliminary line illustrations, Alexandre Monro allowed us to use his photos of living specimens of *B. monroi*, and Kanchi Gandhi provided nomenclatural advice. This research was supported by student grants to L.P.L. from the Explorer's Club, the Rockefeller Center for Latin American Studies at Harvard University, and the American Society of Plant Taxonomists, and a National Science Foundation Doctoral Dissertation Improvement Grant (DEB-1210401). Drafts of this manuscript were substantially improved at various stages by comments from Charles C. Davis, Michael Grayum, Barry Hammel, an anonymous reviewer, Associate Editor Ricarda Riina, and Editor-in-Chief James Smith.

LITERATURE CITED

- Antonelli, A. 2008. Higher level phylogeny and evolutionary trends in Campanulaceae subfam. Lobelioideae: Molecular signal overshadows morphology. *Molecular Phylogenetics and Evolution* 46: 1–18.
- Colwell, R., B. Betts, P. Bunnell, F. L. Carpenter, and P. Feinsinger. 1974. Competition for the nectar of *Centropogon valerii* by the hummingbird *Colibri thalassinus* and the flower-piercer *Diglossa plumbea*, and its evolutionary implications. *The Condor* 76: 447–452.
- Erbar, C. and P. Leins. 1995. Portioned pollen release and the syndromes of secondary pollen presentation in the Campanulales-Asterales complex. *Flora* 190: 323–338.
- Garzón Venegas, J. and F. González. 2012. Five new species and three new records of *Burmeistera* (Campanulaceae-Lobelioideae) from Colombia. *Caldasia* 34: 309–324.
- Garzón Venegas, J., F. González, and J. M. Vélez Puerta. 2012. *Burmeistera minutiflora* (Campanulaceae-Lobelioideae), a new species from the high Andes of Antioquia (Colombia) with the smallest flowers in the genus. *Anales del Jardín Botánico de Madrid* 69: 243–246.
- Garzón Venegas, J., J. L. Luteyn, and F. González. 2014. A new species of *Burmeistera* (Campanulaceae, Lobelioideae) from the Western Cordillera of Colombia. *Novon: A Journal for Botanical Nomenclature* 23: 165–170.
- Garzón Venegas, J., J. M. Vélez Puerta, and F. González. 2013. Three new species of *Burmeistera* (Campanulaceae-Lobelioideae) from Colombia. *Brittonia* 65: 119–127.
- Gentry, A. H. 1982. Neotropical floristic diversity: Phytogeographical connections between Central and South America, Pleistocene climatic fluctuations, or an accident of the Andean orogeny? *Annals of the Missouri Botanical Garden* 69: 557–593.
- Janzen, D. H. 1983. *Costa Rican natural history*. Chicago: University of Chicago Press.
- Jeppesen, S. 1981. Lobeliaceae. Pp. 9–170 in *Flora of Ecuador* No 14 eds. G. Harling and B. Sparre. Stockholm: Swedish Natural Science Research Council.
- Kappelle, M., A. M. Cleef, and A. Chaverri. 1992. Phytogeography of Talamancan montane *Quercus* forests, Costa Rica. *Journal of Biogeography* 19: 299–315.
- Knox, E. B., A. M. Muasya, and N. Muchhala. 2008. The predominantly South American clade of Lobeliaceae. *Systematic Biology* 33: 462–468.
- Lagomarsino, L. P., A. Antonelli, N. Muchhala, A. Timmermann, S. Mathews, and C. C. Davis. 2014. Phylogeny, classification, and fruit evolution of the species-rich Neotropical bellflowers (Campanulaceae: Lobelioideae). *American Journal of Botany* 101: 2097–2112.
- Lammers, T. G. 1998. Review of the Neotropical endemics *Burmeistera*, *Centropogon*, and *Siphocampylus* (Campanulaceae: Lobelioideae), with description of 18 new species and a new section. *Brittonia* 50: 233–262.
- Lammers, T. G. 2002. Seventeen new species of Lobelioideae (Campanulaceae) from South America. *Novon* 12: 206–233.
- Lammers, T. G. 2007. *World checklist and bibliography of Campanulaceae*. Richmond, U. K.: Royal Botanic Gardens, Kew.
- Leins, P. and C. Erbar. 2006. Secondary pollen presentation syndromes of the Asterales — a phylogenetic perspective. *Botanische Jahrbücher* 127: 83–103.
- Luteyn, J. L. 1999. Paramos: A checklist of plant diversity, geographical distribution, and botanical literature. Bronx, N. Y.: New York Botanical Garden Press.
- McVaugh, R. 1949. Studies in South American Lobelioideae (Campanulaceae) with special reference to Colombian species. *Brittonia* 6: 450–493.
- Muchhala, N. 2003. Exploring the boundary between pollination syndromes: Bats and hummingbirds as pollinators of *Burmeistera cyclostigmata* and *B. tenuiflora* (Campanulaceae). *Oecologia* 134: 373–380.

- Muchhala, N. 2006a. Nectar bat stows huge tongue in its rib cage. *Nature* 444: 701–702.
- Muchhala, N. 2006b. The pollination biology of *Burmeistera* (Campanulaceae): Specialization and syndromes. *American Journal of Botany* 93: 1081–1089.
- Muchhala, N. 2007. Adaptive trade-off in floral morphology mediates specialization for flowers pollinated by bats and hummingbirds. *American Naturalist* 169: 494–504.
- Muchhala, N. and T. G. Lammers. 2005. A new species of *Burmeistera* (Campanulaceae: Lobelioideae) from Ecuador. *Novon* 15: 176–179.
- Muchhala, N. and A. Pérez. 2015. *Burmeistera zamorensis* (Campanulaceae: Lobelioideae), a new species from southern Ecuador. *Novon* 24: 36–38.
- Muchhala, N. and M. D. Potts. 2007. Character displacement among bat-pollinated flowers of the genus *Burmeistera*: Analysis of mechanism, process and pattern. *Proceedings. Biological Sciences* 274: 2731–2737.
- Nash, D. L. 1976. Campanulaceae. In *Flora of Guatemala*, eds. D. L. Nash and J. V. A. Dieterle. Fieldiana. Botany 24: 396–431.
- Stein, B. A. 1987. Synopsis of the genus *Burmeistera* (Campanulaceae: Lobelioideae) in Peru. *Annals of the Missouri Botanical Garden* 74: 494–496.
- Thiers, B. 2013. Index Herbariorum: A global directory of public herbaria and associated staff. New York Botanical Garden's Virtual Herbarium. Retrieved from <http://sweetgum.nybg.org/ih/>.
- Wilbur, R. L. 1975. A synopsis of the Costa Rican species of *Burmeistera* (Campanulaceae: Lobelioideae). *Bulletin of the Torrey Botanical Club* 102: 225–231.
- Wilbur, R. L. 1976. Family 183. Campanulaceae (Flora of Panama). *Annals of the Missouri Botanical Garden* 63: 593–655.
- Wilbur, R. L. 1981. Additional Panamanian species of *Burmeistera* (Campanulaceae: Lobelioideae). *Annals of the Missouri Botanical Garden* 68: 167–171.
- Wimmer, F. E. 1943. Campanulaceae-Lobelioideae. I. Teil. Pp. 1–260 in *Das Pflanzenreich IV.276b*, ed. R. Mansfeld. Leipzig: Wilhem Engelmann.