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# Six New Species of *Burmeistera* (Campanulaceae) from Ecuador

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**ABSTRACT.** Six species of *Burmeistera* H. Karst. & Triana are described as new from Ecuador: *B. chrysothrix* Mashburn & Muchhala, *B. crocodila* Mashburn & Muchhala, *B. erosa* Mashburn, *B. lingulata* Mashburn & Muchhala, *B. sierrazulensis* Mashburn & Muchhala, and *B. valdiviana* Mashburn. These discoveries bring the total number of *Burmeistera* species in Ecuador to ca. 47. Descriptions are given for each species, as well as diagnoses to differentiate them from other *Burmeistera*. Also provided is a discussion of each species' etymology, phenology, and ecology, a list of all specimens examined, and distribution maps and photos, when available.

**Key words:** *Burmeistera*, Lobelioideae, South America, taxonomy.

The genus *Burmeistera* H. Karst & Triana (Campanulaceae, Lobelioideae) is a group of Neotropical species in a clade with two other closely related genera: *Centropogon* C. Presl and *Siphocampylus* Pohl (Antonelli, 2008; Knox et al., 2008). *Burmeistera* species are classically differentiated from species in these two genera by an inflated corolla tube opening, a dilated anther tube orifice, a deciduous corolla and staminal column after fertilization, baccate fruits, and oblong to fusiform seeds (Lammers, 1998, 2002), though exceptions are possible. *Burmeistera* plants are typically multi-stemmed, non-woody herbs that exhibit either a bush-like or scandent habit, with branches rarely more than 4 m long. All species have alternate leaves. The distinctive floral traits of *Burmeistera* represent adaptations to bat pollination, the pollination syndrome of all but a few species in the genus (Muchhala, 2006; Lagomarsino et al., 2017). Molecular work has shown *Centropogon* and *Siphocampylus* to be non-monophyletic, but consistently upholds the monophyly of *Burmeistera* as sister to these two genera (Antonelli, 2008; Knox et al., 2008; Lagomarsino et al., 2014; Uribe-Convers et al., 2017), and supports an ancestral shift from hum-

mingbird to bat pollination in *Burmeistera* (Lagomarsino et al., 2017).

Species of *Burmeistera* occur in Central and South America, from Guatemala to Peru. The majority of species are found at the center of this range, with ~60 in Colombia, ~47 in Ecuador, and ~21 in Panama and Costa Rica combined (Garzón Venegas & González, 2012; Lagomarsino et al., 2015; Vallejo et al., 2018). Most of these species are found in cloud forests from 1000 to 2500 m in elevation in relatively restricted geographic ranges, although a handful of species are widely distributed (such as *B. cyclostigmata* Donn. Sm. from Costa Rica to Ecuador).

Since the description of the genus in 1854 (Triana, 1854), the number of *Burmeistera* species has continued to grow, coinciding with the efforts of monographers working on Lobeliaceae. The last monograph of the genus as a whole (Wimmer, 1953) recognized 77 species. Recently, the number of species recognized in the genus has grown to ~120 (Vallejo et al., 2018). In Ecuador, the last generic treatment of *Burmeistera* was completed by Jeppesen (1981), in which he recognized 31 species. Since then, 10 new species have been described from Ecuador (Ulloa Ulloa et al., 2017), most recently *B. pterifolia* A. F. Vallejo, Á. J. Pérez & Muchhala, *B. draconis* Á. J. Pérez & Muchhala (Vallejo et al., 2018), and *B. quimiensis* Mashburn & Á. J. Pérez (Mashburn et al., 2020). The six new species described here bring the total number of *Burmeistera* species recognized in Ecuador to 47.

## MATERIALS AND METHODS

The new species described here were discovered through a combination of recent field collections in Ecuador, a thorough revision of the literature, and detailed studies of herbarium material and types. All of this has been done in preparation for a revision of the genus in Ecuador (see Mashburn, 2019), the final ver-

sion of which will include a taxonomic key for all species in the country. We studied material from the following herbaria: HUTI, MO, NY, QCA, and QCNE (acronyms according to Thiers, 2020) and consulted images of the type collections on JSTOR Global Plants (<plants.jstor.org>). Maps were produced in R (R Core Team, 2020) using the package “tmap” (Tennekes, 2018).

All measurements were made on dry material. Flower measurements were made only from mature flowers, where the androecium has emerged and extended from the flower bud. Flower length was measured from the base of the hypanthium, where it emerges from the pedicel, to the farthest tip of the anther tube in a straight line parallel to the flower's axis. Calyx lobe length was measured from their attachment at the distal end of the hypanthium to their tip. The dorsal (two), lateral (two), and ventral (one) corolla lobes were measured from the dorsal, lateral, and ventral sinuses, respectively, in a straight line perpendicular to the flower's axis to the tip of the lobe. Dorsal and ventral sinuses and androecium length were measured from the base of the corolla, at its junction with the hypanthium, to the furthest extent of each part in a straight line parallel to the flower's axis. The androecium includes both filaments and the anthers, which are united in *Burmeistera* to form a continuous tube. Exsertion length (of the androecium) was measured from the ventral sinus of the corolla tube to the furthest extent of the androecium in a straight line parallel to the flower's axis. Anther tube length was measured from the point where the anthers visibly differentiate (bulge) from the filament tube, to the farthest tip of the dorsal anthers. Anther tube width was measured at the distal opening of the anther tube. Fruit measurements were taken from mature fruits, except where noted.

#### NEW SPECIES

**1. *Burmeistera chrysothrix*** Mashburn & Muchhala, sp. nov. TYPE: Ecuador. Carchi: Bosque Protector Golondrinas, on path from Morán to lodge, 2844 m, 00°49'06.06"N 78°04'34.093"W, 3 July 2018 (fl.), N. Muchhala & J. Gruhn 542 (holotype, QCA!; isotypes, HUTI!, MO-6773330!, NY!, QCNE!). Figures 1, 3A, B, 9A.

*Diagnosis.* *Burmeistera chrysothrix* Mashburn & Muchhala is differentiated from *B. aspera* E. Wimm. and *B. loejnantii* Jepesen by the presence of two minute bracteoles at the base of the pedicel, 29–30-mm-long flowers, and a dense pubescence of cream to golden-colored hairs covering all vegetative and reproductive parts.

Scandent herbs, reaching ca. 3 m; latex white. Stems green to violet, terete, up to 4 mm wide on terminal branches, densely pubescent with cream to golden-

colored hairs, internodes 10–40 mm. Leaves alternate, distichous; petiole green to violet, 4–8 mm, pubescent; lamina narrowly ovate to lanceolate, 25–55 × 8–25 mm, base obtuse to rounded, apex attenuate to acuminate, margins shallowly callose-dentate, teeth often irregular in size; adaxial surface green, tinged violet when young, veins sometimes tinged violet, pubescent; abaxial surface green, sometimes tinged violet, densely pubescent; venation craspedodromous, sometimes with a thinner marginal collecting vein, primary and secondary veins light green to yellow, prominent, slightly raised, tertiary veins visible. Pedicels green, 15–30 mm at anthesis, 25–30 mm in fruit, densely pubescent, with 2 minute, persistent bracteoles near the base. Flowers 29–30 mm, solitary in upper leaf axils; hypanthium green to violet, obconical, 7–8 × 7 mm, densely pubescent, with raised ridges; calyx lobes green to violet, deltate, 4–10 × 1–2 mm, densely pubescent, margins dentate with 1 to 5 small teeth, apex obtuse; corolla green to green suffused with violet, densely pubescent; corolla tube 3–4 mm wide basally, throat narrowing to ca. 2 mm wide; corolla lobes lanceolate, margins slightly undulate, dorsal lobes 8–11 × 2–3 mm, arcuate, arched forward, dorsal sinus ca. 14 mm from the corolla base, lateral lobes 4–7 × 1–3 mm, arcuate, slightly recurved, ventral lobe ca. 8 × 4 mm, slightly recurved, ventral sinus 8–9 mm from the corolla base; androecium 20–21 mm, exserted 13–14 mm from the ventral opening, filament tube green spotted with violet, glabrous, anther tube violet, dark green along the sutures, pubescent with cream-colored hairs, top 3 anther tips glabrous, bottom 2 anther tips densely pubescent with cream-colored hairs; style and stigma unknown. Fruits white to pink, obovate, 20–25 × 20–25 mm, spongy, pubescent; seeds light brown, elliptic, 0.2–0.5 mm, surface shiny, shallowly foveate.

*Etymology.* The specific epithet means “with golden hairs,” from the Greek *chrysos*, gold, and *thrix*, hair.

*Phenology.* Specimens have been collected with flowers and fruits throughout the year.

*Distribution.* Collections of *Burmeistera chrysothrix* are concentrated in the northern Ecuador province of Carchi. This region of the country is particularly rich in *Burmeistera* species. The majority of specimens have been collected from roadside forests on the highway northwest from the small town of Tufiño to Maldonado, beginning ca. 30 km west of Tufiño. Nearing Maldonado, the road runs parallel to the border between Ecuador and Colombia. Thus, *B. chrysothrix* possibly occurs in southern Colombia as well, though collections from Colombia have not been seen by the authors. A solitary collection (Reyes *et al.* 4312) has been made



Figure 1. Isotype of *Burmeistera chrysothrix* Mashburn & Muchhala (*N. Muchhala & J. Gruhn 542*, MO).

ca. 70 km southeast of the other collections, in Sucumbíos Province.

**Notes.** *Burmeistera chrysothrix* is only the second *Burmeistera* species from Ecuador known to have persistent bracteoles near the base of the pedicel, the other being *B. formosa* (E. Wimm.) Jeppesen. As a somewhat rare trait, the presence of these bracteoles is quite useful in identifying this new species. Similarities in flower and fruit morphology suggest that *B. chrysothrix* is related to *B. aspera* (from Colombia and Ecuador) and *B. loejnantii* (from Colombia and Ecuador). All three species have white, spongy, globular fruits and flowers that are entirely green or green suffused with violet. *Burmeistera chrysothrix* has the smallest flowers of the three (29–30 mm long), while those of *B. aspera* are intermediate (37–38 mm long) and those of *B. loejnantii* are longest (ca. 47 mm long; note that the holotype of *B. loejnantii* at AAU has mature flowers, whereas the isotype at NY has much smaller, immature flowers that can be confused as mature flowers). Besides flower size, *B. chrysothrix* differs from these other two species in the presence of bracteoles (absent in the other two species), and its densely pubescent vegetative and reproductive parts. Certain parts of *B. aspera* can have strigose hairs, and often these hairs have a bulbous base. Similarly, parts of *B. loejnantii* are sometimes verrucose or sparsely strigose, especially on the petiole, underside of the leaf, and hypanthium. However, neither *B. aspera* nor *B. loejnantii* is entirely densely pubescent, as seen in *B. chrysothrix*.

**Paratypes.** ECUADOR. **Carchi:** Bosque Protector Golondrinas, on path from Morán to lodge, 2750 m, 00°49'11.13"N 78°04'59.663"W, 3 July 2018 (fl., fr.), *Muchhala & Gruhn 544* (MO); Bosque Protector Golondrinas, on path from Morán to lodge, 2704 m, 00°49'03.15"N 78°05'22.883"W, 3 July 2018 (fl.), *Muchhala & Gruhn 546* (MO); carretera Tulcán–Tufiño–Maldonado–Chical, 33–56 km de Tufiño, 2000–2900 m, 00°50'N 78°02'W, 23 Apr. 1993 (fr.), *Freire-Fierro & Andersen 2561* (QCA); carretera Tulcán–Tufiño–Maldonado, Sector La Pradera, 2340–2640 m, 12 Oct. 1986, *Freire-Fierro 374* (QCA); rd. Maldonado–Tulcán, Km. 24, 2575 m, 4 May 1993 (fr.), *Borchsenius 77* (QCA); Tufiño–Maldonado, Km. 42, 2700 m, 19 Feb. 1995 (fl., fr.), *Schwerdtfeger 21923* (QCA); Tulcán–Maldonado rd., 42 km W of Tufiño, 2425 m, 13 Apr. 1978 (fl.), *Luteyn & Lebron-Luteyn 5747* (NY). **Sucumbíos:** Cantón Sucumbíos, parroquia La Bonita, 2600–3000 m, 00°29'N 77°35'W, 26–28 Oct. 2008 (fr.), *Reyes et al. 4313* (QCNE).

**2. *Burmeistera crocodila*** Mashburn & Muchhala, sp. nov. TYPE: Ecuador. Carchi: Bosque Protector Golondrinas, on path from Morán to lodge, 2750 m, 00°49'11.13"N 78°04'59.663"W, 3 July 2018 (fl., fr.), *N. Muchhala & J. Gruhn 545* (holotype, QCA; isotypes, HUTI!, MO-6773329). Figures 2, 3C, D, 9B.

**Diagnosis.** *Burmeistera crocodila* Mashburn & Muchhala is differentiated from *B. resupinata* Zahlbr. by its smaller flowers (36–37 mm long vs. greater than 60 mm), shorter androecium and androecium exertion length, and longer calyx lobes; and from *B. serraniaguae* Garzón & F. González by the presence of leaf and hypanthium indumentum, brochidodromous venation, shorter calyx lobes, longer androecium exertion length, and globose fruits maturing violet.

Scandent herbs, reaching ca. 1 m; latex white. Stems green tinged with violet, zigzag, up to 3 mm wide on terminal branches, glabrous, internodes 15–40 mm. Leaves alternate, distichous; petiole green to violet, 8–12 mm, glabrous basally, becoming pubescent near the lamina, especially abaxially, with white hairs; lamina narrowly ovate to elliptic, 60–100 × 20–35 mm, base obtuse to rounded, apex acuminate 5–10 × 1–2 mm, margins shallowly callose-serrate, teeth intramarginal; adaxial surface green tinged with violet, glabrous; abaxial surface green tinged with violet to entirely violet, pubescent with white hairs; venation brochidodromous, primary vein prominent, raised, secondary veins slightly raised, tertiary veins barely visible or not visible. Pedicels green tinged with violet, 60–85 mm at anthesis, 80–110 mm in fruit, glabrous. Flowers 36–37 mm, solitary in upper leaf axils; hypanthium green to violet, obconical, ca. 6 × 6 mm, puberulent, with smooth ridges; calyx lobes green to violet, liguliform, ascending to patent at anthesis, 9–10 × 1–2 mm, glabrous, margins shallowly callose-serrate, apex obtuse; corolla pale green suffused with maroon-violet, glabrous; corolla tube 5–7 mm wide basally, throat narrowing to 3–4 mm wide; corolla lobes lanceolate, margins smooth, dorsal lobes 15–16 × 4–5 mm, slightly falcate, arched forward, dorsal sinus 18–20 mm from the corolla base, lateral lobes 10–12 × 5–6 mm, falcate, slightly recurved, ventral lobe ca. 13 × 5 mm, ventral sinus 11–14 mm from the corolla base; androecium 29–31 mm, exerted 15–18 mm from the ventral opening, filament tube green with violet striations, glabrous, anther tube green with violet along the sutures, glabrous, top 3 anther tips glabrous, bottom 2 anther tips pubescent with white hairs; style and stigma unknown. Fruits maturing violet outside, interior white, globose, 18–30 × 20–30 mm, slightly inflated; seeds brown, broadly elliptic, ca. 1 mm, surface shiny, shallowly foveate.

**Etymology.** The specific epithet, *crocodila*, is in reference to reptiles of the family Crocodylidae, as the leaves of this species have a consistent brochidodromous venation reminiscent of the scales on a crocodile's back.

**Phenology.** Like many *Burmeistera* species, *B. crocodila* likely flowers and sets fruit throughout the year. Specimens have been collected with flowers in



Figure 2. Isotype of *Burmeistera crocodila* Mashburn & Muchhala (*N. Muchhala & J. Gruhn 545*, MO).

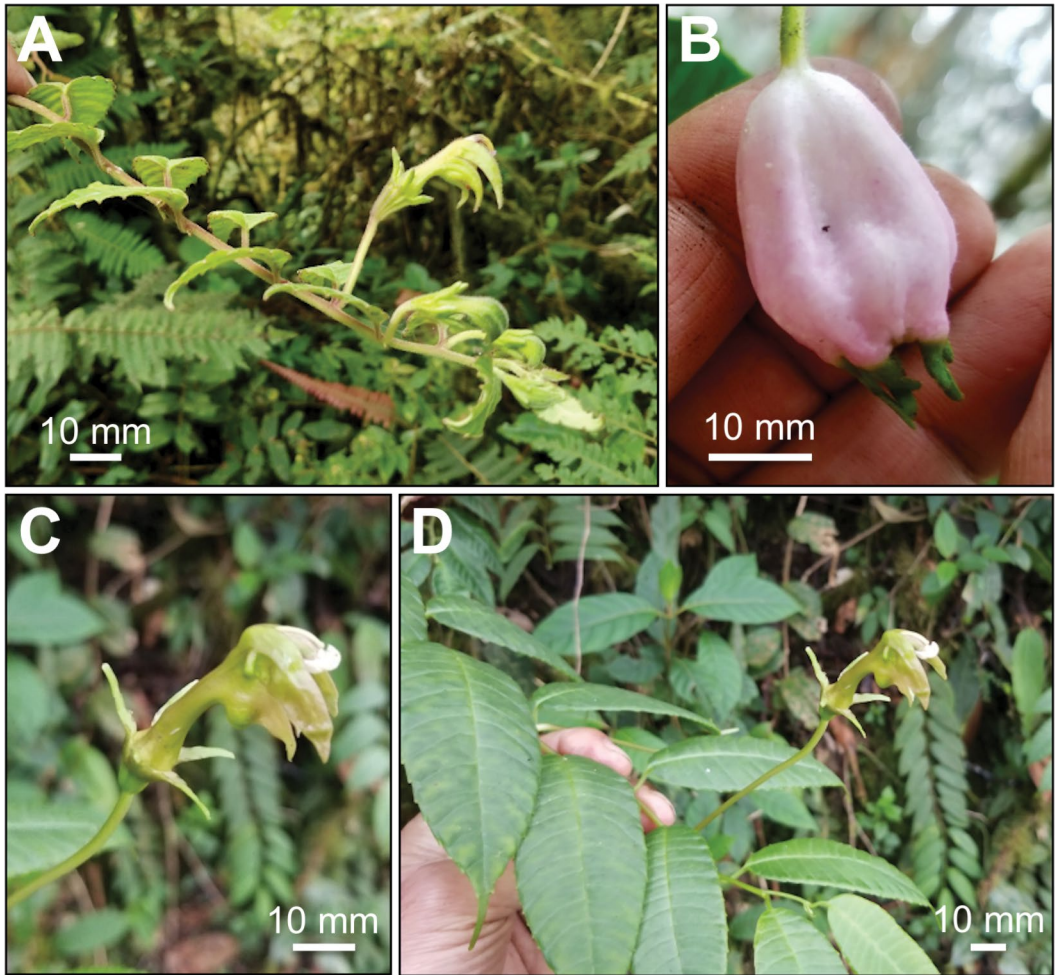


Figure 3. A, B. *Burmeistera chrysothrix* Mashburn & Muchhala. —A. Lateral view of a flowering branch (N. Muchhala & J. Gruhn 546). —B. Mature fruit (N. Muchhala & J. Gruhn 544). C, D. *Burmeistera crocodila* Mashburn & Muchhala. —C. Close-up of flower in female stage (N. Muchhala & J. Gruhn 545). —D. Lateral view of a flowering branch (N. Muchhala & J. Gruhn 545). Photographs A–D by Nathan Muchhala.

January, April, and July. Specimens with fruits have been collected in January and July.

**Distribution.** The few collections of *Burmeistera crocodila* come from a narrow distribution in northwestern Ecuador in Carchi Province. Most specimens have been collected along the road from Tulcán to the small town of Maldonado to the northwest, around elevations of 2500 m or greater. The species possibly occurs just across the border in southwestern Colombia as well, although collections from Colombia have not been seen by the authors.

**Notes.** Vegetatively, *Burmeistera crocodila* appears somewhat similar to *B. resupinata* var. *resupinata* and

*B. resupinata* var. *heilbornii* E. Wimm., both endemic to Ecuador, due to the size and shape of their leaves and the presence of brochidodromous venation. However, *B. crocodila* is easily differentiated from these two species by its much smaller flowers, as both varieties of *B. resupinata* have flowers greater than 60 mm long. In addition, *B. resupinata* has a longer androecium and exertion length (ca. 51 mm and ca. 37 mm, respectively, in variety *heilbornii*, ca. 58 mm and ca. 36 mm in variety *resupinata*), but shorter calyx lobes (5–6 mm in variety *heilbornii*, 2–5 mm in variety *resupinata*).

*Burmeistera crocodila* could be confused with *B. seraniaguae* from central Colombia, due to similarities in general leaf size and shape, as well as certain floral

similarities. However, *B. serraniaguae* can be distinguished by its glabrous leaves and hypanthium, semicraspedodromous leaf venation, longer calyx lobes (13–20 mm), and pyriform fruits, maturing pink. Finally, the two species can be differentiated from each other by their androecium exertion length. We describe this exertion length in *B. crocodila* as 15–18 mm from the ventral corolla lobe. The description of *B. serraniaguae* (in Garzón Venegas & González, 2012) reports an exertion length of 15–20 mm, but this measurement is made from the farthest extent of the dorsal corolla lobes. Our measurement is made from the ventral opening of the corolla. If we used the same exertion measurement as the authors of *B. serraniaguae*, the exertion length of *B. crocodila* would be measured as 4–7 mm, much less than the 15–20 mm described in *B. serraniaguae*. This difference in exertion length is readily seen in the photo provided of *B. crocodila* (Fig. 3C, D) compared with the photos of *B. serraniaguae* found in the figure of Garzón Venegas and González (2012: fig. 3A–C). We are not aware of any consistently accepted method of measuring exertion length in the historical literature. Most historical authors make no quantitative measurements of exertion length, nor do they explain how to apply their descriptions of exertion length. For example, Jeppesen (1981) rarely provides physical measurements, instead using terms such as “long-exserted” or “slightly exerted,” and older authors describe the androecium similarly. We use our method of exertion length measurement, as we find it to be the ecologically informative measurement (see Muchhala, 2006, 2007).

*Burmeistera crocodila* could also be confused with *B. succulenta* H. Karst. & Triana, a widespread species occurring from Venezuela, through Colombia, into Ecuador. The corolla lobes of *B. crocodila*, like the vast majority of *Burmeistera*, are falcate, turning downward and away from the dorsal side of the flower. *Burmeistera succulenta* has corolla lobes that scroll back at maturity, a character only found in two other species: *B. crispiloba* Zahlbr. and sometimes *B. sodiroana* Zahlbr. Additionally, *B. succulenta* can be distinguished by its glabrous leaves, camptrodromous leaf venation, and larger flowers (45–53 mm) with a longer androecium (37–43 mm, exerted 27–33 mm).

**Paratypes.** ECUADOR. **Carchi:** Bosque Protector Golondrinas, on path from Morán to lodge, 2782 m, 00°49'08.09"N 78°04'54.093"W, 3 July 2018 (fl.), Muchhala & Gruhn 543 (MO); sendero desde 0.3–0.5 km WNW de la Cabaña Las Orquídeas (ubicada a 0.14 km W de la intersección con la carretera El Placer–Morán, Km. 19) hasta el Río El Morán entrando por el Km. 19 NW desde El Salado, 2719 m, 00°46'38.8"N 78°03'29.6"W, 22 Nov. 2011, Buenaño et al. 152 (QCA); SE of Maldonado 9–10 km on rd. to Tulcán, 2480–2550 m, 00°51'N 78°02'W, 27 July 1983 (fr.), Thompson & Rawlins 901 (NY); Tulcán–Maldonado rd., 41–45 km

W of Tufiño, 2500–2700 m, 13 Apr. 1978 (fl.), Luteyn & Lebron-Luteyn 5745 (NY); West of Tulcán 62–75 km, 2460–2720 m, 00°50'N 78°05'W, 7 Jan. 1985 (fl., fr.), Luteyn & Cotton 10881 (MO, NY, QCA).

**3. *Burmeistera erosa*** Mashburn, sp. nov. TYPE: Ecuador. Carchi: Forest & ridge area above Río Verde & ridge flanking medium Cerro Golondrinas, 2070–2430 m, 00°52'N 78°07'W, 4 Dec. 1987 (fl., fr.), W. S. Hoover 2301 (holotype, QCA [barcode] 26701!; isotype, MO-3751825!). Figures 4, 9C.

**Diagnosis.** *Burmeistera erosa* Mashburn is differentiated from *B. holm-nielsenii* Jeppesen by its jagged, erose leaf margins and small, delate calyx lobes; and from *B. rostrata* Jeppesen by its larger leaves, longer and thinner tubular hypanthium, and fleshy, opaque corolla lobes.

Scandent herbs, reaching ca. 4 m; latex cream-colored. Stems green, zigzag, up to 3 mm wide on terminal branches, puberulent, internodes 15–35 mm. Leaves alternate, distichous; petiole green, 7–9 mm, puberulent; lamina lanceolate, 120–185 × 20–55 mm, base cuneate to obtuse, apex acuminate to caudate, 25–30 × 0.5–2 mm, margins double callose-dentate, teeth irregular in spacing, size, and direction, tips of the teeth callose, puberulous; adaxial surface green tinged with pale violet, glabrous; abaxial surface pale violet, puberulent along the veins with white hairs; venation brochidodromous, primary and secondary veins prominent, raised, tertiary veins visible, sometimes raised. Pedicels green, 15–34 mm at anthesis and in fruit, puberulent. Flowers 25–28 mm, solitary in upper leaf axils; hypanthium green, tubular, 6–7 × 1–2 mm, base barely distinguishable from pedicel, abruptly widening to 2.5–3 mm wide distally, puberulent; calyx lobes green, deltate, ascending at anthesis, 1–1.5 × 1 mm, puberulent, margins entire; corolla pale green, sometimes lightly tinged with violet, sparsely puberulent; corolla tube 2–3 mm wide basally, throat narrowing to 2–2.5 mm wide; corolla lobes ligulate, margins smooth, dorsal lobes ca. 7 × 1.5 mm, falcate, arched forward, dorsal sinus 10–11 mm from the corolla base, lateral lobes 3–4 × 2 mm, falcate, slightly recurved, ventral lobe ca. 3 × 2 mm, slightly recurved, ventral sinus 8–9 mm from the corolla base; androecium 18–19 mm, exerted ca. 11 mm from the ventral opening, filament tube green, densely puberulent with white hairs, anther tube green, lighter along the sutures, all 5 anther tips glabrous or very sparsely pubescent; style and stigma green, stigma lobes glabrous. Fruits (immature?) green, ca. 6 × 4 mm; seeds unknown.

**Etymology.** The specific epithet, *erosa*, is in reference to the jagged, uneven margins of the leaves of this species.



Figure 4. Holotype of *Burmeistera erosa* Mashburn (W. S. Hoover 2301, QCA).



*Phenology.* Specimens have been collected with flower buds in August and both flowers and fruits in December, suggesting that this species, like many *Burmeistera*, flowers and produces fruits throughout the year.

*Distribution.* Collections of *Burmeistera erosa* come only from a narrow distribution in Carchi Province of northwest Ecuador, within the region of the privately managed Cerro Golondrinas Protected Forest Reserve.

*Notes.* Specimens of this new species have previously been identified as *Burmeistera holm-nielsenii*, endemic to Ecuador, though these two species are easily differentiated. Leaves of *B. erosa* have irregular, jagged, erose margins, while those of *B. holm-nielsenii* are regularly denticulate. In addition, the calyx lobes of *B. holm-nielsenii* are much larger than those of *B. erosa*: 15–20 × 1–1.5 mm, linear with deeply lobed dentate to fimbriate margins. These two species, along with *B. marginata* Triana from Colombia and Ecuador, exhibit a character somewhat unique in *Burmeistera*: a long (6–20 mm) hypanthium that is tubular and equally narrow for almost its entire length, only widening abruptly distally. This character, along with their brochidodromous venation, suggests a close relationship between these three species.

Another species, *Burmeistera rostrata*, is similar to *B. erosa* in having an irregular erose leaf margin. Jeppesen (1981) describes *B. rostrata* in his treatment of the genus in Ecuador, though the type specimen is from Colombia and to our knowledge the species has not been found in Ecuador. *Burmeistera rostrata* can be differentiated by its smaller leaves (55–65 × 10–20 mm) and hypanthium size and morphology (3–3.5 × 2.5 mm, semiovoid to campanulate). In addition, the corolla of *B. rostrata* is green, membranous, and dries somewhat translucent, while the corolla of *B. erosa* is pale green, sometimes tinged violet, fleshy, and dries opaque.

*Paratypes.* ECUADOR. **Carchi:** Espejo, El Gualtal, faldas de Cerro Golondrina Hembra, 2450 m, 00°51'N 78°07'W, 21 Aug. 1994 (fl. bud), *Palacios 12682* (MO); further ascent of Río Verde past stream & waterfall entering from SW and continuing beyond principal drainage stream of large Cerro Golondrinas into drainage streams of medium Golondrinas mts., 1200 m, 00°52'N 78°07'W, 1 Dec. 1987 (fr.), *Hoover 2156* (MO, QCA).

**4. *Burmeistera lingulata*** Mashburn & Muchhala, sp. nov. TYPE: Ecuador. Esmeraldas: Rd. Lita–San Lorenzo, Km. 32, 800 m, 00°30'N 78°53'W, 28 Sep. 1991 (fl., fr.), *B. Øllgaard 99150* (holotype, QCA [bc] 26756!; isotypes, AAU digital image!, QCNE-59219!). Figures 5, 8A, B, 9D.

*Diagnosis.* *Burmeistera lingulata* Mashburn & Muchhala is differentiated from *B. glabrata* (Kunth) Benth. & Hook. f. ex B. D. Jacks. by its smaller (ca. 15 mm diam. vs. 25–30 mm), non-inflated, yellow fruits; and from *B. brachyandra* E. Wimm. by its longer pedicels at anthesis and larger flowers (44–45 mm long vs. 32–37[–41] mm) with larger, tongue-shaped calyx lobes.

Scandent herbs, reaching ca. 1.5 m. Latex white. Stems up to 4–6 mm wide on terminal branches, tan to green, glabrous, striate when dry. Leaves alternate, spiral, internodes 10–40 mm; petiole 15–30 mm, green to brown, glabrous to sparsely puberulent; lamina 50–180 × 15–65 mm, elliptic, base attenuate, apex attenuate, margins shallowly callose-dentate, sometimes nearly entire; adaxial surface green, glabrous; abaxial surface green, puberulent, especially along the main vein, with soft white hairs; venation camptodromous, primary and secondary veins prominent, raised, tertiary veins visible. Pedicels 75–105 mm at anthesis and in fruit, glabrous, green. Flowers 44–45 mm, solitary in upper leaf axils; hypanthium 4–6 × 4–5 mm, cupuliform, green, glabrous; calyx lobes 10–15 × 5–9 mm, tongue-shaped, foliaceous, slightly ascending to patent at anthesis, green, glabrous, margins shallowly callose-serrate; corolla pale green (rarely tinged with red), glabrous; corolla tube ca. 5 mm wide basally, throat narrowing to ca. 2 mm wide; corolla lobes ligulate, margins smooth, dorsal lobes 13–14 × 3–4 mm, arcuate, arched forward, dorsal sinus 20–21 mm from the corolla base, lateral lobes 6–8 × 3–4 mm, arcuate, slightly recurved, ventral lobe 4–5 × 3–4 mm, slightly recurved, ventral sinus ca. 16 mm from the corolla base; androecium 39–41 mm, exerted 25–27 mm from the ventral opening, filament tube green, glabrous, anther tube ca. 5 × 4 mm, green, glabrous, all 5 anther tips glabrous to sparsely pubescent; style and stigma glabrous. Fruits ca. 15 × 15 mm, globose, not inflated, fleshy, maturing yellow; seeds ca. 1 mm, elliptic, tan, surface shiny, shallowly foveate.

*Etymology.* The specific epithet, *lingulata*, comes from Latin, meaning “like a little tongue,” in reference to the tongue-like shape of the calyx lobes.

*Phenology.* Specimens have been collected with flowers and fruits throughout the year.

*Distribution.* *Burmeistera lingulata* is found in the provinces of Carchi and Esmeraldas in northwest Ecuador. The species occurs in wet forests from 380 to 1200 m in elevation and seems to do well in disturbed secondary forests and areas cleared for farmland.

*Notes.* Before the description of this new species, specimens from Carchi and Esmeraldas identified here



Figure 5. Holotype of *Burmeistera lingulata* Mashburn & Muchhala (*B. Ølgaard* 99150, QCA).

as *Burmeistera lingulata* were often annotated as *B. glabrata* (from Colombia and Ecuador), likely due to their relatively long calyx lobes and similarly sized pale green flowers. As a result, Jeppesen (1981) understood *B. glabrata* as occurring on both sides of the Andes: in Carchi and Pichincha Provinces to the west, and in Napo and Morona-Santiago Provinces to the east. With the description of *B. lingulata*, we now understand *B. glabrata* to occur only to the east of the Andes, while *B. lingulata* occurs to the west. Because *B. glabrata* is morphologically similar to its close relative *B. borjensis* Jeppesen, which is found only in Napo Province, both species can possibly be confused with *B. lingulata*. However, *B. lingulata* can be differentiated from both *B. borjensis* and *B. glabrata* by fruit morphology (25–30 mm diam., inflated, and green to green suffused with violet in *B. borjensis* and *B. glabrata*). In addition to these characters, *B. lingulata* has been included in a recent phylogeny (Bagley et al., 2020) and is placed in a separate subclade of *Burmeistera* from *B. borjensis* and *B. glabrata*.

*Burmeistera lingulata* is likely closely related to the Ecuadorian species *B. brachyandra*, *B. domingensis* Jeppesen, and the new species *B. valdiviana* Mashburn, described below. Each of these four species occurs west of the Andes in Ecuador. In the phylogeny of Bagley et al. (2020), a specimen we identify as the new species *B. lingulata* is placed next to *B. domingensis* (the other two species not included). Before the descriptions of *B. lingulata* and *B. valdiviana* (see below), conflicting specimen annotations revealed a difficulty in fitting collections to the existing taxonomy (see Jeppesen, 1981). The descriptions of *B. lingulata* and *B. valdiviana* resolve much of this difficulty. A comparison between these four species is provided in Table 1. *Burmeistera lingulata* can be differentiated from *B. brachyandra* using the characters of size of leaf subtending a flower, flower aggregation, flower length, calyx lobe size and shape, androecium length, exsertion length, fruit size, and geographic distribution. *Burmeistera lingulata* can be differentiated from *B. domingensis* using the characters of indumentum, leaf margin serration, flower length, calyx lobe size and shape, corolla color, androecium length, exsertion length, fruit size and color, and geographic distribution. Finally, *B. lingulata* can be differentiated from *B. valdiviana* using the characters of flower length, hypanthium size, calyx lobe size and shape, fruit color, and geographic distribution.

**Paratypes.** ECUADOR. **Carchi:** border area betw. Prov. Carchi & Esmeraldas, ca. 20 km past Lita on rd. Lita–Alto Tambo, 550 m, 24 June 1991 (fl.), *van der Werff et al. 11911* (MO); plateau above San Marcos de los Coaiqueños, on trail toward Gualpi Bajo, 1000 m, 01°06'N 78°17'W, 7 Feb. 1985 (fl.), *Øllgaard et al. 57355* (QCA, QCNE); Reserva Etnica y

Forestal Awá, San Marcos, 1000 m, 01°05'N 78°15'W, 11 Mar. 1988 (fr.), *Jørgensen et al. 65176* (QCA); San Marcos valley, 600 m, 01°07'N 78°20'W, 20 Nov. 1983 (fl., fr.), *Kvist et al. 48696* (QCA); Tulcán Cantón, Parroquia Chical, Sector Gualpi medio, Reserva Indígena Awá, sendero a San Marcos al N de la casa comunal, 1026 m, 01°02'N 78°16'W, 23–27 May 1992 (fr.), *Tipaz et al. 1039* (MO); Tulcán Cantón, Reserva Etnica Awá, Parroquia El Chical, Sector Gualpi Medio, Río Canumbí, 1150 m, 01°02'N 78°15'W, 19–28 Feb. 1993 (fl.), *Grijalva et al. 466* (MO); Tulcán Cantón, Reserva Indígena Awá, Comunidad San Marcos, 25 km al NW de El Chical, parroquia Maldonado, 1500 m, 01°06'N 78°14'W, 16–30 Nov. 1990 (fl., fr.), *Rubio et al. 905* (MO). **Esmeraldas:** along rd. betw. Lita & San Lorenzo, vic. of Alto Tambo, 6.6 km NW of railroad tracks in Alto Tambo, 684 m, 00°57'34"N 78°37'36"W, 22 Feb. 2005 (fl., fr.), *Croat 95181* (MO); Comunidad Awá Río Bogotá, 11.5 km W of Alto Tambo, 30.5 km W of Río Lita, 3 km by trail to Río Bogotá on S side of Lita–San Lorenzo rd., 380 m, 00°58'57"N 78°35'58"W, 15 Sep. 2002 (fl., fr.), *Croat et al. 87524* (MO); hwy. from Lita to Alto Tambo, 797 m, 00°54.624'N 78°32.736'W, 18 July 2002 (fl.), *Muchhala 142* (QCA); Mun. Lita, Río Lita & tributaries, affluent of Río Mira, 120 km NW of Ibarra, 14 km WNW of Lita, 600 m, 00°52'N 78°29'W, 7 May 1987 (fl.), *Daly & Acevedo 5145* (NY); San Lorenzo Cantón, Alto Tambo, Recinto El Dorado, 2 km al NW del recinto, 340 m, 00°55'N 78°36'W, 26 Oct. 1999 (fl., fr.), *Valenzuela et al. 692* (QCNE).

**5. *Burmeistera sierrazulensis*** Mashburn & Muchhala, sp. nov. TYPE: Ecuador: Napo: private property of William Philips, ca. 2 hr walk from end of rd., W of Cosanga, N slopes of Cordillera de Huacamayos, 2300 m, 00°45'S 77°55'W, 12 Dec. 1989 (fl., fr.), *J. L. Luteyn & S. Cobo 13464* (holotype, NY [bc] 11858571; isotypes, QCA [bc] 267361, QCNE-35913!). Figures 6, 8C, D, 9E.

**Diagnosis.** *Burmeistera sierrazulensis* Mashburn & Muchhala is differentiated from related inflated-fruit species, *B. borjensis* Jeppesen and *B. glabrata* (Kunth) Benth. & Hook. f. ex B. D. Jacks., by its small, deltate calyx lobes (2–3 × 1 mm), which are patent to slightly reflexed at anthesis, and fruits maturing white, tinged and lightly spotted with maroon-violet.

Scandent herbs, reaching ca. 1 m. Latex unknown. Stems up to 5 mm wide on terminal branches, thick-walled, green to green tinged with violet, puberulent, striate when dry. Leaves alternate, spiral, internodes 5–25 mm; petiole 15–20 mm, slender, green to green tinged with violet, puberulent; lamina 35–70 × 15–25 mm, ovate to elliptic, base cuneate to rounded, apex attenuate, margins callose-serrate, serrations not more than 3 mm, sometimes tinged maroon-violet; adaxial surface green, glabrous to sparsely puberulent; abaxial surface green, puberulent along the veins with short white to cream-colored hairs; venation camptodromous, diminishing along the margins or terminating in the marginal teeth, primary and secondary veins prominent, raised, tertiary veins visible. Pedicels 40–65 mm at anthesis, 65–85 mm in fruit, green to green tinged

Table 1. Morphological characters distinguishing *Burmeistera brachyandra* E. Wimm., *B. domingensis* Jeppesen, *B. lingulata* Mashburn & Muchhala, and *B. valdiviana* Mashburn.

	<i>B. brachyandra</i>	<i>B. domingensis</i>	<i>B. lingulata</i>	<i>B. valdiviana</i>
Vegetative indument	stems, petioles, and leaf undersides glabrous to puberulous	stems, petioles, and leaf undersides puberulous with cream-colored hairs, especially on new growth	stems glabrous; petioles and leaf undersides glabrous to sparsely puberulent	stems, petioles, and leaves glabrous
Petiole length	10–45 mm	5–20 mm	15–30 mm	20–50 mm
Leaf size and shape	120–250 × 60–90 mm, broadly elliptic, margins shallowly callose-dentate	(30–)65–120 × (10–)35–65 mm, broadly elliptic, margins increasingly serrate toward the apex	50–180 × 15–65 mm, elliptic, margins shallowly callose-dentate, nearly entire	60–170 × 25–75 mm, elliptic to broadly elliptic, margins shallowly callose-dentate, nearly entire
Leaf subtending pedicel	reduced, 30–75 × 15–40 mm	similar to non-fertile leaves	similar to non-fertile leaves	similar to non-fertile leaves
Flower aggregation	bunched apically with new growth, appearing racemose	solitary in upper leaf axils, not obviously bunching	solitary in upper leaf axils, not obviously bunching	solitary in upper leaf axils, not obviously bunching
Pedicels at anthesis	30–60 mm, glabrous	40–55 mm, basally puberulous, distally becoming glabrous	75–105 mm, glabrous	55–95 mm, glabrous
Flower length	32–37(–41) mm	31–36 mm	44–45 mm	47–50 mm
Hypanthium size and shape	5–6 × 3–6 mm, cupuliform	4–6 × 2–4 mm, cupuliform	4–6 × 4–5 mm, cupuliform	6–8 × 4–7 mm, cupuliform to urceolate
Calyx lobe size and shape	6–7 × 2–3 mm, ligulate	5–8 × 1–3 mm, ligulate, margins serrate	10–15 × 5–9 mm, tongue-shaped, foliaceous	4–10 × 1.5–3 mm, ligulate
Corolla color	green	green streaked or spotted with violet to entirely violet	pale green (rarely tinged with red)	green
Androecium length	27–31(–35) mm	26–29 mm	39–41 mm	38–43 mm
Androecium exertion length	15–23 mm	16–18 mm	25–27 mm	24–26 mm
Fruit size	ca. 10 × 10 mm	ca. 8 × 8 mm	ca. 15 × 15 mm	15–20 × 15–20 mm
Fruit color	pale green to yellow	dark red	yellow	red
Geographic range	provinces of Esmeraldas, western Carchi, western Pichincha, Santo Domingo de los Tsáchilas, northern Los Ríos, and northern Manabí	provinces of Santo Domingo de los Tsáchilas and northern Manabí	provinces of Carchi and Esmeraldas	western Manabí Province in remnants of coastal cloud forest on mountain ridges



Figure 6. Holotype of *Burmeistera sierrazulensis* Mashburn & Muchhala (*J. L. Luteyn & S. Cobo 13464*, NY).

with violet, puberulent. Flowers 42–43 mm, solitary in upper leaf axils, but often with many flower buds bunched apically with new growth; hypanthium 6–7 × 4–5 mm, obconical, green to green tinged with violet, puberulent; calyx lobes 2–3 × 1 mm, deltate, patent to slightly reflexed at anthesis, exteriorly green, interiorly tinged violet, puberulent, margins shallowly callose-dentate, violet, apex acute, violet; corolla pale green, sometimes lightly tinged violet, especially along the margins, puberulent; corolla tube 5–6 mm wide basally, throat narrowing to 2–3 mm wide; corolla lobes ligulate, margins smooth, dorsal lobes 11–13 × 2–3 mm, arcuate, arched forward, dorsal sinus 15–16 mm from the corolla base, lateral lobes 7–8 × 2–3 mm, arcuate, slightly recurved, ventral lobe ca. 5 × 5 mm, slightly recurved, ventral sinus 9–10 mm from the corolla base; androecium 31–36 mm, exerted 23–27 mm from the ventral opening, filament tube green, basally sparsely puberulous with appressed white hairs, distally becoming puberulous, anther tube green, tinged violet along the sutures, puberulent with white to yellow appressed hairs, all 5 anther tips sparsely pubescent with white hairs; style green, sparsely pubescent, stigma green, puberulent. Fruits 35–45 × 25–45 mm, globose to ovoid, inflated, maturing white, lightly spotted with maroon-violet; seeds ca. 1 mm, narrowly elliptic, light brown, surface shiny, shallowly foveate.

*Etymology.* This species is named after the SierrAzul Cloud Forest Reserve in Napo Province, Ecuador, where all of the known collections have been made.

*Phenology.* Specimens have been collected with flowers and fruits in March, May, and December.

*Distribution.* This species is known only from a small distribution in Napo Province, Ecuador, in the SierrAzul Cloud Forest Reserve. It occurs in cloud forest at elevations from 2000 to 2300 m.

*Notes.* *Burmeistera sierrazulensis* is part of a clade of inflated-fruit species in *Burmeistera* and is most closely related to other inflated-fruit species that also occur on the eastern slopes of the Ecuadorian Andes, such as *B. borjensis*, *B. ignimontis* E. Wimm, *B. glabrata* (also found in Colombia), and *B. oyacachensis* Jeppesen (Uribe-Convers et al., 2017). *Burmeistera glabrata* is a widespread species that occurs on the foothills of the Andes, whereas the other species, including *B. sierrazulensis*, occur at higher elevations in restricted ranges. It could be that speciation in this clade has been driven by successive colonization of high-elevation valleys in the Andes, resulting in restricted gene flow between these high-elevation populations. *Burmeistera sierrazulensis* can be differentiated

from each of these species by its much smaller deltate calyx lobes (vs. 13–19 × 6–13 mm, broadly lanceolate in *B. borjensis*; 12–28 × 3–6 mm, ligulate in *B. ignimontis*; 8–15 × 3–6 mm, lanceolate in *B. glabrata*; 11–18 × 3–5 mm, ligulate in *B. oyacachensis*) and mature fruit color (green suffused with violet in the other species mentioned).

*Paratypes.* ECUADOR. **Napo:** private property of William Philips, ca. 2 hr walk from end of rd., W of Cosanga, N slopes of Cordillera de Huacamayos, 2300 m, 00°45'S 77°55'W, 12 Dec. 1989 (fl., fr.), *Luteyn & Cobo 13465* (NY, QCA); Quijos, SierrAzul, Agrícola Industrial Río Aragón, alrededores del Campamento Estero Chico, 2500 m, 00°41'S 77°56'W, 25 Mar. 1992, *Alvarez et al. 224* (MO); Quijos, SierrAzul, Agrícola Industrial Río Aragón, Campamento Aragón, 2050 m, 00°38'S 77°54'W, 28 Mar. 1992 (fr.), *Alvarez & Proaño 258* (MO); Quijos, SierrAzul, Agrícola Industrial Río Aragón, Campamento San Fernando, 2250 m, 00°41'S 77°55'W, 3 May 1992 (fr.), *Alvarez et al. 439* (MO).

## 6. *Burmeistera valdiviana* Mashburn, sp. nov.

TYPE: Ecuador. Manabí: Cantón Jipijapa, Parroquia Jipijapa, Cerro Montecristi, 1 km W of the town of Montecristi, 550 m, 01°03'05.2"S 80°39'42.5"W, 29 Jan. 2001 (fl., fr.), *J. L. Clark, L. Miranda & T. Pilligua 6195* (holotype, QCNE-168918!; isotypes, QCA [bc] 140728!, US [bc] 00713918 digital image!). Figures 7, 8E, F, 9F.

*Diagnosis.* *Burmeistera valdiviana* Mashburn can be differentiated from *B. brachyandra* E. Wimm. by its longer flowers, with longer androecium and exertion lengths, and larger fruits maturing red; and from *B. lingulata* Mashburn & Muchhala by its longer flowers, smaller calyx lobes, and fruits maturing red.

Terrestrial herbaceous shrubs, reaching ca. 1.5 m. Latex unknown. Stems up to 4 mm wide on terminal branches, yellow-green, glabrous. Leaves alternate, spiral, internodes 5–40 mm; petiole 20–50 mm, green, sometimes tinged violet, glabrous; lamina 60–170 × 25–75 mm, elliptic to broadly elliptic, base cuneate, apex acute to attenuate, margins shallowly callose-serrate, sometimes nearly entire; adaxial surface green, glabrous; abaxial surface lighter green, puberulent along the veins; venation camptodromous, primary vein prominent, raised, secondary veins slightly raised, tertiary veins visible. Pedicels 55–95 mm at anthesis and in fruit, glabrous, green to red-violet. Flowers 47–50 mm, solitary in upper leaf axils; hypanthium 6–8 × 4–7 mm, cupuliform to urceolate, yellow-green, glabrous, ridges smooth; calyx lobes 4–10 × 1.5–3 mm, ligulate, ascending to patent at anthesis, green, glabrous, margins shallowly callose-dentate, apex acute; corolla green, glabrous; corolla tube 3–6 mm wide basally, throat narrowing to 2–3 mm wide; corolla lobes ligulate, margins smooth, dorsal lobes 16–20 × 3–4 mm, falcate, arched forward, dorsal sinus ca. 20 mm from the corolla base,



Figure 7. Holotype of *Burmeistera valdiviana* Mashburn (J. L. Clark, L. Miranda & T. Pilligua 6195, QCNE).

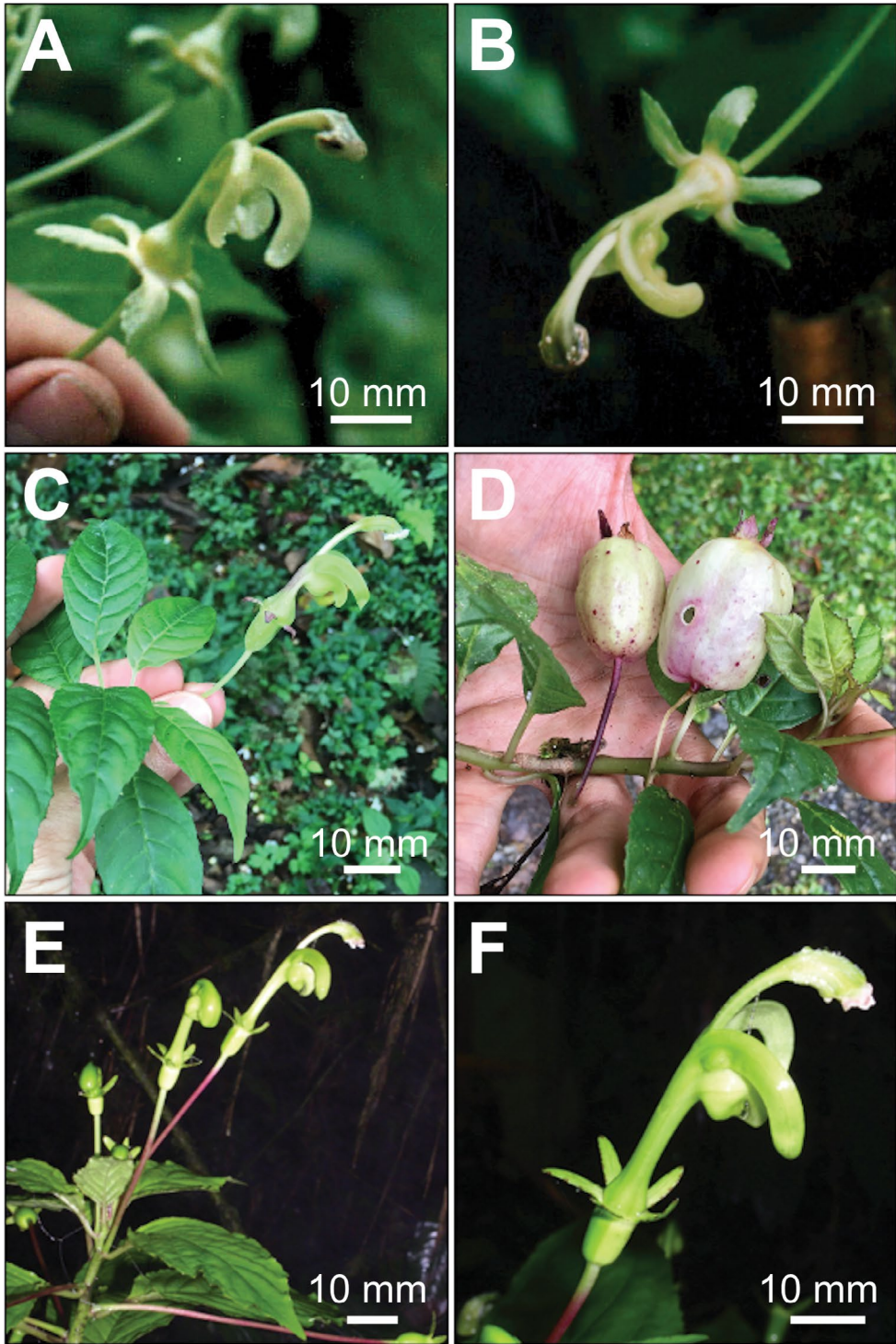


Figure 8. A, B. *Burmeistera lingulata* Mashburn & Muchhala. —A. Ventral view of a mature flower (N. Muchhala 142). —B. Dorsal view of a mature flower (N. Muchhala 142). C, D. *Burmeistera sierrazulensis* Mashburn & Muchhala. —C. Flowering branch with a flower in female stage. —D. Branch with one immature and one mature fruit. E, F. *Burmeistera valdiviana* Mashburn. —E. Flowering branch with red-violet pedicel coloration (N. Muchhala 241). —F. Lateral view of a flower in male stage (N. Muchhala 241). Photographs A, B, E, F by Nathan Muchhala, C, D by Juan I. Moreira-Hernández.



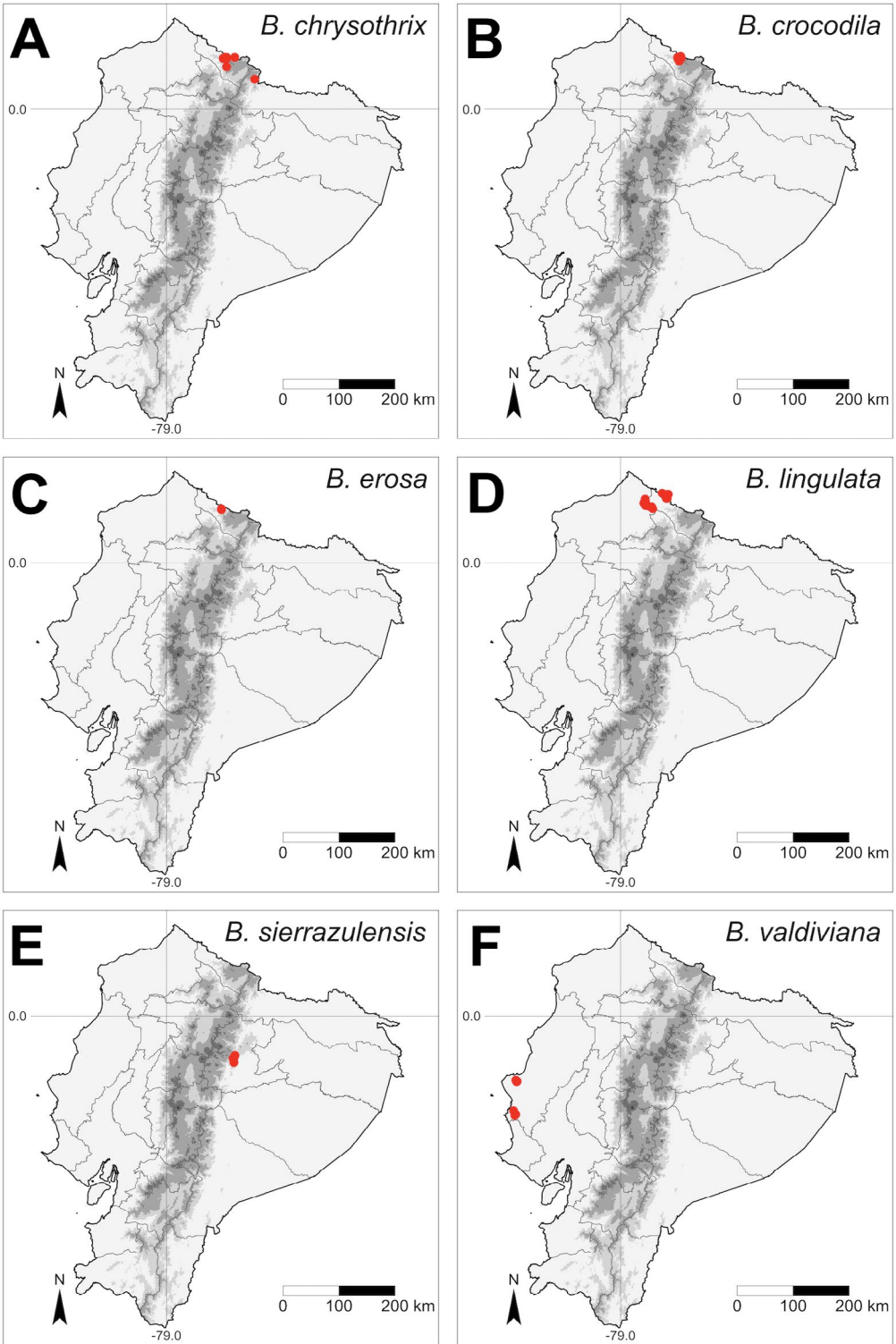


Figure 9. A–F. Geographic distribution maps of known herbarium collections. —A. *Burmeistera chrysothrix* Mashburn & Muchhala. —B. *Burmeistera crocodila* Mashburn & Muchhala. —C. *Burmeistera erosa* Mashburn. —D. *Burmeistera lingulata* Mashburn & Muchhala. —E. *Burmeistera sierrazulensis* Mashburn & Muchhala. —F. *Burmeistera valdiviana* Mashburn.

lateral lobes 9–10 × 3–4 mm, falcate, slightly recurved, ventral lobe ca. 9 × 3 mm, slightly recurved, ventral sinus 15–17 mm from the corolla base; androecium 38–43 mm, exerted 24–26 mm from the ventral opening, filament tube green, glabrous to sparsely pubescent with white hairs, anther tube green, glabrous, all 5 anther tips glabrous to sparsely pubescent; style and stigma cream-colored, glabrous. Fruits 15–20 × 15–20 mm, globose, fleshy, not-inflated, red; seeds ca. 0.5 mm, broadly elliptic, brown, surface shiny, shallowly foveate.

*Etymology.* The specific epithet, *valdiviana*, refers to the Valdivia culture, which flourished from 3500 BCE to 1500 BCE. It is one of the oldest known cultures in the region, and pottery from this period is some of the earliest known in the Western Hemisphere (Bray, 2009). The geographic area in which the Valdivia culture flourished corresponds to the geographic occurrence of *Burmeistera valdiviana*.

*Phenology.* Specimens have been collected with flowers and fruits from September to February.

*Distribution.* *Burmeistera valdiviana* is found in remnants of coastal cloud forests on mountain ridges in Manabí Province, western Ecuador. Locally this type of forest is called “bosque de garua,” in reference to the regular occurrence of fog and drizzling rain.

*Notes.* Based on morphological similarities, *Burmeistera valdiviana* is likely closely related to three other species found in Ecuador, *B. lingulata* (newly described above), *B. brachyandra*, and *B. domingensis*. *Burmeistera valdiviana* occurs disjunct from these other three species, being found only in remnants of cloud forests on the relatively small mountains found on the Pacific coast of central Ecuador. A comparison between *B. valdiviana* and these three similar species is found in Table 1. *Burmeistera valdiviana* can be differentiated from *B. brachyandra* using the characters of size of leaf subtending a flower, flower aggregation, flower length, androecium length, exertion length, fruit size and color, and geographic distribution. *Burmeistera valdiviana* can be differentiated from *B. domingensis* using the characters of indument, flower length, corolla color, androecium length, exertion length, fruit size, and geographic distribution. Finally, *B. valdiviana* can be differentiated from *B. lingulata* using the characters of flower length, hypanthium size, calyx lobe size and shape, fruit color, and geographic distribution.

*Paratypes.* ECUADOR. **Manabí:** Cerro Monte Cristi, 550 m, 8 Sep. 1963 (fl., fr.), *Escuela 330* (MO); Parque Nacional Machalilla, San Sebastián, 8 Feb. 1994 (fl., fr.), *Cornejo*

*1215* (MO, QCNE); Cord. de Chongón, Parque Nacional Machalilla, S of San Sebastian, C. Josse ha plot, 500–600 m, 01°35'S 80°41'W, 24 Mar. 1993 (fr.), *Øllgaard et al. 100778* (AAU, QCNE); Machalilla, San Sebastián, 550–700 m, 01°36'S 80°42'W, 22 Nov. 2004 (fl., fr.), *Muchhala 241* (QCA); Montecristi, Cerro Montecristi, carretera Manta–Jipijapa, entrada por Montecristi o El Chorrillo, 300–600 m, 01°02'S 80°41'W, 11–12 Nov. 1995 (fl., fr.), *Núñez et al. 340* (MO); Montecristi, Cerro Montecristi, crest of mtn., 620 m, 01°03'17"S 80°40'10"W, 7 Feb. 2009 (fl., fr.), *Tepe 2711* (QCNE).

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