

NOTES ON THE GENUS *BACOPA* (PLANTAGINACEAE, GRATIOLEAE) IN THE ORINOQUIA REGION OF COLOMBIA AND VENEZUELA

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Abstract. *Bacopa llanorum*, a new species from the seasonally flooded savannas of the “Llanos” region of Colombia (Arauca department) is described and illustrated, and its morphological relationships are discussed. On the basis of its dimorphic leaves (the innermost blade filiform, uppermost lanceolate-ovate), the new species does not appear to be allied to any other *Bacopa* species. However, it shares several other features with *B. reptans*. A new combination, *Bacopa debilis*, is proposed to replace *Caconapea debilis*. In addition, ecological information of the genus in “Los Llanos” of Colombia and Venezuela, and ecological and floristic notes about the eolic-limose plains, are included. A key for identifying species of *Bacopa* in this region is also provided. *Bacopa llanorum* is remarkable for its foliar dimorphism, in an otherwise predominantly homomorphic-leaved genus, and it increases to 20 the number of species of the genus in the “Llanos del Orinoco” bioregion.

Keywords: *Bacopa*, Plantaginaceae, “Llanos del Orinoco,” foliar dimorphism, wetlands, eolic-limose plains

Resumen. *Bacopa llanorum* de las sabanas estacionalmente inundables de “los Llanos” de Colombia (departamento de Arauca) es descrita, ilustrada, y sus relaciones morfológicas son discutidas. Por su dimorfismo foliar (láminas basales filiformes y lanceolado-ovadas las superiores), *B. llanorum* no se relaciona con ninguna de las otras especies de *Bacopa*. Sin embargo, comparte algunos caracteres morfológicos con *B. reptans*. Se propone la nueva combinación *Bacopa debilis* para substituir *Caconapea debilis*. Adicionalmente, se presenta información acerca de la ecología del género en los Llanos, notas ecológicas y florísticas acerca de la planicie eólica-limosa, y una clave de las especies registradas en la Orinoquia de Colombia y Venezuela. *Bacopa llanorum* es notable por su dimorfismo foliar, en un género donde predominan las hojas homomorfas. Este nuevo hallazgo eleva a 20 el número de especies del género para la bioregión de los Llanos del Orinoco.

Palabras claves: *Bacopa*, Plantaginaceae, “Llanos del Orinoco,” dimorfismo foliar, humedales, planicies eólicas-limosas

Bacopa Aubl. (Aublet, 1795: 128–130), encompassing ca. 60 species, is the largest genus in tribe *Gratioleae* (Fischer, 2004). It is a mostly Pantropical group (Ahedor and Elisens, 2015), with few taxa in temperate areas (Pennell, 1919, 1935; Spencer et al., 1978) and with its highest diversity in the Neotropics (46 species; *vide* Ulloa Ulloa et al., 2018 Onward). The life forms of the genus are variable, including mostly annual prostrate, diffuse, or erect succulent and flaccid stems, aquatic or swamp-inhabiting rhizomatous to completely submerged herbs (Holmgren and Vincent, 2005; Souza, 2012; Sosa et al., 2018). A few taxa are perennial, terrestrial, erect suffrutexes (e.g., *B. angulata* (Benth.) Loefgr. & Edwall; *B. lisowskiana* R. Mielcarek).

The genus has been treated as a member of the tribe *Gratioleae* (Bentham, 1835) of Scrophulariaceae. Molecular-phylogenetic studies have greatly altered concepts of families of the traditional Scrophulariaceae (e.g., Olmstead et al., 2001; Oxelman et al., 2005; Tank et al., 2006; Barker et al., 2012; APG, 2016), placing several genera (e.g., *Bacopa*, *Mecardonia* Ruiz & Pav., and *Scoparia* L.) within Plantaginaceae.

The authors are grateful to Parques Nacionales Naturales de Colombia (PNN) for sponsoring the fieldwork in Arauca Department, and to Gustavo A. Romero-G. (AMES) for his comments on an earlier version of the text and his help locating historical literature. We also thank Liseth Paola Piñeros U. (COL) for preparing the illustration and for providing herbarium and morphological notes, Larry Niño for his help with the Orinoquia map, and the staff of Herbario Nacional de Colombia (COL) and the Gray Herbarium (GH) for making their facilities available for our research. This work could not have been completed without the invaluable JSTOR Global Plants database (<https://plants.jstor.org/>).

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Harvard Papers in Botany, Vol. 25, No. 2, 2020, pp. 195–203.

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ISSN: 1938-2944, DOI: 10.3100/hpib.v25iss2.2020.n7, Published online: 31 December 2020

2013; Sukumaran et al., 2019).

No worldwide monograph of *Bacopa* has been completed; however, several attempts have been made to organize the genus after G. Bentham's treatment of Scrophulariaceae (Bentham, 1846). For instance, von Wettstein (1891) divided the genus into six sections, described two species, and made seven combinations. Edwall (1897) transferred *Herpestis* C.F. Gaertn. to *Bacopa*, and with J. A. C. Loefgren described seven species and made 14 combinations. Pennell (1935) initially placed the species in five genera but later merged them in *Bacopa*, recognizing six sections and six subsections (Pennell, 1946); these form the basis for the most recent taxonomic treatments (Ahedor and Elisens, 2015; Sosa et al., 2018). Since then, 12 new species have been described from the Neotropics (Williams, 1950, 1952; Pennell, 1953; Descole and Borsini, 1954; Alain, 1968; Ichaso and Barroso, 1974; Borhidi and Muñiz, 1975a,b; Rossow, 1986; Souza, 2001).

The genus has been treated for the Flora of Colombia (Pennell, 1920), *Flora of the Venezuelan Guayana* (Holmgren and Vincent, 2005), *Flora Mesoamericana* (Christenhusz, 2014), and *Manual de Plantas de Costa Rica* (Barringer, 2015). In addition, a revision of the genus in Argentina was published by Sosa et al. (2018).

Currently, a third of *Bacopa* species are found in the Orinoco "Llanos" region of Colombia and Venezuela

(Fig. 1), also known as "Orinoquia" in Colombia (Minorta-Cely and Rangel-Ch., 2014). These taxa occur in wetlands (e.g., estuaries, edges of abandoned meanders ["madreviejas"], lagoons, and swamps). In these habitats they constitute ecologically interesting communities of dense aquatic or swamp-inhabiting rhizomatous plants. Their roots are able to penetrate the substrate, and remain submerged or re-emerge, as is the case in swamps. The permanence throughout the year of populations of *Bacopa* spp. and other aquatic plants is highly affected by the marked seasonality in the Orinoquia region, primarily by loss of the water column (Vera-Ospina et al., 2020). These communities are common in the seasonally flooded savannas over the vast eolic-limose plains, which extend from northeastern Colombia through western-central Venezuela (Schargel and Aymard, 1992; Rangel-Ch. et al., 2020). Several taxa of *Bacopa* also occur from Mesoamerica, Amazonia, the Andes, the Guianas, and southeastern and central Brazil to the Southern Cone (Holmgren and Vincent, 2005; Christenhusz, 2014; Barringer, 2015; Sosa et al., 2018).

This contribution increases to 20 the number of *Bacopa* species known from the Orinoco "Llanos" (Table 1). This new species was detected during herbarium research for aquatic vegetation and other physical and biotic studies conducted in seasonally flooded savannas over the eolic-limose plains, Arauca department, Colombia (Rangel-Ch. et al. 2020).

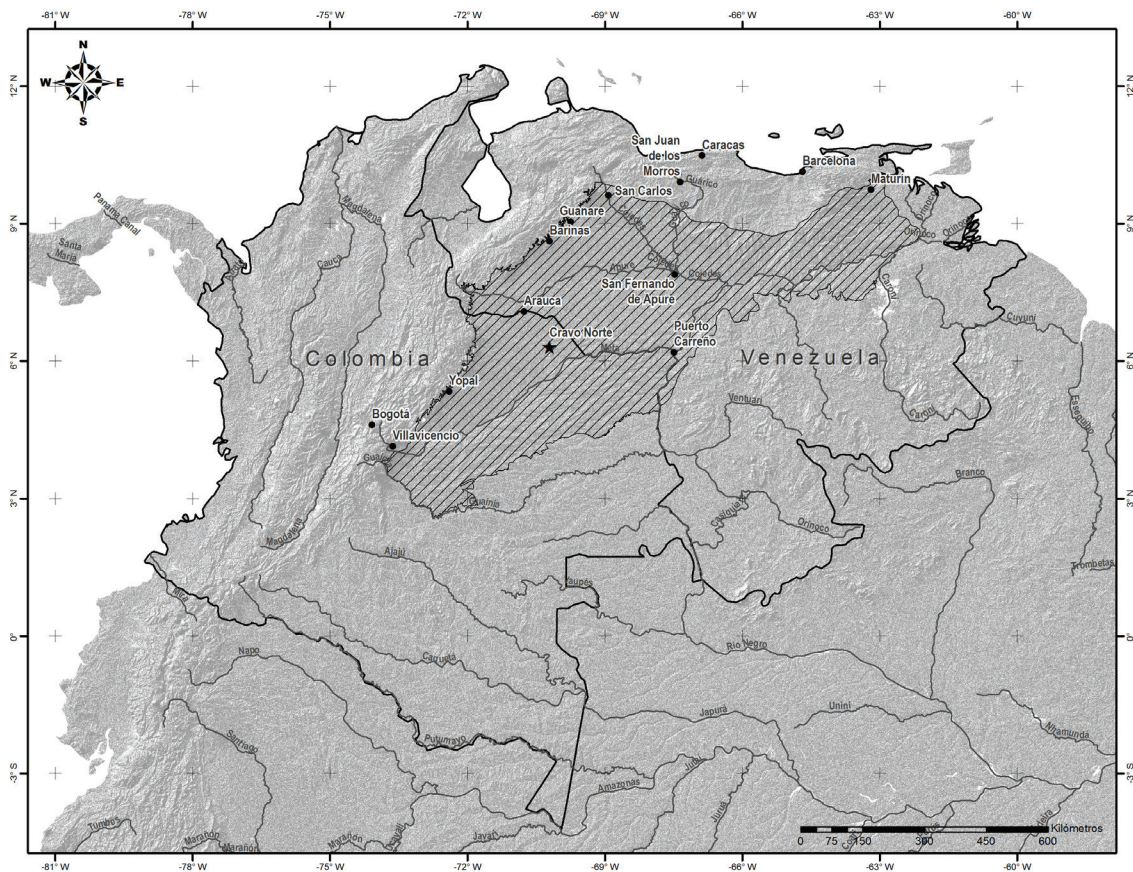


FIGURE 1. "Los Llanos" of Colombia and Venezuela (indicated by oblique black lines [*vide* Aymard, 2017, modified by Larry Niño]) and the geographical distribution of *Bacopa llanorum* (★).

TABLE 1. Comparative checklists of *Bacopa* in the Orinoquia region of Colombia and Venezuela.

TAXA OF <i>BACOPA</i>	MINORTA AND RANGEL (2014); COLOMBIA, 7 TAXA	CÁRDENAS-L. ET AL. (2016); COLOMBIA, 7 TAXA	AYMARD (2017); VENEZUELA, 16 TAXA	BERNAL (2020); COLOMBIA, 7 TAXA	TAXA ACCEPTED IN THIS STUDY: 20 TAXA COLOMBIA (10 SSP.) AND VENEZUELA (18 SSP.)
<i>B. albida</i> (Pennell) Standl.				X	X (COL)
<i>B. aquatica</i> Aubl.			X		X (VEN)
<i>B. axillaris</i> (Benth.) Standl.			X	X	X (COL, VEN)
<i>B. bacopoides</i> (Benth.) Pulle			X		X (VEN)
<i>B. callitrichoides</i> (Kunth) Pennell		X	X		X (COL, VEN)
<i>B. gratioloides</i> (Cham.) Chodat & Hassl.			X		X (VEN)
<i>B. innominata</i> (M. Gómez) Alain					X (VEN)
<i>B. llanorum</i> Aymard & Rangel-Ch.					X (COL)
<i>B. laxiflora</i> (Benth.) Wettst. ex Edwall	X	X	X	X	X (COL, VEN)
<i>B. monnieri</i> (L.) Wettst.			X		X (VEN)
<i>B. monnierioides</i> (Cham.) B.L. Rob.	X	X	X	X	X (COL, VEN)
<i>B. myriophylloides</i> (Benth.) Wettst.	X	X	X	X	X (COL, VEN)
<i>B. reflexa</i> (Benth.) Edwall	X	X	X		X (COL, VEN)
<i>B. repens</i> (Sw.) Wettst.			X		X (VEN)
<i>B. reptans</i> (Benth.) Wettst. ex Edwall	X	X	X	X	X (VEN)
<i>B. salzmännii</i> (Benth.) Wettst. ex Edwall	X	X	X		X (COL, VEN)
<i>B. serpyllifolia</i> (Benth.) Pennell					X (VEN)
<i>B. sessiliflora</i> (Benth.) Edwall	X		X	X	X (COL, VEN)
<i>B. valerii</i> Standl. & L.O. Williams			X		X (VEN)
<i>B. verticillata</i> (Pennell & Gleason) Pennell			X		X (VEN)

MATERIALS AND METHODS

This work is based on a morphological study of specimens in COL, GH, and NY (herbarium codes after Thiers, 2019), and the examination of historical and current taxonomic literature on *Bacopa*. Type specimens of *Bacopa* species were studied through the use of on-line images from

the JSTOR Global Plants database (<https://plants.jstor.org/>). The specific terminology for vegetative characters, vestiture descriptions, inflorescences, flowers, and fruit morphology follow Font-Quer (2001), Harris and Harris (2001), and Endress (2010).

TAXONOMIC TREATMENT

Bacopa llanorum Aymard & Rangel-Ch. *sp. nov.* TYPE: COLOMBIA. Arauca: Cravo Norte, Vereda Campo Abierto, Finca de los hermanos Mojica, estero en la base de médanos, 06°23'49.55"N; 70°25'13.17"W, 105 m. 29 August 2016 (fl

and fr), Vladimir Minorta-Cely, Francisco Castro-Lima, Luis F. Gopar, Andrés Vera-Ospina & Diego Yasnó 2749 (Holotype: COL; Isotype: HORA). Fig. 2.

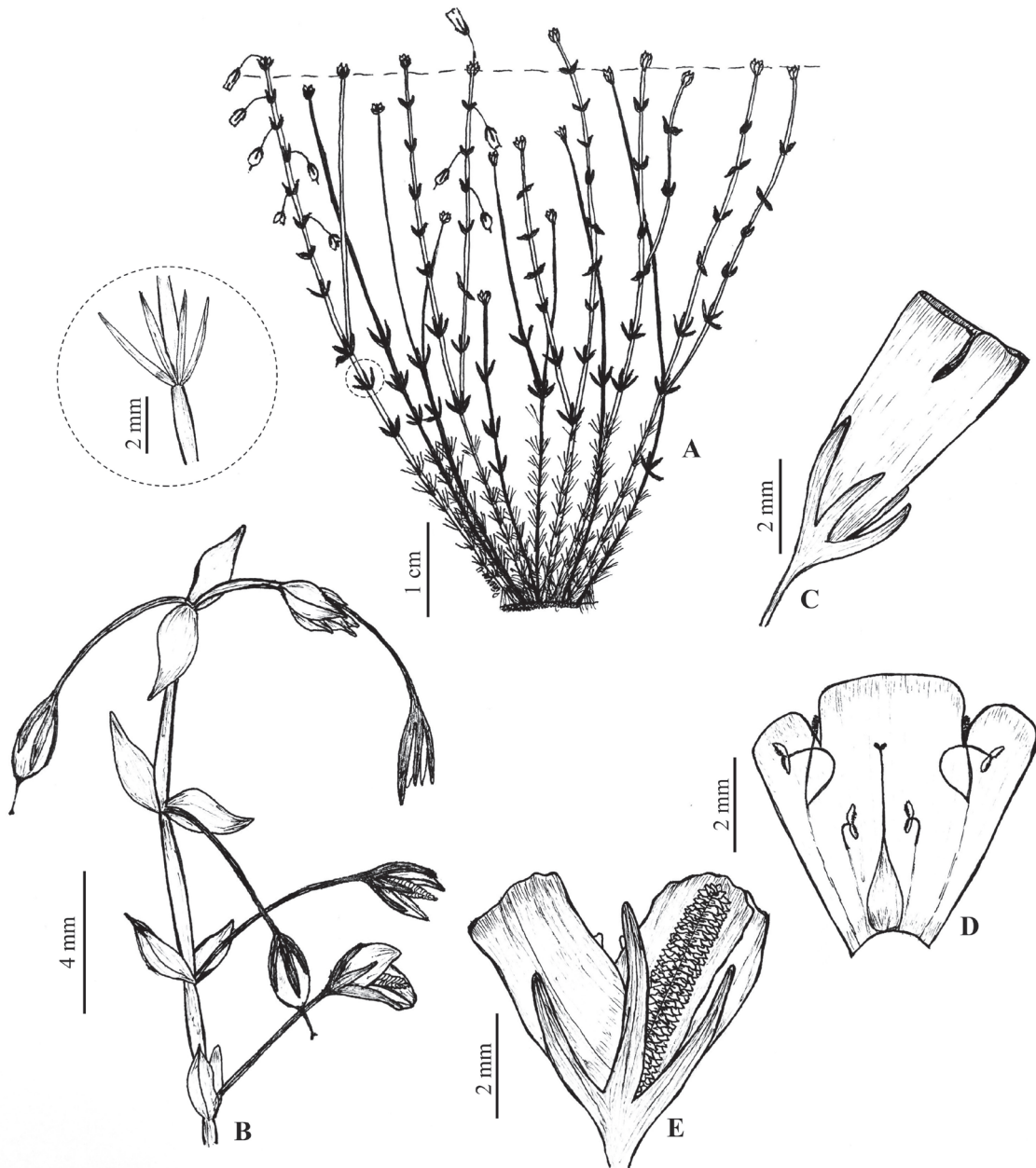


FIGURE 2. *Bacopa llanorum* Aymard & Rangel-Ch. **A**, habit showing the filiform innermost blade; **B**, top of the main stem with capsules showing lanceolate-ovate uppermost blade; **C**, corolla; **D**, inside of corolla showing the stamens and ovary; **E**, mature capsules showing the placenta and seeds.

Bacopa llanorum is morphologically similar to *B. reptans* (Benth.) Wettst. ex Edwall but differs in its habit (stout herbs, 20–40 cm tall), having dimorphic leaves, the innermost blade filiform, the uppermost lanceolate-ovate 3.5–4.6 × ca. 1.9 mm, opposite or 4–6 verticillate, margins entire, apex acute, flowers axillary or terminal, calyx lobes 2.0–2.2 mm long, lanceolate, entire at the margin and the apex acute.

Herbs 20–40 cm, stout, mat-forming, aquatic. *Stems* ascending, becoming erect, branched at the base, quadrangular, glabrate, succulent, creeping and rooting at nodes. *Leaves* dimorphic, opposite or 4- to 6-verticillate, sessile, glabrous and minute punctate on both sides, margin entire, midvein impressed on the upper surface, elevated on the lower surface; the innermost blade filiform, ca. 3.2 × ca. 0.8 mm, base attenuate, apex acute, the uppermost blade lanceolate-ovate, 3.5–4.6 × ca. 1.9 mm, base cuneate, apex acute. *Flowers* solitary, axillary or terminal, pedicel 7.0–7.8 mm long, glabrous, ebracteate; *calyx* 5-lobed, lanceolate, glabrous, apex acute, margins entire, the external dorsal lobe ca 2.2 mm, the 2 lateral and the 2 internal ca. 2 mm long; *corolla* pale lilac, 3-lobed, tube 5–6 mm long, lobes ca. 2 mm, glabrous; *stamens* 4, didynamous; *ovary* ca. 4 mm long, glabrous, style ca. 2.3 mm long, stigmatic apex bifid. *Capsule* ovoid, apex obtuse, ca. 5 × ca. 2 mm. *Seed* ellipsoid, flattened, ca. 0.5 mm.

Phenology: collected with flowers and fruits in August.

Distribution and habitat: the species is known from seasonally flooded savannas over oligotrophic soils, in the eolic-limose plains that extend from northeastern Colombia through western Venezuela, between 100 and 300 m. A recent phytosociological study showed that *Bacopa llanorum* is associated with the *Leersia hexandra* Sw. (Poaceae) and *Pontederia subovata* (Seub.) Lowden (Pontederiaceae) community of the Arauca River floodplains (Vera-Ospina et al., 2020). In estuaries located in Cravo Norte and Puerto Rondón (Arauca department, Colombia), this species forms colonies with high cover values (64%). It is found with other submerged aquatic species, such as *Cabomba furcata* Schult. & Schult. f. (Cabombaceae) and *Eriocaulon setaceum* L. (Eriocaulaceae), and emergent rooted herbs, such as

Sagittaria platyphylla (Engelm.) J.G. Sm. (Alismataceae) (Vera-Ospina et al., 2020). In other cases, this new species was observed in communities of *Cabomba furcata* Schult. & Schult. f. and *Ludwigia sedioides* (Bonpl.) H. Hara (Onagraceae) as an emergent herb with relatively low cover values, between 8 and 50% (Vera-Ospina et al., 2020).

Conservation status: according to IUCN criteria ((IUCN, 2017), this species would be ranked as DD (data deficient). This indicates that, while the species has been overlooked until recently, future research may show that a threatened classification is appropriate. Currently, *Bacopa llanorum* is known only from the type collection; however, we expect this new species to have a wider distribution across seasonally flooded savannas that extend from northeastern Colombia through western Venezuela. Notwithstanding, “Los Llanos” have experienced intense human activity in the last six decades, which has led to changes in the species composition and structural complexity of its vegetation (Aymard, 2017). However, the region remains in a good state of conservation, the main threats being the transformation of savannas into pastures and selective logging. Currently, these activities are relatively local and with low impact, but transformation into pastures is the greatest pressure because of the removal of biomass and soils.

Given its dimorphic leaves (the innermost blade filiform, uppermost lanceolate-ovate), in a predominantly homomorphic-leaved genus, *Bacopa llanorum* is not evidently allied to any other *Bacopa* species. This new species does share several features with *B. reptans* (Benth.) Wettst. ex Edwall from Honduras, Colombia, Venezuela, Guyana, and Bolivia (Santa Cruz) south to Brazil (Minas Gerais): both species have succulent stems, leaf blade minute punctate on both sides, inflorescences of solitary flowers, pedicels ebracteate, and capsules ovoid. Nevertheless, this new species differs from *B. reptans* in the vegetative and reproductive characters discussed in the diagnosis, in Table 2, and in the Key to the Species presented here.

Dimorphism or phenotypic plasticity in leaf form is a remarkable feature among aquatic plants (Deschamp and Cooke, 1983). How aquatic plants form such different leaves has been largely investigated among Eudicots

TABLE 2. Comparison of diagnostic morphological characters of *Bacopa llanorum* Aymard & Rangel-Ch. and *B. reptans* (Benth.) Wettst. ex Edwall.

CHARACTER	<i>BACOPA LLANORUM</i>	<i>BACOPA REPTANS</i>
Habit	Herbs 20–40 cm tall, stout	6–20 cm, slender
Leaves	Dimorphic (the innermost blade filiform, uppermost lanceolate-ovate), opposite or 4–6 verticillate, margins entire	Homomorphic (all linear-lanceolate), opposite or 4-verticillate, margins dentate
Uppermost leaves	Lanceolate-ovate, 3.5–4.6 × ca. 1.9 mm, apex acute	Linear-lanceolate, 6–9 × 3–4 mm, apex obtuse
Inflorescence	Flowers axillary or terminal	Always axillary
Calyx lobes	2–2.2 mm long, external and internal lanceolate, margin entire, apex acute	Ca. 6 mm long, external oblong-lanceolate, internal linear, margin ciliate, apex obtuse

(e.g., Lamiales and Ranunculales), monocots (e.g., Alismatales and Poales), and basal angiosperms such as Nymphaeales (for a review see Koga et al., 2020). This feature is common in several genera, such as *Callitriche* L. (Plantaginaceae), *Elatine* L. (Elatinaceae), *Hydrophila* R. Br. (Acanthaceae), *Potamogeton* L. (Potamogetonaceae), and *Ranunculus* L. (Ranunculaceae). However, dimorphism in *Bacopa* is an uncommon morphological attribute; of the ca. 60 known species, dimorphic leaves has been reported only in *B. verticillata* (Pennell & Gleason) Pennell (Gleason, 1929; Sosa et al., 2018) and in *B. llanorum* herein (see couplets 2a and 2b in the key that follows for differences between these two species).

Caconapea Cham. is one of the genera that Pennell (1946) placed in the synonymy of *Bacopa*. The genus was described by L. K. A. von Chamisso (1833) on the basis

of a single species, *C. gratioides* Cham. Over the years, species of *Caconapea* were transferred to *Bacopa*, except for *C. debilis* Pennell, a species originally collected by F. W. Pennell (1886–1952) in the Colombia Llanos, which is formally combined here:

Bacopa debilis (Pennell) Aymard & Rangel-Ch., *comb. nov.*
Basionym: *Caconapea debilis* Pennell, Proc. Acad. Nat. Sci. Philadelphia 75:151. 1920. TYPE: COLOMBIA. Intendencia del Meta: Villavicencio, shallow pools, 450 m, 1–2 September 1917, Francis W. Pennell 1623 (Holotype: NY; Isotypes: GB, K, PH).

Current taxonomic status: *Caconapea debilis* is currently treated as a synonym of *Bacopa reptans* (Pennell, 1946; Holmgren and Vincent, 2005).

KEY TO *BACOPA* SPECIES OF THE ORINOQUIA REGION

Based on Holmgren and Vincent (2005); distribution outside Orinoquia not included.

- 1a. Leaves dimorphic along the stems 2
- 1b. All leaves homomorphic along the stems 3
- 2a. Leaves filiform only at the base and lanceolate-ovate at the top of the stem, blade punctate, the base attenuate or cuneate; flowers with pedicels 7–7.8 mm long, ebracteate *B. llanorum* (Colombia: Arauca)
- 2b. Leaves pinnatisect or pinnatifid at the base and pinnatifid to entire at the top of the stem, the base amplexicaul or auriculate, epunctate; flowers sessile or with brief pedicels ca. 5 mm long, bracteate *B. verticillata* (Venezuela: Guárico)
- 3a. Leaves deeply pinnately dissected into filiform divisions 4
- 3b. Leaves linear, oblong-lanceolate, narrowly lanceolate, lanceolate or broader 5
- 4a. Leaves 10–14 leaves per node, 0.9–1.5 × ca. 3 mm, with 5–7 segments on each side; pedicels 2–3 cm, with 2 bracteoles; calyx unequal, the external lobes ovate-lanceolate, the internal linear, disc 4- to 8-dentate *B. myriophylloides* (Colombia: Arauca, Meta, Vichada; Venezuela: Apure)
- 4b. Leaves 6–8 leaves per node, 0.2–3.5 × 0.1–1.4 cm, with 5–20 segments on each side; pedicels 0.05–1.80 cm, ebracteate; calyx equal, disk 5- to 10-dentate *B. reflexa* (Colombia: Casanare, Meta; Venezuela: Cojedes, Guárico, Portuguesa)
- 5a. Leaves linear, relatively thick and conduplicate-folded; calyx segments barely differentiated; pedicels 1.0–2.5(–3.5) mm long; flowers often in pairs in each axis, sometimes only 1; bractlets present *B. gratioides* (Venezuela: Guárico, Portuguesa)
- 5b. Leaves oblong-ob lanceolate, obovate, lanceolate or broader, if narrower neither thick nor conduplicate-folded; calyx segments distinctly differentiated except in *B. callitrichoides* and some *B. repens* and *B. reptans*, flowers in fascicles of 4–8 or solitary; bractlets present or absent 6
- 6a. Pedicels < 1.5 mm long or absent 7
- 6b. Pedicels > 1.5 mm long 11
- 7a. Inflorescences of 1 or 2 axillary flowers; calyx 3.5–7.0 mm long; corolla 3–5 mm long; stems glabrous 8
- 7b. Inflorescences in fascicles of 1–8 flowers in leaf axils; calyx 1.5–3.0 mm long, corolla 1.5–3.0 mm long; stems hispid with conspicuous spreading trichomes 9
- 8a. Leaves linear to narrowly oblanceolate, the margins entire or shallowly dentate, pedicels 0.2–1.5 mm *B. sessiliflora* (Colombia: Meta; Venezuela: Apure, Guárico, Monagas)
- 8b. Leaves ovate to lanceolate, obovate-spathulate, the margins serrulate in the upper part; pedicels 5–15 mm 10
- 9a. Leaves 1–5 mm wide, narrowly oblong, margins entire or minutely denticulate; the outer lobes of the calyx ovate, punctate with sessile glands, the inner minutely ciliate; stigma convolute, crestlike *B. monnieroides* (Colombia: Meta; Venezuela: Apure, Cojedes, Guárico, Portuguesa)
- 9b. Leaves 6–12 mm wide, narrowly lanceolate, margins obtusely serrate in the distal part, entire at the basal half; the outer lobes of the calyx broadly ovate, sometimes ciliate, glandular-punctate, the inner densely glandular-punctate; stigmas flattened *B. axillaris* (Colombia: Meta; Venezuela: Guárico, Portuguesa)
- 10a. Plants dried brown in herbarium specimens; leaves ovate to lanceolate, apex acuminate, the midvein with 2 veins on each side; pedicels with bracteoles 2 *B. bacopoides* (Guárico, Portuguesa)
- 10b. Plants dried black in herbarium specimens; leaves obovate-spathulate, apex obtuse, the midvein without 2 veins on each side; pedicels ebracteolate *B. valerii* (Venezuela: Portuguesa)
- 11a. Bractlets present at the summit of the pedicel or attached to the base of the calyx 12
- 11b. Bractlets absent (or rudimentary in some *B. salzmännii* and *B. serpyllifolia*) 15
- 12a. Stems prostrate to decumbent or trailing 13
- 12b. Stems erect or ascending 14
- 13a. Leaves, lanceolate to oblong-lanceolate; 3–9 × 1–2 cm, margins obtusely serrate in the distal part, entire at the basal half; pedicels 1.8–3.6 cm long; calyx 8.5–13.5 mm long; stamens 5 *B. aquatica* (Venezuela: Anzoátegui, Apure, Cojedes, Guárico)
- 13b. Leaves obovate, 0.5–2.0 × 0.1–0.8 cm, margins entire or minutely denticulate; pedicels 0.5–1.0(–3.5) cm long; calyx 4–7 mm long; stamens 4 *B. monnieri* (Venezuela: Portuguesa)

KEY TO *BACOPA* SPECIES OF THE ORINOQUIA REGION CONT.

Based on Holmgren and Vincent (2005); distribution outside Orinoquia not included.

- 14a. Stems 20–45 cm long, with a few short gland-tipped hairs near the apex; posterior calyx segment ovate, scrabrous at the margin; leaves opposite *B. laxiflora* (Colombia: Casanare, Meta; Venezuela: Apure, Guárico, Portuguesa)
- 14b. Stems 3–15 cm long, glabrous; posterior calyx segment (the largest one) lanceolate to broadly lanceolate; glabrous at the margin, leaves opposite to 4-whorled *B. reptans* (Colombia: Meta; Venezuela: northwestern Amazonas, Anzoátegui, Cojedes, Guárico, Portuguesa)
- 15a. Calyx 3.5–7.5 mm long, the posterior segment truncate-rounded to cordate at the base, becoming reticulate-venose; capsule firm-walled 16
- 15b. Calyx 1.2–4.2 mm long, the posterior segment broadly cuneate at the base, not strongly reticulate; capsule membranous-walled 19
- 16a. Stems appressed to ascending-pubescent or glabrous; outer calyx segments glabrous; pedicels 1.5–14.0 mm long 17
- 16b. Stems spreading-pubescent; outer calyx segments pubescent; pedicels (4.5–)8.0–22.0 mm long 18
- 17a. Stems appressed to ascending-pubescent; pedicels 1.5–6.5 mm long; stamens 2(–4) *B. innominata* (Venezuela: Portuguesa)
- 17b. Stems glabrous; pedicels 7–14 mm; stamens 4; capsule elliptic-oblong *B. albida* (Colombia: Meta)
- 18a. Pubescence of the stems, pedicels, and calyx-segment margins of fine, yellowish hairs; corolla 3–6(–7) mm long, mostly concealed by the calyx; stems 5–20 cm long *B. salzmanni* (Colombia: Casanare, Meta; Venezuela: Apure, Cojedes, Guárico, Monagas, Portuguesa)
- 18b. Pubescence of the stems, pedicels, and calyx-segment margins of coarse, whitish, multicellular hairs; corolla 6–7 mm long, the limb exerted from the calyx; stems usually shorter, 3–6 cm long *B. serpyllifolia* (Venezuela: northwestern Amazonas)
- 19a. Leaves > 12 × 7 mm; calyx 2.7–4.2 mm long, usually consisting of 5 segments, 3 broad ones and 2 narrow ones, sometimes reduced to 4 with 1 slightly broader than the others; capsule 2.5–3.5 mm long *B. repens* (Venezuela: Barinas, Guárico, Portuguesa)
- 19b. Leaves < 7 × 5.5 mm; calyx 1.2–2.3 mm long, reduced to 4 segments, 1 slightly broader than the others; capsule 1.2–1.8 mm long *B. callitrichoides* (Colombia: Vichada; Venezuela: Apure, Barinas, Guárico, Portuguesa)

NOTES ABOUT THE ORINOCO “LLANOS” REGION AND ITS EOLIC-LIMOSE PLAINS

The broad lowland region that extends from northeastern Colombia to eastern Venezuela, occupying an area of ca. 532,000 km² (ca. 240,000 in Colombia and ca. 292,000 in Venezuela; Fig. 1), is known as “Los Llanos del Orinoco,” or as “Orinoquia,” particularly in Colombia (Minorta-Cely and Rangel-Ch., 2014); elsewhere, Orinoquia refers to the entire Orinoco River basin. The “Llanos” are regarded as the largest savanna area in northwestern South America, with rich sedimentary deposits of Quaternary origin (Huber et al., 2006; Schargel, 2015), and they are considered one of the most biodiverse regions in the Neotropics (Rangel-Ch., 2014, 2015; Aymard, 2015). This large region is a flat, almost uninterrupted expanse that gradually descends from the base of the Andes (250–500 m) in a west–east direction, ending on the left bank and the deltaic plain of the Orinoco River. The southwestern boundary of the Venezuelan llanos extends from the Arauca and Meta rivers in the direction of the Vichada and Guaviare basins, a region known as “Llanos Orientales Colombianos” (Cortés-Lombana, 1981). Nonetheless, recent evidence indicates that the Vichada and Guaviare watersheds contain a large belt of Amazonian vegetation rather than “Llanos” vegetation itself (Minorta-Cely et al., 2020).

Currently, the vegetation of “Los Llanos” is composed of a mosaic of savannas mixed with pastures, shrubby vegetation, gallery forests, an array of thorn dry forest communities, and a transition of dry semideciduous to

evergreen forests highly transformed by human activity.

The eolic-limose plains located in Colombia and Venezuela Llanos are notable for their physical and biological characteristics and their ancestral inhabitants, and lately there has been particular interest in conserving their ecosystems (Rangel-Ch. et al., 2020). Moreover, these plains are recognized as having a fluvial network composed of several rivers (e.g., the Capanaparo, the Cinaruco, and the Cravo Norte) that are part of the Orinoco River basin. This large sector is characterized by numerous gallery forests and by its large and continuous area of dunes and savannas over oligotrophic soils (Schargel, 2007). Perhaps one of the most peculiar features of these extensive plains is the presence of large, dense tree communities of *Caraiipa llanorum* Cuatr., *C. savannarum* Kub. (Calophyllaceae, “Saladillo”), and *Leptolobium nitens* Vogel (Fabaceae, “Congrio”), the former called “Saladillales” and the latter “Congriales” (Aymard and Campbell, 2008; Montes et al., 2013). This region is important biologically because of its endemics elements, such as *Cuphea apurensis* Lourteig (Lythraceae) and *Xyris apureana* Kral & L.B. Sm. (Xyridaceae), and because it is the northwestern limit of distribution of many Amazonian taxa, such as *Leptobalanus wurdackii* (Prance) Sothers & Prance (Chrysobalanaceae), *Spathanthus unilateralis* (Rudge) Desv. (Rapateaceae), and *Salacia negrensis* Lombardi (Celastraceae) (Aymard, 2015, 2017).

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