

BESLERIA NAQUENENSIS (BESLERIEAE, BESLERIACEAE), A NEW SPECIES FROM SERRANÍA DE NAQUÉN, GUIANÍA RIVER BASIN (COLOMBIA)

GERARDO A. AYMARD C.,^{1,2} HENRY ARELLANO-P.,^{1,3} ADELA LOZANO,¹ MARÍA C. MONTILLA,¹ ALBEIRO CALERO-CAYOPARE,¹ AND REINALDO A. GÓMEZ-YUVABE⁴

Abstract. *Besleria naquenensis* is described and illustrated on the basis of a collection from the understory of seasonally flooded forests drained by black waters located in the lower “Río (Caño) Naquén,” northwestern base of “Serranía de Naquén,” upper Guainía River basin, Guainía Department, Colombia, and its relationships with related species are discussed. This new species shares features with three species (*B. gibbosa*, *B. neblinae*, and *B. yatuana*) of section *Neobesleria* subsection *Axillares*. Morphologically, it is closest to *B. yatuana*, but it differs in its leaves, inflorescences, calyx, and corolla. In addition, habitat information, a distribution map, and data of its conservation status are included. An identification key of 27 species of *Besleria* found in the Rio Negro basin (Brazil, Colombia, and Venezuela) and adjacent regions is also provided. This new species elevates to 66 the number of *Besleria* taxa for the flora of Colombia, the country with the highest diversity of the genus.

Keywords: Guainía River basin, “Serranía de Naquén,” black water, seasonally flooded forests, *Besleria*, Gesneriaceae

Resumen. *Besleria naquenensis* se describe e ilustra a través de una colección en bosques estacionalmente inundables sobre aguas negras, situados en el río (caño) Naquén, noroeste de la base de la Serranía de Naquén, alto río Guainía, Departamento del Guainía, Colombia, y sus relaciones con las especies afines son discutidas. La nueva especie presenta similitudes morfológicas con tres especies (*B. gibbosa*, *B. neblinae* y *B. yatuana*) de la sección *Neobesleria* subsección *Axillares*. Sin embargo, está más relacionada con *B. yatuana*, de la cual difiere en sus hojas, inflorescencias, cáliz y corola. Se incluye información acerca de su hábitat, un mapa de distribución, datos del status de conservación, y una clave para la identificación de las 27 especies de *Besleria* presentes en la cuenca del río Negro (Brasil, Colombia y Venezuela) y regiones adyacentes. Esta nueva especie eleva actualmente en 66 el número de especies de *Besleria* para la flora de Colombia, el país con la mayor diversidad del género.

Palabras clave: Cuenca del río Guainía, Serranía de Naquén, aguas negras, bosques periódicamente inundables, *Besleria*, Gesneriaceae

Yaakuti iipena (Abstract in Kuripako). *Besleria naquenensis*, padana jnete pakajñeta linapjian nerikuda jnaja paniwampe jaikulima alape likuperi uni itajnai liko, aperi Naquén liko, noroeste de la base de la Serranía de Naquén, alto río Guainía, Departamento del Guainía, Colombia. Pakajñeta padeniri linakuapana jlieje *B. naquenensis* jnete kuameka napidzawaka jnaja likaishuperi. Jlieje waline jaiko wadepe pakuaka likapakana naine jnaja madalina jaiko (*B. gibbosa*, *B. neblinae* y *B. yatuana*) de la subsect. *Axillares*. Metsa, kadzu likapakana *B. yatuana* kametsa puadzalika jnaja lipje, liwi, jnete liwi idakipeda. Wakaita kuamekawaka litawiñawa, kuamekawaka jipai lipedzu litawiñakawa, jlinapjian, jnete papera inipu pajneshopa jnakani jnaja 27 nadzawaka *Besleria* aperi itawiña waja rio negro liko (Brasil, Colombia y Venezuela). Jlieje waline waaketaka jaiko 66 shupa namanupeka jnaja *Besleria* Colombia isruwa, katsa jipai isrukada pja manupena.

The genus *Besleria* Plumier ex Linnaeus (Gesneriaceae) currently includes 167 species (Ulloa Ulloa et al., 2018; Clark et al., 2020) of terrestrial, perennial herbs, suffrutexes, or shrubs with fibrous roots, growing in the understory of rainforests (Feuillet and Steyermark, 1999; Skog and Feuillet, 2008). It is rarely epiphytic (e.g., *B. macropoda* Donn Sm.) or small trees not taller than 7 m (e.g., *B. arborescens* C.V. Morton, *B. decipiens* C.V. Morton). The genus has a Neotropical distribution and ranges from southern Mexico (Chiapas, Oaxaca, Puebla, Tabasco, and Veracruz States) through Central America, the Caribbean, Colombia, Venezuela, Guianas, Ecuador, Peru, Brazil, and Bolivia (Morton, 1939; Ferreira et al., 2016; Ferreira, 2019).

Besleria is most diverse throughout the foothills to the high mountains of the Andes (Wiehler, 1975) and the Coastal

Cordillera in Venezuela, where 57% (95) of the species are found growing in nutrient-rich soils. The remaining species appear to require more specific habitats, as is the case with the Amazon/Guayana lineage (e.g., *B. neblinae* Feuillet, *B. saxicola* C.V. Morton, *B. yatuana* Feuillet), which occurs in vegetation that grows on rocky slopes and oligotrophic soils derived from the Precambrian crystalline basement of the Guayana Shield and drained by black waters. Some taxa are found along the Pacific Coast of Colombia and Ecuador. Several species have wide geographic distributions (e.g., *B. aggregata* [Mart.] Hanst., *B. pauciflora* Benth., *B. solanoides* Kunth), whereas others are endemic to particular geographical areas, such as some species found only in Caribbean islands, or in Southeast Brazil (Ferreira et al., 2016).

We gratefully acknowledge the support provided by Compensation International Progress S.A.–Greenlife (Ciprogress–Greenlife) and the Kuripako indigenous alliance for our botanical expedition to the Cui(y)arí, Isana, and Naquén Rivers. The trip was sponsored by the Flor de Infrida REDD+ Project of the Guayana–Amazonian Transition Region, which made this undertaking possible. We also thank Germán Bernal Gutiérrez, Daniel S. Bernal Linares, Juan S. Bernal García, Martha Rivera, and Claudia Restrepo for logistic support, and Alfrío Yavinape, Roberto Garrido, and Jahir Bedoya for their field assistance. We are indebted to the Kuripako people of the communities of Berrocal, San José del Guainía, and Manacal (Guainía River) for their help during different stages of the expedition. Finally, we thank Sylvania Mota de Oliveira (L) for her help finding literature, and Gustavo A. Romero-G. (AMES) for his help finding literature and his comments on early versions of this text. This work would not be possible without JSTOR Global Plants (<https://plants.jstor.org/>).

¹ Compensation International Progress S.A. Ciprogress–Greenlife, Bogotá, D.C., Colombia

² Corresponding author: gaynard@ciprogress.com

³ Nuevo Estándar Biotropical NEBIOT SAS, Bogotá, D.C., Colombia

⁴ Comunidad Kuripako Manacal, Río Guainía, Corregimiento departamental Puerto Colombia, departamento del Guainía, Colombia

Ethnobotanical information about *Besleria* in the lowlands is scarce. However, Lizot (1978) reported that in the Upper Orinoco River (Venezuela), the leaves of *B. laxiflora* Benth. are used by children and teenagers of the Yanomani nation as a tobacco substitute. This species is known in their language as “Tescho kënahekf” (hummingbird’s tobacco).

Recent phylogenetic studies indicate that the genus is monophyletic and belongs in the also-monophyletic tribe *Beslerieae* Bartl. within subfamily Gesnerioideae Link (Perret et al., 2013; Weber et al., 2013). According to these authors, *Beslerieae* diverged about 30 million years ago within the Gesnerioideae. Moreover, diversification rates of Gesneriaceae have increased through time since the Early Miocene (25 Ma), a time frame coinciding with the evolution of hummingbird-adapted flowers and their arrival in South America (Serrano-Serrano et al., 2017).

Besleria is characterized by its mostly terrestrial habit, opposite leaves, stomata of the abaxial leaf surface well-spaced, axillary, pedunculate, or sessile inflorescences, bractless, campanulate or urceolate calyx, conspicuous, ventricose or subcampanulate succulent corollas, nectary in the majority of species evenly ring-shaped, superior ovary, and fleshy berries (Morton, 1939; Wiehler, 1975; Skog, 1978a).

Besleria was monographed worldwide by Morton (1939), who divided the genus into four sections (*Eubesleria* [Hanst.] Benth. & Hook., *Gasteranthus* [Benth.] Benth. & Hook. f., *Neobesleria* Morton, and *Rhynchobesleria* [Hanst.] Benth.

& Hook.) and 18 subsections, recognizing 141 species and describing 43. Later, on the basis of vegetative and fruit features, Wiehler (1975) recognized *Gasteranthus* Benth., to which he also transferred five subsections of section *Neobesleria* (Skog and Kvist, 2000).

Molecular phylogenetic studies in *Besleria* have demonstrated that the four sections proposed by Morton (1939) were not monophyletic (Roalson and Clark, 2005; Clark et al., 2010). Therefore, the circumscription of many species of *Besleria* is still unclear, and the genus needs a detailed revision (Ferreira et al., 2016). Since C. V. Morton’s contributions (Morton, 1939, 1944, 1968), 22 new species have been described (Steyermark, 1970; Skog, 1974, 1978a,b, 1982, 1987; Nowicke, 1974; Skog and Steyermark, 1991; González et al., 2001; Feuillet, 2008; Salinas, 2008; Ferreira, 2017, 2019; Ferreira et al., 2016; Cortés-C. et al., 2017; Sánchez-Taborda et al., 2020). The genus has been treated for Peru (Morton, 1968), *Flora of Panama* (Skog, 1978a), *Flora of the Venezuelan Guayana* (Feuillet and Steyermark, 1999), *Flora of the Guianas* (Skog and Feuillet, 2008), and *Manual de Plantas de Costa Rica* (Kribel, 2010). The present contribution increases to 66 the number of *Besleria* species known from Colombia, the country with the highest diversity of the genus. This new species was detected during fieldwork for forest studies being conducted in the upper Guainía River, Guainía Department, Colombia.

MATERIALS AND METHODS

This work is based on morphological (using a dissecting stereomicroscope) and herbarium studies in COAH, COL, GH, NY, and PORT (herbarium codes after Thiers, 2019) of a specimen collected on a botanical expedition to the Río (Caño) Naquén in 2019, Guainía Department, Colombia. In addition, historical and current taxonomic literature on *Besleria* were examined, mainly the treatment of Gesneriaceae in *Flora of Venezuelan Guayana* (Feuillet and Steyermark, 1999), the original descriptions of *B. neblinae* Feuillet and *B. yatuana* Feuillet (Feuillet, 2008), and the

checklists *Catálogo de plantas y líquenes de Colombia* (Clavijo et al., 2016) and *Catálogo de las plantas con flores de la Amazonia colombiana* (Infante-Betancour and Rangel-Ch., 2018). Type specimens of *Besleria* species involved in this study were examined using on-line images from JSTOR Global Plants (<https://plants.jstor.org/>). The specific terminology for vegetative characters, vestiture description, inflorescences, flowers, and fruit morphology follow Font-Quer (2001), Harris and Harris (2006), and Endress (2010).

TAXONOMY

Besleria naquenensis Arellano-P. & Aymard. *sp. nov.* TYPE: COLOMBIA. Guainía: Corregimiento departamental Puerto Colombia. Sector noroeste de la base de la Serranía de Naquén, río (Caño) Naquén, bosques estacionalmente inundables sobre aguas negras, 2°42'04.5"N; 68°16'41.2"W, 100 m. 15 March 2019 (fl and fr), Gerardo Aymard, Adela Lozano, María C. Montilla, Albeiro Calero Cayopare & Reinaldo A. Gómez Yuvabe 15087 (Holotype: COL; Isotypes: COAH, FMB). Fig. 1–2.

Besleria naquenensis is morphologically similar to *B. yatuana* Feuillet but differs in its larger ovate or elliptic to lanceolate-elliptic leaves, sparsely appressed-pubescent on both sides (denser in midrib abaxially), subtended by petioles 2.8–7.5 cm long, its 5–10-flowered inflorescence, 8- to 10-mm long pedicels, 3–3.5 mm long calyx lobes, broadly lanceolate, appressed-pubescent outside, glabrous inside, and its 3.5- to 3.8-cm long corolla, glabrous outside.

Suffrutescent herb, 1.0–1.5 m tall, spreading branches. Stem terete, somewhat succulent, ca. 0.5 cm diam., appressed-pubescent, trichomes 5–10 mm long. Leaves

dimorphic, opposite, membranaceous, appressed-pubescent on both sides, denser in midrib abaxially, trichomes ca. 1 mm long, margin serrulate; the uppermost pair equal, ovate, 10–12 × 4.0–5.5 mm, base slightly asymmetric, rounded, apex long acuminate, acumen ca. 15 mm long, 8–9 secondary veins on each side, petiole 8–10 mm long, appressed-pubescent. The innermost pairs mostly unequal; smaller leaves lanceolate-elliptic, ca. 17.8 × ca. 5.4 cm, base asymmetric, attenuate, apex long acuminate, acumen ca. 15 mm long, 11–12 secondary veins on each side, petiole 1.2–2.3 cm long, appressed-pubescent; larger leaves elliptic to lanceolate-elliptic, ca. 24.7 × ca. 7.8 cm, base asymmetric, attenuate, apex long acuminate, acumen ca. 15 mm long, 12–15 secondary veins on each side, petiole 2.8–7.5 cm long, appressed-pubescent. *Inflorescences* sessile or with short peduncle up to 2 mm long, appressed-pubescent, 5- to 10-flowered; pedicels 0.8–10.0 mm long, sparsely appressed-pubescent. *Flowers* with calyx sparsely appressed-pubescent, lobes free to base, broadly lanceolate, 3.0–3.5 × ca. 2.5 mm, attenuate at apex; *corolla* horizontal

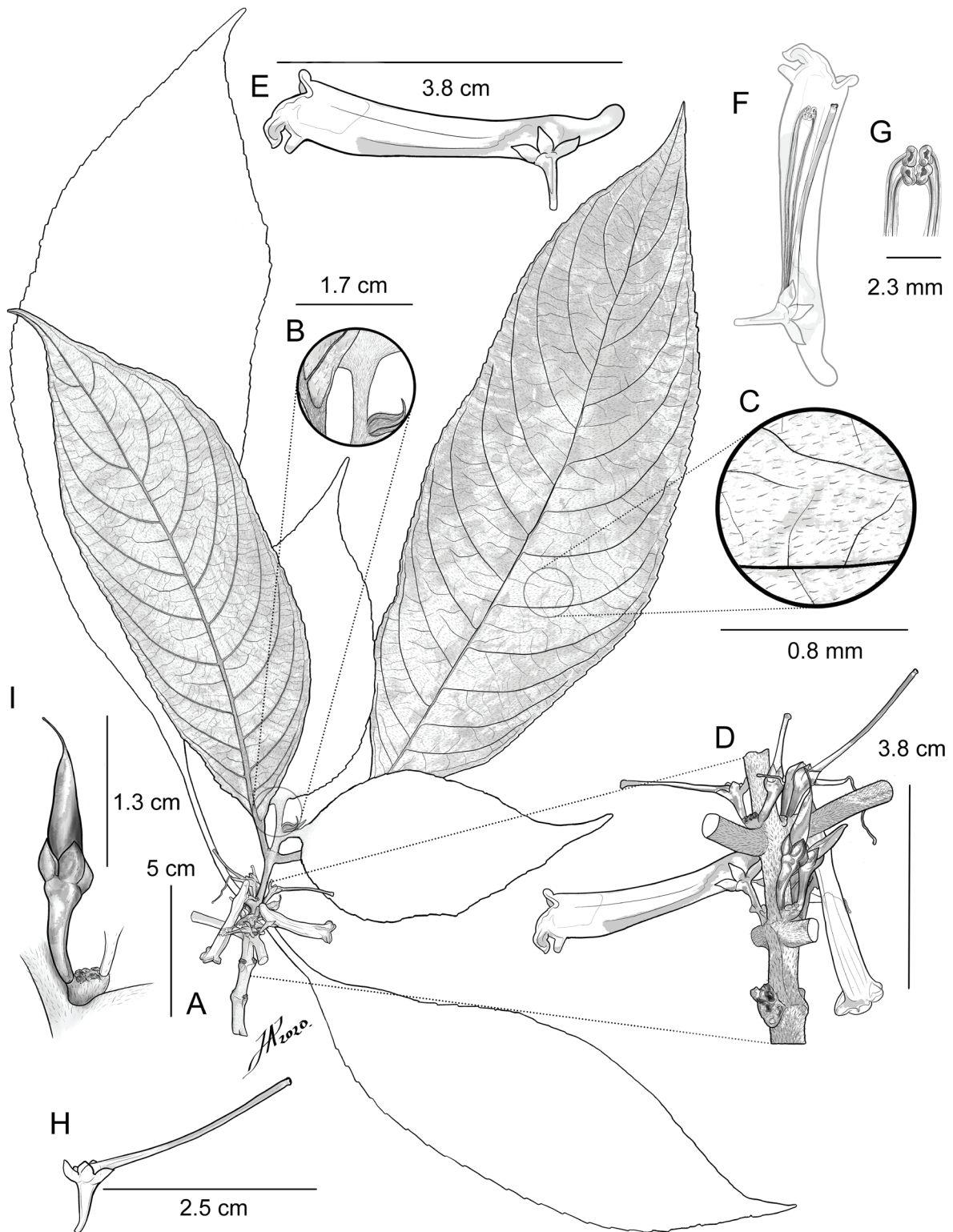


FIGURE 1. *Besleria naquenensis* Arellano-P. & Aymard. **A**, habit showing the unequal leaves and inflorescence; **B**, base of petiole and axillar bud; **C**, adaxial leaf surface showing the sparsely appressed pubescence; **D**, view of the inflorescence; **E**, calyx and corolla in lateral view; **F**, calyx and corolla showing the four stamens and the style and stigma; **G**, anthers view; **H**, calyx and style in lateral view; **I**, immature fruit.

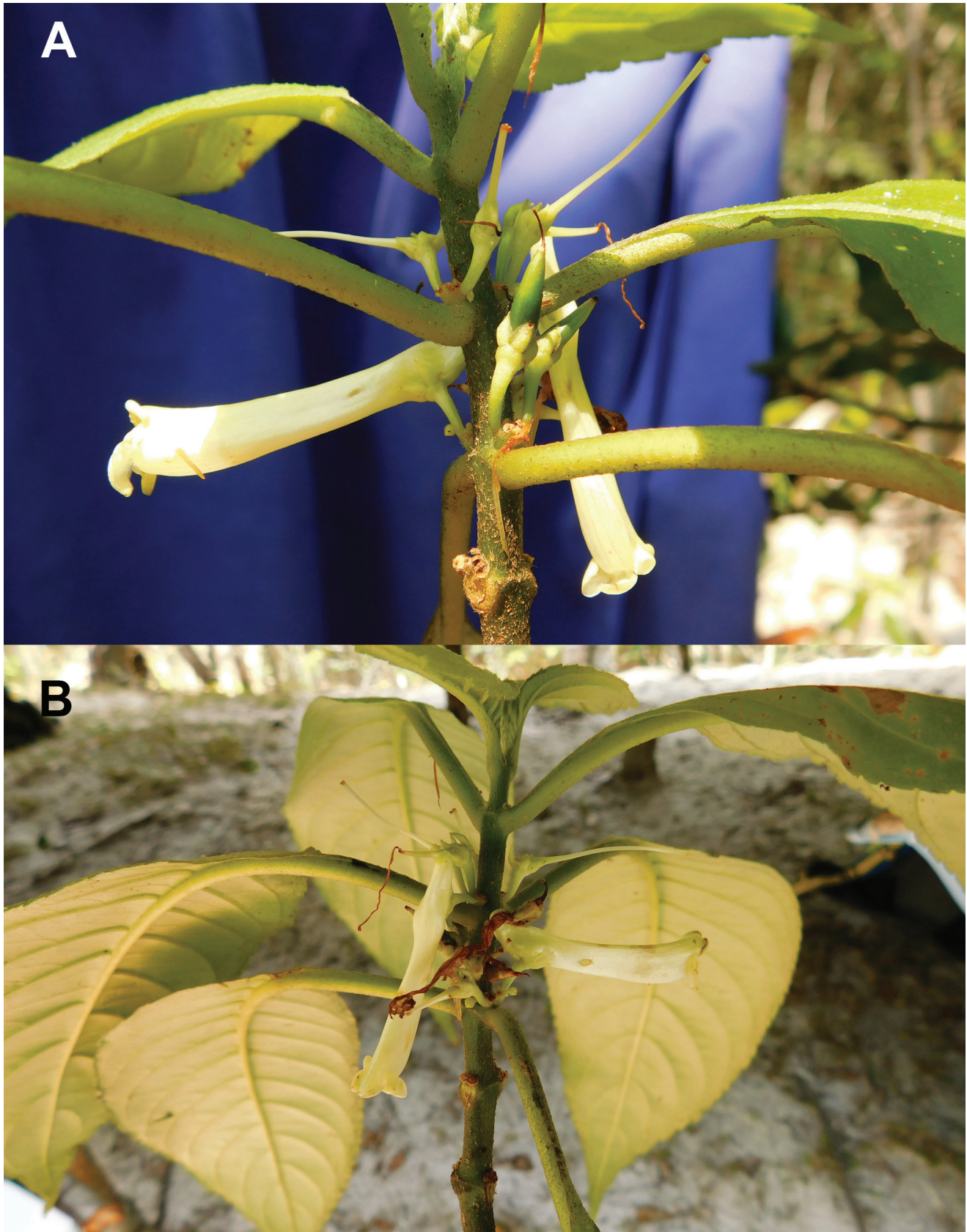


FIGURE 2. *Besleria naquenensis* Arellano-P. & Aymard. **A**, lateral views of the calyx and corolla and young fruits; **B**, flowering branch showing the glaucous leaves on the lower surface and lateral views of calyx and corolla. Based on Aymard *et al.* 15087. Photographs by María C. Montilla. ©Ciprogess Greenlife.

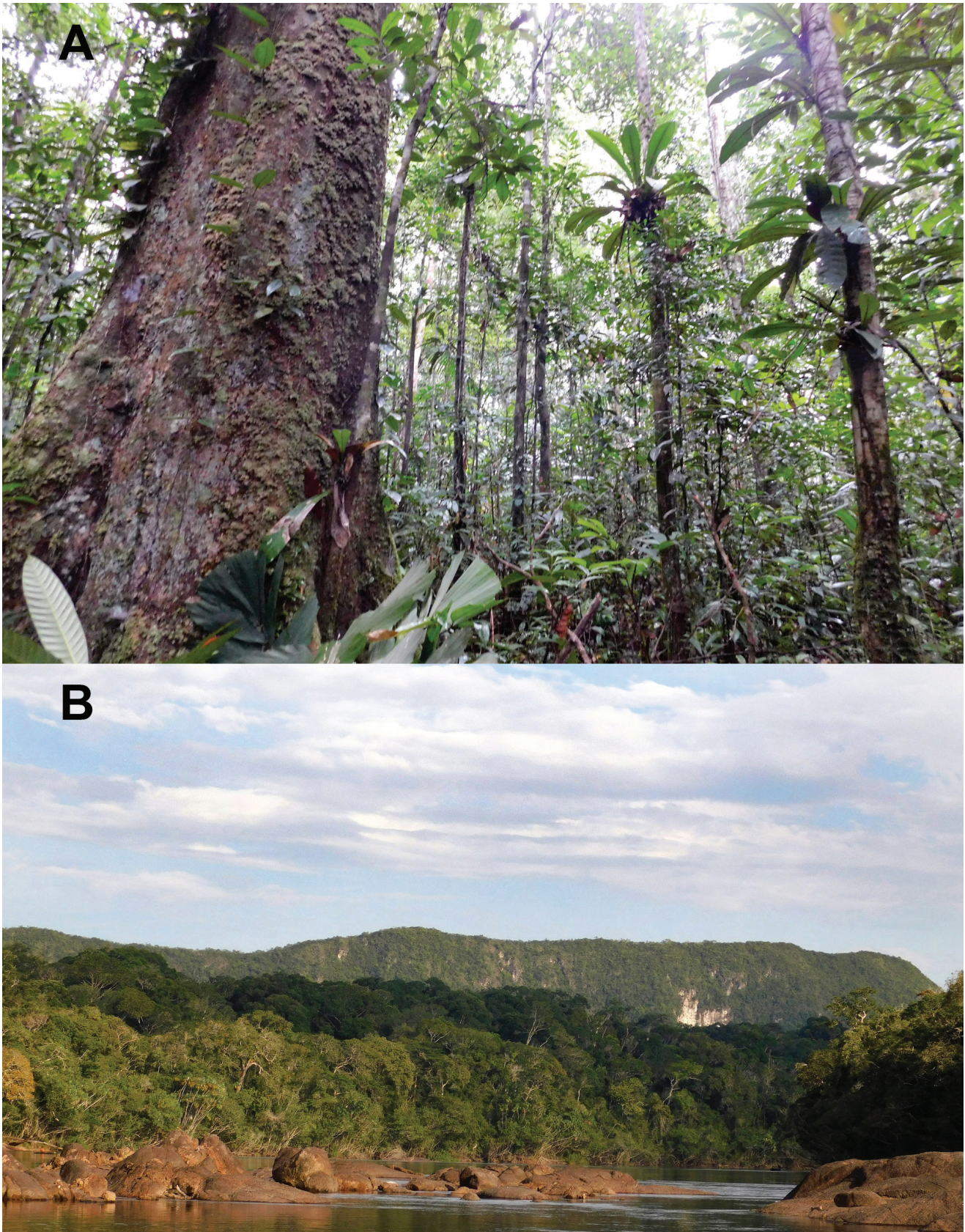


FIGURE 3. **A**, habitat of *Besleria naquenensis*—seasonally flooded forests on alluvial plains drained by black waters of the lower Río (“Caño”) Naquén. Photograph by Adela Lozano. ©Ciprogress Greenlife; **B**, Río (“Caño”) Naquén and a view of the “Serranía de Naquén.” Photograph by María C. Montilla. ©Ciprogress Greenlife.

in the calyx, white, glabrous outside, prominently spurred, spur 5–6 × 4–5 mm, ovoid-oblong, rounded, protruding upward at an angle of ca. 25°; tube 3.5–3.8 × ca. 4 mm at the base and up to 1 cm at the mouth, lobes suborbicular, ca. 5 × ca. 2 mm; 4 stamens, ca. 2.3 cm long, anthers orbicular-reniform, dorsal glands fused into one, staminode not seen; ovary superior, ovoid, glabrous, ca. 2 mm long, style ca. 2.5

cm, glabrous. *Immature fruits* 1.0–1.3 cm, conical, glabrous.

Phenology: the type specimen with flowers and young fruits was collected in March (Fig. 2).

Etymology: *Besleria naquenensis* is named after “Serranía de Naquén,” the type locality. The “Serranía de Naquén” or “Caparro” (also known as Naquén Mountains) is located in the southeastern portion of Guianá Department

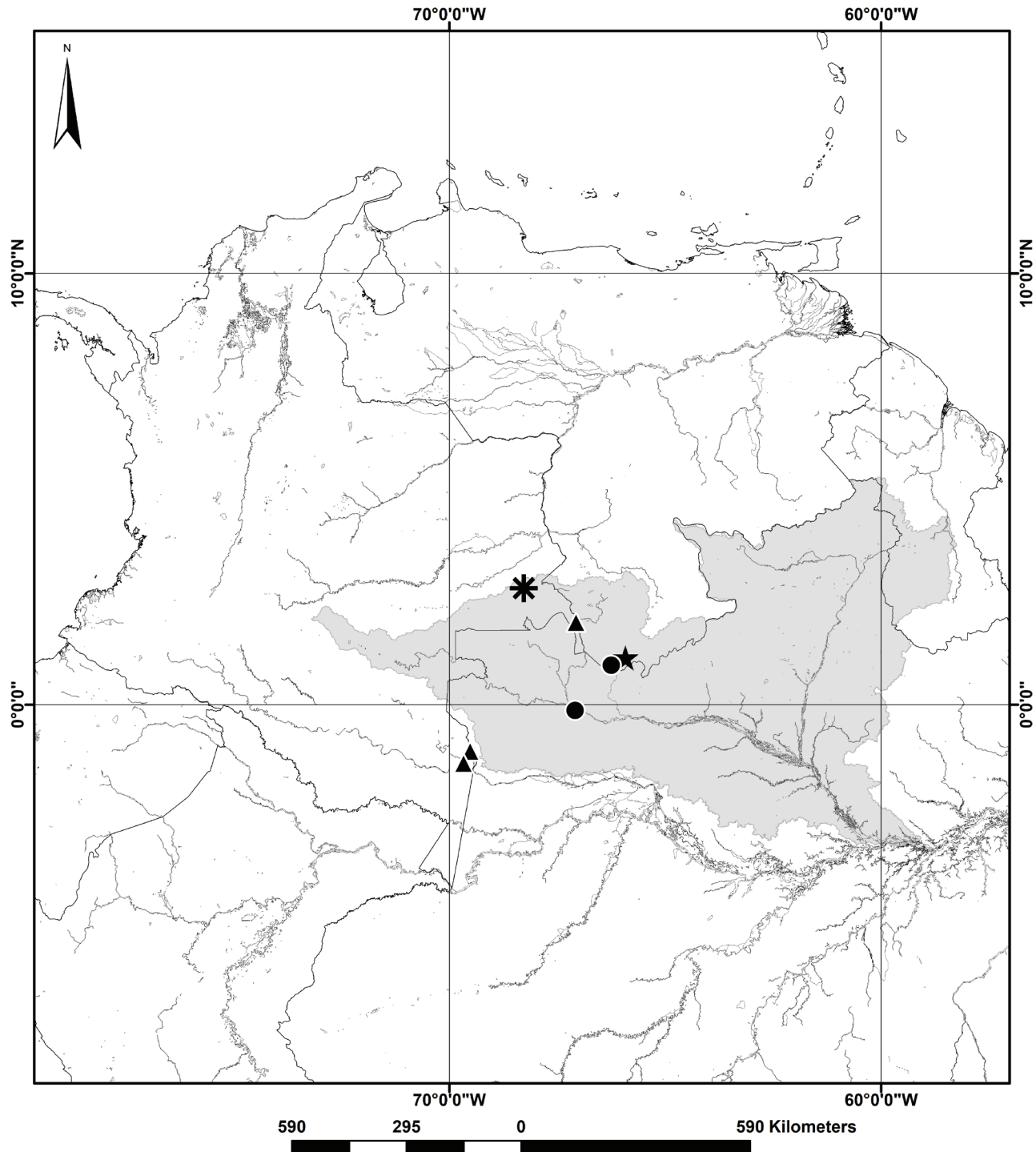


FIGURE 4. The Río Negro basin region of Brazil, Colombia, and Venezuela is outlined by gray shadow; symbols show geographical distribution of *Besleria* species belonging to subsection *Axillares* present in Río Negro basin: *B. gibbosa* (Poepp.) Hanst. (▲), *B. naquenensis* Arellano-P. & Aymard (*), *B. neblinae* Feuillet (●), and *B. yatuana* Feuillet (★).

along the border of northwestern Brazil and southern Colombia. It is ca. 70 km long (ca. 40 km in Colombia, the remaining portion in Brazil), 1–2 km wide. This Precambrian geological formation belongs to the Statherian basement that conforms the Mitú Complex (Bonilla et al., 2020). This metasedimentary sequence is associated with the Tunui Group in Brazil that was deposited around 1720–1600 Ma and extended north into the Naquén and Caranacoa Mountains (for a review see Bonilla et al., 2019, 2020). The Naquén area harbors several endemic species (e.g., *Steyerbromelia naquenensis* Betancur & Aguirre-Santoro, Bromeliaceae), and it forms part of the system of highlands of the Guayana Shield known as “tepuis.” The tepuis are areas rich in numerous endemic species and unique habitats (Maguire, 1970; Riina et al., 2019).

Distribution and habitat: the species is known to occur only along small channels in the understory of seasonally flooded forests growing on oligotrophic and acid soils drained by black waters (Fig. 3A) in the type locality (Fig. 3B, 4). These plant communities are common in alluvial plains of the upper Rio Negro basin in Brazil, Colombia, and Venezuela. A recent phytosociological study (Arellano-Peña et al., in press) showed that *Besleria naquenensis* grows in forest associations that exhibit medium tree statures and densities, composed of trees with an average DBH greater than 10 cm. The species of these forests that presented a high physiognomic expression are: *Micrandra sprucei* (Müll. Arg.) R.E. Schult. (Euphorbiaceae), *Aspidosperma*

verruculosum Müll. Arg. (Apocynaceae), *Henriquezia nitida* Spruce ex Benth. (Rubiaceae), *Caraipa longipedicellata* Steyererm. (Calophyllaceae), *Moronobea riparia* Planch. & Triana (Clusiaceae), *Parahancornia surrogata* Zarucchi (Apocynaceae), and *Pradosia schomburgkiana* (A. DC.) Cronquist (Sapotaceae).

Conservation status: according to IUCN criteria (IUCN, 2017), this species would be ranked as DD (data deficient), suggesting that future research may show that a threatened classification is appropriate. Currently, *Besleria naquenensis* is known only from the type collection, but we expect this species to have a wider distribution along seasonally flooded forests drained by black waters in the upper Rio Negro basin. This region copes with legal and illegal exploitation of minerals (mainly surface gold mining), as well as other economic activities that threaten the territorial rights of indigenous people and promote soil and habitat degradation and toxic contamination by heavy metals (e.g., mercury).

On the basis of its corolla with a spur at the base protruding from the tube at an angle of ca. 25° (Fig. 1) and its thickened, glabrous disk, *Besleria naquenensis* belongs in section *Neobesleria* C. V. Morton. Its sessile inflorescence, axillary pedicels, the corolla horizontal in the calyx, limb regular, not over 10 mm wide, and glabrous ovary place it in subsection *Axillares* C. V. Morton (Morton, 1939). This new species is morphologically similar to three others in subsection *Axillares* (Feuillet, 2008), that is, *B. gibbosa* (Poepp.) Hanst.,

TABLE 1. Comparison of diagnostic morphological characters of *Besleria* species in subsection *Axillares* present in the basin of the Rio Negro.

CHARACTER	<i>BESLERIA GIBBOSA</i>	<i>BESLERIA NAQUENENSIS</i>	<i>BESLERIA NEBLINAE</i>	<i>BESLERIA YATUANA</i>
Stems, petioles, and pedicels	Strigose	Appressed-pubescent	Densely villous with lax spreading trichomes	Appressed-pubescent
Leaves	Blade equal or subequal, broadly elliptic, 8–12 cm wide, sparsely strigose adaxially, the midrib and main veins abaxially densely strigose with patent white trichomes, apex acute to acuminate	Blade strongly unequal, ovate or elliptic to lanceolate-elliptic, 4.0–7.8 cm wide, sparsely appressed-pubescent on both sides (denser in midrib abaxially), apex long acuminate	Blade strongly unequal, lanceolate to elliptic, 3.0–5.5 cm wide, appressed-pubescent on both sides (denser and spreading on midrib and main veins on both sides), apex acute to acuminate	Blade strongly unequal, lanceolate to elliptic, 4–6 cm wide, glabrous on both sides, the midrib and main veins abaxially sparsely appressed–short pilose, apex long acuminate
Petioles on larger leaves	1.5–5.0 cm long	2.8–7.5 cm long	1.5–4.5 cm long	3–5 cm long
Inflorescence	3- to 6-flowered, pedicels 6–8 mm long, strigose	5- to 10-flowered, pedicels 8–10 mm long, appressed-pubescent	2-flowered, pedicels 3–5 mm long, densely villous	1- to 2-flowered; pedicels 3–6 mm long, appressed-pubescent
Calyx lobes	Free to base, ca. 4.5 mm long, ovate or ovate-lanceolate, glabrous or with few long trichomes outside, glabrous inside	Free to base, 3.0–3.5 mm long, broadly lanceolate, minutely appressed-pubescent outside glabrous inside	Connate, 5–6 mm long, lanceolate, hirsute on both sides	Free to base, 6–10 mm long, narrowly lanceolate, minutely appressed-pubescent on both sides
Corolla	2.4–3.0 cm long, pilosulous outside, spur acute at the apex	3.5–3.8 cm long, glabrous outside, spur rounded at the apex	2.5–3.5 cm long, puberulent outside, spur rounded at the apex	Ca. 2.5 cm long, sparsely to moderately pilose outside, spur rounded at the apex

B. neblinae, and *B. yatuana*, but it is most closely related to *B. yatuana* from the upper Rio Negro basin of Venezuela. Both species have stems, petioles, and pedicels appressed-pubescent; leaf blades strongly unequal, apex long acuminate and calyx lobes free to base. However, *B. naquenensis* differs from *B. yatuana* in the characters discussed in Table 1 and

the key to the species represented here.

This new species for the flora of Colombia in an unexplored portion of the upper Guainía River is an incentive to continue vegetation studies in the region, an area unique in the Amazonian basin that deserves more research and conservation efforts.

KEY TO THE SPECIES OF *BESLERIA* TO RIO NEGRO BASIN AND ADJACENT REGIONS INTO THE AMAZON BASIN
(Modified from Feuillet and Steyermark, 1999; distribution outside Amazon basin and the Guianas not included)

- 1a. Inflorescence with a peduncle 0.5–7.0 cm long 2
 1b. Inflorescence without a peduncle, or with short peduncle not longer than 3 mm 13
 2a. Leaf blade with 16–18 primary veins; peduncle 3-branched at apex, pedicels borne throughout the length of the branches *B. minutiflora* (Brazil, Colombia, Peru)
 2b. Leaf blade with 5–14 primary veins; peduncle 1-branched at apex, pedicels being crowded near the apex 3
 3a. Pedicels 4–6 mm long; calyx 2–3 mm long, the lobes suborbicular or oval; corolla white, 3–8 mm long *B. flavovirens* (Brazil, Colombia, Venezuela)
 3b. Pedicels 6–35 mm long; calyx 3–15 mm long, the lobes linear-lanceolate, lanceolate, lanceolate-ovate, oblong, oblong-lanceolate, ovate, ovate-oblong or suborbicular (in *B. mucronata*); corolla yellow, orange, or red, 13–40 mm long 4
 4a. Calyx lobes connate near base or in the middle of the tube, rarely free 5
 4b. Calyx lobes always free, or nearly so 7
 5a. Calyx lobes connate to middle of the tube, without a conspicuous mucro in the apex *B. patrisii* (Guianas)
 5b. Calyx lobes connate near base of the tube, rarely free, with a conspicuous mucro in the apex 6
 6a. Leaf blades lanceolate-elliptic, 11–13 × 4–5 cm, the midrib and lateral veins in the lower surface finely strigillose; the calyx lobes ca. 4 mm long, suborbicular, mucro arising below the apex; corolla 13–14 mm long *B. mucronata* (Brazil, Venezuela)
 6b. Leaf blades elliptic or narrowly oblong, 15–21 × ca. 8.5 cm, the midrib and lateral veins in the lower surface slightly pubescent; calyx lobes 7–15 mm long, oblong-lanceolate, attenuate into a mucro, corolla 17–22 mm long *B. laxiflora* (Brazil, Colombia, Venezuela)
 7a. Leaf blades subentire, inconspicuously shallowly serrulate or crenate at the margin; corolla yellow 8
 7b. Leaf blades serrulate, serrate, minutely denticulate or sharply denticulate at the margin; corolla red or orange 9
 8a. Stems, lower surface of the leaf blade, and petioles densely sericeous; calyx lobes unequal; corolla 35–40 mm long, spurred at base; ovary finely pilose *B. penduliflora* (Brazil?, Venezuela)
 8b. Stems, lower surface of the leaf blade, and petioles densely hirsute, hirsute tomentose; calyx lobes equal; corolla 14–16 mm long, not spurred at base; ovary glabrous *B. trichiata* (Brazil, Peru)
 9a. Leaf blade broadly elliptic; calyx lobes ovate or oblong 10
 9b. Leaf blade elliptic or oblanceolate; calyx lobes linear, linear-lanceolate to subulate-attenuate 11
 10a. Stem stout, hirsute; petioles 2–4 cm long; pedicels ca. 1 cm long; calyx lobes oblong, long white ciliate *B. barbata* (Colombia)
 10b. Stem slender, glabrous; petioles 4–11 cm long; pedicels 2.0–3.5 cm long; calyx ovate, short brown ciliate *B. variabilis* (Colombia)
 11a. Primary veins of the leaf blades 13–14, lobes of the calyx glabrous inside; corolla 12–15 mm long, glabrous outside; ovary glabrous *B. concinna* (Brazil, Venezuela)
 11b. Primary veins of the leaf blades 8–11, lobes of the calyx hirsute inside; corolla 14–22 mm long, pilose outside; ovary pilose 12
 12a. Leaf blades obliquely elliptic; calyx lobes hirsute inside; corolla equal size throughout the length *B. pauciflora* (Colombia, Peru)
 12b. Leaf blades elliptic or oblanceolate; calyx lobes glabrous inside; corolla ventricose upwardly *B. sprucei* (Brazil, Colombia)
 13a. Leaves of a pair equal to subequal, stem internodes straight 14
 13b. Leaves of a pair unequal (at least the petiole), stem internodes at an angle to each other 27
 14a. Stem and petioles densely hirsute or densely long villous 15
 14b. Stem and petioles glabrescent, strigose, sericeous, hirsute, or with short pubescence 21
 15a. Leaf blades elliptic or elliptic-oblong; lobes connate about 2/3 their length *B. insolita* (Brazil, French Guiana, Guyana)
 15b. Leaf blades oblanceolate, elliptic-oblanceolate, oblong, lanceolate, elliptic-lanceolate to elliptic or narrowly elliptic; lobes free, nearly so or connate 1/3 their length (*B. iara*) 16
 16a. Petioles 4–8 mm long; calyx lobes narrow-lanceolate, ovate lanceolate, lanceolate, or linear 17
 16b. Petioles 10–45 mm; calyx lobes rounded, ovate, or linear-lanceolate 19
 17a. Stem and petiole strigose; leaf blade ca. 10 × ca. 3.5 cm, margin entire; pedicels stout; lobes of calyx unequal, narrow-lanceolate or ovate lanceolate, densely pilose externally *B. inaequalis* (Colombia)
 17b. Stem and petiole densely hirsute; leaf blade 12–19 × 4–7 cm, margin crenulate or lightly serrate, pedicels slender; lobes of calyx equal, lanceolate or linear hirsute, externally 18
 18a. Margins of the leaves lightly serrate; calyx lobes 10–11 mm long, corolla ca. 13 mm long, slightly ventricose *B. immitis* (Colombia, Ecuador, Peru)
 18b. Margins of the leaves minutely crenulate; calyx lobes ca. 4.5 mm long, lanceolate, corolla ca. 17 mm long, ventricose upwardly *B. leucostoma* (Colombia)
 19a. Stems very densely long-villous; leaf blade elliptic-oblanceolate, petioles 5–15 mm long; calyx ca. 4 mm long, the lobes rounded; corolla equal size throughout its length *B. villosa* (Colombia)
 19b. Stems densely hirsute, with short hairs, leaf blade oblanceolate or oblong; petioles 1–4 cm long; calyx 10–14 mm long; lobes linear-lanceolate or ovate; corolla slightly ventricose 20

KEY TO THE SPECIES OF *BESLERIA* TO RIO NEGRO BASIN AND ADJACENT REGIONS INTO THE AMAZON BASIN CONT.

(Modified from Feuillet and Steyermark, 1999; distribution outside Amazon basin and the Guianas not included)

- 20a. Leaf oblong, 15–19 × 5.5–6.4 cm, cuneate at the base, margins entire; calyx lobes linear-lanceolate; corolla orange to scarlet *B. aggregata* s. l. (Brazil, Colombia, Peru)
- 20b. Leaf oblanceolate, 18–30 × 7.3–11.4 cm, long-attenuate at the base, margins serrate; lobes of the calyx ovate; corolla yellow *B. iara* (Brazil, Peru)
- 21a. Leaf blade elliptic, broadly elliptic, elliptic-lanceolate, elliptic to oblanceolate or obovate, lateral veins of the leaf blade 5–9 on each side of the midrib, margin entire, minutely denticulate toward apex 22
- 21b. Leaf blade narrowly oblong or obliquely elliptic, lateral veins of the blade leaf 10–15 on each side of the midrib, margin serrate toward apex 26
- 22a. Leaf blade broadly elliptic or elliptic to lanceolate; pedicels 2–10 mm long 23
- 22b. Leaf blades narrow elliptic or elliptic to oblanceolate; pedicels 12–25 mm long 25
- 23a. Stem hirsute throughout the length; lobes of the calyx oblong, long white ciliate; corolla orange or red *B. barbata* (Colombia)
- 23b. Stem strigose or pubescent near apex; lobes of the calyx lanceolate to ovate or ovate-oblong, short brown ciliate; corolla white, greenish white to yellow 24
- 24a. Leaf blades broadly elliptic, thin membranous calyx lobes free, ovate-oblong; corolla white. *B. gibbosa* (Brazil, Colombia, Venezuela)
- 24b. Leaf blades elliptic to lanceolate, subcoriaceous to papery when dry; calyx lobes connate 1/4 to 1/3 their length, lanceolate to ovate; corolla greenish white to yellow *B. parviflora* (Brazil, Venezuela)
- 25a. Leaf blades narrow elliptic; inflorescence fasciculate; calyx lobes green, oblong; corolla 13–15 mm long *B. solanoides* (Colombia)
- 25b. Leaf blades elliptic to oblanceolate, sometimes falcate; inflorescence in congested cymes; calyx lobes white or bluish, rounded; corolla 5–7 mm long *B. stricta* (Colombia)
- 26a. Leaf blade narrowly oblong, 12–22 × 5–7 cm; lobes of the calyx connate in the middle; corolla 3–6 mm long *B. flavovirens* (Brazil, Colombia, Venezuela)
- 26b. Leaf blade obliquely elliptic, 20–30 × 7–13 cm; lobes of the calyx free; corolla 12–20 mm long *B. saxicola* (Guyana)
- 27a. Calyx, pedicels, petioles, and stems either sparsely strigose or appressed-pubescent 28
- 27b. Calyx, pedicels, petioles, and stems densely villous with lax spreading hairs 30
- 28a. Stems, petioles, and pedicels sparsely strigose; leaf blades with apex acute to acuminate; calyx lobes ovate or ovate-lanceolate *B. gibbosa* (Brazil, Colombia, Venezuela)
- 28b. Stems, petioles, and pedicels appressed-pubescent; leaf blades with apex long acuminate; calyx lobes narrowly lanceolate or broadly lanceolate 29
- 29a. Leaves lanceolate to elliptic, glabrous on both sides, the midrib abaxially with sparse, appressed, short hairs, petioles on larger leaves 3–5 cm long; inflorescence 1- to 2-flowered; pedicels 3–6 mm long; calyx lobes 6–10 mm long, narrowly lanceolate, minutely appressed-pubescent in both sides; corolla ca. 2.5 cm long, sparsely to moderately pilose outside *B. yatuana* (Colombia, Venezuela)
- 29b. Leaves ovate or elliptic to lanceolate-elliptic, with sparse, appressed hairs on both sides (denser in midrib abaxially), petioles on larger leaves 2.8–7.5 cm long; inflorescence 5- to 10-flowered, pedicels 8–10 mm long; calyx lobes 3.0–3.5 long, broadly lanceolate, with appressed pubescence outside, glabrous inside, corolla 3.5–3.8 cm long, glabrous outside *B. naquenensis* (Colombia)
- 30a. Large leaf blade 3.0–5.5 cm wide, lanceolate to elliptic, base acute to obtuse, occasionally nearly rounded, apex acute to acuminate, margins ciliate, with lax spreading hairs; calyx tube 1.5 mm long; corolla white, spurred, ovary glabrous *B. neblinae* (Brazil, Venezuela)
- 30b. Large leaf blade 3.0–5.5 cm wide, 6–7 cm wide, base narrowly cuneate, apex attenuate, margin not ciliate; calyx lobes free to base; corolla red, not spurred, ovary pilose *B. immitis* (Colombia, Ecuador, Peru)

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