THREE NEW EPIPHYTIC SPECIES AND A NEW VARIETY IN *CERATOSTEMA* (ERICACEAE: VACCINIEAE) FROM SOUTHEASTERN ECUADOR

Xavier Cornejo
Herbario GUAY
Departamento de Botánica, Facultad de Ciencias Naturales
Universidad de Guayaquil
Av. Raúl Gómez Lince s.n. y Av. Juan Tanca Marengo
(campus Mapasingue), Guayaquil, ECUADOR
orcid.org/0000-0002-4081-4047
Corresponding author: xcornejoguay@gmail.com

James L. Luteyn
The New York Botanical Garden
2900 Southern Blvd., Bronx, New York 10458-5126, U.S.A.
https://orcid.org/0009-0006/1316-118X
Current address:
32075 East Side Drive
Beaver Island, Michigan 49782, U.S.A.

ABSTRACT

Ceratostema guachizacae, Ceratostema portillae, Ceratostema portillae var. **lucida,** and **Ceratostema glandipedicellata** (Ericaceae: Vaccinieae), three new species and a new variety of pendulous epiphytic shrubs, from southeastern Ecuador of ornamental potential are described and illustrated.

RESUMEN

Ceratostema guachizacae, Ceratostema portillae, Ceratostema portillae var. **lucida,** y **Ceratostema glandipedicellata** (Ericaceae: Vacciniae), tres nuevas especies y una nueva variedad de arbustos péndulos epífitos, del sur este de Ecuador y con potencial ornamental, son descritas e ilustradas.

Key Words: Extrafloral nectaries, horticulture, Morona Santiago, Neotropics, Zamora Chinchipe

Ceratostema Juss. (Ericaceae: Vaccinieae) is a genus of Andean blueberries currently consisting of 39 species and one variety, ranging from Venezuela to northern Peru. Thirty-two species of *Ceratostema* are endemic to Ecuador, one to the Guayana Highland of Guyana, and three to northern Peru; only two species are shared between southern Colombia and eastern Ecuador. The genus was first described by A.L. de Jussieu in 1789 and named after the "horned stamens" (the "horns" being the elongated anther tubules). It was treated by A.C. Smith (1952), who gave a brief discussion and a key to the 16 species then recognized, and again in 1986 by Luteyn, who provided a key to the 23 species then recognized. An updated key and accompanying taxonomic treatment to the 28 species of Ecuador was later published by Luteyn (1996). Jiménez et al. (2021, 2024) and Cornejo et al. (In press) have recently added an additional three species to Ecuador.

Ceratostema is characterized by its calyces being articulated with the pedicels and its large corollas (2–5.5 cm long) that are often conspicuously ventricose at the base and with very long, narrow lobes (to nearly 1/2 of the overall corolla length). Its stamens have anther thecae that are strongly papillate and anther tubules that are very long and thin, dehiscing by short, oblique clefts. In habit the plants are pendent epiphytes or terrestrial shrubs up to 3.5 m tall, often arising from large superficial or subsurface lignotubers (to 1.5 m diameter in *C. loranthiflorum* Benth.). Some species have large, green floral bracts (up to 7 cm long in *C. megabracteatum* Luteyn). Their corollas are often fleshy, waxy, and come in striking shades of bright red or orange with contrasting lobes that are dark blue-black within. All have flowers adapted to hummingbird pollination (Luteyn 2002). The fruits of *C. alatum* (Hoer.) Sleumer are locally known as "pera silvestre" or "manzanilla" in Tungurahua Province, Ecuador, where they are eaten—the flavor suggested that of the pear (Popenoe 1924); the fruits of *C. calycinum* (Benth. & Hook.f. ex A.C.Sm.) Sleumer (Ecuador, *Luteyn & Lebrón-Luteyn 5812*, NY) are the largest of the genus and of all known neotropical Vaccinieae and may measure 3–3.5 cm in diameter—they were very juicy although not particularly sweet (Luteyn pers. obs.). Most species have excellent ornamental value, those described herein are currently sold by Ecuagenera.

Within Neotropical Vaccinieae, a tribe with more than 800 species, *Ceratostema* is morphologically most closely related to *Semiramisia* Klotzsch (1851), as was discussed by Luteyn (1984). In a preliminary,

J. Bot. Res. Inst. Texas 18(2): 321–332. 2024
https://doi.org/10.17348/jbrit.v18.i2.1369

phylogenetic molecular analyses of the entire tribe Vaccinieae, based on sequence data from the chloroplast *matK* gene and the nrITS region for 93 species of Vaccinieae (including 2 spp. *Ceratostema*), Kron et al. (2002) placed *Ceratostema* in a strongly supported "Andean Clade", but therein with poor generic resolution. Powell and Kron (2003) analyzed sequence data from *matK*, *ndhF*, *rps4*, and nrITS for 55 species strictly from the Andean Clade (including 4 spp. of *Ceratostema*) that identified a small, but strongly supported (95%) *Ceratostema-Macleania-Psammisia* clade within the larger "Andean Clade." Pedraza et al. (2015) sampled six species of *Ceratostema* in a study that looked at 91 species of Vaccinieae. In a taxon sampling double in size with any previous analysis, her *Ceratostema-Macleania-Psammisia* clade, similar to that of Powell and Kron (2003), failed to form a well-supported clade and evolutionary relationships were still unclear. The phylogenetic study by Ortiz (2017) sampled 42 species of Vaccinieae from the "Andean Clade" (including the same six species of *Ceratostema* used by Pedraza et al. 2015) and other different Andean genera/species overall. It also confirmed *Ceratostema* in the "Andean Clade" but failed to add more to our general understandings of the phylogenetic relationships of *Ceratostema*. All of these studies also found *Ceratostema* to be polyphyletic, and Pedraza et al. (2015) noted that because "… these studies differ in their generic sampling and the groups in which they disagree are either poorly supported or sampled, making detailed comparisons [are] difficult." Clearly, more data is required before any conclusions can be made about the detailed relationships among *Ceratostema* and other Neotropical Vaccinieae.

The Neotropical flora is still relatively unknown given its vast biodiversity. This leads us to predict with some degree of certainty that many additional species await discovery in areas that are botanically unexplored or little explored. Many more collections need to be made, species examined, and then the variation in both morphological and molecular data need to be compared before the phylogenetic make up Vaccinieae in general, and the position of *Ceratostema,* in particular, are known. Furthermore, the fact that seven new discoveries of native *Ceratostema* (Jiménez et al. 2021, 2024; Cornejo et al. 2024, herein) from a high-diversity country such as Ecuador are being cultivated *ex situ* for ornamental and research purposes demonstrates the importance of collecting programs as a method of conservation and protection of biodiversity.

1. Ceratostema guachizacae Cornejo & Luteyn, **sp. nov.** (**Fig. 1**). TYPE: ECUADOR. ZAMORA CHINCHIPE: Canton Yacuambi, Yacuambi environs, 3°36′S 78°57′W, 1800 m, 16 Feb 2024 (fl), *X. Cornejo 10166* [HOLOTYPE: GUAY (mounted and spirit); ISOTYPE: QCA].

Diagnosis.—*Ceratostema guachizacae* is similar to *C. pedunculatum* Luteyn (1996), but differs by having leaf blades lorate-lanceolate, 0.7–1 cm wide (vs. falcate, 2–2.5 cm wide), abaxially concave (vs. flat), the secondary nerves inconspicuous (vs. plinerved); bracteoles located along lower third of pedicel, glabrous (vs. strictly basal, short-pilose); calyx 5–7 mm long, glabrous (vs. 7–10 mm long, pilose to short-pilose), the lobes short-apiculate (vs. long-acuminate); corolla 32–45 mm long (vs. 51–55 mm long); filament of stamens fused (vs. distinct or slightly coherent); and petioles, pedicels and calyces glabrous (vs. densely pilose to short-pilose).

Description.—**Epiphytic shrubs** with lateral branches patent to subpendulous, glabrous; roots not seen; branches terete to subterete, purple to green, smooth, glabrous. **Leaves** loosely spiral, spreading to subpendulous; leaf blades coriaceous (fresh), becoming chartaceous (dry), lorate-lanceolate, 8–13 × 0.7–1 cm, basally cuneate, apically tapering to short-caudate, marginally revolute, green to dark green and somewhat glossy (fresh), becoming opaque brown to grayish (dry), the midvein adaxially sulcate, glabrous, concave, pale green (fresh), becoming brown (dry), the midvein abaxially prominent, glabrous, the secondary nerves inconspicuous on both sides; petioles 3–5 mm long, subterete, rimulose, pale green, glabrous. **Inflorescence** terminal on lateral branches, racemose, ca. 5-flowered; peduncle subterete, 4.5–6 cm long, purple (fresh), brown (dry); floral bract deltoid to short-lanceolate, 1–3 × 0.7 mm (fresh), ca. 1–3 × 0.5 mm (dry); pedicel articulate with calyx, straight to slightly incurved, 25–35 × 1.5–2 mm (fresh), 20–33 × 1–1.5 mm (dry), subterete (fresh), becoming flattened (dry), purple, glabrous (fresh); bracteoles 2, located along lower third of pedicel, short-lanceolate to linear-lanceolate or oblong-lanceolate, 1.5–3 × 0.8 mm (fresh), ca. 1–1.5 × 0.5 mm (dry), glabrous. **Flowers** 5-merous, pendulous; calyx ca. 7 × 10 mm, light-green, purple at base and lobes, glabrous (fresh); hypanthium broadly obconic, truncate at base, subterete, ca. 3.5–4 × 4 mm (fresh), ca. 2–3 × 2–3 mm

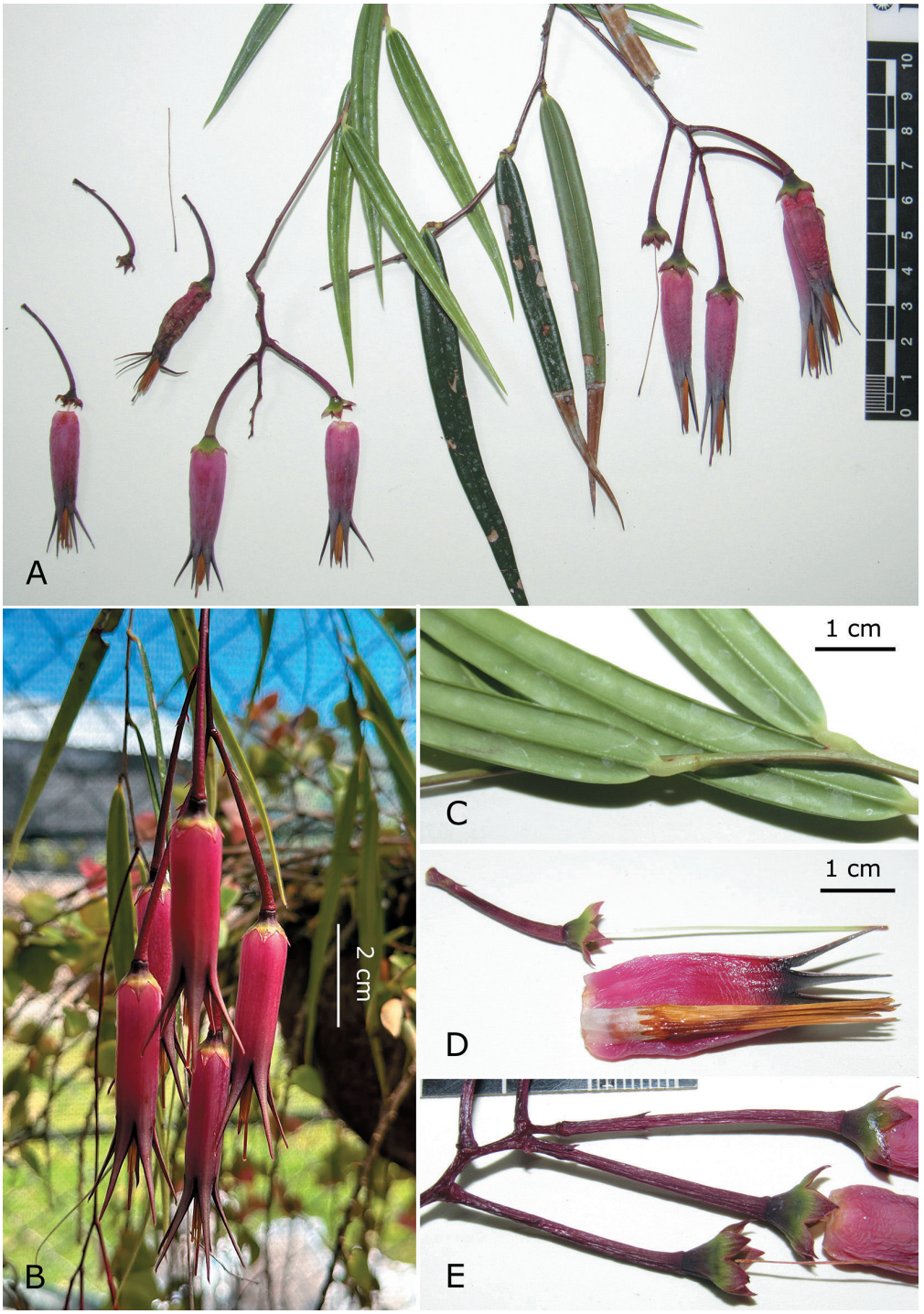

Fig. 1. *Ceratostema guachizacae* Cornejo & Luteyn. **A.** leafy terminal branch and inflorescences. **B.** a pendulous inflorescence. **C.** abaxial view of leaves and petioles. **D.** longitudinal section of corolla exhibiting inner colors, stamens with a white staminal tube, detached pedicel, calyx, and style. **E.** rachis, pedicels, calyx, and base of corollas. (A–E, based on the type. Photos: A, C–E, X. Cornejo; B, José Portilla).

(dry); limb open, spreading, ca. 1 × 5–6 mm (fresh); lobes deltoid, short-apiculate, 3 × 2.5 mm, without basal glands; corolla fleshy, the tube cylindric, 26–35 mm long, 10 mm diam. at base, 7–9 mm diam. at throat when fresh (vs. 23–32 mm long, 6–10 mm diam. at base, and 6–8 mm diam. at throat when dry), carnation-pink to fuchsia, glabrous, the lobes spreading, narrowly-lanceolate, 16–20 × 3 mm, purple-black to black within, glabrous without (fresh), without basal glands; **stamens** 10, nearly equaling the corolla, slightly unequal with each other, 38–45 mm long, the filaments fused into a staminal tube, 6–7 mm long, white, glabrous; anthers 30–40 mm long, the thecae ca. 6–7 mm long, papillose, the tubules distinct, 24–32 mm, long, dehiscing by terminally oblique pores, ca. 1.8 mm long; style equaling stamens, 35–45 mm long, light-green at distal half, reddish at apex, glabrous, the stigma truncate. **Berry** not seen.

Distribution.—*Ceratostema guachizacae* is known only from the type locality, in the environs of Yacuambi, in montane wet forest at 1800 m elevation. Flowering plants have been observed in February.

Discussion.—*Ceratostema guachizacae* resembles *C. pedunculatum,* but is easily recognized by the numerous, characters mentioned in the diagnosis. The lorate-lanceolate shape and very narrow width of the leaf blades (8–13 × 0.7–1 cm) characterize this new species with these features being unique in *Ceratostema*.

Etymology.—*The species is named after Gerardo Guachizaca, who helped to find this beautiful species with flowers and fruits in the field.

Uses.—*This new species is cultivated as an ornamental by Ecuagenera.

2a. Ceratostema portillae Cornejo & Luteyn, **sp. nov.** (**Fig. 2**). Type: ECUADOR. Zamora Chinchipe: Gualaquiza, Parroquia Bemejos, 3°14′S 78°43′W, 1600 m, Andean eastern slopes, 16 Feb 2024 (fl), *X. Cornejo 10165* [holotype: GUAY (mounted and spirit); isotype: QCA].

Diagnosis.—*Ceratostema portillae* is similar to *C. aggetiorum* M.M. Jiménez & H. Garzón (Jiménez et al. 2024), but differs by its solitary, axillary inflorescences (vs. terminal racemes); floral bracts 1 × 0.8 mm (vs. 5.8–34 × 3.7–18.4 mm); and calyx hypanthium smooth (vs. 10-ribbed).

Description.—**Epiphytic shrubs** with branches loosely pendulous to 2 m long, tomentulose with eglandular, white hairs; roots not seen; young branches terete to subterete, somewhat flattened to blunty angled or occasionally longitudinally sulcate, minutely papillose, green, villose to tomentulose with white trichomes (fresh), maturing terete to occasionally somewhat flattened, maroon, with trichomes light brown and somewhat deciduous (dry). **Leaves** spirally arranged, divergent from stem, conduplicate, spathaceous, overlapping each other forming a loosely pendulous subtubular arrangement; blades chartaceous, ovate to short ovate-lanceolate, 3.5–5 × 2.5–3.5 cm, basally subcordate (terminal leaves basally amplexicaule), apically caudate-acuminate, marginally flat but inrolled and forming a tube hiding the stem and base of flowers, opaque green, papillose and white-tomentulose adaxially (fresh), becoming opaque grayish-green to grayish-brown (dry), paler green, papillose, white tomentulose (fresh), grayish-green to grayish-brown, tomentulose to pilose abaxially (dry); weakly 5-plinerved from base, the nerves faintly prominent to often becoming inconspicuous adaxially (fresh), weakly prominent on both surfaces (dry); subsessile or with petioles to 1 mm long, subterete, pale green, white-villose (fresh), becoming brown and pilose to tomentulose (dry). **Inflorescence** axillary or barely supraxillary, 1(–2?)-flowered, short-pedunculate; the peduncle subterete, 1 mm long, pale green (fresh), brown (dry); floral bract broadly ovate, ca. 1 × 0.8 mm (fresh), ca. 0.5 × 0.5 mm (dry); pedicel articulate with calyx, straight, 3–4 × 1.5–2 mm (fresh), ca. 3 × 1 mm (dry), thickly narrowly-obconical (fresh), somewhat compressed (dry), light-green, white-tomentulose to villose (fresh); bracteoles 2, inserted near base of pedicel, lanceolate, ca. 2.2 × 0.8 mm, tomentulose. **Flowers** 5-merous, pendulous; calyx ca. 16–17 × 5 mm, light-green, white-tomentose to villose (fresh); hypanthium obconic, truncate at base, terete, ca. 5 × 6.5 mm (fresh), 3–4 × 2.5–3.5 mm (dry), eglandular; limb divergent, ca. 1 × 7 mm (fresh); lobes narrowly lanceolate, 11–12 × 2.5 mm, caudate, inrolled at tip; corolla fleshy, the tube cylindric, 30–35 mm long, 7 mm diam. at base, 6 mm diam. at throat when fresh (vs. 28–30 mm long, 4–5 mm diam. at base, 3–5 mm diam. at throat when dry), bright pink, tomentulose with hairs white, erect, ca. 0.5–0.7 mm long (fresh), the lobes divergent, mostly straight, narrowly-lanceolate, 18–19 × 2–3 mm, bright pink, white-tomentulose without (fresh); **stamens** 10,

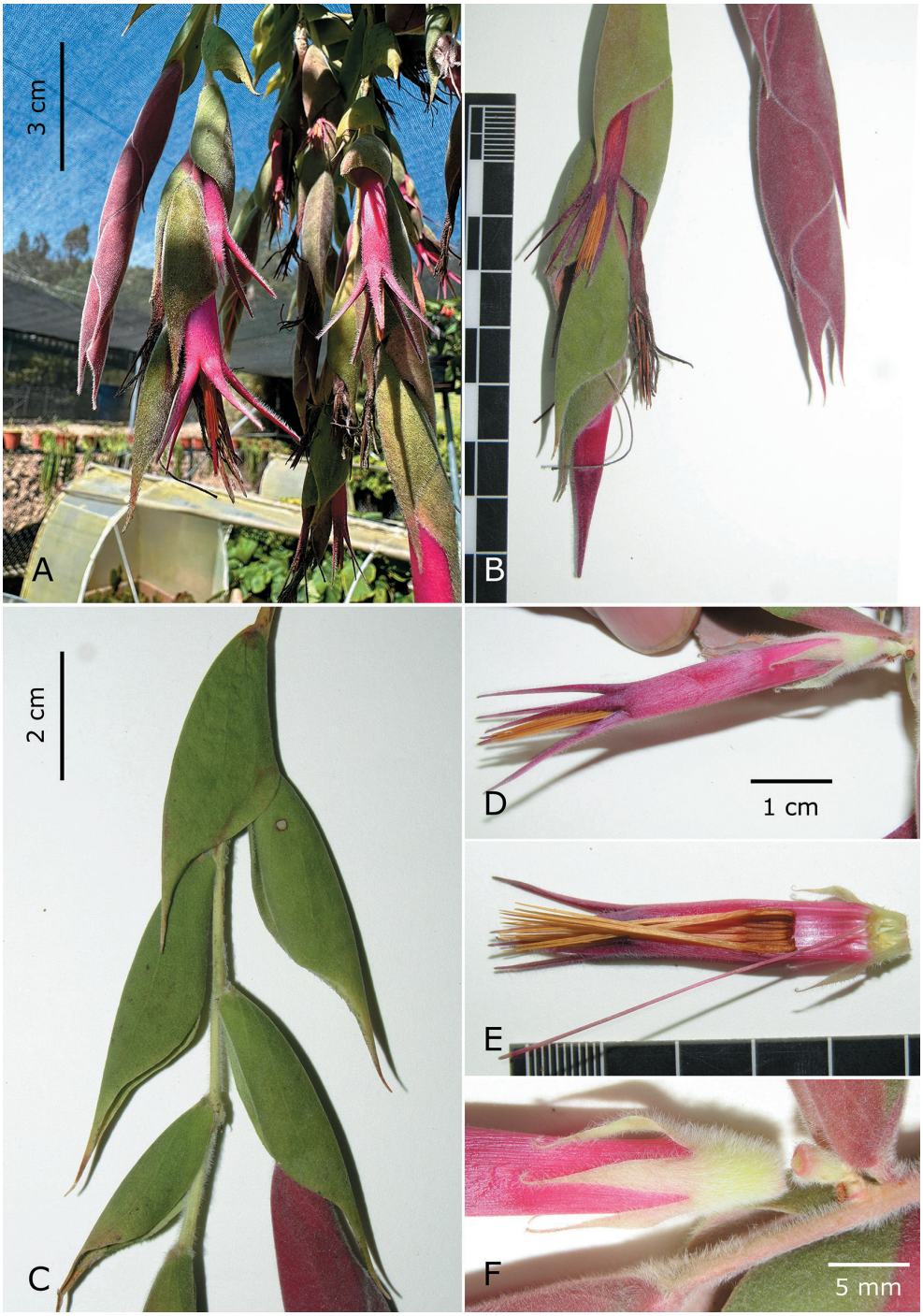

Fig. 2. *Ceratostema portillae* Cornejo & Luteyn. **A.** pendulous leafy branches and flowers. **B.** terminal younger spathaceous leaves, inrolled and overlapping each other forming a pendulous subtubular leafy arrangement hiding the stem and base of flowers. **C.** older conduplicate leaves, divergent from and exhibiting stem. **D.** flower nearly to anthesis. **E.** longitudinal section of flower exhibiting stamens and pink staminal tube. **F.** pedicel, calyx, base of corolla, and white tomentulose stem. (A–F, based on the type. Photos: A, José Portilla, B–F, X. Cornejo).

nearly equaling the corolla, slightly unequal with each other, ca. 48 mm long, the filaments fused into a tube ca. 10 mm long, pink, glabrous; anthers ca. 38 mm long, the thecae 5–7 mm long, papillose, the tubules distinct, ca. 30 mm, long, dehiscing by terminally oblique pores 0.8–1.3 mm long; style barely exceeding stamens, more or less equaling the corolla, 30–50 mm long, pink to rose-red, but green at tip, glabrous, the stigma truncate. **Berry** not seen.

Distribution.—*Ceratostema portillae* is known only from the type locality in the Parroquia Bermejos of Gualaquiza, in montane wet forest at 1600 m elevation. Flowering plants were observed in February.

Discussion.—*Ceratostema portillae* resembles the recently described *C. aggetiorum* (Jiménez et al. 2024), another species endemic to southeastern Ecuador. The new species differs sharply from the latter by the suite of characters given in the diagnosis. It is interesting to speculate that the characteristic conduplicate and inrolled spathaceous leaves of *C. portillae* are a morphological adaptation to protect the ovary of flowers against herbivores. Those leaves exhibit a deeper green color on the outer (abaxial) surface that is observable in fresh material, in contrast to the distinctively paler green color on the closed or mostly hidden adaxial surface, and perhaps results in a higher chloroplast density and consequently greater photosynthetic activity on the permanently exposed abaxial surface.

Etymology.—*The species is named after José Portilla, Executive Director of Ecuagenera, who provided field images and fresh specimens used for the type collections from cultivated plants of the three new species presented in this paper.

Uses.—*This plant is cultivated as an ornamental by Ecuagenera.

2b. Ceratostema portillae var. lucida Cornejo & Luteyn, **var. nov.** (**Fig. 3**). Type: ECUADOR. Morona Santiago: Parroquia Chiguinda, ca. 3°10′S 78°40′W, 2000 m, Andean eastern slopes, 16 Feb 2024 (fl), *X. Cornejo 10164* [holotype: GUAY (mounted and spirit); isotype: QCA].

Diagnosis.—*Ceratostema portillae* var. *lucida* is similar to the typical variety of *C. portillae*, but differs by its leaf blades glossy and glabrous to pilose along the veins abaxially (vs. opaque, tomentulose); terminal leaves maturing conduplicate and spreading to open thus not hiding the flowers at anthesis (vs. maturing spathaceous-imbricate, more-or-less tubular and surrounding the pedicel, calyx, and basal 1/3 of the corolla thus hiding most of the flower at anthesis); calyx 9–13 mm long (vs. 16–17); and corolla tube distally pilose (vs. tomentulose), with the lobes ca. 1/3 corolla length (vs. more than 1/2 in the typical variety).

Description.—**Epiphytic shrubs** with branches loosely pendulous to 2 m long, tomentulose to densely pilose, the white hairs eglandular; roots not seen; branches terete to subterete, minutely papillose, green, villose to tomentulose with white trichomes (fresh), maturing terete to occasionally somewhat flattened, maroon, with trichomes light brown and somewhat deciduous (dry). **Leaves** spirally arranged, divergent from stem, initially conduplicate becoming flat-open along stem, the terminal immature ones spathaceous inrolled and overlapping the next otherwise flat and spreading; blades chartaceous, ovate to short ovate-lanceolate, 2.8–5 × 2–3.5 cm, basally broadly cuneate to subcordate, apically caudate, marginally flat, adaxially pale green, glossy, papillose and glabrous (fresh), abaxially bright green, papillose, glabrous (fresh), grayish to grayish-brown (dry); weakly 5-plinerved from base, the nerves adaxially impressed to inconspicuous, abaxially faintly prominent (fresh), weakly prominent on both sides (dry); subsessile otherwise petioles to 2 mm long, subterete, pale green, white-villose to pilose (fresh) becoming grayish-brown to brown, and tomentulose to pilose (dry). **Inflorescence** axillary, 1-flowered, short-pedunculate; the peduncle subterete, 1 mm long, pale green (fresh), brown (dry); floral bract triangular, ca. 1 × 0.8 mm (fresh), ca. 0.5 × 0.5 mm (dry); pedicel articulate with calyx, straight, 5 × 2 mm (fresh), 3–5 × 0.7–2 mm (dry), thickly narrowly-obconical (fresh), linear or oblong (dry), light-green, white-tomentulose (fresh); bracteoles inserted along pedicel below the middle, triangular to lanceolate, 1.5–3 × 0.7 mm, pilose. **Flowers** 5-merous, pendulous; calyx 9–13 × 5.5–6 mm, light-green, white-tomentose (fresh); hypanthium obconic, truncate at base, terete, ca. 4 × 5 mm (fresh), ca. 3 × 2.5 mm (dry), eglandular; limb divergent, ca. 0.8 × 7 mm (fresh); lobes lanceolate, 5–8.5 × 2.7–3 mm, acuminate, inrolled at tip; corolla fleshy, the tube cylindric, 30–40 mm long, 7–11 mm diam. at base, 7–9 mm diam. at throat when fresh (vs. 30–40 mm long, 5–9 mm diam. at base, 5–8 mm diam. at throat when dry), bright

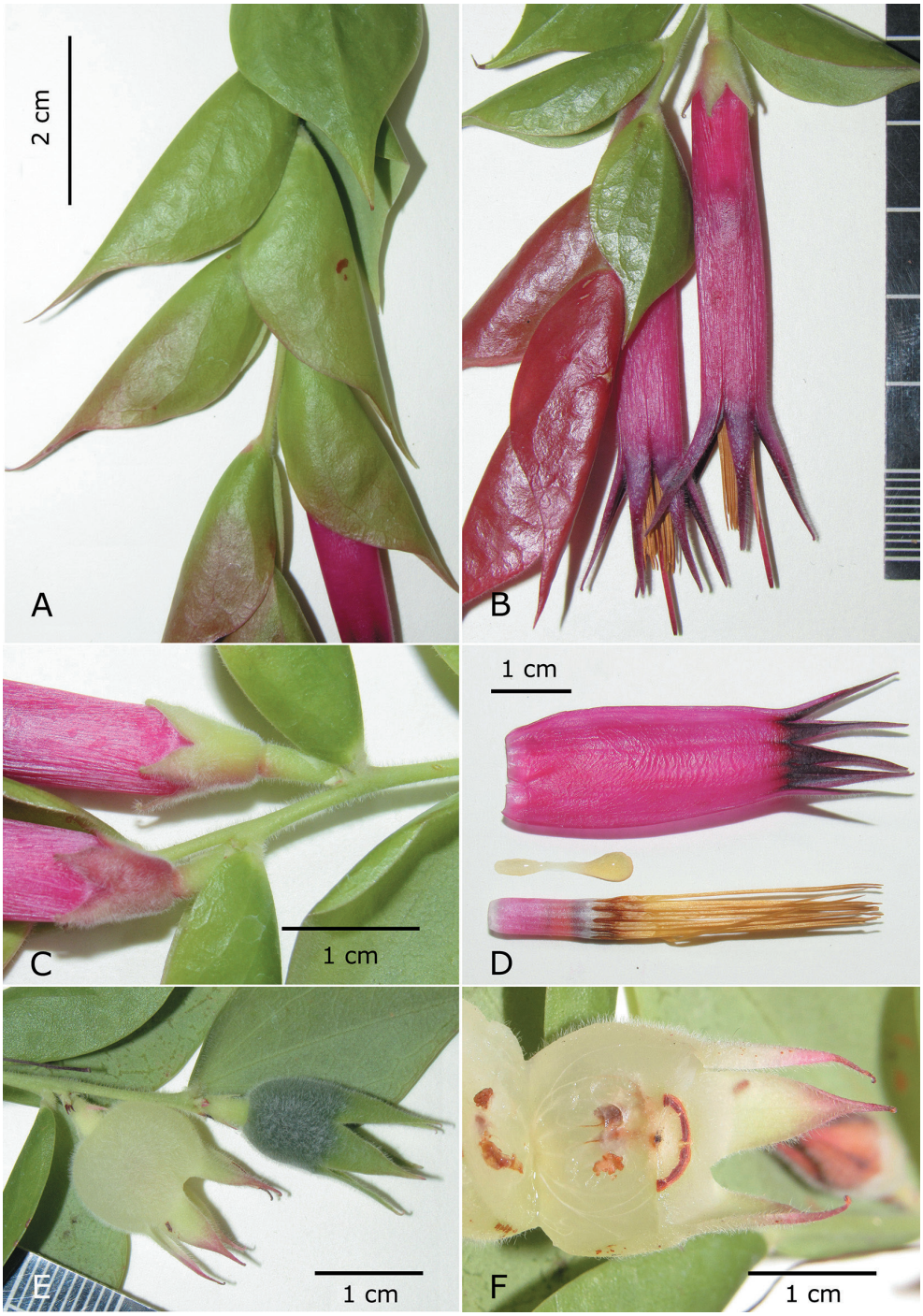

Fig. 3. *Ceratostema portillae* var. *lucida* Cornejo & Luteyn. **A.** branchlet with conduplicate leaves. **B.** branchlet with younger conduplicate leaves and flowers. **C.** tomentulose leafy stem, thick pedicels, calyx, and base of corolla. **D.** longitudinal section of corolla, detached androecium, stamens with a fused pink staminal tube, and in between a nectar drop that was held within the staminal tube. **E.** immature and mature fruits. **F.** longitudinal section of mature fruit, note the white mesocarp and brown seeds. (A–D, based on the type; E–F, based on *Cornejo 10159* (GUAY). Photos: A–F, X. Cornejo).

persian rose, basal third glabrous but distal two-thirds pilose with erect, white hairs ca. 0.5–0.8 mm long (fresh), the lobes more or less divergent, mostly straight, narrowly-lanceolate, 13–17 × 3–4 mm, pinkish purple to purple, papillose, densely white-pilose without and dark purple within (fresh); **stamens** 10, nearly equaling the corolla, slightly unequal with each other, 40–50 mm long, the filaments fused into a tube 10–13 mm long, white or pink, glabrous; anthers 35–38 mm long, the thecae 5–6 mm long, papillose, the tubules distinct, 30–34 mm long, dehiscing by terminally pores 1–2 mm long; style exceeding stamens and corolla, 50–60 mm long, distal half red or light green, glabrous, the stigma truncate, red. **Berry** white at maturity, subglobose, ca. 1 × 1.2 cm (fresh), white tomentose, mesocarp white; seeds brown, embryo whitish (fresh).

Paratype.—**ECUADOR. Morona Santiago:** Canton Gualaquiza, Chiguinda, 1700–2000 m, *X. Cornejo 10159* (GUAY, fl, fr).

Distribution.—*Ceratostema portillae* var. *lucida* is known only from the two cited collections from the type locality, in montane wet forest at 1700–2000 m elevation. Flowering plants and fruits have been observed in February.

Discussion.—*Ceratostema portillae* var. *lucida* resembles the typical variety *portillae*, but the characters mentioned in the diagnosis give the plants a very different overall appearance especially when fresh that allows taxonomic differentiation. The recognition of this new variety for ornamental purposes lies primarily in the visual impression of its distinctive glossy leaves and conspicuous exposed flowers. It was also observed that nectar was stored within the tube formed by the connate staminal filaments thus making it available for floral visitors and pollinators and suggesting this type of tube as an adaptation to pollination (Fig. 3:D).

Etymology.—The epithet *lucida* is derived from the Latin adjective "*lucidus*," which refers to the bright green color of the abaxial surface of the leaves that characterizes this new variety.

Uses.—This plant is cultivated as an ornamental by Ecuagenera.

3. Ceratostema glandipedicellata Cornejo & Luteyn, **sp. nov.** (**Fig. 4**). Type: ECUADOR. Zamora Chinchipe: El Pangui, 3°37′S 78°35′W, 1500 m, Andean eastern slopes, 16 Feb 2024 (fl), *X. Cornejo 10161* [holotype: GUAY (mounted and spirit)].

Diagnosis.—*Ceratostema glandipedicellata* is similar to *C. amplexicaule* A.C. Sm. (1943), but differs primarily by its larger floral bracts, 12–20 × 3–5 mm (vs. 2–8 × ca. 2 mm or shorter); conspicuously larger bracteoles 14–22 × 4–5 mm, inserted along the distal half of the pedicels (vs. 3–10 × 1.3–2 mm, inserted in the lower half of the pedicels); larger calyx lobes 15–22 × 4.5–8 mm (vs. 3–7 × 1–3 mm); and presence of a swollen semi-annular gland at base of pedicels (vs. lack of gland).

Description.—**Epiphytic shrubs** with branches pendulous; branches terete to subterete, somewhat flattened, green, short-pilose with white eglandular hairs (fresh), becoming terete to occasionally somewhat flattened, maroon, the trichomes light brown and somewhat deciduous (dry); roots not seen. **Leaves** spirally arranged, amplexicaule; blades thinly chartaceous, short-lanceolate to elliptic-lanceolate, 8.5–13 × 3.5–5 cm, basally cordate, the rounded basal auricles imbricate, apically acuminate, marginally revolute, adaxially olive-green, somewhat glossy, glabrous (fresh), becoming opaque grayish to grayish-brown (dry), abaxially pale green, abundantly papillose, glabrous (fresh), becoming light brown (dry); pinnatinerved, midvein prominent at base, impressed to sulcate at apex, secondary nerves (3 pairs) impressed to sulcate adaxially, prominent abaxially; subsessile otherwise petioles to 3 mm long, subterete, rimulose, pale green, inconspicuously short-pilose (fresh), becoming brown (dry). **Inflorescence** axillary, a stout pendulous raceme, ca. 10-flowered; the peduncle subterete, longitudinally sulcate, somewhat compressed, 2–3 cm × 3–5 mm, the rachis 3–4 cm × 3–5 mm, pale green, shortly puberulent (fresh), becoming brown (dry); floral bract lanceolate, 12–20 × 3–5 mm, green, margin ciliate with short, dark glandular trichomes, abaxially glabrous (fresh), 10–18 × 3 mm, becoming brown (dry); pedicel articulate with calyx, more or less curved, apically swollen, 30–40 × 4–5 mm (fresh), 25–40 × 2 mm (dry), subterete, shallowly sulcate (fresh), ribbed, sulcate and slightly compressed (dry), light-green, papillose, short-pilose to puberulent (fresh), basally with a swollen asymmetric, semi-annular, laterally 2-lobed gland (adaxial surface of pedicel); bracteoles 2, inserted along distal half of pedicel, lanceolate, ca. 14–22 × 4–5 mm, ciliate with short, dark glandular trichomes at apex, glabrous abaxially. **Flowers** 5-merous, pendulous; calyx ca. 23–30 × 13–18 mm, light-green, inconspicuously short

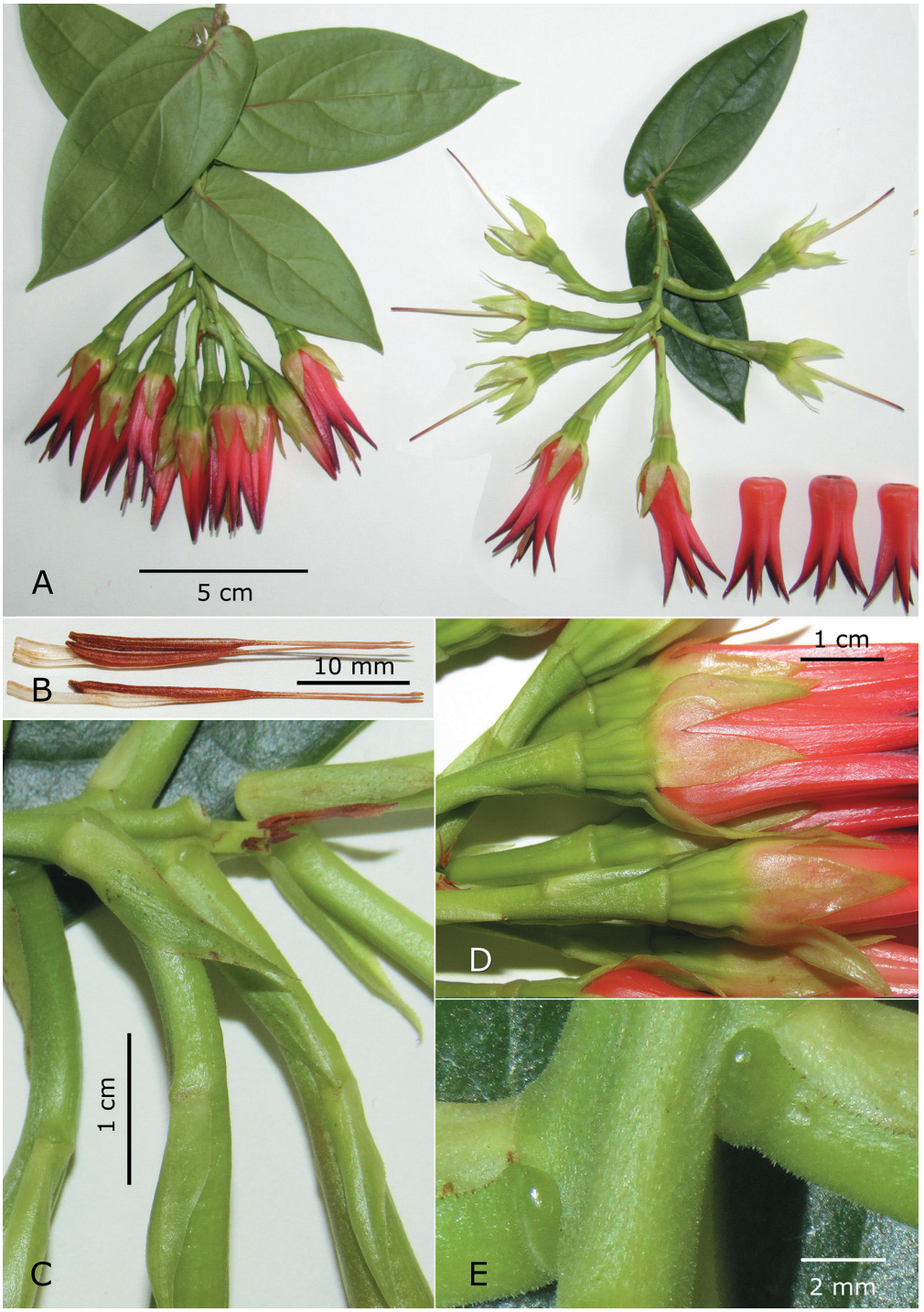

Fig. 4. *Ceratostema glandipedicellata* Cornejo & Luteyn. **A.** leafy branches and inflorescences. **B.** stamens. **C.** floral bracts, pedicels, and bracteoles. **D.** pedicels, calyx, and corolla base. **E.** view of rachis, base of floral bracts, and base of pedicels with swollen axillary gland. (A–E, based on the type. Photos: A–E, X. Cornejo).

papillose-pilose at base otherwise glabrous (fresh); hypanthium obconic, truncate at base, 10-sulcate, ca. 7–8 × 9–11 mm (fresh), 6–7 × 7–9 mm (dry), eglandular; limb divergent, ca. 1–3 × 10 mm (fresh); lobes lanceolate, acute to acuminate, 15–22 × 4.5–8 mm, weakly costate, inconspicuously papillose, with few occasional glands; corolla thickly fleshy, the wall 2–3 mm thick, 5-angled, the tube short-cylindric, ventricose, 24–28 mm long, 14–17 mm diam. at base, 15–17 mm diam. at throat when fresh (vs. 22–25 mm long, 10–15 mm diam. at base, 8–12 mm diam. at throat when dry), bright red, usually glabrous, rarely with suberect, pluricellular glandular trichomes ca. 1.5 mm long (fresh), the lobes 5(–6), divergent, slightly curved, narrowly-lanceolate, 20–24 × 5–6 mm, dark red, short-glandular-pubescent, dark purple at margins without, dark purple within (fresh); **stamens** 10, nearly equaling the corolla, slightly unequal with each other, ca. 40 mm long, the filaments distinct, ca. 10 mm long, white, glabrous; anthers ca. 40 mm long, the thecae 14–18 mm long, papillose, the tubules distinct, ca. 15–17 mm, long, dehiscing by terminally oblique pores ca. 1 mm long; style exceeding stamens and corolla, 42–53 mm long, distally reddish, glabrous, the stigma truncate. **Berry** not seen.

Distribution.—*Ceratostema glandipedicellata* is known only from the type locality, in montane wet forest at 1500 m elevation. Flowering plants have been observed in February.

Discussion.—*Ceratostema glandipedicellata* resembles *C. amplexicaule s.s.*, but is separated from the latter by the characters provided in the diagnosis. *Ceratostema amplexicaule s.l.* is a complex characterized by the distinctively shorter bracteoles inserted in the lower half of pedicels, and shorter calyx lobes; it also includes collections from Napo province with slender inflorescences and shorter corollas with lobes reflexed (e.g., *Neill 18043*, MO), as well as one collection with unusually elongated floral bracts, ca. 23–25 mm long (e.g., *Palacios 6267*, MO; see https://www.tropicos.org/image/100743681). Further taxonomic studies of Ecuadorian populations, using fresh material and involving field observations, may reveal additional taxonomic variants within this complex.

Ceratostema glandipedicellata is also characterized by what we observed to be an extrafloral nectary (EFN)—a glossy, swollen, asymmetric, laterally 2-lobed gland on the basal adaxial surface of the pedicel where it articulates with the rachis (Fig. 4:C, E). Foliage EFNs are rarely mentioned in the descriptions of neotropical Vaccinieae, even when prominent on the specimens. The exudate from these glands has most likely not been noticed before on plants in their natural habitat because nobody was looking for it, it was only secreted at certain times, the amounts were so small, or it was removed by insects or by the "cleansing effect" of the daily rains that characterize the habitats of most Vaccinieae. This cleansing effect has been noted previously in another related ericad, *Macleania pentaptera* Hoer., by one of us (JLL pers. obs. 2011) and figured in Pedraza-Peñalosa et al. (2013:10, fig. 4). We have also noticed that the recently described *C. zamorana* has pedicellary glands on the basal adaxial surface where it articulates with the rachis—not mentioned by the original authors (see Jiménez et al. 2021:fig. 1D). In general, the secreted exudate of EFNs acts as a food source by attracting beneficial insects such as ants which, in part, act as "protectionists" often removing herbivorous insects and seed predators from the plants or protecting flower-nectar from other nectar-feeding organisms such as fungi, bacteria, ants, birds, etc. (Bentley 1977; Koptur 1992; Blüthgen & Reifenrath 2003)—occasionally, hummingbirds also lick extrafloral nectaries—but more field observations are needed. EFNs not associated with pollination, may be found on leaves, petioles, pedicels, floral bracts, and bracteoles, and despite the fact that more than 93 plant families bear EFNs (see Elias 1983 and Koptur 1992 for reviews) and have ecological, evolutionary, and taxonomic importance in many plants, their descriptions have often been overlooked (but see Luteyn 1983, 1996; Blüthgen & Reifenrath 2003; Pedraza-Peñalosa et al. 2013).

Etymology.—*The epithet *glandipedicellata* refers to the swollen semi-annular gland present at the base of each pedicel—a very unusual feature in *Ceratostema*.

Uses.—*This plant is cultivated as an ornamental by Ecuagenera.

ACKNOWLEDGMENTS

The authors are indebted to José Portilla, the executive Director of Ecuagenera, for sending field images of cultivated plants and fresh specimens used as type material for the four new taxa formally presented in this publication. We also thank the anonymous reviewers for helpful comments.

REFERENCES

Bentley, B.L. 1977. Extrafloral nectaries and protection by pugnacious bodyguards. Ann. Rev. Ecol. Syst. 8:407–427.

Blüthgen, N. & K. Reifenrath. 2003. Extrafloral nectaries in an Australian rainforest: structure and distribution. Austral. J. Bot. 51:515–527.

Cornejo, X. & P. Pedraza-Peñalosa. 2019. *Sphyrospermum grandiflorum* (Ericaceae: Vaccinieae): a new epiphytic shrub from southeastern Ecuador. Phytotaxa 409(2):66–70. (doi: 10.11646/phytotaxa.409.2.2).

Cornejo, X., J.L. Luteyn, & G. Tello-Hidalgo. 2024. *Ceratostema loucianae* and *Disterigma chriscanadayi* (Ericaceae: Vaccinieae)—new epiphytic species from eastern Ecuador. J. Bot. Res. Inst. Texas 18(1):87–3.

Cronquist, A. 1978. Once again, what is a species? In: J.A. Romberger, ed. Biosystematics in agriculture. Allanheld, Osmun & Co., Montclair. New Jersey, U.S.A. Pp. 3–20.

Elias, T.S. 1983. Extrafloral nectaries: their structure and distribution. In: B.L. Bentley & T.S. Elias, eds. 1983. The biology of nectaries. Columbia University Press, New York,, U.S.A. Pp. 174–203.

Jiménez, M.M., L. Vélez-Abarca, L. Ocupa Horna, N. Jaramillo, & L.E. Baquero. 2021. A new species of *Ceratostema* (Ericaceae: Vaccinieae) from Ecuador. Phytotaxa 520(3):265–272. (doi: https://doi.org/10.11646/phytotaxa.520.3.5).

Jiménez, M.M., A. Fierro Minda, L. Vélez-Abarca, G.A. Iturralde, & H.X. Garzón-Suárez. 2024. A new species of *Ceratostema* (Ericaceae: Vaccinieae) from the province of Morona-Santiago in Ecuador. Phytotaxa 650(1):73–82. (https://doi.org/10.11646/phytotaxa.650.1.6).

Jussieu, A.L. de. 1789. Genera plantarum secundum ordines naturales disposita, juxta methodum in Horto Regio Parisiensi exaratum, anno M.DCC.LXXIV. Herissant & Barrois, Paris. Website (https://www.biodiversitylibrary.org/item/32208). [*Ceratostema*, p. 163]

Klotzsch, J.F. 1851. Studien über die natürliche Klasse Bicornes Linné. Linnaea 24:1–88. (https://www.biodiversitylibrary.org/item/109424). [*Ceratostema*, p. 27]

Koptur, S. 1992. Extrafloral nectary-mediated interactions between insects and plants. In: E. Bernays, ed. 1992. Insect-plant interaction, vol. 4. CRC Press, Boca Raton, FL, U.S.A. Pp. 81–129.

Kron, K.A., E.A. Powell, & J.L. Luteyn. 2002. Phylogenetic relationships within the blueberry tribe (Vaccinieae, Ericaceae) based on sequence data from *matK* and nuclear ribosomal ITS regions, with comments on the placement of *Satyria*. Amer. J. Bot. 89:327–336. (https://doi.org/10.3732/ajb.89.2.327).

Luteyn, J.L. 1983. *Cavendishia*. Fl. Neotrop. Monogr. 35:1–290.

Luteyn, J.L. 1984. Revision of *Semiramisia* (Ericaceae: Vaccinieae). Syst. Bot. 9:359–367.

Luteyn, J.L. 1986. New species of *Ceratostema* (Ericaceae: Vaccinieae) from the northern Andes. J. Arnold Arbor. 67:485–492.

Luteyn, J.L. 1992. A new *Ceratostema* (Ericaceae: Vaccinieae) from northern Peru. Bull. Torrey Bot. Club 119(3):314–315.

Luteyn, J.L. 1996. Ericaceae. In: Harling, G. & L. Andersson, eds. Flora of Ecuador. Council for Nordic Publications in Botany, Berlings, Arlöv, Sweden. 54:1–404, viii plates.

Luteyn, J.L. 2002. Diversity, adaptation, and endemism in neotropical Ericaceae: biogeographical patterns in the Vaccinieae. In: K. Young, C. Ulloa Ulloa, J.L. Luteyn, & S. Knapp, coauthors & eds. Plant evolution and endemism in Andean South America. Bot. Rev. 68(1):55–87. (doi: 10.1663/0006-8101(2002)068[0055:DAAEIN]2.0.CO;2 []).

Ortiz, E.M. 2017. Evolutionary patterns and processes of the high Andean genera *Demosthenesia*, *Pellegrinia*, *Polyclita*, *Rusbya*, and *Siphonandra* (Vaccinieae: Ericaceae). Unpubl. Ph.D. dissertation. The University of Texas at Austin, Texas, U.S.A.

Pedraza-Peñalosa, P. 2008. Three new species of *Disterigma* (Ericaceae: Vaccinieae) from western Colombia, with comments on morphological terminology. Brittonia 60(1):1–10. (doi:10.1007/s12228-008-9006-3).

Pedraza-Peñalosa, P. 2009. Systematics of the neotropical blueberry genus *Disterigma* (Ericaceae). Syst. Bot. 34:406–413. (https://doi.org/10.1600/036364409788606352).

Pedraza-Peñalosa, P. 2010a. *Disterigma* (Ericaceae: Vaccinieae). Fl. Neotrop. Monogr. The New York Botanical Garden Press, New York, U.S.A. 108:1–130.

Pedraza-Peñalosa, P. 2010b. Insensitive blueberries: a total evidence analysis of *Disterigma s.l* (Ericaceae) exploring transformation costs. Cladistics 26:388–407. (doi:10.1111/j.1096-0031.2009.00293.x).

Pedraza-Peñalosa, P., N.R. Salinas, & W.C. Wheeler. 2013. Venation patterns of neotropical blueberries (Vaccinieae: Ericaceae) and their phylogenetic utility. Phytotaxa 96(1):1–53. (https://doi.org/10.11646/phytotaxa.96.1.1).

Pedraza-Peñalosa, P., N.R. Salinas, A.L.S. Virnig, & W.C. Wheeler. 2015. Preliminary phylogenetic analysis of the Andean clade and the placement of new Colombian blueberries (Ericaceae, Vaccinieae). PhytoKeys 49:13–31. (doi: 10.3897/phytokeys.49.8622).

Popenoe, W. 1924. Economic fruit-bearing plants of Ecuador. Contr. U.S. Natl. Herb. 24:101–134.

Powell, E.A. & K.A. Kron. 2003. Molecular systematics of the northern Andean blueberries (Vaccinieae, Vaccinioideae, Ericaceae). Int. J. Pl. Sci. 164:987–995. (doi: 10.1086/378653).

Smith, A.C. 1943. Studies of South American plants—X. Noteworthy Myristicaceae and Vacciniaceae. J. Arnold Arbor. 24:460–471.

Smith, A.C. 1952. Plants collected in Ecuador by W.H. Camp—Vacciniaceae. Mem. New York Bot. Gard. 8:41–85.